



Widespread delayed mixing in early to middle Cambrian marine shelfal settings

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ABSTRACT

The radiation of burrowing metazoans in the early Phanerozoic dramatically altered the properties of marine sediment, an event commonly referred to as the “Cambrian substrate revolution” or “agronomic revolution.” The advent of infaunalization, and especially biogenically-mediated sediment mixing, profoundly impacted the development of Phanerozoic biogeochemical cycling, including nutrient fluxes, organic carbon burial, seafloor oxygenation and sediment ecology. However, the timing of the development of mixed seafloor sediment has, historically, not been well constrained. Mixing has been assumed, in the absence of data, to occur at the Precambrian–Cambrian boundary with the appearance of the index fossil and three-dimensional burrow *Treptichnus pedum*. Herein we present new ichnological, stratigraphic and taphonomic data suggesting that, although significant developments in infaunalization—paleobiologically complex animal–substrate interactions, particularly burrow construction—occurred during the early and middle Cambrian, mixing remained suppressed throughout this interval. We demonstrate, using a novel multi-proxy approach, that shelfal sediment in the earliest Cambrian was essentially unmixed. Moreover, our findings indicate that even as late as the middle Cambrian—30 million years after the Precambrian–Cambrian transition and well after the appearance of supposedly deposit-feeding trilobites—seafloor heterolithic shelfal sediment remained largely unmixed on a global scale. These findings challenge the current assumption that mixing occurred with the first appearance of three-dimensional burrows and hold important implications for the advent and development of modern-style biogeochemical cycling.

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1. Introduction

The physical and chemical mixing of sediment, known as bioturbation, by burrowing (infaunal) animals plays a critical role in modern marine biogeochemical cycling. Infaunal churning, particularly by bilaterian macrofauna, is responsible for heightened nutrient recycling—including the reoxidation of buried reduced compounds—and the deep and widespread oxidation of seafloor sediment in the modern ocean (Aller, 1982, 1984, 1994; Ziebis et al., 1996). The activity of burrowing animals also significantly impacts substrate consistency and thus the character of benthic communities (Rhoads and Young, 1970; Thayer, 1979, 1983). The modern seafloor and the majority of the Phanerozoic stratigraphic record are characterized by biogenically reworked, well-churned sediment (Bromley and Ekdale, 1986; Boudreau, 1998; Teal et al., 2008, 2010). In contrast, the lack of widespread or penetrative burrowing in Neoproterozoic strata, along with an abundant and diverse record of organic surface textures, suggests that the Ediacaran seafloor was commonly microbially sealed and populated by a fauna of limited mobility (Gehling, 1999; Seilacher, 1999;

Bottjer et al., 2000; Jensen, 2003; Jensen et al., 2005; Gehling and Droser, 2009).

The ecological and geochemical character of the modern seafloor is strongly influenced by the nature and depth of the mixed layer—the zone of biogenically homogenized sediment, which today extends 3–10 cm below the sediment–water interface (Ekdale et al., 1984; Boudreau, 1998; Teal et al., 2008, 2010). The modern mixed layer consists of sediment of ‘soupy’ or flocculent consistency, high water content and low shear strength. The mixed layer is densely populated by infaunal meiofauna and macrofauna and heavily exploited by both infauna and epifauna for its high nutritional content. The mixed layer and its associated infaunal communities are not, however, well represented in the stratigraphic record; due to continual homogenizing activity by burrowing infauna and resulting low sediment shear strength, burrows collapse once they are vacated (Ekdale et al., 1984). The trace fossil record, therefore, is heavily skewed toward the underlying transition and historical layers—the deeper zones of sediment in which the structures produced by deep-burrowing (maintaining open burrows of up to 2.5 m depth in modern seafloor environments), ‘elite tier’ fauna are preserved (Pemberton et al., 1976; Ekdale et al., 1984; Bromley, 1996).

The geologic timing of the development of the mixed layer has not been well constrained. The diversification of burrowing marine bilaterian animals and the onset of sediment mixing, an episode commonly referred

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to as the “Cambrian substrate revolution” (Bottjer et al., 2000) or “agronomic revolution” (Seilacher and Pflüger, 1994) are considered to have played a major role in the transformation of the seafloor. And it has commonly been assumed, without evidence beyond the appearance of the index fossil and three-dimensional burrow *Treptichnus pedum* and the disappearance of widespread matground structures, that the development of well-mixed sediments (“mixgrounds”) occurred at the Precambrian–Cambrian boundary, or even during the latest Neoproterozoic (e.g., Seilacher and Pflüger, 1994, Fig. 1). This assumption has become engrained in the literature. Although several workers have suggested that the development of sediment mixing may have been a more protracted process or have documented gradual increases in local stratigraphic successions (e.g., Droser and Bottjer, 1988; McIlroy and Logan, 1999; Bottjer et al., 2000; Droser et al., 2002a), the ‘Precambrian–Cambrian boundary model’ has remained the classic and most widely cited view (e.g., Rydell et al., 2001; Meysman et al., 2006; Teal et al., 2010; Erwin and Tweedt, 2012; Pawlowska et al., 2013). Moreover, there is a conspicuous paucity of data constraining how rapidly the global development of an appreciable mixed layer, typical of modern seafloor sediment, followed the evolution of infaunal metazoans. And although certain authors, such as Droser et al. (2002a,b), Jensen et al. (2005) and McIlroy and Logan (1999) have described earliest Cambrian advances in infaunalization, systematic documentation of trends in sediment mixing, made from a jointly ichnological and sedimentological perspective, and consideration of post-lower Cambrian strata have largely been lacking (but see Marengo and Bottjer, 2008).

