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A multiple baseline approach for marine heatwaves

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Abstract

Marine heatwaves and other extreme temperature events can drive biological responses, including mass mortality. However, their effects depend on how they are experienced by biological systems (including human societies). We applied two different baselines (fixed and shifting) to a time series of North Sea water temperature to explore how slowly vs. quickly adapting systems would experience extreme temperatures. We tested if the properties of marine heatwaves and the association with atmospheric heatwaves were robust to a change in baseline. A fixed baseline produced an increase in the frequency and duration of marine heatwaves, which would be experienced as the new normal by slowly adapting systems; 7 of the 10 most severe heatwaves occurred between 1990 and 2018. The shifting baseline removed the trend in the frequency but not duration of heatwaves; the 1990s appeared as a period of change in the frequency of strong and severe heatwaves as compared to the 1980s. There were also common patterns among baselines: marine heatwaves were more frequent in late summer when temperatures peak; temperature variability was characterized by low frequency, large amplitude fluctuations (i.e., as red noise), known to drive extinction events. In addition, marine heatwaves occurred during or just after atmospheric heatwaves. Our work highlights the importance of identifying properties of marine heatwaves that are robust or contingent on a change in baseline.

Increasing frequencies of heatwaves occurring over the past decades in association with global change are currently a concern for both ecology and society (Campbell et al. 2018; Smale et al. 2019). Heatwaves are extreme events characterized by a period of increased temperature, the frequency and intensity of which are associated with global warming (Frölicher et al. 2018; Laufkötter et al. 2020). Heatwaves are more visible in terrestrial systems, where temperatures may change rapidly. However, also in the aquatic realm, relatively sudden changes in temperature occur. The clear definition of a heatwave is not trivial, but in recent contributions, Hobday et al. (2016) developed a workable definition for marine heatwaves, that is, periods of time equal to or longer than 5 d when seawater temperature exceeds a predetermined threshold (e.g., 90th quantile of a baseline temperature time series). Marine heatwaves are not small-scale phenomena but typically constitute a disturbance operating at a regional scale (> 1000 km: Jacox et al. 2020; Oliver et al. 2021). Such temperature increases are important, as evidenced by mass mortalities and reductions in biodiversity associated with longer period heatwaves with high intensities (Arias-Ortiz et al. 2018; Smith et al. 2023).

A critical point in the characterization of heatwaves (either marine or atmospheric) is the definition of the baseline used to calculate threshold temperature. There are different views on whether such a baseline should be fixed or if, instead, it should be shifting (Amaya et al. 2023; sen Gupta 2023). The application of a fixed baseline would enable the quantification of the effects of long-term temperature trends in the frequency and characteristics of marine heatwaves (Oliver et al. 2018). From the ecological standpoint, a fixed baseline is important to understand how species with limited capacity for adaptation experience thermal fluctuations in the context of warming (Oliver et al. 2021). In contrast, a shifting baseline (Jacox 2019) enables the exploration of how such fluctuations would be experienced by species able to adapt during, for example, periods of directional temperature change, such as those currently occurring as a result of global warming. The application of the shifting baseline is needed, for example, to account for underlying trends in the temperature time series

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Additional Supporting Information may be found in the online version of this article.

and for the exploration of changes in the statistical properties of extreme events at a period in the future.

Understanding the impact of the baseline choice is important for three reasons: First, we expect important interspecific variation in how marine organisms cope with extreme thermal fluctuations. Interspecific differences with regard to the ability of species to show phenotypic plasticity (i.e., the capacity of a genotype to exhibit phenotypic variation: DeWitt and Scheiner 2004) are expected, as plastic responses can occur at different time scales, within generations (e.g., acclimation, developmental plasticity) or between generations (transgenerational plasticity). Besides, the capacity to evolve (through genetic change) is favored by high-standing genetic variation, in combination with short generation time and high fecundity (Botero et al. 2015).

Second, the baseline affects the "threshold anomaly," that is, the thermal deviations from the threshold temperature defining marine heatwaves (i.e., five or more consecutive days with positive values of threshold anomalies: Hobday et al. 2016). The nature of the variability of the threshold anomalies is likely to drive the evolution of upper thermal tolerance limits, contingent on life history and generation time. For instance, for some fish, a winter marine heatwave might be irrelevant. However, for species with complex life cycles, specific life phases occur at different seasons, and reproductive events require low winter temperatures; in some populations, winter marine heatwaves might be important (e.g., Smith and Thatje 2013; Crickenberger and Wethey 2018). In general, life history theory predicts that environments characterized by predictable fluctuations promote phenotypic plasticity; parents may produce warm, acclimated offspring through transgenerational plasticity (Donelson et al. 2018). By contrast, random fluctuations can promote bet-hedging (Joschinski and Bonte 2020), whereby parents produce offspring differing in environmental tolerance so that at least some offspring may survive the future conditions. Furthermore, time series may be noisy, but characterized as a "colored" instead of as a "white noise." Such "color" is assigned to a time series with an analogy to light, that is, where red color denotes a dominance of low frequencies (= long periods) and blue–violet refers to a dominance of high frequencies (Heino and Sabadell 2003; Mustin et al. 2013). For instance, environmental time series in the marine habitat are often "pink to red" because they contain fluctuations of large amplitude (= extreme) and long periods. Importantly, environmental noise color reflects the extinction risk (Mustin et al. 2013). However, the type of effect can depend on the life history (Heino and Sabadell 2003). Environmental red noise can promote adaptive plasticity and population persistence in species with low fecundity (Romero-Mujalli et al. 2021). The important point is that the choice of baseline could theoretically affect the noisy nature of the threshold anomalies. The threshold anomalies should be noisy because predictable temperature fluctuations (e.g., seasonal patterns) are filtered out in its computation. However, depending on the baseline, periodicities may appear if fluctuations increase in amplitude or frequency over time, beyond the (fixed) baseline, or along the shifting (or fixed) baseline.

The third point concerns whether a change of baseline affects the *relationship* between marine heatwaves and their potential predictors. Those relationships will point toward the mechanisms driving marine heatwaves and extreme temperatures (Oliver et al. 2021). Marine heatwaves may be produced by advection in aquatic systems (Schaeffer and Roughan 2017). However, for shallow coastal systems the most likely drivers are high atmospheric temperatures in combination with reduced wind speeds, as suggested by studies of events of warm atmospheric and seawater temperature (Sparnocchia et al. 2006; Olita et al. 2007). In a system with a strong sea–air coupling marine heatwaves may be predicted, at least for short periods of time ahead, through forecast of atmospheric heatwaves. The relationships between marine and atmospheric heatwaves may be robust (or contingent) to a change in the baseline.

