




Quo Vadimus

Grand challenge for habitat science: stage-structured responses, nonlocal drivers, and mechanistic associations among habitat variables affecting fishery productivity

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Spatial management has been adopted worldwide to mitigate habitat impacts while achieving fisheries management objectives. However, there is little theory or practice for predicting the impact of spatial regulations on future fishery production; this would provide scientific basis for greater flexibility in fisheries management when balancing fishery and conservation goals. We propose that predicting changes in fishery production resulting from human activities within specific habitats is a “Grand Challenge” for habitat science in the coming decade(s). We then outline three difficulties in resolving this Grand Habitat Challenge, including: (i) stage-structured responses to habitat impacts, (ii) nonlocal responses, and (iii) mechanistic associations among habitat variables. We next discuss analytical approaches to address each difficulty, respectively: (i) ongoing developments for spatial demographic models; (ii) individual movement models and rank-reduction approaches to identify regional variability; (iii) causal analysis involving structural equation models. We demonstrate nonlocal effects in detail using a diffusion-taxis movement model applied to sablefish (*Anoplopoma fimbria*) in the Gulf of Alaska and discuss all three approaches for deep-sea corals. Despite isolated progress to resolve individual difficulties, we argue that resolving this Grand Habitat Challenge will require a coordinated commitment from science agencies worldwide.

Keywords: advective-diffusive movement, Grand Habitat Challenge, habitat-selection function, structural equation model

Introduction

Modern efforts to provide a scientific basis for fisheries management can be traced back over 150 years (Smith, 2007). During

this time, fisheries scientists have adopted ecological, mathematical, econometric, and statistical techniques (among others) to predict future changes in fishery production arising due to

present-day changes in fishery regulations. In the United States, a long history of co-development has resulted in legislation obligating fisheries managers to maintain catch levels (with few exceptions) below the rate that corresponds to scientific advice regarding maximum sustainable yield, MSY, and to develop rebuilding plans for species with a biomass far below the level producing MSY (Methot, 2009); there is a similar regulatory emphasis upon “stock status” within the ICES fisheries management framework (ICES, 2019). This framework gains legitimacy in part from a long history of predicting changes in future fishery production resulting from present-day regulations, through a theoretically grounded and empirically validated understanding of individual growth using per-recruit models (Beverton and Holt, 1957) as well as empirically derived biomass-dynamic or age-structured production models (Schaefer, 1954). These two methods for predicting future fishery production have subsequently been synthesized within “integrated” assessment models that combine model structures and parameters derived from process research with information from monitoring data (Maunder, 2008). Integrated stock-assessment models are typically used to identify stock status while leaving fisheries managers free to identify the set of regulations needed to achieve annual catch targets that are consistent with long-term management objectives. There is extensive research to empirically evaluate the successes and failures of stock assessment to predict productivity and thereby support effective fisheries management (Gutiérrez et al., 2011; Cardinale et al., 2013; Neubauer et al., 2013).

Simultaneously, there is a parallel history for science to prioritize the conservation or restoration of habitats as well as mitigate impacts from the fishing industry (e.g. trawl exclusion areas) as well as other sectors (e.g. eutrophication from agriculture, offshore and nearshore development projects, noise from shipping). In the United States, this history resulted in a legal requirement for fisheries managers to periodically consider updates to areas designated as essential fish habitat (EFH) and habitat areas of particular concern (HAPC), as well as scientific interpretation regarding multiple levels of habitat information that can be used as scientific support for EFH designation (Yoklavich et al., 2010). Information regarding EFH and HAPC is then used during consultations with fisheries management councils (when regulating fishing sectors) and other government agencies (regarding regulations upon agriculture, shipping, nearshore development, and other activities). However, EFH is typically designated on the basis of habitat-specific distribution and density for target (commercially harvested) and nontarget (captured as bycatch) fishes in fishery management plans, rather than predicting how habitat impacts will affect future fishery productivity. Alternatively, there is a growing interest in “benthic habitat-impact assessments” predicting fishery impacts on benthic organisms based on their recovery rates after disturbance, combined with maps of benthic communities and fishing (Hiddink et al., 2017; Rijnsdorp et al., 2018; Sciberras et al., 2018). These assessments are mandated by the European Marine Strategy Framework Directive (Rice et al., 2012), as implemented within the ICES Working Group on Fisheries Benthic Impact and Trade-Offs (Eigaard et al., 2020), and separately in the United States, e.g. during EFH designations in waters near Alaska (Smeltz et al., 2019). Although benthic habitat-impact assessments predict recovery rates for biogenic habitat after human disturbance, they do not typically predict the likely impact of contemporary spatial regulations on future fishery production. While there are periodic efforts to develop heuristic

and statistical models predicting future changes in fishery production from habitat impacts (e.g. fig. 2 of McConnaughey et al., 2020), these are not as widely used or enacted in national policy to the same extent as analogous efforts for stock assessment.

From this brief history, we conclude that stock assessment is tasked with predicting likely changes in fishery production from regulatory changes, while habitat science remains primarily focused on describing habitat-specific distribution, density, demography, and benthic recovery rates. In the following, we argue that the task of predicting likely future changes in fishery production arising from spatial regulations of both fishing and non-fishing sectors at fine-spatial scales is a “Grand Challenge” for habitat science. We further argue that such predictions would increase the relevance of habitat science to fisheries managers, both because it allows participatory evaluation of likely impacts of habitat changes on fishery productivity (i.e. sustainable fishing opportunities) and because it encourages validation and refinement of scientific information (Stephenson and Lane, 1995). We first outline a “biomass-dynamic habitat model” via analogy to biomass-dynamics models used for stock assessment. This model predicts changes in future population biomass at different locations, given the prevailing biological and environmental conditions defining habitats at those locations. This model could be used to predict future production of nontarget species (e.g. benthic infauna), thus resembling benthic habitat-impact assessments and thereby informing trade-offs between exploitation and conservation, or targeted species (e.g. commercial fishes), thereby predicting changes in sustainable fishery harvest from habitat impacts. However, we acknowledge that some modification is likely needed for specific applications (for example individual movement likely is less important for benthic infauna than migratory fishes). We then define three difficulties that must be addressed to resolve this Grand Habitat Challenge and explore approaches to each difficulty via extensions to the biomass-dynamic habitat model. This includes a detailed illustration of how fine-scale habitat usage can be inferred from movement analysis and tagging data. We note limitations resulting from data and knowledge gaps, and how these can be addressed, while also illustrating application for deep-sea corals. Finally, we recommend future efforts to coordinate research in the United States and worldwide to address this Grand Habitat Challenge by 2030.

