

Response of macrobenthic communities to the Toarcian Oceanic Anoxic Event in northeastern Panthalassa (Ya Ha Tinda, Alberta, Canada)



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ABSTRACT

In the Early Jurassic, the late Pliensbachian through early Toarcian interval exhibits significant environmental perturbations and biotic extinctions. This study documents the macrobenthic community during this interval in a region that has previously received comparatively little study: northeastern Panthalassa. The relicts of benthic communities from the Ya Ha Tinda Lagerstätte (Ferne Formation) in Alberta, Canada are primarily composed of bivalves and brachiopods, and exhibit taxonomic and ecological similarities with coeval black shale faunas from Europe.

At Ya Ha Tinda, the initiation of the carbon isotope excursion that occurred during the Toarcian Oceanic Anoxic Event (T-OAE) is coincident with major faunal change. The pre-T-OAE community is composed of large epifaunal suspension-feeders (bivalves and brachiopods), lobsters, crinoids, and burrowing organisms represented as trace fossils. The onset of the isotope excursion coincided with a wholesale turnover of bivalve and brachiopod genera as well as with a significant diminution in body size of the community members as a whole. The intra-T-OAE community largely consisted of opportunistic, low-oxygen-tolerant benthic taxa that colonized the seafloor periodically along with some facultatively pseudoplanktonic taxa. Unlike the contemporary deposits in Europe, there is no sign of recovery at Ya Ha Tinda in the middle Toarcian Planulata Ammonite Zone; abundance, richness, and functional diversity of benthic taxa remained extremely low and the size of community members remained small. The primary stress on this system is interpreted to have been oxygen limitation. The minimal ecological effect on the benthic community at the Pliensbachian-Toarcian stage boundary and delayed recovery from the T-OAE of the benthos are in marked contrast to the pelagic record from northeastern Panthalassa. This suggests a decoupling of the benthic and pelagic communities in this region during the Early Jurassic.

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1. Introduction

The Early Jurassic was a critical interval in the evolution of marine communities and was marked by several intervals of rapid environmental change and biological crises. Specifically, the late Pliensbachian and early Toarcian stages exhibit elevated extinction rates (Bambach, 2006) and significant reef collapse (Kiessling and Simpson, 2011). Multiple global carbon isotope excursions coincident with extinction events in the Pliensbachian and Toarcian stages provide evidence that major perturbations to the Earth system were occurring (e.g., Caruthers et al., 2014). One of these carbon isotope excursions in the Early Toarcian (~183 Ma) is coincident with an interval of expanded oceanic anoxia and black shale formation, known as the Toarcian Oceanic Anoxic Event, or T-OAE (Jenkyns, 1988, 2010). The duration of the T-OAE is

estimated at 620–900 kyr (Suan et al., 2008; Huang and Hesselbo, 2014), quite short-lived by geological standards.

The global Pliensbachian and Toarcian environmental perturbations have been related to the eruption of massive flood basalts, i.e. the Karoo-Ferrar-Chon Aike large igneous province (Pálffy and Smith, 2000; Wignall, 2001; Jourdan et al., 2008, 2009; Wignall and Bond, 2008; Sell et al., 2014; Burgess et al., 2015; Al-Suwaidi et al., 2016). Intense volcanism is thought to have introduced large volumes of volatiles such as CO₂ and SO₂ into the atmosphere and oceans. The sudden injection of these volatiles would have caused a cascade of environmental effects across the globe, including warming (McElwain et al., 2005; Gómez and Goy, 2011), ocean acidification (Kiessling and Simpson, 2011; Trecalli et al., 2012; Bush and Pruss, 2013), and widespread oceanic anoxia (e.g., Jenkyns, 1988, 2010; Röhl et al., 2001; Schmid-Röhl et al., 2002; Aberhan and Baumiller, 2003; Pancost et al., 2004; van de Schootbrugge et al., 2005; Wignall et al., 2005; Gill et al., 2011; Gómez and Goy, 2011; Izumi et al., 2012; Danise et al., 2013, 2015; Hermoso and Pellenard, 2014). The synergistic effects of these environmental stressors would have had severe consequences for marine ecosystems.

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While there have been numerous studies regarding the environmental dynamics of the T-OAE, less is known about how exactly the Pliensbachian and Toarcian perturbations shaped the trajectory of organismic and ecosystem evolution. Most quantitative faunal analyses of the T-OAE come from pelagic ammonites or from microfossils, such as radiolarians and benthic foraminifers (Dera et al., 2010; Guex et al., 2012; Caruthers et al., 2013, 2014; Goričan et al., 2013); in addition, research on macrobenthic communities has mostly focused on European sites, which represent the Tethyan or Boreal oceans (Little and Benton, 1995; Hallam, 1996; Röhl, 1998; Röhl et al., 2001; Gahr, 2002; Schmid-Röhl and Röhl, 2003; Morten and Twitchett, 2009; Caswell and Coe, 2012; Danise et al., 2013; Posenato et al., 2013; Bassi et al., 2015). A few studies from European localities have also addressed potential reductions in body size in selected marine invertebrates, a pattern expected with the development of hypoxia and temperature stress as well as reduced primary productivity (Fürsich et al., 2001; Morten and Twitchett, 2009; Caswell and Coe, 2013).

Given that the biotic crises and environmental perturbations in the late Pliensbachian and early Toarcian were global, there is a critical need to obtain quantitative paleobiological and paleoecological data from regions outside of Europe, particularly North and South America (the Panthalassa Ocean). While the ecological composition and evolution of South American macrobenthic faunas has been explored in some detail (Damborenea, 1987; Aberhan and Fürsich, 1996, 2000;

Aberhan and Baumiller, 2003; Ros et al., 2011), analogous studies for North American macrobenthic communities are lacking.

The current study focuses on macrobenthic assemblages of the newly described Pliensbachian-Toarcian Ya Ha Tinda Lagerstätte from the Fernie Formation of Alberta, Canada (Fig. 1). Herein, we present a high-resolution quantitative paleoecological analysis of benthic (and facultatively pseudoplanktonic) faunas in the Ya Ha Tinda area (Fig. 2). The particular aims of our study are (1) to document the taxonomic composition, abundance, and stratigraphic distribution of late Pliensbachian to middle Toarcian macrobenthic invertebrates, especially bivalves and brachiopods; (2) to identify recurring faunal assemblages, characterize and interpret them ecologically, and compare them to time-equivalent assemblages from other continents; (3) to document potential changes in body size across the T-OAE; and (4) to assess the ecological and evolutionary effects of the T-OAE in the study area.

2. Geological setting, depositional environment, and chronostratigraphy

During the Early Jurassic, the area that is now western Alberta was the eastern margin of the Panthalassa Ocean, part of the Western Canada Sedimentary Basin (Fig. 1). Marine Lower Jurassic strata of the Fernie Formation crop out in the foothills of the Canadian Rockies and are

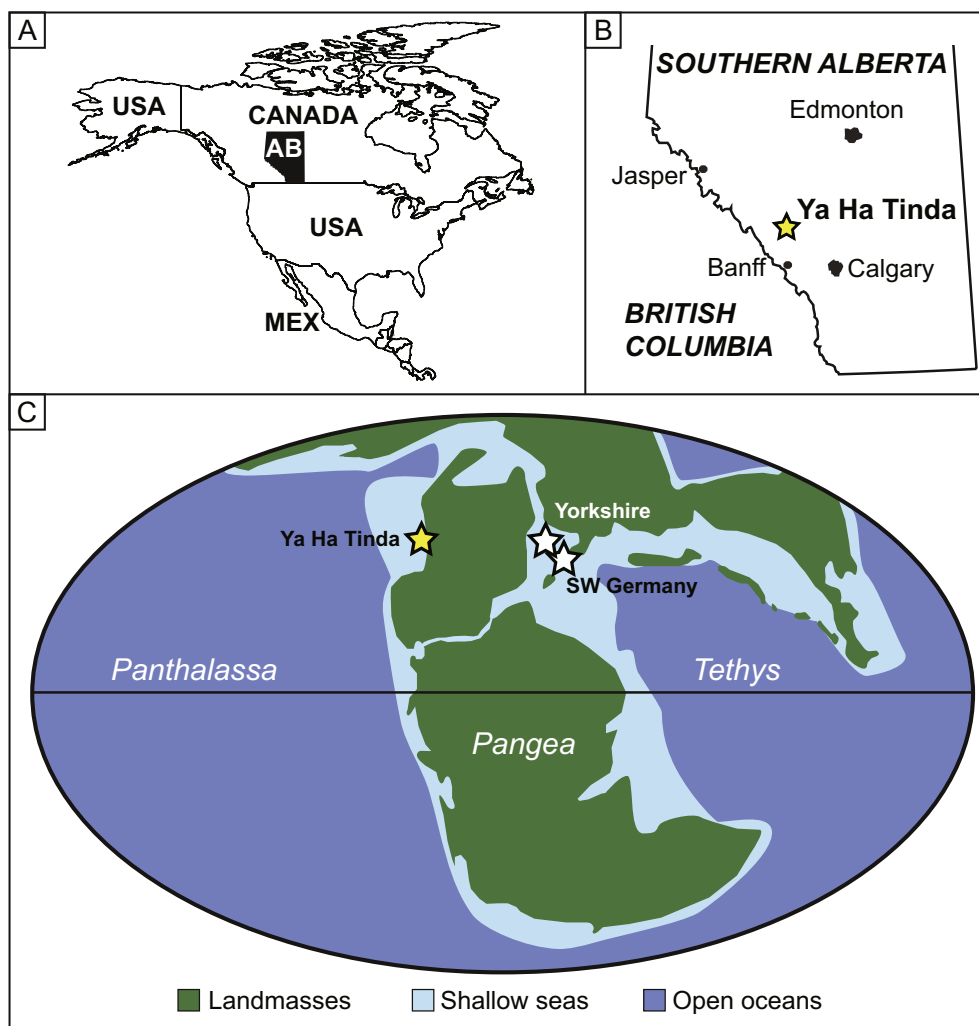


Fig. 1. Location of the studied site at Ya Ha Tinda Ranch. A) Position of Alberta, Canada, within North America. B) Map of southern Alberta with location of Ya Ha Tinda and major cities. C) Global paleogeography of the Toarcian (modified from Them et al., 2017) with the location of Ya Ha Tinda and other well-known Toarcian sections in Yorkshire (UK) and southwest Germany (stars).

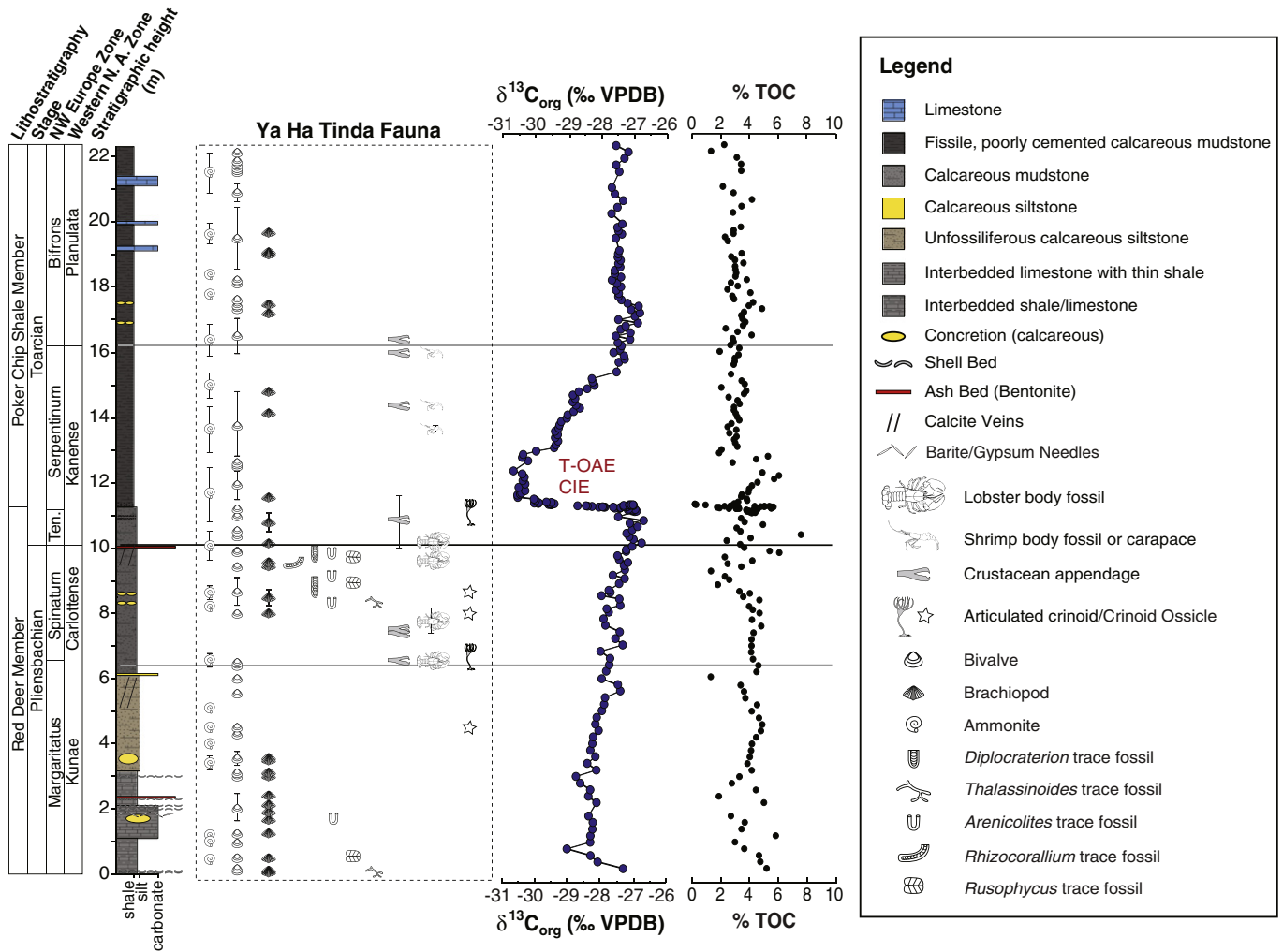


Fig. 2. Stratigraphic column of the East Tributary of Bighorn Creek section (RTMP locality L2428). Lithostratigraphy, organic carbon ($\delta^{13}\text{C}_{\text{org}}$) chemostratigraphy, total organic carbon (%TOC), and ammonite biostratigraphy from Them et al. (2017). Distributions of ammonites, benthic macroinvertebrates, and trace fossils are noted to right of lithostratigraphy. Zones refer to the northwestern European and Western North American ammonite zones; CIE = the carbon isotope excursion associated with the Toarcian Oceanic Anoxic Event (T-OAE); ten. = tenuicostatum; org = organic; VPDB = Vienna Pee Dee belemnite. The horizontal lines indicate ammonite zone boundaries; the black line is the stage boundary.