Here, we apply both fixed and shifting baselines using the 57-yr time series of the Helgoland Roads (54.12°N, 7.9°E, Germany) to quantify the frequency of heatwave events in the German Bight. We evaluated if key characteristics of the heatwaves, such as intensity, duration, and noise color are either robust or contingent on a change in the baseline. Likewise, we quantify associations between marine and atmospheric heatwaves and the robustness of a change in baseline. We take the opportunity of a unique time series (de Amorim et al. 2023) of in situ daily measurements of temperature to resolve and catalog marine heatwaves occurring between 1962 and 2018. Importantly, because our time series is based on high-resolution in situ readings made with the same methods, it does not suffer from issues associated with data obtained from satellites, where, for example, the frequency of measures can affect patterns, especially around the 1980s (Xu et al. 2022). Marine heatwaves are likely to be critical in the German Bight (South Eastern North Sea), which has experienced a considerable rate of temperature increase, especially after the 1990s (Becker and Pauly 1996; Huthnance et al. 2016). Projected changes in temperature for the North Sea include further increases in average temperature (1–3°C for the end of the century: Schrum et al. 2016). Because of the mixing of the water column at the coast (Otto et al. 1990), marine heatwaves are likely to impact bottom habitats as well as surface waters. Decadal-scale changes have already occurred in the North Sea, in species phenology and abundance (Kirby et al. 2007; Petitgas et al. 2012; Scharfe and Wiltshire 2019), community and ecosystem (Kröncke et al. 2011; Reid et al. 2016). In particular, variability in SST has consequences for year-to-year variability in phytoplankton dynamics in the southern North Sea (McQuatters-Gollop and Vermaat 2011); important changes occurred in the plankton dynamics associated with changes in SST of the German Bight (Schlüter et al. 2008; Scharfe and Wiltshire 2019). The recent increase in the number of European atmospheric heatwaves experienced in continental Europe (Russo et al. 2015) is likely to be reflected as fluctuations in seawater temperature, perhaps accelerating change. The association between monthly temperatures at Helgoland Roads (North Sea, German Bight) and temperatures in mainland Germany (de Amorim et al. 2023) suggests a coupling between marine and atmospheric temperatures. Our paper also provides a catalog of heatwaves to be used in the future, to study time series of plankton collected in parallel to temperature readings, since 1962.

Methods

Data sources

The seawater temperature time series (Fig. 1, top panel) corresponds to the daily temperature values of the Helgoland Roads time series (de Amorim et al. 2023) from January 1962 to December 2018 (measured at ~8:00 h; depth < 1 m). On days when temperature data was not taken (e.g., weekends or periods with bad weather), estimations were made through linear interpolation. Linear interpolation was carried out after preliminary simulations showed that such a method performs equally well or better than fitting nonlinear functions. Air temperature data (daily averages, at height = 2 m) were obtained from four weather stations around the German Bight (Helgoland, List, Sankt Peter-Ording, and Nordeney), part of the German national grid from the Climate Data Centre of the German Weather Service (DWD 2021).

Computation of heatwaves

All analyses were carried out in R using RStudio. Heatwave events for both seawater and air temperatures were defined following Hobday et al. (2016) for the fixed baseline, with modifications for the shifting baseline, and computed using the package heatwaveR (Schlegel and Smit 2018). A heatwave event was defined as a period of five or more days where the temperature was higher than the threshold 90th quantile (Q_{90}) of different baselines (*see* below); events of that extent separated by a period of less than 48 h were considered as a single heatwave event. Events that are not categorized as heatwaves, but still surpassed the Q_{90} were defined as "heat spikes." The Q_{90} was calculated using a moving window of 11 d of half-width over which all values of temperature corresponding to the baseline years are pooled into a frequency distribution.

Definition of baselines

The above calculations were carried out based on a fixed and shifting baseline of 30 yr of duration for both seawater and air temperatures. The fixed baseline was set between 01 January 1962 and 31 December 1991, and we computed the heatwave events of the full-time series. The shifting baseline was then applied to years of the period 1992–2018. For this period, we defined a baseline of 30 yr and computed the heatwave statistics only for the last year of that period. For instance, for the year 1992, the baseline used was the period

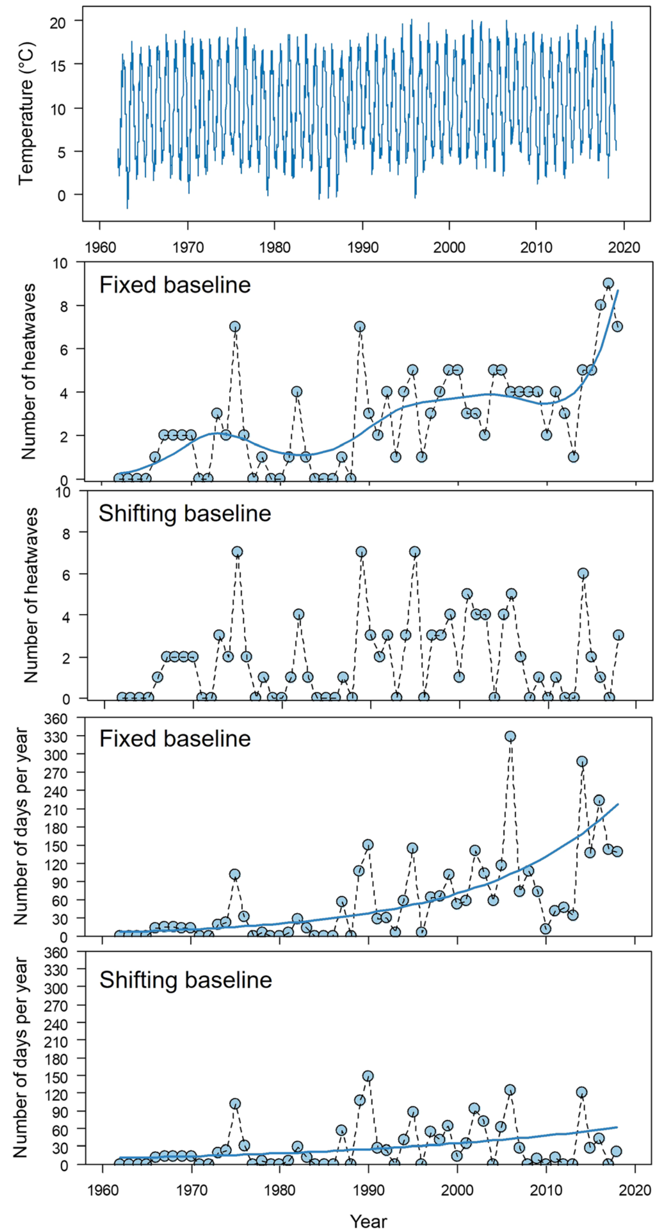

Fig. 1. Time series of daily temperature, the number of marine heatwave events, and number of days per year included in a marine heatwave, computed using fixed and shifting baselines. Curves were added when temperature smooths were retained after the model selection procedure (details in Supporting Information Table S4).

