Investigation of marine temperature changes across temporal and spatial Gradients: Providing a fundament for studies on the effects of warming on marine ecosystem function and biodiversity

Amorim, Felipe de Luca Lopes de; Wiltshire, Karen Helen; Lemke, Peter; Carstens, Kristine; Peters, Silvia; Rick, Johannes; Gimenez, Luis; Scharfe, Mirco

Progress in Oceanography

DOI:
10.1016/j.pocean.2023.103080

Published: 01/08/2023

Progress in Oceanography 216 (2023) 103080

Contents lists available at ScienceDirect

Progress in Oceanography

journal homepage: www.elsevier.com/locate/pocean

Investigation of marine temperature changes across temporal and spatial Gradients: Providing a fundament for studies on the effects of warming on marine ecosystem function and biodiversity

Felipe de Luca Lopes de Amorim [a,1,*], Karen Helen Wiltshire [a,b,1], Peter Lemke [a], Kristine Carstens [b], Silvia Peters [b], Johannes Rick [a], Luis Gimenez [b,c], Mirco Scharfe [d]

[a] Alfred-Wegener-Institut Helmholtz-Zentrum für Polar- und Meeresforschung, Wattenmeerstation Sylt, Hafenstrasse, 43, 25992 List/Sylt, Germany
[b] Alfred-Wegener-Institut Helmholtz-Zentrum für Polar- und Meeresforschung, Biologische Anstalt Helgoland, Kurpromenade, 201, 27498 Helgoland, Germany
[c] School of Ocean Sciences, Bangor University, LL59 5AB Anglesey, United Kingdom
[d] in Memoriam

A B S T R A C T

A current critical issue in climate change studies is how temperature changes and shifts on different spatial and temporal scales can affect organisms in terms of trends, variability and frequency of extremes. In this paper, we analysed marine temperature data on different temporal and spatial scales. We related the sea surface temperature data from the Helgoland Roads Time Series, one of the most important and detailed long-term in situ marine ecological time series, to the Sylt Roads, North Sea, Germany, Europe, North Atlantic and Northern Hemisphere surface temperatures. All time series showed a distinct upwards shift in temperature in the late 1980s, early 1990s, with positive trends in overall for the period between 1962 and 2019 ranging from 1 to 2 °C over 57 years. We quantified changes in temperature variability by comparing the years before and after 1990, on both long-term and seasonal scales. At Helgoland and Sylt, an increase in the number of warmer days in summer and a decrease in extremely cold days in winter are the new characteristics of the temperature pattern after 1990; higher than expected temperatures now also occur earlier during the year. For these locations, we observed the highest trends overall, i.e. of around 0.3 °C/decade. The observed bimodal shape of the probability density functions, characterized by winter and summer modes, had become more heterogeneous, with the cold mode peak moving to higher values and the steepness to the peak increasing, which is a consequence of a decrease in extremely cold days. North Atlantic Oscillation (NAO) and Multidecadal Oscillation (AMO) large-scale phenomena had no significant correlations or, for the NAO, were limited to the winter season at the regional and local scales. The closest landmass (mainland Germany) temperature was highly correlated with the North Sea sites. Taken together, our results suggest that marine pelagic ecosystems and their species are subject to temperature shifts with similar patterns but with variations in magnitude at the different scales. Temperature is one of the main drivers of species diversity and distribution, and this manifests on different spatial and temporal scales depending on population growth, life stages, cycles and habitat. Accordingly, we here present the temperature changes on the appropriate spatio-temporal scales, and thus provide the suitable and useful fundament for studies on the effects of warming on marine ecosystem function and biodiversity.

1. Introduction

The future of human kind is closely linked to the sustainability of coastal and shelf seas and their ecosystems. Global Ocean warming is fact and the effects of warming on marine ecosystem services presents a threat to long-term coastal sustainability and population stability. (IPCC, 2018; IPCC, 2019). Concomitantly, the vulnerability of human survival and livelihoods on coastal and marine systems becomes ever clearer as climate-related problems such as sea level rise, ocean acidification, loss of economically important species, invasive species and the"race for space" for energy parks, manifest in shelf seas (Barnard et al., 2021; Billé et al., 2022).

The trends from 1962 to 2019 in the whole Global Surface and Global Ocean temperatures is, respectively, given as 0.97 and 0.71 °C/57 years (GISTEMP Team, 2022). These values are based on the compilation of direct measurements at land and sea surface e.g. from simple thermometers, Argo data, ship data and meteorological stations (Lenssen et al., 2019). However, while large-scale projections and especially mean trends values are helpful, especially in the political sense, these alone are not particularly useful when considering direct human and organism responses, food web change and ecosystem disruption issues. More humans will live at, or close to, coasts and shelf seas and, as these

* Corresponding author.
E-mail address: felipe.amorim@awi.de (F.L.L. Amorim).
[1] joint first authors.

https://doi.org/10.1016/j.pocean.2023.103080
Received 14 May 2022; Received in revised form 28 March 2023; Accepted 27 June 2023
Available online 29 June 2023

populations are dependent on marine ecosystem integrity and ecosystem services, detailed data and information on marine warming, in appropriate time and spatial scales, facilitating mitigation and protection strategies on human and biological time scales are urgently required.

Marine ecosystems and organisms also react to shifts in environments on a variety of time scales. The potential death, fitness, resilience and adaptation of species is dependent on intensity, duration and frequencies of environmental shifts/ events. Predictability and understanding of temperature-related organism health, fitness, and reactions such as heat shock, depend on dense information of maximum temperatures, variability, frequency and duration of periods characterized by specific temperatures (Wiltshire and Manly, 2004).

Detailed long-term data and accompanying statistical information are fundamental for the development of highly flexible regional marine models (Androsov et al., 2019; Baracchini et al., 2020) needed for ecosystem predictability (e.g., for the estimation of warm water entrainment, marine pathogen dispersal, fish deaths in anoxic zones or sea level rise) in a warmer world. Regional management and realistic local decision taking require that these are operable on very small spatial scales, ranging from 0.5 km to 100 km, also requiring verification and explanatory data on the appropriate scales.

Marine data from ship cruises exist since the 1800 s for some coastal and shelf seas, and impressive large-scale biological change data sets from the continuous plankton survey of Sir Alister Hardy Foundation for Ocean Science's Continuous Plankton Recorder (SAHFOS CPR) are available. However, few continuous and dense time series (i.e., >20 years old) are available for connection with ecological information and biology, even for simple abiotic parameters such as temperature and salinity (Ostle et al., 2021; Philippart et al., 2003; Wiltshire and Manly, 2004). Indeed, dense continuous data from long-term ecological research (LTER) sites are rarely available (Edwards et al., 2010). Without such data, exact changes in environmental drivers are statistically difficult to define and the differentiation of change types including so-called "regime shifts" is often based on poorly defined time scales and system knowledge. Explanatory and predictive models are then difficult and less reliable.

The pressure is on to provide knowledge founded upon detailed real data on appropriate spatial and time scales, in order to predict and understand organism and ecosystem reactions and resilience. It is imperative to relate warming into evinced and graspable effects and consequences, on relevant biological scales. Otherwise, scenario discussions, predictions and management strategies for shelf and coastal seas are difficult/impossible to carry out.

In this paper, we take the sea surface temperature (SST) in situ data from one of the most important and detailed long-term marine ecological time series, the Helgoland Roads Time Series (HR), and relate the data with its nearest neighbour SST time series, the Sylt Roads Time Series (SR). We incorporated to the in situ data spatially averaged SST anomalies time series for the greater North Sea (NS), as well as: Northern Hemisphere (NH) Surface Air Temperature anomalies (SAT), Europe SAT, Germany SAT, North Atlantic (NA) SST anomalies (40°N-60°N belt of latitudes) and the Yellow Sea (YS) SST anomalies time series. These are all spatially averaged and derived from HadCRUT4 and HadSST3 SAT and SST anomalies products, available from the Hadley Meteorological Centre (Kennedy et al., 2011a, 2011b; Morice et al., 2012). The hierarchical and comparative statistical evaluation of all of these time series relative to one another will allow us to relate marine ecosystem change to temperature in terms of time and spatial scales. The objectives are:

1. to investigate the warming in the North Sea in terms of different geographical scales and typical weather indices,
2. to document the different types of changes observed: trends, anomalies and variability
3. to differentiate seasonal shifts,
4. to evaluate anomalies and frequency distributions of temperature over time, and
5. to evaluate hot and cold spells and their variability.

2. Materials and methods

2.1. Data sets

The data sets were divided into in situ and reanalysis products. Fig. 1 shows the areas and sites of interest in this article. Not highlighted, but no less important, are the European and German geographical areas, also analysed in terms of spatially averaged temperature anomalies.

2.1.1. Helgoland Roads time series (HR)

The renowned Helgoland Roads time series was set up in 1961 with the aim to evaluate change in the North Sea and its pelagic food webs over time. The evaluation scale available is from days to decades. Since 1962, surface water samples have been taken (before 9 a.m.) on working days at the "Kabeltonne" site (54° 11, 3'N, 7° 54, 0'E) between the two islands at Helgoland using a bucket. The data from these samples constitute one of the richest temporal marine data sets available, i.e., a pelagic data comprising of salinity, Secchi disk depth, nutrient analyses, phytoplankton and zooplankton analyses (Wiltshire 2004). The temperature at the sea surface was measured to date using calibrated reversing thermometers (Thomas and Dorey, 1967). The data is archived in PANGAEA (Data Publisher for Earth & Environmental Science). See Wiltshire and Manly (2004) for details on the time series.

2.1.2. Sylt Roads time series (SR):

The Sylt Roads time series (55.03° N, 8.46° E) was set up in 1973 to augment Helgoland Roads and German Bight transects with information from a shallow water location. Since 1973, surface water samples have been collected twice a week (except in 1977, 1978 and 1983 when it was suspended), temperature was measured using reversing thermometers and water was analysed for physical, chemical and biological parameters. Data are archived in PANGAEA (Rick et al., 2020e, 2020d, 2020c, 2020b, 2020a; Rick et al., 2017a; Rick et al., 2017b). In order to extend the SR Sea Surface Temperature (SST) time series to cover the same period as the HR series and to fill gaps, the SR data were merged with an additional (until now unpublished) SST data set from a neighbouring station located in List harbour (55.017° N, 8.44° E). This data was provided by Landesbetrieb für Küstenschutz, Nationalpark und Meeresschutz Schleswig-Holstein (LKN.SH, Husum, Germany). The two stations are situated 1.93 km apart in the Sylt-Rømø Bight.

The List harbour data set comprises daily water temperature taken from 1946 to 2003. For the period of overlap (1973–2003) between the two series, the data were compared statistically on a monthly basis applying a double-sided *t*-test. The overlapping data showed no significant differences (p values range 0.22–0.93) and their patterns were well-matched. The harbour data, due to its sheltered position, was insignificantly warmer by an average of + 0.11 °C compared to the SR site. Details on the merged datasets are provided in the supplementary material (S1). Using this approach, we managed to assign monthly mean SST data to all but three months (March 1999; April 1999; October 2000). These missing values were filled in with HadISST SST (Rayner et al., 2003) monthly average values from the closest grid point to the Sylt Roads position (https://www.metoffice.gov.uk/hadobs/hadisst/data/download.html, downloaded on 20 Jul 2020). The resulting time series is depicted in Fig. 2, highlighting the different data sources.

2.1.3. HadCRUT4 and HadSST3 datasets

Land and Sea Surface Temperature anomalies (ST) and Sea Surface Temperature anomalies (SST) were obtained from two products: HadCRUT4 (Morice et al., 2012) and HadSST3 (Kennedy et al., 2011a, 2011b) respectively, provided by Met Office Hadley Centre (https://www.metoffice.gov.uk/hadobs/, downloaded on 03/12/2020). Using

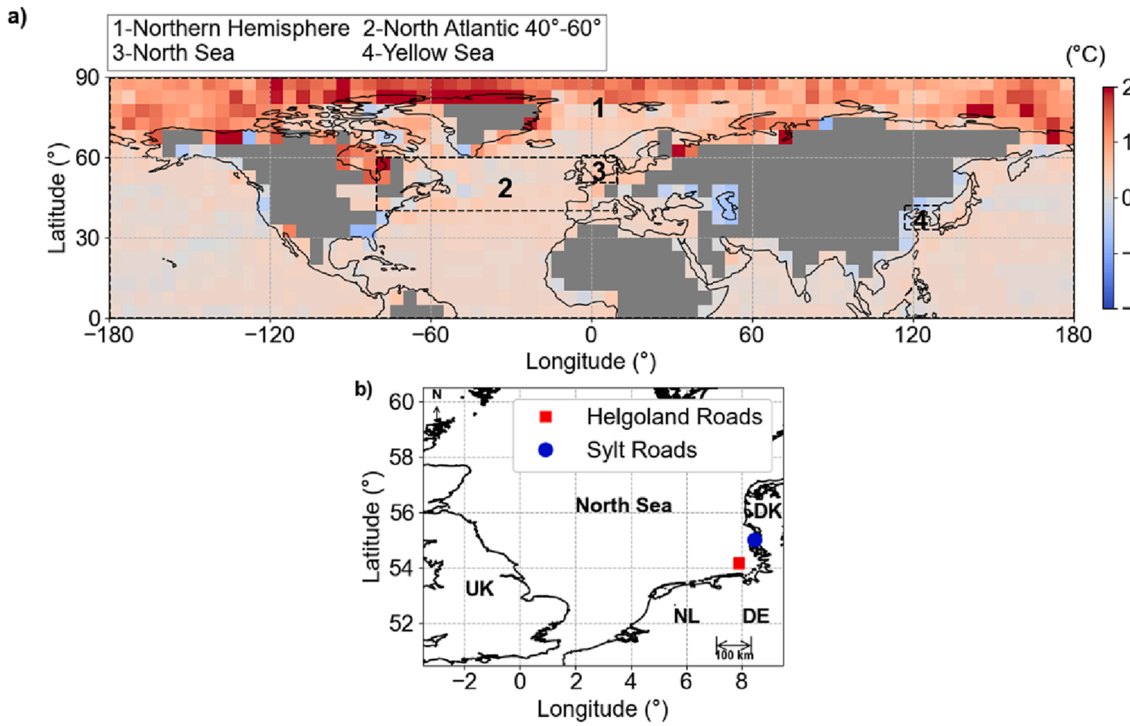

Fig. 1. Regions a) and locations b) analysed in this study. a) 1-Northern Hemisphere, 2-North Atlantic (latitude belt 40°-60°), 3-North Sea, 4-Yellow Sea. b) North Sea area and the two in situ stations – Helgoland Roads (red square) and Sylt Roads (blue circle). UK - United Kingdom; NL - Netherlands; DE - Germany and DK - Denmark. The colour background in a) represents the HadSST3 averaged SST anomalies for the period 1962 to 2019.

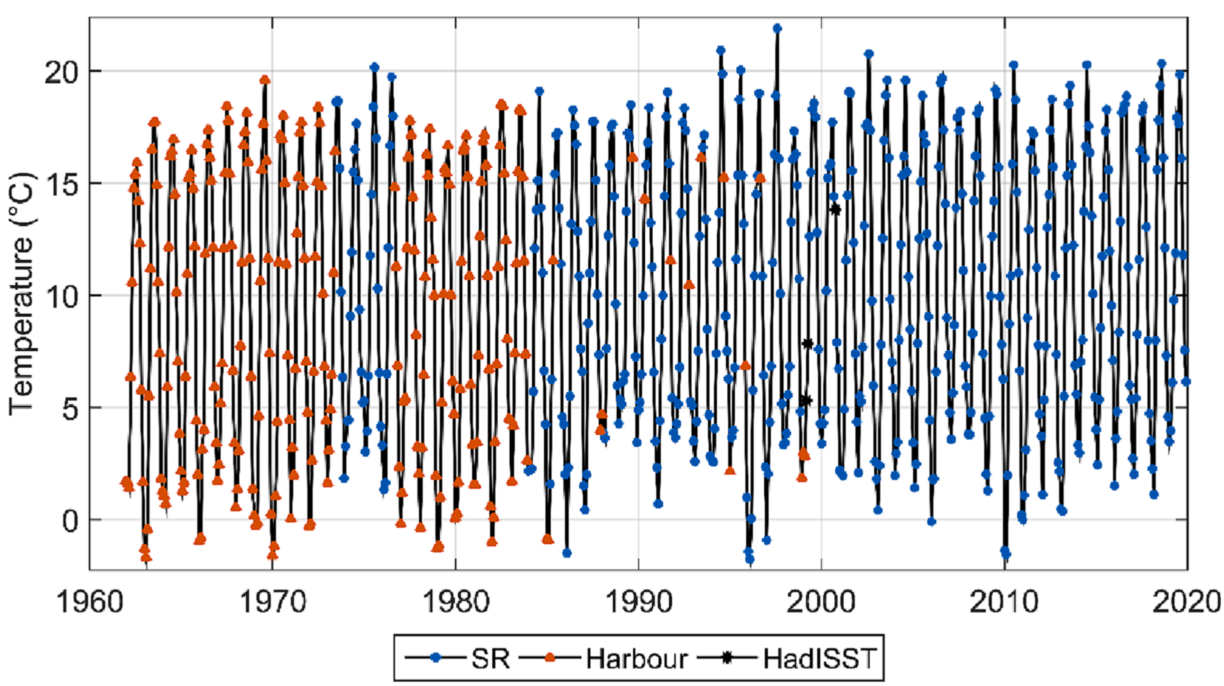

Fig. 2. Sylt Roads SST Time Series – merged from three data sources (solid black line). SR (blue circle), Sylt harbour (orange triangle) and HadISST (black star).

these two products we ensured consistency with atmospheric and sea surface temperature anomalies. Surface temperature anomalies were spatially averaged for 4 regions: Northern Hemisphere (NH ST), North Atlantic (limited by latitudes 40° and 60°N) (NA SST)**,** North Sea (NS SST) and Yellow Sea (YS SST) (Fig. 1).

The temperature anomalies for HadCRUT4 and HadSST3 data are relative to the period of 1961 to 1990 and the limits used for the seas were defined to be as close as possible to the ones defined by the Limits of Oceans and Seas (IHO, 1953).

