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Mestrado em Biologia Marinha

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Resumo

Nos últimos anos, tem havido um reconhecimento crescente da necessidade de aprimorar as metodologias para avaliar as funções dos ecossistemas bentónicos devido ao seu papel crítico na manutenção da biodiversidade marinha e da saúde dos ecossistemas. Avaliar essas funções é essencial para compreender a dinâmica dos ecossistemas, apoiar esforços de conservação e orientar a gestão de recursos. No entanto, a complexidade e variabilidade inerentes aos ambientes marinhos apresentam desafios significativos para o desenvolvimento de abordagens amplamente aplicáveis e padronizadas. Este estudo avalia três principais metodologias — abordagens baseadas em estrutura, processos e funções — cada uma oferecendo vantagens e limitações distintas na pesquisa ecológica marinha.

As metodologias baseadas em estrutura, como a análise de características biológicas (BTA – Biological Trait Analysis), permitem perceber melhor as funções dos ecossistemas ao vincular características das espécies a processos ecológicos. A BTA concentra-se em caracterizar os componentes estruturais dos ecossistemas, incluindo a composição, abundância e características particulares das espécies, para inferir as suas contribuições relativamente às funções ecológicas. Ao examinar as relações entre as características funcionais das espécies e os processos que elas influenciam, a BTA contribui para a compreensão da biodiversidade e do funcionamento dos ecossistemas. No entanto, a padronização dos métodos baseados nas estruturas apresenta desafios significativos. A ampla gama de espécies e características requer um gasto de tempo considerável, colaboração e construção de consensos na comunidade científica para alcançar consistência nas definições das características, medições destas e na estratégia de tratamento de dados. A variabilidade dos dados e a subjectividade inerente complicam ainda mais os esforços para padronizar esses métodos. Apesar desses desafios, os métodos baseados na estrutura permanecem cruciais, especialmente quando medições diretas não estão disponíveis ou são impraticáveis. Eles fornecem uma ampla compreensão de como as espécies contribuem para as funções dos ecossistemas e são particularmente valiosos quando combinados com outras metodologias para alcançar um entendimento mais abrangente.

A integração de métodos baseados em estrutura com outras abordagens, como metodologias baseadas em processos e funções, melhora sua utilidade e eficácia. Por exemplo, a incorporação de técnicas não invasivas, como análise de DNA ambiental (eDNA) ou monitoramento por vídeo subaquático, permite a colheita de dados de interações de espécies e composição da comunidade com distúrbio mínimo. Essa integração oferece novas oportunidades para monitorização de ecossistemas e fornece uma compreensão mais robusta dos mecanismos subjacentes que impulsionam os processos ecológicos observados. Além disso, a BTA pode ser aplicada a estruturas físicas criadas pelos organismos, como refúgios e recifes, servindo como proxies funcionais e ampliando sua

aplicabilidade em diversos ambientes ecológicos. Esforços contínuos para harmonizar as definições das características e protocolos de recolha de dados ajudarão a melhorar a comparabilidade e a integração entre estudos, maximizando o potencial dos métodos baseados em estrutura na ecologia marinha.

As metodologias baseadas em processos oferecem medições diretas de atividades dinâmicas dentro dos ecossistemas bentónicos, como filtração, bioturbação, produção primária e modificação de habitats. Esses métodos abrangem tanto técnicas visuais — como sistemas de vídeo remoto iscado subaquático (BRUVs - Baited Remote Underwater Video Systems), câmeras autónomas iscadas e imagens de perfil de sedimentos (SPI – sediment profile images) — quanto sistemas controlados, como incubações e mesocosmos, para fornecer dados altamente padronizados e comparáveis. As abordagens baseadas em processos beneficiam de protocolos estabelecidos e equipamentos padronizados, permitindo a coleta de dados confiáveis e reprodutíveis em vários estudos e regiões. Por exemplo, BRUVs e câmeras autónomas iscadas capturam efetivamente comportamentos de escavadores e interações de espécies, fornecendo dados de alta resolução com um mínimo viés provocado pelo observador. Da mesma forma, as câmeras SPI oferecem visualizações detalhadas da estratigrafia do sedimento e das atividades dos organismos bentónicos, como bioturbação e bioirrigação, tornando-as adequadas para monitoramento ecológico de longo prazo.

Apesar de seu alto potencial de padronização, as metodologias baseadas em processos também enfrentam vários desafios, particularmente relacionados à complexidade operacional e analítica. O uso de ferramentas como remote operated vehicles (ROVs), autonomous underwater vehicle (AUVs) e câmeras SPI requer conhecimentos especializados, planeamento substancial e equipamentos sofisticados para garantir a recolha correcta de dados. Os custos associados a esses métodos — equipamentos, manutenção e análise de dados — podem ser proibitivos, especialmente em ambientes com recursos limitados, restringindo sua aplicação mais ampla. Além disso, embora os métodos baseados em processos forneçam medições diretas de funções específicas, estes podem não capturar todo o espectro de processos que contribuem para essas funções. Integrar metodologias baseadas em processos com abordagens baseadas na estrutura pode ajudar a superar essas limitações, proporcionando uma compreensão mais abrangente da dinâmica dos ecossistemas. Por exemplo, entender a composição de características das espécies observadas por meio de métodos visuais pode melhorar as interpretações de seus papéis ecológicos e contribuições. Esforços futuros devem-se concentrar em superar os desafios operacionais e relacionados aos custos associados a esses métodos, garantindo que sejam acessíveis a uma gama mais ampla de pesquisadores.

As metodologias baseadas em funções, particularmente aquelas que utilizam câmaras de fluxo bentónicas (BFCs - Benthic Flux Chambers), oferecem os meios mais diretos e padronizados de avaliar as funções dos ecossistemas bentónicos. As BFCs medem diretamente resultados como

ciclagem de nutrientes, estabilização de sedimentos e troca de gases, fornecendo dados de alta resolução essenciais para compreender a saúde e a dinâmica dos ecossistemas aquáticos. A principal vantagem das BFCs reside na sua capacidade de gerar observações *in situ* de sistemas relativamente não perturbados, preservando a integridade dos processos naturais e minimizando os vieses introduzidos por distúrbios amostrais. Essas câmaras demonstraram versatilidade em uma variedade de ambientes, desde habitats subtidais rasos até regiões de mar profundo, capturando processos biogeoquímicos críticos.

No entanto, apesar de suas vantagens, os métodos baseados em funções, como as BFCs, ainda são subutilizados, especialmente em escalas temporais e espaciais mais amplas. Custos elevados, a necessidade de conhecimentos especializados e desafios logísticos associados à sua implantação limitam seu uso generalizado. Para expandir a aplicação das BFCs, esforços devem ser feitos para abordar essas barreiras, como o desenvolvimento de versões mais económicas desses instrumentos e o aproveitamento de avanços tecnológicos, como capacidades de transmissão remota de dados. Incentivar a integração das BFCs com métodos complementares, como abordagens baseadas em estrutura e processos, também pode melhorar o escopo e a profundidade das avaliações ecológicas, apoiando modelos preditivos mais robustos e estratégias de conservação eficazes.

Olhando para o futuro, a investigação nesta área deve concentrar-se em ampliar a aplicação dessas ferramentas inovadoras, ao mesmo tempo em que promove colaborações interdisciplinares e parcerias para melhorar a comparabilidade dos dados em diferentes contextos. Ao integrar múltiplas metodologias, os investigadores podem capitalizar os pontos fortes de cada abordagem, proporcionando uma compreensão abrangente das funções dos ecossistemas. Essa abordagem integrada apoiará estratégias de conservação mais eficazes e decisões políticas, garantindo a preservação da biodiversidade marinha e da saúde dos ecossistemas.

Palavras-chave: Funções de ecossistemas bentônicos, metodologias estruturais, metodologias de processos, câmaras de fluxo bentônico, análise de traços biológicos, métodos de avaliação ecológica, biodiversidade marinha, conservação marinha

Abstract

Assessing benthic ecosystem functions requires methodologies that provide comprehensive, reliable, and standardized data across various settings. Structural-based methods, such as trait-based analysis (BTA), offer valuable insights into species' roles in ecosystem functioning but face challenges in standardization due to species and trait diversity. Process-based methods, including visual techniques like baited remote underwater video systems (BRUVs), autonomous baited camera landers, and sediment profile imaging (SPI) cameras, as well as controlled systems like incubations and mesocosms, deliver direct measurements with high standardization potential, although they are often constrained by operational complexity and costs. Function-based methodologies, such as benthic flux chambers (BFCs), enable precise measurements of ecosystem functions, such as nutrient cycling and gas exchange, but their broader application is limited by financial and logistical barriers. This study emphasizes the need for an integrated approach that combines these methodologies, leveraging their complementary strengths to improve the comprehensiveness and reliability of ecosystem assessments. Future research should prioritize expanding the use of innovative tools like BFCs, developing more cost-effective versions, and fostering interdisciplinary collaborations to enhance global data comparability and support conservation strategies. Such an integrated framework is crucial for generating high-quality data that inform policy decisions aimed at preserving marine biodiversity and ecosystem health.

Keywords: benthic ecosystem functions, structural-based methods, process-based methods, function-based methods, trait-based analysis (BTA), benthic flux chambers (BFCs), management, marine biodiversity

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List of Abbreviations

AUV – Autonomous Underwater Vehicle

BEF – Benthic Ecosystem Functions

BFC – Benthic Flux Chambers

BTA – Biological Traits Analysis

BRUV – Baited Remote Underwater Video Systems

eDNA – Environmental DNA

EOM – Electro-Optical-Mechanical

ROV – Remotely Operated Vehicle

SPI – Sediment Profile Imaging

CHAPTER 1: INTRODUCTION

Marine benthic ecology, pivotal for ecosystem functions through biotic and abiotic interactions, ensures marine environments' dynamic equilibrium (Griffiths et al., 2017; Villnäs et al., 2012). This study is part of the MARBEFES project, an ambitious initiative funded by the European Union's Horizon Europe program, which aims to estimate ecosystem functions and services across a broad geographic range by incorporating various habitats using a landscape approach. The project's goals underscore the significance of our research in developing a unified framework for assessing these functions and services, crucial for advancing effective management and conservation strategies globally.

Within the framework of MARBEFES, Work Package 3.4 targets the detailed exploration of benthic ecosystem functions. This work package is dedicated to developing innovative tools and methodologies that enhance our understanding and quantification of these functions, allowing us to evaluate their variability and impacts across Europe's diverse marine landscapes. The findings from this research are expected to offer new insights into the management of marine resources, potentially influencing environmental policies at national and European levels.

Benthic-pelagic coupling exemplifies the types of interactions studied within this project by facilitating carbon exchange between the seafloor and pelagic zones, influencing both local and global biogeochemical cycles (Griffiths et al., 2017; Rowe et al., 1975). Alongside the roles of benthic organisms in organic carbon burial and nutrient recycling, this process underscores the significance of carbon sequestration and biomass production in providing essential ecosystem services such as food provision and water filtration (Granek et al., 2010). Understanding the mechanisms through which benthic ecosystems deliver these services is crucial for their conservation and the sustainable management of marine resources. However, the accurate monitoring and quantification of these ecosystem functions are challenged by the diversity of benthic habitats, necessitating varied methodologies that complicate data comparison and synthesis. The lack of standardized monitoring approaches and a unified ecological lexicon further exacerbates these challenges, hindering effective policy and decision-making.

To address these challenges directly, our study delineates key ecological concepts essential for understanding benthic ecosystems, focusing on “structure”, “process”, and “function”. Structure refers to the physical and biological composition of the ecosystem, encompassing the arrangement and spatial distribution of biotic and abiotic elements within a habitat. This includes everything from sediment composition and topography to the distribution and diversity of organism communities. Process denotes the dynamic ecological activities that occur within these structures, driven by the organisms themselves. An example of such a process is bioturbation, which involves both the dispersal of sediment particles and the transport of interstitial porewater by benthic organisms. Finally, function relates to the ecological outcomes of these processes, which contribute to ecosystem stability and productivity. In this example, bioturbators would enhance biogeochemical cycling and sediment stabilization. Our research aims to not only clarify these complex interactions but also provide actionable data that can guide the sustainable management of benthic environments, thus ensuring their continued role in supporting global biodiversity and human well-being.

1. Importance of benthic ecosystems

Marine benthic ecosystems, composing the vast expanse of the ocean floor that covers an immense 362 million km² or about 70% of Earth's surface, play a pivotal role in global biodiversity and ecosystem functionality (Ramirez-Llodra et al., 2010). Derived from the Greek word for "depth," the term "benthos" classifies the rich tapestry of life residing on, in, or near the aquatic ecosystems bottom (Reynolds, 2013). This includes both flora and fauna, making the marine benthic zone a cornerstone of oceanic ecological productivity and economic potential (Walag, 2017). The benthic zone's ecological value extends beyond its biological richness; it underpins vital ecosystem goods and services, from supporting fisheries to purifying water (Gutow et al., 2014; Walag & Del Rosario, 2018).

The diversity of the benthic environment is shaped by a complex interplay of factors such as depth, light availability, temperature, salinity, and substrate type, leading to a broad spectrum of living regimes for benthic organisms, each with its unique community and ecological role (Lalli & Parsons, 1997; Smith & Smith, 2003). Figure 1 shows the ecological divisions of the seafloor based on depth and topography, along with some of their associated benthic habitats. Some of these ecological-depth divisions have well-defined boundaries, while others are more arbitrary zones. However, each benthic habitat presents distinctly different living conditions (Lalli & Parsons, 1997). Coastal areas, rich in photosynthetic activity, contrast with deep-water zones where life thrives in the absence of light, dependent on organic material settling from above—each illustrating the contrasting dynamics within the benthic landscape (Walag, 2022). This range not only illustrates the physical diversity of the seafloor but also demonstrates the significant role of environmental dynamics in shaping these habitats, with water depth being a particularly influential factor (Pilditch et al., 2015).

Within this intricate mosaic of species and habitats, the multiplicity of life forms—encompassing an array of phyla from poriferans, cnidarians, annelids, and arthropods to echinoderms, and larger vertebrates such as fish— displays not only varied physical forms but also a spectrum of life strategies. Their disparate ways of feeding, reproducing, and moving contribute to the dynamic processes that underlie the benthic zone's functionality. For example, mangroves, seagrass beds and shallow coral reefs construct extensive reefs that provide shelter and breeding grounds for numerous marine species, while echinoderms like sea urchins often play a critical role in controlling algal populations, thereby influencing nutrient cycling (Nagelkerken et al., 2000; Pearse, 2006). However, this taxonomic and trait diversity does not always correspond to functional diversity in a predictable or linear fashion (Cadotte et al., 2011; Covich et al., 2004; Hooper et al., 2005). While some species may fulfil unique roles within the ecosystem, others might have overlapping functions, creating a complex network of interactions rather than a straightforward relationship between diversity and ecosystem function.

This complexity highlights the critical need for a nuanced understanding and precise measurement of ecosystem functions to ensure effective management and conservation of these vital systems. By delving deeper into the specific roles and contributions of benthic habitats, we can better ensure the proper functionality of these environments is maintained and protected, thus

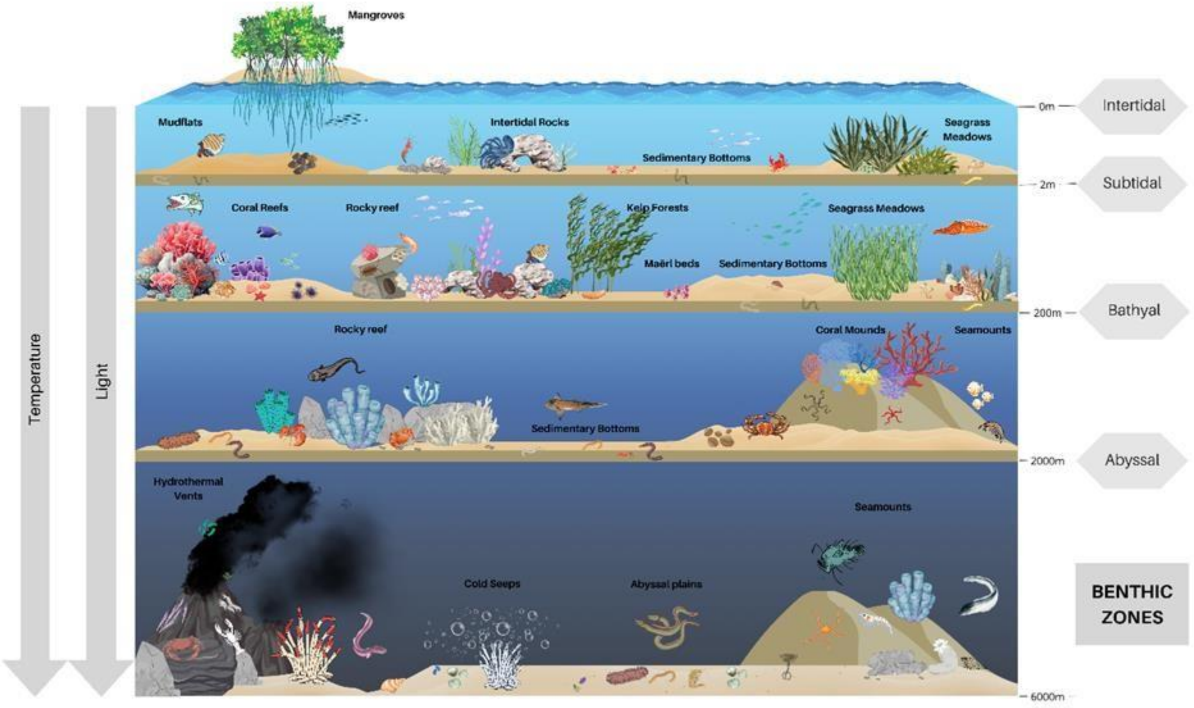

Figure 1. Overview of marine benthic zones and their associated habitats. This cross-sectional diagram depicts the diversity of marine benthic environments from the intertidal zone to the abyssal plain, illustrating key habitats such as mudflats, intertidal rocks, seagrass meadows, coral reefs, kelp forests, maërl beds, rocky reefs/outcrops, sedimentary bottoms, coral mounds, seamounts, hydrothermal vents, cold seeps, and abyssal plains. The diagram highlights the gradient of light and temperature, which significantly influence the distribution and ecological roles of benthic organisms. Each zone supports a unique community of life forms, contributing to the intricate mosaic of species and ecological processes that underpin marine ecosystem functionality. Note: The hadal zone (6000m to 11000m) has not been represented in this figure.

safeguarding the health and productivity of marine environments.

1.1. Benthic ecosystem functions and ecosystem services

The diversity of benthic habitats is intrinsically linked to their contribution to ecosystem functionality. These habitats' structures, defined by their physical and biological composition, directly influence ecosystem processes—dynamic ecological activities driven by the organisms themselves. These processes result in ecosystem functions, which are attributes related to the performance of an ecosystem and the outcomes of one or multiple processes (Lovett et al., 2005). Ultimately, these functions translate into ecosystem services (fig. 2), which are the benefits to human populations, either directly or indirectly (Costanza et al., 1997). For example, substrate types can vary widely, from hard, rocky surfaces to soft, sedimentary bottoms. Hard, rocky substrates provide critical components for building reef structures and offer sites of attachment for sessile organisms like corals, barnacles, and mussels, which remain in one place throughout their adult life. These substrates also create crevices and depressions that serve as refuges for mobile animals, protecting them from predators (Lalli & Parsons, 1997). This extensive habitat engineering supports a wide array of marine life, enhancing biodiversity and increasing ecosystem resilience and stability (Bellwood et al., 2019; Graham et al., 2013). In contrast, soft, sedimentary bottoms are home to burrowing species that play crucial roles in bioturbation. Through this process, organisms rework the sediment, enhancing nutrient cycling and sediment aeration (Queirós et al., 2013). This activity is vital for maintaining the health of the seafloor ecosystem, supporting a diversity of life forms both above and within the sediment. Another key process is organic matter decomposition, driven by microbial communities within the sediment and scavengers. This process breaks down organic material, releasing nutrients that support primary production and maintain nutrient cycles (Rieling et al., 2000).

