

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

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1 Investigation of Marine Temperature Changes across Temporal and Spatial Gradients:
2 Providing a Fundament for Studies on the Effects of Warming on Marine Ecosystem Function
3 and Biodiversity

4

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25 ABSTRACT

26

27 A current critical issue in climate change studies is how temperature changes and shifts on
28 different spatial and temporal scales can affect organisms in terms of trends, variability and
29 frequency of extremes. In this paper, we analysed marine temperature data on different temporal
30 and spatial scales. We related the sea surface temperature data from the Helgoland Roads Time
31 Series, one of the most important and detailed long-term in situ marine ecological time series,
32 to the Sylt Roads, North Sea, Germany, Europe, North Atlantic and Northern Hemisphere
33 surface temperatures. All time series showed a distinct upwards shift in temperature in the late
34 1980s, early 1990s, with positive trends in overall for the period between 1962 and 2019 ranging
35 from 1 to 2°C over 57 years. We quantified changes in temperature variability by comparing
36 the years before and after 1990, on both long-term and seasonal scales. At Helgoland and Sylt,
37 an increase in the number of warmer days in summer and a decrease in extremely cold days in
38 winter are the new characteristics of the temperature pattern after 1990; higher than expected
39 temperatures now also occur earlier during the year. For these locations, we observed the
40 highest trends overall, i.e. of around 0.3°C/decade. The observed bimodal shape of the
41 probability density functions, characterized by winter and summer modes, had become more
42 heterogeneous, with the cold mode peak moving to higher values and the steepness to the peak
43 increasing, which is a consequence of a decrease in extremely cold days. North Atlantic
44 Oscillation (NAO) and Multidecadal Oscillation (AMO) large-scale phenomena had no
45 significant correlations or, for the NAO, were limited to the winter season at the regional and
46 local scales. The closest landmass (mainland Germany) temperature was highly correlated with
47 the North Sea sites. Taken together, our results suggest that marine pelagic ecosystems and their
48 species are subject to temperature shifts with similar patterns but with variations in magnitude
49 at the different scales. Temperature is one of the main drivers of species diversity and
50 distribution, and this manifests on different spatial and temporal scales depending on population

51 growth, life stages, cycles and habitat. Accordingly, we here present the temperature changes
52 on the appropriate spatio-temporal scales, and thus provide the suitable and useful fundament
53 for studies on the effects of warming on marine ecosystem function and biodiversity.

54 Keywords: Sea Surface Temperature, Helgoland Roads, Sylt Roads, Atlantic, NAO, AMO,
55 Climate Change, Warming

56

57 1 INTRODUCTION

58

59 The future of human kind is closely linked to the sustainability of coastal and shelf seas and
60 their ecosystems. Global Ocean warming is fact and the effects of warming on marine
61 ecosystem services presents a threat to long-term coastal sustainability and population stability.
62 (IPCC, 2018; IPCC, 2019). Concomitantly, the vulnerability of human survival and livelihoods
63 on coastal and marine systems becomes ever clearer as climate-related problems such as sea
64 level rise, ocean acidification, loss of economically important species, invasive species and the
65 "race for space" for energy parks, manifest in shelf seas (Barnard et al., 2021; Billé et al., 2016)
66 The trends from 1962 to 2019 in the whole Global Surface and Global Ocean temperatures is,
67 respectively, given as 0.97 and 0.71 °C/57 years (Data.GISS: GISS Surface Temperature
68 Analysis (GISTEMP V4), 2020). These values are based on the compilation of direct
69 measurements at land and sea surface e.g. from simple thermometers, Argo data, ship data and
70 meteorological stations (Lenssen et al., 2019). However, while large-scale projections and
71 especially mean trends values are helpful, especially in the political sense, these alone are not
72 particularly useful when considering direct human and organism responses, food web change
73 and ecosystem disruption issues. More humans will live at, or close to, coasts and shelf seas
74 and, as these populations are dependent on marine ecosystem integrity and ecosystem services,
75 detailed data and information on marine warming, in appropriate time and spatial scales,
76 facilitating mitigation and protection strategies on human and biological time scales are urgently
77 required.

78 Marine ecosystems and organisms also react to shifts in environments on a variety of time
79 scales. The potential death, fitness, resilience and adaptation of species is dependent on
80 intensity, duration and frequencies of environmental shifts/ events. Predictability and
81 understanding of temperature-related organism health, fitness, and reactions such as heat shock,

82 depend on dense information of maximum temperatures, variability, frequency and duration of
83 periods characterized by specific temperatures (Wiltshire & Manly, 2004).

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

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

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

107 In this paper, we take the sea surface temperature (SST) in situ data from one of the most
108 important and detailed long-term marine ecological time series, the Helgoland Roads Time
109 Series (HR), and relate the data with its nearest neighbour SST time series, the Sylt Roads Time
110 Series (SR). We incorporated to the in situ data spatially averaged SST anomalies time series
111 for the greater North Sea (NS), as well as: Northern Hemisphere (NH) Surface Air Temperature
112 anomalies (SAT), Europe SAT, Germany SAT, North Atlantic (NA) SST anomalies (40°N-
113 60°N belt of latitudes) and the Yellow Sea (YS) SST anomalies time series. These are all
114 spatially averaged and derived from HadCRUT4 and HadSST3 SAT and SST anomalies
115 products, available from the Hadley Meteorological Centre (Kennedy et al., 2011a, 2011b;
116 Morice et al., 2012). The hierarchical and comparative statistical evaluation of all of these time
117 series relative to one another will allow us to relate marine ecosystem change to temperature in
118 terms of time and spatial scales. The objectives are:

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

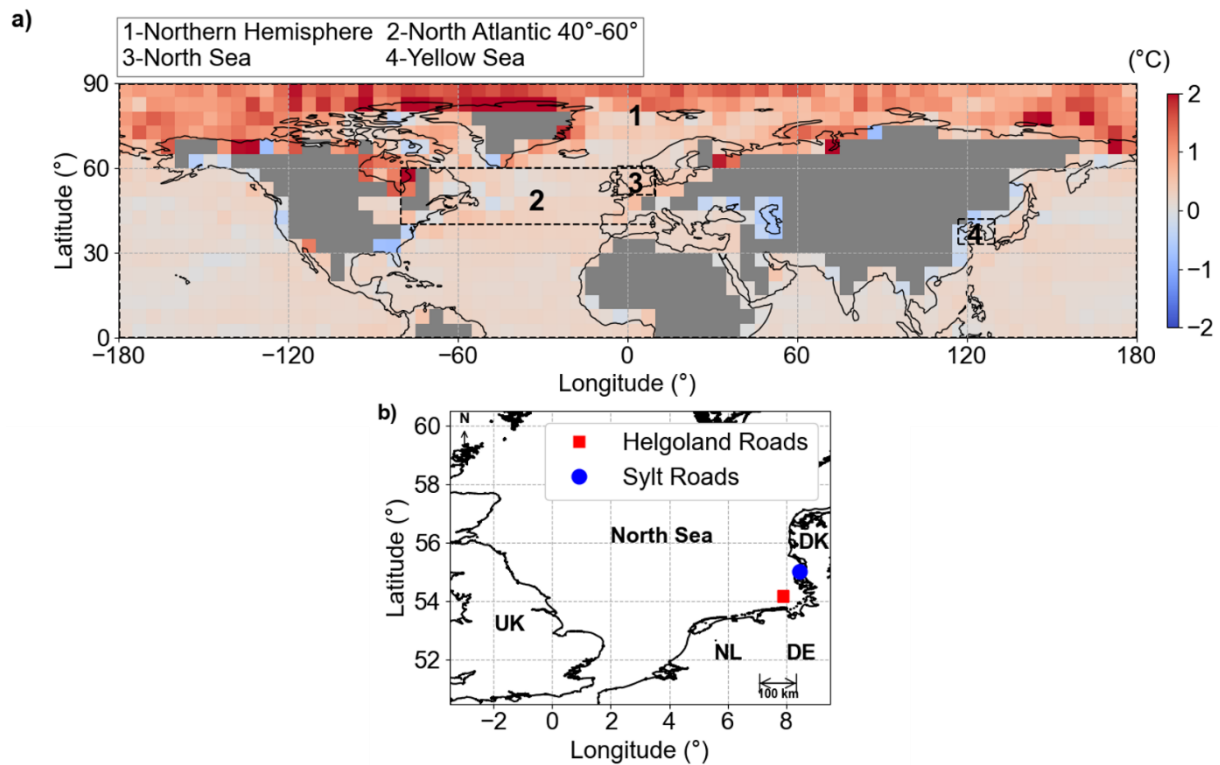
125

126 2 MATERIALS AND METHODS

127

128 2.1 Data Sets

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



132

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

138

139 2.1.1 Helgoland Roads Time Series (HR)

140 The renowned Helgoland Roads time series was set up in 1961 with the aim to evaluate change
 141 in the North Sea and its pelagic food webs over time. The evaluation scale available is from
 142 days to decades. Since 1962, surface water samples have been taken (before 9 a.m.) on working
 143 days at the “Kabeltonne” site (54° 11, 3’N, 7° 54, 0’E) between the two islands at Helgoland
 144 using a bucket. The data from these samples constitute one of the richest temporal marine data
 145 sets available, i.e., a pelagic data comprising of salinity, Secchi disk depth, nutrient analyses,
 146 phytoplankton and zooplankton analyses (Wiltshire 2004). The temperature at the sea surface

147 was measured to date using calibrated reversing thermometers (Thomas & Dorey, 1967). The
148 data is archived in PANGAEA (Data Publisher for Earth & Environmental Science). See
149 Wiltshire & Manly (2004) for details on the time series.

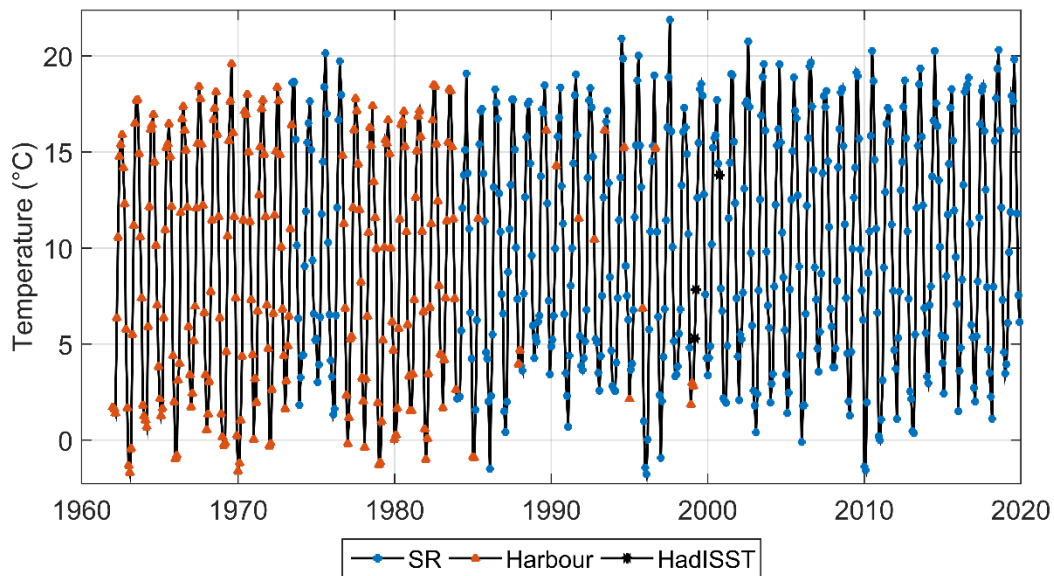
150

151 2.1.2 Sylt Roads Time Series (SR):

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

164 The List harbour data set comprises daily water temperature taken from 1946 to 2003. For the
165 period of overlap (1973-2003) between the two series, the data were compared statistically on
166 a monthly basis applying a double-sided t-test. The overlapping data showed no significant
167 differences (p values range 0.22-0.93) and their patterns were well-matched. The harbour data,
168 due to its sheltered position, was insignificantly warmer by an average of + 0.11 °C compared
169 to the SR site. Details on the merged datasets are provided in the supplementary material (S1).
170 Using this approach, we managed to assign monthly mean SST data to all but three months
171 (March 1999; April 1999; October 2000). These missing values were filled in with HadISST

172 SST (Rayner et al., 2003) monthly average values from the closest grid point to the Sylt Roads
173 position (<https://www.metoffice.gov.uk/hadobs/hadisst/data/download.html>, downloaded on
174 20 Jul 2020). The resulting time series is depicted in Figure 2, highlighting the different data
175 sources.



176
177 Figure 2 - Sylt Roads SST Time Series – merged from three data sources (solid black line). SR
178 (blue circle), Sylt harbour (orange triangle) and HadISST (black star).

179

180 2.1.3 HadCRUT4 and HadSST3 Datasets

181 Land and Sea Surface Temperature anomalies (ST) and Sea Surface Temperature anomalies
182 (SST) were obtained from two products: HadCRUT4 (Morice et al., 2012) and HadSST3
183 (Kennedy et al., 2011a, 2011b) respectively, provided by Met Office Hadley Centre
184 (<https://www.metoffice.gov.uk/hadobs/>, downloaded on 03/12/2020). Using these two products
185 we ensured consistency with atmospheric and sea surface temperature anomalies. Surface
186 temperature anomalies were spatially averaged for 4 regions: Northern Hemisphere (NH ST),
187 North Atlantic (limited by latitudes 40° and 60°N) (NA SST), North Sea (NS SST) and Yellow
188 Sea (YS SST) (Figure 1).

189 The temperature anomalies for HadCRUT4 and HadSST3 data are relative to the period of 1961
190 to 1990 and the limits used for the seas were defined to be as close as possible to the ones
191 defined by the Limits of Oceans and Seas, 1953. ("Limits of Oceans and Seas, 3rd edition"
192 International Hydrographic Organization. 1953).

193 2.1.4 European Land Surface Air Temperature Anomalies 194

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

201

202 2.1.5 German Surface Air Temperature Anomalies

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

208

209 2.1.6 North Atlantic Oscillation Index (NAO)

210 The North Atlantic Oscillation Index (NAO) is regularly used to explain variability in
211 temperature and Long-Term Ecological Research (LTER) time series (Becker, 1996; Hurrell et
212 al., 2001; Pozo-Vázquez et al., 2001). According to the National Center for Atmospheric
213 Research (NCAR), the principal component (PC)-based NAO is the time series of the leading
214 Empirical Orthogonal Function (EOF) of Sea Level Pressure anomalies over the Atlantic sector,

215 20°-80°N, 90°W-40°E, limited by the Icelandic Low and Azores High (Hurrell North Atlantic
216 Oscillation (NAO) Index (PC-Based) | NCAR - Climate Data Guide). In this work, we use the
217 PC-based NAO monthly time series to match with the monthly SST time series in frequency.

218

219 2.1.7 Atlantic Multidecadal Oscillation (AMO)

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

225

226 2.2 Statistical Methods

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

237 All data were used as anomaly time series, and for the two in situ stations (HR and SR), absolute
238 SST was also analysed. For the in situ SST data, the anomalies were calculated removing the
239 seasonal signal calculated as average of individual months from 1962 to 1991. For yearly time
240 series, the mean temperature from 1962 to 1991 was subtracted from the absolute temperature

241 time series. Temperature anomalies were used instead of absolute temperatures because one
242 assumes to first-order that the seasonal cycle is a more or less deterministic consequence of the
243 varying zenith angle of the sun, and all differences from the seasonal cycle (i.e. the anomalies)
244 tell us something about the internal dynamics of the system.

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

251 3 RESULTS

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

253

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

258 2. Long-term changes in seasonality with focus on LTOs.

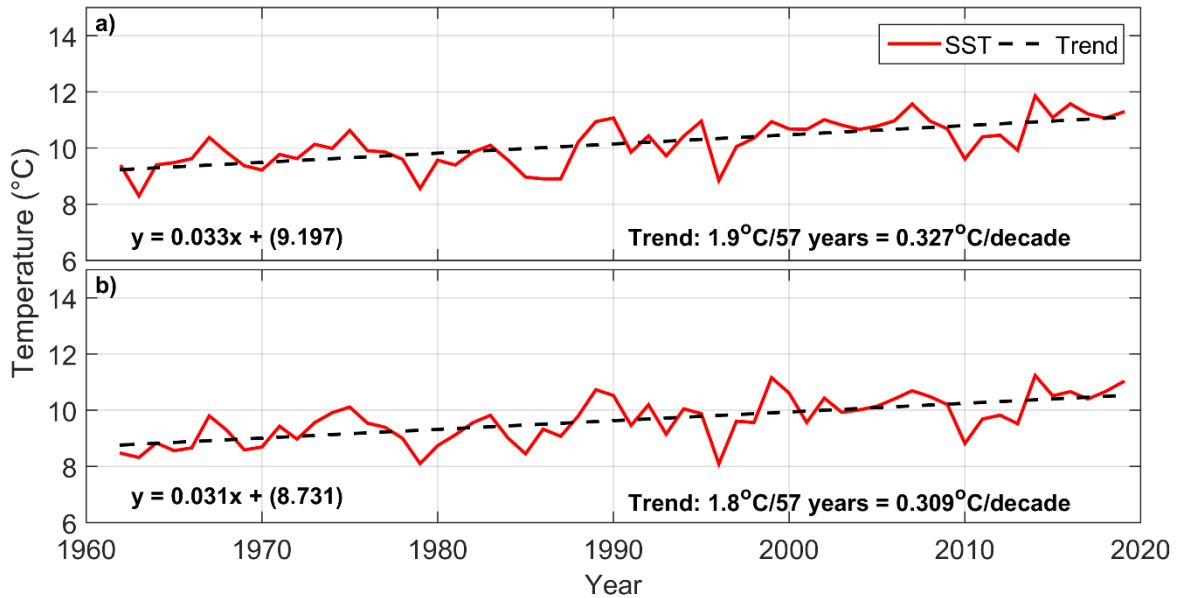
259 3. Comparison of seasonal variability between early (1962-1990) and late (1991-2019)
260 years of the time series.

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

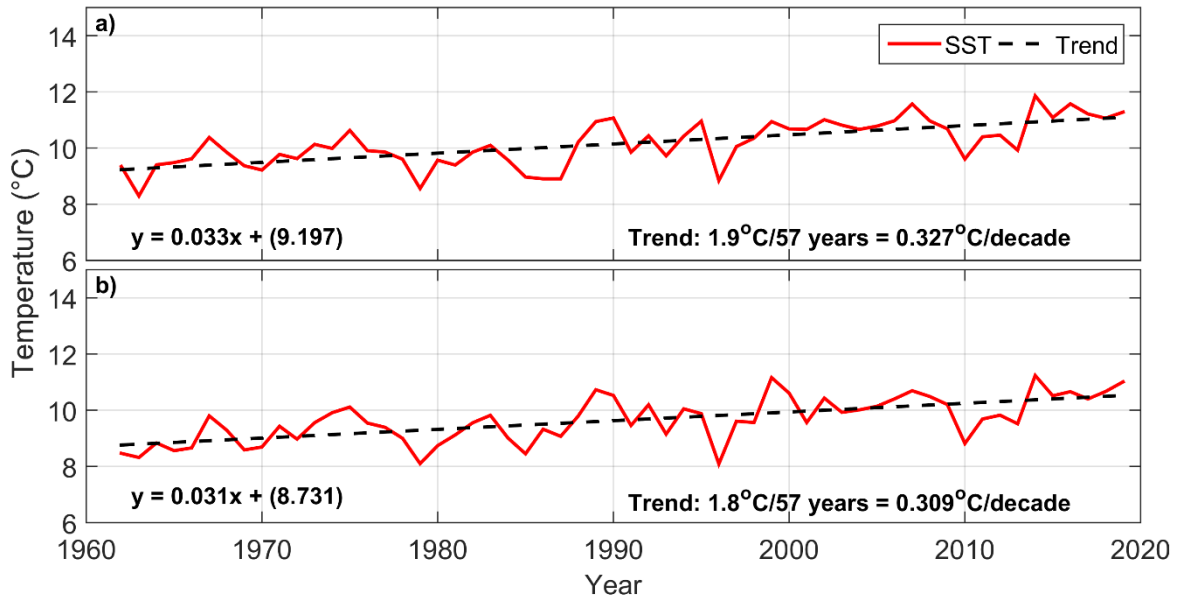
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264 3.1 Overall Trends and Cross-Correlation

265 The data from the two long-term in situ stations at Helgoland Roads and Sylt Roads lend
266 themselves to simple linear calculations of trends based on yearly average (



267
268 Figure 3). The increase in sea surface temperature is clear for both stations. Although the sites
269 are hydrographically completely different, with Helgoland being offshore in the open water of
270 the German Bight and Sylt being a shallow water coastal station in the Wadden Sea, the
271 magnitude of trends are almost the same for both sites.

