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Foraminifera associated with cold seeps in marine sediments

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Cold seep foraminifera have attracted considerable attention as they provide valuable insights into the study of cold seeps. This study provides a comprehensive overview of the manifestations of foraminifera in cold seep environments and methane seepage activities. Certain taxa of benthic foraminifera, such as *Uvigerina*, *Bolivina*, *Bulimina*, *Chilostomella*, *Globobulimina*, *Nonionella*, *Melonis*, *Epistominella*, *Cibicidoides*, and *Globocassidulina*, are known to inhabit geochemical conditions induced by methane-rich environments and may feed on associated methanotrophic microbial communities. Secondary mineralization on foraminifera shells is a widespread manifestation in seep sediments, and alters the microstructure, elementary composition, and isotopic signatures of foraminifera. On one hand, the precipitation of secondary authigenic Mg-rich, Mn-rich, Sr-rich, and Ba-rich calcite coatings have been observed on microfossils. On the other hand, micron-sized crystal pyrite and gypsum aggregates can also grow on the foraminifera walls. The negative $\delta^{13}\text{C}$ and positive $\delta^{18}\text{O}$ anomalies in both planktonic and benthic foraminifera from seep-associated sediments can serve as proxies for tracing past seepage activities, either in their live form or being adulterated by methane-derived authigenic carbonate after deposition. Seeping activities are recognized with a significant impact on benthic foraminifera, and the presence of cold seep-related species and significant isotopic anomalies in shells can be used to reconstruct past methane seepage events. Intensive methane seepage tends to suppress benthic foraminifera populations, while moderate intensity seepage may lead to a thriving benthic foraminiferal community, with hypoxia-enduring taxa such as *Uvigerina*, *Melonis*, and *Bulimina* being predominant. In contrast, oxygen-loving epibenthic taxa such as *Cibicidoides* often occur in areas of low methane flux. Compared to planktonic foraminifera, the single species of benthic foraminifera can provide a more comprehensive record of seepage evolution. Live benthic specimens are preferred for *in-situ* seep studies, while the superimposition of secondary minerals on the original shells should not be ignored when observing dead individuals. The significance of the evolution of methane seepage, changes in environmental parameters of the living habitat, and species sensitivity in cold seeps are emphasized in explaining the variation in foraminiferal assemblages and fluctuations in stable isotopes.

KEYWORDS

cold seep, marine foraminifera, methane seepage, species composition, secondary mineralization, stable isotopes

1 Introduction

Marine cold seeps, frequently observed in the vicinity of active and passive continental margin slopes, have been linked to the destabilization of gas hydrate reservoirs (Ceramicola et al., 2018; Suess, 2020). Variations in sea level increase in bottom water temperature, tectonic activity, and fluctuations in deposition rates can trigger instability in gas hydrate reservoirs and lead to repeated episodes of methane seepage (Karstens et al., 2018; Wallmann et al., 2018; Ketzner et al., 2020; Suess, 2020; Sultan et al., 2020). The seep fluids often saturate the pore water with hydrocarbon gases, an essential process of methane oxidation in methane-charged sediments *via* the action of anaerobic oxidation of methane (AOM, Eq. 1, Caldwell et al., 2008; Knittel and Boetius, 2009). This process is performed by a consortium of anaerobic methane-oxidizing archaea (ANME) and sulfate-reducing bacteria (SRB) (Knittel and Boetius, 2009). The AOM and methane aerobic oxidation processes (Eq. 2, Paull et al., 2005; Reeburgh, 2007) generate carbon dioxide (CO₂) and hydrogen sulfide (H₂S), which, in turn, resulting in local acidic and anoxic conditions (Niewöhner et al., 1998; Aharon and Fu, 2000; Joye et al., 2010). Elevated carbonate alkalinity promoted by AOM results in the formation of authigenic carbonate minerals. Typically, methane-derived authigenic carbonate (MDAC) is a universal mineral indicator in seep areas and is primarily composed of acicular aragonite, high-Mg calcite, and dolomite (Boetius et al., 2000; Judd et al., 2007; Naehr et al., 2007; Buckman et al., 2020; Judd et al., 2020). However, in some cases, Fe- and Mn-carbonates may also be present (Suess, 2020). Meanwhile, a direct consequence of such stressful conditions is the occurrence of symbiotic benthic seep communities. Tube worms, clams, mussels, and microbial mats, are indicator organisms to survive in seep ecological environments (Suess, 2020), and these organisms may provide carbon and energy *via* AOM (Boetius et al., 2000). Implications are that the association of methane fluids, authigenic minerals, and benthic biota has been regarded as a biogeochemical footprint to identify cold seeps.

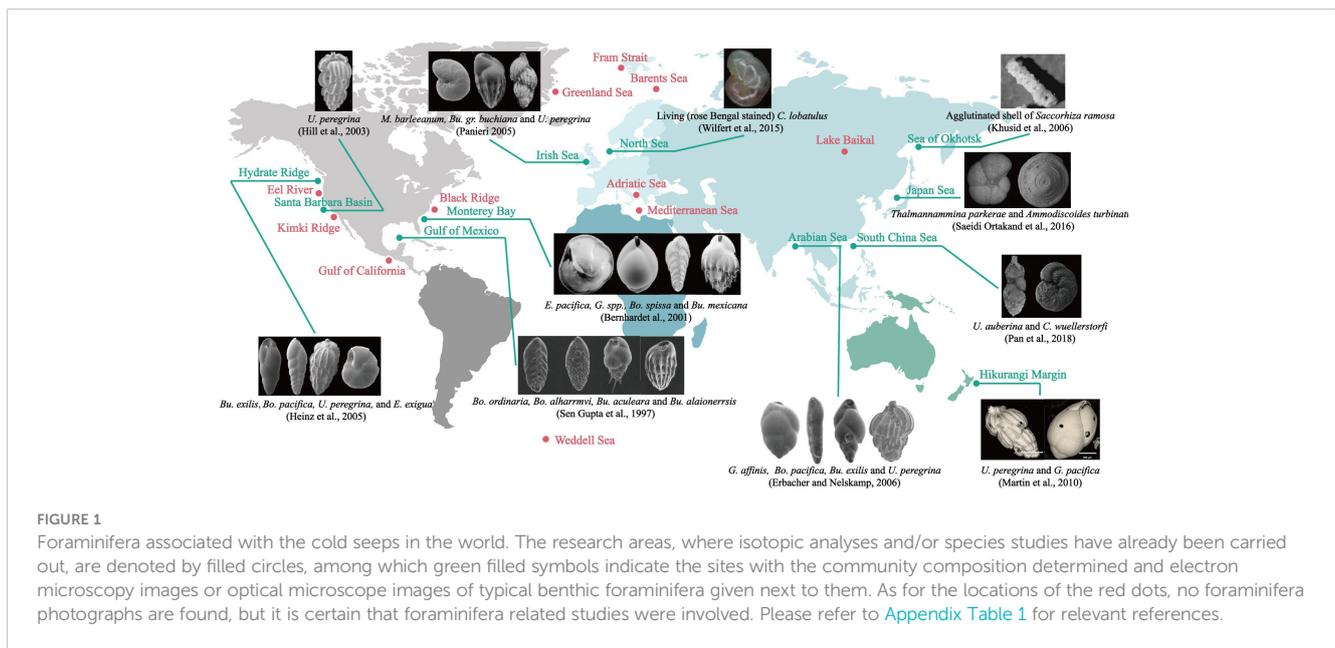


Foraminifera, single-celled eukaryotes widely distributed in seawater and deep-sea sediments, have been established as a crucial micro-paleontological foundation for the study of paleoceanography and paleoclimatology (Jorissen, 1992; Schiebel et al., 2018). Environmental information can be obtained through the examination of foraminifera assemblage on a macro-scale, and as well as shell elements and isotopic compositions on a micro scale (Gooday, 1994; Kucera, 2007; Ravelo and Hillaire-Marcel, 2007; Pawlowski and Holzmann, 2008; Schiebel et al., 2018). In recent decades, evidence of deep-sea benthic foraminifera in seep areas has been discovered (e.g. Brooks et al., 1991; Sen Gupta and Aharon, 1994; Martin et al., 2010), and growing interests begins to focus on the identification of seep environments and methane seepage activities *via* foraminifera research. Apparently, cold seep foraminifera have been served as archives of seep activity, and

differences in foraminiferal assemblages, secondary minerals alteration on the shells, and isotopic compositions between seep and non-seep areas can be detected.

