Selective calcareous nannoplankton survivorship at the Cretaceous-Tertiary boundary

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ABSTRACT

Calcareous nannoplankton underwent devastating diversity loss at the Cretaceous-Tertiary boundary (65.5 Ma), but recovered rapidly in the early Paleocene from a small number of survivor species. An understanding of this survivorship has been hampered by uncertainties introduced by reworking and mixing, but new high-resolution assemblage data from the northwest Pacific (Shatsky Rise, Ocean Drilling Program Site 1210) allow the unequivocal identification of 10 survivors. Evidence of shared adaptive strategies among these species provides the first indication that the extinctions were selective, with survival limited to a few neritic and/or opportunistic species, probably facilitated by hardiness and/or life-cycle escape strategies.

Keywords: Cretaceous-Tertiary boundary, calcareous nannoplankton, survivorship, extinction, selection.

INTRODUCTION

The Cretaceous-Tertiary (K-T) boundary is arguably the best-documented mass-extinction event, yet disputes remain over the intensity, rapidity, and selectivity of the biotic losses. In most cases, these debates concern the veracity of its fossil record, particularly the effects of sampling biases and reworking. There is good evidence for selectivity across a range of vertebrate and invertebrate fossil groups, and the event appears to have been strongly selective for those in food chains dependent on primary productivity. Animals in detritus-based food chains, and taxa with resistance to starvation, were most likely to survive (Sheehan et al., 1996). Among the primary producer groups, both the terrestrial plants and marine calcareous nannoplankton underwent significant extinctions, but there were much greater survival rates within the diatom and dinoflagellate phytoplankton, possibly facilitated by benthic, nonplanktonic cyst or spore resting stages (Kitchell et al., 1986; Knoll, 1989; Wendler and Willems, 2002).

The calcareous nannoplankton arguably provide the most striking record of abrupt and catastrophic K-T extinctions (Bramlette and Martini, 1964; Pospichal, 1996), but an understanding of their survivorship has been hampered by uncertainties introduced by the reworking and mixing evident in high-resolution data sets. Increasingly sophisticated separation and geochemical techniques have documented the ubiquity of abundant reworked microfossils in Danian sediments (e.g., MacLeod et al., 2001; Minoletti et al., 2005). A second approach, applied here, focuses on documenting greatly expanded post-extinction paleobiogeographic distributions.

Calcareous nannofossils are microscopic (1–20 μm) calcitic cell-wall coverings that occur in the millions in most post-Paleozoic marine sedimentary rocks, providing a stratigraphically continuous record of biotic change. Of 131 late Maastrichtian species, only 10–12 survived into the Danian (>90% species loss) (Bown et al., 2004), and the majority of extinctions occurred in a single geologically instantaneous event (Pospichal, 1996; Gartner, 1996; Gardin and Monechi, 1998). Recovery was characterized by a short interval dominated by atypical abundances of survivor species (''disaster'' taxa), often considered to represent acmes responding to continued environmental stress (Perch-Nielsen, 1985). However, because such small, dust-sized fossils are easily mixed or remobilized, details of this general pattern are poorly resolved.

Ocean Drilling Program (ODP) Leg 198 recovered K-T boundary sections from Shatsky Rise (northwest Pacific Ocean) that allow these uncertainties to be addressed. The sections are stratigraphically complete, carbonate rich, and relatively little affected by reworking, except for a short interval in the lowermost Paleocene. They provide one of the most complete records of nannoplankton survivorship and recovery yet reported, including almost all known survivor and incoming Cenozoic species. Survivor species can be unambiguously identified, and the patterns of extinction and survivorship (i.e., extinction selectivity) have significant implications for our comprehension of primary and secondary mass-extinction kill mechanisms.

MATERIAL AND METHODS

Shatsky Rise is an igneous plateau that was located at 10°N at 65.5 Ma, in water depths of 1.0–2.3 km. K-T sections were recovered from four ODP Leg 198 sites (Sites 1209–1212), all with comparable lithological successions, as follows: uppermost Maastrichtian white to pale orange nannofossil ooze overlain by a darker band of lowermost Paleocene grayish-orange foraminiferal ooze (~10 cm), grading into white foraminiferal-nannofossil chalk (20 cm), then grayish-orange nannofossil ooze. The sediments are bioturbated, with burrows ranging from 2 to 5 cm in depth (Bralower et al., 2002).

