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## 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-lying) 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

and Thomsen, 2001); (4) initial regenerative growth of asymmetrical fragments is five times more rapid than colony growth at any other time, implying an urgency in the need to create a circular colony (O'Dea, 2006); and (5) fragments that fail to achieve circularity demonstrate higher rates of mortality (O'Dea, 2006, 2009).

Thus, living freely on the sea floor in bryozoans is facilitated by maintaining a symmetrical colony. As such, relatively high levels of asymmetry in fossil free-living bryozoans may be used as an indication that unfavourable environmental conditions have challenged the attainment of optimal symmetry.

#### 2.4. Colony size

This metric assumes that larger colonies within free-living bryozoan species reflect more favourable environmental conditions because larger colonies have greater numbers of feeding and reproductive zooids.

#### 2.5. Avicularian density

Avicularia are polymorphic zooids with hypertrophied opercula found in a wide array of cheilostome families (McKinney and Jackson, 1989). They include vibracula which have stiff, whip-like setae that extend above the colony surface and whose functions include: (1) deterring epibiotic organisms from settling on colony surfaces; (2) cleaning fine sediment from the colony surface; and (3) removing or impeding the growth of epibionts (Winston, 1988; Carter et al., 2010). In the free-living bryozoans vibracula also physically lift the colony above the surface of the sea floor (Cook, 1963; Cook and Chimonides, 1978; Winston, 1988; O'Dea, 2009), and can be used to dig colonies out of the sediment if accidentally buried (Håkansson and Winston, 1985).

Many groups exhibit varying densities of avicularia within and between colonies of the same species, and such variation is often considered to be induced by local environmental cues (Harvell, 1986, 1991, 1992; Harvell and Helling, 1993; Carter, 2008; Carter et al., 2010), although the precise factors that control the development of avicularia remain largely unknown and are likely to be multiple (Carter, 2008; Carter et al., 2010). Avicularian density may be a response to predation intensity or the intensity of ectosymbiotic activity. Alternatively, the abundance of avicularia in bryozoan colonies may reflect a trade-off between the need for defence vs. the need to feed. Either way, increasing avicularia density should correlate with greater planktonic productivity.

### 3. Study site

#### 3.1. Locality information and depositional environment

The Late Cretaceous experienced rising sea levels (Kominz et al., 2008 and references therein), so that most of Europe was immersed, with coccolith-rich Chalk accumulating over vast areas (Surlyk, 1997). Towards the end of the Maastrichtian, the accumulation of Chalk became restricted to basins in northwest Europe, and as sea level fell even further at the very end of the Cretaceous marine conditions may have persisted in only a narrow seaway that connected the Proto-Atlantic in the northwest to the Tethys in the southeast, bounded by the Ringkøbing-Fyn high to the south and the Fennoscandian Shield to the north (Håkansson and Thomsen, 1999), although precise palaeobiogeography and extent of sub-aerial terrains at this time remains unresolved.

Of the several K–T sections exposed in Denmark, the section near Nye Kløv in northern Jylland (Fig. 1), is most suitable for the analysis used in this study because it is an essentially complete, fairly uniform and fully marine succession containing a diverse, abundant and well-preserved bryozoan fauna (Surlyk and Johansen, 1984; Håkansson and Thomsen, 1999). Furthermore, the stable isotope composition of foraminifera from the section has been studied (Keller et al., 1993). The section is characterised by a succession of pelagic highly

bioturbated chalks with flint nodules preserving the burrows of *Thalassinoides* and *Zoophycos*. Macrofossils make up around 1% by weight of this chalk, with bryozoans dominating (Håkansson and Thomsen, 1999). A 3 cm-thick, clay-rich layer lies sharply on the Chalk and contains the iridium anomaly defining the K–T boundary (Nazarov et al., 1983; Hansen et al., 1986).

#### 3.2. Biostratigraphy and chronostratigraphy

Zonal resolution of Maastrichtian Chalk in northwestern Europe is somewhat coarse, with fewer than ten planktonic zones distinguishable in the up to 700 m-thick succession (Stenestad, 1972). It is therefore unsurprising that the topmost 5 m of Maastrichtian Chalk exposed at Nye Kløv is not easily subdivided. Due to the lack of characteristic low latitude planktonic elements, Keller et al. (1993) simply designated the Maastrichtian succession at Nye Kløv as “unzoned”. However, several other Danish K–T boundary sections are correlatable to Nye Kløv by means of both benthic and planktonic biotas (Surlyk and Johansen, 1984; Håkansson and Thomsen, 1999; Rasmussen et al., 2005), including the coccolith species *Micula murus* characterising the very latest Maastrichtian zone (Perch-Nielsen, 1979). Since no hiatus are evident in the Maastrichtian – and, indeed, the lower part of the Danian – at Nye Kløv (cf. Håkansson and Thomsen, 1999, Fig. 3), the assumption of continuous accumulation up to and including the K–T boundary is made.

