Climatic changes cause synchronous population dynamics and adaptive strategies among coastal hunter-gatherers in Holocene northern Europe

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Abstract

Synchronized demographic and behavioral patterns among distinct populations is a well-known, natural phenomenon. Intriguingly, similar patterns of synchrony occur among prehistoric human populations. However, the drivers of synchronous human ecodynamics are not well understood. Addressing this issue, we review the role of environmental variability in causing human demographic and adaptive responses. As a case study, we explore human ecodynamics of coastal hunter-gatherers in Holocene northern Europe, comparing population, economic and environmental dynamics in two separate areas (northern Norway and western Finland). Population trends are reconstructed using temporal frequency distributions of radiocarbon dated and shoreline dated archaeological sites. These are correlated to regional environmental proxies and proxies for maritime resource use. The results demonstrate remarkably synchronous patterns across population trajectories, marine resource exploitation, settlement pattern and technological responses. Crucially, the population dynamics strongly correspond to significant environmental changes. We evaluate competing hypotheses and suggest that the synchrony stems from similar responses to shared environmental variability. We take this to be a prehistoric human example of the “Moran effect”, positing similar responses of geographically distinct populations to shared environmental drivers. The results imply that intensified economies and social interaction networks have limited impact on long-term hunter-gatherer population trajectories beyond what is already proscribed by environmental drivers.

Keywords: *Synchronicity; Moran effect; human ecodynamics; hunter-gatherers; paleodemography; maritime adaptation; Fennoscandia.*

1. Introduction

Synchronized demographic and behavioral patterns among distinct and geographically separate populations is a well-known natural phenomenon that has been demonstrated across animal and plant populations. The study of spatial synchrony has thus become a key topic in population ecology. “Spatial synchrony” refers to coincident changes in the abundance or adaptive response of geographically disjunct populations (Liebhold et al., 2004). Three primary mechanisms have been offered to explain such synchrony: (a) dispersal or migration among populations, (b) trophic interactions with populations of other species that are themselves spatially synchronous or mobile, and (c) spatially correlated environmental influences (Liebhold et al., 2004). This last phenomenon is known as the “Moran effect”, remarking upon the tendency of spatially separated populations to fluctuate in synchrony when exposed to similar environmental conditions (Moran 1953). The Moran effect is often thought to be the result of synchronous weather or climate influences acting on spatially disjunct populations (Moran, 1953; Koenig, 2002; Rosenstock et al., 2011; Kahilainen et al., 2018).

For prehistoric humans, Shennan et al. (2013) were the first to identify synchrony in ^{14}C date-based human population proxies across mid-Holocene Europe. This synchrony was attributed to migration and population growth, induced by the introduction of agriculture 8000–6000 cal yr BP. Recently, Freeman et al., (2018) argued that synchronous patterns in ^{14}C-time series observed across the globe during the Holocene were the result of intensified networks of trade and migration within continents, while convergent cultural evolution towards more energy-consuming political economies with higher carrying capacities account for global synchrony. However, as Freeman et al. (2018) admit, they omit climate change as the driving force behind the observed synchrony, despite it being the explanation most commonly used in ecology. This is critical, as climate can influence human growth rates either directly (extreme events) or indirectly by affecting environmental productivity and, consequently, food availability. We suggest that evaluating the role of climate change in driving synchronous human demographic and adaptive responses requires analyses sensitive to regionally specific ecological conditions.

Here, we compare Holocene hunter-gatherer ecodynamics in two northern European regions: western Finland and northern Norway. We investigate the role of climate in controlling coastal hunter-gatherer population trends and changes in adaptive strategies between the two regions. We show that population size and adaptive strategies change synchronously between western Finland and northern Norway. These changes coincide with climate changes and consequent changes in food availability. Thus, our results highlight the role of environmental factors in creating spatial synchrony in long-term human population dynamics across space.

2. Regional setting

The data catchment areas of our study are the coasts of northern Troms and western Finnmark Counties, constituting the north-westernmost margin of Norway (69°-71° latitude), and the Ostrobothnian coast in western-central Finland (63°-65° latitude) (Fig 1).

-insert figure 1

The study areas occupy northern coastal ecotones while simultaneously being different systems in terms of ecology and geography. These areas are positioned along different aquatic systems: Northern Norway is on the oceanic interface of the North Atlantic and the Barents Sea, in which upwelling, salinity and significant tidal actions produce a highly productive coast. Western Finland is adjacent to the more enclosed Gulf of Bothnia in the Baltic Sea, marked by relatively low salinity and minimal tides. Also, the topography of these areas differ: Western Finland is a flat continuous coastline, while northern Norway is a rugged, mountainous coastline scattered with islands and deep-cutting fjords.

By the time of the mid-Holocene, the two areas had quite different ecological systems. The Finnish area has a significantly more productive terrestrial ecosystem compared to that of northern Norway, primarily due to latitudinal differences. Major changes occurred in the terrestrial environment during the mid-Holocene, as the previously species-rich mixed forest of the Finnish terrestrial system became increasingly dominated by spruce (*Picea abies*). This turned the forest ecosystem into a modern boreal taiga dominated by spruce and pine (Seppä et al., 2009a).

