

Response of copepod communities to ocean warming in three time-series across the North Atlantic and Mediterranean Sea

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ABSTRACT: The rapid warming of the world's oceans during the last few decades has affected distributional patterns of marine planktonic communities. Here, we analyse links between sea warming and changes in copepod community composition over the last 3 decades (1980–2012). We used zooplankton time-series data which included 79 species of copepods collected at 3 sites in the eastern North Atlantic (Bay of Biscay and the Kattegat Sea) and the Mediterranean Sea (Gulf of Saronikos). First, using community β -diversity metrics, we analysed temporal patterns of copepod community composition changes over time and its relation to local environmental conditions. Second, to test whether the changes in copepod community composition correspond to community thermal preferences, we used the community temperature index (CTI) and compared CTI interannual changes with local temperature trends. The β -diversity analysis reveals a high temporal turnover in the copepod community composition at the 3 sites (30–45%), with a significant similarity decrease over time ('decay') associated with both niche descriptors and demographic stochastic processes. CTI results reveal that both in the Kattegat and Saronikos, where the ocean warming rate was the highest amongst sites, copepod community changes are linked to temperature variability, suggesting that the community is tracking their thermal niche over time. Our findings unveil the fundamental role of abiotic factors structuring copepod biodiversity over time and reveal that the local velocity of ocean warming and the species thermal thresholds are key to rearranging copepod community composition in coastal ecosystems.

KEY WORDS: Community structure · Warm-adapted · Cold-adapted · β -diversity

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1. INTRODUCTION

The global ocean warming over the last decades (IPCC 2013) has fostered interest in testing how the temperature increase is affecting temporal patterns of marine communities (Poloczanska et al. 2016, Thackeray et al. 2016). A large number of studies have reported covariations between climate change and alterations in the abundance, spatial range and phenology of plankton over the last decades (Aebischer et al. 1990, Walther et al. 2002, Edwards & Richardson 2004, Beaugrand & Helaouët 2008, Kahru et al. 2011, Melle et al. 2014, Villarino et al. 2015, Barton et al. 2016). When environmental change occurs, species are expected to shift geographically by tracking their climatic niches in time and space (Beaugrand et al. 2002, Poloczanska et al. 2013, Rivero-Calle et al. 2015) (Fig. 1). For example, planktonic species from equatorial latitudes with warmer thermal affinities replace cold adapted species that occur closer to the poles (Botsford et al. 1997, McCann et al. 2003). However, under ocean warming, species can also remain in the site and adapt to local conditions phenotypically or evolutionarily (Poloczanska et al. 2016, Chivers et al. 2017). The different species responses to climate change, hence, lead to local extinctions and invasions, triggering changes in temporal patterns of community assembly (Poloczanska et al. 2013, Thackeray et al. 2016).

One approach to detecting community composition change in response to ocean warming is to characterize communities by a collective thermal preference, or community temperature index (CTI), and then to compare changes in CTI with changes in local sea temperatures. Under increasing sea temperatures, a temporal increase in CTI directly reflects that the species assemblage of the site will increasingly be composed of individuals with warmer sea water affinities. However, communities are composed of multiple species with unique environmental performance curves, and we cannot necessarily assume that CTI and temperature change will be linearly correlated. Other than sea temperature, factors such as biotic interactions and dispersal limitation also play a key role in shaping the structure of marine communities (Watson et al. 2011, Chust et al. 2016, Villarino et al. 2018). Nevertheless, CTI has been used in variety of recent studies as a metric for evaluating how well communities are suited to their thermal environments and for comparing community structure changes on regional and global scales

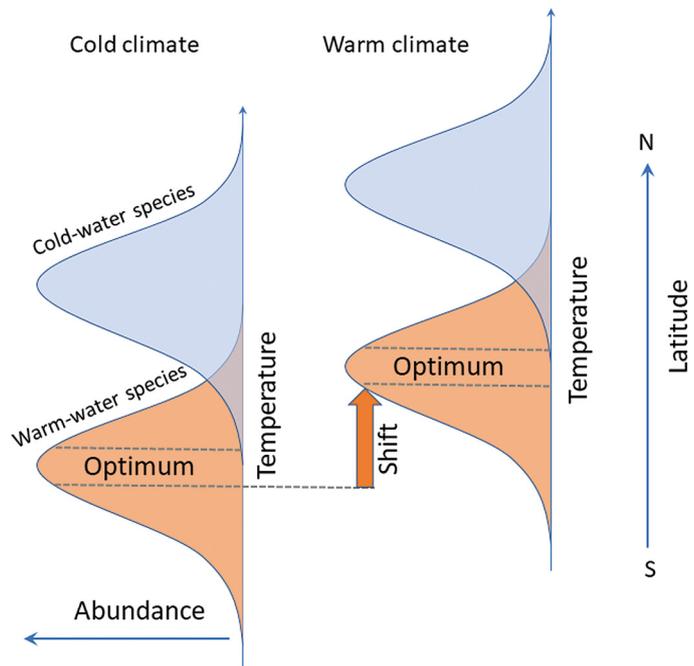


Fig. 1. Illustration of the expected abundance response curve of a cold and warm water species at cold and warm climate conditions in each site, under the assumption of niche tracking

(Devictor et al. 2008, Cheung et al. 2013, Stuart-Smith et al. 2015).

Zooplankton monitoring through long-term time series is useful for examining climate-ecosystem interactions. Zooplankton population dynamics and physiological rates are tightly linked to temperature (Hays et al. 2005, Richardson 2008), which results in a fast species response to environmental change. Zooplankton dynamics studies are also of particular interest as they constitute a key link between primary producers and large predators, supporting commercially important fisheries (Sundby 2000, Orlova et al. 2005). Zooplankton time series extending >10 yr are now available for many regions, carried out as part of different monitoring and research programs (Mackas & Beaugrand 2010). Today, however, across-site studies comparing time series trends are scarce.

Here, we analysed temporal patterns of copepod community assembly, as a representative group of zooplankton, using time-series data including 79 copepod species from 1980 to 2012 across the North Atlantic and the Mediterranean Sea, where sea temperature has significantly increased since the 1980s (deCastro et al. 2009, Palmer & Haines 2009, Shaltout & Omstedt 2014, Costoya et al. 2015). First, using a community β -diversity approach, we explored copepod assemblage composition variation over time as well as their relation to environmental change. Second, using a CTI approach, we tested whether the copepod community changes, whether it is respond-

ing to the ongoing ocean warming over time, and whether this response is consistent with species thermal niche tracking. We also analysed the amplitude of the responses (e.g. 'by how much') and its timing and spatial scales (e.g. 'when and where are rates of change strongest'). Both the temporal β -diversity and CTI approaches are complementary tools to study patterns of community assembly. The former provides specific information on the community turnover rate, whilst the latter is an indicator of the community thermal preferences, and its temporal change is used to test if ocean warming triggers a change in community composition. In both analyses, we expect a decrease in community similarity over time that could eventually be related to ocean warming if the copepod communities are tracking their temperature niches.

2. MATERIALS AND METHODS

2.1. Study sites

The study sites are located in 3 coastal zones of the North Sea and Mediterranean: the Kattegat, which is a sub-area of the North Sea, the mouth of the estuary

of Urdaibai in the southern Bay of Biscay, and the Gulf of Saronikos, in the eastern Mediterranean Sea (Fig. 2). For the Kattegat, we merged 3 separate stations (Aalborg Bay, Ven, and Griben) into one station, due to their proximity.

