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Daily ocean monitoring since the 1860s shows record warming of northern European seas

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Abstract:

Ocean temperatures in most parts of the world are increasing and are expected to continue to rise during the 21st century. A major challenge to ecologists and marine resource managers is to understand and predict how these global changes will affect species and ecosystems at local scales where temperature more directly affects biological responses and species interactions. Here, we investigate historical variability in regional sea surface temperature in two large heavily-exploited marine ecosystems and compare these variations with expected rates of temperature change for the 21st century. We use four of the world's longest calibrated daily time series to show that trends in surface temperatures in the North and Baltic Seas now exceed those at any time since instrumented measurements began in 1861 and 1880. Temperatures in summer since 1985 have increased at nearly triple the global warming rate which is expected to occur during the 21st century and summer temperatures have risen 2-5 times faster than those in other seasons. These warm temperatures and rates of change are due partly to an increase in the frequency of extremely warm years. The recent warming event is exceeding the ability of local species to adapt and is consequently leading to major changes in the structure, function and services of these ecosystems.

Introduction:

Knowledge of how local temperatures have varied in the past, relative to biotic responses, and how temperatures will vary in the future, is fundamental for predicting biotic responses to temperature rise (Drinkwater 2006). However, due to sparse sampling in the past, most datasets used to describe changes in sea temperatures or marine biota are short (usually < 50 years) or are averaged over large time and space scales (e. g. annual means over entire ocean basins; IPCC 2001; Stenseth *et al.* 2004; Barnett *et al.* 2005). As a consequence, the historical biological and physical oceanographic context of the recent warm temperature period is unclear, as is the potential for local biota to have experienced similar conditions in the past, and therefore, to possess physiological and evolutionary mechanisms to facilitate adaptation to warmer temperatures (Somero 2005; ICES 2005; Pörtner and Knust 2007). Moreover, biota respond most directly to local conditions in their immediate habitats, rather than temperatures averaged over large space and time scales (Walther *et al.* 2002; Somero 2005). Interpreting and predicting how individual populations and species in a local ecosystem respond to temperature variations is, therefore, more likely to be reliable when data are scaled closely to their perceived environments and lifehistories (e. g. a regional average by season for particular depth ranges).

Here, we investigate long-term variations in sea surface temperature (SST) in the North Sea, the Baltic Sea and their transitional waters (Skagerrak, Kattegat, Øresund and Belt Sea; Appendix Figure 1). Records of *daily* direct temperature measurements using standardized and calibrated sampling techniques are available here since the mid-late 1800s (Sparre 1984; van Aken 2003; Ottersen *et al.* 2003; MacKenzie and Schiedek 2007). These data are collected in programmes designed specifically for recording oceanographic conditions using standardized instruments at permanent sampling locations (e. g. harbour wharves, lightships, lighthouses MacKenzie and Schiedek 2007). We supplemented these data with opportunistically collected data contained in large international hydrographic databases (Table 1).

We have chosen to use SST data in this study because it is an important indicator of the quality and variability of habitats for marine species. A vast number of these species from many trophic levels inhabit the surface layer either as fertilized eggs, juveniles or adults; the timing of reproduction and the survival of early life history stages of many of these species are coupled to interannual variations in SST either directly via physiological effects, or indirectly via interactions with other species (prey, predators, competitors). SST can be equal to temperatures at much greater depths (e. g. 10s of metres as in tidally mixed areas such as most of the southern North Sea and English Channel during the entire year; during winter when storms mix water masses throughout the water column, and during summer months in the upper 5-20 m mixed layer of the water column), despite being measured in the upper m of the water column. Variations in SST are commonly used in climatological-physical oceanographic studies of air-sea heat fluxes and heat budgets (IPCC 2001; Rayner *et al.* 2003; Döscher and Meier 2004; Stenseth *et al.* 2004; Barnett *et al.* 2005).

We wish to answer three questions related to the long-term variability of SST: how warm are sea temperatures now compared to previously observed maxima, how unique is the recent period of warming, and have some seasons warmed at faster rates than others? Answers to these questions are a pre-requisite for estimating which species can adapt and which must emigrate to other areas.

Materials and methods:

Datasets:

The temperature data used in this study are fully described elsewhere (MacKenzie and Schiedek 2007), and only a brief description is presented here. "Surface" in this study refers to water in the upper 1 m of the water column. The time scale and period of interest is multi-decadal during the past 100+ years.

Two main data sources were used in analyses. One data source is based on daily long-term monitoring programmes (Sparre 1984; Ottersen *et al.* 2003; van Aken 2003; MacKenzie and Schiedek 2007). Temperatures were recorded by professional staff of meteorological, naval or zoological/fisheries institutes as part of oceanographic and meteorological monitoring programmes. All measurements were made using calibrated standard instruments (MacKenzie and Schiedek 2007). Four sites which had some of the longest sea temperature monitoring records in Europe were used in this study: Marsdiep (Netherlands), Torungen (Norway), Skagen (Denmark) and Christiansø (Denmark). Locations and the years of measurements are summarized in Table 1 and Appendix Figure 1). The locations of the sites represent a diverse range of hydrographic situations and are influenced by a variety of large-scale hydrographic and climatological processes (Stenseth *et al.* 2004) including the North Atlantic Oscillation, inflows of Atlantic water to the North Sea, runoff of Baltic water to the North Sea and regional and local climatic phenomena (Otto *et al.* 1990; Dippner 1997; Helcom 2002; MacKenzie and Schiedek 2007). The SST monitoring data from Marsdiep and Torungen are, to the authors' knowledge, the longest daily-recorded, calibrated sea temperature series in the world.

The second data source we used were opportunistically collected data contained in large international hydrographic databases. One database is held by the International Council for the Exploration of the Sea (ICES) and a second database (HADISST1) is maintained by the Hadley Centre of the UK Met Office (Rayner *et al.* 2003). These databases use data from heterogeneous sources including merchant vessels, research vessels, other sampling platforms and satellite imagery, and the sampling coverage varies strongly in time and space. In addition, the sampling methods (depths, time of day, thermometers, etc.) differ (Rayner *et al.* 2003; MacKenzie and Schiedek 2007). Despite these sampling differences these databases are widely used within the oceanographic, climatological and meteorological communities. We have used these data in our analyses to supplement and support results based on the long-term monitoring data. Opportunistic temperature data were obtained from ICES and the Hadley Centre for several regions of the North Sea, Baltic Sea and their transitional waters (Appendix Figure 1).

The monitoring data have not been submitted to either ICES or the Hadley Centre, so comparisons of these data with trends and results from ICES' or the HADISST1 datasets involve independent data sources. We calculated seasonal and annual averages from the monthly data available from monitoring programmes, ICES and the Hadley Centre (MacKenzie and Schiedek 2007). In total, 55 time series are used in this study (11 sites with 4 seasonal and 1 annual series per site). All time series are available on the internet (http://dx.doi.org/10.1016/j.jmarsys.2007.01.003).

We have shown elsewhere that there are high correlations in SST among the monitoring sites, and among these sites and the HADISST1 dataset (MacKenzie and Schiedek 2007). These findings indicate that the single-site temperature measurements associated with long-term monitoring data are representative of major temperature fluctuations over much larger spatial scales (at least 1200 km) than those in the immediate vicinity of where temperature measurements were made. The spatial representativeness of the monitoring data is likely due to the fact that several large-scale climatic and hydrographic processes and phenomena (regional cooling/warming, inflows of Atlantic water, the North Atlantic Oscillation) affect thermal conditions over large areas of northern Europe. The common regional forcing of temperature in this area has been documented previously (Otto *et al.* 1990; Hurrell 1995; Stenseth *et al.* 2004; Sutton and Hodson 2005).

Homogeneity of time series:

Interpretations of long-term trends and variations in time series assumes that the time series themselves are not subjected to sampling and instrument biases or that such biases are small compared to real variations and trends. The monitoring data are considered to be of high quality because of consistent measuring techniques, use of calibrated instruments and employment of professionally-trained personnel (Fonselius 2002; van Aken 2003; Ottersen *et al.* 2003; MacKenzie and Schiedek 2007). The Hadley HADISST1 dataset has been created by applying extensive processing to minimize the likelihood that potential sources of sampling bias contaminate this data series (Rayner *et al.* 2003), and is, therefore, one of the most important marine datasets used in the climatological-oceanographic modelling communities. The ICES data are comparatively raw because they do not represent a gridded, interpolated dataset similar to the HADISST1 dataset. Although we accomodated temporal variations in sampling intensity when calculating averages from ICES data (MacKenzie and Schiedek 2007), we use these data only to support results obtained with the monitoring and Hadley datasets. Our major conclusions are based on the monitoring and Hadley Centre data and are, therefore, very likely based on real variations and trends.

