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Benthic habitat mapping: A review of three decades of mapping biological patterns on the seafloor

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Abstract

What is benthic habitat mapping, how is it accomplished, and how has that changed over time? We query the published literature to answer these questions and synthesize the results quantitatively to provide a comprehensive review of the field over the past three decades. Categories of benthic habitat maps are differentiated unambiguously by the response variable (i.e., the subject being mapped) rather than the approaches used to produce the map. Additional terminology in the literature is clarified and defined based on provenance, statistical criteria, and common usage. Mapping approaches, models, data sets, technologies, and a range of other attributes are reviewed based on their application, and we document changes to the ways that these components have been integrated to map benthic habitats over time. We found that the use of acoustic remote sensing has been surpassed by optical methods for obtaining benthic environmental data. Although a wide variety of approaches are employed to ground truth habitat maps, underwater imagery has become the most common validation tool – surpassing physical sampling. The use of empirical machine learning models to process these data has increased dramatically over the past 10 years, and has superseded expert manual interpretation. We discuss how map products derived from these data and approaches are used to address ecological questions in the emerging field of seascape ecology, and how remote sensing technologies and field survey logistics pose different challenges to this research field across benthic ecosystems from intertidal and shallow sublittoral regions to the deep ocean. Outstanding challenges are identified and discussed in context with the trajectory of the field.

Keywords

Seabed mapping; acoustic remote sensing; optical remote sensing; benthic ecology; species distribution modelling; marine spatial planning

1. Introduction

The global ocean, covering more than 70% of the earth, plays a central role in the structure and function of the biosphere and is critical for achieving sustainable development of human society as a whole (Hoegh-Guldberg *et al*., 2019). However, marine systems face significant pressures from human activities ranging from climate change, ocean acidification, over-exploitation of natural resources, and biodiversity loss (IPCC, 2022). In 2015, the United Nations set 17 Sustainable Development Goals (SDG) as a framework to develop strategies for sustainability, with goal 14: *Life Below Water* aiming to "*conserve and sustainably use the oceans, seas and marine resources for sustainable development*" (UN General Assembly, 2015). It is widely recognized that many of the UN SDGs are inter-related, but SDG 14 is particularly far-reaching due to the important role that the ocean plays in global social-ecological systems (Singh *et al*., 2018); the success of many of the SDGs depends on reaching the targets set under SDG 14. Key technical, organizational, and conceptual scientific barriers have been identified that pose challenges for implementation of transformative policy action to achieve SDG 14, with improved global ocean observation and stronger integration of sciences identified as key elements to success (Claudet *et al*., 2020). The acquisition and use of geospatial environmental and biological data to understand spatial patterns within ecosystems, monitor changing conditions, and assess the health of systems relative to sustainability goals is a critical component to success of SDG 14.

Given a recognized need for spatial data products to inform sustainable development, management, and conservation goals, the field of benthic habitat mapping has progressed substantially over the past three decades. Technological advances in remote sensing methods, increased computing power, and improvements to geospatial data analytics are preeminent among innovations over this period (Pijanowski & Brown, 2022). The immediate result of such progress is increased precision; high resolution thematic seafloor maps have emerged as the primary means for describing spatial patters and processes of seafloor ecosystems, and for informing management and policy frameworks across a diverse range of applications. These outputs are well-suited to support action towards sustainable development goals, such as those outlined by the United Nations.

Developments in the field of benthic habitat mapping have produced a diversity of approaches, data types, technologies, and models that are used to understand and map distributions of biological patterns on the seafloor. It is informative and interesting to review the variety of ways in which these patterns may be mapped, and retrospection of these themes also reflects a change in values over time. We aim to objectively describe these recent changes to chronicle the trajectory of the benthic habitat mapping field leading up to this Decade of Ocean Science for Sustainable Development (Ryabinin *et al*., 2019). Established benthic habitat mapping practitioners may find such retrospective useful for conceptualizing the current state of the field in the context of its recent development (section 4), and may also find value in the clarification of terminology and frameworks presented in section 3. New and early career scientists may benefit from the definitions of terminology and coverage of related reviews provided in section 2, the overview of habitat mapping methods and frameworks in section 3, and the synthesis of approaches and best practices offered in section 5. The data derived from review of the benthic habitat mapping literature may also prove a helpful resource (Supplementary Material).

1.1. Scope of the review and literature search

The objective of this review is to provide a descriptive, rather than prescriptive, synopsis of advances within the field of benthic habitat mapping over the past three (or so) decades. Specifically, we pose three questions:

1) What is benthic habitat mapping?

2) How is it accomplished?

3) How has that changed over time?

Ocean mapping technologies have improved dramatically over the past few decades (see reviews by: Kenny *et al*., 2003; Makowski & Finkl, 2016; Kutser *et al*., 2020; Menandro & Bastos, 2020), and this has been accompanied by an exponential increase in publications in this field. Greater availability of high-resolution remotely sensed data, including both electromagnetic and acoustic technologies, combined with rapid advances in geospatial analytics and capacity to handle large data volumes, have generated tremendous advances over this period. In reviewing these, we do not exclude any particular sensors, methods, geographies, environments, or scales.

To address the three review questions, we analyse trends in the literature to outline what is considered benthic habitat mapping (section 2), what methods are applied to accomplish it (section 3), and where advances have been made in this field over time (section 4). We conducted an unbiased sample of the literature using multiple database searches, applying selection criteria to qualify publications for inclusion into compiled literature statistics. The final search was conducted on October 12, 2021, using the term "*benthic habitat mapping*" on both Scopus and Web of Science, and all items published prior to 2021 were retained, totalling 1316 publications. Additional searches were trialled using terms such as "*seabed mapping*", "*seabed habitat mapping*", and "*seascape mapping*", but these returned fewer publications in all cases – most of which were either duplicates of the first search or were beyond the scope of the review. Only the "*benthic habitat mapping*" search results were retained.

Additional criteria were subsequently applied to qualify a publication for inclusion in the review:

1) The publication had to include a *benthic habitat map product*, which could include any one or several of the possibilities outlined in section 3.1. The scope for this criterion favoured inclusivity, and publications were retained that depicted a habitat component generally (e.g., distributions or habitat suitability of single taxa, morphotaxa, groups of taxa, functional groups, physical habitat structure, habitat-forming substrates, habitat surrogates). Maps depicting only single predictor variables (e.g., depth, morphometric attributes, acoustic backscatter, optical values, oceanographic parameters), costs (e.g., dollar values, worth), or fisheries landings (e.g., in numbers, currencies) did not qualify for this criterion.

2) Published maps had to *depict benthic habitats spatially* past discrete point observations. Maps showing distributions of seabed samples (e.g., underwater photographs, physical samples), therefore, did not qualify – even if they have been classified to represent a benthic habitat component. We consider these "sample distribution maps", rather than "benthic habitat maps", which we define here as "spatially continuous predictions of biological patterns on the seafloor" (see section 2 below, cf. Brown *et al*., 2011).

3) Maps published and reviewed in multiple studies were *only tabulated once* as a "qualifying map", which permits an item to be included in the review. Where habitat maps were detected in multiple outlets, with

no novel map product to differentiate them, the information was collapsed into a single entry for the review dataset.

Of the 1316 publications reviewed from the literature database searches, 624 (47.4%) fulfilled the above criteria for quantification as a sample of the benthic habitat mapping literature. For each of the 624 items, the following information was recorded:

1) Thematic map category (section 3.1). The thematic level of the response variable being mapped, assigned to one of the following four categories: *abiotic surrogate*, *single biota*, *community*, or *benthoscape*.

2) Model class (section 3.6). This describes the class and sub-class of the model (or lack thereof) applied to map the response, including expert *manual* interpretation, *analytical* or *mechanistic* models, and *supervised* or *unsupervised empirical* and *semi-empirical* approaches. *Analytical* and *mechanistic* modelling classes were rare and were collapsed into a single field for the purposes of quantification.

3) Modelling algorithm (section 3.6). The (normally) empirical statistical modelling algorithm(s) or method(s) applied to predict the response. See sections 3.6 and 4.6 for the modelling algorithms and methods identified from the review.

4) Predictor remote sensing technologies (section 3.4). The classes of remote sensing technologies used to obtain predictor variables used to map the response, including acoustic data technologies (e.g., *side scan sonar*, *single* and *multibeam echosounding*, *sub-bottom profiling*); and also electromagnetic remote sensing technologies (e.g., *laser scanning* or *LiDAR*, and *spectral*, *multispectral*, or *hyperspectral* cameras). *Compiled* remote sensing data sources were also considered here, which integrate multiple different technologies into a single data product – for example, the General Bathymetric Chart of the Oceans (GEBCO), which incorporates data from a range of sensors and bathymetric sources (GEBCO Compilation Group 2022, 2022).

5) Predictor remote sensing platforms. The platform(s) from which remote sensing data used to predict the response were acquired, including crewed and un-crewed *aerial craft* such as planes or drones, *handheld* systems such as spectral cameras used to produce orthomosaic images, crewed and un-crewed

marine vessels such as ships or AUVs, and *satellites*. The use of *compiled* sources that include multiple different acquisition platforms were also noted.

6) Primary (measured) geospatial predictor data (section 3.2). The environmental variables measured directly or indirectly to obtain predictors used to map the response. These included data such as *acoustic backscatter*, *local* or *traditional ecological knowledge* (LEK/TEK), *oceanographic* (physical or chemical) parameters, interpolated *physical sample* parameters (biological or geological), *spatial* or *temporal* variables, *spectral* or *LiDAR reflectance*, and the *water depth*.

7) Derived geospatial predictor data (section 3.3). Environmental variables derived or calculated from primary measured geospatial data used to map the response. These commonly included *morphometric parameters* (i.e., “terrain attributes”) such as the slope or rugosity calculated from depth measurements; *spectral features* calculated from optical sensors such as the normalized difference vegetation index (NDVI); various *textural parameters* such as grey-level co-occurrence matrices (GLCMs) calculated to characterize acoustic or spectral remote sensing data; and derived *oceanographic* (physical or chemical) *parameters*.

8) Segmentation approaches. Which (if any) approaches were used to segment the predictor data in order to map the response – for example, *manual*, *morphometric*, *value-based,* or *object-based image* segmentations.

9) Ground validation, or ground truth (section 3.5). The data used to measure or validate the mapped response variable, including calibrated *acoustic responses*, *animal telemetry*, “*by-eye*” field observations, *fishing records*, *physical samples* (geological, biological, or chemical), *remote samples* (geological or biological) such as aerial photographs, and *spectral measurements* such as those obtained via handheld spectrometer. Importantly, the same technologies may be used to produce both “predictor” and “ground truth” data, depending on how the data are treated. Aerial imagery, for example, has been applied extensively as both a predictor (e.g., van der Wal *et al*., 2008; Legrand *et al*., 2010; Baumstark *et al*., 2013) and response (e.g., Cho *et al*., 2014; Fallati *et al*., 2020; Poursanidis *et al*., 2021). The designation as “ground truth” therefore depends on the selection of response (i.e., mapped) data, not on the method of acquisition. Data reported that were not used to map or validate the response were not recorded as ground truth.

10) Geographic extent. The extent of the habitat mapping study, quantized into logarithmic bins (i.e., < 1, 1-10, 10-100, 100-1000, > 1000 km). The extent was determined using the length of the major axis of the study area. For example, the Great Barrier Reef was considered to cover an extent of > 1000 km. Where not stated, extent was estimated by measuring published maps using ImageJ (Schneider *et al*., 2012), calibrated to the scale bar or map graticule.

11) Environment. Whether the benthic environment was marine and *intertidal*, *shelf* (< 200 m depth), or *deep sea* (> 200 m depth), or fresh water and *river*, *pond/wetland,* or *lake*.

Several additional descriptive attributes were tracked for each publication. Unit-invariant validation metrics were recorded where provided, including accuracy, kappa, AUC, Pearson or Spearman correlation scores, and the variance explained. Where multiple different scores were provided for a single metric (e.g., in comparative studies), only scores labelled as “final” were retained. If not indicated, the highest score was selected. If the published map was an ensemble of multiple predictions, or multiple different maps were presented, the validation scores were recorded as the mean of individual scores if no “final” value was provided. If multiple statistics were calculated using both “training” and “test” data that were used to produce and evaluate a map, respectively, the “test” data scores were preferred in all cases. Because of the extreme variability in map validation practices encountered in the reviewed literature, the validation statistics recorded are descriptive only. Finally, the licensing status of each publication item was recorded, indicating whether it was freely available or open-access, or available under a traditional subscription license. The entire curated table to of literature reviewed is provided as Supplementary Material. Again, we note that this table represents a random, rather than exhaustive, review of the literature.

2. What is benthic habitat mapping?

2.1. Thematic habitat mapping

The term “benthic habitat mapping” tends to be ambiguously applied in the literature to describe any form of seabed mapping focused on understanding biological patterns. Previously, “benthic habitat mapping” has been more precisely defined as “*the use of spatially continuous environmental data sets to represent and predict biological patterns on the seafloor (in a continuous or discontinuous manner)*”

(Brown *et al*., 2011). In the context of this review, we have modified and simplified this definition to "*spatially continuous prediction of biological patterns on the seafloor*", to encompass changes in the field over the past decade, and the variety of ways that "habitat" can be represented in different forms of thematic maps.

The presence of an organism at the seafloor, and the resulting spatial patterns that are observed for a species, may be explained using the ecological niche concept first developed and defined by Grinnell (1917) and later by Hutchinson (1957). This describes the ecological niche of a species as an n-dimensional hypervolume of biotic and abiotic environmental conditions that meet its habitat requirements (Begon & Townsend, 2021). Overlapping niches of different species, therefore, define a community, and community composition will change as the hypervolume of environmental conditions change along abiotic and biotic gradients. Patterns of community composition are thus complex, and difficult to predict. Patterns of biotic and abiotic seafloor characteristics can be represented by a variety of different thematic maps. Types of thematic benthic habitat maps are discussed in detail below (section 3.1), but they generally comprise: 1) abiotic maps representing changes in seafloor substrata (or other abiotic variables), which can act as a proxy for biological patterns; 2) maps depicting the distribution of a single species or taxa; 3) maps depicting benthic community patterns; or 4) maps displaying "landscape-scale" bio-physical classifications of the seafloor. Each of these categories can be considered a form of "benthic habitat map" based on the above definition, which conforms to the usage of this terminology in the literature.

2.2. Seafloor remote sensing

Regardless of the type of thematic mapping, all benthic habitat maps tend to rely on the availability of environmental geospatial data from which the distribution of biological patterns may be predicted. In both terrestrial and aquatic environments, remote sensing technologies have greatly advanced both the extent and resolution at which we map global ecosystems. Satellite platforms employ a variety of sensors to image the land surface of the planet (Dubovik *et al*., 2021), which are used to advance our understanding of the spatial configuration of ecosystems, how fauna and flora interact through the environment, and what impacts humans may have on these systems. In the oceans, satellite remote sensing has dramatically improved our understanding of biological processes such as plankton production (Platt, 1986; Sathyendranath *et al*., 1991), physical oceanographic phenomenon such as circulation patterns and ocean-atmosphere linkages (Klemas, 2012), and chemical oceanographic processes (Siegel

& Michaels, 1996). Satellite-borne sensors are additionally employed to study tectonic and geomorphic oceanographic processes through the production of broad scale ocean floor Digital Elevation Models (DEMs) using satellite-derived bathymetry (Watts, 1976; Sandwell *et al*., 2003; Watts *et al*., 2006). In coastal waters, satellite-borne optical sensors provide both depth and seafloor reflectance information that is used to characterize the benthic environment at high spatial resolutions (Kutser *et al*., 2020), but their application is limited to the shallow seafloor (e.g., < 30 m). In deeper waters, acoustic remote sensing is the primary means for obtaining high resolution seafloor mapping data (Brown *et al.*, 2011).