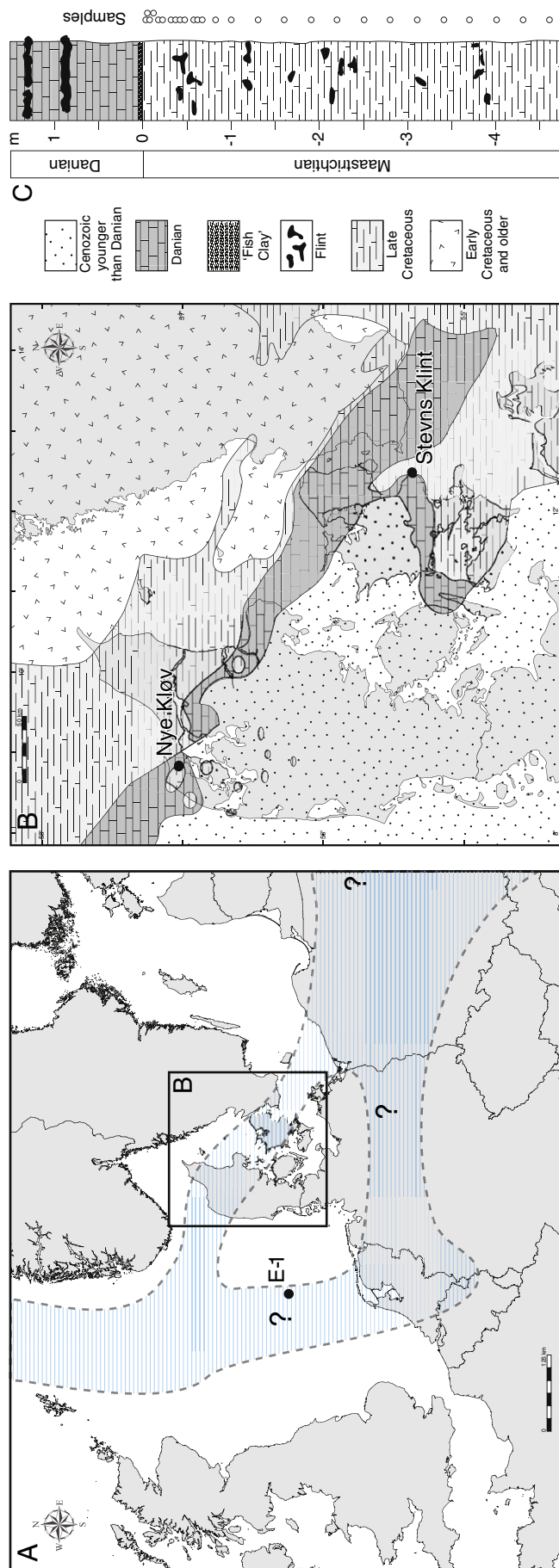
Estimating anything but the most general rate of sedimentation of the Maastrichtian Chalk in the Danish Basin is problematical, not only due to the scarcity of the traditional, low latitude planktonic index taxa, but also because other stratigraphical markers are essentially absent in the uppermost Maastrichtian in the deeper parts of the Danish Basin. Nonetheless, rates of sedimentation for the whole of the Maastrichtian Chalk in the Danish Basin have been estimated to be around 10 cm ka<sup>-1</sup> (Håkansson et al., 1974; Hancock, 1975; Kaminski and Malmgren, 1989). Since these estimates do not take into account hiatus, for which there is evidence of many through the Maastrichtian, (Bromley, 1979) proposed that a figure of around 20 cm ka<sup>-1</sup> is probably closer to the truth for times when sedimentation was continuous. These estimates are deduced from the maximum amount of Maastrichtian sediment accumulation in the Danish Basin, and Bromley's estimate is therefore almost certainly too high to be applied to the section at Nye Kløv where sediment accumulation was considerably slower (Håkansson and Thomsen, 1979). Keller et al. (1993) recognised these problems and accepted a rate of deposition of approximately 4 cm per 1000 years. This study therefore uses a value between those of Bromley (1979) and Keller et al. (1993), close to the original estimate for sedimentation rate of around 10 cm ka<sup>-1</sup>.

### 4. Material

#### 4.1. Sampling details

Twenty-eight bulk samples were collected from successive intervals in the topmost 460 cm of Maastrichtian Chalk leading up to the K–T boundary at Nye Kløv (Fig. 1B). Samples were removed from the section as complete as possible to prevent breakage of bryozoan colonies since large fragments of erect colonies and whole free-living colonies were preferred for analysis. Samples weighed between 2.2 and 5.5 kg when wet.

Bryozoans were extracted from the matrix using a modified technique described by Surlyk (1972). Samples were first air-dried then individually soaked in a supersaturated solution of Glauber's Salt (Na<sub>2</sub>SO<sub>4</sub>·10H<sub>2</sub>O) at a temperature of 43 °C until completely drenched. They were deep frozen to –18 °C, left overnight and then re-heated to 43 °C. This process of freezing and heating was repeated 18–25 times until a fine ooze remained. Samples were then sieved at 1 mm and the residues retained.



**Fig. 1.** A. Marine K–T palaeogeography of Northwest Europe (Modified from Håkansson and Thomsen, 1999). Dashed line represents the inferred extent of marine conditions at the K–T boundary. The narrow seaway in the Danish basin was connected to the Tethys to the Southeast and to the Proto-Atlantic in the Northwest. Location of North Sea Well E-1 marked. B. Geological map of Denmark (Based on Håkansson and Pedersen, 1992) with position of localities referred to in text. C. Sedimentary sequence exposed at Nye Kløv with location of samples taken for this study. K–T boundary is situated at 0 m.