The community assemblage of benthic foraminifera (composition, abundance, diversity, and dominant species) have been recognized as an advantageous indicator for the identification of cold seep environments. Data from different oceanic basins spread across the Pacific Rim shelf (Bernhard and Reimers, 1991; Hill et al., 2003; Heinz et al., 2005; Khusid et al., 2006; Zhou et al., 2009; Chen et al., 2010; Martin et al., 2010; Xiang et al., 2012; Saeidi Ortakand et al., 2016; Pan et al., 2018; Xin et al., 2020; Zhou et al., 2020; Li et al., 2021), the North and east Atlantic (Jones, 1993; Sen Gupta and Aharon, 1994; Sen Gupta et al., 1997; Rathburn et al., 2000; Bernhard et al., 2001; Rathburn et al., 2003; Robinson et al., 2004; Bhaumik and Gupta, 2005; Panieri, 2005; Bhaumik and Gupta, 2007; Lobeguer and Sen Gupta, 2008; Panieri and Gupta, 2008; Wilfert et al., 2015), the North Indian Ocean (Erbacher and Nelskamp, 2006), the Arctic marginal seas (Dessandier et al., 2019; Melaniuk, 2021), and Mediterranean (Panieri, 2003; Panieri, 2006) demonstrate the opportunism of benthic foraminifera associates with cold seep habitats (Figure 1). Some benthic foraminifera, including endobenthic taxa such as *Uvigerina*, *Bolivina*, *Bulimina*, *Chilostomella*, *Globobulimina*, *Nonionella* and *Melonis*, as well as epibenthic taxa such as *Epistominella*, *Cibicidoides* and *Globocassidulina*, are known to withstand methane- and sulfide-enriched seepage conditions. However, no seep-endemic species have been reported to date, as these taxa are well-documented in normal marine environments as well. It should be noted that benthic foraminiferal assemblages (e.g., abundance and diversity) are not congruent in these cold seep areas on a global scale and are influenced by multiple factors. Despite the absence of consistent global patterns in seep benthic foraminiferal assemblages, their sensitive response to seepage environments provides valuable evidence for identifying past methane seepage events (Bhaumik and Gupta, 2007; Zhou et al., 2009; Pan et al., 2018; Li et al., 2021).

Visible changes in the primary microstructure and elemental composition of seep foraminifera due to diagenetic alteration have been obtained through diversified macro-scale observations. This phenomenon has been described by Electron Probe Micro Analysis (EPMA) (Panieri et al., 2017), Energy Dispersive Spectrometer (EDS) (Schneider et al., 2017; Dessandier et al., 2020; Zhou et al., 2020; Miao et al., 2021), Scanning Electron Microscopy (SEM) (Fontanier et al., 2014; Consolaro et al., 2015; Panieri et al., 2017; Schneider et al., 2017; Wan et al., 2018; Dessandier et al., 2020; Zhou et al., 2020; Miao et al., 2021), Transmission Electron Microscopy (TEM) (Panieri et al., 2017), and Electron Back Scatter Diffraction (EBSD) (Panieri et al., 2017). However, the current understanding from *in-situ* observations of seep foraminifera may be deficient, as better micro-observations of specimens after visible diagenetic alteration were just from active seep sites of the Arctic Ocean (Consolaro et al., 2015; Panieri et al., 2017; Schneider et al., 2017; Dessandier et al., 2020), the Atlantic Ocean (Merinero et al., 2008; Fontanier et al., 2014; Dessandier et al., 2020), the South China Sea (Wan et al., 2018; Zhou et al., 2020), and fossil seep sites of the Greenland Sea (Millo et al., 2005), the Barents Sea (Argentino et al., 2021), the Oregon Washington coast and Vancouver Island (Torres et al., 2010). In these methane-charged sediments, the geochemical



cycles of elements are interconnected with authigenic minerals such as carbonate, pyrite, and gypsum (Ritger et al., 1987; Tribouillard et al., 2006; McQuay et al., 2008; Griffith and Paytan, 2012; Large et al., 2017; Smrzka et al., 2020). Available observations indicate that foraminifera shell components are significantly influenced by seep authigenic mineral precipitation, as evidenced by the formation of authigenic Mg-, Sr-, Mn-, and Ba-rich carbonate coatings, and the micron-sized euhedral gypsum and pyrite growth on the exterior and interior walls of seep foraminifera.

Currently, isotopic signals recorded in foraminifera tests are an ideal index for identifying methane release from cold seeps. The isotopic composition of seawater, including both the pore water in seafloor sediments and the upper water body, undergoes significant changes as a result of the reformative processes of seepage fluids and methane-related biogeochemical processes, making the observation of low $\delta^{13}\text{C}$ and high $\delta^{18}\text{O}$ anomalies recorded by foraminifera shells to be widely considered as a marker of methane release at cold seeps (Li et al., 2010; Martin et al., 2010; Panieri et al., 2012). So far, the isotopic composition analysis of foraminifera has revealed the occurrence of methane-release events from various cold seep environments, including the Gulf of California (Keigwin, 2002), the Santa Barbara Basin (Kennett et al., 2000; Hill et al., 2003; Cannariato and Stott, 2004), the Black Ridge (Bhaumik and Gupta, 2007), the Cascadia margin (Hill et al., 2004; Li et al., 2010), the Peru shelf margin (Wefer et al., 1994), the West Svalbard continental margin (Panieri et al., 2014), the Norwegian continental margin (Hill et al., 2012), the Greenland Sea (Smith et al., 2001; Millo et al., 2005), the Fram Strait (Consolaro et al., 2015), the Mediterranean Sea (Panieri et al., 2012), the Japan Sea

(Ohkushi et al., 2005; Uchida et al., 2008), the South China Sea (Lei et al., 2012; Wang et al., 2013; Chang et al., 2015; Zhuang et al., 2016), and the Weddell Sea (Thomas et al., 2002) (Figure 1). Additionally, the application of the isotopic composition analysis of foraminifera has enabled the interpretation of previous methane-release events in various geological settings, including the Northern Apennines (Italy) (Panieri et al., 2009), Western Washington State (USA) (Martin et al., 2007), and the Sunda arc (Indonesia) (Wiedicke and Weiss, 2006). Consequently, reconstructions of methane fluxes and the historical evolution of seepage can be performed through the analysis of fluctuations in foraminifera isotopic ratios (Kennett et al., 2000; Li et al., 2010; Wang et al., 2013; Panieri et al., 2014; Consolaro et al., 2015; Zhuang et al., 2016; Zhou et al., 2020).

While multiple proxies based on cold seep foraminifera offer insights into contemporaneous seep areas and seep activities during geological history, certain issues remain unresolved. For example, the selection of scientifically valuable cold seep-related benthic foraminifera species, the mechanism of the foraminifera community assembly response to dynamic seeping activities, and the explanation of fluctuations in foraminifera isotopic values. Additionally, the ability of foraminifera to fully assimilate seawater or pore water methane-derived carbon during biomineralization, and the differing information recorded by living and fossil, planktonic and benthic foraminifera in cold seep areas also contribute to the uncertainty in interpreting the results. Meanwhile, there still have difficulty in distinguishing the stable isotope signatures between primary biogenic calcite and secondary authigenic calcite precipitate driven by AOM on dead specimens. Thus, while the approach of identifying cold seep environments through

multiple foraminifera proxies offers significant potential, the influence of mixed interference from other factors necessitates further research to resolve these knowledge gaps.

2 Species composition of benthic foraminifera

2.1 Seep-related benthic foraminifera

Benthic foraminifera are widely recognized as valuable indicators of cold seep activities in the seafloor sediment community. In general, the superficial seep sediments exhibit high methane fluxes (up to $90 \text{ mmol m}^{-2} \text{ d}^{-1}$; Hill et al., 2004), sulfide concentrations (up to $63 \text{ mmol m}^{-2} \text{ d}^{-1}$; Heinz et al., 2005), and total organic carbon content (up to 4%; Bhaumik and Gupta, 2005). The stressful microhabitat of active cold seepages presents a challenge for foraminifera to survive. Numerous studies have investigated the responses of benthic foraminiferal assemblages to seep activity in various seep areas, including the Hydrate Ridge (Torres et al., 2003; Hill et al., 2004; Heinz et al., 2005), the Eel River (Rathburn et al., 2000), the Santa Barbara Basin (Hill et al., 2003), the Kimki Ridge (McGann and Conrad, 2018), the Peru shelf margin (Wefer et al., 1994), the Japan Sea (Uchida et al., 2008; Saeidi Ortakand et al., 2016), the Sea of Okhotsk (Khusid et al., 2006), the South China Sea (Zhou et al., 2009; Xiang et al., 2012; Pan et al., 2018; Xin et al., 2020), the Blake Ridge (Robinson et al., 2004; Bhaumik and Gupta, 2005; Bhaumik and Gupta, 2007), the Gulf of Mexico (Sen Gupta and Aharon, 1994; Sen Gupta et al., 1997; Robinson et al., 2004), the Monterey Bay (Bernhard et al., 2001; Rathburn et al., 2003; Martin et al., 2004), the Irish Sea (Panieri, 2005), the North Sea (Wilfert et al., 2015), the Mediterranean Sea (Panieri, 2003; Panieri, 2006), the Adriatic Sea (Panieri, 2003; Panieri, 2006), the Arabian Sea (Erbacher and Nelskamp, 2006), the Arctic shelf margin (Dessandier et al., 2019; Melaniuk, 2021), and the New Zealand shelf margin (Martin et al., 2010). The distribution of benthic foraminifera in seep sediments is remarkably skewed toward adjacent non-seep-affected environments, which suggests that some organisms may opportunistic to adapt to the challenging geochemical conditions brought by methane seepages (Jones, 1993; Bernhard et al., 2001; Panieri, 2005; Bhaumik and Gupta, 2007; Burkett et al., 2016; Dessandier et al., 2019). In these cold seep areas, the foraminifera assemblage is largely hyaline perforate calcitic or aragonitic species, while imperforate porcelaneous and coarsely agglutinated taxa are infrequent. Some hyaline taxa, such as *Uvigerina*, *Bolivina*, *Bulimina*, *Chilostomella*, *Globobulimina*, *Nonionella*, *Melonis*, *Epistominella*, *Cibicidoides*, and *Globocassidulina* have been considered as seep-related species due to their higher adaptation to the high organic, low oxygen, reducing conditions, and hypoxia environments rich in CH_4 and H_2S commonly found in cold seep environments (Appendix Table 1). However, evidence suggests that

these foraminifera may not be restricted to the seep environments (e.g. Sen Gupta et al., 1997; Rathburn et al., 2000; Bernhard et al., 2001).

