

Global Biogeochemical Cycles^a



COMMENTARY

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Key Points:

- New observations should prioritize easier-to-collect variables to rapidly increase temporal and spatial coverage of benthic data
- Multi-variable data sets need to be harmonized to provide comprehensive data sets that can inform gaps in the carbon cycle
- Sediment model comparison is needed to establish recommendations for processes and parameterizations, and support varied modeling efforts

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Elucidating the Role of Marine Benthic Carbon in a Changing World

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Abstract The ocean plays a major role in controlling atmospheric carbon at decadal to millennial timescales, with benthic carbon representing the only geologic-scale storage of oceanic carbon. Despite its importance, detailed benthic ocean observations are limited and representation of the benthic carbon cycle in ocean and Earth system models (ESMs) is mostly empirical with little prognostic capacity, which hinders our ability to properly understand the long-term evolution of the carbon cycle and climate changerelated feedbacks. The Benthic Ecosystem and Carbon Synthesis (BECS) working group, with the support of the US Ocean Carbon & Biogeochemistry Program (OCB), identified key challenges limiting our understanding of benthic systems, opportunities to act on these challenges, and pathways to increase the representation of these systems in global modeling and observational efforts. We propose a set of priorities to advance mechanistic understanding and better quantify the importance of the benthos: (a) implementing a model intercomparison exercise with existing benthic models to support future model development, (b) data synthesis to inform both model parameterizations and future observations, (c) increased deployment of platforms and technologies in support of in situ benthic monitoring (e.g., from benchtop to field mesocosm), and (d) global coordination of a benthic observing program ("GEOSed") to fill large regional data gaps and evaluate the mechanistic understanding of benthic processes acquired throughout the previous steps. Addressing these priorities will help inform solutions to both global and regional resource management and climate adaptation strategies.

Plain Language Summary The ocean plays a large role in shaping atmospheric carbon at timescales from decades to millennia, and ocean sediments not only influence the processes involved but also constitute a long-term storage of oceanic carbon. Despite its importance, benthic (sediment) observations are limited, making it difficult to represent sediment-water interface in climate models and improve our understanding of climate feedbacks. In this manuscript, the Benthic Ecosystem and Carbon Synthesis (BECS) working group recommends a set of priorities to further accelerate sediment research. These include comparing existing sediment models, synthesizing available data, prioritizing cost-effective

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and informative variables for sampling, and coordinating global field campaigns to increase observations in areas where data is lacking.

1. Introduction

The seafloor represents the largest areal habitat on Earth, covering ~71% of the planet's surface, and plays a critical role in regulating surface Earth processes. Human activities and climate variations lead to profound changes in these processes, which in turn influence atmospheric and oceanic concentrations of carbon dioxide (CO_2) and oxygen (O_2) , as well as air-sea fluxes of other important greenhouse gases such as nitrous oxide (N_2O) (Freing et al., 2012) and methane (CH₄) (Rees et al., 2022). Estimates show that \sim 90% of the carbon released to the atmosphere through long-term sources (e.g., volcanism, oxidation of sedimentary bedrock) is ultimately sequestered in the ocean (Regnier et al., 2022). On shorter timescales, Earth's climate is thought to be regulated in part by the biological carbon pump—the sequestration and sinking of organic carbon fixed by phytoplankton in the surface ocean (Archer et al., 2000). The fraction of the organic carbon arriving at the seafloor that is either buried or re-oxidized to inorganic carbon depends on the physical conditions, permeability, biogeochemistry and redox conditions at the sediment surface. Partitioning of CO₂ between the atmosphere and the ocean is also controlled by ocean alkalinity, which at long timescales (millennia) is regulated by reverse weathering (i.e., reactions that consume alkalinity at sediment-water interfaces, producing amorphous clay precursor phases and CO₂) and calcium carbonate (CaCO₃) burial and dissolution in the sediments (Mackenzie & Garrels, 1966; Michalopoulos & Aller, 1995; Middelburg et al., 2020).

Despite their importance to the global carbon cycle, relative to the pelagic environment, benthic sediments and ecosystems are critically under-studied. Consequently, we have only a limited ability to quantify the contribution of each mechanism driving sediment-water exchanges of oxygen, nutrients, and carbon to the global carbon budget. With increasing impacts of climate change and several marine carbon dioxide removal strategies (mCDR) currently involving the storage of carbon in the ocean sediments (NASEM, 2022), it is necessary to quickly quantify and reduce uncertainties related to sediment and their ecosystems to properly manage existing resources and plan mitigation strategies.

Both the vertical and lateral fluxes of carbon to the ocean sediments, and the fate of this carbon, are largely underconstrained. Regarding the biological pump, recent model ensembles estimate that $0.65 \pm 0.24 \,\mathrm{Pg}\,\mathrm{C}\,\mathrm{yr}^{-1}$ reaches depths greater than 1,000 m, contrasted with 0.95 ± 0.25 from observational estimates (Doney et al., 2024), with significant spatial variability (Wilson et al., 2022). Much of the organic matter reaching the seafloor is respired, producing CO₂ and consuming O₂ (Muller-Karger, 2005). This process is especially pronounced in hydrodynamically active shelf regions underlain by permeable sediments (Jahnke et al., 2005), where advective transport enhances solute exchange and microbial remineralization. Further, both the quantity and quality of deposited organic matter play a large role in the processes that link sediments to the water column (benthic-pelagic coupling), with potential implications for global biogeochemical cycles and climate (Freitas et al., 2021). Estimates of particulate inorganic carbon (PIC) flux to the sediments in coastal and shelf areas are scarce but generally agree on a total flux of 0.27–0.29 Pg C yr⁻¹ (Krumins et al., 2013). Estimates of the carbonate burial in these regions, however, range over an order of magnitude from 0.050 to 0.276 Pg C yr⁻¹ (Krumins et al., 2013; Middelburg et al., 2020; O'Mara & Dunne, 2019), indicating that there are substantial gaps in measurements and/or understanding of the balance between coastal inputs and burial. As for particulate organic carbon (POC), not only do flux estimates in coastal and shelf environments have a large range from ~0.2 to 2.2 Pg C yr⁻¹, but there are also significant associated uncertainties (Krumins et al., 2013). Resuspension and lateral transport of particulate carbon and lithogenic material has also been identified as an understudied but potentially significant source of POC to the deep ocean, accounting for $25 \pm 20\%$ of sinking particles globally, serving as a major source of energy to deep ocean ecosystems, and potentially important carbon sequestration path (Kim et al., 2020; Shen et al., 2020).