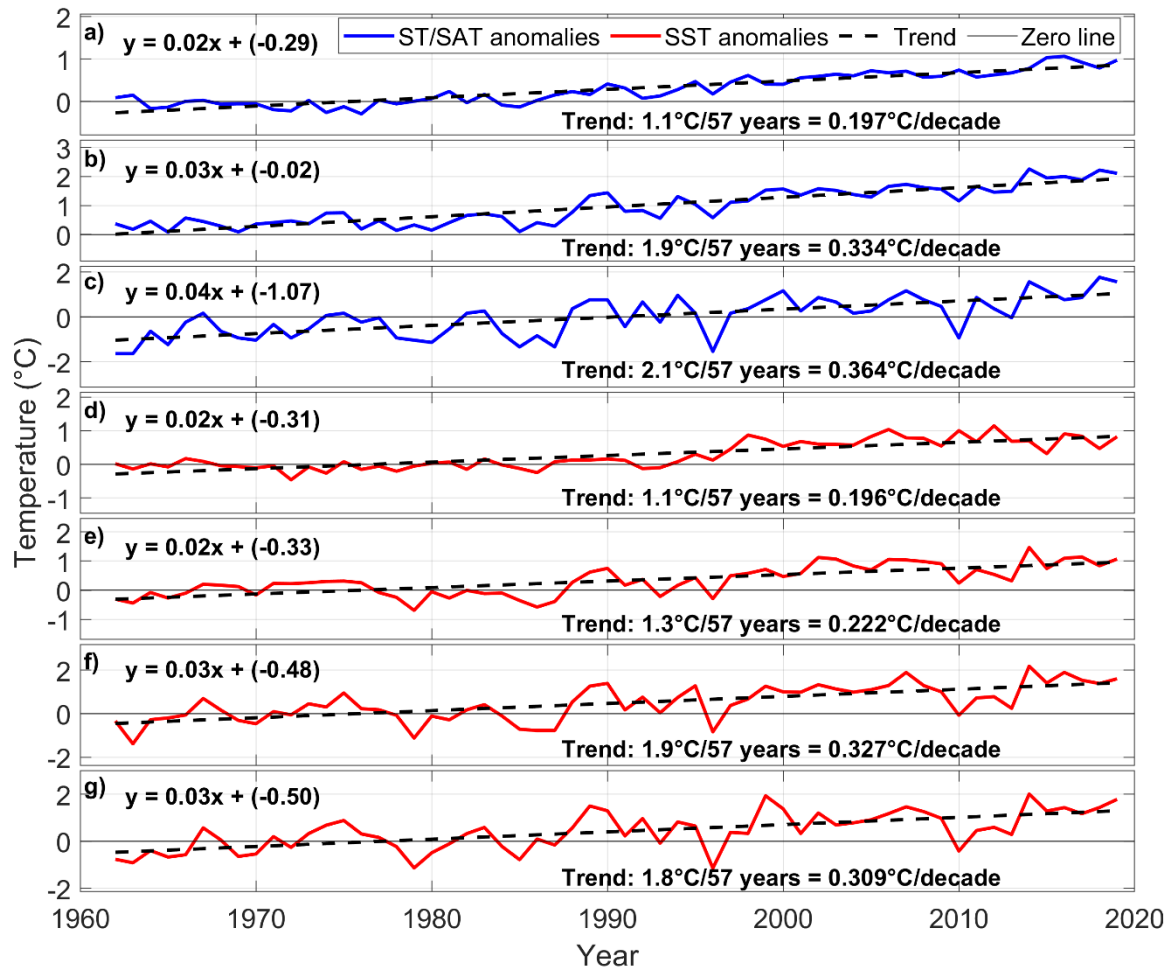


272

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

275

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



281
 282 Figure 4 - Anomaly time series (solid blue and solid red) and their linear trends (dashed black).
 283 From the top: Northern Hemisphere ST (land+sea surface temperature), Europe SAT, Germany
 284 SAT, North Atlantic SST (40°N-60°N belt), North Sea SST, Helgoland Roads SST, and Sylt
 285 Roads SST anomalies. Blue lines, except a), are based on surface air data and red lines are based
 286 on sea surface data.

Temperature Time series	Anomalies	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

287 Table 1 - Trends in °C/period for the various time series with the associated R² (Pearson)
288 coefficient.

289

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

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

295

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

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

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

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

	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
<i>AMO</i>	<i>0.48</i>	<i>0.14</i>	<i>-0.11</i>	<i>0.80</i>	<i>0.18</i>	<i>0.06</i>	<i>-0.11</i>

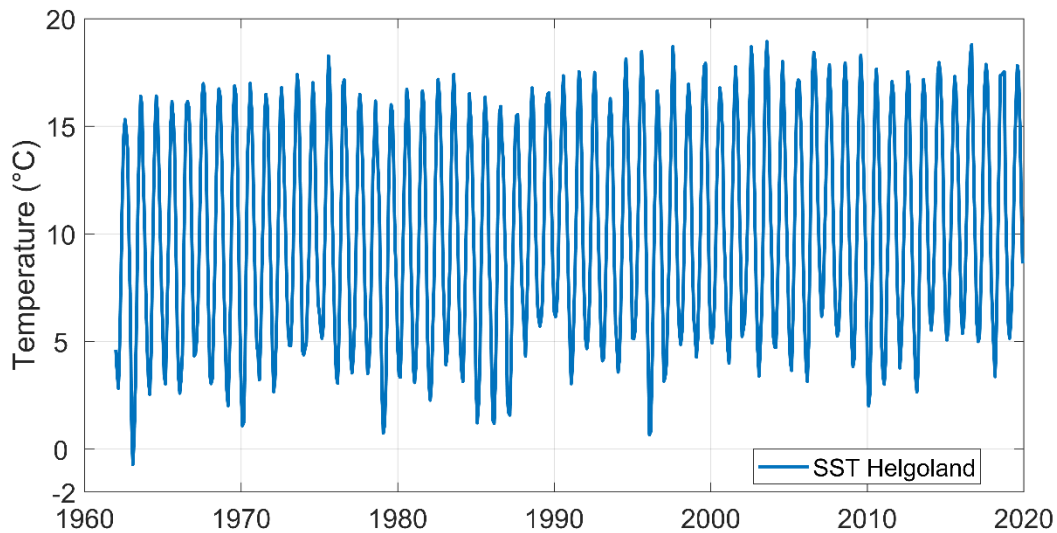
318 Table 2 - Cross-correlations calculated from the detrended anomaly time series. All cross-
 319 correlation values are significant above 95% confidence level. AMO is added for comparative
 320 purposes.

321

322 3.2 Seasonal Patterns

323 The temperate climate zone is characterised by clear seasonality, which defines growth periods
 324 both in terrestrial and marine systems. Having established the cross-correlative relationships
 325 between the data from small to large-scale areas, the next step was to calculate and understand
 326 the seasonal cycle and the anomalies. We concentrated on different time scales, starting with

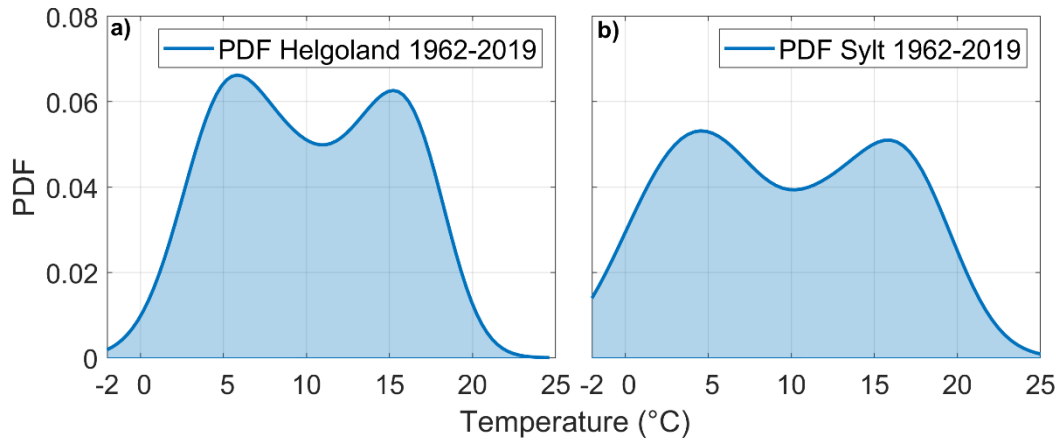
327 seasonality of the in situ LTOs. Thus, we next focused on to understanding variability of the
328 two stations over the past 58 years. Only the results based on the in situ temperature
329 measurements are presented. The sea surface temperature for the data sets were evaluated and
330 show large and variable seasonal evolution. (See example in Figure 5). The variability of the
331 winter minimum displays a much stronger variability than the summer maximum.



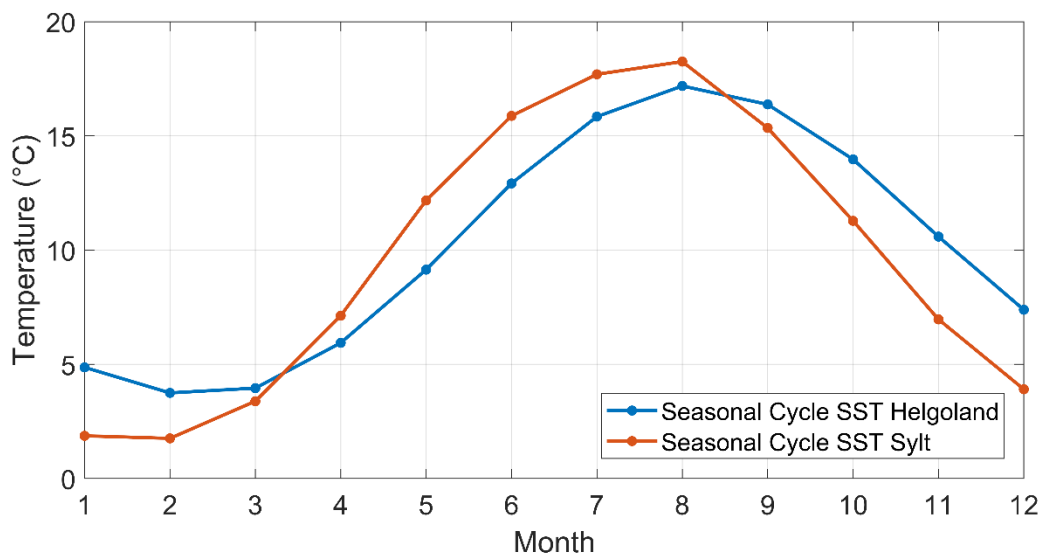
332
333 Figure 5 - Evolution of the sea surface temperature including seasonality as an example:
334 Helgoland Roads.

335
336 When the densities/frequencies of the temperature anomalies for all data sets are resolved, two
337 peaks manifest with bunches (=longer duration of SSTs) of cold temperatures around the winter
338 minimum and warm temperatures around the summer maximum (Figure 6). These peaks
339 represent the time just before and after the winter minimum and the summer maximum. The
340 density curves suggest that the cold peak around the winter is slightly larger compared with that
341 of the summer for both HR and SR. This reflects the slightly longer winter season compared to
342 summer at these latitudes. The corresponding seasonal cycles of HR and SR are shown in Figure
343 7. A smaller curvature of the winter minimum values compared to the summer maximum values
344 is apparent. The winter season is clearly longer by approx. half a month. The winter minimum
345 temperatures at Sylt are colder and the summer temperatures are warmer compared with

346 Helgoland. This, also the difference in timing of the start of spring/ summer between the two
347 sites, reflects the shallow water coastal site at Sylt, vs. the offshore water site at Helgoland.



348
349 Figure 6 – Probability density function curves of sea surface temperatures at a) Helgoland Roads
350 and b) Sylt Roads calculated using Kernel Density Estimates. For a) and b), the x-axis was
351 limited to -2 °C because lower temperatures are an artefact of the PDF.



352
353 Figure 7 - Seasonal cycles for the SST at HR (blue) and SR (orange) for the entire time series.
354
355 Examination of the NA, NS, HR and SR SST anomalies, and as exemplified by HR and SR in
356 Figure 8, indicated positive temperature trends for both summer and winter. The trends for

357 winter and summer were calculated and are presented in Table 3 with their associated R^2
 358 (Pearson) coefficient. The analyses revealed that whereas the summer trends are similar in all
 359 regions, the winter trends are much larger for the two stations Helgoland Roads and Sylt Roads
 360 (reduced cold continental influence in winter) (Table 3). A trend of $0.3^\circ\text{C}/\text{decade}$ for both
 361 seasons was registered for HR (Figure 8a). At the shallow water site SR (Figure 8b) the summer
 362 warming trend was slightly less than for winter.

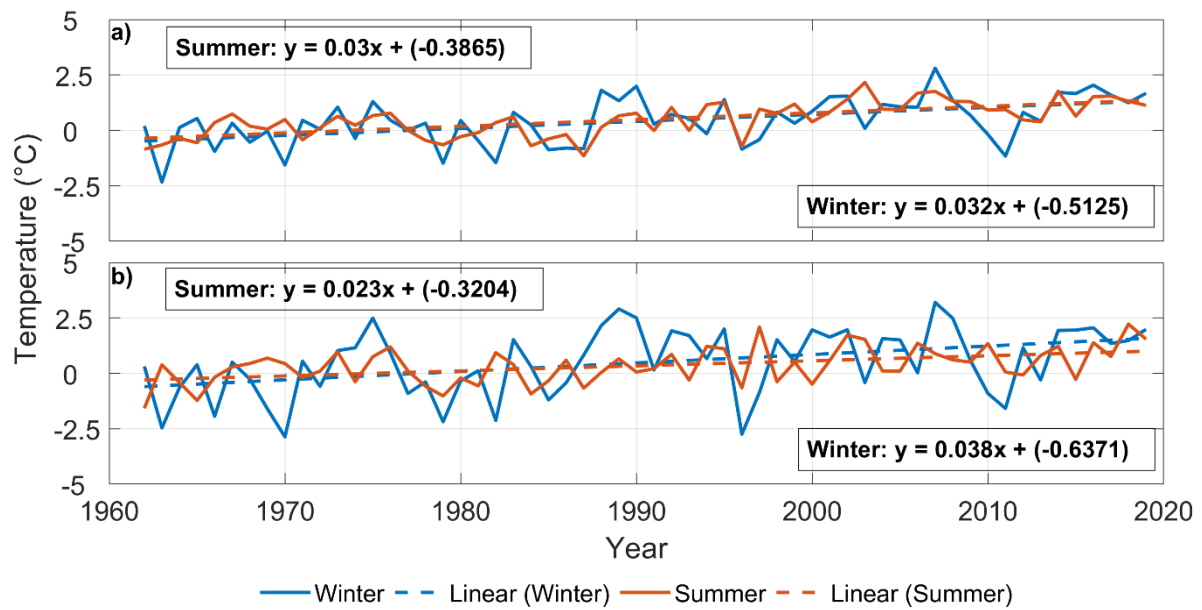


Figure 8 - Temporal evolution and trend of the SST anomalies at a) Helgoland Roads and b) Sylt Roads in summer mean (June-August) (solid orange line) and summer linear trend (dashed orange line), winter mean (December-February) (solid blue line) and winter linear trend (dashed blue line).

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)

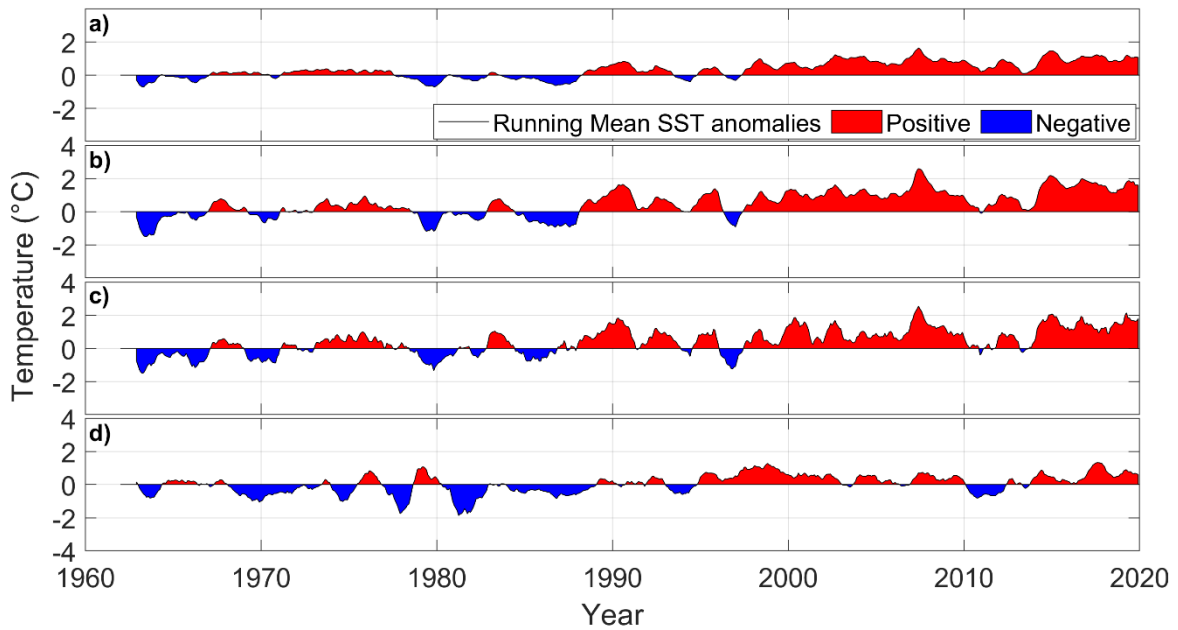
368 Table 3 – SST anomalies trends in °C/decade in summer and winter. The value in brackets is
369 the associated R^2 (Pearson) coefficient.

370

371 3.3 Temperature Variability in First and Second Half of the Time-Series

372 Having evaluated the seasonality, we next turn again to the analyses of the temperature
373 variability, described by the temperature anomalies time. Again, although we calculated these
374 for all data sets in Section 3.1, only the results from NS, HR, SR and YS are depicted here as
375 12-month running means (Figure 9). We kept the y-axis in the same scale for better comparison.
376 The SST anomalies were mostly negative with a small trend until the late 1980s for NA (not
377 shown), NS, HR, and SR, and mostly positive with a larger positive trend thereafter. Figure
378 9a,b,c clearly shows this for NS, HR and SR and this is also aligned with similar evolution
379 found in the European and German surface air temperature anomalies (Figure 4).

