9

10 # Ecological Response of Plankton to Environmental Change – Thresholds for

11 # Extinction

12 Christopher M. Lowery[1*], Paul Bown[2], Andrew J. Fraass[3], Pincelli M. Hull[4]

13

14 [1]University of Texas Institute for Geophysics, University of Texas, Austin

15 [2]Department of Earth Sciences, University College, London

16 [3]School of Earth Sciences, University of Bristol

17 [4]Department of Geology and Geophysics, Yale University

18

19 *Corresponding Author: cmlowery@utexas.edu

20

21 **Abstract**

22   Severe climatic and environmental changes are far more prevalent in Earth history than major

23 extinction events, and the relationship between environmental change and extinction severity has

24 important implications for the outcome of the ongoing anthropogenic extinction event. The response of

25 mineralized marine plankton to environmental change offers an interesting contrast to the overall record

26   of marine biota, which is dominated by benthic invertebrates. Here, we summarize changes in the species

27   diversity of planktic foraminifera and calcareous nannoplankton over the Mesozoic-Cenozoic and that of

28   radiolarians and diatoms over the Cenozoic. We find that, aside from the Triassic-Jurassic and

29   Cretaceous-Paleogene mass extinction events, extinction in the plankton is decoupled from that in the

30   benthos. Extinction in the plankton appears to be driven primarily by major climatic shifts affecting water

31   column stratification, temperature, and, perhaps, chemistry. Changes that strongly affect the benthos, like

32   acidification and anoxia, have little effect on the plankton, or are associated with radiation.

33   **Keywords**: Plankton, Triassic-Jurassic Boundary, Oceanic Anoxic Events, Cretaceous-Paleogene

34   Boundary, Paleocene-Eocene Thermal Maximum, Eocene-Oligocene Boundary

35   **Introduction**

36   Human activity has been causing significant disruption of the biosphere for centuries through

37   over-hunting, over-fishing, habitat destruction, pollution, eutrophication, invasive species introduction,

38   and climate change (e.g., Barnosky et al., 2011). As society seeks ways to mitigate this disruption, it is

39   critical to understand how life responds to and recovers from such perturbations.

40   Paleontology has an important but currently underdeveloped role to play in understanding,

41   predicting, and communicating the changes that are occurring and will occur in the biosphere due to

42   human actions. Just as paleoclimatology has become essential for validating climate models and

43   constraining the effects of different pCO$_2$ concentrations using ancient analogs, paleontology and related

44   disciplines provide the ideal tools for constraining the response of the biosphere at a variety of spatial and

45   temporal scales. This includes developing Holocene baselines of biodiversity and variability within

46   ecosystems, understanding deeper-time response of organisms and ecosystems to particular pressures, and

47   determining post-extinction recovery dynamics and timing. Mass extinctions are each unique events, with

48   different preconditions, drivers, and outcomes, and the ecological response to each has been unique as

49   well. Just as there is no perfect paleoclimate analog for the Anthropocene, there is no perfect

50   paleoecological analog for what is currently happening to the biosphere. Studying and comparing

51   different ancient events, however, can illuminate processes that will affect the future of the biota.

52   Earth has experienced a number of significant mass extinction events from a variety of causes

53   (Raup and Sepkoski, 1982). Although modern losses of biodiversity do not yet equal those of the so-

54   called Big Five mass extinction events (Barnosky et al., 2011), the anthropogenic impact on global

55   biodiversity is undeniable (e.g., Periera et al., 2012), and the recovery from those ancient events may help

56   us understand the mechanisms that will drive recovery in the future. Moreover, Earth has experienced an

57   even larger number of severe environmental and climatic changes which did not result in mass extinction;

58   why do some of these events cause major extinctions while others do not? Are particular environmental

59   changes more damaging, or particular ecosystems more vulnerable?

60   When we discuss major mass extinctions (i.e., the "Big Five" first defined by Raup and Sepkoski,

61   1982) we generally mean declines in the total diversity of marine organisms, a record dominated by

62   benthic invertebrates. But the oceans are an ecologically varied place, and by delving into specific groups

63   we can discover the nuances of the ecological response of marine organisms to environmental change. In

64   particular, how does the record of extinction and origination in those groups differ from the overall

65   marine (mostly benthic invertebrate) record? Marine plankton are both ecologically important to the

66   oceans and robustly represented in the geological record. The ubiquitous presence and high abundance of

67   microfossils in marine sediments, combined with >50 years of scientific ocean drilling, have resulted in a

68   geographically widespread and temporally highly resolved record of species-level diversity for each of

69   the major marine microfossil groups.

70   Cyanobacteria and organic-walled green algae were probably the dominant primary producers in

71   the Paleozoic oceans (Falkowski et al., 2004). The fossil records of photosynthesizing calcareous

72   nannoplankton (coccolithophores), dinoflagellates, and diatoms, as well as heterotrophic planktic

73   foraminifera, indicate that they all evolved in the Mesozoic (Falkowski et al., 2004; Knoll and Follows,

74   2016). This turnover in dominant plankton groups was part of the Mesozoic Marine Revolution (e.g.,

75   Vermeij, 1977) and fundamentally altered ocean ecosystems and energy cycling, as larger cell sizes

76   facilitated more efficient energy transfer to higher trophic levels (Knoll and Follows, 2016).

77   Phytoplankton like diatoms and calcareous nannoplankton form the base of the marine food web, while

78   zooplankton like radiolarians and planktic foraminifera, though themselves less critical to food webs in

79   the modern ocean, can serve as a proxy for non-mineralizing members of this important trophic level.

80   Plankton are also an important part of the carbon cycle, both as vehicles for transporting organic carbon to

81   the sea floor and as pelagic calcifiers (e.g., Henehan et al., 2016).

82   The rise of Mesozoic-Cenozoic plankton groups was influenced by a number of significant

83   environmental changes, including the two most recent major mass extinctions: the Triassic-Jurassic (T-J;

84   201 Ma) and the Cretaceous-Paleogene (K-Pg; 66 Ma). Although these two events had the greatest effect

85   on plankton diversity, they paint an incomplete portrait of turnover in the plankton and the ecological

86   response to environmental change. Extinction events scale from "background extinction" to "mass

87   extinction," and the space between those end members is populated by a range of increasing magnitudes

88   of species loss. This includes some "major extinctions" that are above background rates and felt by

89   certain groups or ecosystems, but are below the scale the catastrophic, global mass extinctions (Bambach

90   et al., 2004).

91   Figure 1 compares the ranked extinction rates of marine genera binned by stage by Bambach et

92   al. (2004) (using Sepkoski's (1998) compilation of marine genera) to the ranked extinction rates of our

93   compilation of planktic foraminifera and calcareous nannoplankton species binned at 1-myr intervals (see

94   Methods, below). Although the magnitude of extinction can be expected to be higher at the species level

95   than the genus level (most genera contain many species, after all), species and genus extinction are

96   strongly correlated (Fraass et al. 2015). Differences in the relative severity of extinction between the

97   plankton and the total marine record can be informative about the response of the plankton compared to

98   the overall marine realm (skewed toward macroinvertebrates and shelf species). In both datasets the K-Pg

99   and T-J clearly stand above the rest, followed by a transitional interval with a steeper slope connecting the

100   major mass extinctions to the background rates, which plot on a long tail with a low slope. Beyond the K-

101   Pg and T-J, there is little similarity between which extinctions were most severe in marine genera overall

102   and in the plankton in particular. In the Bambach et al. (2004) stage-level data, the transition to

103   background extinction values spans the entire Triassic. They interpret this more as a failure of

104   diversification with only moderate rates of extinction than a true "extinction" event, resulting in overall

105   elevated rates of diversity loss (Bambach et al., 2004). A number of events that fall within the background

106   of the Bambach data, such as the Eocene-Oligocene (E-O) boundary and Oceanic Anoxic Event 1b

107   (OAE1b), appear as above-background events in the plankton-only data. The Toarcian OAE (T-OAE), the

108   4th-largest extinction of calcareous nannoplankton, is the 5th-smallest extinction in the total marine

109   diversity data. Conversely, Oceanic Anoxic Event 2 (OAE2) is one of the most severe extinction events

110   overall, but is only the third-most severe OAE among both planktic foraminifera and calcareous

111   nannoplankton, and plots well within the interval of background extinction for these groups.

112   Why do the plankton respond to threshold events in Earth history differently than marine biota as

113   a whole? Open-ocean plankton are adapted to live in specific depth habitats (created by thermal

114   stratification of the water column), nutrient conditions, and biogeographic provinces reflecting latitudinal

115   temperature gradients. In the modern ocean, the greatest diversity of calcareous plankton is in the

116   tropics/subtropics, while that of siliceous plankton is near the poles. Plankton and other open-ocean

117   groups are included in the dataset used by Bambach et al. (2004) but they are diluted by the huge diversity

118   of life on shelves and in shallow seas, which have a fundamentally different response to environmental

119   changes than the deep sea. For example, expanding oxygen minimum zones (OMZs) during OAE2 led to

120   a severe extinction of benthic organisms on carbonate platforms and shallow shelves (e.g., Parente et al.,

121   2008). But many plankton simply lived in habitats above the OMZ, and only a few deeper-dwelling taxa

122   were driven to extinction (e.g., Leckie et al., 2002). Thus, the response of the plankton to major

123   environmental changes can provide additional insight to the susceptibility of particular ecologies to

124   different types of negative environmental forcing. Here, we summarize the open-ocean environmental

125   changes and the response of the plankton during major and minor events from the Triassic to the Neogene

126   to understand how environmental and biotic changes drive turnover, which ecologies are more likely to

127   survive or go extinct due to particular pressures, and the factors controlling the recovery of planktic

128   ecosystems after biodiversity loss.

129   **2. Methods**

130   We compare updated species-level biodiversity records for calcareous nannoplankton and

131   planktic foraminifera from the Mesozoic to the Recent and previously published species level diversity

132   records for radiolarians and diatoms from just the Cenozoic. Calcareous nannoplankton diversity is an

133   updated version of the record of Bown et al. (2004), based on the online atlas Nannotax

134   ([http://www.mikrotax.org/Nannotax3/)](http://www.mikrotax.org/Nannotax3/). New taxa described since 2004 have been added and temporal

135   resolution increased to 1 myr. Planktic foraminifer morphospecies diversity is an update of Fraass et al.

136   (2015), representing a revision of the higher-level taxonomy and the inclusion of key newly erected taxa.

137   As stated in Fraass et al., the pre-Cretaceous planktic foraminifer record is fragmentary and poorly

138   preserved, and should be viewed with that in mind (Figure 2). Cenozoic planktic foraminifer lineage

139   diversity is from Aze et al. (2011). These two datasets differ in that while Fraass et al. was constructed

140   from atlas sources (e.g., Olsson et al., 1999) and contains all recognized morphotaxa of the planktic

141   foraminifera, the Aze et al. (2011) dataset uses a lineage phylogeny to remove the pseudo-extinction and

142   pseudo-origination caused by anagenetic evolution. Cenozoic radiolarian and diatom macroevolutionary

143   rate and diversity data are from Spencer-Cervato (1999) and Renaudie et al. (2018), respectively. Data

144   here are all presented at 1 myr resolution to allow for a shared frame of reference, as previously published

145   work is in that resolution. The species richness is the total number of taxa that occur for some part of, or

146   throughout, each stratigraphic bin, and extinction and origination rates reflect the percentage of taxa not

147   carried over from the previous bin (extinction rate) or new taxa which did not occur in the previous bin

148   (origination rate). As the microfossil record is of the highest quality, singletons have not been excluded

149   from this calculation.

150   Taxonomy in these groups is always shifting, and while there are consistent patterns within each

151   of the groups (compare the diversity curve in Tappan & Loeblich, 1988 to Fraass et al. 2015), stating

152   macroevolutionary rates to a precise tenth of percent is not warranted. Thus, we try to limit our

153   discussions to how rates rank with one another, and not cite precise values when possible (Table 1 is

154   presented for completeness, however). We make an exception for this with non-calcifying plankton in the

155   Mesozoic (when there are no diversity curves at a useful resolution for these groups) and cite examples

156   from the literature of diversity and ecological change at specific intervals.

157   Finally, it is important to note that the lack of standardized methodology for the development of

158   diversity records hampers the inter-comparison of the fossil groups studied here. Most diversity records

159   must take into account unequal sampling and rock volume. Siliceous species are more commonly

160   preserved at high latitudes, except during discrete time intervals (e.g., the Eocene) but the majority of

161   deep sea samples come from tropical and subtropical latitudes. Note that although the radiolarian

162   diversity data used here begin in the Eocene, the record of this group extends back to the Cambrian, and

163   diatoms are known from the mid-Cretaceous onward. There is a clear pull of the recent in both radiolarian

164   and diatom data, but even that masks the true diversity of these groups. For example, Turbovitz et al.

165   (2019) found >500 radiolarian taxa in preliminary results from late Neogene samples from IODP Site

166   U1337, many of which were in a size fraction smaller than commonly used for radiolarian analysis. In

167   addition, the different compilations have distinct characteristics. For example, diatom occurrence data are

168   from the NSB database (http://www.nsb-mfn-berlin.de/), an update of the original Neptune database (e.g.,

169   Lazarus, 1994) and are thus based on species occurrence data from scientific ocean drilling expeditions.

170   The planktic foraminifer morphospecies dataset, on the other hand, is based on first appearance and last

171   appearance datums from atlas compilations (e.g., Olsson et al., 1999) representing a synthesis of

172   foraminifer micropaleontologists' species concepts. These records are measuring similar but distinctly

173   different qualities of the organisms, and should only be compared with that caveat in mind. In addition,

174   there is obvious misfit within our compiled data, as paleoceanographic events are 'felt' in one bin for one

175 group, then 'felt' in a subsequent bin in a different group. This is, again, a function of the above described

176 differences between different microfossil groups and their workers. The micropaleontology community

177 should come together to produce comparisons between these different methods for generating

178 compilations. More importantly, studies using the same methods on multiple groups are needed. Such

179 work would greatly advance our science.

