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Reshaping perspectives of deep-sea benthic function

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Bioturbation is a key ecosystem function with a fundamental role in mediating major biogeochemical cycles. The intensity and depth of bioturbation is influenced by the taxa present, which is often a function of food supply. The deep sea is generally oligotrophic with sediments composed predominantly of small, shallow burrowing macrofauna (<10 cm). Human activity is increasingly introducing POC to the deep-sea, however, organic enrichment of the deep-sea, and the subsequent response of bioturbators is poorly understood. Here we present data on benthic function in deep-sea systems that have experienced organic enrichment. We show that organic enrichment enhances deep-sea bioturbation through larger, advanced successional taxa, and deeper bioturbation depths. Enhanced bioturbation in the deep-sea should confer positive ecosystem functions (nutrient recycling, microbiological activity, remineralization), but adherence to approaches and interpretations guided by the paradigm of small, shallow-burrowing infauna could significantly underestimate deep-sea benthic processes at a global scale.

KEYWORDS

bioturbation, bioturbation activity, macrofauna, deep sea, human disturbance, sediment profile imaging, SPI

Highlights

- Evidence showing anthropogenic organic enrichment of the deep-sea enhances deep-sea function by stimulating bioturbation.

Introduction

The deep sea (>1000 m water depth) is the most extensive habitat on our planet (Snelgrove, 1997; Danovaro et al., 2017) and plays a critical role in global ecosystem function via its influence on the biological pump and nutrient recycling (Snelgrove, 1997;

Ramirez-Llodra et al., 2011; Thurber et al., 2014). More than 60% of the Earth's surface is below 1000 m of water (Glover and Smith, 2003); from about 1000 m to the deepest depths of the ocean floor there is virtually no seasonal variation and water temperatures are consistently ~2°C (Rex and Etter, 2010). This once remote ecosystem is threatened by the cumulative effects of anthropogenic activities (e.g., climate change; fisheries; oil, gas, and mineral extraction), which could result in ecological impairment and potentially catastrophic regime-shifts (Levin and Le Bris, 2015; Wedding et al., 2015; Sweetman et al., 2017). Awareness of increased human disturbances in the deep sea has led to recent calls for the development of an ecosystem-based strategy for global cooperation in deep-sea preservation (Danovaro et al., 2017; Boetius and Haeckel, 2018), but effective conservation requires a robust and accurate understanding of the environment (Le Saout et al., 2013). As our understanding of the deep sea is refined, our perceptions have been reshaped from viewing this environment as homogeneous to one that is complex and diverse (Brandt et al., 2007; Danovaro et al., 2014; Costello and Chaudhary, 2018).

Deep-sea sediments have been traditionally viewed as oligotrophic and food-limited, devoid of the requisite carbon and nutrient input to support large-bodied and deep burrowing macrofauna (Thiel, 1979; Grassle and Grassle, 1994); for this review macrofauna are defined as individuals retained on a sieve size greater than 300 μm, commonly used in deep-sea studies (Supplementary Table SI; Montagna et al., 2016). Chemotrophic production provides organic enrichment in localized instances in the deep sea (Van Dover, 2000), however, the deposition of phytodetritus and/or the horizontal advection of organic matter from the continental shelf supplies carbon and nutrients to much of the deep sea (Jahnke et al., 1990; Honjo et al., 2008). In the latter two instances, the amount of available organic matter to the deep-sea benthos is limited by surface production and the subsequent flux to the seafloor (Honjo et al., 2008). The majority of material transported to the deep seafloor tends to be refractory and a fraction of the quantity that was produced in surface waters (Rowe and Staresinic, 1979), though there are episodic instances where POC produced in surface water is rapidly transported to the deep sea delivering large amounts of fresh (i.e., nonrefractory) material to the sea floor (Smith et al., 2018). As a result of the predominant process of POC transport to the deep sea (Rowe and Staresinic, 1979; Jahnke et al., 1990; Honjo et al., 2008), macrofauna present in deep-sea sediments tend to be small and confined to the upper few centimeters of the sediment column (Rex and Etter, 2010). Thus, methods for sampling deep-sea macrofauna have largely focused on the upper 10 cm of the sediment (Rex and Etter, 2010; Montagna et al., 2016; Supplementary Table SI). This perspective has been challenged recently (Uchman and Wetzel, 2011) but does not appear to have shifted the predominant view of deep-sea ecologists conducting benthic community analysis. The majority of deep-sea benthic community studies employing traditional sampling methods (sediment grabs, box cores, or multi-core arrays) limited the depth of sieving to 10 cm, regardless of the sediment depth cores or grabs were collected (~70% from our literature review presented in Supplementary Table SI; Rex and Etter, 2010). However, there are numerous places in the deep sea that are not oligotrophic (Graf, 1989; Diaz et al., 1994; Witte, 2000) and adherence to approaches (sieving <10 cm) and interpretations guided by a paradigm of small, shallow bioturbators in deep-sea sediments could significantly underestimate deep-sea benthic processes.

