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Shallow marine ecosystem collapse and recovery during the Paleocene-Eocene

Thermal Maximum

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Abstract

The Paleocene-Eocene Thermal Maximum (PETM), the most well-studied transient hyperthermal event in Earth history, is characterized by prominent and dynamic changes in global marine ecosystems. Understanding such biotic responses provides valuable insights into future scenarios in the face of anthropogenic warming. However, evidence of the PETM biotic responses is largely biased towards deep-sea records, whereas shallow-marine evidence remains scarce and elusive. Here we investigate a shallow-marine microfaunal record from Maryland, eastern United States, to comprehensively document the shallow-marine biotic response to the PETM. We applied birth-death modeling to estimate the local diversity dynamics, combined with evaluation of time-variable preservation artifacts. We discovered strong increase of species disappearance and appearance predating the onset and at the final recovery phase of the PETM, respectively. Our paleoecological analyses indicate that bathymetric habitat compression due to extreme warmth and oxygen minimum zone expansion caused shallow-marine benthic species extirpation and ecosystem perturbation during the PETM; and that rapid recovery and diversification followed the PETM disaster, thus contributing new understanding to the shallow-marine biotic changes in a broad context of global warming.
Introduction

The Paleocene-Eocene Thermal Maximum (PETM; ~56 Ma), characterized by a negative carbon isotope excursion (CIE) in both marine and continental sedimentary records, is an abrupt (onset <5 ka (Foster et al., 2018; Turner et al., 2017)) climatic event of extreme global warmth superimposed on long-term greenhouse climate conditions (McInerney and Wing, 2011; Sluijs et al., 2007a). How Earth's biota responded to the PETM has been a prime research question, as the PETM could be the best natural analog to the ongoing and future anthropogenic warming and resulting ecosystem perturbation.

The impacts of the PETM climate anomaly on the pelagic ecosystems seem to be relatively mild in general as most groups underwent prominent but transient changes (Speijer et al., 2012). While calcareous nannoplankton show substantial extinction (Speijer et al., 2012), planktic foraminifera, dinoflagellates, and radiolarians show poleward range shifts (McInerney and Wing, 2011; Speijer et al., 2012). Planktic foraminifera also exhibit rapid evolution of distinctive and short-lived “excursion species” that persisted only during the PETM (Kelly et al., 1996). Deep-sea (bathyal-abyssal) benthic ecosystems were severely perturbed during the PETM as the biotic responses are characterized by strong and rapid benthic foraminiferal extinction marking the end of the “Cretaceous” deep-sea fauna, strong faunal turnover, and the resulting establishment of post-Paleocene faunas (Arreguin-Rodriguez et al., 2018; Kennett and Stott, 1991; McInerney and Wing, 2011; Thomas, 2007). In contrast to the well-studied deep-sea PETM records, relatively less attention has been paid to the shallow-marine (neritic) benthic ecosystems, with varying biotic responses documented yet a synthetic understanding lacking (Self-Trail et al., 2017; Speijer et al., 2012). Shallow-marine mollusks do not show substantial differences between pre-
petas, suggesting an almost imperceptible long-term impact of the PETM (Foster et al., 2020; Ivany et al., 2018). Coral reefs declined at the end of the Paleocene, and larger benthic foraminifera took over the position of dominant carbonate producers in the early Eocene (Kiessling and Simpson, 2011; Scheibner and Speijer, 2008; Speijer et al., 2012). However, the shallow-marine macrofossil record ‘sandwiches’ the PETM without data from the PETM core, because of either poor macrofossil occurrence or preservation, thus lacking documentation of potential transient changes (Foster et al., 2020; Ivany et al., 2018). Therefore shallow-marine benthic PETM records are generally limited to microfossils. Shallow-marine benthic foraminiferal assemblages show changes in species composition and a transient decline in diversity rather than extinction at the PETM (Speijer et al., 2012; Stassen et al., 2015).

Ostracods (seed shrimps: Arthropoda) are the only benthic microfossil other than benthic foraminifera and the only marine metazoan invertebrate that leaves fossil records rich enough to reconstruct a detailed biotic response to the PETM of high temporal resolution. Ostracods are therefore considered the surrogate of other metazoan invertebrates in respect to benthic biotic response (Yasuhara and Cronin, 2008; Yasuhara et al., 2008). Documented deep-sea ostracod responses to the PETM include 1) taxonomic loss of variable magnitude (from 64 to 25% diversity decrease) due to local extinction and/or species geographic range shifts, 2) community restructuring with high dominance of opportunistic and/or generalist taxa, 3) dwarfing, and 4) shell morphological changes (Lewis Steineck and Thomas, 1996; Webb et al., 2009; Yamaguchi and Norris, 2012; Yamaguchi and Norris, 2015; Yamaguchi et al., 2012). A few studies have investigated PETM shallow-marine ostracods and found strong faunal turnovers (Morsi et al., 2011; Speijer et al., 2012; Speijer and Morsi,
2002), but further synthesis of the general patterns of shallow-marine benthic biotic response has been hampered by various uncertainties including the existence of unconformities between depositional units, varying fossil preservation states, and low fossil abundance.

**Fig. 1.** Map showing the location of the South Dover Bridge (SDB) core in the Salisbury Embayment, southeastern Maryland, USA.

