



# Environmental change prior to the K–T boundary inferred from temporal variation in the morphology of cheilostome bryozoans

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## ABSTRACT

Fluctuations in the marine environment just prior to the K–T extinction event have been inferred from several geological sections around the world. Most previous studies have employed isotope or trace element proxies. This study uses morphological changes in erect and free-living cheilostome bryozoans as a proxy to investigate environmental change through the final stages of the Maastrichtian at the Nye Kløv section in Denmark. The metrics used are: (1) mean zooid size as a proxy for temperature; (2) intracolony variation in zooid size as a proxy for degree of seasonality; (3) density of defensive avicularia as a proxy for palaeoproductivity; and (4) colony size and asymmetry as proxies for unfavourable environmental conditions. Three semi-distinct phases in the benthic environment are evident: The lowest 3.5 m of the roughly 4.5 m section experienced apparently normal marine conditions. Next, low estimates of benthic seasonality, and highly symmetrical and large colonies with many avicularia indicate a time of increased environmental stability. Subsequent to this quiescence, the uppermost ~20 cm of the section witnessed environmental volatility and deterioration with mean zooid sizes in all species falling dramatically suggesting a rapid warming or dysoxic event, sharply increasing seasonality estimates implying unusual oceanographical states, and the growth of small, asymmetrical colonies with few avicularia all suggesting unfavourable conditions. These data therefore indicate that strong environmental perturbations occurred just prior to the K–T boundary in the Danish Basin. Such events may have contributed to biotic turnover at the K–T boundary because cause and effect in macroevolution can be delayed. However, potential mechanisms of turnover need to be robustly tested within a detailed palaeoenvironmental framework construct from a suite of independent proxies.

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## 1. Introduction

The mass extinction at the Cretaceous–Tertiary (K–T) boundary has provided controversy for over 30 years. High iridium concentrations (Alvarez et al., 1980), spinels (e.g. Robin et al., 1992), shocked quartz (e.g. Bohor et al., 1987) and a variety of other evidence found at many K–T boundary sections worldwide point to the impact of an extraterrestrial object. Coeval sediments associated with ejecta and the presence of a large crater at Chixculub in the Yucatan Peninsula of Mexico add further support to the hypothesis that extinction was driven by catastrophic environmental changes associated with such an impact (reviewed in Schulte et al., 2010). However, seemingly diagnostic evidence of impact is strongly contested (e.g. Keller and Stinnesbeck, 1996) and patterns of

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biological turnover fail to correlate clearly with a single causal mechanism (Keller et al., 2010), leading several workers to favour other less catastrophic processes, such as prolonged volcanic activity from the Deccan Traps (e.g. Valen, 1984; Officer and Drake, 1985; Keller et al., 2009), as explanations for the K–T mass extinction.

The test to discriminate such contrary hypotheses is seemingly straightforward. A catastrophic mechanism, such as an impact, should produce a sudden extinction of taxa directly associated with rapid environmental change, whilst volcanism should leave evidence of more gradual extinction and prolonged environmental change. Yet both rapid (e.g. Smit, 1982) and protracted (e.g. Keller, 1988) extinctions have been inferred, even from the same samples (Ginsburg, 1997). There is a similar polarisation of conclusions regarding the timing, duration and extent of the environmental changes (e.g. Birkelund and Håkansson, 1982; Sweet et al., 1990; Keller et al., 1993; Keller et al., 1997; Brinkhuis et al., 1998). These contrasting views are likely to reflect idiosyncrasies common to interpreting data from the fossil record (Keller and Abramovich, 2009) and more subtle effects exerted by preconceived conclusions (Valen, 1984). Identifying a single cause for the K–T

extinction has therefore been challenging, and a multicausal scenario remains a viable alternative (Birkelund and Håkansson, 1982; Keller et al., 2003; Archibald and Fastovsky, 2004; Jolley et al., 2010).

The aim of this study is to determine if significant changes in environmental conditions occurred during the period leading up to the K–T boundary in Denmark, as have been observed in several sections from around the world (e.g. Keller et al., 1997; Li and Keller, 1998; Ramkumar et al., 2005). Unlike most K–T marine studies that have used isotopes and trace elements of skeletal material of unitary organisms (e.g. foraminifera, bivalves) as environmental proxies, this study explores environmental conditions using the skeletal morphology of bryozoans whose patterns of colonial growth allow unique insights. The study focuses on the section at Nye Kløv, which is arguably the least complex among the complete K–T boundary sections exposed in the Danish Basin (Håkansson and Hansen, 1979; Birkelund and Håkansson, 1982; Surlyk and Johansen, 1984; Johansen, 1987; Håkansson and Thomsen, 1999), and is therefore considered representative of the final few hundred thousand years of deposition of the Chalk dominating the epicontinental seas covering much of northern Europe during the Late Cretaceous (Surlyk, 1997).

## 2. Metrics of change

This study utilises several morphological metrics from bryozoans as proxies to explore marine conditions leading up to the K–T boundary. This section describes each metric and its application.

