NATURE AND TIMING OF BIOTIC RECOVERY IN ANTARCTIC BENTHIC MARINE ECOSYSTEMS FOLLOWING THE CRETACEOUS–PALAEOGENE MASS EXTINCTION

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Abstract: Taxonomic and ecological recovery from the Cretaceous–Palaeogene (K–Pg) mass extinction 66 million years ago shaped the composition and structure of modern ecosystems. The timing and nature of recovery has been linked to many factors including palaeolatitude, geographical range, the ecology of survivors, incumbency and palaeoenvironmental setting. Using a temporally constrained fossil dataset from one of the most expanded K–Pg successions in the world, integrated with palaeoenvironmental information, we provide the most detailed examination of the patterns and timing of recovery from the K–Pg mass extinction event in the high southern latitudes of Antarctica. The timing of biotic recovery was influenced by global stabilization of the wider Earth system following severe environmental perturbations, apparently regardless of latitude or local environment.

Extinction intensity and ecological change were decoupled, with community scale ecological change less distinct compared to other locations, even if the taxonomic severity of the extinction was the same as at lower latitudes. This is consistent with a degree of geographical heterogeneity in the recovery from the K–Pg mass extinction. Recovery in Antarctica was influenced by local factors (such as water depth changes, local volcanism, and possibly incumbency and pre-adaptation to seasonality of the local benthic molluscan population), and also showed global signals, for example the radiation of the Neogastropoda within the first million years of the Danian, and a shift in dominance between bivalves and gastropods.

Key words: mass extinction, Cretaceous, Palaeogene, Antarctica, biotic recovery.

Mass extinction events have profoundly affected the evolutionary history of life on Earth, and are topics of intense interest due to their links with rapid environmental change, and their longer term ecological and evolutionary effects (Raup & Sepkoski 1982). The recovery of ecosystems following global extinction events is often characterized by a complex set of dynamics operating over an extended (100s of kyr to >1 myr) period (Chen & Benton 2012). Recoveries cause changes in ecological strategy, differences in interactions between organisms, and shifts in the dominance of taxa in both marine and terrestrial environments (Hull 2015). There have been five major mass extinction events in the last 550 million years, the most recent of which occurred at the Cretaceous–Palaeogene (K–Pg) boundary 66 million years ago, with an estimated loss of 75% of marine and 50% of terrestrial species (Bambach *et al.* 2004; Alroy *et al.* 2008; Brusatte *et al.* 2015). This turnover has been convincingly associated with a large (*c.* 6–10 km diameter) bolide impact, which created the 180 km Chicxulub crater in the Gulf of Mexico (Schulte *et al.* 2010). Large Igneous Province volcanism, specifically the eruption of the Deccan Traps in India, is also thought to have contributed to latest Cretaceous and possibly earliest Paleocene environmental change and biological turnover (Schoene *et al.* 2019; Sprain *et al.* 2019). However, the degree to which this is the case is still vigorously debated (Courtillot & Fluteau 2010; Keller *et al.* 2010; Schulte *et al.* 2010; Renne *et al.* 2013).

The severe, rapid and cascading environmental effects of the bolide impact may have included global darkness

(Alvarez *et al.* 1980), rapid climatic changes due to injection of debris and volatiles into the atmosphere (Vellekoop *et al.* 2016; Brugger *et al.* 2017; Artemieva *et al.* 2017), collapse of food chains due to inhibition of photosynthesis (Sheehan *et al.* 1996), and potentially ocean acidification (Alegret *et al.* 2012). The extinction also led to changes in the global carbon cycle (D'Hondt *et al.* 1998; D'Hondt 2005; Esmeray-Senlet *et al.* 2015), which took over 1 myr to recover to pre-boundary conditions (Birch *et al.* 2016). The biological and ecological reorganization that resulted from the K–Pg mass extinction had a profound influence on the nature and structure of modern ecosystems (Krug *et al.* 2009).

Discussion of the timing and nature of recovery following the K–Pg extinction has focused on developing models based on extinction selectivity, where traits shared by different organisms or clades can be shown to provide some advantage when compared to hypothesized short and long-term environmental effects of the mass extinction and its potential causal mechanism(s). Studies vary in terms of temporal and geographical scales, and attempts are often made to compare and link changes in both marine and terrestrial records to build a global picture. One of the earliest models for marine recovery emphasized the preferential survival of benthic detritus feeding organisms over those that were reliant on plant material or photosynthesis (Sheehan & Hansen 1986; Aberhan *et al.* 2007) following evidence for a collapse in primary productivity (Arthur *et al.* 1987). Subsequent work has brought to light a variety of other biotic and abiotic factors which may play a role in extinction selectivity and preferential recovery of certain taxa following the K–Pg mass extinction. These include geographical distance from the impact site and/or palaeolatitude (Raup & Jablonski 1993; Jiang *et al.* 2010; Donovan *et al.* 2016; Tosolini 2017; Lowery *et al.* 2018), palaeoecology (e.g. motility, tiering, feeding strategy; Sheehan & Hansen 1986; Lockwood 2004), geographical range of a given species or clade (Jablonski & Raup 1995; Longrich *et al.* 2012; Landman *et al.* 2014), the effect of incumbency, ecological interactions (Hull *et al.* 2011; Aberhan & Kiessling 2014; Schueth *et al.* 2015) and differing palaeoenvironmental setting (e.g. onshore vs offshore, shallow vs deep water; Sessa *et al.* 2012; Aberhan & Kiessling 2014; Jiang *et al.* 2018) in restoring communities and ecosystem function after the extinction.

Due to this complex array of different factors, an evolving view contends that the effects of the mass extinction on the Earth System were heterogeneous between different regions of the globe, and potentially among different clades and trophic groups, with local pre-boundary environmental conditions, and even chance playing a large role in recovery (Sepúlveda *et al.* 2009; Jiang *et al.* 2010; Hull *et al.* 2011; Sibert *et al.* 2014; Esmeray-Senlet *et al.* 2015; Donovan *et al.* 2016; Tosolini 2017). In this scenario, integrated and temporally constrained fossil datasets from individual localities tied to detailed palaeoenvironmental information are needed to assess the nature of extinction selectivity, and clarify the patterns and timing of recovery around the globe. Such analyses are rare in relatively shallow water continental shelf environments, as there is often a significant time gap over the K–Pg boundary in these settings.

Here we integrate new stratigraphical collections of benthic molluscs (bivalves and gastropods, two of the most common taxa used to understand extinction and recovery in deep time due to their high preservation potential and range of ecological strategies) with palaeoenvironmental and new chronostratigraphic information from Seymour Island, Antarctica, to provide accurate constraints on the timing and nature of biotic recovery following the K–Pg mass extinction event in the southern high latitudes.

GEOLOGICAL SETTING

Seymour Island, Antarctica, 64°15′S, 56°45′W (Fig. 1) is unique due to its high latitude setting in both the modern and Cretaceous–Paleocene interval (Lawver *et al.* 1992; Montes *et al.* 2010; Witts *et al.* 2016) and because it comprises one of the best exposed and most stratigraphically complete Cretaceous–Paleocene sedimentary sequences anywhere in the world. A robustly dated (Bowman *et al.* 2012, 2013, 2016; Tobin *et al.* 2012; Witts *et al.* 2015, 2016), highly expanded stratigraphical succession is contained within the López de Bertodano Formation (LBF) and overlying Sobral Formation (SF) (Bowman *et al.* 2013, 2016; Witts *et al.* 2015, 2016). The composite stratigraphical section through these units presented herein comprises an essentially continuous record of life in the polar seas from the early Maastrichtian (*c.* 69 Ma) through to the Danian (*c.* 65 Ma).