particularly well exposed at the Ya Ha Tinda Ranch near Banff National Park (e.g., Frebold, 1957; Hall, 1984; Poulton and Hall, 1993; Hall et al., 1998; Asgar-Deen, 2003). These outcrops have long been studied for biostratigraphic control (ammonites and coccolithophores) on the Fernie Formation (Hall and Howarth, 1983; Hall, 1984, 1987, 2006; Hall et al., 1998, 2000, 2004; Asgar-Deen et al., 2003, 2004; Them et al., 2017); the biostratigraphic work is complemented by a handful of U-Pb dates from zircons in Ya Ha Tinda ash beds (Hall et al., 2004).

Recent discoveries have greatly expanded the importance of the Ya Ha Tinda sections. Specifically, soft-tissue preservation was discovered in several of the sites at Ya Ha Tinda, making these exposures the first marine Konservat-Lagerstätte documented from the Jurassic of North America (Martindale et al., in press). In addition, high-resolution ammonite biostratigraphy has refined the placement of the Pliensbachian-Toarcian boundary as well as the ammonite zones in these sections (Them et al., 2017). The carbon isotope excursion corresponding to the Toarcian Oceanic Anoxic Event, which will be referred to as the T-OAE CIE interval in this paper, has also been identified in carbon isotope chemostratigraphic analyses (Them et al., 2017). The well-defined initiation and recovery of the T-OAE CIE within the East Tributary section (Fig. 2) allows for excellent correlation of this site to others in Alberta and around the world. The identification of this interval also provides the basis to answer important paleoecological questions,

specifically regarding the effect of the CIE on the benthic and pelagic faunas in this region.

Early Jurassic marine strata at Ya Ha Tinda Ranch are represented by the Red Deer and Poker Chip Shale members (Hall, 2006). The Pliensbachian to early Toarcian Red Deer Member consists of grey to black platy calcareous shales interbedded with fine siltstones and black limestones. In the Red Deer Member, carbonate concretions are common and the shales and siltstones are typically well cemented (Fig. 2). The overlying Toarcian Poker Chip Shale Member is finer-grained, poorly cemented, and fissile. It is composed of black, calcareous shales and mudstones interbedded occasionally with bituminous limestones with TOC values typically between 1 and 7 wt% (Fig. 2) (Them et al., 2017) and as high as 18.5 wt% (Riediger, 2002).

The upper Red Deer and Poker Chip Shale members are interpreted to have been deposited under periodically dysoxic (or even anoxic) conditions (Stronach, 1984; Hall, 1985, 1991; Hall and Neuman, 1989). The main evidence for this interpretation is the paucity of bioturbation and the fine lamination of the beds, particularly within the Poker Chip Shale Member. Furthermore, the preservation of articulated skeletons and lack of scavenging within Lagerstätte-style intervals in the Poker Chip Shale Member support this environmental interpretation (Martindale et al., in press).

3. Material and methods

At Ya Ha Tinda, late Pliensbachian to early Toarcian strata are well exposed at three different sites (at least), namely Scalp Creek, Bighorn Creek, and a site on the eastern tributary of Bighorn Creek, here referred to as the East Tributary locality (Royal Tyrrell Museum of Palaeontology Localities L2430, L2429, and L2428, respectively). Although sedimentological, geochemical, and paleontological data have been acquired from all three sites, this paper focuses primarily on the best-exposed section at East Tributary (Fig. 2) with some additional data from Scalp Creek. High-resolution ammonite biostratigraphy and carbon isotope chemostratigraphy have been generated for the East Tributary site (Them et al., 2017), Bighorn Creek (both), and Scalp Creek (biostratigraphy only). North American ammonite zones have been correlated to the ammonite zones from northwest Europe (Pálffy and Smith, 2000; Them et al., 2017) and provide a good framework for correlating sections throughout this area and globally.

The Ya Ha Tinda fossil localities described in this study cannot be disclosed as they are protected under the Canadian National Parks Act. All fossils and geological samples were collected under a Parks Canada collection and research permit (#YHTR-2014-16156) and fossil excavation permits from the Alberta Government (RTMP Permit #13-058, #14-009, and #15-019). All collected specimens are curated at the Royal Tyrrell Museum of Palaeontology in Drumheller, Alberta, Canada.

Benthic macrofossils (bivalves and brachiopods) were tentatively identified in the field based on Aberhan (1998), and the number of specimens per taxon on individual bedding planes (or bulk samples from single layers of uniform lithology) was recorded. For several shell beds and pavements with abundant specimens, taphonomic data on the orientation of shells was recorded. The stratigraphic position of each paleontological sample is closely tied to the position of geochemical samples (Fig. 2). Altogether >2500 specimens from 109 fossiliferous horizons at East Tributary and Scalp Creek are represented. Well-preserved specimens and the specimens that could not be reliably identified in the field were collected for further study. This involved the comparison of Ya Ha Tinda bivalves with those from Early Jurassic collections housed at the Museum für Naturkunde Berlin, in addition to a survey of the relevant literature. Comprehensive measurements of shell sizes of >1500 specimens are expressed as the geometric mean of two dimensions using calipers accurate to 0.5 mm. The geometric mean is the square root of length multiplied by height in bivalves or by width in brachiopods. In addition to measurements of shell sizes in individual samples, time-averaged body size per ammonite zone was determined with box plot statistics. Cumulative size-frequency distributions per ammonite zone were plotted for each of the most abundant taxa. The significance of differences in bivalve and brachiopod sizes were evaluated

with an analysis of variance (ANOVA) model with the Tukey adjustment (Tukey, 1949) whenever post-hoc analyses were run.

For the analysis of faunal assemblages, samples were only considered if they contained a minimum of 12 specimens. To achieve this quota, stratigraphically adjacent samples were pooled where necessary, provided that lithology remained unchanged (stratigraphic interval height is taken as the midpoint between the lowest and highest beds that were pooled, typically only a few centimeters apart). Overall, this resulted in 48 quantitative samples with relative abundance data for bivalves and brachiopods of, on average, 44 specimens per sample. Samples were grouped into distinct assemblages by means of a two-way cluster analysis based on specimen abundance [average linkage method using the Bray-Curtis similarity coefficient (Bray and Curtis, 1957) to build the similarity matrix]. The significance of differences in average abundance across clusters was evaluated with a multivariate analysis of variance (MANOVA) model of occurrence data (between clusters in general) and an analysis of variance (ANOVA) with the Tukey (1949) adjustment used for post-hoc analyses to compare specific taxa between assemblages. The various assemblages were characterized in terms of dominant taxa, the ecology of the constituent taxa, and taxon richness. Characterization of life habit and feeding mode of taxa is based on comparison with living relatives of similar morphology, functional considerations, and interpretations given in previous studies (see Discussion section). All quantitative analyses were conducted in the R programming environment (www.r-project.org); see the Supplemental data for datasets and R code.

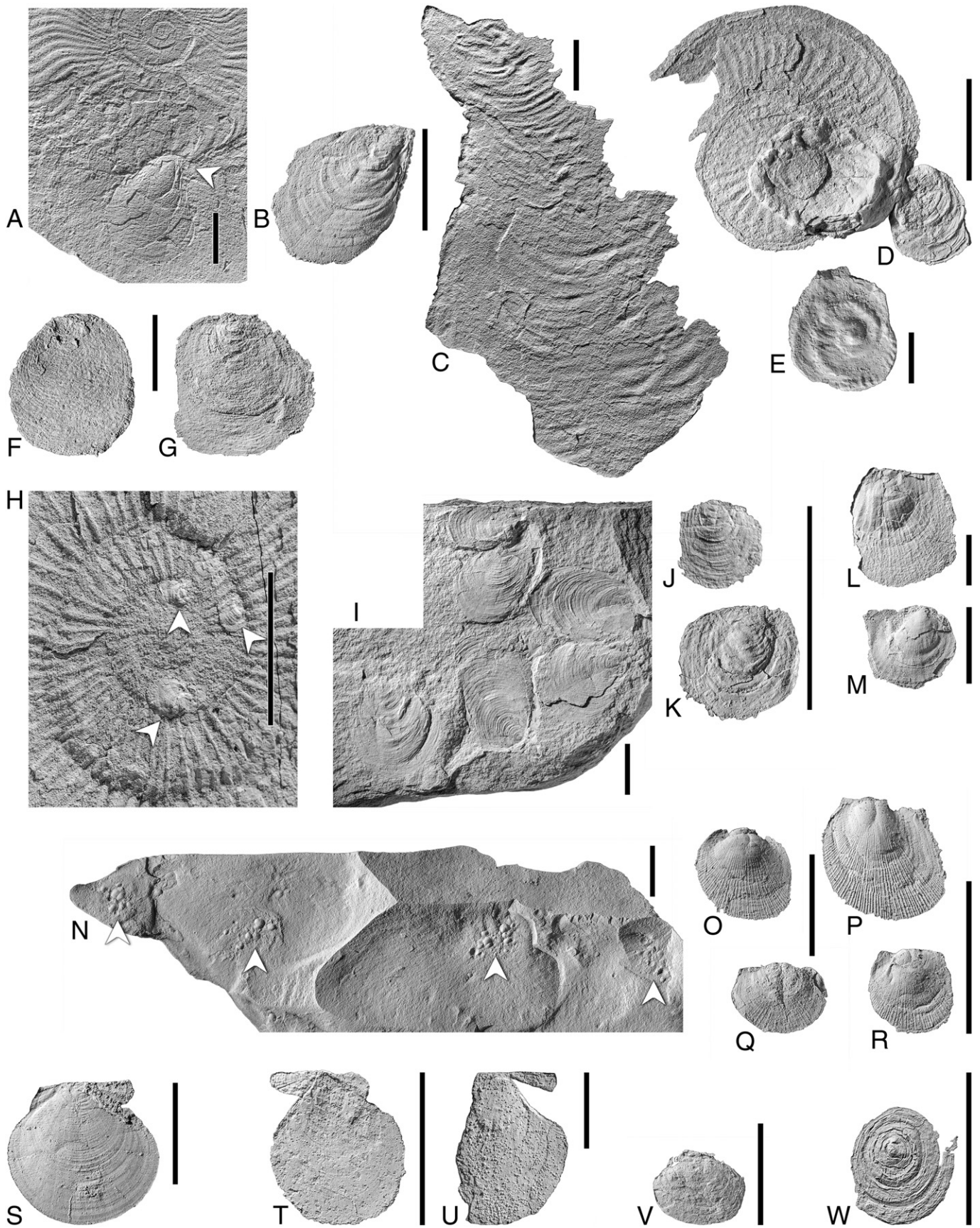
4. Results

4.1. Composition and preservation of the benthic macrofauna

Bivalves strongly dominate the macrobenthos in terms of both abundance and number of taxa; brachiopods occupy the second rank. The bivalve and brachiopod taxa (Figs. 3, 4) are listed in Table 1 along with information on their life habits, feeding modes, and semi-quantitative abundances (number of specimens at each site). Species occurrences and abundance are plotted in Figs. 5 and 6, respectively. Decapod crustaceans (primarily eryonid and uncinid lobsters) and *Seiocrinus* crinoids are rare faunal components. Macroscopic trace fossils in the Red Deer Member include *Arenicolites*, *Thalassinoides*, *Rusophycus*, and *Rhizocorallium* (Figs. 2, 7). Overall, taxon richness of the benthic fauna at Ya Ha Tinda is low, with most bedding planes recording paucispecific communities with two to four taxa.