The Kattegat, 56.95° N, 11.30° E, is a transition zone between the Baltic Sea and the North Sea, with a substantially higher salinity range than the 2 sea areas it connects. Mean sea surface temperatures (SST) range from 0.9°C in February to 17.3°C in September (Mackenzie & Schiedek 2007a,b). Temperatures are influenced by several processes, including incoming solar heat flux and the mixing of warmer saline water from North Sea and outflow of colder brackish Baltic Sea water. The mean depth is ~20 m with a maximum depth > 90 m at the northern boundary, and half the area is shallower than 25 m (Fonselius 1996). The ongoing sampling in the Kattegat is variable in frequency (monthly or seasonal) and is conducted according to the HELCOM COMBINE manual for zooplankton (HELCOM 2010), using a WP-2 net with 180 μ m mesh towed from 25 m to the surface. We analysed monthly data from 1980 to 2012, sampled at irregular intervals, with a total of 257 mo.

The estuary of Urdaibai (43° 22' N, 2° 43' W) is a temperate estuary located on the Basque coast, in the

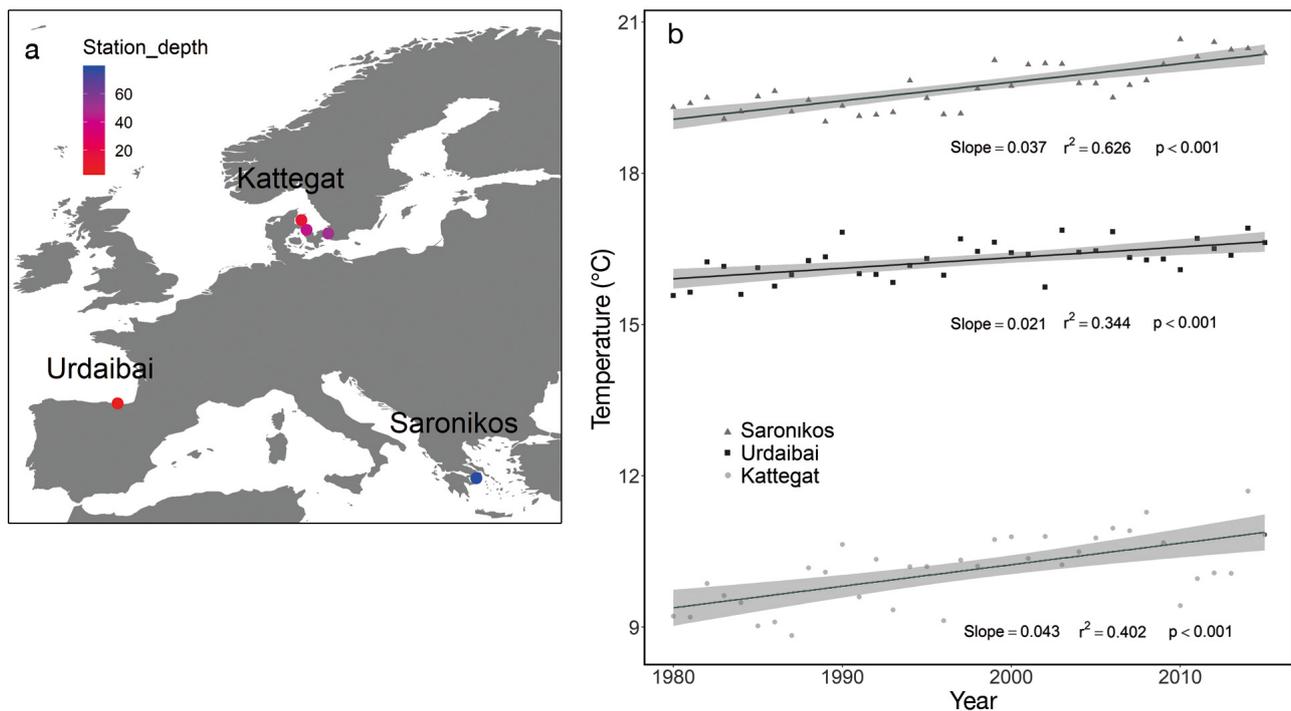


Fig. 2. (a) Site and depth (m) of each station. (b) GODAS SST trend of each station. The temporal development of SST is fitted by a linear model (black solid line), and grey shading shows the 95 % confidence level interval for model predictions. The slopes, r^2 -values and p -values of the linear models are also shown

inner Bay of Biscay. It is a relatively short (12.5 km) and shallow (mean depth of 3 m) meso-macrotidal system, with a maximum width of 1.2 km and <20 m in both outer and inner parts. SST range from 11°C to 23°C (Borja & Collins 2004) and have increased at a rate of 0.019°C yr⁻¹ over the last 50 yr (Goikoetxea et al. 2009, González et al. 2010, 2013). Most of the estuary exhibits marine dominance, with high-salinity waters in the lower half and a stronger axial gradient of salinity towards the head, where it receives most of the freshwater inputs from its main tributary, the Oka River (Villate et al. 2008). The zooplankton time series at Urdaibai estuary was initiated in 1997 (Villate et al. 2008). Surveys are carried out monthly at neap tides in different salinity sites of the estuary. We analysed monthly data from 1999 to 2013 (180 mo) in the marine zone (salinity ~35) from a coastal station at the mouth of Urdaibai estuary. We excluded the 1997–1998 periods from the analysis as some species were not identified to species level in this early time period. Vertical profiles of salinity and temperature were obtained using portable multiparameter meters. Samples for chlorophyll *a* (chl *a*) determination and zooplankton analysis were taken at mid-depth below the halocline. Niskin bottles were used for water samples, and zooplankton was sampled by horizontal hauls with 200 µm plankton nets (Uriarte et al. 2016). Monthly mean values of river flow and precipitation were obtained from the hydrometeorological station of Muxika (County Council of Bizkaia), located nearby the estuary of Urdaibai.

The Gulf of Saronikos is a semi-enclosed embayment on the western coastline of the Aegean Sea. Saronikos Station 11 (Saronikos S11) is located in the Saronikos Gulf at 37° 52.36' N, 23° 38.30' E with a bottom depth of 78 m. Mean monthly SST varies from 8°C in the north during winter up to 26°C in the south during summer. The overall spatial SST and sea surface salinity distribution pattern is controlled by influx of Black Sea waters, advection of the Levantine waters from the south-eastern part of the Aegean Sea, upwelling and downwelling, and, to a lesser extent but locally important, freshwater riverine inflows (Poulos et al. 1997). Saronikos S11 is located 7 km from the Athens domestic sewage outfall. Zooplankton at Saronikos sampling station were sampled with a WP2 net (56 cm diameter, 200 µm mesh) from a depth of 75 m to the surface. Water samples were collected with Niskin bottles. Temperature and salinity were measured with a CTD profiler. Oxygen concentrations were analysed following the Winkler method (Carpenter 1965a,b). Chl *a* measurements were conducted using photometric analyses of material col-

lected on Whatman GF/F filters. Monitoring of zooplankton began in 1987, with variable (monthly or seasonal) sampling frequency and periodic gaps. We analysed data from 1987 to 2007, sampled at irregular intervals, including a total of 71 mo. In all 3 sites, the number of counted specimens are converted to abundance (ind. m⁻³) values using estimated volume of water that is filtered through the net during sampling and any coefficients for dilution (split factors) derived from the subsampling procedure.

