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Marine exploitation and the arrival of farming: resolving the paradox of the Mesolithic-Neolithic transition in Denmark

Check for updates

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ABSTRACT

The transition to farming in the coastal environments of southern Scandinavia remains a key conundrum in European prehistory. This region was heavily exploited by Late Mesolithic communities of the Ertebølle culture, complex hunter-fisher-gatherers who flourished for some 1500 years prior to the arrival of farming at around 4000 BCE marking the start of the Neolithic period. Extensive genetic and isotopic analyses of skeletal remains suggests that the arrival of farming is marked by a rapid demographic change and that incoming populations of 'farmers' had little reliance on marine resources. In contrast, frequent archaeological finds of shell middens and fishing gear in the Early Neolithic supports evidence for continuity in the use of marine resources across the transition.

To assess this apparent paradox, focusing on the Danish evidence, we explore the spatiotemporal trends in the density of some 1500 radiocarbon dates using new informatics tools and modelling strategies. We indeed find strong archaeological indicators of sustained and even intensified patterns of coastal exploitation across and beyond the transition; shell middens, fishing implements, and aquatic residues in ceramics continue well into the Neolithic. Using an agent-based demographic model, we demonstrate how small differences in fertility could rapidly dilute signals of coastal resource use in the context of a growing Neolithic population. More broadly, we suggest that complex palimpsests of archaeological remains and biological information from human remains can only usefully be interpreted through the lens of demography.

1. Introduction

For many years archaeologists have tried to tackle the vexed question of how farming took hold in regions densely occupied by hunter-fishergatherers (Fischer and Kristiansen, 2002; Gron and Sørensen, 2018; Larsson, 2007; Rowley-Conwy, 1999). It is a question that has engaged communities of archaeologists, environmental scientists and more recently geneticists drawn to a process that fundamentally altered the course of human history (Allentoft et al., 2024a). Nowhere else has this question been more probed than Denmark, a country with arguably the

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richest and best studied archaeological record spanning the transition to agriculture in Europe (Fischer and Kristiansen, 2002). In Denmark, as in other parts of southern Scandinavia, hunter-fisher-gatherer communities flourished during the mid-Holocene exploiting the southwest Baltic Sea, Belt Sea and Kattegat, their fjords and their inland waterways, leaving large concentrations of shell middens, often of considerable size, and abundant evidence of occupational activity along these rich aquatic ecotones. Traditionally described as 'complex hunter-gatherers' (Arnold, 1996), these were people who, at their zenith during the Late Mesolithic Ertebølle period (5400-4000 BCE), were capable of sedentary living, the production of pottery and the creation of surpluses, features often associated with early farming societies (Bergsvik, 2001; Boethius, 2017). Between 4000 and 3800 BCE the first evidence of crop cultivation and domesticated animals proliferates, together with changes in material culture, derived from well-established Neolithic farming communities to the south on the North European Plain. Over 150 years since the question was first posed, the processes (i.e. mechanisms and motivations) associated with the transition, a key juncture in prehistory, remain the focus of keen debate.

The movement of people, ideas (e.g., knowledge of farming) and physical resources (e.g., domesticated animals, crops and material culture) provides an alluring model for agricultural transitions, but these different elements need not be inextricably linked. For example, it has been argued that the transition arose through economic and cultural negotiation between foragers and farmers without substantial demographic replacement (Gron and Sørensen, 2018). In contrast, recent genetic analysis of well-dated human remains throughout Denmark points to a more rapid and abrupt demographic change with the arrival of the Neolithic (Allentoft et al., 2024a), a process perhaps entirely driven by the expansion or migration of farming groups from the south. Furthermore, the genetic data show little evidence of a resurgence of hunter-gatherer ancestry following the initial phase of the expansion of farming, as seen in other parts of Europe, until the advent of the non-agricultural Pitted Ware culture later in the 3rd millennium BCE (Mittnik et al., 2018; Rivollat et al., 2020). Far from settling a long-standing debate, this important novel dataset raises new questions as the population turnover demonstrated by genetic evidence is difficult to reconcile with the continued occupation of sites, including shell middens, and similarities in material culture, such as lithic toolkits (Gron and Sørensen, 2018).

In terms of economic change and potential drivers, it has been argued that key fish stocks collapsed due to climate-induced changes to the marine environment (Warden et al., 2017) following a period of increased marine productivity during the Ertebølle period (Lewis et al., 2020). Yet, other sources of archaeological evidence demonstrate the continued use of aquatic resources several hundred years into the Neolithic (Lucquin et al., 2023; Robson et al., 2021a), despite a clear shift to more terrestrial foodstuffs in the isotopic compositions of human remains (Fischer et al., 2007; Tauber, 1981).

Here, focusing on the Danish evidence, we aim to reconcile these different datasets by examining the relationships between cultural, economic, environmental and demographic change from *ca*. 6000–3000 BCE in a new chronological framework. We employ kernel density estimates (KDEs), including time-sliced geospatial KDE models, to assess changes in site density, shell midden activity, and the distribution of artefacts relating to coastline exploitation. Moving average models are used to track diachronic trends in molluscan remains, fishing implements, and isotopic compositions. We examine the timing and intensity of domesticated plant and animal use through modeling the density of directly-dated ecofacts, and evaluate changes in culinary practice using organic residue analysis of pottery. In doing so, we evaluate the most likely drivers of the foraging to farming transition in Denmark and provide an exemplary model for investigating agricultural transitions elsewhere.

2. Materials and methods

2.1. Archaeological sites, chronologies and data sources

We draw upon the following sources of data: the temporal and spatial distribution of shell middens and other archaeological sites; changes in the relative procurement of molluscs (number of shell middens, taxonomic composition and minimal animal units [MAU]); changes in the availability of molluscan resources from dated natural shell banks; material-culture evidence in the form of fishing-related implements such as bone points and eel leisters, fish traps and weirs; zooarchaeological evidence for the exploitation of fish and marine mammals (number of identified specimens [NISP]); biomolecular evidence and isotopic compositions of ceramic vessels and foodcrusts; isotopic compositions of human remains; and dated remains of domesticated plants and animals. Data were obtained from a range of publications, including journal articles, conference proceedings, monographs, newsletters, yearbooks, PhD theses, public repositories, the Danish Sites and Monuments database (Fund og Fortidsminder, https://www.kulturarv.dk/fundogforti dsminder/) and unpublished reports. Duplicate records were removed and the compiled dataset was edited for consistency. These sources of data span the period from ca. 6000 to 3000 BCE across what is today Denmark, encompassing the Jutland Peninsula, its major western Baltic islands and submerged coastal landscapes. The sequence broadly begins at ca. 6500 BCE, the Maglemose-Kongemose transition, when postglacial sea level rise established a fully marine connection between the North and Baltic Seas with the formation of the Littorina Sea (Bailey et al., 2020). The crucial period of change was from the Late Mesolithic Ertebølle culture (ca. 5400-4000 BCE) to the Early Neolithic Funnel Beaker culture (ca. 4000-3300 BCE), particularly the centuries before and after the appearance of domesticated animals at ca. 4000/3900 BCE. The data are deposited in an accompanying repository (http://doi. org/10.5281/zenodo.14019080) while a more detailed description of the datasets and their acquisition is available in Robson et al. (2025).

2.2. Radiocarbon calibration and density modelling

The empirical foundation of our study is the analysis of the temporal density of the various categories of archaeological and ecological data, making use of some 1500 radiocarbon dates (http://doi.org/10.5 281/zenodo.14019080). Numerous 'dates as data' studies have been published in recent years, typically using numbers of dated sites as a proxy for numbers of people (e.g., Shennan et al., 2013), together with an increasing number of methodological innovations addressing criticisms that have been levelled at such studies (Crema, 2022). Major sources of potential bias are different research traditions, the over-representation of sites with well-dated sequences, variability in the function of sites (not all are necessarily settlement sites) and the differential visibility or preservation of different categories of sites and materials (Torfing, 2015). Coastal sites are especially vulnerable to differential visibility because of their location on the shoreline and consequent vulnerability to removal by changes in relative sea-level change; shell middens are also typically liable to over-representation because of the vast bulk and durability of the discarded mollusc shells. We address all these issues in our analysis.

Radiocarbon data were subjected to an initial round of quality screening, removing problematic results and data that could not be reliably matched to their archaeological context. The data were then explored using a number of different statistical techniques. Firstly, summed probability distributions (SPDs) were calculated to determine the general temporal distribution of the data. These were calculated using the appropriate IntCal20 (Reimer et al., 2020) or Marine20 (Heaton et al., 2020) calibration curve for each sample, or a custom mixture of curves for human bone samples with mixed sources of carbon. To model the local marine reservoir effect, we used a ΔR of -234 ± 61 years relative to Marine20, as calculated using Early Neolithic

European oyster (*Ostrea edulis*) samples from the Nekselø fish weir (Fischer and Olsen, 2021). All dates are reported as calibrated years BCE.

