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To cite this article: Giulia La Bianca, Kerry L. Howell, Jazmin Conway, Amanda T. Lombard, Kirsty McQuaid, Holly J. Niner, Kerry Sink, Mathew Upton & Sian Rees (2026) Linking deep-sea biological communities (biotopes), ecological processes and ecosystem services: a systematic literature review, *Ecosystems and People*, 22:1, 2652430, DOI: [10.1080/26395916.2026.2652430](https://doi.org/10.1080/26395916.2026.2652430)

To link to this article: <https://doi.org/10.1080/26395916.2026.2652430>



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REVIEW

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Linking deep-sea biological communities (biotopes), ecological processes and ecosystem services: a systematic literature review

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ABSTRACT

The Kunming–Montreal Global Biodiversity Framework (GBF) encourages the application of area-based management tools for the protection of biodiversity (so-called 30 by 30). The GBF sets out that biodiversity-ecosystem service assessments and information on location and the spatial extent of the ecosystem are needed to ensure understanding and effective management of biodiversity and natural resources. Habitat mapping is an essential element of this, and progress has been made in describing deep-sea benthic assemblages or biotopes for use as mapping units. What is lacking is a clear understanding of the link between mappable units (biotopes) and the ecosystem services (ES) they provide. This study develops a matrix to identify the ES provided by defined deep-sea biological assemblages (biotopes) to support conservation planning in the deep sea. Using a systematic literature review, we collate and summarise evidence of the links between 12 deep-sea biotopes in the Northeast Atlantic and their contribution to 15 ES. We find that cold-water coral reefs, *Desmophyllum pertusum* (formerly *Lophelia pertusa*) reefs, are a well-studied biotope, show contributions to regulating services, such as lifecycle maintenance and climate regulation, and provisioning services, such as food and biomedical benefits. Less or no knowledge exists for the other 11 biotopes. Knowledge gaps relate to their contribution to secondary production and regulating services, particularly how biotopes contribute to benthic–pelagic coupling, long-term climate regulation, cultural services and medical, genetic, and biochemical potential. This study underscores knowledge gaps and research priorities needed to effectively map services provided by these remote yet unique ecosystems.

KEY POLICY HIGHLIGHTS

- Natural Capital Protection: Recognizing deep-sea biota as a key element of climate mitigation and genetic resources is essential for meeting international statutory commitments (e.g., GBF Target 11).
- Precautionary Management: Given the knowledge gaps and high uncertainty regarding deep-sea biogeochemical cycles, policy approaches must account for uncertain knowledge to embed sufficient precaution into decision-making to protect ES.
- Beyond “Hotspots”: Management and research must expand focus beyond cold-water corals to include understudied biotopes like sponge aggregations, burrowing megafauna, holothurians which are putatively critical to regulating services.

ARTICLE HISTORY

Received 2 April 2025
Accepted 24 March 2026

EDITED BY

Sebastian Villasante

KEYWORDS

Deep sea; biotopes; ecological processes; ecosystem services; biodiversity conservation; GBF

1. Introduction

The connection between the marine environment and societal benefit is central to the Kunming-Montreal Global Biodiversity Framework (GBF) (Convention on Biological Diversity, www.cbd.int; adopted 19th December 2022). The GBF invites the application of spatial planning processes to ensure that areas of particular importance for biodiversity and ecosystem function and services are managed effectively, conserved, and ecologically represented by 2030 (Target 3). These targets underscore the importance and international

commitment to not just protect the natural environment but also to account for ecosystem service provision and spatial extent. To ensure implementation, ecosystem service assessments paired with mapping techniques can provide the necessary evidence-based information to meet these global biodiversity strategies. While ecosystem service assessments link biodiversity and ecosystem services (ES) at the local, national and global scale (Brondizio et al., 2019), habitat classification and subsequent mapping (also called bioregionalisation) enables the spatial distribution of biodiversity and ecosystems to

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This article has been corrected with minor changes. These changes do not impact the academic content of the article.

 Supplemental data for this article can be accessed online at <https://doi.org/10.1080/26395916.2026.2652430>.

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be visualised. Thus, this evidence can provide invaluable information to environmental managers on the potential ES provision from sites and their importance to both ecosystems and society.

Although global assessments of biodiversity include all biomes, terrestrial ecosystems have been relatively well studied compared with marine ecosystems and their services (Townsend et al. 2018). Lack of marine ecosystem service assessments is attributed to scarcity of marine spatial data and the spatial disconnect between service supply and beneficiaries (Hattam et al. 2021; Niner et al. 2024). Difficulty in acquiring habitat information and geospatial datasets increases with distance from the coast and increasing depth, particularly for biodiversity found in pelagic and epibenthic ecosystems. Marine habitats and in particular offshore and deep seas are perfect examples where decisions relating to use and potential impacts are often made with little or no biological knowledge, and instead surrogates are used to represent biological diversity when mapping benthic and pelagic habitats (Howell 2010; Clark et al. 2011; McQuaid et al. 2023).

Methods for spatially representing ES can be broadly categorised into direct and indirect approaches (Eigenbrod et al. 2010). Direct methods involve measuring states, quantities, or processes through observations, monitoring, surveys, questionnaires, or remote sensing and earth observation data (Burkhard and Maes 2017; Nahuelhual et al. 2021). In contrast, indirect methods use landscape-based proxies and modeled surfaces informed by prior knowledge and interpretation (Vihervaara et al. 2018; Nahuelhual et al. 2021). For most marine habitats, direct measurements are scarce at the global scale, necessitating the widespread use of indirect methods to map the capacity and delivery of marine ES. One such approach is the habitat–service matrix, which evaluates service provision using ecosystem Service Providing

Units (SPUs). Habitat–service matrices are among the most widely applied tools for assessing ES (Jacobs et al. 2015) and have been instrumental in developing management measures for specific areas (e.g. Tao et al. 2018). SPUs provide a framework to link biodiversity with ES, tracing service provision from individual species or species groups to the ecological functions and processes they underpin (Díaz et al. 2007; Luck et al. 2009) (Figure 1). Translating the ecosystem service contributions of biological components into maps often involves the use of SPU at the level of biological assemblages or biotopes. ‘Biotopes’ encompass both biotic and abiotic factors and ‘habitat’ represent only abiotic conditions (Connor et al. 2004). Biotopes, defined as biological communities and the suite of environmental conditions under which they occur, are fine-scale (at least 25 m²) mapping units (Howell 2010; Davies et al. 2014). They are increasingly used to assess ES in alignment with spatial mapping efforts (Galparsoro et al. 2014; Tempera et al. 2016).

