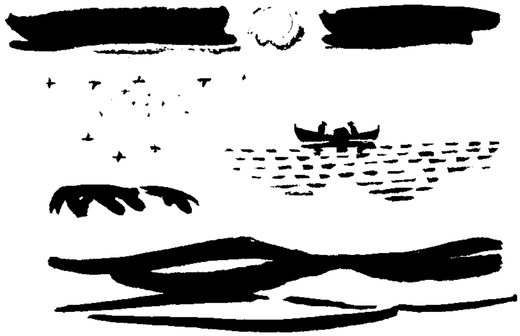


Marine climate, squid and pilot whales in the northeastern Atlantic

Hjálmar Hátún and Eilif Gaard

Abstract

We have identified a clear link between the abundance of long-finned pilot whales and the marine climate in the northeastern Atlantic throughout the last three centuries. During warm periods the whales are observed in high abundances and they can be completely absent from the region during cold periods. The linkage between the marine climate and the abundance of whales probably involves their main prey items, flying squid (*Todarodes sagittatus*) and the large, but highly variable blue whiting (*Micromesistius poutassou*) stock. The latter is preyed upon both by the squid and the whales. The subpolar gyre declined drastically in the late 1990s, resulting in warming and a great increase and a westward shift of the blue whiting stock, but the abundances of *T. sagittatus* and pilot whales in Faroese waters did not increase correspondingly. The post-1980s breaking of this, otherwise stable, multi-century bio-physical link points to anthropogenic interference. We discuss potential causes, rooted in Global Warming and an intensified pelagic fishery, which collectively might explain this breaking rela-

tion. Some new aspects of sub-decadal variability in the marine climate and in the Faroe shelf ecosystem are introduced.

The search for a pilot whale-climate linkage

The time series of long-finned pilot whale catches in the Faroe islands, extending back to 1584 and unbroken from 1709 (Bloch 1994), is one of the longest biological series on record. A strong periodic variability evident in this series has inspired many researchers to look for natural causes. The potential importance of the Faroe Current region to the north of the Faroe Islands (Figs. 1 and 2a) has been acknowledged (Hoydal and Lastein 1993) and a trophic linkage to the abundance of blue whiting in the Iceland-Faroe region has been demonstrated (Hoydal and Lastein 1993), although for a relatively short period (1980-1992). Joensen and Zachariassen (1982) point to the importance of the marine climate in the Rockall region south-west of the Faroe Islands, since the sea surface temperatures (SST) in this region follow the whale catches in the Faroes more closely than does the local SST around the islands (Joensen and Zachariassen 1982). And a comparison between the century-scale fluctuations in the Faroese pilot whale catches and the so-called Dansgaard temperature series from Greenland did not reveal persistent correlations (Hoydal and Lastein 1993).

Building on this knowledge, we have resumed the search

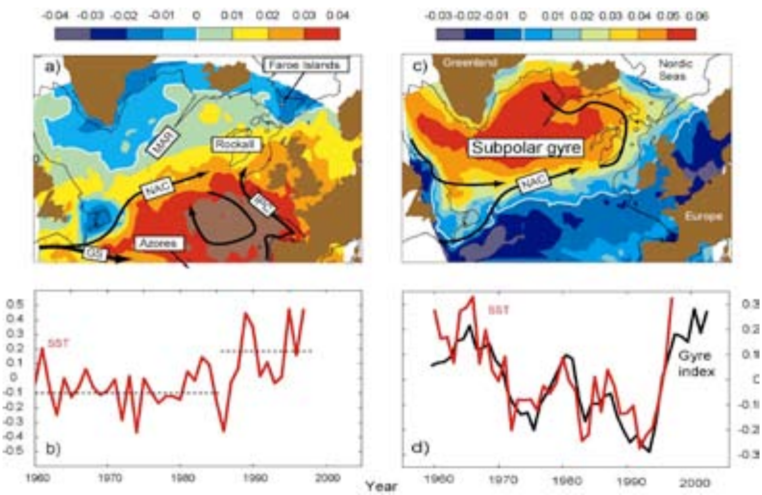


Fig. 1. *Variability sea surface temperature (SST) modes related to Northern Hemisphere Temperature (NHT) and the subpolar gyre, respectively, and the relevant flow systems. a) The spatial imprint of the NHT-like changes, with red colors representing areas with strong impact. b) The NHT-related SST variability over the reddish areas in a). Similarly, c) and d) show the spatial and the temporal gyre-related SST variability. The series are not to scale. The inverted gyre index has been included in d) (black curve). Abbreviations - MAR: Mid-Atlantic Ridge, NAC: North Atlantic Current, GS: Gulf Stream and IPC: Iberian Poleward Current.*