In this study, we investigated the ostracod assemblage from a near-complete PETM section from the Salisbury Embayment of the mid-Atlantic Coastal Plain (Fig. 1). In the Atlantic Coastal Plain, the PETM sections deposited in inner to outer neritic environments are highly expanded due to high sedimentation rates and can be nearly complete (John et al., 2008; León y León et al., 2018; Self-Trail et al., 2017). We employed recently developed process-based birth-death modeling to handle time-
variable and taxon-specific preservation issues, to properly document the shallow-
marine benthic biotic changes in relation to warming, dissolved oxygen decline and
other characteristic ecological stressors of the PETM that might be partially analogous
to those of ongoing anthropogenic warming (Zachos et al., 2008). For example,
bathymetric habitat compression may be occurring in modern shallow-marine
ecosystems due to the interplay between greenhouse gas-driven warming and
deoxygenation (Breitburg et al., 2018; Norris et al., 2013). Decreased gas solubility
and intensified ocean stratification may cause seawater deoxygenation under
greenhouse conditions, leading to the expansion of the oxygen minimum zone (OMZ)
in midwater and shoaling of its upper boundary to shallower depths; consequently, the
well-oxygenated habitat above the OMZ is vertically compressed (Breitburg et al.,
2018; Stramma et al., 2012; Stramma et al., 2010). Global expansion of low-oxygen
marine environments in conjunction with more extreme local seawater deoxygenation
have frequently accompanied major hyperthermal events including the PETM
(Dickson et al., 2012; Nicolo et al., 2010; Vellekoop et al., 2018). Through such
mechanisms, vertical migrations and local extinctions of shallow and midwater
marine biota driven by oxygen availability changes during extremely warm periods
like the PETM may be expected (Breitburg et al., 2018; Stramma et al., 2012;
Stramma et al., 2010).

Material and Methods

Sample processing and data analysis

The PETM sections of the SDB core (210.06-188.06 m core depth) were sub-
sampled at approximately 12 cm intervals, so that 124 sub-samples were analyzed for
their fossil ostracod contents. Carbon isotope values are after Self-Trail et al. (2012).

We adopted the standard sample processing method for ostracod research, i.e., we wet sieved samples with mesh sizes of 63 µm then dry sieved with mesh size of 125 µm, after oven drying (Yasuhara et al., 2017a). Ostracods picked from the >125 µm fraction are usually adults and late molt stage juveniles that can be confidently identified (Yasuhara et al., 2017a). Each articulated carapace was counted as two valves (Yasuhara et al., 2017a).

Non-metric multidimensional scaling (NMDS) analysis was performed to understand the faunal turnovers related to climatic and oceanographic changes during four stages around the PETM: pre PETM, peak PETM, recovery phase and recovery phase II. The NMDS analysis was based on three-point moving sums of ostracod census data and low-abundance data points were excluded (number of valves <10) to address the issues with low sample size (Yasuhara et al., 2008; Yasuhara et al., 2014). The analysis was done using the R package ‘vegan’ (Oksanen et al., 2018), using relative abundances of ostracod species and Bray-Curtis dissimilarity.

Estimation of local appearance and disappearance dynamics

We carried out analyses of the raw ostracod fossil dataset based on the Bayesian framework in the program PyRate (Silvestro et al., 2019; Silvestro et al., 2014). We analyzed the datasets under time-varying birth-death models to simultaneously estimate for each clade (i) the parameters of the preservation process, (ii) the times of local speciation (Ts) and local extinction (Te) of each ostracod species, (iii) the speciation (λ) and extinction (µ) rates and their variation through time, and (iv) the number, timing (= core depths as the surrogate) and magnitude of shifts in
speciation and extinction rates. While some methods can be sensitive to ghost
lineages (a.k.a. the Lazarus effect), the PyRate approach benefits from the estimation
of $Ts$ and $Te$ of the studied species taking into account preservation biases, and thus
provides estimates of species' longevity (i.e., duration or time span of a species),
which therefore reduces the issues pertaining to the estimation of speciation and
extinction rates and so for the number of species through time (Silvestro et al., 2019;
Silvestro et al., 2014). For the purposes of this research, we consider $Ts$ and $Te$ to
indicate appearance and disappearance, respectively, in the SDB core sediments and
not true speciation and extinction events. The preservation process infers the
individual origination and extinction times of each taxon based on all occurrences and
on an estimated preservation rate, denoted $q$, and expressed as expected occurrences
per taxon per meter. We applied a time-variable birth-death model that estimates rate
variations and infers shifts of diversification as well as the $Ts$ and $Te$ for each species.
We first performed the classical BDMCMC (-A 2 option) (Silvestro et al., 2014) and
its recently enhanced version through the reversible-jump MCMC (RJMCMC)
algorithm (-A 4 option) (Silvestro et al., 2019), which allows an accurate estimate of
the speciation and extinction rate shifts.