2.2. Sea temperature time series and trend analysis

To provide a common-method long-term dataset of water temperatures, data from the NCEP Global Ocean Data Assimilation System (GODAS) (www.cpc.ncep.noaa.gov/products/GODAS/) were extracted for each site from the 1980–2015 period. GODAS provides monthly water temperature data on a 0.333° × 1° latitude-longitude grid. Data from the grid closest to each sampling site was selected. We analysed the slope of the temperature trends and its significance using linear regressions and bootstrap cross-validation, which was implemented in the *boot* package of R (Davidson & Hinkley 1997, R Core Team 2019) and has become a standard way to test significance without strong assumptions (normality, independence, and homoscedasticity) (Zeileis & Grothendieck 2005).

2.3. Temporal β-diversity analysis

β-diversity, the spatial and temporal changes in species composition among sampling units, is a measure for quantifying the change (or 'turnover') in species composition across space or time (Whittaker 1960). For each site, we analysed temporal patterns of copepod β-diversity on a seasonal and interannual basis. First, we calculated 3 similarity or distance matrices including (1) biological data on species abundance composition, (2) environmental parameters measured at each site, and (3) the time lapse or time difference at each site. Second, to check whether changes in copepod community composition over time are driven by environmental differences or by random demographic stochastic processes, we correlated each of the matrices pair-wise: first, the community similarity matrix with time and then the community similarity matrix with environmental predictors. We also investigated time-decay (i.e. species similarity decay over time) or environmental-decay

(i.e. species similarity decay over environmental distance) patterns accounting for the degree of community composition change per unit of time.

(1) For the biotic similarity matrix, we calculated pairwise species similarities using the Bray-Curtis dissimilarity (BC) index over time (Legendre & Legendre 2012) with species abundance data at each station:

$$BC_{t_1 t_2} = 1 - \frac{2C_{t_1 t_2}}{S_{t_1} + S_{t_2}} \quad (1)$$

where $C_{t_1 t_2}$ is the sum of the lesser values for only those species in common between time interval t_1 and t_2 . S_{t_1} and S_{t_2} are the total number of individuals counted at both times.

(2) An environmental matrix, which reports the values of each environmental parameter recorded at each site, was used as a predictor to analyse changes in community composition over time. SST, salinity, chl *a*, and oxygen together with other environmental variables unique to each site were considered (precipitation and water flow for Urdaibai, total nitrogen, total phosphorous, dissolved inorganic silicate and Secchi depth for Kattegat). The Euclidean distance of the environmental variables was computed using the environmental differences over time at each site: the squared distances between n environmental variables in multidimensional space are the sum of squared differences in their coordinates. Environmental variables were converted into Z scores ($[x-\text{mean}]/\text{standard deviation}$) to give equal weight in the distance calculation. For example, a large environmental Euclidean distance between 2 given time steps means that the environmental differences over such time steps are large. The environmental variables used in this study have previously been shown to be important for determining copepod distribution (Villarino et al. 2015).

(3) To reveal temporal patterns in copepod communities, a time-lag analysis was used. We quantified the Bray-Curtis dissimilarity between each pair of samples, and the time difference (lag) was plotted against the dissimilarity. A time matrix was calculated with the lag or difference between each pair of months or seasons. For example, the time lag between Month 2 and Month 1 is 1.

To test the statistical relationships between species composition dissimilarity across environmental gradients, we used the Mantel test at both monthly and interannual scale. The Mantel correlation is a well known statistical procedure pertaining to the distance decay relationships framework (Nekola & White 1999). It calculates the correlation between 2

distance matrices computed between pairs of samples and evaluates its significance using random permutations (Mantel 1967). In this randomization, the rows and columns of one of the matrices are randomly permuted n times, and the correlation of each permutation is calculated to assess the significance of any departure from a zero correlation. The Mantel r values fall in the range of -1 to $+1$, where values close to -1 indicate strong negative correlation and $+1$ indicates strong positive correlation. An r value of 0 or near 0 indicates no correlation or little correlation. We performed a set of Mantel tests using the BIOENV (Clarke & Ainsworth 1993) function in the *vegan* R package between environmental distance and biological similarity matrices to find a subset of environmental variables that best correlate to sample similarities. In this case, the similarity matrix of the community is fixed, while subsets of the environmental variables are used in the calculation of the environmental similarity matrix. To check for the individual contribution of SST on community composition change, we built a separate environmental matrix including only temperature differences over time. In addition, we also performed Mantel tests between the biological similarity and time matrix to analyse how the community composition varied over time on a monthly and yearly basis for each station. Since a relationship between community dissimilarity and environment may also result from temporal autocorrelation (Legendre & Legendre 2012), partial Mantel tests were performed: we separated out the influence of the time component over the environment, and vice versa. Multiple regression on distance matrices (MRM) tests were performed using the *ecodist* package in R (Goslee & Urban 2007) to apportion the variability in community composition among the predictor factors (environment and time). MRM involves a multiple regression analysis of a response matrix (community similarity) on any number of explanatory variables (environment and time), where each matrix contains distance or similarities between all pair-wise combination of n objects (Legendre et al. 1994, Lichstein 2007). The test of statistical significance on MRM was performed by permutations.

For each station, we regressed community composition changes over time, on both a month-to-month and year-to-year basis. Subsequently, we obtained the slope of the linear regression as an indicator for the rate of species temporal change ('turnover'). Steeper negative slopes indicate faster temporal species turnover, whereas a slope = 0 indicates no turn-

over over time. We analysed time-decay patterns of community assembly by comparing the similarity of species occurring in the first time-step (month or year) of each time series vs. the similarity of species occurring in the next time-step.

2.4. Characterization of species thermal distributions

We constructed thermal distributions for 79 copepod species matching occurrence records collected from OBIS (Ocean Biogeographic Information System; www.iobis.org) global biological dataset for marine pelagic species, with annual means of GODAS local SST during the 1982–1999 period. The midpoint between the 5th and 95th percentile of the temperature distribution occupied by each species was then calculated, as a measure of central tendency of their realized thermal distribution (Stuart-Smith et al. 2015). We found a strong correlation between species midpoints and the temperatures at which species occurred at their maximum abundance ($r^2 = 0.89$; $p < 0.001$, data not shown); therefore, midpoints were considered a reasonable proxy of species maximum ecological success.

2.5. Community temperature index calculation

CTI was calculated at each station using the thermal midpoint values for each species recorded weighted by their $\log(\text{abundance} + 1)$ (Stuart-Smith et al. 2015). We used log transformation to dampen the influence of highly abundant species on the calculations of CTI. We calculated a CTI per year to analyse the temporal trends of the community abundance and its correspondence with local SST trends. We excluded from the analysis species with occurrences below 100 individuals due to the small sample size.

$$CTI_{t,l} = \sum m sp_n \times \log(a_{s_p} + 1) \quad (2)$$

where CTI for time t and site l is the sum of the midpoints m of species n weighted by the abundance a of species n .

2.6. Correlations between local sea temperature with CTI and time

We analysed correlations between CTI and time and between CTI and SST, calculating their slope

and significance using linear regressions. The slope was measured as the rate of change in community composition per unit of time (year) and per unit of temperature ($^{\circ}\text{C}$).