2.1.4. European land surface air temperature anomalies

We considered the European land mass temperature connection and scale by using the annual mean European Land Surface Air Temperature Anomalies, provided by the European Environment Agency and downloaded from the website https://www.eea.europa.eu/data-and-maps/figures/global-left-and-european-land. As described in the source website, this is a product compiled as the mean of the HadCRUT4, GISTemp v4, and NOAA Tempv5 data sets. The anomalies for this dataset are relative to the pre-industrial period 1850–1900.

2.1.5. German surface air temperature anomalies

The nearest landmass temperature data for both Helgoland and Sylt Roads are the annual mean German Surface Air Temperatures, acquired by meteorological stations around Germany. These were taken from the website of the German Weather Service (DWD, https://www.dwd.de/EN/ourservices/zeitreihen/zeitreihen.html#buehneTop). The anomalies for this dataset are relative to the 1962–1991 period.

2.1.6. North Atlantic Oscillation index (NAO)

The North Atlantic Oscillation Index (NAO) is regularly used to explain variability in temperature and Long-Term Ecological Research (LTER) time series (Becker, 1996; Hurrell et al., 2001; Pozo-Vázquez et al., 2001). According to the National Center for Atmospheric Research (NCAR), the principal component (PC)-based NAO is the time series of the leading Empirical Orthogonal Function (EOF) of Sea Level Pressure anomalies over the Atlantic sector, 20°-80°N, 90°W-40°E, limited by the Icelandic Low and Azores High (NAO, 2022). In this work, we use the PC-based NAO monthly time series to match with the monthly SST time series in frequency.

2.1.7. Atlantic Multidecadal Oscillation (AMO)

The Atlantic Multidecadal Oscillation is defined as the spatial average SST anomalies in the North Atlantic over 0°-60°N (Trenberth and Shea, 2006). The AMO time series is provided by the NCAR Climate Data Guide and it was extracted from https://climatedataguide.ucar.edu/climate-data/atlantic-multi-decadal-oscillation-amo (AMO, 2021).

2.2. Statistical methods

We focused on statistical evaluations of the coastal and pelagic long-term data, considering the period of study from 1962 to 2019, covering a time horizon of 58 years and 696 monthly observations. Statistical analysis was applied to the collection of yearly and monthly surface temperature anomalies time series. Due to the averaging, no missing observations were detected. The methods used were: trend analysis using linear regression; Pearson cross-correlations (significance $p > 0.05$) of detrended time series; variability and seasonality estimated by calculating standard deviation and individual months average; Probability Density Function estimated by Kernel Density Estimate and histograms to observe distribution patterns and changes. All the statistical analyses were performed using the MATLAB® and Microsoft Excel software.

All data were used as anomaly time series, and for the two in situ stations (HR and SR), absolute SST was also analysed. For the in situ SST data, the anomalies were calculated removing the seasonal signal calculated as average of individual months from 1962 to 1991. For yearly time series, the mean temperature from 1962 to 1991 was subtracted from the absolute temperature time series. Temperature anomalies were used instead of absolute temperatures because one assumes to first-order that the seasonal cycle is a more or less deterministic consequence of the varying zenith angle of the sun, and all differences from the seasonal cycle (i.e. the anomalies) tell us something about the internal dynamics of the system.

Trends were quantified by fitting linear models through linear regression. We carried out cross-correlation analyses to investigate the statistical inter-relationships between the temperature data from different geographical regions. We computed the cross-correlation of the detrended time series, as the trends occurring in both time series always contributes to the cross-correlation of two anomaly time series. Seasonal variability was calculated by the standard deviation of specific month temperatures, from January to December.

3. Results

The presentation of the results (and also the discussion) is structured as follows:

Trend and cross-correlation between local Long-Term Observations (LTO) and large-scale time-series in: Northern Hemisphere Surface Temperature (NH ST), Europe SAT (EU SAT), Germany SAT (DE SAT), North Atlantic SST (40°N-60°N belt) (NA SST) and the North Sea SST (NS SST). Here the AMO is also considered.

Long-term changes in seasonality with focus on LTOs.

Comparison of seasonal variability between early (1962–1990) and late (1991–2019) years of the time series.

Means and trends for the above-mentioned periods by seasons, comparing the degree of changes in temperature anomalies related to early and late years.

3.1. Overall trends and Cross-Correlation

The data from the two long-term in situ stations at Helgoland Roads and Sylt Roads lend themselves to simple linear calculations of trends based on yearly average (Fig. 3). The increase in sea surface temperature is clear for both stations. Although the sites are hydrographically completely different, with Helgoland being offshore in the open water of the German Bight and Sylt being a shallow water coastal station in the Wadden Sea, the magnitude of trends are almost the same for both sites.

Because the HR and SR data are used widely for climate and ecological assessments, it was necessary to evaluate these two local sites into the context of larger geographical regions and especially in the context of the warming of the North Sea and the temperatures of the North Atlantic. To achieve this, we used the temperature anomalies data sets already described and the comparative results are shown in Fig. 4 and Table 1.

All the trends were significantly positive and the slopes were larger with decreasing geographical scale (i.e. spatial average) for both surface air temperatures and sea surface temperatures:

- Trend of NH SAT < EU SAT < DE SAT (for the surface/surface air temperature)
- Trend of NA SST < NS SST < HR/SR SST (for the sea surface temperature).

A cross-correlation analysis was carred out to investigate the statistical inter-relationships between the temperature data from different geographical regions. For this, the cross-correlation of the detrended time series was computed, as the cross-correlation of two anomaly time series always has a contribution from the trend occurring in both time series. From Table 2, it is clear that the strongest cross-correlations occurred between Germany/Europe and Europe/NH, as was to be expected. The SST of the North Sea was strongly correlated with the European and the German SAT and, to a lesser extent, with the North Atlantic SST and the Northern Hemisphere ST.

Helgoland Roads and Sylt Roads were strongly correlated with the German SAT and to a smaller extent with the European SAT. The stations were highly correlated with each other and also with the SST of the North Sea. This answers the question as to whether both sites can be considered representative with regard to temperature of the overall North Sea.

Previous studies considered AMO to be related to e.g. rainfall patterns and fish stocks (Alheit et al., 2014; Frajka-Williams et al., 2017). We also considered the AMO data, and its relationships are presented in the bottom line of the correlation matrix in Table 2. Correlations of temperature anomalies with AMO were small, except, unsurprisingly,

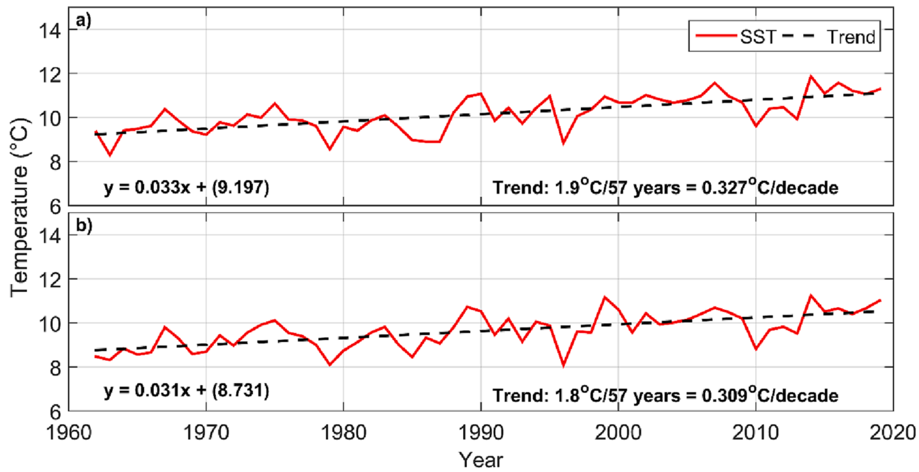

Fig. 3. Yearly averages of temperature time series (solid red) and their linear trends (dashed black), a) Helgoland Roads and b) Sylt Roads.

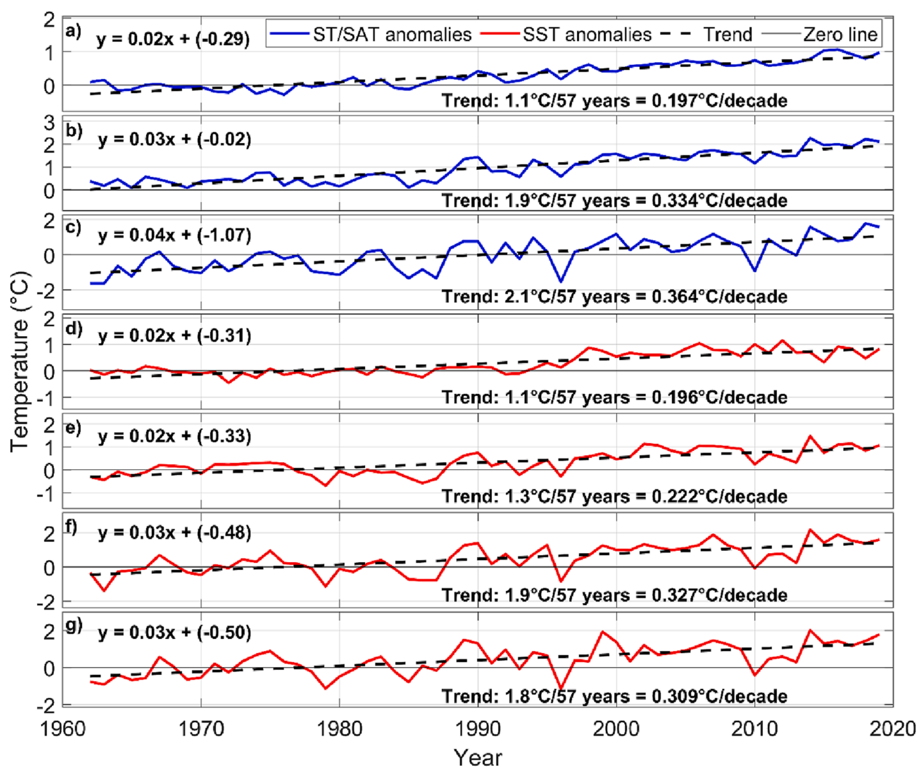

Fig. 4. Anomaly time series (solid blue and solid red) and their linear trends (dashed black). From the top: Northern Hemisphere ST (land + sea surface temperature), Europe SAT, Germany SAT, North Atlantic SST (40°N-60°N belt), North Sea SST, Helgoland Roads SST, and Sylt Roads SST anomalies. Blue lines, except a), are based on surface air data and red lines are based on sea surface data.

Table 1
Trends in °C/period for the various time series with the associated R^2 (Pearson) coefficient.

Temperature Anomalies Time series	Trend per 57 years	Trend per decade	R^2
NH SAT	1.12	0.20	0.82
EU SAT	1.91	0.33	0.80
DE SAT	2.07	0.36	0.49
NA SST	1.12	0.20	0.67
NS SST	1.26	0.22	0.54
HR SST	1.86	0.33	0.47
SR SST	1.76	0.31	0.43

when related with the NH ST and with the NA SST. The AMO and NA SST data sets overlap, partly consisting of the same data. The correlation between HR SST anomalies and the AMO was smaller than between HR SST anomalies and NA SST. This is because the tropical latitudes below 40° N are not included in the latter. Thus, henceforth we concentrated on the NA SST rather than the AMO in all future comparisons with the Northern Atlantic. All cross-correlation values in Table 2 are significant as they are above the 95% confidence levels of uncorrelated white noise.

3.2. Seasonal patterns

The temperate climate zone is characterised by clear seasonality, which defines growth periods both in terrestrial and marine systems.

Table 2
Cross-correlations calculated from the detrended anomaly time series. All cross-correlation values are significant above 95% confidence level. AMO is added for comparative purposes.

	NH SAT	EU SAT	D SAT	NA 40–60	NS	HR	SR
NH SAT	**1**	0.43	0.10	0.55	0.30	0.26	0.09
EU SAT	**0.43**	**1**	0.77	0.30	0.73	0.75	0.71
DE SAT	**0.10**	**0.77**	**1**	0.06	0.67	0.83	0.87
NA 40–60	**0.55**	**0.30**	**0.06**	**1**	0.36	0.24	0.06
NS SST	**0.30**	**0.73**	**0.67**	**0.36**	**1**	0.86	0.72
HR SST	**0.26**	**0.75**	**0.83**	**0.24**	**0.86**	**1**	0.87
SR SST	**0.09**	**0.71**	**0.87**	**0.06**	**0.72**	**0.87**	**1**
AMO	***0.48***	***0.14***	***−0.11***	***0.80***	***0.18***	***0.06***	***−0.11***

Having established the cross-correlative relationships between the data from small to large-scale areas, the next step was to calculate and understand the seasonal cycle and the anomalies. We concentrated on different time scales, starting with seasonality of the in situ LTOs. Thus, we next focused on to understanding variability of the two stations over the past 58 years. Only the results based on the in situ temperature measurements are presented. The sea surface temperature for the data sets were evaluated and show large and variable seasonal evolution. (See example in Fig. 5). The variability of the winter minimum displays a much stronger variability than the summer maximum.

When the densities/frequencies of the temperature anomalies for all data sets are resolved, two peaks manifest with bunches (=longer duration of SSTs) of cold temperatures around the winter minimum and warm temperatures around the summer maximum (Fig. 6). These peaks represent the time just before and after the winter minimum and the summer maximum. The density curves suggest that the cold peak around the winter is slightly larger compared with that of the summer for both HR and SR. This reflects the slightly longer winter season compared to summer at these latitudes. The corresponding seasonal cycles of HR and SR are shown in Fig. 7. A smaller curvature of the winter minimum values compared to the summer maximum values is apparent. The winter season is clearly longer by approx. half a month. The winter minimum temperatures at Sylt are colder and the summer temperatures are warmer compared with Helgoland. This, also the difference in timing of the start of spring/ summer between the two sites, reflects the shallow water coastal site at Sylt, vs. the offshore water site at Helgoland.

Examination of the NA, NS, HR and SR SST anomalies, and as exemplified by HR and SR in Fig. 8, indicated positive temperature trends for both summer and winter. The trends for winter and summer were calculated and are presented in Table 3 with their associated R^2 (Pearson) coefficient. The analyses revealed that whereas the summer trends are similar in all regions, the winter trends are much larger for the two stations Helgoland Roads and Sylt Roads (reduced cold continental influence in winter) (Table 3). A trend of 0.3 °C/decade for both seasons was registered for HR (Fig. 8a). At the shallow water site SR (Fig. 8b) the summer warming trend was slightly less than for winter.

3.3. Temperature variability in first and second half of the Time-Series

Having evaluated the seasonality, we next turn again to the analyses of the temperature variability, described by the temperature anomalies time. Again, although we calculated these for all data sets in Section 3.1, only the results from NS, HR, SR and YS are depicted here as 12-month running means (Fig. 9). We kept the y-axis in the same scale for better comparison.

The SST anomalies were mostly negative with a small trend until the late 1980s for NA (not shown), NS, HR, and SR, and mostly positive with a larger positive trend thereafter. Fig. 9a,b,c clearly shows this for NS, HR and SR and this is also aligned with similar evolution found in the European and German surface air temperature anomalies (Fig. 4).

In order to check whether this was a phenomenon only related to the Northern Atlantic, we searched for other shelf seas comparable with our focus region. The only comparable one, considering latitude limits and bathymetry, was the Yellow Sea (YS) time series. We found the same pattern, which is depicted in Fig. 9d below. The overall temperature trend for the YS was calculated 0.16 °C/decade and 0.9 °C/57 years for the whole period 1962–2019. with a warming rate of 0.12 vs. 0.13 °C/decade in winter vs. summer months, respectively.

The interesting difference between first and second half indicated that an evaluation of the time series in terms of early and recent (late) years separately was necessary. Thus, to avoid bias due to visual interpretation, we simply divided the data series into two halves, from 1962 to 1990 and from 1991 to 2019. We then applied analytical statistics for comparison of early and late years. The anomalies showed distinct differences between these two periods, which were then, examined in detail.

3.3.1. Long-Term changes in SST distributions

Starting with an analysis of the frequency of temperature distribution in the first and second part of the time series, an increase in the occurrence of warmer temperatures during winter was seen in all data sets. In Fig. 10, we show the temperature distribution by period at HR and SR, showing the dislocation of the two lobes peaks (cold and warm modes) representing winter and summer, towards higher temperatures. For both HR and SR, the first half of the time series shows nearly

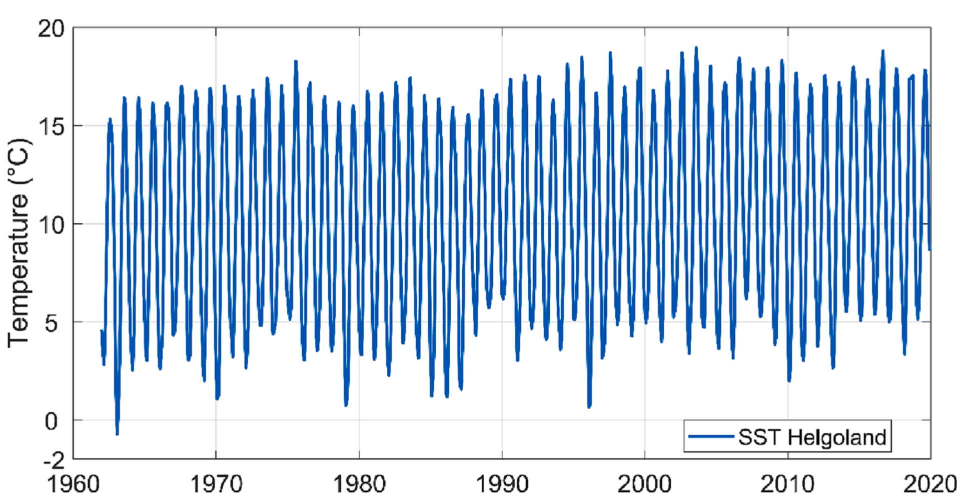

Fig. 5. Evolution of the sea surface temperature including seasonality as an example: Helgoland Roads.