Defining the biomass-dynamic habitat model

Since the 1950s, stock-assessment scientists have used biomass-dynamics (a.k.a. surplus production) models to communicate principles regarding maximum sustainable yield as well as to predict likely change in future fishery production arising from regulations on fishery removals. Modern production models predict the change in biomass ΔB using three variables: current biomass B , measured environmental conditions as well as residual variation X , and catch C (Figure 1). The impact of current biomass on future yield is typically represented using a production function approximating density-dependent and -independent demographic processes, fixed and random effects are estimated to account, respectively, for measured and missing covariates, and catch C typically includes both directed harvest as well as indirect mortality such as catch-and-release mortality rates and bycatch. Importantly, fishery catch is included such that the outcome resulting from an exogenous change in fishery catch (i.e. due to harvest regulation) can be predicted.

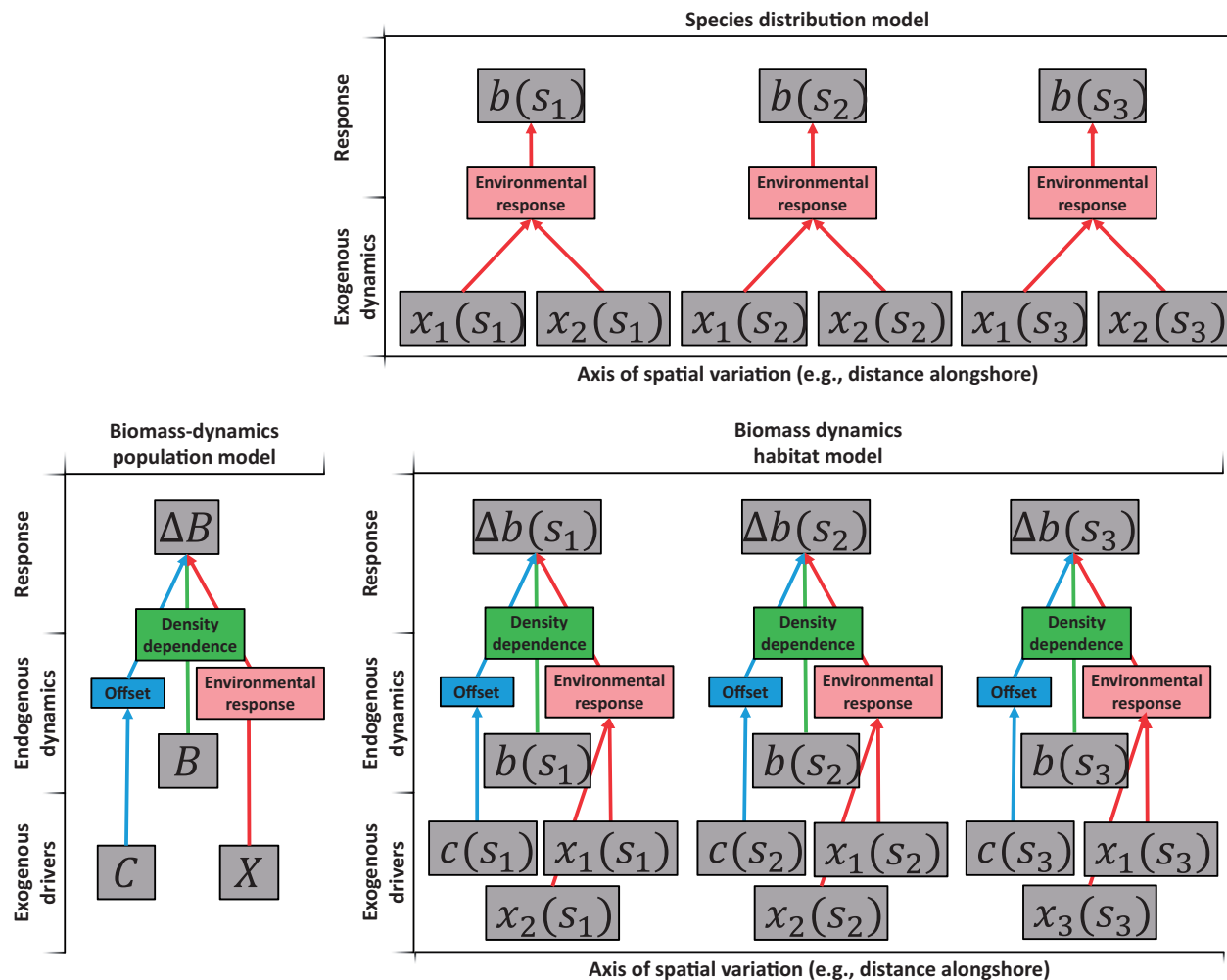


Figure 1. Schematic representations showing the relationship among variables in a conventional biomass-dynamics population model (bottom left panel, a.k.a. “surplus production model”) used for stock assessment and an SDM (top-right panel), and how the two can be combined in a biomass-dynamic habitat model (bottom-right panel). These models include a population biomass, either summed across space B or defined as $b(s)$ for each location s , and the “dynamics” models also include production of biomass ΔB or $\Delta b(s)$. All models include one or more covariates X or $x(s)$, and dynamics models include an additional assumed response to harvest C or $c(s)$. These variables are linked by a specified form for environmental responses (red boxes and arrows), an assumed response to harvest (blue boxes and arrows), and a density-dependent response of production to current biomass (green boxes and arrows).

By contrast, habitat scientists are often trained to fit species distribution models (SDMs) to opportunistic records and field-sampling data, and then use predicted species densities to interpret environmental drivers, plan future sampling, and prioritize areas for protection (Leathwick *et al.*, 2006; Winship *et al.*, 2020). These SDMs often include many covariates and sometimes include residual variation that is spatially correlated. However, SDMs often do not explicitly predict annual production of biomass ΔB , or account for mortality associated with fishery operations (where we proceed using the term “catch” and notation C to represent both harvest and mortality due to gear contact and physical disturbance to maintain similar notation to biomass-dynamic models). They therefore do not include the variables needed to compute the likely change in biomass resulting from changes in spatial distribution of removals. Exceptions exist, including analyses that represent changes in biomass as a function of fishery removals and local productivity (Thorson *et al.*, 2017), or analyses that combine density predictions with subsequent information about fishery impacts and recovery

rates (Smeltz *et al.*, 2019; Rijnsdorp *et al.*, 2020). These exceptions demonstrate that accounting for production of biomass can be as simple as specifying a fixed rate of natural mortality and/or recovery, and typically aggregate data-poor species into assemblages and/or use meta-analysis to identify mortality/recovery rates for these assemblages (Hiddink *et al.*, 2017; Sciberras *et al.*, 2018; Rijnsdorp *et al.*, 2020). However, analyses incorporating fishery removals within an SDM (as advocated here) have not typically been used to designate EFH or otherwise inform spatial management.

