

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

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8 Abstract

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21 past 10 years, and has superseded expert manual interpretation.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

26 Keywords

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

28 1. Introduction

29 The global ocean, covering more than 70% of the earth, plays a central role in the structure and function
30 of the biosphere and is critical for achieving sustainable development of human society as a whole (Hoegh-
31 Guldborg *et al.*, 2019). However, marine systems face significant pressures from human activities ranging
32 from climate change, ocean acidification, over-exploitation of natural resources, and biodiversity loss
33 (IPCC, 2022). In 2015, the United Nations set 17 Sustainable Development Goals (SDG) as a framework to
34 develop strategies for sustainability, with goal 14: *Life Below Water* aiming to “conserve and sustainably

35 *use the oceans, seas and marine resources for sustainable development”* (UN General Assembly, 2015). It
36 is widely recognized that many of the UN SDGs are inter-related, but SDG 14 is particularly far-reaching
37 due to the important role that the ocean plays in global social-ecological systems (Singh *et al.*, 2018); the
38 success of many of the SDGs depends on reaching the targets set under SDG 14. Key technical,
39 organizational, and conceptual scientific barriers have been identified that pose challenges for
40 implementation of transformative policy action to achieve SDG 14, with improved global ocean
41 observation and stronger integration of sciences identified as key elements to success (Claudet *et al.*,
42 2020). The acquisition and use of geospatial environmental and biological data to understand spatial
43 patterns within ecosystems, monitor changing conditions, and assess the health of systems relative to
44 sustainability goals is a critical component to success of SDG 14.

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

54 Developments in the field of benthic habitat mapping have produced a diversity of approaches, data
55 types, technologies, and models that are used to understand and map distributions of biological patterns
56 on the seafloor. It is informative and interesting to review the variety of ways in which these patterns may
57 be mapped, and retrospection of these themes also reflects a change in values over time. This offers
58 insight and hindsight into the goals that motivate exploration of the seabed. Here, we aim to objectively
59 describe these recent changes to chronicle the trajectory of the benthic habitat mapping field leading up
60 to this Decade of Ocean Science for Sustainable Development (Ryabinin *et al.*, 2019).

61 1.1. Scope of the review and literature search

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

65 1) What is benthic habitat mapping?

66 2) How is it accomplished?

67 3) How has that changed over time?

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

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

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

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

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

98 3) Maps published and reviewed in multiple studies were *only tabulated once* as a “qualifying map”, which
99 permits an item to be included in the review. Where habitat maps were detected in multiple outlets, with
100 no novel map product to differentiate them, the information was collapsed into a single entry for the
101 review dataset.

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

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

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

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

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

123 5) Predictor remote sensing platforms. The platform(s) from which remote sensing data used to predict
124 the response were acquired, including crewed and un-crewed *aerial craft* such as planes or drones,
125 *handheld* systems such as spectral cameras used to produce orthomosaic images, crewed and un-crewed
126 *marine vessels* such as ships or AUVs, and *satellites*. The use of *compiled* sources that include multiple
127 different acquisition platforms were also noted.

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

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

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

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

154 10) Geographic extent. The extent of the habitat mapping study, quantized into logarithmic bins (i.e., < 1,
155 1-10, 10-100, 100-1000, > 1000 km). The extent was determined using the length of the major axis of the
156 study area. For example, the Great Barrier Reef was considered to cover an extent of > 1000 km. Where
157 not stated, extent was estimated by measuring published maps using ImageJ (Schneider *et al.*, 2012),
158 calibrated to the scale bar or map graticule.

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

161 Several additional descriptive attributes were tracked for each publication. Unit-invariant validation
162 metrics were recorded where provided, including accuracy, kappa, AUC, Pearson or Spearman correlation
163 scores, and the variance explained. Where multiple different scores were provided for a single metric
164 (e.g., in comparative studies), only scores labelled as “final” were retained. If not indicated, the highest
165 score was selected. If the published map was an ensemble of multiple predictions, or multiple different
166 maps were presented, the validation scores were recorded as the mean of individual scores if no “final”
167 value was provided. If multiple statistics were calculated using both “training” and “test” data that were

168 used to produce and evaluate a map, respectively, the “test” data scores were preferred in all cases.
169 Because of the extreme variability in map validation practices encountered in the reviewed literature, the
170 validation statistics recorded are descriptive only. Finally, the licensing status of each publication item was
171 recorded, indicating whether it was freely available or open-access, or available under a traditional
172 subscription license. The entire curated table of literature reviewed is provided as Supplementary
173 Material. Again, we note that this table represents a random, rather than exhaustive, review of the
174 literature.

175 2. What is benthic habitat mapping?

176 2.1. Thematic habitat mapping

177 The term “benthic habitat mapping” tends to be ambiguously applied in the literature to describe any
178 form of seabed mapping focused on understanding biological patterns. Previously, “benthic habitat
179 mapping” has been more precisely defined as “*the use of spatially continuous environmental data sets to*
180 *represent and predict biological patterns on the seafloor (in a continuous or discontinuous manner)*”
181 (Brown *et al.*, 2011). In the context of this review, we have modified and simplified this definition to
182 “*spatially continuous prediction of biological patterns on the seafloor*”, to encompass changes in the field
183 over the past decade, and the variety of ways that “habitat” can be represented in different forms of
184 thematic maps.

185 The presence of an organism at the seafloor, and the resulting spatial patterns that are observed for a
186 species, may be explained using the ecological niche concept first developed and defined by Grinnell
187 (1917) and later by Hutchinson (1957). This describes the ecological niche of a species as an n -dimensional
188 hypervolume of biotic and abiotic environmental conditions that meet its habitat requirements (Begon &
189 Townsend, 2021). Overlapping niches of different species, therefore, define a community, and community
190 composition will change as the hypervolume of environmental conditions change along abiotic and biotic
191 gradients. Patterns in community composition are thus complex, and difficult to predict. Patterns of biotic
192 and abiotic seafloor characteristics can be represented by a variety of different thematic maps. Types of
193 thematic benthic habitat maps are discussed in detail below (section 3.1), but they generally comprise: 1)
194 abiotic maps representing changes in seafloor substrata (or other abiotic variables), which can act as a
195 proxy for biological patterns; 2) maps depicting the distribution of a single species or taxa; 3) maps

196 depicting benthic community patterns; or 4) maps displaying “landscape-scale” bio-physical classifications
197 of the seafloor. Each of these categories can be considered a form of “benthic habitat map” based on the
198 above definition, which conforms to the usage of this terminology in the literature.

199 2.2. Seafloor remote sensing

200 Regardless of the type of thematic mapping, all benthic habitat maps tend to rely on the availability of
201 environmental geospatial data from which the distribution of biological patterns may be predicted. In
202 both terrestrial and aquatic environments, remote sensing technologies have greatly advanced both the
203 extent and resolution at which we map global ecosystems. Satellite platforms employ a variety of sensors
204 to image the land surface of the planet (Dubovik *et al.*, 2021), which are used to advance our
205 understanding of the spatial configuration of ecosystems, how fauna and flora interact through the
206 environment, and what impacts humans may have on these systems. In the oceans, satellite remote
207 sensing has dramatically improved our understanding of biological processes such as plankton production
208 (Platt, 1986; Sathyendranath *et al.*, 1991), physical oceanographic phenomenon such as circulation
209 patterns and ocean-atmosphere linkages (Klemas, 2012), and chemical oceanographic processes (Siegel
210 & Michaels, 1996). Satellite-borne sensors are additionally employed to study tectonic and geomorphic
211 oceanographic processes through the production of broad scale ocean floor Digital Elevation Models
212 (DEMs) using satellite-derived bathymetry (Watts, 1976; Sandwell *et al.*, 2003; Watts *et al.*, 2006). In
213 coastal waters, satellite-borne optical sensors provide both depth and seafloor reflectance information
214 that is used to characterize the benthic environment at high spatial resolutions (Kutser *et al.*, 2020), but
215 their application is limited to the shallow seafloor (e.g., < 30 m). In deeper waters, acoustic remote sensing
216 is the primary means for obtaining high resolution seafloor mapping data (Brown *et al.*, 2011).

217 For any remote sensing technology, the resolution of the measurements combined with their areal extent
218 determine how the data can be used (Jensen, 2013), and all remote sensing technologies are limited in
219 certain environments based on one or both factors. For example, although satellite platforms are highly
220 efficient for obtaining data at global extents, their application for seafloor mapping is generally limited to
221 either a) high resolution (e.g., metre-scale) mapping of optically shallow coastal waters using spectral
222 sensors (Kutser *et al.*, 2020), or b) low-resolution mapping of the global seafloor using satellite altimetry
223 methods. Acoustic remote sensing, on the other hand, enables high resolution mapping of shallow or
224 deep waters, but at a reduced spatial extent compared to satellite methods. The efficiency of acoustic

225 systems is further limited in shallow waters as a function of the acoustic beam width, which increases as
226 a function of depth and the sonar aperture (Mayer *et al.*, 2018). The data resolution and mapping extent,
227 though, are *inversely* related – the acoustic footprint on the seafloor (i.e., the insonified area) increases
228 with depth and sonar aperture, corresponding to a *decreased* horizontal resolution. Airborne LiDAR may
229 provide high resolution mapping data that are much more efficient to obtain than acoustic data, but
230 which, again, are generally limited to shallow environments.

231 The need for global seafloor data to increase our capacity to map and understand marine biological
232 patterns is well recognized, and increased availability of seafloor data fosters new avenues for marine
233 ecology research. On land, electromagnetic sensors provide direct or indirect indication of biotic (e.g.,
234 vegetation type and cover), and abiotic (e.g., substrate type, morphology, atmosphere) patterns that
235 enable modeling and mapping of terrestrial ecosystems across multiple spatial scales. Increased
236 availability of these methods and technologies has stimulated substantial advances in the field of
237 landscape ecology over the past few decades (Yu *et al.*, 2019). Comparable approaches are now applied
238 using satellite and airborne remote sensing platforms for intertidal and shallow subtidal ecology
239 (Swanborn *et al.*, 2022), leading to emergence of the parallel field of seascape ecology (Pittman, 2017;
240 Lepczyk *et al.*, 2021). This has been largely restricted to shallow ecosystems due to the depth limitations
241 of electromagnetic signals, but in deeper waters, high resolution environmental datasets may be acquired
242 using acoustic methods, or may be accessed from open data compilations and repositories. This enables
243 application of landscape approaches to deep benthic environments (Brown *et al.*, 2011), and it is now
244 feasible to investigate seascape concepts at all depths where data are available.

245 2.3. Previous reviews

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

251 Diaz *et al.* (2004) provide the first comprehensive and cohesive review of benthic habitat mapping and
252 explore in detail the concept of benthic habitat quality. They review habitat mapping approaches,

253 technologies, and terminology, and explore the many methods and indices by which habitat quality is
254 determined. Brown *et al.* (2011) cover the use of acoustic approaches for benthic habitat mapping,
255 providing substantial detail on the acoustic technologies, data layers, and processing pipelines that are
256 commonly applied to map biological patterns on the seafloor. They categorize the strategies by which
257 habitat maps are produced according to a combination of the modelling approach, and at what stage
258 environmental data are segmented spatially. We revisit this scheme here based on the surveyed literature
259 (see sections 3.1 and 3.6 on thematic maps and model class). These reviews were followed in 2012 by the
260 first edition of *Seafloor Geomorphology as Benthic Habitat: GeoHab Atlas of seafloor geomorphic features
261 and benthic habitats* (Harris & Baker, 2012a). The main context of this “Atlas” is a collection of 57 benthic
262 habitat mapping case studies submitted by scientists from around the world. Each case study describes
263 both geomorphic and biotic elements of the seafloor and conforms to a standard template. The atlas
264 additionally identifies common motivations for mapping benthic habitats, such as support for marine
265 spatial planning (see also Cogan *et al.*, 2009), marine protected area (MPA) design, generation of scientific
266 knowledge, and to support resource assessments (Harris & Baker, 2012b). A second edition of the GeoHab
267 Atlas was published in 2020, including an additional 53 habitat mapping case studies conducted between
268 2010-2020 (Harris & Baker, 2020).