## 4.2. Species

From the highly diverse bryozoan residues four cheilostome species were picked (Fig. 2): *Woodipora disparilis* (d'Orbigny, 1851), *Stichopora pentasticha*, *Onychocella nysti* (von Hagenow, 1839), (von Hagenow, 1839) and *Lunulites pseudocretacea* (Håkansson and Voigt, 1996). These species were considered appropriate for study because of their: (1) consistently high relative abundance through the sampled section; (2) relatively unambiguous taxonomy; (3) well-defined and easy to measure morphometric characters; and (4) good preservation of an array of colony sizes.

### 4.2.1. *Woodipora disparilis*

*Woodipora disparilis* (Fig. 2A) is an erect bryozoan with columnar branches of around 1.5 mm in diameter. Zooids are elongate and pyriform in shape with a curved anterior edge. The cryptocyst is often depressed into a proximal–distal furrow. Two opesiules lay proximal of the semi-circular opesia that is situated at the very distal end of the zooecia and is protected by a posterior lip rising from the cryptocyst. Long tapering vibracula are common throughout the colony and are furnished with small, ornamented opesia.

### 4.2.2. *Stichopora pentasticha*

*Stichopora pentasticha* (Fig. 2B) has an atypical colony comprising very few zooids and lacking heterozooids or ovicells. Normal colonies form small, curved 'balls' which were free-living but immobile on top of the sediment, or semi-immersed in the soft mud bottom (Håkansson, 1975). Development of *S. pentasticha* colonies follows a predictable budding pattern and, unless the colony experienced physical disruption during ontogeny, is more or less bilaterally symmetrical along a proximal–distal colony axis. The zooids are hexagonal to oval, depending on their position within the colony. They possess a large, centrally situated oval opesia that often has a flattened proximal rim. The cryptocyst is thick, narrow and granular in texture.

### 4.2.3. *Onychocella nysti*

Colonies of *Onychocella nysti* (Fig. 2C) are heavily calcified with an encrusting base that gives rise to erect, dichotomously branching,

bilamellar fronds. Zooids are fairly irregular in shape, hexagonal to rhomboidal, with a more or less rounded anterior margin. Zooid margins form a raised rim with a medial furrow. The cryptocyst is often depressed and possesses a semi-elliptical opesia with a straight proximal margin. Avicularia are scattered evenly between zooids, have a basic rhomboidal shape with a long tapering distal tip, and can be nearly twice as long as the autozooids.

### 4.2.4. *Lunulites pseudocretacea*

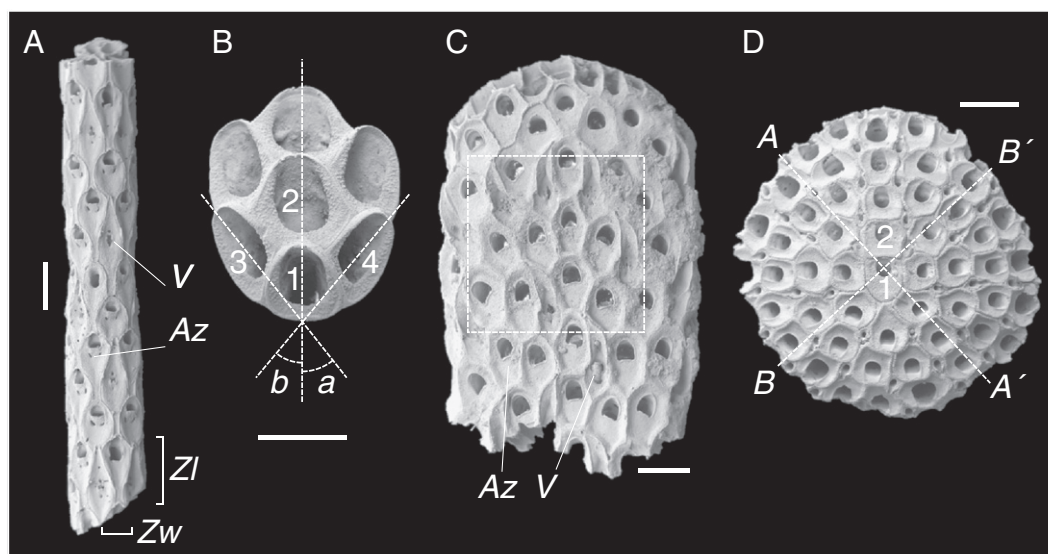
Colonies of *Lunulites pseudocretacea* are circular, slightly concave to flat and disc-like (Fig. 2D). Zooids are budded radially from the central ancestrular zooid, and are more or less rectangular with a depressed cryptocyst and oval opesia surrounded by a coarsely granulated mural rim. Small, slightly tapering vibracula are present between most feeding zooids and feature a rounded opesia. Colonies were probably able to rest freely above the soft sea bed, prevent themselves from being covered by sediment, and move locally to more favourable positions.