Next, Gaussian kernel density estimates (KDE) were modelled to eliminate calibration curve artefacts in the probability distributions (McLaughlin, 2019), resulting in a model with defined confidence limits that can be expressed as absolute density or a dynamic rate of change. We used hierarchical cluster analysis to thin the radiocarbon data to one date per phase of occupation at each site (cf., Crema and Bevan, 2021), to counter any bias towards heavily sampled sites. The resulting models were used to estimate periods of statistically significant growth and decline. A similar analysis was performed separately for certain categories of samples or sites that have special relevance to the aims of our study, such as human remains, fish traps and weirs, spearfishing artefacts, i.e., bone points and composite spears known as 'eel leisters' (which were probably also used for other taxa), and domesticated plants and animals.

Computer code to replicate this analysis is available from http://gith ub.com/rowan-mclaughlin/resolving-paradox, permanently archived via Zenodo at http://doi.org/10.5281/zenodo.15471168.

2.3. Geospatial analysis

Incorporating our database in a GIS, two-dimensional KDE models were calculated for: (i) all known shell midden sites; (ii) all excavated and dated sites in our database including sites that are not shell middens; and (iii) for a series of time-slices. We employed case resampling and model averaging for (iii) to accommodate chronological uncertainty, generating a set of rasters illustrating the changing geography of site density over time. For point pattern analyses, the current Danish coastline was buffered by 5 km to provide an analytical 'window' that accommodated both sea level changes and short journeys by sea. Using UTM coordinates, pairwise distances between each of the sites in a defined 250-year temporal window were calculated and used to work out the average distance between sites and the Clark-Evans R statistic indicating clustering and dispersion. The temporal window was then run through the dataset at 25-year increments, generating a time series that could be compared to the KDE models discussed above. Computer code to replicate this analysis is available from the resources mentioned above.

2.4. Moving average models for exploratory data analysis

The chronological information in our databases includes, in descending order of preference: (i) posterior probability distributions of

Bayesian chronological models, themselves largely based on radiocarbon dates; (ii) radiocarbon dates directly associated with the response variable in question (e.g., paired radiocarbon and stable isotope measurements); and (iii) uniformly distributed age estimates based (primarily) on associated artefactual finds (Table 1). These were used to generate moving average summary models of the archaeological data. This algorithm randomly sampled the posterior distribution of the age estimates or (for entries dated with a broad age range) sampled the uniform distribution. Ordering the resulting scatter plot temporally, a running median was calculated as a means of smoothing, using the R function runmed. Repeating this process many (e.g., 100) times, a moving average summary trend was developed. This has a confidence interval, calculated by approximating the running median simulations to identical timestamps and estimating the variance at each point. For large datasets, an additional step of randomly shuffling the data using sampling with replacement (i.e. 'bootstrapping') expresses variability of the data on top of chronological uncertainty. Computer code to replicate this analysis is also available (see above).

3. Results

3.1. Shell midden activity, molluscan remains and archaeological site density

We begin by exploring the spatio-temporal distributions of shell middens and other types of archaeological deposits in order to track changes in the rates of consumption of different food resources, especially marine molluscs, and changes in human population densities. However, we note at the outset that shell middens are potentially liable to three types of systematic bias that are largely unique to this type of deposit and can severely distort KDE trends in relation to other types of archaeological deposits.

First, being located on the immediate shoreline, they are highly vulnerable to total loss from the record because of destruction or submergence by changes of relative sea-level. These are a major factor in the earliest part of our sequence and continue with an attenuating effect even in later periods. They include the final glacio-eustatic sea-level rise of the Littorina transgression, a rise of *ca.* 10 m between *ca.* 6100 BCE and 4000–3000 BCE, and a component of glacio-isostatic adjustment that tilted the Danish land mass along a northwest–southeast axis, running across northern Jutland and the Danish islands, progressively uplifting shorelines north of this tilt line by as much as 13 m above the present shoreline in the far north of Jutland, and submerging them in the south over the same period by as much as 8 m (Astrup, 2018; Christensen and Nielsen, 2008; Hausmann et al., 2022). The interaction of

Table 1

Sources of data and chronological information for the exploratory models and the statistical methods used.

Dataset	Measurement	Chronology	Modelling approach	Interpretation
Archaeological sites including shell middens, and natural shell banks Fishing-related sites and implements Domesticated plants and animals	Temporal relative frequency	Radiocarbon	Kernel Density Estimation	Settlement density (and density of natural shell banks) Fishing intensity (overall) Timing and scale of farming
Archaeological shellfish, fish and marine mammal remains	NISP per site phase Richness (number of taxa) per site phase	Phase start/end estimates	Running median	Fishing intensity (per site) Specialisation in taxa
	MAU (Minimal Animal Units) of molluscs	Estimates constrained by stratigraphic position in column samples		-
	Bone collagen δ^{13} C and δ^{15} N isotopic compositions (stratified by trophic level)	Sample start/end estimates		Environmental or trophic changes
Human isotopic compositions	Bone collagen δ^{13} C and δ^{15} N isotopic compositions	Radiocarbon		Human protein sources
Biomolecular evidence and isotopic compositions of ceramics	Bulk δ^{13} C and δ^{15} N, and δ^{13} C values of $C_{16:0}$ and $C_{18:0}$ fatty acids Presence/absence of biomarkers	Bayesian chronological model		Food resources
Midden compositions (shell taxa, size and volume)	Spatial autocorrelation	All sites included	Mantel test	Presence or absence of local customs

these two variables means that the marine transgression of pre-existing shorelines and the removal of coastal sites or shell middens located on them by erosion or submergence took place at different times in different regions, creating a major confounding variable in interpreting spatio-temporal trends.

Of course, coastal archaeological sites that are not shell middens, of which there are many in the Danish Mesolithic context, are also vulnerable to this factor, along with the remains of vertebrate marine fauna and other marine indicators recovered from them. However, they are not affected to the same degree, because underwater examples with terrestrial food remains and abundant evidence of fishing and seamammal hunting are quite numerous, whereas underwater shell middens are very rare, and when found have been severely disturbed and truncated by marine erosion (Astrup et al., 2020, 2021; Bailey et al., 2020).

Secondly, because of the vast bulk of shell middens and the huge number of molluscs represented – an estimated 73 million oysters in the Meilgaard shell mound alone (Bailey, 1975a), it is easy to assume that marine molluscs must have been a major food supply and therefore that changes in their rate of consumption must have been closely coupled with changes in the density of the human population dependent on them. However, the high shell-to-meat ratio of molluscs and the large difference in the preservation of their shells compared to all other food remains vastly overestimates their importance. Where measurements have been made to control for this bias, they demonstrate that the molluscs, even the huge numbers in large shell mounds, represent much less in terms of their contribution to the annual food supply, as little as 10 % and sometimes very much less, with other food supplies especially fish providing the major part of the diet (Bailey, 1975b, 1978; Clark, 1975; Meehan, 1982). This means, for example, that an increase in oyster consumption does not necessarily imply a larger human population, nor a decrease in oyster consumption a population decline - in other words rates of mollusc consumption and human population densities can vary quite independently of each other, and the number of shell middens cannot be relied on as a proxy for human population size.

Thirdly, shell middens are liable to over-representation compared to

non-shell sites because of the high labour cost of transporting molluscs in the shell and the high visibility of 'satellite' camps used for seasonal or specialist activities close to localised sources of the molluscs, for processing (de-shelling) and removal of the meat for immediate consumption or removal of the meat elsewhere, or as 'dinner-time' camps. Differences in patterns of settlement and mobility between the Ertebølle and Neolithic are additional potentially confounding variables (see Johansen, 2006).

We control for these potential biases by comparing spatio-temporal trends in shell middens with non-shell-midden sites, natural shell banks, and other independent sources of palaeodietary or palaeoenvironmental data.

Examination of the KDE data (Fig. 1) shows that shell middens are absent in the earliest part of the sequence between 6100 and 5700 BCE (Kongemose culture) most likely because all shorelines of this period were either subsequently uplifted and therefore exposed to erosion or burial under later sediments, or submerged under water, and any sites associated with them have been eroded, buried, or are yet to be recovered by underwater investigation. The subsequent sharp increase in numbers to reach an initial peak at ca. 5100-5000 BCE (early Ertebølle period) is associated with sites that are either underwater, notably the Hjarnø shell middens, or on the highest uplifted shorelines in the far north such as the Brovst shell midden and the Yderhede coastal site (Astrup et al., 2020, 2021, p. 17; Cook Hale et al., 2021). The apparent steepness of this part of the curve from a starting point of zero may therefore be misleading, or exaggerated, because of the loss of sites from the early part of the sequence and their increasing preservation or visibility with the progressive moderation of impacts resulting from relative sea-level change.