269 In their recent review on the application of seascape ecology to the deep sea, Swanborn *et al.* (2022)
270 identify benthic habitat mapping as a tool for studying seascape ecology. They outline fundamental
271 seascape ecology concepts including the use of patch metrics, seascape composition, configuration, and
272 heterogeneity, ecological connectivity, and spatial context and scale (see also the text by Pittman, 2017).
273 These, in most cases, either inform, or are informed by, benthic habitat information, which is therefore
274 prerequisite for most seascape ecology approaches. Seascape ecology has been characterized as the
275 marine counterpart to landscape ecology (Pittman *et al.*, 2021; Swanborn *et al.*, 2022), yet there is no
276 absolute consensus as to what defines landscape ecology (Bastian, 2001; Wu, 2006; Turner & Gardner,
277 2015). Nonetheless, based on the general definitions provided by Wu (2008), Turner & Gardner (2015),
278 and Pittman *et al.* (2017), and on its usage in the marine literature, we adopt the definition that seascape
279 ecology is “*the study of relationships between spatial pattern and ecological processes in the oceans at
280 multiple scales and organizational levels*”.

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

297 Several detailed reviews have been published on specific benthic habitat mapping applications and
298 environments. Kutser *et al.* (2020) chronicle the rise of shallow water remote sensing for bathymetric and
299 habitat mapping around the turn of the century, corresponding to an increase in coral reef research
300 resulting from realization of the full scope of global coral reef decline (Hughes, 1994; Pandolfi *et al.*, 2003;
301 Bellwood *et al.*, 2004; Hoegh-Guldberg *et al.*, 2007). This review focuses primarily on the development
302 and application of passive optical remote sensing, but technologies for mapping shallow areas also include
303 LiDAR, sonar, and synthetic aperture radar. Marcus & Fonstad (2008) provide a review of optical remote
304 sensing methods for riverbed mapping. Optical sensors often enable continuous depth measurements for
305 rivers where clarity permits, and may additionally provide data on river surface features and turbidity. In
306 addition to satellite, balloons, and aircraft, they report early use of drones for optical riverbed mapping,
307 which we believe precedes their widespread uptake for coastal and shallow water mapping. They also
308 report early application of supervised modelling, fuzzy clustering, texture analysis, and object detection
309 for mapping riverbed properties.

310 Finally, we refer the reader to select reviews focused on specific peripheral topics relevant to the field of
311 benthic habitat mapping. In Chapter 5 of the GeoHab Atlas, Harris (2012) reviews the concept of *surrogacy*
312 for benthic habitat mapping – the correspondence and substitution of measurable variables for biotic
313 patterns that are quantified more sparsely (e.g., in space). McArthur *et al.* (2010) also review the use of
314 abiotic surrogates for benthic biodiversity in detail, including the primary surrogates employed in the
315 benthic ecology literature, application of these surrogates for marine management, and the
316 representation of ecological gradients using surrogates (see also Guisan & Zimmermann, 2000; Meynard
317 & Quinn, 2007). Both Makowski & Finkl (2016) and Menandro & Bastos (2020) provide recent perspective
318 on the history of seabed mapping, and the review of seabed mapping technologies for marine habitat
319 classification by Kenny *et al.* (2003) remains highly relevant. Li & Heap (2014) review spatial interpolation
320 methods for the environmental sciences, which, while not strictly marine, includes application to marine
321 environments, and is highly relevant for benthic habitat mapping. Strong *et al.* (2019) review the
322 application and properties of common habitat classification schemes for benthic mapping. Lecours *et al.*
323 (2015) review the concept of spatial scale for benthic mapping contexts, and Lecours *et al.* (2016) describe
324 the related and burgeoning field of marine geomorphometry (both general and specific) – the quantitative
325 study of the seafloor surface. Misiuk *et al.* (2021) synthesized the latter two concepts to provide
326 recommendations for implementing multi-scale geomorphometric techniques for benthic habitat
327 mapping.

328 3. How are benthic habitats mapped?

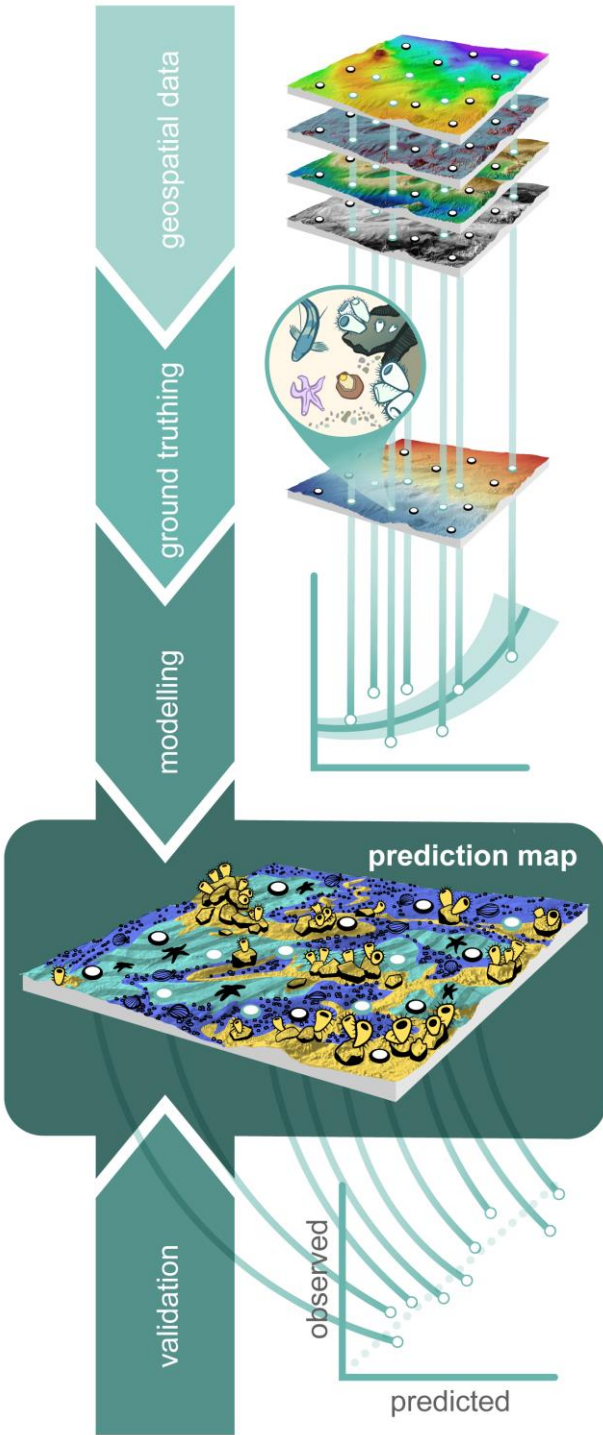
329 Brown *et al.* (2011) provide a detailed overview of how benthic habitats are mapped using acoustic
330 remote sensing methods. Here we update these findings and expand the scope to include additional
331 geospatial datasets, remote sensing technologies, and ground validation approaches that are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

334 Generating benthic thematic maps generally requires the use of continuous coverage environmental data
335 sets, which are used as predictor variables to explain the distribution of the “habitat” response. These can
336 take many different forms, and over recent years the number and diversity of geospatial predictor
337 variables has expanded dramatically (see section 4 below). The general workflow for how these data sets
338 are integrated for benthic habitat mapping is presented in Figure 1. Biological patterns on the seafloor are

339 driven by a complex combination of environmental drivers and biological interactions (Brown *et al.*, 2011).
340 The physical abiotic characteristics of the seabed (e.g., substrate type, morphology), physiographic setting
341 (e.g., depth, distance from shore) combined with the characteristics of the overlying water column (e.g.,
342 temperature, salinity, current speed and direction) all have strong influences on benthic biota, and
343 together define the fundamental niche of each organism. However, obtaining data on these variables
344 through space and time can be extremely challenging.

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

351 The process of generating thematic maps of the seafloor then normally requires some form of direct,
352 usually spatially discrete, in situ observation to record biological or geological measurements at the
353 seabed. These spatially georeferenced in situ observations, commonly referred to as “ground truth” or
354 “ground validation”, define the response variable that is being mapped. The measured response is
355 extrapolated spatially using some form of interpretation or model of the spatially continuous
356 environmental data to generate the final thematic map (Figure 1; see section 3.5).



357

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

363 3.1. Types of thematic maps

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

368 *Abiotic surrogate* approaches describe mapping the distribution(s) of one or several abiotic benthic
369 habitat components, under the implicit assumption that these may act as surrogates for biological
370 distribution patterns (McArthur *et al.*, 2010), or enable biological interpretation (Diaz *et al.*, 2004; Figure
371 2). Previously, the term *abiotic surrogate mapping* has been used to describe the clustering of abiotic
372 environmental data without in situ ground-truth information using unsupervised approaches in order to
373 identify environmental patterns that may be indicative of biological patterns (Brown *et al.*, 2011). Here,
374 we expand the use of this terminology to refer to the thematic mapping subject (i.e., response variable),
375 rather than the classification approach, since unsupervised approaches may be applied using both
376 biological information (e.g., Amorim *et al.*, 2017) and ground-truth data (e.g., Schimel *et al.*, 2010,
377 Proudfoot *et al.*, 2020), and since abiotic environmental surrogates are increasingly mapped using
378 supervised modelling approaches (e.g., Borfecchia *et al.*, 2019; Bravo & Grant, 2020; Zelada Leon *et al.*,
379 2020). Unsupervised clustering of abiotic environmental layers therefore may still be considered abiotic
380 surrogate mapping as long as there is biological or ecological implication. This applies also to
381 characterization of the structural components of benthic habitat, such as sediment distribution modelling
382 (e.g., Gougeon *et al.*, 2017), geomorphological classification (Prampolini *et al.*, 2018; Lavagnino *et al.*,
383 2020), and acoustic facies mapping (Shumchenia & King, 2010), all of which may be applied as forms of
384 abiotic surrogate mapping.