A recent compilation of a large set of pollen cores from across northern Norway indicates a patchwork of vegetation cover, structured both by the inland/coast-axis as well as a west/east-axis, in which the outer coastal area of northwestern Norway was characterized by birch forest cover exceeding current conditions (Sjögren and Damm, 2019). This likely impacted the biogeography of key terrestrial mammals with a shift from post-glacial large herds of migratory ecotype reindeer to smaller herds of sedentary ecotype reindeer (Hood, 2019: 23).

Another important factor in area selection is the fact that Fennoscandia hosts archaeological records of continuous of hunter-gatherer populations throughout the Holocene. These records demonstrate shared adaptive characteristics between the areas with reliance on marine subsistence technologies at an early stage. What is more, there are some indications of participation in extensive interaction spheres, as evidenced by shared material culture traits such as slate technology, ceramics, rock art, imported amber and early metal products (Damm, 2006; Nordqvist et al., 2012; Ramstad et al., 2015). However, very little evidence exists to determine the magnitude of interaction between the areas. On the contrary, there is more separating the areas in terms of culture-history than what is shared.

The areas have some similarities in post-glacial colonization history, but also exhibit important differences. Following the deglaciation of the final Pleistocene, coastal areas of the Fennoscandian/Baltic shield became increasingly accessible for colonization by marine flora and faunas. This process is thought to have triggered a significant incentive for humans to colonize the post-glacial coastal landscape of northernmost Europe. This entailed a radical economic shift: From terrestrially-oriented foraging societies of the Late Glacial Ahrensburgian and Butovo/Veretye groups on the Eurasian plain, moving north/west and developing the maritime adaptations quintessential to the Scandinavian Mesolithic (Schmitt et al., 2006; Bang-Andersen, 2012, 2013; Schmitt, 2015; Schmitt and Svedhage, 2015; Dolukhanov et al., 2017;). The colonization of Norway at the termination of the Younger Dryas (11.700 cal yr BP) occurred along a coastal route requiring seafaring vessels and the know-how of a marine-oriented economy (Bjerck, 2017). The case is somewhat different in Finland, colonized from a terrestrial route. The Finnish case is most in line with the model suggesting maritime adaptations originated in Upper Paleolithic river resource utilization, which was later adapted to larger water bodies that then allowed people to move into the marine niche on the oceanic coasts (Vasil’evskii et al., 1998; cf. Cziesla 2007; Terberger et al., 2013; Cziesla, 2018). At the Pleistocene/Holocene-transition, most of present-day Finland was submerged due to glacio-isostatic loading, yet the ensuing isostatic uplift rapidly transformed the area from a postglacial coast into a patchwork of rivers, lakes and wetlands. The archaeological record also testifies to aquatic economies from the very onset. Complex technologies used for aquatic resource exploitation are evident already from the early Holocene, including the spectacularly well-preserved Antrean fish net dated to 10.500 cal yr BP. During the mid-Holocene, massive stationary fishing structures, such as weirs and lath screen traps recovered from multiple estuaries offer extensive evidence of marine-oriented facilities requiring substantial investment (Koivisto, 2012; Koivisto and Nurminen, 2015; Butler et al., 2019; Groß et al., 2018; Koivisto et al., 2018). The different routes to maritime adaptations underline the comparative relevance of the cases and provide pertinent insight into the evolution of fully-fledged maritime adaptations.

Data-quality is also a vital factor in area selection. Both areas have been intensively investigated archaeologically, including large-scale excavations and surveys. Together with excellent palaeoenvironmental records, the two regions offer robust testing grounds for evaluating changing human ecodynamics.

3. Materials and methods

3.1. Human population size proxies

We reconstruct human population trends in the two areas using temporal frequency distributions of archaeological materials. We consider the timespan from the early Holocene colonization at ~12.000 cal yr BP to about 2000 cal yr BP, at which point farming achieved a more permanent foothold and changes in settlement patterns and economy ensued in northern Fennoscandia. Prior to this, farming made minimal impact on both areas, particularly so in northern Norway.

For western Finland, we use the temporal distribution of 754 shoreline-dated sites as the basis of the population reconstruction (Tallavaara and Pesonen, in press). A gradual and well-established shoreline displacement due to post-glacial isostatic uplift provides high-resolution dating on the basis of elevation above sea level. As with radiocarbon dates, we assume that variation in the number of sites reflects relative changes in past population size. The sites have primarily been identified through LiDAR mapping and the current sample exclusively consists of sites positively confirmed as archaeological remains by field surveying. Included site types range from open-air sites, pithouse sites of variable sizes, to row-house sites and megastructures. Despite a potentially lower chronological resolution, we argue that this approach is justifiable as it substantially boosts sample size in area containing few radiocarbon-dated sites. Further, the approach helps overcome investigation biases, as all identifiable site types are included regardless of the presence of radiocarbon dates. Thus, this site-based proxy sidesteps many of the sampling biases inherent in radiocarbon-based population proxies. The approach also takes advantage of the favorable isostatic properties of the area. Western Finland is positioned near the weight-center of the Fennoscandian ice-cap, resulting in isostatic uplift of more than 200 meters over the past 12,000 years. Given a mostly flat topography, the isostatic rebound of the area provides ideal conditions for high-resolution shoreline dating. Virtually identical trends have been established between the regional site-based reconstruction and the SPD, which is based on the radiocarbon dates covering the total area of Finland. (Tallavaara and Pesonen, in press). This strengthens the reliability of the site-based proxy. Although the population proxies for our two study areas are derived from different source data, we have opted for this strategy as it produced samples of comparable size.