There has been progress in applied research to quantify and map the supply of terrestrial (Maes et al. 2012), and (coastal) marine ES (Rees et al. 2012). This approach has employed best available evidence in published literature and expert opinion to develop habitat–ecosystem service matrices that link ecological and socio-economic systems (Potts et al. 2014; Campagne and Roche 2018; Geange et al. 2019; Armoškaitė et al. 2020; Hattam et al. 2021). Previous studies applying habitat–service matrices show significantly higher numbers of ES provided by habitats found in shallow waters and close to the shore when compared with offshore areas (Milcu et al. 2013; Galparsoro et al. 2014; Cordero-Penín et al. 2023). This is consistent with the fact that humans have easier access to coastal waters than to the deep sea, and data deficiency is particularly evident for deep-sea environments. This is true also for access to benthic habitats where access depends on depth

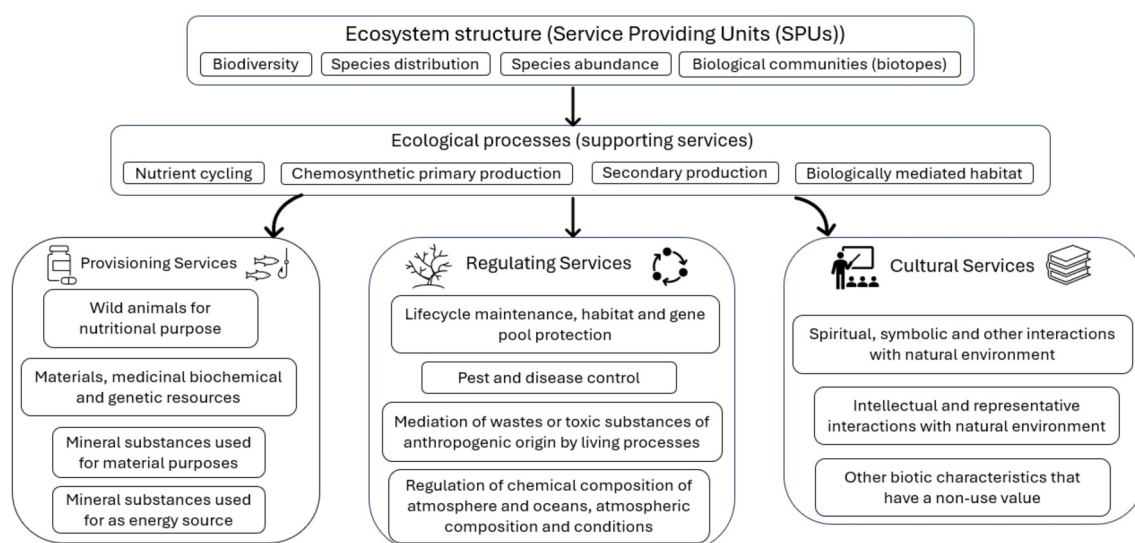


Figure 1. An overview of the linkages amongst biological communities, or biotopes (ecosystem structure), ecological processes and final ecosystem services (adapted from Le et al. 2017).

and distance to the shore, which is evident in research efforts worldwide (e.g. Howell et al. 2020).

However, despite distance and depth affecting access to benthic habitats, the contribution of benthic organisms to ecosystem processes, such as nutrient cycling, and to provisioning services, e.g. bioprospecting, is not to be underestimated (see e.g. Ottaviani 2020). Evidence suggests that there are a wide range of benefits provided by the deep sea including food (Victorero et al. 2018), energy resources (Bravo et al. 2023), climate regulation (Levin 2021) and cultural services (Armstrong et al. 2022) and it is increasingly recognised as a source of potentially beneficial molecules for bioprospecting (Koch et al. 2021; Hesketh-Best et al. 2023). Provision of deep-sea ES has been assessed at the level of broad scale geomorphological features (e.g. open slopes and basins, canyons, seamounts) by means of literature reviews and expert judgements (Armstrong et al. 2012; Salomidi et al. 2012; Potts et al. 2014; Thurber et al. 2014; La Bianca et al. 2018). However, only a single peer-reviewed article is currently available that reviews services provided at the level of biological communities, including deep-sea benthic communities (Salomidi et al. 2012). The study summarises the services provided by just two deep-sea benthic communities, coral reefs and sponge aggregations. It does not align benthic community descriptions to formally described biotopes or biotope complexes, but both cold-water coral reef and deep-sea sponge aggregations can be aligned to defined units at the biotope complex level (European Nature Information System (EUNIS) level 3). Yet, 40 deep-sea biotopes have been described by Howell (2010) that were later adopted into EUNIS. It is unknown what services they provide. Recent research effort has also focussed on ES assessment of just these same two biological community types (Ottaviani 2020; Armstrong et al. 2022; Cordes et al. 2023). There is a general lack of knowledge on the distribution of deep-sea biodiversity, its function, and how function is related to the delivery of services. This knowledge gap hinders wider consideration of the role of deep-sea benthic biological communities in providing services and mechanisms of delivery.

The deep sea is the largest biome on Earth and is heterogeneous consisting of many different ecosystems at different spatial scales. As a foundational step toward identifying and later mapping deep-sea ES, La Bianca et al. (2023) defined the ES relevant to the deep sea in a standardised format informed by a comprehensive literature review. The authors included services that were described in the Common International Classification of Ecosystem Services (CICES) scheme and also presented in the existing deep-sea ES literature (Armstrong et al. 2012; Thurber et al. 2014). The current study now tries to marry service provision to defined SPUs (here biotopes) using a habitat–service matrix approach. We present the results of a systematic literature review, followed by discussion on how this information might

be applied for mapping deep-sea ES and what future research priorities might be. The use of a habitat–service matrix based on existing evidence provides a baseline for consideration of deep-sea ES globally and highlights gaps where research is needed to improve our understanding of these remote ecosystems.

2. Methods

To answer the question ‘what services are provided by deep-sea biotopes?’, a systematic literature review was conducted and a habitat–services matrix was developed. Initial guidance for constructing the matrix was drawn from Salomidi et al. (2012), Potts et al. (2014) and Hattam et al. (2021) (Figure 2).

The first step was to select habitat components or SPUs and their associated ES of relevance. Information on the methodology employed to finalise SPU categories and ES is provided below. The second step was to collate the existing evidence on the ES provided by selected SPUs in a stepwise manner (Evidence review). Finally, the third step, outlined in Habitat–service matrix, was to synthesise the evidence into succinct information and construct the matrix into a visually meaningful and brief output.

2.1. Selecting service providing units (SPUs)

Following Salomidi et al. (2012), Geange et al. (2019) and Hattam et al. (2021), biotopes at a spatial scale in the order of 25 m², were selected as the most suitable SPUs for this study. All benthic biotopes considered in this study were classified according to the European Nature Information System (EUNIS, <https://eunis.eea.europa.eu/index.jsp>, 2025) classification, which is a common habitat scheme used in various published habitat–service matrices to represent ecosystem components in European Seas (Potts et al. 2014; Tempera et al. 2016; Cordero-Penín et al. 2023). The EUNIS deep-sea section provides 40 benthic megafaunal assemblages that were formulated into ‘biotope’ descriptions largely based on Howell (2010). Following Howell (2010), we define a biotope as a seascape characterised by similar environmental conditions and a specific assemblage of animal species. Biotope descriptions in Howell (2010)

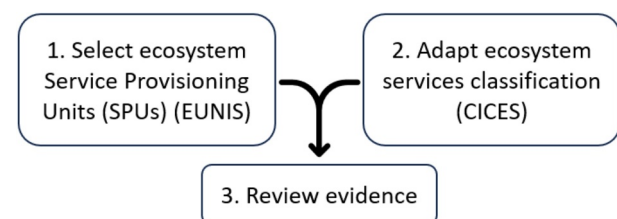


Figure 2. Flow chart of the methods used to summarise the evidence of the links between deep-sea biotopes and ES (modified from Hattam et al. 2021).

were originally adopted into a new deep-sea section of the UK's national habitat classification system (Parry et al. 2015) before being incorporated into EUNIS. The revised deep-sea classification is structured into five hierarchical levels: environment (level 1), biological zone (level 2), substratum (level 3, adapted from EUNIS with the inclusion of biogenic substratum), broad community or biotope complex (level 4), and biological community or biotope (level 5). In this study, 12 deep-sea biotopes (levels 4 and 5) (Figure 3) were selected for consideration. These 12 were chosen on the basis of the potential for mapping their distribution in the Northeast Atlantic in the future, given the availability of point observation data.