For any remote sensing technology, the resolution of the measurements combined with their areal extent determine how the data can be used (Jensen, 2013), and all remote sensing technologies are limited in certain environments based on one or both factors. For example, although satellite platforms are highly efficient for obtaining data at global extents, their application for seafloor mapping is generally limited to either a) high resolution (e.g., metre-scale) mapping of optically shallow coastal waters using spectral sensors (Kutser *et al*., 2020), or b) low-resolution mapping of the global seafloor using satellite altimetry methods. Acoustic remote sensing, on the other hand, enables high resolution mapping of shallow or deep waters, but at a reduced spatial extent compared to satellite methods. The efficiency of acoustic systems is further limited in shallow waters as a function of the acoustic beam width, which increases as a function of depth and the sonar aperture (Mayer *et al*., 2018). The data resolution and mapping extent, though, are *inversely* related – the acoustic footprint on the seafloor (i.e., the insonified area) increases with depth and sonar aperture, corresponding to a *decreased* horizontal resolution. Airborne LiDAR may provide high resolution mapping data that are much more efficient to obtain than acoustic data, but which, again, are generally limited to shallow environments.

The need for global seafloor data to increase our capacity to map and understand marine biological patterns is well recognized, and increased availability of seafloor data fosters new avenues for marine ecology research. On land, electromagnetic sensors provide direct or indirect indication of biotic (e.g., vegetation type and cover), and abiotic (e.g., substrate type, morphology, atmosphere) patterns that enable modeling and mapping of terrestrial ecosystems across multiple spatial scales. Increased availability of these methods and technologies has stimulated substantial advances in the field of landscape ecology over the past few decades (Yu *et al*., 2019). Comparable approaches are now applied using satellite and airborne remote sensing platforms for intertidal and shallow subtidal ecology

(Swanborn *et al*., 2022), leading to emergence of the parallel field of seascape ecology (Pittman, 2017; Lepczyk *et al*., 2021). This has been largely restricted to shallow ecosystems due to the depth limitations of electromagnetic signals, but in deeper waters, high resolution environmental datasets may be acquired using acoustic methods, or may be accessed from open data compilations and repositories. This enables application of landscape approaches to deep benthic environments (Brown *et al.*, 2011), and it is now feasible to investigate seascape concepts at all depths where data are available.

2.3. Previous reviews

A number of complementary reviews have been published previously on topics related to the material covered here. We briefly highlight below key sources providing comprehensive treatment of topics including benthic habitat mapping and seascape ecology, species distribution modelling, ecological surrogacy, and several application- and content-specific subjects, which are highly relevant to the material covered herein, but are beyond the scope of this review.

Diaz *et al*. (2004) provide the first comprehensive and cohesive review of benthic habitat mapping and explore in detail the concept of benthic habitat quality. They review habitat mapping approaches, technologies, and terminology, and explore the many methods and indices by which habitat quality is determined. Brown *et al*. (2011) cover the use of acoustic approaches for benthic habitat mapping, providing substantial detail on the acoustic technologies, data layers, and processing pipelines that are commonly applied to map biological patterns on the seafloor. They categorize the strategies by which habitat maps are produced according to a combination of the modelling approach, and at what stage environmental data are segmented spatially. We revisit this scheme here based on the surveyed literature (see sections 3.1 and 3.6 on thematic maps and model class). These reviews were followed in 2012 by the first edition of *Seafloor Geomorphology as Benthic Habitat: GeoHab Atlas of seafloor geomorphic features and benthic habitats* (Harris & Baker, 2012a). The main context of this “atlas” is a collection of 57 benthic habitat mapping case studies submitted by scientists from around the world. Each case study describes both geomorphic and biotic elements of the seafloor and conforms to a standard template. The atlas additionally identifies common motivations for mapping benthic habitats, such as support for marine spatial planning (see also Cogan *et al*., 2009), marine protected area (MPA) design, generation of scientific knowledge, and to support resource assessments (Harris & Baker, 2012b). A second edition of the GeoHab

Atlas was published in 2020, including an additional 53 habitat mapping case studies conducted between 2010-2020 (Harris & Baker, 2020).

In their recent review on the application of seascape ecology to the deep sea, Swanborn *et al*. (2022) identify benthic habitat mapping as a tool for studying seascape ecology. They outline fundamental seascape ecology concepts including the use of patch metrics, seascape composition, configuration, and heterogeneity, ecological connectivity, and spatial context and scale (see also the text by Pittman, 2017). These, in most cases, either inform, or are informed by, benthic habitat information, which is therefore prerequisite for most seascape ecology approaches. Seascape ecology has been characterized as the marine counterpart to landscape ecology (Pittman *et al*., 2021; Swanborn *et al*., 2022), yet there is no absolute consensus as to what defines landscape ecology (Bastian, 2001; Wu, 2006; Turner & Gardner, 2015). Nonetheless, based on the general definitions provided by Wu (2008), Turner & Gardner (2015), and Pittman *et al*. (2017), and on its usage in the marine literature, we adopt the definition that seascape ecology is "*the study of relationships between spatial pattern and ecological processes in the oceans at multiple scales and organizational levels*".

In their seminal review on *Predictive habitat distribution models in ecology*, Guisan & Zimmerman (2000) synthesized concepts in ecological modelling that would lay the foundation for approaches that have been widely adopted in the field of benthic habitat mapping over the following two decades. We believe their treatment of *empirical* or *statistical* models to have held up particularly well in the context of benthic habitat mapping over this period, for which these models have been adopted almost without exception (see section 3.6 on model class). Their review of regression and classification techniques, ordination, model calibration, spatial prediction, overfitting, and validation procedures remain highly relevant. Additional details on these subjects in the context of ecological applications can be found in subject-specific texts (e.g., by Franklin, 2010 or Drew *et al*., 2011). More recently, Melo-Merino *et al*. (2020) have reviewed the application of ecological niche and species distribution models (ENM; SDM) in marine environments. They unambiguously differentiate these two approaches in a niche theory framework, where ENM refers to modelling the fundamental niche in environmental space and SDM refers to modelling the realized distribution in geographic space (i.e., "E-space" and "G-space", respectively; see also Peterson & Soberón, 2012; Soberón *et al*., 2017). They further elucidate the taxonomic groups and geographic locations that have received the most attention, the methods used to model them, the applications for these models, and also the modelling details peculiar to the marine realm.

Several detailed reviews have been published on specific benthic habitat mapping applications and environments. Kutser *et al*. (2020) chronicle the rise of shallow water remote sensing for bathymetric and habitat mapping around the turn of the century, corresponding to an increase in coral reef research resulting from realization of the full scope of global coral reef decline (Hughes, 1994; Pandolfi *et al*., 2003; Bellwood *et al*., 2004; Hoegh-Guldberg *et al*., 2007). This review focuses primarily on the development and application of passive optical remote sensing, but technologies for mapping shallow areas also include LiDAR, sonar, and synthetic aperture radar. Mandlburger (2020) provides a detailed review of airborne laser bathymetry (i.e., LiDAR), outlining the current state of laser scanning technologies and their applications to shallow and deep-water mapping. Marcus & Fonstad (2008) provide a review of optical remote sensing methods for riverbed mapping. Optical sensors often enable continuous depth measurements for rivers where clarity permits, and may additionally provide data on river surface features and turbidity. In addition to satellite, balloons, and aircraft, they report early use of drones for optical riverbed mapping, which we believe precedes their widespread uptake for coastal and shallow water mapping. They also report early application of supervised modelling, fuzzy clustering, texture analysis, and object detection for mapping riverbed properties. Diesing *et al*. (2016) provide an informative review of terrestrial image-based remote sensing classification methods, which is placed in the context of the methods employed for benthic habitat mapping. They identify key elements of the classification procedure and provide important perspective on feature selection and validation of thematic seafloor maps.

Finally, we refer the reader to select reviews focused on specific peripheral topics relevant to the field of benthic habitat mapping. In Chapter 5 of the GeoHab Atlas, Harris (2012) reviews the concept of *surrogacy* for benthic habitat mapping – the correspondence and substitution of measurable variables for biotic patterns that are quantified more sparsely (e.g., in space). McArthur *et al*. (2010) also review the use of abiotic surrogates for benthic biodiversity in detail, including the primary surrogates employed in the benthic ecology literature, application of these surrogates for marine management, and the representation of ecological gradients using surrogates (see also Guisan & Zimmermann, 2000; Meynard & Quinn, 2007). Both Makowski & Finkl (2016) and Menandro & Bastos (2020) provide recent perspective on the history of seabed mapping, and the review of seabed mapping technologies for marine habitat classification by Kenny *et al*. (2003) remains highly relevant. Steiniger *et al*. (2022) review the use of deep learning approaches for the automatic processing of sonar imagery. Li & Heap (2014) review spatial interpolation methods for the environmental sciences, which, while not strictly marine, includes application to marine environments, and is highly relevant for benthic habitat mapping. Strong *et al*. (2019) review the application and properties of common habitat classification schemes for benthic mapping. Lecours *et al*. (2015) review the concept of spatial scale for benthic mapping contexts, and Lecours *et al*. (2016) describe the related and burgeoning field of marine geomorphometry (both general and specific) – the quantitative study of the seafloor surface. Misiuk *et al*. (2021) synthesized the latter two concepts to provide recommendations for implementing multi-scale geomorphometric techniques for benthic habitat mapping.

3. How are benthic habitats mapped?

Brown *et al*. (2011) provide a detailed overview of how benthic habitats are mapped using acoustic remote sensing methods. Here we update these findings and expand the scope to include additional geospatial datasets, remote sensing technologies, and ground validation approaches that are encountered in the literature. We additionally review the different classes of thematic maps that are used to represent benthic habitats.

Generating benthic thematic maps generally requires the use of continuous coverage environmental data sets, which are used as predictor variables to explain the distribution of the “habitat” response. These can take many different forms, and over recent years the number and diversity of geospatial predictor variables has expanded dramatically (see section 4 below). The general workflow for how these data sets are integrated for benthic habitat mapping is presented in Figure 1. Biological patterns on the seafloor are driven by a complex combination of environmental drivers and biological interactions (Brown *et al*., 2011). The physical abiotic characteristics of the seabed (e.g., substrate type, morphology), physiographic setting (e.g., depth, distance from shore) combined with the characteristics of the overlying water column (e.g., temperature, salinity, current speed and direction) all have strong influences on benthic biota, and together define the fundamental niche of each organism. However, obtaining data on these variables through space and time can be extremely challenging.

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Remote sensing techniques provide tools with which to measure or estimate these environmental variables through space and time, and technologies have advanced tremendously over the past few decades. Challenges remain, though, in how geospatial data are collected, with limitations linked to the environment, type of sensor (e.g., electromagnetic, acoustic), and sensor resolution. Geospatial predictor variables are also commonly modelled where direct remotely sensed spatial data collection is not possible (e.g., physical oceanographic variables). These are outlined and discussed in sections 3.2 and 3.3.

The process of generating thematic maps of the seafloor then normally requires some form of direct, usually spatially discrete, in situ observation to record biological or geological measurements at the seabed. These spatially georeferenced in situ observations, commonly referred to as “ground truth” or “ground validation”, define the response variable that is being mapped. The measured response is extrapolated spatially using some form of interpretation or model of the spatially continuous environmental data to generate the final thematic map (Figure 1; see section 3.5). Finally, the mapped prediction is validated using either subsets of the ground truth dataset (i.e., cross-validation) or an independent validation dataset.

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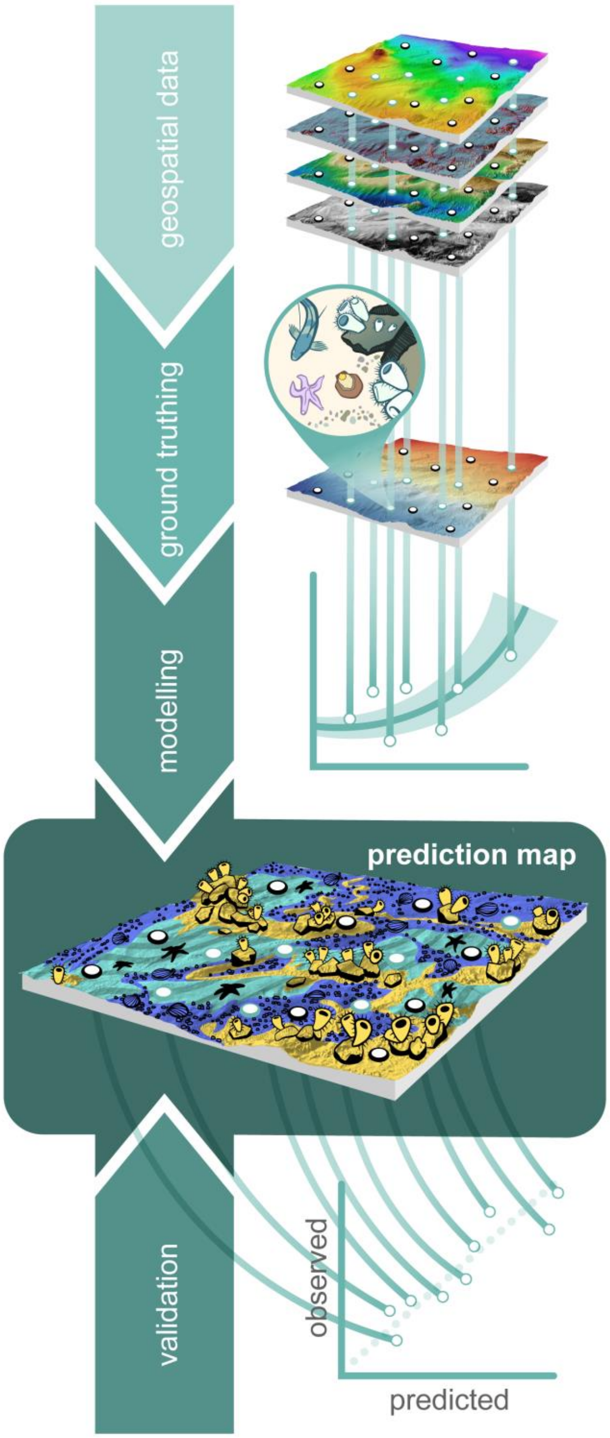


Figure 1. [Single-column] Generalized approach for producing benthic habitat maps. (Top to bottom) Geospatial environmental predictors are obtained, often using remote sensing; in situ ground truth observations of the response variable are obtained over the extent of the environmental data; response observations are modelled or mapped as a function of environmental predictors to generate spatially continuous habitat predictions; the predictions are validated, often using withheld in situ ground truth samples.

3.1. Types of thematic maps

In practice, the term ‘benthic habitat mapping’ is applied liberally to describe the production of several different types of thematic maps. Uses of this terminology in the literature can be grouped into four general categories of benthic thematic map production, which we distinguish based on the mapped response variable (Figure 2).