Some support for this is provided by the other KDE curves in Fig. 1. Natural shell banks were certainly present at the beginning and so too were other types of archaeological sites. Natural shell banks form on the seabed, and are not subject to the same forces of erosion and burial as middens on the coastline, nor are inland archaeological sites. Moreover they both show an increase to an initial small peak similar to the shell midden curve, quite sharply so in the case of the natural shell banks and



Fig. 1. A: Map of the modern coastline of Denmark and the dated sites whose temporal density is shown on the right. The map is based on Natural Earth, www.nat uralearthdata.com; see http://doi.org/10.5281/zenodo.14019080 for site coordinates; the dashed line indicates the approximate palaeoshoreline (after Bailey et al., 2020). B: Density models of Danish radiocarbon data, showing summed probability distributions (SPDs) and kernel density estimates (KDEs) through time for shell middens, natural shell banks and non-shell midden archaeological sites; the KDEs have a bandwidth of 75 years and have associated pointwise confidence bands calculated by resampling the posterior probability distributions of the radiocarbon dates. Note the maxima in activity at *ca.* 4000 BCE in the shell midden density models. The transitional period 4100–3900 BCE is highlighted, representing the division between the Late Mesolithic Ertebølle and the Early Neolithic Funnel Beaker cultures.

less sharply in the all-sites curve, except that the peak of the natural shell bank curve occurs several hundred years earlier than the others. The reasons for this discrepancy are unclear but it may reflect the small sample size of this data set (an order of magnitude smaller than the others) and a noisier signal. The weakest trend is shown by the KDE curve for sites without shell middens, but it nevertheless shows a similar pattern, though much dampened compared to the other curves.

After 5000 BCE, the shell midden KDE curve stabilised, even declining slightly, before increasing again to a higher peak at about 4500-4400 BCE, followed by a further increase to a maximum peak at 4000 BCE (middle to late Ertebølle). The peak in numbers continued across the Ertebølle to Neolithic transition and for several centuries into the Neolithic Funnel Beaker period, indicating high rates of shell accumulation, with shell middens proliferating in the landscape until ca. 3600 BCE. After this, there was a steep decline with a brief reversal of these trends between 3200 and 3000 BCE, when a distinct late-Middle Neolithic phase of intensive shell midden activity occurred in eastern Jutland (see Fig. 2). Between ca. 2700 and 1200 BCE, corresponding to the end of the late-Middle Neolithic period through to the Bronze Age, a steep decline in shell midden activity took place, although shell middens continued to be used sporadically for the burial of human remains in some regions, particularly northern Jutland and the Limfjord (Allentoft et al., 2024a, 2024b; Frei et al., 2019; Price et al., 2007; Sluis et al., 2019; van der Sluis and Reimer, 2021).

As in the earlier part of the sequence, increased preservation or visibility of shell middens may be contributing to the KDE curve at least until about 4000 BCE, but comparison with the curves for natural shell banks and other sites shows a similar general pattern except that, as before, the peak in the KDE of the natural shell banks is several hundreds of years earlier (Fig. 1). Otherwise, the non-shell-midden curve and all-site curves follow quite closely the shell-midden curve, though in more

moderate form, with a sustained increase across the Mesolithic-Neolithic transition. Also, all three curves register a decline and recovery between *ca.* 3600 and 3000 BCE, although the shell midden curve is less pronounced, suggesting that whatever factors caused this cycle of decline and recovery had less impact on shell midden accumulation than other sorts of activities. There are no obvious taphonomic or other biassing factors that would account for the coincidence of time trends in these three curves, apart from the relative displacement between the shell-midden curve and the other archaeological curves. We conclude that the combination of data from these different sources demonstrates a generally rising if occasionally episodic trend of human population increase throughout the Ertebølle and early Neolithic periods *and* a concomitant increase in the rate of consumption of marine molluscs.

Further corroboration of this pattern is the trend towards increased clustering of sites and reduced inter-site distances in tandem with the growth in site KDEs (Fig. 2). Also shown in Fig. 2 is the summed probability distribution (SPD) of radiocarbon dates for oysters in shell middens reported by Lewis et al. (2020). They used this data to suggest that shell midden activity peaked at *ca*. 4400 BCE, and then dwindled when farming arrived in the region. We were unable to replicate their analysis and suspect that the SPD in their study did not correct for the Marine Reservoir Effect. Consequently, the dates in their SPD are too old, resulting in a distribution offset by about 300 years.

The taxonomic composition of molluscs also changed significantly during and after the Mesolithic-Neolithic transition (Fig. 3), though differing in time and place throughout the Danish archipelago (e.g., Larsen et al., 2018). At Norsminde in east-central Jutland and Krabbesholm II in the Limfjord (Laurie, 2008; Nielsen, 2008), where Neolithic shell midden deposits are stratified above Ertebølle layers, the frequency of oysters relative to cockles (*Cerastoderma edule*) fell during the Mesolithic-Neolithic transition. Cockles subsequently declined in



Fig. 2. Spatio-temporal density of shell middens. Left panels show results from KDE modelling temporally (A), and spatially (B). Panel A also shows SPDs for directlydated oyster shells from shell middens, compared to a similar analysis by (Lewis et al., 2020). Panel C shows moving average indicators of the continuous changes in site density. The Clark-Evans statistic is < 1, indicating a clustered (rather than dispersed) settlement pattern. Note how the average distance between sites falls throughout the Ertebølle period, with a minimum occurring shortly before 4000 BCE, at the time of peak intensity in shell midden use. The statistics for Neolithic shell middens indicate an intense but localised phase of activity (see also Supplementary Material: Regional patterns). The steep curves at the beginning of the sequence reflect the rapid proliferation of these sites following changes in their visibility due to sea level stabilisation. Vertical shaded areas highlight the Mesolithic-Neolithic transition.



Fig. 3. Moving average model of molluscan frequency, as minimum animal units (MAU), over time in four column samples from two shell middens, showing the changing MAU per layer (A) and relative compositional change, i.e. percentage of total, in the most important taxa, averaged over the four column samples (B). Note that the MAU increased in the Neolithic layers. Also shown is the KDE for natural shell banks. Note how the decline in oysters relative to other taxa is similar to the decline in natural shell banks, although peak occurrences in both curves are offset. Cockles briefly increase at the expense of oysters before going into long-term decline. And both are overtaken by progressive increases in other taxa after 3500 BCE, especially periwinkles and mussels. Also note that despite the relative decline in oysters and cockles during the Neolithic period, the density of shell remains increases. Differential taphonomic histories of different species may be a confounding variable. See text for further discussion. The individual column samples were assigned sample numbers (Norsminde - N77, Krabbesholm II - 7737, Krabbesholm II - 7738) during excavation, whilst 'Nielsen' refers to the column sample reported in Nielsen (2008) (data after Laurie, 2008; Nielsen, 2008). The Mesolithic-Neolithic transition is shown as a vertical shaded area in the panels.

tandem with a further decline in oysters, eventually giving way to other taxa such as common periwinkles (*Littorina littorea*) and blue mussels (*Mytilus edulis*) (Fig. 3). At the same time the density of molluscan remains, according to the MAU values per unit area of deposit (i.e. layer), actually increased in the Neolithic layers, suggesting that high and increasing rates of shellfish exploitation were sustained despite the decline in oysters (Fig. 3). Since the MAU figures aggregate different molluscan taxa, and these taxa were changing frequency over time, differential fragmentation patterns between different taxa, especially between oysters, cockles and mussels, might be a confounding variable. These density figures are at best suggestive rather than conclusive evidence of intensification, but they are nevertheless consistent with the trends in KDEs and inter-site distances.

Turning to the causes for these changes, Lewis et al. (2020) provide independent evidence from diatoms and other biomarkers in dated marine-sediment cores, suggesting that a major variable contributing to increased rates of shell accumulation in shell middens was changes in the primary productivity of Danish waters. Their data show considerable fluctuations but with peaks coinciding with those of shell accumulation during the Ertebølle period, which they argue contributed to improvements in the productivity of the oyster beds. Lewis et al. (2016) also point to an increased influx of sediments into the shallow bays of the Danish Straits at the Mesolithic-Neolithic transition as a likely factor that inhibited the growth of oysters and contributed to their decline and ultimate replacement by other molluscan species, perhaps accentuated by a reduction in water salinity, to which oysters are especially vulnerable (Lewis et al., 2019).