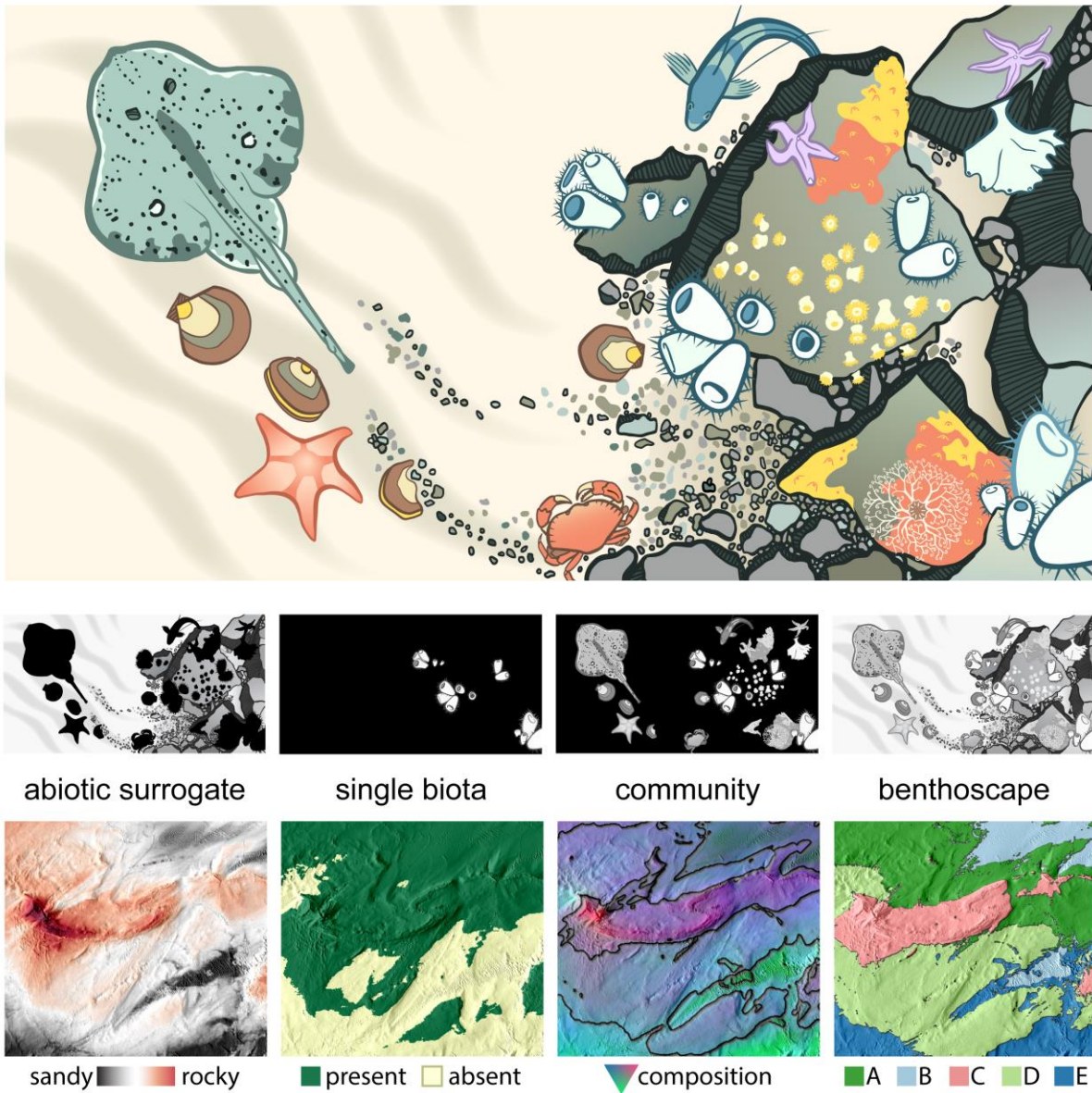
385 *Single biota mapping* is used to estimate the distribution of a single benthic organism at one or multiple
386 spatial scales, which, in practice is often not limited to the taxonomic level of species. By aiming to delimit
387 the habitat requirements of a single organism (e.g., the species’ “ecological niche”), it is by definition the
388 most accurate application of the term “habitat mapping” considered here. This category of benthic
389 thematic mapping includes “species distribution modelling” (Araújo & Guisan, 2006; Elith *et al.*, 2006;
390 Austin, 2007; Franklin, 2010), “ecological niche modelling” (Warren *et al.*, 2008; Melo-Merino *et al.*, 2020),
391 “bioclimatic envelope modelling” (e.g., Midgley *et al.*, 2002; Pearson *et al.*, 2004), and “habitat suitability

392 modelling” (e.g., Rengstorf *et al.*, 2012; Hu *et al.*, 2020). While these terms are often used interchangeably
393 (Franklin, 2010; Melo-Merino *et al.*, 2020), they actually imply different conceptual bases and thematic or
394 spatial scales. “Bioclimatic envelope modelling” generally indicates modelling of the potential climatic
395 distribution of a species (Araújo & Peterson, 2012), which may be applied to problems such as predicting
396 species range shifts or invasions under future climate scenarios (Thuiller *et al.*, 2005; Broennimann *et al.*,
397 2007; Mbogga *et al.*, 2010). “Ecological niche modelling” and “habitat suitability modelling” are concerned
398 with modelling the fundamental niche of an organism (Peterson & Soberón, 2012) – the former perhaps
399 implying a stricter Hutchinsonian interpretation of “niche” (Hutchinson, 1957). “Species distribution
400 modelling”, on the other hand, most often refers to delimiting the “realized” or “actual” niche that a
401 species inhabits, which depends on additional factors that limit the species’ occupation of its fundamental
402 niche, such as biotic interactions (Malanson *et al.*, 1992; Guisan & Zimmermann, 2000; Peterson &
403 Soberón, 2012). There is a tendency towards the use of “species distribution modelling” for fine scale
404 presence-absence studies, which have likely sampled the realized niche, compared to broader regional or
405 continental scale studies that are able to sample along the bioclimatic gradient of a species’ range, or its
406 fundamental niche (Franklin, 2010). These semantics are far from well-accepted, and in practice, these
407 applications share many of the same modelling methodologies and techniques. They are additionally
408 applied at different taxonomic levels in the benthic realm, where the species level either is not required
409 or cannot be resolved (e.g., Bučas *et al.*, 2013), or where higher taxonomic levels are of interest (e.g., Hu
410 *et al.*, 2020). We highlight the recent review on marine species and ecological niche distribution modelling
411 by Melo-Merino *et al.* (2020) for greater detail on this topic in the marine realm.

412 *Benthic community mapping* depicts the distribution of groups of organisms that co-occur, their
413 properties, or macro-ecological metrics describing those groups or properties (i.e., biodiversity metrics;
414 Figure 2). Though this does not imply the use of any particular approach, these applications tend strongly
415 towards supervised empirical modelling (see section 3.6 on model class) – though we note some analytical
416 (e.g., Ichino *et al.*, 2015) and empirical unsupervised (e.g., Hutin *et al.*, 2005; Martins *et al.*, 2014;
417 Uhlenkott *et al.*, 2020) applications. Ferrier & Guisan (2006) distinguish three mechanisms by which
418 community-level mapping may be accomplished. First, independent taxa may be modelled using *single*
419 *biota* strategies as outlined above (e.g., SDM) and then combined to produce community-level metrics in
420 a “predict first, assemble later” framework. For example, in their comprehensive report on the benthic
421 biodiversity of the Great Barrier Reef, Pitcher *et al.* (2007) predicted the distributions of 840 individual

422 taxa using a “hurdle” approach to SDM, whereby the model comprises two sub-models: i) a logistic
423 regression predicting whether a species is present or absent; ii) a linear regression predicting the biomass
424 of the species, conditional on it being present. The results of the 840 individual models were subsequently
425 grouped using Ward’s (1963) hierarchical clustering, enabling the prediction of group biomass across the
426 Great Barrier Reef. Alternatively, information on individual taxa may be aggregated first to produce
427 community-level metrics, which are modelled in aggregate in an “assemble first, predict later” design.
428 Such designs may take several forms: biodiversity metrics (including taxonomic, functional, phylogenetic)
429 may be derived from species data then modelled and predicted spatially (e.g., Huang *et al.*, 2014; Rooper
430 *et al.*, 2014; Doxa *et al.*, 2016; Peterson & Herkül, 2019; Murillo *et al.*, 2020a; Pearman *et al.*, 2020;
431 Wicaksono *et al.*, 2022); or, taxa may be initially clustered into groups based on taxonomic or functional
432 criteria, which are then predicted (e.g., Haywood *et al.*, 2008; Pesch *et al.*, 2011; Moritz *et al.*, 2013;
433 Serrano *et al.*, 2017; Kaminsky *et al.*, 2018; Vassallo *et al.*, 2018). Groups of taxa and/or traits may also be
434 modelled simultaneously in an “assemble and predict together” process that uses interrelationships
435 between individuals to inform the community-level mapping outcome. Again, this may be accomplished
436 using multiple methods. First, biodiversity may be modelled directly using matrix regression approaches
437 such as Generalized Dissimilarity Modelling (GDM; Ferrier *et al.*, 2002) or Gradient Forest (Ellis *et al.*,
438 2012), which predict turnover in β - or γ -diversity as a function of environment and space (e.g., Dunstan *et al.*,
439 *et al.*, 2012; Pitcher *et al.*, 2012; Compton *et al.*, 2013a, 2013b). Alternatively, multivariate community-level
440 responses may be modelled directly using approaches such as Multivariate Regression Trees (MRT;
441 De’ath, 2002) and LINKTREE, which combine community clustering and supervised modelling in a single
442 step that is informed by environmental predictors (e.g., LaFrance *et al.*, 2014; Fontaine *et al.*, 2015;
443 Kaskela *et al.*, 2017; Mazor *et al.*, 2017). Finally, recent approaches have focused on Joint Species
444 Distribution Modelling (JSDM; Clark *et al.*, 2014; Warton *et al.*, 2015), which model joint distributions
445 between species to both account for species co-occurrence and to enable inference at the community
446 level. Specific approaches include Latent Variable Models (e.g., Kraan *et al.*, 2020), and Hierarchical
447 Modelling of Species Communities (HMSC; e.g., Murillo *et al.*, 2020b; Elo *et al.*, 2021; Shitikov *et al.*, 2022),
448 which enables integration of individual species co-occurrences for simultaneous inference at species and
449 community levels, potentially also with information on functional traits and phylogeny (Ovaskainen *et al.*,
450 2017; Tikhonov *et al.*, 2020). The latter approaches offer promising advances for modelling individual
451 species and communities, which are grounded in ecological theory.

452 *Benthoscape mapping* describes the “landscape-scale” bio-physical characterization of the seabed –
453 referring primarily to seafloor classification contexts (Zajac *et al.*, 2003; Figure 2). The term “benthoscape”
454 was introduced by Zajac (2000) as the marine (in particular, seabed) analogue to terrestrial landscapes,
455 which comprise individual “elements” of distinct abiotic (e.g., sediments) and biotic (e.g., infaunal
456 communities) characteristics (Zajac *et al.*, 2003), comparable to terrestrial “land units” (Zonneveld, 1989).
457 Here, again, we invoke the response variable to distinguish different types of thematic habitat maps,
458 rather than the model class (e.g., supervised, unsupervised), which generally conforms with the use of
459 this terminology in the literature (e.g., Godet *et al.*, 2011; Lacharité & Brown, 2019; Proudfoot *et al.*, 2020).
460 Therefore, for the purposes of this review, we consider a “benthoscape map” to depict the distribution of
461 “benthoscape classes”, which are a discrete categorical seafloor bio-physical response often mapped
462 spatially using classification approaches. We note that groups of species and their associated
463 environmental conditions are sometimes also referred to as “biotopes” in the benthic habitat mapping
464 literature (e.g., Foster-Smith *et al.*, 2004; van Rein *et al.*, 2011; Strong *et al.*, 2012; Gonzalez-Mirelis &
465 Buhl-Mortensen, 2015; Lee *et al.*, 2015; Buhl-Mortensen *et al.*, 2020). This has arisen from the use of
466 “biotope” in the Marine Biotope Classification of Britain and Ireland (Connor *et al.*, 1997) – now the
467 Marine Habitat Classification for Britain and Ireland (JNCC, 2022). “Biotope” was appropriated from the
468 ecology literature in the 1990s (Olenin & Ducrotoy, 2006), wherein it was originally used to describe
469 *abiotic* environmental components (Dahl, 1908; Hutchinson, 1957), or the “range of environmental
470 conditions that occur in an area” (Franklin, 2010). Interestingly, the use of “biotope” in the benthic
471 mapping literature has drifted to now refer specifically to biological communities in some cases (e.g.,
472 HELCOM, 2013; Elvenes *et al.*, 2014; Neves *et al.*, 2014, Schiele *et al.*, 2015), which were originally defined
473 by Moebius (1877) as the “biocoenosis” that inhabit the abiotic “biotopes” (Dimitrakopoulos & Troumbis,
474 2008). Meanwhile, this original definition of “biocoenosis” is retained in many places (e.g., Zavodnik *et al.*,
475 2005; Göltenboth *et al.*, 2006; Dauvin *et al.*, 2008a; Maiorano *et al.*, 2011; Sloss *et al.*, 2013). Additional
476 detailed discussion may be found in Olenin & Ducrotoy (2006), Dauvin *et al.* (2008a, 2008b), and Brown
477 *et al.* (2011), who called for greater clarity in the use of terminology for benthic habitat mapping. We
478 avoid use of the terms “biotope” and “biocoenosis” here to reduce ambiguity (e.g., regarding the response
479 variable being mapped), in favour of “benthoscape mapping” (Brown *et al.*, 2012), which refers to
480 mapping bio-physical seabed units comparable to those of terrestrial landscapes (i.e., “land units”;
481 Zonneveld, 1989). This is a useful marine analogue for assessing spatial species-environment
482 relationships, which is a component to the emerging field of seascape ecology (Pittman, 2017).



