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The Danish fish fauna during the warm Atlantic period (ca. 7,000-3,900 BC): forerunner of future changes?

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Abstract:

Vast amounts of fish bone lie preserved in Denmark's soil as remains of prehistoric fishing. Fishing was particularly important during the Atlantic period (ca. 7,000-3,900 BC, i.e., part of the Mesolithic Stone Age). At this time, sea temperature and salinity were higher in waters around Denmark than today. Analyses of more than 100,000 fish bones from various settlements from this period document which fish species were common in coastal Danish waters at this time. This study provides a basis for comparing the fish fauna in the warm Stone Age sea with the tendencies seen and predicted today as a result of rising sea temperatures. One example concerns the anchovy (*Engraulis encrasicolus*) which lived in the Stone Age sea, and has become more numerous in Danish waters since the mid-1990s. Other warm water fishes represented among the Stone Age bone samples include smoothhound (*Mustelus* sp.), common stingray (*Dasyatis pastinaca*), European sea bass (*Dicentrarchus labrax*), black sea bream (*Spondyllosoma cantharus*) and swordfish (*Xiphias gladius*). Surprisingly, Atlantic cod (*Gadus morhua*), whose biomass in the Kattegat and eastern Baltic Sea is presently at record low levels, was one of the most frequently caught species in the Danish Stone Age sea. These results demonstrate that major changes to the fish fauna near Denmark will occur as climate changes. However exploitable cod populations can potentially be maintained in waters near Denmark, including the North Sea, but the vulnerability to climate change and the risk of stock collapse will increase at present high fishing mortalities.

Keywords: Atlantic period, Mesolithic, Stone Age, fish fauna, biodiversity, cod, Baltic Sea, Kattegat, North Sea, climate change

Introduction:

Global and regional climate models predict that air and sea temperatures will rise by approximately 3 °C during the next 70-100 years as a result of increasing concentrations of greenhouse gases (IPCC, 2001; Kerr, 2004; Döscher and Meier, 2004). Such a change will have major implications for species, ecosystems, and food webs: spatial distributions, lifehistories, phenologies, and biotic interactions among species will be altered (Root et al., 2003; Stenseth et al., 2004). Many of these changes already appear to be underway. For example, (1) daily monitoring of sea surface temperatures in the North and Baltic Seas during the last 120-140 years shows that temperatures in the early 2000s are now warmer than at any time since measurements began (MacKenzie and Schiedek, 2007a) (2) a wide variety of marine zooplankton and fish species in the northeast Atlantic are changing their distributions towards northern or deeper waters (Beaugrand et al., 2002; Stebbing et al., 2002; Brander et al., 2003; Beare et al., 2004; Perry et al., 2005), and the production and survival of cold- and warm-adapted species in these regions is respectively decreasing (Beaugrand et al., 2004) and increasing (MacKenzie and Köster, 2004). These ecological changes have occurred following a relatively modest rise in mean annual surface temperature of ca. 0.5 °C since 1985 (MacKenzie and Schiedek, 2007a).

Given that future temperatures may rise ca. 6 fold higher by 2100 (Kerr, 2004; BACC, 2006), it is reasonable to expect that fish faunas in local areas will change even more dramatically. Such changes could include the complete replacement of some cold-adapted species by warm-adapted species. Ecological changes that precede replacement include changes in distributions and lifehistories, which are already occurring. Alternatively, some fish species could adapt genetically and persist in local areas despite a rise in temperature. This possibility could occur in two ways. First, there could be genetic variation for growth, reproduction and survival under warmer conditions present within populations of a given species. This would allow some individuals possessing gene variants providing an advantage under warmer conditions; e.g. physiological capabilities that are more efficient at higher temperatures than at lower temperatures (Pörtner et al., 2001) to have higher reproductive output. By this process of natural selection the “warm” gene variants would then spread to the rest of the population providing overall higher fitness. Secondly, similar to changes in species distributions, different populations within a species may already be differently adapted with respect to their temperature envelope. A rise in temperature could then simply shift the distribution of many genetically different already adapted populations northward.

The future biodiversity of local fish communities will therefore depend on how quickly the temperature changes, how much potential there is within individual species and populations for evolutionary adaptation, and the plasticity of traits (e.g. physiology and life history) of individual species, including those which are predators, prey and pathogens of fish species. In order to understand some of the processes by which global warming might affect the fish fauna in waters near Denmark, we have investigated the fish fauna during one of the warmest prehistoric periods for which ichthyological information is available.

A Holocene climatic optimum can be recognized in, for example, ¹⁸O analyses of carbonated sediments from a lake near the Baltic Sea (Gotland, Sweden). The Holocene warm period lasted from 9000 to 2500 ¹⁴C yr BP (Mörner, 1980), during which time mean summer water temperature was 1.5-2.0 °C higher than today (Fig. 1) and sea levels were also higher (Fig. 2).

More recently pollen analyses have been used to identify "A Holocene thermal maximum (HTM) ..., with generally 2-2.5°C warmer than present day annual mean temperatures between 7000 and 4000 yr BP" (Antonsson, 2006). Several other studies based on fossil chironomid midges (Brooks, 2003) and stable isotopes support the presence of the HTM (Antonsson, 2006). In the Baltic Sea, this warm period was also accompanied by salinities which may have been up to 4 PSU higher than today (Sohlenius et al., 2001; Emeis et al., 2003). Both higher temperatures and salinities will have influenced the fish community in this area.

Here we describe the taxonomic composition of the marine fish community from this period. We hypothesize that these remains could be a useful analog for interpreting present changes in the local fish fauna, for understanding how species invade new habitats, and for forecasting the biodiversity of the fish community which could (re-)appear in Danish waters as global warming progresses.

Fish have been caught and eaten at all times, and when conditions have been favourable, fish refuse in the form of bones has been preserved in the soil as a testimony of both the human activity on the site and of the local fish fauna. Preservation of bones is best if the bones have been deposited in places protected from external influences such as changing weather conditions, hungry dogs, human traffic, bacterial decomposition, etc. The acidity of the sediment is of paramount importance. Optimal conditions for preservation occur, where the bone refuse has been thrown directly into water and has been embedded in oxygen-poor, calcareous, alkaline sediment. This habit of refuse deposition was widespread during the Stone Age (Atlantic) period. An alternative and frequently used solution was to accumulate the refuse in kitchen middens (in Danish: "køkkenmøddinger") on land, together with vast numbers of oyster and other bivalve shells. This habit also provided protected, calcareous conditions.

Material and methods

Our study material consists of fish bones from archeological excavations in Denmark (Fig. 3). Material from each site has been dated using ^{14}C and/or analyses of artefacts (Trolle-Lassen, 1985; Enghoff, 1994; Jensen, 2001; Enghoff, 2006a). On this basis, the majority of the sites have been referred to the Ertebølle culture (EB, ca. 5400-3900 BC), but a few are from the preceding Kongemose culture (KM, 6800-5400 BC). These two culture periods belong to the Mesolithic and together constitute the Atlantic period, which is part of the Holocene period (Aaris-Sørensen, 1998). In addition, a few of the settlements continue into the succeeding Funnel Beaker Culture (TB, 3900-3200 BC) which represents the earliest phase of the Neolithic, Subboreal period. However, only ca. 300 of the studied fish bones are from the Neolithic, including 252 from Bjørnsholm alone.

During the Atlantic period Denmark was a highly fragmented area with numerous islands, bays and inlets (Fig. 2). This difference in landscape and topography was due to the fact that the rise in sea water level during this period, as the temperature reached a maximum and the North American ice-shield retreated, greatly exceeded the contemporaneous land uplift (Christensen, 1995; Aaris-Sørensen, 1998). Fishing opportunities and locations, as well as fish habitats were therefore somewhat different from the present. The fish bones were collected from a number of coastal settlements in six regions of Denmark (Fig. 2).

Region I: Vendsyssel. The fish bones are from two settlements, Østenkær (EB) and Yderhede (EB) (Enghoff, 1994) which both were situated on the north coast of the large Vendsyssel island before the present-day peninsula Skagen Odde was formed. The settlements were located at lagoons which had been formed in connection with sand-bar formations. In this region, the inhabitants have been close to the North Sea and Skagerrak, including deep water.

Region II: Limfjord. The fish bones are from kitchen middens on three settlements: Bjørnsholm (EB) (Enghoff, 1993; Enghoff, 1994), Ertebølle (EB) (*locus classicus*) (Enghoff, 1987; Enghoff, 1994) and Krabbesholm (EB+TB) (Enghoff unpubl.) in the central Limfjord area from where there was then wide connections to the North Sea and Skagerrak towards the west and the north (Petersen, 1981; Petersen, 1985).

Region III: E Jutland, facing the inner waters between Jutland and the north coast of Zealand as well as the west coast of Sweden, i.e., Kattegat and the Belts. The fish bones are from kitchen middens on five sites: Visborg at Mariager Fjord (EB+TB) (Enghoff unpubl.), Nederst on the Djursland peninsula (EB) (Enghoff, 1994), Lystrup Enge (EB) (Enghoff, 1994) at the prehistoric Egå Fjord, Norsminde (EB+TB) at Norsminde Fjord (Enghoff, 1991; Enghoff, 1994) and Vængesø III on the Helgenæs peninsula (EB) (Enghoff unpubl.).

Region IV: NW Funen. The fish bones are from water-covered refuse layers from two settlements: Tybrind Vig (EB) (Trolle-Lassen, 1985) and Ronæs Skov (EB) (Enghoff, 2006a). Both sites are now totally under water due to their position south of the so-called “tiltline”, north of which postglacial land uplift is occurring and south of which the land is being submerged (Christensen, 1995). From these sites fishing could be conducted in the local fjords and inlets connecting to the Little Belt.