180 **3. Extinction Events**

181   Mesozoic-Cenozoic diversity curves for the plankton groups discussed here are plotted in Figure

182 2. A ranking of extinction (Figure 1B) and origination (Figure 1C) rates of calcareous nannoplankton and

183 planktic foraminifera are presented in Figure 1. These clearly show that planktic foraminifera are more

184 sensitive to change than calcareous nannoplankton. It is not clear, however, if this is because of the

185 consistently higher diversity of calcareous nannoplankton, or if planktic foraminifera have ecologies that

186 are more susceptible to extinction (e.g., thermocline/subthermocline niches). It should also be noted that

187 our 1 myr bin size affects these values. For example, planktic foraminifera are commonly cited as having

188 ~90% extinction across the K-Pg (e.g., Olsson et al., 1999), but the appearance of a number of new

189 Paleocene planktic foraminifer taxa within a few hundred kyr of the boundary makes the extinction of

190 foraminifera appear less severe than it truly was.

191 **3.1 Triassic-Jurassic Boundary**

192   The initial rifting of the modern Atlantic Ocean ~200 million years ago (Ma) was associated with

193 the emplacement of the Central Atlantic Magmatic Province (CAMP), possibly the largest flood basalt on

194 Earth (Wignall, 2001). Between 2-4 x 10^6 km^3 of volcanic material (Wignall, 2001) was erupted between

195 580 ± 100 (Olsen et al., 2003) to 840 ± 60 thousand years (kyr) (Schaller et al., 2012) with 3-5 main

196 eruptive pulses (Schaller et al., 2012) that emitted up to 21,000 gigatons (Gt) of carbon and 57,000 Gt of

197 sulfur in total (Beerling and Berner, 2002). This resulted in 3-4°C of warming (McElewain et al., 1999),

198 shifting climate zones, and possibly ocean acidification (Greene et al., 2012). Newly evolved calcareous

199 nannoplankton were severely affected by this event, but this was early in their evolutionary history and

200 diversities were very low: 4 of 5 known Triassic nannoplankton species went extinct, as did 6 of 20

201 species of dinoflagellates (MacRae et al., 1996). Although nearly 20 genera and 130 species of siliceous

202 radiolarians disappeared across the T-J boundary (Carter and Hari, 2005), elevated extinction rates of

203 radiolaria characterized the whole Triassic (something true of the total marine fossil record as well;

204 Bambach et al., 2004), and it is not clear if radiolarian populations were adversely affected by CAMP

205 volcanism in particular (Kiessling and Danelian, 2011).

206   The aftermath of the T-J mass extinction saw a major radiation of calcareous nannoplankton.

207 Within ~10 myr, 9 of 16 Mesozoic families appeared, representing a significant portion of the Mesozoic

208 higher taxa and morphological diversity (Bown et al., 2004). This radiation occurred in two distinct

209 pulses (Figure 2B), the first in the Hettangian, re-establishing the Triassic murolith groups, and the

210 second in the Pliensbachian, which saw the appearance and diversification of new placolith families.

211 Elevated rates of origination and extinction also coincide with the Toarcian OAE (Figure 2B) although

212 this is at least partly an artifact of high numbers of small and fragile species that have only been recorded

213 in the clay-rich sediments associated with the event. However, there are also true nannoplankton

214 extinctions and originations during this interval (Peti et al., 2017)., and these may have resulted from the

215 rapid environmental fluctuations that accompanied the OAE, which included global warming of ~7° C,

216 elevated pCO$_2$, water mass stratification, hypoxia, and elevated nutrients (Cohen et al., 2004; McElwain

217 et al., 2005). Nannoplankton community shifts at this time were likely a response to warming and

218 changing nutrient levels, but carbonate accumulation declines are difficult to distinguish within organic-

219 rich sediments and during intervals of increased weathering and runoff, and the nannolith size fluctuations

220 may not be significantly different to background (Peti and Thibault, 2017).

221   Planktic foraminifera first appeared in the late Early Jurassic, ~20 myr after the T-J, with the

222 evolution of the genus *Conoglobigerina* from a benthic ancestor (Hart et al., 2003; Leckie, 2009). The

223 large oscillations in planktic foraminifer extinction and origination rates in the Jurassic and Early

9

224 Cretaceous (dashed line on Figure 2C) are an artifact of the low number of taxa during this time interval.

225 There are plenty of well-studied Jurassic shelf sections with good carbonate preservation (as evidenced by

226 the diverse nannoplankton record described above), which suggests that planktic foraminifera were not

227 very dispersed or abundant early in their history.

228 **3.2 Cretaceous Oceanic Anoxic Events**

229   The Cretaceous oceans experienced periodic intervals of enhanced burial of organic carbon,

230 resulting in the widespread deposition of black shales, local development of anoxia and euxinia, and

231 corresponding global perturbations of the carbon cycle expressed as positive carbon isotope excursions;

232 these events are known as Oceanic Anoxic Events (OAEs; Schlanger and Jenkyns, 1976; Arthur and

233 Schlanger, 1979; Pratt and Threlkeld, 1984; Leckie et al., 2002; Jenkyns, 2010). The exact number of

234 OAEs depends on how you choose to define them; we focus here on the four that had a significant effect

235 on the plankton: the early Aptian OAE1a, the Aptian-Albian OAE1b, the late Albian OAE1d, and the

236 Cenomanian-Turonian OAE2. A radiation of planktic foraminifera occurred in the Santonian (Premoli

237 Silva and Sliter, 1999), during an interval sometimes called "OAE3." However, this "event" is associated

238 with a ~3-myr interval of black shale deposition in the South Atlantic Ocean, Caribbean Sea, and North

239 American Western Interior Seaway with no clear carbon isotope excursion; because it's not really an

240 event (or, arguably, an OAE; Wagreich, 2012; Lowery et al., 2017), it is not discussed here.

241   OAEs are all associated with the emplacement of large igneous provinces (LIPs) in the marine

242 realm (e.g., Leckie et al., 2002). These events are also associated with significant changes in sea level,

243 water column stratification, and ocean circulation which were likely more important than anoxia in

244 driving plankton turnover. Much of the work summarized in this section represents an update of the

245 review of OAEs and plankton evolution presented by Leckie et al. (2002).

246 **3.2.1 OAE1a**

247   OAE1a was caused by the emplacement of the Ontong Java plateau in the southwest Pacific

248   Ocean (Tarduno et al., 1991; Leckie et al., 2002). The event was preceded by a short, negative carbon

249   isotope excursion thought to reflect the injection of volcanic CO_2 into the atmosphere (Jenkyns, 1995;

250   Erba et al., 2015), or possibly destabilization of methane hydrates (e.g., Jenkyns, 2010). This time period

251   is associated with the "Nannoconid Crisis" (Erba, 1994; Erba et al., 2019) in which the nominate group of

252   calcareous nannoplankton declined for at least a million years, but did not go extinct; this decline began

253   ~40 kyr before the OAE carbon isotope excursion (Giraud et al., 2018). The cause of the 'crisis' is

254   uncertain, not least because this is an entirely extinct non-coccolith nannofossil group, but the decline has

255   been related to a variety of OAE environmental factors, including increased nutrients, elevated pCO$_2$, and

256   trace metal enrichment (e.g., Erba et al., 2019). Nannoplankton were otherwise little affected by this

257   OAE, with origination and extinction rates at background levels (Figure 2).

258   Planktic foraminifera, in contrast, experienced an extinction during OAE1a (Leckie et al., 2002).

259   The early Aptian was preceded by a small radiation (6 species) of planktic foraminifera in the late

260   Barremian, and an equal number of species were lost during the OAE (Figure 2). The OAE1a interval is

261   characterized by depauperate assemblages dominated by the morphologically aberrant *Leupoldina cabri*

262   (Premoli Silva et al., 1999). In the aftermath of this event, planktic foraminifera radiated, with diversity

263   increasing through the late Aptian. Many new species of *Globigerinelloides* and *Hedbergella* appeared;

264   proportionally, this was one of the largest planktic foraminifer speciation events of the Cretaceous (Figure

265   1C).

266   Radiolarians also experienced a turnover during OAE1a. Regional occurrence data from the

267   North Atlantic and western Tethys shows significant local extinction at OAE1a, with a loss of 41% of

268   species (Erbacher and Thurow, 1997). Much like foraminifera, it was deeper-dwelling radiolarians that

269   went extinct during OAE1a, indicating a loss of suitable thermocline habitat due to the expansion of

270   oxygen minimum zones or a break down in water column stratification.

11

271   The rest of the Aptian was characterized by a return to more stable water column stratification

272   and a corresponding increase in species that lived below the mixed layer. Nannoconids reappeared in

273   nannoplankton assemblages (although were generally only common in tropical, shallow water settings;

274   Erba, 1994; Giraud et al., 2018), and new species of deeper-dwelling planktic foraminifera (Leckie et al.,

275   2002) and radiolarians (Erbacher and Thurow, 1997) appeared and diversified. Foraminifer test size also

276   increased following OAE1a (Leckie et al., 2002).

277   **3.2.2 OAE1b**

278   The Aptian-Albian OAE1b saw the largest extinction of planktic foraminifera in the Cretaceous

279   (Premoli Silva and Sliter, 1999; Leckie et al., 2002; Huber and Leckie, 2011; Fraass et al. 2015; Figure

280   1B). OAE1b is comprised of a series of discrete black shale horizons (and corresponding carbon isotope

281   excursions) spanning the latest Aptian to the early Albian. These black shales, which are mainly found in

282   the Tethys/Atlantic region, are associated with the emplacement of the Kerguelen Plateau in the southern

283   Indian Ocean (Whitechurch et al., 1992; Leckie et al., 2002; McAnena et al., 2013). This time period is

284   characterized by cooling and sea level fall in the latest Aptian, followed by sea level rise in the earliest

285   Albian (Leckie et al., 2002; McAnena et al., 2013). OAE1b itself is associated with a breakdown in water

286   column stratification, although the mechanism for this is uncertain. Watkins and Browning (2008) and

287   McAnena et al. (2013) suggest it was related to late Aptian cooling, whereas others have invoked

288   reorganization of North Atlantic deep water circulation following deepening of the gateway linking the

289   North and South Atlantic Ocean (Arthur and Natland, 1979; Huber and Leckie, 2011).

290   Average foraminifer test size fell by 100 μm (Leckie et al., 2002) at the Aptian-Albian boundary,

291   as larger, ornamented, heavily-calcified planktic foraminifera (particularly deeper-dwelling taxa) were

292   replaced with small, simple, thin-walled forms (Leckie, 1989; Premoli Silva and Sliter, 1999; Leckie et

293   al., 2002; Huber and Leckie, 2011). Total abundance of planktic foraminifera also crashed at many sites at

294   this time (Huber and Leckie, 2011). Planktic foraminifer diversity took the entire Albian, ~10 myr, to

295   recover to previous levels. Geographically limited data indicates that the early Albian ocean was weakly

296   stratified, and planktic foraminifera only lived in the mixed layer (Leckie et al., 2002; Huber and Leckie,

297   2011). Planktic foraminifer diversity and test size rose steadily throughout the remainder of the middle

298   and late Albian (Figure 2), as did water column stratification (Leckie et al., 2002).

299   In contrast, nannoplankton show no significant change during this interval, with evolutionary

300   rates falling within the background range. A minor turnover was documented at Blake Nose in the

301   western North Atlantic, but this was likely a regional feature related to local nutrient increases (Browning

302   and Watkins, 2008). Radiolarians passed through the Aptian-Albian boundary unscathed but experienced

303   elevated turnover in the early Albian (42% extinction and 36% origination; Erbacher and Thurow, 1997).

304   **3.2.3 OAE1d**

305   The late Albian OAE1d, first defined by Erbacher et al. (1996), is enigmatic. The exact cause is

306   not currently known, and most black shales recognized from this time are not quite coeval with the

307   relatively minor carbon isotope excursion, suggesting additional carbon burial in an as-yet unidentified

308   region (Petrizzo et al., 2008). Although there are some data indicating increased water column

309   stratification in the Tethys (Gambacorta et al., 2016), most data suggest a weakening of stratification at

310   this time: calcareous nannoplankton indicate a breakdown of stratification at DSDP Site 545 concurrent

311   with an increase in productivity (Watkins et al., 2005), and single species planktic foraminifer isotope

312   data from Blake Nose suggest a breakdown in vertical temperature gradients (Wilson and Norris, 2001;

313   Petrizzo et al., 2008). Whatever the cause, this breakdown in water column stratification led to significant

314   extinction in planktic foraminifera (Nederbragt et al., 2001; Petrizzo et al., 2008; Fraass et al., 2015) and

315   radiolarians (Erbacher and Thurow, 1997; Wang et al., 2019), while calcareous nannoplankton only

316   experienced minor local turnover (Watkins and Bergen, 2003; Watkins et al., 2005).

317   Deeper dwelling planktic foraminifer genera like *Ticinella* and *Biticinella* that had evolved

318   during the gradual increase in water column stratification that followed OAE1b disappeared and new

319   mixed-layer genera like *Praeglobotruncana* and *Paracostellagerina* appeared for the first time. Radiolaria

13

320   also experienced significant turnover, as 15 taxa disappeared during OAE1d, followed by the appearance

321   of 12 new forms typical of Cenomanian oceans (Erbacher and Thurow, 1997).

322   **3.2.4 OAE2**

323   The most significant OAE in the overall marine fossil record (Figure 1A), is the Cenomanian-

324   Turonian OAE2. It was driven by the emplacement of the Caribbean LIP (Leckie et al., 2002; Snow et al.,

325   2005; Turgeon and Creaser, 2008; Monteiro et al., 2012). This volcanism spurred increased productivity

326   either due to direct injection of nutrients from hydrothermal fluids (Leckie et al., 2002) and/or by causing

327   significant warming (e.g., Friedrich et al., 2012), which led to increased flux of terrigenous nutrients into

328   the oceans following a strengthening of the hydrological cycle (Pogge von Strandmann et al., 2013).

329   Ostrander et al. (2017) showed that the OAE2 carbon isotope excursion was preceded by 40 kyr of

330   progressive deoxygenation of the oceans, indicating a gradual onset. It is unclear if such a ramp-up of

331   deoxygenation occurred prior to other OAEs because OAE2 is the only one investigated with the thallium

332   isotope oxygenation proxy (Ostrander et al., 2017) thus far, but this is probably a reasonable assumption.