483

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

488 3.2. Geospatial predictor data

489 The type of thematic map produced depends on the response variable (section 3.1 and Figure 2), but
 490 spatial prediction and mapping of the response variable is achieved using geospatial predictor data (Figure

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

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

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

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

519 Several other forms of geospatial data are measured and implemented as predictor variables for benthic
520 habitat mapping. Spatial measurements such as longitude and latitude coordinates, or distances from
521 geographical features such as coastline, islands, or geological phenomena may serve as surrogates for
522 benthic habitat drivers such as sediment transport, physical or chemical oceanographic parameters,
523 dispersal, or habitat connectivity (McArthur *et al.*, 2010; Giusti *et al.*, 2014; Vassallo *et al.*, 2018; Charlène
524 *et al.*, 2020). These variables also may enable leveraging of spatial autocorrelation of the response variable
525 in order to increase predictive capacity of geospatial models – either by capturing relevant information
526 on unmeasured environmental variables, or by modelling spatial relationships that arise as a function of
527 symbiotic or community processes (Legendre & Fortin, 1989). Spatial autocorrelation may also be utilized
528 explicitly to enable use of discrete geospatial data via geostatistical interpolation to a spatially continuous
529 surface. Examples include kriging sediment parameters from physical samples (e.g., Livingstone *et al.*,
530 2018), or oceanographic measurements obtained via in situ measurement (e.g., CTD casts; Rooper *et al.*,
531 2017). Broad scale temporal oceanographic measurements are made available for much of the Earth
532 through long-term data aggregation efforts such as the World Ocean Atlas (Garcia *et al.*, 2013a, 2013b;
533 Locarnini *et al.*, 2013; Zweng *et al.*, 2013) and the Global Data Analysis Project (GLODAP; Key *et al.*, 2004).

534 3.3. Derived predictor data

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

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

548 Various textural, spectral, and waveform features may be calculated to describe remotely sensed data for
549 subsequent use in benthic habitat mapping. Where acoustic backscatter has been acquired and
550 compensated to produce a raster image, grey-level co-occurrence matrices (GLCMs; Haralick *et al.*, 1973)
551 are commonly calculated to describe the texture of the pixel intensity values (e.g., Cochrane & Lafferty,
552 2002; Blondel & Gómez Sichi, 2009; Che Hasan *et al.*, 2014; Janowski *et al.*, 2018), including metrics such
553 as the homogeneity, contrast, entropy, dissimilarity, and correlation. Trzcinska *et al.* (2020), additionally
554 introduce a range of “spectral” backscatter features that may be calculated to characterize the seabed. It
555 is also possible to retain the angular backscatter response prior to compensation and raster mosaicking
556 to calculate statistics and features that provide a richer acoustic characterization of the substrate (e.g.,
557 Fonseca & Mayer, 2007; Parnum, 2007; Che Hasan *et al.*, 2012, 2014; Misiuk & Brown, 2022; Porskamp *et al.*
558 *et al.*, 2022) – though, this could arguably be considered “primary” rather than “derived” geospatial data. A
559 range of secondary features may also be calculated from spectral remote sensing data acquired using air-
560 or satellite-borne optical sensors. Many of these – including band ratios (e.g., Roelfsema *et al.*, 2013;
561 McIntyre *et al.*, 2018) and various vegetation indices (e.g., Bajjouk *et al.*, 2020; Forsey *et al.*, 2020;
562 Wicaksono *et al.*, 2020) – utilize differences between wavelengths of different spectral bands of multi- or
563 hyper-spectral sensors. Waveform variables calculated from LiDAR also offer potential for increased
564 discrimination of bottom type, for example, by calculating features based on waveform geometry (e.g.,
565 Tulldahl & Wikström, 2012), hue saturation intensity (HSI; e.g., Zavalas *et al.*, 2014) or statistics and
566 vegetation indices comparable to those of spectral data (e.g., Collin *et al.*, 2008; Collin *et al.*, 2012).

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

572 Oceanographic models provide increasingly high-resolution predictions of physical and chemical
573 parameters used to map benthic habitats. These include large-scale global models such as Ocean
574 Circulation and Climate Advanced Modelling (OCCAM; Webb *et al.*, 1998), the Vertically Generalized
575 Productivity Model (VGPM; Behrenfeld & Falkowski, 1997), and HYCOM (<https://www.hycom.org/>), which
576 are used for habitat mapping at broad scales (e.g., Tittensor *et al.*, 2009; Harris & Hughes, 2012; Roberts

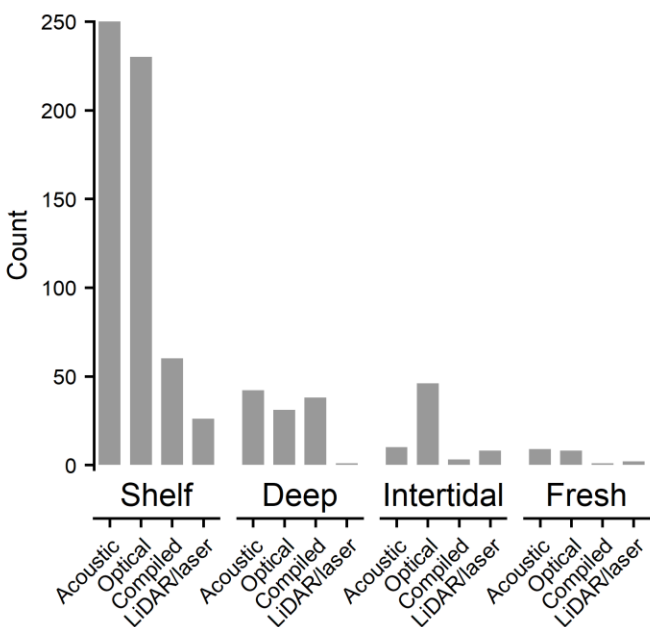
577 *et al.*, 2022), but also bespoke models that are useful for regional applications (e.g., Fabri *et al.*, 2017;
578 Doyle *et al.*, 2018; Peterson & Herkül, 2019; Guillaumot *et al.*, 2020; Murillo *et al.*, 2020b; Pearman *et al.*,
579 2020). The latter are facilitated through a variety of open modelling frameworks and software such as the
580 Regional Ocean Modeling System (ROMS; <https://www.myroms.org/>), the General Estuarine Transport
581 Model (GETM; <https://getm.eu/start.html>), Simulating Waves Nearshore (SWAN;
582 <https://swanmodel.sourceforge.io/>), the COupled Hydrodynamical Ecological model for REgioNal Shelf
583 seas (COHERENS; <https://odnature.naturalsciences.be/coherens/en/>), Finite-Volume Coastal Ocean
584 Model (FVCOM; Chen *et al.*, 2006), and the Nucleus for European Modelling of the Ocean (NEMO; Gurvan
585 *et al.*, 2022). Unlike measurements from satellite, oceanographic models enable prediction of
586 environmental variables throughout the water column, and at or near the seabed. They may also be used
587 to forecast future habitat distributions under different climate scenarios (e.g., Singer *et al.*, 2017; Greenan
588 *et al.*, 2019; Le Marchand *et al.*, 2020).

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

596 3.4. Remote sensing technologies

597 Remote sensing technologies are the primary means by which geospatial predictor data are acquired for
598 benthic habitat mapping, and successful application of any remote sensing method in aquatic
599 environments is dictated by the water depth and turbidity (Figure 3). The development and widescale
600 application of satellite and aerial remote sensing approaches using electromagnetic sensors has changed
601 the way we map the earth (Dubovik *et al.*, 2021), including the seabed (Kutser *et al.*, 2020). These generally
602 include mono-, multi-, and hyper-spectral cameras, and mono- or multi-spectral LiDAR (Hickman & Hogg,
603 1969), which are used to measure reflectance of the seabed in optically shallow waters. We also note
604 development of hyper-spectral LiDAR technologies (Kaasalainen *et al.*, 2007; Chen *et al.*, 2019), which
605 have yet to be deployed for mapping benthic environments to the best of our knowledge. In optically

606 deep waters, spectral measurements may be obtained using underwater vehicles (Foglini *et al.*, 2019), or
 607 by hand (Chennu *et al.*, 2017).



608
 609 Figure 3. [Single column] Number of studies utilizing different remote sensing technologies for different aquatic
 610 environments.

611 Satellite-borne sensors enable highly efficient remote sensing of the oceans and seabed on a global scale.
 612 Water depth may be estimated at a high resolution using multi-band imagery from satellites such as
 613 WorldView (e.g., Cerdeira-Estrada *et al.*, 2012), Sentinel (e.g., Poursanidis *et al.*, 2021), Landsat (e.g.,
 614 Borfecchia *et al.*, 2019), and the Planet Dove constellation (e.g., Li *et al.*, 2019). Altimetry may also be used
 615 to estimate depths over very broader scales (Smith & Sandwell, 1997). Where clarity permits, one of many
 616 satellite- or air-borne spectral cameras may be used to infer habitat characteristics by imaging the seafloor
 617 directly (Capolsini *et al.*, 2003). Several satellites have been specifically designed to provide global
 618 oceanographic measurements. MODIS-Aqua, for example, images the entire Earth every two days across
 619 36 spectral bands, providing reflectance data that may be used to estimate a variety of physical, chemical,
 620 and biological oceanographic variables (Maccherone & Frazier, n.d.; NASA Goddard Space Flight Center,
 621 Ocean Ecology Laboratory, Ocean Biology Processing Group, 2022). These data are available at multiple
 622 resolutions (but as high as 250 m), enabling their use for habitat mapping across multiple spatial scales
 623 (e.g., Fontaine *et al.*, 2015; Jalali *et al.*, 2018; Buhl-Mortensen *et al.*, 2020; Hu *et al.*, 2020). MODIS was

624 preceded by sensors such as the Advanced Very High Resolution Radiometer (AVHRR) and the Sea-viewing
625 Wide Field-of-view Sensor (SeaWiFS), which provide coarser measurements of sea surface temperature
626 and colour (km-scale), but which date back to the 1970s and 1990s, respectively (Earth Resources
627 Observation And Science (EROS) Center, 2017; NASA Goddard Space Flight Center, Ocean Ecology
628 Laboratory, Ocean Biology Processing Group, 2018). Data from these sensors have been applied both prior
629 to, and along with, that of MODIS-Aqua to map benthic habitats over broad extents (e.g., G. Williams *et*
630 *al.*, 2010; Pitcher *et al.*, 2012; Compton *et al.*, 2013a; Mazor *et al.*, 2017; de la Barra *et al.*, 2020). Open
631 cloud computing and hosting platforms such as Google Earth Engine (Gorelick *et al.*, 2017) have greatly
632 increased access to these and other similar global satellite remote sensing datasets.