Typically, endobenthic benthic foraminifera exhibit superior tolerance to the harsh conditions of methane seeps, these methane-loving taxa include *Uvigerina*, *Bolivina*, *Bulimina*, *Chilostomella*, *Globobulimina*, *Nonionella*, and *Melonis*. *Uvigerina* has been observed to be adaptable to high organic matter, low oxygen, and methane-rich conditions and is likely specialized in methane-oxidizing bacteria (Sen Gupta and Aharon, 1994; Rathburn et al., 2000; Bernhard et al., 2001; Torres et al., 2003). *Bolivina* is associated with dysoxic bottom waters due to high methane emissions and is known to be resistant to anoxia and sulfide toxicity (Sen Gupta et al., 1997; Hill et al., 2003; Bhaumik and Gupta, 2005). *Bulimina* is commonly found in seep sediments with high organic matter content (Rathburn et al., 2000; Rathburn et al., 2003; Martin et al., 2004; Wiedicke and Weiss, 2006; Zhou et al., 2009; Xin et al., 2020). *Chilostomella* is noted to tolerate hypoxia and hostile environments rich in methane and hydrogen sulfide (Corliss, 1985; Pan et al., 2018). *Globobulimina* is frequently found in Pacific and Atlantic methane seep areas (Sen Gupta et al., 1997; Rathburn et al., 2000; Rathburn et al., 2003; Hill et al., 2004; Martin et al., 2004; Bhaumik and Gupta, 2007). And food supply provided by microbial mats appears to facilitate the survival of *Melonis* in high-latitude methane-rich environments (Panieri, 2005; Dessandier et al., 2019; Melaniuk, 2021). These hypoxia-tolerant benthic foraminifera are often abundant in methane-rich sediments and serve as proxies for tolerance to stressful seep environments.

However, there are exceptions where densities of a few oxygen-loving epibenthic taxa increase in certain cold seep areas, such as *Epistominella*, *Cibicidoides*, and *Globocassidulina*. *Epistominella* has been observed to be dominant taxa in seep areas of the North Sea (Jones, 1993), the Monterey Bay (Bernhard et al., 2001; Rathburn et al., 2003), the Gulf of Mexico (Robinson et al., 2004), the northern Adriatic Sea (Panieri, 2006), the Hydrate Ridge (Heinz et al., 2005), and the Santa Barbara Basin (Hill et al., 2003). *Cibicidoides* has been found in methane-rich bottom waters of the South China Sea (Pan et al., 2018; Xin et al., 2020), the Hydrate Ridge (Torres et al., 2003; Hill et al., 2004), the Gulf of Mexico (Robinson et al., 2004), and the Vestnesa Ridge (Melaniuk et al., 2022). In some cases, like the East Greenland slope (Smith et al., 2001; Millo et al., 2005), the Blake Ridge (Bhaumik and Gupta, 2005), the Northern North Sea (Wilfert et al., 2015), the Vestnesa Ridge (Dessandier et al., 2019), the Margin of Eastern New Zealand (Martin et al., 2010), and the South China Sea (Zhou et al., 2009; Xiang et al., 2012), *Cibicidoides* also holds a larger advantage. Meanwhile, *Globocassidulina* is dominant in methane seep sediments associated with oxygen depletion and organic-rich conditions (Sen Gupta and Aharon, 1994; Rathburn et al., 2000; Panieri and Gupta, 2008; Zhou et al., 2009). Previous studies have indicated that these benthic foraminifera commonly attach to the wall of the worm tubes and live a few centimeters to tens of centimeters above the bottom sediments (Mackensen et al., 2006; Lobegier and Sen Gupta, 2008;

Rathburn et al., 2009). This attached lifestyle is likely to allow them to escape extreme seep habitats (Gupta et al., 2007).

2.2 Benthic foraminiferal assemblages

Many studies have taken emphasis on the distinction in benthic foraminiferal assemblages between seep and non-seep habitats (Rathburn et al., 2000; Bernhard et al., 2001; Panieri, 2003; Torres et al., 2003; Wiedicke and Weiss, 2006; Dessandier et al., 2019; Li et al., 2021), and environmental parameters such as microhabitat conditions and seepage activities are known to play a crucial role in the survival of these organisms (Figure 2).

Overall, benthic foraminifera are commonly found in a range of seep ecosystems, such as clam beds, microbial mats, mud volcanoes, pockmarks, and algal reefs (Appendix Table 1). The preference of benthic foraminifera for specific seep microhabitats is influenced by substrate type, oxygen level, and total organic carbon content. Fine-grained sediments rich in clay and mud, typically charged with methane, are abundant in endobenthic taxa (e.g. Bhaumik and Gupta, 2005; Zhou et al., 2009; Xin et al., 2020). While epibenthic benthic foraminifera tend to inhabit in coarse and hard areas, such as algal reefs or environments precipitated with carbonate nodules (e.g. Panieri, 2006; Xiang et al., 2012) (Figure 2D). In general, habitats with high oxygen (O_2) levels and low carbon dioxide (CO_2) concentrations are conducive to the survival of foraminifera, as a decrease in O_2 and an increase in CO_2 can limit their survival or symbiotic existence (Herguera et al., 2014). Agglutinate foraminifera thrive in microhabitats with adequate O_2 levels and high CO_2 concentrations, while the growth of calcareous foraminifera is limited in these conditions (Herguera et al., 2014). During periods of high methane flux and anoxic conditions associated with active seepages, endobenthic benthic foraminifera tend to predominate, while with a decrease in seepage activity and

an increase in O_2 levels, epibenthic taxa gradually become dominant (Zhou et al., 2009; Pan et al., 2018). In addition, benthic foraminifera have also been found to show sensitivity to the organic flux to the sea floor (Abu-Zied et al., 2008). In seep areas, organic matter can provide additional food sources for foraminifera, and foraminifera with food tendencies, such as *Cibicidoides*, *Bulimina*, *Uvigerina*, *Nonionella*, and *Melonis*, have been observed (Wefer et al., 1994; Torres et al., 2003; Dessandier et al., 2019; Xin et al., 2020). Compared to non-seep sites, the significantly lower abundance of agglutinate foraminifera (approximately 10% of the total) in seep sites suggests that they may not be well adapted to the seep geochemical environment (Zhou et al., 2009; Martin et al., 2010; Wilfert et al., 2015; Dessandier et al., 2019). There are, however, exceptions, such as the dominance of agglutinate taxa in the Sea of Okhotsk Deryugin seep area (Khusid et al., 2006).

What's more, the point is that the benthic foraminiferal communities in cold seep environments are strongly affected by seepage activities. Studies have shown variable results in terms of foraminiferal abundance in seep areas (from several to thousands per 10 cm^3), with reports of both decreased (e.g. Panieri, 2003; Bhaumik and Gupta, 2007; McGann and Conrad, 2018; Dessandier et al., 2019), increased (e.g. Rathburn et al., 2000; Torres et al., 2003; Wiedicke and Weiss, 2006), as well as no significant differences from non-seepage sites (e.g. Bernhard et al., 2001; Rathburn et al., 2003). Although seep environments are known to be harmful to the survival of benthic foraminifera (Dickens et al., 1995; Dickens et al., 1997; McConnaughey et al., 1997; Bernhard and Bowser, 1999), recent studies suggest that the relationship between seepage activities and benthic foraminifera abundance is more complex (Figure 2). Foraminifera are generally thought to prefer an aerobic methane environment with low methane flux, but the bacteria that flourished during the period of moderate-flux methane seepage may provide a food source for benthic foraminifera, resulting in higher

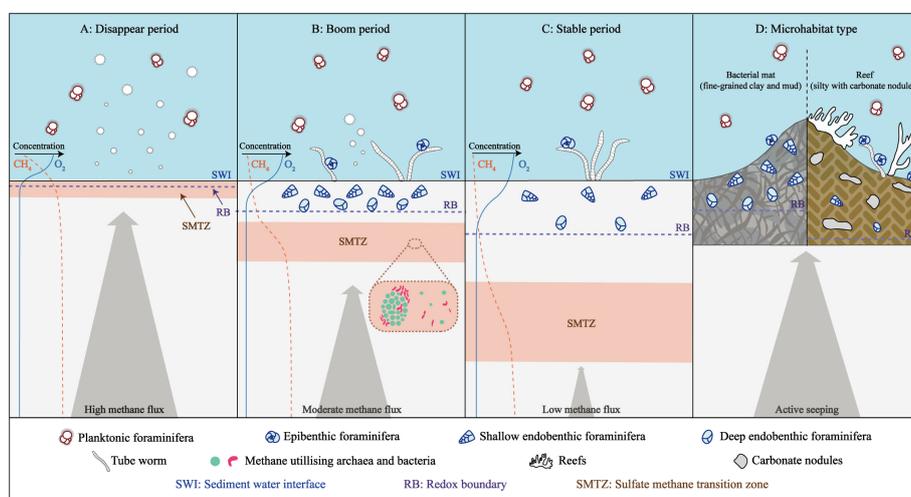


FIGURE 2

Living foraminiferal assemblages associated with methane seepages (after Borowski et al., 1996; Consolaro et al., 2015; Li et al., 2021). (A) Disappear period of benthic foraminifera during times of high methane flux. (B) Boom period of benthic foraminifera during times of moderate methane flux. (C) Stable period of benthic foraminifera during times of low methane flux. (D) Benthic foraminiferal assemblages in different seep microhabitats.