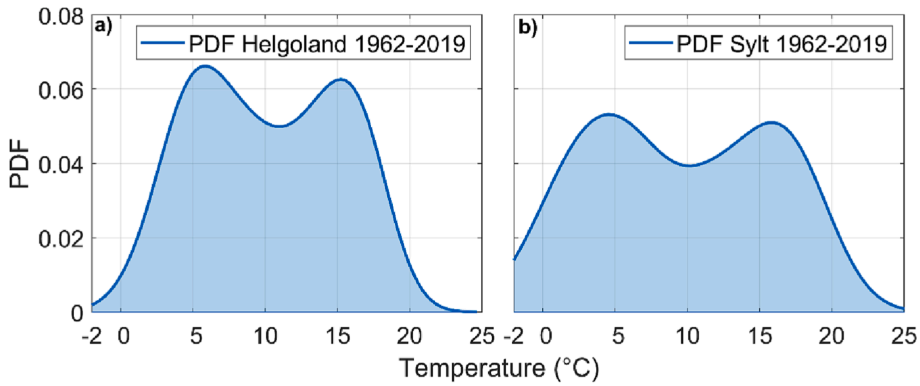

Fig. 6. Probability density function curves of sea surface temperatures at a) Helgoland Roads and b) Sylt Roads calculated using Kernel Density Estimates. For a) and b), the x-axis was limited to −2 °C because lower temperatures are an artefact of the PDF.

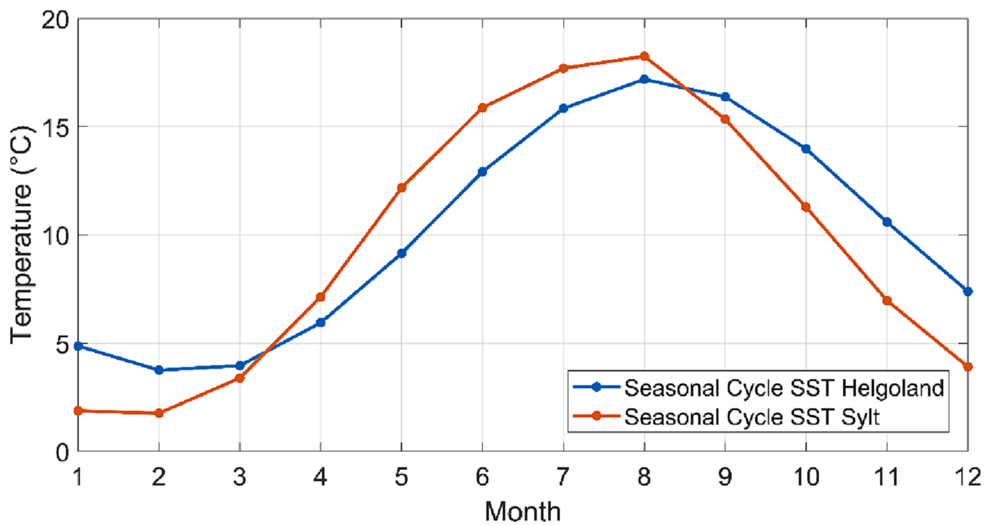

Fig. 7. Seasonal cycles for the SST at HR (blue) and SR (orange) for the entire time series.

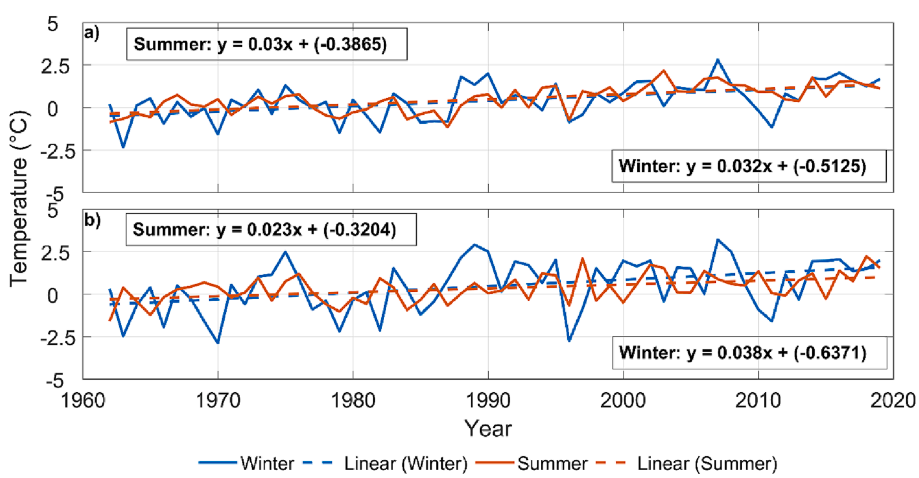

Fig. 8. Temporal evolution and trend of the SST anomalies at a) Helgoland Roads and b) Sylt Roads in summer mean (June-August) (solid orange line) and summer linear trend (dashed orange line), winter mean (December-February) (solid blue line) and winter linear trend (dashed blue line).

perfectly symmetric distributions (Fig. 10a and Fig. 10b, respectively), with peaks around the mean minimum and maximum. In the second half of the time series, the two modes are still visible, but the cold mode is slightly larger than the warm mode. This must be due to the change in the seasonal cycle: the mean minimum in the second half is a little higher and the curvature is steeper, and the mean maximum is a little lower and the curvature is flatter. Because of this change, more values occur around the cold mode and less values around the warm mode, spreading to higher-than-average values.

The HR and SR temperature histograms are shown in Fig. 11 and it is

Table 3
SST anomalies trends in °C/decade in summer and winter. The value in brackets is the associated R^2 (Pearson) coefficient.

Region	North Atlantic	North Sea	Helgoland Roads	Sylt Roads
Summer	0.26 (0.66)	0.25 (0.40)	0.30 (0.44)	0.23 (0.22)
Winter	0.13 (0.44)	0.17 (0.27)	0.32 (0.26)	0.38 (0.18)

possible to observe that temperature distributions have shifted in the later years for both. At Helgoland the distinctive bi-seasonal bimodal shape is still clear, but the peak intervals in winter and summer increased by 1 °C, showing an increase in maximum temperature values. In the shallow inshore waters around Sylt, the seasonal signal has become more homogeneous, as intermediate temperature intervals became enhanced. The low temperature range peak increased also by 1 °C, with a decrease in the counts for the lowest temperature range. These observations underpin the results on the observed long-term shifts in seasonality as presented in Section 3.2. Consideration of the SST anomalies in the North Atlantic, North Sea, HR and SR showed that the temperature density distribution clearly shifted to higher temperatures in the later years in these areas (Fig. 12).

3.3.2. Seasonal means and trends

It seems that the most pronounced difference between the first and the second half of the time series occurs around the winter minimum and the summer maximum (Fig. 10). Thus, we examined the seasonal means and trends of the two sections of time series and the analyses showed that actually all seasons are affected. This can be seen in Figs. 13 to 16 and in all the trend values in Table 4 (HR) and Table 6 (SR).

In both Helgoland and Sylt Roads, the summer long-term trends increased after 1990 (Figs. 13 to 16), and the intercepts increased by roughly 1 °C in both winter and summer in the late years, indicating the increase in SST means for these locations. In Tables 4 and 5, the changes in the SST trends and means at Helgoland Roads and the difference between the first and the second half of the time series are summarized for all seasons. The associated R^2 (Pearson) coefficient, is also provided. In Tables 6 and 7, we summarize the same results for the Sylt Roads. It is clear from Tables 5 and 7 that the mean seasonal SST were significantly higher in late years compared to the early years, especially in spring and

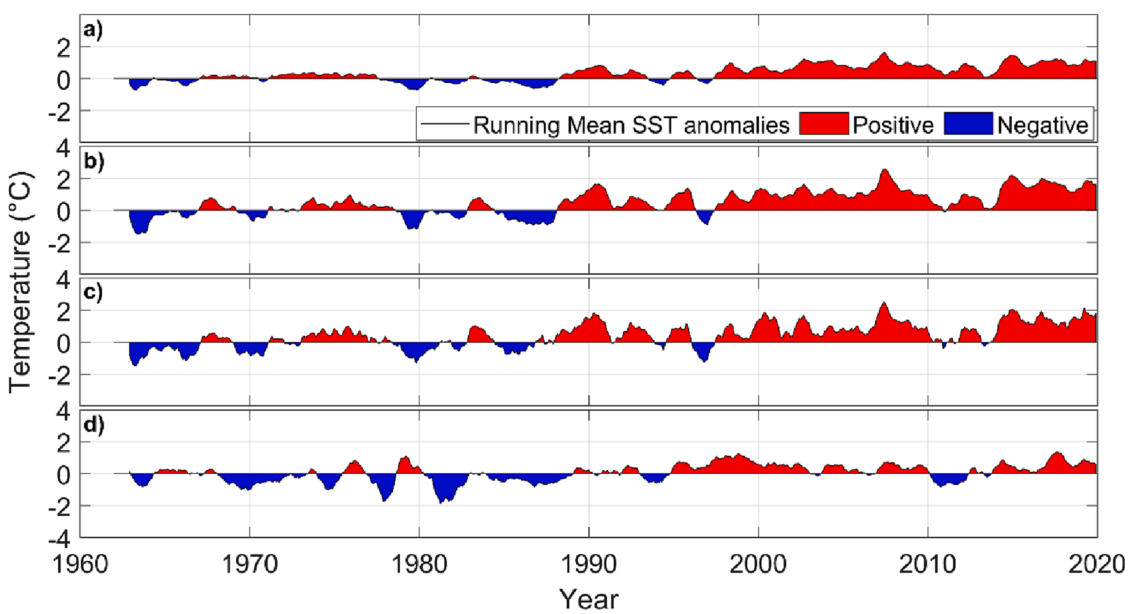

Fig. 9. Twelve-month running mean SST anomalies (black curve). Blue, negative anomalies and red, positive anomalies, respectively. a) NS, b) HR, c) SR and d) YS. It is clear the dominant positive pattern after the end of 1980s.

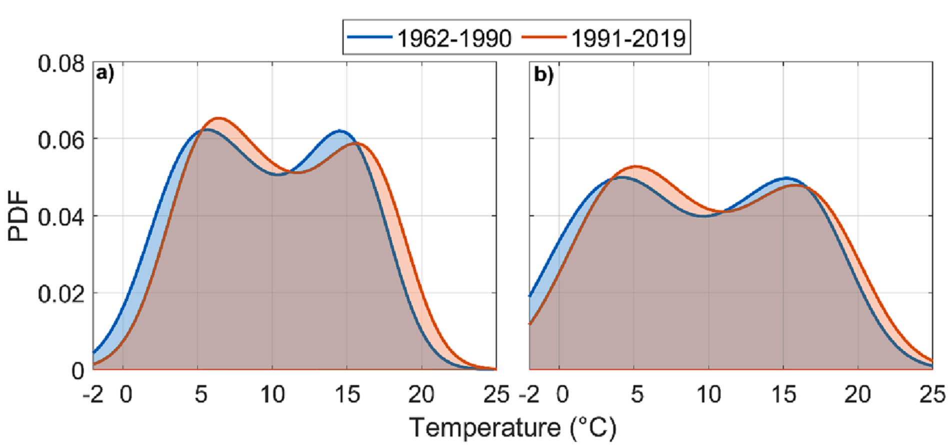

Fig. 10. Distribution of the sea surface temperature at a) Helgoland Roads and b) Sylt Roads, in terms of probability density function, for the first (blue) and second (orange half of the time series. The curves show the bimodality originated from seasonality and the shift when comparing early and late years. For a) and b), the x-axis was limited to −2 °C because lower temperatures are an artefact of the PDF.

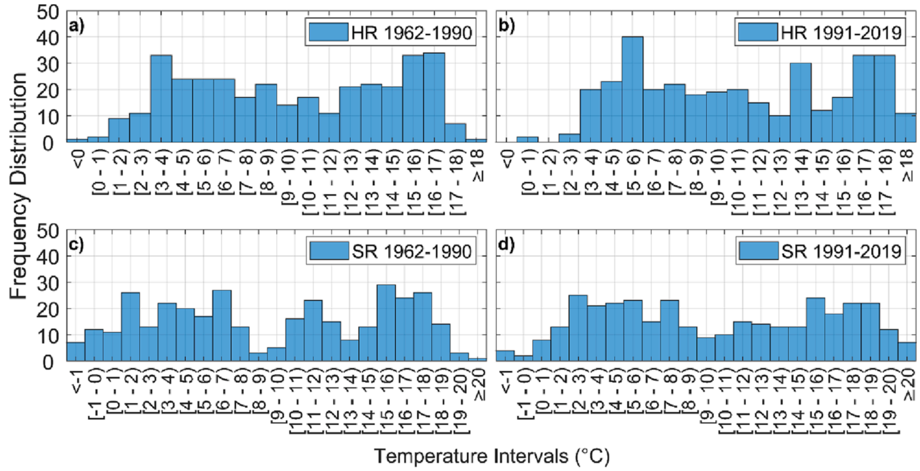

Fig. 11. Frequency of occurrence of temperatures at HR and SR. a) HR SST histogram for the period 1962–1990 and b) HR SST 1991–2019. c) SR SST histogram for the period 1962–1990 and b) SR 1991–2019.The bins are defined as 1 °C intervals, except for the edges. Note the difference in temperature intervals for HR and SR.

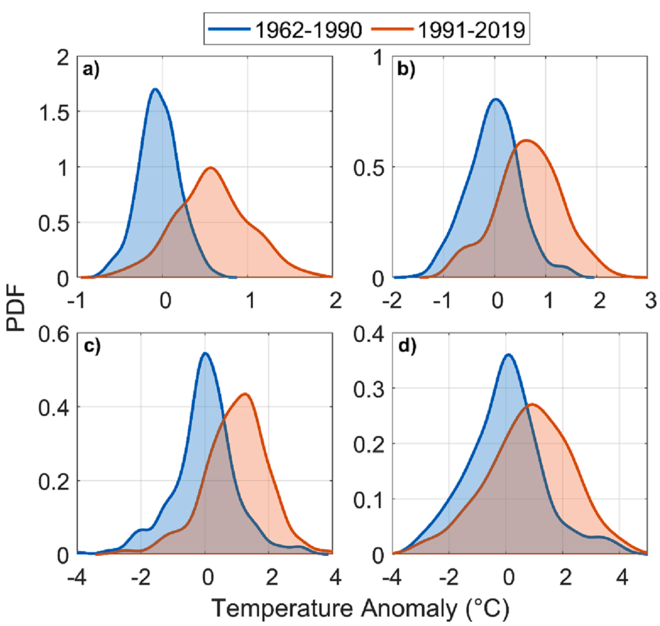

Fig. 12. Probability Density Function (PDF) of sea surface temperature anomalies in the first (blue) and second (orange) half of the time series for the a) NA, b) NS; c) HR and d) SR.

summer (>1 °C) at HR and SR. However, when it comes to the trends (Tables 4 and 6), these were steeper especially in autumn, compared to the summer period in the late years.

3.3.3. Seasonal variability

In order to assess potential shifts in seasonal variability of temperature at the HR and SR sites, we evaluated the seasonal variability of the standard deviation, i.e. we calculate the standard deviation of all Januaries, Februaries, etc. for the total time series and its early and late halves (Fig. 17).

The variability during the winter and spring months was found to be significantly larger than during summer and autumn at both HR and SR. This is especially true for the early half of the time series. In the second half of the time series, the large winter variability has become smaller and the autumn variability has become larger. The same pattern (depicted in Fig. 25 of the Discussion) was found for the North Sea data. However, the data sets for the North Atlantic showed a clear increase in temperature variability for all months since 1991. The Northern Hemisphere and global data sets also show increases in variability in the later years for all months, but with a significantly smaller amplitude.

From Fig. 17, it is clear that the seasonal variability of temperature is different between the first and the second half of the time series. In order to assess how it changes with time, we computed the standard deviation of all months within each year. With this calculation of the seasonal variance, we obtained a measure of the strength of the seasonal amplitude. The results for HR and SR are shown in Fig. 18, and indicate a negative trend in the amplitude of the seasonal cycle.

This means that the seasonal cycle became smaller in magnitude over time, also shown in Tables 4 to 7. For Helgoland, the difference of the mean between the warm seasons (summer, autumn) and the cold seasons (winter, spring) is 8.74 °C in the first half of the time series and 8.56 °C in the second half, i.e. a reduction of the seasonal cycle by 0.2 °C (Table 5), consistent with the trend indicated in Fig. 18a. At SR, the reduction of the seasonal cycle between the first half and the second half of the time series is larger at 0.4 °C (Table 7). Overall, it is clear that the seasonal variability and, concomitantly, the seasonal amplitude has shifted considerably, becoming less in winter and more in autumn; manifesting especially as a reduction of the definite seasonality, both at the open water site at Helgoland and in the shallow Wadden Sea site of Sylt.

3.3.4. Assessment of temperature extremes

The determination of the shifts as the occurrence of low and high temperatures is very important for the assessment of ecological conditions. Thus, the data evaluation relative to maximum and minimum temperatures are presented here. The evaluation of the number of "cold" months and "warm" months based on minimum and maximum thresholds shows large change between the early and late years.

