

Response of marine diatom communities to Late Quaternary abrupt climate changes

PEDRO CERMEÑO^{1*}†, EMILIO MARAÑÓN¹ AND OSCAR E. ROMERO²

¹DEPARTAMENTO DE ECOLOGÍA Y BIOLOGÍA ANIMAL, UNIVERSIDAD DE VIGO, 36310 VIGO, SPAIN AND ²INSTITUTO ANDALUZ DE CIENCIAS DE LA TIERRA, CSIC-UGR, AVENIDA DE LAS PALMERAS 4, 18100 ARMILLA, GRANADA, SPAIN

†PRESENT ADDRESS: INSTITUTO DE CIENCIAS DEL MAR, (CSIC), PASSEIG MARITIM DE LA BARCELONETA, 37-49. E-08003 BARCELONA, SPAIN.

*CORRESPONDING AUTHOR: pedrocermeno@icm.csic.es

Received April 27, 2012; accepted September 23, 2012

Corresponding editor: Roger Harris

The high temporal resolution of the marine microfossil record makes it possible to explore how microbial communities responded to abrupt climate changes in the past. We analysed changes in species richness and total abundance of marine diatoms in sedimentary records from the Mauritanian upwelling system and the Panama Basin spanning the last 100 000 years. The analysis shows instances of community change and recovery linked to episodes of rapid, sub-millennial scale climate change (e.g. Heinrich events). The probability of sampling a given species during the perturbation increased with the mean abundance of the species in the database, indicating that (i) dominant species were persistent through long periods of time and (ii) rare species, with low population densities, accounted for much of the variability in species richness. To the extent that contemporaneous climate change falls within the range of climate variability analysed here, our results point to important changes in the structure of marine diatom communities, yet these changes will be reversible. These results highlight the importance of integrating fossil data and ecological theories to understand the effect of climate change on the ecological and biogeochemical functioning of marine ecosystems.

KEYWORDS: marine diatoms; fossil record; Late Quaternary; abrupt climate change; Heinrich events; dispersal; community stability

INTRODUCTION

The last 100 000 years of Earth history have been a witness to abrupt changes in the functioning of the climate system (Alley, 2000; Andersen *et al.*, 2004). Among these climatic perturbations, Heinrich events have been thoroughly studied because of their possible temporal analogy with projected, human-induced climate scenarios. Heinrich events constitute a suite of rapid, millennial-scale

climate transitions linked to massive discharges of icebergs from Northern Hemisphere melting ice-sheets into the North Atlantic (Heinrich, 1988; Bond *et al.*, 1992; Hemming, 2004). Detailed sedimentary records suggest that these cooling episodes, though each possessing its own peculiarities, gave rise to a rapid shutdown of the Atlantic Meridional Overturning Circulation, Earth cooling and sea level changes with global impact (Alley, 1998; Sachs and Lehman, 1999; Lambeck *et al.*, 2002; Rahmstorf,

2002). These transient states spanned a few thousand years and returned subsequently to previous climatic/oceanographic scenarios through mechanisms still poorly understood. As a whole, these climatic episodes provide an excellent framework to explore (i) the response of microbial plankton communities to abrupt changes in climate and (ii) the potential of these communities for recovery once climatic/oceanographic conditions are re-established.

Two fundamental properties of ecological communities determine their response to environmental perturbations: (i) resistance to change and (ii) resilience or ability to return to previous states after the perturbation (Holling, 1973, 1986; Pimm, 1991). These two ecological properties, in turn, are largely dependent on whether species react to environmental changes individually or collectively as a community (DiMichele, 1994; Pandolfi, 1996). In the former case, community structure primarily depends on species' immigration and local environmental selection, and typically these communities exhibit little resistance to change (Cermeño *et al.*, 2010). In the latter, only a fraction of the regional species pool fits into the local community, which is characterized by strong interspecific dependencies and restricted entry (Pandolfi, 1996). Whereas species' individual responses and immigration provide communities with high resilience, strong interspecific relationships buffer communities against environmental perturbations, increasing their resistance to change (Begon *et al.*, 1986; Margalef, 1986; Hubbell, 2001).