We refer to the simplest version of these models as a biomass-dynamic habitat model (Figure 1) and illustrate that it combines variables used in biomass-dynamics models (from stock assessment) and SDMs (from habitat assessment). We acknowledge two distinctions while noting that the following theory could apply regardless of these choices:

- (1) We use “Eulerian” notation in the following, wherein we track biomass $b(s)$ at each location s ; we could instead use

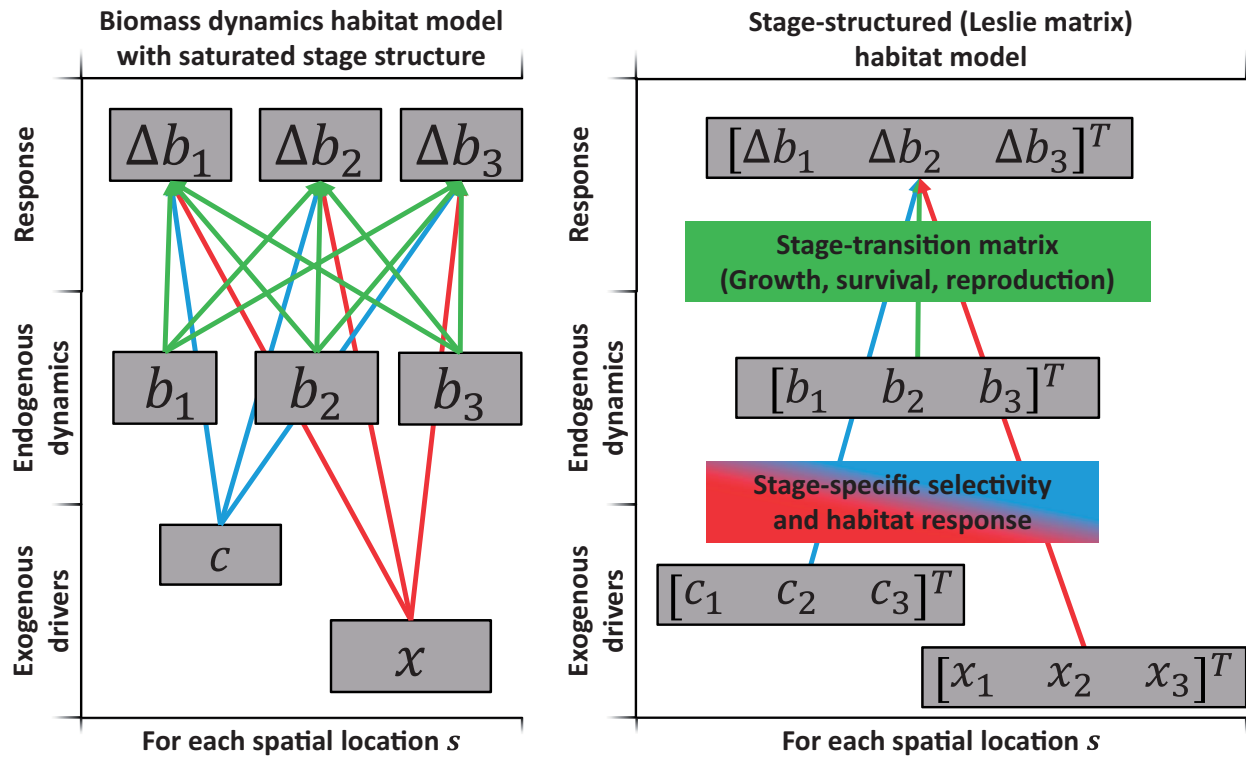


Figure 2. Schematic representation contrasting two approaches to *Challenge # 1: Stage-Structured Dynamics* visualized at a single location: (1) a biomass-dynamic habitat model (see Figure 1 for details) with saturated stage dynamics involving separate effects of biomass, catch, and environmental conditions on productivity for each state (left-hand panel) and (2) a state-structured Leslie-matrix model where productivity follows a stage-transition matrix G , and where responses to covariates and catches are simplified by identifying similar selectivity or environmental responses among adjacent stages (right-hand panel).

“Lagrangian” notation wherein we track the location $s_i(t)$ of each individual i at each time t . Lagrangian notation is often adopted for individual-based models (IBMs), and these IBMs can typically be approximated using Eulerian notation [see Cornell *et al.* (2019) for more details].

- (2) Previous authors have distinguished mechanistic versus correlative SDMs (Kearney and Porter, 2009), where mechanistic (a.k.a. process-based) SDMs involve specifying environmental responses *a priori* based on spatial layers and process research, while correlative (a.k.a. statistical) SDMs involve estimating environmental responses (or spatially correlated residual variation) based upon monitoring and opportunistic data (e.g. Rougier *et al.*, 2015). The biomass-dynamic habitat model could be used as a mechanistic SDM by fixing the value of parameters based on laboratory and field experiments, or a correlative SDM by estimating parameters based on fit to monitoring data. Fixing some parameters while estimating others therefore allows the biomass-dynamic habitat model to include a wide range of behaviours from both mechanistic and correlative approaches, and we advocate incorporating both process-research and monitoring data in this way. We conclude by noting that the following theory (described for the biomass-dynamic habitat model) could therefore be applied to either mechanistic or correlative SDMs.

In the following, we describe the simplest analytical approach for each method; for example by using linear models for stage-structured dynamics (a “Leslie matrix”) or movement rates.

However, these concepts could be extended to include nonlinear functions for survival and movement, and their capacity for extension is part of their benefit.

Three difficulties to addressing this grand habitat challenge

The biomass-dynamic habitat model includes the minimal components necessary for predicting potential future changes in fishery production from spatial regulations; that is an explicit representation at each location s of changing biomass $\Delta b(s)$, endogenous dynamics including density dependence given current density $b(s)$, environmental covariates $x(s)$, and fishery impacts $c(s)$. We note three difficulties to using this simple model to address the full range of habitat-impact and regulatory questions that are often addressed:

- (1) *Stage-structure*: Metabolic rates typically vary as an individual grows in size. For example, individual growth (in units biomass per time) typically accelerates and then decelerates as an individual ages following a von Bertalanffy growth and allometric weight-at-age function, and this underlies classic yield-per-recruit management strategies that identify optimal yield at intermediate exploitation rates (Andersen, 2019). We note that many existing efforts to inform habitat protection using SDMs approximate each stage separately (e.g. Rooney *et al.*, 2018), and then stack resulting stage-structured predictions without explicitly modelling individual transition rates

among stages, and this obscures questions regarding cumulative impacts across multiple stages.