Bioturbation describes the biological displacement or mixing of sediments by flora, fauna or microbial activity (Meysman et al., 2006). In marine sediments macrofauna are predominantly responsible for sediment reworking, which has been shown to play a vital role in regulating marine sediment geochemical and physical properties (Aller, 1978; Rhoads and Boyer, 1982; Nicholaus et al., 2023) as well as affecting ecosystem function (Meysman et al., 2006). Sediment permeability, chemical gradients in pore water, remineralization (supplying electron acceptors that fuel organic mineralization), and inorganic nutrient efflux are a few of the sediment properties and functions regulated by macrofauna bioturbation (Lohrer et al., 2004).

There are two main approaches to assessing bioturbation in marine sediments: as a diffusion process or through direct measurements from cores. The diffusion process is a modelling technique that allows the distribution and exchange rates of pore water solutes, or sediment particles across the sediment-water interface to be quantified and compared by calculating an intensity coefficient and/or a mixed layer depth (Teal et al., 2008). Direct core measurements calculate the depth of bioturbation by measuring the depth of biogenic features in the sediment column relative to the sediment-water interface (Germano et al., 2011). In this study bioturbation was quantified using direct measurements from optical cores (SPI).

Over the years a number of deep-sea benthic surveys have been conducted around anthropogenically disturbed sites using sediment profile cameras (Figure 1[1]*; See S1 to S5). Sediment profile images (SPI) provide a cross-section of the sediment column from the sediment-water interface (SWI) down to ca. 22 cm (Rhoads and Cande, 1971; Solan et al., 2003). The most striking observation from these surveys was the extent of sediment reworking and depth of macrofauna burrowing. Bioturbation depths, the depth beneath the sediment-water interface that biogenic structures (burrows, feeding voids) were detected, exceeded 15–21 cm. Burrows were defined as open or partially filled channels in the sediment surrounded by brownish sediment (oxic halo), and voids as water filled pockets.

These observations indicate larger deeper dwelling macrofauna may play a more important role in biogeochemical cycling in the deep sea than previously assumed. This insight prompted us to revisit current and past paradigms of deep-sea benthic community structure and function. In order to shift from the current shallow-community structure approach to sampling deep-sea sediments, to one that focuses on benthic function, will require sampling deeper than the 10 cm approach commonly applied (Montagna et al., 2016;

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[1] *A linear regression was conducted to determine if there was a correlation between TOC% and Bioturbation Depth. This analysis utilized station location independent data, and the residuals were determined to be random, (i.e. independent variables drawn from a normal [0, sigma] distribution).

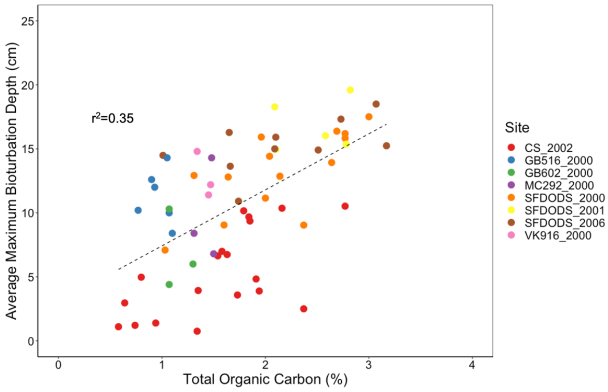

FIGURE 1
Relationship between sediment Total Organic Carbon (%) and maximum bioturbation depth (cm). A significant positive relationship between sediment percent total organic carbon (TOC) and bioturbation depth (df=61, F=33.44, p<0.0005), with bioturbation depth increasing linearly with increasing TOC. Sediment TOC (assessed from sediment grabs) was compared to maximum bioturbation depth, measured by sediment profile imaging, from 8 different deep-sea surveys around the world: CS_2002 – Caspian Sea survey in 2002 related to drilling muds discharge; GB516_2000 and GB602_2000 – surveys around two wells in the Gulf of Mexico in 2000 related to synthetic drilling muds discharge; MC292_2000 and VK916_2000 – surveys around two wells in the Gulf of Mexico in 2000 related to drilling muds discharge; and SFDODS_2000, SFDODS_2001, and SFDODS_2006 – surveys in the eastern Pacific Ocean at a deep-sea dredged material disposal site off the coast of San Francisco Bay.