Field evidence and modelling analyses suggest that on-going climate warming might potentially affect different aspects of marine phytoplankton community structure, including taxonomic composition and size structure (Falkowski and Oliver, 2006; Finkel *et al.*, 2010). Climate warming will enhance the vertical thermal gradient in the ocean, reducing mixing and hence the supply of nutrients into the upper mixed layer. Diatoms rely on intermittent inputs of nutrients to thrive and outcompete other autotrophic plankton, including coccolithophores and flagellates (Litchman, 2006), and therefore reduced mixing is expected to limit their competitive abilities. Likewise, large-sized phytoplankton, with a lower surface to volume ratio, is at a disadvantage over smaller cells for nutrient acquisition, i.e. the nutrient uptake to individual's demand ratio decreases with cell size. Therefore, decreased nutrient supplies are expected to shift the structure of marine phytoplankton communities in favour of taxa with high affinity for nutrients such as coccolithophores and small-sized cells.

It has been suggested that large numbers of melting icebergs in the North Atlantic would have enhanced the vertical density gradient, reducing nutrient renewal, primary productivity and the contribution of diatoms to

community biomass (Ruddiman and McIntyre, 1981). However, other studies have found that diatom productivity increased during Heinrich events, perhaps linked to the input of silica and other nutrients of continental origin, or upwelled through physical mechanisms such as iceberg ploughing (Sancetta, 1992b; Gil *et al.*, 2009). Climatic events initiated at high latitudes might also influence marine primary productivity and the dynamics of tropical phytoplankton communities through interhemispheric teleconnections. Coastal upwelling systems and the equatorial regions receive large amounts of nutrients via upwelling of intermediate and subsurface waters, and contribute enormously to export production, largely dominated by diatom assemblages (Longhurst, 2007). These areas are particularly responsive to climate variability and thus understanding the response of marine diatom communities to such variability is of critical interest to plankton ecologists, biogeochemists and paleoceanographers.

The sinking valves of diatoms which survive dissolution in the water column and at the water/sediment interface finally accumulate in the marine sediments, leaving a fossil record with enough temporal resolution to study community dynamics across episodes of rapid climate change (Romero and Armand, 2010). Here, we analyse data of species richness and abundance of marine diatoms in Late Quaternary sedimentary records from the NW African upwelling system and the easternmost equatorial Pacific. These sedimentary records span the last 44 000 and 100 000 years, respectively, and were studied at a sub-millennial temporal resolution (Romero *et al.*, 2008, 2011). We focus on the analysis of data across Heinrich events, the Younger Dryas (YD) and the transition into the Holocene. Heinrich event 1 (HE1), the YD and the Holocene transition are characterized by changes in climate with no return pathway, and served to test the effect of environmental changes on community structure. In contrast, climatic perturbations linked to Heinrich events 5 and 7 provided an excellent framework to test the community recovery “resilience” hypothesis. These analyses can help us to understand the response of marine microbial plankton communities to rapid changes in climate, their potential to shift back, and the causality/synchrony of climate–biology interactions.

METHOD

Sampling and core stratigraphy

The original data used in this study have previously been reported in two separate studies aimed at investigating

paleoproductivity changes across glacial/interglacial periods (Romero *et al.*, 2008, 2011). Here, we focus on the ecological response of diatom communities to episodes of abrupt changes in climate. Core GeoB7926-2 (20°13'N, 18°27'W, 2500 m water depth) was obtained during R/V Meteor Cruise 53/1c off Mauritania (Romero *et al.*, 2008). The age control for gravity core GeoB7926-2 is based on 17 accelerator mass spectrometry (AMS) radiocarbon dates determined on monospecific samples of the planktonic foraminifer *Globigerina inflata* (>150 mm fraction; Leibniz Laboratory for Radiometric Dating and Stable Isotope Research, Kiel University, Germany; see details in Romero *et al.* 2008). The ¹⁴C ages were converted into calendar years using Calib Execute Version 5.0.2 (<http://calib.qub.ac.uk/>; Stuiver *et al.*, 1998). Calendar ages between dated levels were obtained by linear interpolation between the nearest AMS dating points (Romero *et al.*, 2008).

Core MD02-2529 (08°12.33'N; 84°07.32'W; 1619 m water depth) was collected during the IMAGES VIII/MD 126 MONA oceanographic cruise, off the Costa Rican margin in the Panama Basin (eastern equatorial Pacific; Romero *et al.*, 2011). The age model for core MD02-2529 is based on calibrated radiocarbon ages for the last 40 ka BP. The 60–99 ka BP interval is dated by correlating the benthic $\delta^{18}\text{O}$ record to a reference stack of benthic foraminifera $\delta^{18}\text{O}$ records (Lisiecki and Raymo, 2005).