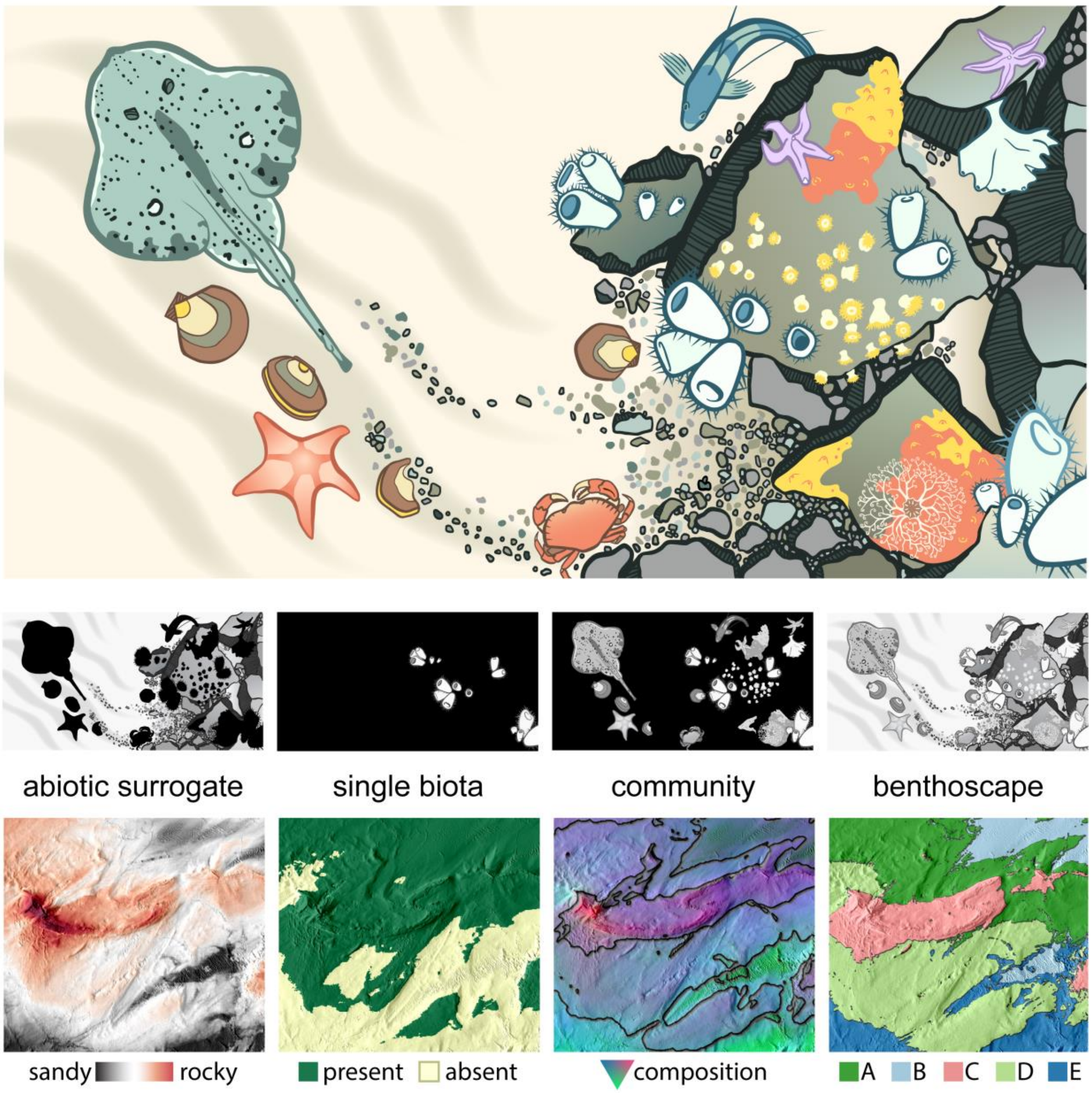
Abiotic surrogate approaches describe mapping the distribution(s) of one or several abiotic benthic habitat components, under the implicit assumption that these may act as surrogates for biological distribution patterns (McArthur *et al*., 2010), or enable biological interpretation (Diaz *et al*., 2004; Figure 2). Previously, the term *abiotic surrogate mapping* has been used to describe the clustering of abiotic environmental data without in situ ground-truth information using unsupervised approaches in order to identify environmental patterns that may be indicative of biological patterns (Brown *et al*., 2011). Here, we expand the use of this terminology to refer to the thematic mapping subject (i.e., response variable), rather than the classification approach, since unsupervised approaches may be applied using both biological information (e.g., Amorim *et al*., 2017) and ground-truth data (e.g., Schimel *et al*., 2010, Proudfoot *et al*., 2020), and since abiotic environmental surrogates are increasingly mapped using supervised modelling approaches (e.g., Borfecchia *et al*., 2019; Bravo & Grant, 2020; Zelada Leon *et al*., 2020). Unsupervised clustering of abiotic environmental layers therefore may still be considered abiotic surrogate mapping as long as there is biological or ecological implication. This applies also to characterization of the structural components of benthic habitat, such as sediment distribution modelling (e.g., Gougeon *et al*., 2017), geomorphological classification (Prampolini *et al*., 2018; Lavagnino *et al*., 2020), and acoustic facies mapping (Shumchenia & King, 2010), all of which may be applied as forms of abiotic surrogate mapping.

Single biota mapping is used to estimate the distribution of a single benthic organism at one or multiple spatial scales, which, in practice is often not limited to the taxonomic level of species. By aiming to delimit the habitat requirements of a single organism (e.g., the species’ “ecological niche”), it is by definition the most accurate application of the term “habitat mapping” considered here. This category of benthic thematic mapping includes “species distribution modelling” (Araújo & Guisan, 2006; Elith *et al*., 2006; Austin, 2007; Franklin, 2010), “ecological niche modelling” (Warren *et al*., 2008; Melo-Merino *et al*., 2020), “bioclimatic envelope modelling” (e.g., Midgley *et al*., 2002; Pearson *et al*., 2004), and “habitat suitability modelling" (e.g., Rengstorf *et al*., 2012; Hu *et al*., 2020). While these terms are often used interchangeably (Franklin, 2010; Melo-Merino *et al*., 2020), they actually imply different conceptual bases and thematic or spatial scales. "Bioclimatic envelope modelling" generally indicates modelling of the potential climatic distribution of a species (Araújo & Peterson, 2012), which may be applied to problems such as predicting species range shifts or invasions under future climate scenarios (Thuiller *et al*., 2005; Broennimann *et al*., 2007; Mbogga *et al*., 2010). "Ecological niche modelling" and "habitat suitability modelling" are concerned with modelling the fundamental niche of an organism (Peterson & Soberón, 2012) – the former perhaps implying a stricter Hutchinsonian interpretation of "niche" (Hutchinson, 1957). "Species distribution modelling", on the other hand, most often refers to delimiting the "realized" or "actual" niche that a species inhabits, which depends on additional factors that limit the species' occupation of its fundamental niche, such as biotic interactions (Malanson *et al*., 1992; Guisan & Zimmermann, 2000; Peterson & Soberón, 2012). There is a tendency towards the use of "species distribution modelling" for fine scale presence-absence studies, which have likely sampled the realized niche, compared to broader regional or continental scale studies that are able to sample along the bioclimatic gradient of a species' range, or its fundamental niche (Franklin, 2010). These semantics are far from well-accepted, and in practice, these applications share many of the same modelling methodologies and techniques. They are additionally applied at different taxonomic levels in the benthic realm, where the species level either is not required or cannot be resolved (e.g., Bučas *et al*., 2013), or where higher taxonomic levels are of interest (e.g., Hu *et al*., 2020). We highlight the recent review on marine species and ecological niche distribution modelling by Melo-Merino *et al*. (2020) for greater detail on this topic in the marine realm.

Benthic community mapping depicts the distribution of groups of organisms that co-occur, their properties, or macro-ecological metrics describing those groups or properties (i.e., biodiversity metrics; Figure 2). Though this does not imply the use of any particular approach, these applications tend strongly towards supervised empirical modelling (see section 3.6 on model class) – though we note some analytical (e.g., Ichino *et al*., 2015) and empirical unsupervised (e.g., Hutin *et al*., 2005; Martins *et al*., 2014; Uhlenkott *et al*., 2020) applications. Ferrier & Guisan (2006) distinguish three mechanisms by which community-level mapping may be accomplished. First, independent taxa may be modelled using *single biota* strategies as outlined above (e.g., SDM) and then combined to produce community-level metrics in a "predict first, assemble later" framework. For example, in their comprehensive report on the benthic biodiversity of the Great Barrier Reef, Pitcher *et al*. (2007) predicted the distributions of 840 individual taxa using a "hurdle" approach to SDM, whereby the model comprises two sub-models: i) a logistic regression predicting whether a species is present or absent; ii) a linear regression predicting the biomass of the species, conditional on it being present. The results of the 840 individual models were subsequently grouped using Ward's (1963) hierarchical clustering, enabling the prediction of group biomass across the Great Barrier Reef. Alternatively, information on individual taxa may be aggregated first to produce community-level metrics, which are modelled in aggregate in an "assemble first, predict later" design. Such designs may take several forms: biodiversity metrics (including taxonomic, functional, phylogenetic) may be derived from species data then modelled and predicted spatially (e.g., Huang *et al*., 2014; Rooper *et al*., 2014; Doxa *et al*., 2016; Peterson & Herkül, 2019; Murillo *et al*., 2020a; Pearman *et al*., 2020; Wicaksono *et al*., 2022); or, taxa may be initially clustered into groups based on taxonomic or functional criteria, which are then predicted (e.g., Haywood *et al*., 2008; Pesch *et al*., 2011; Moritz *et al*., 2013; Serrano *et al*., 2017; Kaminsky *et al*., 2018; Vassallo *et al*., 2018). Groups of taxa and/or traits may also be modelled simultaneously in an "assemble and predict together" process that uses interrelationships between individuals to inform the community-level mapping outcome. Again, this may be accomplished using multiple methods. First, biodiversity may be modelled directly using matrix regression approaches such as Generalized Dissimilarity Modelling (GDM; Ferrier *et al*., 2002) or Gradient Forest (Ellis *et al*., 2012), which predict turnover in β- or γ-diversity as a function of environment and space (e.g., Dunstan *et al*., 2012; Pitcher *et al*., 2012; Compton *et al*., 2013a, 2013b). Alternatively, multivariate community-level responses may be modelled directly using approaches such as Multivariate Regression Trees (MRT; De'ath, 2002) and LINKTREE, which combine community clustering and supervised modelling in a single step that is informed by environmental predictors (e.g., LaFrance *et al*., 2014; Fontaine *et al*., 2015; Kaskela *et al*., 2017; Mazor *et al*., 2017). Finally, recent approaches have focused on Joint Species Distribution Modelling (JSDM; Clark *et al*., 2014; Warton *et al*., 2015), which model joint distributions between species to both account for species co-occurrence and to enable inference at the community level. Specific approaches include Latent Variable Models (e.g., Kraan *et al*., 2020), and Hierarchical Modelling of Species Communities (HMSC; e.g., Murillo *et al*., 2020b; Elo *et al*., 2021; Shitikov *et al*., 2022), which enables integration of individual species co-occurrences for simultaneous inference at species and community levels, potentially also with information on functional traits and phylogeny (Ovaskainen *et al*., 2017; Tikhonov *et al*., 2020). The latter approaches offer promising advances for modelling individual species and communities, which are grounded in ecological theory.

Benthoscape mapping describes the "landscape-scale" bio-physical characterization of the seabed – referring primarily to classification contexts (Zajac *et al*., 2003; Figure 2). The term "benthoscape" was introduced by Zajac (2000) as the marine (in particular, seabed) analogue to terrestrial landscapes, which comprise individual "elements" of distinct abiotic (e.g., sediments) and biotic (e.g., infaunal communities) characteristics (Zajac *et al*., 2003), comparable to terrestrial "land units" (Zonneveld, 1989). Here, again, we invoke the response variable to distinguish different types of thematic habitat maps, rather than the model class (e.g., supervised, unsupervised), which generally conforms with the use of this terminology in the literature (e.g., Godet *et al*., 2011; Lacharité & Brown, 2019; Proudfoot *et al*., 2020). Therefore, for the purposes of this review, we consider a "benthoscape map" to depict the distribution of "benthoscape classes", which are a discrete categorical seafloor bio-physical response often mapped spatially using classification approaches (e.g., Brown *et al*., 2012; Vasquez *et al*., 2015; Montereale Gavazzi *et al*., 2016; Lacharité *et al*., 2018; Butler *et al*., 2020). Benthoscape maps may be useful for marine zonation at scales relevant for management applications that must consider both biological and physical characteristics of the seafloor (Gray & Elliot, 2009). We note that groups of species and their associated environmental conditions are sometimes also referred to as "biotopes" in the benthic habitat mapping literature (e.g., Foster-Smith *et al*., 2004; van Rein *et al*., 2011; Strong *et al*., 2012; Gonzalez-Mirelis & Buhl-Mortensen, 2015; Lee *et al*., 2015; Buhl-Mortensen *et al*., 2020). This has arisen from the use of "biotope" in the Marine Biotope Classification of Britain and Ireland (Connor *et al.*, 1997) – now the Marine Habitat Classification for Britain and Ireland (JNCC, 2022). "Biotope" was appropriated from the ecology literature in the 1990s (Olenin & Ducrotoy, 2006), wherein it was originally used to describe *abiotic* environmental components (Dahl, 1908; Hutchinson, 1957), or the "range of environmental conditions that occur in an area" (Franklin, 2010). Interestingly, the use of "biotope" in the benthic mapping literature has drifted to now refer specifically to biological communities in some cases (e.g., HELCOM, 2013; Elvenes *et al*., 2014; Neves *et al*., 2014, Schiele *et al*., 2015), which were originally defined by Moebius (1877) as the "biocoenosis" that inhabit the abiotic "biotopes" (Dimitrakopoulos & Troumbis, 2008). Meanwhile, this original definition of "biocoenosis" is retained in many places (e.g., Zavodnik *et al*., 2005; Göltenboth *et al*., 2006; Dauvin *et al*., 2008a; Maiorano *et al*., 2011; Sloss *et al*., 2013). Additional detailed discussion may be found in Olenin & Ducrotoy (2006), Dauvin *et al*. (2008a, 2008b), and Brown *et al*. (2011), who called for greater clarity in the use of terminology for benthic habitat mapping. We avoid use of the terms "biotope" and "biocoenosis" here to reduce ambiguity (e.g., regarding the response variable being mapped), in favour of "benthoscape mapping" (Brown *et al*., 2012), which refers to mapping bio-physical

499 seabed units comparable to those of terrestrial landscapes (i.e., “land units”; Zonneveld, 1989). This is a
500 useful marine analogue for assessing spatial species-environment relationships, which is a component to
501 the emerging field of seascape ecology (Pittman, 2017).



502

503 Figure 2. [Two-column] Types of thematic benthic habitat maps differentiated according to the response. “Abiotic
504 surrogate” maps depict abiotic proxies of benthic habitat; “single biota” maps indicate the distribution of a single
505 benthic organism; “community” maps focus on distributions of groups of organisms or on biodiversity; and
506 “benthoscape” maps refer to landscape-scale bio-physical classifications of biotic and abiotic seabed components.