For northern Norway, the reconstruction of population dynamics is based on the summed probability distribution (SPD) method of radiocarbon dated site occupation events (Shennan and Edinborough, 2007; Williams, 2012; cf. Bronk Ramsey, 2017). This method is premised on the proportional relation between population size and datable components of the archaeological record (Rick, 1987; cf.

Haynes, 1969; Kirch, 1980). This so-called dates-as-data premise implies that smaller populations leave behind a smaller sample of archaeologically visible traces, compared to a larger population. Major efforts have been made to test this premise (Surovell and Brantingham, 2007; Surovell et al., 2009; Shennan, 2013; Timpson et al., 2014). Following the results in Edinborough et al., (2017), the method has demonstrated its usefulness in reconstructing palaeodemographic fluctuations. For the current study, archaeological radiocarbon dates were collected for the coast of northwestern Norway, which contains the densest and most recently produced radiocarbon record in northern Norway. The dataset (N=735) exclusively comprises radiocarbon dates from secure archaeological contexts, made on terrestrial carbon (see Supplementary Information). These have further been vetted for taphonomic, investigative and sampling biases (Jørgensen, in press). The dates were then structured into 503 bins of 200 years in order to control for over-representation of more intensively investigated sites. Further details on auditing measures of the current dataset are presented in Jørgensen (in press).

3.2. Palaeoenvironmental data

Holocene environmental changes are represented by eight palaeoecological and palaeoclimatic proxies. We selected available proxies that are related to the productivity of terrestrial and marine environments and, consequently, to food availability for hunter-gatherers. Somewhat different environmental proxy types represent the two areas. This is the result of regional differences in depositional and geomorphic qualities, as well as unequal conditions for preservation of palaeoenvironmental proxy data. The palaeoenvironmental proxies discussed in this paper are summarized in (Table 1).

-Insert table 1

Prehistoric human population dynamics in western Finland are compared to: 1) a measure of annual mean temperature, which is a stack of four pollen-based temperature reconstructions across southern and central Finland. 2) The strength and length of the growing season, which is based on organic matter flux in a varved lake (Ojala and Alenius, 2005; Ojala et al., 2008). 3) Baltic Sea surface temperature (SST) reconstruction, derived from TEX_{86}-paleothermometer (Warden et al., 2017). 4) Baltic Sea salinity levels (‰) based on the compilation of several proxies (Gustafsson and Westman, 2002). Salinity is important in tracking changes in oceanic vs. enclosed, brackish conditions of the Baltic Sea. This has ecological implications, as salinity levels structure aquatic biogeography and affects productivity of the Baltic Sea.

For northern Norway, SST of the North Atlantic Current collected at the offshore shelf break tracks variation in mixing of warm Atlantic and cold Arctic waters at the mid-Norwegian margin (Calvo et al., 2002). Ocean mixing is a significant factor in structuring marine biogeography and for inferring large-scale oceanographic and environmental conditions. Two proxies of inner coastal aquatic conditions in northern Norway are included as the fjord-biome is of great importance to the human populations in the area. Bottom water temperatures (BWT) of a major fjord-system (Malangen fjord) in the study area tracks changes in the coastal current (Husum and Hald, 2004). In addition, we contribute a new palaeoproductivity measure of the same local fjord environment. The fjord productivity proxy is made up of previously unpublished data, courtesy of Jochen Knies at the Norwegian Geological Survey. The percentage of carbonate is used as a direct marker of productivity in the fjord as it relates to the abundance of calcium/chalk-dependent zooplankton, which in turn is the foundation of the marine trophic pyramid. This assumption is justified as the relative proportion of terrigenous-free (biogenic) carbonate has been shown to be a highly suitable indicator of changes in palaeoproductivity in the area (Knies et al., 2003: 1–2; cf. Gardner et al., 1997).

We also include a humification index from the outermost western coast of Norway. The peat humification index is a combined indicator of temperature and precipitation – evapotranspiration – that also reflects changes in terrestrial productivity (Vorren et al., 2012).

3.3. Maritime resource exploitation data

In order to explore potential synchrony between adaptive strategies, population size and environment, we assembled multiple indicators of marine resource use.

To track changes in the subsistence/adaptive strategies in western Finland, we calculate two closely related measures: The proportion of seal bones in archaeofaunal assemblages in coastal sites (seal NISP/total NISP) and the index of seal bones relative to terrestrial mammals (seal NISP/(seal NISP + terr. mammal NISP)) (Grayson, 1984). Although not a direct quantitative measure of seal consumption, we assume that changes in the proportion of seal bones reflect changes in the importance of seals in human diet. As a secondary premise we assume that such variation indirectly reflects adaptive adjustments following either environmental or technological changes. The archaeofaunal data consist of 37,810 burnt bone fragments from 72 archaeological assemblages across the Finnish coast. These data were extracted from the archives of osteological reports compiled by Pirkko Ukkonen and Kristiina Mannermaa at the Finnish Museum of Natural History, and from osteological reports at the National Board of Antiquities. The faunal record was attributed to broad chronological periods based on time constraints given by associated radiocarbon dates or typological artefact attribution: Early Mesolithic (11,000–8500 cal yr BP), Late Mesolithic (8500–7200 cal yr BP), Early Sub-Neolithic (7200–6000 cal yr BP), Middle Sub-Neolithic (6000–5400 cal yr BP), and Late Sub-Neolithic (5400–3500 cal yr BP).

