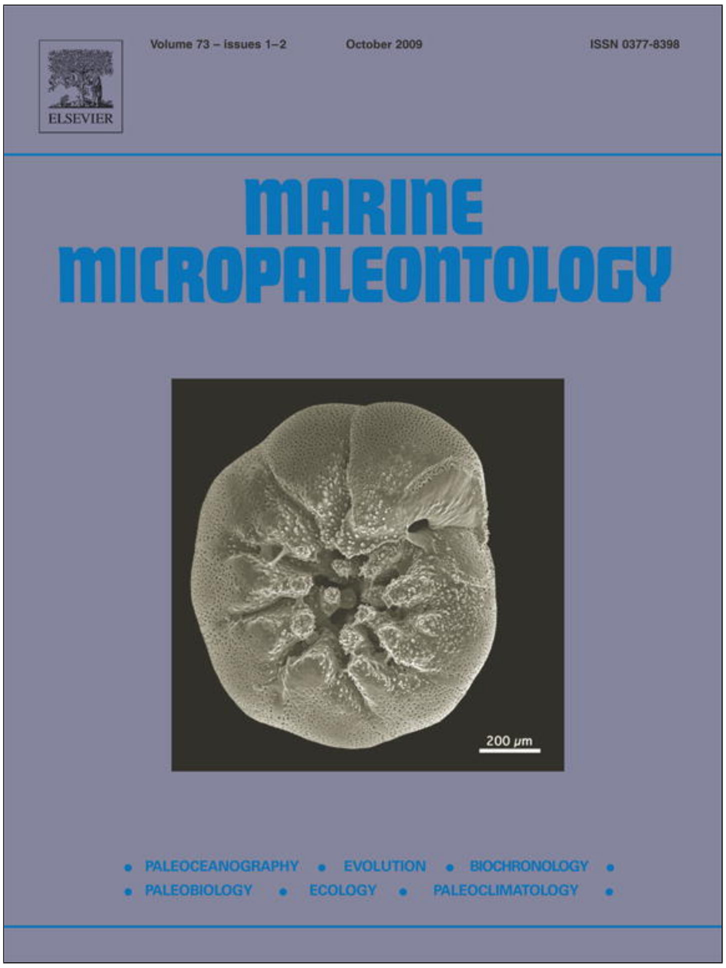
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Food supply to the seafloor in the Pacific Ocean after the Cretaceous/Paleogene boundary event

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ABSTRACT

Deep-sea benthic foraminifera show important but transient assemblage changes at the Cretaceous/Paleogene (K/Pg) boundary, when many biota suffered severe extinction. We quantitatively analyzed benthic foraminiferal assemblages from lower bathyal–upper abyssal (1500–2000 m) northwest Pacific ODP Site 1210 (Shatsky Rise) and compared the results with published data on assemblages at lower bathyal (~1500 m) Pacific DSDP Site 465 (Hess Rise) to gain insight in paleoecological and paleoenvironmental changes at that time.

At both sites, diversity and heterogeneity rapidly decreased across the K/Pg boundary, then recovered. Species assemblages at both sites show a similar pattern of turnover from the uppermost Maastrichtian into the lowermost Danian: 1) The relative abundance of buliminids (indicative of a generally high food supply) increases towards the uppermost Cretaceous, and peaks rapidly just above the K/Pg boundary, coeval with a peak in benthic foraminiferal accumulation rate (BFAR), a proxy for food supply. 2) A peak in relative abundance of *Stensioeina beccariiformis*, a cosmopolitan form generally more common at the middle than at the lower bathyal sites, occurs just above the buliminid peak. 3) The relative abundance of *Nuttallides truempyi*, a more oligotrophic form, decreases at the boundary, then increases above the peak in *Stensioeina beccariiformis*. The food supply to the deep sea in the Pacific Ocean thus apparently increased rather than decreased in the earliest Danian. The low benthic diversity during a time of high food supply indicates a stressed environment. This stress might have been caused by reorganization of the planktic ecosystem: primary producer niches vacated by the mass extinction of calcifying nannoplankton may have been rapidly (<10 kyr) filled by other, possibly opportunistic, primary producers, leading to delivery of another type of food, and/or irregular food delivery through a succession of opportunistic blooms.

The deep-sea benthic foraminiferal data thus are in strong disagreement with the widely accepted hypothesis that the global deep-sea floor became severely food-depleted following the K/Pg extinction due to the mass extinction of primary producers ("Strangelove Ocean Model") or to the collapse of the biotic pump ("Living Ocean Model").

1. Introduction

Evidence that a large asteroid impacted Earth at the Cretaceous/Paleogene (K/Pg) boundary is convincing (e.g., Alvarez et al., 1980; Kring, 2007), but its effects on oceanic ecosystems and the consequences for the global carbon cycle are under debate. The extinction at the end of the Cretaceous was one of the largest of the Phanerozoic (e.g., d'Hondt, 2005; Bambach, 2006; Ocampo et al., 2006). Planktic foraminifera and calcareous nannoplankton suffered severe extinction (e.g., Luterbacher and Premoli-Silva, 1964; Thierstein, 1981; Gardin and Monechi, 1998; Molina et al., 1998; Olsson et al., 1999; Fornaciari et al., 2007; Macleod et al., 2007). In contrast, smaller benthic foraminifera living over a wide depth range did not suffer significant extinction, and only underwent transient assemblage changes in community structure, i.e., relative species abundance and diversity (Kiessling and Claeys, 2001; Alegret et al., 2003, 2004; Culver, 2003; Alegret, 2007). Locations in and around the Gulf of Mexico and North Atlantic were relatively close to the impact site at Chicxulub on the northern Yucatan peninsula. Records from these locations thus cannot give detailed information on the nature of the benthic foraminiferal transient turnover across the K/Pg boundary because of the occurrence of unconformities due to mass wasting processes triggered by the asteroid impact (e.g., Alegret et al., 2001, 2002a,b; Norris and Firth, 2002; Alegret and Thomas, 2004, 2005). The biostratigraphical record is more complete at locations more distal from the impact site.

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The transient changes in deep-sea benthic foraminiferal assemblages in such more complete records varied geographically and bathymetrically (e.g., Thomas, 1990a, b, 2007; Widmark and Malmgren, 1992a, b; Coccioni and Galeotti, 1994, 1998; Alegret and Thomas, 2001, 2005, 2007; Peryt et al., 2002; Alegret et al., 2003, 2004; Alegret, 2007; Coccioni and Marsili, 2007). Many of these authors argued that the transient benthic foraminiferal assemblage changes may have been caused by a severe decrease in food supply to the seafloor, either as the result of collapse of oceanic primary productivity ("Strangelove Ocean" model; Hsü and McKenzie, 1985) or as the result of collapse of the biological pump, i.e., transport of organic matter to the seafloor ("Living Ocean" model; d´Hondt et al., 1998; d'Hondt, 2005; Coxall et al., 2006). In the "Strangelove Ocean" model, this decrease in food to the seafloor was thought to have been caused by the collapse of oceanic primary productivity, with a 'dead ocean' as the result of mass extinction of oceanic phytoplankton, possibly caused by prolonged darkness due to the impact. In the "Living Ocean" model, primary productivity recovered rapidly, but the role of calcifying plankton was taken over by non-calcifiers. In this model, the transport of organic matter to the seafloor collapsed, possibly due to the extinction of fecal pellet producing zooplankton. These fecal pellets have been hypothesized to play an important role in vertical transport of organic matter, because they are much larger than single-celled algae, thus fall through the ocean waters more rapidly, transporting organic matter more efficiently (but see discussion in Thomas, 2007). The severe decrease in food supplied to the deep ocean was thought to have persisted for several hundred thousand years.