The K–Pg boundary occurs within the upper portion of the 1100 m-thick LBF, within a glauconite-rich unit which forms the contact between informal lithostratigraphic units Klb9 and Klb10 (Macellari 1988) (herein referred to as LB9 and LB10) (Elliot *et al.* 1994; Bowman *et al.* 2012). Numerous detailed sedimentary analyses have previously been applied to this succession to decipher local palaeoenvironments accurately (Macellari 1988; Olivero *et al.* 2008; Schoepfer *et al.* 2017). These indicate that the LBF represents a series of palaeoenvironments, ranging from estuarine to shallow marine (mid-shelf) (Macellari 1988; Olivero *et al.* 2008; Olivero 2012). However, both the latest Maastrichtian and early Palaeogene sediments were deposited in a similar mid-shelf environment (Macellari 1988; Olivero 2012). Macellari (1988) suggested the presence of a sudden

FIG. 1. A, map of Antarctic Peninsula, showing location of Seymour Island. B, geology of Seymour Island, with the location of the three section lines along which macrofossils were collected, 1 in 2010, 2 in 1999, and 3 in 2006. The K–Pg boundary (66.04 Ma; Renne *et al.* 2013), shown in red, runs NE to SW across the island. Redrawn from Montes *et al.* (2010) and Witts *et al.* (2016).
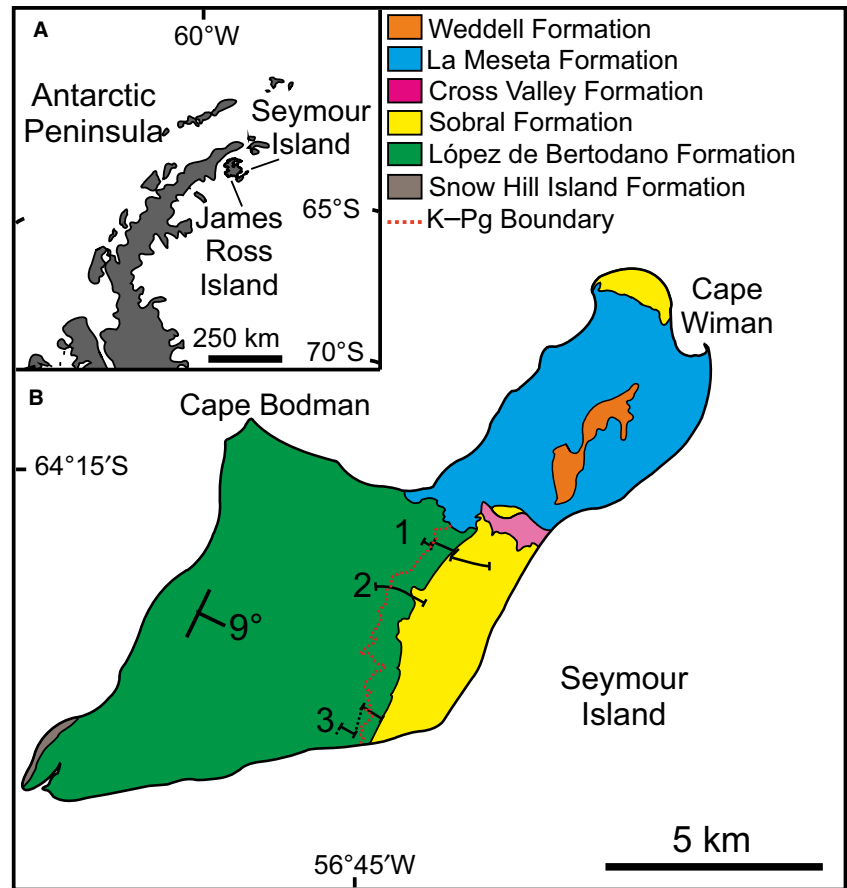
regression, and possible minor depositional hiatus 25–30 m below the K–Pg boundary. However, Tobin (2017) stated that there is little sedimentological variation between LB9 and LB10, and Crame *et al.* (2004) noted that they saw no evidence for a hiatus between these units. As a result, changes to diversity, abundance and ecology of fossil taxa in this interval are likely to be related to the aftermath of the mass extinction, rather than any distinct local change in environment.

The contact between LB10 and the overlying SF is an unconformable sequence boundary (Macellari 1988), with a shift in the local palaeoenvironment from mid-shelf to prodelta. Bowman *et al.* (2016) noted no appreciable change in the dinoflagellate cyst flora across the LB10/SF boundary, and this, as well as the age model for the section, showed that there was not a significant time gap (Bowman *et al.* 2016). However, there is a clear change in environment reflected in the sedimentology of the SF. This shows an overall regressive trend, reflecting eastward progradation of a marine delta with sediments originating from the Antarctic Peninsula more than 100 km to the west (Macellari 1988; Marenssi *et al.* 2012). The SF is mostly Danian in age (Tobin *et al.* 2012; Bowman *et al.* 2016).

A robust age model now exists for this composite LBF and SF sequence (Bowman *et al.* 2012, 2013, 2016; Tobin *et al.* 2012; Witts *et al.* 2015, 2016), which can be correlated with the international timescale using magnetostratigraphy and radiometric dates. This indicates the section is highly expanded compared to many onshore K–Pg successions at lower latitudes.

MATERIAL AND METHOD

Field collecting strategy

Analyses were carried out on benthic mollusc collections made systematically through 550 m of logged sedimentary section lines over three separate field seasons (1999, 2006 and 2010) (Fig. 1B). The 1999 data were collected from section line DJ.953 made through LB9 and LB10 of the LBF in central Seymour Island (Crame *et al.* 2004, 2014). Fossils from the 2006 field season were collected along section line D5.251 in LB9 LBF, LB10 LBF and the SF. A third section was logged in the northern part of Seymour Island in the 2010 British Antarctic Survey (BAS) field season through the uppermost of LB9 LBF, LB10 LBF

(D9.205–207) and the SF (D9.209 and D9.210) (Bowman et al. 2016) (Fig. 1).

Data from 1999 and 2010 were collected systematically, using the same methodology. The 2006 data was collected by a different team; from shorter collecting horizons, at more regular intervals (see Whittle et al. 2019, suppl. data). Occurrences for the 1999 and 2006 collections are given in Witts et al. (2016). New occurrence data presented herein from the 2010 collection is given in Whittle et al. (2019, fig. 1).

For the purposes of this study, primarily concerned with the biotic recovery following the K–Pg mass extinction, the uppermost 200 m of the complete Late Cretaceous dataset was included, the lower units of the LBF having been studied in detail in Witts et al. (2016). Fossil specimens are curated and stored in the BAS collections, Cambridge. Fossil identifications were based on revised molluscan taxonomy (Beu 2009; Crame et al. 2014; Witts et al. 2016).

Fossil data analysis

Mass extinctions affect a variety of aspects of ecosystem structure and function (Hull & Darroch 2013); therefore, analyses were carried out at several different scales ranging from individual fossil occurrences to whole community comparisons across the K–Pg boundary.

Quantitative diversity metrics were calculated from abundance data in individual sampling horizons for each species from the 1999 and 2010 BAS field collections, which were collected using the same methodology. Shannon diversity (H') was calculated using Primer v.6 (Clarke & Warwick 2001). Additional diversity metrics for the 2006 field collection are available in Whittle et al. (2019, fig. 2).