for a climate-pilot whale link, now equipped with much more extensive environmental data (from numerical models, satellites and *in-situ* observations), biological data on plankton and blue whiting, and the recent most additional number of years. The presented results on long-term (multi-decadal to centennial) have previously be presented in two other publications (Hátún et al. 2009a; Hátún et al. 2009b), and will not be reiterated here in their entirety. After a review on the relevant physical oceanography and some important aspects of the blue whiting and squid stocks, we present a relatively tight link between pilot whale abundance in Faroese and the marine climate in the northeastern Atlantic. This links is less clear after the late 1980s, and possible reasons underlying this breaking relation are discussed. Furthermore, a new perspective on this unique whale series is given by considering shorter term (6-10 years) variability in the regional climate, and in the abundance of pelagic fish and squid (prey) on the Faroe shelf.

Ocean Circulation and Climate

Changes in the marine climate in the study region, extending from the Azores in south to the Faroe Islands in north (Fig. 1), have been ascribed to two main drivers – the generally increasing Northern Hemispheric temperatures (NHT) and the subpolar gyre. But before introducing these, a general overview over the main ocean circulation will be given.

Ocean Circulation

The Gulf Stream, which represents the northern periphery of the subtropical gyre proper, leaves the American coast near New Foundland, and flows eastwards to the south of the Azores (Fig. 1a). The North Atlantic Current (NAC) is a poleward branch of the Gulf Stream which crosses the fractures zones in the Mid-Atlantic Ridge (MAR) (Bower et al. 2002) in an eastward direction and turns northward in the vicinity of Rockall (Fig. 1c). This current, which represents the southern and eastern periphery of the subpolar gyre, brings relatively warm and saline *western waters* towards the Rockall region (Holliday 2003). The circulation in the *inter-gyre region* be-