3.2. Geospatial predictor data

The type of thematic map produced depends on the response variable (section 3.1 and Figure 2), but spatial prediction and mapping of the response variable is achieved using geospatial predictor data (Figure 1). In this context, “geospatial predictor data” refers to the primary environmental measurements used to map, or inform mapping of, the response. These data are often acquired using remote sensing methods such as optical cameras or sonar, but may also include direct physical samples (e.g., of geology, biology), which are interpolated or aggregated to a spatially continuous extent for use in predicting the response. Prediction is often, but not always, achieved using statistical models between geospatial datasets and the response, and may also include semi-empirical approaches or manual interpretation, which determines the “model class” (section 3.6).

Measured water depth is commonly used as a source of geospatial data to produce benthic habitat maps. Depth is a gradational variable that is readily measured in a spatially continuous manner using one of several remote sensing techniques (see section 3.4). The utility of depth as a geospatial predictor is two-fold. First, it acts as a surrogate for many physical and chemical oceanographic properties that may influence habitat suitability but are difficult to measure directly at a high resolution. These include variables such as temperature, salinity, light availability, and primary productivity (McArthur *et al*., 2010). Second, it may be used to calculate a range of secondary predictor variables such as terrain attributes (see section 3.3), which are useful for mapping species habitat, segmenting the seabed into morphological units, or identifying relevant geological features (Lecours *et al*., 2016).

Spectral reflectance is another source of geospatial predictor data that is commonly utilized for mapping benthic habitats. Measurements are generally limited to optically shallow waters, but deployment by diver or underwater vehicle enables reflectance measurements at greater depths. LiDAR reflectance may also be used to inform on characteristics of the seabed where clarity permits (Wang & Philpot, 2007; Zavalas *et al*., 2014), or by using underwater vehicles (Collings *et al*., 2020).

Where sonar is employed, acoustic backscatter (i.e., reflectivity) is often recorded to inform on properties of the substrate. The interaction of the sonar signal with the substrate is complex, but if several factors are properly constrained (e.g., beam geometry, sonar electronics and sensitivity, pulse length, signal attenuation, grazing angle), the intensity of the acoustic signal that has reflected off the seafloor depends on the hardness and roughness of the surface (Weber & Lurton, 2015). These properties are characteristic of seafloor substrate composition – a fundamental habitat component for benthic species (McArthur *et al*., 2010).

Several other forms of geospatial data are measured and implemented as predictor variables for benthic habitat mapping. Spatial measurements such as longitude and latitude coordinates, or distances from geographical features such as coastline, islands, or geological phenomena may serve as surrogates for benthic habitat drivers such as sediment transport, physical or chemical oceanographic parameters, dispersal, or habitat connectivity (McArthur *et al*., 2010; Giusti *et al*., 2014; Vassallo *et al*., 2018; Charlène *et al*., 2020). These variables also may enable leveraging of spatial autocorrelation of the response variable in order to increase predictive capacity of geospatial models – either by capturing relevant information on unmeasured environmental variables, or by modelling spatial relationships that arise as a function of symbiotic or community processes (Legendre & Fortin, 1989). Spatial autocorrelation may also be utilized explicitly to enable use of discrete geospatial data via geostatistical interpolation to a spatially continuous surface. Examples include kriging sediment parameters from physical samples (e.g., Livingstone *et al*., 2018), or oceanographic measurements obtained via in situ measurement (e.g., CTD casts; Rooper *et al*., 2017). Broad scale temporal oceanographic measurements are made available for much of the Earth through long-term data aggregation efforts such as the World Ocean Atlas (Garcia *et al*., 2013a, 2013b; Locarnini *et al*., 2013; Zweng *et al*., 2013) and the Global Data Analysis Project (GLODAP; Key *et al*., 2004).

3.3. Derived predictor data

A range of derived geospatial predictors may also be generated from the measured (i.e., “primary) geospatial predictor data for use as explanatory variables for benthic habitat mapping. Derived predictor data are not measured directly, but are calculated from geospatial data measurements such as the depth or reflectance. The slope of the seabed is a common example – it is often employed as a predictor for benthic mapping studies but is seldom measured in situ.

Terrain attributes calculated from a digital terrain model (DTM) are widely derived as predictors for habitat mapping applications. These include the aforementioned slope, but also measures of orientation, curvature, relative position, rugosity, and innumerable variations of these (Lecours *et al*., 2017). The science of terrain characterization is termed “geomorphometry”, which includes calculation of terrain attributes from a DTM. Marine geomorphometry has emerged as a distinct subject of inquiry (Lecours *et al*., 2016), which investigates questions surrounding spatial scale, accuracy, error, and uncertainty in the marine realm (e.g., Wilson *et al*., 2007; Dolan & Lucieer, 2014; Walbridge *et al*., 2018; Misiuk *et al*., 2021; Hansen *et al*., 2022).

Various textural, spectral, and waveform features may be calculated to describe remotely sensed data for subsequent use in benthic habitat mapping. Where acoustic backscatter has been acquired and compensated to produce a raster image, grey-level co-occurrence matrices (GLCMs; Haralick *et al*., 1973) are commonly calculated to describe the texture of the pixel intensity values (e.g., Cochrane & Lafferty, 2002; Blondel & Gómez Sichi, 2009; Che Hasan *et al*., 2014; Janowski *et al*., 2018), including metrics such as the homogeneity, contrast, entropy, dissimilarity, and correlation. Trzcinska *et al*. (2020), additionally introduce a range of "spectral" backscatter features that may be calculated to characterize the seabed. It is also possible to retain the angular backscatter response prior to compensation and raster mosaicking to calculate statistics and features that provide a richer acoustic characterization of the substrate (e.g., Fonseca & Mayer, 2007; Parnum, 2007; Che Hasan *et al*., 2012, 2014; Misiuk & Brown, 2022; Porskamp *et al*., 2022) – though, this could arguably be considered "primary" rather than "derived" geospatial data. A range of secondary features may also be calculated from spectral remote sensing data acquired using air- or satellite-borne optical sensors. Many of these – including band ratios (e.g., Roelfsema *et al*., 2013; McIntyre *et al*., 2018) and various vegetation indices (e.g., Bajjouk *et al*., 2020; Forsey *et al*., 2020; Wicaksono *et al*., 2020) – utilize differences between wavelengths of different spectral bands of multi- or hyper-spectral sensors. Waveform variables calculated from LiDAR also offer potential for increased discrimination of bottom type, for example, by calculating features based on waveform geometry (e.g., Tulldahl & Wikström, 2012), hue saturation intensity (HSI; e.g., Zavalas *et al*., 2014) or statistics and vegetation indices comparable to those of spectral data (e.g., Collin *et al*., 2008; Collin *et al*., 2012).

Oceanographic parameter estimates may be derived indirectly using spectral data from satellites. These commonly include the sea surface temperature, phytoplankton biomass, photosynthetically available radiation, and particulate carbon, chlorophyll, and calcite concentrations. Because these parameters tend to vary over broad spatial scales, data are typically provided on the order of km, or in some cases, 100s of m, and are generally utilized for mapping applications on the order of 100s or 1000s of km.

Oceanographic models provide increasingly high-resolution predictions of physical and chemical parameters used to map benthic habitats. These include large-scale global models such as Ocean Circulation and Climate Advanced Modelling (OCCAM; Webb *et al*., 1998), the Vertically Generalized Productivity Model (VGPM; Behrenfeld & Falkowski, 1997), and HYCOM (https://www.hycom.org/), which are used for habitat mapping at broad scales (e.g., Tittensor *et al*., 2009; Harris & Hughes, 2012; Roberts *et al*., 2022), but also bespoke models that are useful for regional applications (e.g., Fabri *et al*., 2017; Doyle *et al*., 2018; Peterson & Herkül, 2019; Guillaumot *et al*., 2020; Murillo *et al*., 2020b; Pearman *et al*., 2020). The latter are facilitated through a variety of open modelling frameworks and software such as the Regional Ocean Modeling System (ROMS; https://www.myroms.org/), the General Estuarine Transport Model (GETM; https://getm.eu/start.html), Simulating Waves Nearshore (SWAN; https://swanmodel.sourceforge.io/), the Coupled Hydrodynamical Ecological model for RegioNal Shelf seas (COHERENS; https://odnature.naturalsciences.be/coherens/en/), Finite-Volume Coastal Ocean Model (FVCOM; Chen *et al*., 2006), and the Nucleus for European Modelling of the Ocean (NEMO; Gurvan *et al*., 2022). Unlike measurements from satellite, oceanographic models enable prediction of environmental variables throughout the water column, and at or near the seabed. They may also be used to forecast future habitat distributions under different climate scenarios (e.g., Singer *et al*., 2017; Greenan *et al*., 2019; Le Marchand *et al*., 2020).

Finally, previous maps or models derived from primary environmental measurements are sometimes utilized as predictors in subsequent benthic habitat maps. Maps of geological or morphological features are commonly used for this purpose (e.g., Vassallo *et al*., 2018; Linklater *et al*., 2019; Misiuk *et al*., 2019; Uhlenkott *et al*., 2020), although prior biological predictions may also be used (e.g., Knudby *et al*., 2011; Doyle *et al*., 2018). Classification of the seabed into standardized habitat schemes, such as EUNIS, may be accomplished through the combination of prior maps describing individual habitat components (e.g., Vasquez *et al*., 2015).

3.4. Remote sensing technologies

Remote sensing technologies are the primary means by which geospatial predictor data are acquired for benthic habitat mapping, and successful application of any remote sensing method in aquatic environments is dictated by the water depth and turbidity (Figure 3). The development and widescale application of satellite and aerial remote sensing approaches using electromagnetic sensors has changed the way we map the earth (Dubovik *et al*., 2021), including the seabed (Kutser *et al*., 2020). These generally include mono-, multi-, and hyper-spectral cameras, and mono- or multi-spectral LiDAR (Hickman & Hogg, 1969), which are used to measure reflectance of the seabed in optically shallow waters. We also note development of hyper-spectral LiDAR technologies (Kaasalainen *et al*., 2007; Chen *et al*., 2019), which have yet to be deployed for mapping benthic environments to the best of our knowledge. In optically deep waters, spectral measurements may be obtained using underwater vehicles (Foglini *et al*., 2019), or by hand (Chennu *et al*., 2017).

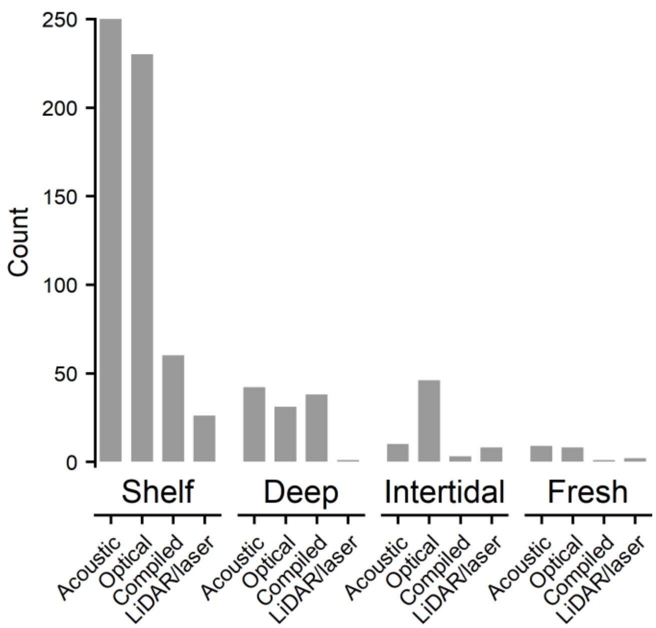


Figure 3. [Single column] Number of studies utilizing different remote sensing technologies for different aquatic environments.

Satellite-borne sensors enable highly efficient remote sensing of the oceans and seabed on a global scale. Water depth may be estimated at a high resolution using multi-band imagery from satellites such as WorldView (e.g., Cerdeira-Estrada *et al*., 2012), Sentinel (e.g., Poursanidis *et al*., 2021), Landsat (e.g., Borfecchia *et al*., 2019), and the Planet Dove constellation (e.g., Li *et al*., 2019). Altimetry may also be used to estimate depths over very broader scales (Smith & Sandwell, 1997). Where clarity permits, one of many satellite- or air-borne spectral cameras may be used to infer habitat characteristics by imaging the seafloor directly (Capolsini *et al*., 2003; Purkis *et al*., 2019). Several satellites have been specifically designed to provide global oceanographic measurements. MODIS-Aqua, for example, images the entire Earth every

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two days across 36 spectral bands, providing reflectance data that may be used to estimate a variety of physical, chemical, and biological oceanographic variables (Maccherone & Frazier, n.d.; NASA Goddard Space Flight Center, Ocean Ecology Laboratory, Ocean Biology Processing Group, 2022). These data are available at multiple resolutions (but as high as 250 m), enabling their use for habitat mapping across multiple spatial scales (e.g., Fontaine *et al*., 2015; Jalali *et al*., 2018; Buhl-Mortensen *et al*., 2020; Hu *et al*., 2020). MODIS was preceded by sensors such as the Advanced Very High Resolution Radiometer (AVHRR) and the Sea-viewing Wide Field-of-view Sensor (SeaWiFS), which provide coarser measurements of sea surface temperature and colour (km-scale), but which date back to the 1970s and 1990s, respectively (Earth Resources Observation And Science (EROS) Center, 2017; NASA Goddard Space Flight Center, Ocean Ecology Laboratory, Ocean Biology Processing Group, 2018). Data from these sensors have been applied both prior to, and along with, that of MODIS-Aqua to map benthic habitats over broad extents (e.g., G. Williams *et al*., 2010; Pitcher *et al*., 2012; Compton *et al*., 2013a; Mazor *et al*., 2017; de la Barra *et al*., 2020). Open cloud computing and hosting platforms such as Google Earth Engine (Gorelick *et al*., 2017) have greatly increased access to these and other similar global satellite remote sensing datasets.

Beyond the limits of light penetration, sonar is generally utilized to provide geospatial predictor data for benthic habitat mapping. Single beam sonar systems emit a single sounding that is typically normal to the vessel, while sidescan sonar is used to acquire a swath of soundings at oblique angles. Multibeam sonars may be used to collect a broad swath of soundings at both normal and oblique angles, which generally include a mapped width on the order of 4 times the water depth, greatly increasing survey efficiency compared to single beam systems. In shallow waters, these systems enable habitat mapping at very high resolutions (e.g., sub-metre; Montereale Gavazzi *et al*., 2016). Remote and autonomous underwater vehicles (ROVs, AUVs) additionally enable very high-resolution mapping at great depths (100s or 1000s of m), providing benthic habitat information at unprecedented levels of detail (cm or m-scale) over broad extents (Robert *et al*., 2014; Pierdomenico *et al*., 2015; Sen *et al*., 2016). Sub-bottom profilers emit a low frequency pulse capable of penetrating the substrate in order to image the subsurface. Each of these technologies has capability to measure both the time and intensity of the echo, yielding estimates of depth and acoustic backscatter, respectively. Recently, the ability to ping at multiple acoustic frequencies simultaneously has enabled so-called “multispectral” backscatter mapping using multibeam sonars (Brown *et al*., 2019), which has potential to increase the resolvability of seabed substrate properties (Feldens *et al*., 2018; Gaida *et al*., 2018; Janowski *et al*., 2018; Misiuk & Brown, 2022). Multifrequency surveys may now be conducted using single beam (e.g., Cutter & Demer, 2014; Mopin *et al*., 2022), sidescan (e.g., Tamsett *et al*., 2016; Fakiris *et al*., 2019), multibeam (e.g., Gaida *et al*., 2020; Menandro *et al*., 2022; Schulze *et al*., 2022), and synthetic aperture (Barclay *et al*., 2005; Rymansaib *et al*., 2019) side scan sonars. A summary of remote sensing technologies and sensors used to collect geospatial data for benthic habitat mapping is provided in Table 1.