Closing the carbon budget in coastal and shelf regions is of critical importance, since these areas account for ~90% of the marine sediment carbon burial (Dunne et al., 2007) and support a large diversity of marine life, despite representing less than 10% of the seafloor. In shallower regions, where benthic-pelagic coupling is stronger, sediment remineralization can be as important of a nutrient source for the pelagic environment as terrestrial fluxes, supplying an average of 15%-32% of N and 17%-100% of P demand in areas up to 10 m depth

SCHULTZ ET AL. 2 of 18 (Boynton et al., 2018). Large uncertainties in coastal benthic-pelagic coupling are compounded by uncertainties in the riverine contributions themselves; a recent estimate suggested an upward revision of ~25% to the global riverine contribution to coastal carbon (M. Liu et al., 2024). The spatial extent of riverine influence also impacts the ultimate fate of the riverine carbon, with discharge from large rivers (e.g., Amazon (Aller & Blair, 2006), Congo (Rabouille et al., 2019)) transported significantly deeper and more offshore than the smaller rivers.

In addition, submarine groundwater discharge (SGD), saline and fresh, has also been estimated to transport quantities of dissolved nitrogen, phosphorus and silica to the coastal ocean comparable to the ones delivered by global rivers (Cho et al., 2018; Rahman et al., 2019), with fluxes exceeding river inputs in \sim 60% of the study sites compiled by a global synthesis (Santos, Burdige, et al., 2021). Discharge volume of submarine groundwater discharge is estimated to be \sim 1.2e14 m³ yr⁻¹, of which 2.4e12 m³ yr⁻¹ is from fresh submarine groundwater discharge, or \sim 3x that of river discharge (Kwon et al., 2014; Zhou et al., 2019). Combined with the inherent uncertainties due to the high diversity of coastal and nearshore systems and their sensitivity to anthropogenic perturbations (Kiro, 2025; Richardson et al., 2024), an estimate of the coastal carbon budget, including alkalinity, is a thorny challenge (e.g., Middelburg et al., 2020).

Among the many anthropogenic pressures on coastal and nearshore systems, bottom trawling has emerged as a particularly important and contentious issue in benthic carbon dynamics. The mixing and resuspension that occurs during trawling can increase the respiration of organic matter, limit sediment settlement and consolidation, and decrease benthic faunal biomass; all changes that could lead to reduced carbon accumulation in the benthos and increased dissolved inorganic carbon (DIC) in the water column. Reductions in faunal biomass, however, could also lower bioturbation and thus oxygen supply to deeper sediments, which would favor carbon burial (Epstein et al., 2022). The impact of trawling to the global carbon cycle, thus, has been heavily debated (Hilborn & Kaiser, 2022; Sala et al., 2021), and extrapolations from site-specific studies are currently difficult to perform since impacts will depend on several factors including size and type of gear (Depestele et al., 2016) and sediment type (Kaiser et al., 2002), which are not always present across available data sets (Paradis et al., 2024). A recent review (Epstein et al., 2022) found that despite consistency in the experimental design, studies that investigated changes in organic carbon stocks due to demersal fishing showed very different results, highlighting the difficulty in assessing the impact of trawling disturbances on the global scale.

Other anthropogenic disturbances that affect sediment transport and benthic dynamics include offshore wind, coastal development, industrial use, river re-routing and damming. Offshore wind, for example, currently comprises more than 13,000 turbines globally (McCoy et al., 2024), and both modeling (De Borger et al., 2021) and observational (Coates et al., 2014) studies have documented organic matter enrichment in these areas due to changes in hydrodynamic processes, leading to increased epifaunal growth. Dams, which grew in numbers since the 1950s, were previously thought to limit the supply of sediments to coastal zones. In North America, however, sediment accumulation in some coastal depocenters currently match or surpass relative sea level rise, although this accumulation is uneven with some areas showing increasing depth (Rodriguez et al., 2020). Characterizing change and understanding the magnitude of these disturbances, therefore, is a needed first step to improve management of coastal and shelf regions.

The high impact of hard-to-sample episodic events, including extreme synoptic events, on the benthic environment (Durrieu De Madron et al., 2011) makes it even harder to quantify elemental budgets in these systems. Storms can impact the physical structure of benthic habitats and change the rates of biogeochemical transformation affecting organic matter, while flood events can lead to changes in dissolved and particulate nutrients and organic matter delivery to estuarine and deltaic systems (Tesi et al., 2013). Marine heatwaves can drive modifications in ecosystem structure and function and increase biogeochemical variability (Gomes et al., 2024). While synoptic events are more impactful in shallower areas, episodic events also impact the deep ocean, where large pulses of organic matter deposition to the seafloor in otherwise low flux regions can have disproportionate impact (Smith et al., 2018). The effect of these deposition events on benthic ecosystems and biogeochemistry can be highly significant (Titelman et al., 2006), but can vary depending on the lability and quantity of organic matter deposited (Lochte & Turley, 1988; Nmor et al., 2025; Stauffer et al., 2022).

The complex role of benthic food webs in driving biogeochemical fluxes has also been receiving increasing attention, highlighting the role of often cryptic organisms that have substantial effects on biogeochemical cycles. For example, the importance of cable bacteria (cm-long chains that can effectively draw energy from redox gradients) in changing redox dynamics has been detected in coastal regions worldwide, which can influence

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various elemental cycles (Dong et al., 2024; Xiong et al., 2024). A recent study showed that benthic denitrifying foraminifera were found in diverse marine environments, contributing significantly to the total benthic denitrification (Rakshit et al., 2025). Another recent study (Glock et al., 2025) reported high intracellular phosphate storage in foraminifera, and estimated that they may buffer riverine phosphorus runoff for approximately a month at the Southern North Sea and Peruvian margin. Further, while the role of burrowing macrofauna in governing diagenetic transformations has been previously explored (Deng et al., 2020; Kristensen et al., 2012), the role of megafauna is now increasingly acknowledged, with demersal fish and rays shown to increase sediment resuspension and bioturbation rates (Nauta et al., 2024; Yahel et al., 2008).

