Recovery of the deep-sea floor after the Cretaceous–Paleogene boundary event: The benthic foraminiferal record in the Basque–Cantabrian basin and in South-eastern Spain

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Abstract

A detailed analysis of the Upper Cretaceous and lower Paleogene benthic foraminiferal assemblages (>63 μm) from the middle bathyal Loya section (Basque–Cantabrian Basin, Southwestern France) has been carried out. The benthic foraminiferal and palaeoenvironmental turnover across the K/Pg boundary at Loya has been compared to that observed in the nearby Bidart section. Both sections exhibit mesotrophic conditions in the uppermost Maastrichtian, and a drastic decrease in the nutrient supply to the sea floor in coincidence with the K/Pg boundary. Moreover, a faunal recovery of the assemblages is observed through the lowermost Danian.

The pattern of faunal and palaeoenvironmental recovery in the Basque–Cantabrian Basin has been compared to that observed in the middle bathyal Agost and Caravaca sections (South-eastern Spain), where a similar decrease in the food supply to the sea floor is observed in coincidence with the K/Pg boundary. However, whereas low oxygen conditions have been recorded in the lowermost Danian in these two sections, no evidence for oxygen deficiency has been found in the Basque–Cantabrian Basin, thus pointing to the regional – and not global – nature of low oxygen conditions following the K/Pg boundary event.

Benthic foraminifera from the G. cretacea Biozone suggest environmental instability in the Basque–Cantabrian Basin and in Southeastern Spain. Such environmental stress has been related not only to the collapse of the food web due to the extinction of calcareous primary producers, but also to a rapidly changing food supply driven by phytoplankton blooms. Although stabilization of the ecosystems in surface waters probably occurred towards the upper part of the G. cretacea Biozone, data available from the Ps. pseudobulloides Biozone at Bidart and Agost indicate that food supply to the benthos had not completely recovered, at least, 200 kyr after the K/Pg boundary.

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1. Introduction

The Cretaceous/Paleogene (K/Pg) boundary marks a period of major faunal turnover on Earth. The numerous extinctions recorded in both terrestrial and oceanic environments have been commonly linked to the effects of a bolide impact that occurred just at the K/Pg boundary (Alvarez et al., 1980; Smit and Hertogen, 1980). The impact hypothesis also accounts for the anomalous enrichment in iridium and other extraterrestrial impact evidence in the boundary sediments globally, as well as for the abrupt changes in δ13C and δ18O values in bulk sediment and in tests of foraminifera...
It has been broadly documented that planktonic foraminifera, among other groups of calcareous plankton, were dramatically affected by the K/Pg boundary event (e.g., Luterbacher and Premoli-Silva, 1964; Smit, 1990), and show a catastrophic mass extinction pattern in coincidence with the boundary (e.g., Molina et al., 1998). However, there is a reduced group of researchers who do not support this model, and suggest that the extinctions were gradual and started in the Maastrichtian (e.g., Keller, 1989a, b, 2003).

In contrast to planktonic foraminifera, deep-sea benthic foraminifera do not show significant extinctions in coincidence with the K/Pg boundary, but drastic changes in their community structure, followed by a gradual and staggered pattern of recovery across the early Danian (e.g., Culver, 2003; Alegret and Thomas, 2005). Such temporary changes in benthic foraminiferal assemblages have been interpreted as resulting from the collapse of the pelagic food web and the subsequent drop in food supply to the benthos (e.g., Thomas, 1990a, b; Kuhnt and Kaminski, 1993; Culver, 2003). However, benthic foraminiferal assemblages exhibit different patterns of recovery through the lowermost Danian depending on their palaeogeographical distribution, and the palaeoenvironmental conditions after the K/Pg boundary are not clear (e.g., Alegret and Thomas, 2005). Since benthic foraminifera are excellent indicators of ocean productivity or oxygenation (e.g., Van der Zwaan et al., 1999), high-resolution analysis of the assemblages is thus needed to perform a detailed reconstruction of the palaeoenvironmental turnover across the K/Pg boundary.