Due to poor preservation of organic remains, there is no representative archaeofaunal sample to draw on from the Norwegian area and we had to devise an alternative measure of marine resource use. In order to map changes in marine resource use, we assembled a "Slate Index", premised on the strong affinity between maritime adaptive strategies and the use of slate tools. The Slate Index tracks the abundance of slate tools relative to other lithic industries, based on the averaged frequencies of slate vs. harder lithic materials from a selection of reliably dated site assemblages. The dataset consists of 37 securely dated lithic assemblages covering the entire local Stone Age chronology, with more than 22,000 lithic objects. Importantly, most of the assemblages stem from multi-phase sites of significant occupation history. This factor helps control for variation in site function. As the ecological properties of a single coastal site are assumed to be more or less stable, any major variation in lithic assemblage composition through time is assumed to reflect changes in subsistence strategies.

Based on the near-universal reliance on slate tools amongst circumpolar maritime hunter-gatherers (Fitzhugh, 1974), we assume that slate tools provide a reliable indication of maritime resource exploitation. There have been multiple attempts at explaining the strong prevalence and assumed superiority of slate tools for maritime economic purposes (Gjessing, 1953; Dumond, 1968; Ritchie, 1969; Fitzhugh, 1974; Clark, 1980, 1982; Morin, 2004; Graesch, 2007; Dinwiddie, 2014). As a basic premise, we follow several arguments and empirical demonstrations (Clark, 1979; Wilhelmsson, 1996; Nuñez, 1998; Morin, 2004) that slate technologies can reduce handling costs and facilitating mass-harvesting of marine resources (sensu Madsen and Schmitt, 1998), and thus alter the energy budget and ranking of marine/terrestrial resources. As a result, slate technology could significantly boost food security and survivorship, and hence population numbers, among maritime hunter-gatherers. In northern Norway, slate tools have an almost exclusively coastal distribution, supporting our assumption that slate tools were used primarily as a maritime technology and thus a relevant proxy for marine resource exploitation. Despite lower sampling density of inland sites potentially contributing to this picture, reviewing existing data suggest two patterns: 1) there is literally no evidence for slate tool production in the interior, indicating import (cf. Hood, 1992, p. 521). 2) In the rare cases of locally procured material, inland slate tools appear to be of a much more silicified raw material and subject to a different reduction sequence, occasionally even made by recycling greenstone tools (cf. Rigajokka site (Helskog, 1974, pp. 4–5)).

4. Results

Figure 2 shows the reconstructed population dynamics/trajectories for northern Norway and western Finland and reveals a clearly synchronous pattern between the two regions. A major feature in both reconstructions is the prominent boom-and-bust cycle between 6500/6000 and 5000 cal yr BP. However, in northern Norway the highest population levels apparently occur c. 300 years earlier than in western Finland. In addition to this major population boom-and-bust, the population proxies further indicate synchronous declines at 8200 and 7000 cal yr BP.

-insert Fig.2

Figure 3 further shows a correspondence between long-term human population dynamics and environmental variability in both areas. In the Finnish dataset, proxies covering both marine and terrestrial productivity show increasing trends culminating around 6000 cal yr BP, concurrent with the prominent population peak (Fig 3. b—e). This is particularly evident in the marked correspondence between the reconstructed population trend, growing season intensity (Fig 3.c) and the Baltic Sea SST (Fig 3.d). The subsequent population decline coincides with declining Late Holocene productivity (see also Tallavaara and Seppä, 2012). Furthermore, population dips observed in both areas at around 8200 and 7000 cal yr BP coincide with shorter-duration downturns in temperature and growing season intensity (Fig 3. b—d).

The pattern is similar in the Norwegian study area, where marine proxies (Fig3. i—k) show peaking sea surface temperatures and marine productivity around 6000 cal yr BP. The North Atlantic Current conveyed higher quantities of warm Atlantic water during the mid-Holocene and the coastal water temperature and marine productivity peaked in the major fjord system within the study area (Fig 3.i). This indicates a mild climate with increased Atlantic water in the fjord system that drove the production of carbonate (either produced in-situ or transported with the Atlantic water).

In accordance with the Finnish data, temperatures and productivity declined after 6000 cal yr BP. The evapotranspiration reconstruction (Fig 3.h) shows a slightly different pattern as the highest values occur between 7500 and 6500 cal yr BP. Nevertheless, very stable conditions are recorded around the 6000 cal yr BP population peak, while a general climate shift towards highly variable conditions occurred with the transition to the late Holocene.

-insert Fig.3

In northern Norway, population declines at 8200 and 7000 cal yr BP coincide with the Storegga tsunami, caused by the massive submarine landslide in the Norwegian Sea (Romundset and Bondevik, 2011), and the Tapes transgression (Sørensen et al., 1987; Romundset et al., 2011), respectively. Thus, taphonomic loss of archaeological material may be responsible for the declines in the Norwegian population proxy (see also Jørgensen, in press, 5). However, this is most likely an insufficient cause as the population declines at 8200 and 7000 cal yr BP perfectly mirror the Finnish settlement data, where no such taphonomic loss is observed. This suggests that these specific declines in northern Norway most likely are actual demographic events.