3. RESULTS

3.1. Temperature trends

Local mean SSTs obtained from GODAS confirm a significant increase in the 1980 to 2015 period at the 3 sites ($p < 0.001$) (Table 1, Fig. 2). The ocean warming rate is faster at the Kattegat (0.43°C per decade) and Saronikos (0.37°C per decade), compared to Urdaibai (0.21°C per decade). During the Urdaibai biological time-series period (1999–2013), no significant trend in SST was observed (Table 1, Fig. 2).

3.2. Temporal β -diversity

The community composition of each site is shown in Table S1 in the Supplement at www.int-res.com/articles/suppl/m636p047_supp.pdf. Community similarity between samples significantly decreased with the increase in time-lag, on both the seasonal and the interannual analysis (Table 2, Fig. 3). Time-decay slopes were higher in the year-to-year analysis compared to month-to-month (Table 2, Fig. 3). The degree of changes in species composition (e.g. turnover rate) varied from site to site, with 45% of the copepod community changing over time in the Kattegat and Urdaibai and 30% in Saronikos, as seen in the similarity values of the first and last year of each time-series (Fig. 3, below). In terms of seasonal patterns, a marked seasonal signal was observed in Urdaibai (Fig. 3, above), followed by the Kattegat, with some irregular seasonal cycles, and Saronikos, where no regular pattern was found (Fig. 3). Community similarity decayed more abruptly with environmental distance, at both month and year analysis, compared to the time-decay slopes (Table 2, Figs. 3 & 4). Environmental-decay slopes were similar to the SST difference slope, except for Urdaibai, where SST was not an important variable driving year to-year community composition change (Table 2).

Mantel tests in the monthly analysis reveals that community similarity was significantly correlated with time at the Kattegat ($r = 0.128$; $p < 0.001$) and Saronikos ($r = 0.064$; $p = 0.033$) but not at Urdaibai ($r = 0.025$; $p > 0.05$). In contrast, in the interannual

Table 1. Local SST trend analysis using GODAS annual means over the 1980–2015 period and over the time-series period. The slope, R^2 and p-value of the linear models between the local SST and time are shown, as well as the non-parametric bootstrap cross-validation confidence intervals (95 %)

Site	Period	Parametric			Non-parametric bootstrap (min, max)	°C increase per decade	Trend (max–min)	Temp. range
		Slope	R^2	p				
Kattegat	1980–2012	0.042	0.360	<0.001	(0.302, 0.792)	0.42	Increase	2.445
	1980–2015	0.043	0.402	<0.001	(0.394, 0.801)	0.43	Increase	2.865
Urdaibai	1999–2013	-0.002	-0.076	0.916	(-0.476, 0.485)	-0.02	No trend	1.127
	1980–2015	0.021	0.344	<0.001	(0.321, -0.769)	0.21	Increase	1.337
Saronikos	1987–2007	0.041	0.397	0.001	(0.416, 0.796)	0.41	Increase	1.218
	1980–2015	0.037	0.626	<0.001	(0.672, 0.872)	0.37	Increase	1.633

Table 2. Slope, p-value and R^2 correlation coefficients of the parametric linear models between Bray-Curtis copepod community similarity (Sim.) and time, environmental distance (Env.), and temperature differences, for each site and period

Frequency	Site	Sim. vs. Time			Sim. vs. Env.			Sim. vs. Temperature		
		Slope	R^2	p	Slope	R^2	p	Slope	R^2	p
Month	Kattegat	-4.586e-04	0.016	<0.001	-9.929e-02	0.144	<0.001	-9.929e-02	0.144	<0.001
	Urdaibai	-1.091e-04	0.001	<0.001	-2.635e-02	0.014	<0.001	-2.635e-02	0.014	<0.001
	Saronikos	-6.131e-04	0.004	0.001	-6.127e-02	0.157	<0.001	-7.268e-02	0.148	<0.001
Year	Kattegat	-7.098e-03	0.078	<0.001	-4.592e-02	0.057	<0.001	-4.592e-02	0.057	<0.001
	Urdaibai	-1.424e-02	0.068	0.004	-5.285e-02	0.055	0.009	1.951e-02	-0.002	0.368
	Saronikos	-1.425e-02	0.143	<0.001	-3.298e-02	0.048	0.013	-5.532e-02	0.020	0.081

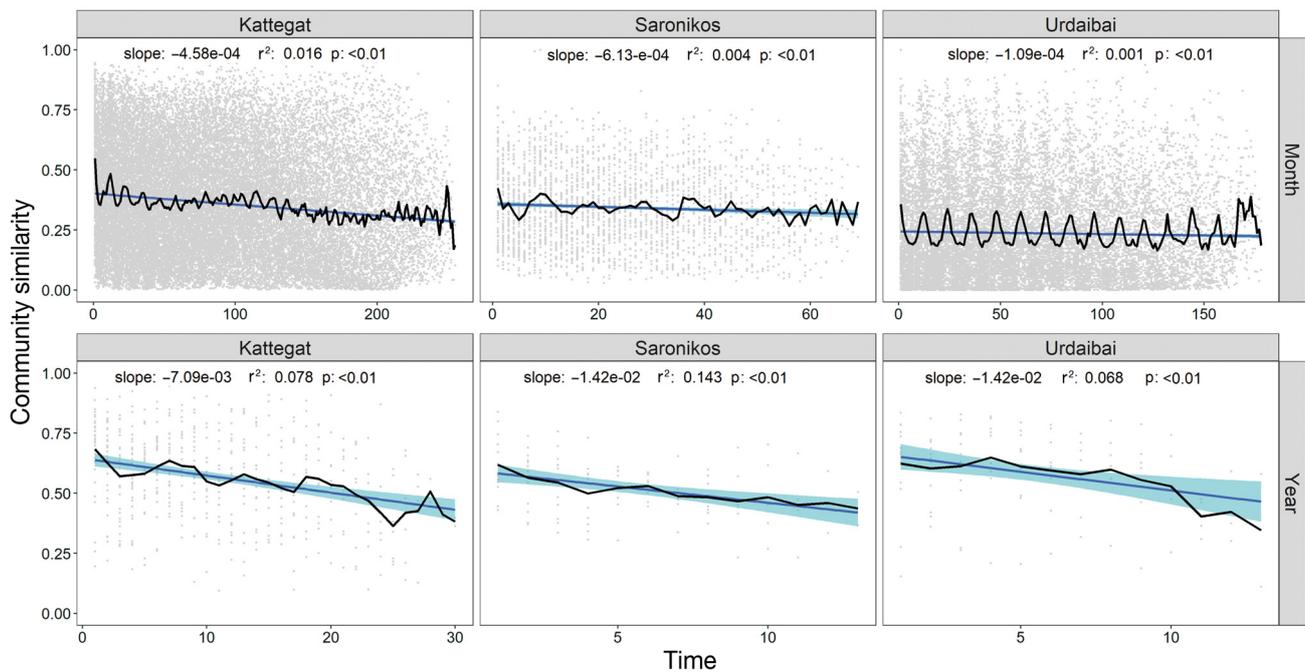


Fig. 3. Relationship between Bray-Curtis community similarity and time at monthly and interannual basis for each site. The grey points show the community similarity values at each consecutive time-step of each time-series. The black solid line depicts for the mean community similarity at each time step. The relationship between community similarity and time is fitted by a linear model (blue solid line), and the smooth shadows shows the 95 % confidence level interval for predictions of a linear model