The Basque–Cantabrian Basin (Northern Spain and Southwestern France) yields some of the most complete K/Pg boundary sections in Southwestern Europe (Seyve, 1990; Haslett, 1994; Molina et al., 1998). Moreover, this area is particularly important because of its palaeogeographical location during the Late Cretaceous and Early Paleogene, between the Tethys and the North Atlantic. Due to these reasons, K/Pg boundary sections from the Basque–Cantabrian Basin have been studied by numerous authors from different points of view such as stable isotope analysis (Romein and Smit, 1981; Renard et al., 1982; Margolis et al., 1987; Nelson et al., 1991), iridium content (Delacotte, 1982; Smit and ten Kate, 1982; Bonté et al., 1984; Rocchia et al., 1988), magnetostratigraphy or biostratigraphy (e.g., Delacotte et al., 1985; Mary et al., 1991; Haslett, 1994; Fondecave-Wallez et al., 1995; Apellaniz et al., 1997; Arenillas et al., 1998), among others. However, detailed analysis on the Upper Cretaceous and lowermost Paleogene benthic foraminiferal assemblages from this area are scarce (e.g., Kuhnt and Kaminski, 1993, Zumaya and Sopelana sections; Alegret et al., 2004, Bidart section).

In order to obtain more detailed information on the benthic foraminiferal and palaeoenvironmental turnover across the K/Pg boundary in this area, and especially on the recovery of primary productivity through the lowermost Danian, a high-resolution analysis of benthic foraminiferal assemblages has been carried out in the Loya section (Southwestern France, 19 km from Bidart, and 70 km and 140 km from the Zumaya and Sopelana sections, respectively; Fig. 1). No detailed studies on K–Pg benthic foraminifera have been carried out in this section, up to now. The aim of this paper is thus to perform a detailed quantitative analysis of the uppermost Cretaceous and lowermost Danian benthic foraminiferal assemblages from the Loya section, and to compare the faunal and the palaeoenvironmental turnover with those inferred from the nearby Bidart section.

Recently, Alegret and Thomas (2005) carried out a correlation of the benthic foraminiferal and palaeoenvironmental turnover across the K/Pg boundary among several basins such as the central North Pacific, the North-western Atlantic, the Gulf of Mexico, and the Tethys area, but no correlation has been shown between the Basque–Cantabrian Basin and other basins, up to now. By means of such a correlation, environmental changes will be assessed and linked to local or global causes. One of the aims of this paper is thus to compare the faunal and palaeoenvironmental turnover in the Basque–Cantabrian Basin (Loya and Bidart sections) with that inferred from two of the most expanded and well preserved K/Pg boundary sections in South-eastern Spain, such as the Caravaca and Agost sections (e.g., Molina et al., 2005; Smit, 2005). Very high-resolution benthic foraminiferal data are available from these middle-bathyal sections, where low oxygen conditions prevailed at the sea floor for the first 10 kyr of the Danian (Coccioni et al., 1993; Coccioni and Galeotti, 1994; Alegret et al., 2003). Correlation between this area and the Basque–Cantabrian basin will provide information on the temporal and palaeogeographical extent of low oxygen conditions at the sea floor, in order to evaluate K/Pg extinction hypotheses that argue for widespread oceanic anoxia (e.g., Kajiwara and Kahi, 1992; Kahi et al., 1999).

2. Material and methods

The Loya section is located in the vicinity of Pointe–Sainte–Anne, close to Hendaye (Southwestern France),
within the Basque–Cantabrian basin. It is situated 19 km southwest of the Bidart section (Fig. 1), close to the French–Spanish border. The outcrop is located at Bay of Loya, close to a cliff situated towards the northeastern side of the beach. Although access is hazardous (Seyve, 1990), the analysis of this outcrop may provide additional information on the K/Pg boundary event, and it may be useful for correlation of the faunal and palaeoenvironmental turnover between the Bidart section and other sections from the Basque–Cantabrian Basin.