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



386

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

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

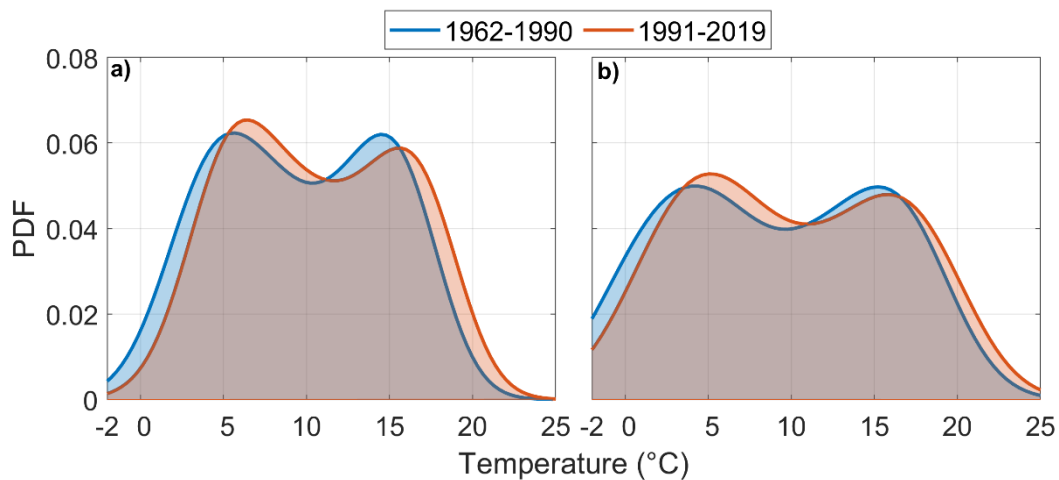
396

397 3.3.1 Long-Term Changes in SST Distributions

398

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

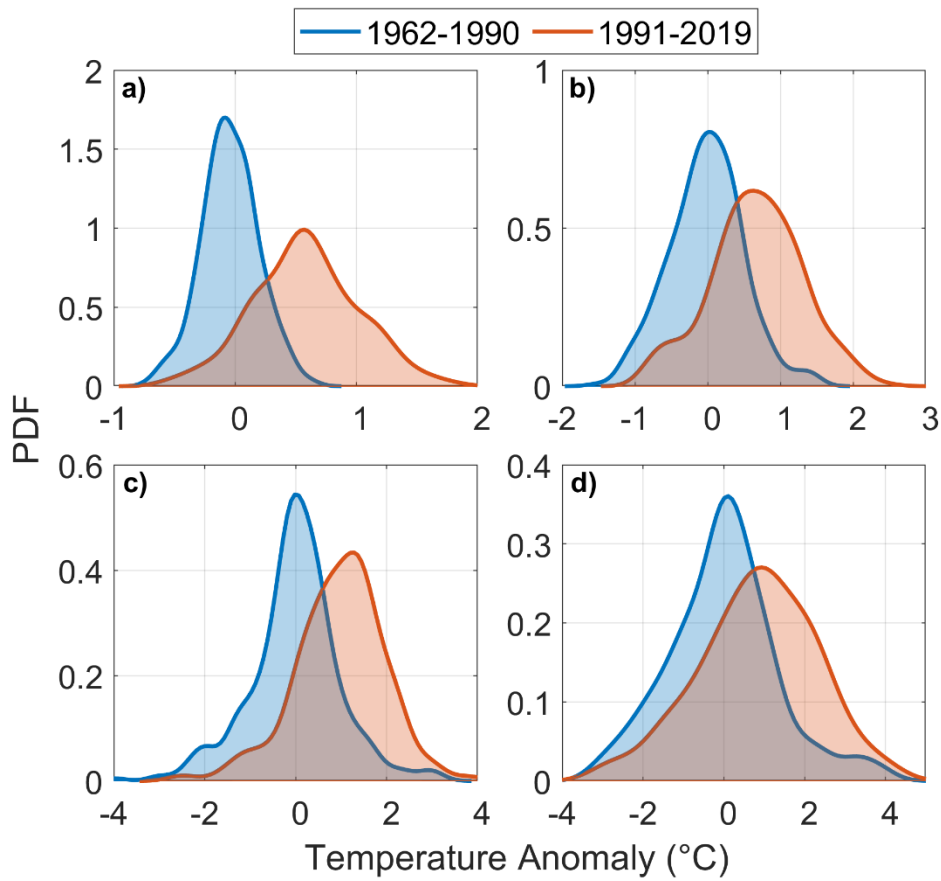
405 peaks around the mean minimum and maximum. In the second half of the time series, the two
406 modes are still visible, but the cold mode is slightly larger than the warm mode. This must be
407 due to the change in the seasonal cycle: the mean minimum in the second half is a little higher
408 and the curvature is steeper, and the mean maximum is a little lower and the curvature is flatter.
409 Because of this change, more values occur around the cold mode and less values around the
410 warm mode, spreading to higher-than-average values.



411
412 Figure 10 - Distribution of the sea surface temperature at a) Helgoland Roads and b) Sylt Roads,
413 in terms of probability density function, for the first (blue) and second (orange half of the time
414 series. The curves show the bimodality originated from seasonality and the shift when
415 comparing early and late years. For a) and b), the x-axis was limited to -2 °C because lower
416 temperatures are an artefact of the PDF.

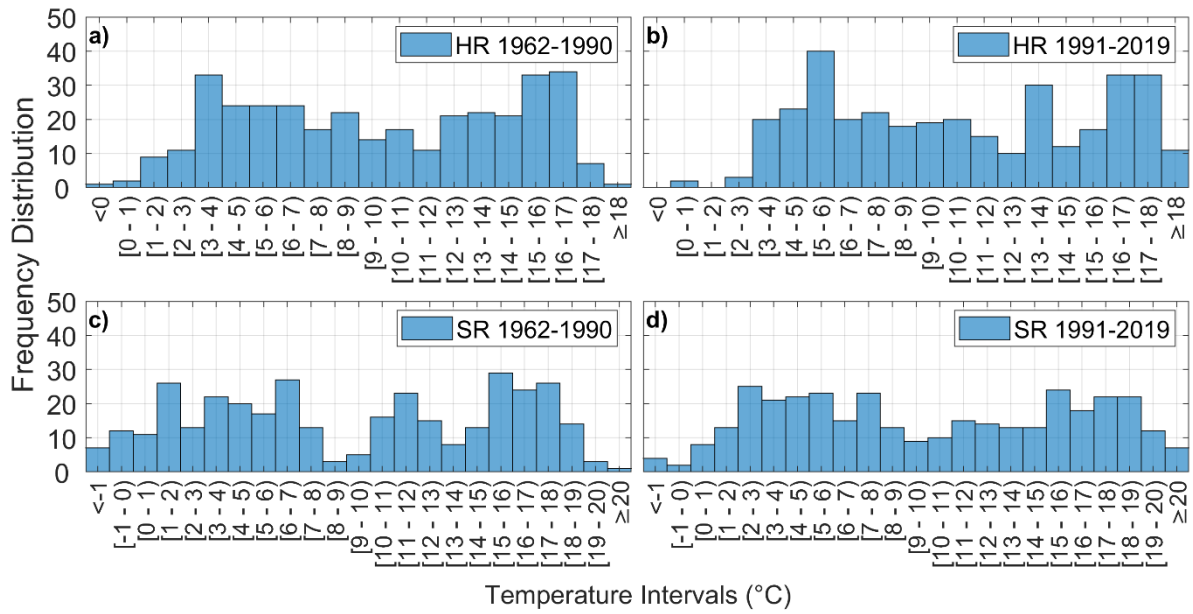
417
418 The HR and SR temperature histograms are shown in Figure 11 and it is possible to observe
419 that temperature distributions have shifted in the later years for both. At Helgoland the
420 distinctive bi-seasonal bimodal shape is still clear, but the peak intervals in winter and summer
421 increased by 1°C, showing an increase in maximum temperature values. In the shallow inshore
422 waters around Sylt, the seasonal signal has become more homogeneous, as intermediate
423 temperature intervals became enhanced. The low temperature range peak increased also by 1°C,

424 with a decrease in the counts for the lowest temperature range. These observations underpin the
425 results on the observed long-term shifts in seasonality as presented in Section 3.2. Consideration
426 of the SST anomalies in the North Atlantic, North Sea, HR and SR showed that the temperature
427 density distribution clearly shifted to higher temperatures in the later years in these areas (



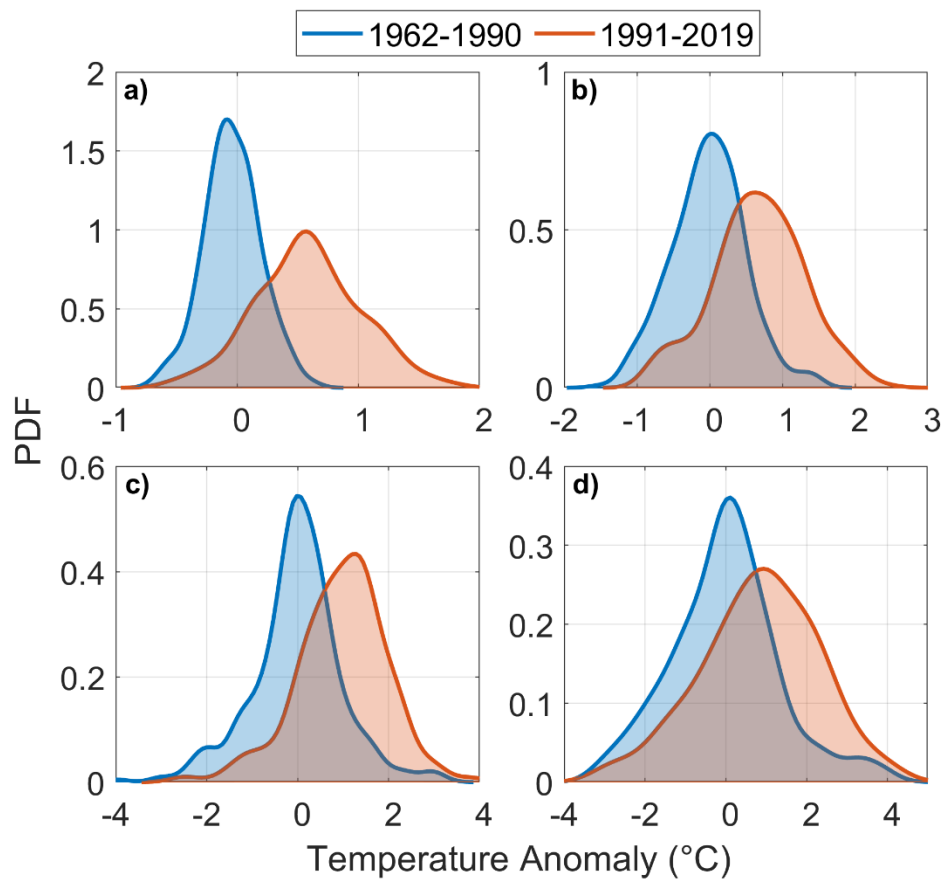
428

429 Figure 12)



430

431 Figure 11 - Frequency of occurrence of temperatures at HR and SR. a) HR SST histogram for
 432 the period 1962-1990 and b) HR SST 1991-2019. c) SR SST histogram for the period 1962-
 433 1990 and b) SR 1991-2019. The bins are defined as 1°C intervals, except for the edges. Note the
 434 difference in temperature intervals for HR and SR.



435

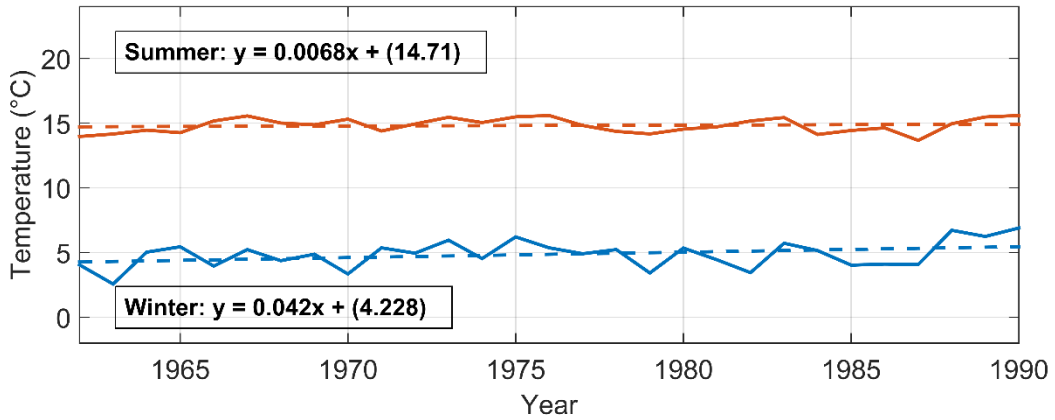
436 Figure 12 – Probability Density Function (PDF) of sea surface temperature anomalies in the
 437 first (blue) and second (orange) half of the time series for the a) NA, b) NS; c) HR and d) SR.

438

439 3.3.2 Seasonal Means and Trends

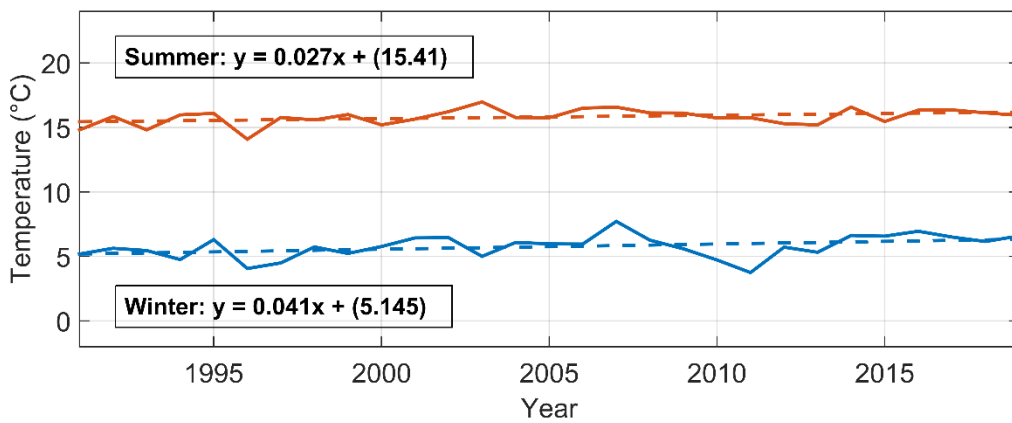
440

441 It seems that the most pronounced difference between the first and the second half of the time
 442 series occurs around the winter minimum and the summer maximum (Figure 10). Thus, we
 443 examined the seasonal means and trends of the two sections of time series and the analyses
 444 showed that actually all seasons are affected. This can be seen in Figures Figure 13 to Figure
 445 16 and in all the trend values in Table Table 4 (HR) and Table 6 (SR).



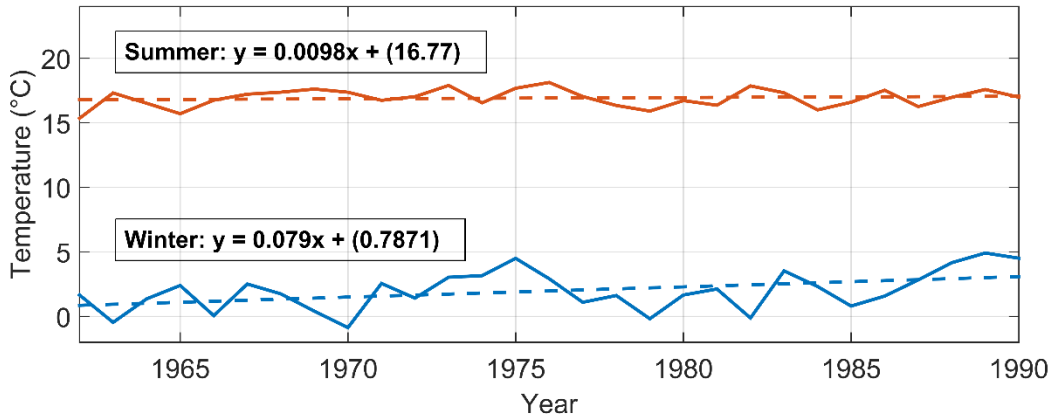
446 Winter (1962-1990) - - Linear (Winter) Summer (1962-1990) - - Linear (Summer)

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



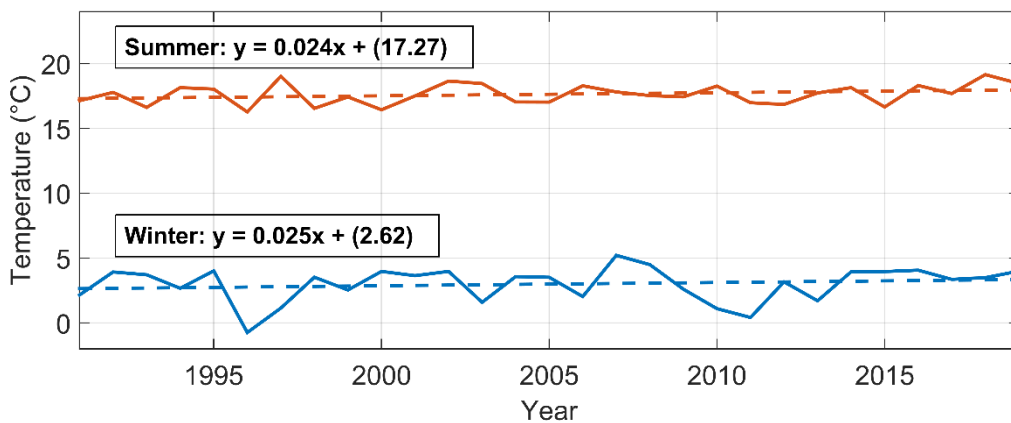
449 Winter (1991-2019) - - Linear (Winter) Summer (1991-2019) - - Linear (Summer)

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



452 — Winter (1962-1990) — Linear (Winter) — Summer (1962-1990) — Linear (Summer)

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



455 — Winter (1991-2019) — Linear (Winter) — Summer (1991-2019) — Linear (Summer)

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

458
 459 In both Helgoland and Sylt Roads, the summer long-term trends increased after 1990 (Figures
 460 Figure 13 to Figure 16), and the intercepts increased by roughly 1°C in both winter and summer
 461 in the late years, indicating the increase in SST means for these locations. In Tables Table 4 and
 462 Table 5, the changes in the SST trends and means at Helgoland Roads and the difference
 463 between the first and the second half of the time series are summarized for all seasons. The
 464 associated R^2 (Pearson) coefficient, is also provided. In Tables Table 6 and Table 7, we

465 summarize the same results for the Sylt Roads. It is clear from Tables Table 5Table 7 that the
 466 mean seasonal SST were significantly higher in late years compared to the early years,
 467 especially in spring and summer (more than 1°C) at HR and SR. However, when it comes to
 468 the trends (Tables Table 4 andTable 6), these were steeper especially in autumn, compared to
 469 the summer period in the late years.

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)

470 Table 4 – Annual and seasonal trends of SST in °C/period at Helgoland Roads for the entire
 471 period, the first and the second half of the time series for the different seasons. The values in
 472 brackets are the associated R² (Pearson) coefficient, which indicates how much of the variance
 473 is explained by the trend.

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

474 Table 5 - Mean annual and seasonal SST in °C at Helgoland Roads for the complete period (A
 475 1962-2019), the first half (B 1962-2019) and the second half (C 1991-2019) of the time series.
 476 The difference of the late data from the early data (C-B) is presented, as it is significantly
 477 positive for all seasons and the whole period.

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)

478 Table 6 – Annual and seasonal trends of SST in °C/period at Sylt Roads for the entire period,
 479 the first and the second half of the time series in the different seasons. The value in brackets is
 480 the associated R² (Pearson) coefficient, which indicates how much of the variance is explained
 481 by the trend.

