Viewpoint Article

The value of remote sensing techniques in supporting effective extrapolation across multiple marine spatial scales

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Running header: Extrapolation supported by remote sensing techniques

Abstract

The reporting of ecological phenomena and environmental status routinely required point observations, collected with traditional sampling approaches to be extrapolated to larger reporting scales. This process encompasses difficulties that can quickly entrain significant errors. Remote sensing techniques offer insights and exceptional spatial coverage for observing the marine environment. This review provides guidance on (i) the structures and discontinuities inherent within the extrapolative process, (ii) how to extrapolate effectively across multiple spatial scales, and (iii) remote sensing techniques and data sets that can facilitate this process. This evaluation illustrates that remote sensing techniques are a critical component in extrapolation and likely to underpin the production of high-quality assessments of ecological phenomena and the regional reporting of environmental status. Ultimately, is it hoped that this guidance will aid the production of robust and consistent extrapolations that also make full use of the techniques and data sets that expedite this process.

Keywords: remote sensing techniques, extrapolation, spatial scaling, monitoring requirement paradox

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Introduction

Traditional methods of sampling typically provide point observations with a high information content, i.e. the characteristics of the seabed at one place. For logistic reasons, these observations typically cannot provide continuous data surfaces over large spatial areas (Gray & Elliott 2009). Consequently, they are poorly suited for detecting the detailed structure within broad-scale gradients (e.g. salinity, depth and propagule dispersal) and representing spatial heterogeneity (e.g. substratum patchiness). Although ecological phenomena occur at various spatial scales (Figure 1), those occurring at broader spatial scales are currently the target of greater attention e.g. species loss, environmental health and climate change impacts (Box 1). This means there is a growing discrepancy between the spatial scales associated with the sampling and reporting of variables (Urban et al. 1987) – this is especially true for observations from traditional sampling techniques.

The assessment and reporting of these broad-scale phenomena therefore requires that observations, sampled at smaller spatial scales, are 'scaled-up' (Miller et al. 2004, Peters et al. 2008, Aertsen et al. 2012) or spatially extrapolated (Box 2 and Figure 2). Although undertaken routinely, the extrapolative process is complex (Levin 1992, Wu, David 2002) and may introduce substantial errors if not undertaken correctly (Miller et al. 2004, Denny & Benedetti-Cecchi, 2012). Of potentially value for extrapolation are the technological developments, often from military and medical sectors, that have generated many remote sensing techniques (i.e. techniques that use sound or light to quantify variables or surrogates of interest) suitable for the marine environment (Solan et al. 2003). The greater spatial coverage captured by many imaging techniques is more closely aligned with the domains of scale (Figure 1) apparent in marine ecology and required by the current suite of international legislation.

Datasets covering multiple spatial scales, such as those provided by remote sensing techniques, are particularly informative about processes and properties occurring at various spatial scales and especially larger and more ecologically relevant scales. Accordingly, here we examine the complexities inherent within the extrapolative process and the information, provided by remote sensing techniques, that can address these difficulties. Specific objectives are:

1. explain the difficulties in producing robust extrapolations;
2. describe the process of spatial extrapolation used within ecology;
3. develop a framework that combines remote sensing datasets within the extrapolation process (provided with examples); and
4. describe remote sensing techniques and indicate their value, in terms of coverage and thematic focus, and limitations.

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Box 1: Research and policy drivers for effective extrapolation

As environmental and ecological information and understanding accumulates at a local level, there is a greater interest and ability to examine broad-scale issues. This has also been driven by increased concern regarding regional and global pressures on ecological phenomena and environmental status (e.g. distributional mitigation and climate change, broad-scale habitat loss and the modification of ecosystem goods and services). Unfortunately, this has coincided with a paradox in marine assessments – that an increasing marine governance is dependent on acquiring greater data across larger spatial scales (Borja et al., 2016) and yet the bodies responsible for data collection are subject to significant resource limitation (Borja and Elliott 2013a). For example, ambitious legislation, such as the EU Marine Strategy Framework Directive (2008/56/EC) and the US Oceans Act (S.C. 1996), are making greater demands from the assessment process, with the current trends including:

(i) the evaluation of health over large spatial scales; increasingly defendable and repeatable measurements of status;
(ii) responsive to management measures, and
(iii) cost-effective implementation (Borja & Elliott 2013a).

Estimating environmental status over larger spatial scales requires that reliable extrapolation is used. While those assessments have been historically centred on point observations that may or may not have been extrapolated to larger areas, this is now acknowledged to create larger uncertainty in policy implementation. It is now apparent that the most effective extrapolations are those drawing on both high-quality point observations (i.e. traditional sampling) and informative, broad-scale sampling (i.e. remote sensing techniques) to be combined to deliver the best outputs possible.

Obstacles to effective extrapolation

The requirement to traverse between many spatial scales (i.e. domains of scale) and account for the localised sources of heterogeneity within each scale complicates the process of extrapolation. Environmental or ecological observations and phenomena (e.g. sampling events, environmental impacts, ecological phenomena and areas for the reporting of environmental status) are all associated with specific spatial scales termed 'domains of scale' (Urban et al. 1987). These domains are not spatially exclusive and can overlap (Figure 1). Changes in ecosystem properties and the dominance of specific processes create discontinuities in the scaling relationship when scaling between domains of scale. For example, sea surface temperature may generally not be expected to vary much 1 – 1000 m, but will vary, and therefore be influential, over 1 – >1000 km. As such, it is important to identify and characterise these domains of scale during extrapolation.

The environmental or ecological properties and processes associated with each domain will be associated with a particular type and range of variation, termed here 'source(s) of heterogeneity' (SoH). An individual SoH can be either qualitative (comprised of differing classes e.g. broad-scale substratum or habitat classes) or quantitative (gradient of a continuous variable e.g. sea surface temperature) (Figure 2). Both natural and anthropogenic properties and processes can generate SoH. Due to the 'nesting' of the domains of scale, a SoH can occur within another SoH present within a larger domain of

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scale. Interactions can occur between nested SoH to generate further heterogeneity. For example, an interaction will occur between substratum patchiness (SoH1 in Figure 2) and biological dispersal (SoH2 in Figure 2) if settlement is only possible on one class of substratum. These interactions complicated the aggregation of response surfaces. Combining all of the individual sources of heterogeneity, and the interactions generated between sources, provides the 'total heterogeneity' observed (Figure 2).

It is therefore apparent that robust extrapolations require information on SoH from several domains of scale. These sources must be represented during extrapolation to avoid scaling errors and provide an accurate spatial representation of the phenomena of interest. Depending of the size of the extrapolation, this may require several sources of information. Of particular value for meeting this requirement are remote sensing techniques that generate continuous data surfaces over large spatial areas.

Extrapolation and a framework for integrating remote sensing

Types of extrapolation in ecology

Observations can be scaled over space, time and ranges of base quantities (Figure 3). Lumping, extrapolation and explicit integration are the three main methods for scaling (King 1991). *Lumping* averages observations within an area and creates a mean value assumed to represent a larger area. *Extrapolation* maintains the detail within the observations through creating a small-scale response function, which either project (empirical approach) or model (mechanistic approach) the extrapolated value based on initial observations and predictor variable(s). *Extrapolation by explicit integration* rescales a smaller scale model to create a new, larger scale model with space as an integrating variable (King 1991, Aertsen et al. 2012). Although simple to undertake, lumping fails to provide spatial detail within the predicted areas and makes assumptions about the homogeneity of an area and the distribution of the data. For most applications, the ability of extrapolation to be able to overcome data gaps and use predictor variables (via a model) to generate detailed spatial outputs has meant it is the most used method for scaling.

A framework for structuring the extrapolative process and integrating remotely sensed data

The conceptual framework given by Miller et al. (2004) for the use of extrapolation in ecology is modified here to integrate and exploit the particular benefits provided by data sets from remote sensing techniques (Figure 4). This framework provides:

(i) A conceptual model: this provides the objectives of the extrapolation. It also identifies influential sources of heterogeneity and predictor variables that best represent these sources within the extrapolation. It also defines the influence of each source of heterogeneity on the extrapolated variable and the interactions between sources that may modify this influence.
(ii) A response function: an empirical or mechanistic relationship between the variable being extrapolated and the predictor variable(s) used to represent source(s) of heterogeneity;
(iii) A response value or surface: quantities, rates or area produced through the combination of a response function and predictor variable(s).
(iv) The extrapolated product derived from the response value or surface with an associated assessment of uncertainty.