Table 1. Examples of geospatial benthic habitat predictor data sets collected using remote sensing technologies. An inventory of predictors found in the reviewed literature is provided in the Supplementary Material.

Remote sensing	Sensor	Geospatial data	Derived predictor examples
Acoustic	SBES[1]	Depth	Terrain
		Backscatter	Waveform/echogram parameters
	SSS[2]	Backscatter	GLCM[7]; focal statistics; power spectra; fractal dimension
		Depth	Terrain
	SBP[3]/seismic	Depth	Terrain; subsurface reflector depth
		Backscatter	Echogram parameters
	MBES[4]	Depth	Terrain; fractal dimension; spectral parameters
		Backscatter	GLCM[7]; angular parameters; focal statistics
	ADCP[5]	Current speed	
		Depth	Terrain
Electromagnetic	Laser/LiDAR	Depth	Terrain
		Reflectance	Waveform parameters
	Spectral	Reflectance	Depth; spectral indices; physical/chemical oceanography
	Radar	Altimetry[6]	Depth

[1]Single beam echosounder
[2]Side scan sonar
[3]Sub-bottom profiler
[4]Multibeam echosounder
[5]Acoustic Doppler current profiler
[6]Altimetry-derived depths are generally accessed via data compilations such as SRTM15+.
[7]Grey-level co-occurrence matrices

The need for higher resolution global seafloor data is well recognized, and there now exist multiple publicly available compilations of bathymetric data for the world's oceans that are accessed for benthic habitat mapping applications. The SRTM15+V2.0 grid provides a 15 arc-second (~500 x 500 m at the equator) compilation of global elevation data (both land and sea; Tozer *et al*., 2019). Satellite altimetry and ship-borne acoustics provide depth estimates for the global oceans, while terrestrial elevation is derived through satellite radar. The SRTM15+ grid is augmented by the General Bathymetric Chart of the Oceans (currently "GEBCO_2023"), which is a global elevation surface developed and provided freely by the International Hydrographic Organization (IHO) and the Intergovernmental Oceanographic Commission (IOC) of the United Nations Educational, Scientific and Cultural Organization (UNESCO). The GEBCO grid is updated annually, providing continuous elevation data for the globe also at 15 arc-second intervals compiled from SRTM15+ and additional data from a variety of acoustic, optical, and historical data sources. The GEBCO grid is further augmented by the Global Multi-Resolution Topography (GMRT) Synthesis hosted by the Columbia University Lamon-Doherty Earth Observatory (Ryan *et al*., 2009), which provides a global compilation of multibeam sonar data at a base resolution of ~100 m, but up to ~25 m in some areas. GMRT is updated regularly, and multibeam grids may be accessed at one of several resolutions, or optionally, may be acquired as an enhanced version of the latest GEBCO grid (https://www.gmrt.org/index.php).

These global compilations have greatly increased the accessibility of global bathymetric data for science, but the true data density and resolution are often deceiving. For example, Mayer *et al*. (2018) point out that the GEBCO_2014 grid, which has a resolution of 30 arc-seconds (926 m at the equator), relies on interpolated depth values for approximately 82% of grid cells, which have no actual bathymetric measurements. Of the 18% of cells with bathymetric measurements, many have only a single bathymetric sounding, and only 9% of cells contain high-resolution multibeam echosounding data. Increased awareness of this data gap has motivated global initiatives such as the Nippon Foundation—GEBCO Seabed 2030 Project, which has the goal of collecting at least one bathymetric measurement in a global grid of depth-variable cells by 2030, which range from 100 m resolution in waters shallower than 1500 m, to 800 m resolution in the deepest parts of the ocean (> 5750 m water depth; Mayer *et al*., 2018). As of 2023, approximately 23% of the global oceans have been mapped according to these criteria (Seabed 2030 Project, 2023).

3.5. Ground validation

"Ground validation" or "ground truth" data are measurements of the response variable that is being mapped. This is used either as training data for producing thematic benthic habitat maps, or to validate them. Recognizing the variety of data used for this purpose (see section 4.5), we consider the terms "ground validation" or "truth" to be non-prescriptive regarding the method by which the data are acquired; in other words, these terms describe data on the response variable, not the methods for acquiring those data (e.g., photography, physical sampling). Owing to the limitations and efficiencies of sampling in marine environments, though, several methods of benthic ground validation predominate.

Underwater imagery is an efficient and non-destructive method for obtaining both biological and geological ground validation, and still or video cameras can be mounted on a variety of platforms for different purposes. Passive camera systems may be lowered via tether from the surface to the seafloor to collect imagery, which are not fitted with any form of propulsion. Drop cameras, for example, are deployed directly beneath a survey vessel, either at one or several discrete points per location for still imaging systems, or for a continuous period of time for video systems, in which the vessel, not under power, is allowed to drift for some interval (e.g., Wilson *et al*., 2021). Similarly, towed imaging systems are deployed from a vessel under power to acquire benthic images from along a path or transect (e.g., Ierodiaconou *et al*., 2007). Sediment profile imaging (SPI) cameras are another specific type of passive drop camera that captures subsurface profile images of the sediment (Rhoads & Cande, 1971). Autonomous and remote underwater vehicles (AUVs, ROVs) are self-propelled platforms that are increasingly utilized for imaging the seabed. AUVs have capacity to efficiently collect large volumes of imagery data over broad extents and are ideal for long term monitoring applications (e.g., S. B. Williams *et al*., 2010, 2012), and ROVs enable image acquisition at deep and often morphologically complex sites such as submarine canyons, vertical walls, and hydrothermal vents, which may be otherwise difficult to sample (Robert *et al*., 2015; Bodenmann *et al*., 2017; Pearman *et al*., 2020). In shallow waters, imagery is commonly collected manually via SCUBA or snorkeling, which may additionally be used to establish precise measurements by using quadrats or transects (e.g., Doxa *et al*., 2016). Several forms of immobile in situ cameras are also used to survey mobile fauna or for monitor environmental health, including baited remote underwater video systems (BRUVS; e.g., Moore *et al*., 2009) and time lapse systems (Kocak *et al*., 2008). A modern comprehensive overview on the use of underwater imagery for benthic habitat mapping is provided by Bowden *et al*. (2020).

Both biological and geological physical samples are commonly used as ground validation for benthic habitat mapping. Physical samples refer to those that are removed from the seabed for analysis at the surface. Bulk substrate extraction is the most common form of physical sampling used to acquire validation data for benthic habitat mapping. Grab sampling is a method for bulk sediment extraction that is often used to acquire surficial geological and infaunal biological data simultaneously. Various coring techniques are also applied that enable profile sampling of the sediment surface and subsurface, such as gravity, piston, vibro- and multi-cores. Box cores may provide both a large planar surficial sample – similar to that of a grab – and also a profile sample, making them highly useful for obtaining simultaneous representative biological and surficial geological samples (e.g., Leduc *et al*., 2015). Targeted sampling is used where feasible to obtain specific biological or geological samples (e.g., McRea *et al*., 1999; Perez *et al*., 2020). Benthic trawls are a method of sampling that may be targeted or indiscriminate, and are often deployed during scientific or fisheries surveys to sample benthic or demersal species (e.g., Montero *et al*., 2020; Murillo *et al*., 2020a).

Several additional methods for acquiring data on the response are found in the literature. Direct observations of benthic biology or geology are commonly acquired in the intertidal zone simply by recording them manually. In shallow waters, observations may be recorded by snorkeling or diving (Wilson *et al*., 2019). Additionally, reflectance properties may be measured using a spectrometer in optically shallow waters to validate electromagnetic remote sensing data (Kutser *et al*., 2020). Some use of previous maps or compiled datasets as ground truth also occurs where they are deemed high quality (e.g., Immordino *et al*., 2019). Occasionally, high resolution remotely sensed optical datasets such as those acquired via airborne hyperspectral sensors or drones are used to ground truth lower resolution optical sensors that may cover a broader extent, such as satellite data (e.g., Wicaksono *et al*., 2020; Poursanidis *et al*., 2021).

3.6. Model class

Spatially continuous benthic habitat maps were traditionally produced by manual expert interpretation, yet geospatial modelling has now become the primary means for achieving these spatial predictions. Three broad classes of models are distinguished in the spatial ecology and biology literature (Guisan & Zimmermann, 2000). *Analytical* or *mathematical* models aim to describe an ecological phenomenon and infer results using one or multiple closed-form mathematical equations, which are not necessarily linked theoretically to any environmental mechanism (Sharpe, 1990). These might be established based on observed ecological trends, but specific models (e.g., regression) are not fit to field observations. The rigidity of analytical models allows them to represent the behaviour of a simplified system, which may be transferred to generate predictions or inferences under particular sets of potentially novel conditions (Pickett *et al*., 2007). These models may target highly specific phenomena such as lateral transport of organic matter to the seabed (Ichino *et al*., 2015), or more general population-level parameters such as species biomass and weight (e.g., Duplisea *et al*., 2002). *Mechanistic* or *process* models, on the other hand, explicitly link behaviours of the model to the ecological processes that drive them (Levins, 1966). The formulation and application of these models is primarily concerned with understanding of ecological processes and interactions and may include qualitative or graphical models that describe the sign (i.e., increasing or decreasing), or general shape of an ecosystem response function (Levins, 1966; MacArthur & Levins, 1964). Like *analytical* models, *mechanistic* models are general, but provide interpretability at the expense of precision (Guisan & Zimmermann, 2000). Unlike *analytical* models, *mechanistic* models attempt to assign causality to ecological processes (Sharpe, 1990), for example, by applying ecological theory that relates life history traits to benthic environmental properties (Kostylev & Hannah, 2007). Finally, *empirical* models are used to fit statistical relationships directly to data observations. These are also known as "predictive" or "statistical" models. They are precise and realistic but may lack generality – failing at extrapolation to novel conditions. Correlations uncovered by *empirical* models do not imply causation between variables. Species distribution models generally fall under this category. A statistical model fit between species observations and environmental variables may be used to accurately predict species presence within the study area, but no mechanistic conclusions can be implied regarding the relationships between environmental variables and species habitat, and it is unlikely that the model is transferable to new locations.

Although model classes are somewhat ambiguous – particularly for cases of apparent combined *analytical-empirical* (e.g., Ceola *et al*., 2014; Paoli *et al*., 2016) and *mechanistic-empirical* (e.g., Harris & Hughes, 2012; Galparsoro *et al*., 2013; Foveau *et al*., 2017; Lewis *et al*., 2019) approaches – *empirical* models fit directly to sample data (i.e., "correlative" models; Melo-Merino *et al*., 2020) are overwhelmingly preferred in the benthic habitat mapping literature (see section 4.6). "Semi-empirical" or "semi-automated" (Costa & Battista, 2013; Lacharité *et al*., 2018) models also appear frequently. These are hybrid models constructed using a combination of empirical statistical analysis of sample data with manual or contextual expert interpretation (e.g., Cruz-Vázquez *et al*., 2019). Both empirical and semi-empirical models may be *supervised* or *unsupervised*. *Supervised* models fit and predict the response (a benthic habitat observation) directly as a function of environmental predictor variables. Generally, all regression models (i.e., a continuous response variable), and also many classifiers found in the benthic habitat mapping literature, are applied in a supervised manner. Examples include generalized linear (e.g., Jansen *et al*., 2018; de la Barra *et al*., 2020), and additive (Serrano *et al*., 2017; Torriente *et al*., 2019) models, and most decision tree-based methods such as classification and regression trees (e.g., Pesch *et al*., 2011), Random Forest (e.g., Lucieer *et al*., 2013; Zhang *et al*., 2013), and recently, XGBoost (Nemani *et al*., 2022) and LightGBM (Mackin-McLaughlin *et al*., 2022). *Unsupervised* models attempt to uncover meaningful patterns in the environmental variables without using information about the response. These models comprise a large number of clustering techniques such as k-means and -medoids (e.g., Węsławski *et al*., 2013; Hoang *et al*., 2016), DBSCAN and OPTICS (e.g., Menandro *et al*., 2022), and specific artificial neural network architectures such as self-organizing maps (e.g., Fendereski *et al*., 2014). Clusters uncovered using these algorithms may be subsequently assigned to classes using ground truth information (e.g., Brown & Collier, 2008; Calvert *et al*., 2015) or may also be used for purposes such as sample site stratification and selection. An exhaustive list of supervised and unsupervised algorithms encountered in the sampled literature are provided in the Supplementary Material.

4. How has benthic habitat mapping changed over time?

4.1. Thematic maps

The types of thematic maps produced over the past couple decades has remained fairly constant (Figure 4). Similar proportions of benthoscape and abiotic surrogate maps have been produced recently compared to two decades ago. Maps focused on the distribution of single biota (such as SDM and ENM) have generally increased during this period – possibly as a result of increased application of these spatial data products as conservation management and planning tools, and also increased focus on issues such as potential range shifts caused by changing climatic conditions (Melo-Merino *et al*., 2020).

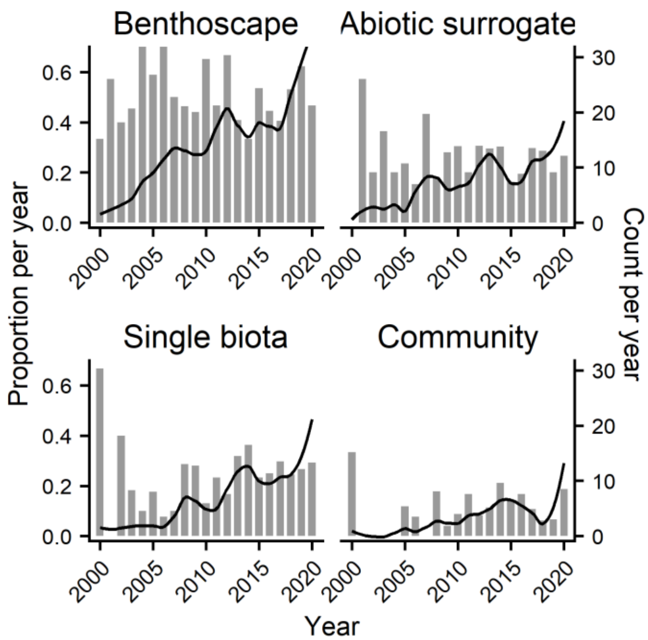

Figure 4. [Single-column] Proportion of thematic map categories produced since 2000 (primary axis; bars), and raw counts per year (secondary axis; lines). Plots are ordered according to prevalence.