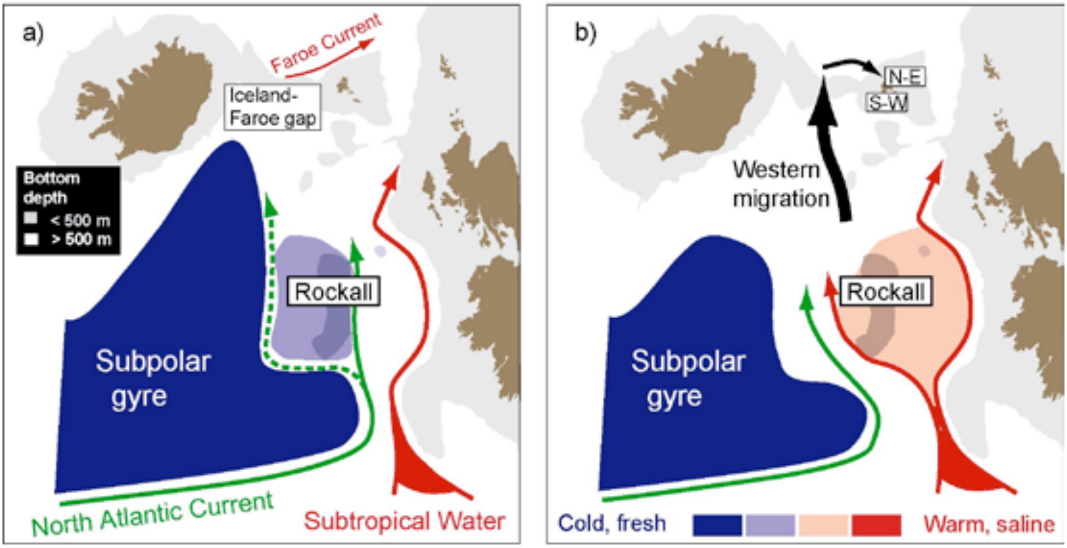


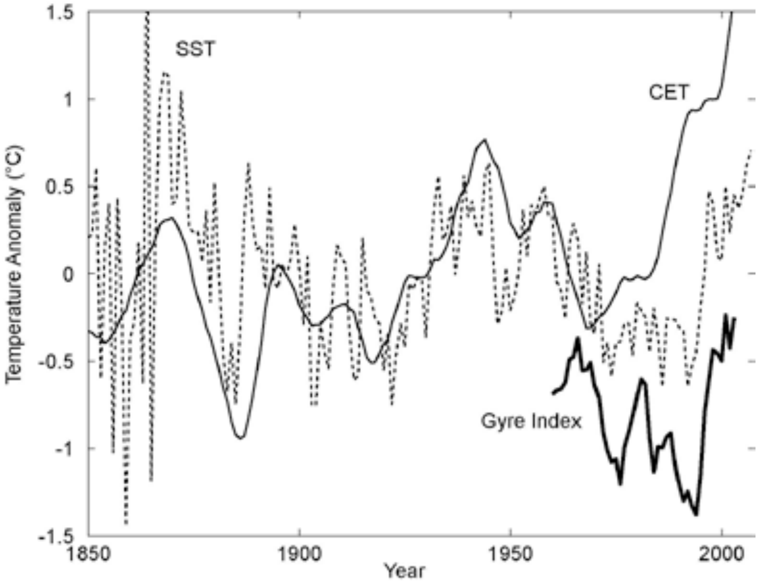
Fig. 2. *Simplified illustration of the source flows to the Rockall Region. a) A strong subpolar gyre results in strong influence of cold subarctic water in the Rockall region. b) A weak gyre results in a warm subtropical anomaly in the Rockal region (based on Hatun et al. 2009b). The variable western migration through the Iceland-Faroe gap, via the Faroe Current and into the northeastern (N-E) bays of the Faroe Islands has been sketched as well.*

tween the subtropical and subpolar gyres is less energetic and more complex (Pollard et al. 1996). A large pool of warm and saline *eastern water* circulates clockwise in an area between the Azores and the Bay of Biscay (Fig. 1a). These saline eastern waters are slowly advected towards the Rockall region (Ellett et al. 1986). An even more saline type of waters flows northwards along the European Continental Shelf in the Iberian Poleward Current (IPC)(Fig. 1a). This water mass, which is influenced by the highly saline Mediterranean outflow, is intermittently entering the Rockall Trough. Finally, the subpolar gyre (Fig. 1c) is a cold and low-saline water mass source for the Rockall area (Wade et al. 1997). So a broad and complex fan of different types of water converges and mixes in the relatively constricted Rockall region. For simplicity, we do here consider the water mass that flows northward past the Faroe Islands to be a mixture of *subtropical* and *subarctic* water.

Temperatures in the inter-gyre region

The NHT has been increasing during the last four decades, likely related to anthropogenic Global Warming. This trend has had a particularly strong imprint on the SST in the inter-gyre region between the Azores and the Bay of Biscay (Beaugrand et al. 2002; Hátún et al. 2009a) (Fig. 1a). The tempera-

Fig. 3. *Climate indices. Annual averages of: the SST west of the British Isles (Rayner et al., 2006) (52.5-62.5°N, 27.5-12.5°W), the inverted gyre index (Hátún et al., 2005). The Central England Temperature (CET) (Parker and Horton, 2005) during the spring months March and April has been plotted over the SST series. The CET is low-pass filtered using an eight-year filter width. The two temperature time series are to scale, the gyre index is not.*



ture trend is characterized by decadal scale fluctuations with a particularly steep increase during the late 1980s (Fig. 1b), a period which led the an ecological regime shift in the North Sea (Reid et al. 2001).

The subpolar gyre

The subpolar gyre is a large body of cold and low-saline subarctic water that circulates counterclockwise south of Iceland and Greenland (Fig. 1c). The circulation strength and the eastward extent of the subpolar gyre are highly variable. Some years it reaches near the European Continental Shelf, where it constricts the northward flow of subtropical water (Fig. 2a). During such years, the subpolar gyre contributes a large proportion of the source water to the mixing region southwest of the Faroes, and the marine climate there becomes both cold and low-saline. When the gyre weakens and retracts westwards, away from the European Continental Shelf, it opens up a „window“ for a northward flush of subtropical water which leads to warming, salinification and a reorganization of the entire marine ecosystem (Hátún et al. 2009a) (Fig. 2b). The weakening can take place relatively suddenly, like it for example did during the mid-1990s, and probably also during the

1920s (Drinkwater 2006). The relative influence of the subpolar gyre on the marine climate in the northeastern Atlantic has been represented by a so-called *gyre index* (Hátún et al. 2005).