Diatom analysis

For the study of diatoms, samples were prepared following the method proposed by Schrader and Gersonde (Schrader and Gersonde, 1978). Qualitative and quantitative analyses were carried out at $\times 1000$ magnification using a Zeiss Axioscope with phase contrast illumination. Counts were carried out on permanent slides of acid cleaned material (Mountex mounting medium). Several traverses across the coverslip were examined, depending on valve abundances (between 400 and 1300 valves per coverslip were counted). At least two coverslips per sample were scanned in this way. Diatom counting of replicate slides indicates that the analytical error of the concentration estimates is <15%. The counting procedure and definition of counting units for diatoms followed those proposed earlier (Schrader and Gersonde, 1978). A full list of species identified can be found in Supplementary data Appendix SI.

Data analysis

Preston's representations, displaying the frequency of species across classes of abundance (Preston, 1960),

were constructed using the global database at each location. These representations show the relative contribution of dominant and rare species to community abundance.

Indices of community similarity were computed for each pair of fossil assemblages across the sedimentary records analysed. The Jaccard index, \mathcal{J} , quantifies the similarity between communities j and k in terms of taxonomic composition, and is calculated as (Legendre and Legendre, 1983),

$$\mathcal{J}_{jk} = \frac{a}{a + b + c},$$

where a is the number of species present in both communities j and k , b the number of species present in community j , but absent in k , and c the number of species present in community k , but absent in j . This index requires that species which are jointly absent from j and k are first removed. \mathcal{J} ranges from 0 (when no species are shared between any two communities) to 1 (when all species are shared) and emphasizes compositional changes. Quantitative estimates of community similarity were determined using the Bray–Curtis (BC) index, which is defined as

$$\text{BC}_{jk} = \frac{\sum_{i=1}^p y_{ij} - y_{ik}}{\sum_{i=1}^p y_{ij} + y_{ik}},$$

where y_{ij} and y_{ik} are the abundances of species ($i = 1, 2, \dots, p$) in samples j and k (Clarke and Warwick, 1994). This index emphasizes changes in the dominant species, i.e. those with large population abundances. Pair-wise community similarities were computed on raw data (not transformed) using SPSS software and the R programming platform.

RESULTS

We studied the dynamics of marine diatom assemblages across HE1, the YD and the transition into the Holocene (Holocene) from the sedimentary record obtained off Mauritania, and Heinrich events 1, 5 and 7 (HE1b, HE5 and HE7) from the core collected in the Panama Basin. Disruption of climatic/oceanographic conditions led to drastic changes in the structure of marine diatom communities in terms of total abundance and species richness (Figs 1 and 2). In the Mauritanian upwelling system, climate change episodes linked to HE1 and the YD increased diatom abundance and species richness, almost certainly as a result of enhanced mixing and nutrient supply to the photic zone (Fig. 1). A higher nutrient

availability increased total diatom (valve) abundance, and most likely the relative contribution of diatoms with respect to slow-growing phytoplankton. Although no counts of other microplankton groups such as coccolithophores are available for the cores described here, the relative dominance of diatoms and calcifiers, respectively, can be inferred to a large extent from changes in the percentages of opal and calcium carbonate in marine sediments. During periods of enhanced wind intensity and upper

ocean mixing, the percentage of opal in sediments increased with respect to calcium carbonate (Romero *et al.*, 2008), underscoring the competitive advantage of siliceous plankton. Conversely, the transition to warmer climates of the Holocene weakened global atmospheric gradients and the intensity of wind-driven upwelling off Mauritania, decreasing diatom abundance and species richness (Fig. 1).