Region V: NE Zealand. The fish bones are from refuse layers, kitchen middens and settlement grounds of nine sites, mostly at the prehistoric fjords connecting with the Belts (Øresund) at Nivå and Vedbæk. The settlements are: Nivågård at Nivå Fjord (KM+EB) (Enghoff unpubl., Jensen 2001), seven settlements at Vedbæk Fjord, viz., Stationsvej 19 (KM), Henriksholm-Bøgebakken (EB), Magleholm (EB+TB), Maglemosegård (EB), Maglemosegårds Vænge (KM+EB), Vænget Nord (KM) and Gøngehusvej 7 (KM) (Enghoff, 1994), and Italiensvej (KM), a now submarine settlement on Amager island (part of greater Copenhagen) (Enghoff unpubl.).

Region VI: Bornholm. The material comes from one settlement, Grisby (EB; Enghoff 1994), which was located at a small bight on the east coast of the island of Bornholm in the Baltic Sea.

Modern excavation techniques were used to extract the fish bones, involving sieving of sediment. Experiments have shown that sieving is essential for retrieving small fish bones because only very fine meshes retain bones from the smallest fish (Enghoff, 2005a). The fish bones were identified using the reference collection at the Natural History Museum of Denmark (Zoological Museum), University of Copenhagen.

When interpreting numbers of identified fish bones from archaeological sites, it is important to bear in mind that some species have more species-specific bones than others, and that within each species, some bones such as those in the head are more characteristic than others, such as vertebrae. For example, almost all bones from eel can be identified to this species. On the other hand, most skeletal elements from species of the plaice/flounder/dab group can only be identified

to this group, and only a few head bones can specifically be assigned to plaice, flounder or dab. The same problem applies to the gadids where most bones can easily be referred to this family but where identification to species (cod, haddock, saith, etc.) is only possible for a limited number of skeletal elements. In addition, different fish species have different numbers of bones (e.g. eel has many more vertebrae than most other species), and bones from different groups of fish have unequal chances of preservation in the sediment. For example, bones of salmonids are poorly ossified, and clupeid bones are fatty and fragile, whereas gadid bones are more robust.

Results

A total of 108,000 fish bones were identified (Table 1; Fig. 4-6, 8-10). Assuming that long-distance fish trade did not occur during this period (Enghoff, 2000; Barrett et al., 2004), the species listed in Table 1 must have been captured in local waters by Holocene era fishermen. The species composition in Table 1 reflects therefore to some extent the species composition of local waters (Enghoff, 1994).

The material includes bones from at least 49 species of fish. Most of the species are common in Danish waters today but there is also a number of exotic species which today have a more southerly distribution. These are: smoothhound (*Mustelus* sp.), common stingray (*Dasyatis pastinaca*), anchovy (*Engraulis encrasicolus*), European sea bass (*Dicentrarchus labrax*), black sea bream (*Spondyllosoma cantharus*) and swordfish (*Xiphias gladius*).

Smoothhound

Smoothhound (*Mustelus* sp.) is represented in the Limfjord (3 bones) and E Jutland (4 bones) regions. It is a cartilaginous fish, meaning that its bones in general have a smaller chance of preservation than those of bony fishes. Particularly good conditions for preservation must therefore have been present at these sites. All smoothhound bones are vertebrae. The three vertebrae from Bjørnholm (Limfjord region; Fig. 4) are from at least two individuals of different sizes. Smoothhound was probably present in this region for a considerable duration because it occurs in both Mesolithic and Neolithic layers (Enghoff, 1993).

There are two closely related species of the genus *Mustelus* in European waters: *M. asterias* and *M. mustelus*. It is impossible to distinguish the two species of smoothhound on the basis of vertebrae. The present distribution of the two species includes the Atlantic from Morocco and Madeira northward to the British Isles; *M. asterias* can also be found near the Shetlands Islands and in the North Sea and Mediterranean (Whitehead et al., 1984). Both species are very rare in Danish waters today, and are only known from the North Sea and Skagerrak (Carl et al., 2004).

Common stingray

A well-preserved tail spine of the common stingray (*Dasyatis pastinaca*) was found in early Neolithic layers of the kitchen midden at Bjørnholm (Limfjord) (Rosenlund, 1986b; Enghoff, 1993) (Fig. 5). There are three further subfossil finds of common stingray from Denmark, probably from the Mesolithic period (Rosenlund, 1986a). The present distribution of common stingray includes Atlantic coastal waters from South Africa northward to the British Isles, southern Norway, and (rarely) the western part of the Baltic; the species is also present in the Mediterranean (Whitehead et al., 1984). Carl et al. (2004) classify common stingray as very rare in Danish waters although it has been found in the North Sea, Skagerrak, Kattegat, the Belts and the Baltic Sea.

Anchovy

Bones from anchovy (*Engraulis encrasicolus*) have only been found at a single site (Krabbesholm, near Limfjord; Fig. 6). Due to the wide connections to Skagerrak during the Atlantic warm period, the environment was probably truly marine. Anchovy bones were recovered by sieving sediment from the kitchen midden through mesh as small as 0.5 mm. A ^{14}C dating of eel bones found together with the anchovy bones indicates a ^{14}C age of 6070 ± 40 BP (Poz-12163) (in calendar years: 4640-4450 BC {68,2% probability}, calibrated with Curve marine04). This dating places the eel bones (and indirectly the anchovy bones) in the Ertebølle culture period. Most of the anchovy bones are from individuals estimated to have been ca. 13 cm long. The present-day distribution of anchovy includes the Sea of Azov, Black Sea, Mediterranean, and extends northwards along the Atlantic coasts of Portugal, Spain, France and into the southern North Sea (Whitehead et al., 1984). According to Carl et al. (2004) the species has recently been relatively frequent in Danish waters and has been recorded from the North Sea, Skagerrak, Kattegat and the Belts. Quantities are now sufficiently large that they are being exploited by commercial fishermen (Fig. 7).

European Seabass

A single bone of European seabass (*Dicentrarchus labrax*) was found in water-covered refuse layers off the Yderhede settlement (Vendsyssel), and 11 bones were found in the Bjørnsholm kitchen midden (Limfjord; Fig. 8). On the latter site there are bones from specimens of 30-40 cm total length as well as from somewhat bigger ones. The vertical distribution of the bones indicate repeated catch incidences, since 10 of the bone are from Ertebølle culture layers, and one from the Funnel Beaker culture layer. The sea bass thus seems to have occurred in this area during an extended period of time (Enghoff, 1993). The present distribution of European sea bass includes the North Atlantic from Norway south to the Mediterranean, Morocco and the Canary Islands (Whitehead et al., 1986). The species is relatively frequent in Danish waters nowadays, especially along the west coast and near cooling water runoffs from powerplants. It has been found in the North Sea, Skagerrak, Kattegat and the Belts (Carl et al., 2004), and Danish commercial landings have risen in the past 10-15 years (Fig. 7).

Black sea bream

Like the preceding species, black sea bream (*Spondyliosoma cantharus*) has been found at Bjørnsholm (Limfjord; Fig. 9). The species is represented by 83 bones and 21 scales, representing at least three individuals, probably more (Enghoff, 1993). All bones except one were found in Ertebølle culture layers, the last in the Funnel Beaker culture layer, indicating that the sea bream occurred in the area during an extended period. The specimens were 30-40 cm long (Enghoff, 1993). Black sea bream lives in inshore waters and its present distribution includes Atlantic coastal waters from Scandinavia to Angola, and the Mediterranean (Whitehead et al., 1986). In Danish waters it is rare, known from the North Sea, Skagerrak, Kattegat and the Belts (Knijn et al., 1993; Carl et al., 2004).

Swordfish

One bone fragment (vomer) from swordfish (*Xiphias gladius*; Fig. 10) was found on the submarine settlement Italiensvej (NE Zealand) (Enghoff unpubl.). In addition, an ornamented swordfish "sword" has been found on the site Bloksbjerg (late Kongemose – early Ertebølle) near Klampenborg in the NE Zealand region (Petersen, 1996). In Europe, swordfish occurs in the Mediterranean and Black Seas and in the east Atlantic from southern Africa to southern Norway. It is rare in the North Sea, Skagerrak, Kattegat, the Belts and the Baltic Sea (Knijn et al., 1993; Carl et al., 2004; Bacevicius and Karalius, 2005).

Thinlip grey mullet

In addition to the species discussed above, thinlip grey mullet (*Liza ramada*) is known from four Mesolithic and Neolithic sites in Denmark. The largest find consists of 11 vertebrae from the Neolithic settlement Kainsbakke (Djursland, E Jutland). The other finds are from Vejleby (EB, N. Zealand), Ordrup Næs (EB, NW Zealand) and Kolind (EB, Djursland, E Jutland) (Richter, 1987). There is also one younger find consisting of 144 bones from an Iron Age-Viking Age market place in Ribe, S. Jutland (Enghoff, 2006b). Thinlip grey mullet is common in southern Europe, along the Atlantic and in the Mediterranean (Curry-Lindahl, 1985). It is presently very rare in Danish waters, although it has been recorded from the North Sea, Skagerrak, Kattegat, the Belts and the Baltic Sea (Carl et al., 2004). Thinlip grey mullet should not be confused with thicklip grey mullet (*Chelon labrosus*) which has become more frequent in Danish waters since ca. 1970 (Curry-Lindahl, 1985). The geographic ranges of both species are similar (Muus and Nielsen, 1999) and the species are presently not distinguished from each other in Danish commercial catches. However landings of this species pair have increased during the 1980s-1990s (Fig. 7).

Other species:

Gadids, including cod

The codfish or gadid family (Gadidae) is represented in the material by cod, haddock, whiting, pollack, saith and ling. Identification to species level of gadid bones is based only on selected bones from the head and the first four vertebrae (Enghoff, 1983), hence the number of unspecific gadid bones is very large. As the vast majority of gadid bones identified to species are from cod (Table 1), one may assume that the vast majority of the unspecified gadid bones are also from cod

Plaice/flounder/dab

Most bones from this group of flatfishes are difficult or impossible to identify to species level. Species identification is mainly possible for several bones from the head. Most bones which could be identified to species are from flounder, and some are from plaice. Dab has not been documented from the study period but since the vast majority of dab bones cannot be distinguished from those of plaice and flounder, we refer to bones from flatfishes as being from the plaice/flounder/dab group.