Supplementary Table SI). Especially as we gain a better understanding of how organic enrichment from human activity or localized organic input reshapes the response and function of deep-sea communities, resulting in sediments with functional characteristics (deep bioturbation) similar to productive shallow coastal systems (Zhang et al., 2024).

Organic enrichment and bioturbation in the deep sea

Large areas of the deep sea are oligotrophic (Druffel and Robison, 1999) and, in these areas, macrofauna are generally small-bodied and primarily reside in the upper 2–3 cm of the sediment column (Snider et al., 1984; Witte, 2000; Rex and Etter, 2010). Macrofauna, relatively sessile organisms that spend the vast majority of their lives inhabiting the sediment, influence many important benthic functions through bioturbation (Solan et al., 2003), and secondary production (Nilsen et al., 2006). Numerous studies have attempted to document the biological response of deep-sea macrofauna to the flux of particulate organic carbon (POC), but the responses are complex, and dependent on the source and type of POC enrichment (e.g., carcass falls, anthropogenic sources, upwelling zones, density flows) (Pfannkuche, 1993; Diaz et al., 1994; Smith et al., 2014). Deep-sea macrobenthic response to POC flux has ranged from limited or nonexistent (Pfannkuche, 1993; Gooday et al., 1996; Drazen et al., 1998; Smith et al., 2002), to a rapid response occurring on the order of days (Graf, 1989; Witte et al., 2003). The contrast in response between these endpoints suggests fine-scale differences in the quantity, quality, and rate of POC deposition to the deep seafloor, even though most carbon hitting the deep sea is well reworked (Honjo et al., 2008).

It is generally accepted in deep sea ecology that 90% of meio- and macrofauna occupy the top few cm of the sediment, and in organically rich continental shelf sediments macrofauna can extend down to 10 cm, but it is not common (Rex and Etter, 2010; Montagna et al., 2016). Our data review suggests an alternative and presents a picture of deep-sea sediment communities where organic enrichment can facilitate deep burrowing often extending well below 10 cm (Figure 1). In a synthesis of deep-sea sites around the globe (S1-S5), we found bioturbation depth to be significantly correlated with the percent of total organic carbon (TOC) in the sediment (df=61, F=33.44, p<0.0005), with TOC explaining more than 35% of the variability in bioturbation depth. Further, there was evidence that organic enrichment of the deep sea facilitated a community of deep burrowing (>10 cm) bioturbators (Figure 2). These findings were consistent with recent observations assessing the influence of organic matter on deep-sea bioturbation (Zhang et al., 2024).

Diaz et al. (1994) found deep-sea bioturbation extending past 10 cm off the coast of Cape Hatteras, NC (Figure 2B). The outer continental shelf and upper slope off Cape Hatteras bight is located at an important hydrodynamic confluence that results in this part of the Atlantic slope receiving high rates of organic and inorganic materials (Blake and Grassle, 1994) supporting high macrofauna production (Blake and Hilbig, 1994). Using x-ray cores, ^{210}Pb, and SPI, Diaz et al. (1994) found surface sedimentary structures to be dominated by the bioturbation activities of deep burrowing macrofauna to at least 30 cm depth in the sediment column at stations up to 2,000 m water depth.

Similar observations were made in the early 2000s along the continental slope in the Gulf of Mexico from 1,000 to 1,075 m depths (Figure 2A) (CSA, 2006). A survey was commissioned by the U.S. Mineral Management Service (now the Bureau of Ocean Energy Management) to assess the physical, chemical, and biological effects of oil and gas development by investigating sediments and biota at several well sites (Supplementary Table S1–1; Supplementary Figure S1–1). SPI results from these studies showed active bioturbation deep within the sediment column both near (in the immediate vicinity of drilling activity) and far (stations located 10 to 25 km away from the well sites) from the wells in all examined scenarios. At each of the four well sites influenced by drilling activity, which included organic-rich synthetic drilling muds (TOC up to 2.6%), the maximum bioturbation depths in SPI ranged from 10.3 to 19.0 cm with a mean of 15.1 cm (SD±2.8) (Supplementary Table S1–1; Supplementary Figure S1–3). Synthetic drilling muds are a nonaqueous emulsion in which the external phase is synthetic fluid rather than petroleum. Synthetic muds were developed as environmentally friendly alternatives to conventional petroleum-derived oil-based muds due to their lower toxicity (Growcock et al., 1994). Due to these properties synthetic muds have become popular for offshore drilling projects because of the environmental acceptance to disposing of synthetic muds into the