abundance (Figure 2B, Li et al., 2021). The poisonous sulfidic environment during high-methane flux periods will lead to the death of the foraminifera, while the benthic foraminifera community in low-methane flux periods may be similar to that of the normal marine sediments (Figure 2, Consolaro et al., 2015; Li et al., 2021; Melaniuk et al., 2022). Additionally, the density of living foraminifera is related to the thickness of microbial mats, with higher taxa observed in thicker mats due to a greater food supply (Robinson et al., 2004). The depth distribution of benthic foraminifera is also influenced by redox conditions in methane-rich sediments. Typically, the redox boundary is close to the sediment-water interface and may be lower than 1 cm (Sen Gupta and Aharon, 1994), which restricts the distribution of living foraminifera within 0.5–3 cm below the sediments, where they are primarily hypoxia-tolerant epibenthic species (Rathburn et al., 2000; Erbacher and Nelskamp, 2006; Melaniuk, 2021).

3 Micro-observation of foraminifera shells

3.1 Authigenic carbonate coatings

The precipitation of authigenic calcite is an anticipated process due to the typically intense AOM and inherent saturation of CaCO_3 in seep-associated sediments (Figure 3A). Authigenic Mg-calcite overgrowth is the dominant form of secondary mineral coatings observed on the macroscopic tests of foraminifera, with a contribution to the shell weight reaching up to 58 wt% (Millo et al., 2005; Schneider et al., 2017; Wan et al., 2018). This microcrystalline Mg-calcite overgrowth may overlay the whole foraminifera surface and is structurally identical to the primary biogenic calcite (Panieri et al., 2017). As diagenetic alteration

intensifies, the precipitation of MDAC on the shell is cumulatively added. The shell surfaces from “glassy” to “translucent,” and even “fuzzy,” eventually forming a solid inorganic carbonate crust, which results in the loss of the shell’s smooth surface texture, with both the interior and exterior walls covered and thicken (Schneider et al., 2017). The “glassy” shells under biomineralization processes usually show low magnesium content below 0.2 wt% MgCO_3 (Blackmon and Todd, 1959; Bentov and Erez, 2006), whereas in modern active seep sites the Mg/Ca ratios of benthic foraminifera tests can be higher than 10 mmol/mol (Panieri et al., 2017; Wan et al., 2018). Furthermore, diagenesis-altered benthic foraminifera tests from ancient seep sites have been reported to exhibit spots with high Mg (*Cassidulina neoteretis*, *Cassidulina reniforme*, and *Melonis barleeianum*, Argentino et al., 2021), and the Mg/Ca ratios could be up to 69 mmol/mol (*Globobulimina pacifica*, Torres et al., 2010). The elevated Mg content of original shells is considered to benefit from Mg-rich interlayers with Mg/Ca ratios even reaching 220 mmol/mol (Panieri et al., 2017) (Figure 3B). To some extent, the increasing Mg/Ca ratio of altered foraminifera shells reflects the heightened activity of AOM and authigenic carbonate precipitation, which in turn signifies changes in the activities of seepage (e.g. Torres et al., 2003; Li et al., 2010).

Secondary mineralization can also be traced with the use of Sr, Mn, and Ba content of foraminifera. Sr and Mn are typical elements to determine the extent of alteration associated with meteoric diagenesis, as Mn can be incorporated into carbonate while Sr will separate from carbonate during diagenetic alteration (Kaufman and Knoll, 1995). The Sr/Ca of benthic foraminifera in seep areas is usually around 1 mmol/mol, but individual tests could reach up to 36.48 mmol/mol (Torres et al., 2010), which may be related to the precipitation of Sr-rich aragonite (Tesoriero and Pankow, 1996; Fontanier et al., 2014).

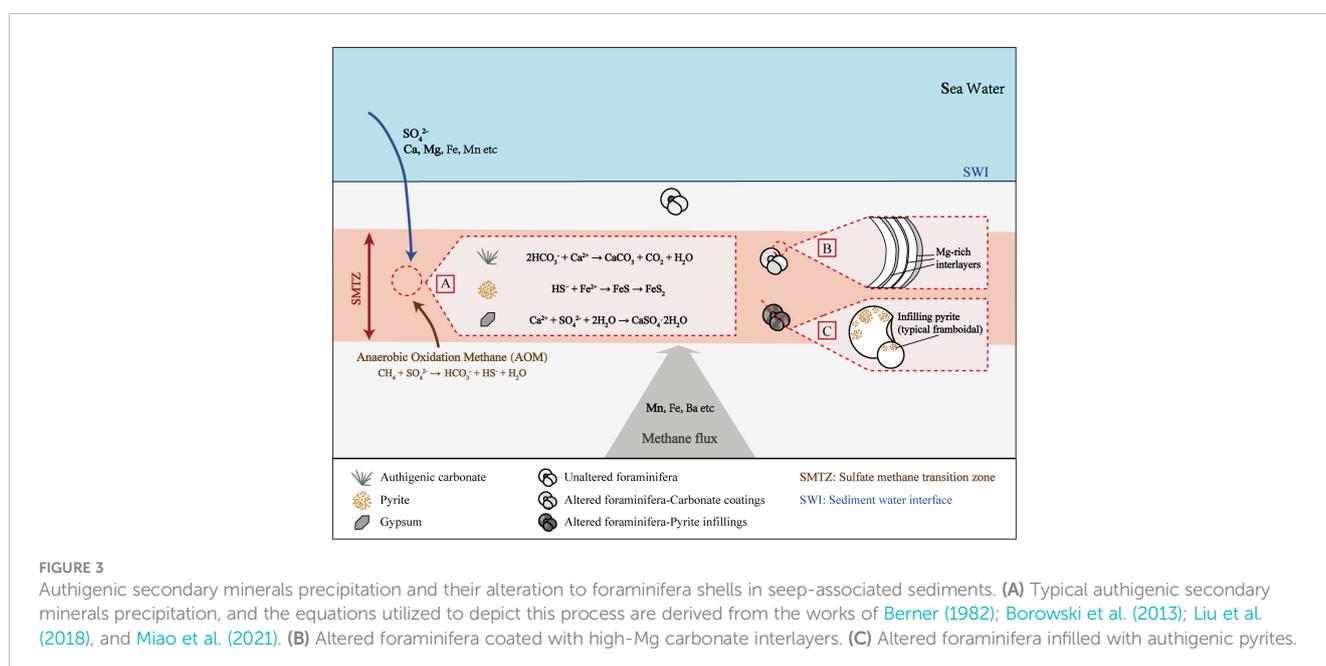


FIGURE 3

Authigenic secondary minerals precipitation and their alteration to foraminifera shells in seep-associated sediments. (A) Typical authigenic secondary minerals precipitation, and the equations utilized to depict this process are derived from the works of Berner (1982); Borowski et al. (2013); Liu et al. (2018), and Miao et al. (2021). (B) Altered foraminifera coated with high-Mg carbonate interlayers. (C) Altered foraminifera infilled with authigenic pyrites.

The Mn/Ca ratio of foraminifera in case of natural calcification ranges from 0.05 to 0.3 mmol/mol (Klinkhammer et al., 2009), while the Mn/Ca ratio of benthic foraminifera in seep-associated sediments can exceed 1 mmol/mol, or even up to 12 mmol/mol (Torres et al., 2010). Moreover, foraminifera modified by cold seeps in high latitudes display spots of high Ba content under EDS images (Dessandier et al., 2020). These trace elements can mask microbial shells by incorporating carbonates after the alteration of diagenesis and may play an important role in seep elemental cycling.

3.2 Self-shaped crystal growth

An association of authigenic gypsum with pyrite tends to occur within the sulfate-methane transition zone (SMTZ), which also marks the methane seepage events (Figure 3A; Lin et al., 2016a, b; Zhou et al., 2020; Dantas et al., 2022). The fluid released by natural gas hydrate decomposition or seepage carries dissolved barium (Ba^{2+}) (Hu et al., 2014), resulting in a higher Ba content in bottom water and usually precipitated in the form of gypsum ($\text{CaSO}_4 \cdot 2\text{H}_2\text{O}$) in surface sediments (Pierre, 2017). Macroscopic observations of gypsum in methane-charged sediments reveal rhombic, bladed, lenticular, or trapezoidal shapes (Kocherla, 2013; Lin et al., 2016a). By now, crystal growth of gypsum microcrystals on foraminifera shells in the seep sediments of the Nansha Trough (Zhou et al., 2020) and the Santos Basin (Dantas et al., 2022) has been observed.