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The conceptual model

The conceptual model is a critical first stage in developing the extrapolation process by defining:

1) the objectives of the extrapolation, i.e. the thematic, temporal and spatial properties of the extrapolated product and a desired level of certainty;
2) the thematic, temporal and spatial properties of the observations to be extrapolated;
3) the sources of heterogeneity that modify the extrapolation of the response variable and the predictor variables that can be used to represent these sources;
4) interactions between sources of heterogeneity that modify the extrapolation of the response variable, and
5) the type of response function (i.e. calculations, geospatial analysis or another model) required to extrapolate the response variable.

Specifying the objectives and classifying the variables to be extrapolated defines the scope of the extrapolation (Figure 4). The conceptual model should identify and detail the properties and processes that influence the response variable within the extrapolation area (Holling, 1992), i.e. identifying influential sources of heterogeneity. It should also state the character of each source of heterogeneity i.e. whether they are qualitative or quantitative variables (Table 1). The model can then pair each SoH with a predictor variable capable of representing it within the extrapolation area. The influence of each SoH does not operate in isolation, i.e. the influence of one source may well be modified by being nested within another source of heterogeneity. As such, the conceptual model should indicate these interactions and the way in which sources of heterogeneity collectively influence the response variable – this may require rules or additional functions on how to aggregate separate SoH into the final output.

Primarily, the conceptual model should guide the selection of predictor variables required. Without this step, there is a temptation to use widely available or routinely used variables without considering their ecological relevance, likely influence or potential interactions. If certain predictor variables are not available then the conceptual model should be used to identify surrogates, or dummy variables or, if the particular source of heterogeneity cannot be addressed, important caveats are required for the extrapolated output.

<u>Response function(s)</u>

A response function provides a relationship between the variable being extrapolated and a property or process that modifies the variable (i.e. sources of heterogeneity as represented by predictor variables). For a spatially-consistent, homogeneous area, a response function is not necessary and only lumping or a linear spatial scaling function may be required for extrapolation (also termed direct scaling: see King 1991, Miller et al. 2004). However, most marine areas for which extrapolation is required are heterogeneous. Response functions can be based on either mechanistic/deterministic or empirical relationships. The former are based on a theoretical and underlying understanding of the response of specific components within the system of interest whereas an empirical relationship is a specific response associated with a set of conditions or projection from a trend that may be statistically shown but have no known underlying theory. Regardless of the approach used, the response function must also be stable over time and dependent of the direction of change i.e.

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responsive to hysteresis should it occur (Denny & Benedetti-Cecchi 2012). Stochastic relationships may also need consideration within the response function.

Common response functions used for extrapolation include:

- Qualitative response variables - deductive (rule-based) or inductive (correlative) modelling methods such as logistic regression, maximum likelihood and decision tree learning (classification trees)
- Quantitative response variables - regression-based (parametric and non-parametric) models such as generalized linear model (GLM), generalized additive model (GAM) or machine learning methods such as decision trees.

The conceptual model will specify whether response functions are qualitative or quantitative. The choice of specific approaches will be determined by the distribution of response variables. Response variables that are normally distributed and homoscedastic (variance does not change as a function of the mean) can be modelled with classical regression methods. For response variables deviating from a normal distribution, newer regression models such as GLM (parametric), and GAM (semi-parametric) for non-linear relationships, are more appropriate (Guisan and Zimmermann, 2000; Guisan et al. 2002).

Response value or surface

Extrapolated products from a response function can be presented as data surfaces (for spatial scaling) or values (for temporal or quantity scaling).Yhey can be determined either (i) directly (with a deterministic function(s) generating a specified value), (ii) by 'expected value' (created empirically by statistical methods and includes moderate stochasticity, associated with the input variables, to generate a probability distribution and therefore a range of possible values) or (iii) driven by chance alone (purely stochastic model) (Denny & Benedetti-Cecchi 2012). The choice of which output type is most appropriate will depend on the relative influence of stochastic sources of heterogeneity on the response variable.

Finally, the extrapolated products should be presented with values of model performance (e.g. adjusted r-squared, Akaike Information Criterion etc.) and/or validation results from an independent data set (e.g. confusion matrices, kappa etc.). These values should form the basis for estimating the uncertainty of the extrapolation. Other information can also contribute to the estimation of uncertainty such as the density, distribution and relevance of the observations that have been extrapolated and the performance of the remotely sensed data in representing the influential SoH within the domains of scale traversed. Furthermore, it is critical that the estimation of uncertainty remains attached to the extrapolated product and is presented in a meaningful and interpretable manner. This will allow the end user to understand the limitations of the output and assess its fitness for purpose for their own use. It is likely many of the largest extrapolations within ecology are naturally associated with a high level of uncertainty. A failure to communicate uncertainty clearly to the end user can lead to unrealistic expectations and misguided management that may ultimately undermine the credibility of the methods and assessments based on the extrapolation products.

Applied examples of extrapolation using remote sensing techniques

Tables 2, 3 and 4 describe extrapolative approaches for three common marine assessments. Each approach progressive includes additional remote sensing techniques,

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which in turn compensate for more sources of heterogeneity. Habitat mapping is a common survey activity, and the resulting maps are used in various activities such as marine spatial planning of anthropogenic activities, the designation of marine protected areas and research into marine landscape ecology. Before hydro-acoustic methods became widely available, habitat mapping relied on manual or interpolative approaches for spatial extrapolation (Table 2). Products from this process, although easy to generate, only provide coarse, indicative maps for the distribution of habitats and species. They typically neglect the additional structure provided by substrata, depth and other influential environmental factors. The inclusion of video transects, and especially hydro-acoustic methods such as MBES within the survey methodology, has allowed mappers to account for substratum (via video observations or acoustic backscatter) and depth (including variables derived from the bathymetry). Consequently, the extrapolated products have greater levels of realism and accuracy, and can now be used for the extraction of summary indicators, such as habitat extent, that can be used for condition monitoring. Finally, the wide-spread use of MBES by habitat mappers means that large areas of the seabed are now mapped acoustically. Such is their combined extent that the inclusion of broad-scale oceanographic variables is now relevant within the extrapolation process. Based on the known influence of bioclimatic variables for species distribution, and the increasing importance of climate change for marine ecosystems, it is likely that the inclusion of satellite-derived data sets will further improve the accuracy of habitat mapping and the accuracy of extrapolated indices from these maps.

Stock assessments are an essential component of fisheries management. Table 3 describes stock assessment methods that incorporate remote sensing techniques. Once again, it is apparent that the inclusion of these techniques addresses a greater number of SoH, such as the patchiness inherent in fish distribution (via hydro-acoustic surveys) and the influence bioclimatic variables (via satellite-based imaging). Furthermore, remotely sensed data sets typically have a larger spatial extent when compared with traditional trawl surveys. This is particularly effective at representing oceanographic sources of heterogeneity and capturing the inherent domain of scale appropriate for national stock assessments. Efforts to include oceanographic variables from satellite sensors within fisheries stock assessments include the development of ecological provinces (Devred et al., 2007; Moore et al., 2009), essential fish habitat (e.g. Reiss et al 2008), modelling temporal variation in recruitment (Stuart et al., 2011) and the direct detection of fishing activity (e.g. the jumbo flying squid fishery by Waluda et al., 2006 and the tracking of fishing fleets through the use of vessel monitoring systems).

Assessments of ecosystem functions and services are routinely used by marine managers and policy makers to provide regional indicators of environmental status. Once again, several sources of heterogeneity hamper the scaling of point observations to regional scales. Using the example of primary production (Table 4), it is evident that remote sensing techniques can capture several sources of heterogeneity across multiple spatial scales. Without representing these sources of heterogeneity with the extrapolation, the process would quickly entrain excessive levels of variance and bias, generated by the dynamic and patchy conditions locally, that would promptly invalidate the final values. Lee et al. (2015) also conclude that the linkage of *in-situ* samples with synoptic and repetitive satellite observations is the only possible and feasible approach for the extrapolation of PP to regional and global scales.