633 Beyond the limits of light penetration, sonar is generally utilized to provide geospatial predictor data for
634 benthic habitat mapping. Single beam sonar systems emit a single sounding that is typically normal to the
635 vessel, while sidescan sonar is used to acquire a swath of soundings at oblique angles. Multibeam sonars
636 may be used to collect a broad swath of soundings at both normal and oblique angles, which generally
637 include a mapped width on the order of 4 times the water depth, greatly increasing survey efficiency
638 compared to single beam systems. Sub-bottom profilers emit a low frequency pulse capable of
639 penetrating the substrate in order to image the subsurface. Each of these technologies has capability to
640 measure both the time and intensity of the echo, yielding estimates of depth and acoustic backscatter,
641 respectively. Recently, the ability to ping at multiple acoustic frequencies simultaneously has enabled so-
642 called “multispectral” backscatter mapping using multibeam sonars (Brown *et al.*, 2019), which has
643 potential to increase the resolvability of seabed substrate properties (Feldens *et al.*, 2018; Gaida *et al.*,
644 2018; Janowski *et al.*, 2018; Misiuk & Brown, 2022). Multifrequency surveys may now be conducted using
645 single beam (e.g., Cutter & Demer, 2014; Mopin *et al.*, 2022), sidescan (e.g., Tamsett *et al.*, 2016; Fakiris
646 *et al.*, 2019), multibeam (e.g., Gaida *et al.*, 2020; Menandro *et al.*, 2022; Schulze *et al.*, 2022), and synthetic
647 aperture (Barclay *et al.*, 2005; Rymansaib *et al.*, 2019) side scan sonars. A summary of remote sensing
648 technologies and sensors used to collect geospatial data for benthic habitat mapping is provided in Table
649 1.

650 Table 1. Examples of geospatial benthic habitat predictor data sets collected using remote sensing technologies. An
 651 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

652 ¹Single beam echosounder

653 ²Side scan sonar

654 ³Sub-bottom profiler

655 ⁴Multibeam echosounder

656 ⁵Acoustic Doppler current profiler

657 ⁶Altimetry-derived depths are generally accessed via data compilations such as SRTM15+.

658 ⁷Grey-level co-occurrence matrices

659 The need for higher resolution global seafloor data is well recognized, and there now exist multiple
 660 publicly available compilations of bathymetric data for the world's oceans that are accessed for benthic
 661 habitat mapping applications. The SRTM15+V2.0 grid provides a 15 arc-second (~500 x 500 m at the
 662 equator) compilation of global elevation data (both land and sea; Tozer *et al.*, 2019). Satellite altimetry
 663 and ship-borne acoustics provide depth estimates for the global oceans, while terrestrial elevation is
 664 derived through satellite radar. The SRTM15+ grid is augmented by the General Bathymetric Chart of the
 665 Oceans (currently "GEBCO_2022"), which is a global elevation surface developed and provided freely by
 666 the International Hydrographic Organization (IHO) and the Intergovernmental Oceanographic

667 Commission (IOC) of the United Nations Educational, Scientific and Cultural Organization (UNESCO). The
668 GEBCO grid is updated annually, providing continuous elevation data for the globe also at 15 arc-second
669 intervals compiled from SRTM15+ and additional data from a variety of acoustic, optical, and historical
670 data sources. The GEBCO grid is further augmented by the Global Multi-Resolution Topography (GMRT)
671 Synthesis hosted by the Columbia University Lamont-Doherty Earth Observatory (Ryan *et al.*, 2009), which
672 provides a global compilation of multibeam sonar data at a base resolution of ~100 m, but up to ~25 m in
673 some areas. GMRT is updated regularly, and multibeam grids may be accessed at one of several
674 resolutions, or optionally, may be acquired as an enhanced version of the latest GEBCO grid
675 (<https://www.gmrt.org/index.php>).

676 These global compilations have greatly increased the accessibility of global bathymetric data for science,
677 but the true data density and resolution are often deceiving. For example, Mayer *et al.* (2018) point out
678 that the GEBCO_2014 grid, which has a resolution of 30 arc-seconds (926 m at the equator), relies on
679 interpolated depth values for approximately 82% of grid cells, which have no actual bathymetric
680 measurements. Of the 18% of cells with bathymetric measurements, many have only a single bathymetric
681 sounding, and only 9% of cells contain high-resolution multibeam echosounding data. Increased
682 awareness of this data gap has motivated global initiatives such as the Nippon Foundation—GEBCO
683 Seabed 2030 Project, which has the goal of collecting at least one bathymetric measurement in a global
684 grid of depth-variable cells by 2030, which range from 100 m resolution in waters shallower than 1500 m,
685 to 800 m resolution in the deepest parts of the ocean (> 5750 m water depth; Mayer *et al.*, 2018). As of
686 2023, approximately 23% of the global oceans have been mapped according to these criteria (Seabed
687 2030 Project, 2023).

688 3.5. Ground validation

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

696 Underwater imagery is an efficient and non-destructive method for obtaining both biological and
697 geological ground validation, and still or video cameras can be mounted on a variety of platforms for
698 different purposes. Passive camera systems may be lowered via tether from the surface to the seafloor to
699 collect imagery, which are not fitted with any form of propulsion. Drop cameras, for example, are
700 deployed directly beneath a survey vessel, either at one or several discrete points per location for still
701 imaging systems, or for a continuous period of time for video systems, in which the vessel, not under
702 power, is allowed to drift for some interval (e.g., Wilson *et al.*, 2021). Similarly, towed imaging systems
703 are deployed from a vessel under power to acquire benthic images from along a path or transect (e.g.,
704 Ierodionou *et al.*, 2007). Sediment profile imaging (SPI) cameras are another specific type of passive
705 drop camera that captures subsurface profile images of the sediment (Rhoads & Cande, 1971).
706 Autonomous and remote underwater vehicles (AUVs, ROVs) are self-propelled platforms that are
707 increasingly utilized for imaging the seabed. AUVs have capacity to efficiently collect large volumes of
708 imagery data over broad extents and are ideal for long term monitoring applications (e.g., S. B. Williams
709 *et al.*, 2010, 2012), and ROVs enable image acquisition at deep and often morphologically complex sites
710 such as submarine canyons, vertical walls, and hydrothermal vents, which may be otherwise difficult to
711 sample (Robert *et al.*, 2015; Bodenmann *et al.*, 2017; Pearman *et al.*, 2020). In shallow waters, imagery is
712 commonly collected manually via SCUBA or snorkeling, which may additionally be used to establish
713 precise measurements by using quadrats or transects (e.g., Doxa *et al.*, 2016). Several forms of immobile
714 in situ cameras are also used to survey mobile fauna or for monitor environmental health, including baited
715 remote underwater video systems (BRUVS; e.g., Moore *et al.*, 2009) and time lapse systems (Kocak *et al.*,
716 2008). A modern comprehensive overview on the use of underwater imagery for benthic habitat mapping
717 is provided by Bowden *et al.* (2020).

718 Both biological and geological physical samples are commonly used as ground validation for benthic
719 habitat mapping. Physical samples refer to those that are removed from the seabed for analysis at the
720 surface. Bulk substrate extraction is the most common form of physical sampling used to acquire
721 validation data for benthic habitat mapping. Grab sampling is a method for bulk sediment extraction that
722 is often used to acquire surficial geological and infaunal biological data simultaneously. Various coring
723 techniques are also applied that enable profile sampling of the sediment surface and subsurface, such as
724 gravity, piston, vibro- and multi-cores. Box cores may provide both a large planar surficial sample – similar
725 to that of a grab – and also a profile sample, making them highly useful for obtaining simultaneous

726 representative biological and surficial geological samples (e.g., Leduc *et al.*, 2015). Targeted sampling is
727 used where feasible to obtain specific biological or geological samples (e.g., McRea *et al.*, 1999; Perez *et*
728 *al.*, 2020). Benthic trawls are a method of sampling that may be targeted or indiscriminate, and are often
729 deployed during scientific or fisheries surveys to sample benthic or demersal species (e.g., Montero *et al.*,
730 2020; Murillo *et al.*, 2020a).

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

741 3.6. Model class

742 Spatially continuous benthic habitat maps were traditionally produced by manual expert interpretation,
743 yet geospatial modelling has now become the primary means for achieving these spatial predictions.
744 Three broad classes of models are distinguished in the spatial ecology and biology literature (Guisan &
745 Zimmermann, 2000). *Analytical* or *mathematical* models aim to describe an ecological phenomenon and
746 infer results using one or multiple closed-form mathematical equations, which are not necessarily linked
747 theoretically to any environmental mechanism (Sharpe, 1990). These might be established based on
748 observed ecological trends, but specific models (e.g., regression) are not fit to field observations. The
749 rigidity of analytical models allows them to represent the behaviour of a simplified system, which may be
750 transferred to generate predictions or inferences under particular sets of potentially novel conditions
751 (Pickett *et al.*, 2007). These models may target highly specific phenomena such as lateral transport of
752 organic matter to the seabed (Ichino *et al.*, 2015), or more general population-level parameters such as
753 species biomass and weight (e.g., Duplisea *et al.*, 2002). *Mechanistic* or *process* models, on the other hand,
754 explicitly link behaviours of the model to the ecological processes that drive them (Levins, 1966). The

755 formulation and application of these models is primarily concerned with understanding of ecological
756 processes and interactions and may include qualitative or graphical models that describe the sign (i.e.,
757 increasing or decreasing), or general shape of an ecosystem response function (Levins, 1966; MacArthur
758 & Levins, 1964). Like *analytical* models, *mechanistic* models are general, but provide interpretability at
759 the expense of precision (Guisan & Zimmermann, 2000). Unlike *analytical* models, *mechanistic* models
760 attempt to assign causality to ecological processes (Sharpe, 1990), for example, by applying ecological
761 theory that relates life history traits to benthic environmental properties (Kostylev & Hannah, 2007).
762 Finally, *empirical* models are used to fit statistical relationships directly to data observations. These are
763 also known as “predictive” or “statistical” models. They are precise and realistic but may lack generality –
764 failing at extrapolation to novel conditions. Correlations uncovered by *empirical* models do not imply
765 causation between variables. Species distribution models generally fall under this category. A statistical
766 model fit between species observations and environmental variables may be used to accurately predict
767 species presence within the study area, but no mechanistic conclusions can be implied regarding the
768 relationships between environmental variables and species habitat, and it is unlikely that the model is
769 transferable to new locations.