Abundance counts were performed on 32 samples from Hole 1210A, with sample spacing of 2–3 cm at the boundary (every ~6 k.y.), increasing to 10 cm above (every ~28 k.y.) (Bralower et al., 2002). The first 300 specimens or more were counted over at least five fields of view (FOV), and the count extended through the next 50 FOV, ignoring the most abundant taxa. The abundance of foraminifers and calcisphere fragments (>5 μm) was also estimated but not included in the 300 count.

RESULTS

The K-T boundary is identified at Site 1210 and other Shatsky Rise sites by the first occurrences of calcispheres and planktonic foraminifer debris in nannofossil smear slides, by characteristic planktonic foraminifer assemblages of the basal Danian P0 and Pα bio-

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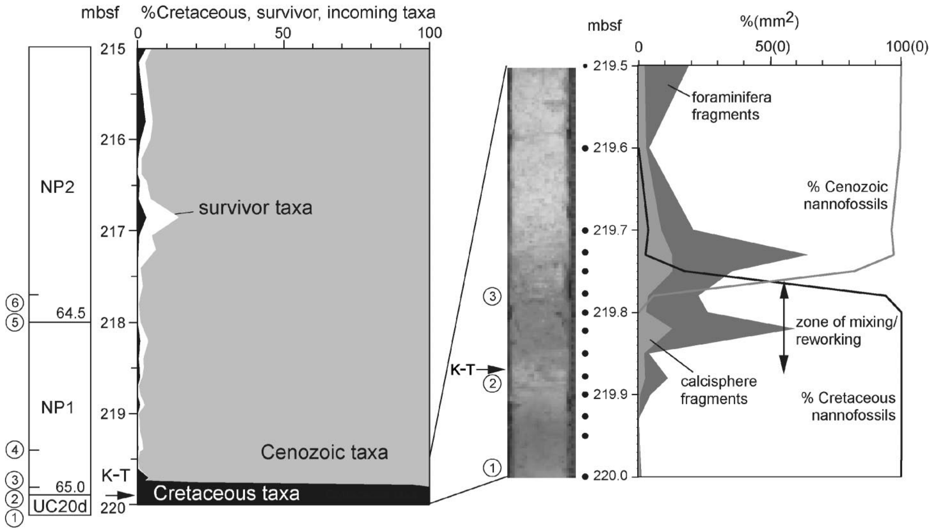

Figure 1. Percentages of Cretaceous, survivor, and Cenozoic calcareous nannofossils through studied section (left), and high-resolution data from Cretaceous-Tertiary (K-T) boundary interval (right), with core image, and sample locations shown by black dots; mbsf—meters below seafloor. Right plot also shows abundance estimates (specimens/mm^2) for calcisphere and foraminifer fragments. Also shown, at left, are nannoplankton (NP) zones of Martini (1971) and Upper Cretaceous (UC) subzone of Burnett (1998). Far left column: short dashes show subzonal boundaries of Jiang and Gartner (1986), and numbered bioevents are as follows: (1) presence of *Micula prinsii*; (2) calcisphere abundance increases; (3) first occurrence of (FO) *Neobiscutum*; (4) FO *Cruciplacolithus primus*; (5) FO *Cruciplacolithus intermedius*; (6) abundant *Futyania petalosa*.

zones, together with a subtle, yet distinct, lithological change to darker foraminiferal ooze with rare dispersed spherules at 219.85–219.87 m below seafloor (mbsf) (Fig. 1) (Bralower et al., 2002). Stratigraphic completeness is demonstrated by the presence of all apposite nannofossil zonal and subzonal marker species, i.e., *Micula prinsii*, calcispheres, *Neobiscutum* spp., *Cruciplacolithus primus*, *C. intermedius*, and *Futyania petalosa* (Perch-Nielsen, 1985; Jiang and Gartner, 1986) (Figs. 1 and 2). Nannofossil preservation was moderate to good throughout, and the presence of very small coccoliths (1–2 μm) is strong evidence for good preservation.