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The three case studies provided exemplify the assessments that are commonly required for the routine monitoring and management of the marine environment. They also demonstrate that a failure to account for the most influential sources of heterogeneity during the extrapolative process can decisively undermine the outputs, and in turn, discredit the assessment process relying on these outputs. Furthermore, uncertainty associated with the outputs of extrapolation could results insufficient regulation of the underlying causative pressures, which could result in a further deterioration of status in the marine environment. Modern remote sensing techniques can cost-effectively capture and represent these sources of heterogeneity, thereby increasing accuracy and resolution (spatial and temporal), as well as providing more direct mechanistic relationships between the response variable and the predictor variables within extrapolations.

Useful remote sensing techniques for extrapolation within marine science

When compared with traditional observational methods, remote sensing techniques demonstrate greater (i) cost-effectiveness per replicate, (ii) non-destructive sampling capabilities, (iii) levels of replication and, most notably, (iv) spatial coverage (e.g. McClain 2009, Alverez et al. 2014, Fretwell et al. 2015). Given that remote sensing techniques undertake data collection from a very large spatial range (i.e. <1 cm to near-global scales), here we group the imaging techniques into fine, medium and coarse spatial ranges before describing their thematic content, value and coverage.

<u>Remote sensing techniques observing at small spatial scales (10^{-1} – 10^{1} m^2)</u>

The remote sensing techniques operating at the finest spatial scale are often the most comparable to the scale of observation provided by traditional point samples (Figure 5). Table 5 describes eight remote sensing methods that are particularly informative about SoH at the smallest spatial scale for pelagic and benthic applications. The main sources of heterogeneity addressed within benthic habitats concerns the variation in sediment structure. Imaging methods such as Sediment Profile Imaging (SPI) (Solan et al. 2003) (Table 5), and Computed Tomography (CT) scanning provide important information about the size, density and spatial (horizontal and vertical) arrangement of bioturbation from both macrofaunal (Solan et al. 2003) and meio-faunal species (CT scanning only - Mazik et al. 2008). This in turn provides valuable contextual information for understanding the biogeochemical regime of sediments, such as redox (oxidation-reduction conditions), traditionally gathered as point samples with profiling electrodes (Gray & Elliott 2009). The combined use of CT with Positron Emission Tomography (PET) can observe and explain the distribution of burrowing processes, bioturbation and sediment heterogeneity (Delefosse et al. 2015). As such, these imaging techniques can complement traditional techniques of benthic sampling (physical and biological) using grabs and corers, which provide high quality composite data of structural variables, with valuable functional information from both the macro- and meio-faunal assemblages even if grab samples homogenise the vertical patterns (Figure 5).

Pelagic imaging techniques mostly address the heterogeneity that stems from small-scale dispersal and patchiness (e.g. split-beam target tracking (Klevjer and Kaartvedt, 2003) and laser scattering and transmissometry (Anglès et al. 2006)). These techniques are particularly valuable for providing context for point sampling of plankton and suspend material within water column profiles.

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Many fine-scale imaging techniques (Table 5) are also capable of providing: (i) variables measured in real-time for the direct assessment of environmental status (e.g. optical planar optodes combined with SPI (Glud et al 2001) and *in situ* spectrophotometric techniques), (ii) *in situ* observations (e.g. SPI (Rosenberg et al. 2001, Solan et al. 2003), laser scattering and transmissometry and Spectrophotometric techniques), and (iii) *ex-situ* non-destructive observations (e.g. CT scanning (Rosenberg et al., 2008; Weissberger et al. 2009, Salvi et al. 2013)).

Therefore, the remote sensing techniques operating at the finest spatial scale often provide the most compatible datasets for the initial extrapolation from traditional point samples. However, at the finer spatial scales, it is likely that the need for extrapolation is driven by research interests and the need to understand benthic processes rather than for assessments of environmental health. Equally, the high cost, low replication and reduced availability of many of these techniques (e.g. CT and PET) suggests that they are better suited as research tools and currently have a limited value as routine methods of environmental health. Sediment Profile Imaging is, however, being increasingly used for environmental monitoring with the development of quality indices such as the Marine Sediment Quality Index (MSQI) (Gries 2006, Rosenberg et al. 2009).

<u>Remote sensing techniques observing at medium spatial scales (10^2 – 10^5 m^2)</u>

The multiple sources of heterogeneity occurring at this spatial scale are often a product of both physical heterogeneity (e.g. benthic substratum patchiness, bedform morphology, and water body features or local gradients) and biological processes (e.g. patchy distributions from settlement behaviour or grazing pressure). The interaction between these processes can generate high levels of influential heterogeneity that are particularly difficult to sample and describe using traditional methods. Acoustic techniques are well suited for data collection at intermediate spatial scales. Table 6 describes five remote sensing techniques that have added greatly to our understanding of heterogeneity at intermediate spatial scales.

As well as providing high resolution soundings of bathymetry, acoustic mapping systems, such as multibeam echo-sounders, have also been used to map superficial substrata (Table 6) and biological features (e.g. seagrass - Komatsu et al. 2003, Shono et al. 2004, Di Maida et al. 2011, and macroalgae - McGonigle et al. 2011). They can also provide valuable spatial information on the distribution of organisms within the water column (Benoit–Bird & Au, 2009) thereby indicating the level of heterogeneity generated by biological dispersal at intermediate scales (Table 6). Advances in autonomous underwater vehicle (AUV) availability, endurance, and reliability will further increase the spatial coverage of both acoustic and optical sensors mounted on these platforms. This combination of detailed observations and high spatial coverage is especially well suited to detect heterogeneity within both surficial substrata and the distribution of epifaunal species.

The use of video and photographic stills cameras to observe seabed habitats is an established survey practice which provides footage at the <1 m scale but can also cover transects of many km (Table 6). This information can be expensive to collect and process. Although problematic for many reasons (Lebart et al. 2000, Bernhardt & Griffing, 2001, Dawkins et al. 2013), automated seabed image analysis is likely to assist greatly these surveys by improving the objective classification and counting of benthic features in a cost-effective manner (e.g. Chailloux et al. 2008, Dawkins et al. 2013). Reflectance spectroscopy

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has also been used with image analysis for automatically detecting and counting specific species (Table 6). For pelagic environments, *in situ* techniques combining flow cytometry, machine-learning algorithms and image analysis have flourished recently (e.g. the Video Plankton Recorder (Davis et al., 1992, 1996) and the In Situ Ichthyoplankton Imaging System (Cowen et al., 2008, 2013)) can increase replication and/or sample volume over large areas.

Given the above, many of the remote sensing techniques are well suited for sampling, and therefore representing, sources of heterogeneity within intermediate spatial scales in both benthic and pelagic realms (Table 6 and Figure 5). Consequently, many imaging techniques already provide predictor variable data for the spatial scaling of benthic and pelagic point observations, e.g. predictive habitat mapping and species distribution modelling. Many of the acoustic and optical techniques are widely adopted and cost-effective enough to be routinely used for research and monitoring. The continued development and uptake of autonomous platforms and image analysis will both reduce acquisition and processing costs and increase coverage. Finally, the resulting data sets often relate directly to the SoH relevant for common extrapolations, e.g. substratum patchiness in benthic habitat surveys and turbulent advection induced patchiness in planktonic communities (Abraham 1998, McManus and Woodson 2012).

Remote sensing techniques observing at large spatial scales (10^5 – 10^{10} m^2)

Sampling and representing this spatial scale hitherto has been the most challenging for traditional forms of marine sampling. Fortunately, satellite and aerial imaging sensors provide unparalleled imaging at the broadest spatial scales on a range of important physical and chemical variables (see Table 7 for an overview of these techniques). This is especially the case for the pelagic realm through the reporting of important variables such as temperature, turbidity and the distribution of chlorophyll. The detection of biological features is however, limited to the direct detection larger marine mammals in surface waters (Abileah 2002) and seabirds at sea and in colonies (e.g. Hughes et al. 2011, Fretwell et al. 2015) (Table 7).