1963–1992; for the year 1993, the baseline was the period 1964–1993 (Supporting Information Fig. S1). Hence, in both approaches, the number of heatwaves was the same for the first 30-yr period but was expected to vary after 1991. We adopted this specific shifting baseline because we wanted to keep a time period of 30 yr in order to obtain solid estimates of the Q_{90} and be able to compare the results of both baselines. We defined the target year as the last of each 30-yr period because, at any given time, whether a fluctuation is experienced by organisms as "extreme" depends on the past temperatures (not on the future). Note that mathematically, it would be better to have a target year toward the middle of the 30-yr period of the shifting baseline; however, this would mean that organisms should be responding to future conditions, which, of course, is not possible.

Characteristics of marine heatwaves

This analysis was carried out in three sections. First, trends in the frequency, intensity, and duration of heatwaves were quantified using generalized linear and additive modeling (GAM; Woods 2017). GAMs were fitted with the package "mgcv" using thin plate spline smoothers and considering Gaussian, Poisson, and negative binomial residuals. Second, temporal variation in the full set of heatwave traits (Supporting Information Tables S1, S2) was explored using principal components analysis (PCA) with emphasis on differentiating between pre-1991 vs. post-1991 periods in order to better quantify and visualize the effects of different baselines on the results. The main traits are indicators of intensity, duration, and rate of temperature change. PCA was based on the correlation matrix in order to take into account variables measured in different units and scales (e.g., intensity in °C and time duration in days). Third, we focused on the most intense events: marine heatwaves were classified using the scheme of increasing intensity (from moderate to extreme) developed by Hobday et al. (2018), and then the distribution of the 10 most intense heatwaves was studied. In addition, we searched for information on atmospheric heatwaves in order to determine whether our top 10 events were identified with critical periods of unusually high temperatures in Europe.

Variability in threshold anomalies

The daily threshold anomaly was calculated as the daily temperature minus the daily threshold temperature (here the daily Q_{90} as defined above). We studied temporal patterns in threshold anomalies because they define marine heatwaves (when positive for five or more consecutive days). We differentiate between threshold anomalies and the so-called average, maximum, and cumulative "threshold intensities" (Hobday et al. 2016); threshold intensities are properties of the marine heatwaves and are calculated as the maximum, average, or cumulative threshold anomalies during a marine heatwave. Temporal patterns in threshold anomalies were characterized using wavelet and spectral analyses (Cazelles et al. 2008) using the package waveletComp (Roesch and Schmidbauer 2018). For this analysis, the seasonal patterns of temperature are not present in the time series because they are filtered out when the Q_{90} is subtracted from the temperature values of each time series. In order to characterize the "color" of the time series, we carried out spectral analysis (function *spec* in R) of the time series of threshold anomalies and fitted linear statistical models to the relationship between spectral values and frequencies (both variables log-transformed). For such log–log relationship, red noise is characterized by negative slopes (e.g., slope $= -1$ is defined as "pink noise") while blue noise is characterized by positive slope values (white noise has 0 slope value).

Marine and atmospheric temperatures

Associations between marine and atmospheric extreme temperatures were studied after applying the same baseline (either fixed or shifting) to both time series. Associations were studied at two different levels. First, we explored associations between threshold anomalies of each temperature time series, but transformed into binary (= 1 if threshold anomalies $> Q_{90}$, 0 otherwise), as representing the presence/absence of heatwaves and heat spikes. Second, we explored associations between heatwave events in paired time series (on daily time steps) also with data transformed to binary (1 = heatwave, 0 otherwise). Associations were quantified with cross-correlation (Chatfield 2004) and co-occurrence analysis (Veech 2013; Griffith et al. 2016). Cross-correlation was used to determine if association peaked at specific time lags; we intended to *hypothesize* causal links between atmospheric and marine heatwaves. The use of cross-correlations for binary variables is justified because Pearson correlation transforms into the φ-association coefficient used in the analysis of contingency tables (definition in Sokal and Rohlf 1995, pp. 741–743, *see* Supporting Information S1). For cross-correlation analysis, time series were previously detrended (by differentiation) and prewhitened (function *prewhiten* of package TSA: Chan and Ripley 2020). Co-occurrence and quantification of overlap were helpful in our case because cross-correlation analysis gave peak correlations between atmospheric and marine heatwaves at very short time lags. Co-occurrence analysis has been used in ecology to quantify and test whether patterns of species co-occurrence are random or structured. We use it here (package *cooccur* in R: Griffith et al. 2016) because it is well suited for binary data and enables a test of whether observed co-occurrences deviate from those expected under random distribution of heatwaves. In addition, the overall overlap between marine and atmospheric heatwaves was quantified by the Schoener index of niche overlap (Broennimann et al. 2012), which ranges between 0 (no overlap) and 1 (complete overlap).

Results

A fixed baseline gave more marine heatwaves (= 153) than a shifting baseline (= 106; Supporting Information Tables S1, S2), which was due to a higher number of events for the period 1992–2018 (110 vs. 63), where the calculations based on the fixed and shifting baselines differ (details in Supporting Information Fig. S1). With the fixed baseline, the number of marine heatwaves per year increased over time, but no such increase was evident with the shifting baseline (Fig. 1; Supporting Information Tables S3, S4). In both cases, the number of days and the average duration per marine heatwave per year increased over time, especially after 1990 (Fig. 1;

Supporting Information Fig. S2), although the shifting baseline led to a less pronounced increment. Trends on yearly average and maximum threshold intensities (i.e., the average and maximum threshold anomalies during the heatwave) were evaluated using the full-year data because not all years had marine heatwaves; threshold intensities increased through time (Supporting Information Fig. S3; Supporting Information Tables S3, S4) although the increment was lower after application of the shifting baseline. Average threshold intensities increased at a rate twice as high for the fixed vs. shifting baselines (0.32 vs. 0.16°C decade^{-1}). The shifting baseline highlighted the period between the years 1990 and 2000 as dominated by marine heatwaves characterized by high threshold intensities (Supporting Information Fig. S3); the same pattern was observed in the number of marine heatwaves per year, but it was not retained in the statistical model. In addition, when taken together, heatwave components (including threshold intensities, duration, and rates increase and decrease in temperature) were more variable in the latter three decades. This is shown especially after the