We ran PyRate for 5 million MCMC generations with sampling frequency of
5,000 for the whole dataset. All analyses were set with the best-fit preservation
process after comparing (-PPmodeltest option) the homogeneous Poisson process (-
$mHPP$ option), the non-homogeneous Poisson process (default option), and the time-
variable Poisson process (-$q$ option). The time-variable Poisson process estimated a
preservation rate every 2 meters of sediments. We also accounted for varying
preservation rates across taxa using the Gamma model (-$mG$ option), that is, with
gamma-distributed rate heterogeneity (Silvestro et al., 2014). We monitored chain
mixing and effective sample sizes by examining the log files in Tracer 1.7.1 (Rambaut et al., 2018) after excluding the first 10% of the samples as the burn-in period. We then combined the posterior estimates of the origination and extinction rates across all replicates to generate rates-through-time plots (origination, extinction, and net diversification) and the 95% credibility intervals (CI) of each rate.

We replicated all the analyses on ten randomized datasets and calculated estimates of $T_s$ and $T_e$ as the mean of the posterior samples from each replicate. Thus, we obtained ten posterior estimates of the $T_s$ and $T_e$ for all species and we estimated the past diversity dynamics by calculating the number of living taxa at every point in time based on the $T_s$ and $T_e$. For all the subsequent analyses, we used the estimated $T_s$ and $T_e$ for all species, which avoids re-modeling preservation and re-estimating times of speciation and extinction, therefore focusing exclusively on the estimation of the birth-death parameters for specific models. This procedure reduced drastically the computational burden, while still allowing to account for the preservation process and the uncertainties associated with the fossil ages.

To statistically identify a Lazarus taxon that has a range termination within the peak PETM in the SDB core, we used the Bayesian birth-death model to show the 95% confidence intervals of the disappearance and re-appearance horizons are not overlapped within the peak PETM for a Lazarus taxon. We treated a Lazarus taxon as two evolutionary entities in operation (e.g., Hazelina1_pre and Hazelina1_post for the first and second appearance periods, respectively) in our Bayesian birth-death modeling to fully reconstruct local extinction and speciation processes. By doing so, we considered initial disappearances of Lazarus taxa at the PETM onset as local extinction events and their subsequent re-appearances in the recovery phases as local speciation events. We also showed the results of the original dataset in the online
supplementary material (i.e., treating a Lazarus taxon as one evolutionary entity, fig. S1) for comparison.

**Oceanographic and geological setting**

Highly-expanded sections of shallow marine PETM sediments (210.06–188.06 m core depth) were obtained in the South Dover Bridge (SDB) core in the Salisbury Embayment of the mid-Atlantic Coastal Plain in Maryland, USA (38.74704º N; 76.00697º W) (Fig. 1) (Self-Trail, 2011; Self-Trail et al., 2012). The Paleocene-Eocene boundary sequence of the SDB core consists of three depositional units: the upper Paleocene Aquia Formation (210.06–204 m), the lower Eocene Marlboro Clay (204–188.4 m) and the lower Eocene Nanjemoy Formation (188.4–188.06 m) (Self-Trail et al., 2012). In the Aquia Formation, a pre-onset excursion (POE: 206.6-205.9 m) is marked by a 2‰ negative shift in bulk δ¹³C and partial dissolution of benthic calcareous fossils (Fig. 2a) (Robinson and Spivey, 2019). The contact between the Aquia Formation and the overlying Marlboro Clay at 204 m corresponds to the base of the CIE with a rapid 3-4‰ negative shift in bulk δ¹³C over a 1.3-m dissolution zone, which marks the onset of the PETM (Fig. 2a). This 1.3-m dissolution zone (204-202.7 m) at the base of the Marlboro Clay with trace amount of calcareous fossils is most likely caused by the shoaling of the lysocline to the middle shelf in the Salisbury Embayment, coinciding with the rapid CIE onset (Fig. 2a) (Bralower et al., 2018; Self-Trail et al., 2012).

Based on lithological analyses, calcareous nannofossils and the carbon isotope signal (Self-Trail, 2011; Self-Trail et al., 2012), we further divide the Paleocene-Eocene boundary sequence into four sections corresponding to different stages of
PETM development: pre PETM (Aquia Formation, 210–204 m), peak PETM (lower Marlboro Clay, 204–196.6 m), recovery phase I (middle Marlboro Clay, 196.6–191 m), and recovery phase II (upper Marlboro Clay and Nanjemoy Formation, 191–188 m) (Fig. 2a). The PETM onset, peak and initial recovery are nearly, if not entirely, complete in terms of sedimentary sequence. Nannofossil biostratigraphy indicates some missing time (<0.9 My) at the Aquia/Marlboro Clay contact (and none at the Marlboro Clay/Nanjemoy contact) (Self-Trail et al., 2012), but this hiatus is most likely restricted to the upper Aquia Formation, as the basal Marlboro Clay contains the dissolution zone that accompanies the PETM-onset acidification event (Self-Trail et al., 2012). The only disconformity within PETM sediments is situated at the top of the calcareous nannofossil zone NP10 at 188.05 m (Self-Trail et al., 2012) at the very top of our study interval, which therefore has no effect on our discussion.