Imaging from satellite and airborne sensors is mostly restricted to observations of the sea surface. Nevertheless, although highly constrained in temperate areas due to the increased turbidity, satellite-derived imagery can be used to determine shallow bathymetry and broad-scale seabed features (Reshitnyk et al. 2014). This can greatly reduce the costs of collecting large areas of seabed information in a zone typically falling between the coverage of two other remote sensing methods i.e. MBES and LiDAR (Table 7). Despite this, there are practically no broad-scale imaging techniques for deeper benthic habitats.

Overall, the current suite of satellite and airborne imaging systems provides a clear representation of many of the most influential SoH within surface waters. Mid-water and benthic SoH are poorly represented at this scale and still rely on remote sensing methods associated with the small and medium scales. With regard to the availability of this information, satellite and airborne imaging is becoming cheaper and more available due to the increasing number of commercial suppliers of satellite imagery and low cost airborne platforms such as Unmanned Aerial Vehicle (UAVs). This has facilitated not just an increase in spatial coverage but also the ability to routinely resample large areas and hence provide greater temporal resolution on influential sources of pelagic heterogeneity. As such, these

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information sources are an extremely helpful when structuring regional and global extrapolation.

Summarising the descriptive and scalar properties of remote sensing

Many remote sensing methods provide observations across multiple spatial scales, and are even capable of collecting information at continental and global scales (e.g. satellite observations of pelagic habitats). Pelagic sources of heterogeneity can be observed almost across all spatial scales (Tables 5 – 7 and Figure 5). Benthic sources of heterogeneity can be observed between small and medium spatial scales, and occasionally at larger scales for shallow water habitat although as yet it is not possible to observe benthic sources of heterogeneity at the larger scales with sufficient resolution. This deficiency is likely to remain a significant hindrance for spatially extrapolating benthic observations and will limit the scale of assessment to regional levels. Despite this, remote sensing techniques will enhance several phases within spatial extrapolation, such as:

1) Accurate and objective representation of sources of heterogeneity, across broad spatial scales, within ecologically relevant predictor variables (Figure 3 and Table 8).
2) High-frequency sampling that enables cost-effective trend analysis and temporal prediction.
3) A direct assessment of variables representing the status of the environmental.
4) A cost-effective means of obtaining many broad-scale variables e.g. sea surface temperature, when compared with traditional sampling techniques obtaining similar levels of coverage.

Many of these benefits are often gained at the expense of traits common to traditional methods of sampling, i.e. certainty, specificity and the direct detection of the primary variables of interest. It is, therefore, apparent that information from traditional sampling and remote sensing must be combined to generate the best results from the extrapolative process. A framework is provided below for the integration of remotely sensed data within the extrapolative process.

Conclusions and recommendations

There has been a sustained scientific effort to examine environmental and ecological phenomena at larger, and typically, more appropriate spatial scales. The marine policy community has also driven this by requiring assessments of environmental status at larger spatial scales. For example, the EU Water Framework Directive and the Marine Strategy Framework Directive (2008/56/EC) require sub-regional and regional assessments of status (Borja et al., 2013b, c). Similarly, the US Clean Water Act and Oceans Act requires large-scale assessments of environmental quality (US Congress 2002; Crowder et al. 2006). The challenge is compounded as the marine environment is a complex mosaic of activities, each changing the environmental status within a homogeneous system, interspersed by areas where no impacts occur (Boyes et al 2016). In turn, governance requires the environmental status to be summarised across that heterogeneous area. Extrapolation is therefore required for both observing, assessing, interpreting and predicting ecological phenomena at their appropriate scales and delivering marine research and policy objectives.

If undertaken incorrectly, extrapolation can introduce substantial error and bias that ultimately undermines assessment and hence extrapolation must be reliable and repeatable.

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The basic framework for the extrapolation process provided by Miller et al. (2004) has been expanded here to help guide, formalise and make more objective these calculations. In support, remote sensing techniques are overcoming some of the limitations associated with traditional techniques and now make a significant contribution to the observation of marine systems at previously unimaginable spatial scales. The variety of valuable remote sensing techniques for the extrapolative process described here and the framework adapted to show how these data sets could be used to support extrapolation.

The adoption and greater use of existing imaging data sources are likely to provide a cost-effective approach for undertaking necessary assessments of environmental status and helping to overcome the monitoring requirement paradox highlighted by Borja and Elliott (2013a) – that more assessments are required but within decreasing resources for making those assessments. The concurrent development of spatial statistics within flexible platforms such as geographic information systems (GIS) has also greatly facilitated the uptake and analysis of imaging datasets and its use in extrapolation (Miller et al. 2004).

Future work is needed on (i) how to delineate units of heterogeneity in a meaningfully and consistently manner, (ii) the best way to sample response variables within units of heterogeneity, and (iii) capture uncertainty within extrapolation. Despite these difficulties, extrapolation remains a critical component for the appropriate reporting of ecological phenomena and environmental status and remote sensing techniques are essential for supporting this process. Alternative processes of scaling, such as lumping, are unlikely to provide values or surfaces of sufficient accuracy or resolution to be effective for ecological or assessment purposes. As such, scientists and managers of the marine environment working on related issues are encouraged to adopt and support the use of remote sensing techniques within their work and especially when extrapolating observations.

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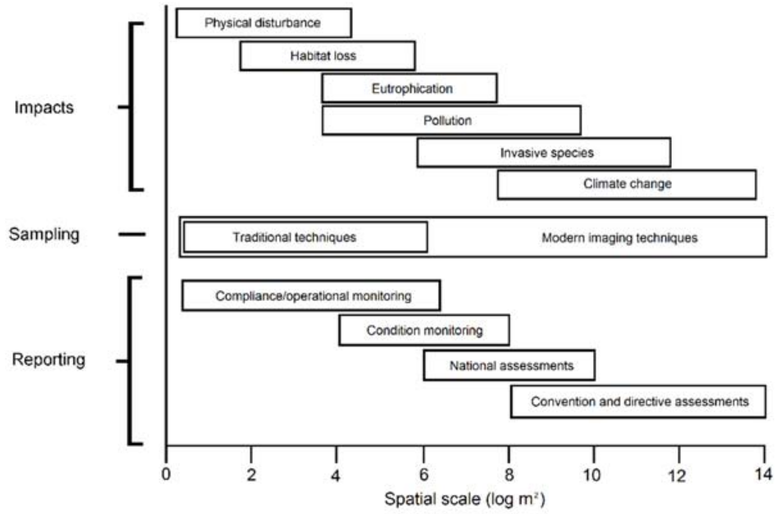

Figure 1. Domains of scale for examples of marine sampling, anthropogenic pressures and the reporting of environmental status.

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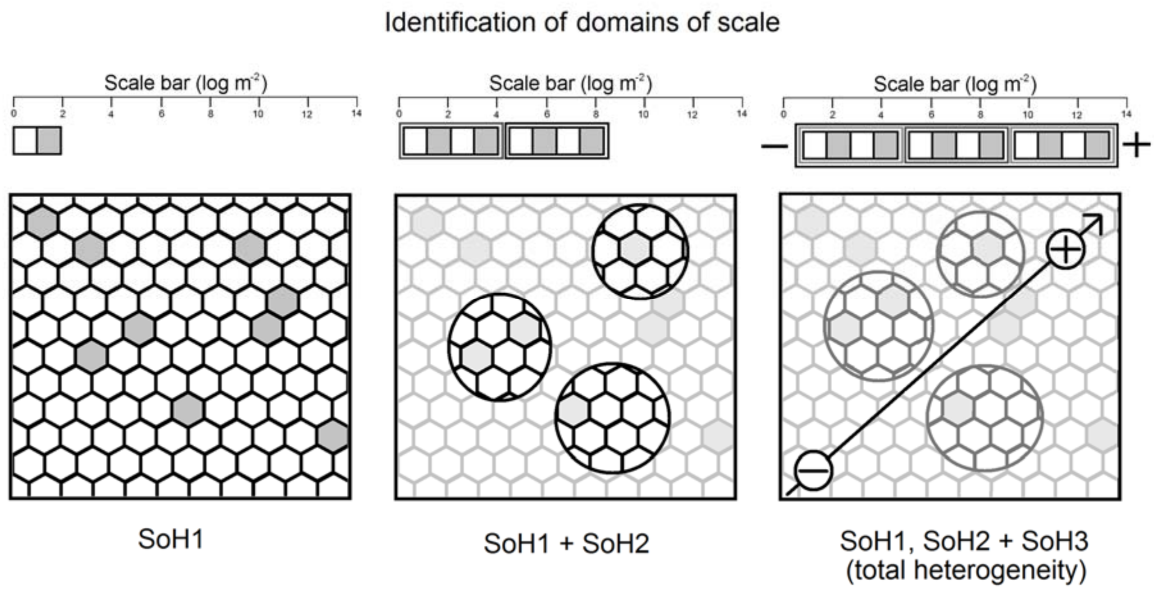

Figure 2. The nesting of three sources of heterogeneity and the generation of the total heterogeneity observed. Source of heterogeneity (SoH) 1 is a fine-scale qualitative variability occurring across an area (e.g. patches of different substratum classes), SoH 2 is a broad-scale qualitative variability occurring across an area (e.g. dispersal range of a species) and SoH 3 is quantitative gradient in variability that occurs across an area (e.g. temperature).