To assess initial recovery, occurrences of species in sampling horizons within LB10 were also illustrated from the three BAS collections, as well as occurrences taken from the literature (Zinsmeister 1998; Stilwell et al. 2004) mentioned above. For diagrammatic purposes the mid points of collecting horizons were plotted.

The first and last occurrence data of species from the 1999, 2006 and 2010 collections, with additional data from the study of Zinsmeister (1998) and some stratigraphically constrained species ranges from Stilwell et al. (2004) (correlation to BAS section lines described in Crame et al. (2014) and Witts et al. (2016)), were used to construct a composite range chart. Several stratigraphic tie points were used to correlate different sedimentary section lines, such as glauconite beds in the LBF, and the base of the SF. Changes in stratigraphic bin size were accounted for by taking the base of the stratigraphic bin in which a species first occurred as the first appearance, and the top of the stratigraphic bin in which a species last occurred as the last appearance (as in Witts et al. 2016). These were plotted against the stratigraphy and age model from Bowman et al. (2016). The ecological categories of tiering, feeding and motility from Bambach et al. (2007) were combined to provide a mode of life for each species.

To examine broader ecological patterns, proportional taxonomic richness (based on the number of species) and proportional abundance (based on specimen numbers) for tiering, feeding and motility categories were calculated using all datasets for three binned intervals and shown for LB9, LB10 and the SF.

Ecological community structure for the Cretaceous and Palaeogene was analysed using modes of life for species and abundance data in individual sampling horizons, from the three BAS field collections (1999, 2006 and 2010). For abundance, sampling horizons with at least 22 individuals were used. These were analysed below and above the K–Pg boundary, as in the methodology outlined by Aberhan & Kiessling (2015) to allow for direct comparison with data from other sites at lower latitude. Non-parametric multidimensional scaling (nMDS) was performed using a Bray–Curtis similarity index to visualize patterns in the multivariate data using Primer v.6 (Clarke & Warwick 2001). The significance of the stratigraphic groupings (LB9 Cretaceous, LB10 Palaeogene, SF Palaeogene) based on ecology for the species numbers and abundance data was assessed using the ANOSIM test. The similarity percentages routine (SIMPER) was used for the ecology based on species numbers and abundance data to determine which ecological strategies were responsible for the greatest similarity within the stratigraphic periods.

RESULTS

Timing of taxonomic and ecological recovery in Antarctica based on stratigraphic data

Our data show that the extinction event in Antarctica is associated with a drop in both standing species richness of benthic molluscs and quantitative diversity metrics (Fig. 2) coincident with the K–Pg boundary, defined by dinoflagellate cyst biostratigraphy (Elliot et al. 1994; Bowman et al. 2012, 2016), and a small iridium (Ir) anomaly in a parallel section (Elliot et al. 1994). The extinction interval on Seymour Island is several metres thick (1007.5–1013 m in the composite stratigraphic section), including a layer with disarticulated and articulated fish debris (Zinsmeister 1998), with the upper limit here coincident with the last appearance of Cretaceous holdover taxa, as defined by Witts et al. (2016) (Fig. 3). Due to the large difference in sampling strategy, diversity analysis through the section appeared dramatically different in the

2006 collection, highlighting the importance of standardizing sampling methods for comparing different data sets (see Whittle *et al.* 2019, fig. 2).

Taxonomic recovery from the extinction initiated rapidly in the earliest Palaeogene, with the occurrence of three new species of benthic mollusc immediately above the extinction horizon at the base of LB10 (1007.5 m in the composite section) (Figs 2, 3). There is no indication for any size reduction (i.e. a 'Lilliput effect') in the benthic molluscan fauna above the K–Pg boundary in Antarctica. Both diversity and standing species richness of the benthic molluscan fauna increase during LB10 (Fig. 2). A total of four new taxa appear throughout LB10, with a concentration of first occurrences and appearance of three new species towards the top of the unit, stratigraphically *c.* 50 m above the extinction interval (Fig. 4).

The most dramatic ecological change in benthic molluscan faunas is a distinct shift in tiering. Infaunal taxa preferentially survived and proliferated immediately following the extinction event, in LB10, and apart from a single specimen of the semi-infaunal bivalve *Pinna*, the only molluscs in this ecological category occur in a 40 m-thick interval in the early Paleocene of LB10 (Fig. 3). These taxa were generally facultatively motile shallow infaunal suspension feeders or slow motile shallow infaunal surface deposit feeders (Fig. 3). The taxonomic richness of species each ecological category remained similar over the K–Pg boundary (Fig. 5A) but the abundance of specimens within each ecological category changed dramatically over the boundary (Fig. 5B). Infaunal organisms dominated on abundance, but not on species numbers. This is because there was an
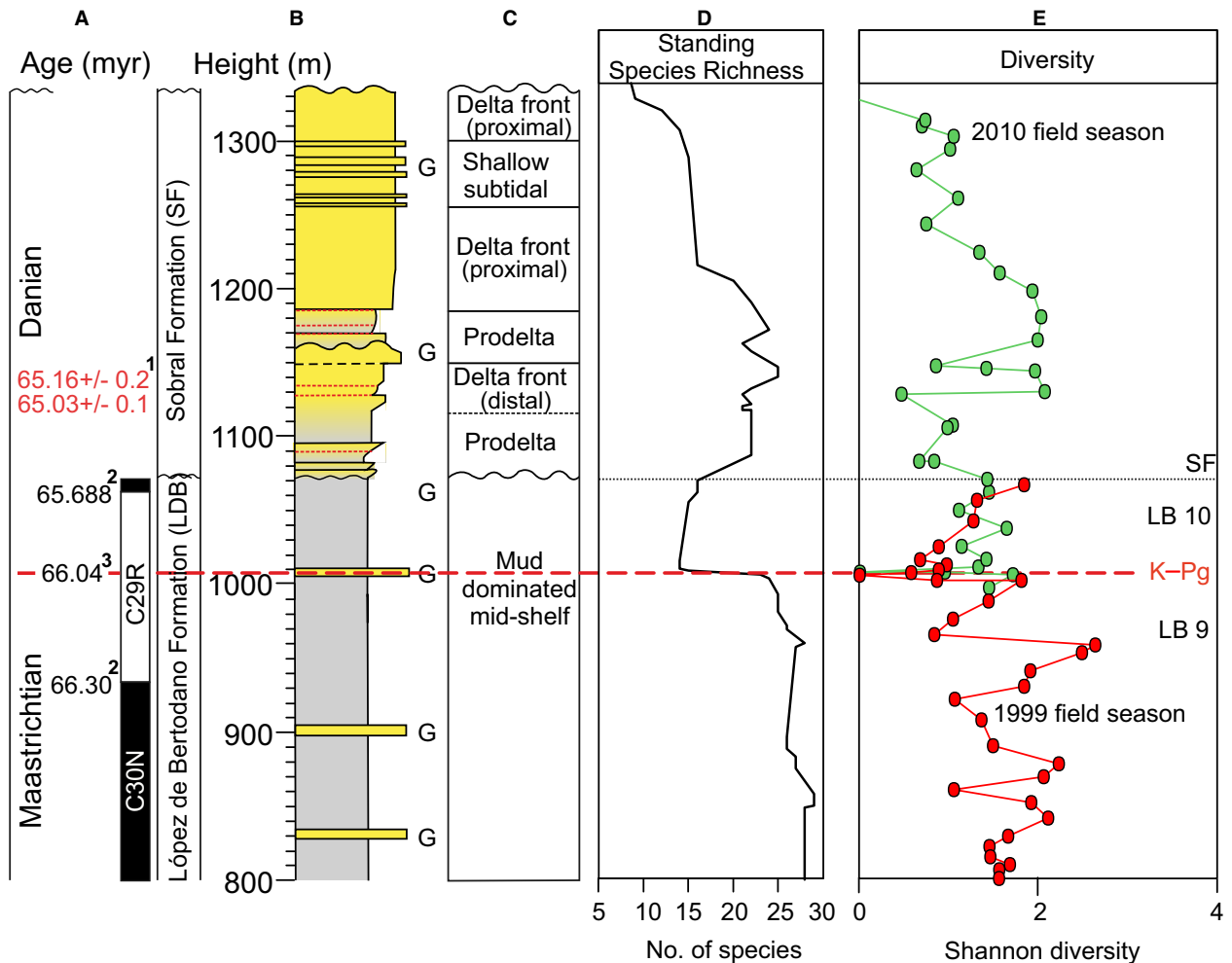