2.2. Selecting ES

In the development of a habitat-service matrix that is specific for local- and regional-scale ES mapping and

assessment, it was necessary to first select an appropriate ES classification (Heink et al. 2016). ES classifications relevant to the deep sea were described in La Bianca et al. (2023). These authors discussed deep-sea ES and with an additional literature review, aligned the terminology to internationally agreed ES frameworks CICES v5.1 (Haines-Young and Potschin 2018) and IPBES (Brondizio et al. 2019). This new standard identified a total of 15 ES provided by the deep sea and was adopted for use in this study.

Distinction between ecological processes and ES has been a highly contested topic since the inception of the MEA framework (2005), and more recent habitat-service matrix studies have advocated for the explicit categorisation of these two components when assessing natural capital (Hattam et al. 2015). To maintain a holistic approach and account for ecosystem complexity and integrate existing ecological knowledge in the habitat-service matrix, ecological processes described

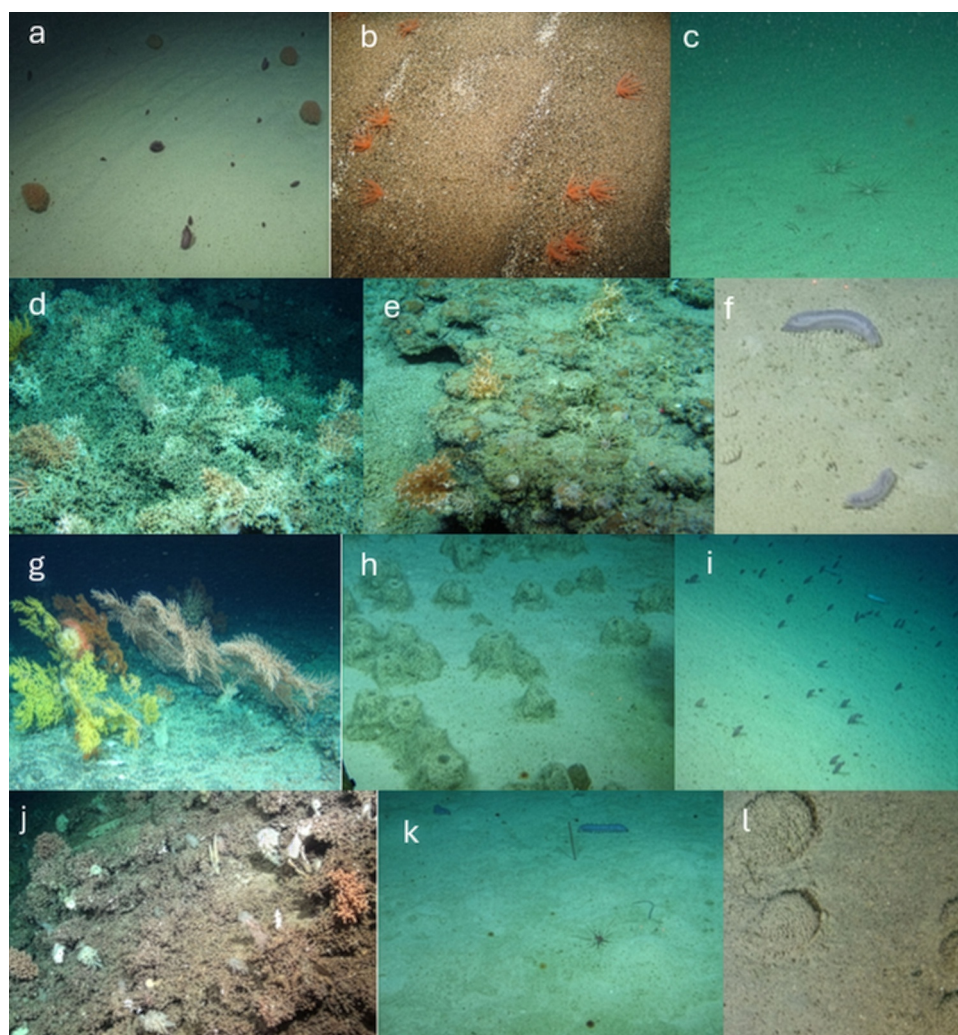


Figure 3. The biological communities (biotopes) selected for this study: a. *Acanella arbuscula* assemblage on mud; b. burrowing anemone fields on coarse sediment; c. *Cidarid* urchin assemblage on coarse sediment and sand; d. *Desmophyllum pertusum* reef; e. discrete *Desmophyllum pertusum* colonies; f. holothurian-dominated community; g. mixed cold water coral community (coral gardens); h. *Pheronema carpenteri* field on mud; i. sea pens and burrowing megafauna on mud; j. *Solenosmilia variabilis* reef; k. solitary scleractinian fields; l. *Syringammia fragilissima* fields on mud, mixed and coarse sediment. Photos credits: (a, d, e, f, g, h, i) SeaRovers 2018 & 2019 marine Institute, Ireland. (b) Crown copyright 2006 SEA/SAC surveys. (c, j, k, l) NERC funded Deeplinks project 2016, Plymouth University, Oxford University, BGS, JNCC.

in La Bianca et al. (2023), *Nutrient cycling*, *Biologically mediated habitat*, *Chemosynthetic primary production* and *Secondary production*, were included within the assessment. Evidence shows that these ecological processes are important for deep-sea fauna (Armstrong et al. 2012; Thurber et al. 2014). Given that the scope of this study is to understand the role of deep-sea biological communities to provide services, ecological processes were retained within the assessment to understand what deep-sea organisms do and highlight knowledge gaps. However, as *per* Hattam et al. (2015), Tempera et al. (2016) and Galparsoro et al. (2021), when mapping ES, only final ES should be used to avoid double counting.

2.3. Evidence review

This study seeks to collate current evidence of the ecological processes and ecosystem services provided by deep-sea biological communities. Specifically, it develops understanding of what knowledge exists on the contributions of biological communities toward ecosystem services, identifies knowledge gaps and the research priorities identified in the literature.