Data analyses:

Analysis of trends and variability:

Analyses were conducted to investigate long-term variability and trends in both seasonal and annual data. All seasonal and annual time series were plotted and visually inspected to observe variations and trends. Linear regression analyses were conducted to investigate whether overall increases or decreases in temperature occurred in individual time series. These analyses used the raw seasonal or annual data.

In order to visualise and quantify multi-year variability in the series, general additive models (GAMs) were used (Hastie and Tibshirani 1995). This modelling approach is particularly useful for exploratory visualisation of major trends and variations in datasets, including time series and spatial distributions because they can model nonlinearities using nonparametric smoothers. Examples of applications in the marine ecological literature include analyses of fish feeding (Porter *et al.* 2005), distributions (Swartzman *et al.* 1992; Begg and Marteinsdottir 2002; Hedger *et al.* 2004) and population dynamics (Ciannelli *et al.* 2005). Unlike other time series approaches (e. g. autoregressive and moving average, or ARIMA, models; Chatfield 1989), GAMs can be applied to time series with missing observations and long gaps. These characteristics were common in some of the time series used in this study. In addition, and again unlike ARIMA models, GAMs do not require autocorrelation and can therefore be an effective quantitative modelling tool when autocorrelation is weak or absent, as was also the case for the data series used in this study (MacKenzie and Schiedek 2007).

Lastly, the fitted trends can be derived using fully objective approaches. As a result, the smoothed estimates yielded by GAMs do not depend on arbitrary user choice of a smoothing window, as is the case when moving (or "running") averages are calculated and applied to time series.

GAMs were fitted to each time series using locally weighted least squares regression (LOESS), an identity link function and Gaussian error distribution. The amount of data used to fit the local regression for each data point was objectively determined using a cross-validation technique (Swartzman *et al.* 1992; SAS Inc. 2000). Analyses were conducted using SAS software (SAS Inc. 2000); the outputs included the GAM estimate of a best fit trend through the data, 95% confidence limits for the trend and a measure of residual deviance of the fitted model. The significance of the fitted trend from GAM was evaluated two ways. First, if a horizontal line can be drawn between the 95% confidence limits of the fitted trend, then the model is insignificant ($P > 0.05$; (Swartzman *et al.* 1992)). Second, significance was assessed quantitatively using the deviance estimates and the pseudo-R^2, which expresses the fraction of total deviance (variance) explained by the model (Swartzman *et al.* 1992). The explained deviance depends partly on the amount of smoothing (i. e. degrees of freedom) used to fit the model and must be accommodated when calculating the pseudo-R^2. The adjustment of pseudo-R^2 was done in a fashion similar to adjusting the classical R^2 for the number of independent variables in a multiple regression model (Zar 1999). The adjustment used the following formula (Prof. E. McKenzie, Dept. Statistics and Modelling Science, University of Strathclyde, Glasgow, Scotland; personal comm.):

$$\text{pseudo-}R^2 = 1 - \{(\text{residual deviance} / (N - DF_{\text{smoothing}} - 1)) / (\text{deviance of null model} / N)\}.$$

The deviance of the null hypothesis model is estimated by fitting the GAM to the overall mean of the time series. Statistical significance of the pseudo-R coefficients was assessed using t-tests, with degrees of freedom given by $N - DF_{\text{smoothing}} - 1$. Residual variation from the GAM fits was checked for autocorrelation for lags between 0 and N/5 (Thompson and Page 1989; Pyper and Peterman 1998) as a further evaluation of goodnesss of fit. When present, significant autocorrelation would indicate temporal variability still remaining in the series and a suboptimal fit of the model. Autocorrelation is considered significant if it exceeds the 95% confidence limit for autocorrelation in a random time series containing the same number of observations as a given temperature time series (Chatfield 1989).

The most recent warming period is of particular interest because its influence on local species and ecosystems has been described in many recent studies (Reid *et al.* 2001; Brander *et al.* 2003; Beaugrand *et al.* 2002; Beaugrand *et al.* 2004; Beare *et al.* 2004; Genner *et al.* 2004; MacKenzie and Köster 2004; Perry *et al.* 2005). The precise start date differs slightly from place to place and among seasons. In addition, in some situations the warming occurred after a relatively stable period when temperatures only fluctuated by small amounts. Visual inspection of the time series suggests that the most intensive warming occurred after the mid-1980s in most time series, which also corresponds to increasing evidence of a regime shift in the North Sea (Reid *et al.* 2001; Reid *et al.* 2003). Rates of temperature warming ($^{o}C\ yr^{-1}$) were calculated for the period beginning in 1985 until the next maximum temperature as described by GAM. Because the GAM smoothes individual years' data, occasionally there were several consecutive years which had the same maximum temperature. In these cases, the warming period was defined as ending with the first of a series of consecutive years having identical GAM-fitted high temperatures.

Temperatures during the recent warm period (since the mid-late 1980s; see Results below) were compared with previous periods of warm temperatures since 1861. This comparison was done two ways. First, meta-analysis was used to evaluate the hypothesis that recent temperatures have now exceeded historically observed maxima. Within each time series, the warmest temperature during the last warm period was compared with the maximum temperature observed previously anytime during the time series. This comparison was conducted for each seasonal and annual time series. The frequencies of exceeding or not exceeding the historic maxima were then compared using chi-square analysis with a random distribution of exceed events. The random distribution (null hypothesis) assumed that half of the time series would exceed their historical maximum. GAM-fitted temperatures were used in these comparisons.

The second analysis quantified by how much the recent period of warming exceeded peak temperatures observed during previous warm periods. Temperature differences between warm periods were compared within and between time series for all seasons and for annually averaged data. Because it is possible that the magnitude of warming in summer may be larger in absolute magnitude than the warming in winter, or warming at some sites could be larger than at other sites, all time series were first converted to standardized temperatures using the following formula:

$$x_{i,stand.} = \frac{x_i - \bar{x}}{\sigma_x}$$

This standardization only rescales the data to common units, does not alter the pattern of variability and therefore faciliates comparisons among datasets.

GAMs were then fitted to the standardized time series. The peak standardized temperatures in three time periods were then extracted from each time series. The time periods were defined based on visual inspection of the time series, literature descriptions of hydrographic variability in the area (Danielsson *et al.* 1996; Helcom 2002; ICES 2004; Stenseth *et al.* 2004; Sutton and Hodson 2005) and are chosen to enclose peak temperatures in different areas and seasons. The periods correspond to the following: pre-1900 (corresponding approximately to the warm period observed in the 1860s-1880s), 1925-1965 (corresponding approximately to the warm period observed in the mid-1900s) and 1985-2005 (representing the most recent warm period). Standardized temperature differences were then calculated between maximum temperatures observed during the recent warm period and each of the previous warm periods for each time series according to the equation:

$$\overline{\Delta T_{st}} = \frac{\sum_{1}^{5} (t_{\max, last} - t_{\max, j})}{N},$$

where N = 5 (4 seasonal and 1 annually-averaged time series per site), $t_{\max, last}$ denotes the maximum temperature in the period 1985-2005 and $t_{\max, j}$ denotes the maximum temperature during one of the previous *j* time periods (1925-1965 or 1861-1899).

One-way ANOVA was used to evaluate the hypothesis that differences in standardized temperature maxima between warm periods were similar for different datasets and geographic locations (Marsdiep, Torungen, Skagen, Christiansø, entire North Sea and Baltic Sea).

Estimating probability of occurrence of extreme events:

Global climate change models predict not only changes in average conditions, but also an increase in the frequency of extreme climatic events such as exceptionally warm temperatures (IPCC 2001). We investigated the hypothesis that the frequency of extreme sea temperature conditions has increased during the 120-140 year period of our study.

We defined an extreme warm (cold) temperature event as a season whose temperature was in the upper (lower) 10% of the frequency distribution of all observations in a given seasonal time series. We then constructed chronologies of the extreme warm (cold) years for the winter and summer seasons. Similar chronologies were developed using annually-averaged data. These chronologies revealed when the extreme events occurred and therefore allowed us to investigate whether the frequencies of mild winters and hot summers have changed.

We calculated the decadal probability of extreme temperature events in the winter, summer and for annually-averaged data. Probabilities were calculated by summing the number of extreme events in each decade observed in all six time series (i. e. the four monitoring series and the two Hadley Centre series) and dividing by the total number of years within the decade for which temperature observations were available in the same six time series:

$$P(extreme)_k = \frac{\sum_{j=1}^{6} E_i}{\sum_{j=1}^{6} N_j}$$

where E_i = the occurrence of an extreme temperature year *i* within a given decade *k*, N_j = the number of years withn the same decade *k* for which seasonal or annual temperature data are available and *j* represents the six time series for a given season or annual mean.

Chi-square analysis was used to evaluate the significance of changes in the frequency of extreme and non-extreme years across decades. In order to meet the requirement of a minimum of 5 expected events per cell in the chi-square analysis (Zar 1999) in decades when too few years were sampled, frequencies in the 1860s and 1870s were summed, and frequencies in the 1990s and 2000s were summed. Frequencies of extreme events were low in the 1860s and 2000s because the number of years containining measurements was low in these decades. We conducted a total of six chi-square analyses as follows: 1 analysis was conducted each for extremely cold and warm years for winter, summer and annually-averaged data.