Despite limitations in observational coverage, our understanding of biogeochemical processes in ocean sediments continues to evolve. Long-term studies are highlighting the dynamic nature of benthic fluxes and their sensitivity to local and global anthropogenic changes (Boynton et al., 2023; Robinson W. Fulweiler & Heiss, 2014; Tucker et al., 2014), and models with improved benthic representation and spatiotemporal resolution (Nmor et al., 2022) yield a better fit to available observations (Siedlecki et al., 2021). While a number of recent syntheses have compiled benthic quantities and fluxes (Boynton et al., 2018; Jørgensen et al., 2022; Solan et al., 2019; Stratmann et al., 2020), the sparse spatiotemporal coverage of benthic data has limited their utility for both closing biogeochemical budgets (Boynton et al., 2018) and quantifying variability in dynamic coastal areas (Jørgensen et al., 2022). Still, new developments use machine learning to extrapolate sparse benthic data to the global scale (Lee et al., 2019). While new numerical technologies to grid existing data and create global maps are needed, care must be taken to ensure that the amount of available data is adequate and to evaluate conditions under which the algorithms are prone to error, including areas of large disturbance due to anthropogenic activities. When combined with large-scale biogeochemical constraints (Brandes et al., 2007; Dunne et al., 2007), these new methodologies could be a promising way to increase benthic understanding.

An improved understanding and quantification of benthic-pelagic fluxes and burial in the ocean sediments is imperative in the face of its increased use for a series of societal needs. For example, assessing the effectiveness and permanence of mCDR methods will require better characterization of the benthic ecosystem and degradation rates (Raven et al., 2024) and of feedbacks between sediments and the surface ocean. The Benthic Ecosystem and Carbon Synthesis (BECS) working group, with the support of the US Ocean Carbon & Biogeochemistry (OCB) Program, consists of over 40 scientists from different disciplines conducting benthic research in eight different countries across four continents. As a working group, we coalesced around a set of key challenges to, and opportunities for, improved understanding of the benthic environment and its role in the global carbon cycle (Figure 1). We present action plans needed to advance the understanding of benthic carbon's role in the global carbon budget and address challenges, including the ones identified in Lessin et al. (2018). These include (a) a benthic model intercomparison activity with existing benthic models to inform users and support future model developments; (b) recommendations for data synthesis products geared toward informing both model parameterizations and future observations; (c) new experimental efforts and development of platforms and technologies in support of in situ benthic monitoring; and (d) recommendations for coordinated global benthic observational programs. Some of the emphasis of the proposed solutions rely on increasing coverage of benthic variables, with an accessible plan that prioritizes measurements that are cost-effective and do not rely on complicated logistics or sophisticated resources.

2. Comparing Existing Benthic Models and Working Toward a Mechanistic Global Model

Benthic biogeochemical models are essential for understanding and predicting biogeochemical processes within the seafloor and at the water-sediment interface, as well as for scaling up observations to estimate global carbon budgets and for informing crucial decisions related to mCDR strategies (NASEM, 2022; Siegel et al., 2021). Benthic systems, however, are characterized by high spatial heterogeneity in both the horizontal and vertical scales (Glud et al., 2009; Figure 2). While benthic models have significantly advanced over the last two decades (Brady et al., 2013; Butenschön et al., 2016; Munhoven, 2021; Soetaert et al., 1996; Sulpis et al., 2022), they differ widely in their complexity, application, domain (local, regional, or global), and terminology, making cross-comparisons difficult (Lessin et al., 2018; Paraska et al., 2014). Further, the inclusion of benthic food webs that interacts with the sedimentary biogeochemical cycles is increasingly recognized as important, particularly in coastal systems (Butenschön et al., 2016; Ehrnsten et al., 2020; Lessin et al., 2018), but is still rare in most models.

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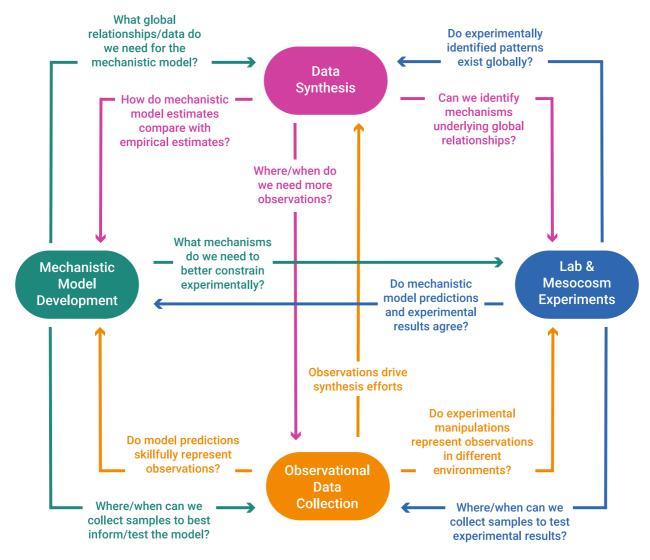


Figure 1. Diagram showing four interlinked key initiatives to improve the understanding of benthic ecosystem and diagenetic dynamics, and benthic-pelagic interactions. Arrows connecting different initiatives highlight the relationship between two individual initiatives.

Due to the significant variability in the complexity and structure of available models, there is currently little consensus on how benthic processes should be represented to achieve the goals of closing gaps in the global carbon budget and informing climate and ecosystem management solutions at large scales (Planchat et al., 2023), making assessments of particular scenarios challenging. Global ocean and Earth System models (ESMs) have historically relied on empirical relationships to close global budgets at the seafloor rather than mechanistic process representation (Hülse et al., 2017; but see Heinze et al., 1999), in part due to a lack of observational and theoretical constraints as well as computational limitations.