Upper Cretaceous sediments at Loya consist of a grey to brown marly sequence that contains abundant and well-preserved benthic and planktonic foraminifera. The uppermost 3 m of the Maastrichtian have been sampled and analysed. The K/Pg boundary is marked by a sharp contact between the Maastrichtian marls and a 26-cm-thick dark grey to reddish clay level that contains a ∼2-cm-thick dark rusty layer at its base. This clay level is overlain by two tabular, 30-cm-thick levels of massive limestones, and higher in the section, by a tabular, heterogeneous breccia.

In order to perform a detailed analysis of the benthic foraminiferal and palaeoenvironmental recovery after the K/Pg boundary, high-resolution sampling was carried out in the lowermost 26 cm of the Danian.

All samples were disaggregated in water with diluted H₂O₂ and washed through a 63 μm sieve. Quantitative studies were based on representative splits of 300 or more specimens of benthic foraminifera from the >63 μm fraction when possible, which were obtained with a modified Otto microsplitter. All specimens were picked, identified, counted and mounted on microslides for a permanent record. Benthic foraminifera were identified at the generic level largely following Loeblich and Tappan (1987) and at the specific level following Alegret and Thomas (2001) and Alegret et al. (2003). The Fisher-α index and the H(S) Shannon-Weaver index were calculated as proxies for diversity and heterogeneity of the assemblages; the percentages of calcareous and agglutinated benthic foraminifera were also worked out. Furthermore, morphotypic analysis was performed following Corliss (1985), Jones and Charnock (1985) and Corliss and Chen (1988). All specimens were allocated to infaunal (living at >1 cm depth) and epifaunal morphogroups (living at the sediment surface or in its uppermost cm). Although caution must be taken with microhabitat assignments (Buzas et al., 1993), the relative abundance of morphotypes has been commonly used as an indicator of delivery of food to the sea floor (e.g., Gooday, 2003).

The faunal turnover across the K/Pg boundary at the Loya section has been compared to that inferred by Alegret et al. (2004) from the nearby Bidart section. The faunal and palaeoenvironmental recovery during the lowermost Danian in the Basque–Cantabrian basin was then correlated to the high-resolution benthic foraminiferal analysis performed by Coccioni et al. (1993) and Alegret et al. (2003) in the Caravaca and Agost sections (Southeastern Spain, Tethys Region). The later two sections are located in the Betic Cordilleras, and consist of pelagic gray marls with abundant microfossils that were deposited in middle bathyal environments (Coccioni et al., 1993; Coccioni and Galeotti, 1994; Alegret et al., 2003). The K/Pg boundary in these sections is located in the contact between the Maastrichtian marls and a ∼10 cm-thick layer of black clays, with a 2–3 mm-thick, ferruginous level at its base. The clay layer contains an anomalous concentration in iridium, a very low CaCO₃ content, a negative shift in bulk δ¹³C values, and trace elements indicative of low oxygen conditions (Smit, 1990; Martinez-Ruiz et al., 1992, 1999). Scattered
samples from the Caravaca section were analysed in order to ensure that the taxonomy and size fraction used by Coccioni et al. (1993) are consistent to those used in this study and by Alegret et al. (2003, 2004) in the Agost and Bidart sections.

3. Benthic foraminifera from the Loya section (Southwestern France)

3.1. Palaeobathymetry

Benthic foraminiferal assemblages at Loya are dominated by calcareous tests (Fig. 2), and indicate deposition well above the calcite compensation depth. The planktonic/benthic ratio is high (90%) in all samples except for those from the lowermost Danian, which are dominated by benthic foraminifera.

Detailed palaeobathymetric assignments have been based on the upper depth-limits and depth distribution of benthic foraminiferal species as reviewed by Van Morkhoven et al. (1986), Alegret and Thomas (2001), and Alegret et al. (2003).

Benthic foraminiferal assemblages contain abundant representatives of the bathyal and abyssal Velasco-type fauna (Berggren and Aubert, 1975), namely Cibicidoides velascoensis, Gaudryina pyramidata, Gyroidinoides globosus, Nuttallides truempyi, Nuttallinella floreais, Osangularia velascoensis, or Stensioeina beccariiformis. Other taxa typical from upper and middle bathyal depths (e.g., Bolivinoides delicatulus, Coryphostoma incrassata.