The gyre index extends back to 1960 (Hátún et al. 2005), but other climatic indices with longer available time series have been used to characterise the gyre dynamics further back in time in place of the gyre index (Fig. 3). The gyre index is close-

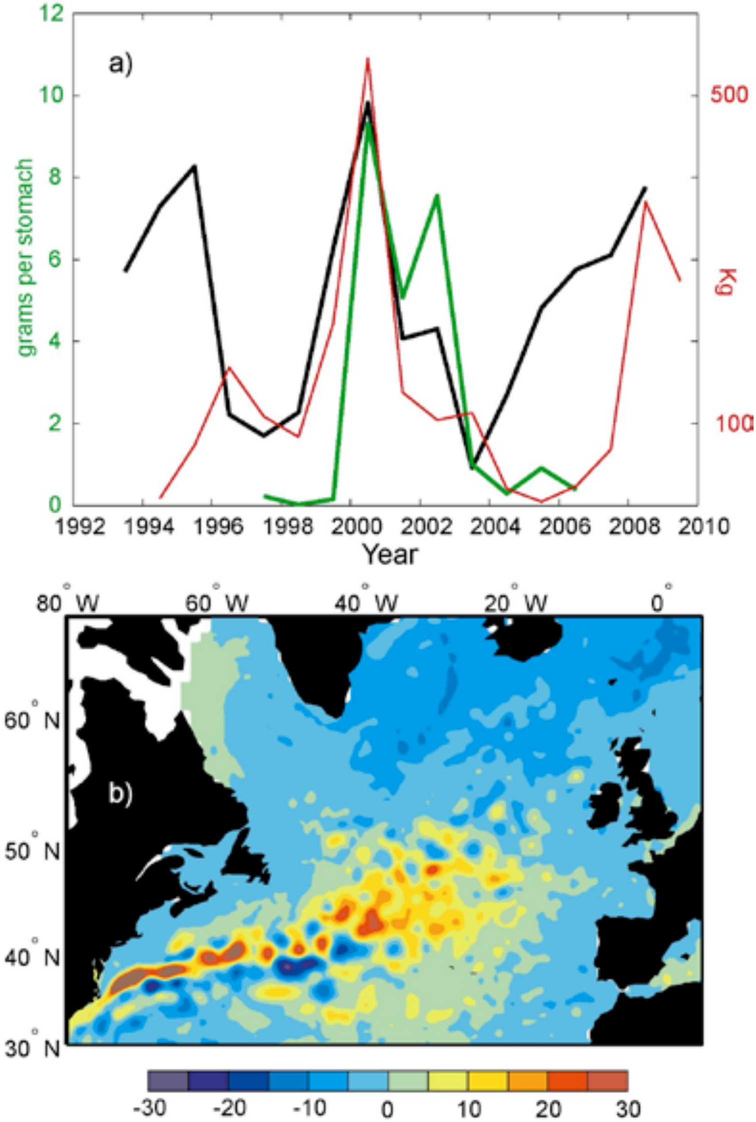


Fig. 4 The sub-decadal oscillations (SDO) in the subpolar Atlantic and biology on the Faroe shelf. a) The SDO index (black), total catches of T. Sagittatus on the Faroe shelf (red) and the abundance of sandeel from stomach samples (green). The amount of sandeel has increased after 2006, although not to the levels around 2000 (pers. comm. Petur Steingrund), b) The associated spatial pattern, showing that the SDO has a coherent impact on the water south of Iceland and within the Nordic Seas (bluish colors).

ly related to SST over the north-eastern Atlantic and this parameter has therefore been used as a gyre proxy (Hátún et al. 2009b). To infer the state of the gyre even further back in time, a second alternative proxy is required. The Central England Temperature (CET) (Parker and Horton 2005) during the spring months March and April represents the Hadley Centre SST series fairly well until around 1980 (Fig. 3) when the relationship breaks down, probably due to anthropogenic warming (Intergovernmental Panel on Climate Change 2007).

Sub-decadal Oscillations in the subpolar Atlantic

Clear sub-decadal oscillations are riding on the slower decadal to multi-decadal variations of the subpolar gyre as represented by the gyre index (Häkkinen and Rhines 2004; Hátún et al. 2005).