333   Warming at the Cenomanian-Turonian boundary led to a breakdown of vertical stratification in the oceans

334   and an increase in upwelling (Arthur and Natland, 1979; Leckie et al., 1998; Huber et al., 1999; Trabucho

335   Alexandre et al., 2010).

336   Despite causing a major extinction among other marine groups (e.g., Bambach et al., 2004;

337   Parente et al. 2008; Figure 1A), OAE2 is associated with only minor turnover in the planktic foraminifera,

338   with the loss of just a few thermocline/subthermocline taxa (Figure 2). Deeper-dwelling planktic

339   foraminifera, notably *Rotalipora* and *Thalmanninella*, disappeared during the event, but this decrease in

340   diversity was offset by the radiation of new forms before, during, and after the OAE, as the first double-

341   keeled taxa, which were common throughout the rest of the Cretaceous, appeared in the late Cenomanian

342   (Premoli Silva and Sliter, 1999).

343   The Cenomanian-Turonian boundary interval is associated with a drop in calcareous

344   nannoplankton diversity, a rare interruption of the long-term increase that had continued unabated through

345   previous OAEs (Figure 2). However, this decline began in the mid-Cenomanian (as noted by Bown et al.,

346   2004) and continued into OAE2, which is associated with a series of extinctions (~9 species), but overall

347   the evolutionary rates are at background levels. A step-wise extinction of radiolarians also began in the

348   mid-Cenomanian and culminated during OAE2 (Erbacher and Thurow, 1997) with 29 taxa disappearing

349   during the event; 20 new forms appear within or just after the OAE2 interval in the Umbria-Marche

350   region of Italy (Erbacher and Thurow, 1997; see Musavu-Moussavou et al. 2009 for a more recent report

351   on this same region).

352   **3.3 Cretaceous-Paleogene Boundary**

353   The most recent of the "Big Five" mass extinctions (Raup and Sepkoski, 1982) is the Cretaceous-

354   Paleogene boundary event. It was caused by the impact of an asteroid on the Yucatán carbonate platform

355   in the southern Gulf of Mexico (e.g., Alvarez et al., 1980; Smit and Hertogen, 1980; Hildebrand et al.,

356   1991; the best review of the impact hypothesis remains Schulte et al., 2010; see also Lowery et al., 2019

357   for an update of current results from recent scientific drilling in the crater). The Chicxulub impact lofted

358   gigatons of dust, soot from widespread fires, and, most importantly, sulfur from the evaporite-rich target

359   rock, into the stratosphere, resulting in a sharp reduction in solar insolation and a coincident crash in

360   photosynthesis, which led to a collapse of marine food webs (Zachos et al., 1989; Toon, 1997; D'Hondt et

361   al., 1998; Coxall et al., 2006; Brugger et al., 2017; Artemieva et al., 2017). A side effect of this severe

362   cooling was a major breakdown in open ocean stratification; one recent model (Brugger et al., 2017)

363   indicates that the ocean's mixed layer plunged from its normal depth of <100 m to >2500 m at 60°

364   latitude and >1000 m in the tropics (Brugger et al., 2017). Other stressors on the pelagic realm include

365   ocean acidification and hypoxia. Although geographically limited evidence exists for the expansion of

366   intermediate depth oxygen minimum zones at the K-Pg boundary, particularly at Caravaca, Spain (e.g.,

367   Kaiho et al., 1999; Mizukami et al., 2013), it is unclear how widespread this may have been. Meanwhile,

368   recent work with Boron isotopes shows rapid, severe surface ocean acidification (drop of 0.2-0.3 pH

369   units) right at the boundary followed by a rebound and overshoot of surface ocean pH (increase of 0.5 pH

370   units) within 40 kyr (Henehan et al., 2019). However, a similar magnitude of surface ocean acidification

371   has been observed at the PETM (decrease of 0.3 pH units; Penman et al., 2014), which is only associated

372   with minor extinction in the plankton (see below). This is in line with model results of sulfate and nitrate

373   production from the impact, which suggest that these were too low to cause acidification severe enough to

374   drive extinction in the plankton, unless nearly all of it was put in the oceans within a year (which is

375   unlikely) (Tyrell et al., 2015). Despite this, the K-Pg was selective for calcareous taxa despite. This could

376   be explained by the higher latitude habitat of most non-calcareous microfossils, or the many cyst-forming

377   groups of diatoms and dinoflagellates that may have been better equipped to withstand a short period of

378   global darkness and unstable waters. Early recovery assemblages were characterized by acmes of

379   calcareous dinoflagellates like *Cervisiella* (e.g., Lamolda et al., 2005; Alvarez et al., 2019); if these were

380   indeed resting cysts this was likely a useful attribute for survival.

381   Although it is difficult to determine the specific lethality of any one of these extreme

382   environmental changes, together they drove severe extinction in the marine realm: ~75% of marine

383   species went extinct at the K-Pg (e.g., Jablonski, 1995). However, the extinction was selective for species

384   living in the upper ocean, while deep sea biodiversity was barely affected (e.g., Culver, 2003). Greater

385   than 90% of planktic foraminifera went extinct, leaving just four survivors with clear Paleocene

386   populations: *Guembelitria cretacea*, *Muricohedbergella holmdelensis, M. monmouthensis*, and

387   *Rectuvigerina cretacea*; of these, only the first three had descendants (Olsson et al., 1999). A fifth

388   survivor, *Zeauvigerina waiparaensis,* was the ancestor of a genus that ranged into the Eocene before

389   going extinct, but its isotope paleobiology plots more closely to benthics than other planktics, and this

390   genus may be polyphyletic (Huber et al., 2006). Approximately 93% of calcareous nannoplankton also

391   went extinct, with ~10 survivor species (Bown et al., 2004). Survivors from both planktic foraminifera

392   and calcareous nannoplankton were shallow water, often neritic, taxa with a more opportunistic trophic

16

393 strategy (Leckie, 1987; D'Hondt and Keller, 1991; Bown, 2005a). A good example of this is the planktic

394 foraminifer *Guembelitria cretacea,* which was common in nearshore waters during the Cretaceous

395 (Leckie, 1987) but dominated open ocean assemblages in the earliest Paleocene (D'Hondt and Keller,

396 1991; Arenillas et al., 2000).

397   Records of siliceous and organic-walled fossils are more poorly developed at the K-Pg (D'Hondt,

398 2005). Dinoflagellates lost ~40% of their diversity (~200 species; MacRae et al., 1996), although this

399 occurred across a broader interval. Sims et al. (2006) show that 63% of diatom species went extinct at the

400 K-Pg; the majority of survivors were high latitude, neritic species capable of forming resting cysts (Sims

401 et al., 2006). Radiolarian extinction rates suggest little extinction (Hollis et al., 2003), but recent upward

402 revisions of dinoflagellate and diatom extinction rates (e.g., MacRae et al., 1996; Simms et al., 2006)

403 suggest this should be taken with a grain of salt. However, the species loss in these three groups is still

404 well below the catastrophic level (>90%) suffered by calcareous plankton.

405   The most important change in the open ocean at the K-Pg is the weakening of the biological

406 pump, which removes organic matter from the surface ocean to the deep sea. Photosynthesis favors ^{12}C;

407 sinking of dead organic matter therefore preferentially removes ^{12}C from the upper water column and thus

408 creates a carbon isotope gradient from the surface waters to the seafloor. This gradient collapsed after the

409 K-Pg (D'Hondt et al., 1998) and was not repaired for at least 1.8 million years (Birch et al. 2016).

410 Although the collapse of this gradient was originally taken as evidence of the complete shutdown of the

411 biological pump (the so-called Strangelove Ocean, e.g., Hsü and MacKenzie, 1985), subsequent work has

412 shown that an increase in the amount of organic matter remineralized in the upper water column from 90

413 to 95% (D'Hondt et al., 1998; Henehan et al., 2019) can explain the observed isotope values. Calcareous

414 nannoplankton were one of the dominant primary producers of the Cretaceous, and the sharp decline in

415 this group left a gap in ocean food webs. Biomarkers indicate blooms of algae and other non-fossilizing

416 phytoplankton just above the boundary in the Fish Clay of Denmark (Sepulveda et al., 2009). Given the at

417 least partial continuity of marine food webs in the early Danian (e.g., Hull and Norris, 2011; Alegret and

418 Thomas, 2012) and the early recovery of productivity in nearshore marine environments (Sepulveda et al.,

419 2019), it may be presumed that blooms of non-fossilizing primary producers occurred elsewhere in the

420 ocean, too, but thus far such data exists only from the Fish Clay, and further investigation is needed.

421). The final recovery of the biological pump also appears related to calcareous nannoplankton

422 diversity. A highly-resolved nannoplankton record from Pacific Ocean Site 1209 (Shatsky Rise), shows a

423 post-extinction interval of almost 2 million years of highly unstable communities, characterized by

424 a succession of acme events (100s of kyr scale), before a more stable, equilibrium-state

425 community emerged that displayed indicators of resilience (Alvarez et al., 2019). The transition to this

426 equilibrium-state community occurred as cell sizes and species richness increased and was coincident

427 with restoration of a fully functioning biological pump, suggesting a fundamental link between

428 ecosystem recovery and biogeochemical cycling (Birch et al., 2016; Alvarez et al., 2019). On shorter

429 timescales, export productivity reconstructions based on the biogenic barium proxy have found that some

430 open ocean sites experienced an increase in export production in the earliest Danian (Hull and Norris,

431 2011). This may have been driven by local differences in the efficiency of the biological pump, and there

432 is evidence to suggest that these differences were a factor in the initial recovery of calcareous

433 nannoplankton assemblages. For example, at Chicxulub a reduction in initially-high post-extinction

434 export productivity is associated with turnover in the nannoplankton from a *Braarudosphaera*-dominated

435 assemblage of survivor species to more diverse assemblages of new Paleocene taxa (Jones et al., 2019).

436 Reduced biological pump efficiency would result in the concentration of nutrients in the upper

437 water column and thus may have actually increased local primary productivity (Jones et al., 2019).

438 The recovery of nannoplankton following the K-Pg mass extinction was an explosive radiation

439 with a handful of Cretaceous survivor species quickly joined by miniscule incoming new taxa that formed

440 a striking series of global acmes (Bown, 2005a). Origination rates are some of the highest in the history of

441 the group (Figure 1C), with ~25 species added in the first million years of the Danian, although full

442 recovery of pre-extinction diversities took another 10 million years (Figure 1C; see also Alvarez et al.,

443   2019). The synchrony of some of these nannoplankton acmes has been questioned, with lags explained by

444   incumbency or environmental heterogeneity (Jiang et al., 2010; Schueth et al., 2015; Jones et al., 2019).

445   However, some of these events are widely applied in biostratigraphy (e.g., Varol, 1989; Agnini et al.,

446   2014), suggesting roughly synchronous timing across ocean basins, and it may be that reported

447   discrepancies are caused by taxonomic inconsistency (unavoidable among incoming, minute groups with

448   similar morphologies), inconsistent preservation of small, fragile species, problems with age models, or

449   localized effects. These issues will likely become clearer as further sections are studied at high resolution

450   (e.g., Jones et al., 2019, Alvarez et al., 2019).

451   The recovery of planktic foraminifera from the K-Pg mass extinction is also frequently cited as an

452   example of explosive adaptive radiation (e.g., Smit et al., 1982; Coxall et al., 2006; Hull et al., 2011;

453   Birch et al., 2012). Our data show that it is characterized by only moderately elevated origination rates

454   (Figure 1C), although this may be a function of the binning scheme. The timing of planktic foraminiferal

455   recovery is synchronous across the oceans, with a succession of dominant taxa observed across the

456   Tethys/North Atlantic within relatively diverse populations (Arenillas et al., 2000; Alegret et al., 2004).

457   Within the Chicxulub Crater, where nannoplankton disaster taxa (*Braarudosphaera* spp. and *Cervisiella*

458   spp.) remained the longest, the full diversity of early Danian planktic foraminifera appeared essentially

459   immediately, within 30 kyr of the boundary (Lowery et al., 2018). Thus, the mechanisms driving the

460   recovery of autotrophic calcareous nannoplankton and heterotrophic planktic foraminifera appear to be

461   disconnected.

462   Recovery of both planktic foraminifera and calcareous nannoplankton diversity to roughly mid-

463   Cretaceous levels took roughly the entire Paleocene (10 myr; Figure 2).

464   **3.4 Paleocene-Eocene Thermal Maximum**

465   The Paleocene-Eocene Thermal Maximum (PETM) was the most extreme hyperthermal event of

466   the Paleogene, and probably the best ancient analog for the current rate of CO_2 release, with an initial

467 onset of the event occurring in as little as 4,000 years (still an order of magnitude lower than modern

468 rates) (Zeebe et al., 2016). Although the mechanism for carbon release (indicated by a negative carbon

469 isotope excursion that defines the event) is still debated, with many in favor biogenic methane as the main

470 culprit (e.g., Dickens et al., 1995, 1997; DeConto et al., 2012), although Gutjahr et al. (2017) argue that

471 volcanic sources are sufficient. Either way, between 2000 and 6000 Pg carbon were released (Panchuk et

472 al., 2008; Zeebe et al., 2009), resulting in significant ocean acidification (e.g., Hönisch et al., 2012) and

473 the shoaling of the calcite compensation depth (CCD) by as much as 2 km (Zachos et al., 2005). Surface

474 pH dropped by 0.3 pH units (Penman et al., 2014). This acidification had a severe effect on the biosphere,

475 resulting in a major extinction of deep sea benthic foraminifera (Thomas, 2007), a turnover of shallow

476 water larger benthic foraminifera (Scheibner and Speijer, 2008), and a collapse of coralgal reefs

477 (Scheibner and Speijer, 2008).