Helgoland Roads, an exposed open water site, showed minimum cold thresholds of mean monthly temperatures < 2 °C and < 3 °C. The maximum warm thresholds at HR were mean monthly temperatures > 17 °C and > 18 °C. The number of months with mean values above/ below these thresholds is shown in Fig. 19. It can clearly be seen that there has been a significant shift towards very many warm months with values over 17 °C and 18 °C at Helgoland Roads since 1991. The very cold months (mean values below < 2 °C and < 3 °C) have become significantly less common. The percentages of the mean number of cold and warm months relative to the total number of months of the different time periods are given in Table 8. The percentage of months with mean temperatures below 3 °C has gone down from 6.6 % to 1.4% of the total months in the early/ late years, respectively. At the same time, the percentage of months with mean temperatures above 17 °C has gone up from 2.3 % to 12.4 % of the total months in the early/ late years,

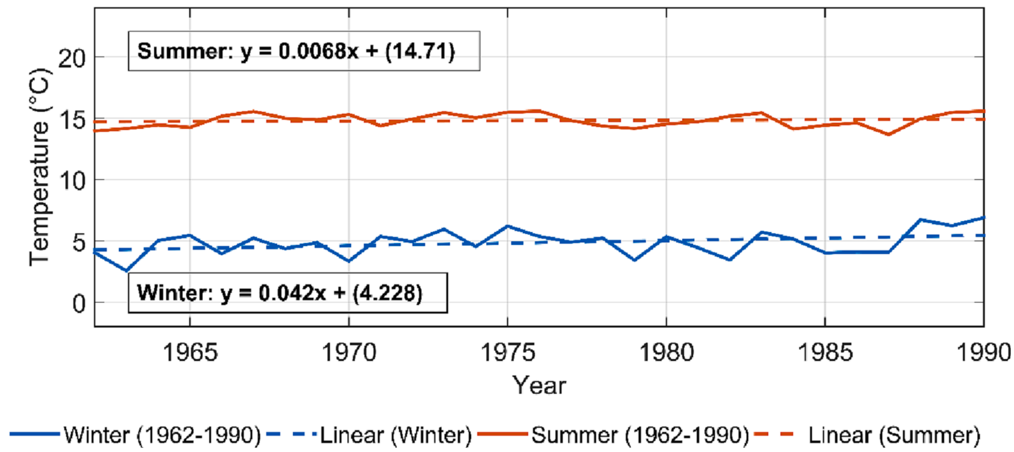

Fig. 13. Trends of the summer (dashed orange line) and winter seasons (dashed blue line) mean temperatures at HR for the first half (1962–1990) of the time series.

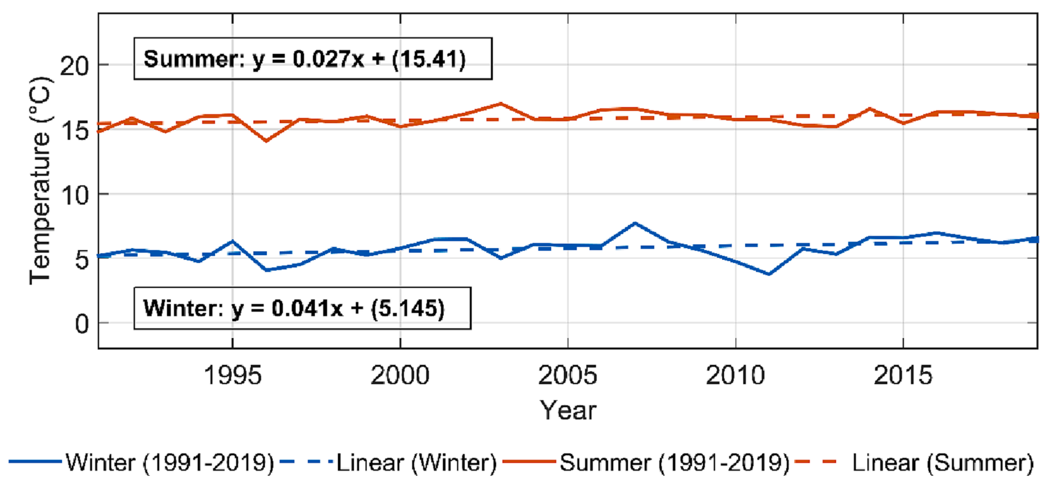

Fig. 14. Trend of the summer (dashed orange line) and winter seasons (dashed blue line) mean temperatures at HR during the second half (1991–2019) of the time series.

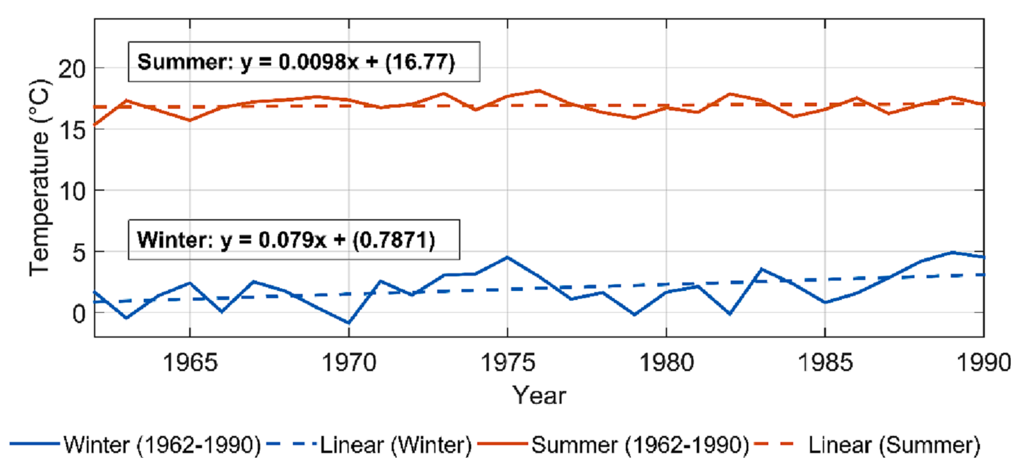

Fig. 15. Trends of the summer (dashed orange line) and winter seasons (dashed blue line) mean temperatures at SR for the first half (1962–1990) of the time series.

respectively.

Sylt Roads, the shallow water Wadden Sea site, showed minimum cold thresholds of mean monthly temperatures < 1 °C, < 2 °C and < 3 °C. The SR maximum warm thresholds were mean monthly temperatures > 17 °C and > 18 °C. The number of months with mean values above/below these thresholds is presented in Fig. 20 for SR. It is obvious that there has been a significant shift towards more warm months at Sylt since 1991 and the very cold months (mean values below < 2 °C and < 3 °C) have become significantly less (for percentages of total, see Table 9). For example, the percentage of months with mean temperatures below 2 °C has gone from 16.6% to 7.8% of the total months in the early/ late years, respectively. At the same time, the percentage of

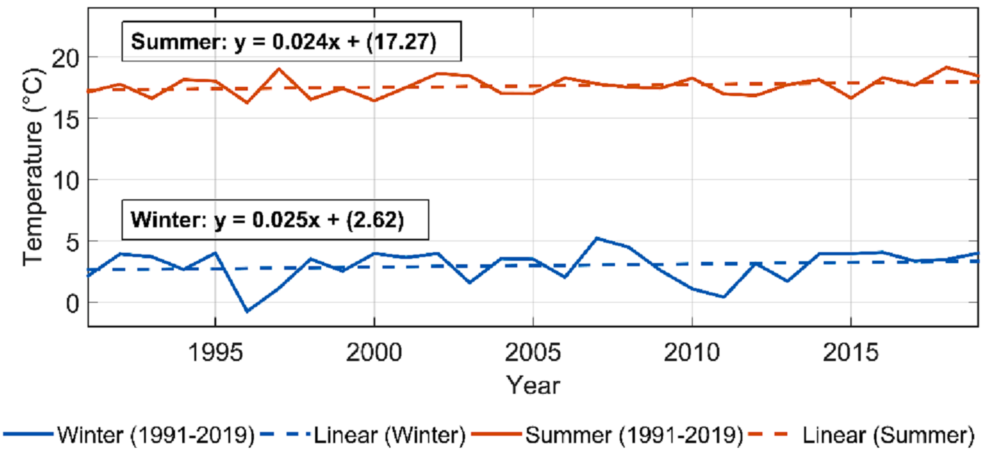

Fig. 16. Trend of the summer (dashed orange line) and winter seasons (dashed blue line) mean temperatures at SR during the second half (1991–2019) of the time series.

Table 4
Annual and seasonal trends of SST in °C/period at Helgoland Roads for the entire period, the first and the second half of the time series for the different seasons. The values in brackets are the associated R^2 (Pearson) coefficient, which indicates how much of the variance is explained by the trend.

Season Period	Spring	Summer	Autumn	Winter	Annual mean
1962–2019	0.405 (0.28)	0.307 (0.45)	0.265 (0.37)	0.335 (0.29)	0.335 (0.48)
1962–1990	0.372 (0.08)	−0.068 (0.01)	−0.006 (0.0001)	0.423 (0.12)	0.243 (0.10)
1991–2019	0.293 (0.05)	0.291 (0.16)	0.541 (0.35)	0.407 (0.15)	0.361 (0.24)

Table 5
Mean annual and seasonal SST in °C at Helgoland Roads for the complete period (A 1962–2019), the first half (B 1962–2019) and the second half (C 1991–2019) of the time series. The difference of the late data from the early data (C-B) is presented, as it is significantly positive for all seasons and the whole period.

Season Period	Spring	Summer	Autumn	Winter	Annual mean
A 1962–2019	6.35	15.32	13.63	5.31	10.29
B 1962–1990	5.73	14.82	13.25	4.86	9.79
C 1991–2019	6.97	15.83	14.02	5.76	10.79
Difference: **C-B**	**1.24**	**1.01**	**0.77**	**0.90**	**1.00**

Table 6
Annual and seasonal trends of SST in °C/period at Sylt Roads for the entire period, the first and the second half of the time series in the different seasons. The value in brackets is the associated R^2 (Pearson) coefficient, which indicates how much of the variance is explained by the trend.

Season Period	Spring	Summer	Autumn	Winter	Annual mean
1962–2019	0.406 (0.32)	0.228 (0.22)	0.202 (0.16)	0.393 (0.19)	0.307 (0.44)
1962–1990	0.683 (0.28)	0.098 (0.01)	−0.083 (0.02)	0.795 (0.19)	0.365 (0.23)
1991–2019	0.357 (0.08)	0.240 (0.07)	0.611 (0.27)	0.250 (0.03)	0.369 (0.21)

months with mean temperatures above 17 °C has gone up by over 6% of the total months in the early/ late years at Sylt Roads.

It is interesting to note that these data clearly show that the sites at Helgoland and Sylt, because of their different hydrographic situation (i.e. open North Sea vs. shallow Wadden Sea), have different temperature

Table 7
Mean annual and seasonal SST in °C at Sylt Roads complete period (A 1962–2019), the first half (B 1962–2019) and the second half (C 1991–2019) of the time series. The difference of the late data from the early data (C-B) is presented, as it is significantly positive for all seasons and the whole period.

Season Period	Spring	Summer	Autumn	Winter	Annual mean
A 1962–2019	7.56	17.27	11.20	2.49	9.64
B 1962–1990	7.03	16.92	10.93	1.98	9.22
C 1991–2019	8.10	17.63	11.46	2.99	10.05
Difference:					
C-B	**1.07**	**0.71**	**0.53**	**1.01**	**0.83**

extremes. Sylt water heats up faster and cools down more. On the long run, it may be expected that this difference will become even more pronounced.

3.3.5. Relationship of the North Atlantic Oscillation (NAO) and temperature

Evaluation of how the NAO relates to temperature data in the Northern Hemisphere is of importance and is often used in the ecological literature. The NAO only relates well to the winter temperatures (December-February) because the difference between the two pressure systems that characterizes the NAO index are more pronounced during winter months (Rodwell et al., 1999). From previous analyses of North Sea data (Lohmann and Wiltshire, 2012; Wiltshire et al., 2010), it was clear that NAO index was also only useful for explaining variability in the North Sea winter temperatures. After checking that indeed the temperature of the summer months at HR and SR barely correlated with the NAO, we concentrated on the winter months. The analysis of the Hurrell winter NAO index (December to February means) from the first principle component (PC) as per web download, is depicted in Fig. 21.

In the PC NAO, there is a positive trend toward positive NAO (more frequent westerly winds and warmer temperatures in winter in Europe) (Trigo et al., 2002). As can be seen from the histograms in Fig. 22, in the first half of the time series there are 7 years with strongly negative values (<-1), and in the second half there are only 3 years with strongly negative values (equivalent to a smaller number of cold winters). The correlation analyses of temperature with the NAO was highly significant for all the data sets except the North Atlantic data set. This was the case for all years and both early and late years (Table 10).

3.4. Summary of results

Table 11

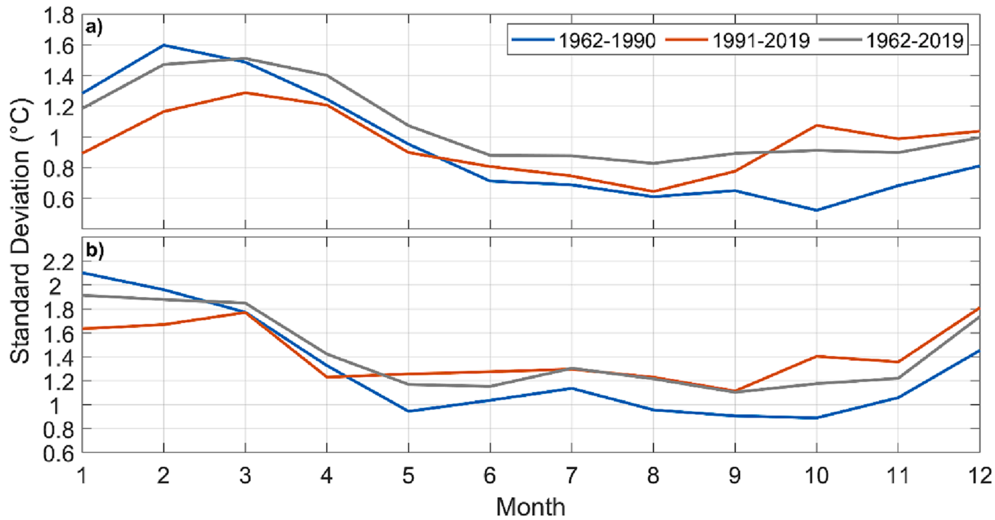

Fig. 17. The seasonal variation of the standard deviation of the SSTs at a) Helgoland Roads and b) Sylt Roads for the entire time series (grey) and for the first (blue) and second half (orange).

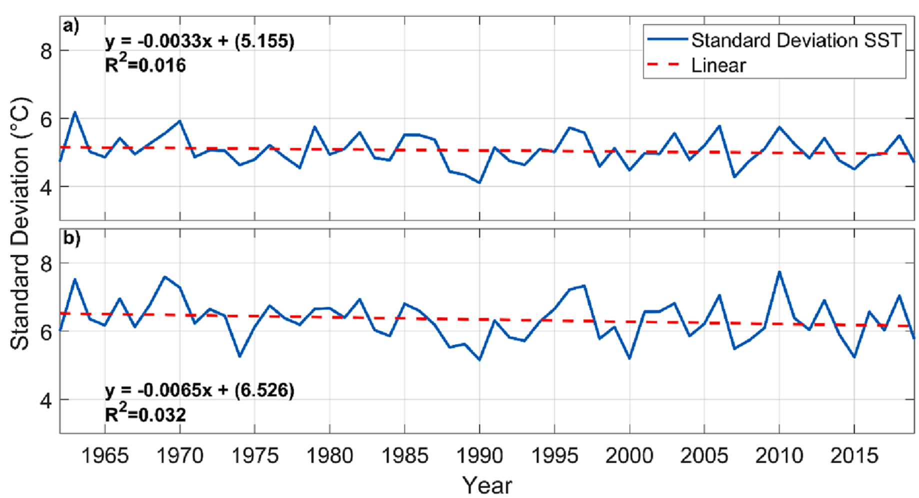

Fig. 18. The seasonal standard deviation (solid blue line) with trend (dashed red line) – a measure of the seasonal amplitude – at a) Helgoland Roads and b) Sylt Roads, calculated per year using monthly SST in situ datasets.

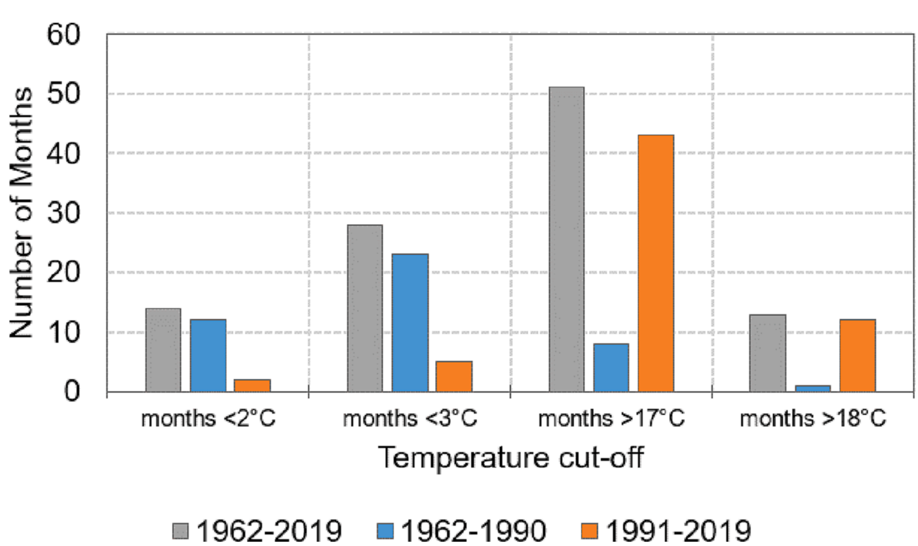

Fig. 19. Number of “cold” and “warm” months for total (grey), early (blue) and late years (orange) of the Helgoland Roads data set.

Table 8
Percentages of the mean number of cold and warm months relative to the total number of months of the late and early time periods at Helgoland Roads (HR).

HR %	1962–2019	1962–1990	1991–2019
months < 2 °C	2.0	3.4	0.6
months < 3 °C	4.0	6.6	1.4
months > 17 °C	7.3	2.3	12.4
months > 18 °C	1.9	0.3	3.4

4. Discussion

In this study, we have critically considered long-term temperature data sets on increasing spatial scales: from local, regional, continental, oceanic to hemispheric, in order to investigate the different trends, frequencies, variability and correlations when moving from small to large temporal and spatial scales. We report on analyses carried out relating the sea surface temperature (SST) data from the Helgoland Roads Time Series, one of the most important and detailed long-term in situ marine ecological time series, to the Sylt Roads, North Sea, Germany, Europe, North Atlantic and Northern Hemisphere surface temperatures. The following discussion of these findings is directed to the needs of biologists using long-term data of marine temperature in conjunction with considerations on effects of temperature shifts, events, and variabilities on ecosystems, biodiversity, species adaptation, etc., over many different temporal and spatial scales.