Summing up, several exotic fish species obviously occurred regularly in Danish waters during the Atlantic climatic optimum. However, the relative frequencies of fish species shown in Table 1 leave no doubt that the most important species caught by the stone age people were gadids (primarily cod; Fig. 11), flatfish (plaice/flounder/dab), and eel.

Discussion

The material assembled and presented here represents the largest collections of fish bones recovered from the Atlantic period in Denmark as well as in the whole of Scandinavia. We document that coastal societies in Denmark contained active fishers who were able to catch a wide variety of marine fish species; marine fishing was clearly established at a subsistence level already during the warm Atlantic period. This observation is supported by the vast amounts of fish bones recovered from the Kongemose and Ertebølle sites, which indicates that fish constituted a large share of the marine menu (Enghoff, 1994). Furthermore, ¹³C analyses of bones of Kongemose and Ertebølle humans have shown that their diets were predominantly of marine origin (Tauber, 1981; Tauber, 1987). Intensive exploitation (i. e.,

for trade and commercial purposes) of marine fishes in the North Sea and adjacent Wadden Sea only began several millennia later (ca. 1000-1200 AD; (Enghoff, 2000; Barrett et al., 2004; Lotze, 2007).

The extent to which our archaeological material represents the fish fauna of local waters potentially depends on many factors, including taphonomy and fishing practices. Regarding the former, we have only used material obtained from sites with good preservation conditions, and excavated by modern recovery methods, including sieving of sediments to ensure recovery of small fishbones. The additional taphonomic factors mentioned under methods are not believed to influence the results significantly and we therefore maintain that our sample provides a roughly representative picture of the local faunas. The main fishing gear used by Ertebølle fishermen was probably stationary selv-fishing traps deployed in shallow nearshore waters during summer (Enghoff, 1994). The traps were deployed in a variety of locations around Denmark and captured a large number of especially small, coastal and migratory fish species as well as small individuals of bigger fish species like cod (Enghoff, 1994). These observations suggest that the gear was a relatively unselective means for catching fish which entered and inhabited coastal waters. As the remains of the many different fish species are found in situations indicating they are leftovers from meals, the Stone Age people seem to have been unselective consumers of the fish that were caught. As a consequence, the fish community represented by our archaeological material is a good indicator of the fish community of coastal Danish waters during the Atlantic warm period.

Faunistic composition of Danish waters during the Stone Age:

Our sample of 108,000 fish bones, which originates from coastal fishing activity in different regions of Denmark during the postglacial maximum gives an impression of which fish were commonly present in the local fish fauna. In order to be represented in archaeological material, we assume that the species must have been very common in the waters around Denmark. This assumption is based on the fact that only portions of investigated settlements (e. g., a ditch or a few square metres) have been examined, yet the recovered species were nevertheless present in these small areas that were chosen for excavation. The relative frequencies of fish species (Table 1) indicate that the commonest species caught by the Stone Age people were gadids (primarily cod), flatfish (plaice/flounder/dab), and eel. These fish were major dietary components and probably among the most abundant and easily captured species near human settlements.

It is useful to compare our archaeological sample with the changes occurring presently and which will likely happen in future as sea temperatures rise due to global warming. Our archaeological evidence shows that there were several exotic species present during this period, which are not present or only recently have become present in waters near Denmark. These species presently have a more southerly distribution, and their presence near Denmark during the postglacial optimum was presumably due partly to the warmer temperatures at that time. Smoothhound, common stingray, anchovy, European sea bass, black sea bream and swordfish were in fact *only* found during the postglacial optimum and have never been seen again in archaeological remains in Denmark. Although most of these species have been occasionally caught in waters near Denmark since then as indicated by zoological and museum records (Nilsson, 1855; Wright, 1892; Bacevicius and Karalius, 2005), their presence among Atlantic warm period archaeological remains indicates that their relative abundance must have been greater at that time than in subsequent periods. Some of these same species have now been, or are being, captured regularly by Danish fishermen in commercially

important quantities in the past 10-15 years. For example, anchovy and sea bass landings are much higher now than they were 10-20 years ago (Fig. 7). The increase in Danish commercial landings is consistent with many observations in both research surveys and commercial landings of increases in abundance of these same species in neighbouring waters (Heessen and van de Kamp, 1996; Beare et al., 2004; Genner et al., 2004; Perry et al., 2005).

The presence of anchovy in the Danish remains in the Limfjord indicates that sea temperatures during this period were relatively warm. The main distributional range of anchovy is from Morocco through the Mediterranean and north to the southern North Sea; it is usually rare in the Skagerrak and Kattegat (Muus and Nielsen, 1999). Anchovy has become more common in the North Sea (Beare et al., 2004), and in the Kattegat and Belt Sea since 1994 (MacKenzie et al., 2007b), after many decades when it was rare. The most recent period when it was abundant in Danish waters was during the late 1930s and early 1940s, when the species reproduced in the Kattegat (Heegaard, 1947); anchovy also reproduced in the German Bight of the North Sea during the 1940s (Aurich, 1953). These decades were part of a warm period during the mid-20th century (Drinkwater, 2006; MacKenzie and Schiedek, 2007a). The observations of anchovy reproduction in the Kattegat and southern North Sea during the mid-20th century warm period are consistent with the archaeological evidence of anchovy presence also during a warm period. Dietary evidence from the mid-1800s in the Skagerrak-Kattegat shows that cod occasionally preyed on anchovy (Nilsson, 1855).

The findings of southern species at Danish settlements is supported by findings at Swedish sites for the same time period. A large number of bones of the bogue (*Boops boops*; Sparidae) were found in the Mid-Neolithic period (Subboreal); many bones from several small individuals (ca. 6 months old) were found at Ånneröd, Sweden. The presence of small bones suggests that the species reproduced in the North Sea at that time (Jonsson, 1995; Jonsson, 2005). Presently bogue is distributed in the Mediterranean and along the east Atlantic coast from Angola to the Bay of Biscay (Whitehead et al., 1986; Muus and Nielsen, 1999).

The fish community represented by the remains at Danish sites also includes some large highly migratory species such as bluefin tuna (one vertebra from Italiensvej, one vertebra on each of two Medieval sites; (Rosenlund, 1976; Enghoff, 2005b)) and swordfish. It is not clear how these species were captured but they may have become stranded on beaches or entangled in coastal fish traps, as has occurred in the past (Bacevicius and Karalius, 2005; MacKenzie and Myers, 2007). Bluefin tuna has an efficient thermal regulatory system for maintaining core muscle and vital organ temperatures above ambient temperatures (Graham and Dickson, 2001; Dickson and Graham, 2004); as a result, its presence in northern boreal waters during and outside the warm Atlantic period is not unexpected (Mather et al., 1995; MacKenzie and Myers, 2007). Swordfish have less extensive endothermy, which is primarily directed to heating the eyes and brain (Dickson and Graham, 2004; Fritsches et al., 2005), and therefore may be less likely to inhabit local waters unless temperatures are warm.

The presence of a fish community near Denmark with warmer temperature tolerances during this period is supported by other faunistic evidence. Archaeological excavations of settlements, as well as finds in bogs, have revealed numerous remains of exotic bird and reptile species. These include, for example, Dalmatian pelican (*Pelecanus crispus*), European pond turtle (*Emys orbicularis*), and Aesculapian snake (*Elaphe longissima*) which were present in Denmark during the warm period, but which now have a more southeasterly range (Llungar, 1995; Aaris-Sørensen, 1998). Remains from this period of southern species of

dolphins (*Delphinus/Stenella* sp.) have also been recovered from Danish settlements (Jensen and Kinze unpubl.; Enghoff 2006). Two ostracod species, *Aurila arborescens* and *Callistocythere badia*, which normally are only associated with the Mediterranean, were also present in northern Denmark during the Atlantic warm period (Vork and Thomsen, 1996).

Species composition in warming habitats and species assembly rules:

Our comparison of the Atlantic period and the contemporary fish community in Danish waters shows that the fish community is changing in a direction which partly resembles that which was present during the earlier warm period. However there are several differences in the two fish communities. For example, black sea bream was found in the Holocene material but is still rare in Danish waters. Moreover, black sea bream (as of 2003) still had not been captured in Scottish trawl surveys conducted annually since 1925, despite increasing captures of other southern species such as anchovy and sardine (Beare et al., 2004). In the case of black sea bream, it is possible that temperatures have not yet become warm enough for this species in Scottish and Danish waters. Research surveys and commercial catch data show that red mullets have increased in abundance in the North Sea (Beare et al., 2004; Brander et al., 2003) during the late 1990s. Landings of this species by Danish fishermen from the North Sea have also increased during the 1990s (Fig. 7). However, this species is absent from our archaeological finds. We have no reason to believe that the bones of red mullet are less likely than other bony fish species to be preserved in Danish soil and believe that the differences could be due to ecological factors controlling the abundance and colonisation of new habitats by these species.

In the case of red mullet, its recent invasion could perhaps have been promoted both by warm temperature and by the relative absence of potential resident predators, such as cod, which were otherwise abundant in the Holocene waters near Denmark. The successful immigration and colonisation by nonlocal species of new habitats depends not only on abiotic variables, but also on species interactions at all stages of the lifehistory. As a result the patterns by which species assemble in local habitats can differ over time, depending partly on abundances and functional roles of existing resident species and the immigrating species. These considerations suggest that a niche in the North Sea – Kattegat area recently became vacant and was filled by red mullet.