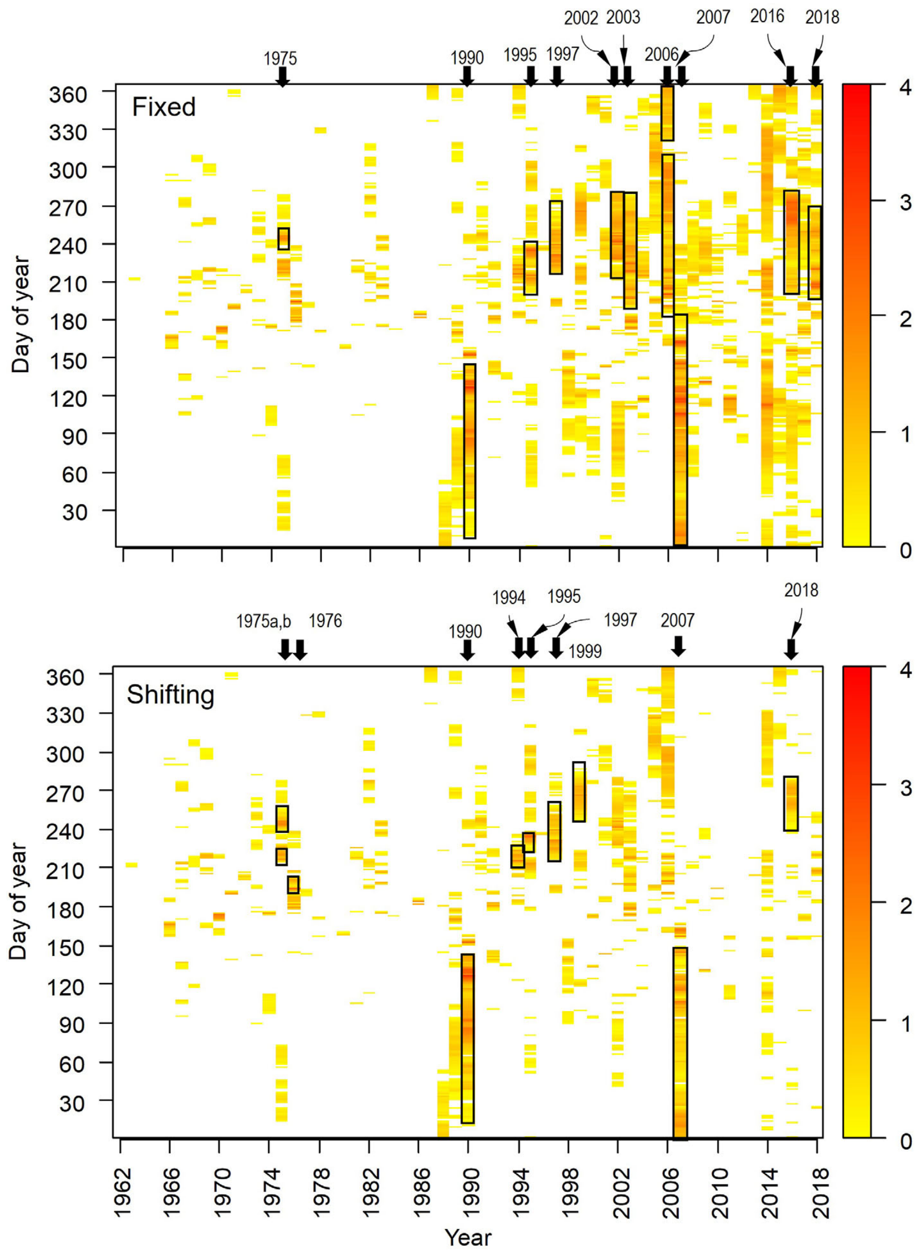

Fig. 2. Heatmap of marine heatwaves and spikes after the application of a fixed (upper panel) or shifting baselines (lower panel). The scale color is in °C above the threshold temperature. Rectangles: approximate timing of the 10 most important heatwaves (details in Table 1 and Supporting Information Table S5); note that for the fixed baseline, there was an event starting in 2006 that continued in 2007.

application of the fixed baseline (PCA in Supporting Information Fig. S4: note that the cloud corresponding to the period 1992–2018 filled a larger portion of the multivariate space). Such effect reflected higher intensities and duration contributing to the first axis (> 50% of total variance); rate onset and decline contributed mostly to the second component (17–22%). The majority of marine heatwaves (70%) had a duration < 30 d but some extended for > 100 d (Supporting Information Fig. S5). The application to the shifting baseline resulted in shorter heatwaves, with some of them being a fragmentation of long events detected by the fixed baseline (e.g., years 2002, 2003, 2006, 2007, and 2018; Supporting Information Tables S1, S2). Heatwave intensities and rates did not differ much between the fixed and shifting baselines (Supporting Information Figs. S6, S7), and most heatwaves were classified as moderate; however, there were more severe heatwaves after the application of the fixed than the shifting baseline (9 vs. 3 events).

For the second part of the time series (years 1992–2018), where the application of the baselines differs, there were slightly different patterns of severity. The fixed baseline led to an increased number of marine heatwaves and spikes along the 30-yr period (Fig. 2) and resulted in eight out of nine severe events (Supporting Information Fig. S8). With the shifting baseline, there was still a change between the 1980s and 1990s in the number of marine heatwaves and spikes (Fig. 2) and in the number of strong and severe marine heatwaves (Supporting Information Fig. S8). With the shifting baseline, the period between 1990 and 2007 had 14 strong marine heatwaves (~ 7 strong events per decade) in contrast to a single event in the decade of the 1980s and three events in the period 2008–2018.

Marine heatwaves and spikes occurred all year round (Fig. 2; Supporting Information Fig. S8) but were concentrated March–April and July–September (Supporting Information Fig. S9). The third quarter of the year had the highest frequency of marine heatwaves for both the fixed and shifting baselines (fixed: 35%, shifting: 42% of all heatwaves). The winters were characterized by negative threshold anomalies, except for two long mild winters (1990, 2007; Fig. 2; Supporting Information Fig. S8) detected as very long heatwaves.

The top 10 marine heatwaves obtained by applying the fixed baseline were nine severe events (i.e., maximum threshold intensities were larger than three times the difference between the Q_{90} and climatological baseline). In addition, there was a very long event extending from Autumn 2006 to Spring 2007 (Fig. 2; Table 1; Supporting Information Fig. S10). In contrast, only three events were classified as severe after applying the shifting baseline (Supporting Information Table S5). With both baselines, most of the top 10 events identified occurred in summer to early autumn (Fig. 2; Supporting Information Figs. S8, S9). The most important heatwaves identified with the fixed baseline (Supporting Information Fig. S9) coincided with known warm atmospheric events occurring at the continental scale. The most intense marine heatwave (duration: 84 d Summer–Autumn 2016) was associated with a long atmospheric heatwave over Europe (Zschenderlein et al. 2018). Other events that were clearly associated with atmospheric heatwaves were the mild winters of the years 1990 and 2007 (Luterbacher et al. 2004; Twardosz and Kossowska-Cezak 2016), summer heatwaves of years 2003 (Schär et al. 2004), 2006 (Russo et al. 2015), and 2018 (Li et al. 2020). There were other marine heatwaves of lower intensity coinciding with known atmospheric heatwaves in Europe (Russo et al. 2015). For instance, two events detected in 1976 (June and August) and two events in 1994 coincided with single atmospheric heatwaves for each year (1976: British Isles; 1994: NE Europe). Two marine heatwaves were detected in Autumn 2015, followed by high temperatures in northern Germany and positive August SST anomalies in the German Bight (Ionita et al. 2017). The application of the shifting baseline led to the identification of similar events post-1991, but they were detected as shorter events or as a sequence of several marine heatwaves and spikes (Supporting Information Fig. S9: period 1991–2018).