In studies on the effects of changing temperature in temperate marine environments such as the North Sea, one must consider shifts in a) long-term trends over decades, abrupt regime shift-like and relationships with greater global ocean drivers (e.g., AMO; NAO; b) seasonality; c) shifts in max/min temperatures and frequencies, and d) changes in variability of temperature, which need to be primarily considered in terms of changed biology and ecosystems. Above, we analysed the overall temperature trends, anomalies, seasonal shifts, variabilities and frequency distributions, frequency of occurrence of extremely hot and cold temperatures and the relationship of the temperature measurements with the climate index NAO. For completeness, we also considered the AMO index in the context of the time series.

The impacts of warmer ocean waters on marine organisms are one of the biggest scientific topics of our time and have been subject of many studies over the past two decades (Fellous et al., 2022; Gittings et al., 2018; Jorda et al., 2020; Lima and Wethey, 2012; Wiltshire and Manly, 2004). The need for scenario development and management strategies is pivotal to Earth System sustainability. For this, dense long-term data and an excellent understanding of this data are required, otherwise, modelling of systems and scenarios is impeded. However, most studies on how global warming manifests with regard to marine organisms are laboratory or, more rarely, in situ habitat observations during/after weather extremes. When it comes to direct in situ causal linkage of temperature shifts in the ocean and long-term shifts in ecosystems, this has proven difficult simply because the relevant long-term measurements are not available on the appropriate temporal and spatial scales, and those available are not temporally and spatially dense enough. Data sets based on LTER at one site can be considered to be under-representative of a region and the only data sets which are spatially available are often interpolative both in terms of space and time. Remote sensing data, with around 40 years of surface temperature measurements, is an efficient option to represent temporal and spatial changes, but it is still constrained by biases in sensors and retrieval algorithms, in addition to the lack of agreement between the products of different satellite missions (Yang et al., 2013). Reanalysis products give robust information combining different observations from multiple sources, including remote sensing, and they are spatially complete, physically consistent and bias adjusted (Dee et al., 2014).

In this study, we place our findings, which are summarised in Table 11, in the marine ecological context and deliberate these in terms of time and space, as scale plays a fundamental role when linking drivers to ecosystem function, species distributions and biodiversity (Margalef, 1958). When considering habitat and population resilience in the context of drivers of change, such as temperature and particularly when based on observations, understanding scale in terms of time and space is paramount. Without this, the evaluation of temperature to ecosystem relationships, predictability and for example models of climate with biological relationships are tenuous (Addicott et al., 1987; Levin, 1992; Mackas et al., 1985; Peterson and Parker, 1998; Steele, 2004). With changes in scale, statistical relationships and correlations can change. Variability, at lower scales, can show a lot of noise and at high spatial scales a lack of detail.

Observations, which are made too far apart (in space or time), can result in one missing essential ecosystem detail such as life cycle information or diel vertical migration patterns. Observations, which are too close together (in space or time) might merely, reflect a moment of variability rather than being related to the big picture. Moreover, environmental and ecosystem variables and especially different species with differing adaptations, drivers and niches may not be intercomparable in terms of time and spatial scales. Mackas et al. (1985) showed that in a one-dimensional transect of the North Sea temperature, chlorophyll and zooplankton had very different variabilities and thus,

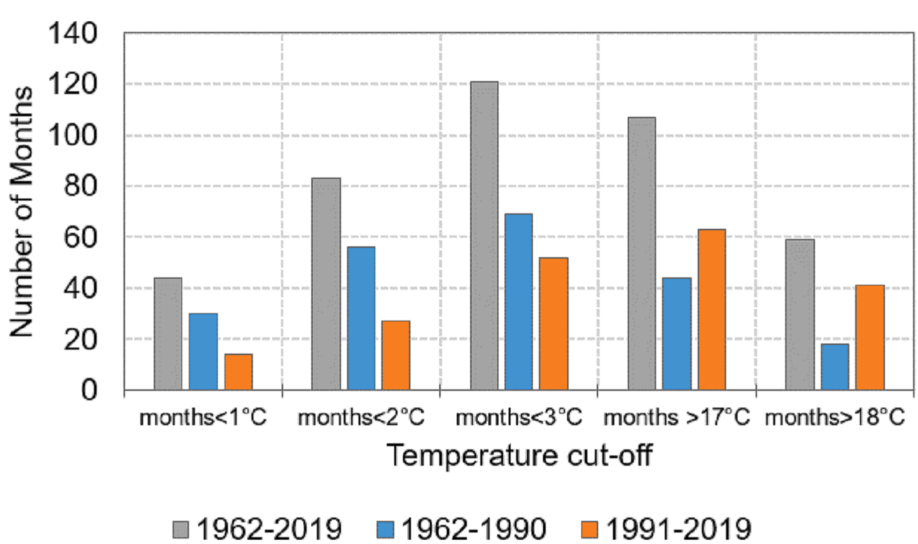

Fig. 20. Number of "cold" and "warm" months for total (grey), early (blue) and late years (orange) of the Sylt Roads data set.

Table 9
Percentages of the mean number of cold and warm months relative to the total number of months of the late and early time periods at Sylt Roads (SR).

SR %	1962–2019	1962–1990	1991–2019
months < 1 °C	6.3	8.6	4.0
months < 2 °C	11.9	16.1	7.8
months < 3 °C	17.4	19.8	14.9
months > 17 °C	15.4	12.6	18.1
months > 18 °C	8.5	5.2	11.8

obviously were controlled by different drivers. The complexity of interrelating different species, which have widely different spatial ranges and different patchiness, is well illustrated by Bertrand et al. (2014). The very basis of organism succession, competition and co-occurrence in pelagic temperate environments is based on different scaling in time and space of organisms. Temperature related match-mismatch phenomena (Cushing, 1990) between predators and their prey however, are founded up on the opposite situation, as the organisms are dependent on the exact timing of their prey. Similarly, diurnal migration of for example zooplankton is also very dependent on timing related to light and stable/ particular triggers on mesoscales.

Obviously, there is no one overarching dimension in space or time, which is applicable to all ecosystem questions related to temperature. For example, if scales in time and space in terms of temperature trends are too large, one loses life cycle details (time) or patterns related to local climatic conditions in one's considerations. If, on the other hand, one merely considers effects of temperature on ecosystems and their components, e.g., using short-term or local observations of temperature for future scenarios, these may simply reflect small-scale variability of the system. To paraphrase Levin (1992) "we trade off the loss of detail or heterogeneity within a group for the gain of predictability".

To summarise, marine pelagic ecosystems and their species are subject to temperature on different scales in time and space, with temperature being one of the main drivers of species diversity and distribution. We have summarized the relationships of the biology of marine systems to temperature on different temporal and spatial scales in Fig. 23, which underpins this discussion.

Depending on the type of reaction and adaptation, and especially if these are required to deal with daily variability (e.g. day-night temperatures) or long-term life cycle shifts and biogeographical changes in habitat, such as movement of organisms to cooler waters, the time scales can range from days to decades. Organisms also react to temperature shifts on time scales of generations, which can be anything upwards from days (e.g. phytoplankton and bacteria) through years and decades (e.g. fish, crustaceans) via epigenetics or evolutionary processes between generations (Cohen, 1967; Marshall and Burgess, 2015; Shama et al., 2016; Slatkin, 1974; Wilson and MacArthur, 1967). The biological distribution of species both in terms of latitude and height/ depth has, since the studies by Humboldt and Bonpland (1805), been accepted to be related to global temperature gradients, and in marine phytoplankton it is not different (Righetti et al., 2019). This is not only the case for terrestrial environments; marine organisms and their habitats are also dependent on the temperature of their environment and its variability. A few excellent studies have shown how life cycles of marine organisms are shifted along biogeographical gradients (e.g., shore crabs and cod) (Giménez, 2011; Perry et al. 2005; Pörtner et al., 2017). The effects of in situ heat shock are well documented for corals and effects of cold winters or sudden cold on exposed marine tidal flats are another example (Büttger et al., 2011; Barceló et al., 2016; Giménez et al., 2021; Hackerott et al., 2021). How marine organisms react and adapt depend very much on their living environment and whether they can move away from stress. Thus, plankton and nekton or sessile benthic organisms will react differently and with different tolerance and long-term resilience (for review on this see Harvey et al. (2021)) dependent on their life cycles. The manner in which marine organisms react to climate shifts and change is diverse. Most papers are interested in fish, however organisms at the bottom of the food web, i.e., plankton, which are at one with the waterbodies, are affected directly and cannot move well/ far in aquatic environments.

4.1. Long-term trends and the role of Indices: Biogeographical shifts over multiple decades and potential regime Shifts.

In this study, all temperature trends were significantly positive, in agreement with the global literature (IPCC, 2018; IPCC, 2019). The trends were larger with decreasing geographical scale (i.e., spatial average) for both surface air temperatures and sea surface temperatures (Fig. 24).

When we examined the surface air temperature, it was clear that the strongest cross-correlations occur between Germany/Europe and Europe/NH, as was to be expected. In congruence with the rise in global atmospheric temperatures, the oceans are warming steadily. And as can be seen from Fig. 24, rise in temperature of the North Sea is considered especially high. It has repeatedly been shown that, based on long-term data (Edwards et al., 2010) and models (Holt et al., 2012; Kjellström et al., 2018; Pierce et al., 2006), the North Sea temperatures have been rising steadily in the last decades.

The SST of the North Sea is strongly correlated with the European

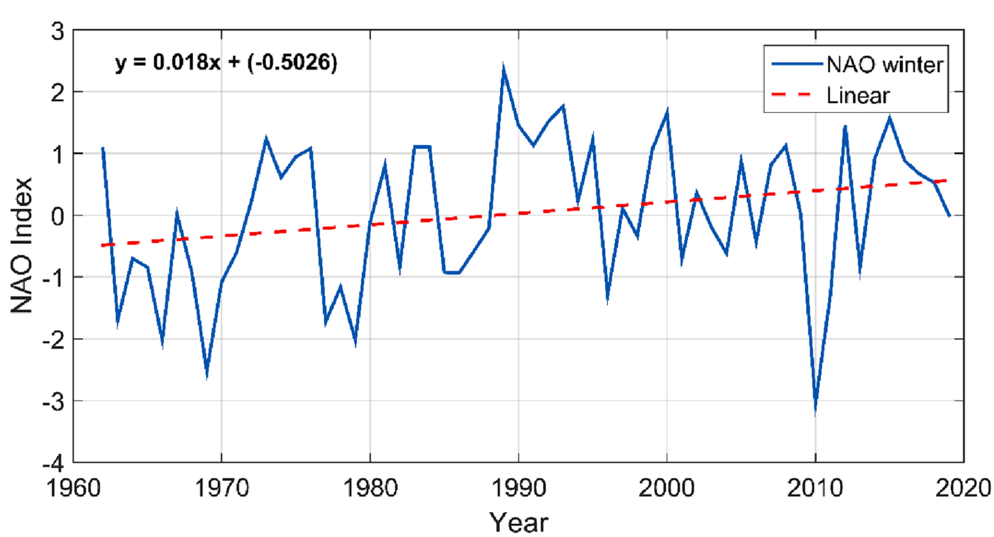

Fig. 21. First PC Winter mean NAO evolution over time (solid blue line) with linear trend (dashed red line).

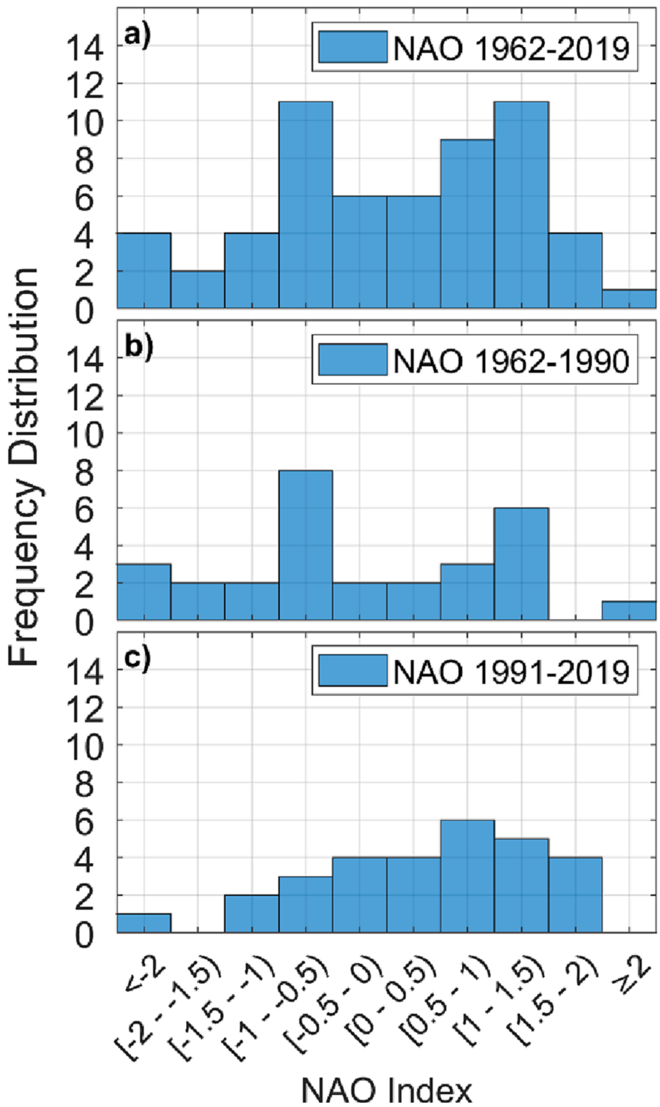

Fig. 22. Frequency of occurrence of winter mean (Dec-Feb) NAO index values for the whole period (1962–2019, top), early (1962–1990, middle) and late (1991–2019, bottom) years.

and the German SAT and, to a lesser extent, with the North Atlantic SST and the Northern Hemisphere SAT. This shows that, like the data for the Dutch Wadden Sea, analysed by van Aaken in 2008, the two LTER sites in the German Bight are more driven by the terrestrial temperature regime than by the Atlantic temperature regime. This can be expected for a shallow sea bounded by land. It also explains why areas in the Southern North Sea are warming faster that the areas in the Northern North Sea (Scottish coast) (see Holliday et al., 2008).

We found that the two stations, Helgoland Roads and Sylt Roads, are strongly correlated with the German SAT and, to a lesser extent, with the European SAT. The stations are highly correlated with each other and also with the SST of the North Sea. This answers affirmatively the question as to whether both sites can be considered representative with regard to temperature of the overall North Sea.

We showed that the NAO index only relates well to the winter temperatures (December-February) in both HR and Wadden Sea SR sites, due to the fact that the Icelandic low pressure system is deeper during winter, showing strong gradient related to the Azores High (Rodwell et al., 1999). Similar results have been found for the western Wadden Sea and Marsdiep area by van Aken (2008), who also pointed out that, since 1982, the NAO does not show any persistent trends. This was also seen here, and previously Wiltshire et al. (2010) showed that the NAO

Table 11
Overall summary of Results.

Trends:	**Summary**
All areas	Trends were significantly positive for all surface temperature anomalies data sets examined.
HR & SR	Of all, HR and SR showed highest warming trend of 0.3 °C/decade.
Correlation all areas	All data sets were significantly correlated with each other.
Correlations HR & SR	HR and SR are most correlated with EU and GE temperature anomalies time series.
AMO	AMO was found to be unsuited for comparisons and was replaced by NA SST.
HR & SR (early vs late years)	Trends have increased significantly in late years.
Seasonal Analyses:	**Summary**
HR & SR	Strong seasonal cycle, increased mean in late years (warmer temperatures earlier in time).
Frequency distributions	Bimodal frequency distribution of temperature (cold and warm modes) becoming more heterogeneous, with the cold mode peak moving to higher values and becoming steeper.
Comparison all areas	Summer trends are similar, winter trends much larger for HR & SR (lower thermal inertia compared to deeper and larger areas).
Winter vs Summer	Winter peaks larger than summer for both HR & SR = slightly longer winter season.
HR	HR seasonal cycle reflects open water situation with modulated winter and summer temperatures.
SR	SR seasonal cycle reflects shallow water situation, higher variance between winter and summer.
Variability	Variability of winter minima displays greater variability than the summer maxima.
HR & SR (early vs late years)	Late years: winter variability became smaller and autumn variability became larger. For both sites, the seasonal standard deviation (i.e. the seasonal amplitude) decreased with time.
Anomalies:	**Summary**
All areas	SST anomalies had a strong positive trend after the 1980s. Clear separation of early and late years. Late years warmer.
Comparison Yellow Sea (YS)	Clear separation of early and late years. Late years warmer.
NAO all areas except NA	Winter NAO highly correlated with winter anomalies.
Temperature Extremes:	**Summary**
HR & SR warmest months	Highly significant shift towards more warm months with mean values over 17 °C.
HR & SR coldest months	Very cold months (means < 2 °C and < 3 °C) decreased frequency.

Table 10
Detrended winter mean SST anomalies and winter mean NAO correlation (Pearson) for the different regions and HR and SR stations, showing all (1962–2019), early (1962–1990) and late (1991–2019) years. Winter mean considers December, January and February months. NA - North Atlantic (40°-60° belt); NS - North Sea; HR - Helgoland Roads and SR - Sylt Roads. Except for NA, all correlations are significant (p<0.05).