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Fig. 2. Benthic foraminiferal indices across the K/Pg boundary at Loya. A, Percentage of calcareous and agglutinated taxa; B, H(s) Shannon–Weaver index; C, α–Fisher diversity index; D, Relative abundance of infaunal and epifaunal morphotypes. G. cre. = G. cretacea Biozone; Pv. eu. = Pv. eugubina.
forma gigantea, Oridoridals plummerae, Osangularia plummerae, Praebuliminina reussi), and from middle bathyal to abyssal depths (e.g., Buliminella beaumonti, Cibicidoides hyphalus, Marssonella oxycoa, Spiroplectammina spectabilis) are also common. The upper depth limit of some of the species is located at ~500–700 m depth (e.g., Nuttallinella floraeals, Stensioeina beccariiformis, Spiroplectammina spectabilis). These data suggest that the upper Maastrichtian and lowermost Danian sediments at Loya were deposited in the middle part of the slope.

Loxostomum eleyi makes up 0.3 to 4.4% of the assemblages in the upper Maastrichtian, and the specimens analysed show no evidence for reworking. Although this species is typical of outer shelf environments (MacNeil and Caldwell, 1981; Nyong and Olsson, 1984), its depth occurrence may increase under a high food supply, as suggested by Alegret et al. (2003, 2004) at the Agost and Bidart sections. Moreover, the high percentage of infaunal morphotypes in the upper Maastrichtian indicates a high food supply to the sea floor; under such conditions, the depth of occurrence of L. eleyi may have been somewhat greater than at other locations. The occurrence of L. eleyi at Loya might indicate that deposition occurred in the uppermost part of a middle bathyal environment.

3.2. Benthic foraminiferal assemblages

Uppermost Maastrichtian benthic foraminiferal assemblages from the Loya section are highly diverse and heterogeneous, and they are strongly dominated by calcareous taxa (Fig. 2). The percentage of infaunal morphotypes (e.g., Gyroidinoides beisseli, laevidentalinids, Lenticulina spp., Loxostomum eleyi, Praebuliminina reussi, Pyrulinoides spp.) makes up 60% of the assemblages; Osangularia spp., Stensioeina beccariiformis, Cibicidoides hyphalus and Nuttallinella spp. are most abundant among epifaunal taxa (Fig. 3).

Four benthic foraminiferal species, namely Globulina prisca, Loxostomum eleyi, Praebuliminina reussi and Stiella sp., have their uppermost occurrence at the K/Pg boundary (where they make up 4.7% of the assemblage). In spite of the scarcity of significant extinctions, benthic foraminifera underwent a major faunal turnover in coincidence with the boundary, where a drastic decrease in the percentage of infaunal morphogroups, as well as in diversity and heterogeneity of the assemblages, have been recorded (Fig. 2).

A stepped pattern of recovery is observed in the lowermost Danian (Fig. 4). Assemblages from the lowermost part of the G. cretacea Biozone are clearly dominated by epifaunal taxa (61% of the assemblages), mainly by the species Stensioeina beccariiformis (30% of the assemblages); among the infaunal morphogroups, Recurvoides makes up to 23% of the assemblages (Fig. 4). The highest percentage of agglutinated taxa (43%) is observed during this interval.

The second step corresponds to the middle part of the G. cretacea Biozone. In addition to the high percentages of Stensioeina beccariiformis and Recurvoides spp., this interval is also characterised by peaks in the relative abundance of Cibicidoides hyphalus, Karrerulina spp., Osangularia spp. and trochamminids. Heterogeneity and diversity of the assemblages are low during this interval.

In the upper part of the G. cretacea Biozone and the lower 3 cm of the Pv. eugubina Biozone, the former dominant Stensioeina beccariiformis becomes a minor component of the assemblages, and the percentages of Globorotalites sp. and Osangularia spp., as well as the diversity and heterogeneity of the assemblages, significantly increase (Figs. 2, 4).