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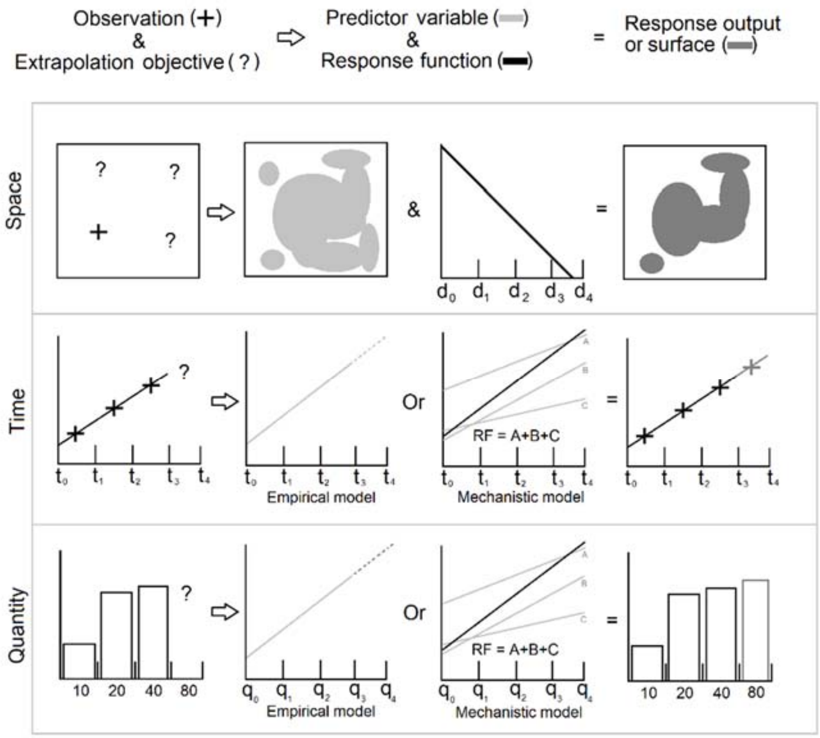

Figure 3. Basic types of extrapolation used in ecology.

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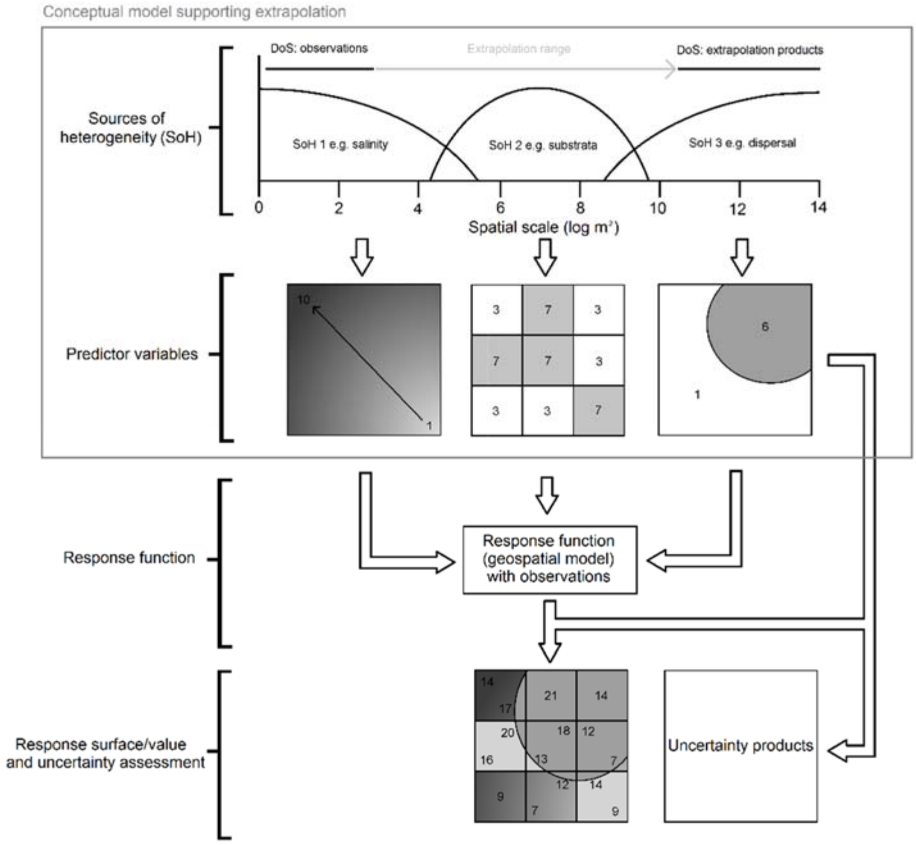

Figure 4. A framework for extrapolation (modified extensively from Miller et al. (2004)). The example depicts how species richness could be extrapolated across an area containing three sources of heterogeneity. Within the example, substrata patchiness constitutes the fine-scale heterogeneity, which is itself nested within a larger zonation of biological dispersal (medium-scale heterogeneity). Finally, a temperature gradient provides a broad-scale source of heterogeneity across the entire site. The example provides hypothetical response functions for species richness for each source of heterogeneity (or a combine response function in ‘route B’). The response functions can then be used to convert values of heterogeneity, provided as predictor variables from remote sensing techniques, into predicted values of species richness. The individual response surfaces are aggregated to produce a combined response surface (unless route B has been used).

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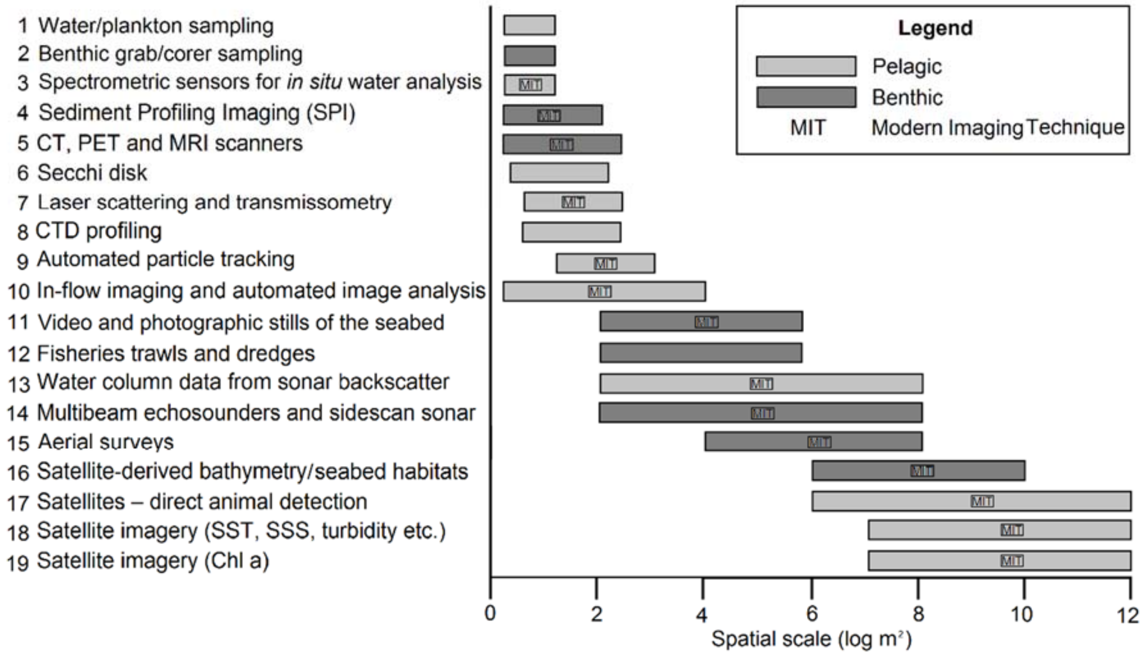

Figure 5. Domains of scale associated with traditional sampling and remote sensing techniques.