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

482 Table 7 - Mean annual and seasonal SST in °C at Sylt Roads complete period (A 1962-2019),
 483 the first half (B 1962-2019) and the second half (C 1991-2019) of the time series. The difference

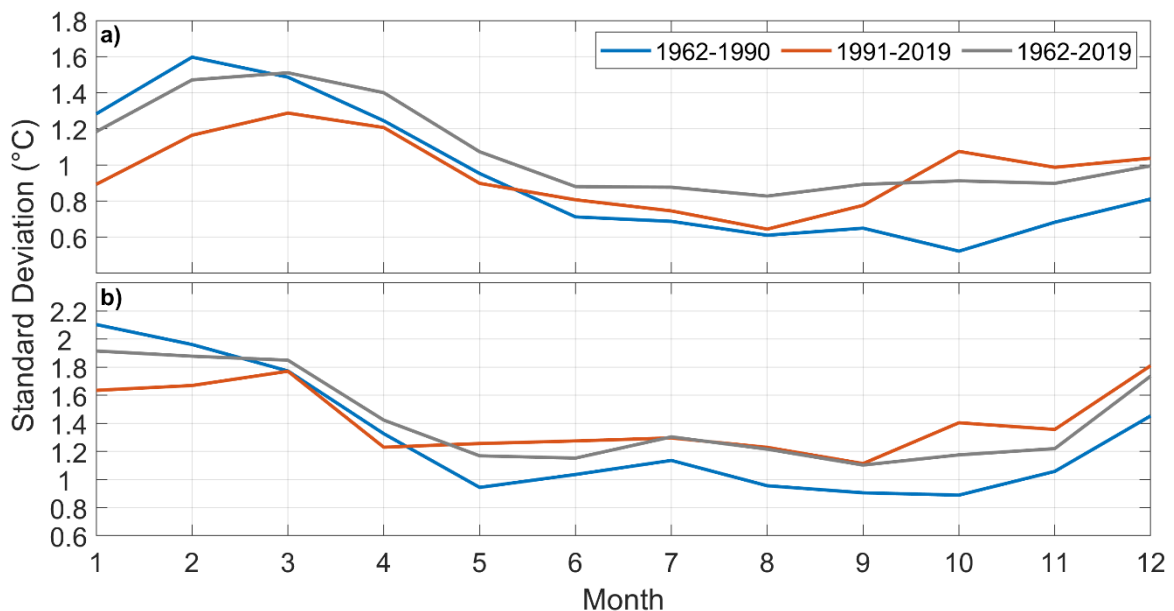
484 of the late data from the early data (C-B) is presented, as it is significantly positive for all
485 seasons and the whole period.

486

487 3.3.3 Seasonal Variability

488

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



493

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

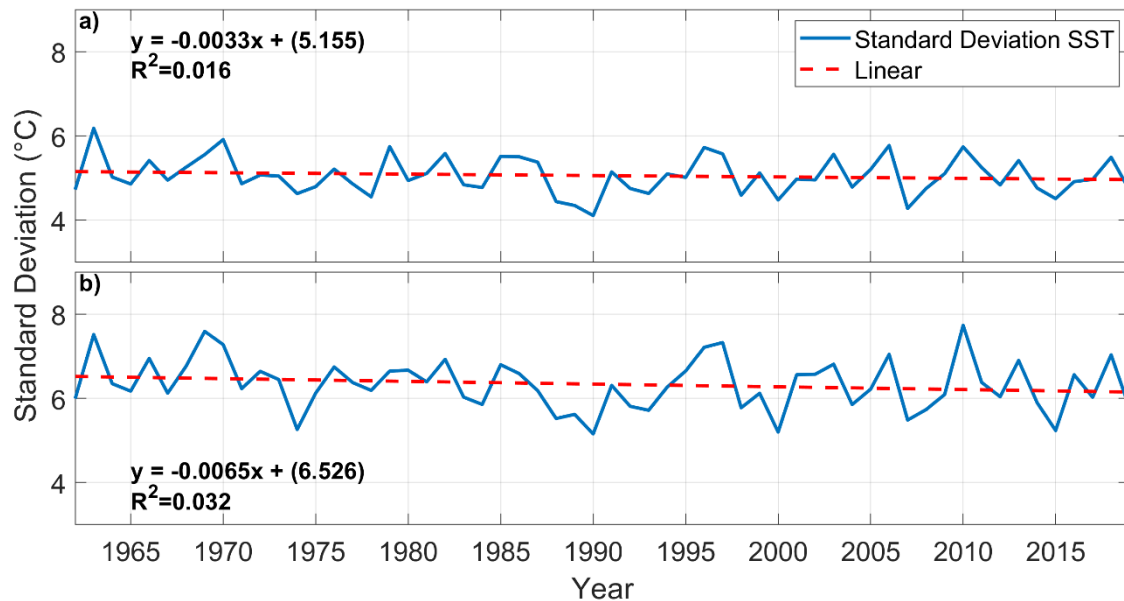
497

498 The variability during the winter and spring months was found to be significantly larger than
499 during summer and autumn at both HR and SR. This is especially true for the early half of the
500 time series. In the second half of the time series, the large winter variability has become smaller
501 and the autumn variability has become larger. The same pattern (depicted in Figure 25 of the

502 Discussion) was found for the North Sea data. However, the data sets for the North Atlantic
503 showed a clear increase in temperature variability for all months since 1991. The Northern
504 Hemisphere and global data sets also show increases in variability in the later years for all
505 months, but with a significantly smaller amplitude.

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

512 This means that the seasonal cycle became smaller in magnitude over time, also shown in Tables
513 Table 4Table 7. For Helgoland, the difference of the mean between the warm seasons (summer,
514 autumn) and the cold seasons (winter, spring) is 8.74°C in the first half of the time series and
515 8.56°C in the second half, i.e. a reduction of the seasonal cycle by 0.2°C (Table 5), consistent
516 with the trend indicated in Figure 18a. At SR, the reduction of the seasonal cycle between the
517 first half and the second half of the time series is larger at 0.4°C (Table 7). Overall, it is clear
518 that the seasonal variability and, concomitantly, the seasonal amplitude has shifted
519 considerably, becoming less in winter and more in autumn; manifesting especially as a
520 reduction of the definite seasonality, both at the open water site at Helgoland and in the shallow
521 Wadden Sea site of Sylt.



522

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

526

527 3.3.4 Assessment of Temperature Extremes

528

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

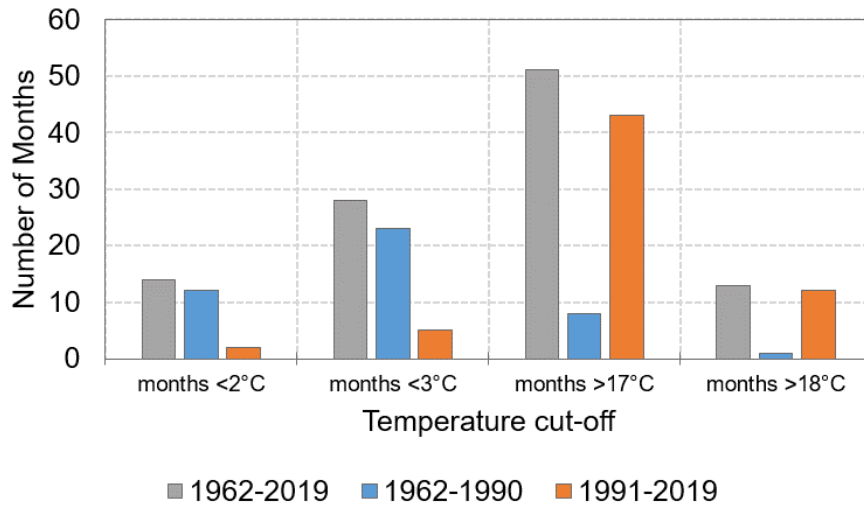
534 Helgoland Roads, an exposed open water site, showed minimum cold thresholds of mean
 535 monthly temperatures $< 2^{\circ}\text{C}$ and $< 3^{\circ}\text{C}$. The maximum warm thresholds at HR were mean
 536 monthly temperatures $> 17^{\circ}\text{C}$ and $> 18^{\circ}\text{C}$. The number of months with mean values
 537 above/below these thresholds is shown in Figure 19. It can clearly be seen that there has been a
 538 significant shift towards very many warm months with values over 17°C and 18°C at Helgoland
 539 Roads since 1991. The very cold months (mean values below $< 2^{\circ}\text{C}$ and $< 3^{\circ}\text{C}$) have become

540 significantly less common. The percentages of the mean number of cold and warm months
541 relative to the total number of months of the different time periods are given in Table 8. The
542 percentage of months with mean temperatures below 3°C has gone down from 6.6 % to 1.4%
543 of the total months in the early/ late years, respectively. At the same time, the percentage of
544 months with mean temperatures above 17°C has gone up from 2.3 % to 12.4 % of the total
545 months in the early/ late years, respectively.

546 Sylt Roads, the shallow water Wadden Sea site, showed minimum cold thresholds of mean
547 monthly temperatures <1°C, < 2°C and <3°C. The SR maximum warm thresholds were mean
548 monthly temperatures > 17°C and >18°C. The number of months with mean values
549 above/below these thresholds is presented in Figure 20 for SR. It is obvious that there has been
550 a significant shift towards more warm months at Sylt since 1991 and the very cold months
551 (mean values below < 2°C and <3°C) have become significantly less (for percentages of total,
552 see Table 9). For example, the percentage of months with mean temperatures below 2°C has
553 gone from 16.6% to 7.8% of the total months in the early/ late years, respectively. At the same
554 time, the percentage of months with mean temperatures above 17°C has gone up by over 6% of
555 the total months in the early/ late years at Sylt Roads.

556 It is interesting to note that these data clearly show that the sites at Helgoland and Sylt, because
557 of their different hydrographic situation (i.e. open North Sea vs. shallow Wadden Sea), have
558 different temperature extremes. Sylt water heats up faster and cools down more. On the long
559 run, it may be expected that this difference will become even more pronounced.

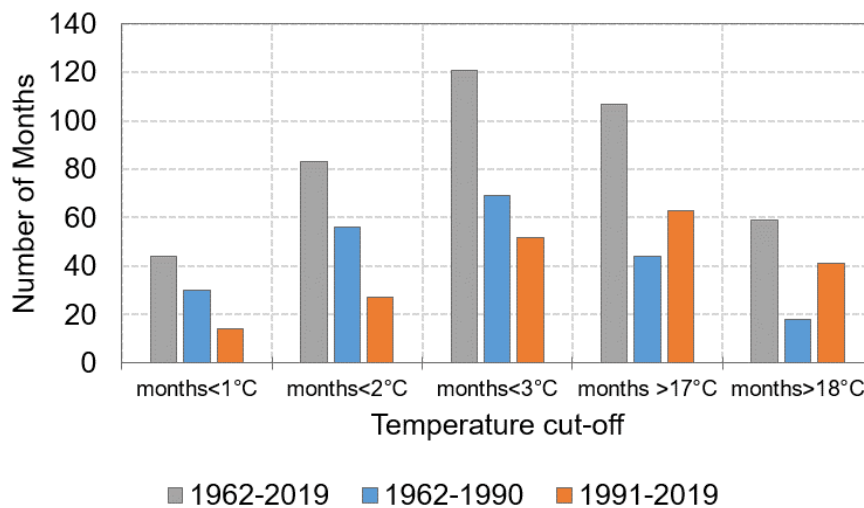
560



561

562 Figure 19 - Number of “cold” and “warm” months for total (grey), early (blue) and late years

563 (orange) of the Helgoland Roads data set.



564

565 Figure 20 - Number of “cold” and “warm” months for total (grey), early (blue) and late years

566 (orange) of the Sylt Roads data set.

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

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

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

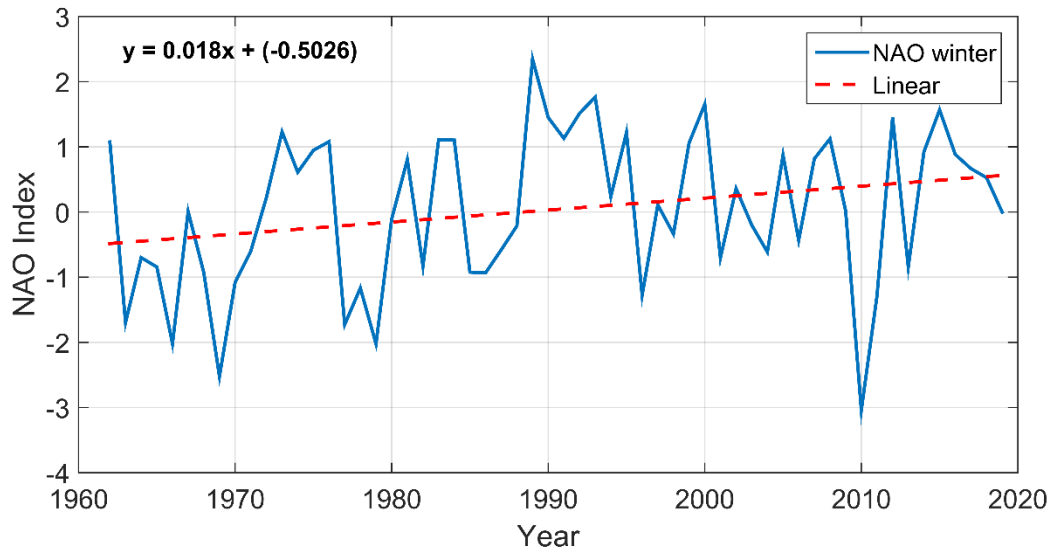
569 Table 9 - Percentages of the mean number of cold and warm months relative to the total number
570 of months of the late and early time periods at Sylt Roads (SR).

571

572 3.3.5 Relationship of the North Atlantic Oscillation (NAO) and Temperature

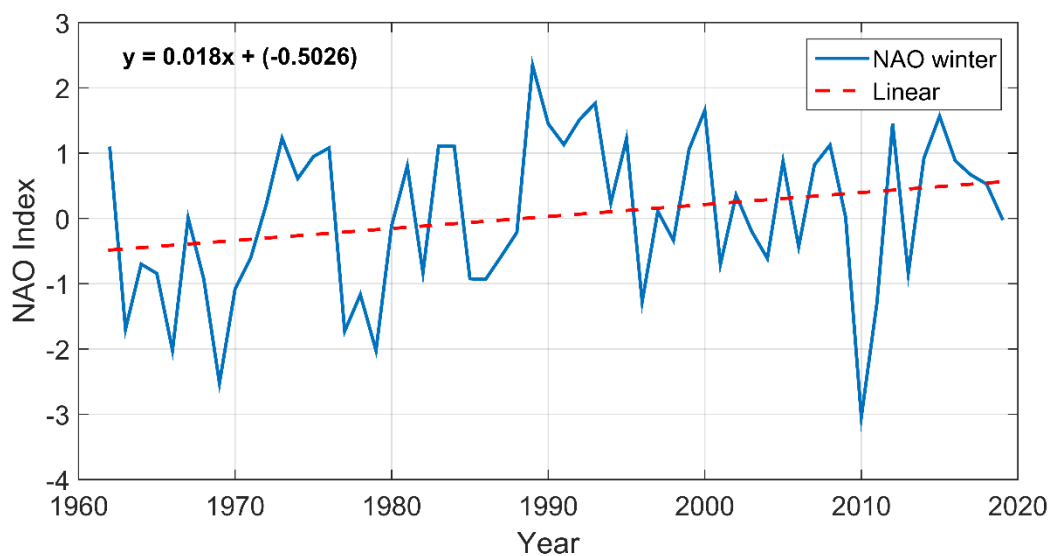
573

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



584

585 Figure 21.



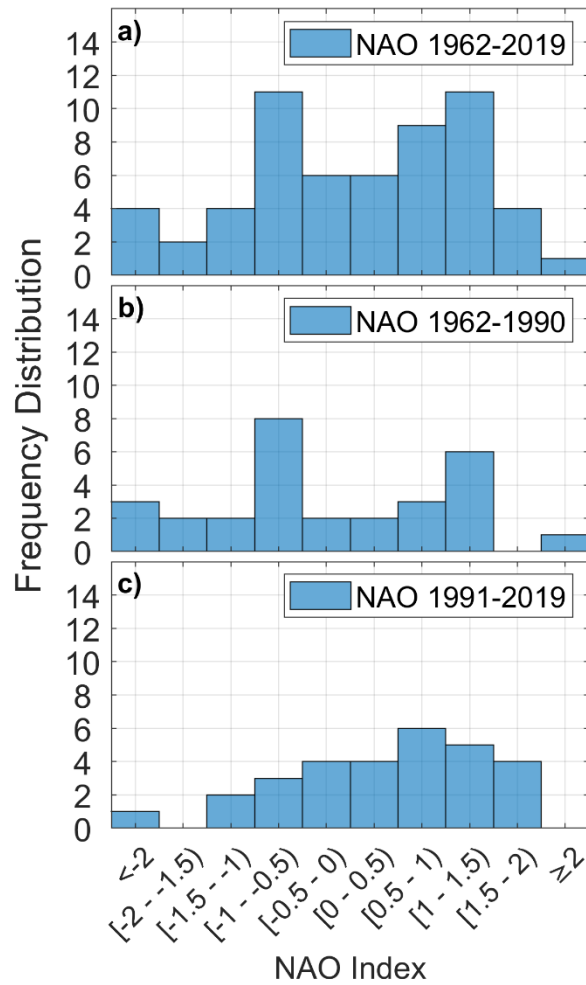
586

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

589

590 In the PC NAO, there is a positive trend toward positive NAO (more frequent westerly winds
 591 and warmer temperatures in winter in Europe) (Trigo et al., 2002). As can be seen from the
 592 histograms in Figure 22, in the first half of the time series there are 7 years with strongly
 593 negative values (< -1), and in the second half there are only 3 years with strongly negative
 594 values (equivalent to a smaller number of cold winters). The correlation analyses of temperature

595 with the NAO was highly significant for all the data sets except the North Atlantic data set. This
 596 was the case for all years and both early and late years (Table 10).



597
 598 Figure 22 - Frequency of occurrence of winter mean (Dec-Feb) NAO index values for the whole
 599 period (1962-2019, top), early (1962-1990, middle) and late (1991-2019, bottom) years.

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
Significance		***	***	***		***	***	***		***	***	***
p-values	0.478	0.001	0.000	0.000	0.512	0.008	0.001	0.000	0.788	0.020	0.002	0.000

600 Table 10 - Significance of detrended SST anomalies and NAO correlation (Pearson) for
601 different regions and the stations HR and SR showing all (1962-2019), early (1962-1990) and
602 late (1991-2019) years. Winter mean considers December, January and February months. NA -
603 North Atlantic (40°-60° belt); NS - North Sea; HR - Helgoland Roads and SR - Sylt Roads.