It appears, however, improbable that the observed transient, relatively minor changes in benthic faunal assemblages could be the response to a long-term collapse of the food supply, because deep-sea benthic foraminiferal assemblages in the present-day ocean are strongly coupled to productivity in the surface waters (bentho–pelagic coupling; Gooday, 2003; Jorissen et al., 2007). A prolonged lack of food should have led to severe extinction. In addition, post-extinction assemblages in the central North Pacific (DSDP Hole 465A, Hess Rise) do not indicate a decrease in food supply just above the K/Pg boundary (Alegret and Thomas, 2005). Benthic foraminiferal data from this site (Fig. 1) are so far the only ones available from the Pacific Ocean (Widmark and Malmgren, 1992a; Alegret and Thomas, 2005). The sedimentary record at that site appears to be biostratigraphically complete and an Ir-anomaly is present, but rotary drilling caused irregular disturbance of uppermost Maastrichtian and lowermost Danian sediments in a 20–30-cm-thick zone across the K/Pg boundary (Kyte et al., 1980; Widmark and Malmgren, 1992a), and there was no high-resolution age model available for the site (Alegret and Thomas, 2005). The sections drilled by hydraulic piston coring at Ocean Drilling Program (ODP) Site 1210 at Shatsky Rise (Leg 198, northwest Pacific) represent some of the least-disturbed and complete deep-sea records of the K/Pg extinction event. The extinction of calcareous plankton has been well documented (Bralower et al., 2002; Bown, 2005), and an orbitally-tuned age model is available (Westerhold et al., 2008). We present a second benthic foraminiferal data set across the K/Pg boundary from the Pacific Ocean, and compare the data from Site 1210 with those from Site 465, in order to investigate benthic paleoecological and paleoenvironmental changes across the K/Pg boundary in the largest ocean on Earth.

2. Material and methods

We quantitatively analyzed benthic foraminiferal assemblages from ODP Site 1210, drilled on the Southern High of Shatsky Rise (Fig. 1), and located at tropical latitudes (~10ºN) during the Maastrichtian (Larson et al., 1990; Bralower et al., 2002). The sedimentary succession includes uppermost Maastrichtian white to pale orange nannofossil ooze overlain by lowermost Paleocene, grayish-orange foraminiferal ooze (10 cm) that grades upwards into a white foraminiferal nannofossil chalk (20 cm), and then into a grayish-orange nannofossil ooze (Fig. 2). Abrupt changes in nannofossil and planktonic foraminiferal assemblages have been documented across the K/Pg boundary, although intense bioturbation disturbs the record, with up to 5-cm-

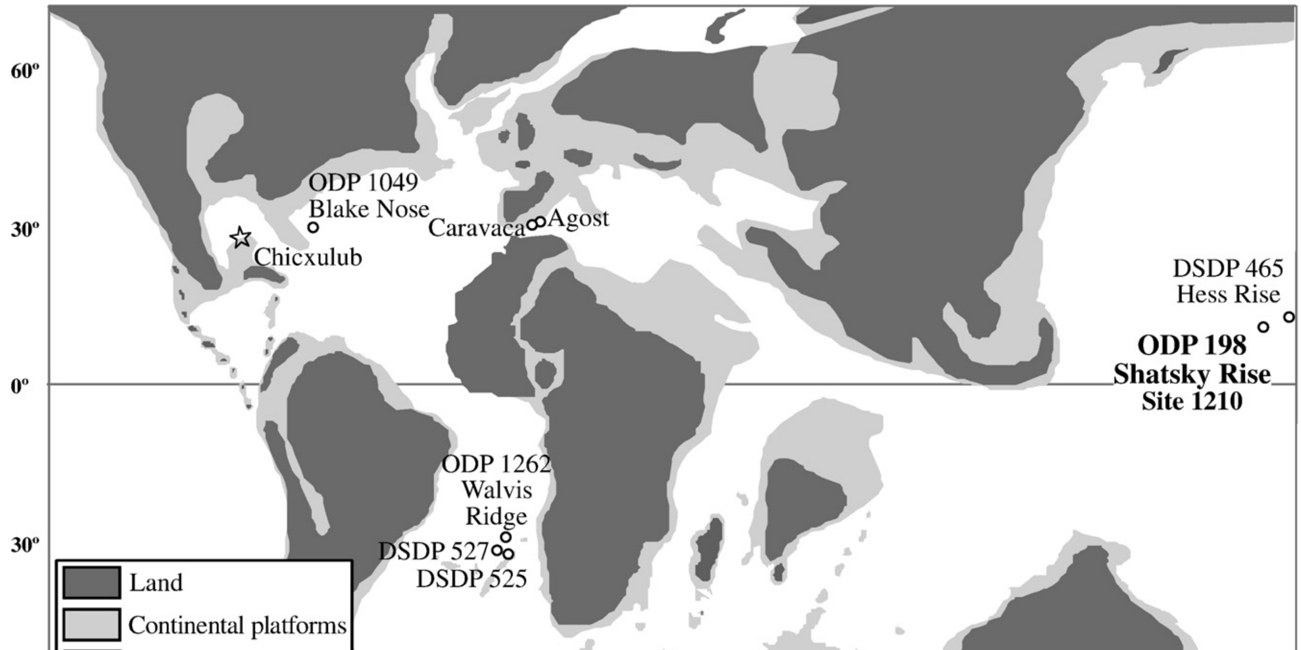


Fig. 1. Paleogeographical distribution of land masses, shallow seas and deep ocean basins at the end of the Cretaceous, showing the location of ODP Site 1210 (Shatsky Rise), the K/Pg Chicxulub structure (Yucatan peninsula, Mexico) and other K/Pg boundary sections and sites referred to in the text. Modified from Denham and Scotesse (1987).

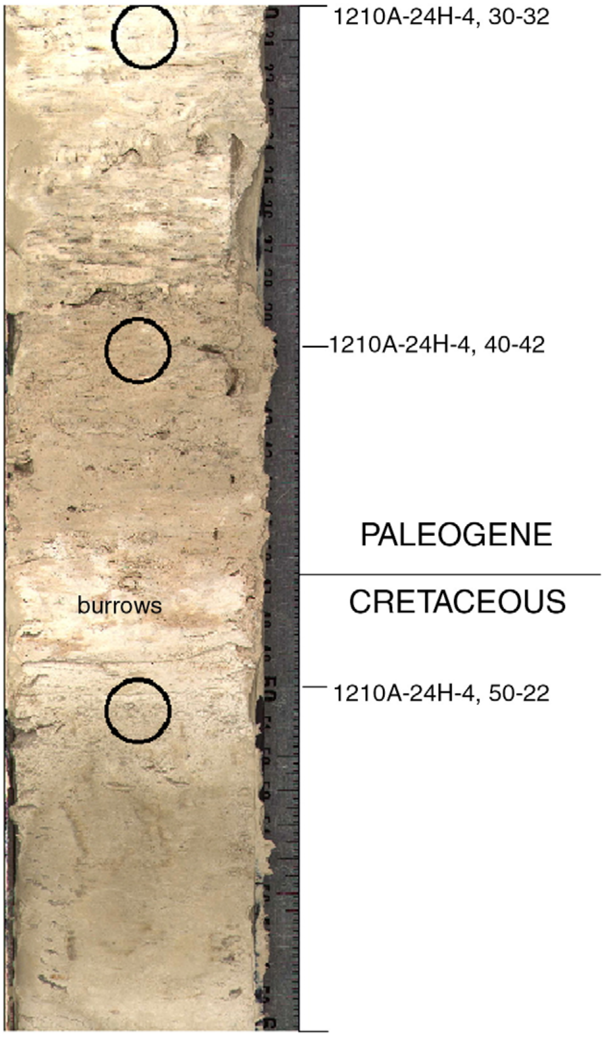


Fig. 2. Detail of the K/Pg transition at ODP Site 1210, showing the 5 cm-thick burrowed interval across the boundary, and the location of our samples (black circles with sample level). Note that our samples were not taken within the burrowed interval across the boundary.

long burrows across the boundary. For biostratigraphical control, we follow the zonations of Bralower et al. (2002), and Bown (2005). The substantial thickness of the uppermost Maastrichtian *Micula prinsii* (CC26) Zone and the lowermost Danian *Parvularugoglobigerina eugubina* (P) Zones indicates that the K/Pg boundary is paleontologically complete.