Constraining the timing of this transformation in seafloor substrate is, however, essential, given that bioturbation has long been considered the cause of a plethora of geochemical, ecological and taphonomic phenomena, including changes in bioessential nutrient fluxes, the cycling of redox-sensitive elements and seafloor oxygenation; declines in the diversity and abundance of microbialites; the disappearance of the Ediacara Biota, Ediacara-style preservation and matgrounds; the advent of the Cambrian Explosion; changes in lipid biomarker preservation; changes in the stratigraphic character of event bedding and the decline of Burgess Shale-type preservation (Awramik, 1971; Brasier, 1990; Sepkoski et al., 1991; Allison and Briggs, 1993; McIlroy and Logan, 1999; Orr et al., 2003; Dornbos et al., 2005; Meysman et al., 2006; Callow and Brasier, 2009; Canfield and Farquhar, 2009; Brasier et al., 2011; Erwin and Tweedt, 2012; Pawlowska et al., 2013).

Previous work (Droser et al., 2002a, b; Jensen, 2003; Jensen et al., 2005) has documented that burrowing in the latest Ediacaran, at the Precambrian–Cambrian transition and in the earliest

Cambrian (Terreneuvian Epoch) was shallow (≤ 2 cm depth). The exceptions, such as *Skolithos* and *Arenicolites*, common in early Cambrian and younger nearshore, sandy, high-energy environments (e.g., Sepkoski et al., 1991) attained much greater depths. However, these structures, which have been attributed to static filter-feeding rather than mobile deposit-feeding organisms (Thayer, 1979; Droser et al., 2002b), would have merely statically increased advection of bottom-waters into the sediment on a very localized scale (Aller, 1982; Droser et al., 2002a), rather than mediating physical or chemical homogenization. Therefore, even densely colonized ‘pipe rock’ does not represent well-mixed sediment. In contrast, it would be expected that with the appearance of trilobites—mobile, benthic organisms long considered to be largely deposit feeders and thus sediment mixers (Seilacher, 1985, 2007)—in the late early Cambrian, the mixed layer should have become well developed in open marine, oxygenated environments. This study represents the first systematic test of this prediction.

2. Assessment of mixed layer development

2.1. Geologic setting

Data were collected from lowermost Cambrian through lower middle Cambrian successions across the Great Basin (USA), in southern Spain and in Newfoundland (Fig. 1). Shallow marine siliciclastic deposits were targeted because siliciclastic sediment and strata represent the vast majority of both the modern seafloor and the stratigraphic record, respectively (e.g., Bluth and Kump, 1991), and generally contain better preserved and more abundant trace fossils. Shallow marine environments, long considered to be both modern diversity ‘hotspots’ and cradles of early seafloor diversity (Jablonski et al., 1983), would be the expected locus of the earliest and most dynamic changes in seafloor communities and thus sediment mixing. Additionally, emphasis was placed upon lithologic heterogeneity—thinly (mm- to dm-scale) bedded and interbedded mudstone, siltstone and sandstone—in order to maximize resolution of mixing trends (see Section 2.3).

The lower Cambrian Wood Canyon and lower to middle Cambrian Pioche (and correlative Bright Angel Shale) formations (Great Basin) and the lower Cambrian Torreárboles Sandstone (Spain) are characterized by thinly bedded, fine-grained heterolithic lithologies (Palmer, 1971; Gozalo et al., 2003). They are interpreted, on the basis of facies, fauna and paleogeographic reconstructions, to have been deposited under shallow, oxygenated marine waters. Data from the lowermost Cambrian Chapel Island Formation—a well-exposed succession of thinly



Fig. 1. Study localities. Areas of study (marked by stars) include the Great Basin, western USA (see inset map; from west to east: Salt Spring Hills, CA [Wood Canyon Fm.]; Frenchman Mountain, NV [Pioche Fm.]; Pioche Mining District, NV [Pioche Fm.]; House Range, UT [Pioche Fm.]); Newfoundland, Canada (Fortune Head [Chapel Island Fm.]) and southern Spain (Guadajira [Torreárboles Sandstone]).

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