The computational capabilities of many modeling centers have advanced to the point where sediment models with centimeter-to-decimeter scale vertical resolution can be used to simulate global biogeochemical cycles over centennial timescales. ESMs have progressed significantly in their representation of exchanges in the land to ocean continuum (Lee et al., 2024; Xu et al., 2024) and of coastal and shelf processes (Mathis et al., 2024), such that the inclusion of process-based benthic biogeochemistry becomes increasingly critical. Additionally, with new carbon management needs such as modeling and verifying mCDR (Kwiatkowski et al., 2023; Wu et al., 2023), global ocean and Earth System Models (ESMs) are being stretched to new applications without sufficient process refinement, with few benthic models parameterized to represent the global domain or a wide range of habitats (Heinze et al., 1999; Munhoven, 2021; Sulpis et al., 2022). Of these models, it is unclear how they compare

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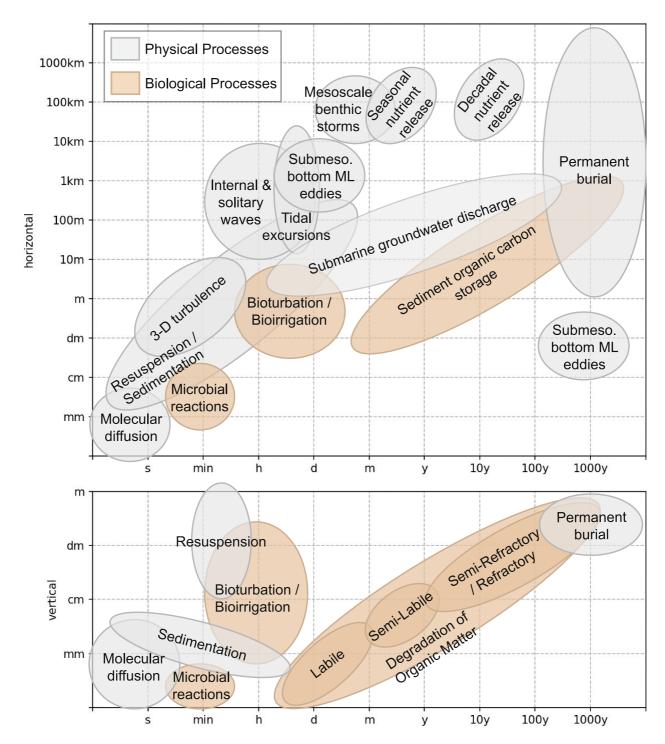


Figure 2. Stommel diagram representing horizontal (top) and vertical (bottom) distribution of key benthic processes across spatiotemporal scales. Processes that are primarily physically driven are in gray, whereas processes that are primarily biologically driven are in brown.

against a common set of observational constraints or behave when forced under a common set of environmental conditions.

There are a number of important steps needed to address the disconnect between existing model capability and emerging demands, such as creating more global data synthesis products (Section 2) and collecting ex situ and in situ observations at scales relevant to sediment processes (Sections 3 and 4). Challenges to advance benthic modeling by addressing specific knowledge gaps have recently been described by Lessin et al. (2018), which

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advocates an interdisciplinary, fully integrated framework for collaboration between modelers and empirical scientists, and traceable and hierarchical complexity for benthic-pelagic models. Building intra-community dialog can be done through a community of practice among modeling teams. Specifically, model-intercomparison projects (MIPs) are a common and useful approach (e.g., Eyring et al., 2016; Orr et al., 2017; Tittensor et al., 2018) and could be tailored to the needs and challenges of benthic ecosystem modeling. A benthic MIP may consist of a set of common experiments, with shared forcings and output variables, or it could utilize an existing experimental design (e.g., climate change scenarios) and request a set of relevant output variables. Such an exercise would allow the sediment modeling community to benchmark large suites of state-of-the-art benthic models and evaluate the essential processes, phenomena, or parameters that give rise to systematic differences among models. Furthermore, a rigorous model comparison would facilitate a better understanding of the structural uncertainties inherent in simulating benthic biogeochemical dynamics, as well as identifying the essential fields needed for global benthic biogeochemistry modeling.

In a recent related manuscript, Siedlecki et al. (2025) lay out the scientific justification and guidance for a sediment biogeochemistry MIP (SedBGC-MIP). Addressing the need for traceable and hierarchical complexity for benthic models (Lessin et al., 2018; Siedlecki et al., 2025) propose a framework that classifies models relative to their biogeochemical and ecosystem complexity. To facilitate maximum involvement from a wide range of sediment models, Siedlecki et al. (2025) recommend that this sediment intercomparison exercise not be limited to global ESMs but would be inclusive of 1-D, local, and regional sediment models. Such an exercise can coalesce community effort in identifying focal variables or processes critical for models to simulate and properly capture, thereby accelerating model development toward fully coupled benthic biogeochemical and ecosystem models within global ESMs.

3. Recommendations for Data Synthesis Products

A comprehensive global data synthesis that encompasses different benthic elemental cycles and ecosystem characteristics is a critical step toward a better understanding of the role of ocean sediments in planetary-scale exchanges of carbon. Additionally, integrated and self-consistent data sets with global coverage would significantly accelerate model development efforts, by providing modelers with critical data constraints that could be used to tune and validate models. An essential part of such an effort would be to harmonize different data sets collected with disparate methods within a common database in a manner easily accessible to non-experts. The synthesized data could be used to identify gaps, develop quantitative relationships among variables, evaluate correlates of key rate processes, and build gridded data sets that could help inform and validate models (Section 1). While there have been many recent synthesis efforts (Bourgeois et al., 2017; Boynton et al., 2018; Freitas et al., 2021; Jahnke, 1996; Jørgensen et al., 2022, 2024; Seiter et al., 2004; Solan et al., 2019; Stratmann et al., 2020), additional challenges remain. These include the need to integrate across the coastal-deep ocean divide, co-locate biogeochemical and ecosystem information, and recover additional data in gray and unpublished sources.

To fill data gaps without directly measuring important benthic variables that might not be accessible, existing data synthesis efforts have relied on quantities that are relatively easy to measure (e.g., sediment carbon) and can be used as proxies for more challenging or time-consuming to sample pools or fluxes. This approach has been particularly important in less accessible habitats such as the deep sea. For example, water depth and POC content have been linked to bathymetric and spatial patterns in benthic biomass and community structure (Carney, 2005; Rex et al., 2006; Wei et al., 2010), as well as benthic remineralization rates and other fluxes (Jørgensen et al., 2022; Middelburg et al., 1997; Smith et al., 2001). On the continental shelf, the presence of muddy versus highly permeable sandy sediments can be an important proxy for many processes, including sediment denitrification (Chua et al., 2022), and carbon burial and preservation (Burdige, 2007).