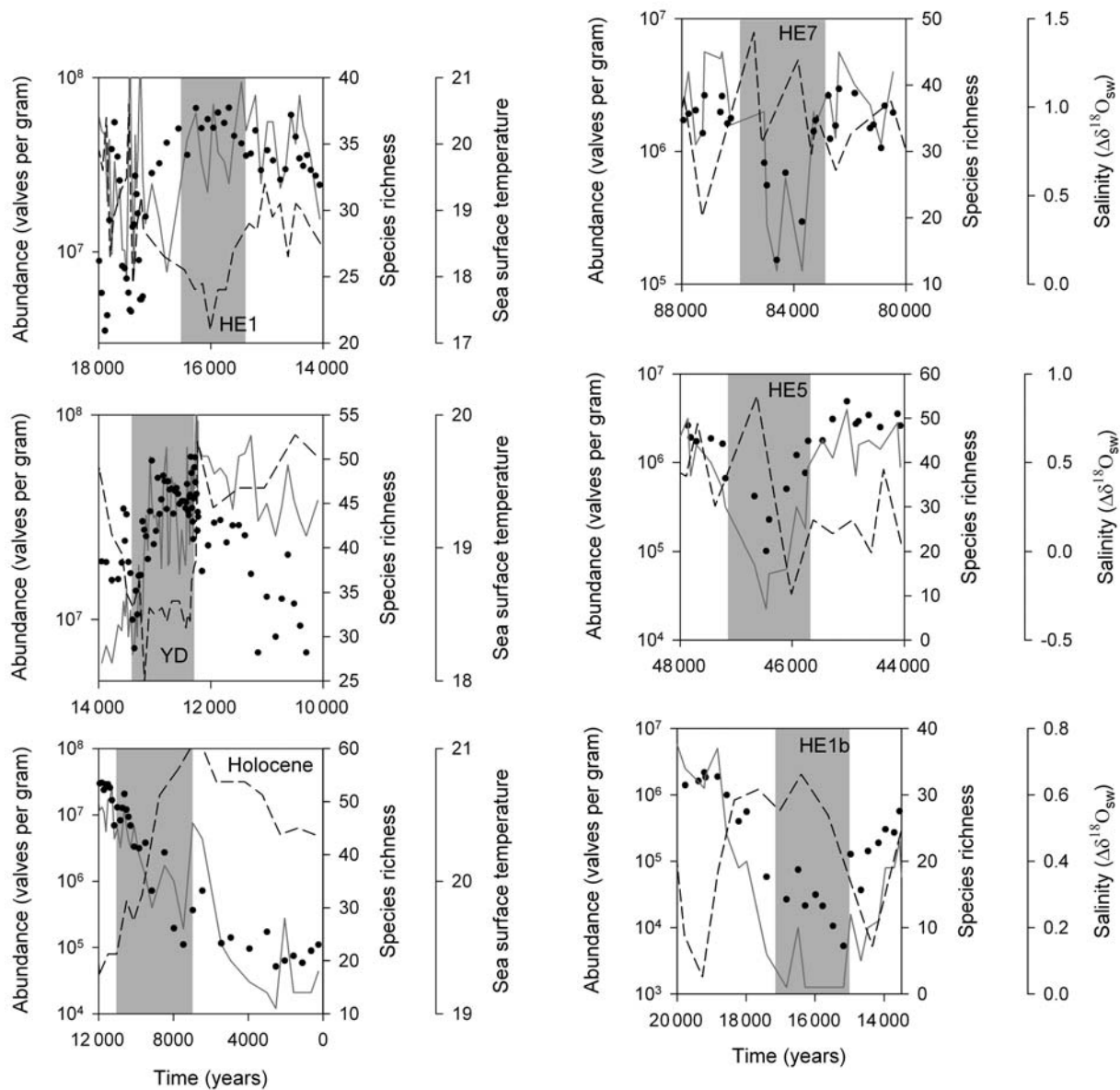


Fig. 1. Temporal evolution of diatom abundance (dots), species richness (grey line) and sea surface temperature (black dashed line) in the Mauritanian upwelling system during HE1, the YD and the transition into the Holocene; upper, middle and bottom panel, respectively. The shaded areas denote the time interval of the corresponding climatic episode. Higher values of sea surface temperature are indicative of reduced nutrient delivery.

Fig. 2. Temporal evolution of diatom abundance (dots), species richness (grey line) and sea surface salinity (black dashed line) in the Panama Basin during HE7, HE5 and HE1b; upper, middle and bottom panel, respectively. The shaded areas denote the time interval of the corresponding climatic episode. The variations in $\delta^{18}\text{O}_{\text{sw}}$ represent a proxy for regional changes in salinity with higher values indicative of enhanced subtropical influence and meso/oligotrophic conditions.

The patterns observed in the Panama Basin were radically opposite (Fig. 2). In core MD022529, diatom abundance and species richness during the perturbation dropped to values $<50\%$ relative to those observed before the climate events. The response of marine diatom assemblages to HE1b, HE5 and HE7 in the Panama Basin sharply contrasted with the response of diatom communities to H1 and the YD off Mauritania (Figs 1 and 2). We found that these patterns of community change in the Panama Basin coincide with periods of higher sea surface salinity, which is indicative of enhanced subtropical influence in this region. Remarkably, our data analysis shows that, except for HE1b, individuals' numbers and species richness rapidly recovered once hydrographic conditions were re-established.