Benthic primary production, a process performed by benthic algae and seagrasses, converts sunlight into energy, forming the base of the food web and sustaining higher trophic levels (Dierssen et al., 2010) . These habitats play a crucial role in the provision of habitat to other marine species, as well as in nutrient cycling and carbon sequestration (fig. 2)(Duarte, 2002; Unsworth et al., 2022). Seagrass meadows enhance biogeochemical cycling by trapping and holding nutrients within their dense root and rhizome systems, preventing resuspension and making nutrients available for plant uptake and microbial processing (Cullen-Unsworth & Unsworth, 2013; Duffy, 2006).This supports the growth of seagrasses and other primary producers, which provide food and habitat for diverse marine life. Through photosynthesis, seagrasses absorb CO2 and convert it into organic carbon, which is then incorporated into their biomass. Decomposed seagrass leaves contribute to long-term carbon storage in sediments, reducing atmospheric CO2 levels and mitigating climate change. The dense vegetation and root systems stabilize sediments, promoting the long-term storage of carbon in the seafloor (Röhr et al., 2018).

Furthermore, the deep seafloor, characterized by its high pressure, low temperatures, and absence of light, is formed by hundreds of millions of square kilometres of continental slopes and abyssal plains. These areas support a broad range of geological structures with varying complexities, fostering unique microbiological and faunal communities, each contributing uniquely to ecosystem functions and processes (Ramirez-Llodra et al., 2010). Seamounts, for instance, are underwater mountains that provide solid substrates for coral and sponge attachment, creating biodiverse habitats that support various marine life, from invertebrates to large pelagic species (DOSI, 2023). These structures interrupt ocean currents, creating localized upwellings that enhance nutrient availability, thus supporting high levels of primary and secondary production. The presence of these complex habitats promotes biodiversity and ecological resilience, which are crucial for maintaining ecosystem stability (Thurber et al., 2014). Hydrothermal vents, on the other hand, are hotspots of chemical energy in the deep sea, where mineral-rich water supports chemosynthetic communities. These vents host unique organisms that rely on the oxidation of chemicals like hydrogen sulphide for energy, driving primary production in an otherwise nutrient-poor environment (Thurber et al., 2014). The biogenic habitats formed around these vents, including tube worms and other specialized fauna, play a critical role in nutrient cycling and carbon sequestration, illustrating the direct link between geological structures and ecosystem functions. Abyssal plains, covering vast areas of the ocean floor, are predominantly soft-sediment habitats that support benthic processes such as bioturbation, carried out by organisms like polychaetes and echinoderms.

Collectively, these marine habitats demonstrate the integral role of structural composition in supporting ecological processes that underpin essential ecosystem functions (fig. 2). The dynamic interplay between the physical environment and biological activities in the ocean ensures the provision of vital ecosystem functions such as nutrient cycling, carbon sequestration, and habitat provision, which are fundamental to the health and sustainability of marine ecosystems.

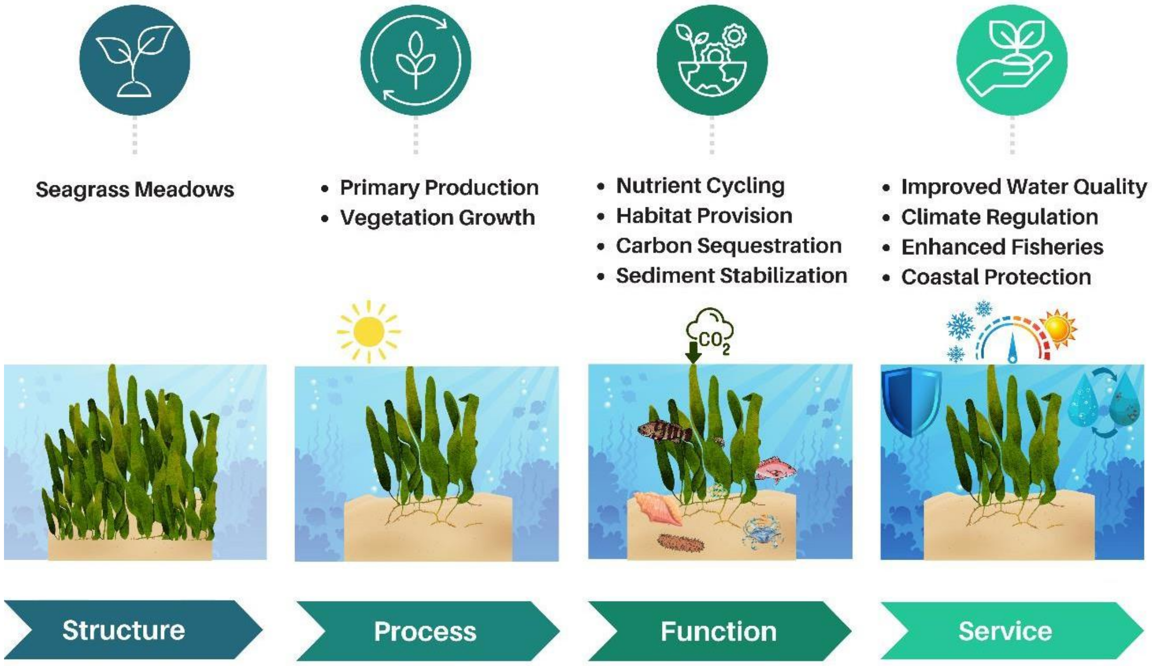

Figure 2. The relationship between structure, process, function, and service in seagrass meadows. Seagrass meadows provide the physical foundation with dense vegetation. Primary production and vegetation growth occur through photosynthesis. These processes result in crucial ecosystem functions such as nutrient cycling, habitat provision, carbon sequestration, and sediment stabilization. The benefits to human populations include improved water quality, climate regulation, enhanced fisheries, and coastal protection.

These benthic habitats provide several ecosystem services that benefit human populations. The structural complexity of rocky substrates and reef formations enhances biodiversity, which supports commercial and recreational fisheries by providing habitat for various fish species (Bellwood et al., 2004). The sediment stabilization provided by soft-bottom substrates prevents coastal erosion and protects shorelines, reducing the risk of damage to coastal infrastructure (Duarte et al., 2013). Additionally, organic matter decomposition processes, which result in nutrient cycling, enhance water quality by preventing the buildup of organic waste and maintaining clear waters, crucial for both marine life and human activities such as tourism and fishing (Rieling et al., 2000). Carbon sequestration by these habitats also plays a significant role in mitigating climate change by capturing and storing carbon dioxide, thus helping to regulate global climate patterns (Krause-Jensen & Duarte, 2016; Röhr et al., 2018)(fig. 2). This diversity illustrates the unique contributions of each environment to the functionality of marine ecosystems, offering crucial ecosystem services.

Understanding the ecosystem services provided by benthic habitats highlights the direct and indirect benefits to human societies. When communities recognize and appreciate these benefits, there is often greater support for conservation measures. This acceptance is crucial for the successful implementation of policies aimed at preserving marine ecosystems.

1.2. Threats that human activities pose towards functions and services

While benthic ecosystems offer a multitude of benefits through their ecological functions and services, these vital habitats are increasingly threatened by human activities. Such threats encompass pollution (Llacuna, 2016; Trannum et al., 2019), destructive fishing practices (Hinz et al., 2009; Lambert et al., 2014; Ramirez-Llodra et al., 2011), and climate change (Doney et al., 2009; Hoegh-Guldberg et al., 2007). Understanding these threats is crucial not only for maintaining the health and stability of marine environments but also for preserving the ecosystem services that support human societies.

Chronic pollution, including nutrient run-off, heavy metals, and plastics, severely impacts benthic habitats. Nutrient run-off from agricultural and urban areas can cause eutrophication, leading to hypoxic conditions that suffocate marine life and disrupt ecosystem processes (Diaz & Rosenberg, 2008). Heavy metals and other toxic substances accumulate in the sediment, posing long-term health risks to benthic organisms and affecting their reproductive and feeding behaviours (Chapman et al., 1998). Plastic pollution, particularly microplastics, has become pervasive in marine environments, where it can be ingested by benthic organisms, leading to physical harm and the introduction of toxic substances into the food web (Wright et al., 2013).

Overfishing and destructive fishing practices, such as trawling and dredging, have severe impacts on benthic ecosystems. Trawling disturbs the seabed, causing physical damage to habitat structures such as coral reefs and seagrass beds, which are essential for various marine species. This disturbance not only reduces biodiversity but also impairs the ecosystem functions these habitats provide, including nutrient cycling and carbon sequestration (Hiddink et al., 2017; Kaiser et al., 2006). Additionally, bycatch – the unintended capture of non-target species – further depletes marine populations and disrupts the ecological balance of benthic communities (Alverson, 1994).

Climate change poses another significant threat to benthic ecosystems. Rising sea temperatures, ocean acidification, and changes in ocean currents impact the distribution and health of benthic species. Warmer waters can lead to the bleaching and death of coral reefs, while acidification affects organisms with calcareous shells and skeletons, such as molluscs and some species of plankton (Doney et al., 2009; Hoegh-Guldberg et al., 2007). These changes can alter the composition of benthic communities, leading to the loss of biodiversity and the disruption of ecosystem functions, such as primary production and habitat provision (Gattuso et al., 2015).

2. Milestones and limitations

In recent years, there has been a significant rise in research dedicated to enhancing our understanding of benthic ecosystem functions (Bellwood et al., 2019; Elise et al., 2019; Griffiths et al., 2017; Hinz et al., 2021; Kristensen et al., 2014; Lambert et al., 2014; Link et al., 2013; Pettorelli et al., 2018). Some of these latest studies delve into the intricate relationship between biodiversity and ecosystem performance, shedding light on how diverse marine life contributes to the health and efficiency of these habitats (Belley & Snelgrove, 2016; Cadotte et al., 2011) and introducing innovative methodologies to explore this relationship.

Among these, the Benthic Trait-Based Approach (BTA) stands out for its focus on the traits of benthic organisms, providing a complementary perspective on how biodiversity underpins ecosystem functions (De Juan et al., 2022; Hinz et al., 2021). This methodological diversity, including both broad-scale biodiversity studies and trait-focused analyses, underscores the multifaceted nature of ecological research in benthic environments.

Significant progress has been made in identifying and studying various functions and processes within benthic environments. Our knowledge of key habitats, including seagrass meadows (Burgos et al., 2017; Dolbeth et al., 2013; Harborne et al., 2006) and coral reefs (Micheli et al., 2014; Richardson et al., 2020; Tebbett et al., 2021), has particularly expanded, offering new insights into their ecological significance and contributions. These new insights not only underscore their roles in maintaining marine biodiversity but also highlight their critical contributions to human well-being (Moberg & Folke, 1999; Mtwana Nordlund et al., 2016; Orth et al., 2020; Ruiz-Frau et al., 2017; Sanchez-Vidal et al., 2021; Woodhead et al., 2019). For example, by supporting fisheries and protecting coastlines from erosion, seagrass meadows and coral reefs directly sustain economic activities and communities that rely on marine resources. Furthermore, their ability to sequester carbon plays a vital role in climate regulation, underlining the interconnectedness of benthic habitats with global environmental health. Conversely, less accessible habitats, particularly those along the continental slope and deeper ocean regions, have received comparatively minimal attention. The logistical and technological demands of studying these areas, compounded by the substantial financial investment required for deep-sea research, have been significant barriers (Brandt et al., 2016; Glover et al., 2010). Despite these obstacles, this area of research has seen a notable increase propelled by advancements in technology that have begun to bridge these gaps (Brandt et al., 2016; Feng et al., 2022).

2.1. Addressing conceptual variation in benthic ecosystem studies

The ongoing discourse around how ecosystem functions are defined has long been a source of contention due to unclear and overlapping terminologies (Paterson et al., 2012; Roe et al., 2012). This challenge is particularly acute in marine studies, including benthic environments, where disparate definitions hinder effective comparison and synthesis of research findings. The term “function” itself lacks a universally accepted definition, thereby clouding our understanding of its ecological and conservation implications (Bellwood et al., 2019). The growing adoption of trait-based ecology, which focuses on the relationship between species’ ecological traits and ecosystem functionality, further emphasizes the need for precise language (Mcgill et al., 2006; Violle et al., 2007).

Pettorelli et al. (2018) illustrates these terminological challenges by showing how “ecosystem functions” often blend with or are mistaken for “ecosystem services” (Lamarque et al., 2011; Srivastava & Vellend, 2005), “ecological processes” (Lawton & Brown, 1994), and “ecosystem processes” (Dominati et al., 2010; Mace et al., 2012). Each term carries its own definitions and applications across different ecological studies, highlighting the complexity and potential for confusion. Moreover, Paterson et al. (2012) argue for a deeper understanding of these terms across disciplines, noting their varied use in environmental science and policy. This complexity is further magnified by the adoption of similar or identical terms across different disciplines, complicating the intersection between environmental science and policymaking. The authors describe a co-evolution of terminology and scientific understanding that often precedes and shapes policy decisions, emphasizing how the diverse definitions of “ecosystem functions” and their relation to “ecosystem services” can lead to varied interpretations in policy contexts. Such differences in terminology can result in policies that may not fully capture the scientific nuances of ecosystem functionality, potentially leading to misaligned or ineffective management strategies.

This variability and broad interpretation of ecosystem functions underscore the urgent need for establishing a standardized terminological framework in marine ecosystem research, particularly for benthic studies. Clarity in defining ecosystem functions and services could significantly enhance the comparability and integration of research findings and support more coherent policy development. By “speaking the same language,” researchers, policymakers, and practitioners can more effectively share knowledge, synthesize findings, and collaborate on addressing the complex challenges facing marine ecosystems. Moving forward, the establishment of a consensus-based framework for terminology in marine ecology, facilitated through workshops, symposiums, and collaborative publications, can serve as a cornerstone for this endeavour. Such efforts should aim not only to define terms but also to elucidate the scope and limitations of these definitions, ensuring they are inclusive and adaptable to the breadth of research within the field. This shared language will enable us to weave individual studies into a larger, more comprehensible tapestry of marine ecosystem understanding.

2.2. Methodological limitations

This fragmentation is further exacerbated by the methodological diversity present in benthic ecosystem studies. Researchers often employ varied approaches tailored to specific habitats or research objectives, making cross-study comparisons and data aggregation challenging. For instance, studies on coral reefs may utilize remote sensing and diver surveys to assess habitat structure and function (Hedley et al., 2016), while deep-sea research relies on submersibles and sophisticated oceanographic instruments to explore the abyssal plains (Brandt et al., 2016). This variance in methodologies, although necessary due to the distinct nature of each habitat, hinders the creation of a cohesive picture of benthic ecosystem functionality on a global scale. Additionally, the endeavour to achieve a holistic understanding is often constrained by the sheer diversity of benthic habitats, from shallow seagrass beds to the depths of the ocean floor. Each habitat presents unique challenges in terms of accessibility, requiring specialized equipment and substantial financial resources for thorough investigation.

The quest for a more integrated view of benthic ecosystems also grapples with the temporal and spatial scales at which these systems operate. Many studies focus on localized, short-term observations (Raffaelli, 2006; Rapacciuolo & Blois, 2019), which may not capture the full dynamism of ecosystem processes that unfold over larger spatial extents and longer temporal durations. As a result, our current knowledge tends to be piecemeal, lacking the scalability necessary to inform broader ecological models or global conservation strategies.

To navigate these challenges, future research must strive for greater standardization in methodologies and terminologies used across benthic ecosystem studies. This effort could be facilitated by the development of universally accepted frameworks that allow for the integration of data from disparate studies, thereby enhancing our collective ability to model ecosystem functions and predict responses to environmental changes. Furthermore, embracing emerging technologies and interdisciplinary collaboration could unlock new pathways for enhancing our understanding and management of marine benthic ecosystems.

In light of the challenges outlined, including the need for methodological standardization and the expansion of research scopes to encompass the true dynamism of benthic ecosystems, this study proposes a comprehensive approach designed to bridge these gaps and foster progress within the field.

3. Objectives

Our objectives are twofold: first, to conduct a thorough literature review of existing methodologies for assessing ecosystem processes and functions within benthic environments, identifying their core advantages and limitations. This review will serve as an essential foundation, compiling an inventory of methods that have been applied across different benthic studies. Second, we aim to critically evaluate the suitability of these methods—and possible combinations thereof—for conducting cost-effective, large-scale sampling that can yield standardized, comparable data. This evaluation will not only consider the logistical aspects of various methodologies but also their ability to address the temporal and spatial scales that are crucial for understanding ecosystem processes comprehensively. Furthermore, this study seeks to highlight emerging technologies and interdisciplinary approaches that hold promise for improving how we assess ecosystem functions across expansive spatial and temporal scales.

By providing a critical evaluation of current methods, proposing integrative research strategies, and embracing technological advancements, we aspire to lay the groundwork for a new perspective of benthic ecosystem studies. This holistic approach will not only enhance our ability to comprehend the complex interplay of processes within these ecosystems but also equip policymakers and conservationists with the insights needed to protect these vital components of the marine environment effectively.

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CHAPTER 2: A COMPREHENSIVE REVIEW OF EXISTING AND NEW METHODS AND APPROACHES TO ASSESS BENTHIC ECOSYSTEM FUNCTIONS

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Keywords: benthic ecosystem functions, ecosystem processes, structure, methodologies, biological traits.

Abstract

Assessing benthic ecosystem functions requires methodologies that provide comprehensive, reliable, and standardized data across various settings. Structural-based methods, such as trait-based analysis (BTA), offer valuable insights into species' roles in ecosystem functioning but face challenges in standardization due to species and trait diversity. Process-based methods, including visual techniques like baited remote underwater video systems (BRUVs), autonomous baited camera landers, and sediment profile imaging (SPI) cameras, as well as controlled systems like incubations and mesocosms, deliver direct measurements with high standardization potential, although they are often constrained by operational complexity and costs. Function-based methodologies, such as benthic flux chambers (BFCs), enable precise measurements of ecosystem functions, such as nutrient cycling and gas exchange, but their broader application is limited by financial and logistical barriers. This study emphasizes the need for an integrated approach that combines these methodologies, leveraging their complementary strengths to improve the comprehensiveness and reliability of ecosystem assessments. Future research should prioritize expanding the use of innovative tools like BFCs, developing more cost-effective versions, and fostering interdisciplinary collaborations to enhance global data comparability and support conservation strategies. Such an integrated framework is crucial for generating high-quality data that inform policy decisions aimed at preserving marine biodiversity and ecosystem health.

Keywords: benthic ecosystem functions, structural-based methods, process-based methods, function-based methods, trait-based analysis (BTA), benthic flux chambers (BFCs), management, marine biodiversity

Introduction

Benthic fauna, residing on the ocean floor—a vast expanse covering 362 million km² of the 510 million km² that constitutes Earth's surface (Ramirez-Llodra et al., 2010)—play a pivotal role in the functionality of marine ecosystems. They influence carbon, nitrogen, and phosphorus fluxes, thus affecting elemental ecosystem dynamics (Ehrnsten et al., 2022). The diversity of benthic habitats is intrinsically linked to their contribution to ecosystem functionality. For example, sandy areas, despite their apparent simplicity, often serve as critical zones for juvenile fish and invertebrate larvae, contributing to species development and energy transfer in the ecosystem in coastal waters (Menéndez et al., 2023). On the other hand, more complex ecosystems like coral reefs provide extensive habitat engineering, supporting a wide array of marine life and enhancing biodiversity. This in turn increases ecosystem resilience and stability (Bellwood et al., 2019; Graham et al., 2013). Furthermore, the deep seafloor is formed by hundreds of millions of square kilometres of continental slopes and abyssal plains. They support a broad range of geological structures with varying complexities, supporting unique microbiological and faunal communities (Ramirez-Llodra et al., 2010). This diversity of benthic habitats illustrates the unique contributions of each to the functionality of marine ecosystems, offering crucial ecosystem services from shoreline protection, water quality improvement, fisheries resources, and habitat and food for migratory and resident animals (Levin et al., 2001). Yet, human activities like trawling, waste disposal and climate change threaten these ecosystems, impairing their long-term functionality (Hinz et al., 2009; Lambert et al., 2014; Ramirez-Llodra et al., 2011) and the ecosystem services they provide.