We used the raw SST time series for identification of extreme events instead of the GAM fits because the GAM fits by their nature are smoothed versions of raw data and because we were specifically investigating the occurrence of large anomalies.

Results:

Visual inspection and linear regression analysis of four monitoring (Marsdiep, Torungen, Skagen and Christiansø) and two opportunistically-collected (Hadley Centre, UK (Rayner *et al.* 2003)) data series shows that there is little evidence of a gradual linear increase or decrease in temperature since the mid-late 1800s (Figure 1). Linear regression explained no significant variability in most of the series (i. e. R^2 = 0% in 26 and P > 0.05 in 29 of 55 series; Appendix Table 1). In contrast, nearly all of these data series display significant warming and cooling at shorter (multi-annual) time scales. In particular, most time series show a warm period in the mid-1900s and that warming has occurred during the last 10-15 years. This latest warming is detectable in all seasons and in annually-averaged data. In addition to this warm period, the four long-term monitoring time series indicate that there was another warm period in the mid-late 1800s (ca. 1861-mid 1880s; Figure 1). Temperatures during this first warm period were in many years similar to, and in some individual years, even higher than those measured in the late 1990s and early 2000s.

Inspection of the GAM-derived fits shows that the recent warming period in most time series is unprecedented (Figure 1, Table 2): 25 of the 30 monitoring and Hadley Centre time series now have temperatures which exceed all measurements since 1861. In addition, 22 of 25 time series based on opportunistic data held in the ICES Hydrographic database are now warmer than ever before (Appendix Figure 2). Both frequencies are higher than expected by chance (chi-square tests: P < 0.005). The GAMs effectively removed all significant time trends as residuals showed no significant autocorrelation for lags between 0 and N/5 (Appendix Figure 3).

The magnitude and rate of warming for the monitoring and Hadley Centre data (i.e. the longest series with most consistent temporal coverage) were calculated for the period between 1985 and the year subsequently having the highest temperature (typically in the early 2000s based on GAM fits; Figure 1). Annual mean temperatures rose on average 0.6 ^{o}C (standard error = 0.06 ^{o}C) during this period (Figure 2 and Appendix Figure 4). However, temperatures rose significantly faster and higher (> 1.4 ^{o}C) in the summer than in other seasons and for annually-averaged data (1-way ANOVA: F = 18.74, P < 0.0001, R^2 = 0.75). There was no significant difference among the six data sets in the change in temperature (seasonal or annual averages) between 1985 and the early 2000s (1-way ANOVA: P > 0.50).

The probability of extremely warm winters, summers and years has increased by 2-4 fold in the 1990s and 2000s relative to the probability in nearly all previous decades; this change in frequency of extreme events is statistically highly significant (Figure 3). Since 1990 there has been a ca. 50% chance that any given winter or summer has had a temperature in the warmest 10% of all measurements since at least 1880. Similarly, the probability of having extremely cold winters, summers and years has *decreased* to < 10% in these same decades (Figure 3).

The magnitude of the recent warming relative to historical temperature maxima differs between datasets: based on monitoring data, the latest warming period has in most seasons recently exceeded all previous historical maxima by a few tenths of a degree. In contrast, the Hadley Centre data series suggest that recent temperatures are much warmer (ca. 1 ^{o}C) than historical maxima in these time series (Figures 1, 4). One-way ANOVA showed that standardized temperature differences between the recent and previous warm periods within individual time series differed significantly depending on the time series (F = 8.48, P < 0.0001, R^2 = 64% ; F = 9.71, P < 0.0001, R^2 = 67% for comparisons involving respectively the recent and mid-1900s warm period, and the recent and late-1800s warm period; Figure 4). The difference in perception of warming is most noticeable relative to the warm period in the 1860s-1880s where the Hadley datasets suggest a warming 2-3 times larger than that based on the monitoring series (Figure 4, lower panel).

Discussion:

Species and marine ecosystems in the North and Baltic Seas are becoming exposed to warm temperatures which are unprecedented in the history of instrumented measurements in this region. Sea temperature trends in all seasons and annual mean temperatures since the late 1980s have exceeded the measured maxima in 143 years of daily observations. Moreover, the rate of sea temperature rise since 1985 is due at least partly to large changes in the occurrence of extremely warm and cold conditions during summer and winter. The frequency of occurrence of extremely warm and cold years has respectively increased and decreased. This pattern is consistent with changes in the frequency of extremes of European air temperatures (Luterbacher *et al.* 2004; Moberg *et al.* 2005). For example, several mild winters in this same time period (Helcom 2002; ICES 2004; Luterbacher *et al.* 2004; MacKenzie and Köster 2004) would have reduced the losses of heat remaining from the previous summer across the air-sea interface that usually occurs in winter (Otto *et al.* 1990). Major inflows of warm Atlantic water to the North Sea in 1988 and 1998 have also increased North Sea temperatures (Reid *et al.* 2001).

Summer warming rates since 1985 are nearly triple those which could be expected on the basis of the emerging consensus view of global warming of air temperatures (Kerr 2004), and assuming that SST responds in a similar magnitude as air temperature. It must be emphasized, however, that the consensus view is a *global annual average* for *air temperatures,* and that air temperatures may not always track all scales of variability in SST. Data compiled here show significant deviations from this view at seasonal and regional scales, even though the annual average warming rate is consistent with the consensus rate. The evidence from the North and Baltic Seas shows that local biota are therefore experiencing very different warming rates from those expected from global annual averages. Summer warming rates also exceed warming rates during other seasons. Similar seasonal differences in warming were observed in the 1930s-1950s in the southern North Sea (Becker and Kohnke 1978) and elsewhere in the north Atlantic (K. Drinkwater, Norwegian Institute of Marine Research, pers. comm. 2005).

Temperatures prior to the instrumental record are available from paleo-climatic sources. For example, temperatures in a central Swedish lake and the Skagerrak during the Holocene Optimum were 3-4º C higher than at present (Mörner 1980; Emeis *et al.* 2003). The increase in annual (ca. 0.5º C) and summer (ca. 1.5º C) mean SST in the North Sea and Baltic Sea regions since the mid-1980s, therefore, corresponds to ca. 12-15% or 37-50% of the maximal warming seen in the last 10,000 years. The warm temperatures and rates of change since the late 1980s-early 1990s are exceeding the ranges of habitat preferences and scopes for thermal physiological acclimation and evolutionary adaptation in many local species. As a result, numerous zooplankton (Stenseth *et al.* 2004), benthic (Stenseth *et al.* 2004) and fish (Genner *et al.* 2004; Stenseth *et al.* 2004; Perry *et al.* 2005; Drinkwater 2006) species in these ecosystems are responding to increasing temperatures by relocating to cooler habitats. The warm temperatures are also directly affecting lifehistories of diverse marine taxa, such as the timing (Philippart *et al.* 2003; Edwards and Richardson 2004; Greve *et al.* 2005) and success of reproduction (Thompson and Ollason 2001; Philippart *et al.* 2003; MacKenzie and Köster 2004), and the links between trophic levels (Philippart *et al.* 2003; Beaugrand *et al.* 2004; Edwards and Richardson 2004). These changes are analogous to responses associated with earlier warm periods such as those during the warm Atlantic period (Enghoff *et al.* 2007) and the mid-1900s (Drinkwater 2006), and are consistent with predictions based on thermal

considerations of biogeographical patterns (Walther *et al.* 2002) and physiological responses to temperature stress (Pörtner and Knust 2007).
The strength of this study is that the trends and variations in SST are evident in datasets designed intentionally to monitor sea temperature at regular intervals using standardized sampling methods over long periods of time. The fluctuations cannot be attributed to potential biases associated with opportunistic sampling (e. g. sporadic temporal and spatial coverage) or uncertainties associated with some proxy indicators to represent true temperature (Moberg *et al.* 2005).

Based on the different datasets, there is a difference in perception of the amount of warming *relative* to historical temperatures, and the implied temperature stress to which living organisms are now being exposed. The difference is perhaps due to sparse data coverage in the Hadley data for the specific locations and years of this investigation. Nevertheless, the difference in perception of temperature change among datasets affects our interpretation of the sensitivity of biota to recent temperature changes, and our expectation of the changes that can occur in future. Regional prognostic models of SST development during the next 80-100 years suggest that temperatures can be expected to be 2-4 ^{o}C higher in the latter decades of the 21st century in both the North (Sheppard 2004) and Baltic Seas (Döscher and Meier 2004), relative to the temperatures observed during 1961-1990. Late 21st century temperatures may, therefore, be similar to those during the Holocene Optimum (Mörner 1980; Emeis *et al.* 2003).