Benthic foraminiferal assemblages from the uppermost part of the studied section (Pv. eugubina Biozone) are clearly dominated by the epifaunal Osangularia spp. and Globorotalites sp. (Fig. 4); among the agglutinated taxa, which make up 33–39% of the assemblages, Recurvoides spp., trochamminids and Karrerulina spp. dominate. Diversity and heterogeneity of the assemblages, and the percentages of infaunal morphotypes, are low compared to the Maastrichtian values (Fig. 2).

4. Benthic foraminiferal and palaeoenvironmental turnover across the K/Pg boundary

4.1. Basque–Cantabrian Basin (Loya and Bidart sections, Southwestern France)

Agglutinated benthic foraminifera make up 10% of the assemblages at the Bidart section (Alegret et al., 2004), whereas at Loya ~20% and ~40% of the foraminifera belong to agglutinated forms in the Upper Maastrichtian and lowermost Danian, respectively. According to Kuhnt and Kaminski (1993), agglutinated forms make up two thirds of the assemblages at the coeval Sopelana and Zumaya sections (Basque Country), which may indicate a greater supply of terrigenous material as compared to Bidart and Loya (Kaminski et al., 1988).

Upper Maastrichtian benthic foraminiferal assemblages at Loya consist of a mixture of infaunal and epifaunal morphogroups, suggesting mesotrophic conditions at the sea floor. Similar palaeoenvironmental conditions occurred at Bidart, where infaunal morphogroups
Fig. 3. Percentages of the most abundant benthic foraminiferal taxa in the upper Maastrichtian and lowermost Danian sediments from Loya.

<table>
<thead>
<tr>
<th>MAASTRICHTIAN</th>
<th>DANIAN</th>
<th>AGE</th>
<th>BIOZONES</th>
<th>LITHOLOGY</th>
<th>THICKNESS (cm) &amp; SAMPLES</th>
</tr>
</thead>
<tbody>
<tr>
<td>A. mayaroensis</td>
<td>G. cretacea</td>
<td>P. eugub.</td>
<td>L.</td>
<td>L.</td>
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</table>
also make up ~60% of the assemblages in the uppermost 4 m of the Maastrichtian (Alegret et al., 2004). Although the percentage of agglutinated taxa is slightly lower at Bidart, the relative abundance of agglutinated species increases in both sections towards the uppermost 10 cm of the Maastrichtian, where they make up 25% to 32% of the assemblages.

Benthic foraminiferal assemblages underwent a significant faunal turnover in coincidence with the K/Pg boundary. The percentage of infaunal morphogroups, as well as the diversity and heterogeneity of the assemblages, drastically decreased at the boundary in both sections. The epifaunal *Stensioeina beccariiformis* bloomed just after the K/Pg boundary (lowermost part of the *G. cretacea* Biozone) at Loya and Bidart (Figs. 4, 5). However, whereas *Recurvoides* also dominated the assemblages during this interval at Loya, quantitative peaks in the abundance of *Cibicidoides hyphalus* and *Coryphostoma incrassata forma gigantea* are recorded at Bidart (Fig. 5). Overall, assemblages from the lowermost part of the *G. cretacea* Biozone are dominated by epifaunal morphotypes, indicating oligotrophic conditions at the sea floor. Such a decrease in the nutrient supply to the sea floor has been related to the decrease in organic flux from the surface waters as the result of the mass extinction of primary producers (e.g., D'Hondt et al., 1998). The collapse of the food web is thought to have been the main parameter that determined the benthic foraminiferal turnover directly after the K/Pg boundary. The high percentages of certain infaunal taxa within the CaCO₃ depleted boundary layer,
such as *Recurvoides* at Loya or *Coryphostoma incrassata forma gigantea* at Bidart, might be related to high-productivity conditions driven by phytoplankton blooms, such as the dinoflagellates *Thoracosphaera operculata*, *Cyclagelosphaera reinhardii* and *Braadurosphaera bigelowii* blooms reported from the dark clay layer at Bidart (Peybernés et al., 1996). Under such conditions, *Recurvoides* and *C. incrassata forma gigantea* might have behaved as opportunistic taxa, taking over the infaunal niche whenever other taxa could not compete.