478   Among the plankton, however, the PETM resulted in relatively muted levels of speciation and

479 extinction (e.g., Gibbs et al. 2006a), although turnover across the broader interval was high in

480 nannoplankton (Figure 1B and C). Although a few planktic foraminifera species disappeared, overall

481 diversity rose significantly across the Paleocene-Eocene boundary (Figure 2) (Kelly et al., 1996, 1998;

482 Pardo et al., 1999; Gibbs et al., 2006a,b; Sluijs et al., 2006; Bown and Pearson, 2009; Speijer et al., 2012).

483 Unusual morphologies occur in a minor number of nannoplankton during the PETM (Raffi and De

484 Bernardi, 2008; Bralower and Self Trail 2016) and planktic foraminifera and calcareous nannoplankton

485 both produced several "excursion taxa" (Kelly et al., 1998) which only lived during the carbon isotope

486 excursion (e.g., *Morozovella alisonensis; Coccolithus bownii*). Changes in assemblage structure have

487 been reported in both organic-walled dinoflagellates (Sluijs and Brinkhuis, 2009) and calcareous

488 nannoplankton (Gibbs et al., 2006a, b), the former of which, at least, were widespread and inferred to be a

489 response to stratification in the open ocean and nutrient increases in shelf seas. Tropical and subtropical

490 planktic foraminifer and nannoplankton assemblages expanded poleward due to warming (Thomas and

491 Shackleton, 1996; Pardo et al., 1999; Sluijs et al., 2006), while extreme warmth in the tropics (up to

492   40°C) may have led to exclusion ("dead zones") of both calcareous and organic-walled plankton at some

493   locations due to thermal stress (Aze et al., 2014; Frieling et al., 2017)

494   Radiolaria also experienced evolutionary radiation during the PETM, with the extinction of a few

495   species and the appearance of more than a dozen (Sanfillipo and Blome, 2001; Hollis et al., 2006; Liu et

496   al., 2011). Note that our radiolarian record in Figure 2 (from Spencer-Cervato et al., 1999) begins in the

497   Eocene, and thus this turnover is not documented.

498   Subsequent Eocene warming events also had no negative effect on planktic foraminifer or

499   nannoplankton diversity but assemblage shifts are evident (e.g., Gibbs et al., 2013). The magnitude of the

500   hyperthermals (i.e., the size of the carbon isotope excursion) scales with evidence of community variance

501   in the nannoplankton and, to a lesser extent, planktic foraminifera and dinoflagellates, suggesting

502   perturbation of the plankton communities even if these events didn't exceed the threshold to drive

503   extinction (Gibbs et al., 2013; Alvarez et al., 2019). There is evidence for "bleaching" (i.e., loss of

504   symbionts) in symbiont-bearing planktic foraminifera due to warming during the Middle Eocene Climate

505   Optimum (MECO) hyperthermal and a concurrent reduction in average test size, but this ecological stress

506   did not result in any extinction (Edgar et al., 2013). In fact, the middle Eocene was the Cenozoic high

507   point for diversity of both planktic foraminifera and calcareous nannoplankton (Figure 2). Warming

508   during the MECO is also associated with a significant increase in accumulation rates of siliceous plankton

509   in the Southern Ocean (Witkowski et al., 2012) and North Atlantic (Witkowski et al., 2014). The

510   proportionate response of the plankton communities to these environmental perturbations and rapid

511   recovery after each event suggests that these plankton groups were resilient to environmental changes of

512   this magnitude throughout the Paleocene and Eocene (Alvarez et al., 2019).

513   **3.5 Eocene-Oligocene Boundary**

514   The Eocene-Oligocene boundary event, also known as the Eocene-Oligocene Transition (EOT),

515   was the first major step in the progressive cooling that characterized the second half of the Cenozoic. It is

516 associated with a global benthic oxygen isotope shift of about 1.5‰ (Zachos et al., 1996, 2001) that

517 corresponds to about 2.5°C cooling in the deep sea (Lear et al., 2008) and the inception of the East

518 Antarctic Ice Sheet (DeConto and Pollard, 2003). Early thinking held that the cooling was related to a

519 thermal isolation of Antarctica with the opening of the Drake Passage (e.g., Kennett, 1977), but it has

520 since been demonstrated that orbital controls on temperature and CO_2 concentration played a primary role

521 in the appearance and growth of the ice sheet (DeConto and Pollard, 2003) and, importantly, that the

522 Drake Passage opened at a different time, beginning around 41 Ma, or the late middle Eocene (Scher and

523 Martin, 2006).

524   The transition resulted in fundamental changes in the global ocean. Indeed, given that there were

525 no major ice ages in the Mesozoic, we would argue that most major eukaryotic plankton groups

526 originated and diversified in a greenhouse world that ended at the EOT. The CCD deepened by roughly a

527 kilometer (Coxall et al., 2005), and North Atlantic Deep Water began to form, resulting in a significant

528 reorganization of global circulation (Scher and Martin, 2008; Cramer et al., 2009; Katz et al., 2011).

529 These events led to the decline of warm water groups and the diversification of cold water groups.

530 Planktic foraminifera suffered their 3rd worst extinction (Figure 1B), with more than half of species,

531 mostly warm water tropical and subtropical taxa, going extinct in the early Oligocene. Calcareous

532 nannoplankton had a more drawn-out but similarly severe extinction, losing ~33 species across the EOT

533 and into the early Oligocene, with overall diversity declining through the rest of the epoch. Among both

534 groups, this was a protracted loss of species over ~1 myr or more, rather than a mass extinction event

535 focused at the boundary.

536   Conversely, diatoms added ~30 new species during this event (Lazarus et al., 2014). Radiolarian

537 diversity stayed fairly consistent across the EOT (the large increase in Figure 2 is likely an artifact of

538 available datasets and the aforementioned pull of the recent), with declines in tropical taxa offset by the

539 appearance of new cold-water adapted species (Funkawa et al., 2006). There are records of very

540 significant local losses of radiolarian diversity at the E/O boundary (e.g., Palike et al., 2009), and

22

541   Kamikuri and Wade (2012) report a decline in the late Eocene that is not reflected in the Spencer-Cervato

542   et al. (1999) global diversity data plotted here. Overall, while there is a clear need to improve existing

543   diversity compilations, the oceanographic and climatic reorganization that began in the Oligocene clearly

544   suited non-calcareous plankton (Bown, 2005b; Lazarus et al., 2014). It is possible that changes in

545   circulation resulted in increased productivity at higher latitudes, favoring siliceous taxa and displacing

546   calcareous nannoplankton equatorward. Perhaps, because cooler waters at high latitudes are more

547   corrosive, the cooling at the E-O boundary pushed calcareous plankton out of those environments,

548   allowing non-calcareous plankton to thrive in their place. Kidder and Erwin (2001) demonstrated that

549   biogenic silica is more widespread in the oceans during colder periods, when more vigorous circulation

550   caused more widespread upwelling, stimulating increased productivity and silica production, although

551   low and mid latitude biogenic cherts were widespread during the warmest part of the Paleogene

552   greenhouse (Muttoni and Kent, 2007).

553   Our diversity data show that planktic foraminifer diversity remains low for the duration of the

554   Oligocene, ~11 myr, before rebounding in the Miocene and diversifying up to the present day high.

555   Diatoms also diversified throughout the Neogene, achieving their maximum biodiversity in the Recent

556   (although this may be an artifact of the pull of the recent). Calcareous nannoplankton, however, have not

557   seen their diversity rebound after the E-O boundary although they are still key primary producers in the

558   Neogene ocean. This reduced diversity may partly reflect smaller size ranges and more fragile coccoliths

559   in many of the later Cenozoic nannoplankton groups, and reduced preservation potential in many

560   Neogene and modern taxa (Young et al., 2005).

561   **4. The Ecological Response of Plankton to Environmental Change**

562   Each of these environmental events affected the plankton in unique ways, and the response of

563   each group was not always consistent from extinction to extinction. What aspects of plankton ecology are

564   important during and after mass extinctions?

565   Does shell material (e.g., calcareous vs. siliceous/organic) explain the observed differences? It's

566   necessary to preface this discussion with the disclaimer that the record of siliceous and organic walled

567   microfossils is currently much poorer than the record of calcareous microfossils, and these trends will

568   likely change when higher quality records of those groups are developed. With that caveat, the answer is

569   "no." Only the K-Pg and E-O boundaries were strongly selective against calcareous taxa only. Other

570   extinctions, like OAEs, were not selective for wall type but drove extinctions of planktic foraminifera and

571   radiolarians but not calcareous nannoplankton.

572   Calcareous taxa tend to dominate in the tropics, where warm waters and low productivity result in

573   high carbonate saturation. Siliceous taxa tend to dominate in the higher latitudes, where colder water,

574   higher productivity, and, often, seasonal upwelling result in lower carbonate saturation. The extinctions

575   which were selective for calcareous taxa (K-Pg, E-O) were also ones that generally favored cold-adapted

576   taxa. Although there is evidence for ocean acidification at the K-Pg (Henehan et al., 2019), it is of the

577   same magnitude as acidification observed at the PETM (Penman et al., 2014) which is not associated with

578   elevated extinction rates, and thus we think it is more likely that the K-Pg extinction was driven primarily

579   by global darkness and, to a lesser extent, stratification changes. High latitude organisms must have been

580   already adapted to cold and months of darkness in unstratified waters, and were therefore more likely to

581   survive than species living in the warm, sun-bathed Maastrichtian tropics. The E-O boundary was marked

582   by the first significant glaciation of the Antarctic, and this major cooling event resulted in a significant

583   expansion of cool water taxa at the expense of warmer water groups. As discussed above, cool water taxa

584   tend to be siliceous and warm water taxa tend to be calcareous, so the former diversified while the latter

585   declined. In both cases, survival vs. extinction was not dictated by shell material directly (e.g.,

586   susceptibility to acidification). Instead, the traits that were related to survival (e.g., adapted to living in

587   cool polar/subpolar waters) were ones that are more common in non-calcareous groups.

588   Water column structure has always been considered an important control on planktic foraminifer

589   diversity (e.g., Hart, 1980; Premoli Silva and Sliter, 1999; Leckie et al., 2002; Ezard et al., 2011; Fraass et

24

590   al., 2015). Many open-ocean species are adapted for a specific depth habitat, associated with a certain

591   salinity, temperature, level of sunlight, and food supply; a breakdown of stratification would push these

592   species out of their comfort zone and, if sustained, lead to extinction. A consistent through-line of many

593   of the extinction events discussed is a breakdown of stratification. OAEs are associated with the (local)

594   collapse of water column stratification at each event and the coeval decline or disappearance of deeper-

595   dwelling taxa (e.g., Leckie et al., 1998, 2002; Browning and Watkins, 2008; Petrizzo et al., 2008; Huber

596   and Leckie, 2011; McAnena et al., 2013). The local disappearance of such taxa is often diachronous with

597   the local onset of black shale deposition, suggesting that stratification, not anoxia, was the primary

598   stressor in the turnovers of the mid-Cretaceous. It is likely that changes in water column stratification

599   played an important role in the Cenozoic mass extinctions as well. The K-Pg was characterized by a

600   complete breakdown of water column stratification in addition to the collapse of food webs, and all the

601   survivor species and most of the first generation of new Paleocene foraminifer taxa were mixed layer

602   species. Water column structure remained fairly intact during the PETM, and this event was more of a

603   turnover than an extinction, despite significant surface ocean acidification. The EOT was characterized by

604   a major reorganization of ocean circulation and water column structure, and corresponding severe

605   extinctions among planktic foraminifera and calcareous nannoplankton. Changes in water column

606   stratification have a stronger affect on the plankton than benthic organisms, most of which occupy niches

607   unrelated to water column structure, and the importance of water column changes in driving extinction in

608   the plankton likely explains much of the difference between the overall record of marine biodiversity and

609   that of the plankton studied here.

610   Ezard et al. (2011) found that climate and ecology are the primary drivers of extinction in

611   Cenozoic macroperforate planktic foraminifera. This appears to be true across all the plankton groups

612   studied here. Warming and gateway changes led to breakdown of water column stratification during

613   Cretaceous OAEs and drove the extinction of taxa adapted to a deeper habitat. Cooling and darkness led

614   to the collapse of ocean food webs and the elimination of water column stratification following the K-Pg

615   mass extinction, driving severe extinction in photosynthesizing calcareous nannoplankton and deep-

616   dwelling (and most mixed layer) planktic foraminifera. Bown et al. (2004) suggested that the ecological

617   response of calcareous nannoplankton to cooling was different during the Mesozoic and Cenozoic.

618   Cooling events superimposed on the greenhouse climate of the Cretaceous stimulated diversification by

619   increasing biogeographic partitioning in the oceans. The Cenozoic shift from greenhouse to icehouse,

620   however, contracted the viable range of calcareous nannoplankton taxa to only the temperate to tropical

621   latitudes and allowed the proliferation of diatoms in high latitude waters (Bown et al., 2004; Bown

622   2005b). We observe a similar process in the planktic foraminifera, although while calcareous

623   nannoplankton diversity remained low after the onset of late Cenozoic cooling, planktic foraminifera

624   began to diversify again in the Neogene, as icehouse conditions intensified.

625   Ezard et al. (2011) also found that diversity was the primary control on speciation (although

626   climate and ecology play key roles in their model as well). Diversification begins immediately following

627   all the major extinctions discussed here, but full post-extinction diversification often takes about 10 myr.

628   Calcareous nannoplankton diversified in several pulses in the 10 myr following the T-J mass extinction,

629   each of which involved the origination of new families, indicative of significant evolutionary innovations

630   (Bown et al., 2004). Planktic foraminifera took ~10 myr to rebuild diversity following the severe OAE1b

631   extinction and ~11 myr (roughly the entire Oligocene) to rebuild diversity after the E-O. Both groups took

632   ~10 myr to rebuild diversity following the K-Pg. An average 10 myr delay in the recovery of diversity

633   following mass extinctions is well known from the Phanaerozoic marine invertebrate record (e.g.,

634   Kirchner and Weil, 2000; Alroy, 2008). Kirchner and Weil (2000) speculated that this was driven by the

635   need to rebuild ecospace following mass extinctions, as life strategies disappear along with species during

636   such events. Lowery and Fraass (2019) tested this hypothesis with the record of planktic foraminifer

637   morphological complexity (essentially ecospace occupation in simple groups like foraminifera) following

638   the K-Pg mass extinction and found that ecospace expansion does indeed pace diversification. This

639   suggests a fundamental macroevolutionary speed limit on diversification after mass extinctions. Our

640 review here shows that the lag in diversification is present among other plankton groups and after other

641 extinction events. Because we lack detailed morphological data for other groups of plankton we can only

642 speculate that these delays are also driven by the same need to rebuild ecospace.