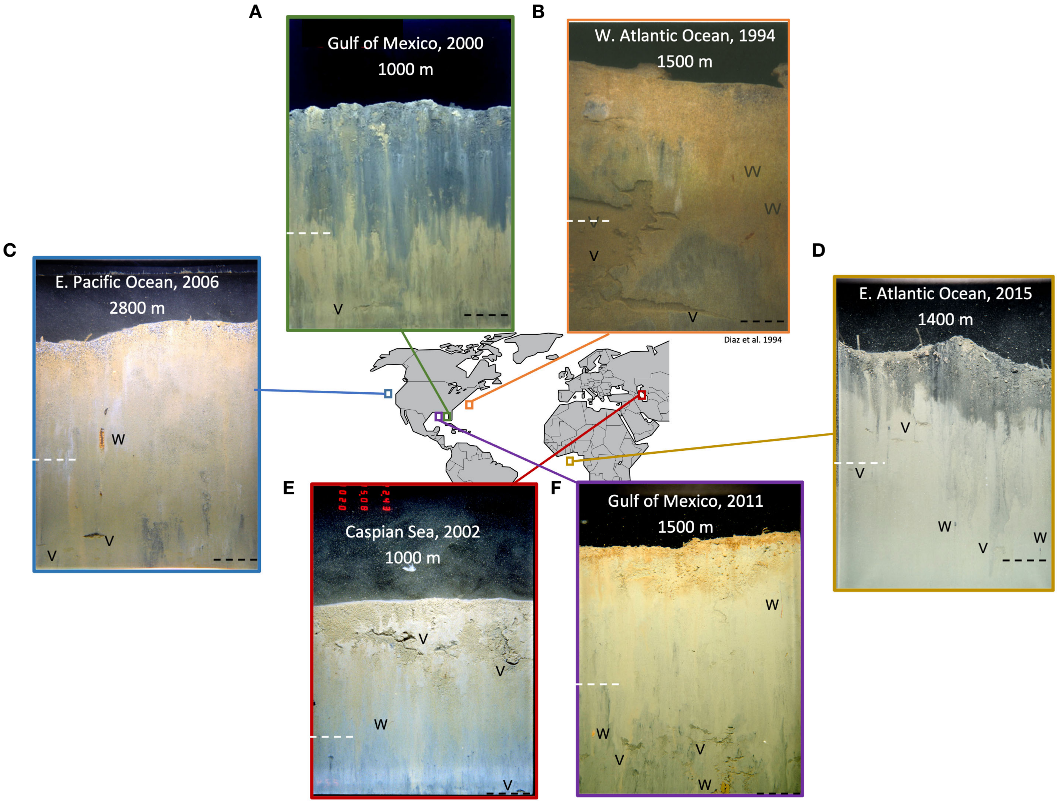

FIGURE 2
Locations around the globe where deep-sea organic enrichment and enhanced deep-sea bioturbation were observed. Organic enrichment of the deep sea and subsequently enhanced bioturbation documented at a number of locations around the globe. The mechanism of enrichment varied between location, but the process in each instance was similar (large input of organic material to the deep sea over a short timeframe). The dotted white lines denote 10 cm depth in the sediment column, representing the depth to which traditional deep-sea sampling studies process the sediment. The black dotted lines are the maximum depth of bioturbation observed in each SPI; on occasion the black line is at the bottom edge of the field of view (FOV), suggesting bioturbation extends deeper than the FOV of the SPI. Feeding voids [V] and active burrows [W] are also indicated. **(A)** Enrichment of the deep-sea Gulf of Mexico from synthetic drilling muds. The signature of disturbance (synthetic drilling muds) was visible in the sediment profile (gray sediment), and feeding voids were present deep within the sediment column. **(B)** Enrichment of the outer continental shelf and upper slope off Cape Hatteras bight due to hydrodynamic confluence. Numerous voids and burrows were visible throughout the sediment column. **(C)** Enrichment of the Eastern Pacific deep sea following the disposal of dredged material. Signatures of dredged material were visible at the sediment-water interface (gray coarse grains and grayish white mottled clay), a large worm was visible in its burrow extending deep into sediment, and there was a presence of feeding voids near the bottom edged of the FOV. **(D)** Enrichment of the eastern Atlantic continental slope from drilling muds. Drill cuttings were visible in the sediment profile (black sediment just below the sediment-water interface), and numerous voids and burrows were present deep in the sediment column. **(E)** Enrichment in the Caspian Sea around a well from drilling activity. Drilling muds were visible in profile image (brown surface sediment) with voids observed in the drilling mud. A worm was observed in its burrow just below the drilling muds, and a void is visible at the bottom edge of the FOV. **(F)** Enrichment of the deep-sea Gulf of Mexico following the Deepwater Horizon oil spill. Numerous feeding voids were observed deep within the sediment column, and a large worm was visible against faceplate near the penetration maximum of the prism. Scale of the images is 21 x 15 cm.

environment. These observations show that use of synthetic drilling muds organically enriches deep-sea sediments resulting in deep bioturbation.