The maximum abundance of *Cibicidoides hyphalus* at Loya and Bidart is recorded in the middle part of the *G. cretacea* Biozone (∼5 cm above the K/Pg boundary), where the percentage of *Stensioeina beccariiformis* drops (Figs. 4, 5). In spite of the common occurrence of some infaunal taxa such as *C. incrassata forma gigantea* at Bidart, or *Recurvoides* spp. and *Karrerulina* spp. at Loya, assemblages are still dominated by epifaunal morphotypes, indicating oligotrophic conditions represented by this interval.

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**Fig. 5.** Percentages and scanning electron-micrographs of the most significant benthic foraminiferal taxa in the lowermost Danian sediments from Bidart. Biostratigraphy by Haslett (1994), Peybernés et al. (1996), and Apellaniz et al. (1997). 1, 2, 3, *Stensioeina beccariiformis*; 4, *Coryphostoma incrassata forma gigantea*; 5, 6, 7, *Cibicidoides hyphalus*; 8, 9, *Globorotalites* sp.; 10, 11, *Nuttallides truempyi*; 12, *Spiroplectammina israelskyi*. Scale bars 200 μm.
Diversity and heterogeneity of the assemblages significantly recover through the upper part of the G. cretacea Biozone and the lowermost part of the *Pv. eugubina* Biozone, although they are still low compared to the upper Maastrichtian values. The percentages of *Globorotalites* sp. and *Osangularia* spp. gradually increase during this interval at Loya and Bidart. These two taxa become dominant through the *Pv. eugubina* Biozone, where the food supply is still low as inferred from the abundance of epifaunal taxa. Data available from the Bidart section indicate that food supply to the benthos had not recovered by the *Ps. pseudobulloides* Biochron, more than 200 kyr after the K/Pg boundary (Alegret et al., 2004; this paper).

This pattern of recovery is compatible with that described by Kuhnt and Kaminski (1993) in the Zumaya and Sopelana sections (Fig. 1). These authors inferred a period of reduced primary productivity after the K/Pg boundary, with epifaunal, *Gavelinella* and *Stenstoeina*-dominated assemblages in the lower part of the boundary clay layer, and high percentages of the infaunal *Spirelectammina israelskyi* at the top of it. They also documented increased percentages of opportunistic species just after the K/Pg boundary. This fact may indicate that, in addition to the drastic decrease in primary productivity by calcareous plankton just at the K/Pg boundary, blooms of certain primary producers (e.g., *Thoracosphaera operculata*, *Cyclagelosphaera reinhardii* and *Braadurosphaera bigelowii*; Peybernés et al., 1996) might have spread throughout the Basque–Cantabrian basin during the lowermost Danian.

### 4.2 Comparison to the faunal turnover in Southeastern Spain, Tethys area

A comparison between the stepped pattern of recovery of benthic foraminiferal assemblages during the lowermost Danian in the Basque–Cantabrian basin (Bidart and Loya sections) and in Southeastern Spain (Agost and Caravaca sections) is here shown. Uppermost Maastrichtian and lowermost Danian sediments from all these sections were deposited at middle bathyal depths (Coccioni et al., 1993; Coccioni and Galeotti, 1994; Widmark and Speijer, 1997; Coccioni et al., 2003, 2004).

A temporary faunal turnover consisting of the reorganization of the benthic foraminiferal community structure — but no major extinctions — starting at the K/Pg boundary has been reported from Southeastern Spain. Coccioni et al. (1993) documented a very short interval (<1 cm of sediment) of high-food, low oxygen conditions in the lowermost Danian at Caravaca, where the assemblages (fraction >125 μm) are dominated by *Bolivina* (*Coryphostoma*) and *Spirelectammina* (Fig. 6). Since the latter results cannot be directly compared to the studies here reported, which are based on the fraction >63 μm, some scattered samples of the fraction larger than 63 μm have been here analysed; assemblages from the lowermost 2 cm of the Danian are mainly—but not exclusively—dominated by laevidentalinids and *Coryphostoma*. Other taxa such as *Gyroidinoideas depressus*, *Valvalabamina lenticula*, *Anomalinoideas*, *Pleurostomella*, *Stilosomella*, *Fursenkoina* are common components of the assemblages (Fig. 6). The latter three taxa, together with *Coryphostoma*, present small, tapered and non-ornamented tests with abundant pores, and are common in dysaerobic environments (e.g., Leutenegger and Hansen, 1979; Bernhard, 1986). Moreover, assemblages from the lowermost 2 cm of the Danian are dominated by infaunal taxa (62% of the assemblages), which may indicate low oxygen conditions at the sea floor (Jorissen et al., 1995).