The thinlip and thicklip grey mullet species also show contrasting results between the Atlantic period and contemporary fish communities. Thinlip grey mullet was present but thicklip grey mullet was absent in the archaeological material, but according to Curry-Lindahl (1985), only the thicklip species has become more common around Denmark. If this is true, then most of the landings of the combined thicklip and thinlip grey mullets (Fig. 7) could be composed of thicklip grey mullets. Both species historically are more typically associated with warmer waters than those near Denmark (Muus and Nielsen, 1999). Why both species were not present during the Holocene and at the present is not clear.

One possible explanation for these apparent discrepancies is that the archaeological data are from a period which was relatively warm for several 1000s of years. This long period would have given sufficient opportunity for species to change their geographical distributions, new species interactions to develop and new species assemblies to occur. Given that fish species with different lifehistories (e. g., maximum body length; age/size at maturity) respond to ocean warming at different rates (Perry et al., 2005), and that regional sea surface temperatures in this region have only recently exceeded historical highs in the instrumented

temperature record (MacKenzie and Schiedek, 2007a), it is perhaps too early to expect that the archaeological representation of the Atlantic period fish fauna would fully represent the dominant characteristics of the fish fauna near Denmark at the present time.

We are also aware that the fish community of the North Sea-Baltic Sea region has been heavily influenced by exploitation during the past century: the abundances of several formerly abundant species (e. g., cod, plaice, dab, eel) has declined, and the overall species and size composition of these fish communities have changed (Knijn et al., 1993; Bianchi et al., 2000; Jennings et al., 2002). As a result, the trophic structure and species interactions (competition, predation) have also changed. These changes may have indirectly facilitated or hastened immigration and establishment of “southern” species.

Cod and Stone Age climate:

A notable finding of the archaeological material is the presence of species which are abundant in waters near Denmark both at the present time and during the postglacial warm period. These species include cod. The presence of cod, together with many warm-adapted species, during the warm period is particularly relevant to recent studies of the relative influence of fishing and climate change on cod population dynamics.

Cod biomasses in the eastern Baltic Sea (ICES Subdivisions 25-32), Kattegat (ICES Subdivision 21) and North Sea (ICES Subdivision IV) are presently very low compared to biomass estimates available since the 1960s-1970s (ICES, 2005). The main reason why cod biomasses are low in these regions is fishing, although environmental conditions are partly responsible (ICES, 2005; Drinkwater, 2005). In particular warm surface temperatures have been associated with declining recruitment of the North Sea cod stock (Beaugrand et al., 2004), and warm temperatures can cause reduced growth in juveniles even when food supplies are not limiting (Björnsson and Steinarsson, 2002). Carrying capacity for cod in 20 ecosystems inhabited by this species also decreases with increasing bottom temperature (Myers et al., 2001). However analytical modelling studies of the influence of fishing and temperature on production of the North Sea population show that, if exploitation was lower, this population could be much larger even given the warm temperatures observed recently and to be expected in the coming 2-3 decades (Cook and Heath, 2005; Kell et al., 2005).

Our archaeological evidence, although based primarily on finds near the Kattegat and Belt Sea, whose seasonal and annual mean surface temperatures are strongly correlated with those in the North and Baltic Seas (MacKenzie and Schiedek, 2007b), demonstrates that cod can indeed grow and survive in large numbers at relatively warm temperatures. This evidence suggests that the Kattegat and North Sea cod populations could become much larger and sustainable than at present, if fishing mortality rates were reduced. Moreover the presence of anchovy and cod together in the Kattegat and North Sea in the 1940s-1950s and during the Stone Age period demonstrates that a moderately large cod population can thrive in relatively warm conditions in these waters.

We believe that the cod populations in the Kattegat and Belt Sea, and probably also the North Sea, during the warm postglacial period were probably much larger than at present, and perhaps had a different genetic composition than at present. This conclusion is based on several considerations. First, fishing activity and fishing mortality rates must have been extremely low compared to present levels. Overall mortality rates were probably lower than today, which would have allowed the population to attain higher biomass, unless there was

intense compensatory mortality due to other predators (e. g. marine mammals, larger fish including cannibalism). This latter possibility seems unlikely given that recent historical reconstructions of cod biomass in other areas show that cod biomass can be much higher when fishing mortality rates are lower (Rose, 2004; Rosenberg et al., 2005).

Secondly, the higher abundance of cod during the warm postglacial period could be caused by processes related to the genetic population structure of cod and the distribution of these populations in space and time. A number of recent studies have demonstrated genetic differences among local cod populations at spatial scales of 10s-100s of km in waters near Denmark and more generally in the northeast Atlantic (Nielsen et al., 2001; Nielsen et al., 2003; Knutsen et al., 2003; Case et al., 2005). Such temporally stable genetic differences imply demographic independence of cod populations; i.e. limited or lacking exchange of genetic material among them. Isolated populations allow for genetically based adaptations to local abiotic or biotic conditions to develop. The occurrence of such “local adaptations” have been strongly suggested in a number of studies of cod ranging from examination of apparently complex traits such as sperm mobility and egg buoyancy (Nissling and Westin, 1997), to variation in single genes playing a major role in a physiological process such as hemoglobin (e.g. (Petersen and Steffensen, 2003)). Three different, but not mutually exclusive, population responses can provide a possible explanation for the apparent discrepancy between high temperature and high cod abundance.

The local population(s) in Danish waters at that time could have adapted genetically to the gradually increased temperatures, resulting in very different optimal temperature(s) (warm adapted) compared to present Icelandic cod (Björnsson and Steinarsson, 2002). Likewise, local adaptations to a range of other correlated environmental changes including species assemblages could have been apparent. With the drop in temperature after the Atlantic Warm Period, the genetic composition changed again, and “cold adapted” genotypes were favored until recently, when the process was again reversed. Whether the present cod population will be able to adapt to changing environmental conditions depends on a number of factors including: the magnitude of the temperature change, the number of traits that have to be changed, how much standing genetic trait variation is found in the population (is there something for selection to work on?), the architecture of the trait (are many or a few genes involved in regulating the trait?), and the (genetically effective) population size. The larger the population the more genetic variation will be present and there will be more individuals for selection to work on. Heavy fishing pressure, as has been the case in the past decades, will reduce the population size and could thereby impede future adaptability.

Another option is that different local populations of cod, similar to the processes at the species level presented here, have shifted their ranges over time in response to environmental changes. In times of low temperature, a large number of populations (a metapopulation) with different temperature optima have slowly shifted their distributions and “migrated” southwards. A similar northward migration should then be apparent in warmer periods. This scenario is intuitively simple and appealing, since it does not seem to require evolution to take place, only migration. However, many local adaptations may not have any relation to temperature, and tradeoffs between different locally adapted traits likely exist (Davis et al., 2005). For example, Baltic cod possess a number of traits related to salinity (mentioned above), which would be maladaptive in the North Sea environment even under the same temperature regimes. Some populations which are demographically isolated may therefore not be able to migrate (e. g., when temperatures change), even if optimal temperature conditions become the norm in neighboring waters.

Finally, the in situ persistence of large Danish cod population(s) under varying temperatures could simply be due to the plasticity of the species; i.e. if changing climate remains within the species' tolerance limits. As mentioned above, sub-optimal conditions may reduce the population abundance, but large undisturbed populations could be sustained under current climate scenarios (Cook and Heath, 2005; Kell et al., 2005) even without inferring genetically based adaptation or migration. The clue to be able to make better predictions of future distribution and abundance is an improved understanding of thermal (local) adaptation in cod; i.e. to establish a functional link between temperature and trait variation – and ultimately the underlying genetic variation. For instance, little is known of which aspect of temperature is important; i.e. is it the average, maximum or life-history specific temperatures? Further, is it temperature *per se*, or other drivers correlated with temperature which are important (e.g. copepod community; Beaugrand et al. 2004).

Our archaeological results have also shown that cod were probably a dominant species in coastal waters near Bornholm (southern Baltic Sea) during the Atlantic warm period. The influence of temperature on cod population dynamics in the eastern Baltic Sea is unclear but may be negative via its influence on oxygen concentrations in deep water layers where cod eggs are neutrally buoyant (MacKenzie et al., 1996). Recent studies show that recruitment in this population is negatively related to the winter index of the North Atlantic Oscillation (Brander and Mohn, 2004), which in turn is positively related to surface and halocline temperatures in the Baltic Sea (MacKenzie and Köster, 2004; MacKenzie and Schiedek, 2007b). These relationships suggest that warm temperatures are detrimental to the eastern Baltic cod population (MacKenzie et al., 2007a). Contemporary process studies of how the environment affects this cod population show that salinity and oxygen concentrations are the main environmental drivers of variability in this population (Köster et al., 2003; Köster et al., 2005). The salinity of the Baltic Sea 8000-3000 year BP (Litorina period) was similar to (Emeis et al., 2003) or ca. 4 PSU higher than at present (Sohlenius et al., 2001); given present understanding of cod recruitment processes in the eastern Baltic, a potentially higher salinity during this period would have promoted reproductive success in this population. This influence may have been sufficient to offset the potential negative effect that warmer temperatures may have had on this population.

The remains of cod recovered from several of our archaeological sites also included otoliths. Future analyses of these subfossil cod otoliths may identify a correlation between age and size, and the seasonality of cod growth, thus adding information on estimates of growth rates of the Stone Age cod. These rates and seasonal patterns could be compared with those observed in recent decades and during the post-Medieval period (van Neer et al., 1998; Bolle et al., 2004).

Conclusions:

Archaeological evidence shows that there were many warm-water fish species present in waters near Denmark during the Atlantic warm period, and that these species co-habited with species now considered to be more boreal (e. g., cod). When temperatures cooled after the warm period ended, most of these species disappeared from the archaeological record, suggesting that local abundances declined. However, many of the warm-water species evident in the archaeological remains from the Atlantic period have recently reappeared in waters around Denmark as temperatures have risen in the last 10-15 years. These results indicate that zoo-archaeological evidence can contribute to ongoing scientific discussions of the dynamics of marine fish populations during future climate change.