The recent ecological changes in these ecosystems, while important and significant, may therefore be relatively minor compared to future ecological events, particularly if further analyses show that the recent ecological changes have been induced by temperatures which exceed historical maxima by only few tenths of a degree. Expectations of biodiversity and ecosystem changes which assume that sea temperature warming rates will follow the global consensus view of warming (Kerr 2004) will likely underestimate the magnitude of such changes because the global annual average dampens local, seasonal and multi-annual variability to which biota are more sensitive. Moreover, changes in the seasonality of warming or the frequency of extremely warm and cold seasons or years, such as those documented here using long-term datasets, increase the probability that some biota will (or fail to) complete their lifehistories or increase (or decrease) the number of generations per year. For example, temperatures in extreme years may be reaching thresholds for successful completion of key physiological processes (e. g. gonadal development, survival of early lifehistory stages), for production of important prey species or becoming sub-optimal for feeding by predators. Mechanisms such as these will also promote changes in distributions of populations and species.

Conclusions:

The recent warm period, regardless of cause or the data source (i. e. monitoring or oppportunistic data) used for its documentation, is unique in the past 120-140 years, and is already having major ecological consequences. As a result, this event and the prospects for continued warming (Kerr 2004; Barnett *et al.* 2005), even though there are uncertainties in the rate and duration of future warming (IPCC 2001; Bryden *et al.* 2005), are challenging stakeholders (e. g. scientists, policymakers, the fishing industry) responsible for managing, exploiting and conserving species and ecosystems (Root *et al.* 2003; Garcia *et al.* 2006). Management frameworks and regulations for protecting marine species and ecosystems will increasingly need to be designed to accommodate such uncertainties and, in due course, to incorporate the likelihood that long-term environmental change in a given direction will occur. In some cases, this will mean acknowledging that populations or ecosystems for long periods of time (e. g. decades) could be on trajectories towards new states.

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Table 1. Summary of sea surface temperature used in this study. See Appendix Figure 1 for geographic locations and MacKenzie and Schiedek (2007) for further details. Websites containing updated data are listed with references in the bibliography.

Location	Latitude	Longitude	Source	Data type	Period of Measurements
Marsdiep, NL	52.983°N	4.75° E	(van Aken 2003)	Daily monitoring	1861-2003
Torungen, N	58.333° N	8.883° E	(Ottersen *et al.* 2003)	Daily monitoring	1867-2003
Skagens Reef, DK	57.775° N	10.725° E	(Sparre 1984)	Daily monitoring	1880-1979
Christiansø, DK	55.317° N	15.20° E	(Sparre 1984)	Daily monitoring	1880-1998
North Sea (HADISST1)	51° N – 58° N (54.5° N)	2° W – 9° E (3.5° E)	(Rayner *et al.* 2003)	Opportunistic sampling	1870-2003
Baltic Sea (HADISST1)	54.0° N – 60.5⁰ N (56.75° N)	14.5° E – 23.5° E (19.0° E)	(Rayner *et al.* 2003)	Opportunistic sampling	1870-2003
Northeast North Sea-Skagerrak	55° N – 60° N (57.5° N)	5° E – 10° E (7.5° E)	ICES www. ices.dk	Opportunistic sampling	1914-2001
Central North Sea	55° N – 60° N (57.5° N)	0° – 5° E (2.5° E)	ICES	Opportunistic sampling	1905-2001
Northwest North Sea	55° N – 60° N (58° N)	5⁰ W – 0° (1° W)	ICES	Opportunistic sampling	1904-2001
Bornholm Basin	55.916° N – 54.75° N (55.333° N)	16.333° E – 14.8° E° (15.565° E)	ICES	Opportunistic sampling	1923-2003
Kattegat-Øresund-Great Belt	55° N – 60° N (56.25° N)	10° E – 15° E (11.5° E)	ICES	Opportunistic sampling	1911-2002

Table 2. Results of locally weighted least squares regression (LOESS) of variability in sea surface temperatures in the North and Baltic Seas as represented by different data sets for the four seasons (January-February-March, April-May-June, July-August-September and October-November-December) and annually-averaged data. Regressions were fitted using General Additive Modelling (GAM) with degrees of freedom (DF) chosen objectively with a cross-validation technique (Swartzman *et al.* 1992; SAS Inc. 2000). Table entries are pseudo-R^2 values which have been adjusted for the number of degrees of freedom used to fit the models. Subscripts are the model DF and the sample size N; superscripts are significance levels, where ns, *, **, ***, **** indicate significance levels (respectively P >0.05, <0.05, <0.01, <0.001 and < 0.0001. Entries with pseudo-R^2 values in italics (4 time series) resulted in DF between 23-31 and fitted models which overemphasized short-term variability. These time series were then re-analysed using the mean DF objectively selected by GAM for all other time series (i. e. DF = 4).

Area	JFM	AMJ	JAS	OND	Annual
Marsdiep, NL	$0.05_{3, 143}^{***}$	$0.20_{5, 143}^{***}$	$0.25_{5, 143}^{***}$	$0.18_{8, 143}^{***}$	$0.23_{4, 143}^{***}$
Torungen, NO	$0.06_{2, 132}^{**}$	$0.20_{3, 135}^{***}$	$0.36_{9, 137}^{***}$	$0.15_{3, 136}^{***}$	$\mathit{0.31}_{4, 130}^{***}$
Skagen, DK	$0.02_{1, 116}^{ns}$	$0.05_{4, 114}^{**}$	$0.19_{9, 114}^{***}$	$0.12_{5, 115}^{***}$	$0.10_{4, 112}^{***}$
Christiansø, DK	$0.03_{2, 114}^{ns}$	$0.04_{3, 113}^{*}$	$0.14_{5, 114}^{****}$	$0.02_{3, 117}^{ns}$	$0.06_{3, 107}^{*}$
North Sea (HADISST1)	$0.10_{2, 136}^{****}$	$0.26_{4, 135}^{****}$	$0.36_{8, 135}^{****}$	$0.19_{6, 135}^{****}$	$\mathit{0.31}_{4, 135}^{****}$
Central Baltic Sea (HADISST1)	$0.09_{1, 136}^{****}$	$0.15_{1, 135}^{****}$	$\mathit{0.21}_{4, 135}^{****}$	$0.11_{2, 135}^{***}$	$\mathit{0.23}_{4, 135}^{****}$
Northeast North Sea-Skagerrak	$0.09_{13, 69}^{*}$	$0.02_{2, 68}^{ns}$	$0.15_{5, 65}^{**}$	$0.19_{3, 70}^{***}$	$0.05_{3, 59}^{ns}$
Central North Sea	$0.00_{1, 60}^{ns}$	$0.14_{2, 70}^{**}$	$0.18_{5, 71}^{***}$	$0.23_{6, 59}^{**}$	$0.19_{4, 46}^{ns}$
Northwest North Sea	$0.11_{4, 50}^{*}$	$0.10_{1, 61}^{*}$	$0.21_{3, 66}^{***}$	$0.44_{7, 53}^{***}$	$0.11_{2, 29}^{ns}$
Kattegat-Øresund-Great Belt	$0.09_{2, 59}^{*}$	$0.09_{3, 63}^{*}$	$0.22_{4, 60}^{***}$	$0.00_{2, 61}^{ns}$	$0.09_{2, 48}^{*}$
Bornholm Basin	$0.05_{1, 38}^{ns}$	$0.07_{2, 43}^{ns}$	$0.05_{1, 35}^{ns}$	$0.06_{1, 33}^{ns}$	$0.35_{2, 16}^{*}$

Figure legends:

Figure 1. Time series of SST measured at Marsdiep (Netherlands), Torungen (Norway), Skagens Reef (Denmark; intersection of the Skagerrak and Kattegat**),** Christiansø (Denmark, southern Baltic Sea), the North Sea and the Baltic Sea. Panels from top to bottom represent the four seasons (January-February-March, April-May-June, July-August-September and October-November-December) and annually-averaged data. The thin solid line and dots represent observations. The thick solid line is the trend fitted by General Additive Modelling (GAM; (Hastie and Tibshirani 1995). The dashed lines are the 95% confidence limits for the fitted GAM trend. See Table 2 for results of significance tests.

Figure 2. Seasonal and annual rates of temperature change (mean + 2 standard errors) between 1985 and the year with the subsequent maximum temperature for six SST time series in the North-Baltic Sea region. Data shown are means across the six datasets for each season and for annually-averaged data. Means with the same letter at top of panels are not significantly different ($P > 0.05$). Horizontal dashed line is the consensus estimate of the expected global annual rate of increase of air temperature during the 21st century (Kerr 2004).

Figure 3. Probabilities of the occurrence of extremely cold (left panels) or warm (right panels) years per decade for winter, summer and annually-averaged SST as estimated from six long-term datasets in the North and Baltic Seas. Extremely cold and warm years are respectively those < 10th and > 90th percentiles of distributions. The differences in decadal probabilities within each panel are statistically significant in all cases (chi-square analysis: $P < 0.001$). Decades with no bars are those in which no extreme events occurred (i. e. decadal probability = 0).