However, these simple formulations are less applicable in more dynamic nearshore settings where benthic processes are complex. Jørgensen et al. (2022) observed no clear depth-dependence of O_2 flux across the sediment-water interface in areas shallower than 10 m and assumed a constant value in their global estimate of sediment oxygen consumption (and ultimately sediment organic carbon remineralization). This was even though sediment oxygen demand varies substantially over space and time in nearshore regions (Boynton et al., 2023; Mazur et al., 2021). Other potential predictors of benthic fluxes such as benthic invertebrate community composition (Mermillod-Blondin & Rosenberg, 2006) and groundwater discharge (Cho et al., 2018; Rahman

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et al., 2019) are not incorporated in existing analyses, and their relationship with nutrient and carbon cycles are not well understood.

Currently, multiple repositories house benthic data, including the National Science Foundation's Biological and Chemical Oceanography Data Management Office (BCO-DMO; https://www.bco-dmo.org/); PANGAEA (https://www.pangaea.de/); the Ocean Biodiversity Information System (OBIS; (Stratmann et al., 2020), https://manual.obis.org/index.html); and the Modern Ocean Sediment Archive and Inventory of Carbon (MOSAIC; (Paradis et al., 2023)), which contains data from more than 21,000 individual sediment cores across the global continental margins. However, accessing data stored in such locations involves sorting through individual repositories for isolated measurements and specialized knowledge regarding the quantities measured and their methodological limitations. Without harmonized and gridded data in a uniform and easily accessible format, it remains challenging for users (e.g., global modelers) to fully benefit from existing benthic data.

A benthic data product that supports a broad range of applications and communities should be based on a core set of variables collected with standardized methodologies and with common units and metadata, highlighting the need for unified variables and approaches to be used by the community. For example, benthic invertebrate biomass estimates that could be more easily incorporated into models could rely on existing data, power-law relationships between abundance and body size, and length-to-weight relationships (Ruhl et al., 2023). In the case of benthic flux estimates, more experiments and observational studies that employ multiple methodologies are needed to better constrain these estimates and more carefully assess the methods and their limitations, as well as assumptions in different environments. Ex situ measurements should also be used to inform these assumptions and help collate data collected using different methods. For example, in situ studies have revealed substantial differences between methodologies due to factors such as advective flow in permeable sediments and sediment resuspension (Camillini et al., 2021; Huettel et al., 2014). Efforts in other fields to urge method standardization are ongoing (White et al., 2020), and in some cases have led to substantial changes in our understanding of important biogeochemical processes.

4. The Role of Ex and In Situ Experiments, and New Observational Technologies

Continual, critical assessments of existing techniques are necessary to advance benthic research. Here, in situ measurements refers to measurements taken at the observation site, while ex situ refers to measurements taken in a laboratory or under a controlled environment. Along with standardization of measurements and development of methodology that would allow us to compare existing data sets, advances in observational technologies and ex and in situ measurements can change the way we understand ocean sediment processes by providing coverage at spatiotemporal scales not previously observed. New in situ data should also be complemented by ex situ measurements to quantify how reaction rates from different methodologies relate to each other (e.g., Jørgensen et al., 2022). In this section, we highlight priorities toward expanding the use of in situ and ex situ measurements and address the role of new technologies to cover spatiotemporal scales that were previously difficult to observe.

4.1. Expanding the Use of Ex Situ Measurements to Quantify Transformation Rates and Influence of Different Stressors

As the ocean undergoes rapid change, we need to experimentally determine how multiple concurrent stressors and forcings alter benthic process rates, so that response of early diagenesis to subtle changes in environmental conditions such as temperature and pH can be properly represented in ESMs. Ex situ experiments are key to disentangling these complex biogeochemical interactions and determining kinetics, and core incubations and mesocosms are two approaches that could be used to further our understanding of these dynamic processes (Fulweiler et al., 2007).

Core incubations are a common method for measuring benthic process rates and have been successfully used in experimental manipulations to examine the effects of controlling factors (e.g., temperature, organic matter concentrations) across a wide-range of variables (e.g., oxygen, nutrients, carbon). Core incubations, however, may isolate sediments from other ecosystem processes (physical mixing, water-column processes). Mesocosms, in contrast, offer an experimental approach to measure sediment process rates in the context of a more representative ecosystem. e.g., to test the impact of both warming and changes in organic matter deposition to benthic processes, a mesocosm approach would allow scientists to examine metabolism, infauna changes, microbial community dynamics, water column processes, etc. Like all methods, mesocosms have their limitations: they can

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be expensive, they cannot represent all environments (e.g., deep sea), and care must be taken to mimic field hydrodynamics and limit artifacts. However, they also provide a unique opportunity for control and replication as well as access.

Incorporating data from experimental manipulations in core incubations and mesocosms in model parameterizations relies on improving communication between different scientific communities to properly weigh the method's benefits and limitations against observations. Outfitting the mesocosms with sensors would provide real time data acquisition in a protected environment; data that are not only useful to scientists from different disciplines but for education and outreach as well. Compared to the financial costs and logistical constraints that limit widespread participation on research cruises, mesocosms provide an unparalleled experimental and educational platform.

4.2. Creating a Priority System to Increase Global Benthic Data Coverage

While other oceanographic fields have significantly increased their spatial coverage through remote sensing and autonomous platforms such as Argo floats (Jayne et al., 2017), focused on subsurface physics and biogeochemistry, and global surveys such as Tara Oceans (Gorsky et al., 2019), for plankton biodiversity, similar technological developments are missing to scale up sediment flux measurements, resulting in limited understanding of their variability and significant unevenness in data coverage. As an example, over 47% of the sediment nitrate flux data (Boynton et al., 2018) is from the northeast coast of the US (39-46°N), while the whole South Atlantic Ocean (40°S to equator, 15–60°W), which includes major river deltas and large continental shelf regions, accounts for ~0.84% of the data. This disparity exemplifies the currently common practice to widely apply understanding and values for benthic fluxes from Northern Hemisphere temperate systems (often in the Atlantic) to the rest of the globe. However, caution is needed when extrapolating locally measured flux data from a specific time to larger spatial scales and periods, as benthic processes can exhibit significant variability on daily to-multiannual and ocean margin-to-open ocean scales (e.g., Sultan et al., 2020; Yin et al., 2021, 2023). Different ecosystems, for example, with organisms adapted to live under different temperature ranges and sources of organic matter, can show different responses to warming rates and anthropogenic perturbations. For example, recent studies have documented how extrapolations of oxygen utilization rates in the deep ocean are confounded by differences in organic matter types (Luo et al., 2024; Sulpis et al., 2023).