DISCUSSION

Survivor Record

The K-T boundary interval at Site 1210 is characterized by the abrupt disappearance of Cretaceous nannoplankton taxa and their rapid replacement by Cenozoic species (219.75–219.90 mbsf) (Figs. 1 and 2). At high resolution, however, the lowermost 12 cm of the Paleocene (219.78–219.90 mbsf) is dominated by Cretaceous taxa that are interpreted here as reworked-mixed (Fig. 1). This interpretation is based on integrated stratigraphic identification of the boundary, as described previously, together with direct evidence for mixing, as shown by burrows in the core. Above this mixed interval, the Cretaceous taxa show two distinct distribution patterns that allow for unequivocal differentiation between victims and survivors of the extinction event. First, the survivor species show continuous distributions that continue well into the Paleocene. In contrast, victim taxa disappear, or are infrequent and rare before disappearing (Fig. 2). Second, the survivors show discrete abundance trends that are clearly distinct from each other and those of reworking (Fig. 2). Third, of the 10 survivors, only one, *Zeugrhabdotus sigmoides*, is present at all in the Cretaceous sediments at Shatsky Rise, and so their presence above the boundary cannot be explained by local reworking or mixing (Fig. 2; for Maastrichtian assemblage data, see Lees and Bown, 2005).

Using these observations, the lower Paleocene of Site 1210 verifies the presence of 10 Cretaceous survivor species, including several not previously recognized as such. The first survivor assemblages occur directly above the mixed interval (219.80 m) and comprise a *Cyclagelosphaera reinhardtii* acme, as seen in many mid-latitude sections (Pospichal, 1996). *Watznaueria* and *Markalius* are consistently present, with varying abundances (Fig. 2). *Neocrepidolithus* and *Zeugrhabdotus* species appear in the assemblages ~1.5 m above the boundary. *Zeugrhabdotus sigmoides* increases in abundance until it dominates the survivor assemblage at +3.0 m (Fig. 2), a distinctive recovery distribution that is widely observed in the Tethys (Gardin, 2002), South Atlantic, Indian, and Southern Oceans (Pospichal, 1996), and in the Boreal North Sea Basin (Varol, 1989).

Incoming Cenozoic Taxa

The first of a succession of new Cenozoic species floods the assemblages ~10 cm above the K-T boundary (219.75 mbsf) (Fig. 2). The minute, low-birefringence *Neobiscutum* coccoliths are exceptionally abundant (~5500/mm^2), but are replaced by successive acmes of *Cruciplacolithus* and *Coccolithus*, along with *Praeprinsius* and *Futyania*. The size and relative simplicity of the coccolith architecture render inferences of ancestral affinities difficult, although these closely comparable morphologies strongly suggest shared ancestry. Current phylogenetic models suggest that the Mesozoic placolith family, Biscutaceae, gave rise to these incoming placolith taxa (Perch-Nielsen, 1985; Bown et al., 2004).

K-T Boundary Survivorship

Most nannoplankton survivors were holdover species that gave rise to few or no descendant taxa, but they were persistent, sometimes fleetingly abundant, and globally distributed in the Danian; notably, *Braarudosphaera* and *Calciosolenia* survive to the present day. Of the 10 survivors at Shatsky Rise, only *Z. sigmoides* was present, though infrequently, in the underlying Maastrichtian assemblages. Absence of the other nine taxa from the low-latitude, oceanic environment of Shatsky must have resulted from ecological or competitive exclusion. Their ocean-wide Danian distribution was therefore a remarkable geographical expansion from their Cretaceous range, presumably exploiting vacated photic-zone environments, cleared of oceanic nannoplankton that had made up most of the Maastrichtian biodiversity. It is unclear whether this expansion was simple opportunism, exploiting an ecological vacuum that was nevertheless a recovered and habitable environment, or alternatively a record of continued survivorship in a still hostile, but gradually recovering, ecosystem. That the post K-T colonization appears to have been incremental, first by small calcispheres and *Cyclagelosphaera* (with *Braarudosphaera* on the shelves), and then later by other survivors and incoming taxa, perhaps indicates a period of environmental amelioration prior to full recovery and subsequent recuperation of diversity.