## 5. Data collection and analysis

### 5.1. Mean zooid size

Zooid size was measured in one of two different ways depending on the growth habit of the species. For the two erect species, *Onychocella nysti* and *Woodipora disparilis*, the five largest, most complete and well-preserved colony fragments were selected for analysis from each sample. Twenty zooids were randomly selected for measurement in each specimen of *O. nysti*, and ten for the smaller fragments of *W. disparilis*. For each zooid selected, maximum length was measured. Mean zooid length within a colony was then calculated, from which an overall mean zooid size (mean of the means) per stratigraphical 'population' was determined.

For the two smaller free-living species, *Lunulites pseudocretacea* and *Stichopora pentasticha*, up to 30 colonies per sample were used for analysis. Where there were fewer than ten colonies per sample, adjacent samples were combined to provide adequate data, although abundance was sufficient enough through the section that this only



**Fig. 2.** Colonies of the cheilostome species used in this study. A. *Woodipora disparilis*, Zl = Zooid length and Zw = Zooid width. B. *Stichopora pentasticha*. Dashed lines illustrate measurement of angles *a* and *b* that describe the angle of budding of the 3rd and 4th budded zooids from ancestral (1st) and 2nd zooid that was used to calculate bilateral asymmetry of colonies. C. *Onychocella nysti*. Dashed box illustrates area used to calculate avicularian density. D. *Lunulites pseudocretacea*. Dashed lines illustrate the calculation of colony asymmetry as the eccentricity from a true circle using the major (A–A') and minor (B–B') axes. Scale bars on all = 500  $\mu$ m. V = Avicularia; Az = autozooid.

occurred on one occasion and only with *L. pseudocretacea*. Data collection for these species had to be modified from the approach outlined by Okamura and Bishop (1988) because astogenetic variation in zooid size is expressed across a relatively large proportion of the colony, presumably as an accommodation to their unique modes of life (Håkansson, 1975). Thus, for these two unusual species only the first two zooid generations were measured; the ancestral zooid (ancestrula) and the second zooid budded immediately distally from the ancestrula (see Fig. 2B and D). For both zooids, length was measured and changes in the mean length of each zooid within species tracked through time.

Comparing trends in the data of zooid size from all species was assisted by normalising all zooid metrics for each species and compiling them in one plot to reveal shared trends in zooid size through time.

### 5.2. Intracolony variation in zooid size

For *Onychocella nysti* and *Woodipora disparilis* the five largest, most complete and well-preserved colony fragments were selected for zs-MART analysis from each stratigraphical sample from 460 to 0 cm below the boundary, where sufficient colonies were available. For each colony fragment, twenty zooids were haphazardly selected for measurement in *O. nysti* and ten in *W. disparilis*. Maximum length and width were measured, from which a proxy of zooid frontal area (length × width) was derived. The mean CV of zooid frontal area from all colonies per stratigraphical sample was used to estimate MART by applying the equation  $MART (^{\circ}C) = -3 + 0.745(b)$  (O'Dea and Okamura, 2000b).

### 5.3. Colony asymmetry

Because of their differing modes of life, colonies of *Lunulites pseudocretacea* are radially and *Stichopora pentasticha* bilaterally symmetrical. For *L. pseudocretacea* all unbroken colonies were analysed in samples from 250 to 0 cm below the boundary. Each colony was digitally photographed and threshold-isolated using ImageJ software (Abramoff et al., 2004). A script was run to determine the lengths of the major and minor axes of each colony based upon an ellipse. Asymmetry was measured as eccentricity ( $\epsilon$ ) of the ellipse from a true circle using  $\epsilon = \sqrt{1 - \left(\frac{b}{a}\right)^2}$  where  $a$  = half the major axis and  $b$  = half the minor axis (Fig. 2D). Mean  $\epsilon$  was calculated per stratigraphical level and plotted through time.

For *Stichopora pentasticha* bilateral asymmetry was determined as the difference in degrees between the two angles described by the 3rd and 4th dextral and sinistral zooids relative to the ancestrular zooid (respectively  $a$  and  $b$  in Fig. 2B). This was achieved by first drawing a line that bisects the ancestrula and then locating the most distal point of the 3rd and 4th zooids from which the angles could be measured.

### 5.4. Colony size

ImageJ software was used to calculate the area of *L. pseudocretacea* contained within the outline of the margin of the colony. This value was used as a proxy for frontal area assuming that colonies are flat discs. This assumption is reasonable as *L. pseudocretacea* colonies are flatter than those of most other lunulitiform species. No damaged or fragmented colonies were included in the analysis. Mean colony frontal area was plotted through time.

### 5.5. Avicularian density

The mean density of avicularia in colonies of *Onychocella nysti* and *Woodipora disparilis* was measured for each colony fragment used for

the analysis of intracolony variation in zooid size. Five randomly selected 3.2 mm<sup>2</sup> areas were located on the colony surfaces (Fig. 2C). Within each square, the number of whole avicularia plus the number bisected by the proximal and dextral lines of the square were counted.