Pyrite (FeS_2) is a ubiquitous sulfide mineral in marine sediments and plays a crucial role in the global Fe-S cycle (Berner, 1985). In cold seep environments, the formation of pyrite is closely linked to the presence of methane upwelling, as hydrogen sulfide produced by AOM action may be the main electron donor for pyrite formation (Schippers and Jorgensen, 2002; Zhang M. et al., 2018). Framboidal pyrite, which forms *via* authigenic crystallization, is known as the typical morphology in methane-charged sediments (Peckmann et al., 2001; Lin et al., 2016b). Additionally, pyrite may also precipitate in bacterial forms, such as spheroids, rod-chains, and worm-like structures (Chen et al., 2006). Pyrite infill in foraminifera chambers is not extraordinary and typically exhibits framboids and aggregates forms (Figure 3C). In recent years, numerous studies have reported the presence of pyrite infillings in foraminifera shells from various cold seep sites, including the western Svalbard (Panieri et al., 2017), the Haima seep (Miao et al., 2021), the Nansha Trough (Zhou et al., 2020), the South China Sea (Zhuang et al., 2016), and the Gulf of Cadiz (Merinero et al., 2008). From another perspective, many trace elements can incorporate into the pyrite structure as solid solution or as sulfide/metal microinclusions (e.g. As, Cu, Zn, Pb, Sb, Mo, Ag, Cd, Mn, Hg, Au) or directly through ionic substitution (e.g. Ni^{2+} , Co^{2+} , Cu^{2+} , Se^{2-} , Te^{2-}) (Large et al., 2017). These pyrite-filling aggregates can influence the elemental composition of foraminifera shells, but the quantification of trace element cycling processes remains challenging due to a lack of relevant findings.

4 Isotope anomalies of foraminifera

4.1 Negative carbon-isotope anomalies

It is generally believed that the apparent lack of ^{13}C in foraminifera shells is invoked as an indicator of methane seepages. There have been published that use foraminifera carbon isotopic signatures to reconstruct ancient seepages and variable methane fluxes (e.g. Consolaro et al., 2015; Panieri et al., 2016; Zhou et al., 2020). During the destabilization of hydrate reservoirs, large amounts of ^{13}C -depleted methane are released and anaerobically consumed when they reach the seafloor (Ruppel and Kessler, 2017; Egger et al., 2018). Carbon isotope signals will be conveyed into the pore water dissolved inorganic carbon (DIC) pool in the form of HCO_3^- *via* AOM (Ussler and Paull, 2008). And by so doing, benthic foraminifera often have low $\delta^{13}\text{C}$ values by incorporating ^{13}C -depleted DIC during calcification (Hill et al., 2003; Rathburn et al., 2003). Given that AOM mainly occurs within the SMTZ near the top of the sediments, the carbon isotope deficit is most pronounced in this region (e.g. Torres et al., 2003; Ussler and Paull, 2008).

Most carbon isotopic composition of benthic foraminifera shells, both living and fossil, from methane seepage environments have been observed to range from 3‰ to -22‰ PDB, with one exception of -35.7‰ PDB (Martin et al., 2010), in contrast, the isotopic composition of ancient seep specimens have been observed to be lower than -50‰ PDB (Appendix Table 2, Figure 4). Methane in gas hydrates can have a variety of sources, such as thermogenic, biogenic or a mixture, with a typical carbon isotope value of methane ranging from -30‰ to -110‰ PDB, and typically lower than -60‰ PDB (Sackett, 1978; Kvenvolden, 1993; Whiticar, 1999). The carbon isotope of pore water DIC ($\delta^{13}\text{C}_{\text{DIC}}$) in normal marine sediments is typically between -1 and 1‰ PDB (Tagliabue and Bopp, 2008), but can become lower than -45‰ PDB when incorporate by methane-derived carbon (Rathburn et al., 2003; Torres et al., 2003). Apart from that, the carbon isotope of authigenic carbonate ($\delta^{13}\text{C}_{\text{carbonate}}$) precipitates related to methane oxidation processes is commonly lower than -40‰ PDB (Whiticar, 1999). Although carbon isotopic values of benthic foraminifera ($\delta^{13}\text{C}_{\text{BF}}$) in seep sediments exhibit discernable negative shifts compared to those living in normal marine sedimentary environments (-1 to 1‰ PDB, McCorkle et al., 1990), the shifts still remain far from the magnitude observed in $\delta^{13}\text{C}_{\text{DIC}}$ or $\delta^{13}\text{C}_{\text{carbonate}}$ influenced by methane (Figure 4). Overall, most bulk values of $\delta^{13}\text{C}_{\text{BF}}$ have been observed to be concentrated between 0‰ and -16‰ PDB, which suggests a disequilibrium between $\delta^{13}\text{C}_{\text{BF}}$ and methane-derived $\delta^{13}\text{C}_{\text{DIC}}$.

Planktonic foraminifera living in the upper water column are generally considered to be isolated from the light carbon isotope signals from methane seepage, due to processes such as AOM in sediments, diffusion, and dissolution in seawater, as well as consumption by methanotrophic microbes (Damm et al., 2005;

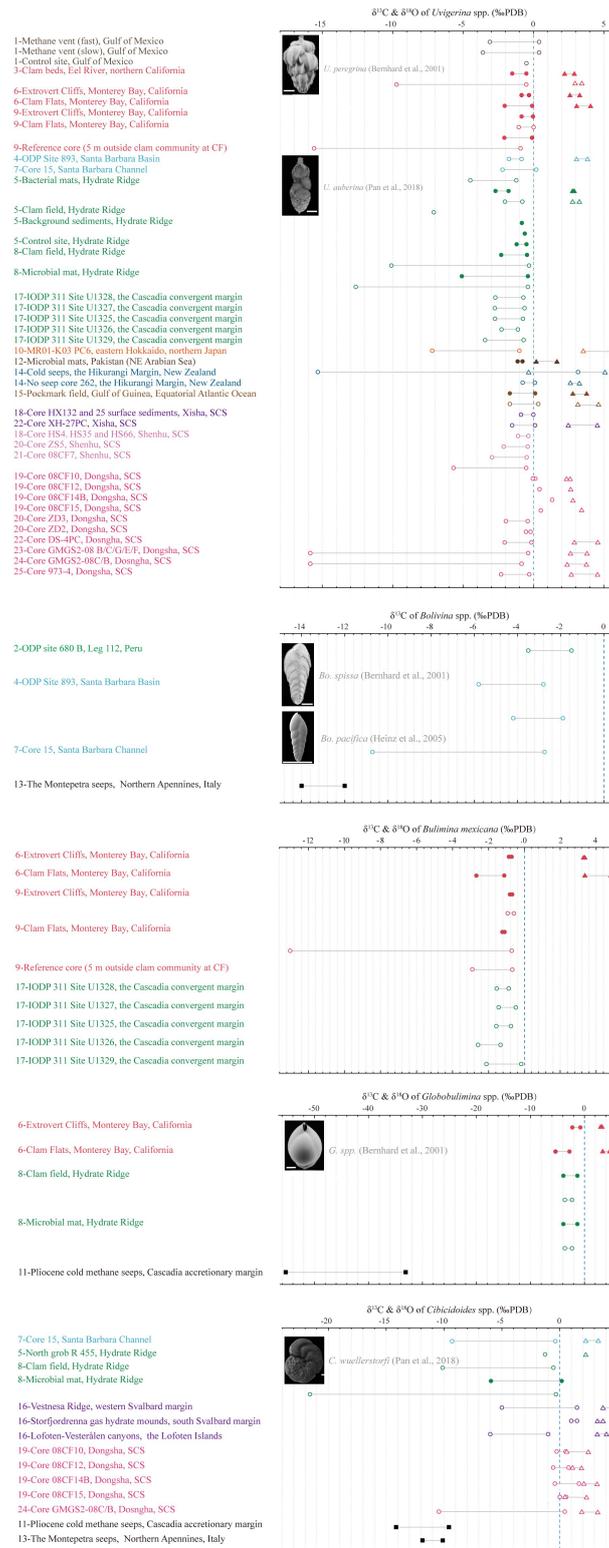


FIGURE 4

Summary of carbon and oxygen isotopic records of benthic foraminifera in seep sediments. The most commonly adopted endobenthic species (*Uvigerina* spp., *Bolivina* spp., *Bulimina mexicana*, and *Globobulimina* spp.) and epibenthic species (*Cibicides* spp.) are selected. $\delta^{13}\text{C}$ values of live and dead benthic specimens are represented by solid dots and open circles, respectively. Similarly, $\delta^{15}\text{O}$ values are represented by triangles. The black square represents the $\delta^{13}\text{C}$ results of ancient seep samples. The solid gray line in the middle of two symbols represents the fluctuation range of the isotopic value, but it does not mean continuous change. Dotted blue line is a guide for the normal marine average $\delta^{13}\text{C}_{\text{BF}}$ value, which is selected as 0‰ PDB here. Please refer to Appendix Table 2 for data sources.