An important consideration when developing new guidelines to expand data coverage is to recognize the financial and logistical constraints many scientists face and prioritize measurements that can offer the most significant amount of information without relying on methods that are either too costly, take too much time, or involve equipment or supplies that are not widely accessible. The Global Ocean Observing System (GOOS) has promoted the Essential Ocean Variable (EOV) concept to identify variables that have both high feasibility and impact (Tanhua et al., 2019). In agreement with the EOV concept, and with past global observational campaigns such as the Joint Global Ocean Flux Study (JGOFS) and the Marine Biogeochemical Cycles of Trace Elements and Isotopes Program (GEOTRACES), we developed a priority set of recommended benthic variables that would facilitate the collection of globally distributed and consistent data sets (Figure 3).

The BECS working group agreed on a minimum set of "core variables" (Priority 1) for water column, sediment and sediment-water fluxes to better constrain global models. These variables were chosen for their ease of collection and standardization, and relevance in characterizing benthic-pelagic coupling with respect to the variables that are currently included in global models. By prioritizing easier-to-collect variables, a larger number of groups throughout the world would be able to collect at least first priority variables, thus increasing the coverage of benthic data. By not requiring time-consuming and highly specialized measurements, this prioritization also facilitates collection of benthic data during cruises focused on water column processes. However, whenever possible, we also recommend adding Priority 2 and Priority 3 measurements to further constrain the mechanisms driving benthic carbon budget and to validate model predictions.

While inorganic carbon variables, including DIC and total alkalinity, would provide extremely valuable information to constrain the benthic carbon budget, these variables are relatively challenging and resource intensive to measure and would lower the frequency of sampling. For Priority 1 variables, therefore, we focus on characterizing the benthic environment more generally and on oxygen fluxes, which provides valuable information on different pathways for carbon assimilation and consumption. Water column variables for Priority 1 consist of temperature, salinity, pH, oxygen, total suspended solids, and water depth. pH information alone is not enough to

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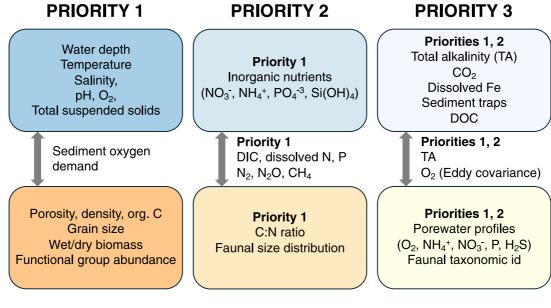


Figure 3. Outline of recommended best practices and priority measurements that all researchers can make when deployed in the field. Priority 1 measurements aim to characterize the benthic environment and provide information on oxygen consumption. Priority 2 measurements include measurements from Priority 1 with added information to characterize nutrient dynamics and greenhouse gases, while Priority 3 includes all measurements plus methods that provide higher resolution in time and space but that are more expensive and/or require more expertise and logistical support.

constrain the carbonate system, yet it is easily measurable and, coupled to reasonable assumptions about alkalinity, could be used for qualitative assessment of models or to estimate other carbonate system variables. Total suspended solids or POC were added to address the need to spatially and temporally characterize resuspension and potential respiration in the bottom water, assuming the transition between sediment and the water column is not always well defined. To represent sediment-water flux, the Priority 1 measurements include sediment oxygen demand (SOD), which can be measured with a relatively straightforward core incubation, making it more accessible than sediment oxygen profiles. SOD also provides a rate, which is preferable to stationary numbers for model evaluation and for process understanding. Sediment variables include porosity, density, and grain size to characterize the environment, organic carbon to provide information on organic carbon content, and wet and dry biomass and functional group abundance to characterize the epifauna and infaunal communities. While the dynamic nature of the benthos is not fully described with these variables, it is possible to infer the importance of transport, sedimentation and resuspension from sediment characteristics.

When possible, Priority 1 measurements should be collected along with Priority 2 (Figure 3), which include inorganic nutrients in the water column, sediment-water fluxes of dissolved inorganic C, N and P, N_2O , N_2 , and methane, and C:N ratio (obtained from dry biomass) and faunal size distribution. These added measurements are aimed at improving our understanding of carbon assimilation in the benthos and of diagenetic fluxes of nutrients to the water column, which can be achieved by better constraining the sediment nitrogen budget. We include N_2O and CH_4 since these are relatively easy to measure and are important greenhouse gases. While fully understanding the processes involved in their generation would need further measurements, there is value in improving our knowledge of the spatiotemporal variability of these concentrations and fluxes, particularly in shallower regions.

Priority 3 measurements (Figure 3) include resource intensive variables, new technologies, and measurements that require specialized regional knowledge (benthic organism classification), but when coupled with measurements in Priorities 1 and 2, would provide the most information about benthic processes. Adding sediment traps also provides added information about sedimentation and resuspension processes. The inclusion of dissolved iron in this list is due to the importance of better understanding diagenetic sources of iron to the water column, rather than to characterize the redox cascade. Lastly, when feasible, we recommend proper storage of unamended sediment samples for future analysis. This could allow for later genomic analysis, for example, that would help connect benthic microbial and metazoan biodiversity with benthic biogeochemical fluxes.