Considering the precise synchrony of these events between western Finland and northern Norway, it is of interest that the main population event appears to occur slightly earlier in northern Norway, with a more gradual build-up and more abrupt collapse, compared to the Finnish population cycle. The slight variation in dating of these events may be the result of the methods used to reconstruct population dynamics. This has been indicated previously, as a similar age-shift in the highest population levels between different population proxies has been observed in the Finnish data (Tallavaara and Pesonen, in press). Another possibility is that the timing of the main population cycles correspond to different timings of the most favorable environmental conditions in the separate areas. This is supported by the identification of a latitudinal gradient in the timing and duration of the peak Holocene Thermal Maximum (HTM), occurring earlier in the higher latitudes of Fennoscandia (Eldevik et al., 2014, p. 228). Future efforts should aim at discriminating between methodological and climatic effects in explaining this lag, as well as further issues of data resolution.

In addition to the correspondence between population and environmental proxies, proxies indicating marine resource use also correlate with population and environmental proxies in both areas. Marine resource use increases along with increasing population size and environmental productivity until around 6000 cal yr BP, and decline as population size and productivity proxies decrease. The Finnish archaeofaunal record (Fig 3.f) shows that during the boom phase of the mid-Holocene population event, seal bones make up more than 70% of the coastal archaeofaunal assemblages. The trend of seal exploitation intensity corresponds both to the growth and decline phases of the population trajectory.

In Norway, the use of slate intensified from 7000 cal yr BP and became the dominant lithic industry by the time of the population peak (Fig 3.i). By this time, slate concentrations often reached up to about 80% of coastal assemblages. We assume that this reflects a change in adaptive strategies towards more intensified use of marine resources in the region. A shift away from slate in favor of a more expedient technology based on local quartz occurred simultaneously to the population decline. Slate is still important for some time after the 5500 cal yr BP population decline, but the slate component is reduced from 70-80% to about 30%. In addition to the slate index, several other characteristics of the Norwegian archaeological record support the idea of increased marine resource use during the population boom. From 7000 cal yr BP, larger coastal sites consisting of multiple pit-houses emerge. Despite there being some indications of pit house construction occurring prior to this period, this represented a marked change in settlement longevity (Damm et al., in press; Gjerde and Skandfer, 2018), indicating increased locational investment in coastal sites and a shift in coastal settlement pattern and organization. Furthermore, recent investigations of differences in coast and inland human presence clearly demonstrate an almost complete lack of inland occupation concurrent with the major population peak at the coast (Jørgensen and Riede, 2019; Hood et al., In press). This corroborates the previous impression that major population packing occurred on the coast and that activity in the interior was minimal at this time (Hood, 2012). Given the significant difference in magnitude between inland and coastal settlements, packing does not seem a sufficient explanation. We suggest actual population growth followed coastal packing, although this is in need of further enquiry.

Highlighting this, the archaeological and rock art records suggest technological and organizational intensification of marine resources through the introduction of more efficient hunting/processing tools and (most likely) corporative hunting strategies (cf. Gjerde, 2018). Dietary investigations of the only mid-Holocene human individual currently known from northern Norway (Måløy Island) demonstrate a spectacularly high intake of marine protein (Günther et al., 2018: S1, 12). Discriminating the isotopic signature of marine mammal protein from that of migratory cod is difficult due to comparable trophic levels (Schulting et al., 2016), but migratory cod is by far the most dominant species in the region´s faunal record during the time of the population boom (cf. Olsen, 1967; Utne, 1973; Engelstad, 1983; Renouf, 1989). Tentatively, this may indicate adaptive adjustments towards lower ranked fish resources. Systematic diachronic sampling of biochemical dietary proxies may help resolve these issues in the future.

5. Discussion

Our main finding is the clear spatial synchronicity in demographic trends and adaptive strategies between two geographically separate human populations. Our results also strongly suggest that this synchronicity is related to the variability in terrestrial and marine productivity, which themselves are correlated between the two areas. While the details of these human ecodynamics and the pathways towards increased populations and maritime adaptations differ between the two focus regions, the outcomes are comparable. This suggests that the long-term demographic trajectories in both areas were ultimately regulated by climate and its downstream effect on both terrestrial and marine productivity and hence food availability for hunter-gatherers. The high productivity of the mid-

Holocene would have increased the environmental carrying capacity, and in concert with highly stable climatic conditions, offered unprecedented potential for human population growth. This seemingly mechanistic climate forcing of human populations is further supported by the synchronous decline in population numbers and environmental productivity after 5500 cal yr BP, as well as by short-term declines at 8200 and 7000 cal yr BP. Thus, our results apparently demonstrate Moran effects in action among human populations. The implication being that climate has the potential to synchronize long-term human population trajectories among foraging economies. Future research would have to investigate to what extent this relation also holds for food producing populations.