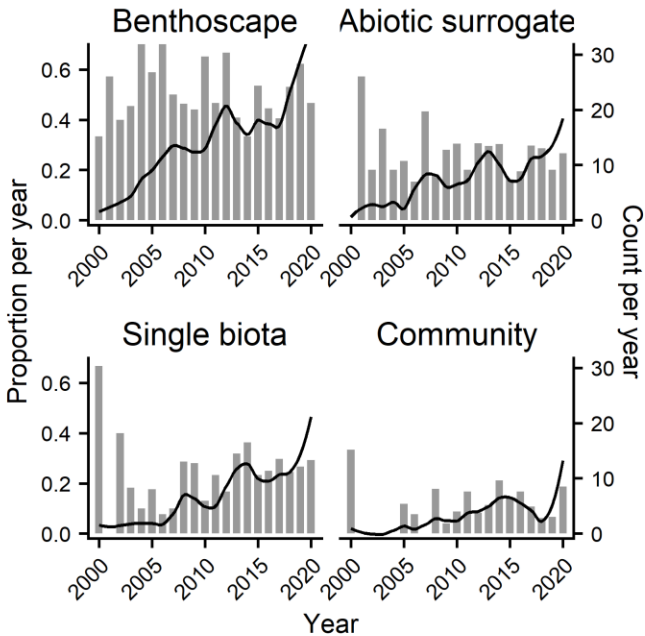
770 Although model classes are somewhat ambiguous – particularly for cases of apparent combined
771 *analytical-empirical* (e.g., Ceola *et al.*, 2014; Paoli *et al.*, 2016) and *mechanistic-empirical* (e.g., Harris &
772 Hughes, 2012; Galparsoro *et al.*, 2013; Foveau *et al.*, 2017; Lewis *et al.*, 2019) approaches – *empirical*
773 models fit directly to sample data (i.e., “correlative” models; Melo-Merino *et al.*, 2020) are
774 overwhelmingly preferred in the benthic habitat mapping literature (see section 4.6). “Semi-empirical” or
775 “semi-automated” (Costa & Battista, 2013; Lacharité *et al.*, 2018) models also appear frequently. These
776 are hybrid models constructed using a combination of empirical statistical analysis of sample data with
777 manual or contextual expert interpretation (e.g., Cruz-Vázquez *et al.*, 2019). Both empirical and semi-
778 empirical models may be *supervised* or *unsupervised*. *Supervised* models fit and predict the response (a
779 benthic habitat observation) directly as a function of environmental predictor variables. Generally, all
780 regression models (i.e., a continuous response variable), and also many classifiers found in the benthic
781 habitat mapping literature, are applied in a supervised manner. Examples include generalized linear (e.g.,
782 Jansen *et al.*, 2018; de la Barra *et al.*, 2020), and additive (Serrano *et al.*, 2017; Torriente *et al.*, 2019)
783 models, and most decision tree-based methods such as classification and regression trees (e.g., Pesch *et al.*
784 *et al.*, 2011), Random Forest (e.g., Lucieer *et al.*, 2013; Zhang *et al.*, 2013), and recently, XGBoost (Nemani

785 *et al.*, 2022) and LightGBM (Mackin-McLaughlin *et al.*, 2022). *Unsupervised* models attempt to uncover
786 meaningful patterns in the environmental variables without using information about the response. These
787 models comprise a large number of clustering techniques such as k-means and -medoids (e.g., Węśławski
788 *et al.*, 2013; Hoang *et al.*, 2016), DBSCAN and OPTICS (e.g., Menandro *et al.*, 2022), and specific artificial
789 neural network architectures such as self-organizing maps (e.g., Fendereski *et al.*, 2014). Clusters
790 uncovered using these algorithms may be subsequently assigned to classes using ground truth
791 information (e.g., Brown & Collier, 2008; Calvert *et al.*, 2015) or may also be used for purposes such as
792 sample site stratification and selection. An exhaustive list of supervised and unsupervised algorithms
793 encountered in the sampled literature are provided in the Supplementary Material.

794 4. How has benthic habitat mapping changed over time?

795 4.1. Thematic maps

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

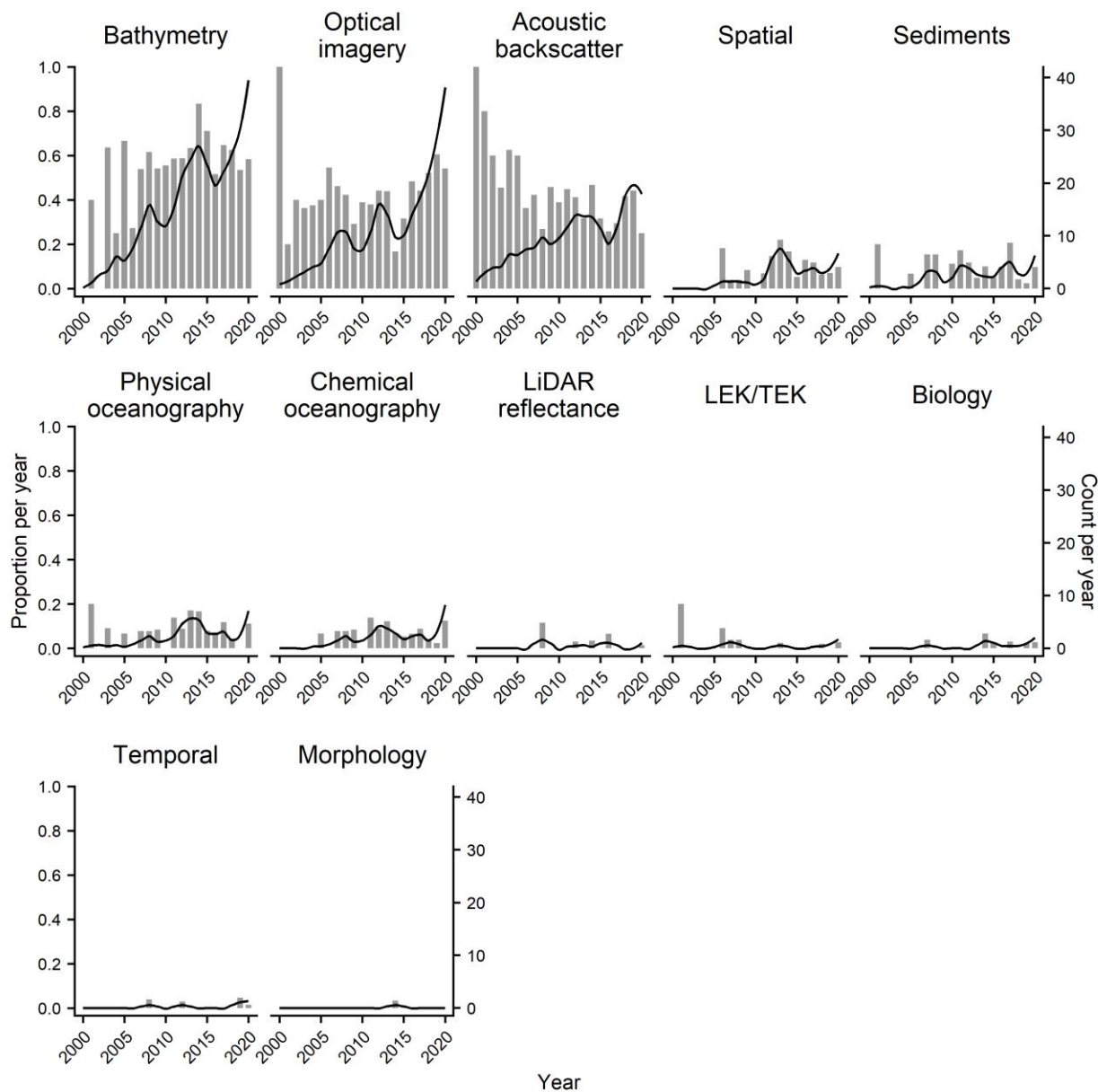


802

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

805 4.2. Geospatial predictor data

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

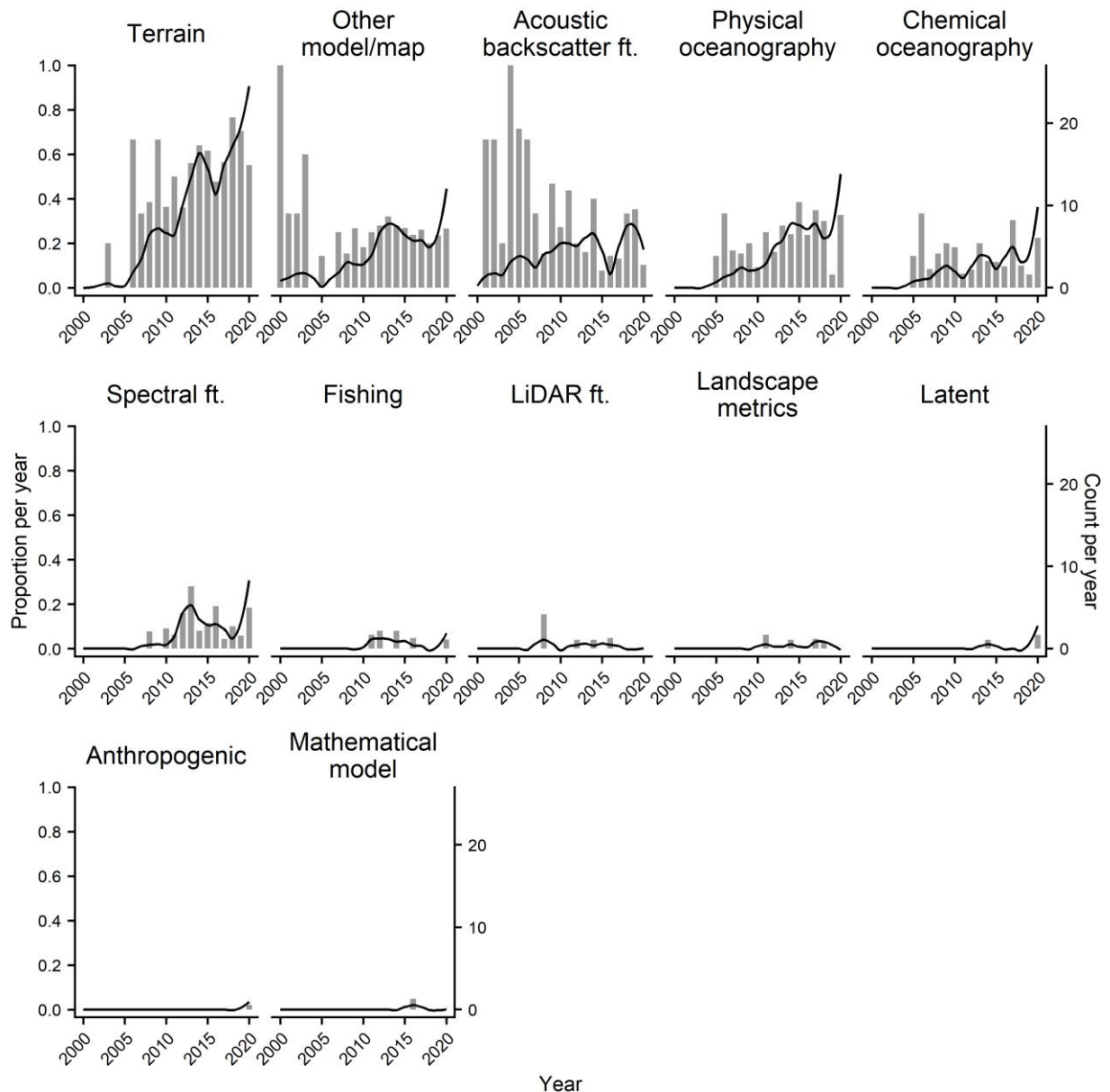


818
 819 Figure 5. Proportion of studies utilizing different types of geospatial predictor data since 2000 (primary axis; bars),
 820 and raw counts per year (secondary axis; lines). Plots are ordered according to prevalence.