Literature was subject to a systematic review applying a deductive framework centred around the ecological processes and ES provided by deep-sea biota as described in La Bianca et al. (2023). The systematic review was based on the main principles of the PRISMA framework (Preferred Reporting Items for Systematic Reviews and Meta-analysis) (Moher et al. 2015) and adapted to the scope of our review. The search terms were selected according to existing frameworks that describe the ecological processes and ES (La Bianca et al. 2023) and are included in the Supplementary Table S1. Review and analysis were conducted by a single reviewer (GLB). Primary literature, secondary literature and databases (only for natural products used for medicine and biotechnology: Marine Pharmacology database (marinepharmacology.org, 2025), Comprehensive Marine Natural Products Database (cmnpd.org, 2025), Natural Products Magnetic Resonance Database (Wishart et al. 2025), Natural Product Activity and Species Source Database (bidd.group/NPASS/search.php, 2025), were considered relevant for this review. Studies were included for further eligibility assessment if they specifically addressed ecological processes and ecosystem services that deep-sea biotopes provide. Evidence was included only if the title and/or abstract contained the terms 'deep sea' and one or more of the search terms listed in Supplementary Table S1. Studies were excluded if they investigated exclusively human impacts, habitat classification, ecotoxicology, eDNA, community structure, description of new species, environmental status, shallow and mesophotic papers, climate change predictions, not the taxa group of interest, dispersal models, conservation. The search was

undertaken using the internet search engines, Google Scholar, Web of Science and Scopus, selecting article title and abstract. Queries included search terms with Boolean strings. Due to limitations in Google Scholar's Boolean functionality, complex nested search strings were simplified, and ecosystem function terms were searched separately in combination with habitat descriptors. In Google Scholar, owing to the large number of results, evidence was sorted by relevance and the first 100 results (title and snippet) were scanned for each combination of search terms. Non-English publications were omitted from this review. To ensure the reproducibility of this review, only studies with full-text availability were considered. We excluded citations where the primary data remained inaccessible via open-access channels or the authors' institutional library access. To ensure relevant knowledge was included, the search was conducted on evidence published between 1 January 1980 and 12 December 2024. The criteria were that the literature should not be published prior to 1980 to allow us to access all full papers. However, here it is acknowledged that there may be relevant evidence published before and after this date that is not included in our review.

Full reference and type of evidence (peer-reviewed and grey literature e.g. reports, website) were included in a Microsoft Excel sheet for each relevant piece of evidence. All text of relevant studies was reviewed. Additional evidence was supplemented by snowball strategies (e.g. papers that matched our inclusion criteria were scanned for relevant references and included in this study). Review papers were scanned to identify the most relevant primary literature to answer the study's question. When full text was scanned, research priorities were noted for each evidence and later compiled in one succinct table.

The evidence search aimed to collate information related to the specific biotope described in the habitat classification; however, due to large knowledge gaps at this level, the evidence search was also considered at the biotope complex level in some cases. This was true for most biotopes, except for *Desmophyllum* reefs, where evidence was robust, and it was not considered necessary to widen the search pool. Dominant taxa within the biological assemblages were extracted from the Joint Nature Conservation Committee (JNCC) habitat classification (database available online). Selected biotopes and their higher hierarchical levels are included in the search terms list (Supplementary Table S1). This review gathered information on the dominant taxa within the biological assemblage, thus evidence on the less abundant epifauna and infauna living within the same community was not within the scope of this study. Some evidence was used more than once when it showed relevance to more than one service.

2.4. Habitat–service matrix

Based on the evidence collated, publications that provided relevant information for the scope of the present research were summarised and tabulated. Two matrices were produced. The first matrix contained a summarised description of the evidence found, categorised *per* service and complemented with a reference list (Supplementary Table S1). A second, combined matrix was also developed to show succinctly evidence gaps. Information on the capacity of 12 seabed biotopes to provide ES was extracted from the literature review. Sources are provided in Supplementary Table S1. Once the literature review was concluded, each habitat–service link was reported in the matrix, according to three potential findings: (1) evidence exists, (2) no evidence found and (3) ecological processes or service not applicable to the biotope.

All ecosystem services are connected to ecological processes in a variety of ways, and one function/process provides a diversity of services (Thurber et al. 2014). Given the difficulty in linking ecological processes to final services, when evidence was found on the ecological processes carried out by a biotope, it is assumed that the same biotope also delivers its linked biotic final services. For cultural services, no distinction of biotopes was made in the review process owing to the difficulty of finding evidence that was biotope specific; therefore, any evidence that discussed cultural services in the context of the deep sea was included in all biotopes.

3. Results

3.1. Habitat–service matrix

Existing evidence and knowledge gaps of ecological processes and final services provided by 12 deep-sea biological communities is summarised in the habitat–service matrix (Table 1). Broad understanding of each service is summarised, bringing together the *status quo* of services provided by selected deep-sea biotopes. Table 1 provides a quick-data visualisation. Full details of the evidence found *per* biotope/service are attached in Supplementary Table S1. One hundred and forty-one studies provided evidence to support linkages between deep-sea biotopes to ES (Figure 4).

This study found 321 linkages between 12 deep-sea biotopes and ES. The matrix demonstrates that the majority of the deep-sea biotopes (11/12) play a role in all ecological processes to varying degrees depending on the particular component of the biotope. Substantial knowledge exists on the nursery and nutrient cycling processes provided by deep-sea cold-water coral reefs, coral gardens, sea pen fields and sponge aggregations (Figure 5a). In contrast, evidence of most final services exists only for deep-sea cold-water coral *D. pertusum* reefs than for any other biotopes (Figure 5b). For the remaining deep-sea biotopes analysed there is some

understanding of the contributions to material for biotechnology and bioprospecting. Additionally, 104 of 141 papers selected in this review are peer-reviewed articles, of which 49 papers are on the role of cold-water coral reefs. Blank cells in Table 1 show the missing links between biotopes and direct services to society. Although this does not imply that biotopes do not provide a service, it indicates that no studies were found that provide evidence for that linkage.

3.2. Ecological processes

This review found 88 linkages between 12 deep-sea biotopes and four ecological processes. Ecological processes are fundamental for the functioning of deep-sea ecosystems, primarily categorised into nutrient cycling and habitat provisioning. Habitat provisioning was most documented in cold-water corals (CWC) and sponges, which serve as structural engineers. *D. pertusum* and *Pheronema* spp. fields provide complex microhabitats that support diverse taxa, including *Brosme brosme* and various echinoderms, by altering localised water flow and stabilising substrates.

Nutrient cycling is driven by both sessile and mobile fauna. CWC-associated microbes enhance carbon and nitrogen fixation, while sponges facilitate nitrogen cycles through nitrification and anammox. Epibenthic megafauna, such as *Cidarid urchins* and holothurians, influence nutrient cycling and sediment oxygenation. Sea urchins play a role in coral carbonate budgets and organic carbon flux, though overpopulation can damage coral reefs (Stevenson and Rocha 2013). Holothurians recycle nutrients through sediment bioturbation, releasing ammonium and dissolving calcium carbonate (Williamson et al. 2021), but direct studies on the role of holothurians in bioturbation impacts are sparse. Sea pens and burrowing megafauna stimulate ammonium flux through sediment bioturbation, enhancing microbial activity and nutrient cycling (Miatta and Snelgrove 2021). Foraminifera, particularly xenophyophores, contribute to global carbon cycling by processing particulate and dissolved organic matter, creating carbon deposition hotspots (Levin and Gooday 1992; Tsuchiya and Nomaki 2021). Despite these roles, research remains disproportionately focused on CWCs and sponges, leaving significant gaps in our understanding of carbon processing in less-studied biotopes.