- (2) *Nonlocal effects*: The biomass-dynamic habitat model also assumes that environmental covariates $x(s)$ and fishery impacts $c(s)$ affect production $\Delta b(s)$ at each location s separately and in isolation. However, this assumption precludes considering how habitat changes at one location (e.g. where pelagic larvae settle and grow as juveniles) affects production at distant locations (e.g. subsequent juvenile and adult production).
- (3) *Mechanisms affecting environmental conditions*: The biomass-dynamic habitat model does not explicitly model potential dependencies among habitat variables, and therefore cannot identify the cumulative effect of changing covariates impacting productivity via both direct and indirect pathways. For example, many demersal fishes are associated with a specific range of seafloor depths (bathymetry). However, this pattern could arise due to a preference for a specific level of light, seafloor temperature, or many other factors. Therefore, predicting the likely consequences of changing temperature (due to climate change) or light levels (due to increased suspended sediment associated with coastal development) requires understanding both the impact of each habitat variable on population productivity (“direct effects”), and also the impact of each habitat variable on other habitat variables (“indirect effects”).

In the following, we propose minimal extensions to the biomass-dynamic habitat model that are required to address each of these difficulties, while noting previous studies that provide preliminary illustration for each method.

Difficulty # 1: stage-structured effects

The first extension involves specifying that habitat effects (“exogenous dynamics”) and density dependence (“endogenous dynamics”) vary widely for different stages of marine organisms (Figure 2). We refer to different demographic rates among sizes, ages, or sexes as “stage-structure”. Stage-structured habitat modelling requires tracking densities $b_c(s)$ for each stage c at each location s , as well as distinguishing how stage-specific productivity $\Delta b_c(s)$ changes due to densities of that and other stages as well as environmental conditions. Similar to population-dynamics models, it is easy to incorporate stage-structured endogenous dynamics by including a stage-transition matrix:

$$\Delta b_{c1}(s) = \sum_{c2=1}^{n_{\text{stages}}} g_{c1,c2} b_{c2}(s), \quad (1)$$

that is $\Delta \mathbf{b}(s) = \mathbf{G}\mathbf{b}(s)$, where stage-transition matrix \mathbf{G} includes the effect $g_{c1,c2}$ of biomass for each other stage $c2$ on productivity of stage $c1$. The stage-transition matrix can be interpreted as representing growth and mortality rates under particular growth and mortality models (Kristensen *et al.*, 2014), expanded to separately track empirical moulting and growth rates (Cao *et al.*, 2020), re-interpreted to represent multi-species interactions (Thorson *et al.*, 2019), or replaced with a nonlinear function representing delayed recruitment and individual growth (Thorson *et al.*, 2015b).

Importantly, process research can reveal how elements of the stage-transition matrix (including size, growth rate, and natural mortality) vary among different habitats, such that stage-transition matrix $\mathbf{G}(s)$ can be approximated for each location. It is then easy to calculate intrinsic growth rate $r(s)$ as the dominant eigenvalue of $\mathbf{G}(s)$ (McAllister *et al.*, 2001). Intrinsic growth rate then serves as a “common currency” for comparing habitat quality across different habitats and species (Chesson, 2000; Shoemaker and Melbourne, 2016). Intrinsic growth rate is already used to calculate management target and limit reference points for marine populations (Zhou *et al.*, 2012), so it also provides a ready-made reference point for comparing habitat importance or evaluating alternative regulatory scenarios using the biomass-dynamics habitat model. However, calculating $r(s)$ also has drawbacks. Most importantly, it fails to account for nonlocal population drivers (resulting from seasonal or ontogenic movement), e.g. how production in adult feeding groups is associated with survival at geographically distant juvenile habitat. We therefore address this difficulty next.

Difficulty # 2: nonlocal effects

The biomass-dynamic habitat model specifies that covariates $x(s)$ and catch $c(s)$ affect production $\Delta b(s)$ at that single location and no other; we call this the “local dynamics” assumption. We envision separate ways to relax this assumption for covariates and for catches (Figure 3).

Nonlocal covariates

Nonlocal covariates will be important whenever habitat quality is associated with atmospheric or oceanographic “teleconnections”. For example, bowhead whales in the Chukchi Sea prey upon euphausiids that grow in the Bering Sea and are then advected northward (Berline *et al.*, 2008), such that bowhead habitat selection is mechanistically correlated with environmental conditions at geographically distant conditions that drive Bering Sea euphausiid abundance. We refer to these nonlocal correlations as “ecological teleconnections”. Ecological teleconnections can be estimated from time-series data by applying empirical orthogonal function (EOF) analysis to the matrix of covariates at each location and time, extracting the dominant mode(s) of variability, and then including the resulting indices in a spatially varying coefficient model. EOF analysis is widely used to identify oceanographic indices such as the Pacific Decadal Oscillation (Thorson *et al.*, 2020b), while spatially varying coefficient models have been adapted previously for use in SDMs (Bacheler *et al.*, 2012; Hunsicker *et al.*, 2013; Thorson, 2019). Combining these two approaches allows $\Delta b(s_1)$ at a location s_1 to be highly correlated with a covariate $x(s_2)$ even when these locations are geographically distant. Importantly, regional indices identified using EOF may be predictive of local processes during some oceanographic regimes but not others (Litzow *et al.*, 2018), and EOF can be generalized to maximize predictive power for individual species or processes (Thorson *et al.*, 2020a).

Advective-diffusive movement involving a habitat suitability function

By contrast, nonlocal density dependence and catches can be incorporated by explicitly modelling individual movement. Movement rates are often estimated by models using Lagrangian notation (Jonsen *et al.*, 2003; Johnson *et al.*, 2008), whereas