Acknowledgements:

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- 1 Table 1. Relative frequencies (percentages) of bones identified to individual fish species/species groups from the studied archaeological sites.
 2 Numerical entries in the top row of the table indicate number of bones identified. The letter x in the table body indicates that bones for a given
 3 species were present but the share of the given species represented less than 1% of all identified fishbones found at the site.
 4
 5
 6
 7

	Region	Vendsyssel	Limfjord	E Jutland	NE Funen	NE Zealand	Bornholm
N_{total} = 108390		N=553	N=24355	N=28133	N=2513	N=51156	N=1680
Marine species							
porbeagle	<i>Lamna nasus</i>	x		x			
smoothhound	<i>Mustelus</i> sp.		x	x			
topeshark	<i>Galeorhinus galeus</i>	1		x			
spurdog	<i>Squalus acanthias</i>	30	x	x	3	1	
thornback ray	<i>Raja clavata</i>					x	
common stingray	<i>Dasyatis pastinaca</i>		x				
ray unspecified	<i>Raja</i> sp.		x				
cartilaginous fish, unspecified				x			
anchovy	<i>Engraulis encrasicolus</i>		1				
herring	<i>Clupea harengus</i>		2	4	1	1	x
clupeids unspecified	Clupeidae		x				
shad	<i>Alosa</i> sp.					x	
garfish	<i>Belone belone</i>		1	x		x	
garfish/Atlantic saury	<i>B. belone/Scomberesox saurus</i>		x				
pipefish unspecified	Syngnathidae			x	x		
cod	<i>Gadus morhua</i>	1	1	3	1	4	18
haddock	<i>Melanogrammus aeglefinus</i>					x	
whiting	<i>Merlangius merlangus</i>			x		x	
pollack	<i>Pollachius pollachius</i>			x		1	

saith	<i>Pollachius virens</i>		x	x		x	
pollack/saith	<i>P. pollachius/P. virens</i>		x			x	
ling	<i>Molva molva</i>	1					
gadids unspecified	Gadidae	1	7	40	75	43	69
European sea bass	<i>Dicentrarchus labrax</i>	x	x				
Atlantic horse-mackerel	<i>Trachurus trachurus</i>		x				
black sea bream	<i>Spondyllosoma cantharus</i>		x ²				
cuckoo wrasse	<i>Labrus bimaculatus</i>				x		
goldsinny-wrasse	<i>Ctenolabrus rupestris</i>					x	
sand-eel	<i>Hyperoplus/Ammodytes</i>		x	x		x	
greater weever	<i>Trachinus draco</i>	1	3	1		x	
dragonet	<i>Callionymus lyra</i>			x			
Atlantic mackerel	<i>Scomber scombrus</i>		1	x	1	1	
bluefin tuna	<i>Thunnus thynnus</i>					x	
swordfish	<i>Xiphias gladius</i>					x	
viviparous eelpout	<i>Zoarces viviparus</i>	1	x	x	x	x	
black goby	<i>Gobius niger</i>				1	x	
gobiids unspecified			x	x		x	
tub gurnard	<i>Trigla lucerna</i>					x	
grey gurnard	<i>Eutrigla gurnardus</i>	1	x	x		x	
gurnard unsp.		x	x	x		x	
bull-rout	<i>Myoxocephalus scorpius</i>	x	x	x	x	x	
three-spined stickleback	<i>Gasterostus aculeatus</i>	1	7	x	3	x	
fifteen-spined stickleback	<i>Spinachia spinachia</i>		x			x	
turbot	<i>Psetta maxima</i>		x ⁴			x	
brill	<i>Schophthalmus rhombus</i>				x		
turbot/brill	<i>P. maxima/S. rhombus</i>			x		x	1
plaice	<i>Pleuronectes platessa</i>			x		x	
flounder	<i>Platichthys flesus</i>	x	x ⁵	1 ³		1	
plaice/flounder /dab	<i>P. platessa/P. flesus/Limanda limanda</i>	50	1	36	15	44	12

flatfish unsp.	Heterosomata	x	x	1		x	
Catadromous and anadromous species							
sturgeon	<i>Acipenser sturio</i>	x				x	
shad	<i>Alosa</i> sp.						
trout	<i>Salmo trutta</i>		x				
trout/salmon	<i>Salmo</i> sp.	1	x	x	x	x	x
whitefish	<i>Coregonus</i> sp.	1 ¹	x			x	
salmonids unspecified	Salmonidae		x		x		
eel	<i>Anguilla anguilla</i>	8	39	12	1	1	x
Freshwater species							
pike	<i>Esox lucius</i>	2	x	x		x	
tench	<i>Tinca tinca</i>		x				
roach	<i>Rutilus rutilus</i>		2			x	
rudd	<i>Scardinius erythrophthalmus</i>		x			x	
common bream	<i>Abramis brama</i>					x	
cyprinids unspecified	Cyprinidae		32	x		1	
perch	<i>Perca fluviatilis</i>		1			x	

8

9 1 : 227 scales not included

10 2 : 21 scales not included

11 3 : 237 scales/dermal denticles not included

12 4 : 2 scales/dermal denticles not included

13 5 : 67 scales/dermal denticles not included

Figure captions

Figure 1. Palaeotemperature curve from Lake Tringstäde Träsk (Gotland, Sweden) as established via stable isotopes in the sediments (Mörner 1980). Present-day temperature indicated with arrow on the base line. Major events noted to the right.

Figure 2. Map of Denmark during the Atlantic period with present-coastline indicated (Helleisen and Tuxen, 1988), showing locations of archaeological sites from where fish bones were recovered. Region I: Vendsyssel. 1: Østenkær, 2: Yderhede. Region II: Limfjord. 1: Bjørnsholm, 2: Ertebølle, 3: Krabbesholm. Region III: E Jutland. 1: Visborg, 2: Nederst, 3: Lystrup Enge, 4: Norsminde, 5: Vængesø. Region IV: NW Funen. 1: Ronæs Skov, 2: Tybrind Vig. Region V: NE Zeland. 1: Nivågård, 2: Vedbæk Fjord (Stationsvej 19, Henriksholm-Bøgebakken, Magleholm, Maglemosegård, Maglemosegårds Vænge, Vænget Nord, Gøngehusvej 7), 3: Italiensvej. Region VI: Bornholm. 1: Grisby. Map provided by K. Rosenlund, Zoological Museum, University of Copenhagen.

Figure 3. A sediment sample from Krabbesholm. An example of a sediment sample as it appeared before the sorting of fish bones started. One can see several small fish bones among pebbles and bivalve and snail shells. It turned out that a new species was hiding in this sample. Each scale unit equals 1 cm. Photo provided by G. Brovad, Zoological Museum, University of Copenhagen.

Figure 4. Vertebra of smoothhound from Bjørnsholm (Enghoff 1993). The scale corresponds to 5 mm. Photo G. Brovad.

Figure 5. Tail spine of common stingray. Bottom: subfossil spine from Bjørnsholm. Top: recent spine for comparison (Enghoff 1993). Length of the subfossil spine is 15 cm (base and tip are missing). Photo G. Brovad.

Figure 6. Anchovy. Vertebrae of anchovy caught by the stone age people at Krabbesholm. Two connected vertebrae from a recent anchovy are shown for comparison. Scale 10 mm. Photo G. Brovad.

Figure 7. Annual landings during 1978-2005 by Danish commercial fishermen of four fish species (anchovy, European seabass, thicklip-thinlip mullet, and red mullet and striped red mullet) commonly associated with southern warmer waters (Heessen and van de Kamp 1996; Muus and Nielsen, 1999). The Danish landings database does not distinguish between thicklip and thinlip mullets, nor between red mullet and striped red mullet.

Figure 8. A vertebra and praevomer of European seabass from Bjørnsholm (Enghoff 1993). The scale corresponds to 10 mm. Photo G. Brovad,

Figure 9. Articulare, parasphenoideum and two vertebrae of black sea bream from Bjørnsholm (Enghoff 1993). The scale corresponds to 10 mm. Photo G. Brovad.

Figure 10. Vomer of swordfish from Italiensvej (Greater Copenhagen). Photo provided by W. Karrasch, Viking Ship Museum, Roskilde, Denmark.

Figure 11. Part of the fishbones from 1 m² of the Maglemosegård excavation. 48% of the 12784 identified fish bones were from gadids, mainly cod (Enghoff 1994). Photo G. Brovad.