3.3. Regulating services

Results indicate that some deep-sea biotopes contribute to regulating services, such as *Lifecycle maintenance, habitat and gene pool protection, mediation of wastes or toxic substances of anthropogenic origin by living organisms* and *regulation of chemical composition of atmosphere and oceans*. To date, no Pest control services examples exist for deep-sea benthic

Table 1. A summary of the existing evidence on deep-sea ES for twelve biotopes. ✓ = evidence exists; blank cell = no evidence found; X = eco-process or service does not apply to this biotope. Please note that blank cells indicate where evidence does not exist, however, this does not imply that a biotope does not provide a service. No expert opinion was used to compile this table. All evidence relates to deep-sea biotopes only. Further information on each individual link is provided in the Supplementary of this manuscript.

Final services																
Eco-process			Regulating			Provisioning			Cultural							
Biological community or Biotope	Depth range (m)	Nutrient cycling	Secondary production	Chemosynthetic primary production	Biologically mediated habitat	Lifecycle maintenance, habitat and gene pool protection	Mediation of wastes or toxic substances of anthropogenic origin by living processes	Pest and disease control	Regulation of chemical composition of atmosphere and oceans; atmospheric composition and conditions	Material, medicinal biochemical and genetic resources	Wild animals used for nutritional purposes	Mineral substances used for material purposes	Mineral substances used for as energy source	Intellectual and representative interactions with natural environment	Spiritual, symbolic and other interactions with natural environment	Other biotic characteristics that have a non-use value
<i>Acanella arbuscula</i> assemblage	900–1200			X	✓	✓				✓		X	X	✓	✓	✓
Burrowing anemones fields	600–1300	✓		X						✓		X	X	✓	✓	✓
<i>Cidarid urchins</i>	184–1062	✓		X	✓							X	X	✓	✓	✓
<i>Desmophyllum pertusum</i> reef	191–229	✓		X	✓	✓	✓		✓	✓	✓	X	X	✓	✓	✓
Discrete <i>Desmophyllum pertusum</i> colonies	457–960	✓		X	✓					✓		X	X	✓	✓	✓
Holothurian-dominated community	3100–4100	✓		X						✓		X	X	✓	✓	✓
Mixed cold water coral community (Coral Garden)	457–960	✓		X	✓					✓		X	X	✓	✓	✓
<i>Pheronema</i> spp. field	1000–1500	✓		X	✓	✓				✓		X	X	✓	✓	✓
Sea pens and burrowing megafauna	200–600	✓		X	✓	✓	✓			✓	✓	X	X	✓	✓	✓
<i>Solenosmilia variabilis</i> reef	1198–1766			X	✓	✓						X	X	✓	✓	✓
Solitary scleractinian fields	200–600			X	✓	✓						X	X	✓	✓	✓
<i>Syringammina fragilissima</i> fields	1042–1375	✓		X	✓							X	X	✓	✓	✓

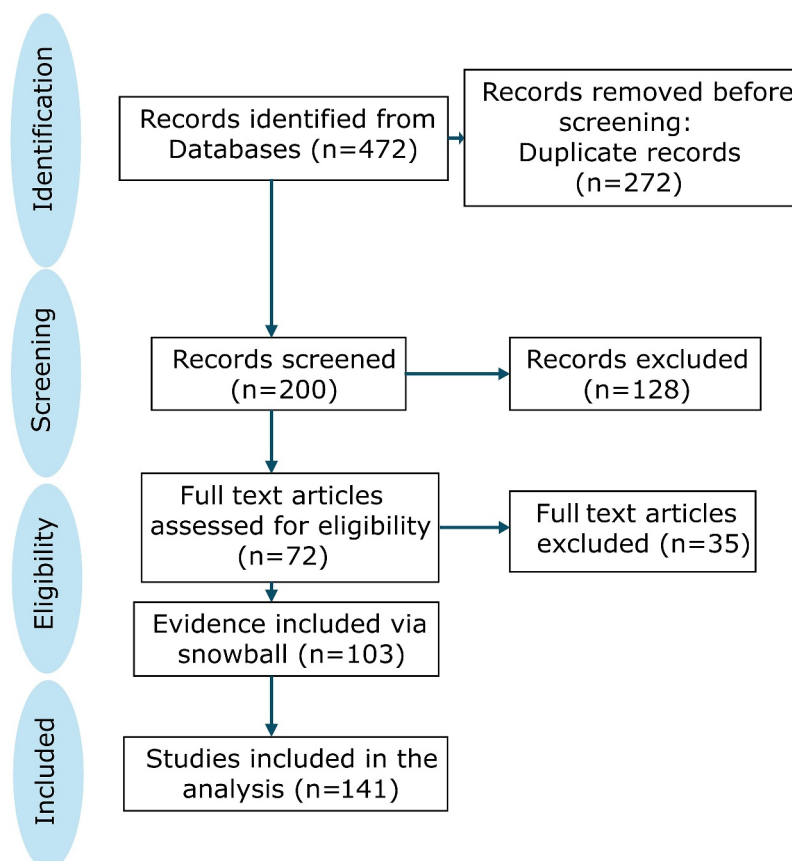


Figure 4. Presents the review results following the PRISMA protocol.

biotopes (La Bianca et al. 2023). This study found 66 linkages between 12 deep-sea biotopes and three regulating services.

This review found 13 articles available on lifecycle maintenance services by coral gardens (combining *Acanella arbuscula* assemblages, sea pens aggregations and mixed cold-water coral community (Coral Garden)) and 22 articles on reef forming CWCs. For some biotopes, CWC reefs, sponge aggregations, coral gardens and sea cucumber fields, there is more information than the other biotopes. For example, it is known that cold-water scleractinians are exceptional ecosystem engineers that support an ample range of associates. Available evidence suggests that CWC reefs play an important role in providing habitat complexity, forming the so-called animal forests of the world (Rossi and Bramanti 2020).

Results on *mediation of wastes or toxic substances of anthropogenic origin by living organisms* show that this service is provided by deep-sea *D. pertusum* reefs, holothurian communities, coral gardens and sea pens and burrowing megafauna, and it depends on biotope composition and microbial activity. Biological communities that host burrowing species or complex 3D structures have an impact on waste remediation. For example, coral frameworks intercept organic matter that would otherwise not settle on the seafloor, increase turbulence and augment influx to the coral community (Van Oevelen et al. 2009). Bioturbation