To derive sedimentation rates for the Danian and Maastrichtian we used numerical ages as derived from the orbitally-tuned age model described by Westerhold et al. (2008). We used these sedimentation rates combined with density data in Bralower et al. (2002) to calculate sediment mass accumulation rates. We modified the age model for Site 465 somewhat from that used by Alegret and Thomas (2005). In order to derive this age model, we correlated the planktic foraminiferal carbon isotope values (Boersma and Shackleton, 1981) with the bulk carbon isotope data for Site 1262 (Zachos et al., 2004); both records show the well-documented global decline in surface ocean carbon isotope values across the K/Pg boundary. The Site 1262 record was correlated to the Site 1210 record by Westerhold et al. (2008), so that we could indirectly correlate the Site 465 record to the Site 1210 record. Numerical ages for the samples from both sites are presented in Table 1 (Supplementary material).

We analyzed 25 samples, spaced at 10 cm-intervals in the uppermost Maastrichtian and lowermost Danian, and at 50 cm-intervals below and above the K/Pg transition. Because our samples are spaced 10 cm apart, we did not sample the 5 cm-thick burrowed interval across the boundary (Fig. 2). We analyzed benthic foraminifera from the >63 µm fraction (Plates I and II), and calculated the relative abundances of foraminiferal species (Table 2 in Supplementary material; Fig. 3). In order to quantify changes in diversity and heterogeneity, we calculated the Fisher-α index, and the H(S) Shannon–Weaver information function (Fig. 4). The percentages of agglutinated taxa and buliminid taxa (species of the genera *Aragonia, Bolivina, Bolivinoides, Bulimina, Buliminella, Coryphostoma, Eouvigerina, Fursenkoina, Praebulimina, Pyramidina, Quadratobuliminella* and *Reussella*) were also calculated (Fig. 4). We allocated all specimens to epifaunal (living at the seafloor or in the uppermost cm of the sediment) and infaunal (living in deeper layers of the sediment) morphogroups (Fig. 4), following Corliss (1985), Jones and Charnock (1985) and Corliss and Chen (1988), and in agreement with Alegret and Thomas (2005). The morphogroup analysis may help to infer probable microhabitat preferences and environmental parameters such as nutrient supply to the seafloor or seawater oxygenation (e.g., Bernhard, 1986; Jorissen et al., 1995). The benthic foraminiferal accumulation rate (BFAR, number of foraminifera per cm^2 per kyr) is shown in Fig. 5 for both sites, with data for Site 465 adjusted to the new age model. The BFAR data are plotted together with abundances of a few important taxa. BFAR values are generally used to infer delivery of food to the seafloor, because food is generally the limiting factor for benthic foraminiferal productivity in the deep ocean (Gooday, 2003; Jorissen et al., 2007).

3. Results

3.1. Paleobathymetry based on benthic foraminiferal assemblages

The strong dominance of benthic foraminifera with calcareous tests throughout the studied section indicates deposition above the calcite compensation depth, which was reconstructed at about 3 km in the Maastrichtian Pacific (Barrera and Savin, 1999). Partial dissolution of planktonic forms, especially in the Maastrichtian, suggests that the Maastrichtian lysocline may have been close to paleodepth of Site 1210 (Bralower et al., 2002).

Benthic foraminifera are useful indicators of paleobathymetry because their depth distribution in the oceans is controlled by several depth-related parameters, including food supply (e.g., Nyong and Olsson, 1984; Van Morkhoven et al., 1986). The comparison between fossil and recent assemblages, the occurrence and abundance of depth-related species, and their upper depth limits (e.g., Van Morkhoven et al., 1986; Alegret and Thomas, 2001; Alegret et al., 2003) thus allowed us to infer the paleobathymetry of the uppermost Cretaceous through lowermost Paleogene sediments at Shatsky Rise.

Representatives of the cosmopolitan deep-water Velasco-type fauna, such as *Nuttallides truempyi, Nuttallinella florealis, Osangularia velascoensis* and *Stensioeina beccariiformis* (Berggren and Aubert, 1975) are common to abundant. The assemblages contain abundant species that are characteristic for deep-bathyal to abyssal settings, such as *Aragonia velascoensis*, *Gyroidinoides globosus*, *Paralabamina lunata, Oridorsalis umbonatus* and buliminid taxa such as *Bulimina kugleri, Praebulimina reussi, Bulimina velascoensis* and *Buliminella beaumonti* (e.g., Tjalsma and Lohmann, 1983; Widmark and Malmgren, 1992a, b; Widmark, 1997; Alegret and Thomas, 2001, 2004; Alegret et al., 2003). Other buliminids observed at Site 1210, such as *Pyramidina rudita,* show greatest abundances at sites of intermediate paleodepth (Tjalsma and Lohmann, 1983). These data suggest a lower bathyal–upper abyssal (~1500–2000 m) depth of deposition for upper Maastrichtian–lower Danian sediments at Site 1210.

We thus infer a somewhat shallower depth for the studied interval than has been assessed for the Maastrichtian sediments at that site, which according to shipboard benthic foraminiferal data and backtracking were deposited at upper abyssal (2000–3000 m) depths (Bralower et al., 2002). *Paralabamina hillebrandti* is common across the K/Pg transition, but much less abundant than in the Maastrichtian, thus supporting a slightly shallower depth of deposition across the K/Pg interval. This is somewhat more than paleodepths arrived at for Site 465, estimated to be ~1500 m (Alegret and Thomas, 2005).

3.2. Benthic foraminifera as environmental indicators at Sites 1210 and 465

3.2.1. Upper Maastrichtian

Benthic foraminiferal assemblages from Site 1210 are dominated by calcareous taxa (~87–100%), and consist of mixed infaunal and epifaunal morphogroups for most of the studied interval, with assemblages slightly dominated by infaunal taxa (Figs. 3, 4). Assemblages from the lowermost part of the studied section (upper Maastrichtian) are diverse and heterogeneous, with mixed infaunal (*Praebulimina reussi, Bulimina simplex*) and epifaunal (e.g., *Nuttallinella ripleyensis, Paralabamina lunata, Osangularia* spp.) taxa. Heterogeneity and diversity decreased strongly for a short interval in the upper Maastrichtian (222 to 221 mbsf), where the percentage of infaunal taxa overall increased. The percentage of the infaunal buliminids increased to ~67% at 221 mbsf (Fig. 3), where *Pyramidina rudita* makes up 49% of the assemblages (Fig. 2). *Adercotryma kuhnti,* a species first described from Site 1210 (Alegret and Thomas, 2009), is scarce in the lower part of the section and peaks in relative abundance in the uppermost Maastrichtian.