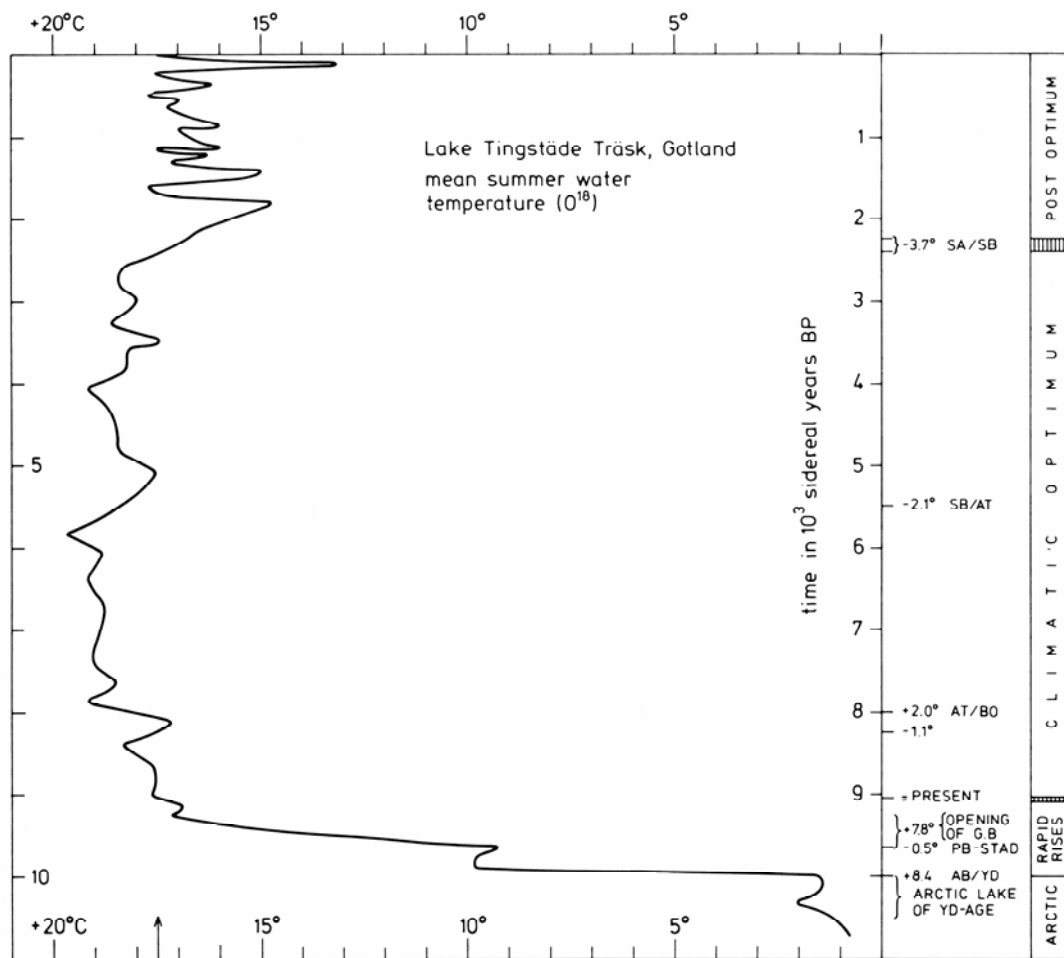


Figure 1

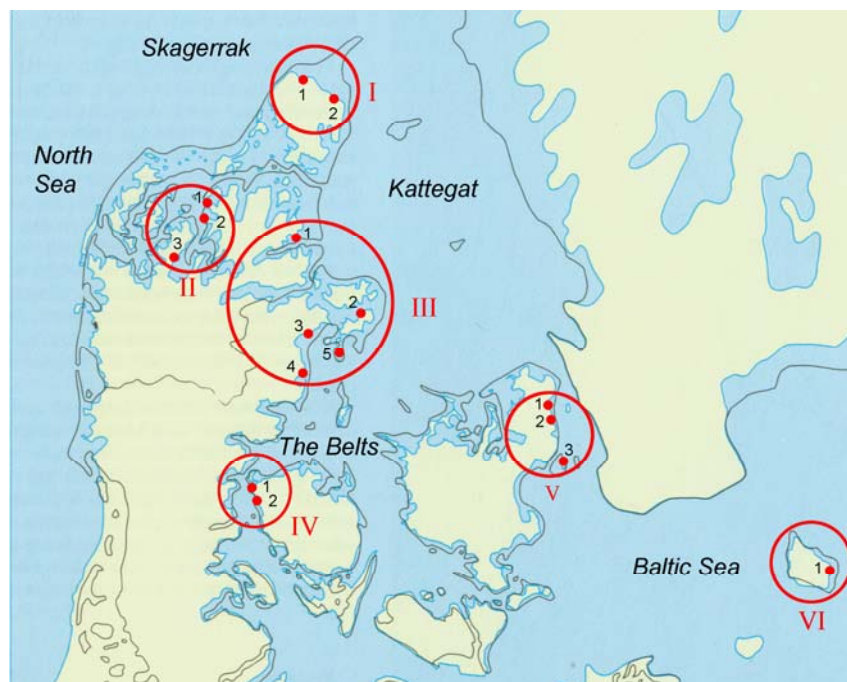


Figure 2



Figure 3



Figure 4

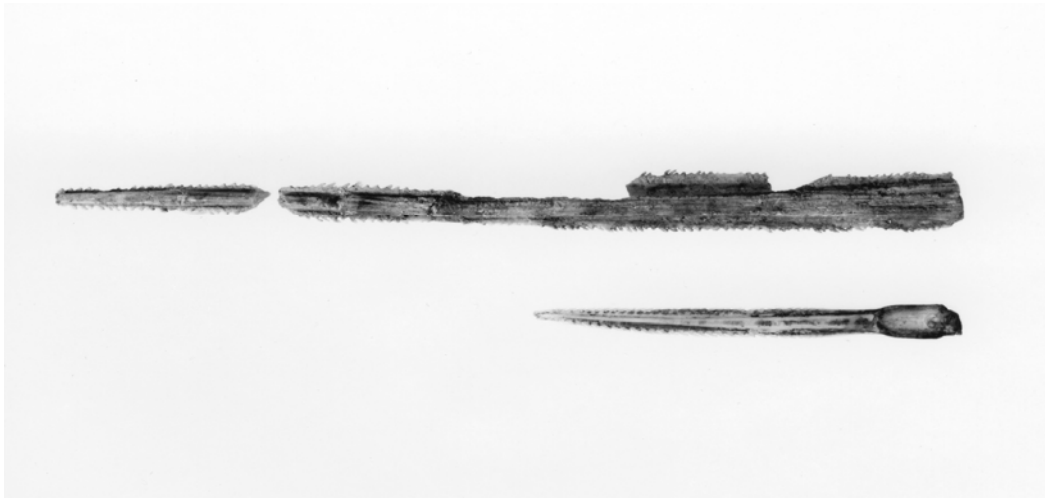


Figure 5



Figure 6

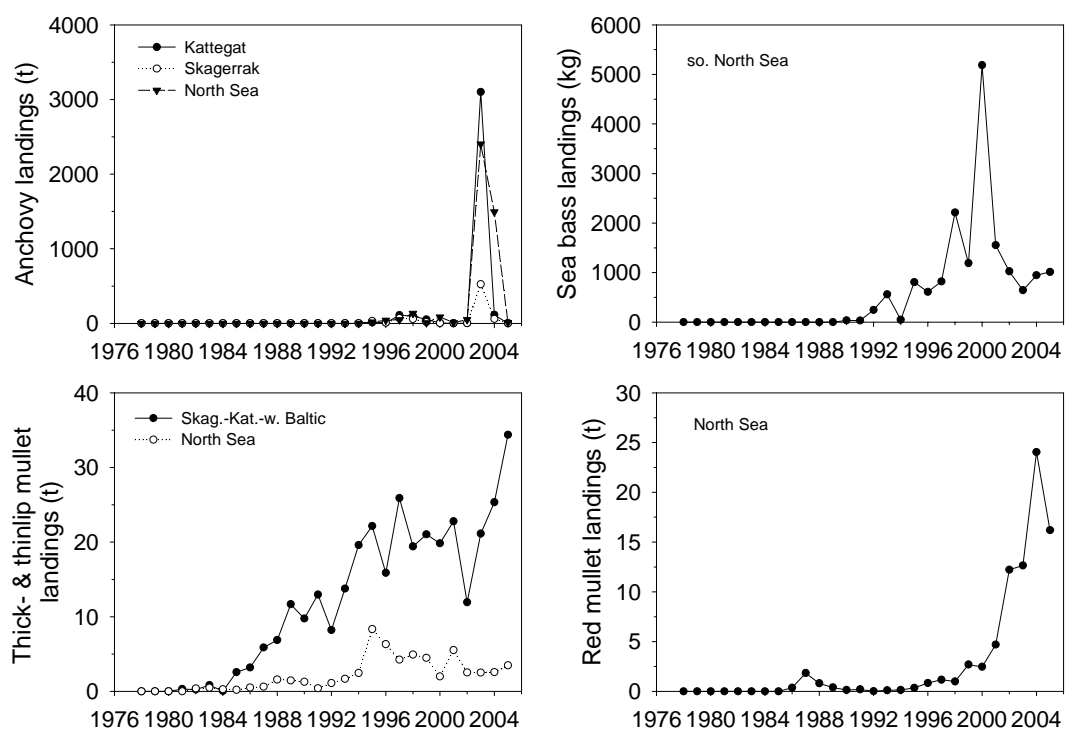


Figure 7

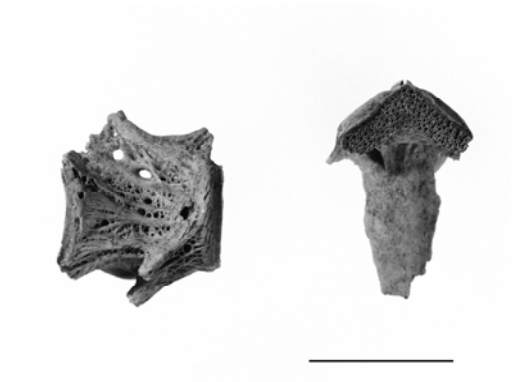


Figure 8



Figure 9



Figure 10



Figure 11

Reference List

- Aaris-Sørensen, K., 1998. Danmarks Forhistoriske Dyreverden. Gyldendal.
- Antonsson, K. Holocene climate in central and southern Sweden. Digital comprehensive summaries of Uppasala Dissertations from the Faculty of Science and Technology 168. Acta Universitatis Upsaliensis. Ph. D. thesis, Uppsala University, Uppsala, Sweden.
- Aurich, H. J., 1953. Verbreitung und Laichverhältnisse von sardelle und sardine in der südöstlichen Nordsee und ihre Veränderung als Folge der Klimaänderung. Helgoländer wiss. Meeresunters. 4, 175-204.
- BACC, 2006. Assessment of Climate Change for the Baltic Sea Basin - the BACC Project (International Conference, Gothenberg, Sweden, May 22-23, 2006). IKSS, Gestacht, Germany.
- Bacevicius, E., Karalius, S., 2005. A survey of the data on swordfish (*Xiphias gladius* L.) in the southern and southeastern Baltic Sea. Bull. Sea Fish. Inst. 165, 63-72.
- Barrett, J. H., Locker, A. M., Roberts, C. M., 2004. The origins of intensive marine fishing in medieval Europe: the English evidence. Proc. R. Soc. Lond. B 271, 2417-2421.
- Beare, D. J., Burns, F., Greig, T., Jones, E. C., Peach, K., Keinzle, M., McKenzie, E., Reid, D. G., 2004. Long-term increases in prevalence of North Sea fishes having southern biogeographic affinities. Mar. Ecol. Prog. Ser. 284, 269-278.
- Beaugrand, G., Brander, K. M., Lindley, J. A., Souissi, S., Reid, P. C., 2004. Plankton effect on cod recruitment in the North Sea. Nature 426, 661-664.
- Beaugrand, G., Reid, P. C., Ibañez, F., Lindley, J. A., Edwards, M., 2002. Reorganization of North Atlantic marine copepod biodiversity and climate. Science 296, 1692-1694.
- Bianchi, G., Gislason, H., Graham, K., Hill, L., Jin, X., Koranteng, K., Manickchand-Heileman, S., Payá, I., Sainsbury, K., Sanchez, F., Zwanenburg, K., 2000. Impact of fishing on size composition and diversity of demersal fish communities. ICES J. Mar. Sci. 57, 558-571.
- Björnsson, B., Steinarsson, A., 2002. The food-unlimited growth rate of Atlantic cod (*Gadus morhua*). Can. J. Fish. Aquat. Sci. 59, 494-502.
- Bolle, L. J., Rijnsdorp, A. D., Neer, W. v., Millner, R. S., Leeuwen, P. I. v., Ervynck, A., Ayers, R., Ongenae, E., 2004. Growth changes in plaice, cod, haddock and saithe in the North Sea: a comparison of (post-)medieval and present-day growth rates based on otolith measurements. Journal of Sea Research 51, 313-328.
- Brander, K., Mohn, R., 2004. Effect of the North Atlantic Oscillation on recruitment of Atlantic cod (*Gadus morhua*). Can. J. Fish. Aquat. Sci. 61, 1558-1564.
- Brander, K. M., Blom, G., Borges, M. F., Erzini, K., Henderson, G., MacKenzie, B. R., Mendes, H., Santos, A. M. P., Toresen, P., 2003. Changes in fish distribution in the eastern North Atlantic: are we seeing a coherent response to changing temperature? ICES Mar. Sci. Symp. 219, 260-273.
- Brooks, S. J., 2003. Chironomid Analysis to Interpret and Quantify Holocene Climate Change. In: A. MacKay, R. Battarbee, J. Birks, F. Oldfield (Eds.), Global changes in the Holocene. Arnold, London, pp. 328-341.
- Carl, H., Nielsen, J. G., Møller, P. R., 2004. En kommenteret og revideret oversigt over danske fisk. Flora og Fauna 110, 29-39.

- Case, R. A. J., Hutchinson, W. F., Hauser, L., Van Oosterhout, C., Carvalho, G. R., 2005. Macro- and micro-geographic variation in pantophysin (*PanI*) allele frequencies in NE Atlantic cod *Gadus morhua*. Mar. Ecol. Prog. Ser. 301, 267-278.
- Christensen, C., 1995. The Littorina Transgressions in Denmark. In: A. Fischer (Ed.), Man and sea in the Mesolithic: coastal settlement above and below present sea level., pp. 15-22.
- Cook, R. M., Heath, M. R., 2005. The implications of warming climate for the management of North Sea fisheries. ICES J. Mar. Sci. 62, 1322-1326.
- Curry-Lindahl, K., 1985. Våra Fiskar. Havs- Och Sötvattensfiskar i Norden Och Övriga Europa. Stockholm.
- Davis, M. B., Shaw, R. G., Etterson, J. R., 2005. Evolutionary responses to climate change. Ecology 86, 1704-1714.
- Dickson, K. A., Graham, J. B., 2004. Evolution and consequences of endothermy in fishes. Physiol. Biochem. Zool. 77, 998-1018.
- Döscher, R., Meier, H. E. M., 2004. Simulated sea surface temperature and heat fluxes in different climates of the Baltic Sea. Ambio 33, 242-248.
- Drinkwater, K. F., 2005. The response of Atlantic cod (*Gadus morhua*) to future climate change. ICES J. Mar. Sci. 62, 1327-1337.
- Drinkwater, K. F., 2006. The regime shift of the 1920s and 1930s in the North Atlantic. Prog. Oceanogr. 68, 134-151.
- Emeis, K.-C., Struck, U., Blanz, T., Kohly, A., Voss, M., 2003. Salinity changes in the Baltic Sea (NW Europe) over the last 10,000 years. Holocene 13, 411-421.
- Enghoff, I. B., 1983. Size distribution of cod (*Gadus morhua* L.) and whiting (*Merlangus merlangus* L.) (Pisces, Gadidae) from a Mesolithic settlement at Vedbæk, North Zealand, Denmark. Vid. Medd. Dansk Naturhist. Forening 144, 83-87.