In contrast to Caravaca, a drastic decrease in the percentage of infaunal morphotypes has been recorded in coincidence with the K/Pg boundary at Agost (Alegret et al., 2003). These authors also documented several peaks of opportunistic taxa in the lowermost Danian dark clay layer (Fig. 6), and interpreted them as indicators of an overall decrease in primary productivity combined with environmental instability, with benthos receiving food from short-lived, local blooms of primary producers. Although benthic foraminifera are rare in the dark clay layer, faunas show a series of short-term peaks of low-oxygen tolerant, opportunistic taxa (e.g., Kaminski et al., 1996; Fig. 6). Moreover, geochemical data suggest that low oxygen conditions occurred at Agost and were even more severe than at Caravaca (Martinez-Ruiz et al., 1992, 1999); such conditions prevailed at the sea floor at Agost during the deposition of the dark clays (i.e., during the first 10–15 kyr of the Danian; Alegret et al., 2003).

Whereas faunal and geochemical data indicate low oxygen conditions during the earliest Danian in Southeastern Spain (Agost and Caravaca sections), no evidence for oxygen deficiency at the sea floor has been found in sections from the Basque–Cantabrian Basin. Instead, benthic foraminiferal assemblages show clear evidence for a drastic decrease in the food supply to the benthos in coincidence with the K/Pg boundary, and environmental instability during the earliest Danian (e.g., Kuhnt and Kaminski, 1993; Alegret et al., 2004; this paper). These data are compatible with the results presented by Alegret and Thomas (2005), who argued that only local or regional — not global — anoxia occurred at the sea floor after the K/Pg boundary. Alegret
Fig. 6. Percentages and scanning electron-micrographs of the most significant benthic foraminiferal taxa in the lowermost Danian sediments from Agost and Caravaca. (A) Myr according to Molina et al. (1996). (B) Biostratigraphy by Molina et al. (1996) and Coccioni et al. (1993).

- **Stensioeina excolata**
- **Stilostomella sp.**
- **Spiroplectammina spectabilis**
- **Haplophragmoides spp.**
- **Anomalinae acuta**
- **Pyramidina rudita**

Agost

- **Globorotalites sp.** (11-13)
- **Pleurostomella spp.** (14-15)
- **Stensioeina beccariiformis** (5-7)
- **Coryphostoma incrassata forma gigantea** (10)
- **Repmanina charoides** (8-9)
- **Globoconulina grybowskii**

Caravaca

- Politaxic assemblages with complex trophic structure

- Epifaunal: Bathysiphon, Gyroidinoideas, Osangularia, Stensioeina, Repmanina
- Infaunal: Dorothis, Bolivinoides
- Mobile infaunal: Trochamminoides, Recurvoides (20)

- **Laevidentalinae, Coryphostoma spp., Valvulabamina lenticula, Gyroidinoideas depressus** (18-19)
- **Anomalinae, Pleurostomella (16), Stilostomella (17), Fursenkoidea**

*This study (>63 microns): Laevidentalinae, Coryphostoma spp., Valvulabamina lenticula, Gyroidinoideas depressus (18-19), Anomalinae, Pleurostomella (16), Stilostomella (17), Fursenkoidea.*

Scale bars 100 μm.
et al. (2003) suggested that the dissociation of gas hydrates that occurred along the western North Atlantic margin due to a K/Pg meteorite impact might account for the low oxygen conditions, as well as to a locally enhanced bacterial food supply to the benthos.