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4.3. Expanding the Use of New Technologies for in Situ Sampling

The recommendations above do not preclude investments in new technologies to provide in situ measurements of key benthic quantities, which are still limited but are increasingly available. One key biogeochemical rate measurement that provides substantial insight into benthic carbon processing is the dissolved O_2 flux across the sediment-water interface (Hartnett et al., 1998; Woulds et al., 2007). This flux is a useful proxy for benthic rates of organic-inorganic carbon transformations due to the nearly 1:1 ratio between respiratory carbon oxidation and oxygen consumption (Jørgensen et al., 2022) in a large majority of sediments. Various methods exist to conduct these measurements with differing associated technical and financial challenges: Winkler titrations, oxygen sensor measurements and profiles, sediment core incubations, or benthic chamber deployment on the seafloor. These approaches work reasonably well for non-permeable sediments but likely do not accurately capture O₂ fluxes from permeable sediments (Huettel et al., 1996). Instead, over the last two decades, the non-invasive aquatic eddy covariance (AEC) technique has emerged as a powerful tool for measurements of O₂ fluxes under true in situ conditions over relatively large areas (10–100 m²) without disturbing the natural flow, light, and exchange of nutrients with the overlying water, which are particularly useful in permeable sediments, macrophyte beds, and hard-bottom reefs (Berg et al., 2022), although characterizing above sediment respiration in high turbidity regions could be needed to properly interpret results. Widespread application of this technique is currently limited by challenges such as cost, expertise, the slow development of instrumentation that can withstand high pressures, and other aspects that could be more readily addressed by the scientific community, such as the lack of data treatment protocols and user-friendly software packages. Training workshops could inform potential users of this relatively new and powerful technology, develop a more extensive community aimed at developing this method, and create collaborations that would ease the financial burden on new interested groups and expand data collection.

5. Global Coordination for a Benthic Observing System—Toward a Benthic "GEOSed"

International observational programs such as the JGOFS, GEOTRACES, and the Global Ocean Shipboard Hydrographic Investigations Program (GO-SHIP) have greatly expanded our understanding of large-scale biogeochemical cycling in the ocean interior. However, despite the critical role the benthos plays in pelagic processes and in closing marine mass balances, benthic measurements were often excluded from these efforts due to logistical constraints (Hayes et al., 2021; Lam et al., 2018; Pavia et al., 2024). Ship-based benthic sampling methods are well suited for spatial coverage of the coastal-open ocean continuum; however, complete transects from nearshore to abyssal plains are rare, so data from multiple sources (each with potential biases) must be compiled into a more extensive data set or model. Ship-based transects are not ideal for capturing the temporal variability in benthic conditions, especially abrupt seasonal changes, dynamic biotic assemblages, and extreme events. Reconciling the discrepancies in spatiotemporal scales from coastal observations (often cm-m scale) to the open ocean (km scale) at short (day) to medium (year) timescales is a non-trivial challenge to better model sediment processes from the land to open ocean. To fill the gaps in our understanding of sediment and benthic ecosystem processes, we recommend the establishment of a large-scale international program with both shipbased efforts and observational arrays for future benthic studies (The GEOSed project). The following components should be integrated into the framework to facilitate effective translation from observation-based data to models.

5.1. Sampling the Land-Ocean Continuum to Lower Uncertainties Across Spatiotemporal Scales Under the GEOSed Framework

The first overall goal of the proposed GEOSed program would be to achieve meshing across different oceanic environments, including the land-ocean continuum. Indeed, some studies have presented full transects from river to trough (Bao et al., 2019), from delta to slope (Nmor et al., 2022) or from shelf to abyssal plain (Rowe et al., 2008). We recommend that similar transects be prioritized and include regions where the connection with land takes different forms. This would include estuaries, deltas, and upwelling regions. Cross-shelf sampling of different environments would aid interpretation of laboratory and mesocosm experiments and improve estimates of lateral transfer of carbon in different environments. It could also help solve for potential biases including the role of submarine groundwater discharge, which tends to be sampled in regions where it is assumed to have heightened importance (Santos, Chen, et al., 2021).

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The residence time of water, and consequently its oxygen, nutrients and organic matter, can influence benthic processes from estuaries to shelves (Fuchsman et al., 2015; Russoniello et al., 2018). Estimated residence times for different coasts and shelves range from days to years (Liu et al., 2019), with high heterogeneity within each system. With this in mind, bathymetry and residence time could be weighed to prioritize cross-shelf transects in less sampled regions to compare with better sampled areas with similar characteristics. Increased sampling in the broad and shallow Patagonian shelf (residence time 1–3 years), for example, could be compared to benthic properties of the better sampled Northeast Atlantic to isolate underlying drivers and processes. Increasing sampling in tropical and polar regions should also be prioritized, considering the disproportionate representation of temperate latitudes in data syntheses.

Benthic sampling programs guided by pelagic sampling or satellite analysis to target oceanic features (e.g., oxygen minimum zones or bathymetric features (Berkenbusch et al., 2011; Gier et al., 2016) are also highly valuable since the water column information provides context for benthic observations in regions of interest. When including these observations in models, however, it is important to evaluate whether the product used to prescribe the bathymetry is appropriate for the features in focus. Hotspots in the deep ocean (hydrothermal vents, cold seeps, canyon terminal zones) deserve special attention due to their extreme fluxes and require separate models with distinctive resolutions that can be coupled offline (Rabouille et al., 2019).

In the GEOSed program, interdisciplinary sampling should be promoted, with a commitment to sample as many variables as feasible following an agreed-upon tiered system (e.g., Figure 3). Following the GEOTRACES framework (Aguilar-Islas et al., 2024), we recommend that a sediment-based program adheres to a common set of Essential Benthic Variables (EBVs) with common sampling protocols and includes the collection of intercalibration samples that are easily comparable between cruises. The co-location of different variables and a rigorous sampling protocol would facilitate the interpretation and use of the data by different scientific communities and projects not directly involved with the sampling.

5.2. Investment in Comprehensive Time-Series

In addition to the large international effort covering the coastal-open ocean continuum, we consider augmentation with benthic time-series cruises and stations ideal to capture event-driven particulate and dissolved fluxes and recommend expanded use of new observing instruments and integrated platforms. Fixed and mobile platforms have been used for over a decade to estimate oxygen and carbon dynamics related to benthic metabolism (Gallo et al., 2020; Grégoire et al., 2021; Toussaint et al., 2014). Biogeochemical parameters and camera observations taking advantage of cabled observatories can deliver real-time observations and extend from land to the deep-sea. Adaptive sampling strategies can also be used in which sampling would be triggered once a defined threshold for a key parameter was exceeded, allowing sampling of stochastic events (Toussaint et al., 2014). Specific tools should be used to monitor bioturbating macrofauna from the observation platforms (e.g., Sediment Profiling Imagery).