For a comprehensive understanding of benthic ecosystems' diversity and their critical roles in marine ecosystem functionality, it becomes of great importance to delve deeper into the availability of monitoring tools and quantification methods (Bellwood et al., 2019; Ehrnsten et al., 2022). Gaining insights into how each different benthic habitat contributes to the overall functionality of the ecosystem and consequently to the benefits we derive from them in the form of ecosystem services, underscores the significance of addressing the threats that endanger their sustainability (Hinz et al., 2009). This depth of understanding is essential, not only for quantifying the contribution of diverse functions to the health and resilience of the ecosystem, but also for informing and refining conservation strategies and management practices (Lambert et al., 2014). By integrating these insights into policy and decision-making, we can ensure the sustainable use of marine resources, protect biodiversity, and maintain the ecological processes that underpin ecosystem services critical to human and environmental well-being (European Parliament and Council, 2008). This comprehensive approach not only facilitates the achievement of Good Environmental Status as defined by the European Marine Strategy Framework Directive, but also targets a global strategy to standardize methods and ensure data comparability (European Parliament and Council, 2008).

Among these, the Biological Traits Analysis (BTA) stands out for its focus on the traits of benthic organisms, providing a complementary perspective on how biodiversity underpins ecosystem functions (De Juan et al., 2022; Hinz et al., 2021). This methodological diversity, including both broad-scale biodiversity studies and trait-focused analyses, underscores the multifaceted nature of ecological research in benthic environments and the application of a seascape approach (Boström et al., 2011). The seascape approach refers to the analysis and management of ecological processes at the scale of entire seascapes, rather than isolated habitats or smaller geographic units. By considering ecological interactions and biodiversity patterns across large spatial scales, the seascape approach allows for a more comprehensive understanding of ecosystem dynamics. This is particularly relevant in broad-scale biodiversity studies, where the goal is to capture the complexity of ecological networks and their contributions to ecosystem services. The seascape perspective also facilitates the identification of key areas for conservation and informs more effective management strategies by considering the connectivity between different marine habitats (Boström et al., 2011).

Significant progress has been made in identifying and studying various functions and processes within benthic environments. Our knowledge of key habitats, including seagrass meadows (Burgos et al., 2017; Dolbeth et al., 2013; Harborne et al., 2006) and coral reefs (Micheli et al., 2014; Richardson et al., 2020; Tebbett et al., 2021), has particularly expanded, offering new insights into their ecological significance and contributions. These new insights not only underscore their roles in maintaining marine biodiversity but also highlight their critical contributions to human well-being (Moberg & Folke, 1999; Mtwana Nordlund et al., 2016; Orth et al., 2020; Ruiz-Frau et al., 2017; Sanchez-Vidal et al., 2021; Woodhead et al., 2019). For example, by supporting fisheries and protecting coastlines from erosion, seagrass meadows and coral reefs directly sustain economic activities and communities that rely on marine resources. Furthermore, their ability to sequester carbon plays a vital role in climate regulation, underlining the interconnectedness of benthic habitats with global environmental health.

Conversely, less accessible habitats, particularly those along the continental slope and deeper ocean regions, have received comparatively minimal attention. The logistical and technological demands of studying these areas, compounded by the substantial financial investment required for deep-sea research, have been significant barriers (Brandt et al., 2014; Glover et al., 2010). Despite these obstacles, this area of research has seen a notable increase propelled by advancements in technology that have begun to bridge these gaps (Brandt et al., 2016; Feng et al., 2022).

However, as we navigate through this expanded body of knowledge, the question persists: Do these studies address ecosystem “processes” or “functions”? Clarifying this distinction is crucial for aligning research outcomes with the ecosystem services they support. Although numerous studies have ventured into this debate proposing definitions tailored to specific ecosystems or broader (Bellwood et al., 2019; Paterson et al., 2012; Pettorelli et al., 2018), more inclusive terminologies and consensus remains elusive. Most discussions, while insightful, tend to be ecosystem-specific, thereby limiting their applicability in fostering a unified understanding across different marine environments.

This fragmentation is further exacerbated by the methodological diversity present in benthic ecosystem studies. Researchers often employ varied approaches tailored to specific habitats or research objectives, making cross-study comparisons and data aggregation challenging. For instance, studies on coral reefs may utilize remote sensing and diver surveys to assess habitat structure and function (Hedley et al., 2016), while deep-sea research relies on submersibles and sophisticated oceanographic instruments to explore the abyssal plains (Brandt et al., 2016). This variance in methodologies, although necessary due to the distinct nature of each habitat, hinders the creation of a cohesive picture of benthic ecosystem functionality on a global scale. Additionally, the endeavour to achieve a holistic understanding is often constrained by the sheer diversity of benthic habitats, from shallow seagrass beds to the depths of the ocean floor. Each habitat presents unique challenges in terms of accessibility, requiring specialized equipment and substantial financial resources for thorough investigation.

The quest for a more integrated view of benthic ecosystems also grapples with the temporal and spatial scales at which these systems operate. Many studies focus on localized, short-term observations (Raffaelli, 2006; Rapacciuolo & Blois, 2019), which may not capture the full dynamism of ecosystem processes that unfold over larger spatial extents and longer temporal durations. As a result, our current knowledge tends to be piecemeal, lacking the scalability necessary to inform broader ecological models or global conservation strategies.

To navigate these challenges, future research must strive for greater standardization in methodologies and terminologies used across benthic ecosystem studies. This effort could be facilitated by the development of universally accepted frameworks that allow for the integration of data from disparate studies, thereby enhancing our collective ability to model ecosystem functions and predict responses to environmental changes. Furthermore, embracing emerging technologies and interdisciplinary collaboration could unlock new pathways for enhancing our understanding and management of marine benthic ecosystems.

In light of the challenges outlined, including the need for methodological standardization and the expansion of research scopes to encompass the true dynamism of benthic ecosystems, this study proposes a comprehensive approach designed to bridge these gaps and foster progress within the field. Our objectives are twofold: first, to conduct an extensive qualitative literature review of existing methodologies for assessing ecosystem processes and functions within benthic environments, identifying their core advantages and limitations. This review will serve as an essential foundation, compiling an inventory of methods that have been applied across different benthic studies. Second, we aim to critically evaluate the suitability of these methods—and possible combinations thereof—for conducting cost-effective, large-scale sampling that can yield standardized, comparable data. This evaluation will not only consider the logistical aspects of various methodologies but also their ability to address the temporal and spatial scales that are crucial for understanding ecosystem processes comprehensively. Furthermore, this study seeks to highlight emerging technologies and interdisciplinary approaches that hold promise for improving how we assess ecosystem functions across expansive spatial and temporal scales.

By providing a critical evaluation of current methods, proposing integrative research strategies, and embracing technological advancements, we aim to lay the groundwork for a new perspective on benthic ecosystem studies. It is important to clarify that this study does not focus on benthic habitat mapping through remote sensing techniques. While some of the methods discussed may serve dual purposes, our primary aim is to explore techniques that assess the functions of organisms, communities, and habitats. Although habitat mapping is a prerequisite for extrapolating measurements made on finer scales, broad-scale mapping techniques are beyond the scope of this paper. Instead, we concentrate on methods that directly or indirectly access functional aspects, acknowledging that some structural approaches discussed may also provide functional insights.

This research is conducted as part of the MARBEFES project (Marine Biodiversity and Ecosystem Functioning for Ecosystem Services), specifically contributing to Work Package 3: Biodiversity and Ecosystem Tools. The findings are relevant to the project's goal of developing and refining tools to assess and monitor marine biodiversity and ecosystem functions, ultimately supporting the sustainable management of marine resources. This holistic approach enhances our understanding of the complex interplay of processes within these ecosystems and equips policymakers and conservationists with the insights needed to protect these vital components of the marine environment effectively.

Defining Ecosystem Functions: Terms and Methodologies

The ongoing discourse around how ecosystem functions are defined has long been a source of contention due to unclear and overlapping terminologies (Paterson et al., 2012; Roe et al., 2012). This challenge is particularly acute in marine studies, including benthic environments, where disparate definitions hinder effective comparison and synthesis of research findings. The term "function" itself lacks a universally accepted definition, thereby clouding our understanding of its ecological and conservation implications (Bellwood et al., 2019). The growing adoption of trait-based ecology, which focuses on the relationship between species' ecological traits and ecosystem functionality, further emphasizes the need for precise language (Mcgill et al., 2006; Violle et al., 2007).

Pettorelli et al. (2018) illustrates these terminological challenges by showing how "ecosystem functions" often blend with or are mistaken for "ecosystem services" (Lamarque et al., 2011; Srivastava & Vellend, 2005), "ecological processes" (Lawton & Brown, 1994), and "ecosystem processes" (Dominati et al., 2010; Mace et al., 2012). Each term carries its own definitions and applications across different ecological studies, highlighting the complexity and potential for confusion. Moreover, Paterson et al. (2012) argue for a deeper understanding of these terms across disciplines, noting their varied use in environmental science and policy. This complexity is further magnified by the adoption of similar or identical terms across different disciplines, complicating the intersection between environmental science and policymaking. The authors describe a co-evolution of terminology and scientific understanding that often precedes and shapes policy decisions, emphasizing how the diverse definitions of "ecosystem functions" and their relation to "ecosystem services" can lead to varied interpretations in policy contexts. Such differences in terminology can result in policies that may not fully capture the scientific nuances of ecosystem functionality, potentially leading to misaligned or ineffective management strategies.

The broad interpretation of ecosystem functions in marine research highlights the need for a standardized terminological framework, particularly for benthic studies (Borja et al., 2010; Costanza et al., 1997). Clear definitions of ecosystem functions and services would enhance the comparability and integration of research findings, supporting more coherent policy development (Potschin & Haines-Young, 2016). A consensus-based framework, developed through workshops, symposiums, and collaborative publications, can help establish a common language for marine ecology (Díaz et al., 2015). These efforts should aim not only to define terms but also to clarify their scope and limitations, ensuring they are adaptable to diverse research needs (Borja et al., 2010). A shared language would allow researchers, policymakers, and practitioners to effectively communicate, synthesize findings, and collaborate on addressing the challenges facing marine ecosystems.

Due to these terminological inconsistencies and the reliance on diverse proxies, accurately measuring ecosystem functions has historically presented significant challenges. Paterson et al. (2012) also discusses the implications of proxy use, noting that while necessary, these often lead to errors in analysis due to oversimplifications. For instance, the process of photosynthesis, involving complex biochemical pathways, provides critical ecosystem functions such as carbon fixation and oxygen production. Proxies like PAM fluorescence measurements, which assess energy transfer through photochemical pathways in chloroplasts, are frequently used to estimate biomass or photosynthetic activity (Consalvey et al., 2005; Hicks et al., 2011; Jesus et al., 2006). However, this method relies on assumptions that may not fully capture the nuances of ecosystem functions, blurring the lines between ecological processes and functions. Such measures demonstrate the intricate relationship between proxy-based assessments and ecosystem function evaluations, emphasizing the need for clear definitions and methodological precision.

A similar issue arises within the Biological Traits Analysis (BTA), where trait diversity is often equated with functional diversity, contributing to ecosystem functions. This assumption can be problematic because studies sometimes claim to work on ecosystem functions without clearly defining or quantifying them (Petchey & Gaston, 2006). For example, while BTA can provide valuable insights into the relationship between species traits and ecosystem processes, the connection to actual ecosystem functions is often implied rather than explicitly demonstrated. This can lead to a loose and unspecific link between trait diversity and functional outcomes, underscoring the need for precise definitions and robust methodologies.

To address these challenges from a methodological viewpoint, our study delineates key ecological concepts essential for understanding benthic ecosystems, focusing on “structure”, “process”, and “function”. This approach distinguishes between what different methods actually measure: the physical and biological composition of the ecosystem (structure), the activities or actions related to ecological processes (activity related to a process), and the ecological outcomes as directly measured fluxes resulting from both structure and activity. This distinction is not merely academic but has practical implications for ecosystem research and management as it enables more precise measurements, enhances methodological approaches, and facilitates interdisciplinary research (Banerjee et al., 2013; De Groot et al., 2002; Fu et al., 2013).

For example, preserving the structure (like maintaining vegetation cover) is essential for supporting the processes (such as pollination) that lead to vital ecosystem functions (like food production and biodiversity support) (Banerjee et al., 2013). Therefore, *structure* refers to the physical and biological composition of the ecosystem, encompassing the arrangement and spatial distribution of biotic and abiotic elements within a habitat. This includes everything from sediment composition and topography to the distribution and diversity of organism communities. *Ecosystem process* denotes the dynamic ecological activities driven by organisms within these structures, such as bioturbation, which involves both sediment reworking and bioirrigation by benthic organisms (Maire et al., 2008), contributing to ecosystem functions. Finally, *ecosystem function* relates to the ecological outcomes of these processes — attributes related to the performance of an ecosystem that is the consequence of one or of multiple ecosystem processes (Lovett et al., 2006) —, which contribute to ecosystem stability and productivity. In the case of the bioturbation process, the functions are manifested as the stabilization of sediment and the enhancement of biogeochemical cycling of carbon and nutrients.

Understanding these refined definitions is crucial for framing our research objectives and guiding the selection and evaluation of methodologies used to assess and quantify the integral roles of benthic environments. By clearly defining the terms “structure”, “process”, and “function”, we can more accurately determine what we are actually measuring and how we are measuring ecosystem functions either through proxies or directly. This clarity helps in evaluating whether our measurements represent proxy or absolute values of ecosystem functions. For instance, assessing bioturbation might involve measuring sediment reworking rates (a proxy measure) or directly quantifying the enhancement of biogeochemical cycles (an absolute measure). Linking these definitions directly to our methods ensures that our study's objectives—such as understanding the impacts of various benthic processes on ecosystem stability—are precisely addressed through robust and well-defined methodologies.

As a result, a clear categorization of the methodologies employed in marine ecosystem research becomes indispensable. We therefore categorize these methodologies into three distinct types, each addressing different aspects of ecosystem analysis **(**fig. 1):

1. **Type 1. Structural-based methodologies**: These methodologies primarily evaluate the physical and compositional aspects of ecosystems, focusing on the architecture and configuration of benthic habitats. They examine the arrangement of biotic and abiotic elements to establish a baseline understanding of the habitat's structural integrity and variability. While these methodologies often involve the extraction of physical samples from the ecosystem, such as through substrate analysis, they also encompass non-invasive methods, including image observations and trait-based analyses. Image observations provide valuable data on the spatial distribution and structural complexity of benthic habitats, as well as some of the species inhabiting the photographed habitat. BTA can be applied to the resultant data from these image observations, as well as to the extractive type samples, translating structural information into estimations of ecological processes, subsequently linked to specific ecosystem functions (Hinz et al., 2021). This approach allows researchers to infer how structural characteristics influence broader ecological dynamics and contribute to the functionality of the ecosystem.

2. **Type 2. Process-based methodologies:** Focused on the dynamic ecological processes that underpin ecosystem functionality. These methodologies assess these processes primarily through both *in-situ* and *ex-situ* observations and measurements. Key tools used include sensors, (baited) underwater surveillance cameras, and benthic flux chambers. These tools are instrumental in examining processes such as primary production, scavenging, and bioturbation (Dunlop et al., 2021; Migné et al., 2004; Solan et al., 2004a). By understanding these ecological processes, researchers can better determine how ecosystems sustain their resilience and productivity, thereby providing insights into the mechanisms that support ecosystem health and stability.

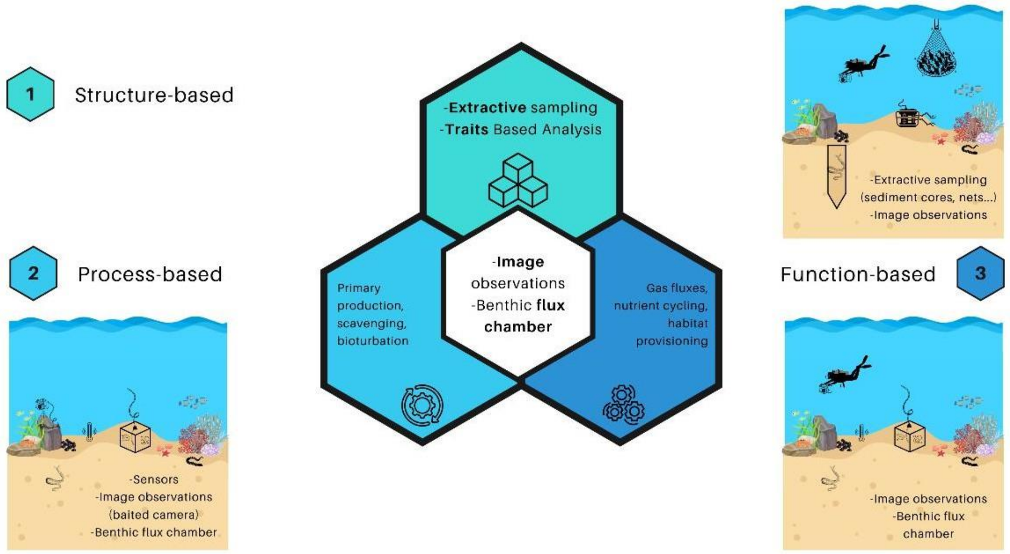


Figure 1. Overview of Methodologies for Evaluating Benthic Environments. Illustration of examples of the three types of methodologies: (1) Structural-based methodologies focus on physical composition of the ecosystem; (2) Process-based methodologies focused on the dynamic ecological processes that underpin ecosystem functionality; (3) Function-based methodologies which measure ecosystem functions directly. The central hexagon highlights tools and techniques common to multiple types of methodologies, emphasizing the interconnected nature of these approaches and how the categorization of certain methodologies can vary depending on the research objective.

3. **Type 3. Function-based methodologies**: This category focuses on the direct measurement of ecosystem functions and may also incorporate the measurement of associated ecosystem processes, either directly or indirectly. The specific objective of the study often determines whether a method is classified under this category or as a Type 2 process-based methodology. For example, benthic flux chambers can be utilized to measure primary production in terms of overall ecosystem productivity -a process- (Migné et al., 2004), or more specifically, they can be used to measure the flow of gases within the chamber which might not be directly related to primary productivity assessment but is crucial for understanding specific ecosystem functions like gas exchange rates (Villnäs et al., 2012). This distinction highlights how methodologies can be adapted to focus either on broader process dynamics or specific functional outcomes, depending on the research goals.