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Table 1. Information required from qualitative and quantitative sources of heterogeneity for the construction of response and scaling functions (P/A: presence/absence data).

		Sources of heterogeneity with example parameter	
		Qualitative (P/A, state or class) e.g. patches of different classes of substratum	Quantitative (range of values on a continuous scale) e.g. sea surface temperature
Response variable to be extrapolated with example variable	Qualitative (P/A, state or class) e.g. categorical levels of environmental status	Determine the response variable state or class for each class within a SoH	Determine the response variable state or class for discrete ranges of values within the SoH
	Quantitative (range of values on a continuous scale) e.g. change in extent	Determine the response variable value for each class within a SoH	Determine the response variable value across the range of values within a SoH

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Table 2. A comparison of possible approaches for the extrapolation of habitat extent using remote sensing techniques.

Extrapolation approach and information required	Sources of heterogeneity (SoH) addressed				Processing and response function required	Advantages	Disadvantages
	Distributional patchiness[1]	Substratum	Depth	Oceano-graphic variables[2]			
Interpolation from grabs or photographic stills	No	Partially (broad-scale only)	Partially (from platform only)	No	Manual segmentation, buffering or Thessian polygons (qualitative data) or geospatial interpolation (quantitative data) followed by spatial summation	Minimal data requirement Simple to undertake	Simplistic classification surface and inaccurate extrapolation products The extrapolated values will be biased by sampling distribution, allocation and effort Extrapolation beyond the survey site is not possible Fails to fully account for any SoH Expert judgement required for some processing steps
Interpolation from video transects	Partially (via burrow entrances observed in footage)	Partially (broad and fine-scales)	Partially (from platform only)	No	As above	Partial correction for distributional and substratum patchiness Few assumptions	Extrapolation beyond the survey site is not possible This approach fails to account fully for any SoH The extrapolated values will be biased by sampling distribution, allocation and effort Expert judgement required for some processing steps
Full coverage photo/video-mosaic surface (AUV or ROV)	Partially (via burrow entrances observed in footage)	Yes	Yes	No	Segmentation of the image followed by spatial summation	Full correction for substratum and depth improves the accuracy of the extrapolation No interpolation or assumptions required Full coverage products are generated	Expensive to collect and therefore limited to small survey areas Extrapolation beyond the survey site is not possible
Geospatial modelling of grabs, stills and/or video with hydro-acoustic data (e.g. MBES)	Partially (via burrow entrances observed in footage)	Yes	Yes	No	Geospatial modelling (regression or machine learning methods) followed by spatial summation	An established mapping approach Full correction for substratum and depth improves the accuracy of the extrapolation Full coverage, high resolution products Depending on transferability, the model can be applied to other local acoustic data sets lack grab/video observations	This approach is complex and requires specialist skills Assumptions linking environmental variables and 'potential habitat' are required during the geospatial modelling An acoustic survey represents a significant survey cost
Geospatial modelling of grabs, stills and/or video, hydro-acoustic data (e.g. MBES) and oceanographic observations (in-situ or satellite sources)	Partially (via burrow entrances observed in footage)	Yes	Yes	Yes	Geospatial modelling (regression or machine learning methods) followed by spatial summation	Full correction for substratum, depth and oceanographic variables results in high level of accuracy for the extrapolated values Depending on transferability, the model can be applied to other regional acoustic data sets lack grab/video observations	This approach is complex and requires specialist skills Assumptions linking environmental variables and 'potential habitat' are required during the geospatial modelling An acoustic survey represents a significant survey cost

[1] Example based on a habitat supporting a burrowing mega-infaunal assemblage
[2] For example, temperature, salinity, currents, chlorophyll, SPM etc.

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Table 3. A comparison of possible approaches for the extrapolation of fish abundance, from various stock assessment (SA) methods, using remote sensing techniques.

Extrapolation approach and information required	Sources of heterogeneity addressed			Processing and response function required	Advantages	Disadvantages
	Local patchiness (shoal)	Regional patchiness (distributional)	Oceanographic variables[3]			
Landings data (fishery dependent)	No	No	No	Direct or ratio SA expansion method and spatial summation	Well replicated input data	Extrapolated values biased by landings size, under-reporting and port avoidance No SoH are specifically addressed, and extrapolated values are likely to be skewed
Gridded trawl survey (fishery independent)	No	Yes	No	Direct or ratio SA expansion method and spatial summation	Greater sampling of size classes and a broader assessment area addresses the regional distribution of species and leads to a more representative extrapolation of the stock	Aspects of local patchiness or broad-scale environmental drivers are not assessed, hence reducing the accuracy of the extrapolated value
Trawl and hydro-acoustic survey (fishery independent)	Yes	Yes	No	Area SA expansion method and spatial summation	Local distribution (shoal size and distribution) is estimated, via the hydro-acoustic survey, and the trawl observations corrected (improving the final extrapolated value) Greater sampling of size classes and a broader assessment area addresses regional distribution of species and leads to a more representative extrapolation	The influence of broad-scale environmental drivers are not assessed, hence reducing the transferability of the extrapolation approach across large spatial areas
Trawl and hydro-acoustic survey with remotely sensed oceanographic variables	Yes	Yes	Yes	Meta-analysis SA method and spatial summation	All of the influential SoH are observed and used to correct the extrapolation The use of satellite-derived oceanographic variables allows the modelling/extrapolation of other probable fish locations and the incorporation of the 'ecosystem-based' approach to fisheries management	The combination of multiple data sources requires a complex SA/extrapolation approach The incorporation of ecosystem drivers requires further calibration and additional assumptions within the stock assessment method

[3] e.g. Sea surface temperature and phytoplankton type / abundance

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Table 4. The extrapolation of total primary production (PP) using extrapolation approaches including progressively more remote sensing techniques. The advantages and disadvantages associated with each approach, and the sources of heterogeneity captured, are discussed for each approach.

Extrapolation approach and information required	**Sources of heterogeneity addressed**			**Processing and response function required**	**Advantages**	**Disadvantages**
	Local patchiness (horizontally and vertically)	**Oceanographic variables (regional patchiness)**	**Temporal variation**			
In-situ point sampling of chlorophyll and the light field	Partially	Partially (broad-scale interpolation only)	No	Mechanistic or empirical modelling of PP, linear spatial integration followed by volumetric summation	Simple and established assessment of PP using chlorophyll concentration	Unable to extrapolate beyond the extent of the point samples (horizontally or vertically) Fails to fully account for any SoH and the resulting extrapolation is likely to be inaccurate in heterogeneous areas Extrapolations biased by sampling distribution, sampling depth, effort and survey timing
Moored, *in-situ* spectrometric sensors of chlorophyll, light field, temperature and nutrients	No	No	Yes	Mechanistic or empirical modelling model of PP, linear spatial integration followed by volumetric summation	Temporal variation at the sensor station is observed and integrated into the extrapolated value	Multi-sensor moorings are expensive and subsequently networks typically have a very limited spatial coverage Unable to extrapolate beyond the extent of the sensor network (horizontally or vertically) Extrapolations biased by the number and location of moorings, sensor depth and observation interval/timing
Aerial-derived chlorophyll fluorescence, light field, temperature	Yes	Partially (full coverage of a subset or partial coverage of the full area)	No	Mechanistic or empirical modelling and volumetric summation	Full coverage, high-resolution mapping of parameters relevant for PP generate accurate extrapolations	The spatial coverage is insufficient for regional extrapolations of PP *In situ* profiling is still required to account for vertical heterogeneity Repeated surveys are required to capture temporal trends within extrapolated values
Satellite-derived chlorophyll fluorescence, light field, nutrients and temperature	Yes	Yes	Yes	Mechanistic or empirical modelling followed by volumetric summation	All of the most influential SoH are observed and compensated for within the extrapolation The spatial scale of the observations is broadly aligned with the domain of scale relevant for PP	*In situ* profiling is still required to account for vertical heterogeneity The combination of multiple data sources requires a complex extrapolation approach The incorporation of oceanographic variables requires further calibration and additional assumptions within the extrapolation

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Table 5. Description of remote sensing techniques observing at small spatial scales (typical survey coverage 10^{-1} – 10^{2} m^2).