Taking the evidence as a whole, we conclude that the rate of shell accumulation, especially when oysters were the dominant midden constituent, increased significantly during the Ertebølle period, mainly because of environmentally driven increases in the availability or productivity of oyster beds, but also to some extent because of increased demand by a growing human population, reaching a peak during the Funnel Beaker period. The most important point is that shell middens continued in use across the Neolithic transition and for some centuries beyond, with ongoing and perhaps more intensive levels of shellfish procurement, during a period when domesticated plants and animals were becoming well established in the economy, and the local human population had been replaced by incoming farmers. Shell midden accumulations, far from being a Mesolithic phenomenon, continued at almost the same level during the early part of the Neolithic, and persisted into the Early Iron Age to Viking Age, albeit on a smaller scale compared to the Mesolithic and Neolithic (Andersen, 2007).

3.2. Fishing-related implements and marine vertebrates

The temporal density of directly-dated artefacts related to fishing such as bone points and eel leisters, fish traps and weirs provides an alternative perspective on coastline exploitation. The distinctive phase of Ertebølle growth in shell midden activity at 4500 BCE is also reflected in sharp increases in the amount of artefactual fishing evidence. Importantly however, these traditions peaked during the Early and Middle Neolithic (Fig. 4), bone points and eel leisters at 3600 BCE and fish traps and weirs at 3400 BCE. In this context, it is worth noting that remains of Early and Middle Neolithic fish weirs, perhaps rebuilt over their Mesolithic predecessors, are more numerous and appear to have been more efficiently constructed. Some were rebuilt on successive occasions, with evidence for a line of supporting poles extending many tens of metres out from the shoreline and intervening wattle panels made of tightly woven hazel withies, well suited to the mass capture of smaller fish (Fischer, 2007; Pedersen, 2013; Pedersen et al., 2017).

To assess the economic significance of fishing, we compiled the results of zooarchaeological analysis of fish remains from 113 sites or unique phases of occupation at the same site, and mammals from 116 sites (http://doi.org/10.5281/zenodo.14019080). The NISP per site for fish strongly declined throughout the period, averaging over 1000 at 5500 BCE but reducing to 100 by 4000 BCE (Fig. 4). There is no reason to assume that the size of excavation varied substantially with the age of the site, and the same pattern is evident when we consider the NISP density per square metre of excavation (volumetric calculations proved impractical; see Supplementary Information: Midden area and volume). The NISP values of terrestrial and marine mammals provide a useful control on these results and remain relatively stable, suggesting that the decline in fish remains is a genuine feature and not the result of a record biassed by sampling strategies or differential preservation.

Overall, the pattern suggests that finfish became less economically important as shellfish increased. A similar diachronic change is also present in the richness data, which points to the specialisation in fewer fish taxa over time (Fig. 4). Moreover, marine vertebrate isotopic compositions remain stable across the period when the organisms measured are stratified by their theoretical adult trophic level (see Fig. 4). This observation is based on significant datasets (n = 74, 169 and 117 for



Fig. 4. The archaeological record of marine resources, showing the temporal frequency of bone points and eel leisters, fish traps and weirs compared to shell middens (A), and the changing composition of vertebrate remains found in archaeological sites (B–D). Note how both the NISP and richness (i.e. number of different taxa present) of fish strongly declines throughout the millennia, whereas the relative abundance of mammals is static. Also note how the frequency of fishing-related implements *increases* during the Neolithic transition, indicated by the shaded area around 4000 BCE. Panels E and F show average stable isotope values from fish, stratified by their adult trophic level, indicating little change over time. For details on the sample sizes and the taxa involved, see http://doi.org/10.5281/zeno do.14019080. The vertical lines mark the transition to the Neolithic.

trophic levels 3.2, 3.6 and 4.1 respectively). Trophic level 3.2 is comprised principally of righteye flounders (Pleuronectidae); 3.6 mostly European eels (Anguillidae) and 4.1 mostly cods and haddocks (Gadidae) but significant numbers of other taxa are present in the sample too (see http://doi.org/10.5281/zenodo.14019080). The moving average

approach therefore integrates various isotopic perspectives into a signal of broader trends that indicate no clear evidence for perturbation in the marine trophic ecology. Marine mammals, whose remains are always much less frequently encountered at sites compared to fish, were exploited throughout the period, but as the evidence of fish exploitation



Fig. 5. Diagram of the sitewise relative proportion (% NISP) of the 12 most frequent finfish families found in the archaeological sites. Diadromous/freshwater families have a darker shade. Note the appearance of Anguillidae (European eel) after 4600 BCE and the temporary decline in Gadidae (cods and haddocks) around the transition period at 4000 BCE. The Mesolithic-Neolithic transition is shown as a horizontal line.

waned, the relative importance of marine mammals increased, dramatically so from *ca.* 4300 BCE (Fig. 4).

Disaggregation of the NISP temporal trend for finfish into taxonomic groupings produces too noisy a signal because of the small sample size, but examination of the percentage representation of taxa at individual sites demonstrates that certain key species are not evenly distributed through time (Fig. 5). Gadidae (cods and haddocks) have enduring importance but temporarily decline around the time of the arrival of agriculture. Anguillidae (European eel) are sporadic before 4600 BCE, but are well represented in the later part of the Ertebølle sequence and throughout the Neolithic period. Conversely Squalidae (dogfish sharks) are common in the early part of the sequence but become sporadic after 4600 BCE. All taxa vary in their relative proportion quite considerably, reflecting significant differences between sites. There is, however, no evidence that the sites were specialised according to local conditions or traditions, as mantel tests reveal little spatial autocorrelation in terms of the fish, marine mammals or molluscan taxa exploited (see Supplementary Information: Midden composition and Mantel tests).

Overall, the evidence of artefacts and faunal remains related to the exploitation of marine vertebrates indicates not simply a continuity of exploitation patterns across the Mesolithic-Neolithic transition, but an actual intensification in the Neolithic period, particularly regarding fishing, at least according to the evidence of bone points and eel leisters, fish traps and weirs and the rate of shell accumulation in shell middens. The progressive reduction in the relative abundance of fish remains and the reduced taxonomic richness of fish bone assemblages further reinforces this interpretation of intensification, at least to the extent that such trends are consistent with intensifying economic pressure on available fish stocks. At the same time, this overall trend is super-imposed on a background pattern of considerable fluctuations in the abundance of different categories of evidence both before and after the transition. Moreover, there is some evidence that the three main groupings - shellfish, finfish and marine mammals - were fluctuating in a

complementary manner, reductions in one category being offset by an increase in one of the other two, underscoring the overall resilience of an economy with a variety of marine sources at its disposal.

3.3. Isotopic compositions and biomolecular evidence

3.3.1. Human diet

We compiled stable carbon and nitrogen isotope data for 425 human individuals from prehistoric Denmark, from a diverse range of sites including shell middens, coastal, submerged and wetland settlements and find spots as well as long barrows, dolmens and passage graves (http://doi.org/10.5281/zenodo.14019080). Although the spatial and temporal distribution of this material is not uniform (Fig. 6), this nonetheless represents a significant dataset, especially given that 261 samples are directly associated with radiocarbon dates, enabling moving average models of diachronic change. These models rehearse the longestablished observation that the Neolithic period in Denmark appears to have been associated with a strong, rapid shift away from marine food resources (Fischer et al., 2007; Tauber, 1981). When the shell midden and non-shell midden individuals were considered separately (Fig. 6), there were some nuances; shell midden humans had slightly lower δ^{15} N values than their counterparts from other sites, as would be expected if they were more heavily dependent on marine resources with a low trophic level (e.g. shellfish), or marine taxa residing in eelgrass meadows which are likely to be 15 N depleted and might have become more intensively exploited in step with the proliferation of shell middens (Guiry and Robson, 2024; cf. Meadows and Fischer, 2024).

Whilst fewer in number in our synthesis, it seems that non-shell midden Ertebølle individuals were less dependent on marine resources in general, with a greater range of δ^{13} C values from individuals discovered in these contexts (Fig. 6). This reflects the inland burial location for some of these cases, where a greater reliance on terrestrial and freshwater resources is expected, although many burial sites



Fig. 6. Human isotopic compositions interred in shell middens and other Danish archaeological sites. Left panels show the temporal density (A), and location (B). Moving average models (C and D) illustrate the 'sudden' shift from marine to terrestrial sources in the Neolithic. Biplots in the right panels illustrate the variability by archaeological context (E, ellipses showing standard deviation) and genetic cluster compared to other taxa from the region (F). Note that vertical lines mark the date of the first indications of farming.

without middens are also close to or in some cases below the modern shoreline and there is no general correlation between the isotopic results and distance to coast (see Supplementary Information: Human stable isotopes and distance to coast). In the Neolithic, shell midden humans had slightly higher δ^{13} C values than those from other contexts, hinting at the continued consumption of a relatively small amount of marine protein. However, the strongest signal by far is the shift to terrestrial protein sources, with the average δ^{13} C values for shell midden humans dropping from -12.0 to -19 ‰ over the 200-year period from 4000 to 3800 BCE. Using the Bayesian mixture model simmr (Parnell et al., 2013) to explore how these values relate to the relative abundance of source dietary protein, we estimate this represents a shift from 63 to 94 % marine protein to only 3-36 % (Table 2). It is notable that the posterior probabilities estimated using the mixture model accommodate some input from marine protein in the Neolithic, as previously noted (Milner et al., 2004). For details of the modelling and the source values used, see Supplementary Information: Palaeodietary mixture modelling.