Survivor Paleoecology

The distribution of calcareous nannoplankton in surface waters, and subsequently seafloor sediments, reflects the environmental preferences of the individual taxa (Winter et al., 1994). Although most Cretaceous species are long extinct, their paleoecologies can be

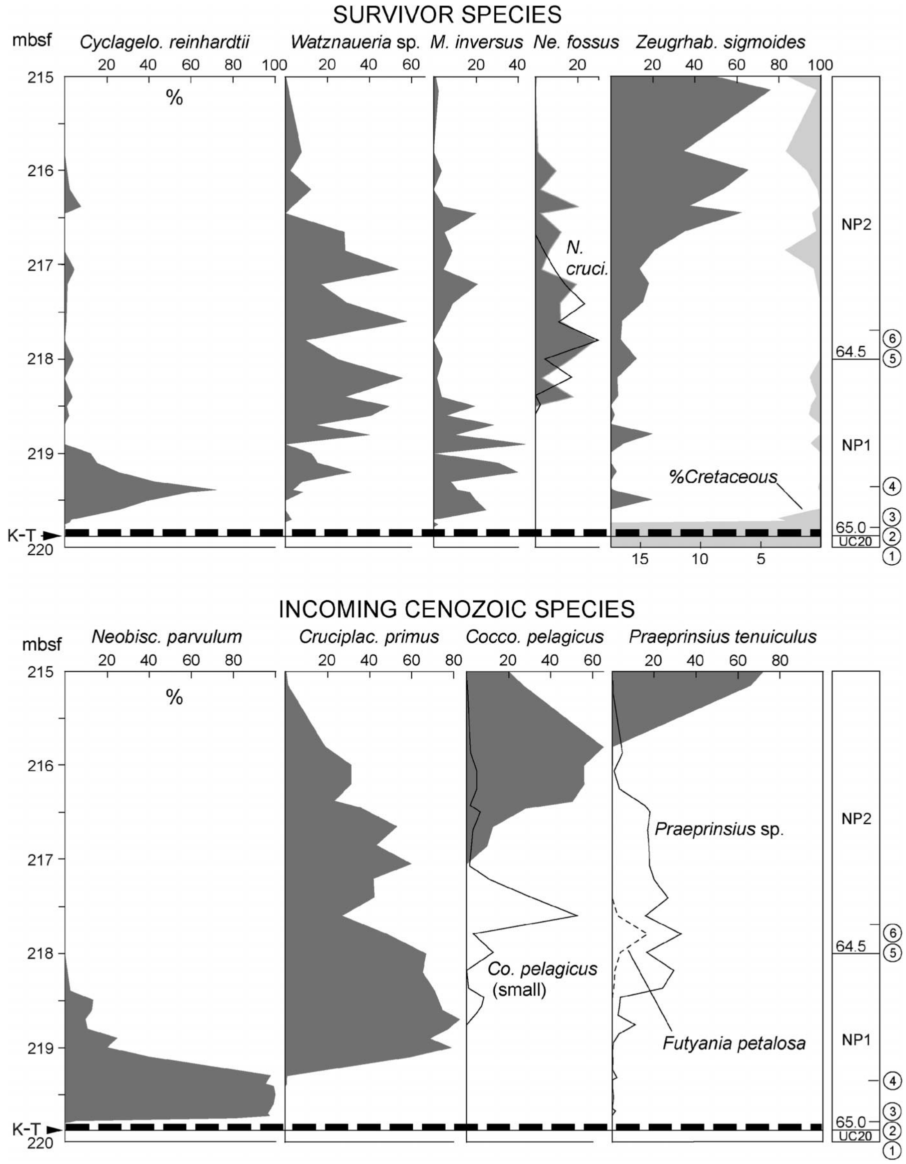

Figure 2. Abundances of principal survivor and incoming Cenozoic nannofossils. Survivor species counts are percentages of survivor assemblage. Incoming Cenozoic species counts are percentages of total assemblage. Additional taxa are shown as line plots. Interval of mixed-reworked nannofossil taxa is shown as dashed line, and Cretaceous-Tertiary (K-T) boundary level is shown by black line. Biostratigraphic information as for Figure 1 (mbsf—meters below seafloor). Full taxonomic names as follows: *Cyclagelosphaera margerelii*, *Markalius inversus*, *Neocrepidolithus fossus–cruciatus*, *Zeugrhabdotus sigmoides*, *Neobiscutum parvulum*, *Cruciplacolithus primus*, *Coccolithus pelagicus*.