Some species of *Gyroidinoides* adopt an opportunistic lifestyle in the recent oceans (e.g., Schmiedl et al., 2003). Buliminids may indicate a high and fairly stable food supply, and/or reduced oxygen concentrations at the seafloor (e.g., Thomas, 1990b; Bernhard and Reimers, 1991; Sen Gupta and Machain-Castillo, 1993; Jorissen et al., 1995; Bernhard et al., 1997). A high relative abundance of buliminid taxa, however, is more commonly caused by an abundant and continuous food supply than by low-oxygen conditions (e.g., Jorissen et al., 1995; 2007; Fontanier et al., 2002; Gooday, 2003). There is no sedimentological evidence for severe low-oxygen conditions (e.g., dark laminated sediments) at Site 1210, where the sediments are bioturbated across the boundary (Fig. 2). Therefore we interpret the high relative abundance of buliminids as caused by a high food supply. A fairly high supply of food to the seafloor would allow some infaunal taxa that were scarce earlier in the Late Cretaceous to proliferate during the latest Maastrichtian, thus accounting for the peaks in relative abundance of such taxa as *Adercotryma kuhnti, Aragonia velascoensis, Gyroidinoides globosus* and *Buliminella beaumonti* (Fig. 2). Peaks in abundance of buliminids lower in the Maastrichtian at Site 1210 (Frank et al., 2005) have been explained as caused by a relatively high surface productivity. The high percentages of infaunal morphogroups (Jorissen et al., 1995), together with the presence of abundant, heavily calcified buliminids, indicates that the nutrient flux to the seafloor was relatively high at least for some periods in the Maastrichtian. Similar conditions of a high food supply to the seafloor have been inferred from Maastrichtian benthic foraminiferal assemblages for central North Pacific DSDP Hole 465A (Hess Rise, paleodepth ~1500 m; Alegret and Thomas, 2005). According to Widmark and Malmgren (1992b), this site had a relatively high productivity because of its proximity to the Cretaceous equatorial upwelling zone, and there may have been widespread episodes of higher productivity in the Pacific Ocean in the later Maastrichtian, with blooming of high productivity species resulting in overall lower diversity.

3.2.2. The K/Pg transition

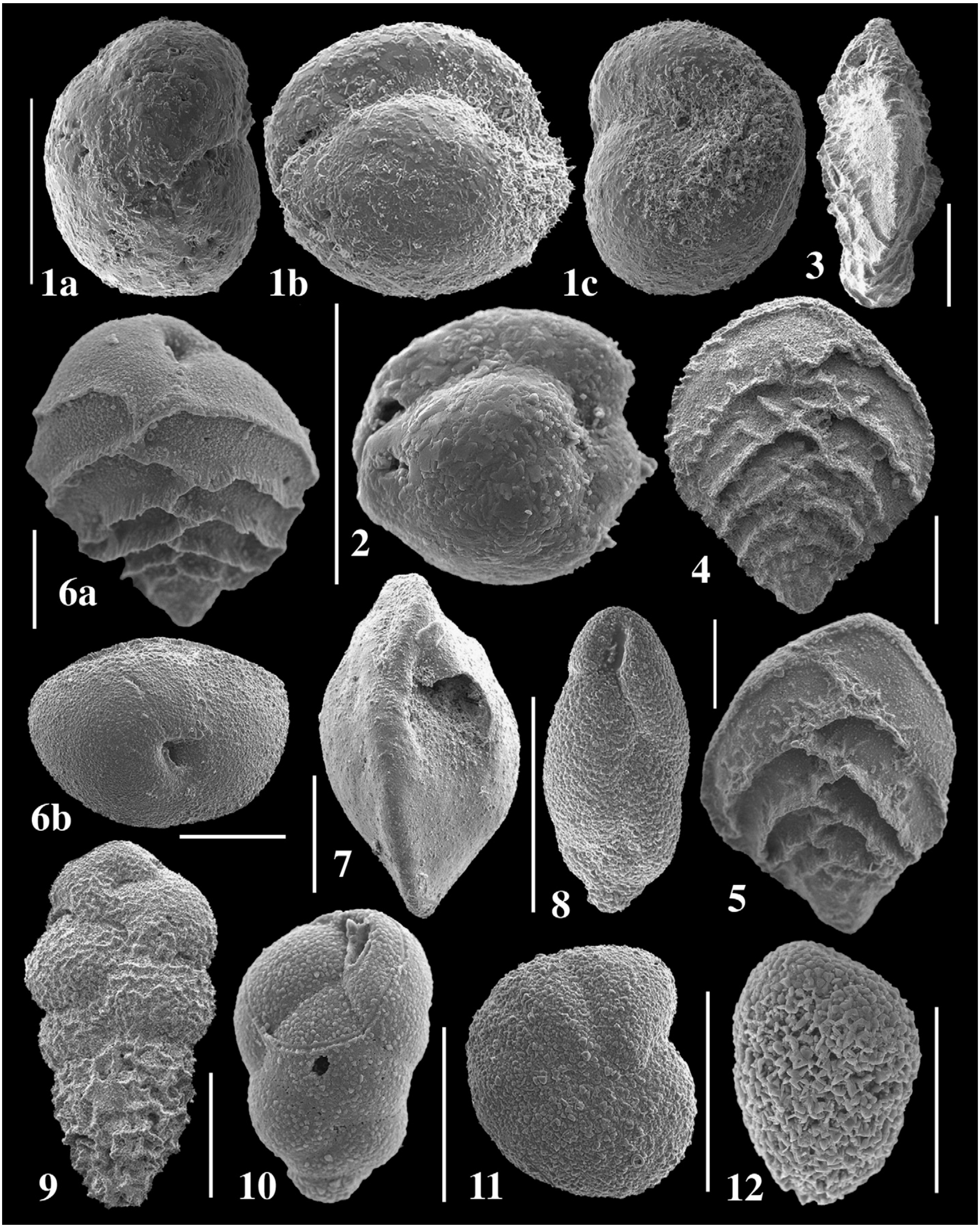
In the uppermost Maastrichtian sample, however, more oligotrophic conditions returned, as indicated by a higher relative abundance of more oligotrophic species such as *Nuttallides truempyi*, lower percentages of buliminids (33–45%), and the rapid recovery of diversity and heterogeneity. Assemblages in this interval have a slight dominance of infaunal taxa over epifaunal taxa, with common infaunal taxa such as *Praebulimina reussi, Aragonia velascoensis, Bulimina simplex*, and *Buliminella beaumonti*. Among the epifaunal taxa, *Anomalinoides* spp., *Paralabamina lunata* and *Nuttallides truempyi* are common (Fig. 2). *Adercotryma kuhnti, Praebulimina reussi* and *Scheibnerova* sp. have their highest occurrence at the K/Pg boundary, coeval with a drop in heterogeneity and diversity. Changes in the assemblages at the K/Pg boundary at Site 1210 include a rapid increase in the percentage of buliminids (*Bulimina kugleri, Bolivinoides* sp. 1), the disappearance of three species, and a sharp decrease in heterogeneity and diversity of the assemblages, that lasted about 200 kyr at Site 1210, but only 100–150 kyr at Site 465 (Fig. 5). The Fisher-α values are the lowest of the studied interval in the lowermost Danian, and the heterogeneity of the assemblages is very low in the lowermost 1.5 m of the Danian at Site 1210, then recovers towards the top of the studied interval.

At Site 1210 the percentage of buliminids (*Bolivinoides* sp. 1, *Bulimina kugleri*) is very high immediately above the K/Pg boundary (219.80 mbsf; Figs. 3, 4, 5). The spike in percentage of buliminids was coeval with peak values of BFAR, and both persisted for about 10–30 kyr. Similar peaks are present at Site 465 (Fig. 5). We argue that the peak abundance of buliminids coeval with the peak in BFAR indicates an unusually high food supply to the seafloor just after the K/Pg extinction event at both locations in the Pacific Ocean.

Above this interval is a peak in abundance of *Stensioeina beccariiformis*, which persisted until about 100 kyr after the K/Pg boundary event at Site 1210, coincident with the bloom of the calcareous nannofossils *Neobiscutum parvulum* and *Cyclagelosphaera reinhardtii* (Bown, 2005). This species is very scarce throughout the Maastrichtian part of the section, and it has its highest occurrence in the lowermost Danian, just above this peak in relative abundance. At the slightly shallower Site 465, *S. beccariiformis* was generally somewhat more frequent (Alegret and Thomas, 2005; Fig. 4) than at Site 1210, and its relative abundance peaked slightly later, persisting for about 130 kyr (Fig. 5). This species usually is abundant at somewhat shallower paleodepths than that of Site 1210 (Tjalsma and Lohmann, 1983). We argue that *S. beccariiformis* may have become more frequent at greater depths, because a persistant high food influx (though decreased from the flux during formation of the buliminid peak) allowed it to thrive at deeper sites, which are more oligotrophic (similar to the modern 'delta effect', where more eutrophic species are seen at greater depth at locations with increased food supply; Jorissen et al., 2007).