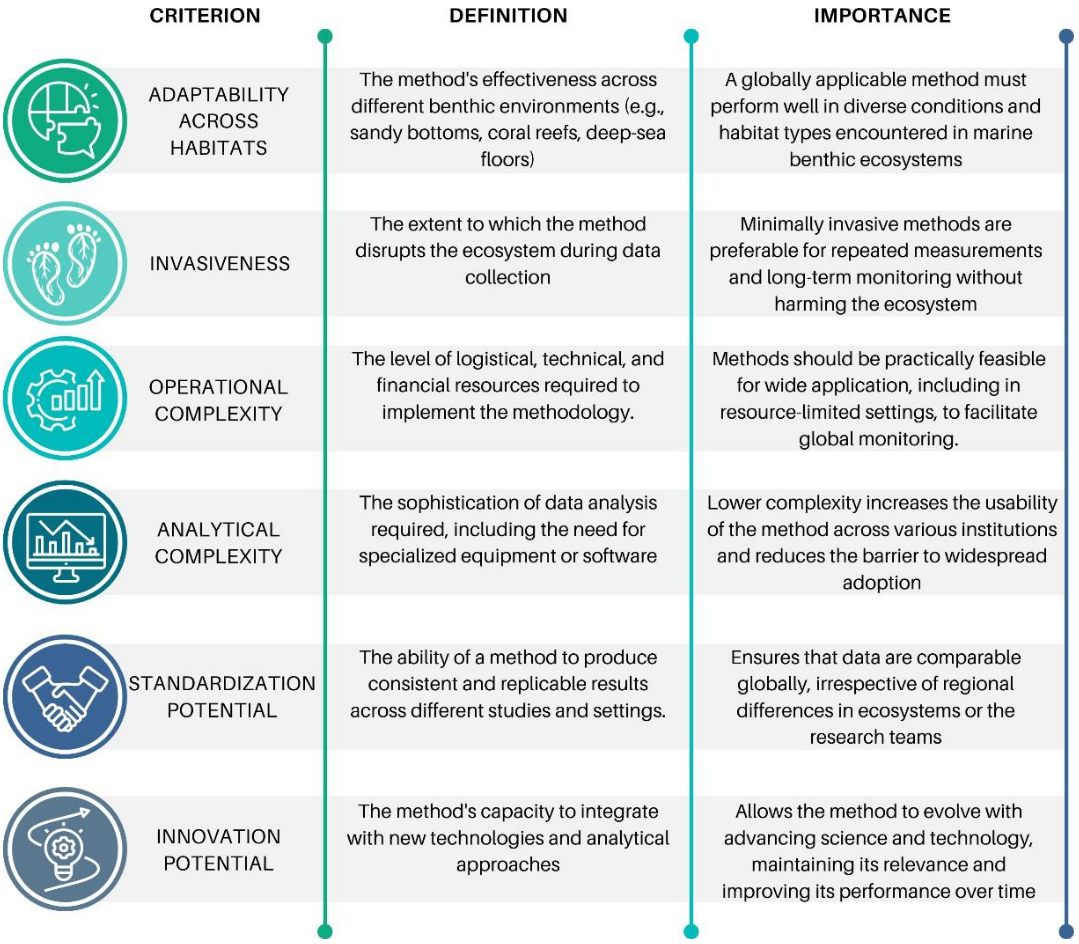
In light of these considerations, this study’s primary objective is to conduct a rigorous evaluation and comparison of methodologies used to quantify ecosystem functions in benthic environments, focusing on their standardization potential, operational and analytical complexities, and adaptability. Our goal is to pinpoint the most effective methods that provide reliable, reproducible, and scalable metrics suitable for broad-scale ecosystem assessments. Such metrics are crucial for developing a global indicator of benthic ecosystem functions, which will ultimately inform and enhance conservation strategies and management practices, ensuring the sustainability of marine benthic ecosystems worldwide.

Materials and methods

Evaluation Criteria for Methodologies in Quantifying Benthic Ecosystem Functions

To enhance the precision and relevance of our study, we have defined a set of criteria crucial for evaluating various methodologies used to assess ecosystem functions within benthic environments. These criteria are integral to selecting methodologies capable of contributing robustly to a global indicator of benthic ecosystem functions.

The criteria address both the scientific rigor required for accurate and reliable data and the practical applicability necessary for global scalability. This dual focus ensures that selected methodologies can be effectively implemented across diverse global contexts, supporting the development of a universally applicable framework.



CRITERION	DEFINITION	IMPORTANCE
ADAPTABILITY ACROSS HABITATS	The method's effectiveness across different benthic environments (e.g., sandy bottoms, coral reefs, deep-sea floors)	A globally applicable method must perform well in diverse conditions and habitat types encountered in marine benthic ecosystems
INVASIVENESS	The extent to which the method disrupts the ecosystem during data collection	Minimally invasive methods are preferable for repeated measurements and long-term monitoring without harming the ecosystem
OPERATIONAL COMPLEXITY	The level of logistical, technical, and financial resources required to implement the methodology.	Methods should be practically feasible for wide application, including in resource-limited settings, to facilitate global monitoring.
ANALYTICAL COMPLEXITY	The sophistication of data analysis required, including the need for specialized equipment or software	Lower complexity increases the usability of the method across various institutions and reduces the barrier to widespread adoption
STANDARDIZATION POTENTIAL	The ability of a method to produce consistent and replicable results across different studies and settings.	Ensures that data are comparable globally, irrespective of regional differences in ecosystems or the research teams
INNOVATION POTENTIAL	The method's capacity to integrate with new technologies and analytical approaches	Allows the method to evolve with advancing science and technology, maintaining its relevance and improving its performance over time

Figure 2. Comprehensive overview of the criteria used to evaluate the suitability of various methodologies for quantifying ecosystem functions in benthic environments. Each criterion is defined with its corresponding importance, reflecting its contribution to ensuring the methods are scientifically rigorous and practically applicable globally. This evaluation framework is crucial for developing a global indicator of benthic ecosystem functions, facilitating standardized, reliable, and scalable ecosystem assessments.

Methodological Evaluation Process

Our evaluation employs these criteria to systematically review and score methodologies identified in the literature. These criteria, detailed in Table 1, involves a qualitative assessment that facilitates direct comparison and nuanced discussion regarding each methodology's merits and limitations. Through this evaluation, we aim to pinpoint the most effective techniques for broad implementation, highlighting areas that need innovation or further research.

By applying these criteria, we aim to establish a framework that will significantly enhance the capacity to monitor and sustain marine ecosystem health globally. The assessment of methodologies delineated in this section is designed to inform targeted decision-making in marine conservation, ensuring that strategies are based on the most reliable and applicable scientific data available.

Literature Review

The methodologies used to quantify benthic ecosystem functions were evaluated using an integrated approach (fig. 3) that combines AI-enhanced tools with traditional research databases. Ensuring a consistent application of terminology and theoretical frameworks was a priority throughout the research to maintain the rigor and clarity of our analysis.

Data Search and Article Selection

The literature review commenced with a comprehensive data search using advanced AI platforms such as Scite.ai and Connected Papers, along with established scholarly databases like Google Scholar. The searches were guided by specific keywords including “methodologies”, “benthic”, “ecosystem functions”; process-specific terms like “bioturbation”, “scavenging”, and “filtration”, as well as function-specific terms such as “gas fluxes,” “nutrient cycling,” and “habitat provision”, among others. This initial filtering aimed to capture studies relevant to ecosystem processes and functions within these specific habitats.

Initial Screening

Articles initially chosen based on their relevance to the designated keywords underwent a further screening process. This phase involved a meticulous review of the research objectives outlined in each study, followed by an examination of the methodologies detailed in the "Methods" section of the papers. This ensured that the chosen articles utilized equipment and approaches relevant to our study’s needs. AI tools, such as dashboards within Scite.ai and mainly Chat.pdf, were employed to scan large quantities of articles rapidly, focusing on those that aligned with the specific objectives of our study—mainly, studies where ecosystem functions or processes were assessed and quantified. This tool's algorithm is designed to pinpoint relevant information within articles to answer questions from the user, providing page references for extracted data. To ensure accuracy, the information provided by these algorithms was meticulously verified by manually checking the referenced pages in the original articles. This double-checking process ensuring accurate extraction and interpretation by the AI and maintaining the integrity and reliability of our literature review.

Detailed Evaluation and Selection

From an initial pool of approximately 116 articles, about 71 were deemed suitable based on their methodological alignment with our research criteria. Articles that provided detailed insights into the operational and analytical methodologies, particularly those detailing equipment used in sampling and analysis, were prioritized. In total 44 peer reviewed articles were selected for the final evaluation providing a broad spectrum of current methodologies used. The studies selected can be viewed as exemplifier for the different methodologies and

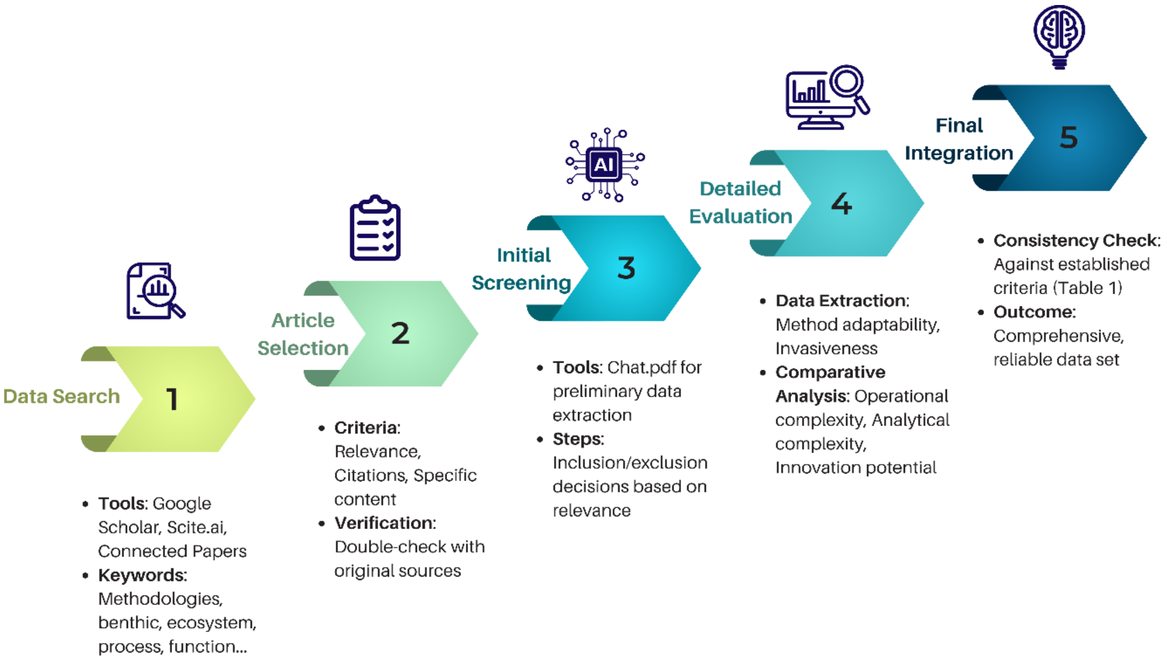


Figure 3. Workflow of the Literature Review Process for Evaluating Methodologies in Benthic Ecosystem Studies. Outlined structure of the systematic approach used for sourcing, evaluating, and integrating scientific articles into the research framework. The process begins with a comprehensive data search using platforms such as Google Scholar and Scite.ai, followed by article selection based on predefined relevance criteria. Initial screening ensures only pertinent articles proceed to detailed evaluation, where data extraction and comparative analysis are conducted. The final step involves integrating these findings into the existing body of knowledge, ensuring consistency and reliability of the data set.

technologies presented and evaluated by this study.

Data Extraction

Data relevant to our established evaluation criteria (fig. 2) were methodically extracted from selected articles. We gathered direct data on the adaptability of methods across various habitats and their invasiveness. More subjective metrics, such as operational and analytical complexity and the innovative potential of each methodology, were assessed through a comparative analysis informed by a comprehensive review of the field (see Appendix A for a summary of the studies reviewed). This balanced approach ensured that our evaluations remained objective and reflected current scientific standards.

Integration and consistency check

The final integration of the articles was conducted with an emphasis on consistency and relevance to the overarching research objectives. This process involved synthesizing data from various sources to form a cohesive understanding of the methodologies used in assessing benthic ecosystem functions. This synthesis was critical in forming a robust foundation for evaluating the subjective criteria in our criteria table, such as standardization and innovation potential.

The integration of AI tools significantly enhanced the depth and efficiency of our literature review. By rigorously applying these advanced tools in conjunction with traditional research methods, we established a robust framework that supports accurate, scalable, and globally applicable assessments of benthic ecosystem functions.

Challenges

Early stages of the review process were hindered by confusion between similar ecological terms, which initially complicated the categorization of ecosystem processes and functions. This issue was mitigated by adopting a more rigorous definitional framework, ensuring clarity and precision in the selection and analysis of literature. Furthermore, deciding which methodologies to include presented a challenge, particularly in distinguishing between generalizable methods and those too specific for broad application. The focus was refined to prioritize methodologies with significant standardization potential, excluding those specific to unique research objectives or ecological functions.

Results

The evaluation categorizes these methodologies into three distinct types: structural, process-based, and function-based. Each category is examined to determine its effectiveness in capturing the dynamics of benthic ecosystem functioning.

Type 1. Structural-based methodologies

The primary method of assessing community structure in benthic ecosystems involves compiling species lists, a traditional proxy for biodiversity. By understanding the variety and abundance of species, researchers can begin to approximate the ecological interactions and processes occurring within the ecosystem. This approach has historically equated taxonomic diversity with functional diversity, positing that a richer array of species implies a broader range of ecological functions (Covich et al., 2004). However, this assumption is increasingly questioned as new research suggests that similar taxonomic diversity can yield disparate functional outcomes (Hooper et al., 2005). These limitations necessitate advanced methodologies like the Biological Traits Analysis, which provides a more nuanced understanding of how species traits contribute to ecosystem functions beyond mere taxonomic diversity (De Juan et al., 2022). BTA has become an essential tool in benthic marine studies for bridging the gap between taxonomy and functionality. It enhances our understanding by linking community structure to ecological functions through species' attributes, revealing that species within the same genus, and even the same species, can exhibit diverse ecological functions, while distantly related species may perform similar roles in their respective ecosystems (Cadotte et al., 2011). This method delves deeper than mere species identification; it integrates data on life history, behaviour, and morphology to interpret ecosystem dynamics (Bremner et al., 2003).

Adaptability Across Habitats and Invasiveness

The evaluation of these parameters varies greatly with the selection of the sampling method. Epibenthic samplers such as sleds, trawls, and dredges might decrease the adaptability across different benthic habitats, being restricted mainly to soft substrates like sandy and muddy bottoms. Furthermore, grabs and box corers, which are mainly used to extract infauna (H. L. Rees et al., 2009) and small sedentary epifauna (McArthur et al., 2010), are not ideal for use on coarse-grained sediments as the grains can prevent closure (Jørgensen et al., 2011), resulting in sample loss and underestimation of the density or richness of taxa (Lozach et al., 2011). These more traditional methods have their own advantages. For instance, sleds and trawls are advantageous when large spatial coverage is desired as they collect information over transects and can target large epifauna, enabling species-level and genetic analysis (Flannery & Przeslawski, 2015).

However, they come with their own set of disadvantages, where invasiveness plays a crucial role. These methods are destructive, often biased towards collecting more visible or easily accessible species while potentially overlooking cryptic or smaller fauna. Additionally, they can cause considerable disturbance to the benthic environment, potentially impacting the ecosystems being studied (Jørgensen et al., 2011; H. Rees, 1999).

However, BTA can be integrated with non-invasive data collection methods, such as underwater video cameras and environmental DNA (eDNA) through water collection samples. Underwater imagery systems can be stand-alone units, which include towed video remotely operated vehicles (ROV) baited remote underwater video systems (BRUVs) and autonomous underwater vehicles (AUV), where navigation is pre-programmed (Flannery & Przeslawski, 2015). A significant problem when using these methods is the variable data quality due to environmental conditions (i.e. turbidity), issues might include increased cost, limitations of sampling depth by the attached cable, instability of the ROV in rough waters, and observer bias (Azis et al., 2012). eDNA methods, while powerful for detecting biodiversity, it can be diminished by its potential for contamination and degradation of DNA in the environment, which can affect the accuracy of species detection (Takahara et al., 2012).

Despite these challenges, non-invasive methods like eDNA provide significant advantages. They allow researchers to describe benthic structural elements and assess ecosystem functions without significantly altering the ecosystem, demonstrating considerable adaptability across various benthic environments, including sandy bottoms, coral reefs, and deep-sea floors. These approaches are less disruptive, provide high-resolution data, and can be repeated over time to monitor changes in the ecosystem (Marques et al., 2021).

Operational Complexity

Operational complexity refers to the logistical, technical, and financial challenges associated with implementing BTA. Conducting a BTA involves several steps, including the collection of biological samples, trait data measurement, and the subsequent analysis to link these traits to ecosystem functions (Bremner et al., 2006). The complexity of operations can vary depending on the chosen data collection methods. Traditional methods like trawls and grabs, while logistically demanding, provide extensive datasets on species composition and abundance but require considerable effort and expertise to minimize ecological disturbance and sample processing errors.

On the other hand, non-invasive methods such as underwater video cameras and eDNA analysis, although less intrusive, come with their own operational challenges. For instance, deploying and managing underwater cameras requires specialized equipment and expertise to handle environmental factors like water turbidity and current. Similarly, eDNA analysis necessitates meticulous sample handling to prevent contamination and precise laboratory protocols to ensure accurate DNA extraction and amplification (Marques et al., 2021). Additionally, the financial cost of these advanced technologies can be significant, potentially limiting their widespread application in resource-constrained settings.

Analytical Complexity

Analytical complexity in BTA involves the processing and interpretation of large datasets to derive meaningful ecological insights. BTA requires integrating data from various sources, including morphological, behavioural, and life history traits, to assess their collective impact on ecosystem functions. This integration demands sophisticated statistical and computational tools to analyse multivariate data and model ecological processes accurately (Bremner et al., 2006), requiring a high level of expertise in data science and ecology.

The variability in trait expression can lead to significant uncertainties, necessitating robust analytical frameworks to ensure reliable and reproducible results. Standardizing trait definitions and measurement protocols across studies is essential to minimize analytical discrepancies and enhance the comparability of BTA findings (De Juan et al., 2022). These advancements reduce the analytical burden, enhancing the usability of BTA across various institutions.

Standardization Potential

Standardization potential is crucial for ensuring data comparability across studies and regions. For example, the Bioturbation Potential (BPc) and Reworking Rate Index (RRI) are derived from inventories of species, abundance, and biomass data, alongside functional classifications of organism traits related to sediment mixing (Queirós et al., 2013). These metrics provide a standardized approach to estimate the community bioturbation potential, which is crucial for understanding sediment stability and nutrient cycling in marine ecosystems. It has also been applied to understand how community composition influences ecosystem resilience and recovery potential (Hinz et al., 2021) and for developing a Vulnerability Index to assess the impacts of fishing practices (De Juan et al., 2020). To illustrate the extensive applications of BTA, figure 4 encapsulates a comprehensive summary of the various ecosystem processes and functions assessed using this method across different studies.

Despite its promise, BTA faces challenges in standardization due to inconsistencies in trait reporting and reliance on expert judgment (De Juan et al., 2022). Nonetheless, its flexibility allows it to be applied retroactively to existing datasets and adapted to various technological advancements, enhancing its potential for future standardization.

Importantly, BTA can also be applied to physical structures created by animals—such as burrows, reefs, and Lebensspuren (trace fossils)—which are linked to functional aspects of the ecosystem. This flexibility enables the use of simple habitat descriptors as functional proxies, thus broadening the scope of BTA beyond traditional biological traits (Norkko et al., 2013).