reconstructed by examining distributions, abundances, and relationships with other paleoenvironmental proxies (Mutterlose et al., 2005). There are two categories of K-T nannoplankton survivors: those that were long ranging and widely, often commonly, distributed in the Cretaceous seas (*Watznaueria*, *Cyclagelosphaera*, *Biscutum*, *Zeugrhabdotus*), and those that were typically rare and infrequent (*Braarudosphaera*, *Calciosolenia*, *Markalius*, *Neocrepidolithus*, *Goniolithus*, *Lapideacassis*, holococcoliths) (Lees, 2002). The paleoecologies of the first group, in particular, reveal commonalities that suggest that survivorship success may have been selective.

The genera *Biscutum* and *Zeugrhabdotus* are widely recognized as the most extreme Cretaceous examples of *r*-selected (opportunistic) taxa that were adapted to eutrophic, cold-water environments (Roth and Bowdler, 1981; Watkins, 1989; Erba, 1992), and they were also significantly more abundant at high latitudes, both prior to and immediately after the K-T extinction event (Pospichal and Wise, 1990; Pospichal, 1996). Similarly, *Cyclagelosphaera* was most abundant in eutrophic, neritic, and even lagoonal settings through the Jurassic and Cretaceous (Tribovillard et al., 1992; Lees et al., 2004). *Watznaueria* was the most abundant and widely distributed Mesozoic coccolithophore and a eurytopic, hardy, probably broadly *r*-strategist taxon (Negri et al., 2003; Lees et al., 2004).

Paleoecologies of the second group of survivors are less well understood, but they were more consistently and abundantly present in Late Cretaceous shelf settings and, in some cases, at higher latitudes (Pospichal and Wise, 1990; Lees, 2002). *Calciosolenia* has a neritic distribution at present and is competitive with diatoms, and therefore is almost certainly an *r*-strategist (Andruleit et al., 2003). *Braarudosphaera* was, and still is, a sporadic bloom taxon with strongly neritic biogeography, probably related to nutrient enrichment and/or low salinity, and is generally absent in oceanic settings (Peleo-Alampay et al., 1999; Kelly et al., 2003).

Survival Strategy

The survivor paleoecologies reveal striking evidence of shared adaptive strategies and the first indication that K-T nannoplankton extinctions were selective. Of the 12 nannofossil survivor species, at least half, and possibly all, were *r*-selected opportunists that were more abundant in, and in some cases restricted to, neritic and high-latitude environments during the Late Cretaceous. Following the extinctions, most survivor species continued abundantly at high-latitude and shelf sites, but extended their distribution into oceanic habitats that were previously dominated by Cretaceous species with K-selected (specialist) taxa. These oceanic taxa, adapted to stable, stratified, oligotrophic ocean habitats, were the principal victims of the extinction event.

Clearly, the dramatic decline of calcareous nannoplankton throughout the global ocean required environmental perturbation that is compatible with the hypothesized major impact-winter event, and it is likely that survival was limited to those species able to temporarily endure or escape disruption in the upper water column. Most living cocco lithophores are truly open-ocean adapted, without the escape strategies employed by some diatoms and dinoflagellates, such as encystment, resting spores, and/or benthic lifecycle stages. However, such strategies have been adopted by a number of extant coastal nannoplankton (Billard, 1994). If similar adaptations were present in Cretaceous taxa living in shelf or coastal settings, then this ability may have promoted survival through the K-T boundary event. It is notable that the most abundant survivors in the nannoplankton size range were calcareous dinoflagellates, albeit dwarfed populations, and this group was clearly able to encyst when encountering stressful environmental conditions. However, two of the nannoplankton survivors, *Braaru-*

dosphaera and *Lapideacassis*, also had unusual, imperforate, cystlike morphologies, and these may have provided similar encystment refuges. That the remaining coccolith survivors included the most abundant, widespread, eurytopic, and opportunistic Cretaceous species also indicates that hardiness alone was enough to ensure survival for some species, although this may have entailed the ability to survive deeper in the photic zone and/or to endure extreme and widely variable surface-water parameters such as temperature, light intensity, and pH.

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