Ecologically, virtually all specimens are epifaunal suspension-feeders (Table 1). The two bivalve taxa categorized as infaunal, and doubtfully assigned to the Lucinidae and Astartidae, are very rare (one

Fig. 3. Bivalves and brachiopods from the Early Jurassic of the Ya Ha Tinda area; scale bars equal 1 cm. All specimens are housed at the Royal Tyrrell Museum of Palaeontology (RTMP). A) *Pseudomytiloides cf. dubius*; internal view of left valve (arrow) attached to periphery of ammonite (*Cleviceras exaratum*); Toarcian, Kanense (Serpentinum) Zone; East Tributary of Bighorn Creek – L2428; TMP 2015.050.0248; $\times 1$. B) *Pseudomytiloides cf. dubius*; composite mold of right valve; Toarcian, Kanense (Serpentinum) Zone; Scalp Creek – L2430, TMP 2015.051.0095; $\times 2$. C) *Inoceramid* bivalve; internal mold of left valve; Toarcian, Kanense (Tenuicostatum) Zone; East Tributary of Bighorn Creek – L2428, TMP 2015.050.0256; $\times 1$. D) *Liotrota* sp.; two specimens associated with ammonite (*Hildaites cf. subserpentinus*); Toarcian, Kanense (Tenuicostatum) Zone; East Tributary of Bighorn Creek – L2428, TMP 2015.050.0139; $\times 2$. E) *Liotrota* sp.; internal view of right valve exhibiting xenomorphic sculpture of ammonite to which left valve was attached; Toarcian, Kanense (Serpentinum) Zone; Scalp Creek – L2430, TMP 2015.051.0005; $\times 1$. F) *Placunopsis?* sp.; external mold of left valve; Toarcian, Kanense (Serpentinum) Zone; East Tributary of Bighorn Creek – L2428; TMP 2015.050.0253; $\times 1.5$. G) *Placunopsis?* sp.; external mold of left valve; Toarcian, Kanense (Serpentinum) Zone; Scalp Creek – L2430, TMP 2015.051.0088; $\times 1.5$. H) Several small valves of *Placunopsis?* sp. (arrows) on ammonite (*Dactylioceras cf. semicelatum*); Toarcian, Kanense (Serpentinum) Zone; Scalp Creek – L2430, TMP 2015.051.0027; $\times 3$. I) *Pseudomytiloides cf. dubius*; slab with several specimens; Toarcian, Planulata Zone; Bighorn Creek – L2429; TMP 2013.036.0029; $\times 1$. J) *Bositra* sp.; external mold of single valve; Toarcian, Kanense (Serpentinum) Zone; East Tributary of Bighorn Creek – L2428; TMP 2015.050.0279; $\times 4$. K) *Bositra* sp.; internal mold of single valve; Toarcian, Kanense (Serpentinum) Zone; Scalp Creek – L2430, TMP 2015.051.0067; $\times 4$. L) *Oxytoma* sp.; external view of left valve; Toarcian, Kanense (Tenuicostatum) Zone; Scalp Creek – L2430, TMP 2015.051.0094; $\times 1$. M) *Oxytoma* sp.; external view of right valve; Toarcian, Kanense (Tenuicostatum) Zone; Scalp Creek – L2430, TMP 2015.051.0128; $\times 1.5$. N) *Meleagrinnella* sp.; many specimens clustered in nests (arrows); Toarcian, Kanense (Serpentinum) Zone; Scalp Creek – L2430, TMP 2015.051.0082; $\times 1$. O) *Meleagrinnella* sp.; external view of left valve; Toarcian, Kanense (Serpentinum) Zone; Scalp Creek – L2430, TMP 2015.051.0096; $\times 2$. P) *Meleagrinnella* sp.; silicon cast of external mold of left valve; Toarcian, Kanense (Serpentinum) Zone; Scalp Creek – L2430, TMP 2015.051.0108; $\times 2$. Q) *Meleagrinnella* sp.; external view of right valve; Toarcian, Kanense (Serpentinum) Zone; East Tributary of Bighorn Creek – L2428; TMP 2015.050.0216; $\times 2$. R) *Meleagrinnella* sp.; silicon cast of external mold of left valve; Toarcian, Kanense (Serpentinum) Zone; Scalp Creek – L2430, TMP 2015.051.0073; $\times 3$. S) *Camptonectes subulatus*; internal mold of right valve; Toarcian, Kanense (Serpentinum) Zone; Scalp Creek – L2430, TMP 2015.051.0076; $\times 2$. T) *Canadonectites* sp.; external mold of right valve; Toarcian, Kanense (Serpentinum) Zone; Scalp Creek – L2430, TMP 2015.051.0042; $\times 3$. U) *Canadonectites* sp.; composite mold of right valve; Toarcian, Kanense (Serpentinum) Zone; Scalp Creek – L2430, TMP 2015.051.0113; $\times 1.5$. V) Lucinid? bivalve; silicon cast of external mold of left valve; Toarcian, Kanense (Serpentinum) Zone; Scalp Creek – L2430, TMP 2015.051.0116; $\times 2$. W) *Discinisca* sp.; internal mold of brachial valve; Toarcian, Kanense (Serpentinum) Zone; East Tributary of Bighorn Creek – L2428; TMP 2015.050.0254; $\times 3$.



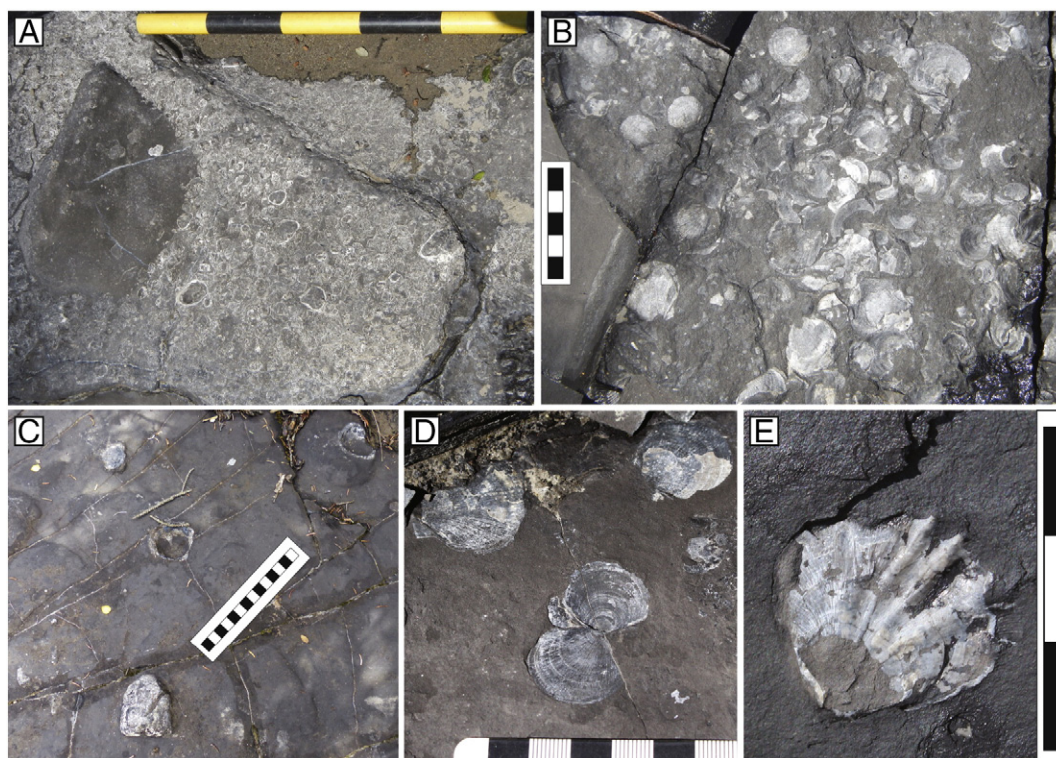


Fig. 4. Field photos of Pliensbachian bivalves and brachiopods from the East Tributary site. A) Shell concentration at base of section (0 m), with *Gryphaea* cf. *rockymontana*, *Oxytoma* sp., and rhynchonellid brachiopods; yellow and black scale bar is in decimeters. B) Pavement of *Ochotochlamys* cf. *bureiensis* at 3 m; white and black scale bar is in cm. C) *Gryphaea* cf. *rockymontana* shells from 0.05 m in section; white and black scale bar is in centimeters. D) Pavement of articulated and inarticulated *Ochotochlamys* cf. *bureiensis* at 2.1 m in section; white and black scale bar is in cm (small ticks are mm). E) Rhynchonellid brachiopods found in float; white and black scale bar is in cm.

and two specimens, respectively). The majority of taxa were fixosessile, either attached with a byssus or pedicle or cemented to the substrate. These taxa were either fixed benthic or facultatively pseudoplanktonic, i.e. attached to ammonites, driftwood, or floating algae in the water column (see [Discussion](#) section). The remaining taxa were reclining unattached on the seafloor.

Bivalves and brachiopods are mostly preserved with shell or relics of shell, less commonly as internal, external, or composite molds. Pyritization occurs extremely rarely as coatings on internal molds, mostly in *Meleagrinnella* of the middle Toarcian Planulata Zone. The degree of fragmentation is generally low, but in-situ breakage and compression

of valves during diagenesis are common features. Overall, preservation quality is moderate owing to (modern) erosion on exposed bedding planes of Pliensbachian strata and the fissile nature of the Toarcian Poker Chip Shale Member. As a consequence, unequivocal identifications at the species level are rarely possible. Except for the chitinophosphatic linguliform brachiopod *Discinisca*, all common taxa had calcitic or bimineralic shells. Aragonitic benthos is missing except for the very few infaunal specimens mentioned above. Regardless, the ubiquitous presence of ammonites, which originally had aragonitic shells and are well preserved as molds, indicates that a bias in benthic composition by the selective dissolution of aragonitic shells can be ruled out.

Table 1
List of benthic (and facultatively pseudoplanktonic) bivalves and brachiopods in late Pliensbachian to middle Toarcian strata from the East Tributary and Scalp Creek sections in the Ya Ha Tinda area, along with information on the autecology of taxa. Number of specimens in abundance categories: Rare (1–4); occurs (5–14); common (15–50); abundant (>50).

	Specimen numbers at East Tributary	Specimen numbers at Scalp Creek	Life habit	Feeding mode
Bivalves				
<i>Pseudomytiloides</i> cf. <i>dubius</i>	Abundant	Common	Epifaunal byssate	Suspension-feeding
<i>Inoceramid</i> gen. et sp. indet.	Rare	–	Epifaunal free-living	Suspension-feeding
<i>Liostrea</i> sp.	Common	Common	Epifaunal cementing	Suspension-feeding
<i>Gryphaea</i> cf. <i>rockymontana</i>	Abundant	–	Epifaunal free-living	Suspension-feeding
<i>Placunopsis</i> ? sp.	–	Rare	Epifaunal cementing	Suspension-feeding
<i>Bositra</i> sp.	Abundant	Common	Epifaunal free-living	Suspension-feeding
<i>Oxytoma</i> sp.	Rare	Occurs	Epifaunal byssate	Suspension-feeding
<i>Palmoxytoma cygnipes</i>	–	Rare	Epifaunal byssate	Suspension-feeding
<i>Meleagrinnella</i> sp.	Abundant	Abundant	Epifaunal byssate	Suspension-feeding
<i>Camptonectes subulatus</i>	–	Occurs	Epifaunal byssate	Suspension-feeding
<i>Canadonectites</i> sp.	–	Rare	Epifaunal byssate	Suspension-feeding
<i>Ochotochlamys</i> cf. <i>bureiensis</i>	Abundant	Abundant	Epifaunal byssate	Suspension-feeding
luciniid? gen. et sp. indet.	–	Rare	Deep infaunal	Suspension-feeding/chemosymbiotic
astartid? gen. et sp. indet.	Rare	–	Shallow infaunal	Suspension-feeding
Brachiopods				
<i>Discinisca</i> sp.	Occurs	Occurs	Epifaunal pedically attached	Suspension-feeding
Rhynchonellid gen. et sp. indet.	Abundant	Common	Epifaunal pedically attached	Suspension-feeding