821 4.3. Derived predictor data

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

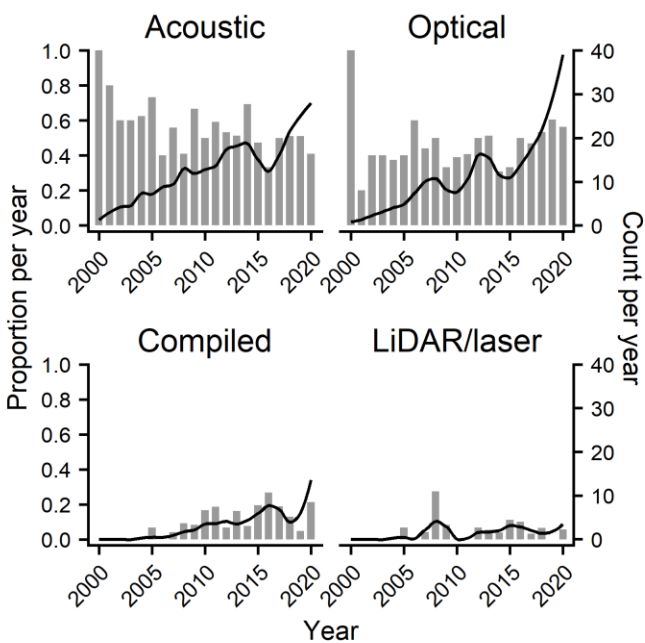
826 of the QTC software for sonar data processing, which included calculation of backscatter features for
 827 seabed characterization (Preston, 2009; Brown *et al.*, 2012). Oceanographic features are increasingly
 828 calculated and applied, likely as a function of increased availability of high-quality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



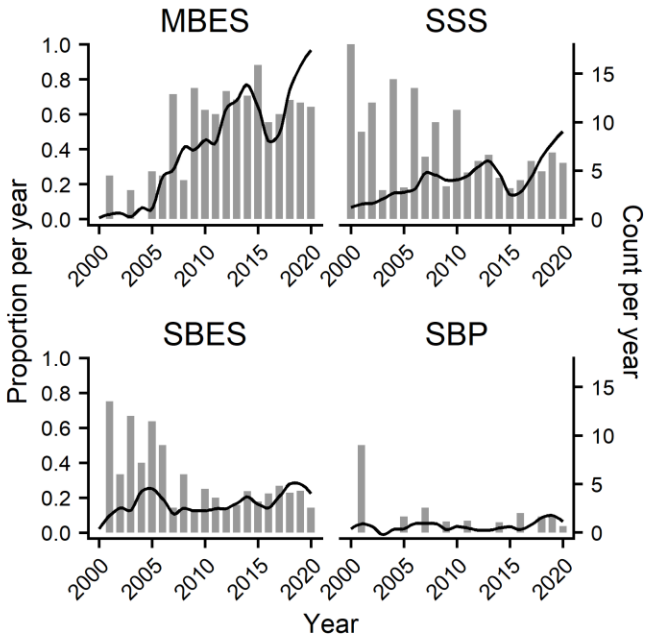
831
 832 Figure 6. Proportion of studies utilizing different secondary features derived from geospatial data since 2000
 833 (primary axis; bars), and raw counts per year (secondary axis; lines). Plots are ordered according to prevalence.

834 4.4. Remote sensing technologies

835 The prevalence of remote sensing technologies encountered in the sampled benthic habitat mapping
836 literature has changed since the year 2000 (Figure 7). Acoustic technologies were the preferred remote
837 sensing tool up until about 2005, after which optical technologies were increasingly utilized. Past 2015,
838 the implementation of optical technologies has surpassed acoustic ones. Access to compiled remote
839 sensing datasets has increased over this period, likely as a result of increased accessibility to large public
840 data repositories such as GEBCO (GEBCO Compilation Group 2022, 2022), the World Ocean Atlas (Garcia
841 *et al.*, 2013a, 2013b; Locarnini *et al.*, 2013; Zweng *et al.*, 2013), and Google Earth Engine (Gorelick *et al.*,
842 2017), including the datasets therein. LiDAR and laser technologies have been applied consistently but in
843 a small number of cases. There was substantial heterogeneity among the acoustic methods employed
844 over this period (Figure 8), which differ technologically. Side scan and single beam sonar (SSS, SBES) were
845 greatly preferred in the first decade, but increased accessibility to multibeam echosounders (MBES) has
846 somewhat superseded these technologies for mapping optically deep waters.



847
848 Figure 7. Proportion of different remote sensing technologies employed since 2000 (primary axis; bars), and raw
849 counts per year (secondary axis; lines). Plots are ordered according to prevalence.