FIG. 2. Benthic molluscan standing species richness and diversity metrics. A, age model (Bowman *et al.* 2013, 2016); 1, U–Pb zircon dates from airfall tuff beds (Bowman *et al.* 2016); 2, dates for magnetochron boundaries (Ogg *et al.* 2012); 3, date for the K–Pg boundary (Renne *et al.* 2013). B, lithostratigraphy; G, glauconitic horizon. C, palaeoenvironmental setting. D, standing species richness. E, Shannon (*H'*) diversity for the 1999 and 2010 field collections; the 2006 field collection had a different sampling strategy; diversity for this is shown in Whittle *et al.* (2019, fig. 2).
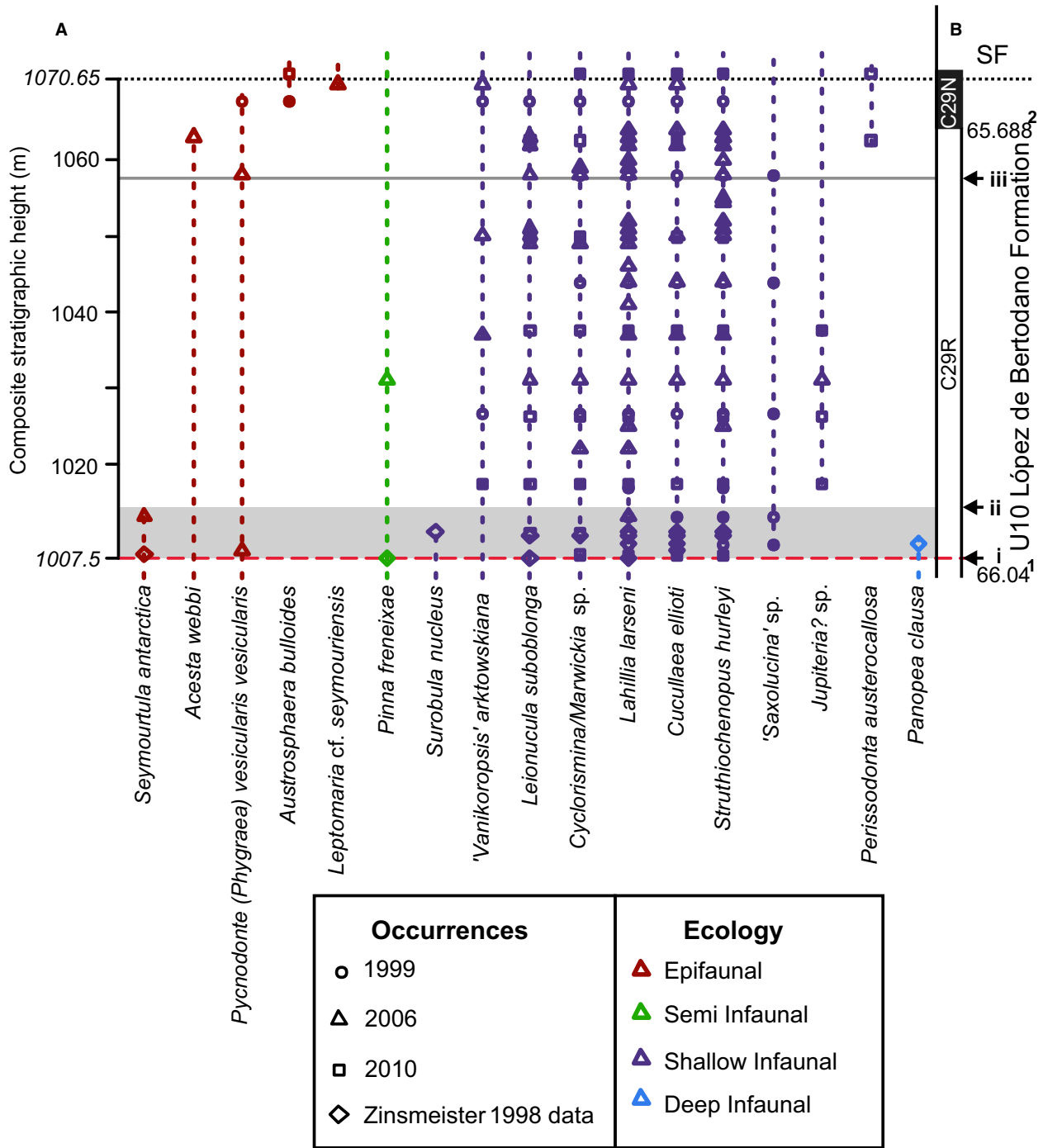
FIG. 3. Occurrences and palaeoecology of benthic molluscan species in LB10 of the LBF. A, point shape refers to collection, colour refers to ecology (tiering), and dashed lines indicate ranges (for additional versions of this figure relating to feeding strategy and motility see Whittle *et al.* 2019, figs 3–4). B, stratigraphy and age model; i, K–Pg boundary located at a height of 1007.5 m in the composite section, defined by dinoflagellate biostratigraphy (Bowman *et al.* 2012, 2013) and appearance of Ir anomaly in parallel section (Elliot *et al.* 1994); ii, last appearance datum of Cretaceous holdover taxa, defining the top of the extinction interval on Seymour Island (Witts *et al.* 2016); iii, stratigraphic horizon where epifaunal taxa return to the composite section; 1, date for the K–Pg boundary (Renne *et al.* 2013); 2, date of C29R/29N reversal (Ogg *et al.* 2012).
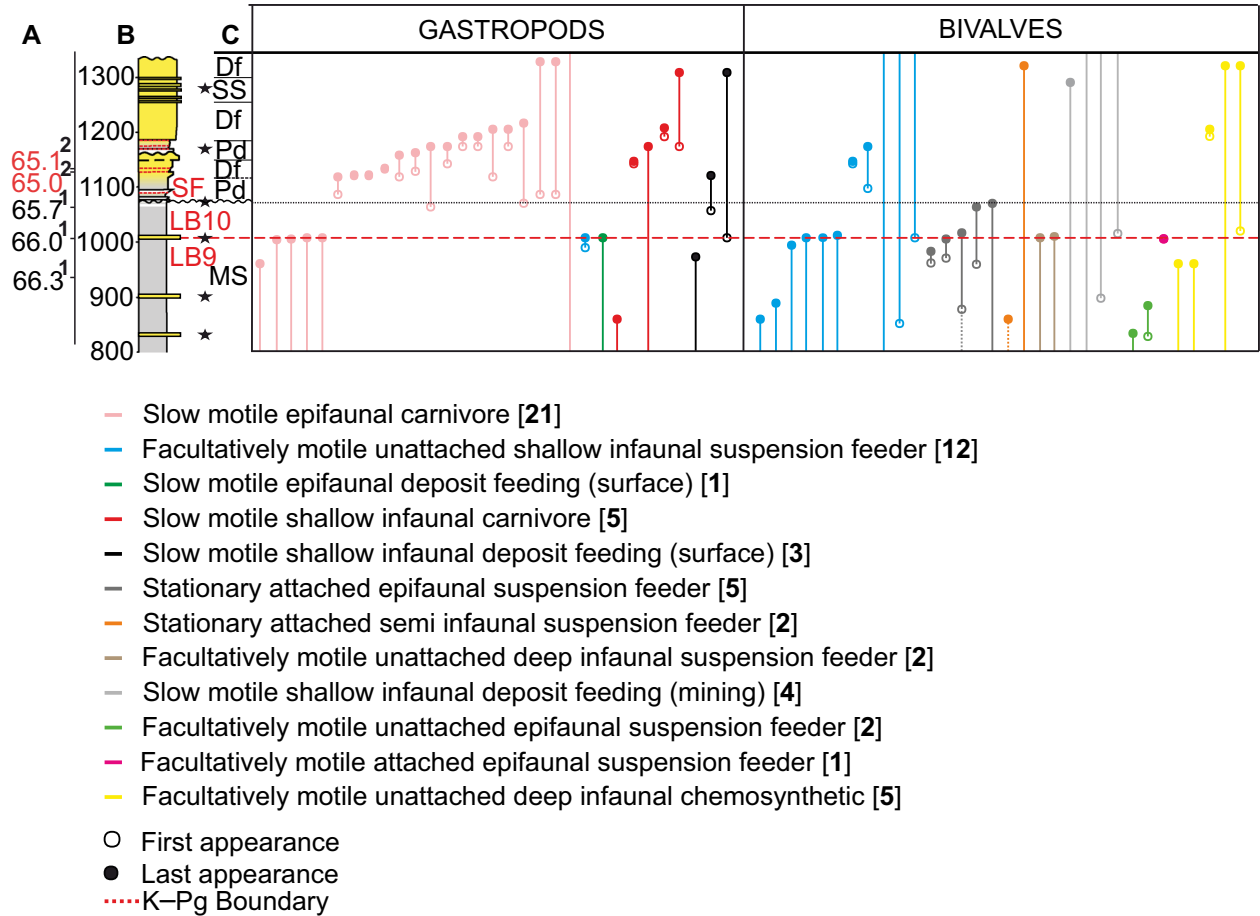
FIG. 4. Composite Stratigraphic Range for benthic molluscan taxa in the upper two units of the LBF (LB9 and LB10) and SF. A, age model; B, lithostratigraphy; star, glauconitic horizon; age dates: 1, magnetochron reversals (Gradstein *et al.* 2012; Tobin *et al.* 2012); 2, U–Pb dates from ash horizons in the SF (Bowman *et al.* 2016). C, palaeoenvironmental setting: Df, delta front; MS, mid-shelf; Pd, prodelta; SS, shallow subtidal. Lines on range chart are coloured according to mode of life of benthic molluscan taxa, number in brackets following mode of life indicates number of species. Data from 1999, 2006, 2010 BAS field collections, supplemented by Zins-meister (1998) and Stilwell *et al.* (2004), occurrences detailed in Crame *et al.* (2014). Whittle *et al.* (2019, fig. 5) shows taxon names for ranges.