The return to food supply conditions similar to those in the Maastrichtian is indicated by the increase in relative abundance of epifaunal taxa including *Nuttallides truempyi* at both sites, *Nuttallinella ripleyensis* at Site 1210, and *Paralabamina lunata* at Site 465 (Alegret and Thomas, 2005). Above the interval with relatively high abundance of *Stensioeina beccariiformis,* epifaunal morphogroups at Site 1210 are dominated by *Nuttallinella ripleyensis* (36% of the assemblages),

Plate I. SEM illustrations of benthic foraminifera across the K/Pg transition at Site 1210, Shastky Rise. Scale bar = 100 µm. 1, *Adercotryma kuhnti* Alegret and Thomas, sample 198-1210A-24H-5(10–12), 221 mbsf; 1a, ventral side: 1b, apertural view; 1c, dorsal (spiral) side. 2, *Adercotryma kuhnti* Alegret and Thomas, sample 198-1210A-24H-5(110–112), 222 mbsf, apertural view. 3, *Aragonia aragonensis* (Nuttall), sample 198-1210A-24H-5(110–112), 222 mbsf, lateral view. 4, *Aragonia aragonensis* (Nuttall), sample 198-1210A-24H-5(110–112), 222 mbsf, front view. 5, *Aragonia aragonensis* (Nuttall), sample 198-1210A-24H-5(110–112), 222 mbsf, front view. 6, *Aragonia velascoensis* (Cushman), sample 198-1210A-24H-7(5–7), 223.25 mbsf; 6a, side view; 6b, apertural view. 7, *Nuttallides truempyi* (Nuttall), sample 198-1210A-24H-4(110–112), 220.50 mbsf, apertural view. 8, *Bulimina kugleri* Cushman & Renz, sample 198-1210A-24H-4(10–12), 219.50 mbsf. 9, *Bolivinoides* sp. 1, sample 198-1210A-24H-4(30–32), 219.70 mbsf. 10, *Bulimina simplex* Terquem, sample 198-1210A-24H-7(5–7), 223.25 mbsf. 11, *Anomalinoides* cf. *acutus* (Plummer), sample 198-1210A-24H-7(5–7), 223.25 mbsf, ventral side. 12, *Bolivina huneri* Howe, sample 198-1210A-24H-7(5–7), 223.25 mbsf.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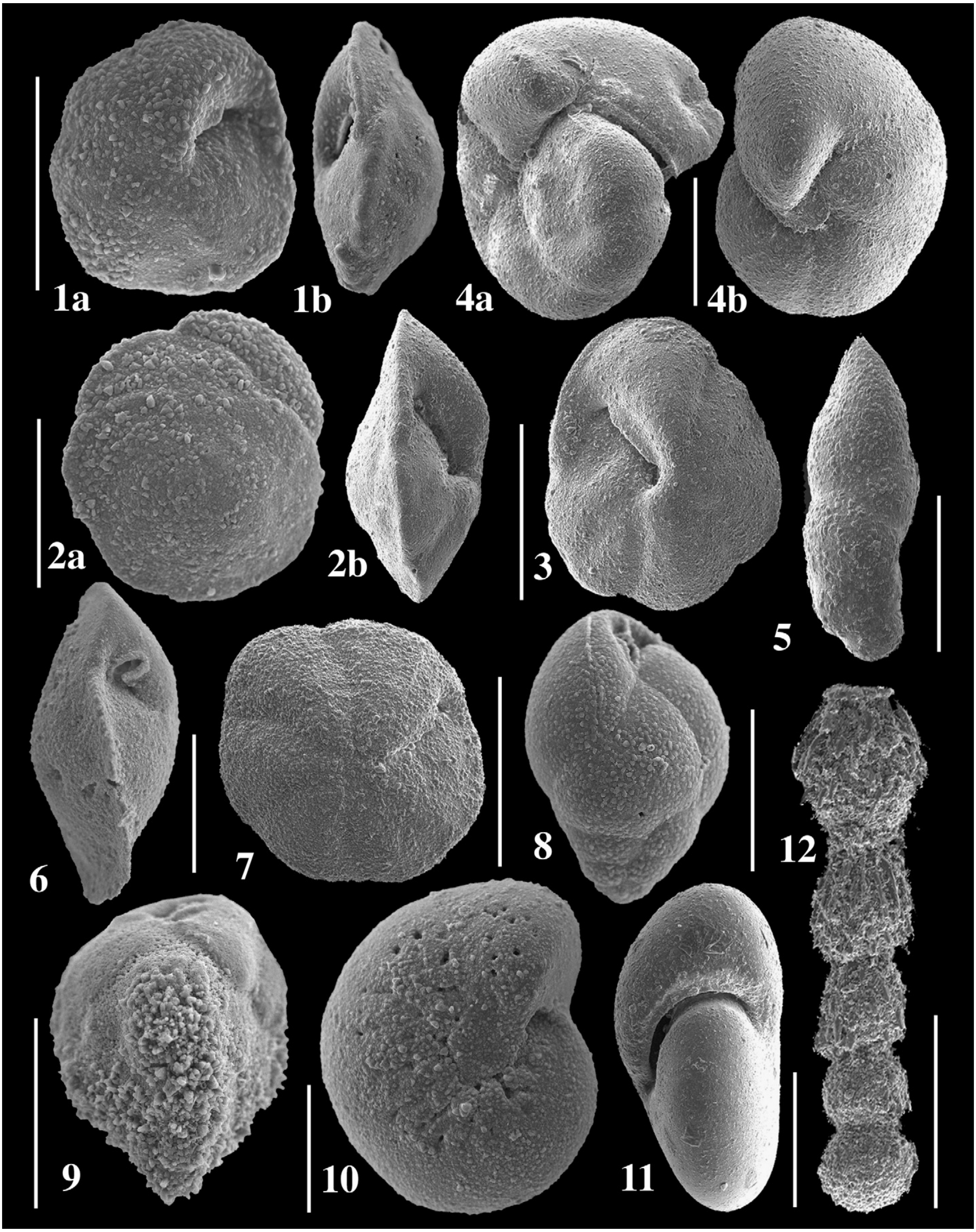
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whereas *Bulimina kugleri* is most abundant (~20%) among the infaunal morphogroups (Fig. 2). The relative abundance of *Nuttallides truempyi* increases towards the top of the studied interval. The uppermost sample (215 mbsf) contains the lowest percentages of buliminids (14%) in the studied interval, with abundant epifaunal taxa (68% of the assemblages), including *Nuttallides truempyi, Nuttallinella florealis* and *Paralabamina hillebrandti.* These assemblages indicate the return to oligotrophic conditions at the seafloor towards the top of the studied interval.

We thus argue that at two Pacific sites the benthic foraminiferal evidence strongly supports an increase in food supply to the benthos just after the K/Pg extinction of calcifying calcareous primary producers, instead of a collapse of primary productivity or the biological pump or both.

4. The global carbon cycle across the K/Pg boundary

The diversity and heterogeneity of benthic foraminiferal assemblages decreased directly after the K/Pg boundary in the Pacific and Atlantic Oceans as well as in Tethyan sections (Widmark and Malmgren, 1992a,b; Coccioni and Galeotti 1994; Coccioni and Marsili, 2007; Alegret et al., 2003, 2004; Alegret and Thomas, 2005, 2007; Alegret, 2007), but there are pronounced biogeographical differences in the nature of the benthic foraminiferal turnover after the K/Pg boundary (e.g., review in Culver, 2003).