Period	1962–2019				1962 – 1990				1991 – 2019			
	NA	NS	HR	SR	NA	NS	HR	SR	NA	NS	HR	SR
Winter mean	−0.10	0.41	0.54	0.73	−0.13	0.49	0.57	0.78	0.05	0.43	0.54	0.69

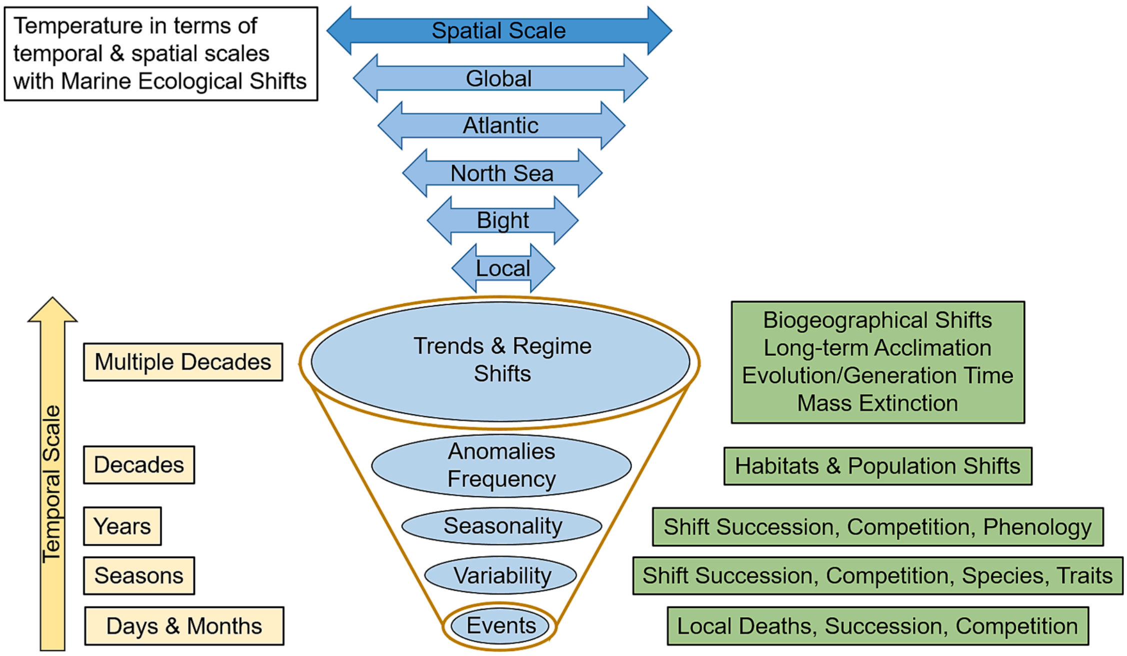

Fig. 23. Temporal and spatial scales of temperature in relation to marine biological systems.

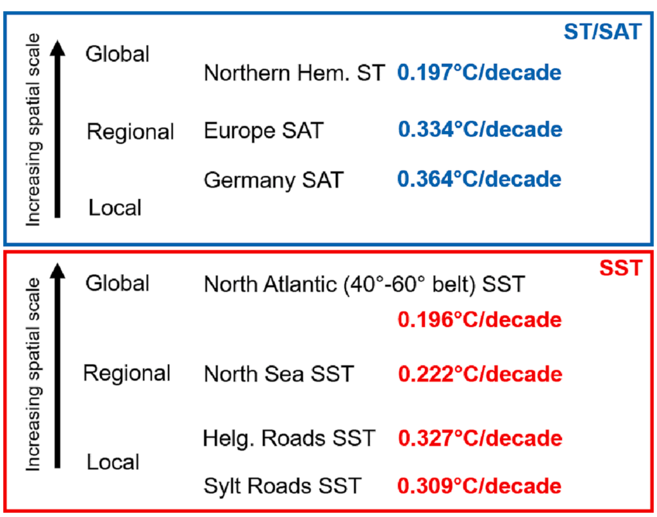

Fig. 24. Results of trends and the direction of increase concerning the different spatial scales for Surface Temperature/Surface Air Temperature anomalies (blue rectangle) and Sea Surface Temperature anomalies (red rectangle).

index was also only useful in the winter months for explaining variability at Helgoland Roads. In addition, we speculate that the Atlantic Multidecadal Oscillation (AMO), used to explain biological phenomena in the North Sea and Atlantic (Alheit et al., 2014; Edwards et al., 2013), would not be causal regarding biological shifts in the North Sea at regional and local scales. The AMO, with its broad spatial distribution (0°-60°N, 80°W-0°), was minimally useful for explaining any anomalies or variability in all of our temperature data. Therefore, the driver of biological shifts would rather be the shifts in water masses. The North Atlantic (40°N-60°N) data was more representative for comparisons with the North Sea and HR and SR time series. The AMO was considered to be an oscillatory index in the past, however its validity is currently being questioned, based on recent literature by the original authors (Mann et al., 2021).

We have avoided discussion of so-called regime shifts in ecosystem drivers (temperature) here, because of the temporal tenuousness of such identifications in time series of merely a few decades. However, other authors have identified temporal shifts in the 1960s, 1980s and during the period 1996 to 2003 in the North Sea (Beaugrand et al., 2008, 2014; Edwards et al., 2002; Siegismund and Schrum, 2001). Beaugrand et al. (2014) suggests that these three shifts impacted 40% of the plankton species or taxa considered in a study of data of the CPR in the North Sea.

We highlight that in all of the temperature time series analysed for the Northern Hemisphere, a distinct upwards shift in temperature trend can be seen in the late 1980s. One explanation for this could be found in a decrease in cold spells and an increase in heat waves due to blocking systems (Brunner et al., 2018).

Our comparisons of the temperature trends from local through to hemispheric scales, showed comparable trends/ patterns over large spatial scales. We showed overall warming, which is highest in the southern North Sea at HR. These trends will result in new biogeographical gradients and redistribution of species, with cold adapted species moving further north, as is currently being seen with for example cod (Drinkwater, 2005). This is where it becomes important to link up with such spatial data sets as the CPR provides, where indeed, strong evidence of species shifts on large spatial scales have been found (Beaugrand, 2004; Heath, 2005; Weijerman et al., 2005). However, data is exceedingly rare on species diversity overall, and daily LTER data are non-existent. Therefore, we can only make the links through statistical comparison of the drivers and shifts on different spatial scales and then add the knowledge we have on organisms also via models.

4.2. Shifts in Seasonality: Local to regional shifts of Succession, competition and phenology

Overall, the daily variability has declined at HR and SR. Wiltshire et al. (2010) showed that the number of growth days (defined as days with temperatures over 5 °C) have increased significantly at HR. This was also found in the present study for both HR and SR. When subtracting the annual minimum from the annual maximum, we found a negative trend, indicating that the difference between cold and warm days of the year has become smaller, meaning that the strong seasonality of our regions has weakened. The positive temperature trend in the cold season (winter and spring) was also larger than the positive trend in the warm season (summer and autumn), i.e., again evidence that the seasonal cycle has become smaller with time. Because the overall trend is a warming trend, with extension of warmth into the cooler months, the growing period has become longer. This affects the timing and succession of particularly microalgae (phytoplankton) and their predators (zooplankton). Investigations of seasonal shifts in temperature, in units of days, weeks, months and seasons are required to understand how temperature drives marine ecosystems. Growth rates, number of growth days, phenology, ennichement of new species may then be related to long-term changes (Beaugrand et al., 2014; Chivers et al., 2020; Scharfe and Wiltshire, 2019; Wiltshire et al., 2010). The complex nature of the wind, tide and current interactions at Helgoland and Sylt result in large daily variability of water conditions, both at HR and SR. We had no means of comparing marine daily data with other regions, because unfortunately this is currently unavailable. It would be interesting to compare our results with data from the Dutch Wadden Sea (van Aken, 2008) and with the compilation of data for the Baltic Sea (Mackenzie and Schiedek, 2007) where it seems that variability in the systems may have shifted considerably in the past 50 years. It is often precisely this variability which results in growth triggers and controls (e.g. turbulence, resuspension of sediments and nutrient recycling) and which are associated with seasonal shifts (Philippart et al., 2003; Scharfe and Wiltshire, 2019; Wiltshire and Manly, 2004).

Wiltshire et al. (2015) have shown how the timing of the spring bloom of phytoplankton at HR has shifted based on daily values and that this could be related to the continued overwintering grazing of herbivorous zooplankton. Based on these works, Sommer and Lengfellner (2008) carried out experiments in mesocosms with a modelling backdrop, to demonstrate how temperature regulated the interaction of microzooplankton, zooplankton and phytoplankton growth. Scharfe and Wiltshire (2019), in an analysis of key phytoplankton species, showed that the timing, in days, of late winter/early spring (e.g. *Skeletonema spec.*), spring (e.g. *Ditylum brightwellii*) and early summer species (e.g. *Rhizosolenia setigera*) have shifted forward in the last 50 years, also often evincing longer periods of occurrence. However, the timing of others, for example *Odontella sinensis* and *Thalassionema nitzschioides*, late summer/ autumn species respectively, shifted towards central winter reflecting longer warm periods in autumn, as shown in the temperature analyses of this paper. The work by Scharfe and Wiltshire (2019) and some work by the CPR groups of SAHFOS (Hinder et al., 2012) have shown that the reaction of species is specific to their ennichement time. Based mostly on weekly data, Beaugrand et al. (2014), Greve et al. (2004) and Heath (2005) provide evidence that the phenology and succession of species of zooplankton (copepods) have shifted at HR and in the greater North Sea. As the timing of zooplankton and its life cycle stages are very dependent on the available phytoplankton food, shifts in phytoplankton timing and species composition can be detrimental to food web function, as proposed in the match-mismatch hypothesis by Cushing (1990). As with the timing of land plants and the occurrence of pollinating insects or pests (Solga et al., 2014) such timing relationships are often just as narrow in marine systems; in the order of days or maximally weeks.

Whether or not shifts in phenology based on days and weeks are spatially ubiquitous/transferable to wider areas across the northern latitudes depends on the species ranges and the adaptability of organisms. Plants driven by photosynthesis adapt differently to animals. The link to greater spatial areas is given when, as shown in this study, trends/ shifts observed in detailed long-term data can be related to the same trends/ shifts at other spatial scales.

4.3. Maximum and minimum Temperatures- hot and cold Spells: Physical and behavioural adaptation; competition with neobiota; local species extinction

We found that there was a significant shift towards much more presence of very warm months with values over 17 °C and 18 °C at HR and SR since 1991, while the very cold months (mean values below < 2 °C and < 3 °C) have become significantly less common. An associated study (Gimenez et al., 2022), based on HR, showed that the frequency of marine heatwaves has increased, especially after the 1990 and that the major heatwaves coincide with large atmospheric European summer heatwaves or mild winter spells. Hence, different forms of data analyses highlight the increasing prevalence of warm periods for the German Bight.

Maximum and minimum temperatures and the number of days with specific temperatures are very important to the adaptation, (both on the short term and longer term over generations) and survival of species in marine systems. Heat waves and their consideration are currently very important in the literature (Ainsworth et al., 2020; Frölicher and Laufkötter, 2018). Marine heatwaves in particular have led to a number of changes in marine ecosystems, ranging from mass mortality of foundations species to changes in the food web (Arias-Ortiz et al. 2018, Hayashida et al. 2020). The latitudinal or climatic temperature regime which organisms are acclimatised to will also make a big difference in how they react to heat (Boersma et al., 2016). Minimum temperatures can regulate the difference between survival and non-survival of indigenous vs. neobiota (Lenz et al., 2011). When it gets too warm, the thermal tolerance will indicate species vulnerability to climate warming (Madeira et al., 2012). The majority of species found in the German Bight, whether they are plankton, fish, crustaceans or mammals have very large ranges of occurrence and for example, many phytoplankton have been around for millennia (see fossil records, Dale, 2001).

Based on this data for the increased number of months/days with maximum temperatures plus the evinced trends for HR, SR, the North Sea and North Atlantic it is clear that "warm waters are the new normal". Species, no matter when they occur, will have to cope with warmer waters and many more days with much warmer maximum and minimum temperatures. Brunner et al. (2018) have examined the cold spells and especially the increase in warm spells in Europe and related these to blocking systems. They found that over 80% of cold spells in south-eastern Europe occur during blocking and that warm spells are correlated with blocking mostly in northern Europe. They suggest that, in future, cold snaps are likely to become even more important in these new warmer normal, as they seem to be associated to each other.

However, marine organisms are not merely enniched between maximum and minimum temperatures or the number of days making a heat wave or cold snap. The frequency with which organisms are confronted by a specific temperature will be central to its acclimatisation and range of occurrence (Boersma et al., 2016). Thus, it is incorrect to assume that species adjustment to temperature has mostly to do with maximum and minimum temperatures of the system where the organism is enniched. It is also not realistic to simply project a line between min and max temperatures and use this for experimental evaluations of temperature acclimation. Unfortunately, due to the lack of frequency distribution analyses many studies, which have been carried out on how organisms react to temperature change, both on the short and long-term, may be based on false assumptions on distributions of temperature in nature (Boyd et al., 2013; Pörtner, 2002; Thomas et al., 2012). Instead, we should consider experiments that manipulate realistic temperature scales and levels of intensity, defined accordingly to empirical temperature distributions.

Interestingly, the frequency distributions of temperature over the years have changed substantially in the later years. At Helgoland and Sylt, the homogeneous bimodal shape, besides the shift of the two distinct lobes peaks to higher temperature values, has flattened in the warm mode and got steeper in the cold mode. This indicates that more values occur around the cold mode and less so around the warm mode. Especially, autumn and winter months have become warmer and the number of very hot days/ months has increased significantly.

Plots of the frequency distributions of the temperature anomalies for the North Atlantic, North Sea and HR and SR (Fig. 12) showed that the anomalous temperature density distribution clearly shifted to higher temperatures in the later years in all spatial areas. Interestingly, especially in the North Atlantic, the maximum and minimum values of the anomalies have moved significantly further apart, indicating that the variability of the anomalies has become higher. The shape of the distribution of the temperature anomalies has also flattened considerably for the North Atlantic data, much more so than the other regions. This may reflect the very large spatial area considered in the North Atlantic and the wide range of temperatures, which have different shifts and because of the high spatial variability of temperature evinced across the different latitudes.

4.4. Variability on the Long-Term: Physical and behavioural adaptation; local species Extinction, shifts in growing season and biogeographical species distribution

The variability during the winter and spring months was found to be significantly larger than during summer and autumn at both HR and SR, particularly for the early half of the time series. In the later part of the time series, the large winter variability became smaller and the variability of temperature in the autumn became larger (Fig. 17 and Fig. 25e,f). The same pattern, but slightly smaller in amplitude, was found for the North Sea data (Fig. 25d). The North Atlantic showed a significant increase in temperature variability for all seasons since 1991 (Fig. 25c). In comparison, the Global and Northern Hemisphere datasets show a smaller increase in variability in the later years for all months (Fig. 25a,b).

Aquatic ecosystem variability can be considered a driver of species diversity, thus, it is important to evaluate the magnitude of variability changes in climate change studies (Borics et al., 2013; D'Odorico et al., 2008; Dornelas, 2010; Flöder and Sommer, 1999). Indeed, explanation of species diversity as a function of ecosystem variability is subject of a long-term discussion in the literature (e.g., Collins, 1990; Connell, 1978; Grime, 1973; Robinson and Minshall, 1986). Sarker et al. (2018) describe the 1980s as the period of high ecosystem variability at the Helgoland Roads Time Series station, with a considerably less variable period identified after the 1990s. They also showed that both diversity and species occurrence probability declined with the increase of ecosystem variability. The occurrence of more species was seen at low ecosystem variability without a loss of rare species already in the system. This implies a high level of niche differentiation, reducing interspecies competition and lack of exclusion and this directly increases species diversity. Indeed, increasing species diversity and the co-existence of neo biota and indigenous species has been going on in the North Sea and especially the German Bight for the past 20–30 years (Buschbaum and Gutow, 2005; Greve et al., 2004; Reise et al., 2017; Wiltshire et al., 2010). This reflects the ecosystem theory that the warming of a cold temperate sea will allow for more species. Beaugrand et al. (2008) also showed that the 1980s overall were a period of high variability, whereas the 1990s were identified with a low variability in the North Atlantic region. Conversi et al. (2010) observed similar change in the late 1980s in long-term records of Mediterranean ecological and hydro-climate variables.

Temperature variability induced by shifts in larger weather patterns, including storm patterns such as El Nino and Blocking Systems, can be translated to shifts in hydrography, turbulence, stratification and, in coastal systems, freshwater input from rivers. Such shifts affect e.g., primary productivity, fish distribution, spawning timing and species distribution of planktonic organisms (Dippner, 1997; Mackenzie and Schiedek, 2007; Root et al., 2003; Stenseth et al., 2004). Here, we also considered the indicator indices of large Northern Hemisphere climate patterns, namely the NAO and the (in the meantime questionable) AMO (Mann et al., 2021). These indices are often used in the literature to explain events and as links to organism distribution e.g. fish, bivalves and copepods (Alheit et al., 2014; Dippner, 1997; Philippart et al., 2003; Reid et al., 2003). It is not logical to link the large-scale climate indices such as NAO to marine organisms directly, as these are not drivers in themselves. Rather, it is the effect of the large-scale weather patterns on hydrography and temperature, which can be drivers of the pelagic distribution and species life cycles (van Aken, 2008). For example, it is not the NAO that drives the shift of *Calanus helgolandicus* vs. *Calanus finmarchicus*, but rather the inflow of the Atlantic Ocean into the North Sea, which transports the Atlantic species *C. finmarchicus* more or less into the North Sea. This inflow is related to large-scale weather pattern fluctuations of which the NAO is an indicator (Heath et al., 1999). This can also be seen in the study on timing of spawning of *Limecola (Macoma) baltica*, by Philippart et al. (2003) and van Aken (2008). Phillipart et al. (2003) postulated that this was related to the NAO index, but later it was found by van Aken that it is not likely that the NAO is directly related to spawning and it is certainly as an index, not the trigger. They consider the long-term trend in temperature to be the reason for earlier triggering and not zonal winter winds reflected by the NAO pressure index.