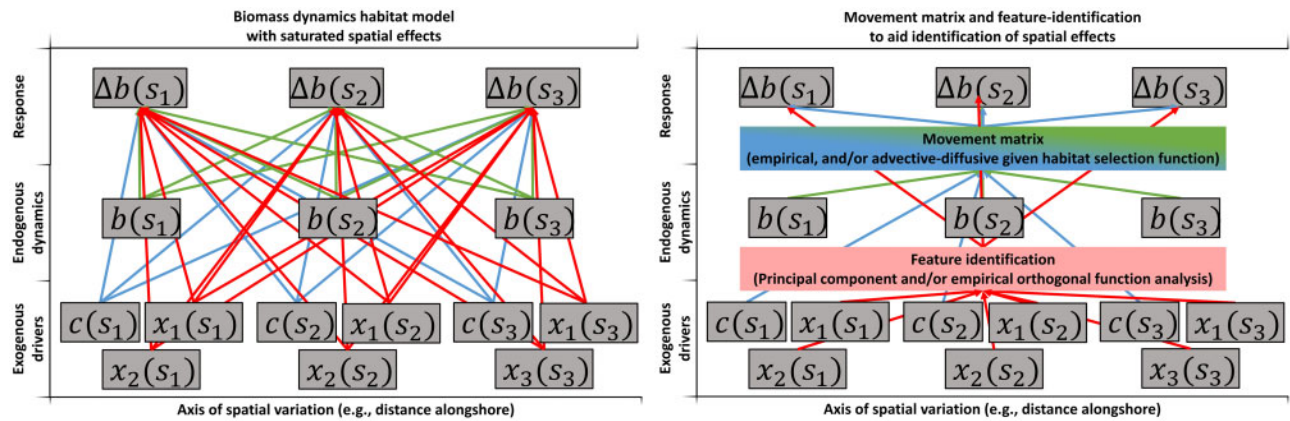


Figure 3. Schematic representation contrasting two approaches to *Challenge # 2: Nonlocal Effects*: (1) a biomass-dynamic habitat model (see Figure 1 for details) visualizing saturated spatial dynamics involving an impact of covariates and density at any location s on productivity at any other location s^* (left-hand panel) and (2) a rank-reduced approach that links productivity and biomass using a movement matrix (either empirical or predicted from advective-diffusive movement) and links covariates to productivity by identifying dominant features (e.g. as empirical orthogonal functions) and specifying a response to those features such that nonlocal correlations can arise from shared response to regional environmental conditions (right-hand panel).

landscape-level properties and spatial population-dynamics are often studied using Eulerian notation (Skellam, 1951; Bolker and Pacala, 1997; Okubo et al., 2001). For studying habitat-specific production we advocate using Eulerian notation so that we can easily extract a movement matrix \mathbf{M} where $\mathbf{m}(s_1)$ is the probability of moving from location s_1 to s_2 . To do so, we estimate a habitat-selection function $h(s)$ for each location, where:

$$h(s) = \sum_{j=1}^{n_x} \beta_j x_j(s), \quad (2)$$

that is where habitat preferences are modelled as a linear (e.g. basis-spline) function of location environmental conditions. Directional (“advective”) movement then follows the gradient of this habitat-selection function, while the rate of random (“diffusive”) movement d^2 controls the rate at which individuals move between habitats of similar quality. This is sometimes called a “taxis-diffusion” model, recognizing that advection is driven by taxis towards preferred habitat (Potts and Schlägel, 2020), and movement matrix \mathbf{M} is then calculated by integrating these two rates over time. Given sufficient time, densities will converge upon the “stationary distribution” for movement matrix \mathbf{M} , where this stationary distribution could be used to infer the likely long-term distribution of individuals.

We illustrate this approach by exploring seasonal movement of sablefish *Anoplopoma fimbria* in the Gulf of Alaska (see Supplementary Appendix SA for details). A similar approach has been developed for fisheries population-dynamics (Faugeras and Maury, 2005; Lehodey et al., 2008), although a simplified demonstration using R code has not been published previously to our knowledge (see R script in Supplementary Appendix SB). We specify advective-diffusive movement where advection follows a linear habitat-selection function based on bathymetry and bottom temperature; we model “fall” movement from summer (June–August) to the following winter (December–February) and “spring” movement from winter to the following summer, where fall movement is predicted based on fall (September–November) bottom temperatures and spring movement is based on spring (March–May) bottom temperatures. The bathymetry layer is derived from bathymetric soundings (Zimmermann et al., 2019), while the

spring and fall bottom temperatures are derived from a Regional Ocean Modelling System developed for the Gulf of Alaska (Hermann et al., 2009; Cheng et al., 2012; Coyle et al., 2019). We specify separate habitat-selection parameters for fall and spring movement, while both seasons share the same diffusion rate (resulting in five movement parameters total). We model movement between 531 raster cells (each 25 km × 25 km in size), using the domain used in the ROMS model for bottom temperature as the spatial extent. We ignore size-structured effects (i.e. movement rates are identical for all tag records) and catchability effects (i.e. recovery location is treated as ignorable) in this example.

We then fit this model to tag-recapture records from 97 conventional tags (Echave et al., 2013) representing spring movement; that is released in summer (June–August) and recaptured the following winter (December–February), as well as 510 conventional tags representing annual movement; that is released in summer and recaptured the following summer. Spring movement was modelled based on spring movement probabilities, while annual movement was modelled based on the net effect of fall and spring movement probabilities; parameters were estimated using maximum likelihood (see Supplementary Appendix SB for R script implementing approach). We then visualize fall movement $\mathbf{m}(s_1)$ for three simulated release locations (near Sand Point in the Shumagin Islands, Seward in the central Gulf of Alaska, and Dixon Entrance in southeast Alaska) as well as the stationary distribution for annual movement (Figure 4). This predicted wintertime distribution is constrained to the deepest waters, in agreement with wintertime habitat estimates using fishery data (Rooney et al., 2018, figs. 70 and 71), as well as limited mixing between southwest Alaska (False Pass) and southcentral Alaska, but greater mixing (more similar movement probabilities) between the central and eastern Gulf of Alaska.

Importantly, movement matrix \mathbf{M} could be used to determine how local densities and catches re-distribute from one year to the next:

$$\Delta \mathbf{b} = \mathbf{M}(f(\mathbf{b}) - \mathbf{c}), \quad (3)$$

where this model implicitly assumes that density dependence $f(\mathbf{b})$ occurs first, then catches are subtracted, and then