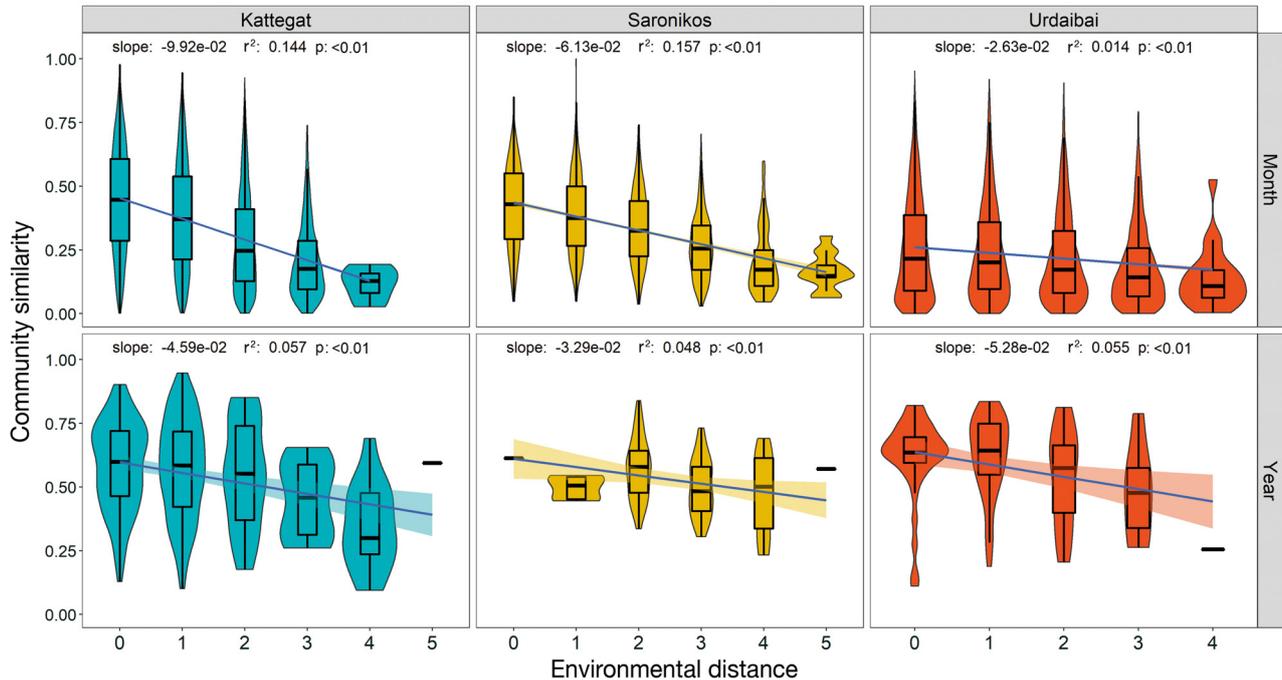


Fig. 4. Relationship between Bray-Curtis community similarity and environmental distance at monthly and interannual basis for each site. The boxplot shows the community similarity at each bin of environmental distance (0 to 5). The bottom and top of the box are the lower (Q1) and upper (Q3) quartiles, and the band inside the box is the median. The whiskers extend up to 1.5-fold the interquartile range (Q3–Q1) from the box. The points outside the whiskers are not drawn. The violin plot shows the kernel probability density of the data at different similarity values. The relationship between community similarity and environmental differences over time is fitted by a linear model (blue solid line), and the smooth shadows show the 95% confidence level interval for predictions of a linear model

analysis, correlations were significant for all 3 sites (Kattegat, $r = 0.282$ and $p < 0.01$; Urdaibai, $r = 0.277$ and $p < 0.05$; Saronikos, $r = 0.389$ and $p < 0.01$) (Table 3a). Mantel correlations between community similarity and environmental distance were significant for the 3 sites and much higher compared to the correlations between community similarity and time (Table 3a). In fact, the seasonal variability of environmental components, namely temperature, salinity, oxygen and chl *a*, was larger than the interannual variability (see Fig. S1 in the Supplement), which explains the greater importance of environment on seasonal community composition change. In turn, the interannual analysis shows a balanced contribution of time and environment, with time being a slightly better descriptor than environment at the 3 sites. In Urdaibai, the environment factor was not significantly correlated to community similarity (Table 3a). In the Kattegat and Saronikos, the partial Mantel correlation in the monthly analysis between community similarity and time, and between environment and SST, remained significant after controlling for each descriptor (Table 3b). In Saronikos, temporal ecological drift is an important factor driving interannual distribution, as seen in

the partial Mantel test (Table 3b). In general, the portion of the variance explaining patterns of community structure slightly increased when we accounted for the joint contribution of time and environment in community similarity, as seen in the multiple regression on distance matrices (MRM) analysis (Table 3c).

Results using the BIOENV model selection reveal SST as the most important factor driving temporal distributions of copepods seasonally. This is clearly seen in the significant Mantel correlations between temperature and community similarity, which are higher relative to the correlations with other environmental factors (Table 4, Fig. 5). To a lesser extent, oxygen variability in the Kattegat and Saronikos is also shown as an important and significant factor driving month-to-month distribution of copepods. In contrast, in the interannual analysis, the relative contribution of SST to community variance varies across sites. For example, SST was the most important factor ruling community composition changes over time in the Kattegat, while in Saronikos, SST was not a significant driver in itself, and a combination of environmental variables was selected by the models (SST, salinity, oxygen and chl *a*). In Urdaibai, SST was neg-

Table 3. (a) Mantel correlations, (b) partial Mantel correlations, and (c) multiple regression on distance matrices (MRM) between copepod community similarity (Sim.), environmental distance, and time difference. Mantel partial correlations are calculated after controlling for the effects of environment, time, and SST, in statistically significant cases. The statistical significance of the Mantel is assessed using 9999 random permutations. MRM involves a multiple regression analysis of a response matrix (community similarity) on any number of explanatory variables (in this case, Environment and Time), where each matrix contains distance or similarities between all pair-wise combination of n objects. The test of statistical significance is performed by permutations

(a)		— Sim. vs. Time —		Sim. vs. Environment		Sim. vs. Temperature			
Frequency	Site	Mantel r	p	Mantel r	p	Mantel r	p		
Month	Kattegat	0.128	<0.001	0.379	<0.001	0.379	<0.001		
	Urdaibai	0.025	0.105	0.119	<0.001	0.119	<0.001		
	Saronikos	0.064	0.033	0.397	<0.001	0.385	<0.001		
Year	Kattegat	0.282	<0.001	0.244	0.050	0.244	0.050		
	Urdaibai	0.277	0.019	0.253	0.090	-0.088	0.636		
	Saronikos	0.389	0.001	0.240	0.046	0.171	0.088		
(b)		Sim. vs. Time (out Env)		— Sim. vs. Env. — (out Time)		— Sim. vs. Time — (out Temperature)		— Sim. vs. Temp — (out Time)	
Frequency	Site	Partial Mantel r	p	Partial Mantel r	p	Partial Mantel r	p	Partial Mantel r	p
Month	Kattegat	0.138	<0.001	0.382	<0.001	0.138	<0.001	0.382	<0.001
	Saronikos	0.078	0.012	0.399	<0.001	0.078	0.011	0.387	<0.001
Year	Kattegat	0.296	<0.001	0.260	0.049	0.296	<0.001	0.260	<0.001
	Saronikos	0.360	0.002	0.183	0.104	–	–	–	–
(c)		MRM (Time + Environment)							
Frequency	Site	MRM r	p						
Month	Kattegat	0.401	0.001						
	Saronikos	0.404	0.001						
Year	Kattegat	0.379	0.004						
	Saronikos	0.424	0.003						