In western Tethyan sections (e.g., the Spanish Caravaca and Agost sections), low-oxygen conditions occurred at the sea floor just after the K/Pg boundary, as indicated by the occurrence of laminated, black sediments (Coccioni and Galeotti, 1994; Alegret et al., 2003). In open marine continental margin settings, such low-oxygen conditions are most probably caused by a high flux of organic matter to the sea floor (e.g., Levin, 2003). In the North African Tethyan sections (including El Kef, Ain Settara and Elles), in contrast, there is no sedimentological, geochemical or micropaleontological evidence for low-oxygen conditions, with the low-diversity benthic assemblages present directly above the K/Pg boundary characterized by abundant large, trochospiral *Cibicidoides pseudoacutus* (Speijer and van der Zwaan, 1996; Peryt et al., 2002; Coccioni and Marsili, 2007). The abundant occurrence of this oligotrophic indicator and the dominance of epifaunal taxa suggest overall low food supply to the seafloor in that region.

In the Southeastern Atlantic Ocean, the K/Pg boundary was followed by a period of strong fluctuations in food supply as reflected in benthic foraminiferal assemblages, but no overall change in the total amount of food (Alegret and Thomas, 2007). Benthic foraminiferal assemblages in the Atlantic sector of the Southern Ocean point to a decrease in nutrient flux after the K/Pg boundary (Thomas, 1990a, b).

With all this biogeographic variability, benthic foraminiferal data indicate high primary productivity after the K/Pg boundary over large areas such as the Pacific Ocean and western Tethys (e.g., Coccioni and Galeotti, 1994; Alegret et al., 2003; Alegret and Thomas, 2005). At Sites 1210 and 465 (Pacific Ocean), the benthic foraminiferal data point to high food supply at the K/Pg boundary, and low diversity and heterogeneity indicate stressed environments. We suggest that this stress may have resulted from a change in taxonomic composition of the primary producers after the severe extinction of the haptophyte calcareous nannoplankton (e.g. Bown, 2005; Fornaciari et al., 2007). The severe extinction of these calcifying primary producers, however, may not have meant a prolonged and severe decrease in primary productivity, as also argued by d'Hondt et al. (1998), because the niches left vacant by the extinction of these producers may well have been filled rapidly by others. At the K/Pg extinction, diatoms did not suffer extreme extinction (Kitchell et al., 1986), and neither did organic-walled dinoflagellates (Brinkhuis and Zachariasse, 1988). The dinoflagellate calcareous cyst *Thoracosphaera* bloomed opportunistically worldwide (e.g., Thierstein, 1981; Perch-Nielsen et al., 1982; Gardin and Monechi, 1998; Bernaola and Monechi, 2007; Fornaciari et al., 2007). Just like benthic foraminiferal assemblages, post-extinction planktic foraminiferal assemblages at many locations are indicative of high productivity (e.g., Koutsoukos, 1994, 1996; Keller and Pardo, 2004; Coccioni and Luciani, 2006).

If primary productivity in the Maastrichtian Pacific Ocean resembled the present primary productivity, a large part of the production of organic matter was not by eukaryote primary producers such as haptophytes, dinoflagellates or diatoms, but by prokaryotes such as *Synechococcus* and *Prochlorococcus* (e.g., Alvain et al., 2008), which may not have been much affected by the mass extinction. Blooms of such opportunistically growing prokaryotes may have brought a fluctuating but high supply of food to the sea floor, resulting in high benthic foraminiferal productivity, but in a stressed environment due to high variability in composition and amount of food (e.g., Alegret et al., 2003).

A high food supply to the seafloor after the K/Pg boundary would be in strong disagreement not just with the hypothesis of prolonged collapse of primary productivity ("Strangelove Ocean Model"; Hsü and McKenzie, 1985), but also with the "Living Ocean Model" (d´Hondt et al., 1998; d'Hondt, 2005; Coxall et al., 2006). This model invokes a lack of food supply to the seafloor due to the extinction of zooplankton which produces fecal pellets that supposedly enhance delivery of organic matter to the seafloor. More recent publications, however, document that a decrease in abundance of zooplankton may lead to enhanced, rather than decreased delivery of organic matter to the seafloor (e.g., Sarmiento and Gruber, 2006). These authors describe that zooplankton break up large phytoplankton aggregates, and such aggregates are much more efficient in the transport of organic matter to the seafloor than the fecal pellets. The potential cause of a collapse of the biological pump invoked in the "Living Ocean Model" thus may not be correct, because the efficiency of the biological pump may have been more affected by factors which were not influenced much by an impact. For instance, coagulation of organic particles by sticky organic compounds may contribute to the formation of large particles for rapid deposition (Jackson, 2001; Armstrong et al., 2001), as well as ballasting particles with biogenic silica or terrigenous dust. If atmospheric pCO_2 levels were very high after the impact (Beerling et al., 2002), calcification of the few surviving calcareous nannofossils may have decreased, but led to increased delivery of organic matter to the seafloor because of increased formation of the sticky polysaccharides (DeLille et al., 2005; Engel et al., 2004).

Extensive phytoplankton blooms have been argued to have characterized the immediate aftermath of the Triassic–Jurassic extinction (van de Schootbrugge et al., 2007). The occurrence of similarly extensive plankton blooms after the K/Pg extinction could explain the global variability of the benthic foraminiferal turnover. Such blooms, which may have been highly variable in time and space, may have caused the low-diversity benthic assemblages indicative of a high food supply, as observed in the Pacific Ocean, and western Tethys.

Plate II. SEM illustrations of benthic foraminifera across the K/Pg transition at Site 1210, Shastky Rise. All scale bars 100 µm. 1, *Nuttallinella ripleyensis* (Cushman), sample 198-1210A-24H-7(5–7), 223.25 mbsf; 1a, ventral side; 1b, side view. 2, *Nuttallinella ripleyensis*, sample 198-1210A-24H-7(5–7), 223.25 mbsf; 2a, dorsal side; 2b, side view; 2a, ventral side. 3, *Nuttallinella ripleyensis*, sample 198-1210A-24H-7(5–7), 223.25 mbsf, ventral side. 4, *Cibicidoides* cf. *westi* (Howe), sample 198-1210A-24H-4(60–62), 220 mbsf; 4a, dorsal and apertural views; 4b, ventral side. 5, *Pleurostomella acuminata* Cushman, sample 198-1210A-24H-7(5–7), 223.25 mbsf. 6, *Osangularia velascoensis* (Cushman), sample 198-1210A-24H-4(30–32), 219.70 mbsf, apertural view. 7, *Paralabamina lunata* (Brotzen), sample 198-1210A-24H-7(5–7), 223.25 mbsf, ventral side. 8, *Praebulimina reussi* (Morrow), sample 198-1210A-24H-7(5–7), 223.25 mbsf. 9, *Pyramidina rudita* (Cushman and Parker), sample 198-1210A-24H-4(110–112), 220.50 mbsf. 10, *Stensioeina beccariiformis* (White), sample 198-1210A-24H-4(30–32), 219.70 mbsf, ventral side. 11, *Pullenia* sp., sample 198-1210A-24H-7(5–7), 223.25 mbsf, apertural view. 12, *Siphonodosaria hispidula* Cushman, sample 198-1210A-24H-4(110–112), 220.50 mbsf.