abundance of specimens within a small number of species.

The reappearance of epifaunal species coincides with an increase in the appearance of new taxa *c.* 50 m above the K–Pg boundary on Seymour Island (Figs 3, 4). This horizon can be dated to *c.* 320 000 yr after the extinction based on correlation to the base of magnetochron C29N (Ogg *et al.* 2012; Tobin *et al.* 2012; Witts *et al.* 2016), and was more recently precisely dated to 328 000 ± 15 000 yr after the mass extinction by Sprain *et al.* (2018). A further increase in standing species richness occurs at the base of the SF (Fig. 2), potentially related to the distinct change in palaeoenvironment. Evidence for broader recovery of the benthos is present at this level, with the return of echinoid spines and serpulid worm tubes (*Rotularia*), which were abundant below the K–Pg boundary in LB9 (Macellari 1988; Witts *et al.* 2016; RJW

unpub. data). Although species richness of benthic molluscs continued to increase above the sequence boundary, it does not recover to pre-extinction values in the basal SF. The highest standing species richness values occur between *c.* 1140 and 1150 m in the composite section, coincident with the highest Paleocene diversity values (Fig. 2). At this horizon, there is a radiation of gastropod species, many with short ranges. Unlike species richness, diversity values do return to values comparable to the late Maastrichtian. Recently published U–Pb dating of ash beds within this interval indicate it was deposited *c.* 65 Ma (Bowman *et al.* 2016), placing this recovery of species richness and diversity values 1 myr after the mass extinction (Renne *et al.* 2013).

Stratigraphically above this level, evidence for further recovery is complicated by localized environmental changes in the SF. Species richness and diversity decrease
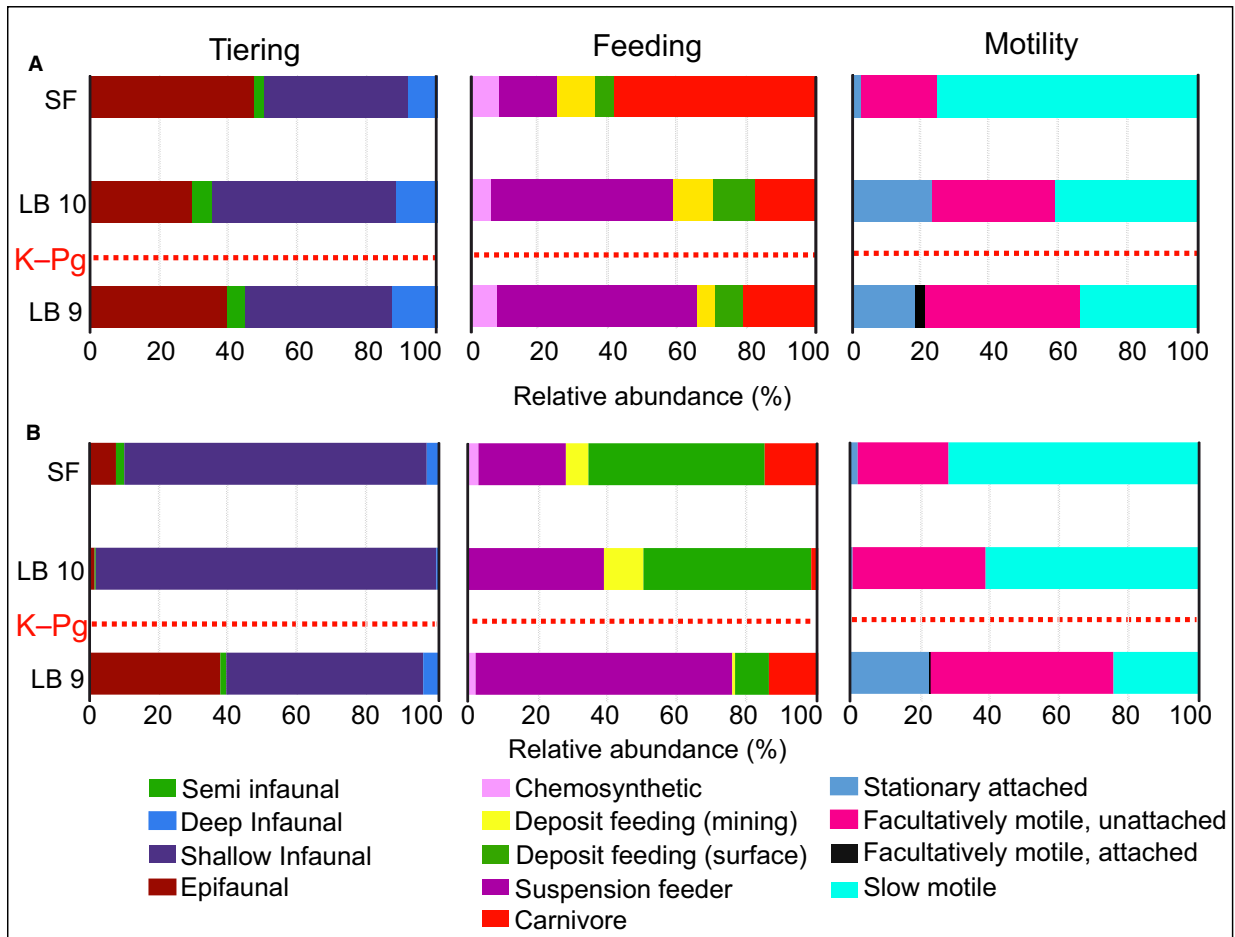
FIG. 5. A, proportional taxonomic richness for tiering, feeding and motility categories based on species numbers in LB9, LB10 and the SF. B, proportional taxonomic abundance based on specimen numbers, for tiering, feeding and motility categories based on specimen numbers in LB9, LB10 and the SF.