3.3.2. Pottery culinary practices

While bone collagen isotopic compositions provide a time-averaged palaeodietary proxy of protein intake, organic residue analysis of ceramic vessels offers information about culinary practice, and indirectly diet, at a more detailed scale. Our meta-analysis of 173 foodcrusts and 86 absorbed lipids in potsherds (Fig. 7; http://doi.org/10.5 281/zenodo.14019080) suggests there was no sudden change in cooking practices associated with the arrival of farming, but rather a record of continuous change spanning the transition. There are consistent differences in the results from coastal versus inland sites, most prominently visible in the bulk $\delta^{13}\mathrm{C}$ values of foodcrusts but also the $\delta^{13}\mathrm{C}$ values of C_{16:0} and C_{18:0} fatty acids (Fig. 7), broadly corresponding to differences in terrestrial versus marine input. Dairy biomarkers were present in the region before the introduction of farming (Courel et al., 2020; Lucquin et al., 2023) and while their relative presence increases slightly with time, no sudden change is evident. Interestingly, during the Neolithic period, dairy residues were more frequently encountered at coastal compared to inland sites, shown by a marked decrease in the Δ^{13} C proxy (Fig. 7F) (Copley et al., 2003).

3.3.3. Radiocarbon-dated ecofacts

At a larger scale, the temporal distribution of directly-dated domesticated plants and animals can be used as a proxy for their relative importance and compared with the KDE of all directly-dated shellfish and other marine animals (Fig. 8), and trends in site distribution (Fig. 2). The curve for marine resources shows a steady increase with an early, small growth peak at 5200 BCE followed by a major peak at 3920 \pm 95 BCE during the Neolithic transition. This peak subsequently slowly declines, significantly around 3650 BCE and again at 3400-3200 BCE. Likewise, the KDE of cereals demonstrates that their cultivation followed a marked boom-bust cycle in Neolithic Denmark, as it did simultaneously at similar latitudes in Europe (McClatchie et al., 2016; Stevens and Fuller, 2012). Domesticated animals appeared and declined at more moderate rates, peaking earlier at 3750 \pm 70 BCE versus 3595 \pm 10 BCE for cereals. This reflects the relative sequence of events (but not the absolute chronology) inferred from recent palynological work at Højby Sø, in northern Zealand (Allentoft et al., 2024a),

Table 2

Results of Bayesian mixture model estimates of the relative proportion of dietary protein sources (median posterior values and 95 % credible interval) for average isotopic values in human bone collagen per context, estimated using *simmr*.

•			•	
	Plants	Terrestrial	Marine	-
Mesolithic shell middens	9 (1–24) %	9 (2–27) %	79 (63–94) %	
Mesolithic non-shell middens	21 (3–53) %	27 (4–61) %	48 (27–73) %	
Neolithic shell middens	37 (4–79) %	46 (6–88) %	16 (3–36) %	
Neolithic non-shell middens	38 (4–81) %	47 (5–89) %	13 (2–33) %	

which shows that early farming in Denmark first had a focus on animal husbandry, and subsequently cereal cultivation. In general, during the 4th millennium BCE, the frequency of marine resources matched fluctuations in domestic animals, including a phase of recovery starting around 3200 BCE. This is the expected pattern if both were driven by changing human population numbers.

4. Discussion

Our analysis of multiple lines of evidence from material culture, archaeozoological assemblages and ceramic residues demonstrates that marine resources continued to be exploited during and after the introduction of agriculture, and in some cases more intensively than before. Our data analysis also indicates sustained human population growth during the Ertebølle period which continued into the subsequent Neolithic period. This raises four major issues: (i) our results cast doubt on those hypotheses that have argued for an environmental decline in marine resources as the trigger that opened the way to the introduction of farming by weakening the pre-existing Ertebølle economy (Lewis et al., 2016; Rowley-Conwy, 1984; Schulting, 2010; Warden et al., 2017); (ii) they appear to stand in direct contradiction to the long-established stable isotopic compositions of human remains, which shows a sharp dietary shift from marine to terrestrial foodstuffs across the Neolithic transition, implying a reduction in the exploitation of marine resources or even their avoidance (Allentoft et al., 2024a; Fischer et al., 2007; Tauber, 1981; Thomas, 2003); (iii) our results need to be reconciled with the new genetic evidence demonstrating a population replacement at the transition, indicating that the introduction of agriculture into Denmark was brought about by the spread of farming communities from the south (Allentoft et al., 2024a); (iv) our results support sustained episodes of population growth before, during and after the introduction of agriculture, raising questions about their potential impact on marine productivity and biodiversity. We consider each of these issues in turn.

4.1. Did marine resources fail?

Exploitation of the marine environment enabled the fluorescence of the Ertebølle culture, so questions naturally arise about how sustainable this economy was, and whether factors such as overexploitation or other environmental factors affecting the productivity of the marine environment led to the adoption of farming. Theories that might account for a decline in marine resources have included changes in seawater salinity or temperature, increased sedimentation rates in shallow water, or increased hypoxia in the inner waters of the Baltic, at or around 4000 BCE (Lewis et al., 2016; Rowley-Conwy, 1984; Schulting, 2010; Warden et al., 2017). However, our data synthesis provides copious evidence for fishing activity after the arrival of domesticated plants and animals: shell midden deposition continued (although gradually began to decline), fish stocks did not appear to collapse, fishing-related implements increased in frequency, and aquatic resources continued to be processed in ceramic vessels (Table 3).

Warden et al. (2017) identified evidence of warmer sea-surface temperatures leading to increased carbon flux and bottom water hypoxia in the Baltic at *ca*. 4000 BCE. They postulated that such increased eutrophication is likely to have been highly detrimental to bottom-feeding fish, which can include Atlantic cod (*Gadus morhua*) and saithe (*Pollachius virens*), leading to their decline and providing a trigger for farming to take hold. Some support for this hypothesis is present in our data, which show a short-lived decline in bones of Gadidae on archaeological sites at *ca*. 4000 BCE, and in some other taxa such as righteye flounders (Pleuronectidae) and European eel (Anguillidae) (Fig. 5). However, other indicators of marine exploitation are sustained and even increase across the Mesolithic-Neolithic boundary (Fig. 4), and Warden et al.'s (2017, p. 4–6) own archaeozoological analysis shows no overall decline in fish remains on Early Neolithic sites. Moreover, the



Fig. 7. Summaries of results obtained from the organic residue analysis of ceramics throughout the region, showing the temporal distribution of the material (A) and moving median summary statistics for the δ^{13} C values of C_{16:0} and C_{18:0} fatty acids, and the presence of biomarkers relative to all samples that yielded lipids (other panels). Coastal and inland sites are modelled separately to show consistent differences in isotopic compositions, especially bulk δ^{13} C (B) and δ^{13} C_{16:0} fatty acids (D), before and after the arrival of farming. Note that the arrival of farming (shown by the vertical lines) had little detectable effect on the culinary use of these vessels.

sediment cores they used to identify evidence of hypoxia within the Baltic Sea are more than 500 km distant from the Danish Straits, which is the regional focus of our analysis, and their 3-D modelling of increased probability of hypoxic conditions does not extend closer than about 300 km. Warden et al. (2017) also did not include any marine samples in their SPD-based proxy of population trends and therefore their results do not reflect the true intensity of coastal activity across the transition to agriculture. Krossa et al. (2017) have produced contradictory evidence indicating cooling of sea-surface-temperatures from cores in the Skagerrak some 100–200 km north of our region; they suggest this weakened the marine basis of the Ertebølle economy but do not specify how or why this should be so. Finally, sediment cores from within the Danish Straits, closest to the archaeological sites of our analysis (Lewis et al., 2020), actually show an increase in proxies of marine primary productivity at the time of the transition (Fig. 9). Further investigation of both the geochemical marine environment proximal to the archaeology and independent signals of marine biodiversity are needed to examine Warden et al.'s (2017) hypothesis further.