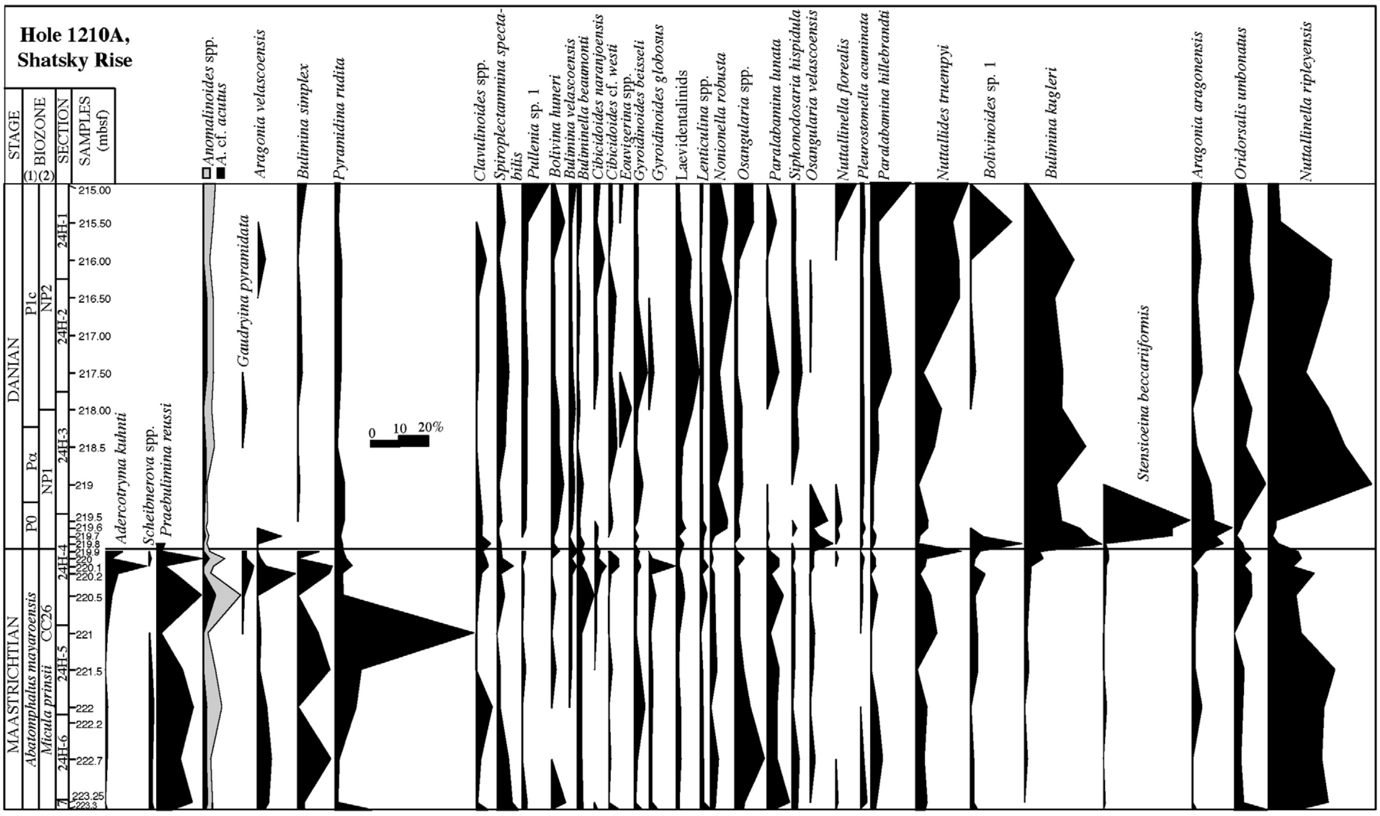

Fig. 3. Occurrence and relative abundance of the most characteristic benthic foraminiferal species across the K/Pg transition at Site 1210, Shatsky Rise. Biostratigraphy according to (1) Bralower et al. (2002), and (2) Bown (2005).

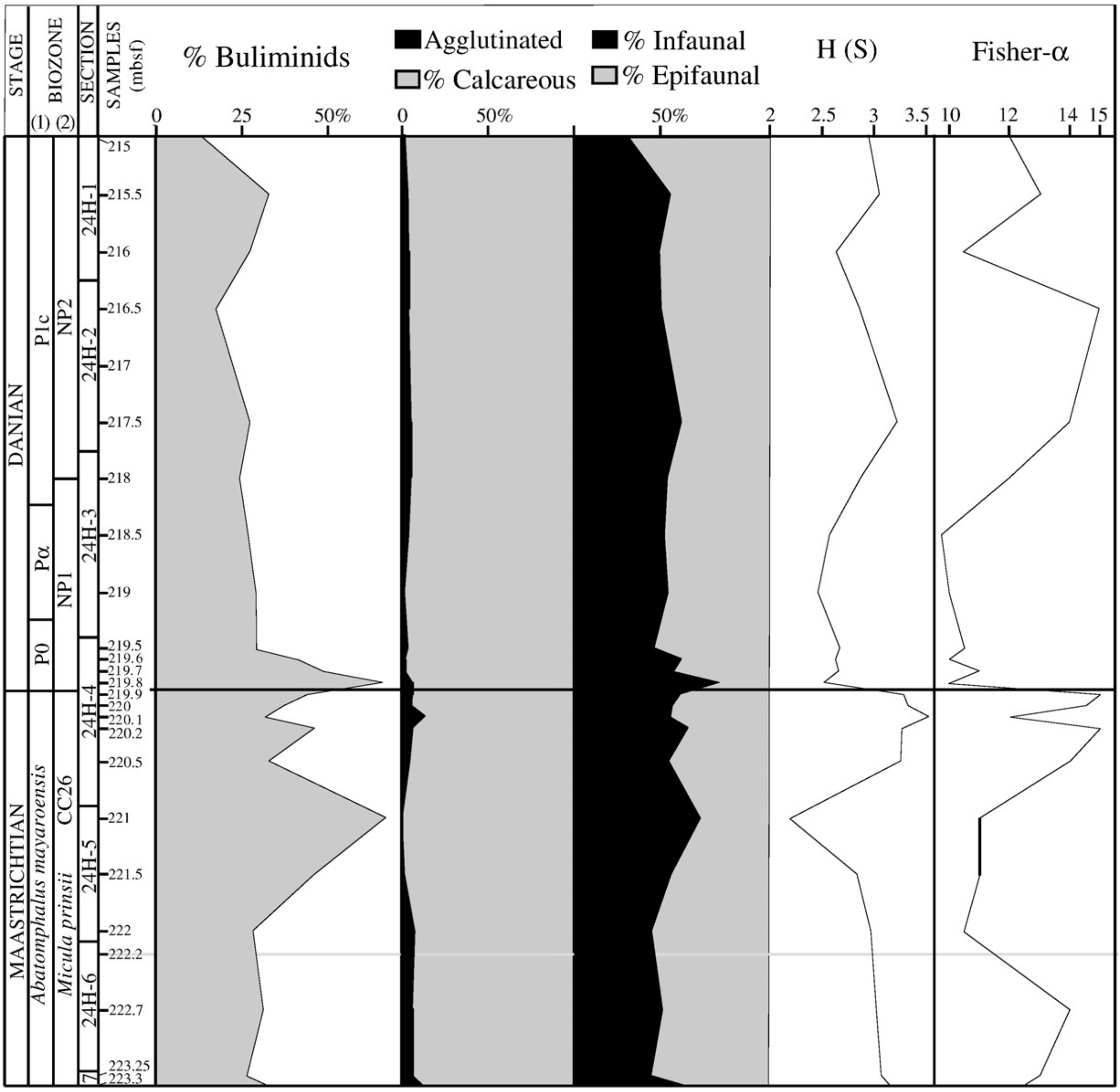

Fig. 4. Percentages of buliminid taxa, agglutinated and calcareous benthic foraminifera, and infaunal and epifaunal morphogroups; H(S) Shannon–Weaver heterogeneity index; and Fisher-α diversity index of benthic foraminiferal species across the K/Pg transition at Site 1210, Shatsky Rise. Biostratigraphy according to (1) Bralower et al. (2002), and (2) Bown (2005).