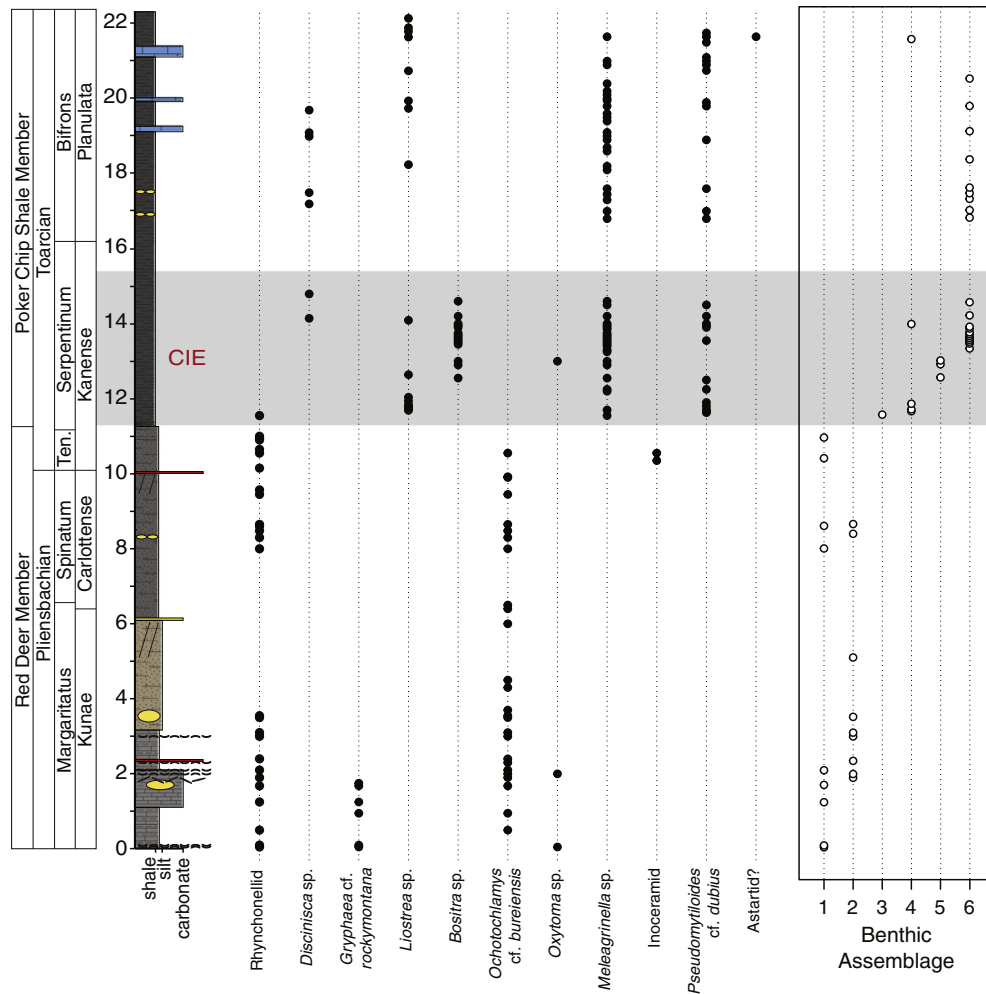


Fig. 5. Occurrences of the bivalve and brachiopod taxa in the Ya Ha Tinda East Tributary section. Also shown is the distribution of six benthic assemblages, as defined through hierarchical clustering on the bivalve and brachiopod abundance data (Fig. 8). Lithostratigraphy, chemostratigraphy, and ammonite biostratigraphy from Fig. 2.

4.2. Stratigraphic distribution of benthic faunas

When the benthic faunas are plotted on a stratigraphic log, clear trends emerge (Figs. 2, 5, 6). In the East Tributary locality, macroscopic trace fossils are only found within Pliensbachian strata (Red Deer Member) and are most abundant at the base of the section (0 m–1.75 m) and between 8.25 m and 10 m. To date, no visible bioturbation has been identified in Toarcian strata.

The crinoid *Seiocrinus* and crinoid ossicles can be found in both Pliensbachian and Toarcian strata but are always found below the T-OAE CIE interval, consistent with previous *Seriocrinus subangularis* discoveries (Hall, 1991). Similarly, articulated lobster body fossils (either carcasses or articulated moults) are only found below the T-OAE CIE interval, some lone appendages (typically claws) occur throughout the section. One articulated shrimp carcass was found within the CIE along with several other potential shrimp appendages.

With respect to bivalves and brachiopods, *Gryphaea* cf. *rockymontana* only occurs in the Kunae Zone of the Red Deer Member (Pliensbachian), together with abundant *Ochotochlamys* cf. *burelensis*, rhynchonellid brachiopods, and rare *Oxytoma* (Fig. 5). In the rhynchonellid-*Gryphaea* shell bed at 0.1 m, 63.3% of the strongly convex left valves of *Gryphaea* (sample size $n = 33$) occur in a convex-down position, which corresponds to the orientation during life and suggests an in-situ biogenic concentration (as opposed to reworking by waves or currents). Within the Pliensbachian strata,

Ochotochlamys is the dominant bivalve and rhynchonellids are the dominant brachiopods (Figs. 5, 6). Together with *Gryphaea* they commonly appear as pavements in the pre-T-OAE interval (Fig. 4). The valves of *Ochotochlamys*, which dominate the pavements at 2.0 and 3.0 m, are preferentially oriented convex-down (79.2%, $n = 144$ and 77.3%, $n = 44$ respectively) rather than the hydrodynamically stable convex-up position. Together with the lack of size sorting (Fig. 6) and the occasional preservation of articulated specimens (Fig. 4D), this orientation suggests concentration of shells within their original habitat through winnowing by gentle currents rather than large-scale transport. Low water-energy at the seafloor is also evident from an accumulation of *Atractites* sp. (a belemnoid) proostraca at 1.68 m ($n = 25$), which do not exhibit a preferred orientation (see Supplemental data). The pattern of *Ochotochlamys* and rhynchonellid dominance in Pliensbachian strata holds in Scalp Creek as well, with rare *Oxytoma* and *Palmoxytoma* (see Supplemental data). Between 3.5 m and 8 m of the section at East Tributary, there is a notably depauperate zone with monospecific beds of *Ochotochlamys*, consisting of <10 individuals, and even some intervals that lack benthic taxa entirely (Figs. 5, 6). This depauperate interval corresponds to a bioturbation gap between 2 and 8 m and is approximately equivalent in time to the second ammonite extinction highlighted by Caruthers et al. (2013, 2014). However, this interval is not associated with a permanent change of the taxonomic composition of the macrobenthos at Ya Ha Tinda (Fig. 5).

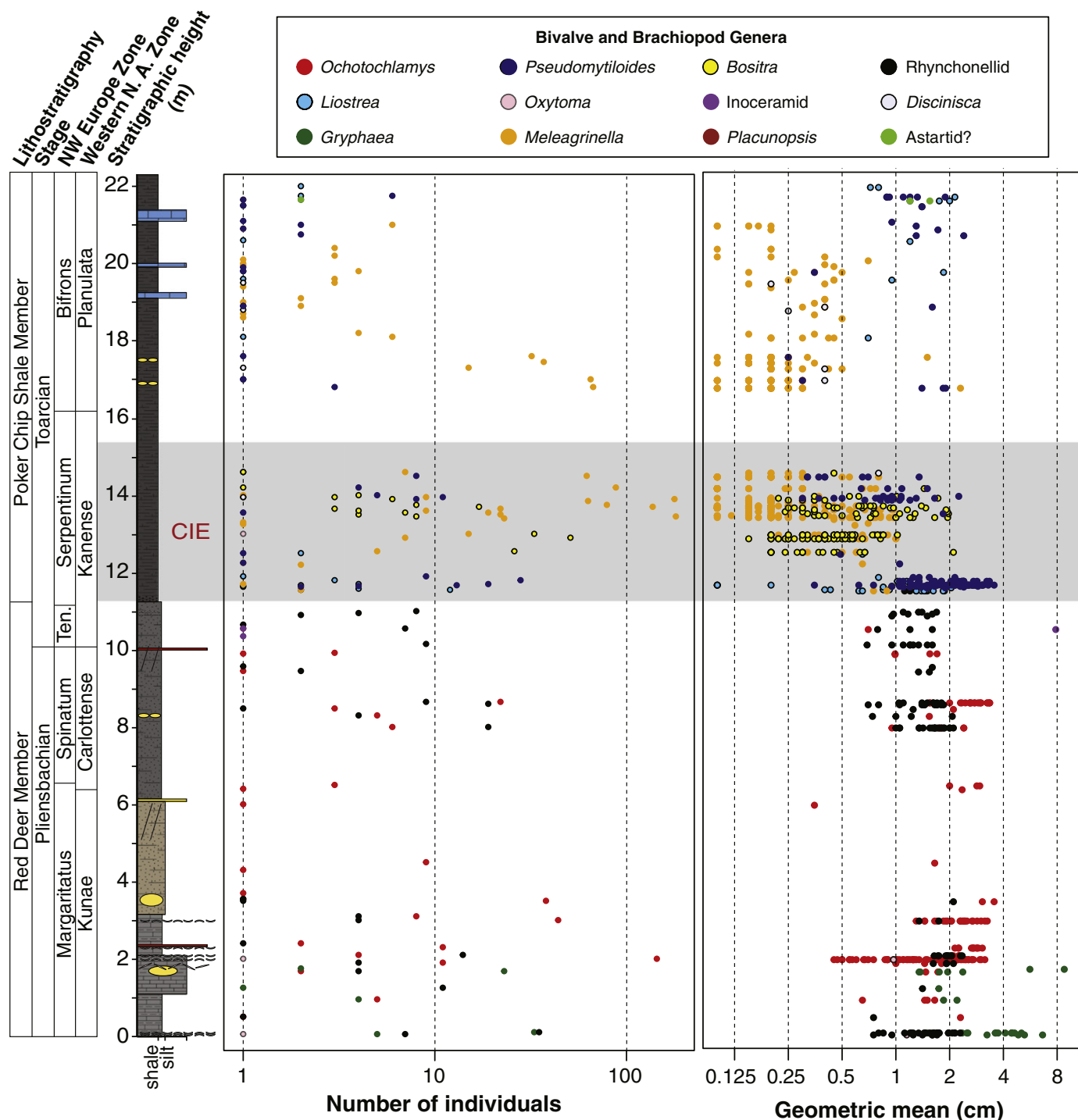


Fig. 6. Abundance and shell size of bivalve and brachiopod taxa at each horizon within the East Tributary section. Column on left displays absolute abundance (number of individuals per bed) and the column on right displays the size measurements of individuals (geometric mean). Note the log scale on both graphs as well as the taxonomic turnover and size decrease across the CIE.

Ochotochlamys and rhynchonellids continue to be dominant across the Pliensbachian-Toarcian boundary (within strata that correspond to the Tenuicostatum Zone in Europe), with the addition of a few large-sized inoceramid bivalves at East Tributary (Figs. 3C, 6) and two individuals of *Oxytoma* at Scalp Creek. *Ochotochlamys* cf. *bureiensis* does not persist through the T-OAE CIE interval and although one *Oxytoma* and one bed with rhynchonellid brachiopods have been identified within the CIE interval, these taxa are also not found above the CIE.

The T-OAE CIE interval itself contains a moderately diverse suite of bivalves and brachiopods (Figs. 5, 6), including *Discinisca*, *Liostrea*,

Meleagrinella, *Bositra*, and *Pseudomytiloides* cf. *dubius* at both sites with additional occurrences of *Placunopsis*?, *Camptonectes*, *Canadonectites*, and one lucinid? at Scalp Creek (see Supplemental data). In the lower part of the CIE interval, corresponding to the carbon isotope minima, *Liostrea* and *Pseudomytiloides* are the most abundant organisms (Fig. 6). Both taxa are closely associated with ammonites, which apparently formed the preferred substrate. *Liostrea* directly cemented its shell onto the umbilical region and the flanks of ammonites (Fig. 3D), and isolated specimens commonly exhibit the coiling and sculpture of their original ammonite substratum (Fig. 3E). Less commonly, valves of

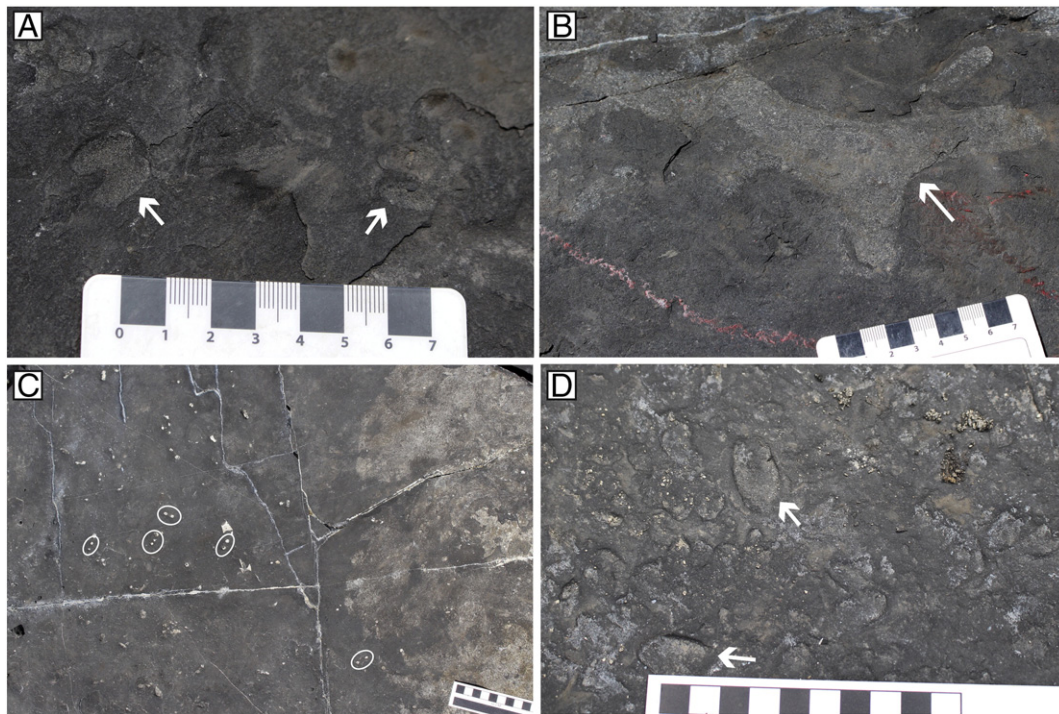


Fig. 7. Field photos of trace fossils at the East Tributary site, Ya Ha Tinda; white and black boxes on scale bar are in cm (small ticks are mm). A) *Rusophycus* traces (arrows) from 0.55 m in stratigraphy. B) *Thalassinoides* burrow (arrow) from 8.33 m in stratigraphy. C) Numerous *Arenicolites* burrows (best examples circled) from 8.30 m in stratigraphy. D) *Rhizocorallium* burrows (arrows) from 9.55 m in stratigraphy.