### 2.1. Mean zooid size

Cheilostome colonies are formed by the iterative budding of zooids that remain fixed in size once budded. The size of these zooids varies inversely with ambient temperature; thus, a zooid budded in warmer waters will be smaller than a genetically identical zooid budded in cooler waters, other factors being equal (Menon, 1972; Hunter and Hughes, 1994; O'Dea and Okamura, 1999; Amui-Vedel et al., 2007). This relationship is the same physiological response expressed widely across invertebrates, known as the temperature–size rule (Atkinson, 1995; Atkinson and Sibly, 1997; Atkinson et al., 2006). The rule almost certainly represents a universal response, whether adaptive or not (see Kingsolver and Huey, 2008, for further discussion). In the Bryozoa it applies at the level of the zooid rather than the colony (Okamura and Bishop, 1988; Hunter and Hughes, 1994; O'Dea and Okamura, 1999, 2000b; O'Dea and Jackson, 2002; O'Dea, 2003, 2005; Amui-Vedel et al., 2007; O'Dea et al., 2007b; Knowles et al., 2009). In general, and provided sufficient care is taken to avoid sampling unrepresentative zooids, changes in zooid size provide a reliable indication of changes in temperature (for detailed discussion see Okamura et al., in press).

The relationship between temperature and zooid size provides an opportunity to infer relative changes in palaeotemperature by observing intraspecific changes in mean zooid size through time. For example, since the Early Pliocene, the mean sizes of zooids in several cheilostome species from shallow seas in northwestern Europe have decreased significantly (Okamura and Bishop, 1988; O'Dea, 2000), paralleling the established cooling of waters in this region and global climate in general (Zachos et al., 2001). The current study examines how mean zooid size within four species of Maastrichtian cheilostome Bryozoa varied in the time leading up to the K–T boundary.

The zooid size–temperature relationship is robust but the ultimate mechanisms accounting for it remain unresolved (Okamura et al. in press). One proposed explanation is that as temperatures increase oxygen demand also increases but oxygen supply is limited because solubility decreases in warmer waters (Atkinson et al., 2006). Oxygen concentration has been demonstrated to determine zooid size in some Recent cheilostomes with smaller zooids expressed in lower oxygen conditions (Atkinson, 1994; O'Dea and Okamura, 1999). Thus,

changes in zooid size may not only reflect temperature but also oxygen levels on the sea floor.

### 2.2. Intracolony variation in zooid size

Variation in zooid size within a colony will, among other things, reflect the variation in temperature the colony has experienced during its growth. As bryozoan colonies often live for more than one year, intracolony variation in zooid size will reflect the local seasonal regime in temperature. This relationship has been quantified by linear regression of the amount of intracolony zooid size variation in over 150 Recent cheilostome colonies against the mean annual range of temperature (MART) from the sites in which these colonies lived (O'Dea and Okamura, 2000b). The regression allows retrospective estimation of MART based on the amount of intracolony variation in zooid size in cheilostomes using the equation:  $MART (^{\circ}C) = -3 + 0.745(b)$ , where  $b$  is the mean intracolony coefficient of variance (CV) of zooid frontal area (O'Dea and Okamura, 2000b).

The zooid size approach to MART (zs–MART) can determine MART to an accuracy of around  $\pm 1^{\circ}C$  (see Okamura et al., in press) if various requirements are met (O'Dea and Okamura, 2000b). The approach has been used successfully to estimate the MARTs of several ancient seas, including the shallow coastal seas of northwestern Europe through the Neogene (O'Dea and Okamura, 2000a, b), a wide array of epicontinental seas across the North Atlantic during the critical Pliocene warm period (Knowles et al., 2009; Williams et al., 2009), and coastal seas of the southwestern Caribbean as upwelling regimes changed dramatically due to the emergence of the Isthmus of Panama (O'Dea et al., 2007a).

### 2.3. Colony asymmetry

Fluctuating asymmetry (FA) is a form of morphological asymmetry resulting from stress experienced during development or developmental instability (reviewed in Dongen, 2006), and is therefore of particular interest to palaeobiologists because it probably represents the best way to estimate the fitness of long-dead individuals (Völlestad et al., 1999). Studies of FA in the fossil record have tended to focus on organisms with bilateral symmetry (see Babcock, 2005 for review), although deviation from radial symmetry has also been related to fitness costs, for instance in mechanical stability and pollinator attraction in plants (Neal et al., 1998).

This study uses variation from either bilateral or radial symmetry in colonies of free-living bryozoans as a proxy for unfavourable environmental conditions. This approach assumes a positive relationship between symmetry and fitness for the majority of free-living (or free-living) taxa, which is supported by several lines of evidence. In the immobile, free-living Maastrichtian species *Stichopora pentasticha*, colonies were more liable to burial or overturning when they were temporarily bilaterally asymmetrical (Håkansson, 1975). In motile, free-living species, radial symmetry is customary in all but a few Late Cretaceous species, even though all other aspects of morphology and patterns of growth vary greatly amongst species (O'Dea et al., 2008; O'Dea and Jackson, 2009), strongly supporting the idea that radial symmetry is highly adaptive. Indeed, experimental data have shown that deviating from radial symmetry is disadvantageous for motile free-living species because: (1) asymmetrical colonies are more likely to be turned over by wave action and are less able to move up through sediment passively if they become buried (O'Dea, 2009), implying that radial symmetry confers hydrodynamic stability and better in-faunal coordination; (2) fragments that are always asymmetrical are more prone to burial than circular colonies of the same size (O'Dea, 2009); (3) when a free-living bryozoan is fragmented, initial regenerative growth is always concentrated in the central portions of the sides of the fragments (O'Dea, 2006; O'Dea et al., 2008), thereby ensuring that a circular, more stable shape is rapidly regained by the colony (Håkansson

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