Sea surface height (SSH) reflects the buoyancy, and thus temperature and salinity, of the entire water column. The gyre index was obtained by applying multivariate statistics on SSH data from satellites (Häkkinen and Rhines 2004) and from a numerical ocean model (Hátún et al. 2005). We have here applied the same analysis to annually averaged and gridded SSH data from AVISO (www.jason.oceanobs.com), but after a linear trend has been subtracted from each data point (Fig. 4). The sub-decadal oscillations appear as the first *mode of variability*, which demonstrates that this has been the most coherent pattern of SSH in the North Atlantic Ocean, since the early 1990s – disregarding the slower trend. These oscillations reflect the high-passed component of the hydrographic variability in the Nordic waters (Holliday et al. 2009)(Paper In Prep.). The statistical SSH analysis produces a time series (principal component), which we term the sub-decadal oscillation (SDO) index (Fig. 4a), and a spatial pattern which illustrates that this type of variability impacts the waters south of Iceland and in the Nordic Seas in a coherent way (bluish colors in Fig. 4b).

Blue whiting, Flying squid and pilot whales

Blue whiting

The gyre-induced changes of the marine climate shift the biogeographical boundaries of key plankton species (Hátún et al. 2009a), which in turn has consequences for planktivorous fish, such as the small pelagic gadoid, blue whiting (*Micromesistius poutassou*). This large fish stock spawns west of the British Isles in early spring and then migrates past the Faroe Islands to its main feeding grounds in the Nordic Seas (Bailey 1982). Blue whiting is of considerable importance for both regional fisheries and as a food source for both flying squid (*Todarodes sagittatus*) (Gaard 1988) and pilot whales (*Globalicephala melas*) (Desportes and Mouritsen 1993). A weak gyre leads to a westward and northward shifted spawning distribution (Hátún et al. 2009b), good recruitment and thus increased blue whiting stock, and a westerly post-spawning migration through the waters between Iceland and the Faroe Islands (Hátún et al. 2009a).

Flying squid

The flying squid, *Todarodes sagittatus,* is widely distributed in the North Atlantic, from the African shelf in the south to the Barents Sea in the north, and from the MAR in the west to the Mediterranean Sea in the east.

Annual spawning events of *T. sagittatus* are thought to occur in deep waters adjacent to the continental slopes. These occur in late winter-spring in north European waters, around March-April in the Bay of Biscay, mainly between October and December in Portuguese waters and September-November in the western Mediterranean (Lordan et al. 2001; Piatkowski et al. 1998) (Learmonth et al. 2006) refs therein. Spawning is also taking place farther west as Shimko (1989) observed newly hatched larvae (2-7 mm) in winter close to the Azores, and subsequent larval and juvenile drifting north-eastwards during spring. Spawning could also occur farther north along the MAR, although this has, to our knowledge, not been document yet.

In the northern Atlantic, *T. sagittatus* is known to undergo extensive seasonal feeding and spawning migration (Shimko 1989), but the occurrence of squid in the Nordic Seas is highly irregular. During the periods late 1950s-late 1960s and from the late 1970s to the mid-1980s, huge aggregations of these squid appear around Iceland, the Faroe Islands and off the north-western coast of Norway (*squid years*) (Jákupsstovu 2002; Sundet 1985; Wiborg 1972), while the squid have been virtually absent during the early 1970s and after the mid-1980s.

The squid that some years invade the Nordic waters are young and immature. Age estimation, based on statolith daily growth rings (Rosenberg et al. 1981) indicate that squid caught on the Faroes in August 1981 in average were 251 days old (n= 303) and that squid caught in September 1985 in average were 269 days (n = 36). This indicates that these individuals have been hatched in November-December. The squid, caught in Faroese in-shore areas in August in early 1980, had mantle lengths of around 18-30 cm. Age estimates from squid caught off northern Norway similarly indicates that the peak spawning of these individuals is in December-January (Sundet 1985). The concurrent squid periods around Iceland, the Faroe Island and off Norway, the observed ages and the fact that dense abundances arrive off northern Norway about 1-2 months after they have passed the Faroe Islands (Gaard 1988), indicates that these squid belong to the same stock and drift/migrate from the same spawning grounds in southern waters. The flow regime is, however, highly non-isotropic in different regions and depths along plausible migration routes, and this makes it difficult to single out any specific spawning location based on ages and mantle lengths alone.