Pseudomytiloides served as secondary hard substrate for *Liostrea*. *Pseudomytiloides* is most abundant on bedding planes that also exhibit a high density of ammonites. In several cases, *Pseudomytiloides* occurs close to or directly at the periphery of an ammonite (Fig. 3A). For an ecological interpretation of its life habit (see Section 5.2) it is also relevant that some large specimens of *Pseudomytiloides* are found on small ammonites, and that *Pseudomytiloides* also attached to isolated ammonite aptychi.

In the last segment of the isotope minima *Bositra* becomes the most dominant bivalve and forms closely spaced shell pavements. As the carbon isotopes begin to return to pre-excursion values, *Bositra* is replaced by *Meleagrinnella*, which occurs in huge abundances (often >100 individuals per bedding plane sample; Fig. 6), mostly as mm-sized juveniles that are concentrated in small clusters, here termed nests (Fig. 3N). As a rule, these *Meleagrinnella* nests are associated with semi-articulated skeletons, skulls, bones, scales, or fin spines of fishes. More rarely, nests and isolated larger specimens also occur on ammonites and their isolated aptychi, shells of *Bositra*, or the interior of *Pseudomytiloides* valves. Apparently, all these biogenic hard parts served as suitable attachment sites for *Meleagrinnella* larvae.

In the post-CIE interval, the Planulata Zone, *Meleagrinnella* individuals and nests of juveniles continued to be abundant until approximately 18 m in section, when most occurrence data drop down to single digits for all taxa. In addition to *Meleagrinnella*, several *Liostrea*, *Discinisca*, *Pseudomytiloides*, and an astartid? bivalve have been found in the post-OAE interval at East Tributary (Figs. 5, 6). At the top of the section, it is not uncommon to only find one or two individuals per bed.

4.3. Quantitative paleoecology of the Ya Ha Tinda macrobenthic communities

Cluster analysis of the 48 quantitative samples with bivalves and brachiopods from East Tributary yields six distinct faunal groups referred to here as benthic assemblages (Fig. 8). Assemblages 1 and 2 occur in Pliensbachian and lower Toarcian strata below the T-OAE

CIE (Margaritatus to Tenuicostatum zones by the European ammonite zonation) (Fig. 5). These assemblages are different from the intra- and post-CIE assemblages due to the dominance of *Gryphaea*, *Ochotochlamys*, and rhynchonellid brachiopods (Fig. 8). In addition, Assemblages 1 and 2 are significantly different from each other [MANOVA $F(3,14) = 5.53$, $p = 0.010$]; the frequencies of *Ochotochlamys* and rhynchonellids are significantly different between Assemblages 1 and 2 [ANOVA $F(1,16) = 5.04$, $p = 0.039$ and $F(1,16) = 15.61$, $p = 0.001$ respectively] and Assemblage 2 lacks *Gryphaea*.

The clusters within the CIE and post-CIE interval (Assemblages 3 through 6) are also distinct, with Assemblages 4, 5, and 6 being significantly different from each other [MANOVA $F(10,46) = 28.58$, $p < 0.0001$]. The lack of data in Assemblage 3 (i.e. a single horizon) makes it difficult to compare it with the others statistically, but this is the only horizon that is dominated by *Liostrea* sp., the last interval containing rhynchonellid brachiopods, and the first interval after the initiation of the T-OAE CIE (Figs. 5, 8). *Pseudomytiloides* and *Bositra* dominate Assemblages 4 and 5, respectively; *Meleagrinnella* dominates Assemblage 6, which is by far the most common assemblage from the middle of the CIE interval onwards. An ANOVA on the occurrences of *Bositra* yielded significant differences between Assemblages 4 and 5 ($p < 0.0001$) and Assemblages 5 and 6 ($p < 0.0001$), and ANOVA on both *Pseudomytiloides* and *Liostrea* occurrences show significant differences for Assemblages 4 and 6 ($p < 0.0001$ in both cases). These results demonstrate that the identified assemblages are clearly distinct from each other and not merely an artifact of hierarchical clustering.

Despite their differences in taxonomic composition, the assemblages share characteristic ecological attributes. The individual as well as the pooled fossil samples are mono- to paucispecific, never exceeding five taxa and mostly yielding no more than three taxa with uneven abundance distributions (Fig. 8). The six assemblages consist entirely of suspension-feeders, which suggests that food was available as suspended particles. The faunal components were stationary, only *Ochotochlamys* potentially being capable of intermittent swimming.

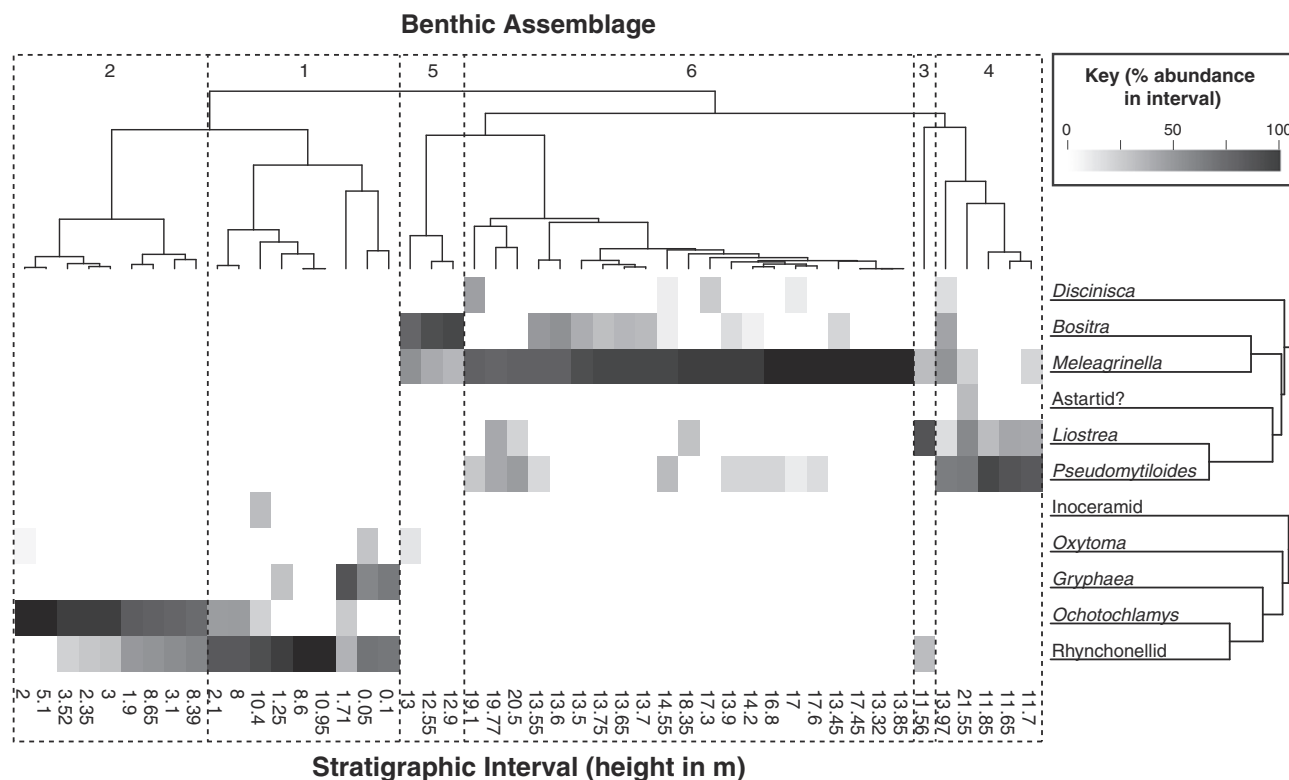


Fig. 8. Two-way cluster analysis of the bivalve and brachiopod taxa at the East Tributary section; average linkage method using the Bray–Curtis similarity coefficient (Bray and Curtis, 1957) to build the similarity matrix. The six main benthic assemblages are highlighted; note that Assemblages 1 and 2 occur in the pre-CIE strata (late Pliensbachian and earliest Toarcian) whereas Assemblages 3 through 6 occur in intra- and post-CIE strata. See text for discussion of cluster analysis and significance of assemblages.

4.4. Size analysis of benthic faunas

As in the case of the taxonomic distribution, clear patterns in bivalve and brachiopod shell size are apparent at the East Tributary locality

(Figs. 6, 9). It should be noted that when significant size shifts are reported, the maximum and minimum values shift in concert with the mean (unless otherwise stated); in some cases (i.e. Kanense vs. Bifrons zones) minima remain the same because the minimum size is the

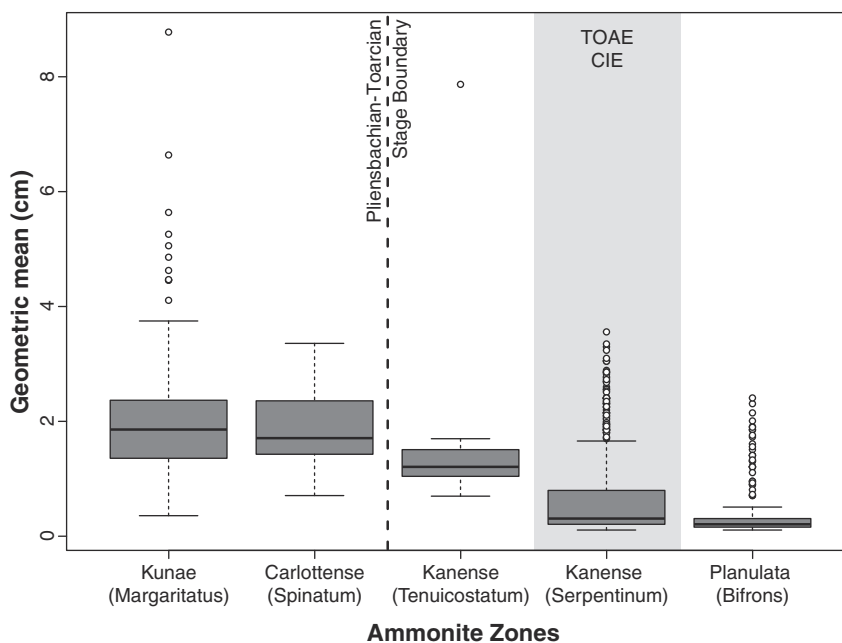


Fig. 9. Shell sizes of bivalve and brachiopod specimens from East Tributary (sample size $n = 1269$) grouped by ammonite zone (North American zones listed on top, northeastern European zones in parentheses). Box plots represent the median value (thick black line), within the 1st and 3rd quartile (grey box), the minimum and maximum (whiskers), as well as outliers (unfilled circles). When outliers are present, the whisker represents $1.5 \times$ the likely range of variation (the IQR), from the 3rd quartile rather than the maximum value. Dashed line = Pliensbachian–Toarcian stage boundary; grey background represents T-OAE CIE interval, which is contained within the upper Kanense (Serpentinum) ammonite Zone (see Fig. 2).

minimum measurable size (i.e. 0.5 mm). The observation that mean, minimum, and maximum values all change together indicates that negative (or positive) changes in size are a result of directional reduction (or enlargement) of shell size rather than an artifact of decreased variance.

Within the Pliensbachian strata, there is no significant size difference between the total faunal assemblage of the Kunae Zone and that of the Carlottense Zone ($p = 0.58$). Across the stage boundary there is also no significant size decrease of assemblages when comparing the pre-CIE Kanense Zone (Tenuicostatum Zone) with the Carlottense Zone ($p = 0.25$). Nevertheless, when the size data from the pre-CIE Kanense Zone is compared with data from the Kunae Zone, significance is achieved ($p = 0.02$). When data from Scalp Creek are incorporated into the ANOVA, none of the pre-CIE size changes are significant [Kunae to Carlottense $p = 1.00$; Kunae to early Kanense (Tenuicostatum) $p = 0.10$; Carlottense to early Kanense (Tenuicostatum) $p = 0.24$]. This suggests a gradual decrease in size leading up to the onset of the T-OAE CIE interval.

The onset of the T-OAE CIE (beginning at 11.27 m in East Tributary) clearly coincides with a major change in the size of faunal assemblages (Figs. 6, 9). The sizes from within the CIE interval of the Kanense (Serpentinum) Zone are always significantly smaller than pre-CIE sizes ($p < 0.0001$, East Tributary data and all data). Similarly, the post-CIE sizes from the Planulata Zone are always significantly smaller than either the intra-CIE or pre-CIE sizes ($p < 0.0001$) in both the East Tributary dataset and the combined dataset (East Tributary and Scalp Creek).