Boersma et al (2016) have shown that it is also very important to understand the frequency distributions of temperature which organisms

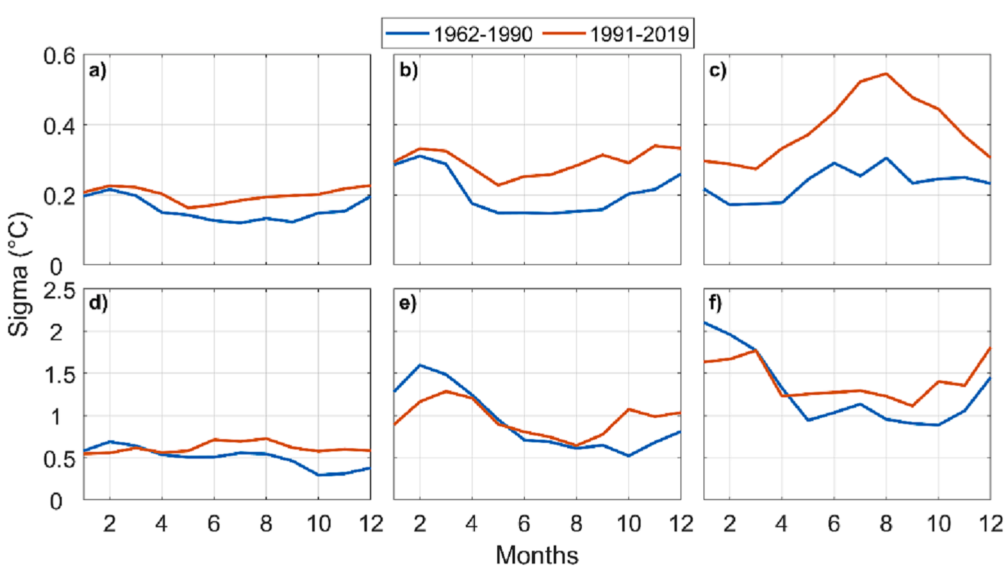

Fig. 25. The seasonal variation of the standard deviation of the SST in all spatial scales (from Global to local) for the first (blue) and second half (orange) of the time series. a) Global; b) Northern Hemisphere; c) North Atlantic 40°-60°; d) North Sea; e) Helgoland and f) Sylt. The y-axis scales are different for top and bottom rows, showing the increase in variability from larger to smaller spatial scales.

are subjected to rather than max/ min curves only. As the frequency distributions for temperature data and their anomalies have shifted considerably over the past 20 years on all the special scales we examined, we can assume that especially animals, which have tight temperature adaptations, will have to move or acclimate in all examined areas.

Animals will react differently to temperature changes than plants. Plants, including marine phytoplankton and macroalgae, moving further north or indeed into cooler deeper waters will also have to adjust their photosynthesis apparatus to deal with different light regimes (Falkowski, 1984; Jorda et al., 2020). The highly significant shifts in seasonality and the associated very much warmer winters and autumns are much more visible at the Wadden Sea (SR) and German Bight (HR) sites than in the North Atlantic, due to the higher heat capacity larger and deeper water bodies, like the latter, present. Even in the North Sea, this is not so pronounced. Such local to regional effects can result in shifts in the phenology, spawning time and/or life cycles of bivalves and other species, and result in match-mismatch food web situations (Edwards and Richardson, 2004).

We have taken one of the densest data series in the world, the Helgoland Roads time series, and we described the statistical and comparative analysis on different scales, from local to hemispheric context, in order to make its data sensibly and accurately available, especially to biologists. With this, we also have demonstrated the usefulness of point-source temperature time series in the North Sea and showed their representativeness to overall temperature time series.

5. Conclusion

Marine ecosystem function is governed by the scale-dependent nature of physical processes. These are also reflected in both coupling and differences among processes occurring in the ocean, the coastal zone and land, requiring reliable temperature data and assessments of this data. Here, we provided a study on how temperature behaves on different spatial scales, the magnitude of changes in trends and variability and the representability of local scales in larger scales and vice-versa. From global to local, all temperature trends are positive, corroborated by the significant positive correlations among the analysed areas and sites. For the local and regional scales, the highest correlations observed between the sea sites and the closest land mass is an important result. This allows us to understand the variability mechanisms of temperature change in the North Sea. The large-scale phenomena such as AMO and NAO which are often considered important do not necessarily have a significant influence on regional and local scales. Evaluations and the observed changes in variability, seasonal as well as inter-annual, cannot be ignored in temperature considerations, as they are part of the significant changes occurring in temperature affecting ecological systems. We provide this information as a basis for marine biological and ecological research, and especially for considerations of responses in organisms and environments to temperature shifts and changes on diverse scales. We thus provided the necessary information to increase the robustness of predictability and assessments of future climate risk to biological systems.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

HadCrut4 and HadSST3 reanalysis data are available online in the Met Office Hadley Centre website. Helgoland Roads and Sylt Roads data are available in PANGAEA Data Publisher and upon request.

Acknowledgements

We acknowledge the immense effort of the Aade and Mya II crews to collect the Helgoland and Sylt Roads data and the Landesbetrieb für Küstenschutz, Nationalpark und Meeresschutz Schleswig-Holstein for the complementary Sylt SST data. We thank the Met Office Hadley Centre, the European Environment Agency, the German Weather Service (Deutscher Wetterdienst) and NOAA National Center for Atmospheric Research (NCAR) for making available the datasets used here. We acknowledge support by the Open Access Publication Funds of Alfred-Wegener-Institut Helmholtz-Zentrum für Polar- und Meeresforschung. We thank the Editor and reviewers for their careful evaluation of our manuscript, the positive feedback, and their comments that helped to further improve the manuscript.

Appendix A. Supplementary material

Supplementary data to this article can be found online at https://doi.org/10.1016/j.pocean.2023.103080.

References

Addicott, J.F., Aho, J.M., Antolin, M.F., Padilla, D.K., Richardson, J.S., Soluk, D.A., 1987. Ecological neighborhoods: scaling environmental patterns. Oikos 49 (3), 340–346. https://doi.org/10.2307/3565770.

Ainsworth, T.D., Hurd, C.L., Gates, R.D., Boyd, P.W., 2020. How do we overcome abrupt degradation of marine ecosystems and meet the challenge of heat waves and climate extremes? Glob. Chang. Biol. 26 (2), 343–354. https://doi.org/10.1111/gcb.14901.

Alheit, J., Licandro, P., Coombs, S., Garcia, A., Giráldez, A., Santamaría, M.T.G., Slotte, A., Tsikliras, A.C., 2014. Reprint of "Atlantic Multidecadal Oscillation (AMO) modulates dynamics of small pelagic fishes and ecosystem regime shifts in the eastern North and Central Atlantic". J. Mar. Syst. 133, 88–102. https://doi.org/10.1016/J.JMARSYS.2014.02.005.

AMO Index Data provided by the Climate Analysis Section, NCAR, Boulder, USA, Trenberth and Shea, 2006. Updated yearly. Accessed 05 June 2021, https://Climatedataguide.Ucar.Edu/Climate-Data/Atlantic-Multi-Decadal-Oscillation-Amo.

Androsov, A., Fofonova, V., Kuznetsov, I., Danilov, S., Rakowsky, N., Harig, S., Brix, H., Wiltshire, K.H., 2019. FESOM-C vol 2: coastal dynamics on hybrid unstructured meshes. Geosci. Model Dev. 12 (3), 1009–1028. https://doi.org/10.5194/gmd-12-1009-2019.

Arias-Ortiz, A., Serrano, O., Masqué, P., et al., 2018. A marine heatwave drives massive losses from the world's largest seagrass carbon stocks. Nat. Clim. Chang. 8, 338–344. https://doi.org/10.1038/s41558-018-0096-y.

Baracchini, T., Chu, P.Y., Šukys, J., Lieberherr, G., Wunderle, S., Wüest, A., Bouffard, D., 2020. Data assimilation of in situ and satellite remote sensing data to 3D hydrodynamic lake models: a case study using Delft3D-FLOW v4.03 and OpenDA v2.4. Geosci. Model Dev. 13 (3), 1267–1284. https://doi.org/10.5194/gmd-13-1267-2020.

Barceló, C., Ciannelli, L., Olsen, E.M., Johannessen, T., Knutsen, H., 2016. Eight decades of sampling reveal a contemporary novel fish assemblage in coastal nursery habitats. Glob. Chang. Biol. 22 (3), 1155–1167. https://doi.org/10.1111/gcb.13047.

Barnard, P.L., Dugan, J.E., Page, H.M., Wood, N.J., Hart, J.A.F., Cayan, D.R., Erikson, L. H., Hubbard, D.M., Myers, M.R., Melack, J.M., Iacobellis, S.F., 2021. Multiple climate change-driven tipping points for coastal systems. Sci. Rep. 11 (1) https://doi.org/10.1038/s41598-021-94942-7.

Beaugrand, G., 2004. The North Sea regime shift: evidence, causes, mechanisms and consequences. Prog. Oceanogr. 60 (2–4), 245–262.

Beaugrand, G., Edwards, M., Brander, K., Luczak, C., Ibanez, F., 2008. Causes and projections of abrupt climate-driven ecosystem shifts in the North Atlantic. Ecol. Lett. 11 (11), 1157–1168. https://doi.org/10.1111/j.1461-0248.2008.01218.x.

Beaugrand, G., Harlay, X., Edwards, M., 2014. Detecting plankton shifts in the North Sea: a new abrupt ecosystem shift between 1996 and 2003. Mar. Ecol. Prog. Ser. 502, 85–104. https://www.int-res.com/abstracts/meps/v502/p85-104/.

Becker, G., 1996. Sea surface temperature changes in the North Sea and their causes. ICES J. Mar. Sci. 53 (6), 887–898. https://doi.org/10.1006/jmsc.1996.0111.

Bertrand, A., Grados, D., Colas, F., Bertrand, S., Capet, X., Chaigneau, A., Vargas, G., Mousseigne, A., Fablet, R., 2014. Broad impacts of fine-scale dynamics on seascape structure from zooplankton to seabirds. Nat. Commun. 5 (1), 5239. https://doi.org/10.1038/ncomms6239.

Billé, R., Chabason, L., Drankier, P., Molenaar, E. J., & Rochette, J. (n.d.). *Making Regional Seas Programmes, Regional Fishery Bodies and Large Marine Ecosystem Mechanisms Work Better Together*. Retrieved February 9, 2022, from www.unep.org/regionalseas.

Boersma, M., Grüner, N., Tasso Signorelli, N., Montoro González, P.E., Peck, M.A., Wiltshire, K.H., 2016. Projecting effects of climate change on marine systems: is the mean all that matters? Proc. R. Soc. B Biol. Sci. 283 (1823), 20152274.

Borics, G., Várbíró, G., Padisák, J., 2013. Disturbance and stress: different meanings in ecological dynamics? Hydrobiologia 711 (1), 1–7. https://doi.org/10.1007/s10750-013-1478-9.

Boyd, P.W., Rynearson, T.A., Armstrong, E.A., Fu, F., Hayashi, K., Hu, Z., Hutchins, D.A., Kudela, R.M., Litchman, E., Mulholland, M.R., 2013. Marine phytoplankton temperature versus growth responses from polar to tropical waters–outcome of a scientific community-wide study. PLoS One 8 (5), e63091.
Brunner, L., Schaller, N., Anstey, J., Sillmann, J., Steiner, A.K., 2018. Dependence of present and future european temperature extremes on the location of atmospheric blocking. Geophys. Res. Lett. 45 (12), 6311–6320. https://doi.org/10.1029/2018GL077837.
Buschbaum, C., Gutow, L., 2005. Mass occurrence of an introduced crustacean (Caprella cf. mutica) in the south-eastern North Sea. Helgol. Mar. Res. 59 (3), 252–253.
Büttger, H., Nehls, G., Witte, S., 2011. High mortality of Pacific oysters in a cold winter in the North-Frisian Wadden Sea. Helgol. Mar. Res. 65, 525–532. https://doi.org/10.1007/s10152-011-0272-1.
Chivers, W.J., Edwards, M., Hays, G.C., 2020. Phenological shuffling of major marine phytoplankton groups over the last six decades. Divers. Distrib. 26 (5), 536–548. https://doi.org/10.1111/ddi.13028.
Cohen, D., 1967. Optimizing reproduction in a randomly varying environment when a correlation may exist between the conditions at the time a choice has to be made and the subsequent outcome. J. Theor. Biol. 16 (1), 1–14. https://doi.org/10.1016/0022-5193(67)90050-1.
Collins, S.L., 1990. Effects of fire on community structure in tallgrass and mixed-grass prairie. Fire in North Am. Tallgrass Prairies 81–98.
Connell, J.H., 1978. Diversity in tropical rain forests and coral reefs: high diversity of trees and corals is maintained only in a nonequilibrium state. Science 199 (4335), 1302–1310.
Conversi, A., Fonda Umani, S., Peluso, T., Molinero, J.C., Santojanni, A., Edwards, M., 2010. The Mediterranean Sea regime shift at the end of the 1980s, and intriguing parallelisms with other European basins. PLoS One 5 (5), e10633.
Cushing, D.H., 1990. Plankton production and year-class strength in fish populations: an update of the match/mismatch hypothesis. In: Blaxter, J.H.S., Southward, A.J. (Eds.), Advances in Marine Biology, Vol. 26. Academic Press, pp. 249–293. https://doi.org/10.1016/S0065-2881(08)60202-3.
D'Odorico, P., Laio, F., Ridolfi, L., Lerdau, M.T., 2008. Biodiversity enhancement induced by environmental noise. J. Theor. Biol. 255 (3), 332–337. https://doi.org/10.1016/j.jtbi.2008.09.007.
Dale, B., 2001. The sedimentary record of dinoflagellate cysts: looking back into the future of phytoplankton blooms. Sci. Mar. 65 (S2), 257–272.
Dee, D.P., Balmaseda, M., Balsamo, G., Engelen, R., Simmons, A.J., Thépaut, J., 2014. Toward a consistent reanalysis of the climate system. Bulletin oft he Am. Meteorol. Soc. 95, 1235–1248. https://doi.org/10.1175/BAMS-D-13-00043.1.
Dippner, J.W., 1997. Recruitment success of different fish stocks in the North Sea in relation to climate variability. Deutsche Hydrografische Zeitschrift 49 (2), 277–293.
Dornelas, M., 2010. Disturbance and change in biodiversity. Philos. Trans. R. Soc., B 365 (1558), 3719–3727. https://doi.org/10.1098/rstb.2010.0295.
Drinkwater, K.F., 2005. The response of Atlantic cod (Gadus morhua) to future climate change. ICES J. Mar. Sci. 62 (7), 1327–1337.
Edwards, M., Beaugrand, G., Hays, G.C., Koslow, J.A., Richardson, A.J., 2010. Multi-decadal oceanic ecological datasets and their application in marine policy and management. Trends Ecol. Evol. 25 (10), 602–610. https://doi.org/10.1016/J.TREE.2010.07.007.
Edwards, M., Richardson, A.J., 2004. Impact of climate change on marine pelagic phenology and trophic mismatch. Nature 430 (7002), 881–884. https://doi.org/10.1038/nature02808.
Edwards, M., Beaugrand, G., Reid, P.C., Rowden, A.A., Jones, M.B., 2002. Ocean climate anomalies and the ecology of the North Sea. Mar. Ecol. Prog. Ser. 239, 1–10. https://www.int-res.com/abstracts/meps/v239/p1-10/.
Edwards, M., Beaugrand, G., Helaouët, P., Alheit, J., Coombs, S., 2013. Marine ecosystem response to the atlantic multidecadal oscillation. PLoS One 8 (2), e57212.
Falkowski, P.G., 1984. Physiological responses of phytoplankton to natural light regimes. J. Plankton Res. 6 (2), 295–307. https://doi.org/10.1093/plankt/6.2.295.
Fellous, A., Wegner, K.M., John, U., Mark, F.C., Shama, L.N.S., 2022. Windows of opportunity: Ocean warming shapes temperature-sensitive epigenetic reprogramming and gene expression across gametogenesis and embryogenesis in marine stickleback. Glob. Chang. Biol. 28 (1), 54–71. https://doi.org/10.1111/gcb.15942.
Flöder, S., Sommer, U., 1999. Diversity in planktonic communities: an experimental test of the intermediate disturbance hypothesis. Limnol. Oceanogr. 44 (4), 1114–1119. https://doi.org/10.4319/lo.1999.44.4.1114.
GISTEMP Team, 2022. GISS Surface Temperature Analysis (GISTEMP), version 4. NASA Goddard Institute for Space Studies. Dataset accessed 2022-02-09 at https://data.giss.nasa.gov/gistemp/.
Frajka-Williams, E., Beaulieu, C., & Duchez, A. (2017). Emerging negative Atlantic Multidecadal Oscillation index in spite of warm subtropics. *Scientific Reports 2017 7: 1*, *7*(1), 1–8. 10.1038/s41598-017-11046-x.
Frölicher, T.L., Laufkötter, C., 2018. Emerging risks from marine heat waves. In: Nat. Commun., Vol. 9, Issue 1. Nature Publishing Group. https://doi.org/10.1038/s41467-018-03163-6.
Giménez, L., 2011. Exploring mechanisms linking temperature increase and larval phenology: the importance of variance effects. J. Exp. Mar. Biol. Ecol. 400 (1–2), 227–235. https://doi.org/10.1016/j.jembe.2011.02.036.
Gimenez, L., Boersma, M., Wiltshire, K.H., 2022. Marine Heatwaves: The new normal? A multiple baseline approach. ICES Symposium on Decadal Variability of the North Atlantic and its Marine Ecosystems: 2010-2019. Bergen, June 20-22nd, 2022. https://decadal2022.imr.no/.
Giménez, L., Chatterjee, A., Torres, G., 2021. A state-space approach to understand responses of organisms, populations and communities to multiple environmental drivers. Commun. Biol. 4 (1), 1142. https://doi.org/10.1038/s42003-021-02585-1.
Gittings, J.A., Raitsos, D.E., Krokos, G., Hoteit, I., 2018. Impacts of warming on phytoplankton abundance and phenology in a typical tropical marine ecosystem. Sci. Rep. 8 (1) https://doi.org/10.1038/s41598-018-20560-5.
Greve, W., Reiners, F., Nast, J., Hoffmann, S., 2004. Helgoland Roads meso- and macrozooplankton time-series 1974 to 2004: lessons from 30 years of single spot, high frequency sampling at the only off-shore island of the North Sea. Helgol. Mar. Res. 58 (4), 274–288. https://doi.org/10.1007/s10152-004-0191-5.
Grime, J.P., 1973. Competitive exclusion in herbaceous vegetation. Nature 242 (5396), 344–347.
Hackerott, S., Martell, H.A., Eirin-Lopez, J.M., 2021. Coral environmental memory: causes, mechanisms, and consequences for future reefs. Trends Ecol. Evol. 36 (11), 1011–1023. https://doi.org/10.1016/j.tree.2021.06.014.
Harvey, B.P., Marshall, K.E., Harley, C.D.G., Russell, B.D., 2021. Predicting responses to marine heatwaves using functional traits. Trends Ecol. Evol.
Hayashida, H., Matear, R.J., Strutton, P.G., 2020. Background nutrient concentration determines phytoplankton bloom response to marine heatwaves. Glob. Chang. Biol. 26 (9), 4800–4811. https://doi.org/10.1111/gcb.15255.
Heath, M.R., 2005. Changes in the structure and function of the North Sea fish foodweb, 1973–2000, and the impacts of fishing and climate. ICES J. Mar. Sci. 62 (5), 847–868. https://doi.org/10.1016/j.icesjms.2005.01.023.
Heath, M.R., Backhaus, J.O., Richardson, K., McKenzie, E., Slagstad, D., Beare, D., Dunn, J., Fraser, J.G., Gallego, A., Hainbucher, D., Hay, S., Jónasdóttir, S., Madden, H., Mardaljevic, J., Schacht, A., 1999. Climate fluctuations and the spring invasion of the North Sea by Calanus finmarchicus. Fish. Oceanogr. 8 (s1), 163–176. https://doi.org/10.1046/j.1365-2419.1999.00008.x.
Hinder, S.L., Hays, G.C., Edwards, M., Roberts, E.C., Walne, A.W., Gravenor, M.B., 2012. Changes in marine dinoflagellate and diatom abundance under climate change. Nat. Clim. Chang. 2 (4), 271–275. https://doi.org/10.1038/nclimate1388.
Holliday, N. P., Kennedy, J., Kent, E. C., Marsh, R., Hughes, S. L., Sherwin, T., & Berry, D. I. (2007). Sea temperature. *Marine Climate Change Impacts Annual Report Card, 2008*.
Holt, J., Hughes, S., Hopkins, J., Wakelin, S.L., Penny Holliday, N., Dye, S., González-Pola, C., Hjøllo, S.S., Mork, K.A., Nolan, G., Proctor, R., Read, J., Shammon, T., Sherwin, T., Smyth, T., Tattersall, G., Ward, B., Wiltshire, K.H., 2012. Multi-decadal variability and trends in the temperature of the northwest European continental shelf: a model-data synthesis. Prog. Oceanogr. 106, 96–117. https://doi.org/10.1016/j.pocean.2012.08.001.
Humboldt, A. von, & Bonpland, A. (1805). *Analysis of the geography of plants*.
Hurrell, J.W., Kushnir, Y., Visbeck, M., 2001. The North Atlantic Oscillation. Science 291 (5504), 603–605. https://doi.org/10.1126/science.1058761.
IHO, 1953. Limits of Oceans and Seas, 3rd. International Hydrographic Organization, Monte-Carlo.
IPCC, 2018. Global warming of 1.5°C: An IPCC special report on the impacts of global warming of 1.5°C above pre-industrial levels and related global greenhouse gas emission pathways, in the context of strengthening the global response to the threat of climate change, sustainable development, and efforts to eradicate poverty. Intergovernmental Panel on. Retrieved from Clim. Change. https://www.ipcc.ch/sr15/.
Jorda, G., Marbà, N., Bennett, S., Santana-Garcon, J., Agusti, S., Duarte, C.M., 2020. Ocean warming compresses the three-dimensional habitat of marine life. Nat. Ecol. Evol. 4 (1), 109–114. https://doi.org/10.1038/s41559-019-1058-0.
Kennedy, J.J., Rayner, N.A., Smith, R.O., Parker, D.E., Saunby, M., 2011a. Reassessing biases and other uncertainties in sea surface temperature observations measured in situ since 1850: 1. Measurement and sampling uncertainties. J. Geophys. Res. 116 (D14), D14103. https://doi.org/10.1029/2010JD015218.
Kennedy, J.J., Rayner, N.A., Smith, R.O., Parker, D.E., Saunby, M., 2011b. Reassessing biases and other uncertainties in sea surface temperature observations measured in situ since 1850: 2. Biases and homogenization. J. Geophys. Res. 116 (D14), D14104. https://doi.org/10.1029/2010JD015220.
Kjellström, E., Nikulin, G., Strandberg, G., Christensen, O.B., Jacob, D., Keuler, K., Lenderink, G., van Meijgaard, E., Schär, C., Somot, S., 2018. European climate change at global mean temperature increases of 1.5 and 2 C above pre-industrial conditions as simulated by the EURO-CORDEX regional climate models. Earth Syst. Dynamics 9 (2), 459–478.
Lenssen, N.J.L., Schmidt, G.A., Hansen, J.E., Menne, M.J., Persin, A., Ruedy, R., Zyss, D., 2019. Improvements in the GISTEMP Uncertainty Model. J. Geophys. Res. Atmos. 124 (12), 6307–6326. https://doi.org/10.1029/2018JD029522.
IPCC, 2019. Summary for policymakers. In: Pörtner, H.-O., Roberts, D.C., Masson-Delmotte, V., Zhai, P., Tignor, M., Poloczanska, E., Mintenbeck, K., Alegría, A., Nicolai, M., Okem, A., Petzold, J., Rama, B., Weyer, N.M. (Eds.), IPCC special report on the ocean and cryosphere in a changing climate. Intergovernmental Panel on Climate Change. Retrieved from https://www.ipcc.ch/srocc/.
Lenz, M., da Gama, B. A. P., Gerner, N. v, Gobin, J., Gröner, F., Harry, A., Jenkins, S. R., Kraufvelin, P., Mummelthei, C., Sareyka, J., Xavier, E. A., & Wahl, M. 2011. Non-native marine invertebrates are more tolerant towards environmental stress than taxonomically related native species: Results from a globally replicated study. *Environmental Research*, *111*(7), 943–952. 10.1016/j.envres.2011.05.001.
Levin, S.A., 1992. The problem of pattern and scale in ecology: the robert H. MacArthur Award Lecture. *Ecol.* 73 (6), 1943–1967. https://doi.org/10.2307/1941447.
Lima, F.P., Wethey, D.S., 2012. Three decades of high-resolution coastal sea surface temperatures reveal more than warming. Nat. Commun. 3 https://doi.org/10.1038/ncomms1713.