Although our results suggest that climate is the most likely explanation for the spatial synchrony between the northern Norwegian and western Finnish hunter-gatherer populations, other mechanisms may still be at play. The trend correspondence between population size, climate and adaptive strategies highlights the more generalized "chicken or the egg" problem of what should be ascribed causal primacy among demographic, technological and environmental factors in bringing about synchronous adaptive strategies: Did marine resource exploitation vary independently of population size, or did the maritime specialization result from changes in population size, thus being density-dependent? The latter option fits the concept of marine resources becoming attractive only when population packing restricts terrestrial hunting capabilities, creating an imbalance between human population growth and its (assumed) preference for a terrestrial resource base (Binford, 2001, p. 188,210; Kelly, 2013). This is thought to follow from the high handling and initial investment costs in aquatic resource exploitation In order to turn a profit, such as the development of boats, specialized fishing equipment and marine hunting gear, as well as bulk processing and storage (Osborn, 1977; cf. Yesner et al., 1980; Steffian et al., 2006; Fitzhugh, 2016).

In our case, however, this seems problematic. First, human population growth and marine resource exploitation appear to increase alongside a coupled marine-terrestrial productivity increase. One might point to the significantly fewer trophic levels in high-latitude, terrestrial ecosystems as a possible limitation to terrestrially based human population growth (cf. Steele, 1985; Carr et al., 2003; Steele et al., 2019). The abundance of ungulates is strictly regulated by density-dependent mechanisms in boreal forests (Bergerud et al., 2012, p. 102), and is arguably less resilient in the face of human overexploitation than marine resources (cf. Minc and Smith, 1989; Gunderson, 2000). It is therefore not clear whether continued terrestrial growth results in a linear increase in resource abundance relevant to human economic exploitation. This is an unresolved issue to consider for future research, yet current data do not support scarce terrestrial resources as the driving factor of the regime shift in marine exploitation. Further lacking support, is the possibility of a significantly earlier terrestrial productivity peak driving the shift towards intensified marine economies (also when considering a wider range of terrestrial proxies from northern Norway (Balascio and Bradley, 2012; Wittmeier et al., 2015; Sjögren and Damm, 2019). Second, the intensity of marine resource use appears to decline along with declining terrestrial (and marine) productivity. Third, if marine resources are secondary to terrestrial resources, it would make it difficult to explain how aquatic resources could support the population growth observed in our data, or how some of the highest population densities in the ethnographic record are found among maritime-adapted hunter-gatherers. For now, we cannot resolve the causal relationship between technological change and population growth. The fact that increase and decrease of marine resource use follow the trends in environmental productivity nevertheless suggests that adaptive changes in our study areas were ultimately subordinate to climate changes.

An alternative to endemic population growth, in ecology, dispersal between populations is another common factor causing spatial synchrony and may pertain to our case as well, e.g. through source-sink dynamics (cf. Kawecki, 2004). Agriculture was broadly adopted across northern parts of continental Europe, southern Scandinavia, and the British Isles c. 6000 cal yr BP. This created an unparalleled population boom roughly synchronous to the pattern observed in the population proxies from western Finland and northern Norway. This suggest that the mid-Holocene population peak in our study area relate to agricultural expansion, either directly through incoming farmers contributing to the population growth, or indirectly by displacing hunter-gatherers into northern 'foraging refugia' as suggested for central Europe (Silva and Vander Linden, 2017). The direct influence of farmers is problematic, however, as solid evidence for agriculture in our study areas is significantly younger than the 6000 cal yr BP population event (Sjögren, 2009: 707; Sjögren and Arntzen, 2013; Lahtinen et al., 2017; cf. Mökkönen, 2009). Indirect influences of agriculture are equally problematic. Firstly, the hunter-gatherer population in northern Norway was already growing some 500 years before agriculture was introduced to southern Scandinavia. The same pattern of pre-agricultural population growth is evident when reviewing the population reconstruction of Holocene Finland in its entirety (Tallavaara et al. 2010; Tallavaara and Seppä 2012). Secondly, displacement of hunter-gatherers from south to north would neither explain the remarkable population decline after 6000 cal yr BP or short-term declines at 8200 and 7000 cal yr BP.

In the case of observed synchronicity among human populations, an additional synchronizing factor of social interactions through trade and networks has been proposed (Freeman et al., 2018). The dissemination of improved subsistence technologies could tentatively drive synchronous demographic and adaptive strategies between our study areas. If so, cultural diffusion might facilitate the observed shift in marine exploitation regime while also contributing to population growth. This is particularly pertinent for two technological industries in the area: slate tools and early pottery.

The Slate Index (Fig 3.i) demonstrates strong correspondence with population dynamics in Norway. Assuming that slate tools are superior in marine resource processing, one might expect a comparable importance of slate industries among the coastal population of the Finnish area. No such quantitative dataset or overview currently exist from Finland. However, there are some similarities in slate technology that may suggest social networking in action between Finland and Norway (cf. Äyräpää, 1950; Huurre, 1983). Such is demonstrated by the long (100-150 mm) and slender (10-15 mm) Pyheensilta/Nyelv lance points, occurring in both areas. A review of a large set of lance points, including a depot containing points at various stages of completion (Hesjedal et al., 1996, p. 70), demonstrates remarkable standardization in production technique and morphometric qualities. The standardized breadth and hafting characteristics of Pyheensilta points, as well as the frequent resharpening of broken distal ends, reflect optimal characteristics for effective marine hunting. Maritime technologies are strongly associated with multi-component and replaceable components, given the complexity of hunting on water and the need for quick replacement/repair of hunting gear – a “maintainable” characteristic within and otherwise mostly “reliable” technology, sensu (Bleed, 1986). We therefore suggest that the Pyheensilta/Nyelv lances provide a telling example of shared marine subsistence technology.