- Enghoff, I. B., 1987. Freshwater fishing from a sea-coast settlement - the Ertebølle, *locus classicus*, revisited. J. Dan. Archaeol. 5, 62-76.
- Enghoff, I. B., 1991. Fishing from the stone age settlement Norsminde. J. Dan. Archaeol. 41-50.
- Enghoff, I. B., 1993. Mesolithic eel-fishing at Bjørnsholm, Denmark, spiced with exotic species. J. Dan. Archaeol. 10, 105-118.
- Enghoff, I. B., 1994. Fishing in Denmark during the Ertebølle period. Int. J. Osteoarch. 4, 65-96.
- Enghoff, I. B., 2000. Fishing in the southern North Sea region from the 1st to the 16th century AD: evidence from fish bones. Archaeofauna 9, 59-132.
- Enghoff, I. B., 2005a. Dyreknogler Fra Vikingetidens Viborg. In: M. Iversen, D.E. Robinson, J. Hjeremind, C. Christensen (Eds.), Viborg Søndersø 1018-1030. Arkæologi og naturvidenskab i et værkstedsområde fra vikingetid. Viborg Stiftsmuseum, Jysk Arkæologisk Selskab., pp. 239-268.
- Enghoff, I. B., 2005b. Fisk Og Fiskeri. In: M. Svart Kristiansen (Ed.), Tårnby, gård og landsby gennem 1000 år. Jysk Arkæologisk Selskab, pp. 469-478.
- Enghoff, I. B., 2006a. Dyreknogler fra Ronæs Skov-bopladsen. Jysk Arkæologisk Selskab (submitted).
- Enghoff, I. B., 2006b. Fiskeknogler Fra Markedspladsen i Ribe, ASR 9 Posthuset. In: C. Feveile (Ed.), Det ældste Ribe. Udgravninger på nordsiden af Ribe Å 1984-2000. Ribe Studier vol. 1. Jysk Arkæologisk Selskab, pp. 157-168.
- Fritches, K. A., Brill, R. W., Warrant, E. J., 2005. Warm eyes provide superior vision in swordfishes. Curr. Biol. 15, 55-58.
- Genner, M. J., Sims, D. W., Wearmouth, V. J., Southall, E. J., Southward, A. J., Henderson, P. A., Hawkins, S. J., 2004. Regional climatic warming drives long-term community changes of British marine fish. Proc. R. Soc. Lond. B 271, 655-661.

- Graham, J. B., Dickson, K. A., 2001. Anatomical and Physiological Specializations for Endothermy. In: B.A. Block, E.D. Stevens (Eds.), Tuna: Physiology, Ecology and Evolution. Academic Press, San Diego, California, pp. 121-165.
- Heegaard, P., 1947. Investigations on the breeding season and the quantities of eggs of the food-fishes of the Kattegat and the Northern Belt Sea. 1929-1941. Meddelelser fra Kommissionen for Danmarks Fiskeri- og Havundersøgelser 11, 3-22.
- Heessen, H., van de Kamp, G., 1996. Changes in abundance of "southern" fish species in the North Sea. ICES J. Mar. Sci. x, x.
- Hellesen, J. P., Tuxen, O., 1988. Historisk Atlas Danmark. Copenhagen.
- ICES, 2005. Report of the ICES Advisory Committee on Fisheries Management, Advisory Committee on the Marine Environment, and Advisory Committee on Ecosystems. ICES Advice 6, 1-275.
- IPCC, 2001. Climate Change 2001: the Scientific Basis. Cambridge University Press, Cambridge, UK.
- Jennings, S., Greenstreet, S., Hill, L., Piet, G., Pinnegar, J., Warr, K. J., 2002. Long-term trends in the trophic structure of the North Sea fish community: evidence from stable-isotope analysis, size-spectra and community metrics. Mar. Biol. 141, 1085-1097.
- Jensen, O. L., 2001. Kongemose- Og Ertebøllekultur Ved Den Fossile Nivåfjord. In: O.L. Jensen, S.A. Sørensen, K.M. Hansen (Eds.), Danmarks jægerstenalder - status og perspektiver. Hørsholm Egns Museum, pp. 115-129.
- Jonsson, L., 1995. Vertebrate Fauna During the Mesolithic on the Swedish West Coast. In: A. Fischer (Ed.), Man and sea in the Mesolithic: coastal settlement above and below present sea level., pp. 147-160.
- Jonsson, L., 2005. *Bogas-Boops boops* (L. 1758) from the Biscay to the North Sea in 2500 BC and 1980 AD. Munibe (Anthropologia-Arkeologia) 57, 5-8.
- Kell, L. T., Pilling, G. M., O'Brien, C. M., 2005. Implications of climate change for the management of North Sea cod (*Gadus morhua*). ICES J. Mar. Sci. 62, 1483-1491.
- Kerr, R. A., 2004. Three degrees of consensus. Science 305, 932-934.
- Knijn, R. J., Boon, T. W., Heesen, H. J. L., Hislop, J. R. G., 1993. Atlas of North Sea fishes. Based on bottom-trawl survey data for the years 1985-1987. No. 194, ICES, Copenhagen
- Knutsen, H., Jorde, P. E., Andre, C., Stenseth, N. C., 2003. Fine-scaled geographical population structuring in a highly mobile marine species: the Atlantic cod. Mol. Ecol. 12, 385-394.
- Köster, F. W., Hinrichsen, H.-H., Schnack, D., St. John, M. A., MacKenzie, B. R., Tomkiewicz, J., Möllmann, C., Kraus, G., Plikshs, M., Makarchouk, A., Aro, E., 2003. Recruitment of Baltic cod and sprat stocks: identification of critical life stages and incorporation of environmental variability into stock-recruitment relationships. Sci. Mar. (Suppl. 1) 67, 129-154.
- Köster, F. W., Möllmann, C., Hinrichsen, H.-H., Tomkiewicz, J., Wieland, K., Kraus, G., Voss, R., MacKenzie, B. R., Schnack, D., Makarchouk, A., Plikshs, M., Beyer, J. E., 2005. Baltic cod recruitment – the impact of climate variability on key processes. ICES J. Mar. Sci. 62, 1408-1425.
- Llungar, L., 1995. First subfossil find of the aesculapian snake *Elaphe longissima* (Colubridae) from a Mesolithic settlement in Denmark. Amphibia-Reptilia 16, 93-94.
- Lotze, H., 2007. Rise and fall of fishing and marine resource use in the Wadden Sea, southern North Sea. Fish. Res. (accepted) x, x.
- MacKenzie, B. R., Gislason, H., Möllmann, C., Köster, F. W., 2007a. Impact of 21st century climate change on the Baltic Sea fish community and fisheries. Glob. Change Biol. 13: 1348-1367.