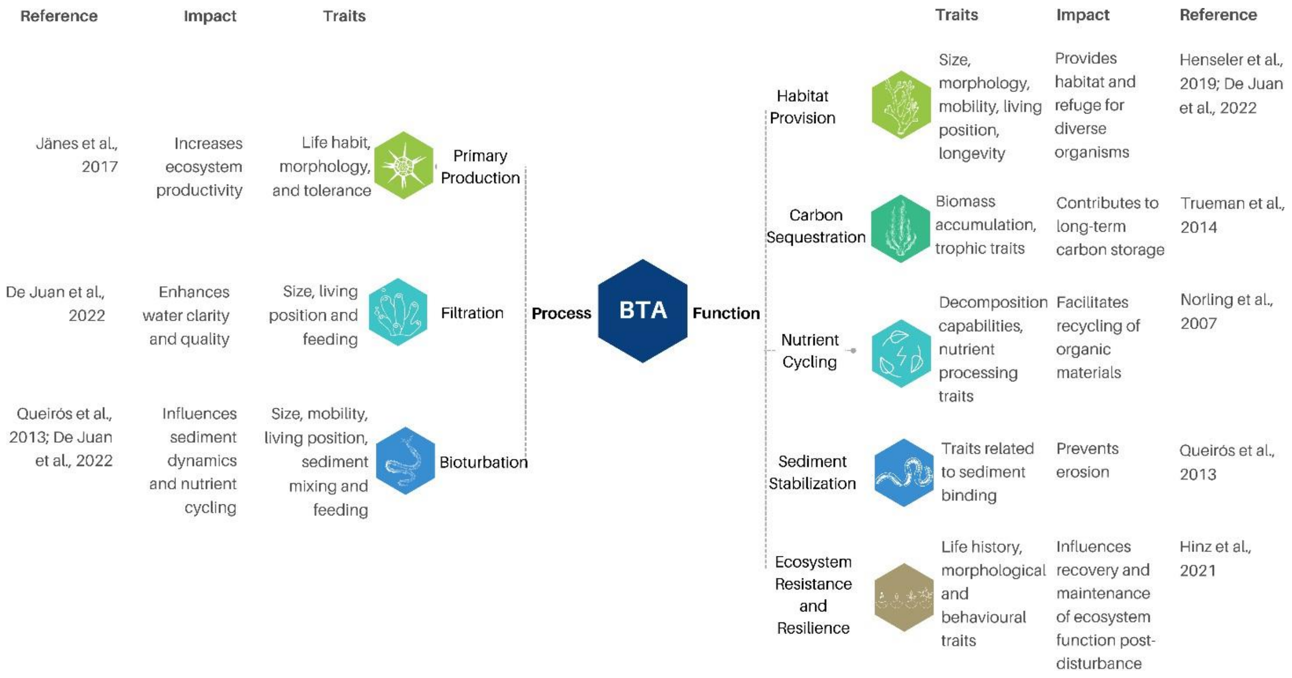


Figure 4. Overview of Ecosystem Processes and Functions Assessed through Biological Traits Analysis (BTA). This figure lists various ecosystem processes and functions that have been studied using BTA, highlighting the specific traits involved and their impacts on ecosystem functionality. The colour coding illustrates the relationships between processes and functions, with each colour representing those that are more closely related. This visual representation emphasizes how different processes support various ecosystem functions, facilitating a comprehensive understanding of BTA's application in marine ecosystem studies.

However, a significant limitation is that the methods commonly used to collect benthic data for BTA often capture only certain segments of the benthic community due to the specific efficiency and capabilities of the sampling gear. For example, infauna sampling methods might miss much of the epifauna or hyperfauna, and camera-based methods are generally limited to larger, more visible organisms (Durden et al., 2016). This selective sampling can result in data imbalances, particularly when comparing different regions, as some areas may lack comprehensive data for all components of the benthic community. Therefore, beyond the standardization of trait data, greater coordination is needed to ensure balanced data collection across different benthic components, with careful selection of sampling gears and methodologies to achieve a more holistic understanding of benthic ecosystems on a broad scale (De Juan et al., 2022).

With such global efforts, BTA could yield more reliable and comparable estimates across different ecosystems.

Innovation Potential

The flexibility of BTA is one of its most compelling features, particularly in its capacity to integrate new technological advancements that enhance both data collection and trait knowledge.

Emerging technologies are revolutionizing how data is collected in marine environments, significantly enhancing the scope and precision of BTA. For instance, environmental DNA (eDNA) allows for the detection of species even at low abundance, making it invaluable for compiling comprehensive species lists that feed into BTA without the need for intrusive sampling methods (Antich et al., 2021; Takahara et al., 2012). Bioacoustic monitoring offers a non-invasive approach to continuously monitor species interactions and behaviours, providing data that can be directly tied to specific biological traits related to ecosystem functions (Birchenough et al., 2006; Elise et al., 2019). Additionally, 3D scanning, and video monitoring technologies afford detailed visualization and analysis of habitat structures and organism morphologies, enhancing the accuracy with which traits can be measured and related to functional outcomes (Ferrari et al., 2022; Marre et al., 2019). Technologies such as tracking devices and species identification from automated image recognition through the use of machine learning, which can aid in species identification from images and video footage, helping in monitoring species and populations over time (Aguzzi et al., 2009; Raphael et al., 2020). This can lead to the attainment of new data that can be seamlessly integrated into existing BTA frameworks.

While these technologies significantly increase the granularity and scope of the data, they also enhance the precision with which traits are related to ecosystem functions. However, it is important to note that most BTA approaches use broad categorical trait data with assumed or estimated relationships with function. These estimates are mostly proxies or relative measures that cannot be easily standardized between studies. This variability presents a significant drawback, as studies are not always comparable, and uncertainties exist due to the way proxies are calculated, considering the variable underlying trait data. Therefore, most estimates will be study and context-specific and are, at best, relative measures of function. By incorporating such technologies, BTA can more precisely estimate the processes and functions crucial for ecosystem management and conservation strategies. However, addressing the standardization challenge remains essential to ensure that these innovative approaches yield comparable and reliable results across different studies and ecosystems.

Type 2. Process-based methodologies

Process-based methodologies are techniques used to study the dynamic activities within benthic ecosystems that are directly or indirectly related to ecosystem functions. These methods aim to observe or measure processes such as filtration, bioturbation, primary production, and habitat provisioning, which are essential for maintaining ecosystem health and stability. Traditional methods of studying these processes often involve direct observations and measurements that can be broadly categorized into visual sampling and controlled systems techniques. The intrinsic differences in the processes being assessed necessitate a dual approach, combining both visual and incubation methodologies to comprehensively evaluate these dynamic activities.

Visual methodologies utilize tools like remotely operated vehicles (ROVs), baited remote underwater video systems (BRUVs), autonomous baited camera landers, and sediment profile imaging (SPI). ROVs have been primarily employed for habitat mapping across diverse benthic settings (Marre et al., 2019). but also show potential for inferring certain functions related to direct observations, such as identifying species behaviour and interactions. However, tools like autonomous baited camera landers and BRUVs are particularly effective in studying scavenging behaviour and species interactions, providing valuable insights into community dynamics and habitat use (Dunlop et al., 2021; Langlois et al., 2018). Additionally, SPI can visualize sediment layering and benthic organism activities like bioturbation and bioirrigation (Maire et al., 2008; Solan et al., 2004b).

Controlled systems methodologies include both incubation and mesocosm techniques, which can be performed in-situ and ex-situ. Incubations involve creating controlled environments to measure specific ecological processes. Benthic flux chambers (BFCs) are a prime example of in-situ incubations, used to quantify processes like bioturbation and primary production by isolating a portion of the sediment-water interface (Needham et al., 2011). While BFCs are effective in measuring ecosystem processes, they are also considered excellent for assessing ecosystem functions and will be discussed in more detail in Type 3 methodologies. Mesocosms, on the other hand, provide larger, semi-controlled systems that replicate natural environments to study broader ecological interactions and processes, such as filtration and bioturbation (Doering & Oviatt, 1986; Maire et al., 2008). The controlled conditions of these methodologies allow for detailed assessments of how benthic organisms influence sediment dynamics.

Visual methodologies offer the advantage of non-intrusive observations over broad spatial scales (Jones et al., 2012), while incubation methodologies provide detailed, quantitative data on specific processes (Kristensen et al., 1995). By combining these approaches, researchers can achieve a comprehensive understanding of benthic ecosystem processes, capturing the full complexity and variability of these dynamic systems.

Adaptability Across Habitats and Invasiveness

Visual methodologies demonstrate significant adaptability across a variety of benthic habitats, ranging from shallow coastal areas to deep-sea regions. These tools allow researchers to gather data without significantly disturbing the habitat.

BRUVs and autonomous baited camera landers are particularly effective for studying scavenging behaviour and species interactions in various sediment types, but their suitability might be decreased in habitats where the field of view is likely to be obscured (e.g., tall kelp habitats, very high relief reefs, or low-visibility, highly turbid waters) (Dunlop et al., 2021; Langlois et al., 2018). These methods are minimally invasive, providing high-resolution data while preserving the natural state of the habitats.

Similarly, SPI cameras offer a unique capability to visualize sediment stratigraphy and the activities of benthic organisms like bioturbation and bioirrigation. They are commonly used in subtidal zones, estuaries, and coastal areas, where they can capture detailed images of sediment layers and biogenic structures with minimal disturbance (Solan et al., 2004b). Despite potential challenges like turbidity affecting data quality, these methodologies enable repeated monitoring over time, making them suitable for long-term ecological studies (Solan & Kennedy, 2002).

Mesocosms allow for the study of interactions and processes in various sediment types, including muddy, sandy, and mixed substrates (Doering & Oviatt, 1986; Maire et al., 2008). They are adaptable to both laboratory and field settings and provide detailed assessments of how benthic organisms affect sediment dynamics under controlled conditions (Maire et al., 2008; Vajedsamiei et al., 2021). While the initial setup of mesocosms may involve some disturbance for in-situ studies, their controlled nature facilitates precise, quantitative measurements of ecological processes.

Operational Complexity

Visual methodologies, while offering high adaptability and minimal invasiveness, present varying degrees of operational complexity. ROVs and AUVs are technologically advanced tools that require significant expertise for operation. Deploying ROVs involves handling sophisticated control systems, ensuring stable navigation in varying water conditions, and managing power and communication cables, which can limit their operational depth (Negahdaripour & Firoozfam, 2006). AUVs, being pre-programmed for autonomous missions, demand meticulous planning and programming skills to ensure accurate data collection and retrieval, especially in complex or deep-sea environments (Johnson-Roberson et al., 2010).

BRUVs and autonomous baited camera landers, although simpler in design compared to ROVs and AUVs, also require careful deployment and retrieval procedures. These systems involve selecting appropriate bait, ensuring stable positioning to capture relevant ecological interactions without camera drift, and handling depth limitations in deeper water habitats, which can be affected by local conditions such as water currents (Dunlop et al., 2021; Langlois et al., 2018).

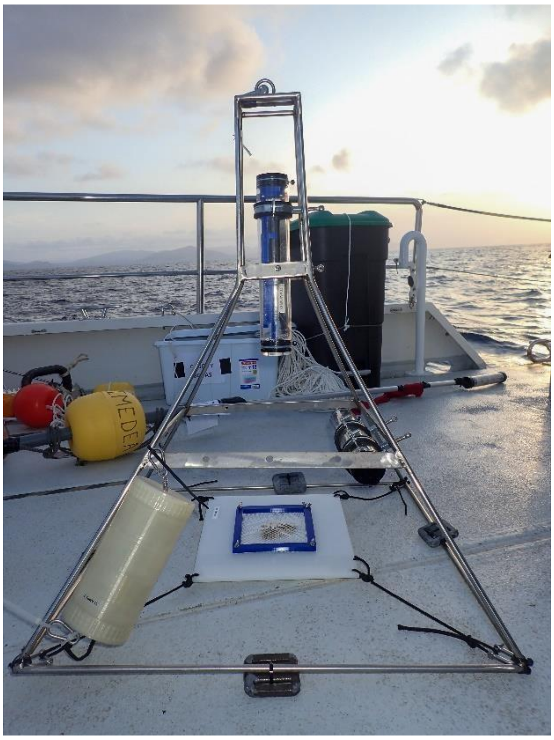


Figure 5. Example of baited remote underwater video systems (BRUVs) deployed during a research cruise of the MARBEFES project, in which the author participated. These systems are used for capturing scavenger behaviour and species interactions in various benthic environments, providing non-invasive visual data for ecological studies.

SPI cameras add another layer of complexity due to the precise deployment and handling of specialized imaging equipment. The SPI camera must be carefully calibrated and inserted into the sediment to avoid disturbing the substrate, which requires technical expertise and often advanced deployment mechanisms (Solan & Kennedy, 2002). Additionally, there are limitations, such as the potential for artifacts introduced by the deployment process and challenges in capturing the full extent of sediment reworking due to spatial and temporal variability (Maire et al., 2008).

Controlled systems methodologies, such as mesocosms, require extensive setup and maintenance. Establishing a mesocosm experiment involves selecting appropriate sites, constructing or installing mesocosm units, and replicating natural environmental conditions as closely as possible (Doering & Oviatt, 1986). This includes controlling variables such as temperature, light, and nutrient levels, which can be logistically challenging and resource intensive. Furthermore, the long-term nature of many mesocosm studies demands ongoing monitoring and adjustment to maintain the integrity of the experimental conditions, adding to the operational complexity (Furukawa et al., 2001).

Analytical Complexity

The primary challenge of visual methodologies lies in the processing and interpretation of large volumes of visual and spatial data. ROVs and AUVs generate high-resolution images and videos that require extensive post-processing. The analytical complexity associated with these visual methodologies is significant, particularly for tasks such as 3D habitat mapping, which involves creating detailed and accurate representations of underwater environments. This process includes capturing fine-scale ecological processes and detecting changes in habitat structure over time (Marre et al., 2019). The challenges faced in underwater imaging include acquiring high-quality georeferenced imagery due to water attenuation of electromagnetic waves, the need for near-bottom, high-resolution imaging, and the limitations of high-bandwidth communications and GPS-based positioning underwater (Johnson-Roberson et al., 2010).

The analytical complexity for BRUVs and autonomous baited camera landers is driven by the need to process long video sequences to extract meaningful ecological data. Identifying and counting species, analysing behaviour, and determining scavenging rates are time-consuming tasks that often require specialized software and manual review (Dunlop et al., 2021; Langlois et al., 2018). The variability in environmental conditions, such as light and turbidity, can complicate the analysis, necessitating correction techniques to standardize the data.

The analytical complexity of SPI arises from the detailed processing and interpretation of the captured sediment profiles. The primary challenge lies in accurately quantifying bioturbation and sediment stratigraphy from these images. This process necessitates the use of advanced image analysis software to measure parameters such as sediment layering and biogenic structures (Solan & Kennedy, 2002). Interpreting these images demands a deep understanding of sedimentology and benthic ecology to distinguish between different bioturbation activities and their impact on sediment structure. Additionally, the temporal aspect of SPI, particularly when using time-lapse imaging, further complicates analysis as it requires tracking changes over time, necessitating robust data management and sophisticated statistical modelling techniques to analyse temporal trends in bioturbation and sediment reworking (Solan et al., 2004b).

Controlled systems methodologies, such as incubations and mesocosms, produce extensive datasets encompassing a wide range of variables, from physical and chemical parameters to biological responses. These studies must account for temporal and spatial variability, necessitating sophisticated statistical methods and models to analyse these variations accurately (Maire et al., 2008). The intricate nature of these studies is well-documented, highlighting the substantial effort required to maintain the integrity and reliability of mesocosm experiments (Furukawa et al., 2001).

Standardization Potential

ROVs and AUVs have high standardization potential due to the widespread availability of standardized protocols for their deployment and operation. Established guidelines for navigation, data collection, and maintenance ensure consistent data quality and facilitate comparability across different research initiatives (Tillin, H.M. et al., 2018). The use of uniform software and data formats further enhances the ability to integrate and compare datasets from different studies. However, variations in vehicle models, sensor configurations, and operational settings can introduce some inconsistencies, requiring careful calibration and validation to maintain standardization.

BRUVs and autonomous baited camera landers also offer considerable standardization potential. There are well-established protocols for bait selection, deployment duration, and camera positioning, which help to ensure consistency in data collection (Langlois et al., 2018). Standardizing video analysis procedures, such as species identification and behaviour classification, is facilitated by the use of specialized software and machine learning algorithms (Mohamed et al., 2018). However, environmental variability and differences in camera specifications can pose challenges to achieving full standardization.

SPI cameras have a high standardization potential due to the consistent methodology used for capturing and analysing sediment profiles. Standard protocols for image acquisition, sediment core insertion, and data interpretation are well-documented, allowing for reproducible and comparable results across different studies. The use of standardized metrics, such as bioturbation depth and sediment layering, further enhances the ability to compare findings across different regions and time periods (Germano et al., 2011).

Mesocosms are widely standardized due to the well-established guidelines for their construction, operation, and monitoring. Standard protocols for setting up mesocosm experiments, including the selection of experimental units, environmental controls, and sampling procedures, help to ensure consistency and reproducibility (Widdicombe et al., 2010). The use of common metrics and standardized data collection methods, such as nutrient concentrations and biological responses, further enhances the ability to compare results across different studies. However, the complexity and variability inherent in mesocosm experiments, such as differences in scale and experimental conditions, can pose challenges to achieving full standardization.

Innovation Potential

The innovation potential for ROVs and AUVs is substantial due to ongoing advancements in robotics, artificial intelligence, and sensor technology. Innovations include sophisticated processing techniques, such as image correction for lighting and colour absorption, and the use of advanced algorithms for image stitching and 3D reconstruction to ensure accurate and reliable data (Johnson-Roberson et al., 2010) as well as 3D modelling of marine habitats through photogrammetry (Marre et al., 2019).

Additionally, the development of machine learning algorithms for automated species recognition, tracking and behavioural analysis can significantly reduce the time and effort required for data processing (Mohamed et al., 2018). These advancements are also beneficial for BRUVs and autonomous baited camera landers, enhancing species identification and behavioural analysis. For ecological assessments, these technologies allow for more detailed and accurate data collection, enabling researchers to explore and monitor previously inaccessible or challenging environments. However, manual validation remains essential to ensure accuracy due to the complexity and variability of natural environments.

The continuous advancements in imaging technology and software for image analysis also enhance the precision and scope of SPI applications. The development of interactive computer software for detailed image interpretation allows for more accurate and comprehensive analysis of sediment profiles (Germano et al., 2011). Additionally, integrating SPI with other geochemical and biological assessment tools can lead to a more holistic understanding of benthic processes, driving further innovation in environmental impact assessments and monitoring studies.

Innovations in environmental control technologies, such as automated systems for regulating temperature, light, and nutrient levels, enable more precise manipulation of experimental conditions. The integration of mesocosms with advanced sensors and data analytics allows for comprehensive monitoring and analysis of ecological processes, providing valuable insights into ecosystem dynamics and responses to environmental stressors.

Type 3. Function-based methodologies

Type 3: Function-based methodologies differ from process-based methods by directly measuring the outcomes or results of ecosystem structures and processes, such as nutrient cycling or sediment stabilization. Unlike process-based methods that often integrate measurements of structure and process, function-based methodologies focus on the final ecosystem functions, sometimes without the need for prior measurements of these components, although integrating both approaches can enhance understanding.

This direct focus on outcomes is particularly relevant in studying benthic–pelagic coupling, where interconnected processes link the bottom substrate and water column habitats through the exchange of mass, energy, and nutrients. This phenomenon is vital in aquatic ecosystems, playing a key role in functions ranging from nutrient cycling to energy transfer within food webs. Monitoring and quantifying benthic ecosystem functions is crucial for gaining insight into the health and dynamics of these ecosystems, which is essential for conservation efforts, sustainable resource management, and predicting responses to environmental changes (Griffiths et al., 2017).