When the size data are taxonomically dissected more finely (see Supplemental data), brachiopods display the same pattern as the overall trends. Rhynchonellid brachiopods exhibit no significant size difference between Pliensbachian ammonite zones ($p = 0.23$) or from the last Pliensbachian ammonite zone to the first Toarcian ammonite zone (Carlottense to early Kanense or Tenuicostatum $p = 0.08$), but there is a significant size decrease from the Kunae Zone to the pre-CIE interval of the Toarcian ($p < 0.001$) suggesting an overall size decrease. Bivalves of the order Pectinida (i.e. *Ochotochlamys* and *Oxytoma* combined) get significantly larger through the Pliensbachian ($p < 0.0001$ in both

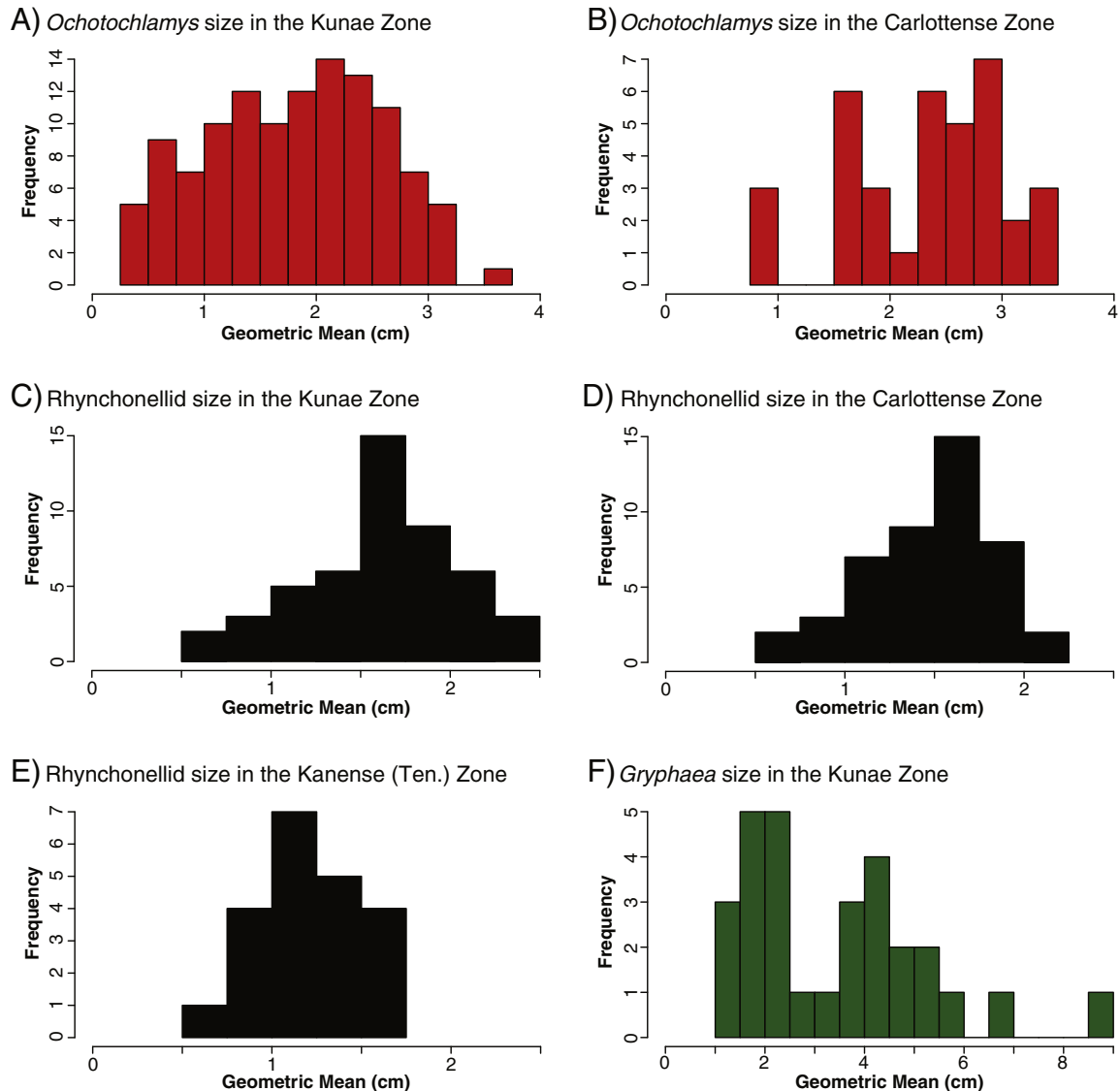


Fig. 10. Cumulative size-frequency histograms (geometric mean) by ammonite zone for the dominant pre-T-OAE bivalves and brachiopods. A) Size distribution of *Ochotochlamys* cf. *bureiensis* from the Kunae (Margaritatus) Zone. B) Size distribution of *Ochotochlamys* cf. *bureiensis* from the Carlottense (Spinatum) Zone. C) Size distribution of rhynchonellid brachiopods from the Kunae (Margaritatus) Zone. D) Size distribution of rhynchonellid brachiopods from the Carlottense (Spinatum) Zone. E) Size distribution of rhynchonellid brachiopods from the Kanense (Tenuicostatum) Zone. F) Size distribution of *Gryphaea* cf. *rockymontana* from the Kunae (Margaritatus) Zone.

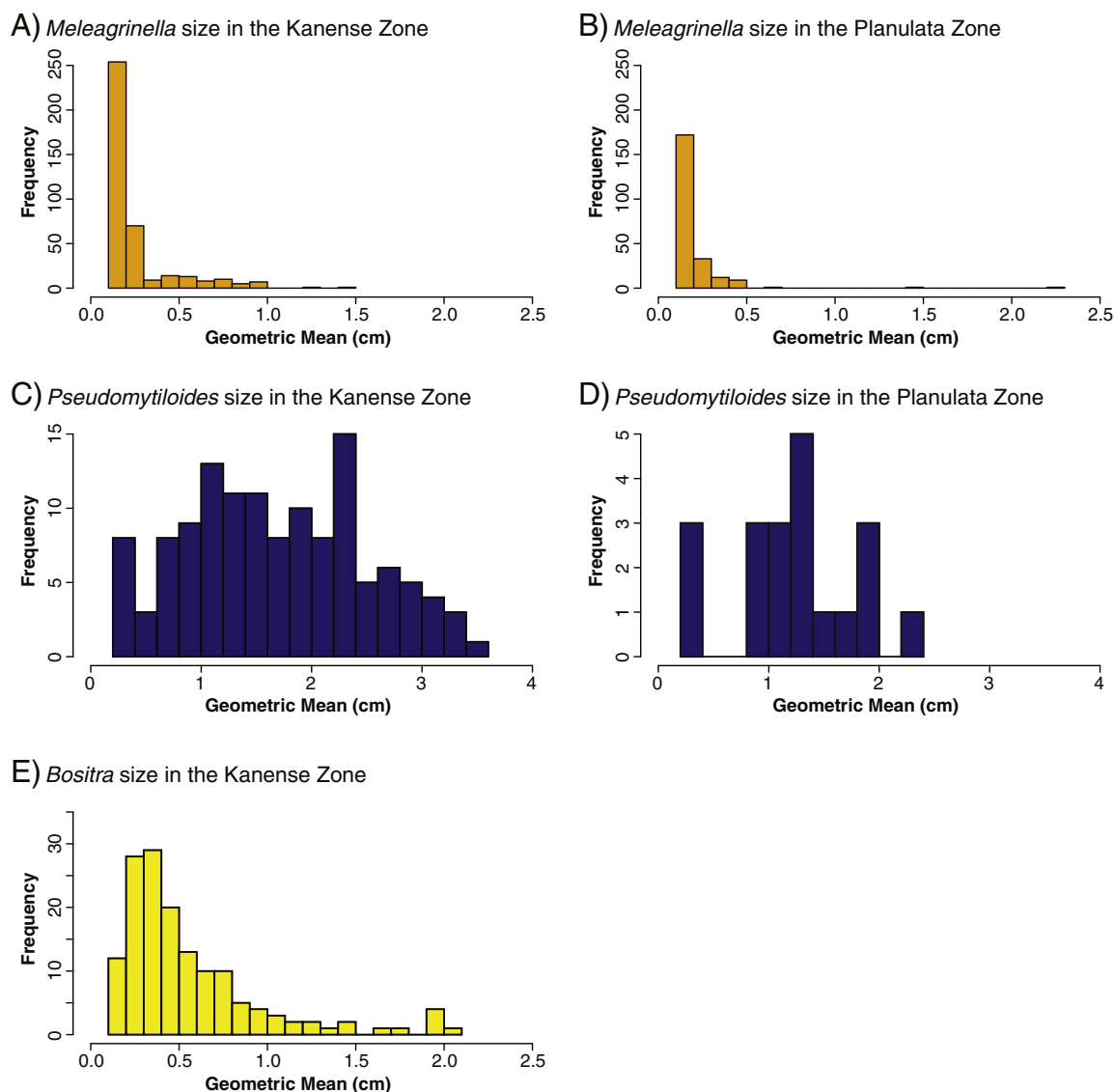


Fig. 11. Cumulative size-frequency histograms (geometric mean) by ammonite zone for the dominant intra- and post-T-OAE bivalves. A) Size distribution of *Meleagrinnella* sp. from the Kanense (Serpentinum) Zone. B) Size distribution of *Meleagrinnella* sp. from the Planulata (Bifrons) Zone. C) Size distribution of *Pseudomytiloides* cf. *dubius* from the Kanense (Serpentinum) Zone. D) Size distribution of *Pseudomytiloides* cf. *dubius* from the Planulata (Bifrons) Zone. E) Size distribution of *Bositra* sp. from the Kanense (Serpentinum) Zone.

East Tributary alone and with all data), which is coincident with a decrease in the variance (increase in minimum size and decrease in maximum size). Toarcian Pectinida (i.e. *Placunopsis*?, *Bositra*, *Oxytoma*, *Palmoxytoma*, *Meleagrinnella*, *Canadonecites*, and *Camptonectes* combined) exhibit a significant size decrease from pre-CIE to intra-CIE strata (equivalent to the Tenuicostatum to Serpentinum ammonite zones in Europe; $p < 0.001$ for the combined dataset), and continue to get smaller between the intra-CIE and post-CIE interval (late Kanense to Planulata zones or Serpentinum to Bifrons zones; $p < 0.001$ for combined data, $p = 0.001$ for East Tributary data).

Size-frequency distributions per ammonite zone of the abundant taxa (Figs. 10, 11) reveal more detailed patterns. During pre-CIE times, *Ochotochlamys*, *Gryphaea*, and rhynchonellid brachiopods exhibit a relatively broad range of size classes and, in the case of *Ochotochlamys* and rhynchonellids, left-skewed size-frequency distributions (Fig. 10), whereas in the CIE interval those of *Meleagrinnella* and *Bositra* are strongly right-skewed (Fig. 11). A right-skewed distribution also holds for *Bositra* after the CIE, whereas *Pseudomytiloides* from both the intra-CIE and the post-CIE intervals have more evenly spread, polymodal distributions (Fig. 11).

5. Discussion

5.1. General interpretation of the Ya Ha Tinda paleo-ecosystem

The fine-grained nature of the late Pliensbachian to middle Toarcian sedimentary rocks, the low degree of reworking, low levels of shell fragmentation, and the spatially clustered in-situ preservation of mm-sized juvenile shells in the Toarcian indicate continuous low water-energy conditions at the seafloor. Occasional shell concentrations within the first three meters of the section most likely resulted from high biogenic production (in case of in-situ accumulations of *Gryphaea* and patchy accumulations of rhynchonellids) and from the winnowing of fine-grained sediment by weak currents (in the case of *Ochotochlamys* pavements).

In terms of substrate conditions, the dominance of mostly fixosessile epifauna should not be used as an indicator of firm or hard substrates. The fine-grained sediments throughout the succession point to a soft substrate, an interpretation supported by occurrences of the reclining oyster *Gryphaea* in Pliensbachian strata, a so-called iceberg strategist adapted to soft bottoms (Thayer, 1975). Because most bivalves and

brachiopods at Ya Ha Tinda are either byssally or pedically attached or cemented forms, these taxa do indeed require firm to hard substrates. The substrates, however, are secondary hard substrates within an otherwise muddy seafloor, provided as sunken skeletal elements of nektonic organisms (ammonite conchs and aptychi, fish remains) and the shells of benthic invertebrates.

The prevalence of soft substrates in Toarcian strata is also suggested by concentrations of juveniles of the ubiquitous *Meleagrinnella* in nests that are separated by unfossiliferous areas (Fig. 3N). Such nests are closely tied to the presence of secondary hard substrates, which, therefore, appear to be a requirement for colonizing a soft seafloor (see also Kauffman, 1978). Nevertheless, an extremely soupy sediment-water interface is unlikely because such conditions are largely produced biologically by the activity of infaunal deposit-feeders, which are missing in the Toarcian interval at Ya Ha Tinda. Non-soupy substrate conditions are also corroborated by the absence of vertically or obliquely embedded ammonites, and only a single rostrum of a Pliensbachian proto-bellerophonite was found in a vertical position at East Tributary (in the Margaritatus Zone).