604

605 3.4 Summary of Results (

<p>3.5 Trends: All areas HR & SR Correlation all areas Correlations HR & SR AMO HR & SR (early vs late years)</p>	<p>Summary Trends were significantly positive for all surface temperature anomalies data sets examined. Of all, HR and SR showed highest warming trend of 0.3°C/decade. All data sets were significantly correlated with each other. HR and SR are most correlated with EU and GE temperature anomalies time series. AMO was found to be unsuited for comparisons and was replaced by NA SST. Trends have increased significantly in late years.</p>
<p>Seasonal Analyses: HR & SR Frequency distributions Comparison all areas Winter vs Summer HR SR Variability HR & SR (early vs late years)</p>	<p>Summary Strong seasonal cycle, increased mean in late years (warmer temperatures earlier in time). Bimodal frequency distribution of temperature (cold and warm modes) becoming more heterogeneous, with the cold mode peak moving to higher values and becoming steeper. Summer trends are similar, winter trends much larger for HR & SR (lower thermal inertia compared to deeper and larger areas). Winter peaks larger than summer for both HR & SR = slightly longer winter season. HR seasonal cycle reflects open water situation with modulated winter and summer temperatures. SR seasonal cycle reflects shallow water situation, higher variance between winter and summer. Variability of winter minima displays greater variability than the summer maxima. 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.</p>
<p>Anomalies: All areas Comparison Yellow Sea (YS) NAO all areas except NA</p>	<p>Summary SST anomalies had a strong positive trend after the 1980s. Clear separation of early and late years. Late years warmer. Clear separation of early and late years. Late years warmer. Winter NAO highly correlated with winter anomalies.</p>
<p>Temperature Extremes: HR & SR warmest months HR & SR coldest months</p>	<p>Summary Highly significant shift towards more warm months with mean values over 17°C. Very cold months (means <2°C and <3°C) decreased frequency.</p>

606 3.6 Table 11):

<p>Trends: All areas HR & SR Correlation all areas Correlations HR & SR AMO HR & SR (early vs late years)</p>	<p>Summary Trends were significantly positive for all surface temperature anomalies data sets examined. Of all, HR and SR showed highest warming trend of 0.3°C/decade. All data sets were significantly correlated with each other. HR and SR are most correlated with EU and GE temperature anomalies time series. AMO was found to be unsuited for comparisons and was replaced by NA SST. Trends have increased significantly in late years.</p>
<p>Seasonal Analyses: HR & SR Frequency distributions Comparison all areas Winter vs Summer HR</p>	<p>Summary Strong seasonal cycle, increased mean in late years (warmer temperatures earlier in time). Bimodal frequency distribution of temperature (cold and warm modes) becoming more heterogeneous, with the cold mode peak moving to higher values and becoming steeper. Summer trends are similar, winter trends much larger for HR & SR (lower thermal inertia compared to deeper and larger areas). Winter peaks larger than summer for both HR & SR = slightly longer winter season. HR seasonal cycle reflects open water situation with modulated winter and summer temperatures.</p>

SR Variability HR & SR (early vs late years)	SR seasonal cycle reflects shallow water situation, higher variance between winter and summer. Variability of winter minima displays greater variability than the summer maxima. 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: All areas Comparison Yellow Sea (YS) NAO all areas except NA	Summary SST anomalies had a strong positive trend after the 1980s. Clear separation of early and late years. Late years warmer. Clear separation of early and late years. Late years warmer. Winter NAO highly correlated with winter anomalies.
Temperature Extremes: HR & SR warmest months HR & SR coldest months	Summary Highly significant shift towards more warm months with mean values over 17°C. Very cold months (means <2°C and <3°C) decreased frequency.

607 Table 11 - Overall summary of Results.

608

609 4 DISCUSSION

610

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

622 In studies on the effects of changing temperature in temperate marine environments such as the
623 North Sea, one must consider shifts in a) long-term trends over decades, abrupt regime shift-
624 like and relationships with greater global ocean drivers (e.g., AMO; NAO; b) seasonality; c)
625 shifts in max/min temperatures and frequencies, and d) changes in variability of temperature,
626 which need to be primarily considered in terms of changed biology and ecosystems. Above, we

627 analysed the overall temperature trends, anomalies, seasonal shifts, variabilities and frequency
628 distributions, frequency of occurrence of extremely hot and cold temperatures and the
629 relationship of the temperature measurements with the climate index NAO. For completeness,
630 we also considered the AMO index in the context of the time series.

631 The impacts of warmer ocean waters on marine organisms are one of the biggest scientific
632 topics of our time and have been subject of many studies over the past two decades (Fellous et
633 al., 2022; Gittings et al., 2018; Jorda et al., 2020; Lima & Wetthey, 2012; Wiltshire & Manly,
634 2004). The need for scenario development and management strategies is pivotal to Earth System
635 sustainability. For this, dense long-term data and an excellent understanding of this data are
636 required, otherwise, modelling of systems and scenarios is impeded. However, most studies on
637 how global warming manifests with regard to marine organisms are laboratory or, more rarely,
638 in situ habitat observations during/after weather extremes. When it comes to direct in situ causal
639 linkage of temperature shifts in the ocean and long-term shifts in ecosystems, this has proven
640 difficult simply because the relevant long-term measurements are not available on the
641 appropriate temporal and spatial scales, and those available are not temporally and spatially
642 dense enough. Data sets based on LTER at one site can be considered to be under-representative
643 of a region and the only data sets which are spatially available are often interpolative both in
644 terms of space and time. Remote sensing data, with around 40 years of surface temperature
645 measurements, is an efficient option to represent temporal and spatial changes, but it is still
646 constrained by biases in sensors and retrieval algorithms, in addition to the lack of agreement
647 between the products of different satellite missions (Yang et al., 2013). Reanalysis products
648 give robust information combining different observations from multiple sources, including
649 remote sensing, and they are spatially complete, physically consistent and bias adjusted (Dee et
650 al., 2014).

651 In this study, we place our findings, which are summarised in

Trends: All areas	Summary Trends were significantly positive for all surface temperature anomalies data sets examined.
-----------------------------	--

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

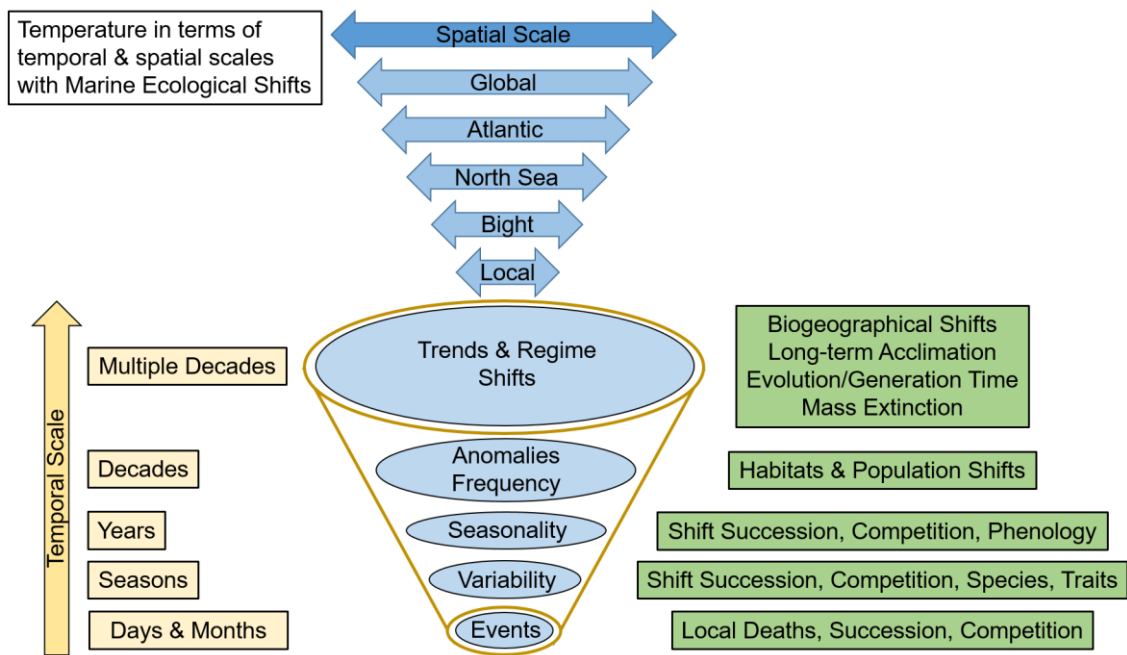
652 Table 11, in the marine ecological context and deliberate these in terms of time and space, as
653 scale plays a fundamental role when linking drivers to ecosystem function, species distributions
654 and biodiversity (Margalef, 1958). When considering habitat and population resilience in the
655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

662 Observations, which are made too far apart (in space or time), can result in one missing essential
663 ecosystem detail such as life cycle information or diel vertical migration patterns. Observations,
664 which are too close together (in space or time) might merely, reflect a moment of variability
665 rather than being related to the big picture. Moreover, environmental and ecosystem variables
666 and especially different species with differing adaptations, drivers and niches may not be inter-

667 comparable in terms of time and spatial scales. Mackas et al. (1985) showed that in a one-
668 dimensional transect of the North Sea temperature, chlorophyll and zooplankton had very
669 different variabilities and thus, obviously were controlled by different drivers. The complexity
670 of interrelating different species, which have widely different spatial ranges and different
671 patchiness, is well illustrated by Bertrand et al. (2014). The very basis of organism succession,
672 competition and co-occurrence in pelagic temperate environments is based on different scaling
673 in time and space of organisms. Temperature related match-mismatch phenomena (Cushing,
674 1990) between predators and their prey however, are founded up on the opposite situation, as
675 the organisms are dependent on the exact timing of their prey. Similarly, diurnal migration of
676 for example zooplankton is also very dependent on timing related to light and stable/ particular
677 triggers on mesoscales.

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

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



691

692 Figure 23 - Temporal and spatial scales of temperature in relation to marine biological systems.

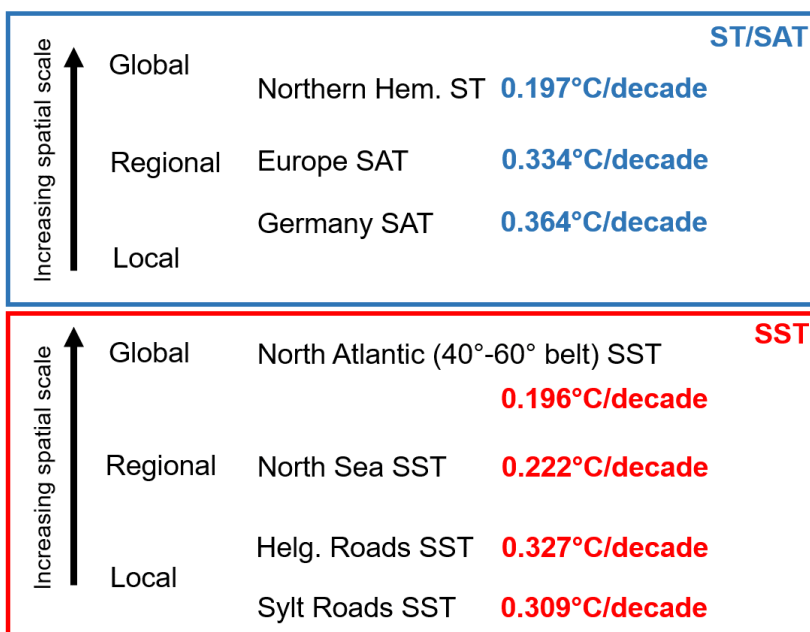
693

694 Depending on the type of reaction and adaptation, and especially if these are required to deal
 695 with daily variability (e.g. day-night temperatures) or long-term life cycle shifts and
 696 biogeographical changes in habitat, such as movement of organisms to cooler waters, the time
 697 scales can range from days to decades. Organisms also react to temperature shifts on time scales
 698 of generations, which can be anything upwards from days (e.g. phytoplankton and bacteria)
 699 through years and decades (e.g. fish, crustaceans) via epigenetics or evolutionary processes
 700 between generations (Cohen, 1967; Marshall & Burgess, 2015; Shama et al., 2016; Slatkin,
 701 1974; Wilson & MacArthur, 1967). The biological distribution of species both in terms of
 702 latitude and height/ depth has, since the studies by Humboldt & Bonpland (1805), been accepted
 703 to be related to global temperature gradients, and in marine phytoplankton it is not different
 704 (Righetti et al., 2019). This is not only the case for terrestrial environments; marine organisms
 705 and their habitats are also dependent on the temperature of their environment and its variability.
 706 A few excellent studies have shown how life cycles of marine organisms are shifted along
 707 biogeographical gradients (e.g., shore crabs and cod) (Gimenez, 2011; Perry et al. 2005; Pörtner

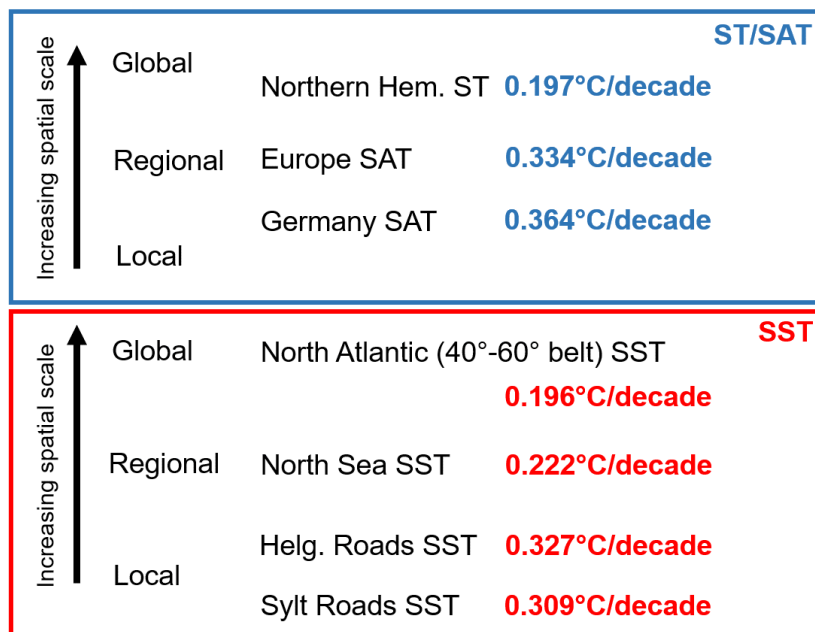
708 et al., 2017). The effects of in situ heat shock are well documented for corals and effects of cold
 709 winters or sudden cold on exposed marine tidal flats are another example (Büttger et al., 2011;
 710 Barceló et al., 2016; Giménez et al., 2021; Hackerott et al., 2021). How marine organisms react
 711 and adapt depend very much on their living environment and whether they can move away from
 712 stress. Thus, plankton and nekton or sessile benthic organisms will react differently and with
 713 different tolerance and long-term resilience (for review on this see Harvey et al. (2021))
 714 dependent on their life cycles. The manner in which marine organisms react to climate shifts
 715 and change is diverse. Most papers are interested in fish, however organisms at the bottom of
 716 the food web, i.e., plankton, which are at one with the waterbodies, are affected directly and
 717 cannot move well/ far in aquatic environments.

718 **4.1 Long-term Trends and the Role of Indices: Biogeographical Shifts Over Multiple Decades**
 719 **and Potential Regime Shifts.**

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



723
 724 Figure 24).



725

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

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

736 The SST of the North Sea is strongly correlated with the European and the German SAT and,
 737 to a lesser extent, with the North Atlantic SST and the Northern Hemisphere SAT. This shows
 738 that, like the data for the Dutch Wadden Sea, analysed by van Aaken in 2008, the two LTER
 739 sites in the German Bight are more driven by the terrestrial temperature regime than by the
 740 Atlantic temperature regime. This can be expected for a shallow sea bounded by land. It also

741 explains why areas in the Southern North Sea are warming faster than the areas in the Northern
742 North Sea (Scottish coast) (see Holliday et al., 2007).

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

748 We showed that the NAO index only relates well to the winter temperatures (December-
749 February) in both HR and Wadden Sea SR sites, due to the fact that the Icelandic low pressure
750 system is deeper during winter, showing strong gradient related to the Azores High (Rodwell et
751 al., 1999). Similar results have been found for the western Wadden Sea and Marsdiep area by
752 van Aken (2008), who also pointed out that, since 1982, the NAO does not show any persistent
753 trends. This was also seen here, and previously Wiltshire et al. (2010) showed that the NAO
754 index was also only useful in the winter months for explaining variability at Helgoland Roads.
755 In addition, we speculate that the Atlantic Multidecadal Oscillation (AMO), used to explain
756 biological phenomena in the North Sea and Atlantic (Alheit et al., 2014; Edwards et al., 2013),
757 would not be causal regarding biological shifts in the North Sea at regional and local scales.
758 The AMO, with its broad spatial distribution (0° - 60° N, 80° W- 0°), was minimally useful for
759 explaining any anomalies or variability in all of our temperature data. Therefore, the driver of
760 biological shifts would rather be the shifts in water masses. The North Atlantic (40° N- 60° N)
761 data was more representative for comparisons with the North Sea and HR and SR time series.
762 The AMO was considered to be an oscillatory index in the past, however its validity is currently
763 being questioned, based on recent literature by the original authors (Mann et al., 2021).

764 We have avoided discussion of so-called regime shifts in ecosystem drivers (temperature) here,
765 because of the temporal tenuousness of such identifications in time series of merely a few

766 decades. However, other authors have identified temporal shifts in the 1960s, 1980s and during
767 the period 1996 to 2003 in the North Sea (Beaugrand et al., 2008, 2014; Edwards et al., 2002;
768 Siegismund & Schrum, 2001). Beaugrand et al. (2014) suggests that these three shifts impacted
769 40% of the plankton species or taxa considered in a study of data of the CPR in the North Sea.
770 We highlight that in all of the temperature time series analysed for the Northern Hemisphere, a
771 distinct upwards shift in temperature trend can be seen in the late 1980s. One explanation for
772 this could be found in a decrease in cold spells and an increase in heat waves due to blocking
773 systems (Brunner et al., 2018).

774 Our comparisons of the temperature trends from local through to hemispheric scales, showed
775 comparable trends/ patterns over large spatial scales. We showed overall warming, which is
776 highest in the southern North Sea at HR. These trends will result in new biogeographical
777 gradients and redistribution of species, with cold adapted species moving further north, as is
778 currently being seen with for example cod (Drinkwater, 2005). This is where it becomes
779 important to link up with such spatial data sets as the CPR provides, where indeed, strong
780 evidence of species shifts on large spatial scales have been found (Beaugrand, 2004; Heath,
781 2005; Weijerman et al., 2005). However, data is exceedingly rare on species diversity overall,
782 and daily LTER data are non-existent. Therefore, we can only make the links through statistical
783 comparison of the drivers and shifts on different spatial scales and then add the knowledge we
784 have on organisms also via models.

785 4.2 Shifts in Seasonality: Local to Regional Shifts of Succession, Competition and Phenology

786
787 Overall, the daily variability has declined at HR and SR. Wiltshire et al. (2010) showed that the
788 number of growth days (defined as days with temperatures over 5°C) have increased
789 significantly at HR. This was also found in the present study for both HR and SR. When
790 subtracting the annual minimum from the annual maximum, we found a negative trend,
791 indicating that the difference between cold and warm days of the year has become smaller,

792 meaning that the strong seasonality of our regions has weakened. The positive temperature trend
793 in the cold season (winter and spring) was also larger than the positive trend in the warm season
794 (summer and autumn), i.e., again evidence that the seasonal cycle has become smaller with
795 time. Because the overall trend is a warming trend, with extension of warmth into the cooler
796 months, the growing period has become longer. This affects the timing and succession of
797 particularly microalgae (phytoplankton) and their predators (zooplankton). Investigations of
798 seasonal shifts in temperature, in units of days, weeks, months and seasons are required to
799 understand how temperature drives marine ecosystems. Growth rates, number of growth days,
800 phenology, enrichment of new species may then be related to long-term changes (Beaugrand
801 et al., 2014; Chivers et al., 2020; Scharfe & Wiltshire, 2019; Wiltshire et al., 2010). The
802 complex nature of the wind, tide and current interactions at Helgoland and Sylt result in large
803 daily variability of water conditions, both at HR and SR. We had no means of comparing marine
804 daily data with other regions, because unfortunately this is currently unavailable. It would be
805 interesting to compare our results with data from the Dutch Wadden Sea (van Aken, 2008) and
806 with the compilation of data for the Baltic Sea (Mackenzie & Schiedek, 2007) where it seems
807 that variability in the systems may have shifted considerably in the past 50 years. It is often
808 precisely this variability which results in growth triggers and controls (e.g. turbulence,
809 resuspension of sediments and nutrient recycling) and which are associated with seasonal shifts
810 (Philippart et al., 2003; Scharfe & Wiltshire, 2019; Wiltshire & Manly, 2004).