Much of the strength of the 'marine-decline' hypothesis has focused on oysters, which would have remained available in a palatable condition throughout the winter months (Yonge, 1960), precisely that lean time of year when other food resources would have been in shortest supply. Seasonality analysis supports this idea, demonstrating that this was the time of year when the majority of oyster collection took place during the Ertebølle period (Milner, 2002, 2013; Milner and Laurie, 2009; Robson, 2015; Robson et al., 2021b). Our own analysis (Fig. 3) shows a long-term decline in oysters, most likely due to a restriction of suitable habitat rather than to over-intensive harvesting pressure



Fig. 8. Kernel Density Estimates (75 year bandwidth) of the directly-dated marine resources, cereals and domesticated animals. Shaded areas represent periods of statistically significant increase or decrease in density, which at the first occurrences of each phenomenon primarily reflects their archaeological visibility; for example the earliest period of growth in the marine resource signal may be illusory because of under-representation due to removal of early coastal sites by sea-level rise. The early signal (pre-4000 BCE) of domesticated animals may represent the misidentification of wild mammals (e.g. Groß et al., 2024; though see Gron, 2023). The cereals peak later than the domesticated animals and decline more rapidly. Shaded areas highlight periods where the rate of change of the KDE is non-stationary at 95.4 % confidence. Decline in the 4th millennium BCE is common to all datasets.

(Robson et al., 2024). Removal or decline of such a critical lean-season resource could conceivably have had a disproportionate impact on the viability of the overall economy, sufficient to require the introduction of new economic strategies and resources. Against this hypothesis is the fact that exploitation of other marine resources could have been intensified to compensate for the decline in oysters as a critical resource, especially fish such as eel and salmon, and marine mammals, all capable of producing storable surpluses of oil- and fat-rich supplies for later consumption in the lean season. In support of this point, our results show that indicators of these resources were indeed increasing concurrently with the decline in oysters (Figs. 3 and 4, Table 3). Overall, there is extensive archaeological evidence for the continuation, and in some cases intensification, of marine exploitation during the Neolithic period, and this presents a trend closely coupled with the increasing density of archaeological sites (Fig. 2).

4.2. Did climate change determine the introduction of agriculture?

Given the absence of evidence for a collapse in fishing, marine mammal hunting and shellfish gathering, two important questions remain. First, what alternative mechanisms explain the delayed arrival of farming in Denmark? Farming economies of the LBK culture with cultivated crops and domestic animals were already established in adjacent regions of the North European Plain for at least 1000 years prior to their introduction to Denmark, providing ample opportunity for an earlier northerly expansion (Gron and Sørensen, 2018). This period has been described by Zvelebil and Rowley-Conwy (1984) as an availability phase, when Ertebølle communities co-existed with farming

Table 3

Summary of archaeological and biomolecular evidence for coastline exploitation
in prehistoric Denmark.

Coastline exploitation	Date range (BCE)	Description
Initial growth	Pre 5800	Fish traps in use. Sporadic shell midden accumulation; gradual increase in natural shell books
	5800–5200	Some increase in shell middens from <i>ca</i> . 5500 BCE indicating increasing dependency on marine resources, but subject to uncertainties because of sea-
Stasis	5200–4500	level change and potential under- representation of coastal sites. Growth in natural shell banks interrupted until 5000 BCE; little change in human patterns of exploitation;
		inshore resources became more important at subsistence level. Early occurrences of pots containing aquatic biomarkers.
Intensification	4500-4000	Bone point/eel leister fishing has become frequent. Shell midden activity intensifies in two pulses of growth, firstly with greater levels of visibility but also activity and nucleation at 4500 BCE, then from 4200 BCE with geographic
		expansion too. Finfish bones reduce in frequency and richness. Human population highly dependent on marine protein, with economic dependency on inshore resources isotopically evident for human remains from shell middens;
		natural shell banks begin to decline, as does the frequency of oysters in middens relative to other molluscs. Domesticated animals appear around 4000 BCE.
Slow decline	4000–3800 (transitional phase)	Peak human activity. Domesticated plants appear and like domestic animals rapidly become more frequent. Rapid human isotopic dietary shift to terrestrial
		resources but continuity in shell midden accumulations and geographic expansion trend continues. Bone points/ eel leisters continue to become more
	3800–3150	frequent. Decline in shell midden accumulation, activity becomes more diffuse in the landscape. followed at 3600 BCE by
		decline in frequency of all sites. Terrestrial resources dominate the diet with a peak in AMS dated cereals at 3600 BCE. at the same time hone points/eel
		leisters also peak in frequency. Evidence for natural shell banks all but disappears. Fish traps and weirs become more frequent, packing at 2400 BCE, Aquatic
		biomarkers in pots persist, slowly declining in frequency as dairy biomarkers increase.
Return	3150–2700	Moderate increase in activity across the landscape. Intense and spatially constrained Neolithic phase of shell midden activity on Jutland; use of fish
	2700–1200	traps and weirs declines. Sporadic shell midden accumulation in northern Zealand and northern Jutland, especially the Limfjord, and use of shell middens for burial.

communities to the south and were in contact with them, but had no reason to adopt agriculture or give way to immigrant farmers until the marine resources that supported large semi-sedentary populations went into decline. By ruling this theory out, it is logical to seek reasons for the delay elsewhere.

One hypothesis is Warden et al.'s (2017) suggestion that climate



Fig. 9. Pigmentation flux from Tempelkrog in northern Zealand (redrawn after Lewis et al., 2020), a proxy of marine primary productivity, compared to the density of directly dated marine organisms from archaeological sites from Figs. 8 and 10, with the Mesolithic-Neolithic transition around 4000 BCE highlighted.

change, identified in their analysis of sea surface temperatures, may have tipped the balance in favour of crop cultivation in previously marginal environments. Cereal crops are quite sensitive to changing climatic conditions and being close to their viable limit in Northern Europe would have been especially vulnerable to crop failure, discouraging the northward expansion of the whole agricultural package until climate changed in their favour. Just one bad season of crop failure or a run of bad seasons might be sufficient to require the total abandonment of the agricultural economy without alternative food supplies to fall back on (see e.g., Halstead and O'Shea, 1989). It is notable that crop cultivation began to increase in other parts of Northern Europe around the same time (Stevens and Fuller, 2012) and then appears to have failed several centuries later perhaps due to small climate fluctuations or decline in soil fertility (Colledge et al., 2019). Subtle changes in growing conditions whether from climate warming (Warden et al., 2017) or cooling (Krossa et al., 2017) might thus have provided the impetus for the expansion of farming into previously marginal and more northerly environments regardless of marine productivity. A climate reconstruction from Lake Belau and Lake Poggensee in northern Germany based on annually-resolved sedimentary changes suggests a phase of increasing summer temperatures from ca. 3850 BCE, thus coinciding with the expansion of farming from this region, although a degree of variability in seasonal weather patterns is also noted (Dreibrodt et al., 2012). Indeed, rather than hindering farming, a reliable alternative means of (marine) subsistence may have mitigated some of the risk and uncertainty in establishing cereal cultivation in climatically marginal environments, the exploitation of which could be intensified in years of poor crop harvests.

4.3. Resolving the paradox of the dietary isotopic evidence: a demographic model

A second question that arises if marine foods continued to make a substantial contribution to diet is how to explain the sudden disappearance of the marine isotopic signal in human bone collagen and the equally rapid population turnover evidenced by ancient DNA analysis (Allentoft et al., 2024a), which shows an almost total replacement of local hunter-gatherer populations at the Mesolithic-Neolithic transition by populations with Anatolian ancestry and a long history of animal husbandry and crop cultivation. The sample of Neolithic human remains analysed for their isotopic compositions is small, a fraction of a percentage of the overall population, but the samples are drawn from a wide range of contexts – shell middens, coastal, submerged and wetland settlements and find spots, and long barrows, dolmens and passage graves. It is therefore hard to sustain the argument that they represent a limited selective sample of individuals with privileged access to

domesticated terrestrial foods (Milner et al., 2004). Similarly, the sample of available Neolithic genomes analysed by Allentoft et al. (2024a) is small, but would be expected to include evidence of 'Western Hunter Gatherer' ancestry if it were present. Here we examine an alternative approach.

Given the evidence presented earlier for major fluctuations in the size of the human population, it is reasonable to examine demographic scenarios across the transition that could be masking the marine dietary isotopic signal while resulting in a 'replaced' ancestry. To explore this idea, we have developed an agent-based model (ABM) to simulate the interaction between two populations, and to estimate the time needed for the economic and/or genetic 'replacement' to occur.