This pattern was also observed in deep-sea sediments surrounding well sites located between 1,200 and 1,400 m depth on the upper continental slope of the Ghanaian continental shelf (Figure 2D) in the Deep Ivorian Basin. SPI were collected as part of a multidisciplinary sampling program to assess impacts of drilling mud discharge on the seafloor near four offshore exploration/production platforms (S2). Sampling around the four production platforms occurred between 150 m and 1000 m from the location where the wells were being drilled. Maximum bioturbation depths ranging from 6.2 to 21.1 cm, with a mean of 14.8 cm (SD±3.2), were observed in the sediments around the four well sites.

Deep bioturbation was also observed in the abyssal plains of the Pacific Ocean following the disposal of dredged spoils (Figure 2C). In the northeastern Pacific Ocean, organically rich dredged material (TOC up to 3.2%) was deposited on an annual basis (material in excess of 16 million cubic yards between 1993 and 2009) at depths of 2,500 to 3,000 m at the San Francisco Deep Ocean Disposal Site (SF-DODS). Monitoring surveys were commissioned by the U.S. Environmental Protection Agency (USEPA) as part of their site monitoring and management plan; those surveys that included SPI took place in 2000, 2001, 2006, and 2009. A synthesis of these four surveys (S3) found maximum bioturbation depths at SF-DODS ranged from 18.6 to 21.7 cm with a mean of 19.5 cm (SD ± 1.0).

A similar pattern of deep bioturbation depths occurred following the Deepwater Horizon oil spill in the Gulf of Mexico

(Figure 2F) (S4). The Macondo wellhead blowout and subsequent activities to control the spill resulted in the deposition of large amounts of hydrocarbons and organic drilling muds to the seabed (Atlas and Hazen, 2011; McNutt et al., 2012; Guarinello et al., 2022). In response to the spill, SPI was collected at depths ranging from 1,040 to 1,689 m in spring 2011 (12 months following the spill), fall 2011 (18 months post-spill), and spring 2014 (37 months post-spill) (Supplementary Figure S4–1). The mean of maximum bioturbation depth from the three surveys ranged from 10.9 to 21.0 cm with a mean of 16.4 cm (SD ± 1.6). At every station sampled from the three surveys, evidence of deep-burrowing macrofauna (>10 cm) were observed (Supplementary Figures S4–2, S4–3, S4–4).

A paradox in deep-sea enrichment and bioturbation

Interpretations of deep-sea benthic community function can be influenced by the methods employed. In comparing assumptions behind traditional methods of sediment collection and selective sieving, with observations from SPI, we postulate traditional methods may potentially lead to an underestimate of benthic function, especially in areas affected by human activities. We found a striking consistency in deep-sea benthic response to organic enrichment at multiple locations around the globe. Each case study represented a different mechanism of anthropogenic enrichment to the deep sea (drilling muds, dredged material, hydrocarbons) with a commonality of large quantities of organic material being deposited on the seafloor over a relatively short period of time. It is precisely these two components, the quantity of material and the timeframe of deposition, that we hypothesize is important for the observations we presented. Within a defined spatial area, over a relatively short-time period human activity can enrich deep-sea sediments in excess of the natural processes supplying carbon to an otherwise oligotrophic seabed. Organic enrichment also occurs in otherwise oligotrophic environments from natural sources such as oil seeps (Levin et al., 2016; Kennicutt, 2017), vents (Marcus et al., 2009), or ocean fronts (Diaz et al., 1994).