Steinle et al., 2015; Ruppel and Kessler, 2017; Egger et al., 2018). Despite this, several studies have reported the occurrence of simultaneous negative shifts in both $\delta^{13}\text{C}_{\text{BF}}$ and carbon isotopic values of planktonic foraminifera ($\delta^{13}\text{C}_{\text{PF}}$), which could potentially be indicative of methane emissions. For example, Kennett et al. (2000) observed that $\delta^{13}\text{C}_{\text{PF}}$ of the Santa Barbara Basin sediments changed over the past 6000 years, but this change was not significant (higher than -3.5‰). Additionally, Hill et al. (2012) found that methane venting not only had an impact on the isotopic composition of benthic foraminifera, but also caused significant negative shifts in the $\delta^{13}\text{C}_{\text{PF}}$ of *Neogloboquadrina pachyderma* in the Nyegga pockmark field. Zhuang et al. (2016) pointed out that the $\delta^{13}\text{C}_{\text{PF}}$ of *Globigerinoides ruber* was depleted (as low as -5.68‰ PDB), but not to the same extent as the benthic foraminifera *Uvigerina peregrina*, which was depleted as low as -15.85‰ PDB. McGann and Conrad (2018) found the same lower $\delta^{13}\text{C}$ peaks in both benthic and planktonic tests, which may provide the evidence of methane releases large enough to influence the water column. Zhou et al. (2020) determined two major paleo-methane seepage events according to anomalously $\delta^{13}\text{C}_{\text{PF}}$ shifts of *Globigerinoides ruber* from seep sediments in the South China Sea. Although benthic foraminifera generally exhibit more obvious shifts in isotopic composition, there are also instances where $\delta^{13}\text{C}_{\text{PF}}$ shifts are significantly depleted (e.g. Smith et al., 2001; Ohkushi et al., 2005). In these cases, careful analysis and consideration of the potential impact of secondary environmental factors on the death of planktonic foraminifera shells is necessary.

4.2 Positive oxygen-isotope anomalies

The high $\delta^{18}\text{O}$ values of foraminifera are also considered as evidence of seep activity due to the release of large amounts of ^{18}O -rich water molecules during hydrate decomposition (Hesse and Harrison, 1981; Davidson et al., 1983; Matsumoto and Borowski, 2000). This process occurs deeper than SMTZ, thus its influence extends deeper than the record of ^{13}C depletion (Dessandier et al., 2020). Positive $\delta^{18}\text{O}$ shifts have been observed in the shells of both living and fossil benthic foraminifera at modern seeps in various locations, such as the South China Sea (Chang et al., 2015), the Barents Sea (Mackensen et al., 2006), the Hikurangi Margin of eastern New Zealand (Martin et al., 2010), the Niger delta (Fontanier et al., 2014), and core records from the Cascadia Margin of northeastern Pacific (Li et al., 2010), the Weddell Sea of Southern Ocean (Thomas et al., 2002), and the Western Mediterranean Sea (Panieri et al., 2012). These shifts of oxygen isotope of benthic foraminifera ($\delta^{18}\text{O}_{\text{BF}}$), which range from 0‰ to 4.5‰ PDB in bulk analyses, are positively correlated with the period of methane emission but not remarkable compared to $\delta^{13}\text{C}_{\text{BF}}$ in the same tests (Appendix Table 2).

The oxygen isotope of planktonic foraminifera ($\delta^{18}\text{O}_{\text{PF}}$) is of critical importance on detecting abnormal climate events since the last glacial period. The marine oxygen isotope record (MIS) has been constructed based on this proxy, which largely reflects the expected changes in paleotemperature (Broecker and Van Donk, 1970; Schiebel et al., 2018). As a result, the $\delta^{18}\text{O}_{\text{PF}}$ is frequently used

to infer both paleotemperature changes and sea-level changes that may have induced methane discharge (Smith et al., 2001; Thomas et al., 2002; Hill et al., 2003). Although some clues of seepage can be detected through $\delta^{18}\text{O}_{\text{PF}}$ tests, it is more likely to be represented by the carbonate deposits precipitated by AOM rather than the original calcification record (e.g. Dessandier et al., 2020).

Compared to $\delta^{13}\text{C}$ records, the $\delta^{18}\text{O}$ signatures of foraminifera are less informative of methane seepages, leading to a lack of correlation between $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ views. Three main factors contribute to this phenomenon. Firstly, there may not be a clear synergy between $\delta^{18}\text{O}_{\text{BF}}$ and $\delta^{13}\text{C}_{\text{BF}}$, as $\delta^{18}\text{O}_{\text{BF}}$ is more prone to isotopic equilibrium zero-point rather than reflecting $\delta^{18}\text{O}$ values in surrounding water bodies (McCorkle et al., 1990). Secondly, $\delta^{18}\text{O}_{\text{PF}}$ is highly sensitive to temperature changes, which is often used to reconstruct seawater temperature. It has been shown that $\delta^{18}\text{O}_{\text{BF}}$ becomes heavier with deeper water depth (lower temperature) (Sen Gupta and Aharon, 1994; Cheng et al., 2005; Erbacher and Nelskamp, 2006; Chang et al., 2015). Finally, the post-depositional alteration to dead individuals during the burial process, such as the precipitation of authigenic carbonates, cannot be disregarded and is difficult to measure.

4.3 Influencing factors

The carbon and oxygen isotopes of foraminifera are primarily influenced by vital effects, ecological preferences and environmental parameters such as pH and temperature *in vivo* (Duplessy et al., 1970; Zahn et al., 1986; Bemis et al., 1998; Barras et al., 2010). However, it is also important to consider the secondary environmental impacts on the shells of dead individuals. In the context of cold seep research, the interpretation of the carbon and oxygen stable isotope values of foraminifera shells remains a subject of controversy and can be summarized into five aspects.

4.3.1 External input of organic matter

Since pore water $\delta^{13}\text{C}$ is often a negative shift due to the decomposition of organic matter in sediments, making $\delta^{13}\text{C}_{\text{DIC}}$ is closely related to organic carbon fluxes from the overlying seawater (McCorkle et al., 1990). In a previous study, Stott et al. (2002) posited that sedimentation of photosynthetically produced organic matter in the upper water column led to the release of HCO_3^- into pore water through anaerobic oxidation (Eq. 3), which ultimately resulted in a negative shift in $\delta^{13}\text{C}_{\text{BF}}$. In low-seepage or non-seepage environments, the anaerobic oxidation of organic carbon was found to be the primary factor affecting the $\delta^{13}\text{C}_{\text{BF}}$ (Chang et al., 2015). On the other hand, some studies have shown that there may not be a direct relationship between the organic carbon content and the $\delta^{13}\text{C}$ of foraminifera in areas with high methane flux, as the $\delta^{13}\text{C}_{\text{BF}}$ is primarily influenced by methane seepage (Wefer et al., 1994; Chen et al., 2007).



Despite previous assumptions, some studies have uncovered that the carbon and oxygen isotope fluctuations of benthic foraminifera

may not necessarily support the presence of methane release events, but rather demonstrate stronger correlations with the glacial-interglacial cycle during the Quaternary period. For instance, Hill et al. (2012) found that the $\delta^{18}\text{O}_{\text{BF}}$ and $\delta^{18}\text{O}_{\text{PF}}$ in a pockmark of the Storegga Slide complex demonstrated a clear transition between glacial and deglacial stages. In Site 973-4 of the South China Sea, benthic foraminifera *Uvigerina* spp. failed to record a methane-derived signature during the last sea-level lowstand, but instead reflected an increase in organic carbon input during the ice age (-2.26% PDB during Last Glacial Maximum, Zhang M et al., 2018). Additionally, the $\delta^{13}\text{C}_{\text{PB}}$ of *Pulleniatina obliquiloculata* showed a positive shift (0.25–1.25‰ PDB) during the seepage period, although the source of short-term light carbon remains uncertain (Zhang B et al., 2018). Similar observations were made in the Shenhu area (Chen et al., 2010) and the Adriatic Sea (Panieri, 2006), where the stable isotope records of foraminifera were deemed to be independent of methane seepages.

4.3.2 Biochemical processes by foraminifera

The carbon and oxygen isotope signals of foraminifera are influenced by various vital activities, including predation, metabolism, and symbionts. During their lifespan, benthic foraminifera exhibit restricted incorporation of ^{13}C depleted methane-derived carbon (Herguera et al., 2014). Spero and Lea (1996) found that food uptake accounted for 8% to 15% of the $\delta^{13}\text{C}_{\text{PF}}$ in *Globigerina bulloides*. Additionally, metabolic processes may mix depleted $\delta^{13}\text{C}$ into foraminifera shells (Erez, 1978; Grossman, 1987; Herguera et al., 2014). Bacteria thriving in methane-influenced environments, such as Beggiatoa (Panieri, 2006), may provide food for benthic foraminifera, and these microbes have a distinct light carbon isotope composition (Jiasheng et al., 2007). Some taxa incorporate the carbon derived from methane into their shells via predation and/or the incorporation of ambient DIC (Bernhard and Reimers, 1991; Panieri, 2006; Melaniuk et al., 2022). Recent studies suggest that benthic foraminifera species, such as *Uvigerina peregrina* (Bernhard et al., 2001; Torres et al., 2003), *Nonionella auris* (Wefer et al., 1994), and *Melonis barleeanus* (Dessandier et al., 2019) could record light $\delta^{13}\text{C}$ values by feeding on methanotrophic bacteria and/or incorporating surrounding DIC (Melaniuk et al., 2022).

Apart from this, the presence of symbiotic bacteria within the foraminifera body may have a significant impact on the isotopic signals of living species. The symbiotic relationship between foraminifera and their endosymbiotic bacteria has been noted by several studies (e.g. Bernhard et al., 2001; Barbieri and Panieri, 2004). Despite the recent discovery of chemoautotrophic symbionts in some living seep-related species in 2010, the positive staining reaction of these endobionts with Rose Bengal raises questions about the reliability of isotopic signals produced by living foraminifera (Bernhard et al., 2010). This highlights the need to further investigate the influence of symbiotic bacteria on the isotopic composition of living foraminifera.