Table 4. Environmental variable selection for copepod community structure. Key environmental variables are selected using the BIOENV function of the 'vegan' package in R, which finds a subset of environmental variables (from a larger set), such that the Euclidean distances of scaled environmental variables have the maximum Pearson correlation with community dissimilarities using Bray-Curtis. T: sea surface temperature ($^{\circ}\text{C}$), S: salinity, DSI: dissolved inorganic silicate (μM), TN: total nitrogen (μM), TP: total phosphorus (μM), O: oxygen (mg l^{-1}), Flow: water flow ($\text{m}^3 \text{s}^{-1}$), Secchi Depth: Secchi depth (m), precipitation: (mm), Chl a: chlorophyll a (μl).

Frequency	Site	Environmental variables	BIOENV- selection	Correlation (selected variables and community similarity)	p
Month	Kattegat	T, S, O, Chl a, TP, TN, DSI, Secchi depth	T	0.379	<0.001
	Urdaibai	T, S, Chl a, Flow, Precip.	T	0.119	<0.001
	Saronikos	T, S, O, Chl a	T + O	0.397	<0.001
Year	Kattegat	T, S, O, Chl a, TP, TN, DSI, Secchi depth	T	0.244	0.050
	Urdaibai	T, S, Chl a, Flow, Precip.	Chl a	0.253	0.090
	Saronikos	T, S, O, Chl a	T + S + O + Chl a	0.240	0.046

atively correlated with copepod community temporal patterns; however, we cannot draw any solid conclusions here due to the short length of the time series.

Instead, Mantel r-values were highest with chl a, the variable selected by the models, but the relationship was not significant (Table 4, Fig. 5).

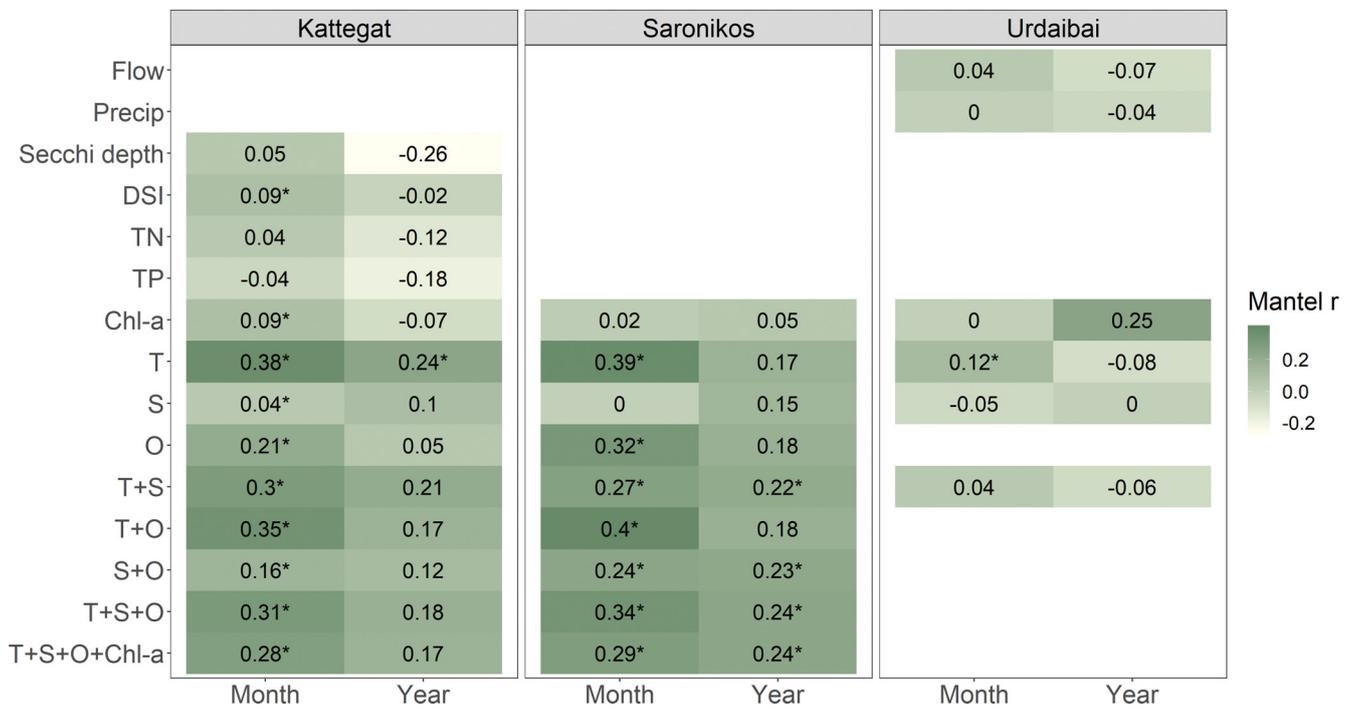


Fig. 5. Tile diagram showing the Spearman's correlations of the copepod community with environmental factors based on Mantel tests. The Mantel r values fall in the range of -1 to $+1$. Brighter cells with negative values in the plot indicate a negative correlation and greener cells with positive values a strong positive correlation. An r value of 0 indicates no correlation between community similarity and environmental variables. T: sea surface temperature ($^{\circ}\text{C}$), S: salinity, DSI: dissolved inorganic silicate (μM), TN: total nitrogen (μM), TP: total phosphorus (μM), O: Oxygen (mg l^{-1}), Flow: water flow ($\text{m}^3 \text{s}^{-1}$), Secchi depth (m), Precip: precipitation (mm), Chl-a: chlorophyll a (μl), *: significant at $p < 0.05$

3.3. CTI temporal analysis

CTI temporal trends varied across sites. The thermal preferences of the Kattegat copepod community are significantly changing over increasing local SST. In fact, a significant increase of CTI over time was observed, governed by a strong and significant local SST increase (Table 5, Fig. 6). As hypothesized, a significant positive correlation between local SST and CTI was found with a CTI increase of 0.55°C for each 1°C increase in local SST (Table 5, Fig. 6). These results confirm that the copepod communities in the Kattegat are following their thermal niches, as the community is shifting towards one with a greater proportion of warm species. In Urdaibai, no trend in CTI over time was observed, nor was there a significant relationship between CTI and local SST, as expected by the low contribution of SST in community variance (Tables 4 & 5, Fig. 6). In Saronikos, despite the significant and relatively strong ocean warming over the time series period, the CTI increase was not significant (Table 5, Fig. 6). However, both the CTI and local SST

followed the same pattern, resulting in a strong correlation between CTI and local SST, with a CTI increase of 0.62°C for each 1°C increase in local SST (Table 5, Fig. 6). The copepod communities of Saronikos are tracking their thermal niches over time, in the same manner as they do in the Kattegat. We also found a clear latitudinal gradient in CTI, as expected, strongly decreasing from south (Saronikos) to north (Kattegat) (Fig. 6).