811 Wiltshire et al. (2015) have shown how the timing of the spring bloom of phytoplankton at HR
812 has shifted based on daily values and that this could be related to the continued overwintering
813 grazing of herbivorous zooplankton. Based on these works, Sommer & Lengfellner (2008)
814 carried out experiments in mesocosms with a modelling backdrop, to demonstrate how
815 temperature regulated the interaction of microzooplankton, zooplankton and phytoplankton
816 growth. Scharfe & Wiltshire (2019), in an analysis of key phytoplankton species, showed that
817 the timing, in days, of late winter/early spring (e.g. *Skeletonema spec.*), spring (e.g. *Ditylum*

818 *brightwellii*) and early summer species (e.g. *Rhizosolenia setigera*) have shifted forward in the
819 last 50 years, also often evincing longer periods of occurrence. However, the timing of others,
820 for example *Odontella sinensis* and *Thalassionema nitzschioides*, late summer/ autumn species
821 respectively, shifted towards central winter reflecting longer warm periods in autumn, as shown
822 in the temperature analyses of this paper. The work by Scharfe & Wiltshire (2019) and some
823 work by the CPR groups of SAHFOS (Hinder et al., 2012) have shown that the reaction of
824 species is specific to their enrichment time. Based mostly on weekly data, Beaugrand et al.
825 (2014), Greve et al. (2004) and Heath (2005) provide evidence that the phenology and
826 succession of species of zooplankton (copepods) have shifted at HR and in the greater North
827 Sea. As the timing of zooplankton and its life cycle stages are very dependent on the available
828 phytoplankton food, shifts in phytoplankton timing and species composition can be detrimental
829 to food web function, as proposed in the match-mismatch hypothesis by Cushing (1990). As
830 with the timing of land plants and the occurrence of pollinating insects or pests (Solga et al.,
831 2014) such timing relationships are often just as narrow in marine systems; in the order of days
832 or maximally weeks.

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

839 4.3 Maximum and Minimum Temperatures- Hot and Cold Spells: Physical and Behavioural 840 Adaptation; Competition with Neobiota; Local Species Extinction

841
842 We found that there was a significant shift towards much more presence of very warm months
843 with values over 17°C and 18°C at HR and SR since 1991, while the very cold months (mean

844 values below $< 2^{\circ}\text{C}$ and $< 3^{\circ}\text{C}$) have become significantly less common. An associated study
845 (Gimenez et al., in prep.), based on HR, showed that the frequency of marine heatwaves has
846 increased, especially after the 1990 and that the major heatwaves coincide with large
847 atmospheric European summer heatwaves or mild winter spells. Hence, different forms of data
848 analyses highlight the increasing prevalence of warm periods for the German Bight.

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

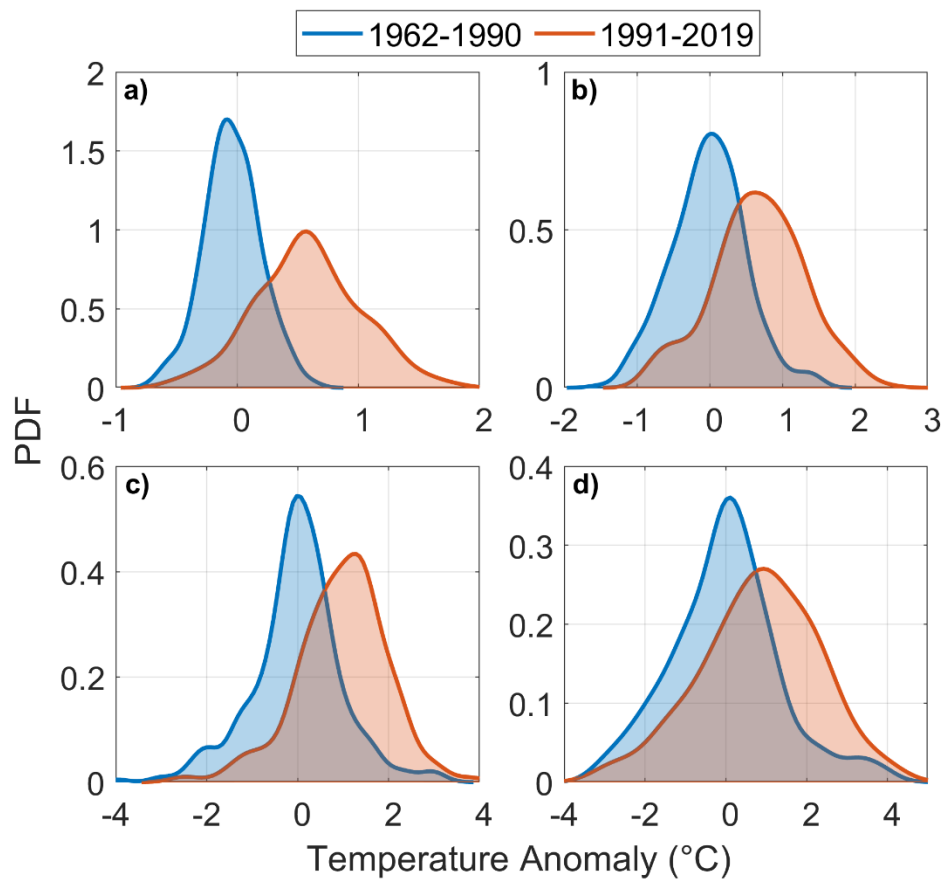
863 Based on this data for the increased number of months/days with maximum temperatures plus
864 the evinced trends for HR, SR, the North Sea and North Atlantic it is clear that “warm waters
865 are the new normal”. Species, no matter when they occur, will have to cope with warmer waters
866 and many more days with much warmer maximum and minimum temperatures. Brunner et al.
867 (2018) have examined the cold spells and especially the increase in warm spells in Europe and
868 related these to blocking systems. They found that over 80% of cold spells in southeastern

869 Europe occur during blocking and that warm spells are correlated with blocking mostly in
870 northern Europe. They suggest that, in future, cold snaps are likely to become even more
871 important in these new warmer normal, as they seem to be associated to each other.

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

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

891 Plots of the frequency distributions of the temperature anomalies for the North Atlantic, North
892 Sea and HR and SR (



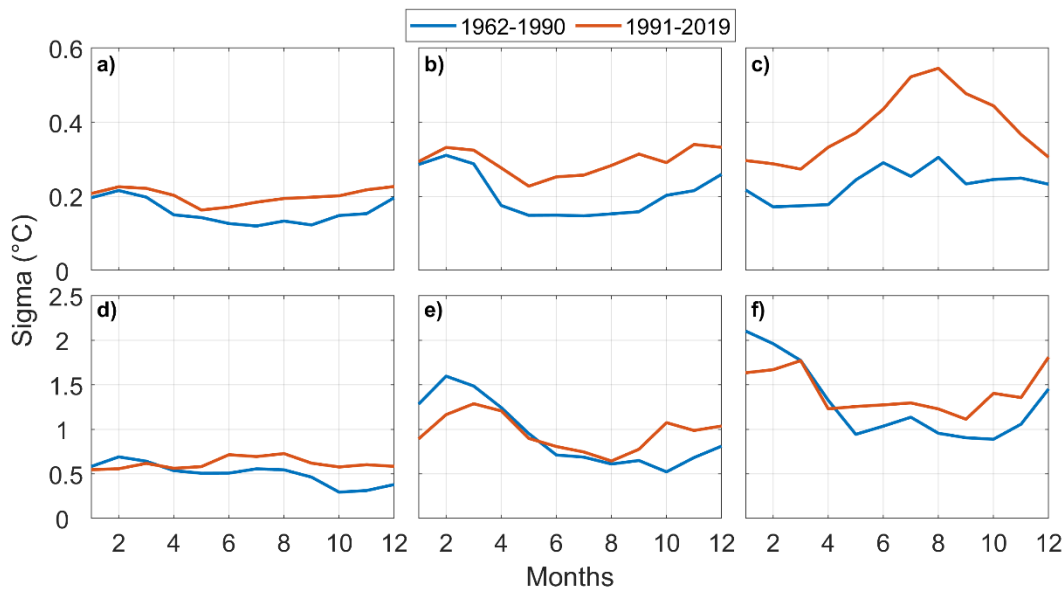
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894 Figure 12) showed that the anomalous temperature density distribution clearly shifted to higher
 895 temperatures in the later years in all spatial areas. Interestingly, especially in the North Atlantic,
 896 the maximum and minimum values of the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

902 4.4 Variability on the Long-Term: Physical and Behavioural Adaptation; Local Species
 903 Extinction, Shifts in Growing Season and Biogeographical Species Distribution

904

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



913
 914 Figure 25 - The seasonal variation of the standard deviation of the SST in all spatial scales (from
 915 Global to local) for the first (blue) and second half (orange) of the time series. a) Global; b)
 916 Northern Hemisphere; c) North Atlantic 40°-60°; d) North Sea; e) Helgoland and f) Sylt. The
 917 y-axis scales are different for top and bottom rows, showing the increase in variability from
 918 larger to smaller spatial scales.

919 Aquatic ecosystem variability can be considered a driver of species diversity, thus, it is
 920 important to evaluate the magnitude of variability changes in climate change studies (Borics et
 921 al., 2013; D’Odorico et al., 2008; Dornelas, 2010; Flöder & Sommer, 1999). Indeed,

922 explanation of species diversity as a function of ecosystem variability is subject of a long-term
923 discussion in the literature (e.g., Collins, 1990; Connell, 1978; Grime, 1973; Robinson &
924 Minshall, 1986). Sarker et al. (2018) describe the 1980s as the period of high ecosystem
925 variability at the Helgoland Roads Time Series station, with a considerably less variable period
926 identified after the 1990s. They also showed that both diversity and species occurrence
927 probability declined with the increase of ecosystem variability. The occurrence of more species
928 was seen at low ecosystem variability without a loss of rare species already in the system. This
929 implies a high level of niche differentiation, reducing interspecies competition and lack of
930 exclusion and this directly increases species diversity. Indeed, increasing species diversity and
931 the co-existence of neo biota and indigenous species has been going on in the North Sea and
932 especially the German Bight for the past 20-30 years (Buschbaum & Gutow, 2005; Greve et al.,
933 2004; Reise et al., 2017; Wiltshire et al., 2010). This reflects the ecosystem theory that the
934 warming of a cold temperate sea will allow for more species. Beaugrand et al. (2008) also
935 showed that the 1980s overall were a period of high variability, whereas the 1990s were
936 identified with a low variability in the North Atlantic region. Conversi et al. (2010) observed
937 similar change in the late 1980s in long-term records of Mediterranean ecological and hydro-
938 climate variables.

939 Temperature variability induced by shifts in larger weather patterns, including storm patterns
940 such as El Nino and Blocking Systems, can be translated to shifts in hydrography, turbulence,
941 stratification and, in coastal systems, freshwater input from rivers. Such shifts affect e.g.,
942 primary productivity, fish distribution, spawning timing and species distribution of planktonic
943 organisms (Dippner, 1997; Mackenzie & Schiedek, 2007; Root et al., 2003; Stenseth et al.,
944 2004). Here, we also considered the indicator indices of large Northern Hemisphere climate
945 patterns, namely the NAO and the (in the meantime questionable) AMO (Mann et al., 2021).
946 These indices are often used in the literature to explain events and as links to organism
947 distribution e.g. fish, bivalves and copepods (Alheit et al., 2014; Dippner, 1997; Philippart et

948 al., 2003; Reid et al., 2003). It is not logical to link the large-scale climate indices such as NAO
949 to marine organisms directly, as these are not drivers in themselves. Rather, it is the effect of
950 the large-scale weather patterns on hydrography and temperature, which can be drivers of the
951 pelagic distribution and species life cycles (van Aken, 2008). For example, it is not the NAO
952 that drives the shift of *Calanus helgolandicus* vs. *Calanus finmarchicus*, but rather the inflow
953 of the Atlantic Ocean into the North Sea, which transports the Atlantic species *C. finmarchicus*
954 more or less into the North Sea. This inflow is related to large-scale weather pattern fluctuations
955 of which the NAO is an indicator (Heath et al., 1999). This can also be seen in the study on
956 timing of spawning of *Limecola (Macoma) baltica*, by Philippart et al. (2003) and van Aken
957 (2008). Philippart et al. (2003) postulated that this was related to the NAO index, but later it was
958 found by van Aken that it is not likely that the NAO is directly related to spawning and it is
959 certainly as an index, not the trigger. They consider the long-term trend in temperature to be the
960 reason for earlier triggering and not zonal winter winds reflected by the NAO pressure index.
961 Boersma et al (2016) have shown that it is also very important to understand the frequency
962 distributions of temperature which organisms are subjected to rather than max/ min curves only.
963 As the frequency distributions for temperature data and their anomalies have shifted
964 considerably over the past 20 years on all the special scales we examined, we can assume that
965 especially animals, which have tight temperature adaptations, will have to move or acclimate
966 in all examined areas.

967 Animals will react differently to temperature changes than plants. Plants, including marine
968 phytoplankton and macroalgae, moving further north or indeed into cooler deeper waters will
969 also have to adjust their photosynthesis apparatus to deal with different light regimes
970 (Falkowski, 1984; Jorda et al., 2020). The highly significant shifts in seasonality and the
971 associated very much warmer winters and autumns are much more visible at the Wadden Sea
972 (SR) and German Bight (HR) sites than in the North Atlantic, due to the higher heat capacity
973 larger and deeper water bodies, like the latter, present. Even in the North Sea, this is not so

974 pronounced. Such local to regional effects can result in shifts in the phenology, spawning time
975 and/or life cycles of bivalves and other species, and result in match-mismatch food web
976 situations (Edwards & Richardson, 2004).

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

983 5 CONCLUSION

984

985 Marine ecosystem function is governed by the scale-dependent nature of physical processes.
986 These are also reflected in both coupling and differences among processes occurring in the
987 ocean, the coastal zone and land, requiring reliable temperature data and assessments of this
988 data. Here, we provided a study on how temperature behaves on different spatial scales, the
989 magnitude of changes in trends and variability and the representability of local scales in larger
990 scales and vice-versa. From global to local, all temperature trends are positive, corroborated by
991 the significant positive correlations among the analysed areas and sites. For the local and
992 regional scales, the highest correlations observed between the sea sites and the closest land mass
993 is an important result. This allows us to understand the variability mechanisms of temperature
994 change in the North Sea. The large-scale phenomena such as AMO and NAO which are often
995 considered important do not necessarily have a significant influence on regional and local
996 scales. Evaluations and the observed changes in variability, seasonal as well as inter-annual,
997 cannot be ignored in temperature considerations, as they are part of the significant changes
998 occurring in temperature affecting ecological systems. We provide this information as a basis

999 for marine biological and ecological research, and especially for considerations of responses in
1000 organisms and environments to temperature shifts and changes on diverse scales. We thus
1001 provided the necessary information to increase the robustness of predictability and assessments
1002 of future climate risk to biological systems.

1003

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1011 CONFLICT OF INTEREST

1012 The authors declare that they have no conflict of interest.

1013 AUTHOR CONTRIBUTIONS

1014 MS and KW initiated this study. KW, FA, and PL developed the research ideas, conceptualized
1015 and designed the study. FA downloaded, compiled and prepared all data. FA, PL, KW, and JR
1016 performed data analysis. KW, JR, KC and SP provided the HR and quality controlled and
1017 validated the in situ data. KW and FA wrote the first draft of the manuscript, PL, KW and LG
1018 provided the global view. All authors contributed substantially to discussion. FA finalized and
1019 edited the manuscript. All authors contributed substantially to revisions.

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1023 REFERENCES

1024

- 1025 Addicott, J. F., Aho, J. M., Antolin, M. F., Padilla, D. K., Richardson, J. S., & Soluk, D. A.
1026 (1987). Ecological Neighborhoods: Scaling Environmental Patterns. *Oikos*, 49(3), 340–346.
1027 <https://doi.org/10.2307/3565770>
- 1028 Ainsworth, T. D., Hurd, C. L., Gates, R. D., & Boyd, P. W. (2020). How do we overcome
1029 abrupt degradation of marine ecosystems and meet the challenge of heat waves and climate
1030 extremes? *Global Change Biology*, 26(2), 343–354. <https://doi.org/10.1111/gcb.14901>
- 1031 Alheit, J., Licandro, P., Coombs, S., Garcia, A., Giráldez, A., Santamaría, M. T. G., Slotte, A.,
1032 & Tsikliras, A. C. (2014). Reprint of “Atlantic Multidecadal Oscillation (AMO) modulates
1033 dynamics of small pelagic fishes and ecosystem regime shifts in the eastern North and Central
1034 Atlantic.” *Journal of Marine Systems*, 133, 88–102.
1035 <https://doi.org/10.1016/J.JMARSYS.2014.02.005>
- 1036 Androsov, A., Fofonova, V., Kuznetsov, I., Danilov, S., Rakowsky, N., Harig, S., Brix, H., &
1037 Wiltshire, K. H. (2019). FESOM-C v.2: coastal dynamics on hybrid unstructured meshes.
1038 *Geoscientific Model Development*, 12(3), 1009–1028. [https://doi.org/10.5194/gmd-12-1009-](https://doi.org/10.5194/gmd-12-1009-2019)
1039 2019
- 1040 Arias-Ortiz, A., Serrano, O., Masqué, P. et al. (2018). A marine heatwave drives massive
1041 losses from the world’s largest seagrass carbon stocks. *Nature Climate Change*, 8, 338–344.
1042 <https://doi.org/10.1038/s41558-018-0096-y>
- 1043 Asch, R. G., Stock, C. A., & Sarmiento, J. L. (2019). Climate change impacts on mismatches
1044 between phytoplankton blooms and fish spawning phenology. *Global Change Biology*, 25(8),
1045 2544–2559. <https://doi.org/10.1111/gcb.14650>
- 1046 Baracchini, T., Chu, P. Y., Šukys, J., Lieberherr, G., Wunderle, S., Wüest, A., & Bouffard, D.
1047 (2020). Data assimilation of in situ and satellite remote sensing data to 3D hydrodynamic lake
1048 models: a case study using Delft3D-FLOW v4.03 and OpenDA v2.4. *Geoscientific Model*
1049 *Development*, 13(3), 1267–1284. <https://doi.org/10.5194/gmd-13-1267-2020>
- 1050 Barceló, C., Ciannelli, L., Olsen, E. M., Johannessen, T., & Knutsen, H. (2016). Eight decades
1051 of sampling reveal a contemporary novel fish assemblage in coastal nursery habitats. *Global*
1052 *Change Biology*, 22(3), 1155–1167. <https://doi.org/https://doi.org/10.1111/gcb.13047>
- 1053 Barnard, P. L., Dugan, J. E., Page, H. M., Wood, N. J., Hart, J. A. F., Cayan, D. R., Erikson,
1054 L. H., Hubbard, D. M., Myers, M. R., Melack, J. M., & Iacobellis, S. F. (2021). Multiple
1055 climate change-driven tipping points for coastal systems. *Scientific Reports*, 11(1).
1056 <https://doi.org/10.1038/s41598-021-94942-7>
- 1057 Beaugrand, G. (2004). The North Sea regime shift: evidence, causes, mechanisms and
1058 consequences. *Progress in Oceanography*, 60(2–4), 245–262.
- 1059 Beaugrand, G., Edwards, M., Brander, K., Luczak, C., & Ibanez, F. (2008). Causes and
1060 projections of abrupt climate-driven ecosystem shifts in the North Atlantic. *Ecology Letters*,
1061 11(11), 1157–1168. <https://doi.org/https://doi.org/10.1111/j.1461-0248.2008.01218.x>
- 1062 Beaugrand, G., Harlay, X., & Edwards, M. (2014). Detecting plankton shifts in the North Sea:
1063 a new abrupt ecosystem shift between 1996 and 2003. *Marine Ecology Progress Series*, 502,
1064 85–104. <https://www.int-res.com/abstracts/meps/v502/p85-104/>
- 1065 Becker, G. (1996). Sea surface temperature changes in the North Sea and their causes. *ICES*
1066 *Journal of Marine Science*, 53(6), 887–898. <https://doi.org/10.1006/jmsc.1996.0111>
- 1067 Bertrand, A., Grados, D., Colas, F., Bertrand, S., Capet, X., Chaigneau, A., Vargas, G.,
1068 Mousseigne, A., & Fablet, R. (2014). Broad impacts of fine-scale dynamics on seascape

1069 structure from zooplankton to seabirds. *Nature Communications*, 5(1), 5239.
1070 <https://doi.org/10.1038/ncomms6239>

1071 Billé, R., Chabason, L., Drankier, P., Molenaar, E. J., & Rochette, J. (n.d.). *Making Regional*
1072 *Seas Programmes, Regional Fishery Bodies and Large Marine Ecosystem Mechanisms Work*
1073 *Better Together*. Retrieved February 9, 2022, from www.unep.org/regionalseas

1074 Boersma, M., Grüner, N., Tasso Signorelli, N., Montoro González, P. E., Peck, M. A., &
1075 Wiltshire, K. H. (2016). Projecting effects of climate change on marine systems: is the mean
1076 all that matters? *Proceedings of the Royal Society B: Biological Sciences*, 283(1823),
1077 20152274.