The ABM simulation allows us to digitally model a growing virtual population, keeping track of the ancestry of each agent and hence its distribution through the population over time. In our illustrative example, we have modelled two populations, representing the 'Mesolithic' and 'Neolithic', but where slightly higher fertility rates among the 'Neolithic' group cause it to expand in number from a small starting population. Once the 'Neolithic' group has grown to twice the size of the 'Mesolithic', each year 1 % of the Mesolithic group leaves, and joins the Neolithic group. The archaeological record at Dragsholm offers a precedent for this scenario. Here, aDNA evidence presents a case where a male individual with Western Hunter Gatherer ancestry adopted a terrestrial diet and was afforded, in burial, the material culture of early farmers (Allentoft et al., 2024a, 2024b; Price et al., 2007). Table 4 lists the parameters of our model. Births, 'marriages' and deaths occur stochastically, controlled by defined probability distributions. Once the

Table 4

Parameters used in the agent-based model (ABM) simulation of the Mesolithic-Neolithic transition in Denmark. See http://doi.org/10.5281/zenodo.15471168 for the computer code in *R* used to create the model. * – The crude birth rate or births per thousand (calculated *post hoc*, as it is not directly modelled), is thus approximately 20 for the 'Mesolithic', and 25 for the 'Neolithic', falling to 15; these numbers are similar to modern populations, which range from around 7–10 for developed countries and 25–40+ for developing countries (UN, 2024).

ABM parameter	Value used in model	Rationale
Initial population size ratio	Set so the groups are equally sized around 4000 BCE, with the Neolithic doubling by 3900 BCE	As indicated by KDE models, the Ertebølle population was relatively high in its Northern European context, given a historic pulse of strong growth at 4500 BCE and subsequent sustained high activity. Allentoft et al. (2024a) found little difference in the homozygosity profile of Danish Mesolithic and Neolithic individuals.
Infant (<5 yrs) mortality rate	1 in 11 odds for both groups	Likely high, set here heuristically to balance the reproduction rate.
Life expectancy at 5 yrs	50 ± 10 for both groups	Likely quite low for prehistoric individuals, with a proportion of women dying before menopause.
Age at reproductive competence	17–44 yrs for both groups	Set heuristically to balance the effect of infant mortality and life expectancy.
Birth rate	Neolithic: 0.096 per woman of childbearing years, falling to 0.060 after 400 years Mesolithic: 0.075*	Set heuristically to match the empirical growth rate of radiocarbon-dated domesticates for the 'Neolithic' and zero net growth for the 'Mesolithic' population.
Rate of one-way mixture	-0.01	Given archaeological finds from Dragsholm, a rate of 1 % of Mesolithic people 'joining' the Neolithic community each year seems plausible.

simulation has run its course, the accumulated data may be probed to calculate the probability of detecting Mesolithic ancestry in an individual sampled randomly from the population. Further, by modelling the Mesolithic 'economy' as something practised by individuals with any degree of Mesolithic ancestry, thus simulating cultural rather than biological transmission, we can estimate its lasting contribution to the total resource base once the population itself becomes extinct.

The results (Fig. 10) illustrate one of many possible scenarios where a population replacement occurs through intrinsic demographic processes, without the need for short episodes of mass migration or elaborate models of cultural replacement, e.g. invasion scenarios. With a 1 % attrition rate per annum, the Mesolithic population becomes effectively extinct around 200 years into our simulations, with very low numbers for the final 3–4 generations. This would pose a challenge to detect using genomic methods (see Fig. 10, top middle panel) from the even considerable human skeletal record of prehistoric Denmark, given the relatively low sampling density and the resolution of radiocarbon dating. The stable isotope evidence for a 'rapid' shift from marine to terrestrial protein, for example, could have taken over 200 years (see Section 3.3 and Fig. 10). The ABM model also illustrates how signals of a given Mesolithic behaviour (e.g. fishing) could persist or even intensify post-extinction: a larger population would generate more archaeological evidence for a given behaviour, even as the overall economic importance of that behaviour became diluted from each individual's perspective.

Whilst the ABM fails to match the empirical KDE in terms of the

directly-dated marine ecofacts in this regard, it does for example quite accurately predict the temporal density of bone points and eel leisters (see Section 3.2. and Fig. 4). In the case of Neolithic Denmark, the model illustrates how fishing-related implements could increase in frequency as the isotopic evidence for fish consumption sinks below the limits of our capacity to detect it using bulk isotopic measurements of bone collagen alone. It also shows that significant population admixture is a short-lived phenomenon, and thus the genetic evidence for it will be slight until several generations into the process, by which time the model predicts that only a relatively small amount of 'Mesolithic' ancestry will be found. Although our model requires additional parameterisation and tuning to fully match all observed archaeological and archaeogenetic phenomena, it is broadly representative of the dynamics inferred from current empirical information, and demonstrates how powerful a mechanism population growth is for shaping the archaeological record. Small differences in birth rates can be compounded by the passage of time and lead to changes that seem dramatic.

The implication of this ABM is that a growing human population sustained by a combination of marine foods and farming products could easily generate an overall economy in which the relative contribution of marine foods to each individual's diet appeared lower than before, even though the total amount consumed by the population remained unchanged or even increased. The model does not address the causality of the transition but is intuitively less supportive of environmental mechanisms based on a decline in marine resources and more supportive of ones that suggest there were better conditions for establishing farming



Fig. 10. KDE models (A) and their first derivative expressed as an annualised growth rate (B) for all directly-dated domesticates and marine ecofacts. The transition to farming is shown by the vertical pink shading. These are used to parameterise the growth rate in an ABM simulation (C) where populations growing at different rates interact. Here, when a small but fast-growing 'Neolithic' population overtakes a 'Mesolithic' one, 1 % of the 'Mesolithic' join the 'Neolithic' each year. The Neolithic reproduction rate eventually falls, to simulate a 'boom-bust' dynamic. Shown are the results in terms of arbitrary population numbers (top-centre), growth rate (bottom-centre), plus the gradual diffusion of 'Mesolithic' socioeconomic (top-right) and genetic (bottom-right) signals. Note that the probability of detecting significant 'Mesolithic' ancestry is only high during the initial decades of the transition although conversely the probability of detecting low amounts of 'Mesolithic' ancestry increases with time. Also note the rapid (200-year) fall in Mesolithic signal per agent (i.e. diet or other culturally-transmitted behaviour) which stabilises here at 10 %.

(Warden et al., 2017). Such demographic increase seems plausible in the light of empirical evidence from around the world that associates agricultural innovations with population growth (e.g. Downey et al., 2014; Gignoux et al., 2011; Page et al., 2016; Shennan et al., 2013).

4.4. Humans impact on marine biodiversity

Given the complex patterning of time trends in many of the marine indicators examined above, the question naturally arises as to how far these changes are the result of increased human impact as opposed to changes in the natural environment. Our data provide both direct evidence in the form of KDE trends for sustained if intermittent growth in human population size, especially in the Early Neolithic, and also indirect evidence from agent-based modelling, which requires a significant increase in population size to account for the dilution of marine palaeodietary signals in individuals of an immigrant population. These population trends are associated with evidence for increased consumption of at least some of the marine foods represented in our data, and we might therefore predict a priori that this increased demand would have had a long-term impact on the marine ecosystem, leading for example to a reduction in taxonomic diversity, depletion or degradation of some resources, or changes in the isotopic composition of marine organisms because of 'fishing down the web' (Pauly et al., 1998). At the same time, there is abundant evidence for a variety of natural changes in the marine environment resulting from changes in sea surface temperature, salinity, primary productivity, tidal regime and sedimentary substrates.

Disentangling the relative influence of these various processes and discriminating between natural and anthropogenic impacts in such circumstances, is especially challenging, and may well lie beyond the resolution of the data currently available. Ideally, we would need evidence for changes in the natural availability of marine resources independent from the changes recorded in archaeological deposits; the archaeological changes might well have been influenced by changes in cultural tradition or technology irrespective of natural availability. However, such independent evidence is currently very limited, especially as regards changes in individual marine taxa. Or it is, at best, indirect and rather generalised as for example in data on primary marine productivity, sea surface temperatures or natural shell banks. Two features invite further comment: changes in the consumption of marine molluscs, in particular oysters, and their ultimate decline; and the progressive decline in the NISP data for fish bones and their taxonomic richness, which appear to be closely coupled.

Changes of marine molluscs are of particular interest because it is the one resource for which we have independent evidence of natural availability in the form of natural shell banks. However, the data are contradictory, with fluctuations in the frequency of the shell banks that are similar to fluctuations in marine mollusc consumption but out of phase with them by 400 years or more. The sharp decline in natural shell banks at a time when the archaeological oyster curve is still increasing at the end of the Ertebølle period, between ca. 4700 and 4300 BCE, is particularly puzzling, especially since oyster shells are a major contributor to the development of natural shell banks because of the preference for their larvae to settle on previously deposited oyster shells, resulting in the creation of substantial oyster reefs. Since the shell-bank data lump together different taxa that cannot reliably be disaggregated due to the small sample size, we suspect that the curve may be masking differential trends in different molluscan species. In any case, the temporal density of natural shell banks is our least robust dataset, with the fewest data points, and cannot be relied on to provide an accurate representation of changes in molluscan availability, let alone changes in individual species.