SDB sediments were deposited at subtropical to temperate paleolatitude, in an environment with seasonal water temperature changes (León y León et al., 2018; Self-Trail et al., 2012). Planktic and benthic foraminiferal data from SDB samples indicate a water depth of ~125 m prior to the PETM onset and ~140 m after the PETM onset (Robinson and Spivey, 2019). While uncertainties and disagreements among PETM water depth proxies in the Salisbury Embayment remain (Stassen et al., 2014), reconstructions based on benthic foraminifer assemblage data agree that sea level may have risen by as much as 30 m across the PETM onset (León y León et al., 2018; Robinson and Spivey, 2019).
Fig. 2. Bayesian estimation of local diversity dynamics of the ostracod community across the PETM. Each Lazarus taxon is divided into two evolutionary entities of the pre-PETM section and post-PETM section. (a) The bulk $\delta^{13}C$ curve for comparison.
Vertical dotted lines at 210 m and 188 m define the interval of study. The division into pre PETM, peak PETM, recovery phase and recovery phase is based on the carbon isotope baseline, excursion, initial recovery and final recovery, respectively (for recovery phase and for recovery phase).

Depositional units of Paleocene/Eocene boundary section are shown in stratigraphic order (N for Nanjemoy Formation). Grey bars at 206.6-205.9 m and 204-202.7 m indicate the POE and the CIE onset, respectively. Inferences of (b) species appearance rates and (e) species disappearance rates with the birth-death model. (d) The net diversification rates as the difference between appearance and disappearance rates (rates below 0 indicate declining diversity). Solid lines indicate mean posterior rates, and the shaded areas show the 95% confidence interval. (e) The local ostracod diversity trajectory. Note that the zero diversity at the beginning and ending of the curve is an analytical artifact as the model assumes the lineages diversified from zero and eventually went extinct (end of the core section).
Fig. 3. Bayesian estimation of the local diversity dynamics of ostracod community throughout the PETM using the RJMCMC model. Each Lazarus taxon is divided into two evolutionary entities of the pre-PETM section and post-PETM section. Red vertical dotted line at 188 m indicates the end of the core section. Black vertical lines at 204 m, 196.6 m, and 191 m indicate the division of the core section into pre PETM, peak PETM, recovery phase and recovery phase. Grey bars at 206.6-205.9 m and 204-202.7 m indicate the POE and the CIE onset, respectively. (a) The species appearance rates. High rate at the beginning of the curve is an analytical artifact as the model assumes the lineages diversified from zero. (b) The frequency of species appearance rates shifts. Frequency > 0.167 (indicated by the upper dashed line) is considered as significant shift (Bayes factor > 6). Significant shift at 207.78 m is likely an analytical artifact. (c) The species disappearance rates. High rate at the ending of the curve is an analytical artifact as the model assumes the lineages eventually went extinct. (d) The frequency of species disappearance rates shifts. Frequency > 0.167 (indicated by the upper dashed line) is considered as significant shift (Bayes factor > 6). Significant shift at 188.79 m is likely an analytical artifact. (e) The net diversification rates as the difference between species appearance and disappearance rates (rates below 0 indicate declining diversity). Solid lines indicate mean posterior rates and the shaded areas show 95% CI. (f) The mean longevity of ostracod lineages. Note that the zero longevity at the ending of the curve is an analytical artifact as the model assumes the lineages eventually went extinct (end of the core section).

Results
Bayesian process-based birth-death model

We analyzed the SDB ostracod fossil record throughout the PETM (1210 specimens, 30 species, 122 samples in total) using a Bayesian process-based birth-death model considering time-variable preservation rates (Zizka et al., 2019). We successfully reconstructed the changes in species appearance and disappearance rates throughout the PETM and its recovery phases in unprecedented detail (Figs. 2 and 3). When estimating the local preservation rates for time bins as represented by 2-m stratigraphic layers, the results clearly demonstrate a time-variable preservation process ranging from 0.037 to 20.58 occurrences per lineage per meter core depth in the POE (q1) and the recovery phase II (q10), respectively (table S1). Importantly, the model estimated a significant shift in species appearance rates at 188.79 m, indicating rapid origination at the end of the PETM (Figs. 2b and 3a-b); it also estimated significant shifts in species disappearance rates at 205.67 m and at 203.56 m with a strong peak between ~205-204 m (Figs. 2c and 3c-d). The net diversification rate indicated a drastic diversity decline initiated at ~206 m (POE) with local diversity dropping from 13 to 5 species during the PETM onset, followed by a slight partial recovery at ~200 m enforced by a local turnover (i.e. appearance equal to disappearance), and a final strong boost in the recovery phase II leading to a local diversity increase from 9 to 16 species (Fig. 2, d and e). Simple presence/absence data gives consistent results that 6 out of 13 pre-PETM species were permanently eliminated from the local assemblages at the PETM onset (46.2% disappearance), and another 5 out of 13 pre-PETM species disappeared during the peak PETM and re-appeared during recovery phases (38.5% Lazarus taxa); on the other hand, 11 out of 22 recovery-phase species first appeared only after the peak PETM (50% new appearance) (Fig. 4).
Fig. 4. Occurrence ranges of all ostracod species. Each dot indicates species presence in the sample. Extinct pre-PETM taxa that do not extend beyond the PETM onset, Lazarus pre-PETM taxa that have range terminations within the peak PETM, and newly occurring post-PETM taxa are highlighted by red, blue, and yellow, respectively. Peak PETM and recovery phase II are shaded by gray ( for recovery
phase). For all Lazarus taxa, the 95% confidence intervals of the disappearance and re-appearance horizons are not overlapped (table S1).