Method
Computed tomography (CT) scanning: Computed tomography (CT) scanners either rotate samples within a stationary x-ray beam or more conventionally, rotate an x-ray source in a spiral around the sample. Magnified images are received onto a detector screen and processed, by computer, into a high-definition, three-dimensional images of the sample. Computed tomography scanners have been used to image burrow morphology within sediment samples and estimate rates of bioturbation (e.g. Perez et al. 1999, Michaud et al. 2003, Rosenberg et al. 2007, Mazik et al. 2008 (including meiofaunal structures), Rosenberg et al. 2008, Weissberger et al. 2009, Salvi et al. 2013).
Positron emission tomography (PET): PET scanning requires the spiking of samples with radionuclide tracers. The PET scan then detects products from the decay of the radionuclide to indicate the movement and accumulation of the tracer within the sample. When used in combination with CT scanning, PET scanning can be particularly informative about the distribution and rate of processes, e.g. sediment/water diffusion induced by bioturbation (Delefosse et al. 2015).
Magnetic resonance imaging (MRI): Magnetic resonance imaging (MRI) use magnetic fields and radio waves to image the internal structure of samples and is especially suited for soft tissues and materials. Magnetic resonance imaging (MRI) has proven well-suited and has been successfully used to image the internal physiology of several species of oyster (e.g. Pouvreau et al. 2006), starfish (Sigl et al. 2013) and estimate gonad maturation in oysters (e.g. Davenel et al. 2006, Smith & Reddy, 2012).
Sediment profile imaging (SPI): Sediment profile imaging collects cross-sectional images of benthic sediments and provides important insights into the sedimentary environment at a greater spatial scale than traditional point sampling. (Rosenberg et al. 2001, Solan et al. 2003). Variables collected include sediment grain size, redox discontinuity depth, gas vesicles, infaunal burrows and epifaunal presence. Many of the variables are calculated automatically by processing software and the resulting values used to calculate various indices of benthic habitat quality specific to SPI-derived data (Solan et al. 2003).
Two and three-dimensional imaging of oxygen and pH: Optical planar optodes can provide two-dimensional quantification of oxygen distribution with a spatial resolution of approximately 0.1 mm over areas of several cm^2 (Glud et al. 1996, Glud et al. 2001). This approach has been shown to be a sensitive and cost-effective tool for assessing the distribution of oxygen for marine sediment samples both in the laboratory (Zhu and Aller 2012) and *in situ* (e.g. combined with SPI by Glud et al. 2001). The same method can also be used to image the distribution of pH values within sediments (Larsen et al. 2011). The three-dimensional imaging of intra- and inter-cellular oxygen concentrations has also become possible through the use of MRI and electron spin resonance (ESR) (Halevy et al. 2010), and the latter has been applied to various marine applications (e.g. the imaging of oxygen fluxes within endolithic algal communities with corals (Kühl et al. 2008).
Automated particle tracking: Split-beam target tracking has been used to both on hull-mount (Røstad 2000 in Klevjer and Kaartvedt, 2003) and *in situ* applications (Klevjer and Kaartvedt 2003) to track individual krill within the water column. Equally, camera-based systems have also been used to autonomously track the movement of plankton in the laboratory Mallard et al. 2013).
Spectrometric sensors for *in situ* water analysis: *In situ* spectrophotometric and fluorescence techniques are quickly providing a proven alternative to traditional analysers using wet chemistry techniques for the monitoring of nutrients, chlorophyll and dissolved gases. Several commercial units utilising ultraviolet spectrophotometric techniques now available and are supported by numerous peer-reviewed studies (e.g. Adornato et al. 2007, Sandford et al. 2007, Zielinski et al. 2011). These *in situ* units are typically capable of detecting nitrogenous compounds between 0 µM and 4000 µM with an accuracy of ± 2 µM (Zielinski et al., 2011). These units can be deployed as either (i) static / buoyed, (ii) profiling or (iii) flow-through instruments. Nitrogenous compounds, and especially nitrate, are extremely influential on coastal and oceanic ecosystems. Sizeable anthropogenic contributions to coastal nitrate are associated with eutrophication and significant environmental perturbation. As such, nitrate concentrations are a core water quality variable and common in many monitoring programmes of water quality. Equally, in situ sensors utilising fluorescence quenching are rapidly replacing traditional, galvanic sensors, for dissolved oxygen.
Laser scattering and transmissometry: Deployable instruments, such as the 'laser in situ scattering and transmissometry' (LISST) 100X, were developed for the automated detection of suspended particle size distribution (Agrawal and Pottsmith 2000). Although originally designed for sediment analysis, studies have demonstrated the potential of these instruments to measure the size distribution of phytoplankton and bacteria (Serra et al. 2001, Rienecker et al. 2008), and for species detection in mixed phytoplankton communities (Anglès et al. 2006).

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Table 6. Description of remote sensing techniques observing at medium spatial scales (typical survey coverage 10^2 – 10^5 m^2).

Method
Underwater stills photography and video transects: Underwater stills photography and video transects collected using various platforms (e.g. epibenthic sledges, drop-down systems, ROVs and AUVs) are well-established techniques and deliver vast amounts of seabed imagery to support various activities such as habitat mapping, stock assessments and condition monitoring. Most photographic and video platforms have an unlimited bottom time and are capable of imaging large spatial areas. As well as documenting the epifaunal community, this footage provides essential information on the physical and biological heterogeneity of seabed habitats. Image analysis systems use various approaches such as shape/outline analysis (Aguzzi et al. 2011), textural assessments, and machine-learning algorithms (Purser *et al*. 2009) to automatically detect and quantify objects within images (Dawkins et al. 2013). Photo mosaicing has also been shown to aid in the mapping of habitat (e.g. Rende et al. 2015). Automated image analysis is facilitating the process of both video and stills imagery and has been successfully applied to cold water coral (Lophelia pertusa) coverage (Purser et al. 2009), sessile benthic species (Beuchel et al. 2010, Teixidó et al. 2011, Trygonis and Sini, 2012), pacific scallops (Dawkins et al. 2013) and the counting of burrows (Nephrops norvegicus) (Lau et al. 2012). Photo mosaicing has also been shown to aid in the mapping of habitat (e.g. Rende et al. 2015).
***In situ* reflectance spectroscopy for benthic mapping:** Hyperspectral radiometers used *in situ* have been used to identify and map individual species, physical substrata and vegetative types based on reflected spectra (Werdell & Roesler 2003, Moline et al. 2007, Caras & Karnieli 2013, Leeuw et al. 2013).
***In situ* imaging of plankton and nekton:** Recent developments have combined *in situ* platforms, flow cytometry, microscopy and image analysis to automate the processing of phytoplankton cells and suspended particles that range from 3 to 3000 um in size. Furthermore, the measurement of phytoplankton abundance and size from imaging-in-flow analyses are precise and considered more reflective of natural size spectra, and often outperform manual microscopy methods (e.g. Sosik & Olson 2007, Alverez et al. 2014) for all but thematic classification (Zetsche et al. 2014). Plankton communities can be imaged and identified *in situ* using towed camera platforms, e.g. the Video Plankton Recorder is able to optically image and automatically identify both phytoplankton and zooplankton taxa (broad groupings), and map their abundance and distribution in real time (Davis et al. 1992, 1996). Similar *in situ* samplers have been developed for other components e.g. ichthyoplanton (Cowen et al. 2008, 2013) and JellyCam (Graham et al. 2003).
Acoustic mapping of the benthos: Acoustic methods such as AGDS, MBES and SSS interpret information from the delay, intensity and/or character of an acoustic pulse returned from the seabed to determine depth and surficial character. The backscatter intensity values obtained during sidescan sonar (SSS) and multibeam echosounder (MBES) surveys have been shown to correlate with several geotechnical properties of the seafloor sediments such as grain size and sorting (e.g. Collier & Brown 2004, Brown & Blondel 2009, Brown et al. 2011). As such, backscatter data, supported by ground-truthing samples, is routinely used to classify the seabed into coarse surficial sediment classes.
Water column backscatter data from multibeam echo-sounders (MBES) and wideband sonars: For MBES, the limitations of detection and storage (Colbo et al. 2014) mean that only the backscatter return from the seabed was typically recorded and processed. Recent advances now allow the collection of backscatter from the water column (both from MBES and single-beam wide-band sonars). Wideband sonars collect backscatter information from a range of frequencies to greatly increase resolution and frequency response, which aids in the discrimination between plankton and fish and facilitates species identification and shoal description. Biological groups that can be clearly imaged within water column backscatter include (i) shoals of fish (e.g. Benoit-Bird & Au 2009), (ii) marine mammals and seabirds (e.g. Benoit-Bird & Au 2009), (iii) zooplankton (e.g. Korneliussen et al. 2009) and (iv) macroalgal biomass (McGonigle et al. 2011). Swim bladders (Foote 1980) and lung cavities for marine mammals (Au 1996) are the primary sources of backscatter. Scattering also occurs between the flesh/water interface thereby allowing the detection of fish without swim bladders (Reeder 2011) – it is for the same reason that concentrations of zooplankton can also be imaged acoustically (Colbo et al. 2014).