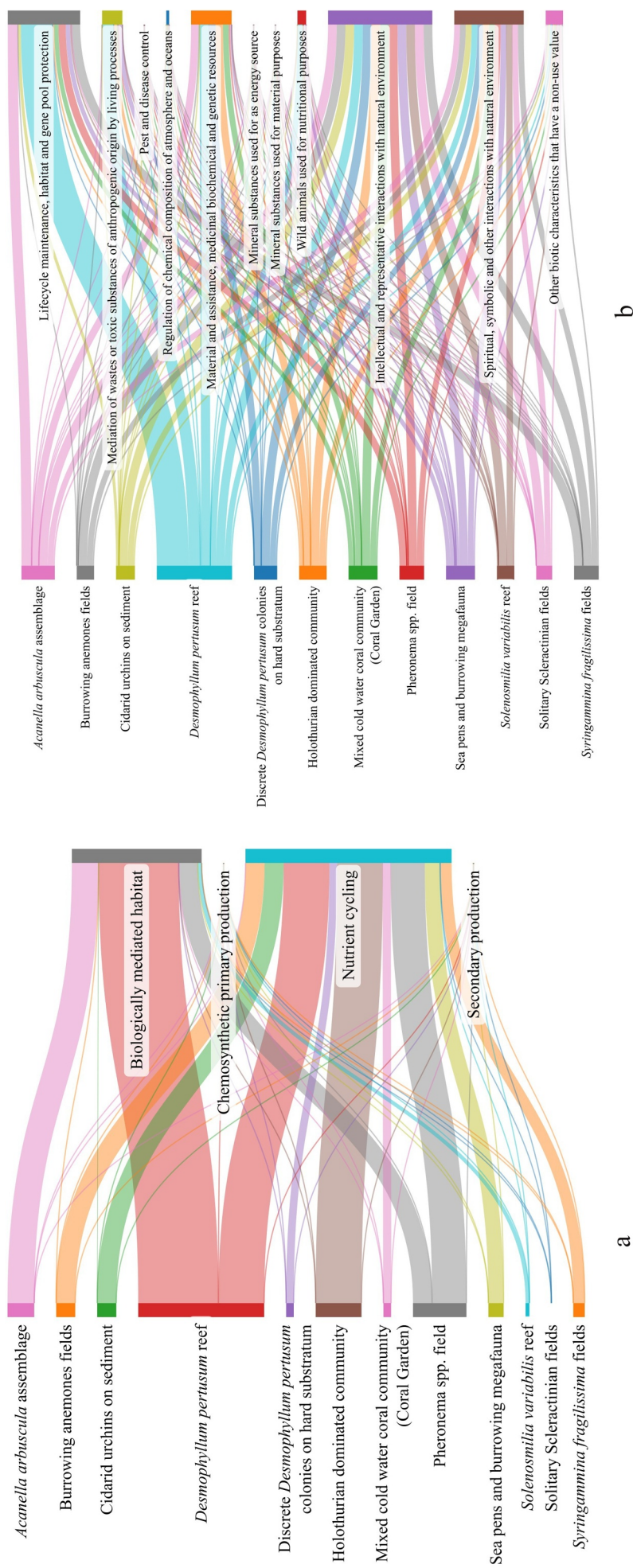
processes play a key role in burial of pollutants, such as radionuclides and heavy metals.

In terms of *Regulation of chemical composition of atmosphere and oceans*, very limited evidence exists on the role of benthic deep-sea biotopes in the long term. CWC reefs are identified as important carbonate sinks or sources (De Clippele et al. 2021). De Clippele et al. (2021) measured the biomass of *D. pertusum* reefs which was fed into the assessments of carbon budgets and evaluated the importance of CWC reefs. This study calculated that live and dead *D. pertusum* frameworks stored a total mean of 126 T C (range 16–303 T C) and 339 T C (range 44–819 T C) providing a considerable contribution to carbon sequestration in the long term.

3.4. Provisioning services

Findings show that deep-sea biotopes are important for (biotic) provisioning services: *Wild animals used for nutritional purposes* and *material, medicinal biochemical and genetic resources*. This review found 34 linkages between 12 deep-sea biotopes and provisioning services.

Bioprospecting of deep-sea species uncovers an extraordinary reservoir of bioactive compounds with significant potential for pharmaceutical, medical and industrial applications. These organisms, adapted to survive under extreme environmental conditions, often produce unique metabolites that can inspire novel treatments and materials. Deep-sea corals, sponges and sea



cucumbers have shown remarkable promise in recent studies. For example, the bamboo coral *Acanella arbuscula* has yielded new sesquiterpenoid derivatives, though their antibiotic activity remains inconclusive. Likewise, *Drifa* sp. from the Irish continental margin produces tuaimenal A, a compound effective against SARS-CoV-2 and cancer. Transcriptomic studies of cold-water anemones (*Bolocera tuediae* and *Hormathia digitata*) identified several novel neurotoxin peptides, advancing the field of digital bioprospecting (Urbarova et al. 2012).

Bacterial symbionts of deep-sea corals are another source of bioactive compounds. For instance, bacteria associated with *D. pertusum* secrete antifouling substances (Galkiewicz et al. 2011), cytotoxic against two human tumors and antibiotics (Brana et al. 2017). These symbionts also cycle nutrients and degrade complex organic materials, providing a foundation for biotechnological exploration. Deep-sea sponges like *Pheronema carpenteri* show antibacterial activity against pathogens, such as *Staphylococcus aureus* and *Escherichia coli* (Hesketh-Best et al. 2023), while cold-water sea pens exhibit potential in treating musculoskeletal diseases through extracts that promote tissue repair (Marchese et al. 2021). A recent study has estimated the full economic evaluation of *Material, medicinal biochemical and genetic resources* of sponge aggregations (Ottaviani 2020). It is noted that the full value is not just from the ecosystem but depends on the addition of inputs from society (other capital inputs), and the value is often context dependent.

Shallow water sea cucumbers complement these findings with established pharmacological properties, including antifungal, anticoagulant, and anticancer activities (reviewed by Bordbar et al. 2011; Khotimchenko 2018). Only one study was found that tested deep-sea holothurians for any biomedical benefit and found that holothurians contain antibacterial compounds (Marginet 2008).

3.5. Cultural services

All deep-sea biotopes also provide *Cultural services*. Three cultural services are considered relevant to deep-sea biotopes and this review found 10 articles and 2 non-for-profit programmes that provide linkages, in the form of virtual interaction, through education and spiritual connection between the deep sea and people. Because of the lack of direct accessibility to the public, the scarce familiarity of the general public with deep-sea ecology and features and the fact that little educational material (e.g. books, documentaries and videos) are available for less charismatic biotopes (e.g. *Cidarid urchins* assemblages) on the market, this assessment is difficult (Ottaviani 2020). The variety of biotopes that are often referred to in scientific research, documentaries, videos and books can make it challenging to link cultural services

to a specific biotope. Nevertheless, the importance of the deep sea has gained particular interest in legal and policy fora in the context of deep seabed mining, highlighting a deep connection of Indigenous Peoples and Local Communities with the ocean, ocean resources and respectful interaction with nature (Escobar et al. 2021). Moreover, new ocean literacy media have pushed the boundaries of public engagement in deep-sea science by using simulated dives and deep-sea exploration through virtual learning (Salazar et al. 2019; Sanchez et al. 2020; Morais et al. 2022). Recent technological advancement on research vessels has equipped ships with live-streaming underwater vehicles (e.g. Nautilus Ocean Exploration Trust and Schmidt Ocean Institute) for the public.

3.6. Knowledge gaps

Significant evidence gaps in the published literature were found on the ecosystem service provision capacity of some deep-sea benthic faunal communities and taxonomic groups. Despite substantial studies, evidence gaps exist for nutrient cycling roles of certain species and habitats. For example, no direct studies examine nutrient cycling in *Solenosmilia variabilis* reefs, though parallels with *D. pertusum* suggest potential roles. Little is known about bioturbation impacts of holothurians in deep-sea ecosystems. Sponge studies rarely address ambient dissolved organic matter uptake beyond specific species. Comparative respiration rates and biogeochemical roles across coral taxa remain unexplored. Research on xenophyophores highlights their ecological importance but lacks clarity on long-term impacts on global carbon cycling. No evidence was found for the ES provided by burrowing anemone fields, and solitary scleractinian fields. Filling these gaps is critical to understanding ecosystem functions and contributing to future management processes, such as marine spatial planning (MSP).