to values lower than those immediately following the K–Pg mass extinction (Fig. 2), coincident with evidence that the depositional environment shallowed due to delta progradation (Bowman *et al.* 2016). Many of the new benthic molluscan taxa, which occur in the lower portion of the SF also have short stratigraphic ranges (Fig. 4).

Community scale changes in ecology over the K–Pg boundary in Antarctica

Overall, the benthic molluscs in this study occupied 12 different modes of life (Fig. 4). Two of these modes of life are present in the Maastrichtian, but do not occur in the Paleocene of Antarctica. There was no significant difference in taxonomic richness in ecological categories across the K–Pg boundary, but there was a substantial change in taxonomic richness from the LBF into the SF (Fig. 5A). Conversely, there was a change in the

abundance of specimens within each ecological category, showing a marked change in dominance of ecological types over the K–Pg boundary, with less of a change over the LBF/SF boundary (Fig. 5B).

The ecological composition of some sampling horizons of the Antarctic Maastrichtian community showed some similarity with Danian horizons, causing a degree of overlap in nMDS analyses (Fig. 6). There was more ecological similarity between the two time periods based on taxonomic richness (Fig. 6A) than there was specimen abundance (Fig. 6B) in the different ecological categories. However, as a whole, the ecological composition of the Maastrichtian was statistically significantly different to the Danian for both datasets ($R = 0.244$ for species data, $R = 0.452$ for abundance data; results significant at $p = 0.001$). Using the same methodology for abundance data from North and South American localities, Aberhan & Kiessling (2015) documented distinct shifts in ecospace utilization at four sites located at different palaeolatitudes over

the K–Pg boundary (Aberhan & Kiessling 2015, fig. S3). In contrast to our results they showed discrete, non-overlapping groups when comparing convex hull surfaces of Maastrichtian and Danian samples from their localities. There was no clear distinction in ecology between the two Palaeogene horizons (LB10 and SF), despite the apparently significant change in the environment of deposition (Fig. 6).

There were more modes of life in the Antarctic Cretaceous community than the Palaeogene (Whittle *et al.* 2019, table 1). Within the Cretaceous community, similarity between sampling horizons was driven by stationary attached epifaunal suspension feeders and slow motile epifaunal carnivores, in addition to the pervasively dominant facultatively motile unattached shallow infaunal suspension feeders. This mode of life was a dominant component of LB9, LB10 and the SF (Whittle *et al.* 2019, tables 1–3), and is probably responsible for the similarity between some individual Cretaceous and Palaeogene samples. The Paleocene communities in LB10 and the SF share a high dominance of slow motile shallow infaunal surface deposit feeders (i.e. *Struthiochenopus*) (Whittle *et al.* 2019, tables 2–3).

DISCUSSION

The timing of recovery following the mass extinction

It has been demonstrated that the K–Pg mass extinction in the southern hemisphere oceans was rapid, and comparable in severity to the northern hemisphere in terms of taxonomic loss of benthic molluscan faunas (Aberhan & Kiessling 2014; Witts *et al.* 2016). Tobin (2017) recently argued that fossil data from Seymour Island is consistent with a two-phased extinction in Antarctica. However, these analyses were based on patterns of last

appearance datums within individual sedimentary section lines. Our composite standing species and diversity data from multiple sections support a single, rapid and severe extinction event at the K–Pg boundary, that is related to the Chicxulub impact (Fig. 2).

Any changes brought about by the Chicxulub impact event (e.g. transient cooling, global darkness, local expansion of anoxic waters; Zinsmeister 1998; Sosa-Montes De Oca *et al.* 2013; Vellekoop *et al.* 2016, 2018; Brugger *et al.* 2017) were probably extremely short-lived. Palaeoclimate data derived from marine (Tobin *et al.* 2012; Bowman *et al.* 2013; Petersen *et al.* 2016) and terrestrial (Bowman *et al.* 2014; Kemp *et al.* 2014) proxies indicate a general continuation into LB10 and the SF of the cool-temperate climatic conditions which characterized the Antarctic Peninsula region during the late Maastrichtian, without any major changes. However, palaeontological data are consistent with the hypothesis that biogeochemical cycling and ecosystem function remained disturbed for an extended period.

There is a large drop in species richness immediately above the K–Pg boundary, and a transient change in the dominance of taxa is seen throughout LB10 until a horizon dated to about *c.* 320 kyr after the extinction event (Figs 2, 3). Previously published microfossil evidence from this interval in the Antarctic has shown an increased number of diatom resting spores (Harwood 1988) and repeated blooms of successive opportunistic dinoflagellate taxa, following a considerable drop in diversity after the boundary (Askin 1988; Bowman *et al.* 2012). Bowman *et al.* (2014) also noted disturbance in the terrestrial palynoflora in LB10, although no 'fern-spike' has been reported from Antarctica at the K–Pg boundary. The apparent recovery of the terrestrial palynoflora occurred towards the top of the LBF and across the unconformity into the SF (Bowman *et al.* 2014). Huber (1988) demonstrated that foraminifera are rare and poorly preserved
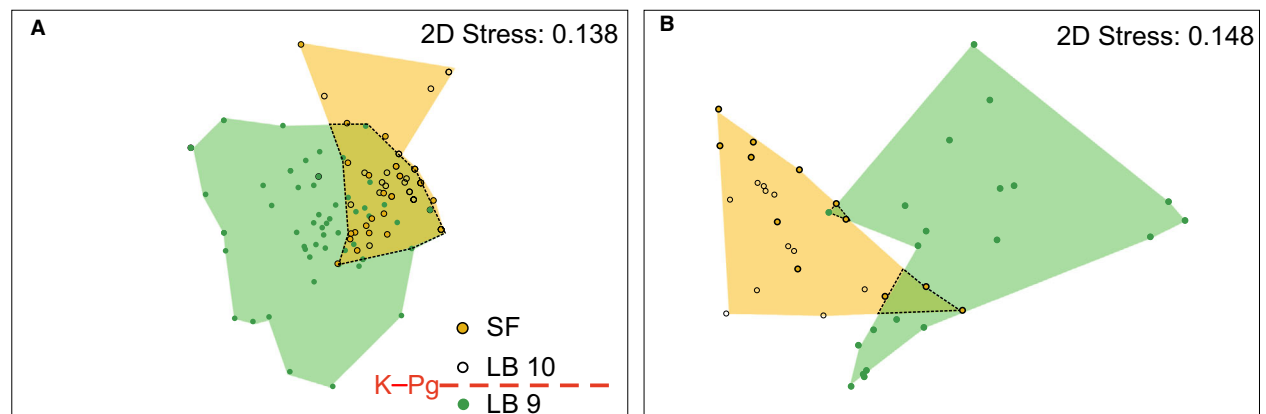