Threshold anomalies were significantly auto-correlated, but the wavelet analysis did not reveal any periodicity that was clear and consistent over the full-time series (Fig. 3). There was, however, a dominance of peaks of spectral density with a period of ~ 1 yr, which is consistent with the increased frequency of positive threshold anomalies in autumn; peaks at longer periods (2–10 yr) were intermittent. The spectral densities were robust to a change in baseline, as shown by the similarities in the period 1992–2018.

Table 1. Main characteristics of the top 10 heatwaves using a fixed baseline and the categorization received for both fixed (F_B) and shifting baselines (M_B). Information for the dates of start, peak, and end (day month), maximum temperature intensity (I_{max}: temperature above the seasonal climatology in °C), and duration (D: in days) corresponds to calculations using a fixed baseline (*see* Supporting Information Table S3 for similar information using the shifting baseline). The categorization of the marine heatwaves of 1975 and 1990 are the same for both windows because they shared the same 30-yr baseline (1962–1991).

ID	Year	Start—Peak—End	I_{max}	D	F_B	M_B
1	1975	20 Aug—01 Sep—14 Sep	2.9	25	III	
2	1990	10 Jan—07 May—25 Jun	5.0	135	III	
3	1995	20 Jul—23 Aug—28 Aug	3.6	39	III	III
4	1997	04 Aug—19 Aug—21 Sep	3.2	49	III	II
5	2002	30 Jul—29 Aug—08 Oct	3.5	70	III	II
6	2003	08 Jul—06 Aug—06 Oct	3.5	90	III	II
7	2006	16 Jul—19 Jul—09 Nov	4.1	116	III	II
8	2007	16 Nov—11 Apr—30 May	4.7	195	II	II
9	2016	18 Jul—28 Sep—10 Oct	3.6	84	III	II
10	2018	19 Jul—25 Jul—25 Sep	3.8	68	III	II

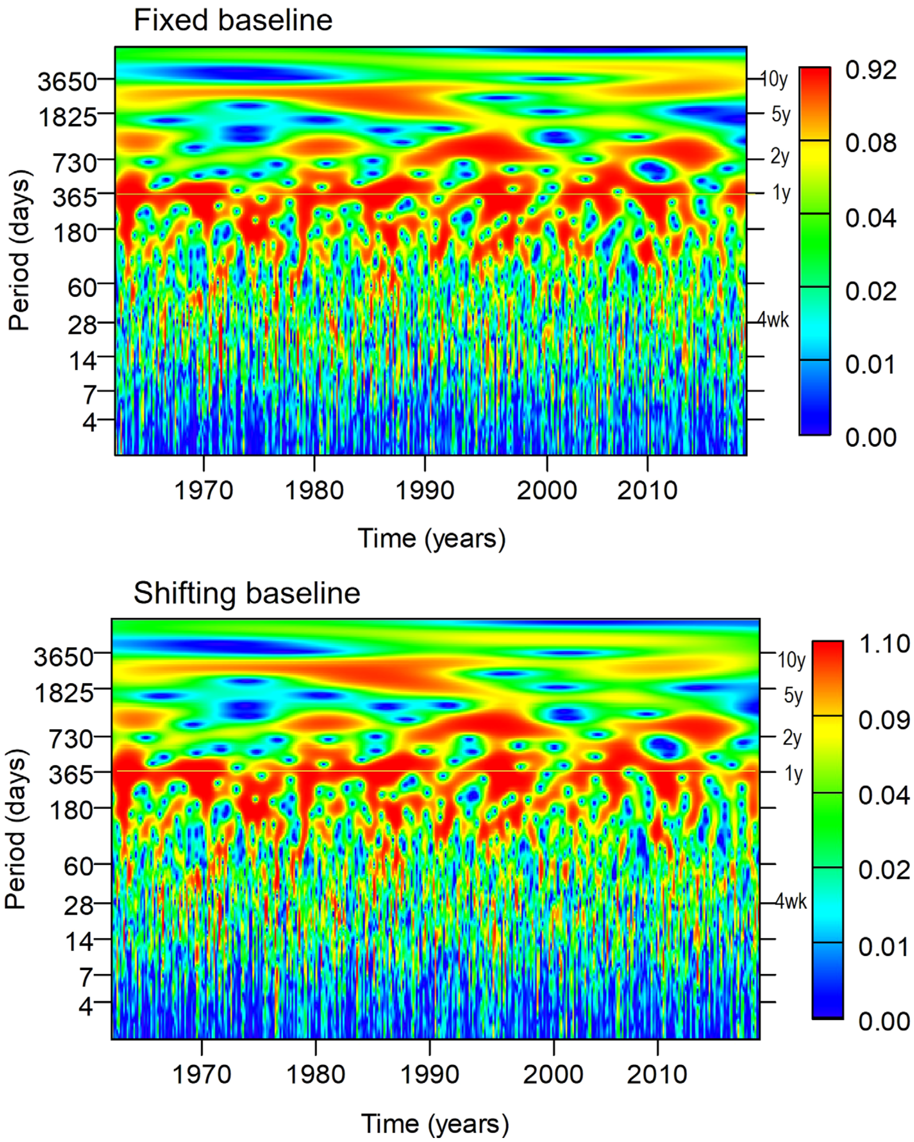

Fig. 3. Spectrogram from wavelet analyses applied to the time series threshold anomalies calculated from the fixed or shifting baselines. Periods were computed following the geometric progression of octaves, but the right and left *y*-axes show selected periods for ease of interpretation. Notice the concentration of high spectral densities along the period of 365 d for most of the length of the time series.

The relationship between spectral densities and frequencies for the threshold anomalies was consistent with red noise for both the fixed and shifting baselines, for the whole time series, and for the period 1992–2018 (Fig. 4). Values of slopes showed a linear pattern that up to frequencies corresponding to a year with the time series shifting to pink and white noise toward to lowest frequency corresponding to 8–30 yr.