Traditional measurements of benthic functions, such as nutrient exchange and organic matter sedimentation, provide some level of quantification. However, there is often a lack of detailed assessment of the magnitude and variability of biological processes, hindering comprehensive quantitative comparisons (Griffiths et al., 2017). Changes in oxygen levels will continue to impact inorganic and organic matter exchange processes across habitats, as oxygen concentration is a main driver of these exchanges (Norkko et al., 2015). Additionally, climate change and reductions in nutrient loads could significantly affect organic matter sedimentation (Bonsdorff & Pearson, 1999). Many biological processes, including predation and bioturbation, are expected to be sensitive to human-induced factors, but their overall impact on ecosystem function remains largely unknown (Griffiths et al., 2017). Crucial ecosystem functions, such as energy transfer within food webs, biogeochemical cycling, and the support of fish nursery areas, depend on various interconnected benthic–pelagic coupling processes (Granek et al., 2010; Seitz et al., 2014). Multiple factors interacting within this system are essential for sustaining these functions. To effectively measure and understand their dynamics, it is imperative to utilize methodologies that can accurately quantify these functions.

Benthic flux chambers (BFCs) offer a robust and versatile solution for quantifying benthic ecosystem functions directly, providing in situ observations of relatively undisturbed systems. These chambers create a controlled environment for measuring the exchange of gases and nutrients between the sediment and the overlying water column. BFCs have been successfully utilized in various studies to measure gas and nutrient exchanges with high precision, demonstrating their robustness in diverse marine environments (Viollier et al., 2003). By isolating a specific area of the sediment-water interface, BFCs allow for precise and reliable measurements of key biogeochemical functions (Tengbergi et al., 1995).

While the primary objective of using BFCs is to quantify ecosystem functions, they also inherently measure the processes that contribute to these functions. For instance, the measurement of photosynthesis, respiration, and calcification rates through BFCs (Yates & Halley, 2003) can provide insights into primary production, energy transfer within food webs, and carbon sequestration. Additionally, nutrient flux measurements, such as those of nitrogen and phosphorus, help to assess nutrient cycling and water quality improvement (Hammond et al., 2004). This dual capability highlights the intricate relationship between ecosystem processes and functions. Understanding this relationship is crucial for comprehensive ecological assessments. However, for the purposes of this evaluation, we will focus on the use of BFCs for the direct assessment of benthic ecosystem functions.

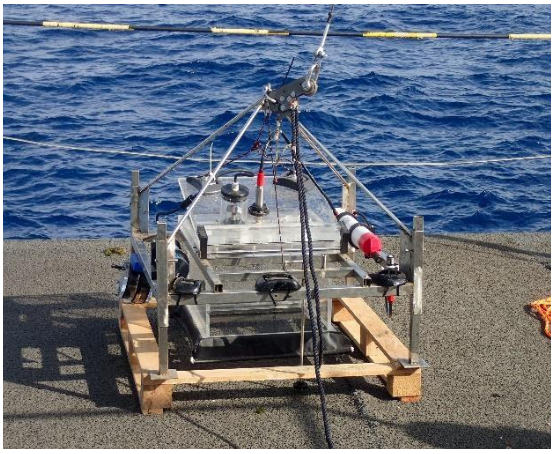


Figure 6. Benthic Flux Chamber (BFC) set up for in situ measurements of gas and nutrient fluxes at the sediment-water interface, demonstrating the controlled conditions created for precise ecosystem function assessments used during a research cruise of the MARBEFES project.

Adaptability Across Habitats and Invasiveness

BFCs exhibit remarkable adaptability across various marine habitats, underscoring their versatility and broad applicability in ecological research. These chambers have been effectively deployed in diverse environments, ranging from subtidal sandy habitats to continental slopes and even deep-sea regions, including oxygen minimum zones.

In subtidal sandy habitats, BFCs have been utilized to measure the impacts of hypoxic disturbances on benthic communities and ecosystem functioning, providing valuable insights into nutrient fluxes and sediment oxygen dynamics under environmental stress (Villnäs et al., 2012). On continental slopes, these chambers have facilitated the study of biogeochemical cycles, revealing critical information about nutrient dynamics and organic matter decomposition under varying hydrodynamic conditions (Viollier et al., 2003). In more extreme environments such as deep-sea regions and oxygen minimum zones, BFCs have proven essential in understanding the role of benthic processes in global nutrient cycles, especially under challenging conditions that significantly influence biogeochemical processes (Hammond et al., 2004).

The design of BFCs ensures minimal invasiveness, which is crucial for preserving the natural state of the habitat and the behaviour of benthic organisms during measurements. When designing and using these instruments, an important goal is to minimize the disturbance they cause to the seabed both during landing and operation (Tengbergi et al.,1995). By enclosing a small section of the sediment-water interface, BFCs allow natural processes to continue undisturbed, ensuring accurate and reliable data collection.

Operational Complexity

The deployment and operation of benthic flux chambers involve several steps that require careful execution but are generally straightforward with proper training and protocols. The chambers need to be securely placed on the sediment to prevent water exchange with the surrounding environment. Sensors and sampling devices within the chambers must be calibrated accurately to ensure reliable data collection (Yates & Halley, 2003). While the initial setup can be complex, especially in challenging environments, the subsequent data collection process is largely automated, reducing the need for continuous manual intervention. Once the lander has been deployed, the ship is free to undertake other operations until it is time for recovery. When designing a lander, numerous factors must be considered to ensure it successfully achieves its designated tasks at the seafloor, including the methods of launching and recovery (Tengbergi et al., 1995).

However, the high cost of sensors and the specialized knowledge required for their operation remain significant challenges, though recent trends suggest these costs may decrease over time (Wang et al., 2019). Additionally, due to these costs and the technical expertise needed, there is currently limited experience in using BFCs, particularly in shelf seas, on broader temporal and spatial scales.

Analytical Complexity

The data collected by BFCs involve continuous monitoring of various parameters such as oxygen, nutrient concentrations, and pH levels. Processing these data requires sophisticated software and analytical tools capable of handling large datasets and performing complex calculations. For example, the study by Hammond et al. (2004) illustrated the use of advanced software for data analysis, highlighting the need for specialized tools to process and interpret the measurements accurately.

Interpreting data from BFCs also involves accounting for environmental variability. Factors such as changes in sediment composition, biological activity, and environmental conditions can introduce variability in the measurements. Advanced statistical and modelling techniques are often employed to parse out meaningful results from the data.

The use of BFCs often necessitates specialized equipment and software for both data collection and analysis. This includes high-precision sensors for measuring nutrient and gas fluxes, as well as advanced analytical software for data processing. The study by Viollier et al. (2003) described the need for specialized equipment to measure nutrient fluxes accurately and compared different analytical approaches to enhance data reliability.

The analytical complexity of using BFCs lies in the need for precise calibration, sophisticated data processing, and advanced analytical techniques to interpret the collected data accurately. This complexity underscores the necessity for specialized equipment and software, as well as a deep understanding of biogeochemical processes and environmental variability.

Standardization Potential

The application of BFCs in diverse habitats, from coastal areas to deep-sea regions, underscores their versatility. Adhering to standardized protocols allows researchers to collect data that are comparable globally, which is crucial for large-scale ecological assessments and understanding environmental impacts on benthic functions.

Standardized deployment and operation steps, including accurate calibration of sensors and sampling devices within BFCs, minimize errors and ensure consistency across different studies (Yates & Halley, 2003). The minimal invasiveness of BFCs and their ability to maintain natural processes within the chamber enhance the reliability of collected data. Advanced analytical tools and high-precision sensors further support this reliability (Viollier et al., 2003).

The use of BFCs is supported by well-established protocols and guidelines that ensure consistency and reproducibility across different studies. These standardized procedures cover all aspects of the methodology, from chamber construction and deployment to data collection and analysis. The high standardization potential of BFCs facilitates comparability of results across various research projects and geographic locations, contributing to a more comprehensive understanding of benthic ecosystem functions on a broader scale.

Innovation Potential

Benthic Flux Chambers (BFCs) continue to evolve, integrating cutting-edge technologies that significantly enhance their functionality and efficiency in ecological research. One of the most promising advancements is the incorporation of remote data transmission capabilities, which allows for real-time monitoring and data collection without retrieving the BFC from the seafloor.

An important aspect of this innovation is the remote data transmission capability. By incorporating acoustic modems and specialized subsea cables connected to telemetry buoys, real-time data can be transmitted from BFCs to shore-based stations or research vessels. This allows researchers to monitor BFC data live, adjust sampling protocols as needed, and download data without the need to retrieve the BFC from the seafloor, significantly reducing environmental disturbance and improving the efficiency of data collection (Yu et al., 2020).

For example, the use of electro-optical-mechanical (EOM) cables connected to surface buoys equipped with renewable energy sources such as solar panels and wind turbines ensures a continuous power supply to the BFCs, facilitating long-term deployments and real-time data transmission. The data transmission systems, including satellite communication and wireless radio, enable high-bandwidth data transfer, making it feasible to transmit large datasets and live video feeds from the benthic environment (Zhang et al., 2022).

Moreover, integrating advanced sensors within the BFCs enhances their ability to measure a broader range of parameters with higher precision. For instance, high-precision sensors can measure nutrient and gas fluxes, providing detailed insights into biogeochemical processes. These sensors, coupled with sophisticated software for data analysis, allow for the processing of large datasets and the application of advanced statistical and modelling techniques to interpret the data accurately (Viollier et al., 2003).

Additionally, combining BFCs with other methodologies, such as environmental DNA (eDNA) analysis, can provide complementary insights into benthic community composition and functional diversity. The integration of function-based methodologies with structural and process-based methods and proxies may enable researchers to define relationships between these different aspects of benthic ecosystems. This approach facilitates more accurate extrapolation of ecosystem functions through modelling, enhancing our understanding and predictive capabilities for broader ecological studies. The continuous evolution of these technologies ensures that BFCs remain at the forefront of marine ecological research, offering new opportunities for exploring and understanding benthic ecosystem function.

Discussion

The primary objective of this study was to identify methodologies that are broadly applicable and capable of providing extensive information about benthic ecosystem functions, either through proxies or direct measurements. This focus is critical in advancing our understanding of ecosystem dynamics, supporting conservation efforts, and guiding resource management. Given the complexity and variability inherent in marine environments, selecting the most suitable methodologies requires careful consideration of each method's ability to deliver comparable data across different settings and scales.

To achieve this, the study evaluated various approaches: structural-based, process-based, and function-based methodologies. While each has unique strengths and limitations, the goal remains to determine which methods offer the greatest potential for standardization, broad-scale application, and integration into current and future research practices.

Structural-Based Methods: Challenges and Opportunities

Structural-based methods, such as trait-based analysis (BTA), play a vital role in understanding ecosystem functions by linking species traits to specific ecosystem processes. These methods focus on characterizing the structural components of ecosystems—like species composition, abundance, and traits—to infer their contributions to ecological functions. BTA has been widely applied to explore relationships between species' functional traits and the processes they drive, offering valuable insights into biodiversity and ecosystem functioning (De Juan et al., 2022).

A key challenge in applying structural-based methods is achieving standardization due to the diversity of species and traits. Consensus on trait definitions, measurements, and data handling requires substantial time and collaboration across the scientific community (De Juan et al., 2022). Inconsistencies in data reporting and reliance on expert judgment can complicate these efforts (Petchey et al., 2006). Despite these hurdles, structural-based methods remain valuable for their capacity to provide a broad understanding of how species contribute to ecosystem functions, particularly when more direct measurements are unavailable.

Combining structural-based methods with other approaches, such as process-based or function-based methodologies, can enhance their utility by providing a more nuanced understanding of ecosystem dynamics. Integrating BTA with non-invasive techniques like environmental DNA (eDNA) analysis or underwater video monitoring offers new opportunities for monitoring species interactions and community composition with minimal disturbance (Norkko et al., 2013; Marques et al., 2021). This combination allows for more robust inferences about ecosystem functions by relating species traits to observed ecological processes.

The flexibility of BTA also enables its application to physical structures created by animals—such as burrows, reefs, and Lebensspuren (trace fossils)—as functional proxies (Norkko et al., 2013). While this adaptability broadens its scope and relevance, it also introduces variability that complicates standardization. Ongoing efforts to harmonize trait definitions and data collection protocols will enhance comparability and integration across studies, maximizing their potential in marine ecology.

Process-Based Methods: High standardization potential with limitations

Process-based methodologies offer robust tools for directly measuring ecosystem functions by observing or quantifying dynamic activities within benthic ecosystems, such as filtration, bioturbation, primary production, and habitat provisioning. The use of tools like visual techniques—such as baited remote underwater video systems (BRUVs), autonomous baited camera landers, and sediment profile imaging (SPI) cameras—and controlled systems, like incubations and mesocosms, demonstrates their capacity to deliver highly standardized and comparable data (Langlois et al., 2018; Solan & Kennedy, 2002).

These methods benefit from established protocols and standardized equipment, allowing for reliable and reproducible data collection across different studies and regions. For example, BRUVs and autonomous baited camera landers are particularly effective in capturing scavenging behaviour and species interactions, providing high-resolution data with minimal observer bias (Dunlop et al., 2021; Langlois et al., 2018). Similarly, SPI cameras offer detailed visualizations of sediment stratigraphy and benthic organism activities, such as bioturbation and bioirrigation, making them suitable for long-term ecological monitoring (Solan et al., 2004b).

Despite their high standardization potential, process-based methods face challenges related to operational and analytical complexity. The deployment of tools like ROVs, AUVs, and SPI cameras requires specialized expertise, considerable planning, and sophisticated equipment to ensure accurate data collection (Negahdaripour & Firoozfam, 2006; Solan & Kennedy, 2002). High costs associated with equipment, maintenance, and data analysis can also limit their application in resource-constrained settings (Dunlop et al., 2021). Moreover, while these methods provide direct measurements of specific functions, they may not capture the full range of processes contributing to these functions (Maire et al., 2008).

To address these limitations, integrating process-based methodologies with structural-based approaches can provide more comprehensive insights. For example, knowing the trait composition of species observed through BRUVs or SPI can help interpret their ecological roles and contributions more accurately (De Juan et al., 2022). Future applications should aim to overcome operational and cost-related challenges, making these methods more accessible to a broader range of researchers (Wang et al., 2019).

Function-Based Methods: Direct Measurements and Broader Applications

Function-based methodologies, particularly those utilizing benthic flux chambers (BFCs), provide the most direct and standardized means of assessing ecosystem functions in benthic environments. By directly measuring outcomes such as nutrient cycling, sediment stabilization, and gas exchange, BFCs offer high-resolution data that are crucial for understanding the health and dynamics of aquatic ecosystems (Viollier et al., 2003; Yates & Halley, 2003).

The primary advantage of BFCs lies in their ability to generate in situ observations of relatively undisturbed systems, thereby maintaining the integrity of natural processes and minimizing biases introduced by sampling disturbances (Tengbergi et al., 1995). These chambers have demonstrated versatility across a range of environments, from shallow subtidal habitats to deep-sea regions, capturing critical biogeochemical processes (Hammond et al., 2004; Viollier et al., 2003). However, their use is currently limited due to high costs, the need for specialized knowledge, and logistical challenges (Wang et al., 2019).

To expand their application, addressing these limitations by reducing costs and developing more accessible versions of these instruments is essential (Yu et al., 2020; Zhang et al., 2022). Integrating BFCs with complementary methods, such as structural-based and process-based approaches, can enhance ecological assessments' scope and depth, supporting robust predictive models and effective conservation strategies.

Comparative Analysis, Recommendations, and Future Directions

While each methodology—structural-based, process-based, and function-based—has unique strengths and limitations, integrating multiple approaches offers the most comprehensive understanding of ecosystem functionality. Structural-based methods provide critical context for interpreting data from process-based and function-based approaches, allowing researchers to develop robust models that capture complex interactions within benthic ecosystems.

Future research should focus on broadening the application of innovative tools like BFCs, developing cost-effective versions, and fostering interdisciplinary collaborations to support global data collection efforts. By harmonizing methodologies and protocols across studies, we can generate high-quality, comparable data that inform effective conservation strategies and policy decisions.

Conclusion

The evaluation of structural-based, process-based, and function-based methodologies in this study highlights the need for an integrated approach to effectively assess benthic ecosystem functions. Structural-based methods like trait-based analysis (BTA) provide valuable insights but face standardization challenges due to species and trait diversity. Process-based methods offer direct measurements of dynamic activities and are highly standardized, yet they are often limited by operational costs and complexity. Function-based methods, such as benthic flux chambers (BFCs), provide reliable measurements of ecosystem functions but are similarly constrained by financial and logistical barriers.

Integrating these methodologies allows for a more comprehensive understanding of ecosystem dynamics, utilizing the contextual insights from structural-based methods alongside the direct measurements from process- and function-based approaches. Future efforts should focus on expanding the use of innovative tools like BFCs, developing more cost-effective versions, and fostering interdisciplinary collaborations to enhance data comparability and support conservation strategies.

By moving towards a more integrated and standardized approach, researchers can generate high-quality, comparable data to better inform policy decisions for preserving marine biodiversity and ecosystem health.