Lohmann, G., Wiltshire, K.H., 2012. Winter atmospheric circulation signature for the timing of the spring bloom of diatoms in the North Sea. Mar. Biol. 159 (11), 2573–2581. https://doi.org/10.1007/S00227-012-1993-7/FIGURES/7.

Mackas, D.L., Denman, K.L., Abbott, M.R., 1985. Plankton patchiness: biology in the physical vernacular. Bull. Mar. Sci. 37 (2), 652–674.

Mackenzie, B.R., Schiedek, D., 2007. Daily ocean monitoring since the 1860s shows record warming of northern European seas. Glob. Chang. Biol. 13 (7), 1335–1347. https://doi.org/10.1111/j.1365-2486.2007.01360.x.

Madeira, D., Narciso, L., Cabral, H.N., Vinagre, C., 2012. Thermal tolerance and potential impacts of climate change on coastal and estuarine organisms. J. Sea Res. 70, 32–41. https://doi.org/10.1016/j.seares.2012.03.002.

Mann, M.E., Steinman, B.A., Brouillette, D.J., Miller, S.K., 2021. Multidecadal climate oscillations during the past millennium driven by volcanic forcing. Science 371 (6533), 1014–1019. https://doi.org/10.1126/science.abc5810.

Margalef, R., 1958. Information theory in biology. General Syst. Yearbook 3, 36–71.

Marshall, D.J., Burgess, S.C., 2015. Deconstructing environmental predictability: seasonality, environmental colour and the biogeography of marine life histories. Ecol. Lett. 18 (2), 174–181.

Morice, C.P., Kennedy, J.J., Rayner, N.A., Jones, P.D., 2012. Quantifying uncertainties in global and regional temperature change using an ensemble of observational estimates: the HadCRUT4 data set. J. Geophys. Res. Atmos. 117 (D8), n/a-n/a. https://doi.org/10.1029/2011JD017187.

NAO Index Data provided by the Climate Analysis Section, NCAR, Boulder, USA, Hurrell, 2002. Updated regularly. Accessed 09 February 2022, https://climatedataguide.ucar.edu/climate-data/hurrell-north-atlantic-oscillation-nao-index-pc-based.

Ostle, C., Paxman, K., Graves, C.A., Arnold, M., Artigas, L.F., Atkinson, A., Aubert, A., Baptie, M., Bear, B., Bedford, J., Best, M., Bresnan, E., Brittain, R., Broughton, D., Budria, A., Cook, K., Devlin, M., Graham, G., Halliday, N., McQuatters-Gollop, A., 2021. The Plankton Lifeform Extraction Tool: a digital tool to increase the discoverability and usability of plankton time-series data. Earth Syst. Sci. Data 13 (12), 5617–5642. https://doi.org/10.5194/essd-13-5617-2021.

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. https://doi.org/10.1126/science.aaa1605.

Peterson, D.L., Parker, V.T., 1998. Dimensions of scale in ecology, resource management, and society. Ecol. Scale: Theory and Applications 499, 503–507.

Philippart, C.J.M., van Aken, H.M., Beukema, J.J., Bos, O.G., Cadée, G.C., Dekker, R., 2003. Climate-related changes in recruitment of the bivalve Macoma balthica. Limnol. Oceanogr. 48 (6), 2171–2185. https://doi.org/10.4319/LO.2003.48.6.2171.

Pierce, D.W., Barnett, T.P., AchutaRao, K.M., Gleckler, P.J., Gregory, J.M., Washington, W.M., 2006. Anthropogenic warming of the oceans: observations and model results. J. Clim. 19 (10), 1873–1900. https://doi.org/10.1175/JCLI3723.1.

Pörtner, H.O., 2002. Climate variations and the physiological basis of temperature dependent biogeography: systemic to molecular hierarchy of thermal tolerance in animals. Comp. Biochem. Physiol. A Mol. Integr. Physiol. 132 (4), 739–761. https://doi.org/10.1016/S1095-6433(02)00045-4.

Pörtner, H.O., Bock, C., Mark, F.C., 2017. Oxygen- and capacity-limited thermal tolerance: bridging ecology and physiology. J. Exp. Biol. 220 (15), 2685–2696. https://doi.org/10.1242/jeb.134585.

Pozo-Vázquez, D., Esteban-Parra, M.J., Rodrigo, F.S., Castro-Díez, Y., 2001. A study of NAO variability and its possible non-linear influences on European surface temperature. Clim. Dyn. 17 (9), 701–715. https://doi.org/10.1007/s003820000137.

Rayner, N. A., Parker, D. E., Horton, E. B., Folland, C. K., Alexander, L. v, Rowell, D. P., Kent, E. C., & Kaplan, A. (2003). Global analyses of sea surface temperature, sea ice, and night marine air temperature since the late nineteenth century. *Journal of Geophysical Research: Atmospheres*, *108*(D14). 10.1029/2002JD002670.

Reid, P.C., Edwards, M., Beaugrand, G., Skogen, M., Stevens, D., 2003. Periodic changes in the zooplankton of the North Sea during the twentieth century linked to oceanic inflow. Fish. Oceanogr. 12 (4–5), 260–269.

Reise, K., Buschbaum, C., Büttger, H., Rick, J., Wegner, K.M., 2017. Invasion trajectory of Pacific oysters in the northern Wadden Sea. Mar. Biol. 164 (4), 68. https://doi.org/10.1007/s00227-017-3104-2.

Rick, J.J., Romanova, T., Wiltshire, K.H., 2017a. Hydrochemistry time series at List Reede, Sylt, Germany, in 2014. PANGAEA. https://doi.org/10.1594/PANGAEA.873549.

Rick, J.J., van Beusekom, J., Romanova, T., Wiltshire, K.H., 2017b. Long-term physical and hydrochemical measurements at Sylt Roads LTER (1973–2013), Wadden Sea, North Sea, links to data sets. PANGAEA. https://doi.org/10.1594/PANGAEA.150032.

Rick, J.J., Romanova, T., Wiltshire, K.H., 2020a. Hydrochemistry time series at List Reede, Sylt, Germany, in 2015 (Version 2). PANGAEA. https://doi.org/10.1594/PANGAEA.918018.

Rick, J.J., Romanova, T., Wiltshire, K.H., 2020b. Hydrochemistry time series at List Reede, Sylt, Germany, in 2016 (Version 2). PANGAEA. https://doi.org/10.1594/PANGAEA.918023.

Rick, J.J., Romanova, T., Wiltshire, K.H., 2020c. Hydrochemistry time series at List Reede, Sylt, Germany, in 2017. PANGAEA. https://doi.org/10.1594/PANGAEA.918024.

Rick, J.J., Romanova, T., Wiltshire, K.H., 2020d. Hydrochemistry time series at List Reede, Sylt, Germany, in 2018. PANGAEA. https://doi.org/10.1594/PANGAEA.918025.

Rick, J.J., Romanova, T., Wiltshire, K.H., 2020e. Hydrochemistry time series at List Reede, Sylt, Germany, in 2019. PANGAEA. https://doi.org/10.1594/PANGAEA.918026.

Righetti, D., Vogt, M., Gruber, N., Psomas, A., Zimmermann, N.E., 2019. Global pattern of phytoplankton diversity driven by temperature and environmental variability. *Science*. Advances 5 (5). https://doi.org/10.1126/sciadv.aau6253.

Robinson, C.T., Minshall, G.W., 1986. Effects of disturbance frequency on stream benthic community structure in relation to canopy cover and season. J. N. Am. Benthol. Soc. 5 (3), 237–248.

Rodwell, M., Rowell, D., Folland, C., 1999. Oceanic forcing of the wintertime North Atlantic Oscillation and European climate. Nature 398, 320–323. https://doi.org/10.1038/18648.

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 (6918), 57–60.

Sarker, S., Lemke, P., Wiltshire, K.H., 2018. Does ecosystem variability explain phytoplankton diversity? Solving an ecological puzzle with long-term data sets. J. Sea Res. 135, 11–17.

Scharfe, M., Wiltshire, K.H., 2019. Modeling of intra-annual abundance distributions: constancy and variation in the phenology of marine phytoplankton species over five decades at Helgoland Roads (North Sea). Ecol. Model. 404, 46–60. https://doi.org/10.1016/J.ECOLMODEL.2019.01.001.

Shama, L.N.S., Mark, F.C., Strobel, A., Lokmer, A., John, U., Mathias Wegner, K., 2016. Transgenerational effects persist down the maternal line in marine sticklebacks: gene expression matches physiology in a warming ocean. Evol. Appl. 9 (9), 1096–1111.

Siegismund, F., Schrum, C., 2001. Decadal changes in the wind forcing over the North Sea. Climate Res. 18 (1–2), 39–45. https://www.int-res.com/abstracts/cr/v18/n1-2/p39-45/.

Slatkin, M., 1974. Hedging one's evolutionary bets. Nature 250 (5469), 704–705.

Solga, M.J., Harmon, J.P., Ganguli, A.C., 2014. Timing is everything: an overview of phenological changes to plants and their pollinators. Nat. Areas J. 34 (2), 227–234.

Sommer, U., Lengfellner, K., 2008. Climate change and the timing, magnitude, and composition of the phytoplankton spring bloom. Glob. Chang. Biol. 14 (6), 1199–1208. https://doi.org/10.1111/j.1365-2486.2008.01571.x.

Steele, J.H., 2004. Regime shifts in the ocean: reconciling observations and theory. Prog. Oceanogr. 60 (2), 135–141. https://doi.org/10.1016/j.pocean.2004.02.004.

Stenseth, N.C., Ottersen, G., Hurrell, J.W., Belgrano, A., 2004. Marine ecosystems and climate variation: the North Atlantic-a comparative perspective. Oxford University Press.

Thomas, R.W., Dorey, S.W., 1967. Protected oceanographic reversing thermometer comparison study. Limnol. Oceanogr. 12 (2), 361–363. https://doi.org/10.4319/lo.1967.12.2.0361.

Thomas, M.K., Kremer, C.T., Klausmeier, C.A., Litchman, E., 2012. A global pattern of thermal adaptation in marine phytoplankton. Science 338 (6110), 1085–1088.

Trenberth, K.E., Shea, D.J., 2006. Atlantic hurricanes and natural variability in 2005. Geophys. Res. Lett. 33 (12), L12704. https://doi.org/10.1029/2006GL026894.

Trigo, R., Osborn, T., Corte-Real, J., 2002. The North Atlantic Oscillation influence on Europe: climate impacts and associated physical mechanisms. Climate Res. 20, 9–17. https://doi.org/10.3354/cr020009.

van Aken, H.M., 2008. Variability of the water temperature in the western Wadden Sea on tidal to centennial time scales. J. Sea Res. 60 (4), 227–234. https://doi.org/10.1016/j.seares.2008.09.001.

Weijerman, M., Lindeboom, H., Zuur, A.F., 2005. Regime shifts in marine ecosystems of the North Sea and Wadden Sea. Mar. Ecol. Prog. Ser. 298, 21–39.

Wilson, E.O., MacArthur, R.H., 1967. The theory of island biogeography Vol. 1, JSTOR.

Wiltshire, K.H., Kraberg, A., Bartsch, I., Boersma, M., Franke, H.D., Freund, J., Gebühr, C., Gerdts, G., Stockmann, K., Wichels, A., 2010. Helgoland roads, north sea: 45 years of change. Estuar. Coasts 33 (2), 295–310. https://doi.org/10.1007/S12237-009-9228-Y/FIGURES/16.

Wiltshire, K.H., Boersma, M., Carstens, K., Kraberg, A.C., Peters, S., Scharfe, M., 2015. Control of phytoplankton in a shelf sea: determination of the main drivers based on the Helgoland Roads Time Series. J. Sea Res. 105, 42–52.

Wiltshire, K.H., Manly, B.F.J., 2004. The warming trend at helgoland roads, north sea: phytoplankton response. Helgol. Mar. Res. 58 (4), 269–273. https://doi.org/10.1007/S10152-004-0196-0.

Yang, J., Gong, P., Fu, R., et al., 2013. The role of satellite remote sensing in climate change studies. Nat. Clim. Chang. 3, 875–883. https://doi.org/10.1038/nclimate1908.