Cross-correlation analyses between heatwaves and threshold anomalies (Fig. 5; Supporting Information Figs. S11–S14) of air vs. seawater temperature showed consistently significant peaks at time lags of 0–3 d irrespective of the baseline or whether the analysis was restricted to the post-1991 period (Supporting Information Fig. S14). Such time lags suggest that the seawater threshold anomalies responded quickly to fluctuation in atmospheric threshold anomalies, although the magnitude of oscillation in temperature was much higher in atmospheric than in marine heatwaves. The frequency of co-occurrence between marine and atmospheric heatwaves was four to seven times higher than expected from a null model (Fig. 5b), which was similar to that found when co-occurrence was calculated based on threshold anomalies (Supporting Information Fig. S13); the overlap between marine and atmospheric heatwaves ranged on 30–40% (Fig. 5c).

The co-occurrence and overlap levels found between any pair of atmospheric heatwaves (as detected in the four meteorological stations) were higher than that observed between

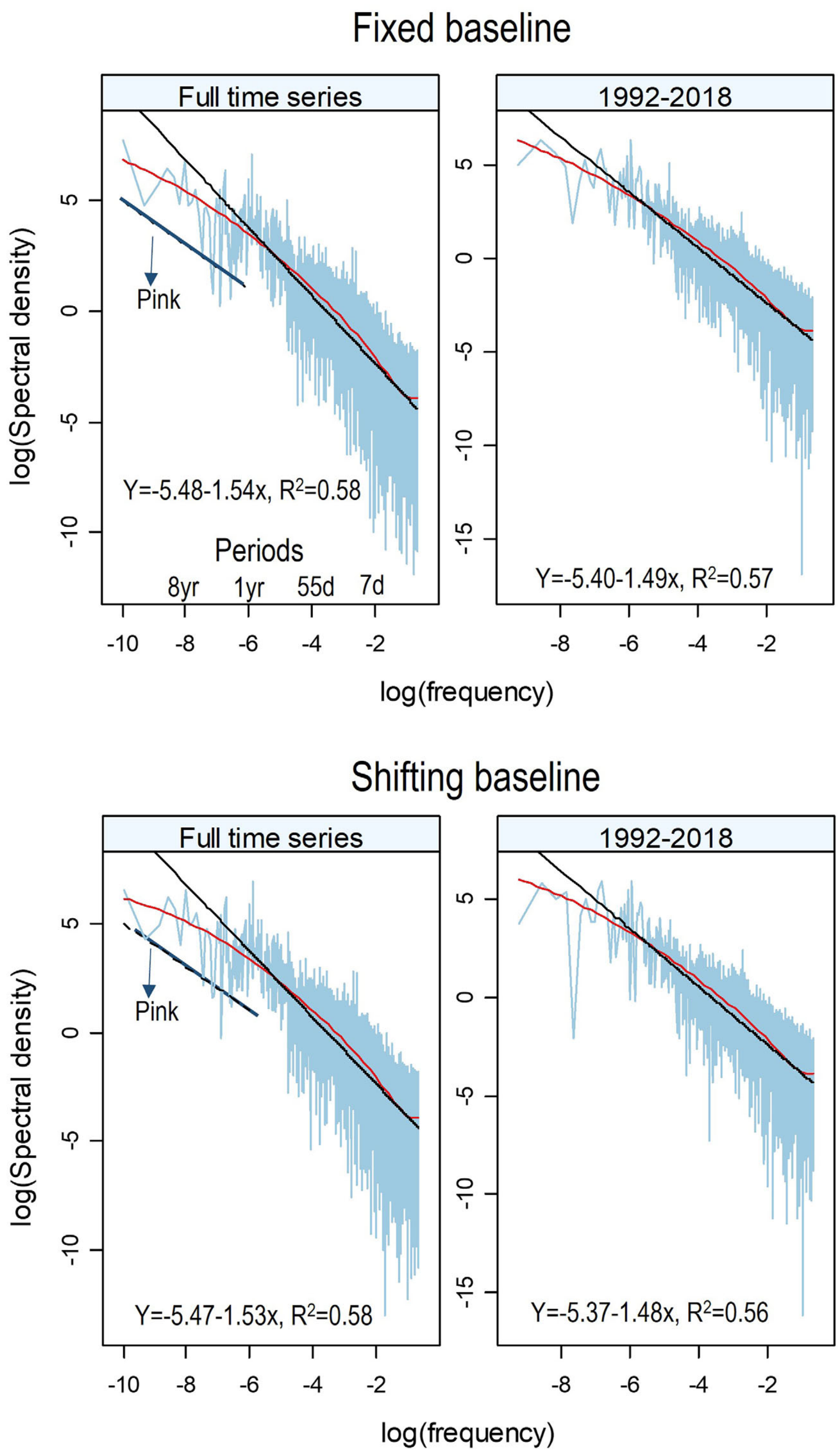

Fig. 4. Spectral analyses of daily threshold anomalies calculated from the fixed or shifting baselines (top and bottom panels, respectively) for the full-time series (1962–2018) and for the second period (1992–2018), reflecting the effect of the different baselines. The straight line fitting the frequencies is the linear model fit (equations in inset, all $p < 0.05$). The curve is the loess smooth of the data. In addition, a separate line for the expected fit of the pink noise (slope $= -1$). The approximate periods corresponding to some of the frequencies (in units of 1/time) are given in the top-left panel for ease of interpretation. Note that the spectral density peaks at period ~ 1 yr, but the peak is not clear. Recall that the seasonal variation in temperature is removed from this time series by subtraction of the threshold temperature (at the 90th quantile).