Another type of evidence that offers some insight into this issue is evidence of changes in oyster size, age-at-death and growth rates. Under heavy human harvesting pressure, we would expect to see reductions in oyster size and age-at-death distributions, while growth rates might vary depending on changes in the natural environment. Analysis of biological age at death, size and growth rate of more than 2000 oyster shells from 20 archaeological sites in the period from 5660 to 2600 BCE has shown that oysters were subject to a consistent level of harvesting pressure throughout the Ertebølle period, with occasional evidence of slightly increased harvesting pressure during the Neolithic period, implying increased demand from a growing human population (Robson et al., 2024; see also Bailey et al., 2008). Where Neolithic shell deposits are stratified above Mesolithic ones, there is little evidence for changes in growth rates, and no evidence for a sharp drop in biological age and size of oysters preceding the shift to cockle-dominated deposits, as would be expected if over-exploitation were the cause of the oyster decline, except at one site (out of five), which appears to be an outlier (Robson et al., 2024). Overall and at the regional scale, there is little evidence that a larger population in the Neolithic period was responsible for changes in the abundance or species-composition of the naturally available mollusc supply, and the oyster decline appears to have been mainly due to reduction in available habitat.

Turning to the fish data, the downward trend in NISP and taxonomic richness seems paradoxical, given the artefactual evidence for increasing emphasis on fishing (Fig. 4). As with the natural shell-bank data, the evidence is too sparse to dissaggregate the general NISP trend into individual taxonomic groups or species, which may be fluctuating independently of each other, but the richness data is consistent with increasing specialisation on fewer species. The percentage representation at individual sites suggests that some taxonomic groupings, such as eel, are especially well represented in the later Ertebølle and Neolithic periods (Fig. 5). Such specialisation is consistent with the evidence for increased construction of fish weirs in the Neolithic period, which are particularly well suited to trap eels in large numbers (Fischer, 2007). The general downward trend of the NISP count must therefore be accounted for in other ways, either by a progressive decrease in the disposal of fish bone at known archaeological sites, perhaps associated with increased off-site processing at fish traps; or there was a consistent downward trend in the natural availability of fish stocks. Notably, however, the stable isotope data show no major changes in nitrogen isotope values of fish, as might be expected if the marine food web had been significantly perturbed (Fig. 4).

In summary, there are suggestive hints of human impact on the marine ecosystem but limited evidence of large-scale or sustained anthropogenic impact, and insufficient data points or chronological resolution to pursue the matter further. The most important conclusion to emerge is that both changes in human economic practices and changes in the natural environment were taking place simultaneously over long periods of time both well before, during and long after the Mesolithic-Neolithic transition, and this represents a continuously moving target of interacting variables that defy easy analysis. From this perspective, the Mesolithic-Neolithic transition looks like an arbitrary line drawn across a continuum, a few freeze-frames in a continuously evolving drama. Further progress will require better independent data on the natural availability of different marine taxa. Perhaps the best chance of achieving that goal is the rapidly developing application of eDNA analysis of marine sediments (Holman et al., 2023), which offers the potential for monitoring biodiversity through the sedimentary sequence.

5. Conclusions

Archaeological data are biassed through preservation and recovery, spatially heterogeneous, highly varied in nature, and associated with significant and mathematically complicated sources of uncertainty. These issues complicate any attempt to understand how past changes in human behaviour impacted the environment or *vice-versa*, even for the rich archaeological record of Denmark. We present here the informatics tools needed to extract signals from the accumulated data and thus recover evidence for changing patterns of human interaction with the environment. In Denmark, some of these changes can be strongly associated with natural processes. The absence of the coastline (by erosion or submergence) in the earliest part of the sequence hampers our understanding of the use of coastal and marine resources in the Maglemose and Kongemose periods, which might have been more intensive than implied by the scant surviving evidence of coastal sites and shell middens. Nevertheless, the slowing rate of relative sea-level change during the Ertebølle period appears to have led to the formation of relatively stable and productive marine environments that offered more abundant supplies of marine molluscs and other marine foods. The human settlement of these environments gradually intensified, with a more rapid pulse in the middle Ertebølle period around 4400 BCE, accepting the KDE data as representative, or more rapidly from earlier in the Ertebølle if coastal sites at that time were still under-represented because of relative sea-level changes. By 4000 BCE in the late Ertebølle, shell middens and other marine indicators reached their zenith, just as the transition to agriculture began.

As the new, agricultural, higher-fertility Neolithic population took up residence in southern Scandinavia, they and their descendants incorporated the old fishing and shellfish foraging lifeways but did so within a society operating at an even larger scale of economic activity. Yet the Neolithic economy, dependent on domesticated plants and animals at the level of subsistence, was not stable over the long term and after 10 generations or so (from *ca*. 3650 BCE), it declined as quickly as it had appeared. This 'boom-bust' dynamic is characteristic of the Early Neolithic across Europe. When growth returned to Neolithic Denmark around 3200 BCE with the appearance of the Pitted Ware culture, so too did traditions of coastal exploitation that echoed those of previous millennia, and these continued in one form or another in the subsequent millennia.

Our agent-based modelling approach offers a demographic explanation for why there was a sharp shift in diet at the onset of the Neolithic despite copious archaeological evidence for persistence of fishing and shell gathering as a cultural tradition. However, it does not fully explain all features of the data; the slow decline of shell middens contrasts with a more sudden reduction followed by a brief resurgence in 'Mesolithic' resource exploitation predicted by the ABM for the Early Neolithic period (Fig. 10). This may be due to the inherent limitations of radiocarbon dating, making it difficult to recover signals varying over shorter timescales, or may simply reflect that the parameters of our model need adjustment. Further modelling and simulation work must attempt to further explore the potential parameter space of culturally and genetically mixing human populations and whether they will be recoverable empirically given the limitations of radiocarbon evidence.

Taken together, our data synthesis and simulation experiments permit a phase, lasting up to 200 years, when indigenous Mesolithic and incoming Neolithic groups would have co-existed in Denmark. During this period, early farming communities may have acquired specific local indigenous knowledge regarding marine exploitation even though evidence of cultural or genetic exchange is limited. Indeed, the apparent ease with which the earliest farmers began fishing and shellfish gathering contrasts sharply with the ability of foragers to adopt farming, of which there is very little isotopic and genetic evidence. This points to fundamental differences in the way that these subsistence strategies were learnt, shared and inherited.

We further suggest that the eventual decline in shell middens in Denmark in the 4th millennium BCE cannot be directly attributed to environmental change, nor the disappearance of the Ertebølle culture (pace Lewis et al., 2020; Warden et al., 2017) but instead reflects the population dynamics of the Neolithic period, especially from 3650 BCE. Early farmers incorporated traditions of coastline exploitation to help feed an expanding human population but one that was ultimately less stable over the long term. A key target for future studies is to directly identify low or sporadic marine consumption in these early farmer groups, which we hypothesise must have been the case, perhaps through stable isotope analysis of serial tooth sections (e.g. Montgomery et al., 2013) or by constructing high-resolution dietary records from collagen

amino acids (e.g. Fontanals-Coll et al., 2023; Soncin et al., 2021).

CRediT authorship contribution statement

T. Rowan McLaughlin: Conceptualization, Data curation, Formal analysis, Investigation, Methodology, Software, Validation, Visualization, Writing - original draft, Writing - review & editing. Harry K. Robson: Conceptualization, Data curation, Formal analysis, Investigation, Methodology, Project administration, Resources, Validation, Writing - original draft, Writing - review & editing. Rikke Maring: Formal analysis, Investigation, Resources, Writing - review & editing. Adam Boethius: Investigation, Resources, Writing - review & editing. Eric Guiry: Formal analysis, Investigation, Resources, Validation, Writing - review & editing. Daniel Groß: Investigation, Resources, Writing - review & editing. Satu Koivisto: Investigation, Resources, Writing - review & editing. Bente Philippsen: Investigation, Resources, Writing - review & editing. Nicky Milner: Conceptualization, Funding acquisition, Methodology, Writing - review & editing. Geoff Bailey: Writing - original draft, Writing - review & editing. Oliver E. Craig: Conceptualization, Funding acquisition, Methodology, Writing - original draft, Writing - review & editing.

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. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.quascirev.2025.109447.

Data availability

All the data analysed in this paper are available from the repository at http://doi.org/10.5281/zenodo.14019080. Code to replicate the analysis has been archived at http://doi.org/10.5281/zenodo.15471168.

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