1078 Borics, G., Várbíró, G., & Padisák, J. (2013). Disturbance and stress: different meanings in
1079 ecological dynamics? *Hydrobiologia*, 711(1), 1–7. <https://doi.org/10.1007/s10750-013-1478-9>

1080 Boyd, P. W., Rynearson, T. A., Armstrong, E. A., Fu, F., Hayashi, K., Hu, Z., Hutchins, D.
1081 A., Kudela, R. M., Litchman, E., & Mulholland, M. R. (2013). Marine phytoplankton
1082 temperature versus growth responses from polar to tropical waters—outcome of a scientific
1083 community-wide study. *PloS One*, 8(5), e63091.

1084 Brunner, L., Schaller, N., Anstey, J., Sillmann, J., & Steiner, A. K. (2018). Dependence of
1085 Present and Future European Temperature Extremes on the Location of Atmospheric
1086 Blocking. *Geophysical Research Letters*, 45(12), 6311–6320.
1087 <https://doi.org/https://doi.org/10.1029/2018GL077837>

1088 Bryndum-Buchholz, A., Tittensor, D. P., Blanchard, J. L., Cheung, W. W. L., Coll, M.,
1089 Galbraith, E. D., Jennings, S., Maury, O., & Lotze, H. K. (2019). Twenty-first-century climate
1090 change impacts on marine animal biomass and ecosystem structure across ocean basins.
1091 *Global Change Biology*, 25(2), 459–472. <https://doi.org/10.1111/gcb.14512>

1092 Buschbaum, C., & Gutow, L. (2005). Mass occurrence of an introduced crustacean (*Caprella*
1093 *cf. mutica*) in the south-eastern North Sea. *Helgoland Marine Research*, 59(3), 252–253.

1094 Büttger, H., Nehls, G. & Witte, S. (2011). High mortality of Pacific oysters in a cold winter in
1095 the North-Frisian Wadden Sea. *Helgoland Marine Research* 65, 525–532.
1096 <https://doi.org/10.1007/s10152-011-0272-1>

1097 Capuzzo, E., Lynam, C. P., Barry, J., Stephens, D., Forster, R. M., Greenwood, N.,
1098 McQuatters-Gollop, A., Silva, T., van Leeuwen, S. M., & Engelhard, G. H. (2018). A decline
1099 in primary production in the North Sea over 25 years, associated with reductions in
1100 zooplankton abundance and fish stock recruitment. *Global Change Biology*, 24(1), e352–
1101 e364. <https://doi.org/10.1111/gcb.13916>

1102 Chivers, W. J., Edwards, M., & Hays, G. C. (2020). Phenological shuffling of major marine
1103 phytoplankton groups over the last six decades. *Diversity and Distributions*, 26(5), 536–548.
1104 <https://doi.org/10.1111/ddi.13028>

1105 Cohen, D. (1967). Optimizing reproduction in a randomly varying environment when a
1106 correlation may exist between the conditions at the time a choice has to be made and the
1107 subsequent outcome. *Journal of Theoretical Biology*, 16(1), 1–14.
1108 [https://doi.org/https://doi.org/10.1016/0022-5193\(67\)90050-1](https://doi.org/https://doi.org/10.1016/0022-5193(67)90050-1)

1109 Collins, S. L. (1990). Effects of fire on community structure in tallgrass and mixed-grass
1110 prairie. *Fire in North American Tallgrass Prairies*, 81–98.

1111 Connell, J. H. (1978). Diversity in tropical rain forests and coral reefs: high diversity of trees
1112 and corals is maintained only in a nonequilibrium state. *Science*, 199(4335), 1302–1310.

1113 Conversi, A., Fonda Umani, S., Peluso, T., Molinero, J. C., Santojanni, A., & Edwards, M.
1114 (2010). The Mediterranean Sea regime shift at the end of the 1980s, and intriguing
1115 parallelisms with other European basins. *Plos One*, 5(5), e10633.

1116 Cushing, D. H. (1990). Plankton Production and Year-class Strength in Fish Populations: an
1117 Update of the Match/Mismatch Hypothesis. In J. H. S. Blaxter & A. J. Southward (Eds.),
1118 *Advances in Marine Biology* (Vol. 26, pp. 249–293). Academic Press.
1119 [https://doi.org/https://doi.org/10.1016/S0065-2881\(08\)60202-3](https://doi.org/https://doi.org/10.1016/S0065-2881(08)60202-3)

1120 Dale, B. (2001). The sedimentary record of dinoflagellate cysts: looking back into the future
1121 of phytoplankton blooms. *Scientia Marina*, 65(S2), 257–272.

1122 Data.GISS: GISS Surface Temperature Analysis (GISTEMP v4). (2022). Retrieved February
1123 9, 2022, from <https://data.giss.nasa.gov/gistemp/>

1124 Data Publisher for Earth & Environmental Science. (2022). Retrieved February 9, 2022, from
1125 <https://pangaea.de/>

1126 de Boeck, H. J., Dreesen, F. E., Janssens, I. A., & Nijs, I. (2010). Climatic characteristics of
1127 heat waves and their simulation in plant experiments. *Global Change Biology*, 16(7), 1992–
1128 2000.

1129 Dee, D. P., M. Balsameda, G. Balsamo, R. Engelen, A. J. Simmons, & J. Thépaut, (2014).
1130 Toward a Consistent Reanalysis of the Climate System. *Bulletin of the American*
1131 *Meteorological Society*, 95, 1235–1248, <https://doi.org/10.1175/BAMS-D-13-00043.1>.

1132 Defriez, E. J., Sheppard, L. W., Reid, P. C., & Reuman, D. C. (2016). Climate change-related
1133 regime shifts have altered spatial synchrony of plankton dynamics in the North Sea. *Global*
1134 *Change Biology*, 22(6), 2069–2080. <https://doi.org/10.1111/gcb.13229>

1135 Dippner, J. W. (1997). Recruitment success of different fish stocks in the North Sea in
1136 relation to climate variability. *Deutsche Hydrografische Zeitschrift*, 49(2), 277–293.

1137 D’Odorico, P., Laio, F., Ridolfi, L., & Lerda, M. T. (2008). Biodiversity enhancement
1138 induced by environmental noise. *Journal of Theoretical Biology*, 255(3), 332–337.
1139 <https://doi.org/https://doi.org/10.1016/j.jtbi.2008.09.007>

1140 Dornelas, M. (2010). Disturbance and change in biodiversity. *Philosophical Transactions of*
1141 *the Royal Society B: Biological Sciences*, 365(1558), 3719–3727.
1142 <https://doi.org/10.1098/rstb.2010.0295>

1143 Drinkwater, K. F. (2005). The response of Atlantic cod (*Gadus morhua*) to future climate
1144 change. *Ices Journal of Marine Science*, 62(7), 1327–1337.

1145 Edwards, M., Beaugrand, G., Hays, G. C., Koslow, J. A., & Richardson, A. J. (2010). Multi-
1146 decadal oceanic ecological datasets and their application in marine policy and management.
1147 *Trends in Ecology & Evolution*, 25(10), 602–610.
1148 <https://doi.org/10.1016/J.TREE.2010.07.007>

1149 Edwards, M., Beaugrand, G., Helaouët, P., Alheit, J., & Coombs, S. (2013). Marine
1150 Ecosystem Response to the Atlantic Multidecadal Oscillation. *PLoS ONE*, 8(2), e57212.
1151 <https://doi.org/10.1371/journal.pone.0057212>

1152 Edwards, M., Beaugrand, G., Reid, P. C., Rowden, A. A., & Jones, M. B. (2002). Ocean
1153 climate anomalies and the ecology of the North Sea. *Marine Ecology Progress Series*, 239, 1–
1154 10. <https://www.int-res.com/abstracts/meps/v239/p1-10/>

1155 Edwards, M., & Richardson, A. J. (2004). Impact of climate change on marine pelagic
1156 phenology and trophic mismatch. *Nature*, 430(7002), 881–884.
1157 <https://doi.org/10.1038/nature02808>

1158 Falkowski, P. G. (1984). Physiological responses of phytoplankton to natural light regimes.
1159 *Journal of Plankton Research*, 6(2), 295–307. <https://doi.org/10.1093/plankt/6.2.295>

1160 Fellous, A., Wegner, K. M., John, U., Mark, F. C., & Shama, L. N. S. (2022). Windows of
1161 opportunity: Ocean warming shapes temperature-sensitive epigenetic reprogramming and
1162 gene expression across gametogenesis and embryogenesis in marine stickleback. *Global*
1163 *Change Biology*, 28(1), 54–71. <https://doi.org/10.1111/gcb.15942>

1164 Flöder, S., & Sommer, U. (1999). Diversity in planktonic communities: An experimental test
1165 of the intermediate disturbance hypothesis. *Limnology and Oceanography*, 44(4), 1114–1119.
1166 <https://doi.org/https://doi.org/10.4319/lo.1999.44.4.1114>

1167 Frajka-Williams, E., Beaulieu, C., & Duche, A. (2017). Emerging negative Atlantic
1168 Multidecadal Oscillation index in spite of warm subtropics. *Scientific Reports 2017 7:1*, 7(1),
1169 1–8. <https://doi.org/10.1038/s41598-017-11046-x>

1170 Frölicher, T. L., & Laufkötter, C. (2018). Emerging risks from marine heat waves. In *Nature*
1171 *Communications* (Vol. 9, Issue 1). Nature Publishing Group. [https://doi.org/10.1038/s41467-](https://doi.org/10.1038/s41467-018-03163-6)
1172 018-03163-6

1173 Giménez, L. (2011). Exploring mechanisms linking temperature increase and larval
1174 phenology: The importance of variance effects. *Journal of Experimental Marine Biology and*
1175 *Ecology*, 400(1-2), 227–235. <https://doi.org/10.1016/j.jembe.2011.02.036>

1176 Giménez, L., Chatterjee, A., & Torres, G. (2021). A state-space approach to understand
1177 responses of organisms, populations and communities to multiple environmental drivers.
1178 *Communications Biology*, 4(1), 1142. <https://doi.org/10.1038/s42003-021-02585-1>

1179 Gittings, J. A., Raitsos, D. E., Krokos, G., & Hoteit, I. (2018). Impacts of warming on
1180 phytoplankton abundance and phenology in a typical tropical marine ecosystem. *Scientific*
1181 *Reports*, 8(1). <https://doi.org/10.1038/s41598-018-20560-5>

1182 Gregory, B., Christophe, L., & Martin, E. (2009). Rapid biogeographical plankton shifts in the
1183 North Atlantic Ocean. *Global Change Biology*, 15(7), 1790–1803.
1184 <https://doi.org/10.1111/j.1365-2486.2009.01848.x>

1185 Greve, W., Reiners, F., Nast, J., & Hoffmann, S. (2004). Helgoland Roads meso- and
1186 macrozooplankton time-series 1974 to 2004: lessons from 30 years of single spot, high
1187 frequency sampling at the only off-shore island of the North Sea. *Helgoland Marine*
1188 *Research*, 58(4), 274–288. <https://doi.org/10.1007/s10152-004-0191-5>

1189 Grime, J. P. (1973). Competitive exclusion in herbaceous vegetation. *Nature*, 242(5396), 344–
1190 347.

1191 IPCC. (2018). Global warming of 1.5°C: An IPCC special report on the impacts of global
1192 warming of 1.5°C above pre-industrial levels and related global greenhouse gas emission
1193 pathways, in the context of strengthening the global response to the threat of climate change,
1194 sustainable development, and efforts to eradicate poverty. Intergovernmental Panel on
1195 Climate Change. Retrieved from <https://www.ipcc.ch/sr15/>

1196 IPCC. (2019). Summary for policymakers. In H.-O. Pörtner, D. C. Roberts, V. Masson-
1197 Delmotte, P. Zhai, M. Tignor, E. Poloczanska, K. Mintenbeck, A. Alegría, M. Nicolai, A.
1198 Okem, J. Petzold, B. Rama, & N. M. Weyer (Eds.), IPCC special report on the ocean and
1199 cryosphere in a changing climate. Intergovernmental Panel on Climate Change. Retrieved
1200 from <https://www.ipcc.ch/srocc/>

1201 Hackerott, S., Martell, H. A., & Eirin-Lopez, J. M. (2021). Coral environmental memory:
1202 causes, mechanisms, and consequences for future reefs. *Trends in Ecology & Evolution*,
1203 36(11), 1011–1023. <https://doi.org/10.1016/j.tree.2021.06.014>

1204 Harvey, B. P., Marshall, K. E., Harley, C. D. G., & Russell, B. D. (2021). Predicting
1205 responses to marine heatwaves using functional traits. *Trends in Ecology & Evolution*.

1206 Hayashida, H., Matear, R. J., & Strutton, P. G. (2020). Background nutrient concentration
1207 determines phytoplankton bloom response to marine heatwaves. *Global change biology*,
1208 26(9), 4800–4811. <https://doi.org/10.1111/gcb.15255>

1209 Heath, M. R. (2005). Changes in the structure and function of the North Sea fish foodweb,
1210 1973–2000, and the impacts of fishing and climate. *ICES Journal of Marine Science*, 62(5),
1211 847–868. <https://doi.org/10.1016/j.icesjms.2005.01.023>

1212 Heath, M. R., Backhaus, J. O., Richardson, K., McKenzie, E., Slagstad, D., Beare, D., Dunn,
1213 J., Fraser, J. G., Gallego, A., Hainbucher, D., Hay, S., Jónasdóttir, S., Madden, H.,
1214 Mardaljevic, J., & Schacht, A. (1999). Climate fluctuations and the spring invasion of the
1215 North Sea by *Calanus finmarchicus*. *Fisheries Oceanography*, 8(s1), 163–176.
1216 <https://doi.org/10.1046/j.1365-2419.1999.00008.x>

1217 Hinder, S. L., Hays, G. C., Edwards, M., Roberts, E. C., Walne, A. W., & Gravenor, M. B.
1218 (2012). Changes in marine dinoflagellate and diatom abundance under climate change. *Nature*
1219 *Climate Change*, 2(4), 271–275. <https://doi.org/10.1038/nclimate1388>

1220 Holliday, N. P., Kennedy, J., Kent, E. C., Marsh, R., Hughes, S. L., Sherwin, T., & Berry, D.
1221 I. (2007). Sea temperature. *Marine Climate Change Impacts Annual Report Card, 2008*.
1222 Holt, J., Hughes, S., Hopkins, J., Wakelin, S. L., Penny Holliday, N., Dye, S., González-Pola,
1223 C., Hjøllø, S. S., Mork, K. A., Nolan, G., Proctor, R., Read, J., Shammon, T., Sherwin, T.,
1224 Smyth, T., Tattersall, G., Ward, B., & Wiltshire, K. H. (2012). Multi-decadal variability and
1225 trends in the temperature of the northwest European continental shelf: A model-data
1226 synthesis. *Progress in Oceanography, 106*, 96–117.
1227 <https://doi.org/https://doi.org/10.1016/j.pocean.2012.08.001>
1228 Humboldt, A. von, & Bonpland, A. (1805). *Analysis of the geography of plants*.
1229 Hurrell, J. W., Kushnir, Y., & Visbeck, M. (2001). The North Atlantic Oscillation. *Science*,
1230 *291*(5504), 603–605. <https://doi.org/10.1126/science.1058761>
1231 *Hurrell North Atlantic Oscillation (NAO) Index (PC-based) | NCAR - Climate Data Guide*.
1232 (n.d.). Retrieved February 9, 2022, from [https://climatedataguide.ucar.edu/climate-](https://climatedataguide.ucar.edu/climate-data/hurrell-north-atlantic-oscillation-nao-index-pc-based)
1233 [data/hurrell-north-atlantic-oscillation-nao-index-pc-based](https://climatedataguide.ucar.edu/climate-data/hurrell-north-atlantic-oscillation-nao-index-pc-based)
1234 Jorda, G., Marbà, N., Bennett, S., Santana-Garçon, J., Agustí, S., & Duarte, C. M. (2020).
1235 Ocean warming compresses the three-dimensional habitat of marine life. *Nature Ecology &*
1236 *Evolution, 4*(1), 109–114. <https://doi.org/10.1038/s41559-019-1058-0>
1237 Kennedy, J. J., Rayner, N. A., Smith, R. O., Parker, D. E., & Saunby, M. (2011a). Reassessing
1238 biases and other uncertainties in sea surface temperature observations measured in situ since
1239 1850: 1. Measurement and sampling uncertainties. *Journal of Geophysical Research*,
1240 *116*(D14), D14103. <https://doi.org/10.1029/2010JD015218>
1241 Kennedy, J. J., Rayner, N. A., Smith, R. O., Parker, D. E., & Saunby, M. (2011b).
1242 Reassessing biases and other uncertainties in sea surface temperature observations measured
1243 in situ since 1850: 2. Biases and homogenization. *Journal of Geophysical Research*,
1244 *116*(D14), D14104. <https://doi.org/10.1029/2010JD015220>
1245 Kjellström, E., Nikulin, G., Strandberg, G., Christensen, O. B., Jacob, D., Keuler, K.,
1246 Lenderink, G., van Meijgaard, E., Schär, C., & Somot, S. (2018). European climate change at
1247 global mean temperature increases of 1.5 and 2 C above pre-industrial conditions as simulated
1248 by the EURO-CORDEX regional climate models. *Earth System Dynamics, 9*(2), 459–478.
1249 Lenssen, N. J. L., Schmidt, G. A., Hansen, J. E., Menne, M. J., Persin, A., Ruedy, R., & Zyss,
1250 D. (2019). Improvements in the GISTEMP Uncertainty Model. *Journal of Geophysical*
1251 *Research: Atmospheres, 124*(12), 6307–6326. <https://doi.org/10.1029/2018JD029522>
1252 Lenz, M., da Gama, B. A. P., Gerner, N. v, Gobin, J., Gröner, F., Harry, A., Jenkins, S. R.,
1253 Kraufvelin, P., Mummelthei, C., Sareyka, J., Xavier, E. A., & Wahl, M. (2011). Non-native
1254 marine invertebrates are more tolerant towards environmental stress than taxonomically
1255 related native species: Results from a globally replicated study. *Environmental Research*,
1256 *111*(7), 943–952. <https://doi.org/https://doi.org/10.1016/j.envres.2011.05.001>
1257 Levin, S. A. (1992). The Problem of Pattern and Scale in Ecology: The Robert H. MacArthur
1258 Award Lecture. *Ecology, 73*(6), 1943–1967. <https://doi.org/10.2307/1941447>
1259 Lima, F. P., & Wethey, D. S. (2012). Three decades of high-resolution coastal sea surface
1260 temperatures reveal more than warming. *Nature Communications, 3*.
1261 <https://doi.org/10.1038/ncomms1713>
1262 Lohmann, G., & Wiltshire, K. H. (2012). Winter atmospheric circulation signature for the
1263 timing of the spring bloom of diatoms in the North Sea. *Marine Biology, 159*(11), 2573–2581.
1264 <https://doi.org/10.1007/S00227-012-1993-7/FIGURES/7>
1265 Mackas, D. L., Denman, K. L., & Abbott, M. R. (1985). Plankton patchiness: biology in the
1266 physical vernacular. *Bulletin of Marine Science, 37*(2), 652–674.
1267 Mackenzie, B. R., & Schiedek, D. (2007). Daily ocean monitoring since the 1860s shows
1268 record warming of northern European seas. *Global Change Biology, 13*(7), 1335–1347.
1269 <https://doi.org/https://doi.org/10.1111/j.1365-2486.2007.01360.x>