Our analysis highlights substantial variations in diatom abundance and species richness, yet it does not provide information about the dynamics of community structure. For instance, what kind of species, if any, persisted through these climatic episodes? Did analogous climate conditions give rise to similar communities? To answer these questions, we computed specific pair-wise community similarity indexes, which provide information on changes in taxonomic structure. The Jaccard similarity index emphasizes changes in community composition giving all species, either dominant or rare, the same weight. The BC index gives a larger weight to dominant taxa as it takes into account the population abundance of species (see Method section for details). We compared the communities through each abrupt climatic episode with the communities just before the perturbation. Assemblages influenced by similar environmental conditions should exhibit more similarities than those experiencing distinct climatic/oceanographic forcing. Consistent with our analysis of total abundance and species richness, the BC similarity index rapidly decreased during the perturbation. In the Mauritanian upwelling system, the index of similarity across HE1, the YD and the transition into the Holocene exhibited a pattern of decrease with no recovery (Fig. 3). In the Panama Basin the index of similarity decreased sharply during the perturbation, yet, increased again after HE5 and HE 7, underscoring the potential of these microbial communities to recover once climatic/oceanographic conditions are fully re-established (Fig. 4). Similar results were obtained by applying the Jaccard similarity index (data not shown).

Ecological communities are usually formed by two types of species: (i) dominant species, which grow locally and attain high population abundances and (ii) rare species (at low population densities), which either persist in the community growing slowly or are recruited via immigration from adjacent communities. We represented the species abundance distribution for

each study site. To the extent that preservation biases allow making paleoecological inferences, the analysis shows that total abundance was dominated by a few dominant taxa in both core sites, yet a large pool of rare species, at low population densities, formed the bulk of species richness (Fig. 5). These species abundance distributions followed a pattern characteristic of communities recruiting a large number of immigrants.

We were interested in understanding the dynamics of dominant and rare species across climate perturbations. To do so, the probability of sampling a given species

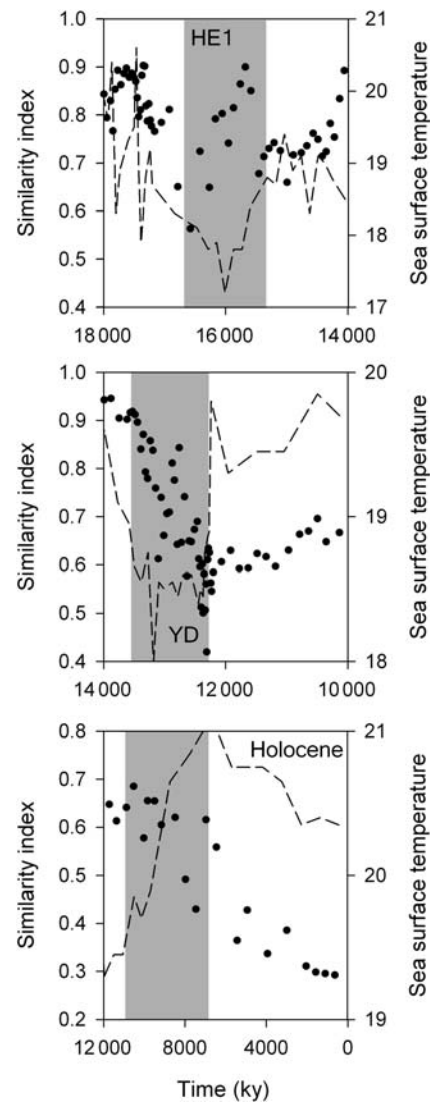


Fig. 3. Community similarity through time (dots) and sea surface temperature (dashed line) in the Mauritanian upwelling system during HE1, the YD and the transition into the Holocene; upper, middle and bottom panel, respectively. The BC similarity index is represented. Each dot represents a pair-wise community comparison between the communities across the period analysed on each panel and the communities before the climate perturbation.