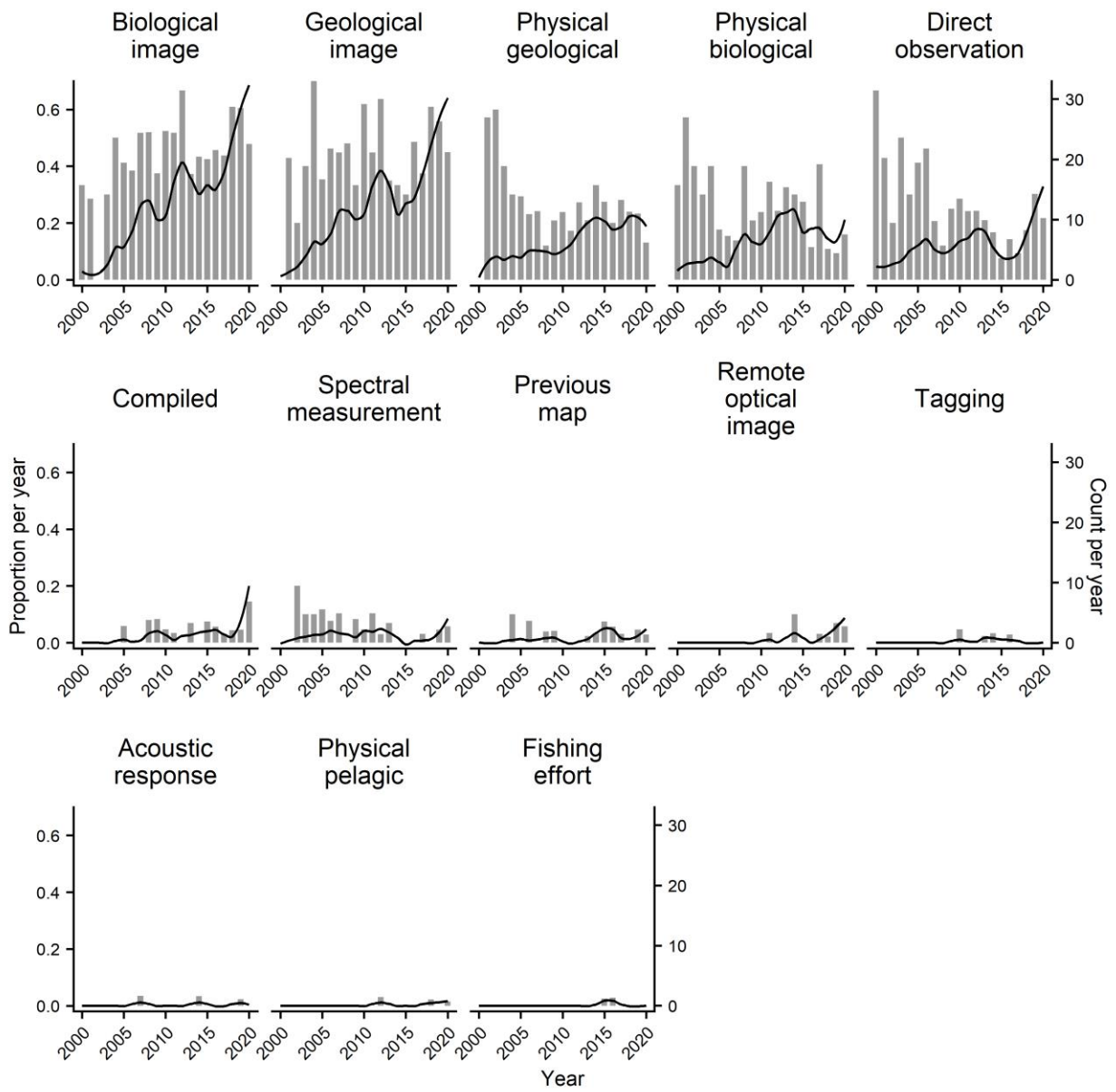


850

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

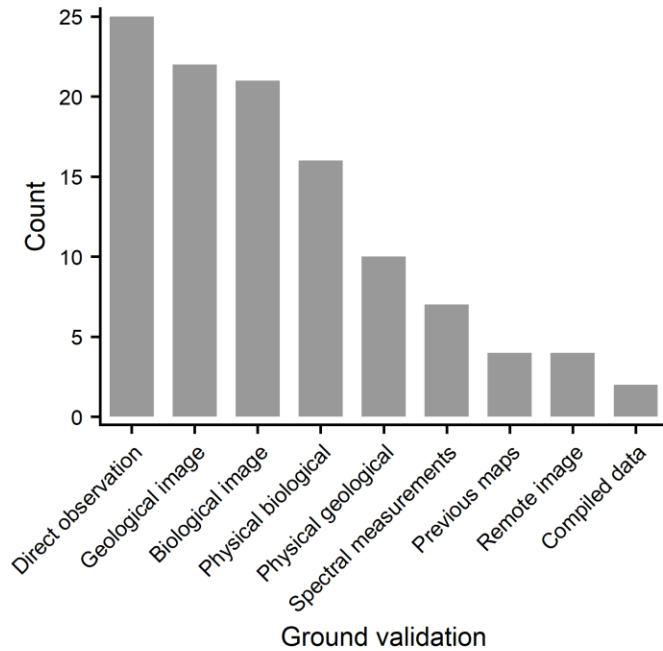
854 4.5. Ground validation

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



862

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



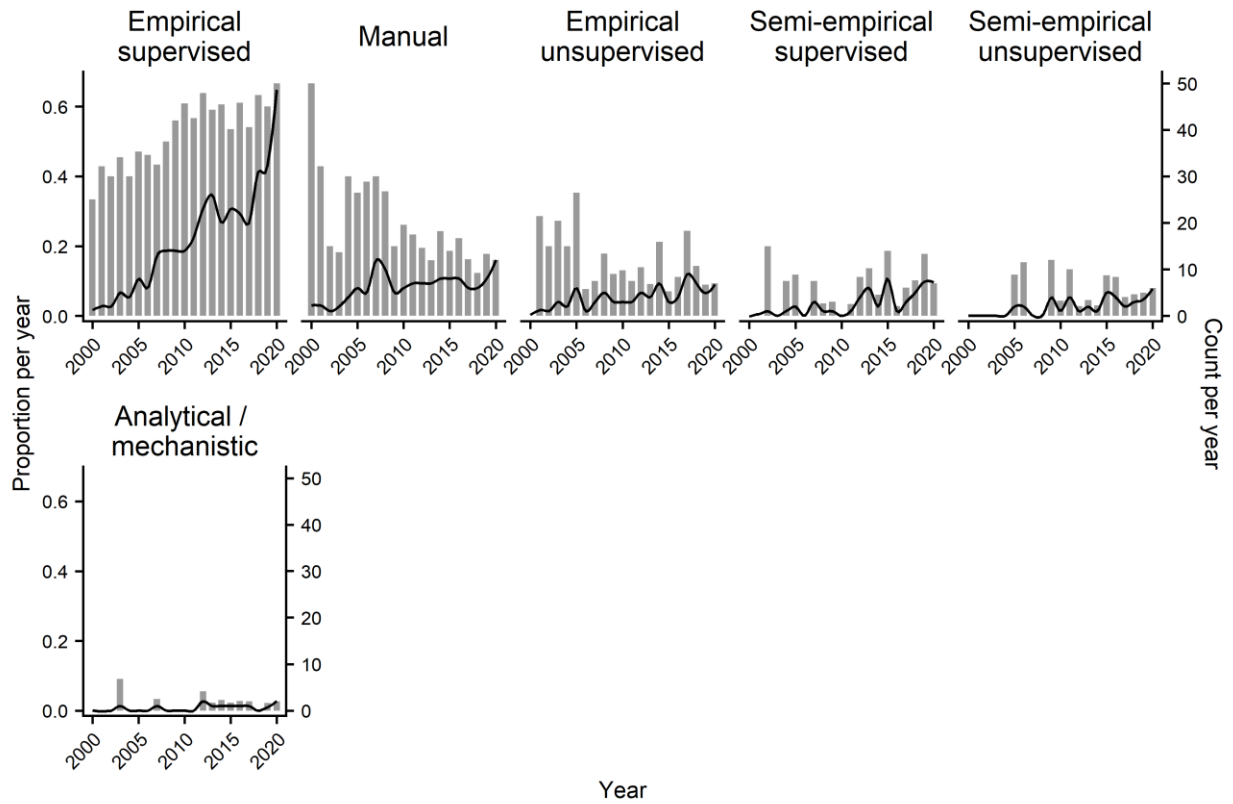
865

866 Figure 10. Number of intertidal studies utilizing different forms of ground validation data.

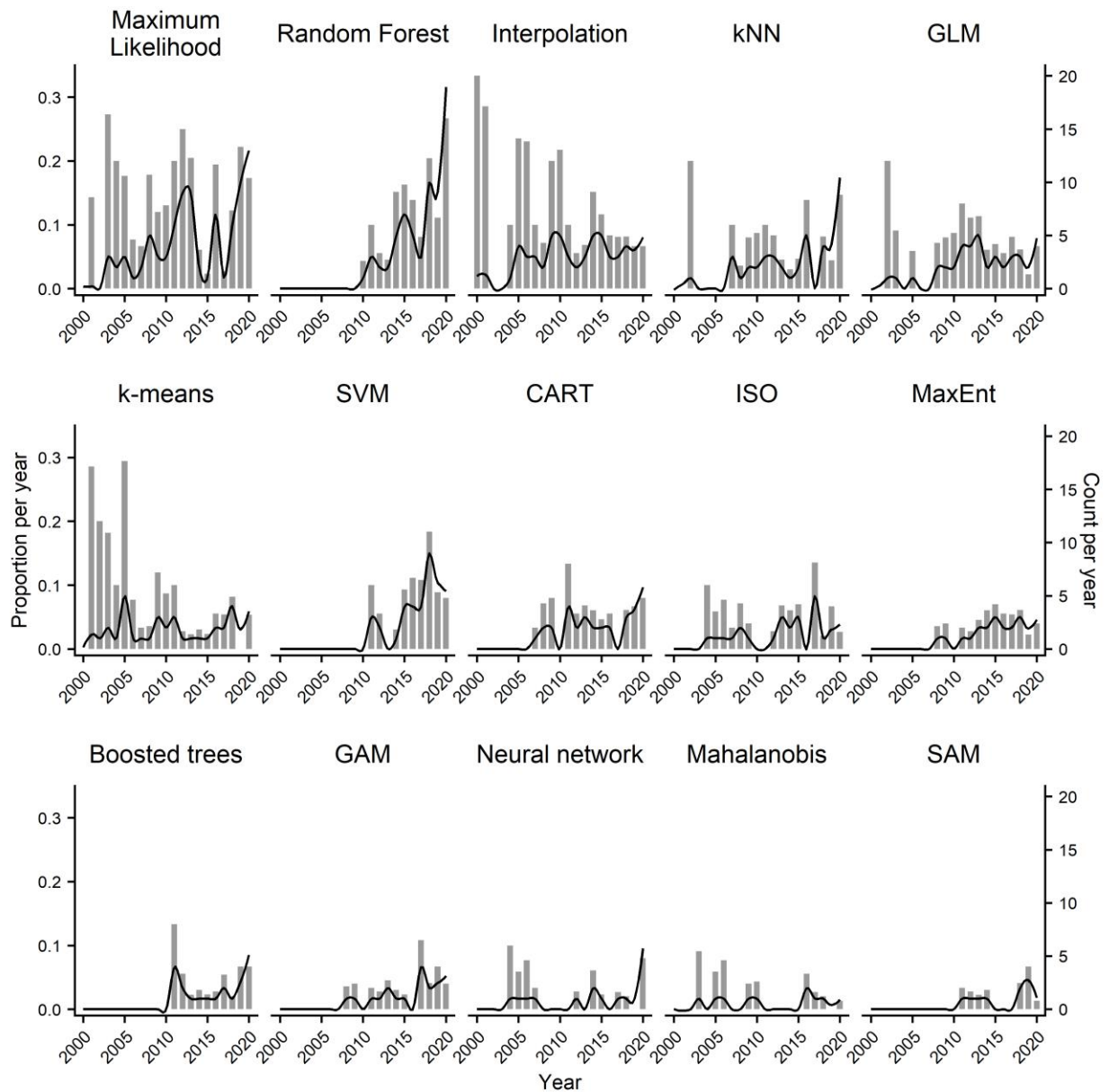
867 4.6. Model class

868 The past two decades have experienced a marked shift away from manual benthic habitat mapping
 869 approaches in favour of empirical ones. Supervised empirical models have been broadly adopted and
 870 were applied to produce the majority of habitat maps sampled from the literature for every year since
 871 2010 (Figure 11). Of these, the Maximum Likelihood classifier is the most common model encountered in
 872 the surveyed literature, and is still included in a large proportion of studies (Figure 12). Various
 873 interpolation approaches (e.g., Kriging, Inverse Distance Weighting, Natural Neighbor) were amongst the
 874 most common techniques used to produce habitat maps in the early 2000s but their use has gradually
 875 subsided over the past decade or so. Unsupervised k-means clustering was also highly popular in the early
 876 2000s, due largely in part to the widespread adoption of the QTC software, which reportedly implements
 877 a modified k-means clustering for classification of acoustic data to produce habitat maps (e.g., Freitas *et*
 878 *al.*, 2003, 2011; Preston & Kirlin, 2003; McGonigle *et al.*, 2010; Brown *et al.*, 2012; c.f. Preston, 2009 and
 879 Preston & Biffard, 2012), which may have changed between versions of the software (Legendre, 2003).
 880 Recently, these methods have been superseded by more automated machine learning approaches such
 881 as Random Forest and Support Vector Machines – the former which comprised over 25% of all habitat
 882 mapping studies surveyed in 2020 (Figure 12). The popularity of Random Forest has undoubtedly arisen

883 as a function of its accuracy and ease of use across a broad range of regression and classification
 884 applications, which have been demonstrated in several comparative studies (e.g., Che Hasan *et al.*, 2012;
 885 Diesing *et al.*, 2014; Le Marchand *et al.*, 2020). Uptake has also been facilitated by increased access to free
 886 and open-source statistical tools such as R (R Core Team, 2021) and Python (van Rossum, 1995).



887
 888 Figure 11. Proportion of studies applying each mapping approach per year since 2000 (primary axis; bars), and raw
 889 counts of application per year (secondary axis; lines). Plots are ordered according to total number of
 890 implementations.



891

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

895 The application of machine learning methods to seabed mapping is not a recent development. Dating back
 896 to at least to the 1990s, the use of neural networks for seabed classification enabled early analysis of
 897 highly dimensional textural and spectral feature sets derived from both acoustic backscatter (Stewart *et*
 898 *al.*, 1994; Müller *et al.*, 1997; Ojeda *et al.*, 2004; Müller & Eagles, 2007) and optical imagery (Bakran-
 899 Petricoli *et al.*, 2006). These methods were somewhat superseded over the following decade by other

900 novel machine learning approaches such as classification and regression trees, Support Vector Machines,
901 k-Nearest Neighbors, Random Forest, and boosted regression trees (e.g., Ierodiaconou *et al.*, 2007;
902 Knudby *et al.*, 2011; Reiss *et al.*, 2011; Che Hasan *et al.*, 2012; Bučas *et al.*, 2013; Prospere *et al.*, 2016;
903 Janowski *et al.*, 2018). The application of neural networks for seabed classification has received renewed
904 interest, though, with the widespread adoption of “deep learning” via convolutional neural networks for
905 image processing (LeCun *et al.*, 2015; Goodfellow *et al.*, 2016), which may be implemented via free open-
906 source software such as Python and the machine learning libraries contained therein. These models differ
907 from early neural networks used for seabed mapping through the application of many convolutional filters
908 that are “learned” as a function of the response being mapped. Using this approach, the texture or terrain
909 of the seabed can be analyzed automatically, rather than by manually “engineering” features that are
910 used to predict the response, which may take many different forms (e.g., Luo *et al.*, 2019; Fincham *et al.*,
911 2020; Shields *et al.*, 2020; Feldens *et al.*, 2021). Convolutional neural networks have demonstrated great
912 discriminatory potential for a variety of terrestrial land cover and vegetation applications (Maggiori *et al.*,
913 2017; Xu *et al.*, 2018; Kattenborn *et al.*, 2021), and adoption of similar methods for seabed mapping
914 appears to be accelerating (Neupane & Seok, 2020; Steiniger *et al.*, 2022). While not geospatial (though,
915 see work by Rao *et al.*, 2014), automated classification of benthic imagery is also increasingly achieved
916 using deep convolutional neural networks (e.g., Diegues *et al.*, 2018; Piechaud *et al.*, 2019; Mahmood *et al.*,
917 2020; D’Archino *et al.*, 2021; Yamada *et al.*, 2021), enabling efficient analysis of data volumes that are
918 orders of magnitude larger than could previously be achieved. We expect to see great advances in this
919 domain over the next decade for all manner of seabed mapping applications.

920 5. Trajectory and challenges

921 Remarkable advances in the field of benthic habitat mapping have been driven by improvements to
922 remote sensing technologies, increased access to remote sensing data sets, improvements to ground
923 validation approaches, and through the capability to effectively process and model these data with
924 modern computing resources and methods. Despite advancement in these areas, several new and
925 outstanding challenges to the field remain that may be addressed through a refocusing of research efforts.

926 The seabed is inherently dynamic, yet habitat mapping data – both in situ and remotely sensed – are
927 normally treated as static products. This occurs out of necessity given the cost of acquisition, particularly
928 in deeper waters using vessel-deployed instrumentation, and implicitly raises two important concerns. First,

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

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

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

972 Finally, we emphasize the importance of interdisciplinary collaboration for the production of better
973 benthic habitat maps. This is not an abstract ideal; there is strong evidence in the recent literature that
974 the use of multiple sensors may increase capacity for mapping benthic habitats across a range of
975 environments and conditions. The simultaneous acquisition of multibeam backscatter and subsea LiDAR
976 by ROV, for example, has enabled enhanced substrate discrimination compared to either technology in
977 isolation (Collings *et al.*, 2020). The combined use of multispectral imagery and LiDAR data has also shown
978 great capacity for discrimination of coastal, shallow, and estuarine habitats, and may be collected by
979 aircraft or a combination of aircraft and satellite (e.g., Chust *et al.*, 2008; Halls & Costin, 2016). Likewise,
980 simultaneous data acquisition using multiple acoustic technologies has enabled efficient and accurate
981 classification of the seabed by exploiting the strengths of different sensors – for example, the horizontal
982 density of sidescan data with the vertical resolution of sub-bottom profiles (Fakiris *et al.*, 2018;
983 Bartholomä *et al.*, 2020). Finally, the use of spectral cameras along with acoustics has been highly
984 effective, and has facilitated mapping across a range of depths generally not achievable using a single
985 acoustic or spectral sensor (e.g., Reshitnyk *et al.*, 2014; Rende *et al.*, 2020). These examples suggest that
986 perhaps a focus on acquiring different data types spanning a range of remote sensing technologies offers

987 greater benefit than acquiring higher resolutions or new forms of a single technology. Given increased
988 accessibility of data from a range of platforms and sensors, and improvements to data acquisition, storage,
989 and processing, we hope to see more collaboration and greater development of multi-sensor benthic
990 habitat mapping over the coming decade.

991 Supplementary material

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