Community composition changes over time are summarized in Fig. 7. In the Kattegat, the relative abundance of warm species dropped at the beginning of the time-series, but afterwards, from 1985 to

Table 5. Parametric linear models between community temperature index (CTI) and time, and between CTI and local GODAS SST for each site, showing the slope, R^2 and p -value of the models

Site	CTI vs. Time			CTI vs. GODAS SST		
	slope	R^2	p	slope	R^2	p
Kattegat	0.042	0.189	0.007	0.551	0.138	0.020
Urdaibai	-0.003	-0.076	0.910	-0.459	0.021	0.273
Saronikos	0.018	0.060	0.382	0.618	0.367	0.009

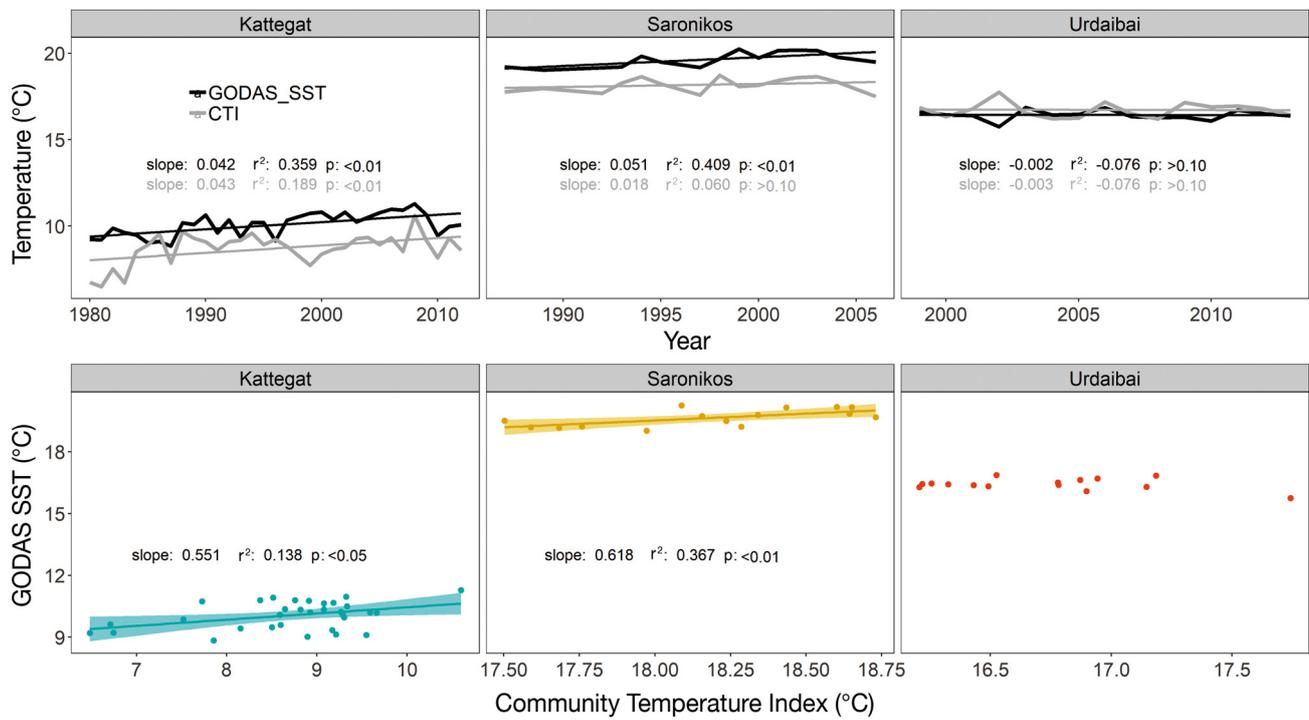


Fig. 6. Top: temporal development of Community Temperature Index (grey) and local GODAS SST (black) for each site. The linear model fit shows the trend, slope r^2 and p-value of each variable. Bottom: relationship between community temperature index and local GODAS SST for each site. When significant, the relationship is fitted by a linear model (solid line), and smooth shadows with the 95% confidence level interval for predictions of a linear model

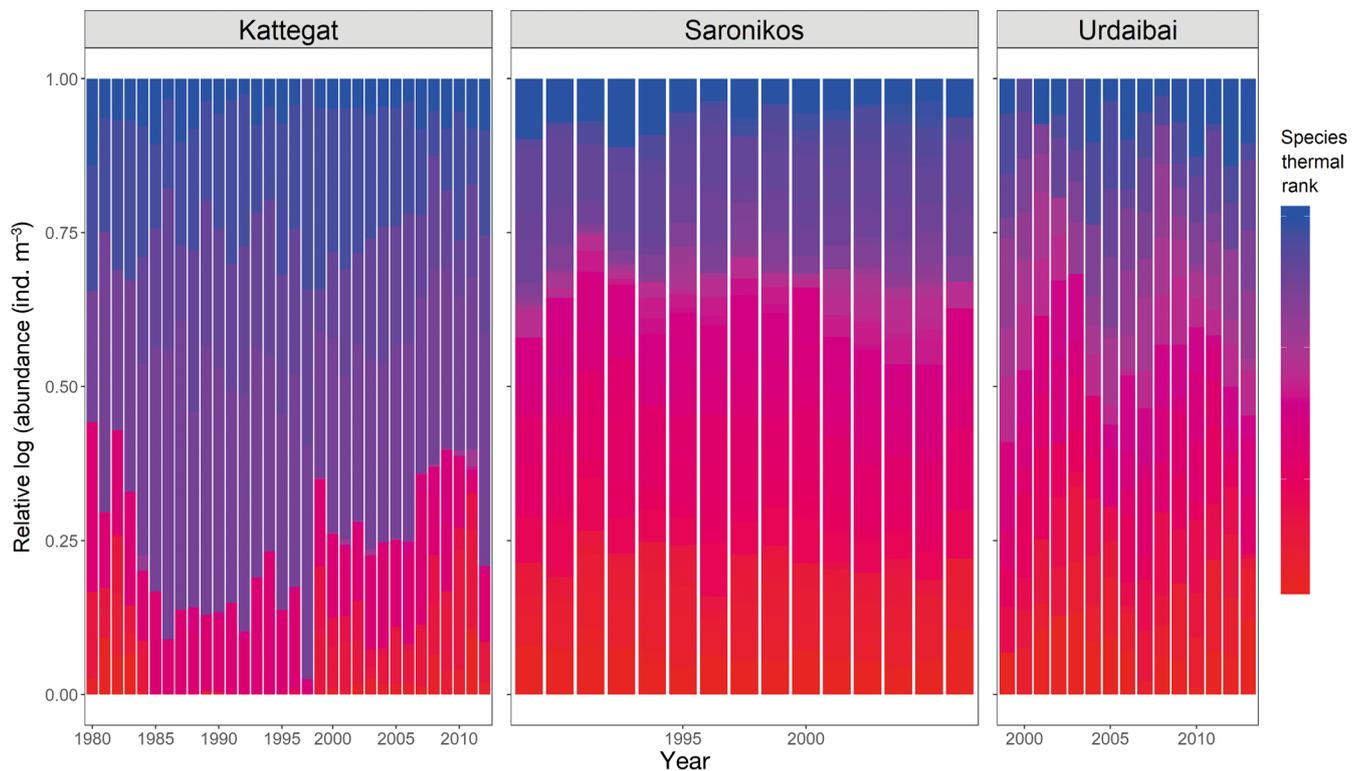


Fig. 7. Vertical barplots showing community composition changes over time at each site. The colorbar shows the species thermal rank for each community. Species are ordered according to their thermal affinities. Red: warm-adapted species, blue: cold-adapted species