Mean avicularian density through the entire section was significantly negatively correlated with mean zooid size in both *O. nysti* ( $r = -0.42$ ;  $t = -2.185$ ;  $df = 22$ ;  $p < 0.05$ ) and *W. disparilis* ( $r = -0.61$ ;  $t = -3.782$ ;  $df = 24$ ;  $p < 0.001$ ). It was therefore necessary to remove the effect of zooid size on avicularian densities to observe patterns of true avicularian density through time. This was achieved by using the residuals of avicularian densities from the correlation in each species.

## 6. Results

### 6.1. Mean zooid size

The patterns of change in mean zooid length in *Woodipora disparilis* and *Onychocella nysti*, and mean length of the ancestrular and second generation zooids in *Stichopora pentasticha* and *Lunulites pseudocretacea* leading up to the K–T boundary at Nye Kløv are presented in Fig. 3A–G. Major trends are best observed in the normalised zooid size data (Fig. 3G). Plotted for comparison are the  $\delta^{18}O$  values of the benthic foraminiferan *Cibicides succedens* from the same section (Fig. 3H) (Keller et al., 1993).

Mean zooid size increases slightly approximately 25 cm below the boundary. This is due only to an increase in size in *W. disparilis* and a slight increase in size in *S. pentasticha*; the other two species did not increase in size at this time. At 15 cm below the boundary, however, zooid sizes in all four species show a dramatic reduction (Fig. 3G). Between 460 cm and approximately 40 cm below the boundary zooid size fluctuates cyclically with a periodicity of around 200 cm (Fig. 3G).

### 6.2. Intracolony variation in zooid size

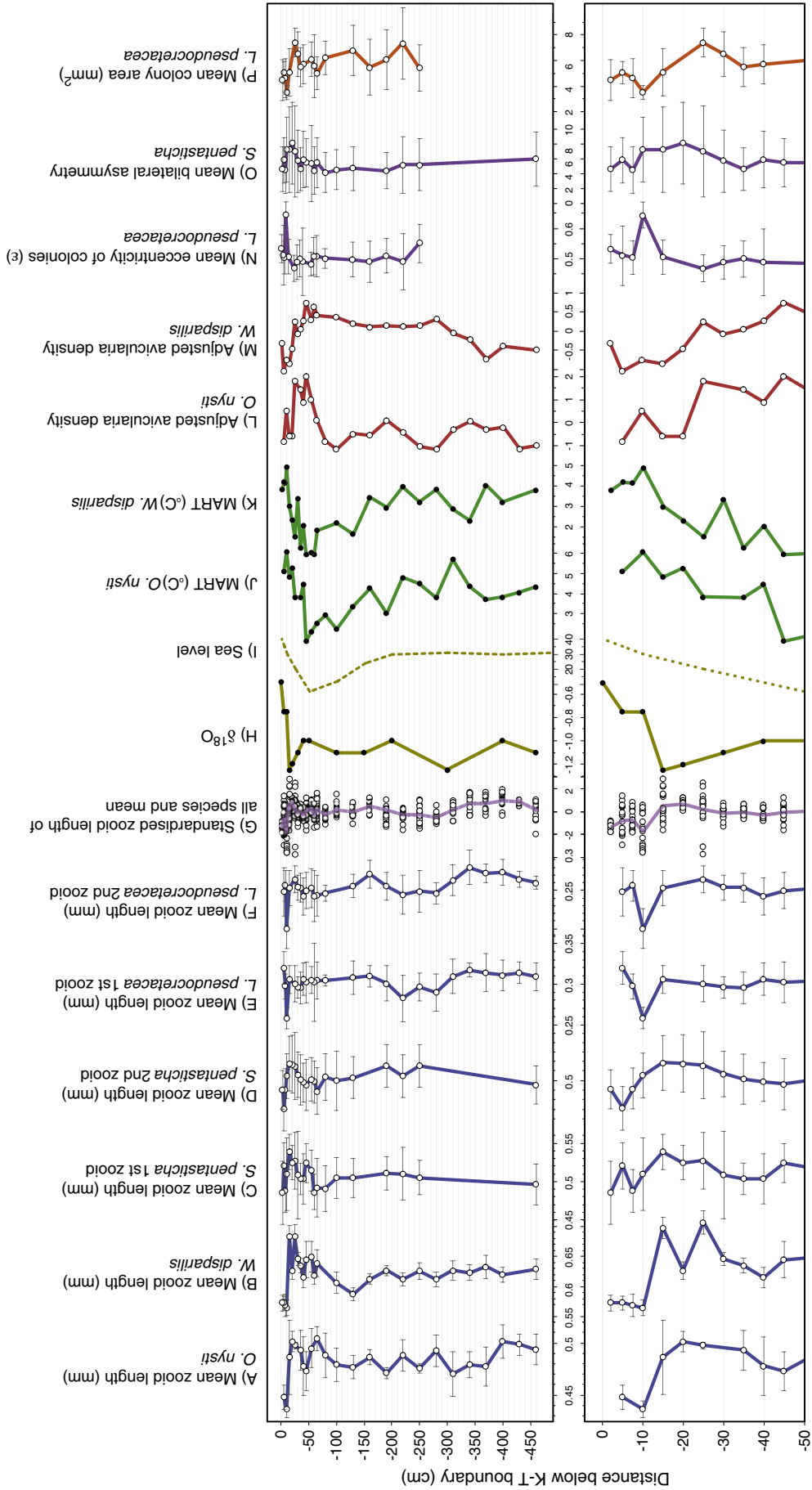
Estimates of MART derived from zs-MART analysis of colonies of *Onychocella nysti* and *Woodipora disparilis* parallel each other through the last 250 cm of the Maastrichtian section at Nye Kløv (Fig. 3J and K). Low MARTs from about 4–6 °C for most of the section suggest an equable climate. As a comparison, benthic environments in northwest Europe today experience MARTs of between 6 and 10 °C. The low MART at Nye Kløv further decreased to 2–4 °C between 100 and 30 cm below the K–T boundary, suggesting even greater equability. However, from about 30 cm below the boundary upwards, MARTs rise sharply to levels similar to and ultimately higher than those prior to the drop at 100 cm.