**NMDS analysis**

The non-metric multidimensional scaling (NMDS) analysis shows that samples from each of the four study intervals (i.e., pre-PETM, peak PETM, recovery phase I and recovery phase II) cluster in two-dimensional space (Fig. 5). The pre-PETM assemblage is most distinguished from all other assemblages, especially from the peak-PETM assemblage, based on their relative positions in NMDS space (Fig. 5), indicating a conspicuous ostracod faunal transition at the PETM onset. From the peak PETM to recovery phase I and then phase II, the three assemblages become progressively more similar to the pre-PETM assemblage in NMDS space with the two recovery assemblages partially overlapping (Fig. 5). Approaching the end of the PETM, the position of recovery phase in-between peak-PETM and pre-PETM assemblages indicates a partial recovery of the ostracod community (i.e., reoccurrence of 5 Lazarus taxa) besides some imprints of remnant peak-PETM faunal elements and first occurrence of post-PETM faunal elements.

Indeed, the down-core trend of NMDS axis 2 values is clearly opposite to that of $\delta^{13}$C (Fig. 6), representing the elimination and recovery process of the pre-PETM type fauna. The peak-PETM and recovery phase fauna have much higher NMDS axis 2 values compared with the pre-PETM fauna, corresponding to the ‘body’ of the CIE with relatively stable and low $\delta^{13}$C values (Fig. 6). The recovery phase fauna quickly decline in the NMDS axis 2 towards the end of the PETM in contrast with the exponential recovery of $\delta^{13}$C to pre-PETM values (Fig. 6). On the other hand, the
down-core trend of NMDS axis 1 values represents the peak PETM fauna, showing highest values between ~202-197 m core depth (Fig. 6). Our high-time resolution down-core NMDS data revealed three distinct, successive maxima in the peak PETM fauna (Fig. 6) indicating repeated small biotic perturbations during the peak PETM.

**Fig. 5.** Non-metric Multidimensional Scaling result showing the PETM-associated faunal changes. Three-point moving sums of ostracod census data are used for the NMDS analysis. Four stratigraphic groupings: pre-PETM (red); peak-PETM (blue); recovery phase (green); and recovery phase (yellow). The grey lines connect one sample to the next in stratigraphic order within each group. Black dashed lines connecting the hull centroid of each group indicate ostracod faunal transitions across the PETM in NMDS space.
Fig. 6. Down-core NMDS axis 1 and NMDS axis 2 scores compared to the bulk δ¹³C curve. Three-point moving sums of ostracod census data are used for the NMDS analysis. Arrows indicate distinct maxima in the peak PETM fauna at ~202 m, 200 m, and 198 m along the NMDS axis 1, respectively. Grey bars at 206.6-205.9 m and 204-202.7 m indicate the POE and the CIE onset, respectively.

Discussion

Disruption and recovery of ostracod community throughout the PETM
We detect significant local disappearance from the pre PETM to the CIE onset in metazoan shallow-marine benthos by the Bayesian process-based birth-death model (Fig. 2). Even if we do not consider a Lazarus taxon as two operational evolutionary entities in the modeling, this disappearance remains significant albeit weaker (*i.e.*, permanent extirpation of 6 non-Lazarus pre-PETM taxa) (table S2 and fig. S1), indicating that a part of this species disappearance event accounted for unrecoverable biodiversity loss in the shallow-marine benthic ecosystem. The disappearance peak indicated by the birth-death model slightly pre-dates the CIE onset, which may reflect the extinction started at the POE as a precursor to the main hyperthermal event.