Numerous biogeochemical parameters are not accessible through autonomous sensors alone and require supplemental campaign-based sampling and measurements. Repeated core sampling to produce a time series of organismal and porewater responses, for example, has proven to be highly useful in validating model results in highly dynamic deposition systems (Ferreira et al., 2024). Given the high heterogeneity in the residence time in different shelves, and the large influence of episodic events, specific observations at individual sites might not be representative of the average conditions at that site. Like frameworks used by large pelagic-focused projects, therefore, we also recommend repeated transects to characterize the variability of benthic versus pelagic fluxes. For benthic observations where a cascade of timescales (from long term change to instantaneous events) must be captured, the maintenance of benthic samples, moorings, and observatories is a crucial but challenging task.

The maintenance of benthic platforms with biogeochemical sensors (including micro-electrodes for porewater), pore fluid extraction and geochemical analysis, and macrofauna determination is time- and labor-intensive. Except for targeted monitoring during special observing periods, long term systematic monitoring of a benthic environment will require adapted observation and sampling facilities with dedicated personnel, including well-trained researchers capable of deploying and maintaining the observational systems, and conducting a series of sampling cruises. As a first step, investment could be made to stations already operating to augment sampling and sensors to include benthic variables.

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6. Summary

The seafloor is critical in shaping global carbon and oxygen budgets at multiple spatiotemporal scales but is underrepresented in ESMs. Increasing our understanding of how benthic systems respond to different perturbations is of growing importance as carbon-releasing activities at the seafloor (e.g., resource extraction) expand, and mCDR methods that rely on benthic carbon burial are increasingly considered. Additionally, coastal benthic regions, which receive the largest amount of organic matter that reaches the seafloor, are highly affected by direct anthropogenic disturbances and by extreme events. Resulting changes in benthic-pelagic fluxes and ecosystem composition can harm ecosystem services provided by the coastal ocean, potentially compromising water quality and fisheries. We are at a critical juncture in benthic ecosystems and process research, with an urgent need to better understand the role of mechanisms driving benthic processes, the influence of multiple stressors, and associated feedbacks with the water column to help inform solutions to both global and regional resource management and climate adaptation strategies.

Despite recent advances in the characterization of benthic-pelagic coupling, significant knowledge gaps persist due to limited sampling coverage of these systems when compared to pelagic biogeochemistry. These gaps include the role of different diagenetic and benthic ecosystem processes in driving benthic-pelagic fluxes, their response to multiple stressors, and the characterization of benthic variability in different environments. Much of the information collected is limited to mid-latitude northern regions and is fragmented between siloed scientific communities. Integrating available benthic data sets and knowledge, therefore, constitutes a priority to further our understanding of the seafloor to current stressors acting on this system. Characterizing spatial and temporal variability is a necessary first step to guide further research aimed at refining choices for regions of interest, characterizing physical transport of sediment, and evaluating the sensitivity of different environments to natural and anthropogenic perturbations. To achieve this goal, it is necessary to increase access of different scientific communities to available data by synthesizing across variables and methods to provide comprehensive, gridded data sets that can be more easily used.

This data synthesis would be crucial to provide guidelines and points of comparison for a proposed sediment model intercomparison project (MIP). Conducting a sediment MIP would allow us to assess which processes and parameterizations are recommended for different purposes, and to provide guidance for adequately incorporating the benthos in ESMs to allow prognostic capacity that could further our understanding of the global carbon cycle. Considering the benthic system as more than a boundary condition is ever more critical to properly simulate climate-related feedbacks in the carbon cycle that include ocean sediments and ecosystem, and to assess the efficacy, permanence, and potential problems associated with several mCDR strategies.

Efforts are needed to conduct targeted experiments aimed at understanding mechanisms driving benthic processes, the influence of different environmental stressors, and to increase spatial and temporal coverage of data, particularly of variables that can be easily measured and that provide useful information. Bridging these gaps requires a multi-pronged approach that includes ex situ experiments, extends the usefulness of existing ocean monitoring stations through benthic sampling, and leverages data synthesis and modeling approaches to inform targeted observational studies.

The boundaries between the water column and sediment are not often well defined, with resuspension-deposition loops leading to large modifications of particulate organic matter in regions of prominent nepheloid layers (Golombek et al., 2024) and large impact of advective processes in the sediment at a variety of scales (Aller & Blair, 2006; Kim et al., 2020; Rabouille et al., 2019). We acknowledge the importance of better characterizing particle dynamics and biogeochemical processes at the sediment-water interface in regions where sedimentation and resuspension processes are more active, and the benefits the knowledge gained from this exercise would be synergistic with the priorities discussed here. Developing a new conceptual definition for the sediment-water interface that better represents this dynamic environment and identifying steps to address this issue, however, would require focused workshops and literature review, and would in turn benefit from well-established model comparison and multi-variable data syntheses.

To address the key challenge of formulating strategies to facilitate the development of global models that mechanistically incorporate the role of the benthos in the global carbon cycle, we prioritize variables and fluxes that could be more easily expanded and incorporated in data syntheses. We suggest a tiered system with priority to more easily obtained pelagic (temperature, salinity, pH) and sediment (loss on ignition, porosity, wet and dry

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80NSSC21K0413). We thank Mai Maheigan and Mary Zawoysky from the biomass) variables, as well as benthic-pelagic fluxes (sediment oxygen demand). These "core variables" can be augmented with more variables if logistics allow. Merging knowledge obtained through process-based observations with wider data coverage would improve the characterization of benthic baselines and their variability across environmental gradients. Finally, in addition to individual projects and data collection sites, coordinated international efforts similar to JGOFS and GEOTRACES should be conducted with a focus on the benthos, since traditional ship-based sampling strategies are not sufficient to understand the spatial and temporal scales in which benthic processes act.

The creation of a truly global scientific community focused on the benthos requires increased awareness of the importance of this system, opportunities for engagement of scientists with different backgrounds and from different regions, and promoting transfer of knowledge and training so that priorities of different regional communities are addressed. Creating opportunities for international training and workshops would also facilitate dialog to foster a common language among researchers from different backgrounds invested in benthic research, and to work on international collaboration projects allowing expanded application of new technologies to a wider range of environments. Addressing these challenges concomitantly will lead to improved knowledge to inform adaptation and mitigation strategies locally and globally.

Conflict of Interest

The authors declare no conflicts of interest relevant to this study.

Data Availability Statement

No data sets were used in the preparation of this manuscript.

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