The consistently low faunal diversity and the high Toarcian juvenile mortality suggest highly stressed environments (see discussions in Sections 5.3 and 5.6). Owing to the presence of stenohaline ammonites throughout the section and of articulate brachiopods, abnormal salinity can be excluded as a stress factor. Also, food supply in the water column and within the sediment seems to have been sufficient based on the abundance of suspension-feeders and high amounts of organic carbon within the sediment (Fig. 2) (Them et al., 2017). In particular, infaunal deposit-feeders such as nuculoid bivalves should have benefitted from a substrate enriched in organic matter. Their absence suggests another factor than limited food supply to be more important.

Several faunal and sedimentary features indicate widespread, albeit variable, oxygen deficiency in bottom waters and within the sediment to be the most important stress factor at Ya Ha Tinda. Evidence includes the lack of shelly infauna; high taxonomic affinity of the bivalve fauna with coeval oxygen-controlled assemblages from Europe (see below for details); the laminated nature and high TOC content of the Toarcian Poker Chip Shale Member (Them et al., 2017); and the restriction of bioturbation in Pliensbachian strata to only a few intervals. Soft substrates probably were an additional stress factor for epifaunal organisms, but the availability of abundant secondary hard substrates suggests that unfavorable substrate conditions were of subordinate importance relative to low oxygen supply.

5.2. Life habits of Ya Ha Tinda invertebrates

Some of the Ya Ha Tinda taxa, particularly those dominant in the T-OAE CIE interval and post-CIE interval, are well known from contemporaneous T-OAE assemblages from northwest Europe, specifically records from Germany (Posidonia Shale), England (Jet Rock) and France (Schistes Cartons).

The fixo-sessile life habit of several dominant bivalves and brachiopods at Ya Ha Tinda (Table 1) implies the possibility of a fully or facultatively pseudoplanktonic rather than exclusively benthic mode of life (Wignall and Simms, 1990). This interpretation is of critical importance to the ecological interpretation, because it affects the suitability of these faunal assemblages as indicators of environmental conditions at the seafloor.

Detailed study of European *Pseudomytiloides dubius* – including analyses of abundance distribution, size-frequency distribution, growth patterns, colonization patterns of biogenic substrates, and geochemical properties of the sediment – suggest an opportunistic, benthic to facultatively pseudoplanktonic lifestyle (Kauffman, 1981; Etter, 1996; Röhl, 1998; Schmid-Röhl and Röhl, 2003; Caswell et al., 2009). Such a mode of life can also be assumed for *Pseudomytiloides* at Ya Ha Tinda. At East Tributary, the following observations support a benthic settlement of *Pseudomytiloides*, mostly on sunken ammonites: mass occurrences at

individual bedding planes (whereas a more even and continuous distribution across the section would be expected if the species lived attached to objects in the water column); large size of specimens in relation to small ammonite and/or high numbers of specimens associated with an ammonite (the cumulative weight probably would have caused sinking of the ammonite); lack of evidence that ammonites were colonized on both flanks (this would be expected if both flanks are available for attachment whilst ammonites reside in the water column, whereas usually just one flank is available when lying on the sea bottom); and attachment to ammonite aptychi or fish skulls (in such cases attachment is impossible or highly unlikely while the organism providing the hard substrate was alive). In contrast, a pseudoplanktonic lifestyle is more likely for specimens oriented with the umbo toward the venter of the ammonite (e.g. Fig. 3A) suggesting a free-hanging life position while the ammonite was in the water column. Rarely, *Pseudomytiloides* specimens are also arranged along a line (not attached to an ammonite) as a “stringer” similar to those documented in Caswell et al. (2009); these *Pseudomytiloides* may have been facultatively pseudoplanktonic and attached to algae. Nevertheless, it is impossible to specify the relative importance of benthic versus pseudoplanktonic occurrences with the present dataset.

Bositra is another dominant bivalve with a controversially interpreted life habit (reviewed in Etter, 1996; Röhl, 1998; Caswell et al., 2009). A pseudoplanktonic lifestyle is, however, unlikely because the shells of *Bositra* lack any visible adaptation that would suggest fixation by a byssus. Rather, an opportunistic, free-lying, benthic life habit is favored based on the dependence of shell growth, body size, and abundance on benthic environmental conditions.

Meleagrinnella is another very common bivalve shared between Ya Ha Tinda and localities in northwest Europe [see Röhl (1998) for a quantitative analyses of the German Posidonia Shale]. *Meleagrinnella* is much more abundant in Alberta than in Yorkshire (e.g., Danise et al., 2015); however, similar proliferations occur in the Posidonia Shale (Röhl, 1998; Röhl et al., 2001; Röhl and Schmid-Röhl, 2005). The abundant juveniles of *Meleagrinnella* in parts of the Ya Ha Tinda sections clearly represent brief phases of benthic settlement because they are closely tied to the presence of biogenic hard parts on the seafloor. In Canada, there is currently no unambiguous evidence of larger specimens having occupied a facultatively pseudoplanktonic lifestyle, but this cannot be excluded.

At Ya Ha Tinda, the cementing oyster *Liostrea* is closely associated with ammonites, either directly as epibionts with preference for the umbilical region of ammonites, or as free valves with a xenomorphic ammonite ornament. Again, these observations correspond well to the occurrences of oysters as encrusters of ammonites in northwest Europe, where a preference for the umbilical region and overgrowth of both flanks of the ammonite shell have been interpreted as indicators of a pseudoplanktonic mode of life of the oysters (Seilacher, 1982; Schmid-Röhl and Röhl, 2003). This interpretation is tentatively adopted for *Liostrea* at Ya Ha Tinda, although in the Canadian material no ammonites have been found with both flanks colonized. It should be noted that the vast majority of ammonites at Ya Ha Tinda were not encrusted. This suggests that living ammonites successfully prevented settlement of most pseudoplankton and supports the general conclusion that pseudoplankton only constitutes a minor portion of the fauna even in organic-rich black shales (Wignall and Simms, 1990; Schmid-Röhl and Röhl, 2003).

For the byssate pectinoid *Ochotochlamys* and the pedunculate rhynchonellids, a benthic rather than pseudoplanktonic mode of life is suggested at Ya Ha Tinda by their co-occurrence with undoubtedly benthic taxa (*Gryphaea*), lack of association with floating objects (ammonites), and strongly fluctuating abundances throughout their stratigraphic range. The thin, equilateral, low-convexity valves define *Ochotochlamys* as a typical flat clam. The high surface to volume ratio of flat clams is interpreted to facilitate oxygen uptake via a large mantle surface (Oschmann, 1994). We consider *Ochotochlamys* cf.

bureiensis as an opportunistic species that was able to tolerate lower than normal but not extreme reductions in oxygen levels. In this respect, its coeval ecological equivalent in Europe and South America is the pectinoid bivalve *Parvamussium pumilum* (Aberhan, 1993; Fürsich et al., 2001).

In conclusion, a primarily benthic mode of life is inferred for the dominant bivalves and brachiopods at Ya Ha Tinda and the faunal assemblages can be interpreted accordingly. The only exception is *Liostrea*, for which colonization of ammonite conchs in the water column seems to be more likely. In addition, the Ya Ha Tinda crinoids are herein interpreted as benthos. Although it is possible that they were (facultatively) pseudoplanktonic, similar to the seirocrinids attached to driftwood in the Posidonia Shale (Röhl et al., 2001; Etter and Tang, 2002), no crinoid or bivalve epifauna have been found on the pieces of wood discovered at Ya Ha Tinda to date.

5.3. Reconstruction of oxygen regimes at Ya Ha Tinda

Faunal characteristics suggest variation in the range and dynamics of oxygen levels at Ya Ha Tinda. In the lowermost 2 m of the East Tributary section, a large portion of individuals reached adult sizes, which, in the case of *Gryphaea*, is combined with very thick shells, indicating unhindered calcification. These assemblages of body fossils along with horizons containing macroscopic trace fossils indicate that oxygen levels at the seafloor were high enough over at least several consecutive years to support mature populations dominated by adults. In principle, this population structure persists for the remainder of the pre-CIE interval. The alternation of unfossiliferous intervals and monospecific assemblages of *Ochotochlamys* in the interval between ca. 4–8 m probably represents more severe oxygen restriction within the pre-CIE interval, but even here oxygenated bottom waters must have prevailed long enough to permit growth to adult size of a monospecific epifauna adapted to low oxygen conditions.

With the onset of the CIE, pseudoplanktonic *Liostrea* dominated the fauna while conditions at the seafloor apparently were mostly inimical to macroinvertebrates. This interpretation is supported by the correlative marked negative shift in carbon isotopes, indicating a major environmental perturbation of the regional ecosystem.

Within the CIE interval at Ya Ha Tinda, the taxonomic and ecological composition of the benthos is strikingly similar to that of contemporaneous assemblages in northwest Europe. The fossiliferous interval with the most negative carbon isotope values (from 11.55 m to 13.0 m) is characterized by assemblages dominated by *Pseudomytiloides* (Assemblage 4) and by *Bositra* (Assemblage 5). *Pseudomytiloides* also dominated the community during the early part of the CIE minima in England (Caswell and Coe, 2013). As low-oxygen opportunists that may have reproduced after just a few months, accumulations of *Pseudomytiloides* and *Bositra* in northwest Europe have been interpreted to indicate fluctuating redox boundaries near the sediment–water interface with at least some oxygen availability for some months to years during which episodic benthic colonization was possible (Röhl et al., 2001; Caswell and Coe, 2013). An analogous interpretation can be applied to Ya Ha Tinda. The unimodal, strongly right-skewed size-frequency distribution of *Bositra* at Ya Ha Tinda suggests high juvenile mortality (Fig. 11E). Death mostly occurred within the first year, and so most individuals represent the first generation after a colonization event. In contrast, the larger sizes and polymodal distribution of *Pseudomytiloides*, as compared to *Bositra*, suggest a different temporal dynamic (Fig. 11C, D). Many individuals persisted into adulthood and the presence of presumably multiple generations suggests fluctuations between anoxic and better-oxygenated periods on the order of several years.

The most short-lived oxygen fluctuations within the CIE interval and continuing to the post-CIE times are inferred for the *Meleagrinea* assemblage (Assemblage 6). The extremely right-skewed size distribution of *Meleagrinea* populations during both the rising limb of the CIE

(Fig. 11A) and the post-CIE interval (Fig. 11B) suggest that long-term anoxia was punctuated by very brief hypoxic periods, no longer than a few weeks in duration. Such accumulations of tiny juvenile bivalves are also documented from northwest Europe and are interpreted as failed benthic colonization events (Röhl et al., 2001).

5.4. The effect of the T-OAE on the composition of Ya Ha Tinda macrobenthic communities

Unlike the multiple, punctuated extinctions of the pelagic and microfossil taxa in northeastern Panthalassa (Caruthers et al., 2013, 2014), there is only one significant faunal turnover in the Ya Ha Tinda benthos: at the Toarcian Oceanic Anoxic Event. At both the Scalp Creek and East Tributary sites, the onset of the T-OAE carbon isotopic excursion is coincident with a major shift in the taxonomic distribution of the fauna, resulting in the wholesale turnover of benthic assemblages (Fig. 5).

No major change occurs in the benthic community across the Pliensbachian–Toarcian stage boundary because the rhynchonellid-dominated assemblage, as well as lobsters and crinoids persist from the Pliensbachian into the earliest Toarcian. This observation is in marked contrast to the ammonite record; one of the largest losses of ammonite species richness (and the lowest generic richness) occurs in the Tenuicostatum Zone, i.e. the earliest Toarcian (Dera et al., 2011; Caruthers et al., 2013, 2014). For ammonites, events around the stage boundary had significant evolutionary consequences, whereas in the Ya Ha Tinda benthic community, no major effects on ecological structure and taxonomic composition can be recognized. The disparity between the macrobenthic and ammonite records could suggest a decoupling of the benthic and the pelagic ecosystem with the more susceptible ammonites reacting earlier to environmental change than the benthic faunas, which were already low-oxygen adapted. In the UK, the loss of benthic taxa starts earlier than in Alberta, beginning in the Tenuicostatum Zone (Caswell et al., 2009; Danise et al., 2013, 2015), or even as early as the late Pliensbachian (Little and Benton, 1995; Morten and Twitchett, 2009), but the majority of taxa disappeared near the top of the Tenuicostatum Zone. In the Posidonia Shale, bioturbation persists into the early Toarcian (Tenuicostatum Zone), longer than at Ya Ha Tinda, but as in Alberta, strata from the Serpentinum (Falciferum) Zone are largely unbioturbated (Röhl and Schmid-Röhl, 2005).

At the onset of the T-OAE, in the falling limb of the CIE, the last rhynchonellids occur with *Liostrea* and *Meleagrinea* (Assemblage 3), and by the carbon isotope minima, the benthic community was completely transformed. Low taxon richness and identification of taxa mostly above the species level prevent a meaningful quantitative analysis of extinction intensity and biogeographic affinities of the benthic fauna. Nonetheless, the species assigned to *Ochotochlamys* cf. *bureiensis*, common in Pliensbachian to Early Toarcian strata of Alberta (Aberhan, 1998), went extinct with the onset of the T-OAE.