643 **4.1 Ecological Response to Future Change**

644 The major environmental perturbations affecting the ocean today – acidification (e.g., Doney et

645 al., 2009) and hypoxia (e.g., Ito et al., 2017) – are the ones that have the most severe effect on the shallow

646 benthos but little or no effect on biodiversity of the plankton. Similar magnitudes of ocean acidification at

647 the K-Pg (Henehan et al., 2019) and PETM (Penman et al., 2014) with vastly different extinction rates

648 among calcareous plankton suggest that ocean acidification alone is not a major driver of extinction in the

649 plankton. Planktic extinction during Cretaceous oceanic anoxic events appears more related to changes in

650 water column stratification than anoxia (e.g., Leckie et al., 2002). While this is likely good news for

651 modern plankton biodiversity, it still bodes ill for coral reefs, commercial fisheries, and the vast array of

652 benthic life on the shelves, which will be devastated by acidification and growing dead zones.

653 This isn't to say that anthropogenic changes won't result in major changes in community

654 structure and biogeography; migrations and assemblage shifts during OAEs and the PETM indicate that

655 the potential for local changes which may cascade through other trophic levels and alter ecosystem

656 function. Indeed, planktic foraminifera assemblages are already shifting poleward due to warming

657 (Jonkers et al., 2019), as are diatoms and dinoflagellates (Barton et al., 2016). The shift from greenhouse

658 to icehouse at the E-O boundary resulted in a significant decline in tropical and temperate plankton

659 diversity; will a shift back toward greenhouse conditions eventually drive an extinction of high latitude

660 plankton (Lazarus et al., 2014)? There is no good analog for this in the paleontological record. Moreover,

661 warming is expected to cause a >20% decline in primary productivity (Moore et al., 2018), likely

662 resulting in additional changes in plankton community structure (and reduced carbon sequestration,

663 fisheries declines, etc.).

4.2 Next Steps

664

665　　　　One of the most important takeaways from this review should be the need for detailed, robust

666　　records of species-level diversity of siliceous and organic-walled microfossil groups. Planktic

667　　foraminifera and calcareous nannoplankton are very well represented from outcrops and deep sea cores,

668　　and so have better constrained histories extending back to the Mesozoic, but the lack of similar records of

669　　other groups limits our ability to fully reconstruct ecological trends in the plankton. Even among the

670　　calcareous plankton, high resolution records tend to focus on events. This is understandable, but means

671　　we have a much poorer understanding of intervals of relative stability and what drives "background"

672　　turnover in these groups.

673　　　　Another key unknown is the response of non-fossilizing plankton to the events discussed here.

674　　Very little work has been done reconstructing the abundance or diversity of other autotrophs like

675　　cyanobacteria and archaea in the past. For example, following the K-Pg, calcareous nannoplankton

676　　declined severely, but food supply to the deep sea remained relatively constant (Culver, 2003; Alegret et

677　　al., 2012). We may assume that non-fossilizing phytoplankton became more abundant at this time, but

678　　there is very little evidence for or against this hypothesis. Sepulveda et al. (2009) showed blooms of non-

679　　fossilizing phytoplankton just about the K-Pg boundary in the Fish Clay of Denmark, but that is the only

680　　such record from this time, and the K-Pg is probably the best studied mass extinction in this regard.

681　　Moreover, what about non-fossilizing zooplankton, or nektonic organisms? The collapse of the marine

682　　food web is the primary hypothesis for the extinction of marine macrofauna like ammonites, plesiosaurs,

683　　and mosasaurs at the K-Pg, but we don't know what the middle step in that extinction was. Did jellyfish

684　　bloom in the earliest Danian? What about during OAEs, or the PETM? If they did bloom, what did this

685　　mean for food webs and the biological pump? Decades of careful research on mineralizing plankton

686　　diversity and ecology has led to a composite dataset that, while still open to improvement, has provided a

687　　uniquely detailed picture of evolution and extinction in the pelagic realm since the Mesozoic. Such

688　　detailed reconstructions may never be possible for non-mineralizing plankton, but those organisms are an

689   integral part of the modern open-ocean ecosystem and even minor improvements in their paleo record

690   would greatly improve our knowledge of the ancient oceans.

691   **Acknowledgements**

697

698   **Figures**
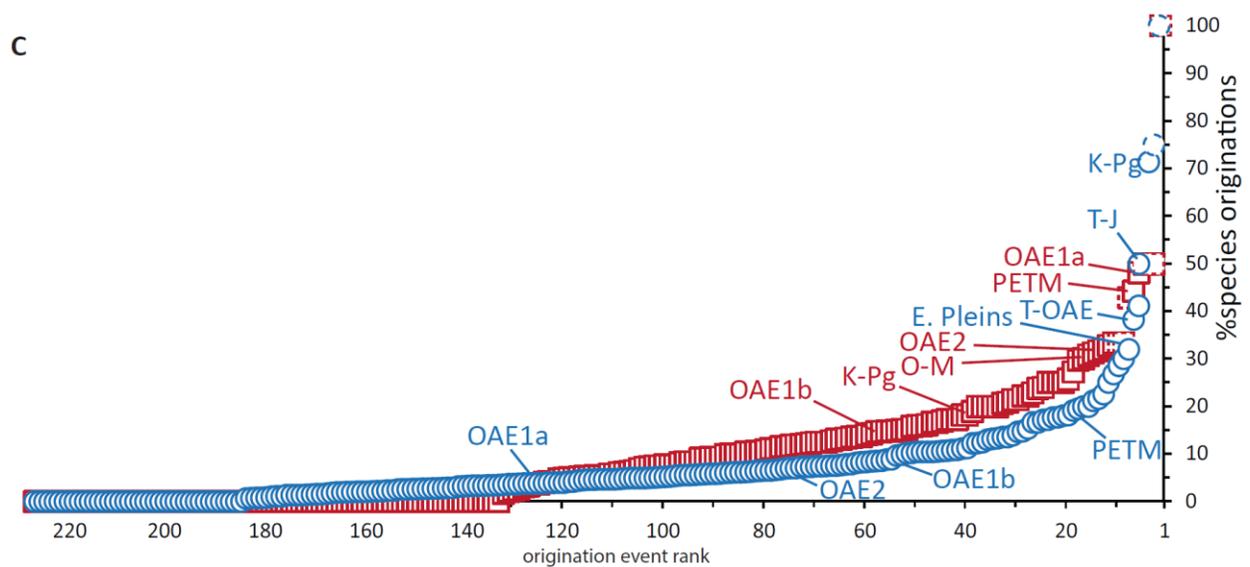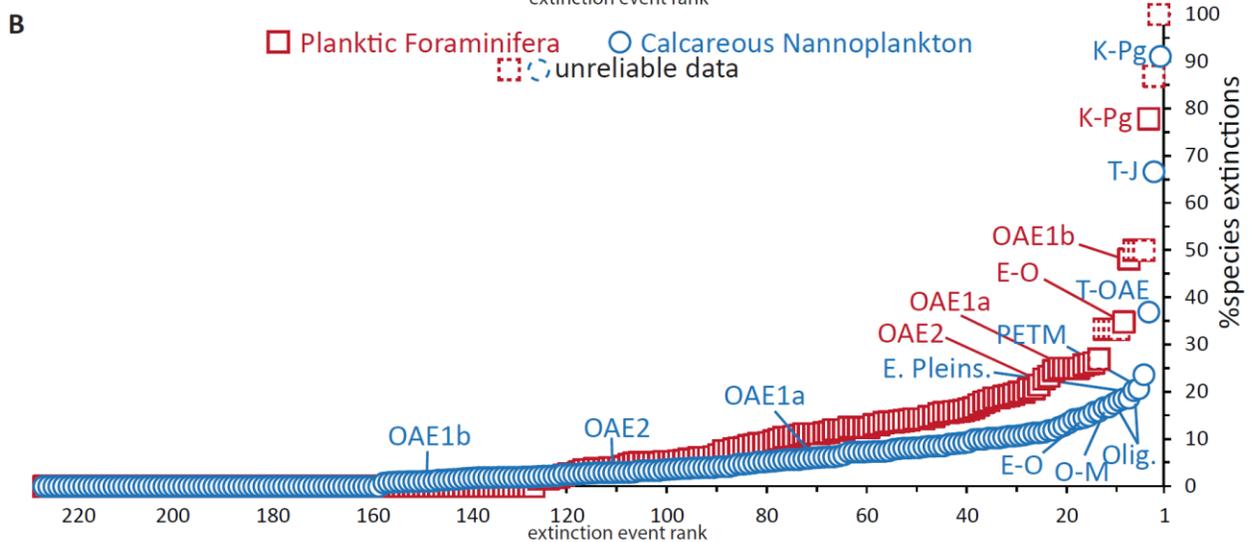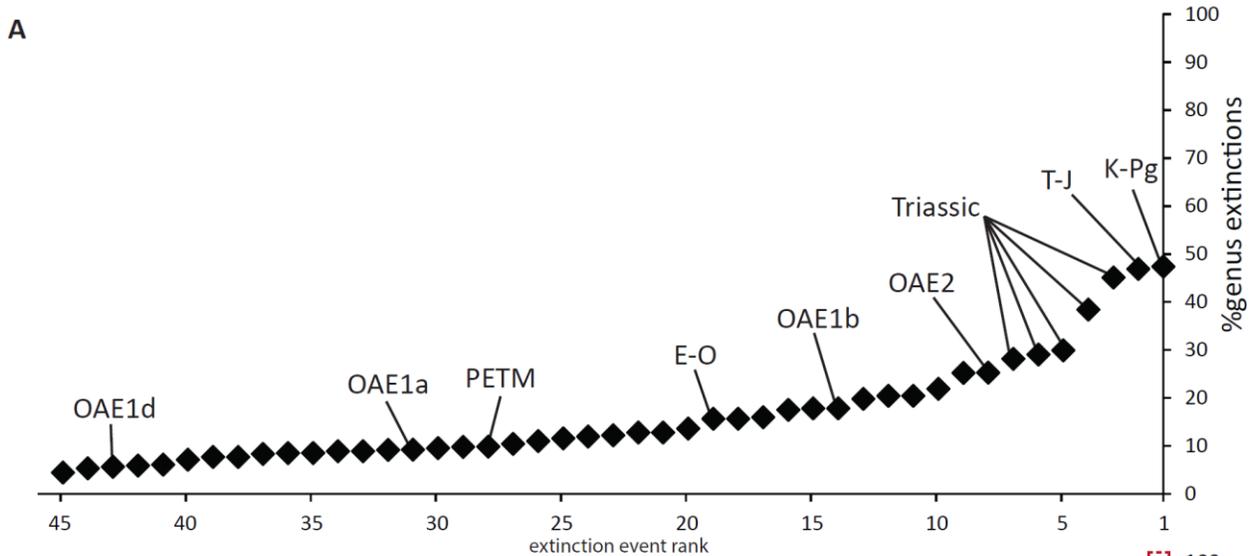
700 **Figure 1.** (A) Extinction rates of all marine genera binned at the stage level and ranked highest (right) to

701 lowest (left) from Bambach et al. (2004). (B) Ranked extinctions and (C) ranked originations of

702 calcareous nannoplankton and planktic foraminifera species binned at 1 myr time intervals this work. The

703 x-axis is the rank of each bin, with 1 being the highest. Outliers in the plankton caused by low diversity

704 (e.g., an extinction where 1 out of 3 total species go extinct, which happened 4 times in the planktic

705 foraminifera, ranked just below the E-O Boundary on part B) are represented by dashed circles/squares.