Appendix A

Name of process or function measured	Sub-Method	Type of Method	Method	Extracted values unit	Standardization potential, comparability and extrapolation	in situ/ ex situ	Community vs Species	Depth range	Habitat type	Invasiveness	Operational complexity and limitations	Analytical complexity and limitations	Inovation potential	References	Notes
Bioturbation sediment reworking	Tracer elements	2	Mesocosm	Bioturbation rates. Depends on the specific tracer being used. For example, radionuclides are often measured in units of activity (Bq g -1 or dpm), while chlorophyll a may be quantified in units of concentration (e.g., µg/g). Isotopically labeled sediment particles or organic matter may be measured in units of mass (e.g., mg or µg). (Ref. 1,2)	High due to the well-established protocols for tracer application, data collection, and analysis.	Majority of tracer experiments *are ex* situ with manipulated single or mulitsepecies mescocoms. Fewer studies appear to measure this in situ.	In general measurements of several species in some instances individual bioturbators have been studied	Experiments in laboratory less limited by depth while in situ so far mostly in shallow waters approx down diver depth. Some deep sea tracer experiments have been done (Ref. 3)	Commonly used in soft sediment environments due to the ease of introducing and tracking labeled particles within the loose sediment.	Minimally invasive. *In-situ* are non invasive as they involve the introduction of labeled particles or substances into the sediment. *Ex-situ* typically requires sediment coring which may involve some disturbance to the sediment structure during retrieval (Ref. 1).	Can go from simple to complex from only analysing tracer distribution in a core visually to measurements by specialized cameras and computer aided systems. Overall, moderately complex due to the selection of tracers, data analysis, modeling, calibration, validation, result interpretation, and integration with complementary methods.	Complex analytical procedures. May require sophisticated laboratory techniques, such as gamma spectrometry, mass spectrometry depending on the type of tracer used (Ref. 1).		1. DOI: 10.3354/ab00053 2. DOI: 0272–7714/98/040531+17 $25.00/0/ec970298 3. Stordal et. al, 1985	Some studies do measure nutrient fluxes alongside or other measurements providing a direct link to one or two functions
Bioturbation sediment reworking	Levelling and microtopography mapping	2	Mesocosm	For Levelling, measurements can include height or depth changes at the sediment-water interface (units of length: cm or mm). In microtopography, measurements include changes in elevation or surface rouhgness at a microscale level (micrometers for vertical and horizontal resolution) (Ref. 1).	Moderate as it may require specialized equipment and data processing techniques. While protocols for data acquisition and analysis can be standardized, variations in equipment and data interpretation may affect comparability across studies.	Levelling can be done *in-situ* but the post-processing of the microtopogrpahy mapping *ex situ,* due to the technological requirements.	In general measurements of several species in some instances individual bioturbators have been studied	Experiments in laboratory less limited by depth while in situ so far moslty in shallow waters approx down diver depth	Muddy, sandy and fine grained sediments mostly. Also in mixed substrates (Ref 1).	Non-invasive . They focus on monitoring temporal changes in sediment surface elevation without direct disturbance to the sediment structure.	Highly complex as it needs specalized equipement and laboratory setup. It also requieres techincal ecpertise and training and data interpretation and validation.	Moderately complex. These techniques require specialized equipment and data processing.	Photogrammetry might be a useful tool to use in addition with microtopography mapping.	1. DOI: 10.3354/ab00053	Potential bias linked to resuspension and sedimentation processes.
Bioturbation sediment reworking	Entrapment	2	Mesocosm	Units related to the volume, weight, density, spatial distribution, temporal changes, and composition of reworked sediment by benthic organisms (Ref 1) .	Low standarization potential due to variations in trap design, placement, and collection protocols.	*in situ / ex situ*	Single species/ individual	Not limited for laboratory experiments. Regading *in-situ* experiments, mostly shallow intertidal zones, althought deep-sea are possible with the appropriate equipment for depolyment and retrieval.	Can be applied in a wide range of marine sediment types (mostly soft, sandy or muddy) and habitats (Ref 1).	Moderately invasive. The placement of traps may disturb the sediment surface and benthic habitats in the immediate vicinity.	Moderatly complex. The deployment of the trap is pretty straight forward, but there are several considerations that contirbute to the method's overall complexity. These include experimental planning and design, data collection and analysis, organism-specific traits, environmental factors.	Not complex. They require sediment processing techniques, such as sieving or weighing, to quantify the amount of reworked sediment		1. DOI: 10.3354/ab00053	Resctrited to sessile or discretely motile organisms, and the presence of the trap may modify local environmental conditions such as hydrodynamics.
Bioturbation sediment reworking	Box core SPI-camera	2	Visual sampling	Biodiffusion Coefficient (D b): The unit is typically in cm^2/yr, representing the rate at which particles are diffused in the sediment . Reworking Activity Constant (a): Typically in cm^-1/yr, indicating the rate of sediment mixing due to bioturbation events . (Ref. 1)	High as it has standarized metrics and protocols (Ref. 5)	*in-situ*	It can be used to assess the bioturbation activity of several species (Ref. 2) as well as a singel individual/species (Ref. 3).	More commonly used in shallow environments, specially subtidal (Ref. 1)	More often used in coastal areas, subtidal zones, estuaries (Ref. 1) or ex-situ (Ref. 4)	Moderately invasive, as the presence of the SPI assembly may act as a refuge and attracted this species to the camera (Ref. 1).	Moderately complex to complex, involve a range of activities, from equipment setup and calibration to data acquisition, processing, analysis, and interpretation (Ref. 3). Also, limitations can involve the potential for attracting non-target species and may induce an underestimation of sediment reworking, since some luminophores may be horizontally displaced away from the monitored sediment area (Ref. 4).	The complexity of SPI methods is influenced by the detailed processing and interpretation of sediment profiles, requiring advanced image analysis software to quantify bioturbation and sediment stratigraphy (Ref. 3). Interpreting these images necessitates expertise in sedimentology and benthic ecology. The temporal aspect, especially with time-lapse imaging, further complicates analysis by requiring robust data management and statistical modeling to track changes over time (Ref. 1).	Acoustic imaging technologies can be used in conjunction with SPI to provide complementary data on sediment structure, bioturbation patterns, and benthic habitat mapping. eDNA analysis can help identify and quantify the presence of specific organisms involved in bioturbation processes, providing molecular insights into community composition	1. DOI: 10.3354/meps271001 2. DOI: 10.1371/journal.pone.0187800.g002 3. DOI: 10.3354/meps228179 4. DOI: 10.3354/ab00053 5. DOI: 10.1201/b11009-7	
Bioturbation sediment reworking	BTA	1	Extractive sampling	Bioturbation Potential (BPc): calculated from inventories of species, abundance, and biomass data, along with a functional classification of organism traits associated with sediment mixing. It provides a standardized metric for estimating community bioturbation potential (Ref. 1). Reworking Rate Index (RRI): Represents different levels of sediment reworking by infaunal invertebrates. It is used to categorize species based on their bioturbation behavior (Ref. 2).	High due to its capacity to establish consistent protocols and trait classifications	Although the sampling is *in situ* the analysis is done *ex situ*	Community	Not limited to a specific depth range and can be applied across different depths in marine benthic habitats where bioturbation processes occur.	Generally on soft bottoms mud to sand sediments	It may vary depending on the sampling method (trawl or physical extraction of species- invasive-, or water sampling for eDNA -non invasive-)	Moderatly complex due to the need for comprehensive biological trait data and the use of statistical or modeling tools to analyze the trait-function relationships.	Can vary from moderately complex to higly complex depending on the other methodologies it is used with. It maya require interdisciplinary collaboration as it combines ecological knowledge with genetics (eDNA) in some instances.	High due to its capacity to be integrated wit other more innovative methodologies such as eDNA and machine learning algorits for the analysis of large complex datasets to identify patterns and predictive models related to bioturbation potential. If combined with visual sampling, it can benefit from the use of AI species-recognition algorithms.	1. DOI: 10.1002/ece3.769 2. DOI: 10.1016/j.ecolind.2021.107692 3. DOI: 10.1002/ece3.9001	Related processes that can be studied: Bioirrigation, Bioerosion. Related Functions: sediment stabilization
Bioturbation sediment reworking	Micro Computed Tomography Scanning	2	Extractive sampling	Number of burrowed galleries, volume, area, radius, orientation... Physical paremeters of the galleries	Standardizing micro-CT scanning for bioturbation assessment may face challenges due to variations in sample types, imaging protocols, and data analysis methods.	Although the sampling is *in situ* the analysis is done *ex situ*	Single species/ individual (Ref. 1)	Not limited for laboratory experiments, sampling is done with cores and the dpeth range depends on the specific equipment and research objectives	There is a range of differente habitat types in which the sampling can be done, considering that the it is typically limited to softer sediments.	Sampling is moderately invasive, as the extraction of cores involves physically removing sediment samples from the environment, which can disrupt the sediment structure and benthic community. However, micro-CT is a non-destructive imaging technique that uses X-rays to create high-resolution 3D images of objects.	Setting up and operating a micro-CT scanner may have a relatively low operational complexity, especially for users familiar with imaging techniques. However, challenges may arise in sample preparation, positioning, and ensuring consistent imaging quality, which can increase operational complexity.	Analyzing basic parameters like orientation and depth of bioturbation structures may have a lower analytical complexity. Quantifying more complex parameters such as volume, porosity, and spatial distribution can increase analytical complexity.	This method by itslef can be considered innovative due to its non-destructive nature, high-resolution imaging capabilities, and ability to provide detailed 3D representations of biogenic structures	1. DOI: 10.1002/rra.4096	
Scavenging	Baited cameras	2	Visual sampling	Rate of carrion removal: typically expressed in grams per hour (g h^-1) (Ref. 1).	There are well-established protocols for bait selection, deployment duration, and camera positioning, which help to ensure consistency in data collection (Ref. 3). Standardizing video analysis procedures, such as species identification and behaviour classification, is facilitated by the use of specialized software and machine learning algorithms (Ref. 4).	*In situ*	Community	Suitable for a wide range of depths (Ref. 1,2)	Not restricted to a certain habitat type, but their suitability is decreased in habitats where the field of view is likely to be obscured (e.g. tall kelp habitats, very high relief reefs or low-visibility, highly turbid waters) (Ref. 3). Habitats included shelf slope, soft sediments and hard substrates (Ref 1,3).	Minimally invasive as it is based on visual observation.	Moderately complex as it requires the need of specialized equipment and it can face ligistical challenges for the deployment and retrieval of the camera depending the depth. (Ref. 3). They also involve selecting appropriate bait and ensuring stable positioning to capture relevant ecological interactions without camera drift (Ref. 1)	Identifying and counting species, analysing behaviour, and determining scavenging rates are time-consuming tasks that often require specialized software and manual review (Ref. 1,3). The variability in environmental conditions, such as light and turbidity, can complicate the analysis, necessitating correction techniques to standardize the data.	Use of AI species recognition algorithms.	1. DOI: 10.1007/s00300-020-02773-5 2. DOI: 10.1098/rspb.2014.2210 3. DOI: https://www.researchgate.net/publication/323688921 4. DOI: 10.3390/rs10050773	Related processes: Deposit feeding. Related functions: decomposition capacity
Scavenging	Stable Isotope Analysis	1	Extractive sampling	δ13C and δ15N Values expressed in per mil (‰) units. (Ref. 1)	Relatively high, considering the method's replicability, the accessibility of necessary equipment and expertise, and the comparability of isotopic data. However, achieving effective standardization requires the development and adherence to detailed methodological guidelines	Although the sampling is *in situ* the analysis is done *ex situ*	More often used to assess the scavenging behaviour of a wider set of species rather than focusing solely on individual species.	Not limited to a certain depth.	Not restricted to a certain habitat type.	May vary from moderately to higly invasive. The use of grabs, sleds and other extrative methods may alter the sampled area.	It may vary depending on the sampling depth and the spatial gradient. The samples do need to be specially prepared for the analysis.	Relatively high, since the analysis of stable isotopes involve precise measurements and calibration and the use of specialized equipment (mass spectometer). Also, it requieres knowledge of isotopic fractionation, trophic enrichment for the correct interpretation of results.	Developing less invasive and more efficient sampling methods, such as using eDNA or remote sampling techniques, could expand the range of species studied with minimal disturbance	1. DOI: 10.1016/j.jembe.2006.06.013 2. DOI: 10.1016/j.epsl.2014.02.053	Also used for the assessment of biogeochemical cycling (Ref. 2)
Filtration	Filtration model	2	Mesocosm	Filtration rates: volume filtered per unit time, such as liters per hour (L/h) or cubic meters per day (m^3/day) (Ref. 1). The amount of particulate matter removed from the water, in dpm, was calculated by multiplying the filtering rate (l d-l) by the dpm 1-' on suspended particles (Ref. 2)	Moderate due to reproducibility, quantifiable parameters, model development, quality control measures. Nevertheless, it would require further validation and calibration (Ref. 1,2). FOFS (Ref. 3) offers transparent and adjustable data processing, enabling precise quantification of filtration and respiration rates. This could be particularly useful for standardizing measurement techniques across studies and improving the comparability of filtration assessment data.	*ex-situ*	Species	Not limited for laboratory experiments (Ref 1,3)	Not restricted to a certain habitat type (Ref. 1,3). Suitable for mixed sediments (Ref.2)	Moderately invasive due to the physical extraction of sediment cores for the mesoscosm studies (Ref.2). Lathough some models have been done without physical extraction of samples (Ref.1)	Moderate considering the chamber set-up and the continuos measurements necessary to obtain filtration rates	Can be considered moderate to high becuase the model invovlds a coupled bentho-pelagic ecosystem model which adds complexity. It also includes various parameters which require carefull calibration (Ref. 1). The method also relies on numercal simulations which can be computationally intensive.	Machine Learning (ML) for predictive modelling. Use of Fluorometer and Oximeter equipped Flow-through Setup (FOFS) approach to simultaneously measure filtration and respiration rates in marine filter feeders under dynamic environmental conditions (Ref. 3)	1. DOI: 10.3390/w10111527 2. Doering & Oviatt, 1986 3. DOI: 10.1002/lom3.10414	Assesment on the effects ofthe filter-feeding on carbon cycling (Ref. 1) and net primary productivity. Ref. 3 studies respiration and filtration simoultaneously
Filtration	Stable Isotope Analysis	1	Extractive sampling	δ13C and δ15N Values were measured in muscle tissues of four filter-feeding mollusc species: expressed in per mil (‰) units. (Ref. 1)	Relatively high, considering the method's replicability, the accessibility of necessary equipment and expertise, and the comparability of isotopic data. However, achieving effective standardization requires the development and adherence to detailed methodological guidelines	Although the sampling is *in situ* the analysis is done *ex situ*	Set of species	Not limited to a certain depth. Ref.1, depth up to 220m.	Not restricted to a certain habitat type. Ref. 1, focuses on the gradient along the continental slope	Varies form moderate to highly invasive. It requires the physical collection and handling of organisms from their natural habitat (dredging, Ref. 1). This disrupts the benthic community to some extent and results in the mortality of the sampled organisms.	Complex due to the need for specialized equipment (e.g., dredging gear, boats capable of reaching various depths, storage facilities for frozen samples) and the coordination of sampling across a large spatial gradient. Limitations include the dependence on weather and sea conditions, the potential for sampling bias due to dredging efficiency across different substrates, and the representativeness of collected samples across different depths and habitats.	Relatively high, since the analysis of stable isotopes involve precise measurements and calibration and the use of specialized equipment (mass spectometer). Also, it requieres knowledge of isotopic fractionation, trophic enrichment for the correct interpretation of results.	Developing less invasive and more efficient sampling methods, such as using eDNA or remote sampling techniques, could expand the range of species studied with minimal disturbance	1. DOI: 10.1016/j.ecss.2011.11.004 2. DOI: 10.1016/j.jembe.2006.06.013	
Filtration	BTA	1	Extractive sampling	Filtration rate based on species traits and abundance. Provides a measure of the ecosystem's ability to filter and clean water (Ref. 1).	High due to its capacity to establish consistent protocols and trait classifications	Although the sampling is *in situ* the analysis is done *ex situ*	Community	Not limited to a specific depth range and can be applied across different depths in marine benthic habitats where filtration processes occur.	Generally on soft bottoms mud to sand sediments	It may vary depending on the sampling method (trawl or physical extraction of species- invasive-, or water sampling for eDNA -non invasive-)	Moderatly complex due to the need for comprehensive biological trait data and the use of statistical or modeling tools to analyze the trait-function relationships.	Can vary from moderately complex to higly complex depending on the other methodologies it is used with. It maya require interdisciplinary collaboration as it combines ecological knowledge with genetics (eDNA) in some instances.	High due to its capacity to be integrated wit other more innovative methodologies such as eDNA and machine learning algorits for the analysis of large complex datasets to identify patterns and predictive models related to bioturbation potential. If combined with visual sampling, it can benefit from the use of AI species-recognition algorithms.	1. DOI: 10.1002/ece3.9001	Related processes that can be studied: Water purification.
Nutrient cycling	Benthic Chamber	3	Incubations	Micromoles per square meter per day (µmol m^-2 day^-1) for oxygen, ammonium (NH4+), nitrate (NO3-), phosphate (PO4^3-), and other nutrients (Ref. 1)	High, as results are generally comparable across studies, especially when standardized protocols for deployment time, chamber size, and analysis techniques are followed. The method can be reproducible if the same protocols and conditions are maintained (Ref. 6,7)	*In-situ*	Community	Benthic chambers can be used across a range of depths (Ref. 1,2,3)	Not limited to a certain habitat type. Studies range from Subtidal sandy habitats (Ref. 1), continental slopes (Ref. 3) , Rise/deep zones, O2 minimum zones (Ref. 2)...	Minimally invasive, since the chambers are deployed directly into the sediment without disturbing the surrounding area extensively, they allow for in-situ measurements of nutrient fluxes while minimizing disruption to the benthic environment (Ref. 8)	Might range from moderatly to higly complex as the deployment of the chamber may inolve some logistical challenges, and depending on the research objective, it may require specialized equipment and vessels. Operational limitations include potential disturbances to the sediments during deployment and retrieval or limitations in the duration of the measurements due to logistical constraints. It requires accurate calibration of sensors (Ref. 7)	This method allows for continuous monitoring of nutrient fluxes under natural conditions. The flux rates are calculated based on the changes in nutrient concentrations within the chamber over time. Processing these data requires sophisticated software and analytical tools capable of handling large datasets and performing complex calculations (Ref.2)	High due to integration of remote data transmission (Ref. 4,5), advanced sensors (Ref. 6), and potential for combining with other methodologies such as eDNA analysis	1. DOI: 10.1371/journal.pone.0044920 2. DOI: 10.4319/lom.2004.2.146 3. DOI: 10.1007/s12601-015-0053-x 4. DOI: DOI: 10.3389/fmars.2022.1018751 5. DOI: 10.3390/jmse8090672 6. DOI: 10.1016/S0022-0981(02)00517-8 7. DOI: 10.1007/s00338-003-0314-5 8. DOI: 0079-6611 (95)00009-7	Related processes: photosynthesis, primary production
Nutrient cycling	Cores	1	Extractive, incubations	Micromoles per square meter per day (µmol m^-2 day^-1) for oxygen, ammonium (NH4+), nitrate (NO3-), phosphate (PO4^3-), and other nutrients (Ref. 1)	High due to established protocols for core extraction and nutrient analysis	Although the sampling is *in situ* the analysis is done *ex situ*	Community	The extraction of sediment cores for *ex situ* incubations can be done across a range of depths (Ref. 1)	There is a range of differente habitat types in which this method can be used, considering that the it is typically limited to softer sediments.	Moderately invasive, as the extraction of cores involves physically removing sediment samples from the environment, which can disrupt the sediment structure and benthic community	Several artifacts resulting from core collection may influence the results. These include changes in macrofaunal irrigation rates and changes in porewater profiles in response to altered temperature, pressure, or oxygen concentration (Ref. 2).	Analitycal limitations may include the effort in mantaining incubation conditons as well as potential biases in flux estimates resulting from differences between in situ and ex situ conditions.	Use of ROV's and Technicon segmented flow auto analyzer III (Ref. 2)	1. DOI: 10.4319/lom.2004.2.146 2. DOI: 10.1371/journal.pone.0151110	
Gas fluxes	Benthic Chamber	3	Incubations	mmol m^-2 h^-1, in a more localized and discrete manner, capturing the fluxes within the chamber over specific time intervals (Ref. 1)	High, as results are generally comparable across studies, especially when standardized protocols for deployment time, chamber size, and analysis techniques are followed. The method can be reproducible if the same protocols and conditions are maintained (Ref. 7,8)	*In-situ*	Community	Benthic chambers can be used across a range of depths (Ref. 2,3,4)	Not limited to a certain habitat type. Studies range from Subtidal sandy habitats (Ref. 2), continental slopes (Ref. 4) , Rise/deep zones, O2 minimum zones (Ref. 3)...	Minimally invasive as they require the placement of chambers on the sediment surface, which can temporarily disrupt the benthic habitat during deployment and sampling (Ref. 9)	Might range from moderatly to higly complex as the deployment of the chamber may inolve some logistical challenges, and depending on the research objective, it may require specialized equipment and vessels. Operational limitations include potential disturbances to the sediments during deployment and retrieval or limitations in the duration of the measurements due to logistical constraints. It requires accurate calibration of sensors (Ref. 8)	Processing these data requires sophisticated software and analytical tools capable of handling large datasets and performing complex calculations (Ref.3)aThe use of BFCs often necessitates specialized equipment and software for both data collection and analysis. This includes high-precision sensors for measuring nutrient and gas fluxes, as well as advanced analytical software for data processing (Ref. 7)	High due to integration of remote data transmission (Ref. 5,6), advanced sensors (Ref. 7), and potential for combining with other methodologies such as eDNA analysis	1. DOI:10.1002/lom3.10038 2. DOI: 10.1371/journal.pone.0044920 3. DOI: 10.4319/lom.2004.2.146 4. DOI: 10.1007/s12601-015-0053-x 5. DOI: DOI: 10.3389/fmars.2022.1018751 6. DOI: 10.3390/jmse8090672 7. . DOI: 10.1016/S0022-0981(02)00517-8 8. DOI: 10.1007/s00338-003-0314-5 9. DOI: 0079-6611 (95)00009-7	Related processes: respiration, calcification
Gas fluxes	Eddy Covariance Hydrogen ion and Oxygen Exchange System (ECHOES)	3	Sensors	mmol m^-2 h^-1, providing continuous and detailed data on the exchange processes at the sediment-water interface (Ref. 1)	High due to its non-invasive nature, high temporal resolution, and ability to integrate measurements over a significant area of the seafloor.	*In-situ*	Community	Deepest AEC measurements to date at 2600 m (Ref. 2) although commercial instrumentation is available for depths down to 4,000 m (Ref. 3).	Suitable for a range of habitat types, including intertidal flats, coral reefs, seagrass meadows, sea ice ...(Ref. 3) as long it is deployed in a relatively flat surface	Non-invasive as it involves deploying sensors at the sediment-water interface without disturbing the benthic environment, allowing for continuous monitoring of gas fluxes without physical interference	The system sensors must be properly placed and calibrated. The ECHOES system may face challenges in high-energy environments with strong currents or sediment resuspension, affecting sensor stability and data quality.	Can be considered of a moderate as analytical requirements post-retrieval involve data processing, quality control, flux calculations, and interpretation	AI algorithms can be used to mine large datasets to identify patterns, trends, and correlations in the flux data andç help in detecting anomalies or outliers in the flux data, enabling researchers to identify and investigate unusual patterns that may indicate sensor malfunctions, environmental disturbances, or other factors affecting data quality	1. DOI:10.1002/lom3.10039 2. DOI: 10.1016/j.dsr.2015.11.007 3. DOI: 10.1146/annurev-marine-042121-012329 4. DOI: 10.3354/meps11780	Also used to study organic carbon cycling (Ref. 3,4)
Gas fluxes	Cores	1	Extractive, incubations	Micromoles per square meter per hour (µmol m−2 h−1) of dissolved oxygen (O2), dinitrogen (N2), and methane (CH4) (Ref. 1).	High due to established protocols for gas flux measurements	Although the sampling is *in situ* the analysis is done *ex situ*	Community	In the case of Ref.1, the extraction was done at a shallow depth (bay), but core extraction can be made across a range of depths (Ref 2.)	There is a range of differente habitat types in which this method can be used, considering that the it is typically limited to softer sediments.	Moderately invasive, as the extraction of cores involves physically removing sediment samples from the environment, which can disrupt the sediment structure and benthic community	Moderate to high due to the steps involved in collecting, preserving, and incubating the cores under controlled conditions to accurately measure gas fluxes	High level of complexity due to the precision required in measuring dissolved gases and interpreting the data. Each method has its limitations: the mass spectrometer system requires specialized technical knowledge and equipment (Ref.1), while optical probes (Ref. 3) might be limited by the specificity and sensitivity of the measurements.	Core incubations: Flow-injection mass spectrometer system (Ref. 1)	1. DOI:10.3389/fenvs.2022.1028405 2. DOI: 10.4319/lom.2004.2.146 3. DOI: 10.5194/bg-10-5911-2013	
Primary Production	Benthic Chamber	3	Incubations	GCP (mg C m⁻-2 h⁻-1)	High, as results are generally comparable across studies, especially when standardized protocols for deployment time, chamber size, and analysis techniques are followed. The method can be reproducible if the same protocols and conditions are maintained (Ref. 7,8)	*In-situ*	Community	Benthic chambers can be used across a range of depths (Ref. 2,3,4)	Not limited to a certain habitat type. Studies range from Subtidal sandy habitats (Ref. 1,2), continental slopes (Ref. 4) , Rise/deep zones, O2 minimum zones (Ref. 3)...	Minimally invasive as they require the placement of chambers on the sediment surface, which can temporarily disrupt the benthic habitat during deployment and sampling (Ref. 9)	Might range from moderatly to higly complex as the deployment of the chamber may inolve some logistical challenges, and depending on the research objective, it may require specialized equipment and vessels. Operational limitations include potential disturbances to the sediments during deployment and retrieval or limitations in the duration of the measurements due to logistical constraints. It requires accurate calibration of sensors (Ref. 8)	The conversion of CO2 flux measurements into estimates of net and gross community primary production involves complex data processing, including adjustments for ambient light and temperature effects. Accurate assessment of primary productivity also requires the integration of additional environmental data (e.g., sediment chlorophyll a content), complicating the analysis.	High due to integration of remote data transmission (Ref. 5,6), advanced sensors (Ref. 7), and potential for combining with other methodologies such as eDNA analysis	1. DOI: 10.1016/j.csr.2004.06.002 2. DOI: 10.1371/journal.pone.0044920 3. DOI: 10.4319/lom.2004.2.146 4. DOI: 10.1007/s12601-015-0053-x 5. DOI: DOI: 10.3389/fmars.2022.1018751 6. DOI: 10.3390/jmse8090672 7. . DOI: 10.1016/S0022-0981(02)00517-8 8. DOI: 10.1007/s00338-003-0314-5 9. DOI: 0079-6611 (95)00009-7	The community photosynthetic response to incident solar radiation and temperature at different periods of the year was characterized and usedto estimate the variation of daily potential primary production and the annual potential primary production (Ref. 1).
Primary Production	Aquatic Eddy Covariance	2	Sensors	mmol m−2 h−1 (Ref. 1)	High due to its non-invasive nature, high temporal resolution, and ability to integrate measurements over a significant area of the seafloor.	*In-situ*	Community	Deepest AEC measurements to date at 2600 m (Ref. 2) although commercial instrumentation is available for depths down to 4,000 m (Ref. 3).	Suitable for a range of habitat types, including intertidal flats, coral reefs, seagrass meadows, sea ice ...(Ref. 3) as long it is deployed in a relatively flat surface	Non-invasive as it involves deploying sensors at the sediment-water interface without disturbing the benthic environment, allowing for continuous monitoring of gas fluxes without physical interference	Operational challenges include deploying in areas with complex topography or substantial biological structures that could interfere with flow and sensor measurements. Also, ensuring the AEC system remains stable and upright throughout the deployment period to avoid data loss or bias adds to the operational complexity.	Accurate estimation of benthic productivity using AEC requires simultaneous measurement of environmental parameters (e.g., light, temperature, salinity) to contextualize the oxygen flux data, necessitating additional sensors and data integration efforts.	Complemented with laboratory studies and seabed image analysis to investigate the importance of benthic fauna for coastal organic carbon cycling (Ref. 1).	1. DOI: 10.3354/meps11780 2. DOI: 10.1016/j.dsr.2015.11.007 3. DOI: 10.1146/annurev-marine-042121-012329	Also used to measure O2 gas fluxes
Primary Production	BTA	1	Extractive sampling	Primary production rate based on species traits and abundance. Provides a measure of the ecosystem's ability to produce biomass (Ref. 1).	High due to its capacity to establish consistent protocols and trait classifications	Although the sampling is *in situ* the analysis is done *ex situ*	Community	Not limited to a specific depth range and can be applied across different depths.	Generally on soft bottoms mud to sand sediments	It may vary depending on the sampling method (trawl or physical extraction of species- invasive-, or water sampling for eDNA -non invasive-)	Moderatly complex due to the need for comprehensive biological trait data and the use of statistical or modeling tools to analyze the trait-function relationships.	Can vary from moderately complex to higly complex depending on the other methodologies it is used with. It maya require interdisciplinary collaboration as it combines ecological knowledge with genetics (eDNA) in some instances.	High due to its capacity to be integrated wit other more innovative methodologies such as eDNA and machine learning algorithms for the analysis of large complex datasets to identify patterns and predictive models related to bioturbation potential. If combined with visual sampling, it can benefit from the use of AI species-recognition algorithms.	1. doi: 10.1111/1365-2435.12798	Related processes that can be studied: Photosynthesis efficiency.
Carbon Sequestration	BTA / Stable Isotope Analysis	1	Extractive sampling	Carbon sequestration rate based on species traits and stable isotope data. Provides a measure of the ecosystem's ability to sequester carbon (Ref. 1).	High due to its capacity to establish consistent protocols and trait classifications	Although the sampling is *in situ* the analysis is done *ex situ*	Community	Not limited to a specific depth range and can be applied across different depths.	Generally on soft bottoms mud to sand sediments	It may vary depending on the sampling method (trawl or physical extraction of species- invasive-, or water sampling for eDNA -non invasive-)	Moderatly complex due to the need for comprehensive biological trait data and the use of statistical or modeling tools to analyze the trait-function relationships.	Can vary from moderately complex to higly complex depending on the other methodologies it is used with. It maya require interdisciplinary collaboration as it combines ecological knowledge with genetics (eDNA) in some instances.	High due to its capacity to be integrated wit other more innovative methodologies such as eDNA and machine learning algorithms for the analysis of large complex datasets to identify patterns and predictive models related to bioturbation potential. If combined with visual sampling, it can benefit from the use of AI species-recognition algorithms.	1. http://dx.doi.org/10.1098/rspb.2014.0669	Related processes that can be studied: Carbon cycling.