4.2. Geospatial predictor data

Bathymetry was the most common form of geospatial data used to produce benthic habitat maps since the year 2000 and was still used in a majority of studies as of 2020 (Figure 5). Optical imagery was also consistently utilized throughout this period. We found acoustic backscatter to be the third most common geospatial data type, but its application appears to have declined relative to other forms of data, ostensibly as a result of increased reliance on optical and compiled remote sensing sources (e.g., Figure 7). Spatial data (e.g., distance from features, coordinates), sediment data (often interpolated), and both physical and chemical oceanographic data have experienced sustained use in a minority of cases since about 2005. Several other forms of geospatial data have been used sporadically since 2000, including LiDAR reflectance, Local or Traditional Ecological Knowledge (LEK, TEK), interpolated biological samples, temporal data (e.g., the year, month), and also what we consider to be a novel application of morphological data obtained directly from in situ measurements by Ceola *et al*. (2014) to model the spatial distribution of fluvial benthic invertebrate species.

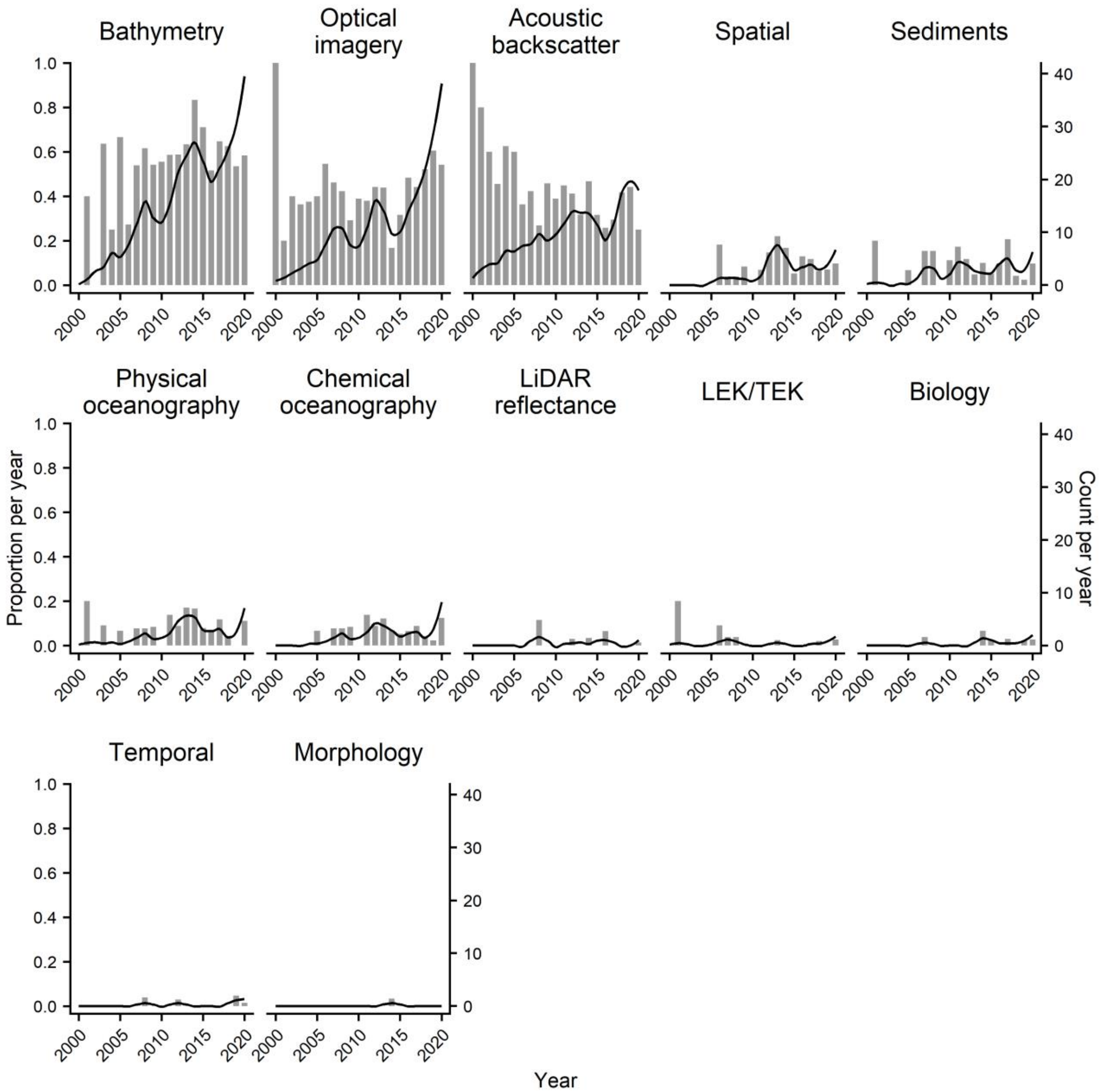

Figure 5. [Two-column] Proportion of studies utilizing different types of geospatial predictor data since 2000 (primary axis; bars), and raw counts per year (secondary axis; lines). Plots are ordered according to prevalence.

4.3. Derived predictor data

The derivation and application of secondary features calculated from the above geospatial predictors has also undergone change since the year 2000 (Figure 6). The use of terrain features has increased notably throughout this period and is now nearly ubiquitous. The application of features derived from acoustic backscatter has declined over the past two decades, at least partially corresponding to reduced utilization

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of the QTC software for sonar data processing, which included calculation of backscatter features for seabed characterization (Preston, 2009; Brown *et al*., 2012). Oceanographic features are increasingly calculated and applied, likely as a function of increased availability of high-quality satellite imagery from which physical and chemical parameters may be estimated. These are differentiated here from spectral features that focus on optical properties and texture of the seabed in optically shallow waters.

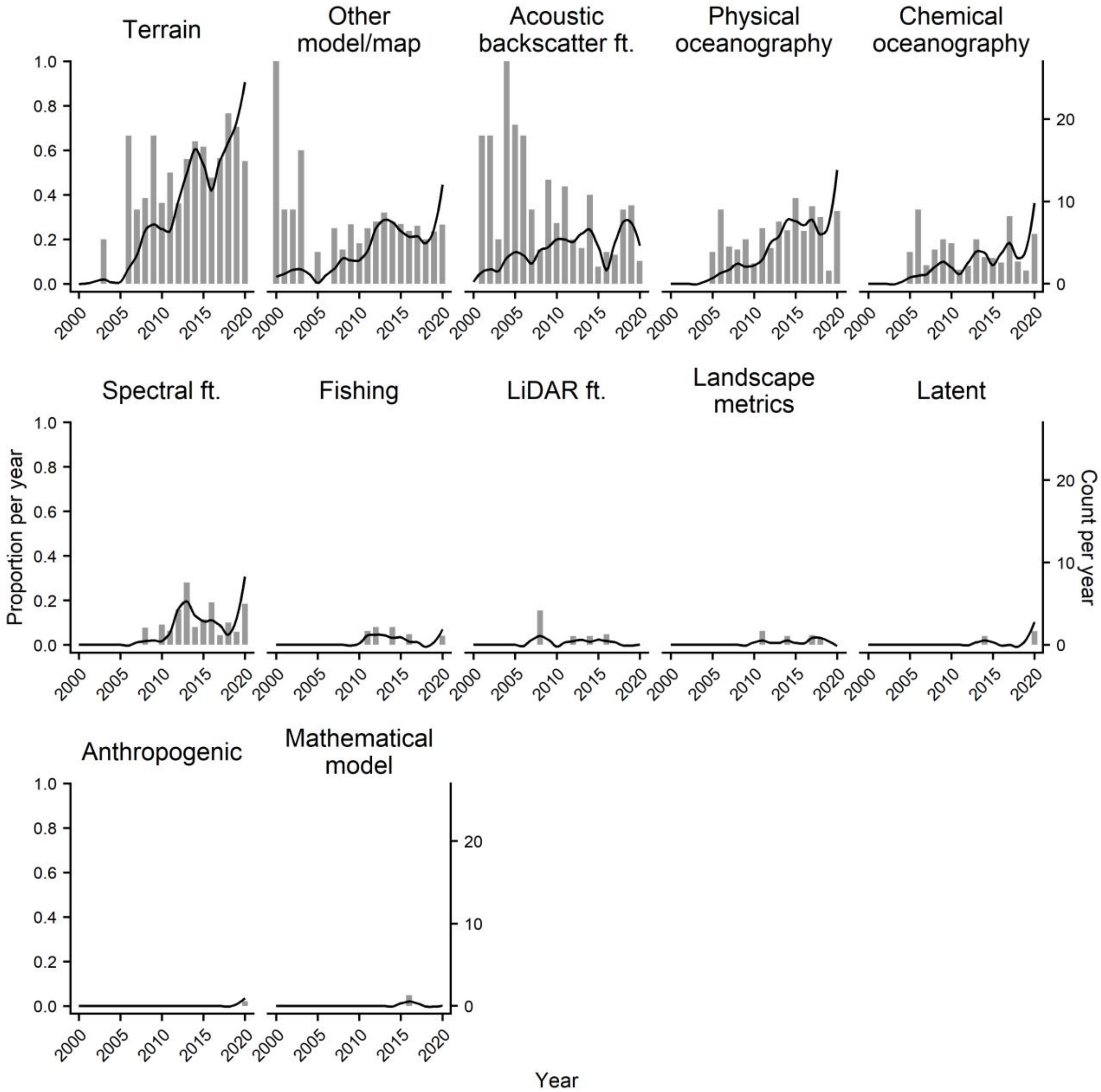

Figure 6. [Two-column] Proportion of studies utilizing different secondary features derived from geospatial data since 2000 (primary axis; bars), and raw counts per year (secondary axis; lines). Plots are ordered according to prevalence.

4.4. Remote sensing technologies

The prevalence of remote sensing technologies encountered in the sampled benthic habitat mapping literature has changed since the year 2000 (Figure 7). Acoustic technologies were the preferred remote sensing tool up until about 2005, after which optical technologies were increasingly utilized. Past 2015, the implementation of optical technologies has surpassed acoustic ones. This is driven at least partially by the efficiency with which optical data may be collected over vast extents, enabling expansive habitat mapping efforts even in remote regions (Purkis *et al*., 2019). Access to compiled remote sensing datasets has increased over this period, likely as a result of increased accessibility to large public data repositories such as GEBCO (GEBCO Compilation Group 2022, 2022), the World Ocean Atlas (Garcia *et al*., 2013a, 2013b; Locarnini *et al*., 2013; Zweng *et al*., 2013), and Google Earth Engine (Gorelick *et al*., 2017), including the datasets therein. LiDAR and laser technologies have been applied consistently but in a small number of cases. There was substantial heterogeneity among the acoustic methods employed over this period (Figure 8), which differ technologically. Side scan and single beam sonar (SSS, SBES) were greatly preferred in the first decade, but increased accessibility to multibeam echosounders (MBES) has somewhat superseded these technologies for mapping optically deep waters.

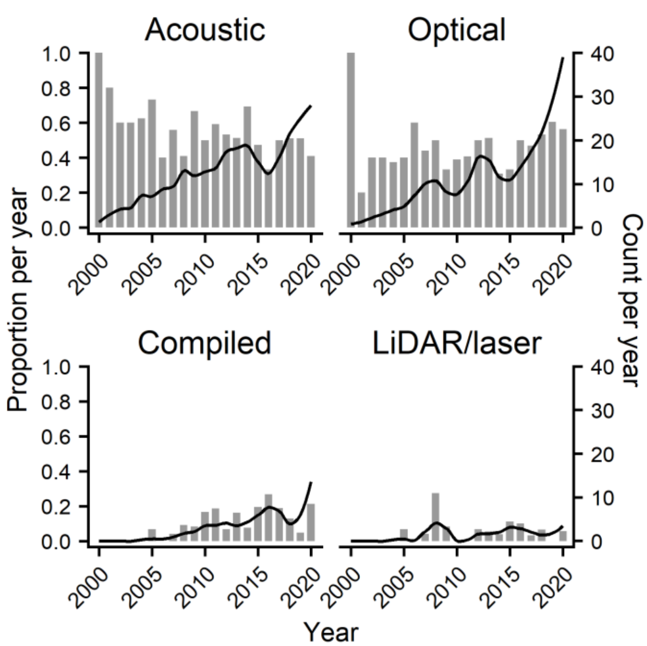

Figure 7. [Single-column] Proportion of different remote sensing technologies employed since 2000 (primary axis; bars), and raw counts per year (secondary axis; lines). Plots are ordered according to prevalence.

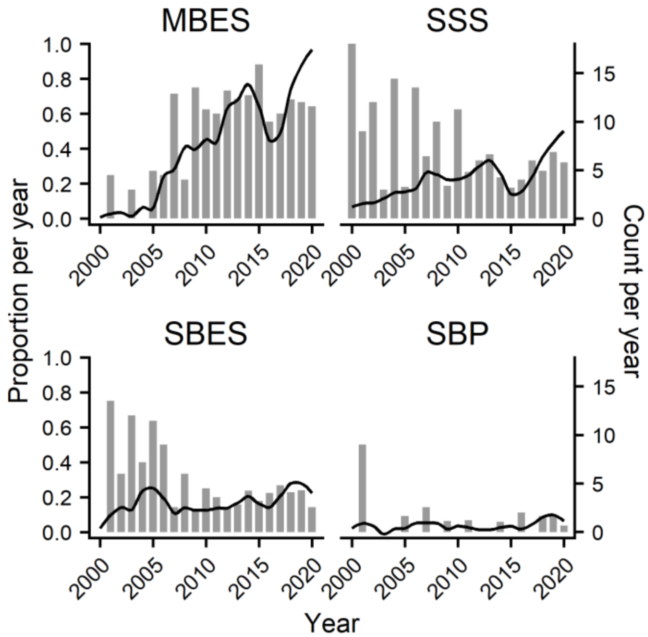

Figure 8. [Single-column] Proportions of acoustic studies employing multibeam echosounders (MBES), side scan sonars (SSS), single beam echosounders (SBES), and sub-bottom profilers (SBP) since 2000 (primary axis; bars), and raw counts per year (secondary axis; lines). Plots are ordered according to prevalence.

4.5. Ground validation

Underwater imagery is the most common form of ground validation obtained to produce or validate benthic habitat maps (Figure 9). Physical samples predominated at the turn of century, but have been largely superseded by imagery, which is often more efficient to acquire in the field and to process. Direct (i.e., “in-person”) observation is still commonly conducted, particularly for intertidal and shallow water studies (e.g., Figure 10). We reiterate that no qualitative judgement was passed on what forms of data constitute ground validation (a.k.a., “ground truth”); here, it is considered to be the sample data that comprise the response variable being mapped.