### 6.3. Avicularian density

Zooid-size adjusted avicularian densities in colonies of *Onychocella nysti* and *Woodipora disparilis* reveal little change through the section until at around 100 cm below the boundary whereupon avicularian densities in both species increase (Fig. 3L and M). Twenty centimetres below the boundary avicularian density in general falls, returning to pre 100 cm levels in *O. nysti* but falling beyond previous values in *W. disparilis*, but both species reveal rather high volatility in adjusted avicularian densities during this time.

### 6.4. Colony asymmetry

The mean eccentricity of colonies of *Lunulites pseudocretacea* reaches a minimum at between 50 and 25 cm below the boundary (Fig. 3N). At 10 cm below the boundary, colonies become highly eccentric just prior to the boundary. Likewise, between around 25 and 10 cm, colonies of *S. pentasticha* become more bilaterally



**Fig. 3.** Patterns of morphological change in bryozoans leading up to the K–T boundary at Nye Kløv, Denmark. Top panel shows the entire section whilst the lower panel expands the final 50 cm for greater resolution. A–G. Zoid length data. H.  $\delta^{18}O$  values of *Cibicides* succedens at Nye Kløv (from Keller et al., 1993). I. Estimated sea level at Nye Kløv (from Keller et al., 1993). J–K. Estimated mean annual range of temperatures (MART) (°C). N–O. Asymmetry data of bryozoan colonies. P. Colony size of *Lumilites pseudocretacea*. All error bars are SDs.

asymmetrical and return to being less asymmetrical in the final 7.5 cm below the boundary (Fig. 3O).

### 6.5. Colony size

The size of *Lunulites pseudocretacea* colonies shows high variation through most of the section but displays a sizeable and sustained reduction in the final 20 cm before the K–T boundary (Fig. 3P).

## 7. Discussion

Substantial changes were observed in zooid and colony morphologies of the four species of cheilostome bryozoans collected from the uppermost Maastrichtian at Nye Kløv. These changes may reflect important events in the latest Cretaceous sea in NW Europe. Each morphological metric is discussed below with reference to their potential environmental or ecological significance. From this evidence, the most parsimonious sequence of events that took place in the final stages leading up to the K–T boundary is inferred. These inferences are compared to previous K–T boundary palaeoenvironmental reconstructions from Nye Kløv, the Danish Basin and worldwide.

### 7.1. Mean zooid size

Normalised data on zooid sizes through the majority of the section at Nye Kløv appear to reveal cyclical fluctuations with a periodicity of approximately 200 cm (Fig. 3G). Cyclical patterns through Upper Cretaceous sediments and fossils have been attributed to environmental variation resulting from orbital forcing, caused either by the 100 ka eccentric, 41 ka oblique, or ~21 ka precessional periods of Milankovitch cycles (Herbert and Dhondt, 1990; Park and Oglesby, 1991; Cunha and Koutsoukos, 2001; Field and Hollis, 2003; Lauridsen and Surlyk, 2008), the latter being most frequently detected (MacLeod et al., 2001). However, cyclicity wasn't tested in this study and the lack of fine biostratigraphical resolution makes it difficult to translate stratigraphical into temporal periodicity and uncover the root cause. However, the data do highlight the potential use of ecophenotypic responses, such as the temperature-size rule, for detecting cyclicity and may even assist in refining biostratigraphic frameworks.

At around 20 cm below the boundary, normalized zooid size increased slightly due to the production of larger zooids in *Woodipora disparilis* and *Stichopora pentasticha*. Because the increase was mirrored in neither *Onychocella nysti* nor *Lunulites pseudocretacea*, it probably does not represent a change in environments. Since *W. disparilis* produced slender, erect and branching colonies while *S. pentasticha* was small and free-living, there are no obvious clues to help construct an alternative explanation for this moderate increase in zooid size.

A collective response to changing ambient conditions, however, is indicated by the striking and rapid decrease in zooid sizes at around 15 cm below the boundary in all four species. In accordance with the temperature-size rule, a zooid size decrease implies a significant warming of bottom waters just prior to the K–T boundary. In contrast,  $\delta^{18}\text{O}$  values of benthic foraminifera from the same part of the Nye Kløv section (Keller et al., 1993) suggest a 2 °C cooling, interpreted as a result of a sudden influx of cold deep water to the Danish Basin. These contrasting results from zooid size and  $\delta^{18}\text{O}$  data could be due to: (1) discrepancies in the isotope data; (2) a response of zooid size to other abiotic or biotic factors; (3) a combination of a warming event and an increase in  $\delta^{18}\text{O}$  values, or (4) insufficient stratigraphical correlation between isotope and zooid size sampling levels.