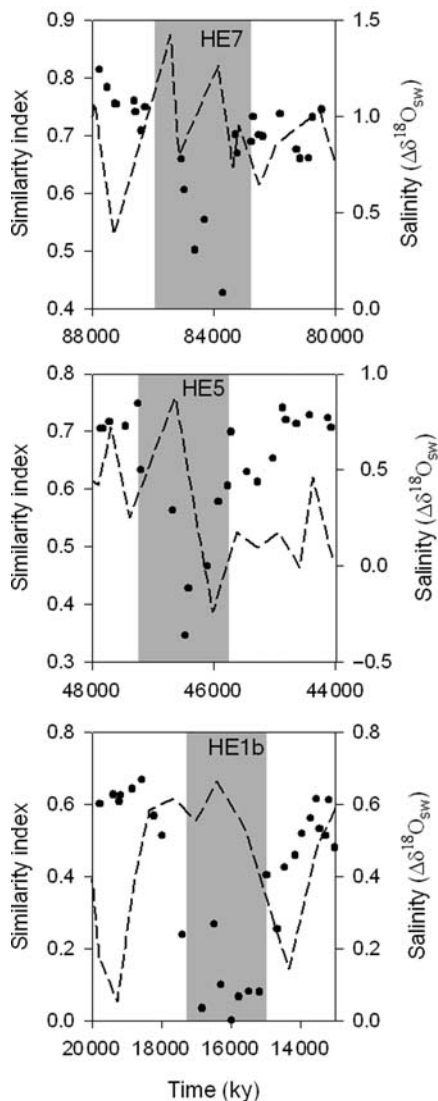


Fig. 4. Community similarity through time (dots) and sea surface salinity (dashed line) in the Panama Basin during HE7, HE5 and HE1b; upper, middle and bottom panel, respectively. As in Fig. 3, the BC similarity index is represented.

during the perturbation was plotted against the mean population abundance of the species before and after the perturbation. Sampling probability, $P(s)$, of a given species, s , was calculated as, $P(s) = n(s)/n(t)$, where $n(s)$ is the number of samples wherein the species is observed, and $n(t)$ is the total number of samples collected during the period of the perturbation. We used the fossil record obtained from the core collected in the Panama Basin wherein fossil assemblages clearly exhibited patterns of recovery after the perturbations. The probability of sampling a given species increased proportionally with the species' mean population abundance in the database (Fig. 6), demonstrating that dominant species were more

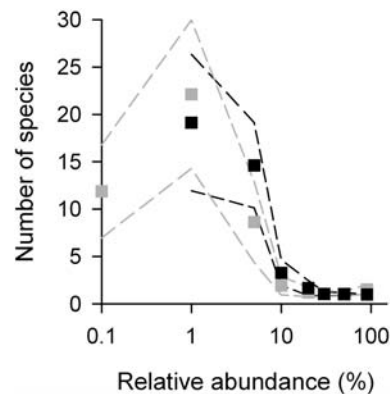


Fig. 5. Species abundance distributions for diatom assemblages in the sedimentary record of Mauritania (black) and Panama (grey). Abundance is expressed as the relative abundance of the species in the sample. Error bars are the mean \pm standard deviation.

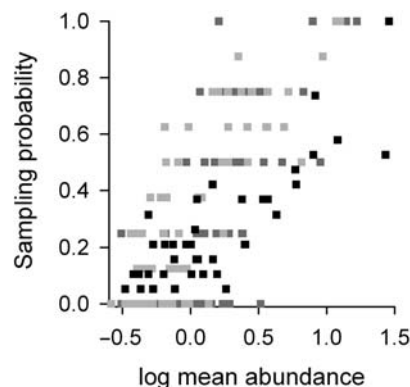


Fig. 6. Probability of sampling a given species during the perturbation plotted against the mean abundance of the species before the perturbation. Black, grey and dark grey squares are for HE1b, HE5 and HE7 from the sedimentary record collected at the Panama Basin. The positive relationship indicates that dominant taxa had a higher probability of continuing across the perturbation events, whereas rare taxa were subject to local extinction.

prone to persist during the perturbation. Conversely, rare species largely fell within the bottom left side part of the panel (Fig. 6), indicating that these species were susceptible to local extinction events and that their temporal dynamics explained much of the variability in species richness during climate perturbations.

DISCUSSION

Microbial plankton dispersal and community dynamics

We have shown that tropical communities of marine diatoms responded through changes in total abundance and species richness to events of rapid changes in