FIG. 6. Nonmetric multidimensional scaling (nMDS) ordination comparing modes of life in Cretaceous and Palaeogene samples. A, ecology based on species numbers from the 1999, 2006 and 2010 BAS field collections. B, ecology based on abundance data, from the 1999, 2006 and 2010 BAS field collections (see Material and Method).

above the K–Pg boundary. The first diagnostic Danian foraminiferal assemblage also occurs at the top of the LBF, 1 m below the contact with the SF (Huber 1988), although this record may be affected by secondary diagenetic decalcification which is a common issue with calcareous microfossil assemblages in the James Ross Basin (Švábenická et al. 2012).

The increase in benthic molluscan species richness in the upper levels of LB10 dated c. 320 kyr after the mass extinction, along with the maximum post-extinction species richness attained c. 1 myr after the mass extinction in the SF, appear to represent significant horizons in the biotic recovery of marine ecosystems in Antarctica. The dates associated with these intervals are also significant when comparing these data with recovery from the mass extinction on a global scale. They coincide closely with timing for the staged recovery of ecosystem function and diversity of various taxonomic groups of primary producers (Coxall et al. 2006; Jiang et al. 2010; Vellekoop et al. 2017), and recovery of the global carbon cycle following the collapse of the deep-sea carbon isotope gradient at the K–Pg boundary (D'Hondt et al. 1998; Esmeray-Senlet et al. 2015; Birch et al. 2016; Witts et al. 2018).

Once thought to represent a total global primary productivity collapse following global darkness after the impact event (Arthur et al. 1987), it is likely that the collapse of the deep-sea carbon isotope gradient instead indicates a loss of efficiency of the biological pump, enhanced nutrient cycling in surface waters, and a significant reduction in organic carbon export and burial globally (D'Hondt 2005; Coxall et al. 2006; Alegret et al. 2012). Such a scenario implies that while nutrients were available for planktonic communities (Lowery et al. 2018), benthic communities and taxa may have been locally starved of food (D'Hondt 2005; Esmeray-Senlet et al. 2015; Vellekoop et al. 2017).

Nearshore and shelf ecosystems, such as those in this study, may have been buffered to a degree from the direct effects of an inefficient biological pump. However, the presence of weak isotope gradients and negative excursions in carbon isotopes in numerous shelf settings as well as the deep ocean, suggest the overall effects were felt worldwide during the early Danian regardless of water depth and latitude (Esmeray-Senlet et al. 2015; Vellekoop et al. 2017). In addition, recent data from Seymour Island suggest the collapse of carbon export and organic carbon burial at the K–Pg boundary also affected the global sulfur cycle, with a prominent negative excursion in sulfur isotopes from biogenic carbonate within LB10 (Witts et al. 2018). Recovery of the sulfur cycle to pre-extinction values occurred at the same time (c. 320 kyr) as the initial recovery of the carbon cycle globally (Witts et al. 2018). These recoveries in geochemical proxies occurred on a similar timescale, and coincide stratigraphically with the appearance of new taxa and the initial stages of full ecological recovery in LB10, with a return of epifaunal taxa occurrences (interval iii in Figs 3, 4).

This similarity in the initial recovery times between geochemical cycles, taxonomic and ecological recovery of marine ecosystems, in a variety of locations and palaeoenvironmental settings following the K–Pg mass extinction, agrees with the 'Earth System Succession' model, where stabilization of biogeochemical cycles is intimately tied to bottom-upward biotic recovery following severe environmental perturbation (Hull 2015). A similar situation has been hypothesized for the aftermath of other Phanerozoic mass extinction events and may represent a general pattern (Payne & Clapham 2012; Foster et al. 2017), with the carbon cycle and marine ecosystems re-stabilizing on a similar timescale (Chen & Benton, 2012; Hull & Darroch, 2013). In all cases, only when the carbon cycle and the base of the marine food chain is restored, can significant biotic recovery begin.

Ecological recovery from the mass extinction

Although the degree of taxonomic loss of benthic molluscan faunas was comparable in severity to the northern hemisphere (data herein; Aberhan & Kiessling 2014; Witts et al. 2016) the shift in ecological dominance across the K–Pg boundary in Antarctica was not as marked as at other locations. A greater degree of change in ecological composition between Maastrichtian and Danian communities was recorded at the Brazos River site (USA), Bajada del Jagüel and San Ramón (Argentina) (Fig. 6; cf. Aberhan & Kiessling 2015, fig. S3). This is consistent with a degree of geographical heterogeneity in the ecological response to the mass extinction event. Ecological trends of K–Pg recovery are especially well-studied in the US Gulf Coastal Plain, proximal to the Chicxulub crater (Schulte et al. 2010). Here, early Danian faunas show a dramatic increase in abundance and number of predatory carnivorous taxa, and a replacement of epifaunal sessile suspension feeders by more active suspension feeders in offshore assemblages (Hansen 1988; Sessa et al. 2012). In contrast, shallow subtidal assemblages did not appear to experience significant ecological reorganization following the K–Pg extinction (Sessa et al. 2012).

Only 2 of the 12 modes of life exhibited by benthic molluscs in the section are present in the Maastrichtian but do not occur in the Paleocene of Antarctica. However, they are known from younger Antarctic fossil deposits (Whittle et al. 2011, 2014), and did not disappear during the Paleocene on a global scale (Aberhan & Kiessling 2014). This is consistent with the hypothesis that global functional diversity is generally retained after mass extinction events, despite severe taxonomic losses

(Dunhill *et al.* 2018). There is little evidence for detritus-based benthos (deposit feeders and bottom dwelling predators) preferentially surviving the K–Pg extinction in Antarctica or proliferating in its immediate aftermath to the detriment of suspension feeders. This is despite the evidence for limitation of benthic food supply and reduction in carbon export globally, and is contrary to the 'classic' models where deposit feeders survive over suspension feeders discussed by Sheehan & Hansen (1986) and Sheehan *et al.* (1996) for primarily North American localities, and Aberhan *et al.* (2007) in South America.

Palaeoenvironmental factors affecting recovery in Antarctica

Despite evidence for no significant shift in palaeoenvironment (i.e. water depth) across the K–Pg boundary, which could overprint changes in species richness and abundance data caused by the mass extinction event, the change in species richness from the LBF into the SF could be partly driven by an environmental shift from mid-shelf to prodeltaic conditions. There is however, not a significant time gap between the two formations based on biostratigraphical dating and calculations based on the rate of sedimentation (Bowman *et al.* 2016).

Although the number of benthic molluscan species increases to its highest level in the section in the lower SF, many of the new taxa which occur in this interval have short stratigraphical ranges (Fig. 4). We argue that these ranges are probably artificially truncated because of changes in water depth due to delta progradation or other local palaeoenvironmental perturbations. For example, the frequent presence of ash layers points to repeated ash falls produced by large volcanic eruptions on the adjacent Antarctic Peninsula during the early Danian (Fig. 4). Because of these environmental fluctuations, it is likely that they are not representative of the true stratigraphical distribution of these taxa. In addition, the majority of benthic molluscan species in this study are endemic to the James Ross Basin, and it should be noted that localities of the same age are not known from elsewhere in onshore Antarctica.