4.3.3 Microhabitat preference and species-specific vital effects

Studies have consistently shown that the analysis of seep activity is often performed by comparing isotopic records obtained from the

same species or taxa of foraminifera. This is because the sensitivity of foraminifera to their microhabitat plays a crucial role in the interpretation of seepage intensity (Zahn et al., 1986; McCorkle et al., 1990; McGann and Conrad, 2018). The shallow infaunal species, such as *Uvigerina peregrina*, are known to reflect the isotopic signature of the pore water below the sediment-water interface, while deep infaunal species, such as *Globobulimina pacifica*, record the isotopic signature in the depth of dissolved oxygen concentration near zero, in contrast, epifaunal species, such as *Cibicides wuellerstorfi*, primarily record the bottom water above the sediment-water interface (McCorkle et al., 1990; Keigwin, 1998; McGann and Conrad, 2018). Similarly, planktonic foraminifera, such as *Globigerinoides ruber*, *Neogloboquadrina dutertrei* and *Pulleniatina obliquiloculata*, mainly record seawater information corresponding to the depth of their living environments (Hemleben et al., 1989). It is suggested that benthic individuals are more likely to *in-situ* record isotopic signals from seep environments compared to their planktonic counterparts, and therefore may have recorded the excursion prior to the latter (Thomas et al., 2002; Martin et al., 2004).

The vital effect refers to the difference in isotopic fractionation between different species of foraminifera, as well as between juveniles and adults of the same species, due to biological processes, such as metabolism. This effect has been shown to result in fluctuations of ~ 1 – 2% $\delta^{13}\text{C}$ values within a single specimen (Rathburn et al., 2000; Rathburn et al., 2003; Panieri, 2006; Melaniuk et al., 2022). Corliss (1985) proposed that reduced absorption of ^{12}C during low-productivity periods leads to the depletion of ^{13}C and lower carbon isotope values of foraminifera. Rathburn et al. (2003) pointed out that different species of benthic foraminifera exhibit distinct ranges of isotope fluctuations, but results from a single species have the potential to be valuable in evaluating methane seepage, assuming no carbonate diagenesis. McGann and Conrad (2018) observed $\delta^{13}\text{C}$ depletion in benthic foraminifera from the Kimki Ridge seep, however, multiple fluctuations were evident among species living above or below the water-sediment interface and in shallow or deep sediments. Additionally, the shell size of planktonic foraminifera has also been proposed as a factor in paleoenvironment reconstruction, with a size of 270–320 μm being suggested as most suitable by Spero and Lea (1996). However, Dessandier et al. (2020) found no significant effect of shell size on the results of stable isotope tests in seep environments. While the mechanisms of microhabitat preference and species-specific vital effects are still unclear, it is widely acknowledged that signals from the same species can provide valuable information in investigating and interpreting cold seep environments.

4.3.4 Methane seepage activities

It can be stated that the $\delta^{13}\text{C}$ values of benthic foraminifera reflect ambient methane concentration to some extent, serving as an indicator of the intensity of methane seepages. Previous studies have demonstrated that a significant negative shift in foraminifera $\delta^{13}\text{C}$ values is commonly associated with high-efficiency AOM during periods of intense methane release (e.g. Millo et al., 2005; Uchida et al., 2008; Consolaro et al., 2015; McGann and Conrad, 2018). On the other hand, normal marine $\delta^{13}\text{C}$ values may be observed during

periods of no or low methane seepage, where AOM cannot affect the shallow pore water DIC and living foraminifera (Sen Gupta and Aharon, 1994; Chen et al., 2007). However, the relationship between methane seepage intensity and foraminifera activity is complex and not straightforward. A recent study thought that foraminifera communities tend to thrive and actively incorporate methane-derived carbon during periods of moderate seepage, whereas high methane discharge could result in the death of foraminifera and secondary signals begin to superimpose (Melaniuk et al., 2022). Additionally, it should be considered that the growth of foraminifera shells is not continuous and that methane seepage events in geological history are dynamic and transient (Thatcher et al., 2013), making it challenging to discern short-term or rapid methane emissions through shell samples (Dessandier et al., 2020).

To explain the mismatch between $\delta^{13}\text{C}$ values of benthic foraminifera and pore water DIC, a lot of research has made the efforts. Early research suggested that periods of excessive methane flux have the potential to induce foraminiferal migration, thereby leading to an imbalance carbon isotope records between the biogenic carbonate and pore water DIC (Bernhard and Bowser, 1999). Another explanation is that the extreme circumstance of active AOM may inhibit the metabolism of foraminifera (Sen Gupta and Aharon, 1994). From the results of methane seepage-emulating culture experiments, it is true that methane release can continue to affect the isotopic composition of deep-sea benthic foraminifera (Wollenburg et al., 2015). As for the variability of foraminifera isotopic values, the mixing of different methane sources (e.g. thermogenic and biogenic) with DIC and marine organic carbon seems to be the most plausible explanation (Martin et al., 2007). Despite numerous studies addressing this discrepancy, there

remains a lack of clarity regarding the mechanism by which foraminifera fail to record equivalent DIC signals in seep areas.

4.3.5 Methane-derived authigenic carbonate (MDAC) secondary overgrowth

It has been confirmed that MDAC can capture methane-derived ^{13}C -depleted (may lower than 60 ‰ PDB) and ^{18}O -enriched signatures (may higher than 8.9 ‰ PDB) from seep environments (Naehr et al., 2007; Feng et al., 2018; Buckman et al., 2020). Foraminifera fossil shells in sediments are susceptible to MDAC secondary overgrowth after diagenetic alteration, which will obscure the original information contained in the shells (e.g. Torres et al., 2003; Millo et al., 2005; Martin et al., 2007; Sexton and Wilson, 2009; Panieri et al., 2012; Edgar et al., 2013; Consolaro et al., 2015). Both planktonic and benthic foraminifera shells can be affected by this process, especially in deep sediments and specimens from ancient cold seep locations (Figure 5).

Indeed, the extreme values in stable isotopes of both benthic and planktonic foraminifera tests are believed to show an information superimposition by secondary overgrowth of MDAC (e.g. Martin et al., 2010; Fontanier et al., 2014; Panieri et al., 2014). These altered shells possess highly variable and extremely depleted $\delta^{13}\text{C}$ signals, ranging from -1.6‰ to -55.3‰ PDB (Torres et al., 2003; Hill et al., 2004; Martin et al., 2007; Uchida et al., 2008; Panieri et al., 2009; Martin et al., 2010; Fontanier et al., 2014; Panieri et al., 2016), and false positive shifts in $\delta^{18}\text{O}$, ranging from 1.5‰ to 5.3‰ PDB (Ohkushi et al., 2005; Uchida et al., 2008; Naehr et al., 2009; Dessandier et al., 2020).

To quantify the relative amount of MDAC overgrowth on foraminifera shells, Schneider et al. (2017) introduced a formula

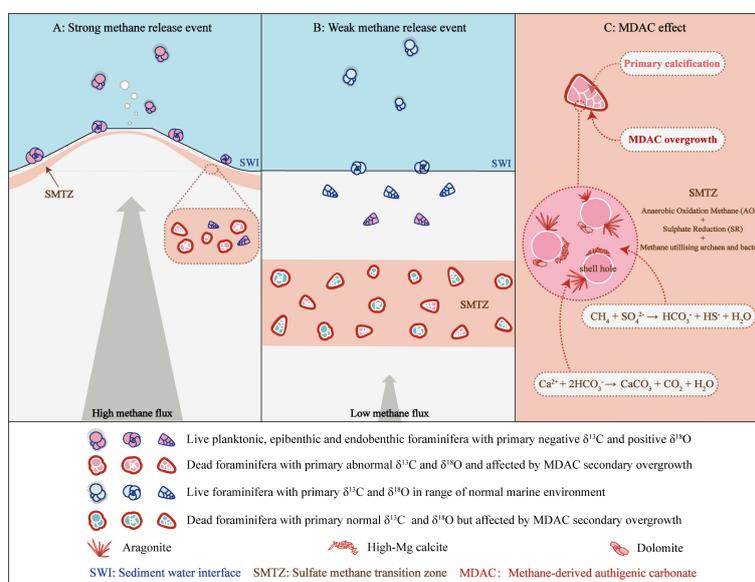


FIGURE 5

Impact on foraminifera stable isotopic signatures from methane seepage intensity and the MDAC-covered coating. (A) Impact during high methane flux period. (B) Impact during low methane flux period. (C) Zoom schematic of the MDAC-covered coating on foraminifera shell.

that takes into account the primary calcification and secondary overgrowth of MDAC (Eq. 4). This method is on the basis that the $\delta^{13}\text{C}$ of foraminifera is composed of two segments: the primary calcification and the secondary overgrowth of MDAC (Figure 5C). Results based on this formula indicate that in the Vestnesa Ridge seep sediments, the $\delta^{13}\text{C}_{\text{BF}}$ signals of *Cassidulina neoteretis* were remarkably mixed by MDAC with a contribution ranging from 55–58% (Schneider et al., 2017). Similarly, in the South China Sea, where seepage activity is relatively weak, MDAC-coupled $\delta^{13}\text{C}$ signals were found to contribute 20–30% in benthic specimens (*Uvigerina peregrina* and *Cibicidoides* spp.) and 11–20% in planktonic specimens (*Globigerinoides ruber* and *Pulleniatina obliquiloculata*) (Wan et al., 2018)

$$\begin{aligned} \text{weight}_{\text{MDAC}}(\%) &= (\delta^{13}\text{C}_{\text{bulk-foram}} - \delta^{13}\text{C}_{\text{pristine-foram}}) / (\delta^{13}\text{C}_{\text{MDAC}} \\ &\quad - \delta^{13}\text{C}_{\text{pristine-foram}}) \times 100 \end{aligned} \quad (4)$$

$\delta^{13}\text{C}_{\text{bulk-foram}}$ represents the $\delta^{13}\text{C}$ of 15 to 28 individual foraminifera, $\delta^{13}\text{C}_{\text{pristine-foram}}$ represents assumed $\delta^{13}\text{C}$ of pristine foraminifera, and $\delta^{13}\text{C}_{\text{MDAC}}$ represents an average $\delta^{13}\text{C}$ of some MADC samples.