Similarly, planktic and benthic foraminifera also showed assemblage changes in terms of faunal composition at SDB and nearby sites prior to the CIE onset (Robinson and Spivey, 2019). Early onset of PETM-associated biotic and environmental changes is not confined to the Salisbury Embayment but also evident in the New Jersey shelf, southwest Pacific Ocean and North Sea (León y León et al., 2018; Sluijs et al., 2007b), consistent with our understanding of the destabilization of ocean-atmosphere system preceding the PETM resulting in perturbed and stressful water conditions. Abrupt local disappearance at the PETM onset may be associated with species habitat range shifts/contraction in response to peak-PETM ecological and environmental stress, and not necessarily global extinction. Recovery and diversification at the end of PETM was unexpectedly strong (*i.e.*, reappearance of 5 Lazarus taxa and first appearance of 11 post-PETM taxa), regardless of the treatment of the Lazarus taxa in the modeling (Fig. 2; fig. S1; table S1 and S2). This post-PETM biodiversity pattern is also evident in earlier studies of benthic biotic response. Ostracod fauna of the Tethyan region show similar recovery in diversity (Yamaguchi and Norris, 2012). Likewise, the Atlantic Coastal Plain mollusks show elevated post-PETM diversity (Ivany et al.,
Indeed, the PETM has been demonstrated to be an origination event in shallow-marine systems (Speijer et al., 2012). The birth-death model therefore clearly reveals a perturbation-recovery pattern of the shallow-marine ecosystem characterized with one peak of species disappearance predating the PETM onset and the other peak of species reappearance combined with first appearance at the final recovery phase. NMDS analysis consistently shows that the greatest faunal turnover occurred at the PETM onset followed by a gradual, partial return of pre-PETM faunal elements and first occurrence of post-PETM faunal elements during the recovery phases such that the ostracod community approached a new state in terms of species composition after the PETM transition (Figs. 5 and 6). Irreversible impacts of climate change on the benthic ecosystem are represented by the difference between recovery phase II and pre-PETM assemblages in the NMDS space. To interpret such shallow-marine biotic responses to the PETM, we suggest deoxygenation and warming during the PETM (see discussion below) may have reset the species assemblages and opened up niches for new colonization both from shallower and deeper depths, resulting in local diversification and possibly true speciation.
<table>
<thead>
<tr>
<th><strong>Genus</strong></th>
<th><strong>Autoecology Summary</strong></th>
<th><strong>References</strong></th>
</tr>
</thead>
<tbody>
<tr>
<td>Acanthocythereis</td>
<td>Deep (outer neritic to bathyal), warm-adapted (i.e., typical warm Paleogene genus), full marine, epifauna (low-oxygen-sensitive)</td>
<td>(Huang et al., 2018; Huff, 1970)</td>
</tr>
<tr>
<td>Brachycythere</td>
<td>Relatively deep (outer neritic), full marine</td>
<td>(Huff, 1970; Morkhoven, 1962)</td>
</tr>
<tr>
<td>Buntonia</td>
<td>Deep (outer neritic to bathyal), warm-adapted (i.e., typical warm Paleogene genus), full marine, epifauna (low-oxygen-sensitive)</td>
<td>(Huff, 1970; Morkhoven, 1962; Yasuhara et al., 2016; Yasuhara et al., 2015)</td>
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<td>Cytherella</td>
<td>Shallow (neritic), warm-adapted (i.e., typical tropical genus), full marine</td>
<td>(Morkhoven, 1962; Shin et al., 2019; Yamaguchi et al., 2014; Yasuhara et al., 2015)</td>
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<tr>
<td>Hazelina</td>
<td>Shallow (neritic), warm-adapted (i.e., typical warm Paleogene genus), full marine</td>
<td>(Huff, 1970; Lord et al., 2009; Van Nieuwenhuise, 2007)</td>
</tr>
<tr>
<td>Hermanites</td>
<td>Shallow (inner neritic), warm-sensitive (i.e., common in extratropical areas), full marine</td>
<td>(Cronin, 1991; Lord et al., 2009; Morkhoven, 1962; Van Nieuwenhuise, 2007)</td>
</tr>
<tr>
<td>Muellerina</td>
<td>Shallow (neritic), warm-sensitive (i.e., typical cold Neogene and extratropical genus), full marine</td>
<td>(Cronin, 1991; Wood and Whatley, 1997; Yasuhara et al., 2019)</td>
</tr>
<tr>
<td>Phractocytheridea</td>
<td>Shallow (inner neritic), brackish</td>
<td>(Morkhoven, 1962; Puckett, 1994)</td>
</tr>
</tbody>
</table>

Table 1. Autoecology summary of important genera.
Fig. 7. Three-point moving summed relative abundance plots of common and ecologically significant ostracod species compared against the bulk δ¹³C curve. Characteristic species of the pre-PETM, peak-PETM, recovery phase and recovery phase are highlighted by corresponding color used in Figure 5 with their environmental preferences shown on the top (see Table 1 for details). Grey bars at 206.6-205.9 m and 204-202.7 m indicate the POE and the CIE onset, respectively.

Biotic response to paleoceanographic changes: sea-level rise, elevated warmth and OMZ expansion

The disruption-recovery pattern of the ostracod community indicated by birth-death model and NMDS analysis can be better understood by examining faunal turnovers across the PETM in detail through changes in the relative abundance of
common and ecologically significant species across the late Paleocene-early Eocene
time series (Table 1; Fig. 7). We consider the pre-PETM assemblage to represent the
ecological and environmental baseline for the region. During the pre PETM,
*Aversovalva, Brachycythere, Cytherella, Hazelina, Hermanites and Muellerina*
sporadically attain high relative abundance. Most species of the pre-PETM
assemblage inhabited shallow-marine environments (neritic zone), but they had
different thermal tolerances as indicated by their latitudinal distribution ranges (i.e.,
extratropical [=sensitive] or tropical [=adapted] taxa): *Hermanites* and *Muellerina* are
warm-sensitive genera, whereas *Cytherella* and *Hazelina* are warm-adapted genera
(Table 1) (Cronin, 1991; Huff, 1970; Lord et al., 2009; Morkhoven, 1962; Shin et al.,
2019; Van Nieuwenhuise, 2007; Wood and Whatley, 1997; Yamaguchi et al., 2014;
Yasuhara et al., 2019; Yasuhara et al., 2015). During the peak PETM, characteristic
species of the pre-PETM assemblage either completely extirpated (*Aversovalva* and
*Muellerina*, extinct taxa) or temporarily disappeared (*Cytherella, Hermanites and
Hazelina*, Lazarus taxa). The genera *Acanthocythereis* and *Buntonia* dominated the
peak-PETM assemblage instead (Figs. 4 and 7). They show ecological affinities to
much greater water depths (outer neritic-bathyal zone) and possibly adapted to
elevated warmth as they are very common, widespread genera throughout the
Paleocene/Eocene greenhouse period (Table 1) (Huff, 1970; Morkhoven, 1962;
Yasuhara et al., 2015). Such abrupt faunal turnovers from the pre to peak-PETM are
represented as major perturbations/excursions of the ostracod community associated
with peak-PETM paleoceanographic conditions. Relative abundances of peak-PETM
taxa rapidly decreased at the transition from the peak PETM to recovery phase I,
coeval with a dramatic increase of *Brachycythere* as a relatively deep and fully marine
opportunistic taxon (Huff, 1970; Morkhoven, 1962) and a slight increase of Lazarus
taxa (Table 1; Figs. 4 and 7). During recovery phase II, the Lazarus taxa reached moderately high abundances (20-40%) while the recovery phase I taxon _Brachycythere_ gradually declined towards the end of PETM; _Phractocytheridea_ as a newly occurring post-PETM taxon that inhabited shallow brackish environments (Morkhoven, 1962; Puckett, 1994) made its first consistent appearance (Table 1; Fig. 7). The assemblage of recovery phase II therefore has high diversity and low dominance with the return of Lazarus taxa and the first occurrence of post-PETM taxa (Figs. 4 and 7), corresponding to the recovery and diversification of the ostracod community when pre-PETM climatic and paleoceanographic conditions resumed (McInerney and Wing, 2011). In addition to above-discussed faunal turnovers, it is noticeable that several taxa (e.g., _Acanthocythereis_ and _Brachycythere_) survived throughout the PETM (Fig. 4).