The other significant change with potential ramifications for the synchronous mid-Holocene population and marine boom-and-bust cycles is the introduction of ceramic technology. Ceramics dispersed throughout northern and eastern Fennoscandia around 7200 cal yr BP in the form of Early Comb Ware - concurrent with the uptake of slate technology in northern Norway. The demographic impact of ceramic technologies is, tentatively, the enhancement of the nutritional uptake of various foodstuffs through cooking, which may reduce child mortality (Jordan and Zvelebil, 2010, p. 54). Interestingly, the beginning of pottery production in our study areas roughly coincide with the beginning of the mid-Holocene population growth and increase in marine resource use proxies, when Finnish sites (<6000 cal yr BP) are characterized by large quantities of pottery (Nuñez, 1990; Pesonen and Leskinen, 2009). Although it has been suggested that the uptake of pottery was related to the intensification of marine resources, lipid analyses of food crusts on pottery walls suggest a wide range of resources were processed in the vessels (Cramp et al., 2014; Pääkkönen et al., 2016; Papakosta and Pesonen, 2019).

Crucially, major discrepancies in the uptake and maintenance of ceramic technologies in the area go against subsistence technologies as a causal factor in the observed synchrony. In Finland, pottery continues to be in use throughout prehistory, despite the reduced importance of marine resources and the population decline after 5000 cal yr BP. In northern Norway however, pottery did not disperse beyond the very easternmost region and was likely a short-lived effervescence based on the short duration and small number of ceramics recovered, with a complete lack of later Comb Ceramic phases (cf. Skandfer, 2003; Hood and Helama, 2010). There are potential functional reasons for this discrepancy, beyond the greater geographical proximity of the Finnish area to dispersive centers of ceramic technology in Eurasia. The eco-setting of the western Finland was likely more conductive to year-round habitation, combined with the evidently strong emphasis on estuarine/riverine fisheries, that could benefit from ceramics for bulk-processing and storage. In Norway, there is to date no evidence to support surplus production of riverine/estuarine resources throughout the Stone Age (cf. Engelstad, 1984; Renouf, 1986: 10). However, mass processing and storage through passive technologies such as preservation through air-drying of stockfish has deep roots in Norway (Perdikaris, 1999; Star et al., 2017). The climatic conditions required for such preservative techniques are very specific to northern Norwegian coast, and are not met in the Finnish area. Although archaeologically elusive, we see no reason why the basic innovation of leaving fish to dry by itself would not have been practiced already during the mid-Holocene. If so, the appeal of pottery may have been offset to the Norwegian population.

We cannot exclude the effects of migration, social interactions or cultural diffusion. It is conceivable that the adoption of new and potentially improved subsistence technologies occurring simultaneously across northern Europe contributed to the growth phase of the 6500/6000 cal yr BP population cycle. The explanatory power of subsistence technology, however, is undermined by the fact that the population decline occurred independently of changes in subsistence technologies in our study areas, and because that both population growth and decline phases coincide with environmental changes. We therefore believe that the observed synchronicity in the long-term population dynamics is better explained by climate-induced variability in environmental productivity acting over large areas, albeit at much larger temporal scales than typically observed in ecological research. This result is at odds with the conclusion of Freeman et al. (2018), who found that environmental variability made no discernable impact on population synchrony. Instead, they suggest that societies dependent on organic sources of energy appear no more synchronous with solar energy fluctuations than fossil-fuel-based economies. However, their conclusions are hampered by the use of sunspot data as a measure of environmental variability. Although solar energy is the primary driver of Earth's climate, the influence of solar activity cycles on climatic variability appears to be limited at best (George and Telford, 2017; Schurer et al., 2014; Telford et al., 2015; Turner et al., 2016).

Instead, net primary productivity (NPP) is the crucial driver of energy availability for immediate return, organic economies, most typical of hunter-gatherers (Tallavaara et al., 2018), as opposed to economies reliant on stored energy reserves (Kander et al., 2013). NPP is controlled by temperature and precipitation, which can be correlated across distances of up to 5000 km, but not globally (Koenig, 2002). Therefore, there is no justification for using any single record of climate or energy availability, such as Greenland ice cores or sunspot data, when analyzing synchrony among prehistoric populations. In addition, taphonomic loss of archaeological material must be taken into account as the exponential-like shape prevalent across the mean trends of human proxy records may well be influenced by taphonomic processes (Surovell and Brantingham, 2007; Surovell et al., 2009).

Consequently, Freeman et al., (2018) do not properly address environmental variability or energy availability as a potential driver of synchrony. However, they demonstrate that spatial synchrony decreases with distance between proxy records. Importantly, the adjacent U.S. states, Arizona and New Mexico could make for a convincing case in which synchrony is best explained by social interaction and cultural diffusion. However, geographical affinity also implies being subjected to similar environmental parameters. Without further investigation of archaeological and environmental records at the regional scale, spatial proximity is not in itself a sufficient condition to come to conclusion about the causes of synchronicity. We therefore reiterate Koenig's (2002) argument, stating that "patterns of spatial autocorrelation in environmental factors should be carefully considered before concluding that synchrony in any particular system is driven by some factor beyond environmental correlation".