Within and above the CIE, some lobster appendages are observed (Fig. 2), but these are limited to claws (some identifiable as *Uncina pacifica*); no articulated lobster specimens have been identified in intra- or post-CIE strata. Research on crustacean taphonomy has demonstrated that the heavily sclerotized claws, the most robust parts of crabs and lobsters, are the most likely to be preserved (Bishop, 1986; Stempien, 2005; Mutel et al., 2008). Additionally, carcasses readily disarticulate, are easily transported by minimal water energy (in the water column, not entrained in the sediment), and can even float, buoyed up by the gases produced during decay (Allison, 1986). Given the lack of articulated lobster specimens following the onset of the T-OAE CIE, it is possible that the lobsters lived in a more oxygenated setting, but claws were occasionally transported into the anoxic environments by weak currents (or even surface currents if they floated). The limitation of lobster fossils to claws points to an extirpation of these crustaceans from the environment represented by the Ya Ha Tinda sections.

Prior to our study, *Pseudomytiloides* cf. *dubius* was poorly known from Canada [figured as ‘unidentified bivalve’ in Hall (1987) (pl. 3, fig. M) and as ‘*Arctomytiloides*? cf. *rassochaensis*’ in Aberhan (1998) (pl. 2, fig. 9)]. Our well-dated occurrences of this species within the CIE, with first appearance in the Kanense (Serpentinum) Zone, suggest that it immigrated to Canada, because older records are known elsewhere, e.g. from the basal Tenuicostatum Zone in northwest Europe (Caswell et al., 2009). Due to the lack of species assignments, the following remains an open question: do *Liostrea* sp., *Bositra* sp., *Meleagrinnella* sp., and *Discinisca* sp., which all make their first appearances within the CIE at Ya Ha Tinda, represent species that originated in Alberta, or species that immigrated from another region?

It is interesting to note that there are significant faunal changes within the CIE interval, which do not necessarily correspond to isotopic shifts, particularly in the lower half of the CIE. The interval of fairly stable isotopic minima (11.55 m to 13.0 m) is characterized by a succession of the largely pseudoplanktonic *Liostrea* assemblage that gives way to the facultatively pseudoplanktonic *Pseudomytiloides* assemblage, which is replaced by the *Bositra* assemblage (Fig. 5). We interpreted these faunal changes to represent different oxygen regimes in terms of magnitude and duration of oxygen restriction (see Section 5.3). In the upper part of the CIE, the first distinct shift within the CIE to more positive carbon isotope values at 13.0 m corresponds well to an almost permanent replacement of the older CIE assemblages by the *Meleagrinnella* assemblage, whereas the final return of carbon isotopes to pre-CIE values at 15.4 m does not affect the long-term continuity of the *Meleagrinnella* assemblage. These findings highlight the potential of faunal analyses to fine-tune environmental interpretations attained with sedimentological and geochemical data. The shortcoming of geochemical data to decipher short-lived environmental fluctuations between anoxic and better aerated bottom conditions in the lower part of the CIE can be explained by differences in the extent of time-averaging of the respective data. Whereas the faunal data, derived from individual bedding planes, most likely represent snap-shots of benthic colonization events at the seasonal to annual scale, the geochemical data, taken from whole rock samples of the black shales, do not have this fine temporal resolution.

5.5. The ecological effects of the T-OAE on the Ya Ha Tinda macrobenthic communities

Even though CIE-related changes in the taxonomic composition are significant, the ecological attributes of the shelly macrofauna remained fairly stable with respect to trophic and life habit composition. Yet, patterns of change are evident in other ecological traits, particularly in motility levels and body size.

The loss of the facultatively mobile *Ochotochlamys*, autochthonous lobsters, and the burrowing infauna (as indicated by the ichnofacies) at the beginning of the CIE indicate a reduction of motility levels of the fauna. Activity is closely related to metabolic rates, and low metabolic costs are beneficial in low oxygen environments. Thus, mobile forms are expected to be more vulnerable under hypoxia than sessile forms (Riedel et al., 2012). The pattern of decreasing mobility along gradients of decreasing oxygen availability (Rhoads and Morse, 1971; Diaz and Rosenberg, 1995; Levin, 2003) is reflected in the succession at Ya Ha Tinda and is compatible with the interpretation of increased oxygen stress with the onset of the CIE and continuing into the studied post-CIE interval.

Similarly, the significant effect of the T-OAE CIE on bivalve and brachiopod size (Figs. 6, 9, 10, 11) implies enhanced oxygen stress. Both intra-CIE and post-CIE taxa are significantly smaller than the pre-CIE taxa. Everything else being equal, larger body (and shell) size means higher metabolic demand (e.g., Payne et al., 2014). As for motility levels, large body size would be selected against under oxygen stress (Diaz and Rosenberg, 1995, 2008), and thus the observed size patterns at Ya Ha Tinda support oxygen deficiency as the main controlling factor. In this respect, our conclusions parallel those attained for the northwest

European Posidonia Shale and Jet Rock. In England, *Pseudomytiloides dubius*, which survived the early Toarcian extinction phase, records its smallest body sizes in the early survival interval owing to low oxygen-induced deceleration of growth rather than dying at younger ages (Morten and Twitchett, 2009). On average, larger specimens of *Pseudomytiloides dubius* and *Bositra radiata* coincided with periods of greater oxygenation and possibly higher primary productivity (Caswell and Coe, 2013). In southwest Germany, Röhl et al. (2001) found environment-dependent variations in shell size of *Bositra buchi*, whereby low absolute oxygen concentrations resulted in retarded growth rates as well as high juvenile mortality. The size trends of *Pseudomytiloides* in Europe conform to the so-called Lilliput effect, i.e. size decrease in a surviving species in the immediate aftermath of an extinction event (Urbanek, 1993; Morten and Twitchett, 2009). The Ya Ha Tinda fauna is not a Lilliput fauna strictly speaking, as there is, instead, complete replacement of assemblages by other, on the whole smaller-sized assemblages.

5.6. The relative role of oxygen deficiency versus other environmental factors

Reductions in body size also have been observed with increased temperature (Atkinson, 1994), ocean acidification (Widdicombe and Spicer, 2008; Parker et al., 2013), and reductions in food supply (Twitchett, 2007). Because the effects of warming, hypoxia, and acidification are often interlinked and reinforce each other (Bijma et al., 2013), they cannot easily be distinguished in laboratory studies and field experiments, let alone the fossil record. Yet, at Ya Ha Tinda several faunal patterns confirm a prominent role for oxygen fluctuations.

Benthic bivalves are relatively tolerant to hypoxia compared with crustaceans (Diaz and Rosenberg, 1995; Vaquer-Sunyer and Duarte, 2008), whereas benthic mollusks seem to be among the first affected by ocean acidification with higher resilience in crustaceans (Ries et al., 2009; Kroeker et al., 2010; Christen et al., 2013). Furthermore, work on modern articulate brachiopods has found that shell growth is hardly affected by ocean acidification (Cross et al., 2015). Similarly, pectinid bivalves seem to be sensitive to hypoxia (Riedel et al., 2014), but not to ocean acidification with respect to their swimming performance and escape behavior from predators (Schalkhauser et al., 2014). Finally, taxa characterized by an active mode of life also have greater capacities to compensate disturbances of the internal acid-base status than sessile organisms with low metabolic rates and thus should be more tolerant toward ocean acidification (Kroeker et al., 2010; Parker et al., 2013). Consequently, at Ya Ha Tinda the shift to less active modes of life, the persistence of benthic bivalves and concomitant loss of decapod crustaceans, articulated brachiopods, and the pectinid *Ochotochlamys*, point to stress via hypoxia rather than ocean acidification.

Compared with mollusks, rhynchonelliform brachiopods appear to fare better if low food supply is an important stressor, because brachiopods are capable of utilizing dissolved organic matter in addition to particulate organic matter (Steele-Petrovic, 1976). The stratigraphic distribution of bivalves and articulate brachiopods at Ya Ha Tinda thus also argues against a major role of reduced food supply.

Thermal stress is difficult to infer from faunal patterns alone, and correlation tests with geochemical proxy data were beyond the scope of this study. Nevertheless, in aquatic invertebrates those with low metabolic rates may have lower maximum heat tolerance because of a low capacity of internal oxygen supply (Pörtner, 2002). Therefore, reduced motility and hence presumably low metabolic rates of the intra- and post-CIE fauna argue against strong temperature-related stress.

5.7. No benthic recovery from the T-OAE at Ya Ha Tinda

One conspicuous feature of the record at Ya Ha Tinda is that there are no signs of benthic recovery in the Planulata (Bifrons) Zone. There are virtually no new taxa that would have originated or immigrated during

the studied post-CIE interval nor is there recolonization of pre-CIE taxa. Furthermore, the abundance of all taxa remains extremely low (often with only 1–3 individuals per horizon), and the overall assemblage-level body sizes are at a minimum (Fig. 9). The presence of almost exclusively juvenile forms of *Meleagrinella*, the dominant bivalve in Assemblage 6, suggests that oxygen stress persisted throughout the study interval, only punctuated by short periods of oxygenation mostly at the subannual scale. Despite the carbon isotopic recovery, the benthic community at Ya Ha Tinda was clearly still extremely stressed in the Planulata Zone.

The lack of benthic recovery at Ya Ha Tinda is in clear contrast to the pelagic ammonite records from this region, which record taxonomic recovery within the Serpentinum and Bifrons zones (Dera et al., 2011; Caruthers et al., 2013, 2014), again suggesting a decoupling of benthic and pelagic ecosystems. Failed benthic recovery at Ya Ha Tinda also contrasts with the faunal patterns seen in northwest Europe. In the UK sections, environmental and ecological recovery occurs in the Bifrons Zone (e.g., Caswell et al., 2009; Morten and Twitchett, 2009; Danise et al., 2013). In contrast to Ya Ha Tinda, in the UK deep infaunal bivalves re-occur, albeit ephemeral and in very low numbers, in the Serpentinum (Falciferum) Zone (Goniomya; Caswell et al., 2009) and recovery of the deep infauna commenced in the Bifrons Zone (common occurrences of *Gresslya*; Harries and Little, 1999). Also, infaunal lingulid brachiopods are present in the Falciferum and Bifrons zones (Harries and Little, 1999). Similarly, trophic composition became more diverse with the recovery of infaunal deposit-feeding bivalves (*Dacryomya*) in the Bifrons Zone and overall diversity increased (Harries and Little, 1999; Caswell et al., 2009). Furthermore, bivalve size minima occur in the Exaratum Subzone (i.e. the T-OAE CIE) and return to pre-extinction levels in the Bifrons Zone (Morten and Twitchett, 2009). In general, size-frequency distributions shift from juvenile-dominated to those dominated by adults in Europe by the middle Toarcian (Röhl, 1998; Fürsich et al., 2001; Caswell and Coe, 2013), whereas in Alberta, sizes continue to decrease through the middle Toarcian (Fig. 9). Although dysoxic-anoxic conditions continued into the Planulata/Bifrons Zone in both Ya Ha Tinda and Europe (e.g., Röhl et al., 2001; Montero-Serrano et al., 2015) it is apparent that benthic faunal recovery was delayed at Ya Ha Tinda.

6. Conclusions

The Lower Jurassic sections at Ya Ha Tinda provide an excellent opportunity to study the ecological changes of the macrobenthic communities through the Pliensbachian-Toarcian interval. The Ya Ha Tinda succession documents faunal changes in northeastern Panthalassa within roughly the same sedimentary environment (e.g., calcareous black shales) as the well-studied localities from northwest Europe. Recent high-resolution ammonite biostratigraphy and chemostratigraphy of Ya Ha Tinda allow the biotic changes to be correlated with the Toarcian Oceanic Anoxic Event, which had the single, most substantial effect on the macrobenthos in this part of northeastern Panthalassa.

The low-diversity benthic assemblages are primarily composed of bivalves and brachiopods. At the onset of the carbon isotope excursion that marks the T-OAE, the benthic communities experienced complete taxonomic turnover, apparently decoupled from the dynamics of pelagic organisms, which experienced multiple taxonomic turnovers before the T-OAE. Ecological change in the benthos includes the loss of burrowing organisms, a reduction in motility levels, and a decrease in body size with a shift in population structure from predominantly mature populations to those dominated by juveniles. Together, these observations suggest a change in the prevailing oxygen regime as the main cause of faunal turnover. During pre-CIE times, we infer that dysoxic bottom waters lasted for several consecutive years, at least intermittently. In contrast, with the onset of the T-OAE anoxic conditions prevailed, only interrupted by very brief hypoxic phases, mostly no longer than a few weeks in duration, which permitted ephemeral benthic colonization events. Only the low-oxygen opportunist *Pseudomytiloides*

seems to have been capable of within-habitat reproduction as suggested by its size-frequency distribution within the Kanense (Serpentinum) Zone. High-frequency oscillations of anoxic-dysoxic conditions persisted into the middle Toarcian Planulata Zone. These inhospitable conditions were responsible for the failed recovery of the macrobenthos at Ya Ha Tinda; at the same time northwest Europe shows an increase in taxonomic richness and functional diversity. Nevertheless, striking similarities are evident in taxonomic composition and ecological structure of the Ya Ha Tinda benthos with assemblages from England, Germany, and France. Such similarities and differences across regions highlight the need for further quantitative paleoecological studies in Panthalassa and other regions outside of Europe to achieve a geographically and environmentally more detailed understanding of the evolutionary dynamics of the T-OAE.

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Appendix A. Supplementary data

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