1270 Madeira, D., Narciso, L., Cabral, H. N., & Vinagre, C. (2012). Thermal tolerance and
1271 potential impacts of climate change on coastal and estuarine organisms. *Journal of Sea*
1272 *Research*, 70, 32–41. [https://doi.org/https://doi.org/10.1016/j.seares.2012.03.002](https://doi.org/10.1016/j.seares.2012.03.002)
1273 Mann, M. E., Steinman, B. A., Brouillette, D. J., & Miller, S. K. (2021). Multidecadal climate
1274 oscillations during the past millennium driven by volcanic forcing. *Science*, 371(6533), 1014–
1275 1019. <https://doi.org/10.1126/science.abc5810>
1276 Margalef, R. (1958). Information theory in biology. *General Systems Yearbook*, 3, 36–71.
1277 Marshall, D. J., & Burgess, S. C. (2015). Deconstructing environmental predictability:
1278 seasonality, environmental colour and the biogeography of marine life histories. *Ecology*
1279 *Letters*, 18(2), 174–181.
1280 Mieruch, S., Freund, J. A., Feudel, U., Boersma, M., Janisch, S., & Wiltshire, K. H. (2010). A
1281 new method of describing phytoplankton blooms: Examples from Helgoland Roads. *Journal*
1282 *of Marine Systems*, 79(1–2), 36–43. <https://doi.org/10.1016/j.jmarsys.2009.06.004>
1283 Morice, C. P., Kennedy, J. J., Rayner, N. A., & Jones, P. D. (2012). Quantifying uncertainties
1284 in global and regional temperature change using an ensemble of observational estimates: The
1285 HadCRUT4 data set. *Journal of Geophysical Research: Atmospheres*, 117(D8), n/a-n/a.
1286 <https://doi.org/10.1029/2011JD017187>
1287 Nye, J. A., Baker, M. R., Bell, R., Kenny, A., Kilbourne, K. H., Friedland, K. D., Martino, E.,
1288 Stachura, M. M., van Houtan, K. S., & Wood, R. (2014). Ecosystem effects of the Atlantic
1289 Multidecadal Oscillation. *Journal of Marine Systems*, 133, 103–116.
1290 <https://doi.org/10.1016/j.jmarsys.2013.02.006>
1291 Ostle, C., Paxman, K., Graves, C. A., Arnold, M., Artigas, L. F., Atkinson, A., Aubert, A.,
1292 Baptie, M., Bear, B., Bedford, J., Best, M., Bresnan, E., Brittain, R., Broughton, D., Budria,
1293 A., Cook, K., Devlin, M., Graham, G., Halliday, N., ... McQuatters-Gollop, A. (2021). The
1294 Plankton Lifeform Extraction Tool: a digital tool to increase the discoverability and usability
1295 of plankton time-series data. *Earth System Science Data*, 13(12), 5617–5642.
1296 <https://doi.org/10.5194/essd-13-5617-2021>
1297 Perkins, S. E., & Alexander, L. V. (2013). On the measurement of heat waves. *Journal of*
1298 *Climate*, 26(13), 4500–4517.
1299 Perry, A.L., Low, P.J., Ellis, J.R. & Reynolds, J.D. (2005) Climate change and distribution
1300 shifts in marine fishes. *Science*, 308, 1912– 915. <https://doi.org/10.1126/science.aaa1605>
1301 Peterson, D. L., & Parker, V. T. (1998). Dimensions of scale in ecology, resource
1302 management, and society. *Ecological Scale: Theory and Applications*, 499, 503–507.
1303 Philippart, C. J. M., van Aken, H. M., Beukema, J. J., Bos, O. G., Cadée, G. C., & Dekker, R.
1304 (2003). Climate-related changes in recruitment of the bivalve *Macoma balthica*. *Limnology*
1305 *and Oceanography*, 48(6), 2171–2185. <https://doi.org/10.4319/LO.2003.48.6.2171>
1306 Pierce, D. W., Barnett, T. P., AchutaRao, K. M., Gleckler, P. J., Gregory, J. M., &
1307 Washington, W. M. (2006). Anthropogenic Warming of the Oceans: Observations and Model
1308 Results. *Journal of Climate*, 19(10), 1873–1900. <https://doi.org/10.1175/JCLI3723.1>
1309 Pontavice, H., Gascuel, D., Reygondeau, G., Maureaud, A., & Cheung, W. W. L. (2020).
1310 Climate change undermines the global functioning of marine food webs. *Global Change*
1311 *Biology*, 26(3), 1306–1318. <https://doi.org/10.1111/gcb.14944>
1312 Pörtner, H. O. (2002). Climate variations and the physiological basis of temperature
1313 dependent biogeography: systemic to molecular hierarchy of thermal tolerance in animals.
1314 *Comparative Biochemistry and Physiology Part A: Molecular & Integrative Physiology*,
1315 132(4), 739–761. [https://doi.org/https://doi.org/10.1016/S1095-6433\(02\)00045-4](https://doi.org/10.1016/S1095-6433(02)00045-4)
1316 Pörtner, H.O., Bock, C. & Mark, F.C. (2017). Oxygen- and capacity-limited thermal
1317 tolerance: bridging ecology and physiology. *J Exp Biol*, 220 (15): 2685–2696.
1318 <https://doi.org/10.1242/jeb.134585>

1319 Pozo-Vázquez, D., Esteban-Parra, M. J., Rodrigo, F. S., & Castro-Díez, Y. (2001). A study of
1320 NAO variability and its possible non-linear influences on European surface temperature.
1321 *Climate Dynamics*, *17*(9), 701–715. <https://doi.org/10.1007/s003820000137>
1322 Rayner, N. A., Parker, D. E., Horton, E. B., Folland, C. K., Alexander, L. v, Rowell, D. P.,
1323 Kent, E. C., & Kaplan, A. (2003). Global analyses of sea surface temperature, sea ice, and
1324 night marine air temperature since the late nineteenth century. *Journal of Geophysical*
1325 *Research: Atmospheres*, *108*(D14). <https://doi.org/https://doi.org/10.1029/2002JD002670>
1326 Reid, P. C., Edwards, M., Beaugrand, G., Skogen, M., & Stevens, D. (2003). Periodic changes
1327 in the zooplankton of the North Sea during the twentieth century linked to oceanic inflow.
1328 *Fisheries Oceanography*, *12*(4-5), 260–269.
1329 Reise, K., Buschbaum, C., Büttger, H., Rick, J., & Wegner, K. M. (2017). Invasion trajectory
1330 of Pacific oysters in the northern Wadden Sea. *Marine Biology*, *164*(4), 68.
1331 <https://doi.org/10.1007/s00227-017-3104-2>
1332 Rick, J. J., Romanova, T., & Wiltshire, K. H. (2017). *Hydrochemistry time series at List*
1333 *Reede, Sylt, Germany, in 2014*. PANGAEA. <https://doi.org/10.1594/PANGAEA.873549>
1334 Rick, J. J., Romanova, T., & Wiltshire, K. H. (2020a). *Hydrochemistry time series at List*
1335 *Reede, Sylt, Germany, in 2015 (Version 2)*. PANGAEA.
1336 <https://doi.org/10.1594/PANGAEA.918018>
1337 Rick, J. J., Romanova, T., & Wiltshire, K. H. (2020b). *Hydrochemistry time series at List*
1338 *Reede, Sylt, Germany, in 2016 (Version 2)*. PANGAEA.
1339 <https://doi.org/10.1594/PANGAEA.918023>
1340 Rick, J. J., Romanova, T., & Wiltshire, K. H. (2020c). *Hydrochemistry time series at List*
1341 *Reede, Sylt, Germany, in 2017*. PANGAEA. <https://doi.org/10.1594/PANGAEA.918024>
1342 Rick, J. J., Romanova, T., & Wiltshire, K. H. (2020d). *Hydrochemistry time series at List*
1343 *Reede, Sylt, Germany, in 2018*. PANGAEA. <https://doi.org/10.1594/PANGAEA.918025>
1344 Rick, J. J., Romanova, T., & Wiltshire, K. H. (2020e). *Hydrochemistry time series at List*
1345 *Reede, Sylt, Germany, in 2019*. PANGAEA. <https://doi.org/10.1594/PANGAEA.918026>
1346 Rick, J. J., van Beusekom, J., Romanova, T., & Wiltshire, K. H. (2017). *Long-term physical*
1347 *and hydrochemical measurements at Sylt Roads LTER (1973-2013), Wadden Sea, North Sea,*
1348 *links to data sets*. PANGAEA. <https://doi.org/10.1594/PANGAEA.150032>
1349 Righetti, D., Vogt, M., Gruber, N., Psomas, A., & Zimmermann, N. E. (2019). Global pattern
1350 of phytoplankton diversity driven by temperature and environmental variability. *Science*
1351 *Advances*, *5*(5). <https://doi.org/10.1126/sciadv.aau6253>
1352 Robinson, C. T., & Minshall, G. W. (1986). Effects of disturbance frequency on stream
1353 benthic community structure in relation to canopy cover and season. *Journal of the North*
1354 *American Benthological Society*, *5*(3), 237–248.
1355 Rodwell, M., Rowell, D. & Folland, C. (1999). Oceanic forcing of the wintertime North
1356 Atlantic Oscillation and European climate. *Nature* *398*, 320–323.
1357 <https://doi.org/10.1038/18648>
1358 Root, T. L., Price, J. T., Hall, K. R., Schneider, S. H., Rosenzweig, C., & Pounds, J. A.
1359 (2003). Fingerprints of global warming on wild animals and plants. *Nature*, *421*(6918), 57–
1360 60.
1361 Sarker, S., Lemke, P., & Wiltshire, K. H. (2018). Does ecosystem variability explain
1362 phytoplankton diversity? Solving an ecological puzzle with long-term data sets. *Journal of*
1363 *Sea Research*, *135*, 11–17.
1364 Sarker, S., & Wiltshire, K. H. (2017). Phytoplankton carrying capacity: Is this a viable
1365 concept for coastal seas? *Ocean & Coastal Management*, *148*, 1–8.
1366 <https://doi.org/10.1016/j.ocecoaman.2017.07.015>
1367 Scharfe, M., & Wiltshire, K. H. (2019). Modeling of intra-annual abundance distributions:
1368 Constancy and variation in the phenology of marine phytoplankton species over five decades

1369 at Helgoland Roads (North Sea). *Ecological Modelling*, 404, 46–60.
1370 <https://doi.org/10.1016/J.ECOLMODEL.2019.01.001>
1371 Shama, L. N. S., Mark, F. C., Strobel, A., Lokmer, A., John, U., & Mathias Wegner, K.
1372 (2016). Transgenerational effects persist down the maternal line in marine sticklebacks: gene
1373 expression matches physiology in a warming ocean. *Evolutionary Applications*, 9(9), 1096–
1374 1111.
1375 Siegismund, F., & Schrum, C. (2001). Decadal changes in the wind forcing over the North
1376 Sea. *Climate Research*, 18(1–2), 39–45. [https://www.int-res.com/abstracts/cr/v18/n1-2/p39-
1377 45/](https://www.int-res.com/abstracts/cr/v18/n1-2/p39-45/)
1378 Slatkin, M. (1974). Hedging one's evolutionary bets. *Nature*, 250(5469), 704–705.
1379 Solga, M. J., Harmon, J. P., & Ganguli, A. C. (2014). Timing is everything: an overview of
1380 phenological changes to plants and their pollinators. *Natural Areas Journal*, 34(2), 227–234.
1381 Sommer, U., & Lengfellner, K. (2008). Climate change and the timing, magnitude, and
1382 composition of the phytoplankton spring bloom. *Global Change Biology*, 14(6), 1199–1208.
1383 <https://doi.org/https://doi.org/10.1111/j.1365-2486.2008.01571.x>
1384 Steele, J. H. (2004). Regime shifts in the ocean: reconciling observations and theory. *Progress*
1385 *in Oceanography*, 60(2), 135–141.
1386 <https://doi.org/https://doi.org/10.1016/j.pocean.2004.02.004>
1387 Stenseth, N. C., Ottersen, G., Hurrell, J. W., & Belgrano, A. (2004). *Marine ecosystems and*
1388 *climate variation: the North Atlantic-a comparative perspective*. Oxford University Press.
1389 Strasser, M., Reinwald, T., & Reise, K. (2001). Differential effects of the severe winter of
1390 1995/96 on the intertidal bivalves *Mytilus edulis*, *Cerastoderma edule* and *Mya arenaria* in
1391 the Northern Wadden Sea. *Helgoland Marine Research*, 55(3), 190–197.
1392 <https://doi.org/10.1007/s101520100079>
1393 Thomas, M. K., Kremer, C. T., Klausmeier, C. A., & Litchman, E. (2012). A global pattern of
1394 thermal adaptation in marine phytoplankton. *Science*, 338(6110), 1085–1088.
1395 Thomas, R. W., & Dorey, S. W. (1967). Protected oceanographic reversing thermometer
1396 comparison study. *Limnology and Oceanography*, 12(2), 361–363.
1397 <https://doi.org/10.4319/lo.1967.12.2.0361>
1398 Thresher, R. E., Koslow, J. A., Morison, A. K., & Smith, D. C. (2007). Depth-mediated
1399 reversal of the effects of climate change on long-term growth rates of exploited marine fish.
1400 *Proceedings of the National Academy of Sciences*, 104(18), 7461–7465.
1401 <https://doi.org/10.1073/pnas.0610546104>
1402 Trenberth, K. E., & Shea, D. J. (2006). Atlantic hurricanes and natural variability in 2005.
1403 *Geophysical Research Letters*, 33(12), L12704. <https://doi.org/10.1029/2006GL026894>
1404 Trenberth, K., Zhang, R., & National Center for Atmospheric Research Staff (Eds.). (n.d.).
1405 *The Climate Data Guide: Atlantic Multi-decadal Oscillation (AMO)*. Last Modified 05 Jun
1406 2021. Retrieved from [https://climatedataguide.Ucar.Edu/Climate-Data/Atlantic-Multi-
1407 Decadal-Oscillation-Amo](https://climatedataguide.ucar.edu/Climate-Data/Atlantic-Multi-).
1408 Trigo, R., Osborn, T., & Corte-Real, J. (2002). The North Atlantic Oscillation influence on
1409 Europe: climate impacts and associated physical mechanisms. *Climate Research*, 20, 9–17.
1410 <https://doi.org/10.3354/cr020009>
1411 van Aken, H. M. (2008). Variability of the water temperature in the western Wadden Sea on
1412 tidal to centennial time scales. *Journal of Sea Research*, 60(4), 227–234.
1413 <https://doi.org/https://doi.org/10.1016/j.seares.2008.09.001>
1414 Weijerman, M., Lindeboom, H., & Zuur, A. F. (2005). Regime shifts in marine ecosystems of
1415 the North Sea and Wadden Sea. *Marine Ecology Progress Series*, 298, 21–39.
1416 Wilson, E. O., & MacArthur, R. H. (1967). *The theory of island biogeography* (Vol. 1).
1417 JSTOR.

1418 Wiltshire, K. H., Boersma, M., Carstens, K., Kraberg, A. C., Peters, S., & Scharfe, M. (2015).
1419 Control of phytoplankton in a shelf sea: determination of the main drivers based on the
1420 Helgoland Roads Time Series. *Journal of Sea Research*, *105*, 42–52.
1421 Wiltshire, K. H., Kraberg, A., Bartsch, I., Boersma, M., Franke, H. D., Freund, J., Gebühr, C.,
1422 Gerdts, G., Stockmann, K., & Wichels, A. (2010). Helgoland roads, north sea: 45 years of
1423 change. *Estuaries and Coasts*, *33*(2), 295–310. <https://doi.org/10.1007/S12237-009-9228->
1424 [Y/FIGURES/16](https://doi.org/10.1007/S12237-009-9228-Y)
1425 Wiltshire, K. H., & Manly, B. F. J. (2004a). The warming trend at Helgoland Roads, North
1426 Sea: Phytoplankton response. *Helgoland Marine Research*, *58*(4), 269–273.
1427 <https://doi.org/10.1007/S10152-004-0196-0>/FIGURES/3
1428 Wiltshire, K. H., & Manly, B. F. J. (2004b). The warming trend at Helgoland Roads, North
1429 Sea: phytoplankton response. *Helgoland Marine Research*, *58*(4), 269–273.
1430 <https://doi.org/10.1007/s10152-004-0196-0>
1431 Yang, J., Gong, P., Fu, R. et al. (2013). The role of satellite remote sensing in climate change
1432 studies. *Nature Climate Change*, *3*, 875–883. <https://doi.org/10.1038/nclimate1908>
1433 Zaiss, J., Boyd, P. W., Doney, S. C., Havenhand, J. N., & Levine, N. M. (2021). Impact of
1434 Lagrangian Sea Surface Temperature Variability on Southern Ocean Phytoplankton
1435 Community Growth Rates. *Global Biogeochemical Cycles*, *35*(8).
1436 <https://doi.org/10.1029/2020GB006880>
1437
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Month	Harbour SST	Harbour SST SD	SR SST	SR SST SD	Delta	SD Delta	n	p-value
January	2.87	1.83	2.90	1.93	-0.03	0.76	111	0.92
February	2.74	2.00	2.69	2.06	0.05	0.70	111	0.86
March	3.77	1.93	3.67	1.99	0.10	0.75	134	0.68
April	7.10	1.92	7.24	2.08	-0.14	1.06	121	0.58
May	12.18	2.10	12.15	1.99	0.03	1.03	105	0.93
June	15.83	1.87	15.65	2.05	0.18	1.10	141	0.43
July	17.79	1.76	17.72	1.78	0.07	0.86	164	0.73
August	18.72	2.03	18.74	1.86	-0.02	0.92	151	0.90
September	15.08	1.86	14.84	2.03	0.24	0.98	130	0.32
October	10.79	2.07	10.47	2.07	0.32	0.94	103	0.28
November	6.48	1.95	6.19	2.04	0.29	0.90	143	0.22
December	3.97	1.89	3.91	1.81	0.06	0.95	97	0.82

1439 Table S1 - Comparison of overlapping SST measurements at Sylt harbour and SR sites.

1440 Monthly averages, differences with SD and p values of monthly t-test comparisons.

1441