Environmental instability after the K/Pg boundary has been recorded not only in the Basque–Cantabrian Basin and Southeastern Spain, but also in many other sites worldwide (e.g., Peryt et al., 2002; Alegret and Thomas, 2005), and it is probably related to a major change in the composition of the food supply as a result of the mass extinction of phytoplankton, as well as a rapidly changing food supply driven by blooms (Alegret et al., 2003). Geographic variability in the composition and extent of the phytoplankton blooms (e.g., Romein, 1977; Thierstein, 1981; Perch-Nielsen et al., 1982; Peybernés et al., 1996) might be a cause of the different patterns of post K/Pg benthic foraminiferal faunal composition at different sites (e.g., Coccioni et al., 1993; Culver, 2003; Alegret et al., 2003, 2004; Alegret and Thomas, 2005).

The slight recovery in the diversity and heterogeneity of the assemblages through the upper part of the *G. cretacea* Biozone and the lowermost part of the *Pv. eugubina* Biozone is probably linked to the recovery of the phytoplankton and stabilization of the ecosystems in surface waters; however, the dominance of epifaunal morphotypes suggests that food supply to the benthos did not completely recover for at least the studied part of the *Pv. eugubina* Biozone. *Globorotalites* sp. is abundant within this interval not only at Loya, Bidart and Agost (Figs. 4–6), but also in other K/Pg boundary sections from Mexico (Alegret et al., 2001a; Alegret and Thomas, 2005) and from the Northwestern Atlantic (Blake Nose Hole 1049C; Alegret and Thomas, 2004). High percentages of this taxon are thus recorded after the beginning of the stabilization of the phytoplankton and under the oligotrophic conditions inferred for the *Pv. eugubina* Biozone, and might thus be useful for biostratigraphical purposes.

Benthic foraminiferal data available from the Bidart and Agost sections indicate that primary productivity had not recovered by the *Ps. pseudobulloides* Biochron, more than 200 kyr after the K/Pg boundary (Alegret et al., 2003, 2004). A similar timing of recovery has been documented from the South Atlantic (Widmark and Malmgren, 1992), Mexico (Alegret et al., 2001a,b), Austria (Peryt et al., 1997) and Tunisia (Peryt et al., 2002), and is compatible with the evolutionary recovery of the phytoplankton (and of the food web that was dependent upon it) after a major disruption at the K/Pg boundary.

5. Conclusions

Benthic foraminiferal assemblages from the Upper Cretaceous to lower Paleogene Loya section (Basque–Cantabrian Basin, South-western France) indicate deposition at middle bathyal depths. The detailed quantitative analysis of the benthic foraminiferal assemblages indicates mesotrophic conditions during the latest Maastrichtian, and a drastic decrease in the nutrient supply to the sea floor in coincidence with the K/Pg boundary. Under these oligotrophic conditions, the composition of the assemblages from the *G. cretacea* Biozone was probably related to the blooms of certain primary producers that spread throughout the Basque–Cantabrian basin during the earliest Danian.

Diversity indices significantly recover towards the upper part of the *G. cretacea* Biozone, although the dominance of epifaunal taxa (e.g., *Globorotalites, Osangularia*) in the *Pv. eugubina* Biozone suggests that the food supply was still low. Comparison between Loya and other middle bathyal sections from the Basque–Cantabrian Basin indicates a similar palaeoenvironmental turnover across the K/Pg boundary.

This pattern of faunal and palaeoenvironmental recovery has been compared to that observed in the middle bathyal Agost and Caravaca sections (South-eastern Spain). In addition to a decrease in the food supply to the sea floor observed just at the K/Pg boundary, low oxygen conditions have been recorded in the lowermost Danian in these two sections. However, the lack of evidence for oxygen deficiency in the Basque–Cantabrian Basin suggests that only regional, and not global low oxygen conditions followed the K/Pg boundary event.

Environmental instability inferred from benthic foraminifera from the *G. cretacea* Biozone in the Basque–Cantabrian Basin and in Southeastern Spain has been related to a rapidly changing food supply driven by phytoplankton blooms. Whereas stabilization of the ecosystems in surface waters occurred probably towards the upper part of the *G. cretacea* Biozone, data available from the *Ps. pseudobulloides* Biozone at Bidart and Agost indicate that food supply to the benthos had not completely recovered more than 200 kyr after the K/Pg boundary.

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