No information was found on the contribution of the following biotopes to *Nutrient cycling*: *Acanella arbuscula* assemblages, *Pheronema carpenteri* fields, *Solenosmilia variabilis* reefs and solitary scleractinian fields. When it comes to other biotopes listed as vulnerable marine ecosystems for instance 'solitary scleractinian fields' on hard and soft-bottom (ICES 2020), also known as cup corals, we found no peer-reviewed papers describing their ecological processes. Additionally, while some knowledge exists on the contribution to *Nutrient cycling* by holothurians (Bett et al. 2001; Amaro et al. 2019), no study was found on the material excreted by them. No evidence was found for the natural products' potential of *Cidarid urchins*, *S. variabilis* reefs, solitary scleractinians or *Syringammina fragilissima* fields.

Another substantial knowledge gap is the lack of understanding in the link between short-term biological processes and long-term climate regulation benefits. Evidence showed that several benthic biotopes play a central and irreplaceable role in biogeochemical processes (e.g. Middelburg 2018), yet there is a disconnect in the effect that these localised ecological processes carried out by benthic biota have in the wider ecosystem.

As previously mentioned, a study was found that calculated the capacity of CWC reefs for storing carbon in their biomass, and therefore contributing to carbon sequestration in the long term (De Clippele et al. 2021). However, this area of research is in its infancy and many questions still remain, particularly when it comes to scaling carbon budgets. While terrestrial studies can exploit remote sensing (e.g. satellite imagery) in combination with field measurements to map biomass at the ecosystem scale (Baccini et al. 2008), this is not feasible for deep-sea habitats (De Clippele et al. 2021). Estimating carbon sequestered by deep-sea biota relies on imagery and with large scaling factors; therefore, error could be considerable (Barnes et al. 2019). The lack of maps depicting CWC reef biomass is also one of the current disadvantages limiting biological carbon budget assessments in the deep sea.

3.7. Research priorities

This study found that knowledge of the ES provided by deep-sea biotopes is unbalanced. The matrix provided herein is a representation of current knowledge; however, gaps in biotope-service linkage are not an indication of lack of importance in delivering that service. On the contrary, it shows that to date no study has been carried out to provide evidence of this linkage. A list of research priorities is provided in Table 2.

4. Discussion

The objective of this study was to demonstrate the ES capacity of deep-sea biota through a systematic evidence review, representing a critical first step toward testing the feasibility of mapping deep-sea ES. By developing a matrix linking Service Providing Units (EUNIS biotopes) to ES provision, this study provides a qualitative baseline of the ecological roles deep-sea biotopes play in natural processes. However, the absence of fundamental biogeochemical information for many benthic assemblages leads to significant uncertainty regarding their contribution to services across vast spatial and temporal scales.

It is evident that deep-sea research has disproportionately targeted cold-water coral (CWC) reefs and sponge aggregations (specifically *Geodia* spp.) at

geomorphological features like seamounts. This focus overlooks the inherent heterogeneity of the deep sea, which represents 63% of the Earth's surface (Thurber et al. 2014). The vast extent of less-studied biotopes suggests they are likely implicated in global biochemical processes, yet research into these areas has lagged. Specifically, information on nutrient remineralisation and *in-situ* benthic fluxes remains scarce. While burrowing megafauna and sea pens influence carbon flux and nutrient recycling via bioturbation (Snelgrove et al. 2014), the lack of quantified activity levels makes scaling this information for spatial mapping applications extremely uncertain.

Furthermore, while the high metabolic activities of CWC reefs and sponge grounds mark them as hotspots for organic carbon cycling (Cathalot et al. 2015), current methodologies present limitations. Recent studies have quantified oxygen consumption to determine organic matter consumption (Khrpounoff et al. 2014; Pierrejean et al. 2020), yet oxygen consumption may not accurately represent the complex inorganic nutrient fluxes at the sediment–water interface. Because these estimates are site-specific, scaling them to wider areas remains problematic. Finally, a major knowledge gap exists regarding the relationship between biological communities and substrata; no identified studies compared the ecological activities of the same community across distinct substrate types, such as bedrock versus coarse sediment, which fundamentally affects how organisms interact with their environment.

4.1. Using biotopes to map deep-sea ES

This study's focus is to connect the disciplines of marine habitat mapping and ES supply; a habitat–service matrix represents a first step toward consideration of ES in spatial management of the deep sea. Notably, it should be questioned whether benthic biological assemblages and their associated environmental conditions (i.e. biotopes) are the most suitable approach for defining service units (Culhane et al. 2018). This approach does not robustly integrate mobile species, and fails to capture the horizontal and vertical movement of species through the water column, or the temporal differences in use of habitats by species at different stages of their lifecycle (Hattam et al. 2021).

Benefits may be realised at multiple spatial scales, from global scales, such as climate regulation, to more local scales, such as habitat provision (Niner et al. 2024). Mapping at a landscape scale using large topographic features, such as submarine canyons allows for large areas to be covered with low-resolution data, which is cost and time effective. However, this approach dismisses the more granular detail,

Table 2. A list of research priorities to fill knowledge gaps and understand deep-sea biotopes contributions to services.

Biotopes	Service	Priority
All	Regulating	Collect <i>in-situ</i> biogeochemistry data of deep-sea assemblages examined in this study using standardised techniques across locations to facilitate comparisons across ecosystems.
All	–	Theoretical efforts should be put into understanding spatial and temporal scales in the deep sea, which are not covered in the literature and generate large uncertainty in ES assessments.
All	Nutrient cycling; climate regulation	Understanding relationships between nutrient cycling and long term effect in regulation of climate.
All	Ecological processes	Assessing ecological processes with substrate characteristics for deep-sea ecosystems. It is expected that deep-sea sediments would contain larger quantities of stored carbon than rocky seafloors. Future work should focus on the integration of ‘carbon storage’, ‘carbon regulation’, ‘sediment carbon’ and ‘seabed carbon’ in the literature search to gather existing evidence of benthic abiotic and biotic relationships.
All	Ecological processes	Integration of the role of mobile species, infauna and particularly microbial communities on ES.
All	All	Linking deep-sea functional groups to ES and understanding the level of service provision <i>per site</i> .
All	All	Include expert opinion to further understand the linkages between deep-sea benthic-coupling mechanisms, biotic and abiotic relationships.
All	Cultural	Trial new interdisciplinary methodology to better account for cultural services provided by remote habitats.
Holothurians	Nutrient cycling; climate regulation; mediation of waste	Material excreted by holothurians in the deep sea. Evidence shows that deep-sea cucumbers are able to assimilate organic matter (Bett et al. 2001; Amaro et al. 2019), but no study was found that tested the link between bioturbation rates and cycle of nutrients for other fauna. Studies on the role of benthic biotopes on nutrient cycling have been conducted for shallow water holothurians. These show that sea cucumbers play an important role in benthic biota productivity by excreting organic nitrogen and phosphorus and are responsible for up to 50% of the dissolution of calcium carbonate in reef systems, which also facilitates scleractinian coral growth (Uthicke 2001; Wolfe et al. 2018; Williamson et al. 2021) (for more details, see Supplementary). Given the distribution of sea cucumbers across several biological assemblages, and their numerical and biomass dominance on abyssal plains (Thurston et al. 1994), this form of nutrient regeneration appears to play a significant role in benthic food webs and the resulting secondary production ultimately important for aquatic oligotrophic ecosystems.
Holothurians	Material, medicinal biochemical and genetic resources	Only one study was found on the tested antibacterial activity of deep-sea holothurians (Marginet 2008). This preliminary research study indicated that each of the holothurians contained several antibacterial compounds against a Gram-positive bacterium. However, to determine if they are known compounds, variants of known compounds or novel compounds, the next phase of the research should focus on the purification of the antibacterial compounds in the active superfractions.
Sponges	Nutrient cycling; regulation of climate	Investigate robust scenarios on the effects of decreasing sponges’ water-pumping capacity. Sponges are one of the major filtering systems of the deep sea, processing a large amount of water and significantly influencing the concentration of nutrients in the environment. Damage or removal of a large number of deep-sea sponges may affect their filtration capacity, with negative consequences to global biogeochemical cycles and causing irreversible climate effects. This is owing to the inability to replace such activity by existing, engineered, advanced technologies, and incurred costs would be prohibitive (Ottaviani 2020).
Sponges	Ecological processes	Evidence on the ecological processes provided by <i>Pheronema</i> spp. is very scarce, yet the vast distribution of this biotope across the Northeast Atlantic is remarkable. One starting point is to investigate the water-pumping capacity across various sizes of <i>Pheronema</i> spp.
Cold-water coral taxa	Ecological processes	Respiration rates and biogeochemical roles across coral taxa.
Xenophyophores	Climate regulation	Research on xenophyophores to demonstrate long-term impacts on global carbon cycling.