2012, a clear increase of warm-adapted species over time was observed. These patterns reflect an abrupt change in the community composition linked to ocean warming, as seen in the CTI significant increase over time. In Saronikos, species with warmer affinities clearly dominated over the entire time-series. The relative abundance of species associated with warm conditions is slightly increasing over time as the ocean warms, at the expense of species with colder affinities, and the community is tracking its thermal niche (Fig. 7). In Urdaibai, the proportion of warmer water species peaked in 2001–2003 and 2008–2011, and the relative abundance changes of warm and cold species alternated over time, despite a lack of a linear trend in local sea temperature (Fig. 7).

4. DISCUSSION

Our study found that community similarity of copepods decreased significantly over time and that copepod assemblage at the end of the time-series differed significantly from the starting period. However, temporal species turnover is the outcome of a variety of dynamic processes: for example, environmental filtering, shaping the communities according to environmental variability, or stochastic demographic processes (e.g. ecological drift), changing the structure of communities with a gain or loss of species through dispersal (Anderson et al. 2011). In the monthly analysis, our results support the hypothesis that environmental selection rather than demographic stochastic processes dominate the copepod temporal distributional patterns. In fact, the proportion of the variance explained by the stochastic replacement of individuals from the community has been substantially lower compared to niche descriptors, particularly SST, at the 3 sites. SST driving seasonal distributional patterns of zooplankton has been described elsewhere (Edwards & Richardson 2004, Richardson 2008). Oxygen is another important variable selected by the models on a monthly basis. Over the last few decades, the extent of bottom water hypoxia has increased in coastal oceans (Diaz & Rosenberg 2008) caused largely by anthropogenic eutrophication and increased nutrient loadings, and oxygen variability predicting the abundances of zooplankton taxa has been well reported in the coastal areas of the Gulf of Mexico (Rabalais et al. 2002, Elliott et al. 2012). In contrast, in the interannual analysis, both environmental and stochastic processes significantly influenced copepod community assembly, and the stochastic contribution was particularly pronounced in

Saronikos. In both periods, a large part of the variance remains unexplained, suggesting that there are other explaining factors unaccounted for or that the variability is purely random. Recent studies showed that 2 types of processes, environmental and stochastic, influence plankton community assembly with varying relative effects depending on geographic scales and strength of environmental gradients (Hanson et al. 2012, Morrison-Whittle & Goddard 2015).

The relative abundance and composition of species has shifted linearly over time. Changes in assemblage similarity over time are not necessarily linear. For example, Hsieh et al. (2005) reported a lack of correlation between fish populations and environmental signals in the coastal and coastal-oceanic assemblages of the Pacific Ocean for the 1951–2002 period, indicating that these species might show non-linear biological responses to external forcing rather than a simple linear tracking of environmental variables. This non-linearity is especially true for intra-annual data sets where similarities may include a seasonal signal. For example, copepod assemblages in spring and autumn may share more species with each other than assemblages in spring and summer, due to lower environmental distance. In these cases, the time-decay shows a nonlinear pattern, as we have seen in the monthly analysis. Inter-annually, all sites show negative linear patterns, as expected, mirroring strong rearrangements of the communities over time (Beaugrand et al. 2002).

A CTI approach was carried out to see if the community change over time corresponded with species thermal niche tracking. We cannot necessarily assume that CTI and temperature change will be linearly correlated, as some species have asymmetrical thermal performance curves (Oksanen & Minchin 2002) or are thermally biased with higher or lower thermal preferences than their local temperatures (Stuart-Smith et al. 2015). However, the scatter plot between CTI and SST suggests either that the fit can also be linear or that there is no relationship between variables. We consider that the calculations of the species thermal optimum or midpoint applied here are a good approximation of the central tendency of their realized thermal distribution (Stuart-Smith et al. 2015). Any increase in local sea temperature may be detrimental for cold-adapted species but beneficial for warm-adapted ones (Kordas et al. 2011), regardless of the shape of the thermal curve. Such species turnover from cold-adapted to warm-adapted species should be somehow mirrored in a change in the community thermal preference or CTI over time. We found that in the Kattegat the significant CTI in-

crease over time is associated with a strong local sea temperature change (Kordas et al. 2011, Berline et al. 2012), which indicates that copepod communities are tracking their thermal niches. This might be because the cold-adapted species of the community, which are at their thermal distribution limits, decreased in abundance, while the warm-adapted species increased. The same niche tracking pattern over time is observed in Saronikos. The Saronikos community is the most biodiverse community among the sites, with a greater resilience capacity to buffer community structure changes due to environmental change (Bernhardt & Leslie 2013). However, the strong local ocean warming is causing important community reorganizations: warm-adapted species are replacing out-migrating and shrinking populations of cold-adapted ones. Plankton community changes towards warmer or cooler compositions that are consistent with historical changes in temperature have been recently reported globally using centennial time series data (Jonkers et al. 2019). Regionally, a number of studies have also found thermal niche conservatism through geographic or compositional shifts in the Mediterranean Sea (Berline et al. 2012) or the North Atlantic (Lucey & Nye 2010, Mackas & Beaugrand 2010, Helaouët et al. 2011, Chust et al. 2014, Villarino et al. 2015, Kleisner et al. 2016). A core problem is that temporal trends in CTI may not only reflect changes in local temperatures. This is because species temperature preferences often covary with other species attributes, and these attributes affect species response to other environmental drivers. In temperate latitudes within the western Bay of Biscay, we found no ocean warming during the biological time series period (1999–2013) and a low yet negative correlation between SST and copepod community composition variability. We consider that in Urdaibai other factors such as dispersal limitation or biotic interactions are playing a more important role than SST in driving temporal change in community composition. Some studies have emphasized the role of species interactions in mediating the impacts of temperature on long-term CTI change in temperate reef communities (Bates et al. 2014, 2017). In general, changes in CTI over time related to temperature increase do not report which species are affected by climate change but integrate the present decline of cold or warm species in the local community. Therefore, changes in CTI provide clues on variations in the dominance structure of species occurring locally.

In summary, we found strong community structure changes in the Kattegat, Urdaibai, and Saronikos, with a significant decrease in community similarity

over time related to both niche and demographic stochastic processes. Patterns of copepod community change in Saronikos and the Kattegat show a slight fingerprint of global warming, where the ocean warming is the fastest among sites. Most of the cold species at these sites are at borderline thermal thresholds; as the local waters warm, these populations must either follow their temperature niche, in space or time, or reduce their abundance. In Urdaibai, no ocean warming is observed during the shorter biological time-series period, so the functional community composition, defined by its thermal preferences, has not changed—as would be expected. Overall, these findings expand current understanding of the ecological mechanisms underlying zooplankton temporal patterns in changing coastal ecosystems.

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