Figure 4. Mean (+ two standard errors) standardized temperature difference between maximum temperature observed between 1985-2005 and 1925-1965 (top panel) and 1985-2005 and 1861-1900 (lower panel) for sea surface temperature measured at six locations. Averages are based on seasonal- and annually-averaged temperature series. Means with the same letter at top of panels are not significantly different ($P > 0.05$; Student-Neuman-Keuls test).

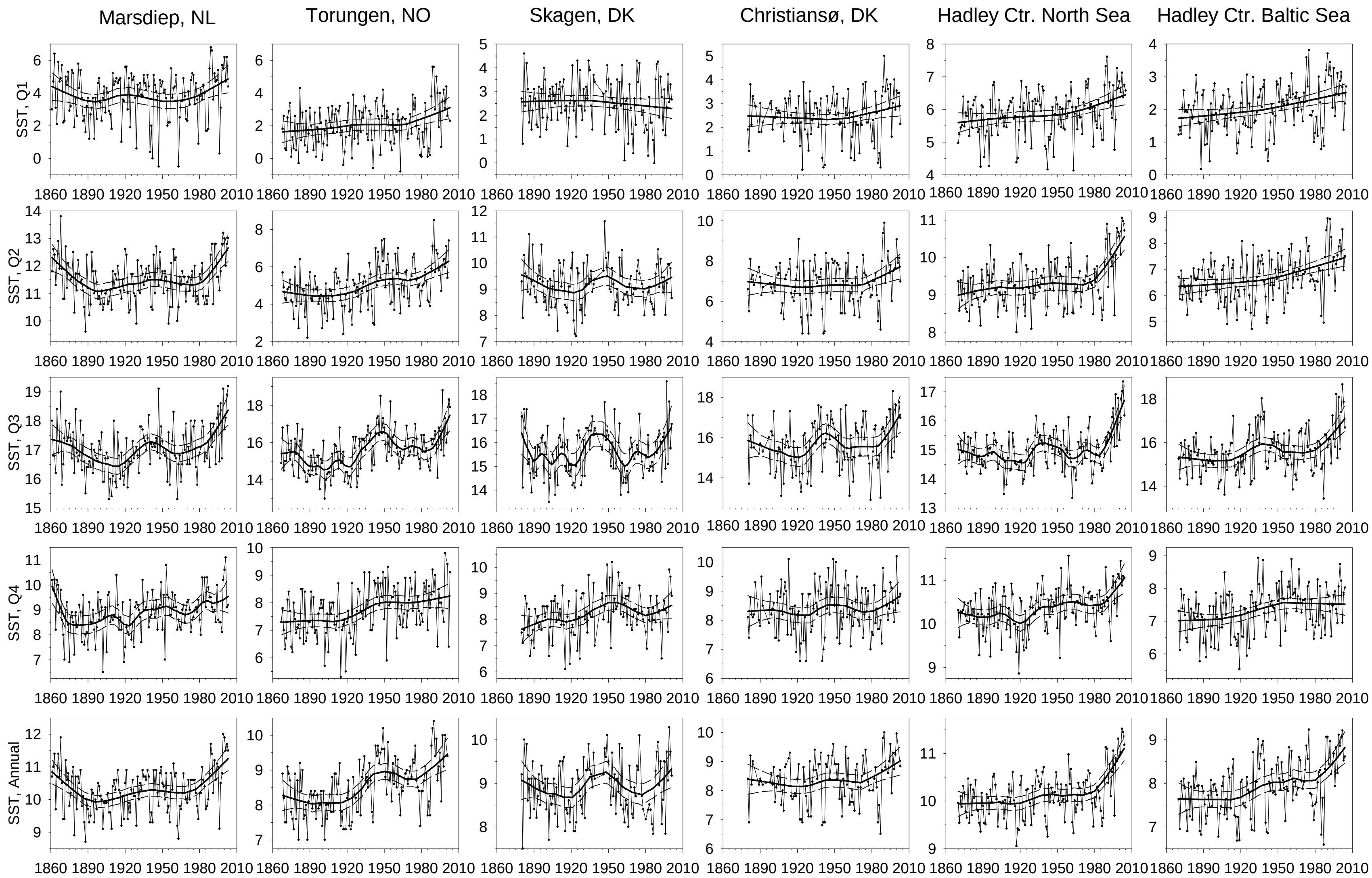

Marsdiep, NL
Torungen, NO
Skagen, DK
Christiansø, DK
Hadley Ctr. North Sea
Hadley Ctr. Baltic Sea
SST, Q1
SST, Q2
SST, Q3
SST, Q4
SST, Annual
1860 1890 1920 1950 1980 2010

Figure 1

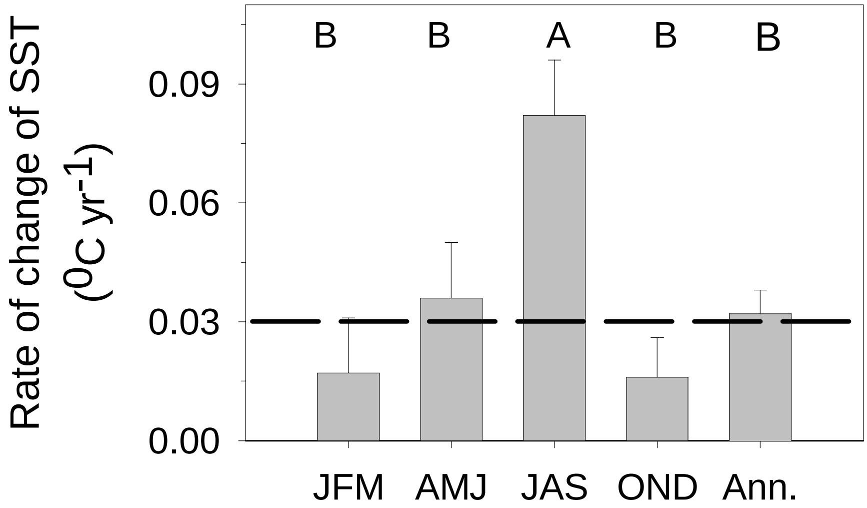

Rate of change of SST
(0C yr-1)
0.09
0.06
0.03
0.00
B
B
A
B
B
JFM
AMJ
JAS
OND
Ann.