706 K-Pg: Cretaceous-Paleogene boundary; T-J: Triassic-Jurassic boundary; OAE: Oceanic Anoxic Event; E-

707 O: Eocene-Oligocene boundary; PETM: Paleocene-Eocene Thermal Maximum; T-OAE: Toarcian OAE;

708 E. Pleins: Early Pleinsbachian. See Appendix for full ranked list.

709

32
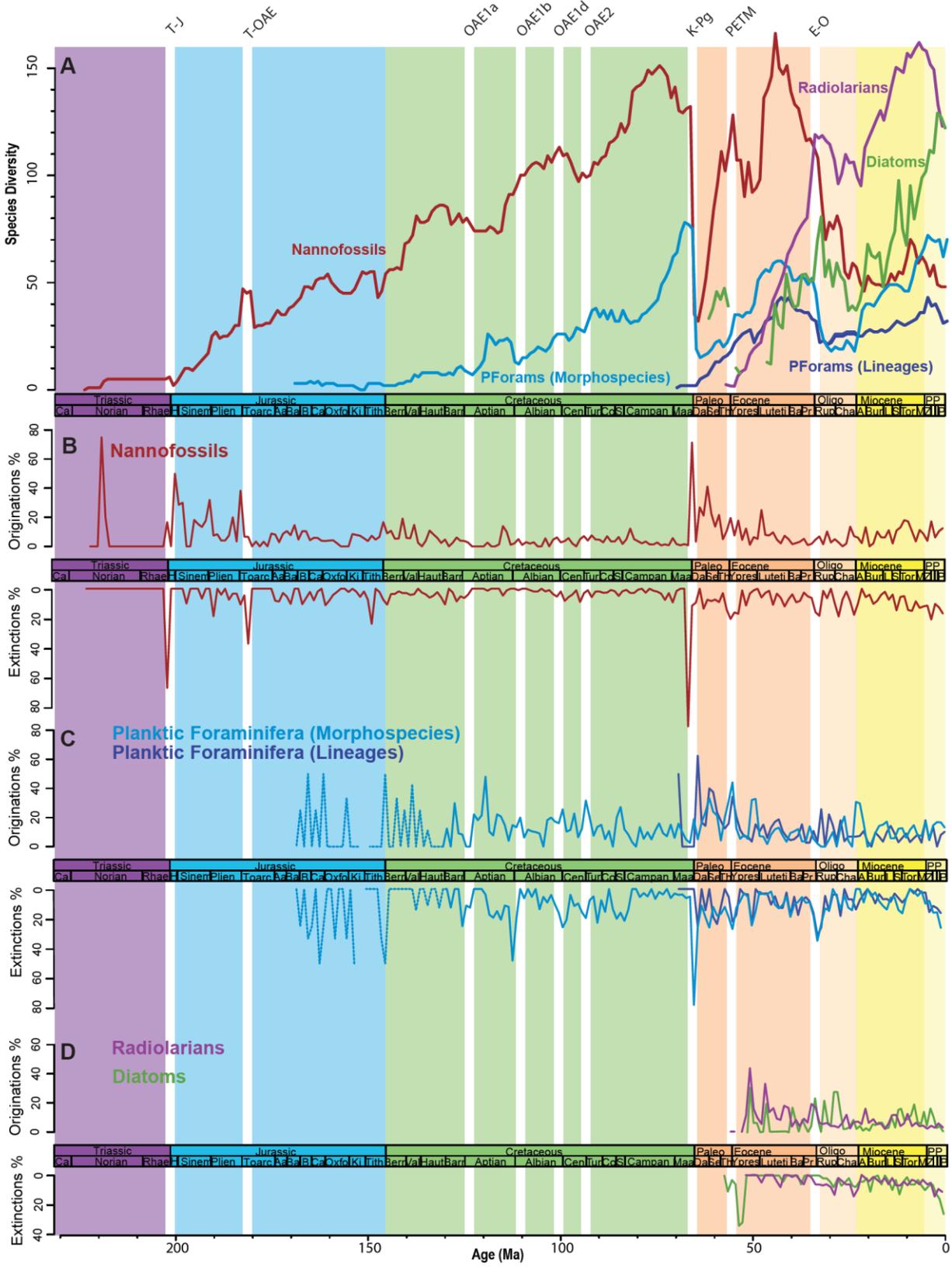
Figure 2. (A) Species diversity of calcareous nannoplankton and planktic foraminifera from the Mesozoic to Recent, and of Diatoms and Radiolarians from the Paleocene to the Recent. Rates of origination (top) and extinction (bottom) of (B) calcareous nannoplankton, (C) planktic foraminifera, and (D) radiolarians and diatoms. 100% originations and extinctions are omitted; the Jurassic and early Cretaceous record of planktic foraminifera extinction and origination is dashed to indicate that they are likely artifacts of low diversity and poor records. Events discussed in this paper are highlighted with white lines (see Figure 1 caption for abbreviations).

REFERENCES

Agnini, C. et al. (2014) Biozonation and biochronology of Paleogene calcareous nannofossils from low and middle latitudes. Newsletters on Stratigraphy. 47, 131–181.

Alegret, L., Arenillas, I., Arz, J. A., & Molina, E. (2004). Foraminiferal event-stratigraphy across the Cretaceous/Paleogene boundary. *Neues Jahrb. Geol. Paläontol. Abh.*, *231*, 25-50.

Alegret, L., Thomas, E., & Lohmann, K. C. (2012). End-Cretaceous marine mass extinction not caused by productivity collapse. *Proceedings of the National Academy of Sciences*, *109*(3), 728-732.

Alroy, J. (2008). Dynamics of origination and extinction in the marine fossil record. *Proceedings of the National Academy of Sciences*, *105*(Supplement 1), 11536-11542.

Alvarez, L. W., Alvarez, W., Asaro, F., & Michel, H. V. (1980). Extraterrestrial cause for the Cretaceous-Tertiary extinction. *Science*, *208*(4448), 1095-1108.

Alvarez, S. A., Gibbs, S. J., Bown, P. R., Kim, H., Sheward, R. M., & Ridgwell, A. (2019). Diversity decoupled from ecosystem function and resilience during mass extinction recovery. *Nature*, 1-4.

Amédro, F., 1992, L'Albien du Bassin Anglo-Parisien: ammonites, zonation phylétique, séquences: Bulletin des Centres de Recherches Exploration-Production, Elf Aquitaine, v. 16, p. 187–233.

Arenillas, I., Arz, J. A., Molina, E., & Dupuis, C. (2000). An independent test of planktic foraminiferal turnover across the Cretaceous/Paleogene (K/P) boundary at El Kef, Tunisia; catastrophic mass extinction and possible survivorship. *Micropaleontology*, *46*(1), 31-49.

Artemieva, N., & Morgan, J. (2017). Quantifying the release of climate-active gases by large meteorite impacts with a case study of Chicxulub. *Geophysical Research Letters*, *44*(20), 10-180.

Arthur, M. A., & Natland, J. H. (1979). Carbonaceous sediments in the North and South Atlantic: The role of salinity in stable stratification of Early Cretaceous basins. *Deep drilling results in the Atlantic Ocean: continental margins and paleoenvironment*, *3*, 375-401.

743   Arthur, M. A., & Schlanger, S. O. (1979). Cretaceous. *AAPG bulletin*, *63*(6), 870-885.

744   Aubry, M. P. (1998). Early Paleogene calcareous nannoplankton evolution: a tale of climatic
745   amelioration. *Late Paleocene-Early Eocene climatic and biotic events in the marine and*
746   *terrestrial records*, 158-203.

747   Bambach, R. K., Knoll, A. H., & Wang, S. C. (2004). Origination, extinction, and mass depletions of
748   marine diversity. *Paleobiology*, *30*(4), 522-542.

749   Barnosky, A. D., Hadly, E. A., Maurer, B. A., & Christie, M. I. (2001). Temperate terrestrial
750   vertebrate faunas in North and South America: interplay of ecology, evolution, and
751   geography with biodiversity. *Conservation Biology*, *15*(3), 658-674.

752   Barnosky, A. D., et al. (2011). Has the Earth's sixth mass extinction already
753   arrived? *Nature*, *471*(7336), 51.

754   Barton, A. D., Irwin, A. J., Finkel, Z. V., & Stock, C. A. (2016). Anthropogenic climate change
755   drives shift and shuffle in North Atlantic phytoplankton communities. *Proceedings of the*
756   *National Academy of Sciences*, *113*(11), 2964-2969.

757   Beerling, D. J., & Berner, R. A. (2002). Biogeochemical constraints on the Triassic-Jurassic boundary
758   carbon cycle event. *Global Biogeochemical Cycles*, *16*(3), 10-1.

759   Birch, H. S., Coxall, H. K., & Pearson, P. N. (2012). Evolutionary ecology of Early Paleocene
760   planktonic foraminifera: size, depth habitat and symbiosis. *Paleobiology*, *38*(3), 374-390.

761   Birch, H. S., Coxall, H. K., Pearson, P. N., Kroon, D., & Schmidt, D. N. (2016). Partial collapse of
762   the marine carbon pump after the Cretaceous-Paleogene boundary. *Geology*, *44*(4), 287-290.

763   Bown, P. R., Lees, J. A., & Young, J. R. (2004). Calcareous nannoplankton evolution and diversity
764   through time. In *Coccolithophores* (pp. 481-508). Springer, Berlin, Heidelberg.

765   Bown, P. R. (2005). Calcareous nannoplankton evolution: a tale of two
766   oceans. *Micropaleontology*, *51*(4), 299-308.

767   Bown, P. Selective calcareous nannoplankton survivorship at the Cretaceous-Tertiary boundary.
768   Geology 33, 653–656 (2005).

769   Bown, P., & Pearson, P. (2009). Calcareous plankton evolution and the Paleocene/Eocene thermal
770   maximum event: New evidence from Tanzania. *Marine Micropaleontology*, *71*(1-2), 60-70.

771   Bralower, T. J., & Self-Trail, J. M. (2016). Nannoplankton malformation during the Paleocene-
772   Eocene Thermal Maximum and its paleoecological and paleoceanographic
773   significance. *Paleoceanography*, *31*(10), 1423-1439.

774   Browning, E. L., & Watkins, D. K. (2008). Elevated primary productivity of calcareous
775   nannoplankton associated with ocean anoxic event 1b during the Aptian/Albian transition
776   (Early Cretaceous). *Paleoceanography and Paleoclimatology*, *23*(2).

777   Brugger, J., Feulner, G., & Petri, S. (2017). Baby, it's cold outside: climate model simulations of the
778   effects of the asteroid impact at the end of the Cretaceous. *Geophysical Research*
779   *Letters*, *44*(1), 419-427.

Cohen AS, Coe AL, Harding SM, Schwark L (2004). Osmium isotope evidence for the regulation of atmospheric CO2 by continental weathering. Geology 32(2):157–160.

Coxall, H. K., Wilson, P. A., Pälike, H., Lear, C. H., & Backman, J. (2005). Rapid stepwise onset of Antarctic glaciation and deeper calcite compensation in the Pacific Ocean. *Nature*, *433*(7021), 53.

Coxall, H. K., D'Hondt, S., & Zachos, J. C. (2006). Pelagic evolution and environmental recovery after the Cretaceous-Paleogene mass extinction. *Geology*, *34*(4), 297-300.

Cramer, B. S., Toggweiler, J. R., Wright, J. D., Katz, M. E., & Miller, K. G. (2009). Ocean overturning since the Late Cretaceous: Inferences from a new benthic foraminiferal isotope compilation. *Paleoceanography*, *24*(4).

Culver, S. J. (2003). Benthic foraminifera across the Cretaceous–Tertiary (K–T) boundary: a review. *Marine Micropaleontology*, *47*(3-4), 177-226.

D'Hondt, S., & Keller, G. (1991). Some patterns of planktic foraminiferal assemblage turnover at the Cretaceous-Tertiary boundary. *Marine Micropaleontology*, *17*(1-2), 77-118.

D'hondt, S., Donaghay, P., Zachos, J. C., Luttenberg, D., & Lindinger, M. (1998). Organic carbon fluxes and ecological recovery from the Cretaceous-Tertiary mass extinction. *Science*, *282*(5387), 276-279.

D'Hondt, S. (2005). Consequences of the Cretaceous/Paleogene mass extinction for marine ecosystems. *Annu. Rev. Ecol. Evol. Syst.*, *36*, 295-317.

DeConto, R. M., & Pollard, D. (2003). Rapid Cenozoic glaciation of Antarctica induced by declining atmospheric CO 2. *Nature*, *421*(6920), 245.

Doney, S. C., Balch, W. M., Fabry, V. J., & Feely, R. A. (2009). Ocean acidification: a critical emerging problem for the ocean sciences. *Oceanography*, *22*(4), 16-25.

Edgar, K. M., Bohaty, S. M., Gibbs, S. J., Sexton, P. F., Norris, R. D., & Wilson, P. A. (2013). Symbiont 'bleaching' in planktic foraminifera during the Middle Eocene Climatic Optimum. *Geology*, *41*(1), 15-18.

Erba, E. (1994). Nannofossils and superplumes: the early Aptian "nannoconid crisis". *Paleoceanography*, *9*(3), 483-501.

Erba, E., Bottini, C., Weissert, H. J., & Keller, C. E. (2010). Calcareous nannoplankton response to surface-water acidification around Oceanic Anoxic Event 1a. *Science*, *329*(5990), 428-432.

Erba, E., Bottini, C., Faucher, G., Gambacorta, G., & Visentin, S. (2019). The response of calcareous nannoplankton to Oceanic Anoxic Events: The Italian pelagic record. *Bollettino della Società Paleontologica Italiana*, *58*(1), 51-71.

Erbacher, J., Thurow, J., & Littke, R. (1996). Evolution patterns of radiolaria and organic matter variations: A new approach to identify sea-level changes in mid-Cretaceous pelagic environments. *Geology*, *24*(6), 499-502.

816   Erbacher, J. V. J. T., & Thurow, J. (1997). Influence of oceanic anoxic events on the evolution of
817   mid-Cretaceous radiolaria in the North Atlantic and western Tethys. *Marine*
818   *Micropaleontology*, *30*(1-3), 139-158.

819   Ezard, T. H., Aze, T., Pearson, P. N., & Purvis, A. (2011). Interplay between changing climate and
820   species' ecology drives macroevolutionary dynamics. *Science*, *332*(6027), 349-351.

821   Falkowski, P. G., Katz, M. E., Knoll, A. H., Quigg, A., Raven, J. A., Schofield, O., & Taylor, F. J. R.
822   (2004). The evolution of modern eukaryotic phytoplankton. *science*, *305*(5682), 354-360.

823   Fraass, A. J., Kelly, D. C., & Peters, S. E. (2015). Macroevolutionary history of the planktic
824   foraminifera. *Annual Review of Earth and Planetary Sciences*, *43*, 139-166.

825   Friedrich, O., Norris, R. D., & Erbacher, J. (2012). Evolution of middle to Late Cretaceous oceans—a
826   55 my record of Earth's temperature and carbon cycle. *Geology*, *40*(2), 107-110.

827   Funakawa, S., Nishi, H., Moore, T. C., & Nigrini, C. A. (2006). Radiolarian faunal turnover and
828   paleoceanographic change around Eocene/Oligocene boundary in the central equatorial
829   Pacific, ODP Leg 199, Holes 1218A, 1219A, and 1220A. *Palaeogeography,*
830   *Palaeoclimatology, Palaeoecology*, *230*(3-4), 183-203.

831   Gambacorta, G., Bersezio, R., Weissert, H., & Erba, E. (2016). Onset and demise of Cretaceous
832   oceanic anoxic events: The coupling of surface and bottom oceanic processes in two pelagic
833   basins of the western Tethys. *Paleoceanography and Paleoclimatology*, *31*(6), 732-757.

834   Gibbs, S. J., Bown, P. R., Sessa, J. A., Bralower, T. J., & Wilson, P. A. (2006a). Nannoplankton
835   extinction and origination across the Paleocene-Eocene Thermal
836   Maximum. *Science*, *314*(5806), 1770-1773.