Analogous to shallow systems that experience organic enrichment, anthropogenic enrichment of the deep sea is a balance between organic enrichment and consumption. Optically, there is a stark contrast in the sediment profiles of deep-sea sediments experiencing enrichment and those from an oligotrophic seafloor (Figure 3). Physical signatures of the enrichment mechanism (dredged material, drilling muds, hydrocarbons) are often visible on the seabed or in the sediment, the sediment column is "pocked" with feeding voids (the products of advanced successional taxa) (Pearson and Rosenberg, 1978; Germano et al., 2011), and bioturbation extends >10 cm beneath the sediment-water interface. The activity of macrofauna is enhanced and positive functions related to enhanced bioturbation should be realized (nutrient recycling, enhanced microbiological activity, remineralization) (Aller et al., 2001; Meysman et al., 2006). While organic enrichment of the deep sea can elicit a positive response in macrofauna activity and function (Baguley et al., 2006),

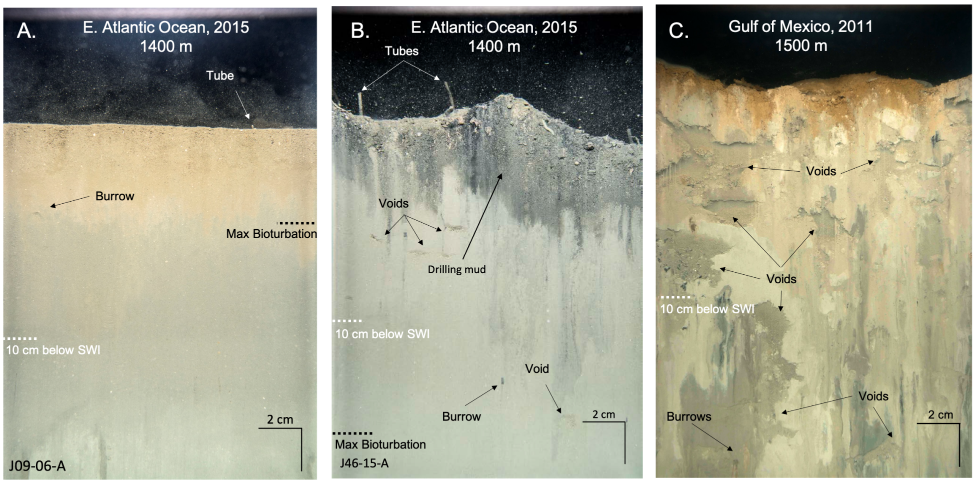

FIGURE 3
Optical comparison between **(A)** oligotrophic deep-sea sediment profile, and **(B, C)** deep-sea sediments experiencing organic enrichment. **(A)** Representation of oligotrophic deep-sea sediments. Image was captured in the Ivorian Basin. The maximum depth of bioturbation is ~2–3 cm below the sediment-water interface, and small tubes were present on the sediment surface. **(B)** Representation of deep-sea sediments experiencing enrichment from drilling muds. Image was captured in the Ivorian Basin located ~150 m from a well. Drilling muds were visible just below the sediment-water interface (black sediment). Numerous voids and burrows were present throughout the sediment column, including deep within the sediment (>10 cm). Medium-sized tubes were present at the sediment surface. **(C)** Representation of deep-sea sediments experiencing enrichment from hydrocarbons and drilling muds. Image was captured in the Gulf of Mexico following the Deepwater Horizon incident in the footprint of the "top-kill" effort (an effort to plug the well by pumping drilling muds into the blowout – resulted in drilling muds with oil particles scattering out in an NW direction from the well). The majority of the sediment profile was drilling muds from "top-kill" and the sediment column was pocked with voids and burrows. Maximum bioturbation depth extended past the prism penetration (see voids and burrows at the lower extent of the field of view). Scale of the images is 21 x 15 cm.

we hypothesize that over-enrichment should promote anaerobic conditions, as frequently occurs in shallow coastal systems (Sturdivant et al., 2011). At a certain threshold of enrichment, deep-sea macrobenthic bioturbation should decline, reduced conditions should become prominent, and microbial processes should dominate (Figure 4). An example of this can be seen in S1, where the impact of synthetic drilling muds on the deep seafloor were assessed. Supplementary Figure S1–5 depicts a SPI captured at a station immediately adjacent the well. In this example, the impact of drilling muds on the surrounding seafloor is a function of distance from the well. Drilling muds and organic enrichment are greatest at stations closest to the well and decreases with increasing distance from the well. The sediment profile in Supplementary Figure S1–5 is entirely composed of organic rich drilling muds. There is low optical reflectance of the sediment in this image indicating high sediment oxygen demand, and the presence of Thiophilic bacteria are visible at the sediment-water interface. These features are evidence of a reduced environment experienced high organic enrichment.