Figure 2

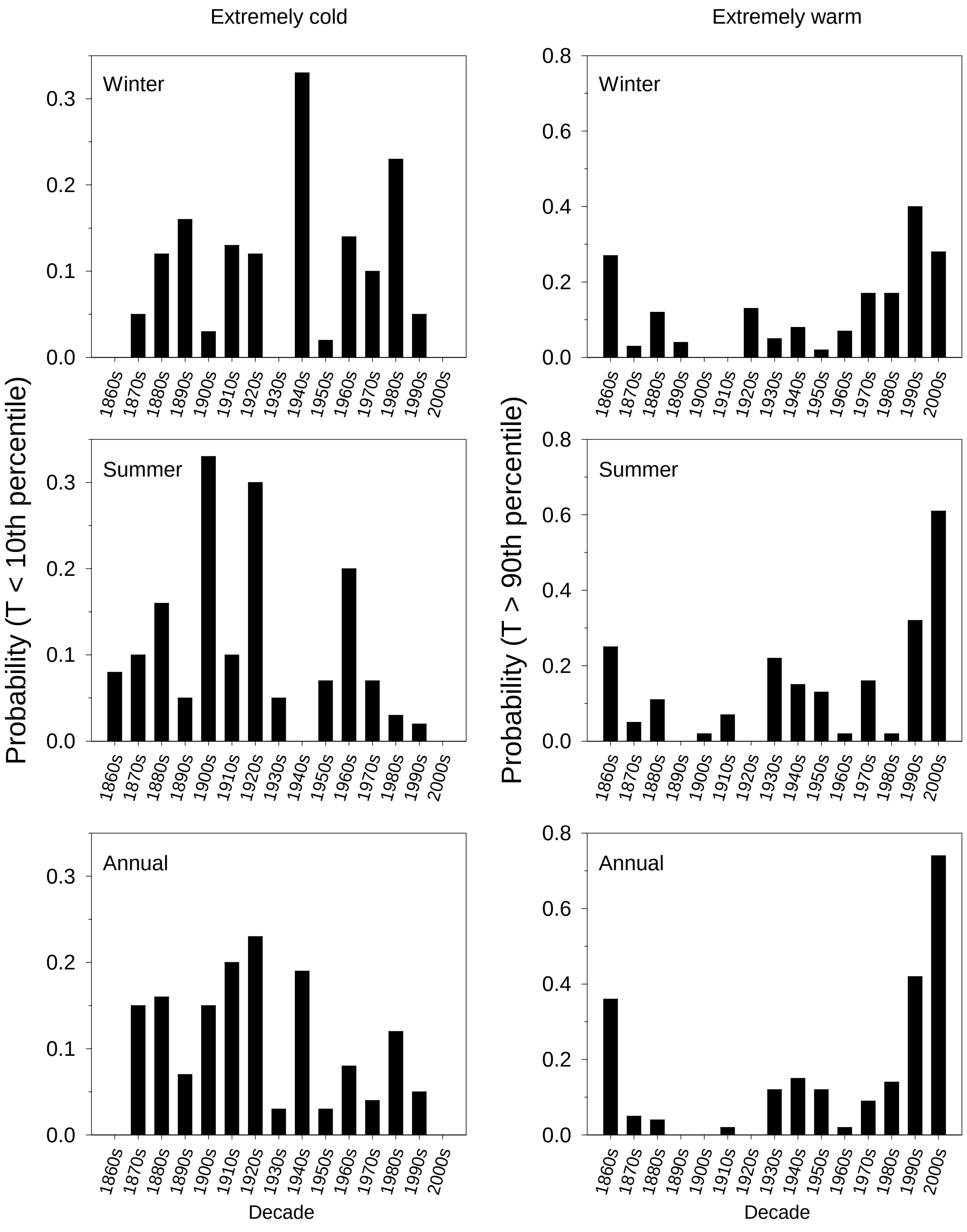

Extremely cold
Extremely warm
Winter
Summer
Annual
Probability (T < 10th percentile)
Probability (T > 90th percentile)
Decade