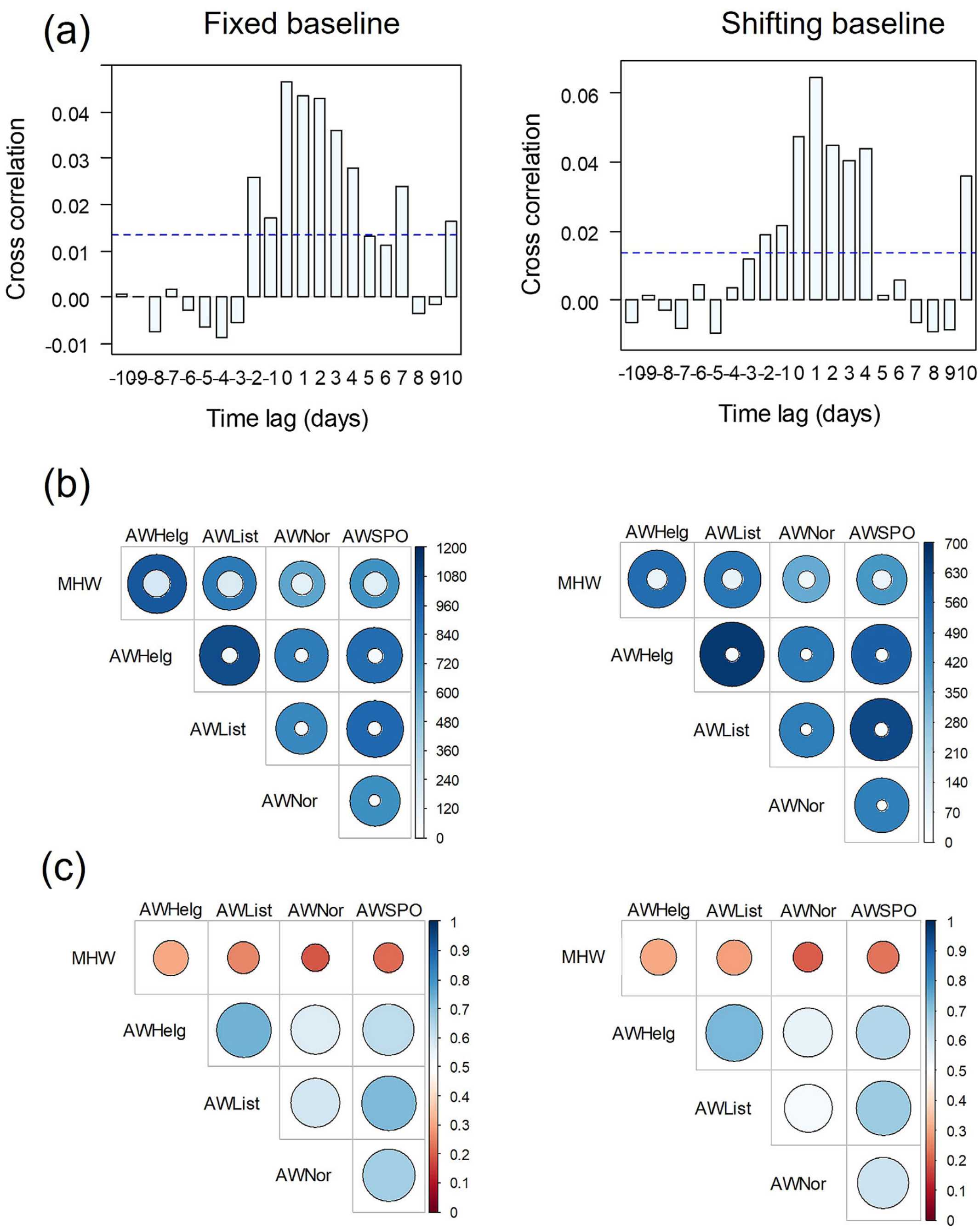

Fig. 5. Association between marine and atmospheric heatwaves after application of a fixed or shifting baseline (left and right panels, respectively). (**a**) Cross-correlation of marine vs atmospheric heatwaves as detected by the meteorological station in Helgoland; plots for the remaining stations are given in Supporting Information Fig. S8 (threshold intensities) and Supporting Information Fig. S9 (heatwaves). (**b**) Observed co-occurrence of heatwaves (outer circles) in relation to those expected based on random patterns of distribution (inner circles). (**c**) Overlap between heatwaves based on the Schoener index. Abbreviations in (b) and (c): MHW: marine heatwaves for Helgoland Roads, AW: atmospheric heatwaves corresponding to Helgoland (Helg), List, Nordeney (Nor) and Sankt Peter-Ording (SPO).

marine and each separated atmospheric heatwave. There was a substantial number of cases where marine and atmospheric events did not fully coincide. Atmospheric threshold anomalies showed stronger oscillations than those based on seawater temperature. There were cases where a single marine heatwave occurred in association with several atmospheric heatwaves (e.g., winter–spring 1990: Supporting Information Fig. S15: days ~ 5–150) or periods when increases in seawater threshold anomalies were associated with atmospheric heatwaves without a marine heatwave event (e.g., year 2002: Supporting

Information Fig. S16: days 1–30 and 2018: Supporting Information Fig. S17 days 60–150). In summary, marine heatwaves were associated with either one or more atmospheric heatwaves, and increments in seawater threshold anomalies were associated with atmospheric heatwaves (or spikes).

Discussion

Heatwaves in aquatic systems are increasingly considered to be game changers in socioecosystems (Campbell et al. 2018; Smale et al. 2019; Smith et al. 2021). The determination of heatwaves is, however, not trivial; different baselines have been discussed in order to define heatwaves (Amaya et al. 2023; sen Gupta 2023). We set the baseline to 30 yr for comparison with other studies using a 30-yr period (as in Hobday et al. 2016, but with a different time period) and to obtain stable estimations of Q_{90} required for the definition of heatwaves. We adopted a multiple baseline approach to study marine heatwaves based on a long-term time series of the German Bight. Our definition of shifting baseline is consistent with the fact that, at a given time of the year, a thermal fluctuation would be experienced by organisms as an extreme event, according to the past temperature conditions only, which would have shaped organismal adaptations. In addition, our definition ensures that heatwaves computed for a given year (e.g., year 2010) are not updated when the baseline is shifted to compute heatwaves for future years (e.g., year 2011). Hence both the shifting and fixed baseline share the same important characteristic that they do not recompute old heatwaves with the addition of new data to the time series. Other types of shifting baseline may use future temperatures to recompute past heatwaves. For example, in a scenario of warming, if heatwaves are computed for the full time series at each time the baseline is shifted (or expanded), then future researchers may erase old heatwaves from the record. However, with our definition, heatwaves computed at a given year are not modified if, sometime in the future, additional years of data are added to the time series.

Differences between the fixed and the shifting baselines are observed in our time series after 1991. The application of the fixed baseline suggests that, from the perspective of slow-adapting species, steady warming is experienced as progressively increasing in intensity and duration of marine heatwaves. Such a trend might continue to foster the influx and breeding success of warm species into the northern North Sea (Reise et al. 2023), while the range distribution of indigenous species might undergo poleward shifts. Under steady warming, only subtle changes in the dynamics of marine heatwaves are seen after the application of a shifting baseline. However, we found that the shifting baseline did not fully remove the temporal patterns and instead found a shift from the 1980s (characterized by only a few strong heatwaves) to the 1990–2007, which contained two of the three severe events and twice as many strong heatwaves per decade than any other period of the time series. The end of the decade of the 1980s and the 1990s was characterized by important changes in the Northern Hemisphere (Beaugrand et al. 2015), including North Sea phytoplankton (Defriez et al. 2016; Di Pane et al. 2022) and zooplankton (Kirby et al. 2007; Deschamps et al. 2023). In the German Bight, the copepod assemblages shifted from a dominance of summer, long-lived herbivores to autumn, short-lived carnivores (Deschamps et al. 2023). We cannot ascribe those changes to marine heatwaves; nutrients are hypothesized to have contributed to the change at least for phytoplankton (Di Pane et al. 2022). However, our data suggest that the 1990s must have been experienced by fast adapting species, as a period of change, as compared to the 1980s. Those changes are likely to reflect a nonlinear long-term temperature trend in the Helgoland Roads and the southern North Sea (Desmit et al. 2020; de Amorim et al. 2023).