Diagenetic alteration is a potential source of discrepancies in the isotope data. Schmitz et al. (1992) noted that pre-boundary foraminifera at Stevens Klint were prone to dissolution and infilling by diagenetic calcite and similar evidence was noted in the samples

taken from Nye Kløv that may account for the pre-boundary positive  $\delta^{18}\text{O}$  shift observed there. Other studies of oxygen isotopes during the time leading up to the boundary in the Danish Basin have given varied results. However, other less well dated boundary sections in the Danish region (Bjerre, North Sea Well E-1; cf. Fig. 1) does indeed show similar drop in  $\delta^{18}\text{O}$  values prior to the boundary, indicating warming (Buchardt and Jørgensen, 1979). Similarly, lighter  $\delta^{18}\text{O}$  values occur close to the boundary in North Sea Well E-1 (Fig. 1) (Buchardt and Jørgensen, 1979). Additionally, the  $\delta^{18}\text{O}$  value of biogenically precipitated calcite is inversely proportional not only to temperature but also salinity (Broecker, 1974), and since freshwater dilution has a greater effect on the oxygen isotopic composition of sea water than does temperature (Hudson, 1990), only a slight decrease in salinity would be required to account for the approximately 0.25 per mil increase of  $\delta^{18}\text{O}$ . The positive  $\delta^{18}\text{O}$  excursion recorded at Nye Kløv by Keller et al. (1993) may therefore not necessarily represent cooling in the Danish Basin.

The universal decrease in zooid size could, however, reflect an environmental signal other than temperature, such as changing oxygen levels. Oxygen concentration in water has been demonstrated to determine zooid size in some Recent cheilostomes (Atkinson, 1994; O'Dea and Okamura, 1999) and temperature driven changes in oxygen solubility in water may, in part, explain body size changes (Atkinson et al., 2006). The shift to the production of smaller zooids just prior to the boundary may, however, be indicative of changes in oxygen conditions that are not driven by temperature. Anoxic events have been inferred to occur on a global scale prior to the boundary as a result of environmental perturbations from Deccan volcanism (see Glasby and Kunzendorf, 1996), and indeed the boundary clay in the Danish Basin has been suggested to represent an anoxic event (Kajiwaru and Kaiho, 1992; Hart et al., 2005). What's more, alternating bioturbated and laminated chalks in other parts of the Danish basin imply the regular occurrence of dysoxic events during the Maastrichtian (Damholt and Surlyk, 2004), although no laminations were observed at Nye Kløv.

### 7.2. Intracolony variation in zooid size

Estimates of MART based upon zooid size variation through the section at Nye Kløv (Fig. 3J and K) represent the first analysis of the benthic seasonal temperature regime during the Maastrichtian in the Danish Basin. MARTs are low throughout the entire section, as expected for an epicontinental benthic setting at 100–200 m depth (Bromley, 1979; Keller et al., 1993). Estimated MARTs from both species fall to very low values between 100 and 30 cm below the boundary,

**Table 1**

Summary of patterns observed in bryozoan morphologies and the inferred environmental conditions leading up to the K–T boundary at Nye Kløv, Denmark.

Approx depth below K–T boundary (cm)	Major patterns	Inferred conditions
25–0	Rapidly declining zooid sizes Rapidly increasing MARTs High colony asymmetry Smaller colonies Decreasing avicularian densities	Unstable and unfavourable environmental conditions. Rapid warming or oceanic anoxia. Low planktonic productivity.
100–25	Low MARTs High avicularian densities Low levels of asymmetry	Stable benthic environmental conditions with low seasonality and high planktonic productivity, favourable for bryozoan growth.
460–100	Cyclical changes in zooid size Intermediate MARTs Low avicularian densities Low levels of asymmetry	Normal depositional environment with possible orbital forcing of sea-floor temperatures. Moderate seasonality



coincident with postulated sea level low. Under normal conditions, a fall in sea level would be expected to increase benthic MARTs as shallow waters are less buffered against the seasonal extremities of the atmospheric climate. Another potential cause of reduced seasonality in mid to high latitudes could be the production of a shallow and permanent thermocline caused by surface water warming, thereby reducing benthic seasonality, although there is no evidence of significant surface warming at this time (Keller et al., 1993). Estimates of MART increase rapidly during the final 30 cm of the section.

Data suggest that the seasonal conditions experienced by benthic organisms in the Danish Basin at the end of the Maastrichtian appear to have changed considerably and in synchrony with postulated sea-level changes. Highly equable seabed conditions between 100 and 30 cm below the boundary are followed by increasing MARTs just prior to the boundary implying benthic instability. Although the oceanographical processes responsible for such potential instability remain speculative, several studies of chalk sea floor morphology suggest an unprecedentedly dynamic benthic system during the Late Cretaceous that may help justify rapid environmental shifts observed (Surlyk and Lykke-Andersen, 2007; Esmerode et al., 2008; Surlyk et al., 2008).