837   Gibbs, S. J., Bralower, T. J., Bown, P. R., Zachos, J. C., & Bybell, L. M. (2006b). Shelf and open-
838   ocean calcareous phytoplankton assemblages across the Paleocene-Eocene Thermal
839   Maximum: Implications for global productivity gradients. *Geology*, *34*(4), 233-236.

840   Greene, S. E., Martindale, R. C., Ritterbush, K. A., Bottjer, D. J., Corsetti, F. A., & Berelson, W. M.
841   (2012). Recognising ocean acidification in deep time: An evaluation of the evidence for
842   acidification across the Triassic-Jurassic boundary. *Earth-Science Reviews*, *113*(1-2), 72-93.

843   Hart, M. B. (1980). The recognition of mid-Cretaceous sea-level changes by means of
844   foraminifera. *Cretaceous Research*, *1*(4), 289-297.

845   Hart, M. B., Hylton, M. D., Oxford, M. J., Price, G. D., Hudson, W., & Smart, C. W. (2003). The
846   search for the origin of the planktic Foraminifera. *Journal of the Geological Society*, *160*(3),
847   341-343.

848   Henehan, M. J., Hull, P. M., Penman, D. E., Rae, J. W., & Schmidt, D. N. (2016). Biogeochemical
849   significance of pelagic ecosystem function: an end-Cretaceous case study. *Philosophical*
850   *Transactions of the Royal Society B: Biological Sciences*, *371*(1694), 20150510.

851   Henehan, M. J., Ridgewell, A., Thomas, E., Zhang, S., Alegret, L., Schmidt, D. N., Rae, J. W. B.,
852   Witts, J. D., Landman, N. H., Green, S. E., Huber, B. T., Super, J. R., Planavsky, N. J., &
853   Hull, P. M. (2019). Rapid ocean acidification and protracted Earth system recovery followed

854 the end-Cretaceous Chicxulub impact. *Proceedings of the National Academy of Sciences*.
855 https://www.pnas.org/cgi/doi/10.1073/pnas.1905989116

856 Hildebrand, A. R., Penfield, G. T., Kring, D. A., Pilkington, M., Camargo Z, A., Jacobsen, S. B., &
857 Boynton, W. V. (1991). Chicxulub crater: a possible Cretaceous/Tertiary boundary impact
858 crater on the Yucatan Peninsula, Mexico. *Geology*, *19*(9), 867-871.

859 Hollis, C. J., & Strong, C. P. (2003). Biostratigraphic review of the Cretaceous/Tertiary boundary
860 transition, mid-Waipara river section, North Canterbury, New Zealand. *New Zealand Journal*
861 *of Geology and Geophysics*, *46*(2), 243-253.

862 Hönisch, B., Ridgwell, A., Schmidt, D. N., Thomas, E., Gibbs, S. J., Sluijs, A., ... & Kiessling, W.
863 (2012). The geological record of ocean acidification. *science*, *335*(6072), 1058-1063.

864 Hsü, K. J., & Mckenzie, J. A. (1985). A "Strangelove" ocean in the earliest Tertiary. *The Carbon*
865 *Cycle and Atmospheric CO2: Natural Variations Archean to Present*, *32*, 487-492.

866 Huber, B. T., Leckie, R. M., Norris, R. D., Bralower, T. J., & CoBabe, E. (1999). Foraminiferal
867 assemblage and stable isotopic change across the Cenomanian-Turonian boundary in the
868 subtropical North Atlantic. *The Journal of Foraminiferal Research*, *29*(4), 392-417.

869 Huber, B. T., Olsson, R. K., & Pearson, P. N. (2006). Taxonomy, biostratigraphy, and phylogeny of
870 Eocene microperforate planktonic foraminifera (Jenkinsina, Cassigerinelloita,
871 Chiloguembelina, Streptochilus, Zeauvigerina, Tenuitella, and Cassigerinella) and
872 problematica (Dipsidripella). *Cushman Foundation of Foraminiferal Research, Special*
873 *Publication*, *41*, 461-508.

874 Huber, B. T., & Leckie, R. M. (2011). Planktic foraminiferal species turnover across deep-sea
875 Aptian/Albian boundary sections. *The Journal of Foraminiferal Research*, *41*(1), 53-95.

876 Hull, P. M., & Norris, R. D. (2011). Diverse patterns of ocean export productivity change across the
877 Cretaceous-Paleogene boundary: New insights from biogenic barium. *Paleoceanography and*
878 *Paleoclimatology*, *26*(3).

879 Hull, P. M., Norris, R. D., Bralower, T. J., & Schueth, J. D. (2011). A role for chance in marine
880 recovery from the end-Cretaceous extinction. *Nature Geoscience*, *4*(12), 856.

881 Ito, T., Minobe, S., Long, M. C., & Deutsch, C. (2017). Upper ocean O2 trends: 1958–
882 2015. *Geophysical Research Letters*, *44*(9), 4214-4223.

883 Jablonski, D. in *Extinction Rates* (eds Lawton, J. H. & May, R. M.) 25–44 (Oxford Univ. Press,
884 Oxford, 1995).

885 Jenkyns, H. C. (1995). Carbon-isotope stratigraphy and paleoceanographic significance of the Lower
886 Cretaceous shallow-water carbonates of Resolution Guyot, Mid-Pacific Mountains.
887 In *Proceedings of the Ocean Drilling Program, Scientific Results* (Vol. 143, pp. 99-104).
888 Ocean Drilling Program, College Station.

889 Jenkyns, H. C. (2010). Geochemistry of oceanic anoxic events. *Geochemistry, Geophysics,*
890 *Geosystems*, *11*(3).

891   Jiang, S., Bralower, T. J., Patzkowsky, M. E., Kump, L. R., & Schueth, J. D. (2010). Geographic
892   controls on nannoplankton extinction across the Cretaceous/Palaeogene boundary. *Nature*
893   *Geoscience*, *3*(4), 280.

894   Jones, H. L., Lowery, C. M., & Bralower, T. J. (2019). Delayed calcareous nannoplankton boom-bust
895   successions in the earliest Paleocene Chicxulub (Mexico) impact crater. *Geology*.

896   Jonkers, L., Hillebrand, H., & Kucera, M. (2019). Global change drives modern plankton
897   communities away from the pre-industrial state. *Nature*, 1.

898   Kaiho, K., Kajiwara, Y., Tazaki, K., Ueshima, M., Takeda, N., Kawahata, H., ... & Lamolda, M. A.
899   (1999). Oceanic primary productivity and dissolved oxygen levels at the Cretaceous/Tertiary
900   boundary: their decrease, subsequent warming, and recovery. *Paleoceanography and*
901   *Paleoclimatology*, *14*(4), 511-524.

902   Kamikuri, S. I., & Wade, B. S. (2012). Radiolarian magnetobiochronology and faunal turnover across
903   the middle/late Eocene boundary at Ocean Drilling Program Site 1052 in the western North
904   Atlantic Ocean. *Marine Micropaleontology*, *88*, 41-53.

905   Kelly, D. C., Bralower, T. J., & Zachos, J. C. (1998). Evolutionary consequences of the latest
906   Paleocene thermal maximum for tropical planktonic foraminifera. *Palaeogeography,*
907   *Palaeoclimatology, Palaeoecology*, *141*(1-2), 139-161.

908   Kennett, J. P. (1977). Cenozoic evolution of Antarctic glaciation, the circum-Antarctic Ocean, and
909   their impact on global paleoceanography. *Journal of geophysical research*, *82*(27), 3843-
910   3860.

911   Kirchner, J. W., & Weil, A. (2000). Delayed biological recovery from extinctions throughout the
912   fossil record. *Nature*, *404*(6774), 177.

913   Knoll, A. H., & Follows, M. J. (2016). A bottom-up perspective on ecosystem change in Mesozoic
914   oceans. *Proceedings of the Royal Society B: Biological Sciences*, *283*(1841), 20161755.

915   Kidder, D. L., & Erwin, D. H. (2001). Secular distribution of biogenic silica through the Phanerozoic:
916   comparison of silica-replaced fossils and bedded cherts at the series level. *The Journal of*
917   *Geology*, *109*(4), 509-522.

918   Kiessling, W., & Danelian, T. (2011). Trajectories of Late Permian–Jurassic radiolarian extinction
919   rates: no evidence for an end-Triassic mass extinction. *Fossil Record*, *14*(1), 95-101.

920   Lamolda, M. A., Melinte, M. C., & Kaiho, K. (2005). Nannofloral extinction and survivorship across
921   the K/T boundary at Caravaca, southeastern Spain. *Palaeogeography, Palaeoclimatology,*
922   *Palaeoecology*, *224*(1-3), 27-52.

923   Lazarus, D., Barron, J., Renaudie, J., Diver, P., & Türke, A. (2014). Cenozoic planktonic marine
924   diatom diversity and correlation to climate change. *PLoS One*, *9*(1), e84857.

925   Lear, C. H., Bailey, T. R., Pearson, P. N., Coxall, H. K., & Rosenthal, Y. (2008). Cooling and ice
926   growth across the Eocene-Oligocene transition. *Geology*, *36*(3), 251-254.

927   Leckie, R. M. (1987). Paleoecology of mid-Cretaceous planktonic foraminifera: a comparison of open
928   ocean and epicontinental sea assemblages. *Micropaleontology*, 164-176.

929 Leckie, R. M. (1989). A paleoceanographic model for the early evolutionary history of planktonic
930   foraminifera. *Palaeogeography, Palaeoclimatology, Palaeoecology*, *73*(1-2), 107-138.

931 Leckie, R. M., Yuretich, R. F., West, O. L., Finkelstein, D., & Schmidt, M. (1998). Paleoceanography
932   of the southwestern Western Interior Sea during the time of the Cenomanian-Turonian
933   boundary (Late Cretaceous).

934 Leckie, R. M., Bralower, T. J., & Cashman, R. (2002). Oceanic anoxic events and plankton evolution:
935   Biotic response to tectonic forcing during the mid-Cretaceous. *Paleoceanography*, *17*(3), 13-
936   1.

937 Leckie, R. M. (2009). Seeking a better life in the plankton. *Proceedings of the National Academy of
938   Sciences*, *106*(34), 14183-14184.

939 Lowery, C. M., Leckie, R. M., & Sageman, B. B. (2017). Micropaleontological evidence for redox
940   changes in the OAE3 interval of the US Western Interior: Global vs. local
941   processes. *Cretaceous Research*, *69*, 34-48.

942 Lowery, C. M., et al., (2018). Rapid recovery of life at ground zero of the end-Cretaceous mass
943   extinction. *Nature*, *558*(7709), 288.

944 Lowery, C. M., Morgan, J. V., Gulick, S. P., Bralower, T. J., & Christeson, G. L. (2019). Ocean
945   Drilling Perspectives on Meteorite Impacts. *Oceanography*, *32*(1), 120-134.

946 Lowery, C. M., & Fraass, A. J. (2019). Morphospace expansion paces taxonomic diversification after
947   end Cretaceous mass extinction. *Nature ecology & evolution*, *3*(6), 900.

948 MacRae, R. A., Fensome, R. A., & Williams, G. L. (1996). Fossil dinoflagellate diversity,
949   originations, and extinctions and their significance. *Canadian Journal of Botany*, *74*(11),
950   1687-1694.

951 McAnena, A., et al. (2013). Atlantic cooling associated with a marine biotic crisis during the mid-
952   Cretaceous period. *Nature Geoscience*, *6*(7), 558.

953 McElwain, J. C., Beerling, D. J., & Woodward, F. I. (1999). Fossil plants and global warming at the
954   Triassic-Jurassic boundary. *Science*, *285*(5432), 1386-1390.

955 McElwain J. C., Wade-Murphy J., Hesselbo S. P. (2005). Changes in carbon dioxide during an
956   oceanic anoxic event linked to intrusion into Gondwana coals. *Nature* 435(7041), 479–482.

957 Meyer, K. M., Ridgwell, A., & Payne, J. L. (2016). The influence of the biological pump on ocean
958   chemistry: implications for long-term trends in marine redox chemistry, the global carbon
959   cycle, and marine animal ecosystems. *Geobiology*, *14*(3), 207-219.

960 Mizukami, T., Kaiho, K., & Oba, M. (2013). Significant changes in land vegetation and oceanic
961   redox across the Cretaceous/Paleogene boundary. *Palaeogeography, Palaeoclimatology,
962   Palaeoecology*, *369*, 41-47.

963 Monteiro, F. M., Pancost, R. D., Ridgwell, A., & Donnadieu, Y. (2012). Nutrients as the dominant
964   control on the spread of anoxia and euxinia across the Cenomanian-Turonian oceanic anoxic
965   event (OAE2): Model-data comparison. *Paleoceanography*, *27*(4).

966   Moore, J. K., et al. (2018). Sustained climate warming drives declining marine biological
967   productivity. *Science*, *359*(6380), 1139-1143.

968   Musavu-Moussavou, B., Danelian, T., Baudin, F., Coccioni, R., & Fröhlich, F. (2007). The
969   Radiolarian biotic response during OAE2. A high-resolution study across the Bonarelli level
970   at Bottaccione (Gubbio, Italy). *Revue de micropaléontologie*, *50*(3), 253-287.

971   Nederbragt, A. J., Fiorentino, A., & Klosowska, B. (2001). Quantitative analysis of calcareous
972   microfossils across the Albian–Cenomanian boundary oceanic anoxic event at DSDP Site 547
973   (North Atlantic). *Palaeogeography, Palaeoclimatology, Palaeoecology*, *166*(3-4), 401-421.

974   Olsson, R. K., Berggren, W. A., Hemleben, C. I., & Huber, B. T. (1999). Atlas of Paleocene
975   planktonic foraminifera. *Smithsonian contributions to Paleobiology*.

976   Ostrander, C. M., Owens, J. D., & Nielsen, S. G. (2017). Constraining the rate of oceanic
977   deoxygenation leading up to a Cretaceous Oceanic Anoxic Event (OAE-2:~ 94 Ma). *Science*

978   Pälike, H., Nishi, H., Lyle, M., Raffi, I., Klaus, A., Gamage, K., & Exp. 320 Scientists (2009).
979   Preliminary Reports of the Integrated Ocean Drilling Program Vol. 320, College Station, TX.