The shifting baseline did not remove seasonal patterns in the frequency of extremely high temperatures, which are relevant in the context of species phenology. Positive threshold anomalies computed from the fixed baseline peaked in spring and late summer, while those computed from the shifting baseline peaked in late summer only. Hence, fast-adapting species would still experience late summer as a critical period of marine heatwaves. In the German Bight, species differ in the timing of bloom or reproduction and in the degree of phenological shifts (e.g., Scharfe and Wiltshire 2019); hence, prediction is not straightforward. Spring marine heatwaves are likely to favor invasive species such as the exotic *Hemigrapsus sanguineus*, which is adapted to warmer conditions than its native competitor *Carcinus maenas* (Espinosa-Novo et al. 2023). The timing, in terms of seasonality of heatwaves is important. Organisms that are adapted to seasons going from cold to warm (e.g., winter to spring and spring to summer) and, especially in temperate systems with high variability in weather conditions, are less likely to be affected by marine heatwaves than those that are adapted to seasons with cooling trends (summer to autumn and autumn to winter). Thus, perhaps the autumn heatwaves are more critical: these may result in developmental traps (Kerr et al. 2020), as organisms may not complete critical life phases before temperatures drop below the lower thermal tolerance limit. Concurrently, cold snaps due to blocking systems may be of importance in spring (*see* de Amorim et al. 2023).

A shifting baseline did not modify the noise color of the time series of threshold anomalies; instead, the time series were red to pink noise, as in previous studies for marine habitats (Mustin et al. 2013), especially from scales of days to ~ 8 yr. However, the change in baseline can be indicative of the different manner in which temperatures are experienced because thermal fluctuations can be experienced as a scenario where rare events are characterized by suboptimal temperatures or the opposite scenario. The noise referred to here will be experienced by organisms as superimposed on the predictable pattern of seasonal temperature variation

(Boersma et al. 2016). This noise is important in relation to adaptive responses of the upper thermal tolerance limits, especially because positive threshold anomalies occur more frequently during late summer when temperatures peak. Events when temperatures matched upper thermal limits have been found in the Wadden Sea (Pörtner and Knust 2007) and even rare bad years can drive the extinction of an annual species (Heino and Sabadell 2003). Biological time scales are central to how fluctuations are experienced at the population level: short generation times (along with, e.g., mutation rate and standing genetic variation) should favor rapid adaptation relative to the decade-scale changes shown here (Fig. 2). Some species with short generation times (days to weeks) can undergo adaptation in response to temperature increase within a year (Dam et al. 2021; Schaum et al. 2022). Longer generation times (few years to decades) are likely to require decades or centuries for adaptation, but transgenerational acclimation (Donelson et al. 2018) might mitigate changes occurring at the scale of years to decades. The shifting baseline used here then gives an approximate representation of how those species experience thermal fluctuations, that is, the post-1991 as a period of slight increase in the duration of marine heatwaves (Fig. 1) and the decade of the 1990s as a period of slight increase in the frequency of strong and severe heatwaves. The shifting baseline is likely to be important for many marine organisms, given that microbes constitute ~ 70% of the total marine biomass (Bar-On et al. 2018) and that those organisms have short generation times (days to weeks). However, the rate of evolution varies among species (Raven and Beardall 2021; Barton et al. 2023), and the ability to evolve or exhibit adaptive plasticity might be limited (Stuart-Smith et al. 2017; Byrne et al. 2020). Hence, for those species with a limited or slow rate of evolution, the temporal patterns in threshold anomalies (Fig. 2) would point toward a shift (in the 1990s), from the scenario of rare bad years to one of rare, good years. Hence, in principle, the fixed baseline is likely to be more important for long-lived organisms (generation times months to decades), such as marine invertebrates and fish, as they are less likely to adapt to changes in temperature within a year. Given that responses are species-specific and contingent on the time scales characterizing the fluctuations (Schaum et al. 2022), we need a screening of thermal performance and tolerance limits under realistic heatwave scenarios in organisms with different life histories if we are to understand responses to fluctuations such as marine heatwaves.

If heatwaves become longer or more frequent, conservation and mitigation approaches will need to rely on the capacity for prediction, which requires mechanistic models. In addition, the adoption of two or more baselines requires that we explore how relationships between marine heatwaves and potential predictors (e.g., atmospheric heatwaves) respond to a change in baseline. Our results suggest a link, at least for the case of long events, where atmospheric heatwaves lead to the increase of seawater temperature and may produce marine heatwaves; such a link was present after the application of both the fixed and the shifting baselines. The positive correlations between atmospheric and marine heatwaves are consistent with a previous analysis of the Helgoland Roads time series, suggesting that the main drivers of temperature in the shallow part of the North Sea are linked to atmospheric conditions (de Amorim et al. 2023). Important marine heatwaves coincided with extensive summer atmospheric heatwaves such as those of 2003 and 2015, which occurred over continental Europe and the Mediterranean, and coincided with atmospheric blocking (i.e., persistent high-pressure anomalies: Ionita et al. 2017; Li et al. 2020). We know that air temperature has a strong influence on the SST of the shallower portions of the North Sea, especially in the German Bight (Dippner 1997; Mathis et al. 2015); the atmospheric contribution is likely to dominate in enclosed shallow seas. Wind speed (in combination with air temperatures) should also be important, and it is considered a driver of the formation of marine heatwaves (Holbrook et al. 2019). Advection of warmer waters might be a contributor, but it should play a stronger role in the Central and Southern North Sea, where the inflow of Atlantic water has been considered a source of temperature increase (Kröncke et al. 2011; McQuatters-Gollop and Vermaat 2011).

In synthesis, a multiple baseline approach was important to identify which properties of the marine heatwaves are either contingent on (or robust to) a change in baseline. The application of the fixed baseline resulted in an increase in the duration and number of marine heatwaves over time, with 9 of the 10 most severe heatwaves occurring after the 1990s, most associated with large European heatwaves. The period after the 1990s might be experienced by slow-adapting species as characterized by many bad years (i.e., with several heatwaves) separated by a few good years. The application of the shifting baselines removed the trend in a number of marine heatwaves, resulting in shorter events of less intensity. However, the shifting baseline did not fully remove long-term trends in the average duration of heatwaves, and still, the 1990s appears as a period of change as compared to the 1980s. Irrespective of the baseline, marine heatwaves peaked in late summer and were associated with atmospheric heatwaves.

Data availability statement

The data is archived in PANGAEA (Data Publisher for Earth & Environmental Science).

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Conflict of Interest

None declared.

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