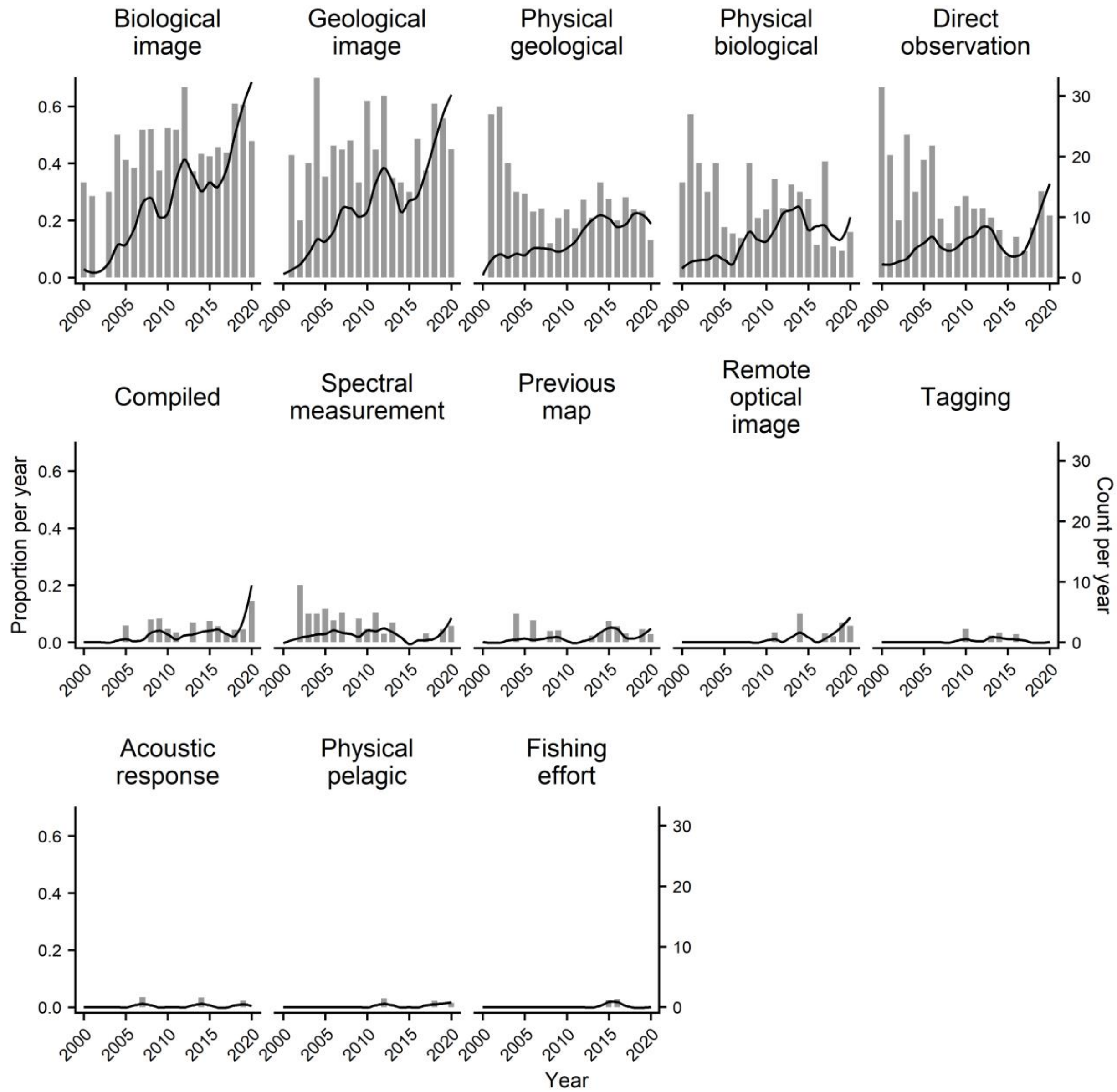

Figure 9. [Two-column] Proportion of studies utilizing different sources of ground validation data since 2000 (primary axis; bars), and raw counts per year (secondary axis; lines). Plots are ordered according to prevalence.

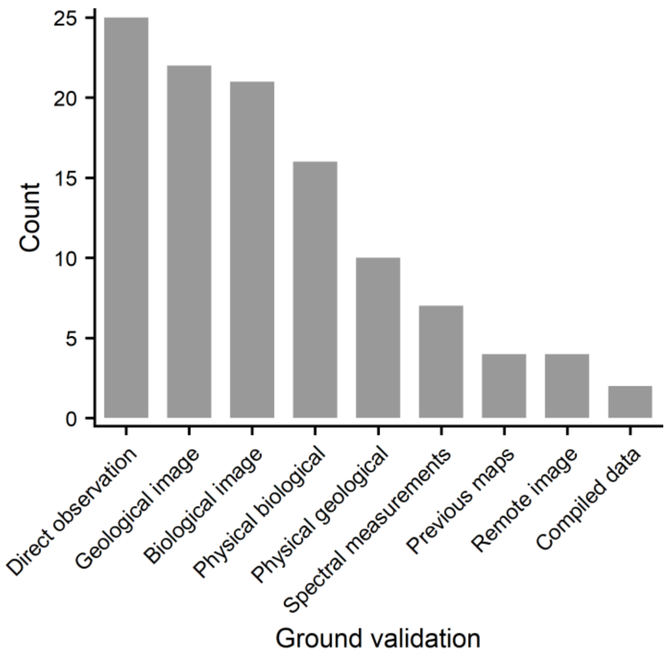

Figure 10. [Single-column] Number of intertidal studies utilizing different forms of ground validation data.

4.6. Model class

The past two decades have experienced a marked shift away from manual benthic habitat mapping approaches in favour of empirical ones. Supervised empirical models have been broadly adopted and were applied to produce the majority of habitat maps sampled from the literature for every year since 2010 (Figure 11). Of these, the Maximum Likelihood classifier is the most common model encountered in the surveyed literature, and is still included in a large proportion of studies (Figure 12). Various interpolation approaches (e.g., Kriging, Inverse Distance Weighting, Natural Neighbor) were amongst the most common techniques used to produce habitat maps in the early 2000s but their use has gradually subsided over the past decade or so. Unsupervised k-means clustering was also highly popular in the early 2000s, due largely in part to the widespread adoption of the QTC software, which reportedly implements a modified k-means clustering for classification of acoustic data to produce habitat maps (e.g., Freitas *et al*., 2003, 2011; Preston & Kirlin, 2003; McGonigle *et al*., 2010; Brown *et al*., 2012; c.f. Preston, 2009 and Preston & Biffard, 2012), which may have changed between versions of the software (Legendre, 2003). Recently, these methods have been superseded by more automated machine learning approaches such as Random Forest and Support Vector Machines – the former which comprised over 25% of all habitat mapping studies surveyed in 2020 (Figure 12). The popularity of Random Forest has undoubtedly arisen as a function of its accuracy and ease of use across a broad range of regression and classification applications, which have been demonstrated in several comparative studies (e.g., Che Hasan *et al*., 2012; Diesing *et al*., 2014; Le Marchand *et al*., 2020). Uptake has also been facilitated by increased access to free and open-source statistical tools such as R (R Core Team, 2021) and Python (van Rossum, 1995).

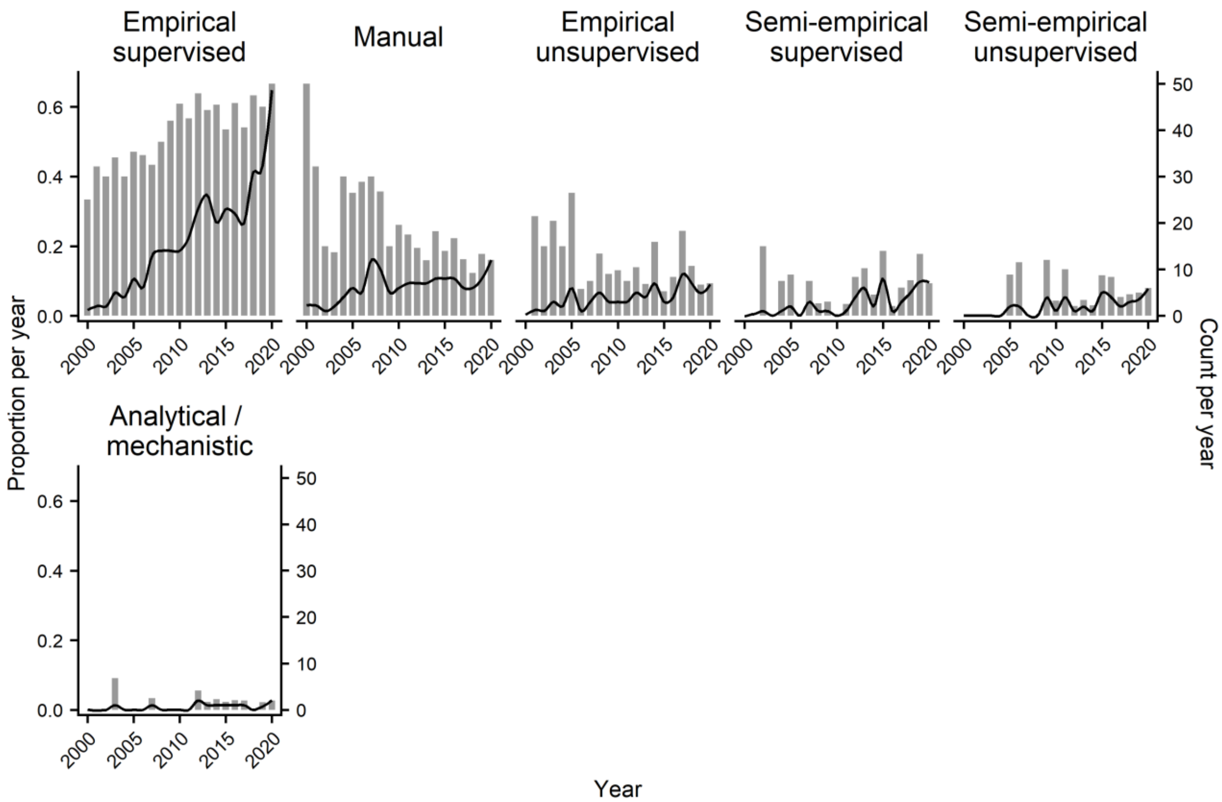

Figure 11. [Two-column] Proportion of studies applying each mapping approach per year since 2000 (primary axis; bars), and raw counts of application per year (secondary axis; lines). Plots are ordered according to total number of implementations.

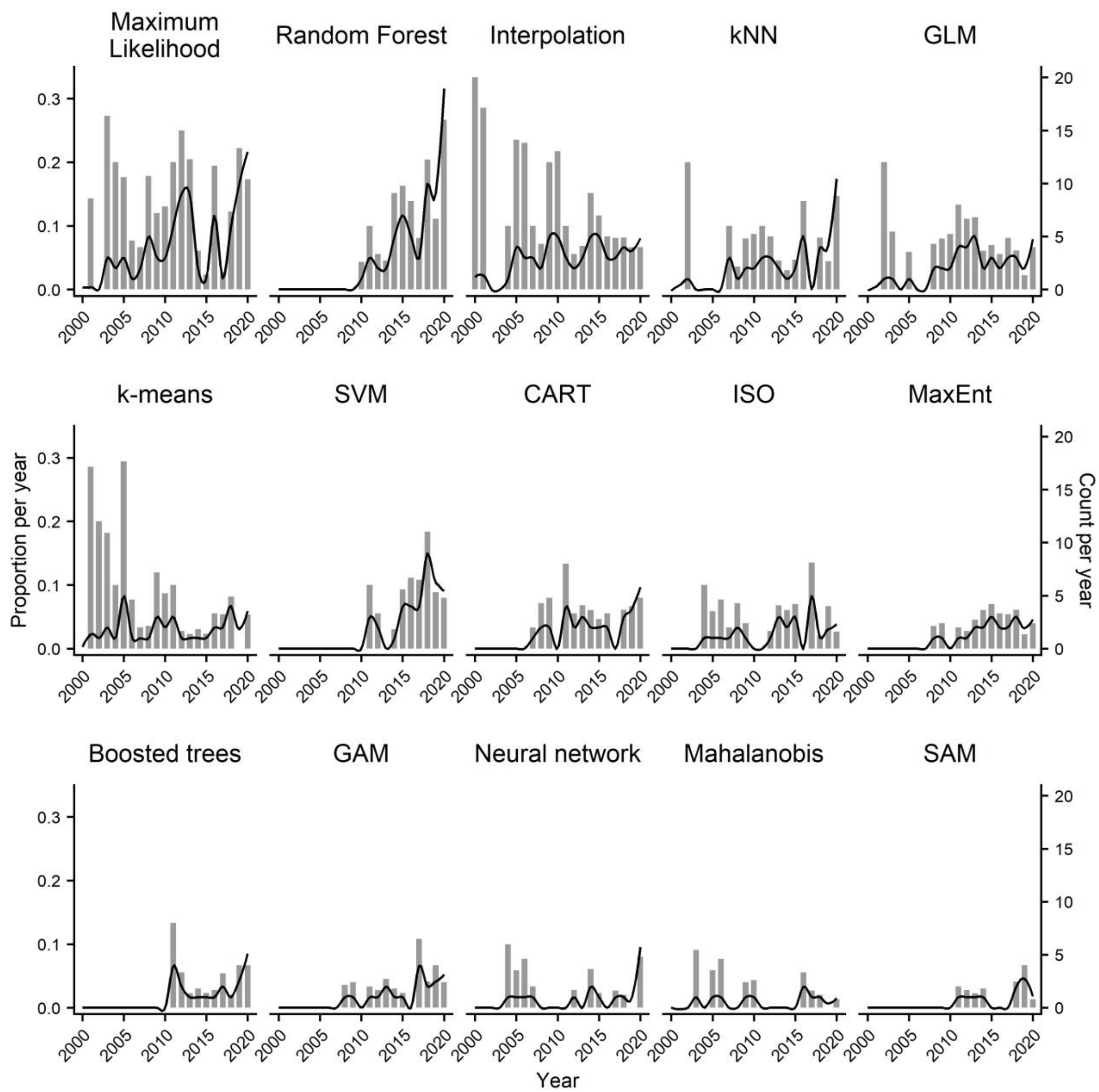

Figure 12. [Two-column] Proportion of studies implementing the top 15 modeling methods per year since 2000 (primary axis; bars), and raw counts of implementation per year (secondary axis; lines). Plots are ordered according to total number of implementations.

The application of machine learning methods to seabed mapping is not a recent development. Dating back to at least to the 1990s, the use of neural networks for seabed classification enabled early analysis of highly dimensional textural and spectral feature sets derived from both acoustic backscatter (Stewart *et al.*, 1994; Müller *et al.*, 1997; Ojeda *et al.*, 2004; Müller & Eagles, 2007) and optical imagery (Bakran-Petricioli *et al.*, 2006). These methods were somewhat superseded over the following decade by other novel machine learning approaches such as classification and regression trees, Support Vector Machines, k-Nearest Neighbors, Random Forest, and boosted regression trees (e.g., Ierodiaconou *et al*., 2007; Knudby *et al*., 2011; Reiss *et al*., 2011; Che Hasan *et al*., 2012; Bučas *et al*., 2013; Prospere *et al*., 2016; Janowski *et al*., 2018). The application of neural networks for seabed classification has received renewed interest, though, with the widespread adoption of "deep learning" via convolutional neural networks for image processing (LeCun *et al*., 2015; Goodfellow *et al*., 2016), which may be implemented via free open-source software such as Python and the machine learning libraries contained therein. These models differ from early neural networks used for seabed mapping through the application of many convolutional filters that are "learned" as a function of the response being mapped. Using this approach, the texture or terrain of the seabed can be analyzed automatically, rather than by manually "engineering" features that are used to predict the response, which may take many different forms (e.g., Luo *et al*., 2019; Fincham *et al*., 2020; Shields *et al*., 2020; Feldens *et al*., 2021). Convolutional neural networks have demonstrated great discriminatory potential for a variety of terrestrial land cover and vegetation applications (Maggiori *et al*., 2017; Xu *et al*., 2018; Kattenborn *et al*., 2021), and adoption of similar methods for seabed mapping appears to be accelerating (Neupane & Seok, 2020; Steiniger *et al*., 2022). While not geospatial (though, see work by Rao *et al*., 2014), automated classification of benthic imagery is also increasingly achieved using deep convolutional neural networks (e.g., Diegues *et al*., 2018; Piechaud *et al*., 2019; Mahmood *et al*., 2020; D'Archino *et al*., 2021; Yamada *et al*., 2021), enabling efficient analysis of data volumes that are orders of magnitude larger than could previously be achieved. We expect to see great advances in this domain over the next decade for all manner of seabed mapping applications.