Notice that the presence of MDAC on foraminifera shells obscure the original information of primary biomass shells, proper cleaning procedures may necessary to obtain the raw isotopic signals. Three cleaning protocols have been established for now, including the use of methanol proposed by Chen et al. (2005), a comprehensive chemical method designed by Barker et al. (2003), and an acid-leaching approach by Millo et al. (2005) and Uchida et al. (2008). The high contribution rates of the MDAC coating to the results may emphasize the importance of properly distinguishing primary and secondary signals in foraminifera shell tests. Results from these procedures revealed that MDAC can dominate up to 10–20% of the $\delta^{13}\text{C}$ signals in foraminifera shells from Quaternary sediments in the Southwest Greenland Sea (Millo et al., 2005), and can contribute up to 22% for planktonic foraminifera and 15% for benthic foraminifera in sediments from Hokkaido, Japan (Uchida et al., 2008). Despite attempts to remove MDAC coatings through leaching experiments, negative $\delta^{13}\text{C}$ and positive $\delta^{18}\text{O}$ values persisted, suggesting that both primary calcification and secondary overgrowth contribute to the excursions of isotopic signatures in foraminifera shells (Panieri et al., 2012; Consolaro et al., 2015). It can be concluded that seepage signatures can be achieved through both primary calcification and secondary overgrowth of MDAC. And by so, foraminifera calcite could still able to exhibit visible excursions in $\delta^{13}\text{C}$ even after cleaning by a standard method, and major ancient methane release events or modern seep environments could be identified (e.g. Millo et al., 2005; Wan et al., 2018; Zhou et al., 2020).

However, the altered specimens may difficult to identify *via* light microscopy, and there still remains arduous to selectively eliminate MDAC from the unaltered shells through the process of exhaustive cleaning (Panieri et al., 2017), making the cleaning process to be a subject of debate. Several publications show specimens with pristine microstructures free from secondary

mineral overgrowths in methane-charged sediments (Hill et al., 2003; Hill et al., 2004; Martin et al., 2007), and the stable isotopic composition of foraminiferal shells may be not significantly affected by authigenic calcite precipitates (Hill et al., 2004; Mackensen et al., 2006; Panieri et al., 2012). To mitigate the influence of secondary minerals on isotope results, some studies have opted to focus exclusively on specimens that are well-preserved, with complete individuals and distinct rims or bright surfaces (e.g. Fontanier et al., 2014; Zhuang et al., 2016; McGann and Conrad, 2018). However, the effort might somewhat limited since the secondary coatings may thin or infill the interior shell walls (e.g. Torres et al., 2003; Hill et al., 2004; Hill et al., 2012). Typically, the diagenetic alteration of foraminifera calcite is comparatively less problematic in benthic as opposed to planktic foraminifera (Uchida et al., 2008; Edgar et al., 2013). There are indeed reports to reconstruct ancient seepage history by distinguishing negative excursions in untreated benthic foraminiferal $\delta^{13}\text{C}$ (e.g. Hill et al., 2012; Panieri et al., 2014; Panieri et al., 2016). Additionally, the negative $\delta^{13}\text{C}$ values of planktonic foraminifera tests buried in seep environments are largely believed to be amplified by diagenetic overprinting with MDAC during methane seepage, rather than a true signal of biogenic carbonates (e.g. Cannariato and Stott, 2004; Ohkushi et al., 2005; Hill et al., 2012; Consolaro et al., 2015; Wan et al., 2018). Incidentally, almost all of the extreme isotopic values reported in prior studies were obtained from dead specimens that appear to have undergone post-depositional alteration (e.g. Torres et al., 2003; Hill et al., 2004; Millo et al., 2005; Martin et al., 2010). However, it is undeniable that the remarkably depleted $\delta^{13}\text{C}$ values of altered foraminifera indirectly confirm the formation of authigenic carbonates in proximity to the shift of the SMTZ and the associated alteration in past methane release events.

5 Summary

- (1) The presence of specific types and assemblages of benthic foraminifera in cold seep sediments reflects the micro-environmental conditions associated with dynamic methane seepages. Despite significant research efforts, the endemic species of benthic foraminifera in seep environments remain to be identified. The dominated assemblages are typically hyaline, some taxa may able to thrive in seep areas due to their high tolerance to the challenging conditions and/or feed on associated methanotrophic microbial communities. These benthic foraminifera, including endobenthic taxa such as *Uvigerina*, *Bolivina*, *Bulimina*, *Chilostomella*, *Globobulimina*, *Nonionella*, and *Melonis*, as well as epibenthic taxa such as *Epistominella*, *Cibicidoides*, and *Globocassidulina*, provide valuable opportunities to study the seep environments.
- (2) The assemblage patterns of benthic foraminifera in cold seep environments are found to be inconsistent and influenced by various environmental factors, such as

seepage activity, oxygen levels, total organic carbon content, substrate type, and microhabitat conditions. In areas of high seeping intensity, hypoxia-tolerant endobenthic species tend to dominate the community within the sediments closest to the seafloor. Meanwhile, agglutinate taxa may experience survival difficulties in these harsh conditions. In contrast, when seepage intensity decreases and environmental conditions become less harsh, oxygen-loving epibenthic species may become abundant. It is expected that benthic foraminifera communities will experience maximal flourishing during periods of moderate seepage intensity, where food supplies are abundant and conditions are more favorable for microbial growth.

- (3) In methane-charged sediments, a pristine shell of foraminifera may undergo widespread alteration by secondary mineralization after the death of the organisms. It can be inferred that foraminifera shells buried in seep-associated sediments may exhibit overprinting signals of secondary authigenic carbonate-bound (Mg, Sr, Mn, Ba) coatings and the growth of gypsum and pyrite microcrystals. The alteration of secondary mineralization to seep foraminifera reveals a magnesium, barium, and strontium incorporation in carbonates formed within SMTZ, and the appearance of gypsum and pyrite shows a typical signature of cold seep environments. Typically, the degrees of secondary mineralization may be served as a valuable proxy for the intensity of AOM and associated post-depositional alteration during methane seepages.
- (4) The detection of abnormal negative $\delta^{13}\text{C}$ and positive $\delta^{18}\text{O}$ values in foraminifera shells is considered a unique fingerprinting of methane release events. Benthic foraminifera, which live above or below the surface of seafloor sediments, are known to be reliable recorders of methane-derived light carbon isotopes and heavy oxygen isotopes released from hydrate decomposition. While this isotopic imprinting may also be observed in planktonic foraminifera tests which are likely to have been altered by methane-derived authigenic carbonate.
- (5) The variations in $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ signatures preserved in foraminifera shells may reflect the influence of external organic matter inputs, biochemical processes, microhabitat parameters, seeping activities, and post-burial secondary authigenic carbonate overgrowth. To minimize these uncertainties, it is advisable to use live foraminifera to study modern cold seep activities, as they provide the best record of *in situ* isotopic data. Benthic species are preferable to planktonic individuals as they are thought to have a higher potential to capture methane-derived light carbon isotopes and heavy oxygen isotopes. To effectively evaluate the evolutionary history of a seepage, the isotopic results of

a single species must be considered in conjunction with other geological and environmental data. Cleaning protocols can be utilized before stable isotopic analyses to distinguish the signals originating from primary biogenic calcite and secondary carbonate coatings. Foraminifera whether after strict cleaning procedures, or selected under microscopic to minimize authigenic contamination, or in their original state, cannot completely eliminate the influence of secondary carbonate isotopes signals, but all have the potential to exhibit a response to the cold seep environments.

Author contributions

YHL: Data collection, Writing original draft; HY: Data collection, Writing–review and editing; BH and YJL: Writing–review and editing; HL: Conceptualization, Supervision, Writing–review and editing. BH supervised the study; YHL wrote the original draft; HY, HL, and YJL contributed to refining the draft. All authors contributed to the article and approved the submitted version.

Conflict of interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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Supplementary material

The Supplementary Material for this article can be found online at: <https://www.frontiersin.org/articles/10.3389/fmars.2023.1157879/full#supplementary-material>

APPENDIX TABLE 1

Summary of cold seeps benthic foraminiferal assemblages.

APPENDIX TABLE 2

Summary of stable isotopic records of cold seep related benthic foraminifera.

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