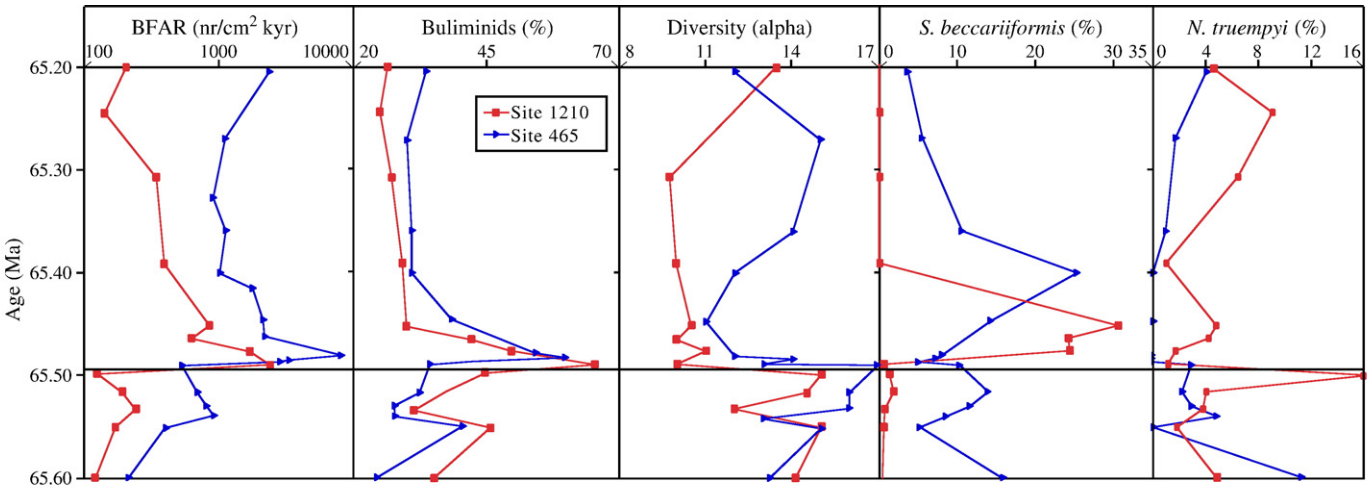

Fig. 5. Benthic foraminiferal accumulation rates (BFAR), percentages of buliminid taxa, Fisher-α diversity index, and relative abundance of *Stensioeina beccariiformis* and *Nuttallides truempyi* across the K/Pg transition at Sites 1210 (Shatsky Rise) and 465 (Hess Rise).

If we are correct in explaining the character of the benthic assemblages by an episode of overall high delivery of food to the seafloor, both primary productivity and food transport to the seafloor recovered much faster than argued by the authors of both the “Strangelove Ocean” and “Living Ocean” models (e.g., Hsü and McKenzie, 1985; Coxall et al., 2006). The recovery of primary productivity in terms of biomass in the oceans thus may have resembled the relatively rapid recovery of productivity on land (Beerling et al., 2001, 2002). The biogeography of the occurrence of plankton blooms may have been controlled by such parameters as the local to regional patterns of upwelling and nutrient run-off from land. For instance, in regions where vegetation was destroyed by the direct and/or indirect effects of the impact, we would expect a strong increase in run-off and in nutrient supply to the oceans, similar to what is observed presently in oceans offshore from deforested regions (e.g., Lü et al., 2007).

Evidence for the collapse of primary productivity (“Strangelove Ocean”) or the biological pump (“Living Ocean) consists mainly of the observation that the vertical carbon isotope gradient ($\Delta\delta^{13}C$) between benthic and planktic foraminifera and/or benthic foraminifera and bulk carbonate collapsed for several hundred thousands of years (e.g., Hsü and McKenzie, 1985; Zachos and Arthur, 1986; Zachos et al., 1989). This collapse of $\Delta\delta^{13}C$ is the result of a very strong decrease in carbon isotope values for surface dwellers, accompanied by a minor increase in values of benthic foraminifera (e.g., Kump, 1991).

We cannot presently explain this collapse in vertical carbon isotope values, but argue that it may have been caused by something else than a lack of transport of organic matter to the seafloor, specifically by diagenetic processes and/or a change in vital effects across the K/Pg boundary (Thomas, 2007). As to diagenesis, sediments with a very low carbonate content such as those directly overlying the K/Pg boundary commonly have extreme negative carbon isotope values because of reactions between the few carbonate grains and the abundant other sediment components (e.g., Zachos et al., 2005).

Vital effects may play a large role in the collapse in $\Delta\delta^{13}C$, because the carbon isotope signal of surface waters is measured in bulk sediment (mainly calcareous nannoplankton) or in planktic foraminifera, both of which suffered massive extinction. Post-extinction planktic records are therefore by necessity obtained from different species than pre-extinction records, possibly with different isotopic signatures (e.g., d'Hondt and Zachos, 1993; Minoletti et al., 2005). For instance, post-extinction calcareous nannoplankton does not dominantly consist of calcite produced by haptophytes, but has a large component of calcite produced by the calcareous dinocyst *Thoracosphaera* (e.g., Thierstein. 1981; Gardin and Monechi, 1998; Fornaciari et al., 2007). Living *Thoracosphaera* species have very light carbon isotope signatures (Zonneveld, 2004; Minoletti et al., 2005).

Similarly, post-extinction records of planktic foraminifera are at many locations derived from *Güembelitria* species (e.g., d'Hondt and Zachos, 1993; Keller, 2002; Minoletti et al., 2005). Maastrichtian triserial *Güembelitria* species have more negative isotope signatures than co-existing benthics (e.g., d'Hondt and Zachos, 1993; Keller, 2002), and the living triserial planktic species *Gallitellia vivans* also has an extremely light carbon isotopic signal (Kimoto et al., 2009). Eocene through Miocene biserial planktonic foraminifera in eutrophic regions with inferred active upwelling also have carbon isotopic signature more negative than the co-existing benthic forms (Resig and Kroopnick, 1983; Sexton et al., 2006; Smart and Thomas, 2006). Modern planktic foraminiferal carbon isotope values are also more negative than those in the benthic foraminifera in regions with high surface productivity due to strongly fluctuating upwelling intensity (Arabian Sea; Naidu and Niitsuma, 2004). There thus are numerous examples where we observe no vertical carbon isotope gradient between planktic and benthic foraminifera, even under high productivity circumstances.

We admit that we do not present a convincing explanation of the collapse in vertical carbon isotope gradient ($\Delta\delta^{13}C$) following the K/Pg extinction, but we argue that the commonly accepted explanation of this feature of the carbon isotopic record (either a collapse of primary productivity or a collapse of the biological pump) is highly unlikely in view of the benthic foraminiferal evidence of persistent food supply to the seafloor. At least part of the explanation for the occurrence of a collapsed gradient in carbon isotope values may be a combination of diagenetic effects, vital effects over an interval of mass extinction of calcifying surface dwellers, and the formation of light carbonate in surface waters during local to regional upwelling with associated large plankton blooms. More research is needed to fully understand the carbon isotopic record across the K/Pg boundary, including the use of Earth System modelling (Thomas et al., in press).

5. Conclusions

- Benthic foraminiferal assemblage data as well as benthic foraminiferal accumulation rates at Pacific Ocean Sites 465 and 1210 present strong evidence for a high food supply to the seafloor just after the K/Pg extinction event.
- During the time of high food supply the faunas had a low diversity and heterogeneity, indicative of stressed environmental conditions.
- Such a combination of stressed conditions and a relatively high food supply could be explained by the occurrence of large blooms of opportunistic primary producers other than calcareous nannoplankton (e.g. prokaryotes), occupying the niches emptied after the extinction, and delivering food to the seafloor that varied in amount and composition over time.
- If primary producers in the oceans recovered quickly, similar to terrestrial floras, the collapse of the vertical carbon isotope gradient must be explained by other factor(s) than prolonged collapse of the primary productivity and/or biological pump after the K/Pg boundary.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at doi:10.1016/j.marmicro.2009.07.005.

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