The deep sea is generally described as an oligotrophic environment with the concept of organic enrichment perceived as somewhat of a paradox (Menzel and Ryther, 1970; Druffel et al., 1989; Rex and Etter, 2010). The notable exceptions to the oligotrophic paradigm are natural seeps and hydrothermal vents (Tunnicliffe et al., 1997) and the occasional phenomena of hydrodynamic confluence (Diaz et al., 1994). Very little is known about macrobenthic communities surrounding seeps and vents and areas of hydrodynamic confluence that enrich the deep sea, such as that observed by Diaz et al. (1994). Based on our observations with SPI, we hypothesize a deep-sea enrichment paradox that counters

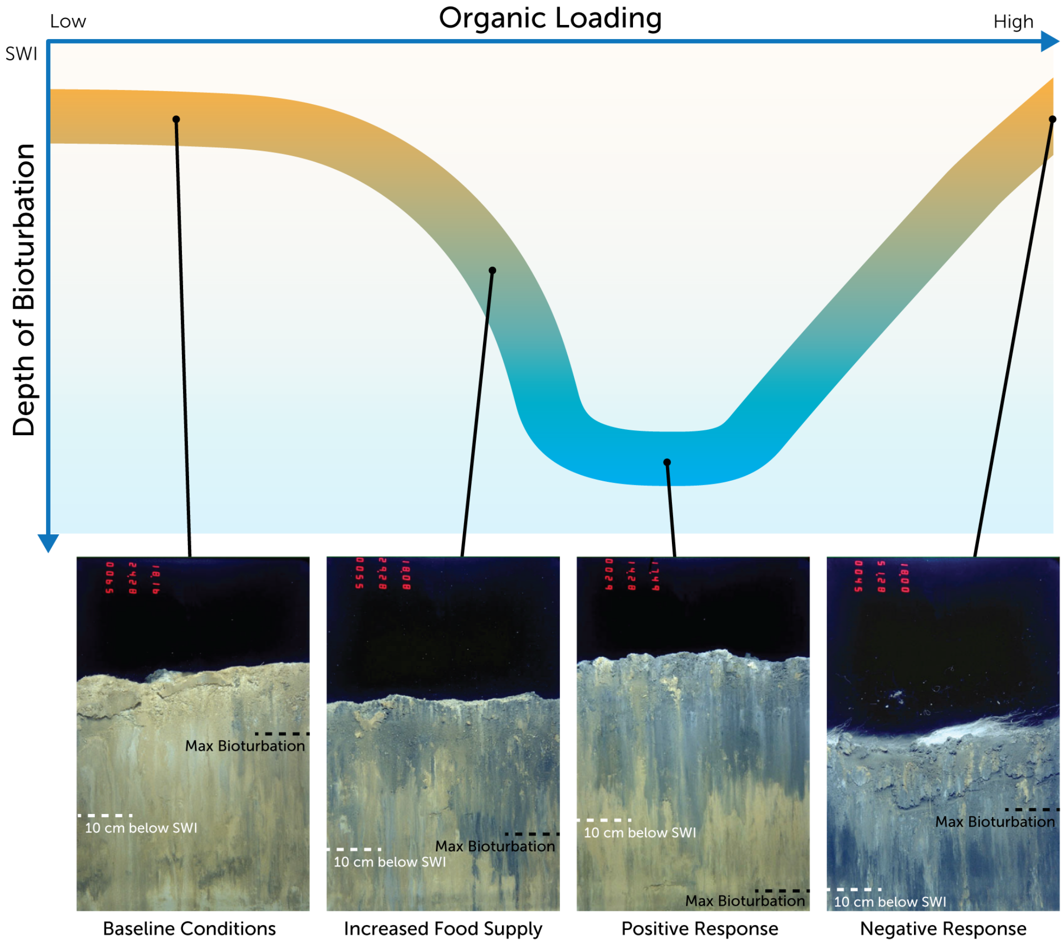

FIGURE 4
The deep-sea enrichment paradox: a theoretical response of bioturbators to organic enrichment of the deep sea. A conceptual model of how deep-sea sediments respond functionally to organic enrichment. The representative sediment profile images (SPI) were captured in the Gulf of Mexico and the mechanism of enrichment was from the deposition of drilling muds onto the deep-sea floor. Traditional oligotrophic deep-sea sediments are represented at the left of the graph and indicated by a profile image (Baseline Conditions) with no drilling mud and shallow bioturbation depth. Moving along the x-axis as organic enrichment increases (in this case the deposition of drilling muds increases on the seafloor) a positive macrobiological response is triggered (Increased Food Supply) and bioturbation increases in depth. As organic enrichment continues to increase this results in the stimulation of deep burrowing bioturbators (Positive Response). Evidence of the enrichment mechanism (drilling muds) is visible in the profile images (grey sediment). As organic enrichment increases to the point of over enrichment a negative macrobiological response occurs (Negative Response) decreasing bioturbation depths and stimulating anaerobic conditions. A key diagnostic feature of over-enrichment visible in the representative profile image is the presence of thiophilic bacterial mats (white filaments at the sediment-water interface) and a darkening of the sediment as sediment oxygen demand increases due to the available organic content. Scale of the images is 21 x 15 cm.