Although decades with squid abundances in Iceland, the Faroes and Norway roughly coincide, indications of an east-west asynchrony have been observed on an *interannual* time-scale. High abundances along Norway are associated with low abundances in Icelandic and Faroese waters, and vice versa (Gaard 1988), which points to an additional east-west shift in the migration route, similar to the east-west migration dynamics of the blue whiting stock, previously related to the dynamics of the subpolar gyre (Hátún et al. 2009b).

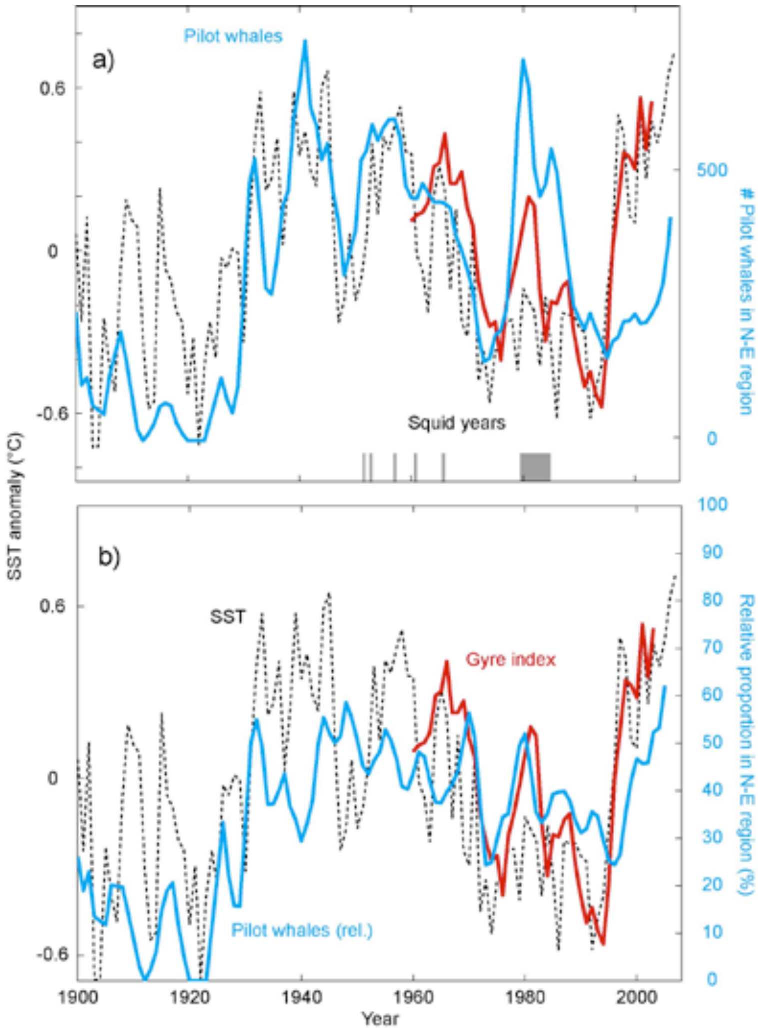


Fig. 5. Pilot whales and the marine climate. a) The number of whales beached at the north-eastern (N-E) bays in the Faroe Islands (low-pass filtered with a three-year band width) (blue), the inverted gyre index (red) and SST anomalies in the north-eastern Atlantic (black dashed). Years when squid were abundant are marked along the bottom axis. b) As a), but with the relative proportion of whales beached in the N-E region of the Faroe Islands (blue).

T. sagittatus enters shallow shelf areas in search of food (Sundet 1985), and probably not due to passive drift. Stomach analysis from squid caught on the Faroe shelf in early 1980s revealed a high diversity of prey items, like crustaceans, worms, fish and squid (cannibalism) (Gaard 1988). Pelagic fish was, however the preferred food item, where sandeel (*Ammodytes tobianus*) and blue whiting ranked on first and second place, respectively.

A special fishery for squid develops during the *squid years* (Jákupsstovu 2002). The fishery always starts in the sounds between the north-easternmost islands, where the catches also are largest, and then progresses gradually further south to the central sounds and fjords of the Faroes (Gaard 1988; Jákupsstovu 2002). This, and the concurrence of squid abundances in Faroese and Icelandic waters, indicates that the squid migrates through the Iceland-Faroe gap (Fig. 2b), drifts eastwards in the Faroe Current from where it makes an on-shelf excursion (Jákupsstovu 2002).