- MacKenzie, B. R., Köster, F. W., 2004. Fish production and climate: sprat in the Baltic Sea. *Ecology* 85, 784-794.
- MacKenzie, B. R., Myers, R. A., 2007. The development of the northern European fishery for north Atlantic bluefin tuna (*Thunnus thynnus*) during 1900-1950. *Fish. Res.* In press. (doi:10.1016/j.fishres.2007.01.013)
- MacKenzie, B. R., Nielsen, E., Lassen, H. In prep. Recent and historical occurrence of anchovy, *Engraulis encrasicolus*, in waters near Denmark and the role of climate variability.
- MacKenzie, B. R., Schiedek, D., 2007a. Daily ocean monitoring since the 1860s shows unprecedented warming of northern European seas. *Glob. Change Biol.* 13: 1335-1347.
- MacKenzie, B. R., Schiedek, D., 2007b. Long-term spatial synchrony of coastal and offshore sea surface temperatures in the North Sea - Baltic Sea region. *J. Mar. Syst.* (in press). (10.1016/j.jmarsys.2007.01.003)
- MacKenzie, B. R., St.John, M. A., Plikshs, M., Hinrichsen, H.-H., Wieland, K., 1996. Oceanographic processes influencing seasonal and interannual variability in cod spawning habitat in the eastern Baltic Sea. *ICES CM* 1996/C+J:4.
- Mather, F. J., Mason, J. M., Jones, A. C., 1995. Historical document: life history and fisheries of Atlantic bluefin tuna. NOAA Technical Memorandum NMFS-SEFSC-370 No. 370, US Department of Commerce, NOAA, NMFS, Southeast Fisheries Science Center
- Mörner, N.-A., 1980. A 10,700 years' paleotemperature record from Gotland and Pleistocene/Holocene boundary events in Sweden. *Boreas* 9, 283-287.
- Muus, B. J., Nielsen, J. G., 1999. Sea Fish. Scandinavian Fishing Year Book, Hedehusene, Denmark.
- Myers, R. A., MacKenzie, B. R., Bowen, K. G., Barrowman, N. J., 2001. What is the carrying capacity of fish in the ocean? A meta-analysis of population dynamics data from the North Atlantic. *Can. J. Fish. Aquat. Sci.* 58, 1464-1476.
- Nielsen, E. E., Hansen, M. M., Ruzzante, D. E., Meldrup, D., Grønkjær, P., 2003. Evidence of a hybrid-zone in Atlantic cod (*Gadus morhua*) in the Baltic and the Danish Belt Sea revealed by individual admixture analysis. *Mol. Ecol.* 12, 1497-1508.
- Nielsen, E. E., Møller Hansen, M., Schmidt, C., Meldrup, D., Grønkjær, P., 2001. Genetic differences among cod populations. *Nature* 413, 272.
- Nilsson, S., 1855. Skandinavisk Fauna (Fjerde Delen: Fiskarna). Bokhandlaren C. W. K. Gleerups Förlag, Lund, Sweden.
- Perry, A. L., Low, P. J., Ellis, J. R., Reynolds, J. D., 2005. Climate change and distribution shifts in marine fishes. *Science* 308, 1912-1915.
- Petersen, K. S., 1981. The holocene marine transgression and its molluscan fauna in the Skagerrak-Limfjord region, Denmark. Special publication International Association of Sedimentologists No. 5
- Petersen, K. S., 1985. Late Weichselian and Holocene marine transgressions in northern Jutland, Denmark. Field conference 1984 of the INQUA subcommission on shorelines of Northwestern Europe No. 35, Eisalter and Gegenwart
- Petersen, P. V., 1996. Fiskeben. *Skalk* 1, 16-17.
- Pörtner, H. O., Berdal, B., Blust, R., Brix, O., Colosimo, A., De Wachter, B., Giuliani, A., Johansen, T., Fischer, T., Knust, R., Lannig, G., Naevdal, G., Nedenes, A., Nyhammer, G., Sartoris, F. J., Serendero, I., Sirabella, P., Thorkildsen, S., Zakhartsev, M., 2001. Climate induced temperature effects on growth performance, fecundity and recruitment in marine fish: developing a hypothesis for cause and effect relationships in Atlantic cod (*Gadus morhua*) and common eelpout (*Zoarces viviparus*). *Cont. Shelf Res.* 21, 1975-1997.
- Richter, J., 1987. Evidence for a natural deposition of fish in the middle Neolithic site, Kainsbakke, East Jutland. *J. Dan. Archaeol.* 5, 116-124.

- Root, T. L., Price, J. T., Hall, K. R., Schneider, S. H., Rosenzweig, C., Pounds, J. A., 2003. Fingerprints of global warming on wild animals and plants. *Nature* 421, 57-60.
- Rose, G. A., 2004. Reconciling overfishing and climate change with stock dynamics of Atlantic cod (*Gadus morhua*) over 500 years. *Can. J. Fish. Aquat. Sci.* 61, 1553-1557.
- Rosenberg, A. A., Bolter, W. J., Alexander, K. E., Leavenworth, W. B., Cooper, A. B., McKenzie, M. G., 2005. The history of ocean resources: modelling cod biomass using historical records. *Front. Ecol. Environ.* 3, 84-90.
- Rosenlund, K., 1976. Catalogue of subfossil Danish vertebrates. Fishes., Zoological Museum, Copenhagen
- Rosenlund, K., 1986a. Hvad en kommodeskuffe kan indeholde. *Dyr i Natur og Museum* 2, 30-31.
- Rosenlund, K., 1986b. The stingray, *Dasyatis pastinaca* (L.) in Denmark. *BAR Intl. Ser.* 124, 123-128.
- Sohlenius, G., Emeis, K.-C., Andrén, E., Andrén, T., Kohly, A., 2001. Development of anoxia during the Holocene fresh-brackish water transition in the Baltic Sea. *Mar. Geol.* 177, 221-242.
- Stebbing, A. R. D., Turk, S. M. T., Wheeler, A., Clarke, K. R., 2002. Immigration of southern fish species to south-west England linked to warming of the North Atlantic (1960-2001). *J. Mar. Biol. Ass. U. K.* 82, 177-180.
- Stenseth, N. C., Ottersen, G., Hurrell, J. W., Belgrano, A., 2004. *Marine Ecosystems and Climate Variation*. Oxford University Press.
- Tauber, H., 1981. ¹³C evidence for dietary habits of prehistoric man in Denmark. *Nature* 292, 332-333.
- Tauber, H., 1987. Argusbopladsen: alder og ernæring belyst ved kulstofanalyser. Fortidsminder og kulturhistorie. Antikvariske studier. No. 8, Kulturarvstyrelsen.
- Trolle-Lassen, T. En zooarchaeologisk analyse af Ertebøllebopladsen Tybrind Vig, primært baseret på knogler af pelsdyr og kronhjort. (Unpublished Master's thesis). Zoological Museum, University of Copenhagen.
- van Neer, W., Løugas, L., Rijnsdorp, A. D., 1998. Reconstructing age distribution, season of capture and growth rate of fish from archaeological sites based on otoliths and vertebrae. *Intl. J. Osteoarchaeol.* 9, 116-130.
- Vork, K. A., Thomsen, E., 1996. Lusitanian/Mediterranean ostracods in the Holocene of Denmark: implications for the interpretation of winter temperatures during the postglacial temperature maximum. *Holocene* 6, 423-432.
- Whitehead, P. J. P., Bauchot, M.-L., Hureau, J.-C., Nielsen, J., Tortonese, E., 1984. *Fishes of the North-Eastern Atlantic and the Mediterranean*. UNESCO, Paris.
- Whitehead, P. J. P., Bauchot, M.-L., Hureau, J.-C., Nielsen, J. G., Tortonese, E., 1986. *Fishes of the North-Eastern Atlantic and the Mediterranean*. UNESCO, Paris.
- Wright, W. v., 1892. *Skandinaviens Fiskar*. P. A. Norstedt & Söners Forlag, Stockholm.