Why did some taxa preferentially survive following the extinction?

One species of bivalve (*Lahillia larseni*) that survived the extinction has been reported to occur in flood abundance above the K–Pg boundary in Antarctica (Crame *et al.* 2004; Stilwell *et al.* 2004). This was suggested as a classic signature of 'disaster taxa', opportunists that proliferate in the immediate aftermath of an ecological crisis due to reduced competition and/or vacant ecospace (Harries

et al. 1996). Our data show an increase in abundance of *Lahillia larseni* after the K–Pg mass extinction (see Whittle *et al.* 2019, suppl. data) and indicate a proliferation of the newly evolved species *Struthiochenopus hurleyi* and *Cucullaea ellioti* immediately following the extinction horizon. These taxa were facultatively motile shallow infaunal suspension feeders or slow motile shallow infaunal surface deposit feeders. *Lahillia larseni* crossed the K–Pg boundary, whilst *Cucullaea ellioti* and *Struthiochenopus hurleyi* had close relatives in the Cretaceous (*Cucullaea antarctica* and *Austroapporhais* respectively). This suggests a role for incumbency, which may have been a significant factor in the survival and phased recovery of southern hemisphere marine fauna and floras following the K–Pg extinction in a variety of clades (Aberhan & Kiessling 2014; Schueth *et al.* 2015). These three taxa remain dominant throughout the following units, until evidence for significant basin shallowing towards the top of the SF, when there is a decrease in the abundance of all taxa, with the exception of the bivalve *Pinna*, apparently adapted to such shallow water conditions.

It is difficult to ascertain the reason for the local dominance of infaunal taxa during the *c.* 320 kyr following the K–Pg mass extinction in Antarctica. Buried species may simply have been more sheltered from environmental perturbation on the sea bed or in the overlying water column than epifauna. Infaunal organisms may also have been pre-adapted to the highly seasonal changes unique to this high latitude environment, probably accentuated in the immediate aftermath of the bolide impact by processes such as global darkness (Alvarez *et al.* 1980) and reduction or change in the quality of food supply to the benthos (Sepúlveda *et al.* 2009; Alegret *et al.* 2012; Vellekoop *et al.* 2017). It is plausible that an adaptation to these conditions was a considerable selective advantage during the earliest Palaeogene.

The aporrhaid gastropod *Struthiochenopus hurleyi* provides a good example, being particularly abundant after the extinction, making up almost 50% of the total Danian fossils collected in the BAS sections (Fig. 3) (Whittle *et al.* 2019). The modern aporrhaid species *Aporrhais occidentalis* alternates between periods of epifaunal activity in the summer and infaunal quiescence in the winter, although experiments and observations showed no evidence for a causal relationship between temperature change and burrowing (Perron 1978). The switch in life habit may therefore be linked to seasonal productivity; a gastropod adapted to such periods of non-feeding quiescence in a time of reduced benthic food supply might have a selective advantage. A recent study (Moss *et al.* 2017) also demonstrated that high latitude Cretaceous and Palaeogene bivalves, including several genera which survived and proliferated in LB10 (*Lahillia*, *Cucullaea*) (Fig. 3), exhibited lifespans of more than 100 years. It is likely that

this longevity was due to slow growth rates linked to slow metabolism, and an adaptation to caloric reduction brought about by the limited availability of food supplies in high latitude environments, ultimately driven by the polar light regime. However, some preadaptation to enhanced seasonality could be argued for all members of the Antarctic K–Pg marine fauna.

Riedel *et al.* (2012) showed through *in situ* experiments that epifauna and predatory taxa are more sensitive to oxygen depletion than infauna. Therefore, the possibility of intermittently anoxic to euxinic conditions on the seafloor and in the water column following the K–Pg mass extinction in Antarctica (Zinsmeister 1998; Witts *et al.* 2016; Schoepfer *et al.* 2017) may have led to the preferential survival, and dominance of infaunal organisms following the extinction horizon in this location. Clapham (2017) found that more motile organisms preferentially survived Mesozoic extinctions, suggesting that greater activity and therefore potentially higher respiratory physiology, controlled survival during extinction periods (Clapham 2017). Our data show little change in the taxonomic richness of facultatively motile taxa; however, abundance trends do show an increase in motility during the early Danian.

Many of the local ecological patterns seen in the recovery of the benthic molluscan fauna on Seymour Island are driven by the near-extinction of slow motile epifaunal carnivorous gastropods at the K–Pg boundary, and a rapid radiation of taxa belonging to this mode of life in the SF (Figs 4, 5). Gastropods belonging to this mode of life may have been somehow more susceptible to environmental change than others, perhaps for the reasons outlined above, or due to some competitive disadvantage not obvious from fossil occurrence data alone. The rapid diversification of gastropods (15 taxa originating in approximately 600 000 years) in the early Paleocene deposits of Seymour Island can be linked to a global event: the rise to dominance in marine molluscan faunas of a single clade, the Neogastropoda (Crame 2013; Crame *et al.* 2014). These new stratigraphically constrained data from Antarctica would suggest that this radiation was well under way less than 1 myr after the K–Pg extinction in the southern hemisphere with the appearance of many new neogastropod taxa in the SF (Stilwell *et al.* 2004; Crame *et al.* 2014).

A well-documented shift in dominance in global molluscan faunas from bivalves to gastropods occurs above the K–Pg boundary (Valentine 1969; Vermeij 1977; Sepkoski 2002; Alroy 2010). This occurs over the same timescale in Antarctica, with the rapid speciation of new gastropod taxa in the SF (Fig. 4, and Crame *et al.* 2014). The patterns seen in the gastropod fauna are in contrast with those exhibited by bivalves, which are dominated by fewer taxa which survived the K–Pg extinction (Fig. 4) (Stilwell *et al.* 2004; Crame *et al.*

2014). Interestingly, the recovery of benthic molluscan species richness in the early Danian of the SF also appears to include the first representatives of several modern Southern Ocean molluscan genera (Beu 2009; Crame 2013; Crame *et al.* 2014). This supports the hypotheses that the K–Pg extinction was instrumental in resetting the evolutionary stage prior to the evolution of the modern marine fauna (Krug *et al.* 2009), and that Antarctica may have acted as an evolutionary source rather than a sink during the Palaeogene prior to the onset of glaciation at the Eocene–Oligocene boundary (Crame 2013; Crame *et al.* 2014).

CONCLUSIONS

Overall, our data show a complex interplay of local environmental factors and broader global patterns in the recovery from the K–Pg mass extinction in Antarctica. The marine recovery in Antarctica is characterized by a shift in abundance and taxonomic richness of benthic molluscan faunas, with infaunal taxa dominating for an initial 320 kyr period of the early Danian. Taxonomic recovery is marked by significant increases in origination and species richness around 320 kyr and 1 myr after the mass extinction. These shifts can be linked to the re-establishment of global biogeochemical cycles and recovery of primary producers over the same timescale worldwide. There is a decoupling of taxonomic and ecological extinction intensity in Antarctica across the K–Pg boundary, and little evidence for the preferential survival of particular ecologies or modes of life following the mass extinction. The degree of ecological change is apparently less than those seen at lower latitudes, which may be explained by a pre-adaptation to seasonally challenging conditions in the Antarctic fauna. The differences in the degree of ecological change between sites supports the hypothesis of geographic heterogeneity in post-extinction ecosystem dynamics.

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DATA ARCHIVING STATEMENT

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