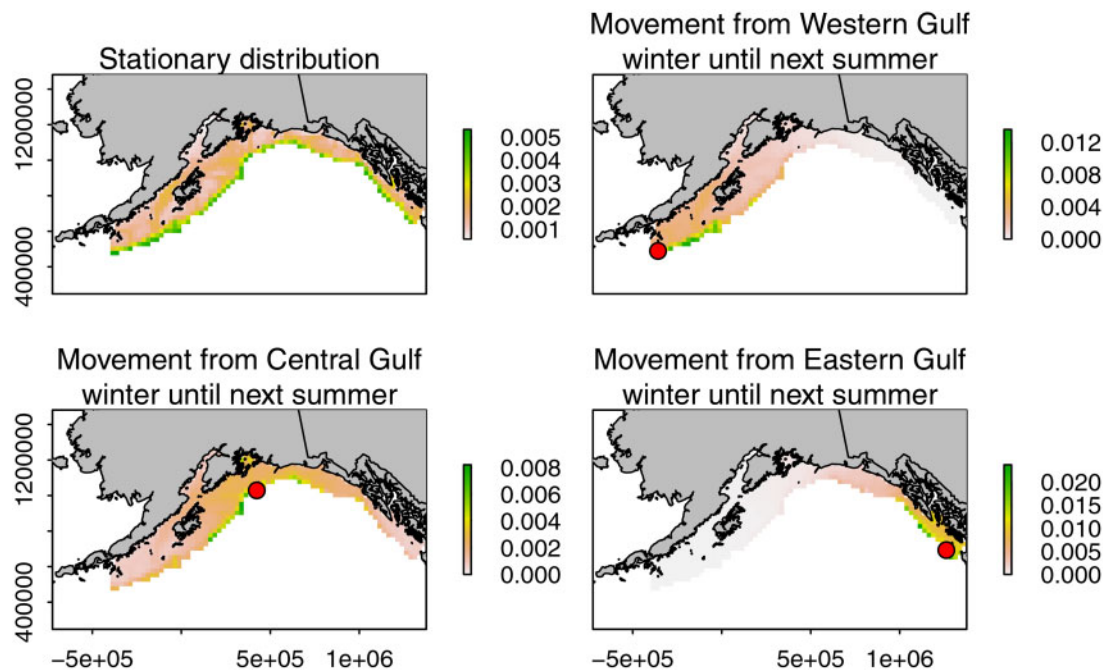


Figure 4. Illustration of output from an advective-diffusive movement model using a habitat-selection function based on bathymetry and bottom temperature, applied to seasonal movement for sablefish restricted to the Gulf of Alaska. Movement is predicted based on locations of tags released in summer and recaptured the following winter (“fall movement”), as well as released in summer and recaptured the following summer (“annual movement”), where the difference is used to infer winter-to-summer (“spring”) movement despite no tags being released during winter for direct measurement. This shows the stationary distribution for numerical density (a.k.a. expected habitat utilization) given annual summer-to-summer movement (top left) as well as spring movement probabilities based on a tag released at one of three locations (red dot) representing releases in the western Gulf of Alaska (top right), central Gulf of Alaska (bottom left), and eastern Gulf of Alaska (bottom right). Note that each panel has a sum of one across all spatial locations.

individuals move such that production is affected by density dependence and catches in proportion to movement between locations (Thorson *et al.*, 2017), and where future research could explore the sensitivity to an alternative assumed sequence of events. Alternatively, movement occurring at fine-spatial scales could be binned across larger areas to calculate movement probabilities between spatial strata defined in stock-assessment models (Hanselman *et al.*, 2015; Berger *et al.*, 2017).

Difficulty # 3: mechanisms affecting environmental conditions

Conventional SDMs and the biomass-dynamic habitat model specify that all covariates $\mathbf{x}(s)$ have an exogenous and independent effect upon production $\Delta b(s)$, termed “direct effects”. However, there are many cases in which covariates arise from a dynamical process, and where ignoring dependencies among covariates (termed “indirect effects”) will result in misunderstanding the relationship between environment and habitat productivity.

For example, productivity for near-bottom habitat is often affected by interannual changes in the proportion of mixing water masses, each with characteristic temperatures and nutrient concentrations, where these drive surface phytoplankton production, which in turn affects near-bottom light levels. In this case, a hypothetical study demonstrating a correlation between light levels and productivity includes a direct (causal) pathway from light levels to consumer productivity (e.g. due to changing visual foraging rates) but also indirect (confounder) pathways where

increased surface production drives changes in the diel-vertical migration of zooplankton prey. Habitat scientists might then be tasked with predicting the likely consequences of an alternative mechanism for changes in light levels; for example arising from increased suspended sediment due to coastal development. This will trigger changes in productivity associated with direct (causal) associations from light levels to productivity but will not necessarily be associated with indirect pathways.

One approach to address this difficulty is to explicitly model the dependencies among variables and covariates using structural equation models, SEM (Kaplan, 2001); this approach has been demonstrated in terrestrial habitat models (Grace and Irvine, 2020; Schoolmaster *et al.*, 2020) but has seen little use in marine habitat sciences [although see van Denderen *et al.* (2014) for an exception] (Figure 5). The SEM approach introduces a new sub-model representing dependencies among latent variables $\mathbf{y}^*(s)$ (i.e. variables that are measured imprecisely and hence never known exactly):

$$\mathbf{y}^*(s) = \mathbf{P}\mathbf{y}^*(s) + \mathbf{\Gamma}\mathbf{z}(s) + \boldsymbol{\delta}(s), \quad (4)$$

where $\mathbf{y}^*(s)$ includes population density $d(s)$ as well as environmental variables $\mathbf{x}(s)$ that have modelled dependencies at each location s , thereby eliminating the distinction arising in linear models between dependent variable $d(s)$ and independent variables $\mathbf{x}(s)$. Meanwhile, \mathbf{P} represents dependencies among these biological and habitat variables, $\mathbf{z}(s)$ is exogenous variables (i.e. experimental treatments) and $\mathbf{\Gamma}$ includes responses to these, and $\boldsymbol{\delta}(s)$ represents residual variability. The SEM is completed by

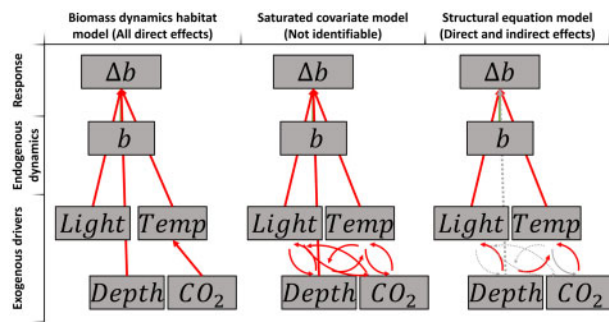


Figure 5. Schematic representation contrasting three approaches to Challenge # 3: *Dependencies among Covariates*: (1) the biomass-dynamic habitat model (left panel) assumes that all covariates are exogenous and independent, (2) the saturated structural model (middle panel) assumes that all covariates are mechanistically linked, resulting in a model that is not identifiable based on observational data, and (3) a structural equation model informed by process research can result in an identifiable model that includes dependencies among covariates (in this case showing the hypothetical impact of atmospheric carbon dioxide and depth on bottom temperature and depth, with resulting impacts on local productivity).

specifying a measurement model for measurements $\mathbf{y}(s)$ of latent variables $\mathbf{y}^*(s)$:

$$\mathbf{y}(s) = \mathbf{y}^*(s) + \boldsymbol{\varepsilon}(s), \quad (5)$$

where $\boldsymbol{\varepsilon}$ is measurement errors, and we simplify presentation by assuming that \mathbf{z} is measured without error and each response is measured individually [see Kaplan, 2001 for details]. This SEM formulation reduces to a linear model in some cases. However, it can also address a broader set of questions, e.g. where fish density $d(s)$ is positively affected by the density of nearby corals $x(s)$ (e.g. by providing refuge from predators), but where coral density is also reciprocally increased by fish density (e.g. by increased nutrient influx from fish digestion or removal of predators). Instances like this involve cyclic dependencies among variables and violate the assumption of exogeneity required by conventional linear models.