Habitat provisioning	BTA	1	Extractive sampling	Habitat complexity and provisioning based on species traits. Provides a measure of the ecosystem's ability to provide habitat for various species (Ref. 1).	High due to its capacity to establish consistent protocols and trait classifications	Although the sampling is *in situ* the analysis is done *ex situ*	Community	Not limited to a specific depth range and can be applied across different depths.	Generally on soft bottoms mud to sand sediments	It may vary depending on the sampling method (trawl or physical extraction of species- invasive-, or water sampling for eDNA -non invasive-)	Moderatly complex due to the need for comprehensive biological trait data and the use of statistical or modeling tools to analyze the trait-function relationships.	Can vary from moderately complex to higly complex depending on the other methodologies it is used with. It maya require interdisciplinary collaboration as it combines ecological knowledge with genetics (eDNA) in some instances.	High due to its capacity to be integrated wit other more innovative methodologies such as eDNA and machine learning algorits for the analysis of large complex datasets to identify patterns and predictive models related to bioturbation potential. If combined with visual sampling, it can benefit from the use of AI species-recognition algorithms.	1. https://doi.org/10.1016/j.ecss.2019.106272	Related processes that can be studied: Habitat diversity.
Habitat provisioning	Under water towed HR camera/ AUVs/ ROVs	2	Visual Sampling	Imaging data (% of coverage)	Used together with ML (Ref. 1), high due to the use of algorithmic processing for classification, which can be consistently applied across different datasets, enhancing comparability and extrapolation of results. ROVs and AUVs, high standardization potential due to the widespread availability of standardized protocols for their deployment and operation (Ref. 6)	Although the sampling is *in situ* the analysis is done *ex situ*	Community	Shallow (Ref. 1). They can be deployed to depths of up to 2,000 meters, allowing for surveys and data collection in a wide range of deep-water environments (Ref. 2) .	Not restricted to a certain habitat type (corals, sediments, seagrass, and algae - Ref.1)	Minimally invasive, as this method does not require the physical extraction of samples from thee environment	The operational complexity may vary depending on the dpeths at which the study is bein made. For shallow habitats, it is quite low as this can be done with divers (Ref. 1). For deeper studies, this may require the use of more specilized equipment and vessels (Ref. 2), which would also increase the cost. At this greater depths, there can be challenges with calibration and measurement accuracy at greater depths due to environmental factors (Ref. 2). Deploying ROVs involves handling sophisticated control systems, ensuring stable navigation in varying water conditions, and managing power and communication cables, which can limit their operational depth (Ref. 4). AUVs, being pre-programmed for autonomous missions, demand meticulous planning and programming skills to ensure accurate data collection and retrieval, especially in complex or deep-sea environments (Ref 5).	Moderate to high, as when done manually it is more than consuming than complex, and might increase the level of subjectivity of habitat identification. When integrated with ML algorithms, the complexity resides in the sleection and trianing of the algorithm, but overall it improves the efficiency, accuracy, and scalability of habitat assessments. However this method is dependant on the quality of video or visual data collected. 3D habitat mapping involves creating detailed and accurate representations of underwater environments. This process includes capturing fine-scale ecological processes and detecting changes in habitat structure over time (Ref. 3). The challenges faced in underwater imaging include acquiring high-quality georeferenced imagery due to water attenuation of electromagnetic waves, the need for near-bottom, high-resolution imaging, and the limitations of high-bandwidth communications and GPS-based positioning underwater (Ref. 5).	Machine Learning (Ref. 1), ROV's (Ref.4), AUV's (Ref. 3,5) and 3D mapping (Ref. 3)	1. DOI: 10.3390/rs10050773 2. DOI: 10.4031/002533208787157624 3. DOI: 10.3389/fmars.2019.00276 4. DOI: 10.1109/JOE.2005.851391 5. DOI: 10.1002/rob.20324 6: ISSN 2517-7605.	
Habitat provisioning	Passive Acoustic Monitoring	2	Acoustic Sampling	Ecoacoustic indices (Hz and DB) (Ref. 1)	Sampling schemes can be repeated identically across multiple spatial and temporal scales and the fully digital raw data produced can be easily compared among localities, stored, exchanged, and re-analysed when needed (Ref. 3)	*In situ*	Community	Most studies regarding benthic habitat are limited to coastal environments, althought this method could also be used for deeper habitats depending on the research objective.	Studies have used this method in coral reefs (Ref.1) and seagrass communities (Ref.2)	Non-invasive or minimally invasive since it involves listening to sounds produced by marine organisms or other sources without introducing additional sounds into the environment, it does not disturb the habitat or the organisms being studied.	Requires low sampling efforts, and can be implemented from the surface without specific technical skills, using recorders moored on the seafloor (Ref. 1) or drifting buoys (Ref. 4)	Processing large amounts of audio recordings, which can be computationally intensive and require specialized software for sound analysis. Limited taxonomic resolution and environmental interference (External factors such as weather conditions, anthropogenic noise, or natural disturbances can interfere with acoustic recordings, affecting the accuracy and reliability of the data collected - Ref. 1)	Automated AI sound identification (CNNs, Ref. 5)	1. DOI: 10.1016/j.ecolind.2019.105623 2. DOI: 10.1002/rse2.72 3. DOI: 10.1111/2041-210X.13101 4. DOI: 10.3354/meps12370 5. DOI: 10.1111/2041-210X.13101	
Ecosystem resilience	BTA	1	Extractive sampling	Ecosystem resilience based on species traits and abundance. Provides a measure of the ecosystem's ability to recover from disturbances (Ref. 1).	High due to its capacity to establish consistent protocols and trait classifications	Although the sampling is *in situ* the analysis is done *ex situ*	Community	Not limited to a specific depth range and can be applied across different depths.	Generally on soft bottoms mud to sand sediments	It may vary depending on the sampling method (trawl or physical extraction of species- invasive-, or water sampling for eDNA -non invasive-)	Moderatly complex due to the need for comprehensive biological trait data and the use of statistical or modeling tools to analyze the trait-function relationships.	Can vary from moderately complex to higly complex depending on the other methodologies it is used with. It maya require interdisciplinary collaboration as it combines ecological knowledge with genetics (eDNA) in some instances.	High due to its capacity to be integrated wit other more innovative methodologies such as eDNA and machine learning algorits for the analysis of large complex datasets to identify patterns and predictive models related to bioturbation potential. If combined with visual sampling, it can benefit from the use of AI species-recognition algorithms.	1. DOI: DOI: 10.1016/j.ecolind.2021.107692	Related processes that can be studied: Recovery rates.
Calcification	Buoyant Weight Technique	1	Extractive Sampling & Laboratory Analysis	Calcification rate (mg/day) (Ref 1.)	Allows for direct comparisons of calcification rates between different organisms or experimental conditions based on changes in skeletal weight. Comparability is facilitated by the non-destructive nature of the method, enabling repeated measurements on the same individuals over time.	*ex situ*	Community	Not limited to a certain depth.	Caution should be exercised in applying the buoyant weighing method to the measurement of calcifi cation in organisms other than corals where the contribution of soft tissue weight to the weight of the calcium carbonate parts may be substantial (Ref 1). See Ries et al. (2009) for an example of the application of this method to a wide range of calcifying benthic organisms.	Non-destructive and minimally invasive	Very simple and easily applied to a large number of replicates.	Limitations include that some of the increase in mass may not be due to building of new skeleton, i.e. some of the increase may be due to an increase in the mass of soft tissue. Also, the accuracy of the method is unknown because it has not been compared with either the AT or Ca2+ depletion methods.		1. Measurements of calcification and dissolution of benthic organisms and communities	
Calcification	Calcification Accretion Units	1	Extractive Sampling & Laboratory Analysis	Calcified biomass (g/cm year) (Ref.1)	High as it provides a cost-effective, standardized protocol for constructing, deploying and processing settlement tiles (Ref.1)	*in situ*	Community	Not limited to a certain depth.	CAUs can be deployed in various coastal marine habitats	Moderatly low, as it involves deploying artificial substrate units to mimic natural habitats, allowing for the collection of data on community structure and calcification withouth directly disturbing the environment	Moderate. Constructing and deploying CAUs require careful planning and execution to ensure standardized data collection. However, the method is considered cost-effective and less time-intensive than some other approaches	Analyzing data collected from CAUs typically involves image analysis to quantify calcium carbonate accretion rates, early successional community structure, and recruitment of marine organisms. While image analysis can be a detailed process, it provides valuable insights into ecosystem functioning and		1. DOI: 10.1111/2041-210X.13867	
Calcification	45Ca Radioisotope	2	Incubations	Calcification rate: dpm/g (disintegrations per minute per gram of calcium carbonate)	Potential for standardizing experimental protocols and data analysis procedures across studies. It involves consistent methods for preparing radioactive solutions, incubating organisms, and measuring radioisotope uptake. Comparability is facilitated by the quantitative nature of radioisotope measurements, enabling researchers to assess and compare calcification rates in a consistent manner. Factors such as species-specific differences in calcium uptake kinetics and environmental variability may limit the direct extrapolation of individual-level data to community or ecosystem scales.	*ex situ*	Single species	As it is a laboratory experiment, it is not limited to a certain depth	Corals	It can be considered invasvie and destrcutive as ot requires the physical extraction of organisms from their environment, followed by the exposure of this organisms to radioactive calcium in a controlled setting	Extremely sensitive so the measurement period can be minutes. It is the only method suitable for studying kinetics and pathways of Ca2+ transport. The weakness of the method is that the organism must be destroyed to be analysed and it is not easily scaled up for use on large organisms or on many organisms in a mesocosm or in the field.	Analyzing the radioactivity levels in the samples requires specialized equipment such as scintillation counters and expertise in handling radioactive materials. Radioisotope methods are destructive, as they involve sacrificing the organisms to analyze the radioactive content. This limits the ability to conduct long-term studies on the same individuals. The method may be challenging to scale up for large organisms or community-level studies due to the logistical constraints of handling radioactive materials and analyzing multiple samples.		1. Measurements of calcification and dissolution of benthic organisms and communities	
Calcification	Alkalinity anomaly	2	Incubations	Calcification rate: units of moles of calcium carbonate (CaCO3) dissolved per unit area per unit time	The method allows for standardization of measurements across different studies, enhancing comparability between research findings. The strengths of the method are that is non-destructive, broadly applicable to small (1 l) and short (1 to 3 h) or large (more than 1000 m3) and long experiments (days to months) and useful for both calcification and dissolution studies (Ref. 1).	Can be applied both in situ and ex situ (in controlled laboratory settings or mesocosms)	Community	Not limited to a certain depth.	Benthic environments where calcifying organisms are present	Non-invasive and does not require direct manipulation of organisms or habitats, minimizing potential disturbances to the ecosystem during data collection	While the method is relatively straightforward in principle, operational complexities may arise in field deployments, sample collection, and data interpretation.	Analyzing alkalinity data and interpreting the results may require specialized analytical techniques and expertise. Limitations may include uncertainties in alkalinity measurements and potential sources of error in calculating net dissolution rates since in certain environments the uptake and release of minerals and organic acids that cuase changes in At unrelated to calcification and dissolution (Ref. 1)		1. Measurements of calcification and dissolution of benthic organisms and communities	Also addresses photosynthesis and respiration

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