### 7.3. Avicularian density

Zooid-size adjusted avicularia densities reveal substantial changes in the uppermost 100 cm of the Nye Kløv section. In general, avicularian densities increased and then decreased just prior to the K–T boundary (Fig. 3). It is assumed that avicularian densities are positively correlated with primary productivity because one would expect a greater need for avicularia during times of greater predation or epibiota pressure which both increase in higher productivity, and likewise a greater capacity by the bryozoan to invest in defence when planktonic food levels are relatively higher.

Avicularian densities in erect colonies like *Woodipora disparilis* and *Onychoella nysti* are unlikely to be a response to sedimentation rates. Their use is more likely to be for defence than for clearing sediment given that sedimentation on vertical fronds elevated above the sea floor and exposed to the stronger currents higher in the water column is likely to be minimal. The increase in avicularian densities observed in the upper 100 cm of the section is therefore assumed to represent an increase in planktonic primary productivity and the subsequent rapid decrease in the final 15 cm prior to the K–T boundary represents a collapse in primary productivity.

### 7.4. Colony asymmetry

Between about 25 and 10 cm below the boundary, colony asymmetry in both free-living bryozoan species *L. pseudocretacea* and *S. pentasticha* increases substantial. This could reflect a direct reaction to unfavourable conditions or an indirect response that caused decreased heterozygosity in both species (Lerner, 1954). Either way, the data suggest deteriorating benthic conditions just prior to the K–T boundary.

### 7.5. Colony size

Reduced colony sizes within the final 20 cm of the Maastrichtian at Nye Kløv also imply that unfavourable benthic conditions prevailed at this time. The most obvious explanation is that levels of available food to the colonies became reduced, given that colony size is highly dependent on quality and quantity of diet (Winston, 1976; Sebens, 1982; O'Dea and Okamura, 1999; Hageman et al., 2009).

## 8. Summary and broader implications

Data from a suite of morphological proxies strongly suggest that benthic conditions in the Danish Basin underwent a series of major changes at the very end of the Maastrichtian. Although timings of

shifts in different metrics do not precisely correlate, these data broadly confer in their major conclusions. Stable conditions with high planktonic productivity are inferred to have dominated from between 100 and ~25 cm below the K–T boundary, as indicated by low seasonality and the growth of large colonies with lots of avicularia and low levels of asymmetry. From 25 cm up to the boundary rapidly deteriorating conditions are inferred as indicated by sharp declines in zooid sizes across all species suggesting widespread warming or anoxia, increased seasonality, and an abundance of small and asymmetrical colonies that had fewer avicularia (Table 1).

It is well known that despite its apparent monotony the Maastrichtian Chalk in the Danish Basin does not represent a homogeneous depositional environment (Håkansson and Thomsen, 1979; Larsen and Håkansson, 2000; Surlyk et al., 2006; Anderskov et al., 2007; Surlyk and Lykke-Andersen, 2007; Esmerode et al., 2008; Lauridsen and Surlyk, 2008; Surlyk et al., 2008) and the data presented here support this by indicating environmental perturbations of great magnitude towards the very end of the Maastrichtian without leaving any apparent sedimentological fingerprint.

Are the inferred major perturbations unique, unprecedented events or did similar events commonly occur in Late Cretaceous Chalk seas? Within the 460 cm section no excursions of similar magnitude to those seen in the last 25 cm were observed in any of the metrics, suggesting that the changes were somehow associated with the boundary. It is not possible however to dismiss the idea that similar rapid perturbations occurred prior to the section studied, and there are no comparable studies with which to compare these results, although this could easily be achieved by applying these approaches to any number of lithologically-similar sections of Late Cretaceous chalk exposed in Northern Europe.

To what extent were these changes caused by global versus regional or local events? Could volcanic activity originating from the Deccan Traps in the Indian Ocean for example have influenced the waters of the Danish Basin leading up the K–T boundary? Carbon black-stained bryozoan colonies are frequently found in the upper part of the Maastrichtian at Stevns Klint and Nye Kløv that may have been caused by the periodic incorporation of volcanic material into the sea water (Hansen et al., 1987) and volcanic soot in the air or water may explain the generally unfavourable conditions for bryozoan growth in the seas at Nye Kløv, but such a hypothesis may be intractable.

Whether pre-boundary environmental perturbations (either global or regional) had a progressive effect on the reduction of biotic diversity is debatable (Jolley et al., 2010). Declining taxonomic diversity is apparent throughout the Maastrichtian in many taxonomic groups (e.g. Birkelund and Håkansson, 1982; Ward, 1990), and there is evidence that some species' extinctions occurred prior to the chronostratigraphical boundary, but a causal correlation between deteriorating conditions and extinction has yet to be demonstrated. To connect major pre-boundary perturbations, such as those discussed here, with extinction event(s) requires the formulation of well-defined mechanistic processes that can be rigorously tested with a suite of palaeoenvironmental proxies (Jackson and Erwin, 2006; O'Dea and Jackson, 2009) and an appreciation that at the temporal scale under observation the structure and composition of biological communities often respond to environmental perturbations in non-linear ways due to threshold effects (Scheffer et al., 2001; Knowlton, 2004; Hsieh et al., 2005; Scheffer et al., 2009).

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