Continuing our previous example, water-mass proportion $x_1(s)$ and nearby coastal development rates $x_2(s)$ both might drive light levels $y_1(s)$ which in turn affects population density $y_2(s)$. In this case, process research might support the assumption that coastal development $x_2(s)$ has no direct effect upon density $y_2(s)$, such that $\gamma_{2,2} = 0$, but is still correlated with densities via its effect upon light levels and resulting indirect effect upon densities, $x_2(s) \rightarrow y_1(s) \rightarrow y_2(s)$. In this example, light levels then “mediate” the mechanism by which coastal development affects population density (Pearl, 2009), and process research is necessary to measure dependencies among variables (\mathbf{P}) in order to accurately predict consequences of coastal development. Relationships among physical variables can be explored or predicted using earth systems models (ESM; e.g. Kearney et al., 2020), but indirect habitat effects resulting from changes in density for other mobile species are not typically represented by ESM and will require ecological research linking habitat to top-down regulation.

Finally, we note that the conventional SDM can in some cases estimate environmental drivers of density using monitoring (observational) data without experimental manipulation; by

extension the biomass-dynamic habitat model can presumably predict some environmental drivers of productivity. However, it is clearly true that monitoring data cannot be used to estimate associations with environmental conditions that have never been observed previously. For example, habitat managers must provide advice regarding permitting commercial activities with new and unknown potential consequences. Increased Arctic shipping can increase ocean noise with resulting behavioural and distributional responses (Ivanova et al., 2020), and new oil dispersants can change the physiological impacts of oil exposure on fishes (Pasparakis et al., 2019). In these cases, analysts must specify the effect of these covariates at known values based on prior process (laboratory and field experimental) research, or apply meta-analytic research to predict unknown effects based on similar conditions elsewhere (Thorson et al., 2015a). This is easily done within structural equation models by treatment as exogenous variables, $\mathbf{z}(s)$. In these and other instances, SEM represents a formal way to include process research informing mechanistic relationships among covariates within habitat models.

Foreseeable limitations to proposed approach

In the preceding, we have outlined three potential approaches to address common difficulties arising when predicting future changes in habitat-specific fishery production arising from spatial regulations. We here note a few limitations that are shared among methods, along with potential directions for research to address these limitations:

- (1) Most importantly, these approaches are constrained by the availability of habitat-specific monitoring data (to measure aggregate $b(s)$ or stage-specific biomass $\mathbf{b}(s)$), tagging data (to measure movement \mathbf{M} and nonlocal impacts), and process research to identify likely mechanisms (for use in structural equation models) and stage-specific rates (for use in growth transition matrix \mathbf{G}). Modelling will never substitute for monitoring data and process research. However, ready-made and widely-accepted models can be used to extend the scope of inference arising from monitoring data and process research, and thereby increase the value (and hence attractiveness for funding) of new data and process research. Despite short-term trade-offs in funds for monitoring, process research, and model development, we therefore see a long-term positive feedback whereby developing habitat-specific productivity models and expanded data collection and process research improves the value of both efforts.
- (2) In cases with limited data (e.g. when modelling habitat-specific production of benthic infauna, secondary producers, or rare/nontarget fishes), these approaches will likely require simplifications to implement in practice. In the case of movement, for example this might involve isotropic and spatially constant diffusion rates, along with meta-analytic information about habitat selection to parameterize (rather than estimate) the habitat-selection function; such an approach could be used to match movement patterns from historical process research, or to generate movement scenarios for use in stock assessment. Similarly, growth and mortality rates in the size-transition matrix \mathbf{G} will be unknown for many species; meta-analysis may again be necessary to define the likely improvement in survival in different potential habitats.

- (3) Finally, there remain some questions about how best to implement habitat-specific models numerically and computationally. This involves improved approximations to spatial modelling (Fuglstad *et al.*, 2014), improved computational methods for estimating parameters (Kristensen *et al.*, 2016), and improved terms of reference to share data between agencies and jurisdictions at relevant scales (Maureaud *et al.*, 2021). We are optimistic that these resources will continue to improve over the coming decade.

An argument for coordinating habitat research

We conclude with several recommendations to coordinate habitat research towards this common goal:

- (1) Coordinate monitoring surveys, process research, and model development, so that these efforts are focused to predict consequences of spatial regulations upon fishery productivity;
- (2) Co-develop these methods in conjunction with decision theory based on stakeholder input (soliciting values, identifying potential management procedures, and collaborative design of management strategy evaluation studies);
- (3) Reduce costs through paradigmatic models, common parameterizations, and sharing information via meta-analyses.

We discuss each of these in detail below.

Coordinate monitoring surveys, process research, and model development

Most importantly, we emphasize that monitoring, process research, and model development are all necessary to resolve these three difficulties. For example, deep-sea corals (Winship *et al.*, 2020) and benthic infaunal communities (Eigaard *et al.*, 2020) have both been analyzed using SDMs to support “benthic habitat-impact assessments”. Translating these SDMs into biomass-dynamic habitat models would likely require aggregating available process research and monitoring data to identify appropriate taxonomic resolution (data-rich species, or higher-level taxa with available information), combined with:

- (1) Some measurement of human impacts used to calculate cumulative impacts [**c** in (3)]; either direct measurements of coral catches from bycatch records, or extrapolating experimentally measured disturbance rates to the entire area impacted by individual fishing gears (Zhou *et al.*, 2009; Rijnsdorp *et al.*, 2020);
- (2) Process research regarding growth rates used to calculate stage-transition rates [**G** in (1)]; for corals either by flagging and periodically re-measuring their individual size or validated growth rings or other physiological markers (Andrews *et al.*, 2002), and for infaunal communities by measuring recovery rates after experimental trawling (Sciberras *et al.*, 2018);
- (3) Process research for habitat connectivity [**M** in (3)], perhaps involving larval advection and settlement rates to parameterize passive advective movement within a stock-recruitment model, or settlement plates to directly measure spatial variation in recruitment for corals (Cowen and Sponaugle, 2009);
- (4) Field experiments measuring the impact of corals and/or benthic infauna on fish demographics/density and vice-versa

[**P** in (4)]; for corals measuring predation and bioenergetics rates of fishes under alternative coral treatments (e.g. Beukers and Jones, 1998) as well as reciprocal impact of fish on coral densities (e.g. Allgeier *et al.*, 2016), and for infauna measuring fish stomach contents and condition before/after experimental trawling;

- (5) Development and testing of models (and associated software) to integrate fishing and non-fishing effects (**c**), larval movement and settlement rates (**M**), individual growth rates (**G**), as well as associations between corals and other habitat variables (**P**).