the typical oligotrophic profile. Given sufficient organic enrichment, the biological response of deep-sea macrofauna can mimic conditions observed in shallow coastal and estuarine systems (Zhang et al., 2024): advanced successional taxa are present (Vetter and Dayton, 1998) and deep bioturbation occurs (Diaz et al., 1994). However, our observations are singular in approach, viewed largely through the "prism" of the sediment profile window. SPI allowed us to document this phenomenon of enhanced benthic function in the deep sea and provide a theoretical conceptualization of deep-sea macrobenthic response to organic enrichment (Figure 4), but questions remain. Does an enhanced deep-sea macrofauna community confer similar positive ecosystem functions to those observed in shallow benthic systems (e.g., nutrient recycling, enhanced microbiological activity, remineralization)? What are the thresholds for organic input (quantity, quality, supply rate) that are necessary to stimulate macrobenthic production and subsequent deep bioturbative activity in the deep sea, and at what point does organic input become over-enrichment with deleterious consequences? When organic enrichment of the deep sea occurs, what proportion of bioturbators occur at depths deeper than 10 cm? All our observations were from large-scale organic inputs over relatively short time frames (days to months). These questions, and more, need to be resolved to better understand the observations we made at the deep-sea sites that were the focus of this study.

Discussion: moving forward in deep-sea ecology

Understanding how a system as important, but difficult to assess, as the deep-sea functions is an imperative. If an area of the deep sea has experienced organic enrichment (anthropogenic or naturally occurring), traditional approaches to benthic community assessment that often do not assess function could lead to underestimating deep-sea benthic function by sampling a small slice (<10 cm) of the sediment. Shallow subsampling can overlook a community that is thriving deep within the sediment and influencing deep-sea sediment processes. This can result in unintentional misinterpretations and misrepresentations of the benthic community and related processes in the deep sea. The ramifications of such underestimations and subsequent misinterpretations can be wide ranging. These have the potential to skew not only our ecological understanding of the deep sea but to distort policy, management, and public opinion related to anthropogenic activity in the deep sea, which has widely been viewed as catastrophically disruptive (Joye, 2016).

Acknowledgement of a paradox in deep-sea enrichment will require ecologists to rethink their approach to deep-sea benthic studies and possibly revisit interpretations of previous studies. Such shifts in approach are most critical in areas where anthropogenic enrichment of the deep-sea may have occurred, especially if such areas are in regions with naturally occurring seeps where benthic communities (microbial and macrofauna) are well-adapted to influxes of carbon (Glover et al., 2010; Smith et al., 2014; Levin et al., 2016). Recent work highlights microbial consumption of hydrocarbons in the global ocean that is occurring on a much larger scale than previously realized (Love et al., 2021). With human influence on the deep sea increasing, our observations are critically relevant for deep-sea ecology moving forward (Ramirez-Llodra et al., 2011). Consideration of ecological and anthropogenic factors will be a critical step in planning deep-sea benthic studies. For assessing community structure, application of the traditional approach and sieving sediments to a depth of 10 cm is acceptable (Montagna et al., 2016). However, to assess community function, it will be important that studies are designed to capture and hopefully provide more data on larger deeper burrowing macrofauna.

Data availability statement

The original contributions presented in the study are included in the article/Supplementary Material. Further inquiries can be directed to the corresponding author.

Ethics statement

The manuscript presents research on animals that do not require ethical approval for their study.

Author contributions

SS: Conceptualization, Data curation, Formal Analysis, Investigation, Methodology, Project administration, Resources, Software, Supervision, Validation, Visualization, Writing – original draft, Writing – review & editing. MG: Formal Analysis, Investigation, Writing – review & editing. JG: Conceptualization, Funding acquisition, Investigation, Methodology, Resources, Supervision, Writing – review & editing. DC: Methodology, Project administration, Resources, Supervision, Writing – review & editing.

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Conflict of interest

Authors SS, MG, JG, and DC founded the company INSPIRE, which was the funding source for the authors' time and the publishing fees. The company had no other involvement in the study.

Publisher's note

Supplementary material

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fmars.2024.1383754/full#supplementary-material

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