Pilot whales

Very little is known about any annual or seasonal migration pattern of pilot whales. The whales occur year-round in Faroese waters, but years with high abundance are typically associated with much elevated numbers during the months July-September (Jákupsstovu 2002), especially in years when *T. sagittatus* are abundant. It is, thus, likely that the whales follow the squid in search for food (Bloch et al. 1990). When squid abundances are low, blue whiting is a preferred prey item for pilot whales, (Desportes and Mouritsen 1993).

The pilot whale catches seem to be concentrated in whaling bays in a particular region of the islands. A clear change in the distribution of catches by whaling bays may indicate a change in the direction from which schools approach the islands, and may thus shed light on pilot whale migration (Zachariassen 1993). In this respect a grouping into north-eastern (N-E) bays and south-western (S-W) bays has been considered appropriate (Zachariassen 1993). The N-E bay proportions seem to correspond with a high grind rate (Zachariassen 1993), and pilot whale catches in the N-E bays (Fig. 2b) closely follow the gyre index and SST variability in the Rockall-Iceland area during the period 1900-1990 (Fig. 5a) (Hátún et al. 2009a) – a weak gyre and warm conditions have been associated with large catches.

A plausible mechanism is that the warm conditions during periods with a weak gyre allow an increased migration of blue whiting through the Iceland-Faroe gap, which attracts both *T. sagittatus* and pilot whales through this passage. This, in turn, leads to high abundances of all species in the eastward flowing Faroe Current, and the probability of on-shelf migration of T. *sagittatus* and pilot whales to the N-E bays increases.

But although the link between environmental indicators and the catch rate are surprisingly close, the very high catch rate around 1980 and the low catch rates after 1995 cannot be explained by environmental variability alone. The total Faroese catches (N-E and S-W) have persistently declined since the 1980s and this decline is strongest in the S-W area (not shown). The proportion of the total catches (%) from the N-E bays follows the main temperature changes during the twentieth century, illustrating that the climate signal is clearer in the N-E region than in the S-W region (Fig. 5b). This N-E/S-W distribution index does show a large post-1995 increase. Hence, although the number of whales caught in the N-E bays did not increase much after 1995, these catches represent a larger proportion of the total catches in recent years than at any-time previously during the twentieth century.

The pilot whale catches in the N-E region and the Central England Temperature (CET), used as a proxy for the long-term oceanic temperature variability west of the British Isles give a temporally unique perspective of the discussed variability. These series co-vary fairly closely from 1709 to the 1980s, except for periods around 1840 and the mid-18th century (Fig. 6). It therefore appears that large pilot whale catches in the N-E region have coincided with periods of warming in England.

Discussion

The relative proportion of whale catches in the N-E compared to the S-W bays in the Faroe Islands, has increased drastically after the large post-1995 decline of the subpolar gyre, which indicates that the east-west regulation of the gyre might still be in force. But the general abundances of whales have remained low after the 1980s, which points to an ocean-basin scale reorganization of the whale population likely linked to low abundances of *T. sagittatus*.

Possible explanations for the post-1980s decline

The pilot whale is categorized as a data deficit species (www.nammco.no) and the information on *T. sagittatus* is also very scarce, so the proposed explanations for the post-1980 decline of squid and pilot whale abundances in Faroese waters should be considered accordingly.

The decline could be a manifestation of an unprecedented poleward bio-geographical shift, due to Global Warming. The late 1980s warming (Fig. 1b) resulted in increased abundances of warmer water whale species in the cetacean community of north-west Scotland, while the number of colder water species, including pilot whales, declined (MacLeod et al. 2005). The bio-geographical range of pilot whale occurrence is *Warm temperate* to *Sub-polar*, following the definition in MacLoed *et al*. (2005), and if the temperature rise continues, it has been predicted that colder water species like the pilot whale might be entire lost from the north-west Scottish cetacean community (MacLeod et al. 2005). This bio-geographical perspective is strong in its demonstration of simultaneous shifts in several whales occupying similar bio-geographical ranges, but perhaps weak due to its ignorance of direct trophic linkages. We consider this explanation as probable, but not satisfactory, since causal mechanisms are preferred.