980   Pardo, A., Adatte, T., Keller, G., & Oberhänsli, H. (1999). Paleoenvironmental changes across the
981   Cretaceous–Tertiary boundary at Koshak, Kazakhstan, based on planktic foraminifera and
982   clay mineralogy. *Palaeogeography, Palaeoclimatology, Palaeoecology*, *154*(3), 247-273.

983   Parente, M., Frijia, G., Di Lucia, M., Jenkyns, H. C., Woodfine, R. G., & Baroncini, F. (2008).
984   Stepwise extinction of larger foraminifers at the Cenomanian-Turonian boundary: A shallow-
985   water perspective on nutrient fluctuations during Oceanic Anoxic Event 2 (Bonarelli
986   Event). *Geology*, *36*(9), 715-718.

987   Pereira, H. M., Navarro, L. M., & Martins, I. S. (2012). Global biodiversity change: the bad, the good,
988   and the unknown. *Annual Review of Environment and Resources*, *37*.

989   Penman, D. E., Hönisch, B., Zeebe, R. E., Thomas, E., & Zachos, J. C. (2014). Rapid and sustained
990   surface ocean acidification during the Paleocene-Eocene Thermal
991   Maximum. *Paleoceanography*, *29*(5), 357-369.

992   Petrizzo, M. R., Huber, B. T., & Wilson, P. A. (2005). Foraminiferal isotope record across the latest
993   Albian Oceanic Anoxic Event 1d at ODP Sites 1050 and 1052 (Blake Nose, western north
994   Atlantic). In *7th international Symposium on the Cretaceous*. Val-impressions.

995   Peti, L. & Thibault, N. (2017). Abundance and size changes in the calcareous nannofossil
996   Schizosphaerella – Relation to sea-level, the carbonate factory and palaeoenvironmental
997   change from the Sinemurian to earliest Toarcian of the Paris Basin. *Palaeogeography,*
998   *Palaeoclimatology, Palaeoecology*, 485, 271-282

999   Peti, L., Thibault, N., Clémence, M.-E., Korte, C., Dommergues, J-L., Bougeault, C., Pellenard, P.,
1000   Jelby, M.E., Ullmann, C.V. 2017. Sinemurian–Pliensbachian calcareous nannofossil
1001   biostratigraphy and organic carbon isotope stratigraphy in the Paris Basin: Calibration to the
1002   ammonite biozonation of NW Europe. *Palaeogeography, Palaeoclimatology, Palaeoecology,*
1003   *468,* 142-161.

Pratt, L. M., & Threlkeld, C. N. (1984). Stratigraphic significance of 13C/12C ratios in mid-Cretaceous rocks of the Western Interior, USA.

Premoli Silva, I., Erba, E., Salvini, G., Locatelli, C., & Verga, D. (1999). Biotic changes in Cretaceous oceanic anoxic events of the Tethys. *The Journal of Foraminiferal Research*, *29*(4), 352-370.

Silva, I. P., & Sliter, W. V. (1999). Cretaceous paleoceanography: evidence from planktonic foraminiferal evolution. *Special Papers-Geological Society of America*, 301-328.

Raffi, I., & De Bernardi, B. (2008). Response of calcareous nannofossils to the Paleocene–Eocene Thermal Maximum: Observations on composition, preservation and calcification in sediments from ODP Site 1263 (Walvis Ridge—SW Atlantic). *Marine Micropaleontology*, *69*(2), 119-138.

Raup, D. M., & Sepkoski, J. J. (1982). Mass extinctions in the marine fossil record. *Science*, *215*(4539), 1501-1503.

Renaudie., J., Drews, E.-L., and Böhne, S. (2018). The Paleocene record of marine diatroms in deep-sea sediments. *Fossil Record,* 21, 183-205.

Schaller, M. F., Wright, J. D., Kent, D. V., & Olsen, P. E. (2012). Rapid emplacement of the Central Atlantic Magmatic Province as a net sink for CO2. *Earth and Planetary Science Letters*, *323*, 27-39.

Scheibner, C., & Speijer, R. P. (2008). Late Paleocene–early Eocene Tethyan carbonate platform evolution—A response to long-and short-term paleoclimatic change. *Earth-science reviews*, *90*(3-4), 71-102.

Scher, H. D., & Martin, E. E. (2008). Oligocene deep water export from the North Atlantic and the development of the Antarctic Circumpolar Current examined with neodymium isotopes. *Paleoceanography and Paleoclimatology*, *23*(1).

Schlanger, S. O., & Jenkyns, H. C. (1976). Cretaceous oceanic anoxic events: causes and consequences. *Geologie en mijnbouw*, *55*(3-4).

Schulte, P., et al., (2010). The Chicxulub asteroid impact and mass extinction at the Cretaceous-Paleogene boundary. *Science*, *327*(5970), 1214-1218.

Schueth, J. D., Bralower, T. J., Jiang, S., & Patzkowsky, M. E. (2015). The role of regional survivor incumbency in the evolutionary recovery of calcareous nannoplankton from the Cretaceous/Paleogene (K/Pg) mass extinction. *Paleobiology*, *41*(4), 661-679.

Sepúlveda, J., Wendler, J. E., Summons, R. E., & Hinrichs, K. U. (2009). Rapid resurgence of marine productivity after the Cretaceous-Paleogene mass extinction. *Science*, *326*(5949), 129-132.

Sepúlveda, J., Alegret, L., Thomas, E., Haddad, E., Cao, C., & Summons, R. E. (2019). Stable isotope constraints on marine productivity across the Cretaceous–Paleogene mass extinction. *Paleoceanography and Paleoclimatology*.

Sims, P. A., Mann, D. G., & Medlin, L. K. (2006). Evolution of the diatoms: insights from fossil, biological and molecular data. *Phycologia*, *45*(4), 361-402.

Sluijs, A., Schouten, S., Pagani, M., Woltering, M., Brinkhuis, H., Damsté, J. S. S., ... & Matthiessen, J. (2006). Subtropical Arctic Ocean temperatures during the Palaeocene/Eocene thermal maximum. *Nature*, *441*(7093), 610.

Sluijs, A., & Brinkhuis, H. (2009). A dynamic climate and ecosystem state during the Paleocene-Eocene Thermal Maximum: inferences from dinoflagellate cyst assemblages on the New Jersey Shelf. *Biogeosciences*, *6*(8), 1755-1781.

Smit, J., & Hertogen, J. (1980). An extraterrestrial event at the Cretaceous–Tertiary boundary. *Nature*, *285*(5762), 198.

Smit, J., Silver, L. T., & Schultz, P. H. (1982). Extinction and evolution of planktonic foraminifera after a major impact at the Cretaceous/Tertiary boundary. In *Geological implications of impacts of large asteroids and comets on the earth* (Vol. 190, pp. 329-352). Geol. Soc. Am. Spec. Paper.

Snow, L. J., Duncan, R. A., & Bralower, T. J. (2005). Trace element abundances in the Rock Canyon Anticline, Pueblo, Colorado, marine sedimentary section and their relationship to Caribbean plateau construction and oxygen anoxic event 2. *Paleoceanography and Paleoclimatology*, *20*(3).

Spencer-Cervato, C. (1999). The Cenozoic deep sea microfossil record: explorations of the DSDP/ODP sample set using the Neptune database. *Palaeontologia electronica*, *2*(2), 270.

Speijer, R., Scheibner, C., Stassen, P., & Morsi, A. M. M. (2012). Response of marine ecosystems to deep-time global warming: A synthesis of biotic patterns across the Paleocene-Eocene thermal maximum (PETM). *Austrian Journal of Earth Sciences*, *105*(1), 6-16.

Von Strandmann, P. A. P., Jenkyns, H. C., & Woodfine, R. G. (2013). Lithium isotope evidence for enhanced weathering during Oceanic Anoxic Event 2. *Nature Geoscience*, *6*(8), 668.

Tappan, H., & Loeblich Jr, A. R. (1988). Foraminiferal evolution, diversification, and extinction. *Journal of Paleontology*, 695-714.

Toon, O. B., Zahnle, K., Morrison, D., Turco, R. P., & Covey, C. (1997). Environmental perturbations caused by the impacts of asteroids and comets. *Reviews of Geophysics*, *35*(1), 41-78.

Tarduno, J. A., Sliter, W. V., Kroenke, L., Leckie, M., Mayer, H., Mahoney, J. J., ... & Winterer, E. L. (1991). Rapid formation of Ontong Java Plateau by Aptian mantle plume volcanism. *Science*, *254*(5030), 399-403.

Thomas, E., & Shackleton, N. J. (1996). The Paleocene-Eocene benthic foraminiferal extinction and stable isotope anomalies. *Geological Society, London, Special Publications*, *101*(1), 401-441.

Trabucho Alexandre, J., Tuenter, E., Henstra, G. A., van der Zwan, K. J., van de Wal, R. S., Dijkstra, H. A., & de Boer, P. L. (2010). The mid-Cretaceous North Atlantic nutrient trap: black shales and OAEs. *Paleoceanography*, *25*(4).

Trubovitz, S., Lazarus, D., Renaudie, J., Noble, P. (2019) NEW CENSUS OF RADIOLARIAN COMMUNITIES IN THE EASTERN EQUATORIAL PACIFIC REVEALS UNPRECEDENTED BIODIVERSITY THROUGHOUT THE LATE NEOGENE, *in* 11th

1081   North American Paleontological Conference Program with Abstracts, *Paleobio*s, 36,
1082   Supplement 1, p. 350.

1083 Turgeon, S. C., & Creaser, R. A. (2008). Cretaceous oceanic anoxic event 2 triggered by a massive
1084   magmatic episode. *Nature*, *454*(7202), 323.

1085 Tyrrell, T., Merico, A., & McKay, D. I. A. (2015). Severity of ocean acidification following the end-
1086   Cretaceous asteroid impact. *Proceedings of the National Academy of Sciences*, *112*(21),
1087   6556-6561.

1088 Varol, O. Palaeocene calcareous nannofossil biostratigraphy. in Nannofossils and their Applications
1089   (eds. Crux, J. A. & van Heck, S. E.) 267–310 (Ellis Horwood, British Micropaleontological
1090   Society Series, 1989).

1091 Vermeij, G. J. (1977). The Mesozoic marine revolution: evidence from snails, predators and
1092   grazers. *Paleobiology*, *3*(3), 245-258.

1093 Wagreich, M. (2012). " OAE 3"-regional Atlantic organic carbon burial during the Coniacian-
1094   Santonian. *Climate of the Past*, *8*(5), 1447.

1095 Wang, T., Li, G., Aitchison, J. C., Ding, L., & Sheng, J. (2019). Evolution of mid-Cretaceous
1096   radiolarians in response to oceanic anoxic events in the eastern Tethys (southern Tibet,
1097   China). *Palaeogeography, Palaeoclimatology, Palaeoecology*, 109369.

1098 Watkins, D. K., & Bergen, J. A. (2003). Late Albian adaptive radiation in the calcareous nannofossil
1099   genus Eiffellithus. *Micropaleontology*, *49*(3), 231-251.

1100 Watkins, D. K., Cooper, M. J., & Wilson, P. A. (2005). Calcareous nannoplankton response to late
1101   Albian oceanic anoxic event 1d in the western North Atlantic. *Paleoceanography and
1102   Paleoclimatology*, *20*(2).

1103 Whitechurch, H., Montigny, R., Sevigny, J., Storey, M., & Salters, V. (1992). K-Ar and 40Ar-39Ar
1104   ages of central Kerguelen Plateau basalts. In *Proc. Ocean Drill. Program Sci. Results* (Vol.
1105   120, pp. 71-77).

1106 Witkowski, J., Bohaty, S. M., Edgar, K. M., & Harwood, D. M. (2014). Rapid fluctuations in mid-
1107   latitude siliceous plankton production during the Middle Eocene Climatic Optimum (ODP
1108   Site 1051, western North Atlantic). *Marine Micropaleontology*, *106*, 110-129.

1109 Witkowski, J., Bohaty, S. M., McCartney, K., & Harwood, D. M. (2012). Enhanced siliceous
1110   plankton productivity in response to middle Eocene warming at Southern Ocean ODP Sites
1111   748 and 749. *Palaeogeography, Palaeoclimatology, Palaeoecology*, *326*, 78-94.

1112 Wignall, P. B. (2001). Large igneous provinces and mass extinctions. *Earth-science reviews*, *53*(1-2),
1113   1-33.

1114 Wilson, P. A., & Norris, R. D. (2001). Warm tropical ocean surface and global anoxia during the mid-
1115   Cretaceous period. *Nature*, *412*(6845), 425.

1116 Zachos, J. C., Arthur, M. A., & Dean, W. E. (1989). Geochemical evidence for suppression of pelagic
1117   marine productivity at the Cretaceous/Tertiary boundary. *Nature*, *337*(6202), 61.

1118   Zachos, J. C., Quinn, T. M., & Salamy, K. A. (1996). High-resolution (104 years) deep-sea
1119   foraminiferal stable isotope records of the Eocene-Oligocene climate
1120   transition. *Paleoceanography and Paleoclimatology*, *11*(3), 251-266.

1121   Zachos, J., Pagani, M., Sloan, L., Thomas, E., & Billups, K. (2001). Trends, rhythms, and aberrations
1122   in global climate 65 Ma to present. *science*, *292*(5517), 686-693.

1123   Zachos, J. C., Röhl, U., Schellenberg, S. A., Sluijs, A., Hodell, D. A., Kelly, D. C., ... & McCarren,
1124   H. (2005). Rapid acidification of the ocean during the Paleocene-Eocene thermal
1125   maximum. *Science*, *308*(5728), 1611-1615.

1126   Zeebe, R. E., Zachos, J. C., & Dickens, G. R. (2009). Carbon dioxide forcing alone insufficient to
1127   explain Palaeocene–Eocene Thermal Maximum warming. *Nature Geoscience*, *2*(8), 576.

1128   Zeebe, R. E., Ridgwell, A., & Zachos, J. C. (2016). Anthropogenic carbon release rate unprecedented
1129   during the past 66 million years. *Nature Geoscience*, *9*(4), 325.