We note that this is not a “complete” list of work needed to measure the impact of corals or benthic infauna on fisheries productivity; presumably habitat assessments will define their scope iteratively in consultation with local resource managers and stakeholders, and this iterative scoping process will be used to define “best available science” for a given policy arena (e.g. Levin *et al.*, 2009).

Evaluate likely performance of spatial management procedures

Stock-assessment scientists developed assessment models at the same time that fisheries managers developed new methods to monitor abundance and enforce regulatory changes. For example, per-recruit analysis co-evolved with international discussions regarding potential versus realized yield (Holt, 1958). Scientists and managers have subsequently co-evolved a toolbox of gear regulations affecting size and age selectivity, annual catch limits, and bycatch regulations that can be represented within conventional assessment models, thereby facilitating simulation testing of likely management performance (e.g. fig. 5 in Carruthers and Hordyk, 2018). Due to this long history, it is therefore unsurprising that trade-offs associated with annual catch limits and other management actions have been thoroughly studied (Worm *et al.*, 2009; Gutiérrez *et al.*, 2011; Melnychuk *et al.*, 2012).

By contrast, spatial regulations include a different set of management tools including (to name a few) move-on rules, permanent and seasonal closures, and cooperative agreements regarding fishing gear (McConnaughey *et al.*, 2020). SDMs have been used to evaluate potential impacts of permanent closures for marine protected area design (e.g. using Marxan; Smith *et al.*, 2009), but there are few options for off-the-shelf software to evaluate likely fishery performance and impacts of spatial regulations. In particular, incorporating stage-structure, movement, and structural-equation modelling approaches into spatial analysis will allow predictions of changing productivity at one location arising from potential management changes at other locations. Models (and associated software) to predict productivity changes from spatial management could then be used independently and transparently to evaluate the likely performance of proposed management procedures (Punt *et al.*, 2016); scientific reviewers and stakeholders will have more confidence in advice from this process in cases where modelling efforts have been well validated (Winship *et al.*, 2020).

Reduced cost through paradigmatic models, common parameterizations, and sharing information via meta-analyses

We recognize that co-developing scientific and management practices that can evaluate spatial regulations by predicting their

likely impact on productivity is a large enterprise. However, we argue that this can be accomplished efficiently through three steps:

- (1) *Paradigmatic models*: First, stock assessment has developed a set of paradigmatic models, including per-recruit, surplus production, delay-difference, and virtual population analysis models (Hilborn and Walters, 1992; Quinn and Deriso, 1999). These models are often used to illustrate different principles for how demographic rates can be measured from field data and represent a diverse set of mechanistic and statistical approaches to understanding population-dynamics. By contrast, habitat analysis typically involves SDMs and IBMs, and neither can clearly illustrate the three difficulties outlined in this paper. We therefore believe that the simple extensions to the biomass-dynamic habitat model presented here can serve as “paradigmatic models” to illustrate these principles, for use in classrooms or stakeholder presentations, and that continued development of “paradigmatic” habitat models will accelerate efforts to connect habitat science with fisheries management.
- (2) *Common parameterizations*: Paradigmatic models for stock assessment typically use a small set of parameters (growth rate k , asymptotic size L_{inf} , catchability coefficient q), where parameters can be easily converted from one model to another (McAllister et al., 2001). Consequently, there is a large literature on how to measure these common parameters given different technologies and field-sampling designs. By contrast, there is less awareness of how to inter-convert parameters within spatial analysis; for example between a state-space movement model (Jonsen et al., 2003), a habitat-selection model with advective-diffusive dynamics (Thorson et al., 2017), or a spatially stratified movement-rate model (Lehodey et al., 2008; Hanselman et al., 2015). This then results in less opportunity to compare parameter estimates between analytical approaches, species, and regions.
- (3) *Sharing information via meta-analysis*: Finally, the common parameterizations within population-dynamics and stock-assessment models lead to easy construction of databases containing results for many stocks (Froese, 1990). Meta-analytic data, in turn, allow for comparative research across stocks, such that general patterns can be identified (Charnov et al., 2013), missing values can be predicted (Thorson, 2020), and meta-analyses can be evaluated and improved (Patrick et al., 2014). Parameters representing movement rates, thermal preferences, and habitat recovery rates are all likely candidates for continued meta-analysis (Hiddink et al., 2017; Burrows et al., 2019).

Grand habitat challenge

We have argued that habitat science should follow stock assessment in developing a theory and practice for predicting the impact of spatial management regulations (including fishing and other sectors) on resulting fishery productivity (a Grand Habitat Challenge). We then introduced the biomass-dynamic habitat model to elucidate how current SDMs can be combined with typical stock-assessment variables to address this Grand Habitat Challenge and then summarized approaches (and associated research programs) to address three difficulties that arise for habitat research.

We end by noting that many difficulties facing fisheries science are expressed spatially and therefore could be aided by coordinated efforts to tackle this Grand Habitat Challenge. For example, climate change is impacting some habitats more than others, while changes in shipping, aquaculture, and offshore energy development are also expressed as spatial impacts. These and other stressors are often listed as components of Ecosystem-Based Management, EBM (NMFS, 2017; see Box 2). Here, however, we have noted several ways that habitat research poses extra analytic difficulties beyond those for EBM in general. We therefore encourage ongoing coordination of habitat research in national and international research venues (NMFS, ICES, PICES, etc.); these unique difficulties will require many lifetimes of scientific research, and therefore requires national and international coordination if they are to be addressed by 2030.

Supplementary data

Supplementary material is available at the *ICESJMS* online version of the manuscript.

Data availability statement

The sablefish tagging example (Figure 4) includes three types of data. The tag release and recovery locations are commercial information and can be obtained from the Alaska Fisheries Science Center upon formal request and approval. A simulated version of these data are provided in Supplementary Appendix SB. The bathymetry and bottom temperature data are obtained from sources listed in Supplementary Appendix SA, and the version of these data used is available in Supplementary Appendix SB.

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