The late 1980s temperature increase in the inter gyre region (Fig. 1a,b) might have spatially shifted the spawning distributions of *T. sagittatus*, resulting in less drift/migration towards Faroese waters. Little is known about the relative importance of the individual spawning grounds around the inter-gyre region. If the main spawning grounds are found along the European continental shelves, then it is difficult to see how the warming can drastically change the drift/migration pattern. If, on the other hand, the most important spawning grounds are found along the MAR, then a northward displacement due to warming could place the offspring into the NAC that would take them along a more westerly route towards Iceland and Greenland. We also consider this explanation as being plausible, but since data on *T. sagittatus* is very scarce, the details mentioned here remain speculative.

The declined in abundances of *T. sagittatus* and pilot whales after the late 1980s could be reinforced by the pelagic fleets primarily targeting blue whiting in west of the British Isles. The efficiency of this fleet has increased dramatically during the 1990s, and the huge trawls are filtering large volumes of water and could thus be decimating the northward drifting/migrating squid. Large specimens of *T. sagittatus* are found hanging from the meshes during years when the squid is present (per. comm. Rógvi Mouritsen and Bogi Jacobsen). But just small biomasses of squid are caught by the trawl, and the damage done to the squid that escape through the meshes is unknown, so this explanation is therefore not well supported.

Prey-limited on-shelf migration of squid and whales

Periods with poor or highly variable production on the Faroe shelf might have limited the degree to which the Faroese pilot whale time series is representative for the open-ocean whale population dynamics. Schools of pilot whales must migrate near land in order to be sighted, and subsequently driven into the whaling bays. The whales follow *T. sagittatus*, and the squid in turn probably enter the shelf in search of sandeel or other pelagic fish (Gaard 1988; Sundet 1985). So *i*) could the biomass of small pelagic fish on the Faroe shelf limit on-shelf migration of squid and pilot whales and *ii*) could such a limitation be related to variability in the marine climate?

A preliminary comparison between total annual catches of *T. sagittatus* made by R/S Magnus Heinason on the Faroe Shelf since 1994, and the abundance of sandeel in cod stom-

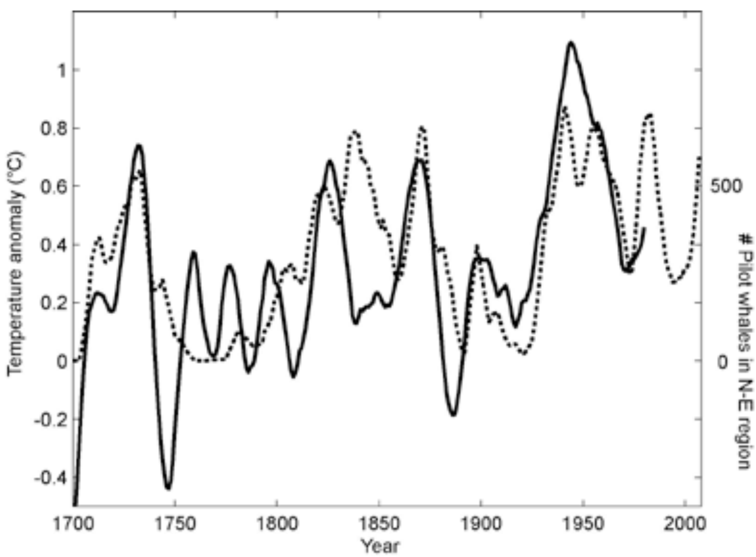


Fig. 6. A three-century perspective. The number of whales beached at the north-eastern (N-E) region of the Faroe Islands (dashed line), and the Central England Temperature (CET) anomaly (solid line). The time series have been low-pass filtered using band widths of 3 and 12 years, respectively. The CET does not represent the SST west of the British Isles after around 1980 (see Fig. 3), and the post-1980 period is thus omitted.

ach samples indicates that there might be a relation (Fig. 4). High abundances of sandeel have previously been associated with increased on-shelf primary production during cold years (Gaard et al. 2002; Hansen et al. 2005) and such years are associated with a high SDO index (Fig. 4). The bio-physical processes represented by the SDO index will be substantiated elsewhere (Paper In Prep.).

Comparing this short-term variability with the whale series did not give any conclusive result (not shown). The statistical quality of these biological series are, however, very low, and these comparisons should merely be regarded as indications.

We are not trying to infer that limitation by the on-shelf ecosystem can explain the large post-1980s decline. But as indicated by cod recruitment variability, the biomass of sandeel or other pelagic prey species has been both smaller and much more variable after 1980s, than previously observed (Steingrund et al. 2010). This mechanism provides a new perspective on the interpretation of the whale series – especially during previous periods when the on-shelf production might have been low.

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