The replacement of the pre-PETM shallow assemblage by the peak-PETM deep, warm-adaptive assemblage is consistent with our background understanding of sea-level rise associated with this hyperthermal event in the Salisbury Embayment (Norris et al., 2013; Robinson and Spivey, 2019; Sluijs and Brinkhuis, 2009; Sluijs et al., 2008; Zachos et al., 2006). In addition, the peak-PETM assemblage includes epifaunal forms sensitive to low-oxygen conditions and lack any infaunal forms typically found at outer neritic-bathyal water depths during the Paleocene-Eocene period, such as _Krithe_, that are adapted to low-oxygen-conditions (Huang et al., 2018; Yamaguchi and Norris, 2012; Yasuhara et al., 2016). We interpret the intrusion of deep, epifaunal (low-oxygen-sensitive) taxa into the SDB site as their upslope migration to avoid the prevalence of low-oxygen conditions, due to OMZ expansion, in deeper waters. In fact, oxygen depletion is one of the most well recognized characteristics of the PETM greenhouse ocean (Breitburg et al., 2018; Gilly et al.,
The expansion of the OMZ in the PETM North Atlantic basin has been revealed by a regional ocean model simulation that a severely hypoxic condition inhospitable for many organisms prevailed on the continental slope below ~200 m while the middle and outer shelf underwent comparatively much milder decline in bottom water oxygenation (Hantsoo et al., 2018), consistent with micropaleontologic evidence of benthic foraminifera in the Salisbury Embayment (Robinson and Spivey, 2019; Self-Trail et al., 2017; Stassen et al., 2015).

**Fig. 8.** Cartoon showing the biotic responses to changes in sea level, water temperature and dissolved oxygen concentration across the PETM. Black bar: SDB core site; hashed area: OMZ, oxygen minimum zone; red circle: shallow taxa; blue
circle: deep taxa; green circle: opportunistic taxa; yellow circle: post-PETM shallow taxa; X: extinction; arrows: downslope migration; blue background: cooler water temperature; orange background: warmer water temperature. (a) Pre-PETM setting. (b) During the peak PETM, deep, low-oxygen-sensitive taxa migrated upslope to the outer neritic SDB site. Intrusion of deep, low-oxygen-sensitive taxa in concert with sea-level rise forced shallow taxa to migrate upslope to extremely warm inner neritic area, where warm-adapted taxa survived and warm-sensitive taxa went regionally extinct. (c) As temperatures cooled and the OMZ constricted during recovery phase I, deep, low-oxygen-sensitive taxa returned to deeper waters, and opportunistic taxa thrived at the SDB site. (d) In recovery phase II, shallow, warm-adapted taxa re-occupied the SDB site, and post-PETM shallow taxa occupied vacant ecological niches left by the extinction of warm-sensitive taxa.