1860s 1870s 1880s 1890s 1900s 1910s 1920s 1930s 1940s 1950s 1960s 1970s 1980s 1990s 2000s

Figure 3

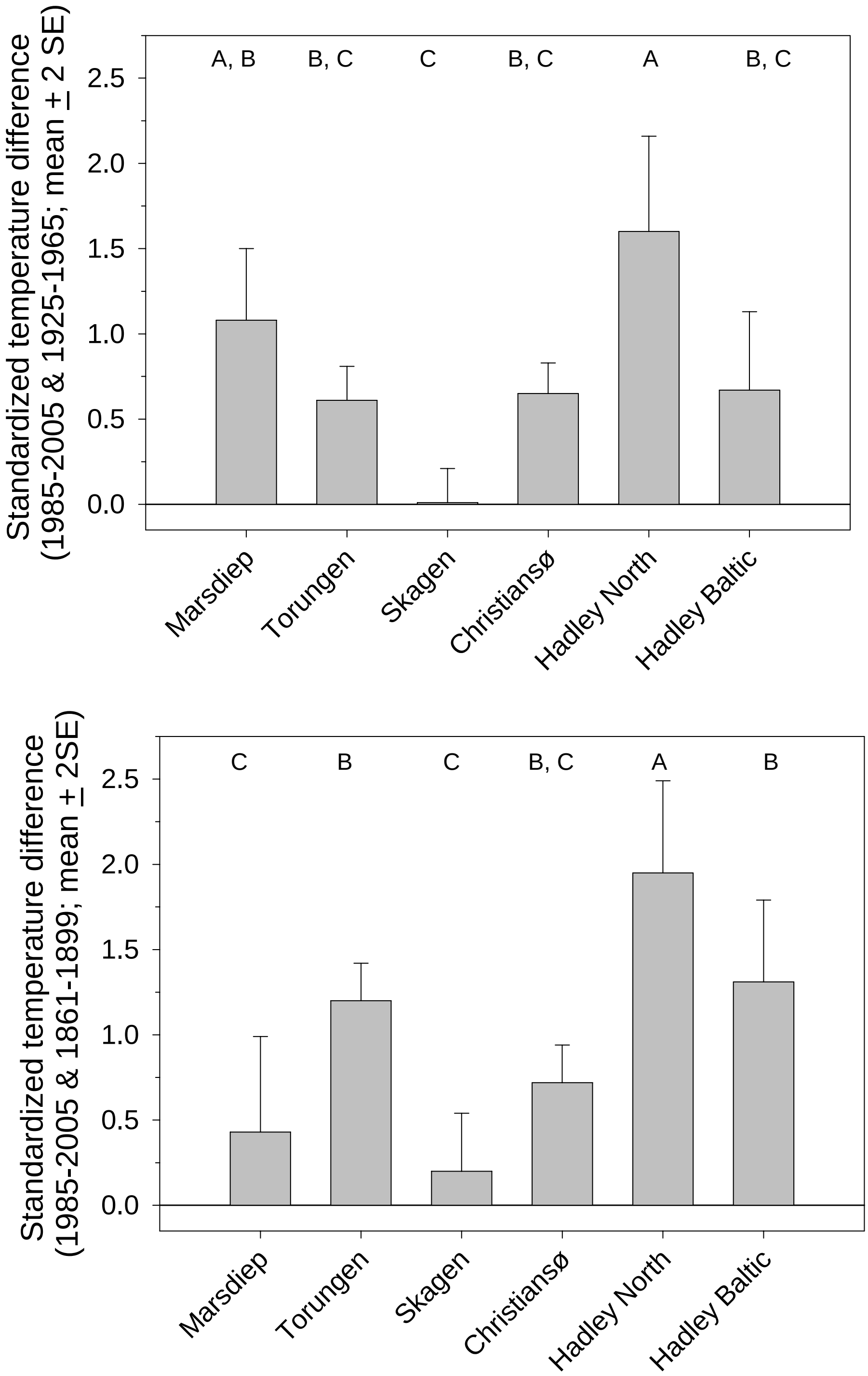
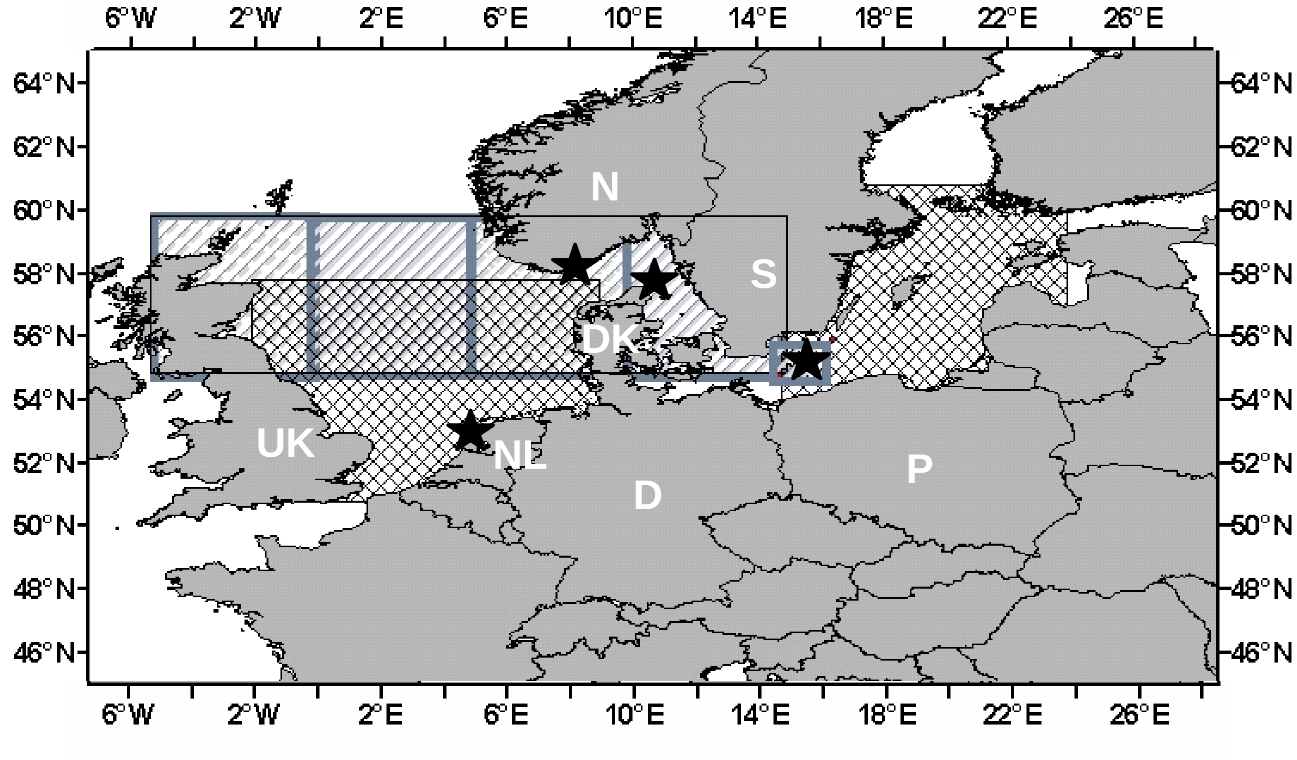
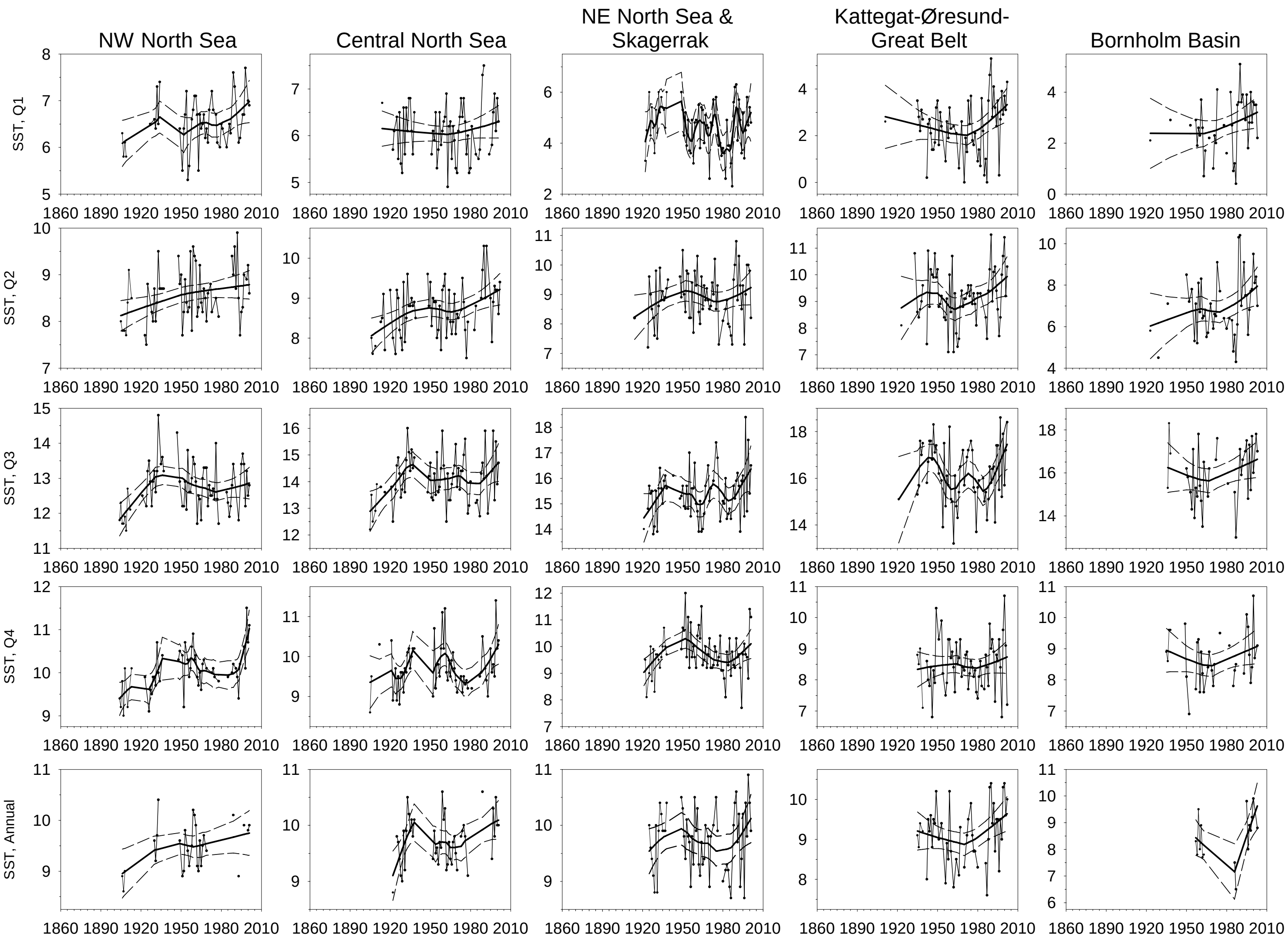