5. Synthesis, trajectory, and challenges

Remarkable advances in the field of benthic habitat mapping have been driven by improvements to remote sensing technologies, increased access to remote sensing data sets, improvements to ground validation approaches, and through the capability to effectively process and model these data with modern computing resources and methods. Despite advancement in these areas, several new and outstanding challenges to the field remain.

Though impressive, the profusion of technological and methodological advances over the past two decades produces challenges for initiates to the field. The widespread adoption of empirical modelling approaches for benthic habitat mapping (e.g., Figures 11, 12) – and for marine remote sensing and geospatial science more generally (Melo-Merino *et al*., 2020) – has yielded a bewildering selection of potential methods from which to choose. The suitability of a given approach is strongly determined by the data characteristics such as the response sample size and design, the availability and extent of geospatial predictor data, the presence of spatial autocorrelation, and the environmental characteristics of the study area – particularly the water depth. The habitat mapping application also strongly influences the selection of methods. Here, we synthesize the most common approaches selected for the four types of benthic habitat mapping based on the literature reviewed to provide examples of how these map products may be generated in practice (Table 2). *Abiotic surrogate mapping* is most commonly performed using ship-borne acoustic data (72% of cases reviewed) – in particular, multibeam backscatter – from which GLCMs and terrain attributes are derived as predictor variables. These data are often clustered using algorithms such as k-means, which are interpreted as geological or physical classes using observations from physical samples of the seabed. Interpolation approaches such as kriging are also commonly used to predict abiotic habitat parameters where geospatial data are lacking. Habitats of *single biota* are frequently mapped using optical data from satellite-borne sensors (44%). The reflectance and water depth returned from these sensors may be used to calculate additional predictors such as physical and chemical oceanographic parameters and terrain attributes. Together, these data may be used to predict occurrence or abundance of species observed from seafloor imagery, most often using supervised approaches such as generalized linear models (GLMs). Benthic *community* patterns measured from physical sampling are most commonly predicted using supervised modelling approaches such as Random Forest or GAMs, trained on combinations of sonar-derived bathymetry and terrain attributes from acoustic data (42%), but also interpolated environmental measurements obtained from compiled data over broad spatial extents (32%). Finally, *benthoscape* maps are produced using a wide variety of datasets and methods. One common approach utilizes observations of habitat classes from biological and geological seafloor imagery to classify optically derived geospatial data layers (53%). One or several multinomial supervised classification algorithms are selected to perform the classification, commonly including maximum likelihood, k-Nearest Neighbors (k-NN), Random Forest, support vector machines, and neural networks. The best of these may be selected via cross-validation, or results can be combined using ensemble approaches (e.g., Huang *et al*., 2012; Diesing & Stephens, 2015; Turner *et al*., 2018; Hossain *et al*., 2020).

Table 2. The most common approaches for producing different benthic thematic habitat maps tabulated from the literature reviewed. Percentages indicate the proportion of applications of the most common remote sensing approaches for each type of thematic map.

Thematic map	Remote sensing	Common geospatial preds.	Common derived preds.	Common response data	Models
Abiotic	Acoustic (72%)	Backscatter	GLCM	Sediment samples	k-means
		Bathymetry	Terrain		Kriging
Single biota	Optical (44%)	Reflectance	Ocean. params.	Biological imagery	GLM
		Bathymetry	Terrain		
Community	Acoustic (42%)	Bathymetry	Terrain	Benthos samples	Random Forest
	Compiled (32%)	Interp. env. measurement	Ocean. params.		Interpolation
			Previous models		GAM
Benthoscape	Optical (53%)	Reflectance	Spectral ft.	Biological imagery	Maximum likelihood
		Bathymetry	Terrain	Geological imagery	k-NN
					Random Forest

In addition to the most common approaches to benthic habitat mapping, a number of best practices and also common pitfalls have emerged from the recent literature that may provide guidance on the selection of appropriate methods. First, we believe there is strong evidence to support the selection of empirical modelling approaches according to data characteristics, rather than according to the apparent superiority of a given modelling method. Indeed, particularly for data-driven machine learning approaches, it appears that many algorithms produce good results when properly calibrated (e.g., Reiss *et al*., 2011; Huang *et al*., 2012; Hu *et al*., 2020), and there is little evidence of the superiority of a given algorithm for all applications (Norberg *et al*., 2019). It is also apparent, though, that the *ease of calibration* has substantially impacted the uptake of particular methods. Random Forest often provides high-quality results with minimal user calibration – commonly performing well with default hyperparameters that control automatic variable selection and regularization, while simultaneously providing unbiased validation estimates as a product of the algorithm itself (Liaw & Wiener, 2002). We argue that this ease of implementation, and not its universal suitability, best explains the rapid and continued uptake of Random Forest in the field (Figure 12). Indeed, given particular data characteristics, such decision tree-based methods may not be optimal. The modelling of a spatially and numerically continuous response with decision trees may produce abrupt linear artefacts in the predicted surface associated with binary splitting of explanatory variables (Li, 2010; Li *et al*., 2011), which in some cases correspond to unrealistic abrupt discontinuities in habitat suitability across environmental gradients (Rooper *et al*., 2017). It is also well-accepted that spatially non-independent ground truth data may severely impact the fitting of these models (Meyer *et al*., 2019). Such non-independent data are commonly encountered in marine science either as a function of sampling design (e.g., transects) or of combining legacy data sources. In these cases, mixed modelling approaches offer a statistically sound solution to handling the non-independent partial pseudo-replication of samples (e.g., Rengstorf *et al*., 2014), yet have received comparatively little uptake in the field – likely as a result of the challenges associated with fitting, calibrating, and understanding these models (Bolker *et al*., 2009). In light of these and other common challenges encountered in the literature, we offer the following perspectives and recommendations for selecting among habitat mapping approaches.

1) Where time and expertise are abundantly available, manual interpretation may be used for effective abiotic or benthoscape classification. This may be performed with minimal, or even no ground truth sampling (Agbayani *et al*., 2015; Harris & Weisler, 2018; Switzer *et al*., 2020). Mapping of a continuous response (e.g., species abundance, grain size) is not generally accomplished via manual interpretation.

2) For a spatially and numerically continuous response (e.g., abundance, mean grain size, species richness), consider testing at least one continuous regression approach (e.g., GLM, neural networks, GAM, MARS). These tend to fit more realistic, albeit rigid, response functions than tree-based methods, often yielding higher quality maps.

3) Decision tree-based algorithms such as Random Forest tend to perform well at categorical classification tasks (e.g., benthoscape classification). Other approaches may also perform well, and it is often useful to compare multiple models via cross-validation and select or aggregate the best results.

4) When using spatially structured ground truth observations for habitat mapping (e.g., clustered sampling, transects), consider a) manual or unsupervised empirical algorithms that are robust to non-independent response observations (e.g., k-means or ISO cluster), or b) a modelling approach in which the structure may be handled explicitly (e.g., via an autoregressive term or specification of random effects). Object-based segmentation may also be useful as a technique to aggregate clustered or repeated samples prior to modelling.

5) Regardless of the modelling approach selected in 4) above, where an independent validation dataset is not available, it is critical to design an appropriate cross-validation that accounts for partial replication of

ground truth observations to estimate the map accuracy (final step, Figure 1). For transect designs, this generally implies considering multiple observations within a transect as replicates of the same measurement; thus, assignment of an entire transect to training or testing data partitions is a sensible approach to validation. There is no consensus on how to best conduct validation using clustered ground truth observations that are not readily assigned as replicates of a single measurement (Meyer & Pebesma, 2022), but potential solutions include spatial validation approaches (Roberts *et al*., 2017), geostatistical simulation (de Bruin *et al*., 2022), and spatial weighting methods (Misiuk & Brown, 2023).

6) The ground truth sample size required for a given application generally scales with the flexibility of the model, and the number of predictor variables. Fairly rigid parametric models such as GLMs (regression) and maximum likelihood (classification) can be effective even given low sample sizes and few predictors. Machine learning models such as artificial neural networks, boosted regression trees, and Random Forest become increasingly useful with more training data. Unsupervised approaches are often robust to low ground truth sample size.

7) It is useful to test or implement a diverse set of environmental predictors across a range of spatial scales. Where feasible, integrating predictor data from multiple different sensors (e.g., sonar systems, both sonar and optical sensors) may provide a greater diversity of useful information than that which is achievable using a single sensor. A wide variety of secondary predictors (e.g., terrain attributes, spectral features) may be derived from geospatial remote sensing data and it can be useful to calculate these at multiple spatial scales (Verfaillie *et al*., 2006; Misiuk *et al*., 2018; Porskamp *et al*., 2018; Trzcinska *et al*., 2020). Many machine learning models contain functionality for automatic variable selection, yet there may be some evidence that performing dimensionality reduction can be beneficial where models are performing poorly due to over-parameterization or low sample size (Diesing *et al*., 2016). This can be accomplished via feature selection approaches (e.g., Stephens & Diesing, 2014; Nemani *et al*., 2022) or ordination (e.g., PCA; Calvert *et al*., 2015; Verfaillie *et al*., 2009). Some deep learning models such as convolutional neural networks include functionality to automate the feature calculation and selection process (Mohamed *et al*., 2020; Shields *et al*., 2020; Arosio *et al*., 2023).

A separate outstanding challenge relates to temporal control. The seabed is inherently dynamic, yet habitat mapping data – both in situ and remotely sensed – are normally treated as static products. This occurs out of necessity given the cost of acquisition, particularly in deeper waters using vessel-deployed instrumentation, and implicitly raises two import concerns. First, that analysis of seabed mapping data generally ignores short-term variability, such as seasonality; and second, that habitat mapping data may become increasingly inaccurate due to changing environmental conditions over longer time scales. The first point may be addressed in some cases through experimental design (e.g., time-series sampling). Increased accessibility of high-resolution satellite imagery has greatly facilitated this in optically shallow waters (e.g., Wicaksono *et al*., 2021). The second point – continued relevance of the data – is a more existential problem. How is it possible to estimate the lifespan of benthic habitat data without re-acquiring it? Given the profound increase in benthic mapping research since the turn of the century (e.g., Figure 4), it appears likely that most existing habitat mapping datasets are less than two decades old. This raises important questions regarding the continued use of legacy data, the continued relevance of existing habitat maps, but also the necessity of repeat surveys to update maps given changing climatic conditions. Re-acquisition of benthic mapping data is difficult to justify given that the vast majority of the oceans remain un-mapped even once. Mayer *et al*. (2018) estimated that to completely map the global ocean using multibeam sonar will take over 900 vessel years, at considerable cost. How is it then possible to balance the need for updating existing datasets that provide scientific knowledge on the status of threatened or vital marine environments with the need to acquire novel data?

While general answers to these questions remain unlikely in the near future, recent advances indicate progress towards addressing the challenges of detecting changes to benthic ecosystems. Establishment of long-term benthic monitoring systems, such as the NEPTUNE cabled observatory on Canada's west coast (Barnes *et al*., 2013), enable investigation of both seasonal and long-term benthic habitat variability (e.g., Command *et al*., 2023). Such monitoring efforts are critical given rapidly changing climate conditions. Though not a habitat mapping exercise, such longitudinal efforts may serve to indicate temporal scales for which regional benthic mapping datasets are relevant. Improvements to the automation of monitoring may also contribute towards these goals. Autonomous monitoring platforms coupled with state-of-the-art computer vision techniques have the potential to greatly enhance the efficiency with which temporal benthic ecosystem dynamics are analysed (Marini *et al*., 2022). The automation of mapping platforms is also developing rapidly, including mobilization of mapping AUVs, but also small, un-crewed surface mapping vessels (Zwolak *et al*., 2020). The increased efficiency and decreased mapping costs associated with such systems may increase the feasibility of balancing repeat mapping efforts with novel ones.

Enhanced efficiency of data acquisition coupled with novel high resolution remote sensing approaches has potential to produce massive data volumes. Datasets such as multibeam water column, synthetic aperture sonar, LiDAR point clouds, and > 4k video provide an unprecedented level of detail on seafloor environments but may easily produce data in the TB or 10s of TB per campaign. Remote sensing time-series quickly become unmanageable for individual researchers, and large-scale repositories such as Google Earth Engine are increasingly necessary to host and process such data volumes, which reach the order of PB. Many of these technologies also have capacity to collect much more data than can be processed using manual approaches. Underwater video is particularly labour-intensive to process (Schoening *et al*., 2016), and efficient acquisition by AUVs and ROVs (S. B. Williams *et al*., 2010) or by crowd-sourcing and collaboration (González-Rivero *et al*., 2014) produces much more imagery in aggregate than may be feasibly processed by humans. This presents a bottleneck to many benthic research workflows, and computer vision platforms such as CoralNet (Beijbom *et al*., 2015) and BIIGLE (Langenkämper *et al*., 2017) are increasingly leveraged to process such data. We expect both trends of increased large-scale cloud-based storage and management, and AI-based automated data processing, to develop further for addressing outstanding data challenges in this field.

Finally, we emphasize the importance of interdisciplinary collaboration for the production of better benthic habitat maps. This is not an abstract ideal; there is strong evidence in the recent literature that the use of multiple sensors may increase capacity for mapping benthic habitats across a range of environments and conditions. The simultaneous acquisition of multibeam backscatter and subsea LiDAR by ROV, for example, has enabled enhanced substrate discrimination compared to either technology in isolation (Collings *et al*., 2020). The combined use of multispectral imagery and LiDAR data has also shown great capacity for discrimination of coastal, shallow, and estuarine habitats, and may be collected by aircraft or a combination of aircraft and satellite (e.g., Chust *et al*., 2008; Halls & Costin, 2016). Likewise, simultaneous data acquisition using multiple acoustic technologies has enabled efficient and accurate classification of the seabed by exploiting the strengths of different sensors – for example, the horizontal density of sidescan data with the vertical resolution of sub-bottom profiles (Fakiris *et al*., 2018; Bartholomä *et al*., 2020). Finally, the use of spectral cameras along with acoustics has been highly effective, and has facilitated mapping across a range of depths generally not achievable using a single acoustic or spectral sensor (e.g., Reshitnyk *et al*., 2014; Rende *et al*., 2020). These examples suggest that perhaps a focus on acquiring different data types spanning a range of remote sensing technologies offers greater benefit than acquiring higher resolutions or new forms of a single technology. Given increased accessibility of data from a range of platforms and sensors, and improvements to data acquisition, storage, and processing, we hope to see more collaboration and greater development of multi-sensor benthic habitat mapping over the coming decade.

Supplementary material

Supplementary_material_1.xlsx. Data recorded from literature review used to support the findings in this study.

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