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Table 7. Description of remote sensing techniques observing at large spatial scales (typical survey coverage $10^5 – 10^8$ m^2)

Method
Satellite-derived surface observation: The detection of oceanic variables from satellite sensors has transformed the observation of large and generally inaccessible sea areas. Satellite sensors are capable of detecting ecologically important variables such as sea surface temperature (Merchant et al. 2012), salinity (Reul et al. 2014), surface waves and currents (Klemas, 2012), and coarse seabed altimetry/bathymetry (Sandwell et al. 2006) over continental and even global scales. Furthermore, ocean colour contains additional variables for pigments (e.g. Chlorophyll a) and particulates (e.g. calcite products for the detection of coccolithophores and the use of reflectance and backscatter for particulate organic matter) in seawater (McClain 2009). It is also possible to estimate surface nutrient concentrations such as dissolved inorganic nitrogen and phosphorus (e.g.Xu et al. 2013, Yu et al. 2016).
Satellite-derived bathymetry and seabed features: The recent availability of satellite imagery of very high resolution with multiple collection bands has generated new possibilities for seabed mapping. For example, WorldView-2 satellite images are being processed to provide the bathymetry and seabed features (e.g. submerged vegetation, topographic features, and very coarse sediment classes) for shallow coastal waters (Reshitnyk et al. 2014). Current estimates of vertical accuracy are approximately 10 % of water depth, suggesting that bathymetry derived from satellite imagery has a lower accuracy than traditional mapping techniques (e.g. MBES). Nonetheless, the vertical error is likely to be acceptable for habitat mapping purposes where relative change is more important than absolute depth. Bathymetry can be currently collected to approximately 30 m in clear, tropical waters. However, in turbid, temperate waters (or tropical areas with poor water quality), penetration is significantly reduced (Reshitnyk et al. 2014), which reduces the current applicability of this technique.
Satellite imagery for the direct observation of marine animals: As the resolution and availability of satellite imagery increases, greater efforts have been made to directly detect marine animals (Abileah 2002) such as whales in specific locations (Fretwell et al. 2014). The detection of marine mammals that use the shoreline is improved greatly as issues relating to turbidity and sea surface roughness are eliminated e.g. LaRue et al. (2011) used satellite imagery to count hauled-out Weddell seals (*Leptonychotes weddellii*) in Antarctica. For seabirds, estimates of population sizes based on ground discolouration (e.g. guano deposits or vegetation fertilised by guano) and were considered successful for king penguins (*Aptenodytes patagonicus*) (Guinet et al. 1995) and emperor penguins (*Aptenodytes forsteri*) (Fretwell and Trathan 2009). Increases in the resolution of satellite imagery now permit the detection of some nests and individual seabirds, hence allowing population estimates to be obtained for several species of penguin (see references in Fretwell et al. 2015) and nests of masked boobies (*Sula dactylatra*) (Hughes et al. 2011).
Aerial optical and multispectral remote sensing: Optical remote sensing techniques are routinely used for imaging shallow water habitats. For example, bathymetric Light Detecting and Ranging (LiDAR) uses both blue-green and near-infrared lasers to obtain shallow water bathymetry. Laser penetration is approximately 2 – 3 times the Secchi disk depth (approximately 40 – 50 m of depth in clear tropical waters but more realistically less than 10 - 20 m in temperate waters). Bathymetric LiDAR is particularly useful for obtaining soundings in areas too shallow for MBES, and yet too deep for standard terrestrial surveying methods. Airborne multispectral methods, such as CASI (Compact Airborne Spectrographic Imager), have also contributed to wide-scale mapping of large intertidal and shallow subtidal areas and are able to discriminate various types of vegetation and substrata.

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Table 8. Common sources of heterogeneity detectable with remote sensing techniques.

Class	Source of heterogeneity	Predictor variable for the source of heterogeneity	Remote sensing technique
Physical	Temperature	Sea surface temperature	Satellite-derived imagery
	Bathymetry	Broad-scale bathymetry (with derived variables)	Satellite-derived altimetry
		Shallow water bathymetry and habitat class (with derived variables)	Satellite-derived bathymetry
		Bathymetry (with derived variables)	Acoustic mapping of the benthos (e.g. MBES)
		Elevation and bathymetry (with derived variables)	LiDAR
	Sediment class	Coarse sediment class	Satellite-derived seabed features
		Surficial sediments/texture	Acoustic mapping of the benthos (e.g. MBES)
		Identity and cover of broad-scale substrata	Underwater stills photography and video transects
		Identity and cover/abundance of substrata and epifaunal species	*In situ* reflectance spectroscopy for benthic mapping
		Identity and cover/abundance of substrata and specific species	Airborne multispectral methods
	Physical disturbance	Burrow structure/bioturbated area	Computed tomography (CT)
		Processes within burrow and bioturbated sediments	Positron Emission Tomography (PET)
		Bioturbation activity and redox depth	Sediment profile imaging (SPI)
		Wave and current energy	Satellite- derived altimetry and mounted synthetic aperture radars
	Light penetration/turbidity	Wavelength reflectance and coefficient of light attenuation (KDPAR)	Satellite-derived ocean colour
Chemical	Gas saturation	Processes within burrow and bioturbated sediments	Oxygen micro-imaging
	Salinity	Radiometric penetration depth (sea surface salinity)	Satellite-derived imagery
	Organic inputs	Reflectance at 555 and 510 nm for particulate backscatter and particulate organic matter.	Satellite-derived imagery
Biological	Distribution and dispersal	Automated particle tracking	Split-beam acoustic target tracking
		Classification and enumeration of planktonic patchiness	*In situ* plankton analysers with in-flow imaging and image analysis
		Distribution of large, mid-water material	Water column data from sonar backscatter
		Extent, density and distribution of specific species	Underwater stills photography and video transects
		Cover and distribution of specific species	Acoustic mapping of the benthos
		Cover and distribution of specific species	*In situ* reflectance spectroscopy for benthic mapping
		Classification and distribution of pelagic material	Wideband sonars (single-beam)
		Cover and distribution of intertidal and shallow subtidal species and habitats	Airborne multispectral methods
		Distribution and abundance of planktonic communities	Satellite-derived ocean colour
		Identity, distribution and abundance of colonies and certain species	Satellites imagery (direct animal detection)

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