As illustrated in Figure 8a–b, when the depositional environment at the SDB site changed from an inner-middle neritic setting to an outer neritic setting because of sea-level rise (Robinson and Spivey, 2019), benthic ostracods, perhaps except deep low-oxygen-adapted taxa (see below), migrated upslope to maintain their preferred depth habitat ranges. Deep, low-oxygen-sensitive taxa may have migrated close to or beyond the shallow limit of their preferred depth range, to the SDB site, to escape the expanded OMZ since the severely hypoxic bathyal OMZ waters were not habitable for them (Gilly et al., 2013; Hantsoo et al., 2018; Huang et al., 2018; Norris et al., 2013; Winguth et al., 2012). Deep, low-oxygen-adapted taxa could have remained in the deeper bathyal zone.
In other words, we propose that habitats of the deep, low-oxygen-sensitive taxa were compressed from the outer neritic-bathyal zones to only the outer neritic layer, a refugium from the expanded OMZ that covered broad bathyal depths in the North Atlantic basin (Hantsoo et al., 2018). The intrusion of deep, low-oxygen-sensitive taxa to the SDB site might have narrowed the ecological niches of the shallow pre-PETM taxa. In conjunction with migration due to sea level rise, this intrusion forced the entire shallow pre-PETM assemblage toward super warm surface waters (Winguth et al., 2012; Zachos et al., 2006) upslope from SDB. Extreme surface warming in the Salisbury Embayment is well documented by previous geochemical and paleoecological studies (León y León et al., 2018; Self-Trail et al., 2012), causing great perturbation of the shallow-marine ecosystem as represented by dramatic faunal turnovers of planktic and benthic foraminifera and malformation of calcareous nannoplankton during the PETM (Bralower and Self-Trail, 2016; Robinson and Spivey, 2019). Among the shallow pre-PETM ostracod taxa leaving the SDB site, only those tolerant to the warmer conditions were able to survive (Fig. 8b). Warm-sensitive pre-PETM taxa could neither survive the elevated warmth of subtropical-temperate surface waters, or escape to higher latitudes as these might be similarly warm due to the flattened latitudinal temperature gradients in anomalous greenhouse conditions (Zachos et al., 2006; Zhang et al., 2019). Such extreme thermal pressure could have driven warm-sensitive taxa to at least regional extinction without cool and shallow suitable habitats or refugia in high-latitude areas. Collectively, we infer that extreme warming in the neritic environment and deoxygenation in the bathyal environment in concert caused the ostracod faunal turnovers from the pre-PETM to peak-PETM. Likely permanent extinction of six warm-sensitive pre-PETM taxa (Fig. 4) indicates that the impacts of habitat compression induced by warming and
deoxygenation might be irreversible, and the PETM as a transient hyperthermal event
punctuated long-term evolution of benthic organisms.

As peak-PETM conditions ended with the initial CIE recovery, *Brachycythere*
as a relatively deep opportunistic taxon temporarily achieved high dominance at the
SDB site during recovery phase I (Table 1; Figs. 7 and 8c). We propose that shallow,
warm-adapted taxa (*Cytherella* and *Hazelina*) and deep, low-oxygen-sensitive taxa
(*Acanthocythereis* and *Buntonia*) migrated downslope from their peak-PETM
positions to their pre-PETM positions during recovery phases I and II as temperatures
cooled, the OMZ constricted, and sea level fell (Fig. 8, c and d) (Self-Trail et al., 2012;
Sluijs and Brinkhuis, 2009). Overall paleoceanographic conditions might not have
fully recovered until shallow, warm-adapted Lazarus taxa eventually recolonized the
SDB habitat during recovery phase II (Figs. 4 and 8d). As the other shallow, warm-
sensitive pre-PETM taxa went extinct due to the unavailability of cooler refugia (Figs.
4 and 8b), vacant ecological niches left by them were occupied by newly occurring
post-PETM taxa like *Phractocytheridea*, a shallow brackish taxon (Table 1; Figs. 4
and 8d).

Interestingly, some deep-water indicator taxa also sporadically appeared in the
recovery phase II assemblage in very low abundances (e.g. *Acanthocythereis*,
*Cytheropteron*, and *Paracypris*) (Figs. 4 and 7) (Huff, 1970; Morkhoven, 1962).
Coexistence of shallow (inner-middle neritic) and deep (bathyal) ostracods is
uncommon in the modern icehouse ocean, as ostracods exhibit strong depth zonation
(Yasuhara et al., 2017b). Taphonomic effects of downslope contamination may
account for minor appearances of shallow species at a deeper site, but it would not
lead to dominance of the shallow species (Kidwell and Holland, 2002). Thus we tend
to prefer the ecological explanation that niche constraints (i.e., deep and shallow
separation) might be overcome in the unusual greenhouse ocean of the early Eocene before the establishment of near-modern ocean circulation and vertical structure (Hutchinson et al., 2019), which may explain the rapid and strong diversification at the end of the PETM identified in the birth-death modeling.

Conclusions

In summary, this four-stage ostracod faunal turnover clearly reflects biotic responses to paleoclimatic and paleoceanographic changes associated with the onset, peak, initial recovery and final recovery of the PETM. Extreme warmth and OMZ expansion as two prominent ecological stressors of the peak PETM together controlled the extirpation and bathymetrical migration of ostracod species by compressing available physical habitats. While upslope migration offers refugia to species with wide depth range habitats, species unable to escape higher temperatures and/or an expanded OMZ are forced to extirpation. Importantly, the PETM offers an example of a threshold event where the recovered shallow shelf benthic community is unlike the one that existed before the ecological collapse. Ostracod (seed shrimp) faunal turnovers throughout the PETM could represent broader metazoan marine benthic community responses and complete the big picture of PETM biotic changes on the shallow shelf in concert with the foraminifera and nannofossil data, which eventually provide a potential analog to future scenarios of short-term and long-term biotic changes in relevance to anthropogenic warming in a greenhouse world.

Data accessibility statement
All data supporting this article has been uploaded as part of the Supplementary Materials and will be deposited in Pangaea (DOI will be added later).

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