Despite some indications that both foraging and early farming communities were equally susceptible to climate change (Bevan et al., 2017; Warden et al., 2017), hunter-gatherer populations are generally assumed to be more directly controlled by NPP (Tallavaara et al., 2018). Still, hunter-gatherers relying on marine resources may take a hybrid form through delayed return systems as bulk processing and storage of energy for lean season consumption is a common characteristic of many northern, maritime groups (cf. Fitzhugh, 2016). Such delayed return economies help overcome the limitations imposed by the direct consumption characterizing organic economies. Either way, the archaeological record suggests that the maritime adaptations under study could only mitigate low-amplitude annual variations and at best delay specific returns on an inter-annual scale. This is not sufficient to significantly boost carrying-capacities or mitigate increased variation in resource abundance like modern economies, that are basically extreme delayed return systems relying on nuclear or fossil fuels (and therefore unsuitable as a comparative case). The limited and short-term mitigation capabilities of pre-industrial economic systems in significantly delaying returns would explain the inability of the populations to avoid decline along with reduced environmental productivity <5000 cal yr BP.

It seems that convergent cultural evolution towards more energy-consuming economies becomes important *after* the adoption of intensified agriculture relying on active niche-construction and yielding reliable surpluses. Consequently, we suggest that intensified economies and social interaction networks have limited impact on long-term hunter-gatherer population trajectories beyond what is already proscribed by external, environmental drivers.

6. Conclusion

This paper reviewed environmental productivity in relation to subsistence strategies in aquatic settings to unpack the drivers of synchrony between separate human populations. We presented a case study of two northern European sub-regions and demonstrated significantly synchronous trends across demographic, adaptive and environmental parameters. Based on an evaluation of different hypotheses, we suggested that the synchronous human ecodynamic trends across Holocene coastal Fennoscandia was result from shared variability in environmental productivity. Considering that the population trajectories of the two separate areas display remarkable synchronicity, and that these follow attendant climate variability in a lock-step manner, the results lend support to the notion that changes in environmental productivity more or less directly results in hunter-gatherer population size changes. The peaking productivity during the mid-Holocene would have drastically increased the environmental carrying capacity and so provided unprecedented human demographic growth potential. In addition, the long-term stability of the environment during the mid-Holocene may also have been a contributory factor to the observed human ecodynamics; dampening the amplitude of fluctuations that may otherwise be difficult to mitigate with short-duration delayed-return risk reduction measures (cf. Riede et al., 2018).

Our results further demonstrate that major economic changes correspond to demographic and environmental dynamics as evidenced by a suite of marine resource exploitation proxies. It is striking that both populations develop similar adaptive strategies, heavily relying on marine resources. Unpacking the causal mechanisms behind this regime shift towards intensive marine exploitation is beyond our ability at this point. The explanatory power of subsistence technology, however, is undermined by the fact that the population decline occurred independently of changes in subsistence technologies in our study areas, as well as that both population growth and decline phases coincide with environmental changes.

Future research should aim at establishing to what extent the mid-Holocene productivity increase was coupled between marine and terrestrial environments or not, and what are the human implications of a potential imbalance in marine vs. terrestrial ecosystem responses to large-scale climate change. If the productivity increase was actually stronger in the marine environment, it may provide a working hypothesis as to why we observe economic, technological and social-organizational shifts in mid-Holocene Northeastern Fennoscandia. However, the palaeoproductivity proxies presented here suggest a coupled response between marine and terrestrial ecosystems.

Another venue for further exploration is potential threshold effects operational in maritime adaptations, making marine resource exploitation more profitable, given all its costs (high handling and initial investments), whenever marine productivity increases above some critical level. The pathways responsible for steering ocean-atmospheric interactions are highly complex (Wunsch, 2005; Yu and Weller, 2007) and may imply more complex climatic drivers of marine productivity compared to terrestrial productivity (Bromley et al., 1967; Behrenfeld et al., 2006; Meehl et al., 2011; Holt et al., 2016; Schmitt, 2018). It is necessary to identify and model various ecosystem components and thermal thresholds to test this properly. Yet, thresholds imply sharp changes in resource use between different system states, while our data indicate rather gradual changes in marine resource use in both areas.

Although a previous study found only minimal evidence for environmental variability as a cause of synchronicity (Freeman et al., 2018), the Fennoscandian archaeological record clearly demonstrates the important role of spatially correlated environmental influences, i.e., Moran effect, in creating spatial synchrony among hunter-gatherer populations. The implication is, contrary to Freeman et al., (2018), that intensified economies and social interaction networks have limited impact on long-term hunter-gatherer population trajectories beyond what is already proscribed by external, environmental drivers.

Supplementary information

The Norwegian radiocarbon record used for modelling palaeodemographic trends in this paper is available at the open-access, data repository:

https://dataverse.no/dataset.xhtml?persistentId=doi:10.18710/AV9R5X

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Individual contributions

Data collection was made by all authors. Idea and analyses by EKJ and MT. Figures were made by MT. EKJ wrote manuscript drafts, commented upon by MT and PP.

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