climate initiated at high northern latitudes. Heinrich events, massive discharges of icebergs into the North Atlantic, are thought to have impacted climate on a global scale, yet, their effects on upper ocean dynamics and plankton ecology varied substantially across regions. In the Mauritanian upwelling system, coastal winds favour the intrusion of nutrient-rich intermediate and subsurface waters into the euphotic layer, increasing primary productivity, primarily associated with diatoms (Blasco *et al.*, 1981). In this area, cooling episodes match with periods of enhanced wind activity, upper ocean mixing and diatom productivity, as inferred from proxies of sea surface temperature and the massive accumulation of *Chaetoceros* spores (Romero *et al.*, 2008). *Chaetoceros* is a genus of diatoms that require high levels of turbulence for growth, and thus their presence in the marine microfossil record is indicative of intense wind conditions and mixing (Romero and Armand, 2010). In the eastern equatorial Pacific, abrupt climate change episodes such as Heinrich events can be tracked through changes in sea surface salinity, with higher values indicative of enhanced subtropical influence (Leduc *et al.*, 2007). These variations in hydrography coincide with rapid shifts in the taxonomic structure of diatom communities towards species typical of meso/oligotrophic conditions (Romero *et al.*, 2011), and striking reductions in diatom abundance and species richness (Fig. 2).

The fossil diatom assemblages in the Mauritanian upwelling system have been shown to be dominated by *Chaetoceros affinis*, *Chaetoceros debilis* and *Chaetoceros* sp 1 (unidentified) (Romero *et al.*, 2008), which are species typical of intense upwelling conditions (Margalef, 1978). Consistent with our analysis of sampling probabilities (Fig. 6), these taxa were present throughout the sedimentary record, reflecting their resistance to local extinction across climate change events. On the other hand, the sedimentary record off Panama was dominated by the species *Thalassionema nitzschioides* var. *nitzschioides* and *Thalassiosira oestrupii*, with large increases in the relative contribution of *Cyclotella littoralis* during Heinrich events (Romero *et al.*, 2011). *Cyclotella littoralis* has been found to increase during episodes of nutrient depletion (Sancetta, 1992a; Romero *et al.*, 2011), which coincides with conditions prevailing during Heinrich events in the Panama Basin.

The broad dispersal of marine microbial plankton species (Cermeño and Falkowski, 2009) and their rapid response to environmental variability (i.e. global phytoplankton biomass turns over every week) confer on microbial plankton communities low resistance to change but enormous potential for recovery. Consistent with this conceptual model, we have shown that communities of marine planktonic diatoms from low-latitude coastal

ecosystems responded to climate perturbations through drastic changes in population abundance, species richness and taxonomic composition. However, our results also show that community structure was rapidly re-established once climatic forcing and oceanographic conditions returned to previous-like states, thus demonstrating that in the marine microbial plankton realm analogous climate conditions produce similar communities. We conclude that these diatom communities have been relatively stable (resilient) over the last 100 000 years despite abrupt changes in climate and hydrographic conditions.

The climate episodes investigated here had a global extent and left clear evidence of change in fossil diatom assemblages from disparate ocean basins. Certainly, the temporal dynamics of these communities was influenced by local determinants as well, including the effect of local topographies on surface currents, continental supply via river runoff, or atmospheric deposition (Zhao *et al.*, 2006; Romero *et al.*, 2008, 2011). Although these local factors might cloud in part the effects of global climate on marine biota, however, our results are consistent with the observation that changes in diatom productivity and community structure are largely controlled by the dynamics of the upper mixed layer and nutrient supply as inferred from proxies of sea surface temperature and salinity.

Our analyses of species abundance distributions confirmed the prevalence of a large pool of species at relatively low population densities (Fig. 5; Cermeño *et al.*, 2010). A number of factors including demographic stochasticity, biotic interactions and climatic variability can potentially drive rare taxa to extinction (van Valen, 1973; Lande *et al.*, 2003), yet the microfossil records from northwest Africa and the Panama Basin show that, in the microbial plankton, rare species survive climate perturbations. We conjecture several potential mechanisms that could facilitate the survival of rare species through time: (i) Passive dispersal with ocean currents and very high population numbers maintain a continuous input of immigrants from adjacent communities, and hence reduce the likelihood of local extinction (Fenchel and Finlay, 2004). Besides, microorganisms can remain metabolically inactive for long periods of time and revive later once environmental conditions turn favourable (Epstein, 2009). (ii) Unlike sexual reproduction, asexual division enables the restoration of a species' population size from a single individual, reducing the likelihood of extinction due to demographic stochasticity. (iii) The low population density of rare species provides refuge from predators and/or viral infections which otherwise would increase their mortality rates (Pedros-Alio, 2006). (iv) Compensatory effects such as predation lower the

biomass of superior competitors (Thingstad, 2000), limiting their ability to exclude rare taxa.