Standardized temperature difference
(1985-2005 & 1925-1965; mean + 2 SE)
A, B
B, C
C
B, C
A
B, C
2.5
2.0
1.5
1.0
0.5
0.0
Marsdiep
Torungen
Skagen
Christiansø
Hadley North
Hadley Baltic
Standardized temperature difference
(1985-2005 & 1861-1899; mean + 2SE)
C
B
C
B, C
A
B
2.5
2.0
1.5
1.0
0.5
0.0
Marsdiep
Torungen
Skagen
Christiansø
Hadley North
Hadley Baltic

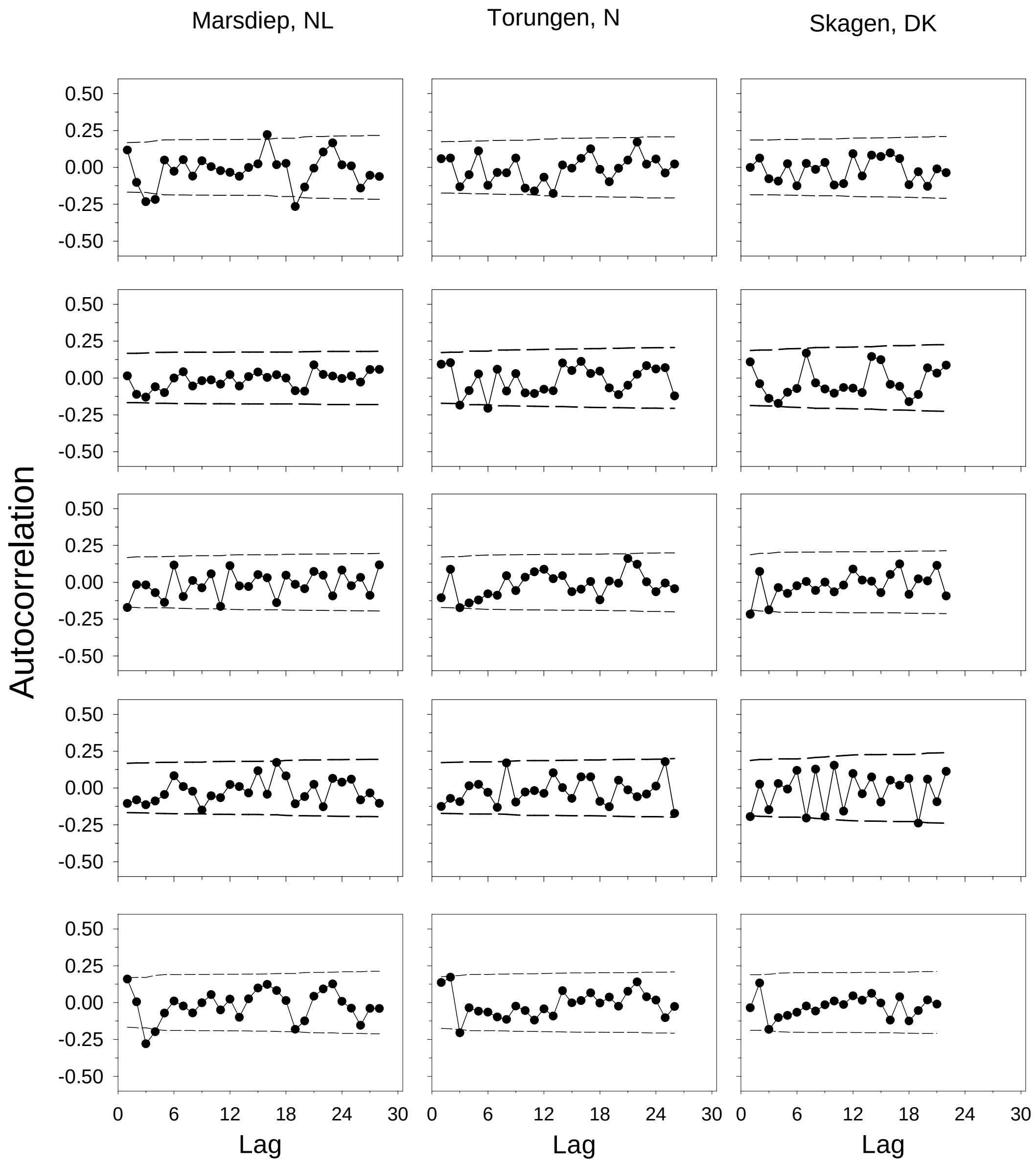
Figure 4



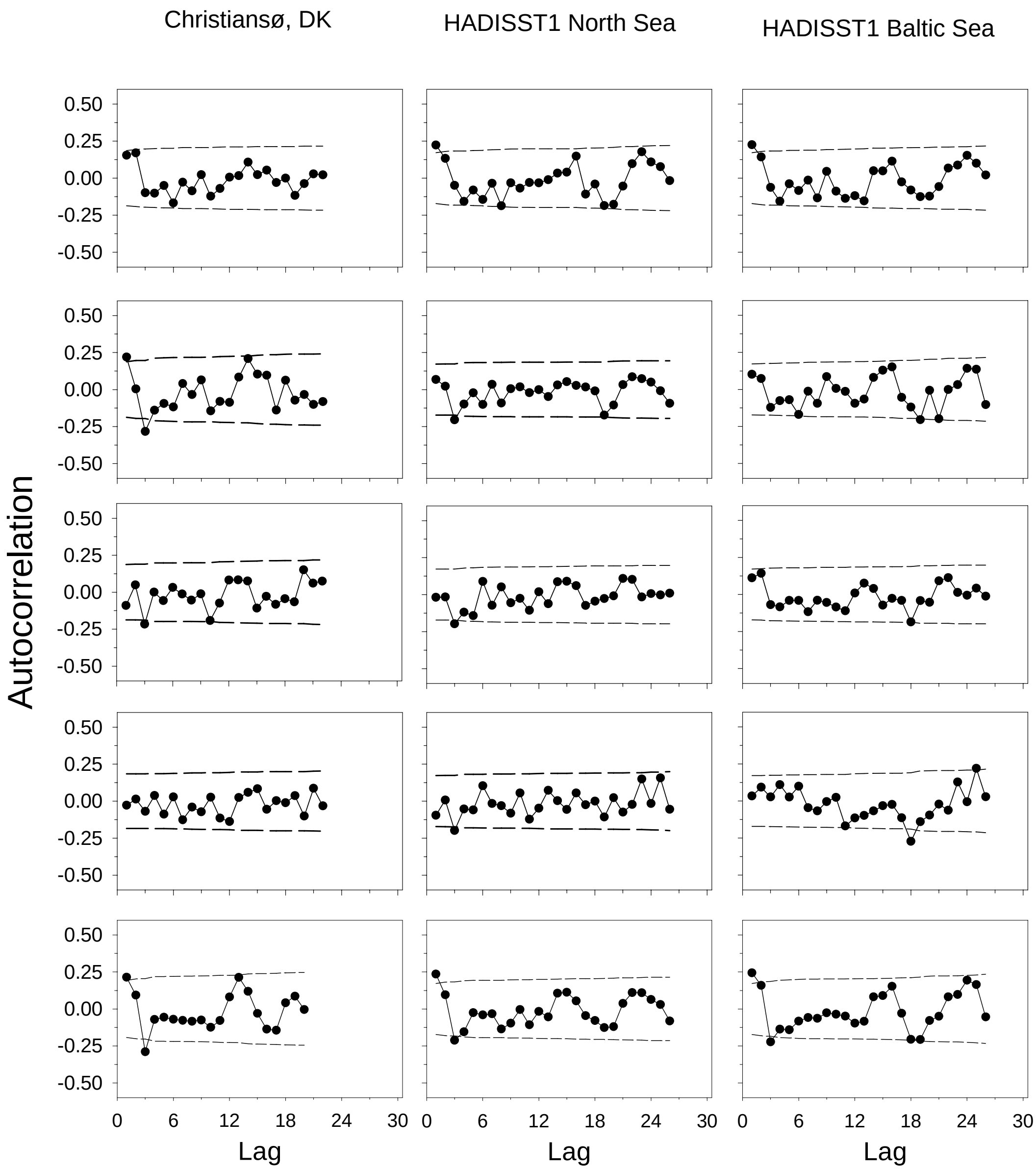
Appendix Figure 1



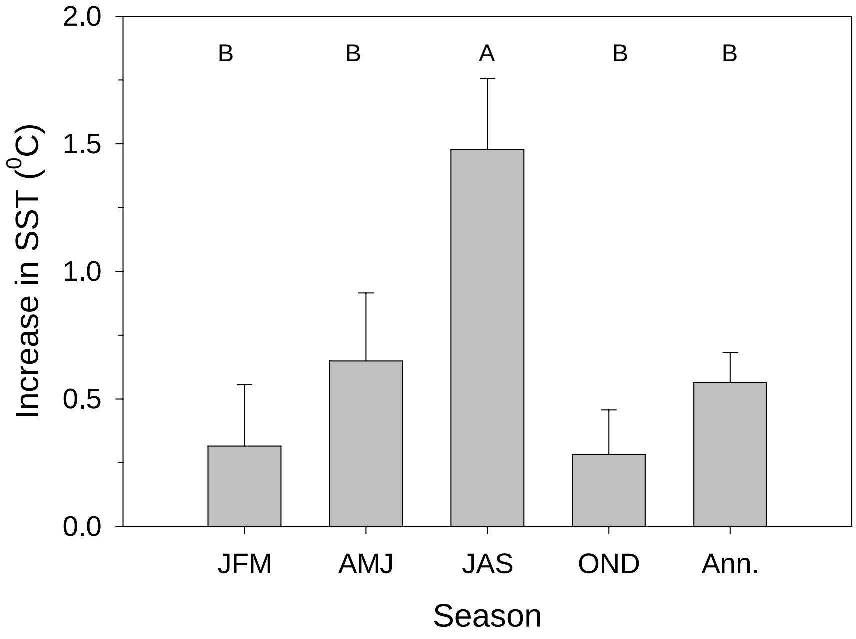
Appendix Figure 2



Appendix Figure 3



Appendix Figure 3 (cont'd.)



Appendix Figure 4

Appendix Table 1. Results of linear regression analysis of the hypothesis of an overall linear increase or decrease in entire time series of sea surface temperature measured at different locations in the North Sea, Baltic Sea and their transitional waters. Data sources available in Table 1.

Area	Season	$R^2_{adj.}$	P	RMSE	N	Equation
Marsdiep, NL	JFM	0	0.46		143	
	AMJ	0	0.34		143	
	JAS	0.04	0.0108	0.79	143	y = 0.0040*x+8.98
	OND	0.05	0.0029	0.81	143	y = 0.0050*x-0.79
	Annual	0.03	0.0176	0.67	143	y = 0.0032*x+4.03
Torungen, NO	JFM	0.06	0.0055	1.264	132	y = 0.0079*x-13.26
	AMJ	0.17	< 0.0001	1.061	135	y = 0.012*x-18.96
	JAS	0.15	< 0.0001	1.021	137	y = 0.011*x-5.48
	OND	0.13	< 0.0001	0.811	136	y = 0.008*x-8.33
	Annual	0.23	< 0.0001	0.683	130	y = 0.01*x-10.23
Skagen, DK	JFM	0	0.37		116	
	AMJ	0	0.97		114	
	JAS	0	0.19		114	
	OND	0.06	0.0059	0.79	115	y = 0.0058*x-3.03
	Annual	0	0.36		112	
Christiansø, DK	JFM	0	0.22		114	
	AMJ	0	0.14		113	
	JAS	0.02	0.048	1.19	114	y = 0.0065*x+3.02
	OND	0	0.33		117	
	Annual	0	0.06		107	
North Sea (HADISST1)	JFM	0.08	0.0006	0.66	136	y = 0.0051*x-4.02
	AMJ	0.14	< 0.0001	0.59	135	y = 0.0061*x-2.53
	JAS	0.09	0.0003	0.65	135	y = 0.0054*x+4.58
	OND	0.12	< 0.0001	0.45	135	y = 0.0044*x+1.72
	Annual	0.18	< 0.0001	0.42	135	y = 0.0052*x+0.01
Central Baltic Sea (HADISST1)	JFM	0.09	0.0002	0.69	136	y = 0.0058*x-9.21
	AMJ	0.13	< 0.0001	0.79	135	y = 0.0081*x-9.03
	JAS	0.1	< 0.0001	0.94	135	y = 0.0084*x-0.77
	OND	0.09	0.0002	0.66	135	y = 0.0056*x-3.54
	Annual	0.19	< 0.0001	0.56	135	y = 0.0070x-5.61
Northeast North Sea-Skagerrak	JFM	0	0.24		69	
	AMJ	0	0.43		68	
	JAS	0	0.1		65	
	OND	0	0.98		70	
	Annual	0	0.8		59	

Central North Sea	JFM	0	0.59		60	
	AMJ	0.11	0.0033	0.6	70	y = 0.0080*x-6.97
	JAS	0	0.0946		71	
	OND	0	0.23		59	
	Annual	0	0.09		46	
Northwest North Sea	JFM	0	0.07		50	
	AMJ	0.10	0.0061	0.54	61	y = 0.0070*x-5.17
	JAS	0	0.27		66	
	OND	0.22	0.0002	0.44	53	y = 0.0084*x-6.31
	Annual	0.11	0.0446	0.44	29	y = 0.0068*x-3.77
Kattegat-Øresund-Great Belt	JFM	0	0.24		59	
	AMJ	0	0.28		63	
	JAS	0	0.85		60	
	OND	0	0.61		61	
	Annual	0	0.18		48	
Bornholm Basin	JFM	0	0.09		38	
	AMJ	0.07	0.0438	1.36	45	y = 0.021*x-35.21
	JAS	0	0.31		35	
	OND	0	0.54		33	
	Annual	0	0.26		16	