where most ecological and biological processes occur (Davies et al. 2014). The use of biotopes, at a smaller spatial scale of 25 m², aligns with mapping methodologies that use habitat classification at the biological community level to map ecosystem components (e.g. Howell et al. 2022) and addresses the need to spatially locate the distribution of biological communities and their services. Used in conjunction with habitat classifications, such as EUNIS, the habitat–service matrix could be applied to map ES at local and regional scales.

4.2. Evidence for policy making

Ramping societal interest in deep-sea biotic and abiotic resources demands an understanding of the ecological benefits of biotopes to support sustainable utilisation and mitigate environmental impacts. This

study demonstrates that the deep sea is important to humans in many ways. Here, we provide evidence of the indirect and direct contributions of deep-sea natural capital assets to human well-being. To the authors’ knowledge, this is the first attempt to gather evidence on the services provided by several benthic deep-sea biotopes at fine scale-resolution, beyond the services provided by well-known cold water coral reefs (Cordes et al. 2023) and cold seeps (Le et al. 2022). Clearly, more deep-sea ecological knowledge relevant to ES assessment exists for these biotopes than for other deep-sea biotopes, such as coral gardens and burrowing megafauna. Filling these gaps is critical to understanding ecosystem functions and contributing to future management processes such as MSP. Tools such as Environmental Impact Assessments and MSP rely heavily on quantified statistically certain data; however, while for some areas

of interest we do have information, a lack of information does not indicate lower importance. Herein, information on other deep-sea biotopes is compiled to widen the research interest towards less studied ecosystems. Literature shows that interconnectivity across depth and space is highly uncertain, and it is also unknown how much ecosystem functioning is provided by deep-sea biological habitats, let alone how this is connected to services to people. This is particularly relevant in the context of human activities and their impacts on deep-sea biodiversity and subsequent ES damage and loss as these are difficult to predict (Niner et al. 2018; Miller et al. 2021).

This study is a response to the need to understand contributions from deep-sea biodiversity to people's benefits. Many countries now have national and international statutory commitments to protect elements of the natural environment from which ES flow (i.e. Aichi Target 11 of the Global Biodiversity Framework, GBF). The (undisturbed) deep sea represents a large long-term reservoir for methane and carbon, important for climate change mitigation. How much selected biological communities contribute to the uptake and storage of methane and carbon is unknown, and evidence suggests that cold-water coral reefs are potentially an important biotope in climate change mitigation (De Clippele et al. 2021). It is also evident that while microbial communities associated with deep-sea biota are diverse and poorly described, they play an important regulatory role in global cycling of carbon, sulphur and heavy metals (Mehta and Baross 2006; Wankel et al. 2011; Holden et al. 2012; Bourbonnais et al. 2014; Fortunato et al. 2018). Potentially vast provisioning resources are provided by deep-sea biota in relation to marine genetic resources and biomaterials, many of which have important applications in human health (Ottaviani 2020). Recent economic valuation of deep-sea natural capital suggests that it is impossible to estimate the (total) value of the deep sea in monetary terms with any confidence, and as Folkersen et al. (2018) suggest, the economic value of the deep sea depends on a multitude of economic aspects not directly related to it, for example tax rates, sales prices, operation costs, equipment, transport efficiency, consumer preferences, and others. While estimating the monetary value of these biotopes could contribute to emphasise their importance, it is perhaps irrelevant given lack of understanding of the ecosystem. Hence, a cost-benefit approach is not appropriate in this context because of fundamental dependencies between humans and the deep sea via regulatory services and widespread biotope implications. There is sufficient knowledge and information to indicate that deep-sea environments are important. We need to develop policy approaches that can account for uncertain knowledge to embed sufficient

precaution into decision-making to protect ES (Niner et al. 2024).

5. Conclusion

This study summarises the existing knowledge of ES provided by deep-sea biotopes providing the first qualitative overview of their ecological roles. Through extensive literature review, the matrix condenses evidence from 12 biotopes to ES, revealing a nuanced understanding of each ES. Despite extensive research on *D. pertusum* reefs, other biotopes remain largely understudied. Deep-sea biotopes, including coral gardens and sponge grounds, play pivotal roles in nutrient cycling, habitat provision, and medicinal resource discovery. Notably, sponges are heavily researched for biochemical resources. While there is some information on the ecological role of these biotopes, there is a lack of data on the link between these biotopes and direct services to society. Major knowledge gaps on biotope's biogeochemical cycles persist, particularly in understanding nutrient cycling and carbon flux effects across all biotopes, as well as their long-term effect on climate regulation. Future research priorities include *in-situ* empirical research of biogeochemical processes by most biotopes; investigation of benthic-coupling mechanisms for deep-sea biotopes; further trialling of the viability of deep-sea biotopes' compounds for bioprospecting; and trials of new methodologies to better account for cultural services. Ultimately, this study establishes a foundational understanding of the potential ES provided by the deep sea and also provides research priorities to better capture the deep sea's role in and contribution to ES. The consolidation and evaluation of the current state of evidence provides a starting point for the integration of deep-sea science data into mapping efforts and supports governance and decision-making that can in turn support positive well-being outcomes for biodiversity and society.

Disclosure statement

No potential conflict of interest was reported by the author(s).

Funding

This work was supported and funded by the University of Plymouth, United Kingdom, and by the University of Plymouth United Kingdom Research and Innovation, Global Global Challenges Research Fund, One Ocean Hub [grant number NE/S008950/1].

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