We recognize that our species abundance distributions at both core sites could be biased by sampling and preservation issues. For instance, rare species, as such, should be poorly represented in the sedimentary record; i.e. the less abundant the species in the surface waters, the lower its probability of being preserved in the sediment. However, even though rare species were unlikely to be well preserved in the sedimentary record, the high proportion of species at relatively low population densities observed in our study suggests that such a left-skewed distribution represents a common pattern of these microbial assemblages. Diatom preservation largely depends on the degree of valve silicification which is species-specific and/or varies with growth conditions (Jordan and Stickley, 2010). This issue is difficult to address as it requires a better knowledge about biochemical aspects of diatom silicification at the species level and under different growth conditions that we currently lack. The degree of valve preservation was assessed in core MD02-2529 according to objective observations of valve silicification (Romero *et al.*, 2011). The analysis indicates a moderate to good preservation state through much of the record, yet, slightly poorer preservation was detected at some events such as H5. Thus, the patterns observed could be related in part to temporal and/species-specific differences in diatom preservation.

An important shortcoming of the microfossil record concerns the commonness of cryptic speciation (Amato *et al.*, 2007 ; Kooistra *et al.*, 2008). Detailed analyses of cell morphology using electron microscopy and molecular data reveal that morphologically defined species are often composed of a number of subspecies/genotypes characterized by subtle morphological differences and/or disparate metabolic functions. We recognize that the pervasiveness of dominant species in the sedimentary record might result from the temporal succession of genotypes exploiting different strategies at different times. Indeed, this genetic variability would reflect the physiological adaptability of dominant morphotypes to changing environmental conditions.

Using the past to predict the future: the case of diatoms

Marine planktonic microbes are central to ocean ecology and global biogeochemical cycles (Falkowski *et al.*, 2008; Fuhrman, 2009). For instance, oxygenic photosynthesis, which is dominated by phytoplankton in the oceans, converts gaseous CO₂ into organic compounds, whereas respiration, largely dominated by

heterotrophic bacteria, accomplishes the reverse. The balance between these two processes contributes to the regulation of the CO₂ exchange between the ocean and the atmosphere. Marine diatoms are responsible for roughly one-fifth of global primary production and contribute disproportionately to the downward export flux into the deep ocean (Smetacek, 1999; Armbrust, 2009). Here, we have shown that marine planktonic diatom communities from low-latitude coastal areas rapidly responded to climate-driven changes in upper ocean mixing and nutrient delivery. This tight connection between climate, upper ocean dynamics and microbial plankton distribution implies that on millennial time scales climate and hydrographic variability control the extent to which these marine microorganisms contribute to modulate ocean biogeochemical cycles. It is probably on longer time scales, of hundreds of thousands to millions of years, that these marine microorganisms potentially influenced the cycling of elements and transformed the composition of the atmosphere, the ocean and the lithosphere at a planetary scale.

The combustion of fossil fuels over the last two centuries is rapidly increasing the concentration of carbon dioxide and other greenhouse gases in the atmosphere with dramatic consequences for the functioning of Earth systems (Falkowski *et al.*, 2000). Marine microorganisms will have to adapt to increases in ocean temperature, changes in upper ocean mixing and the ensuing variations in nutrient supply dynamics (Falkowski and Oliver, 2006), seawater acidification (Doney *et al.*, 2009) or oxygen depletion in deep ocean layers (Shaffer *et al.*, 2009). Historical (instrumental) data usually extend back a century or less, and the records of climate variability available for these periods of time are in general off the range of climate standards foreseen for the coming centuries. A potential way to circumvent this limitation and anticipate the possible response of marine biota to future climate scenarios lies in the analysis of analogue scenarios from the past. The marine microfossil record has an unparalleled temporal resolution and, in conjunction with the analysis of climate proxies, provides a window into the past from which to explore how microplankton communities responded to rapid changes in climate. Our data analysis suggests that marine diatom communities will respond to future, climate-induced changes in ocean hydrodynamics. However, our results also show that these communities will maintain their potential to shift back if environmental conditions are eventually re-established. This is a common feature of microbial plankton communities, which are composed by populations with enormous dispersal ranges.

SUPPLEMENTARY DATA

Supplementary data can be found online at <http://plankt.oxfordjournals.org>.

ACKNOWLEDGEMENTS

PC. was supported by a Juan de la Cierva postdoctoral fellowship from the Spanish government. O.E.R. was partially funded by the Spanish Council of Research (CSIC). The research was funded by Xunta de Galicia through programme Incite (project REFRESCO—10 PXIB312058 PR).

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