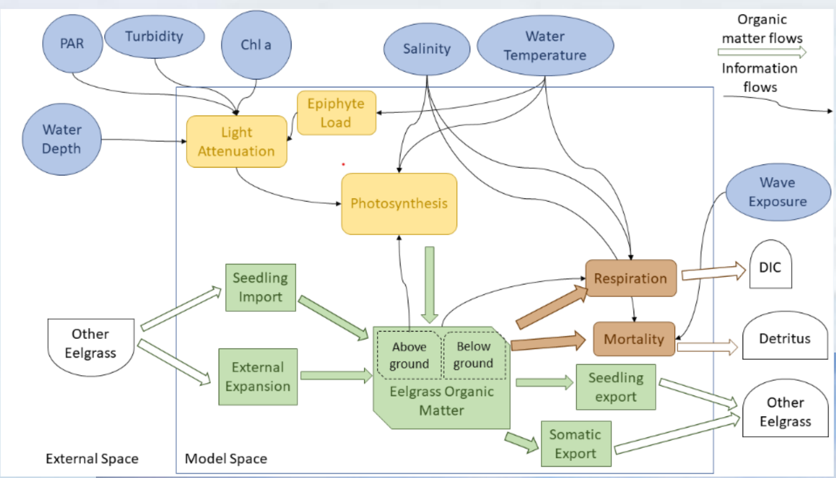
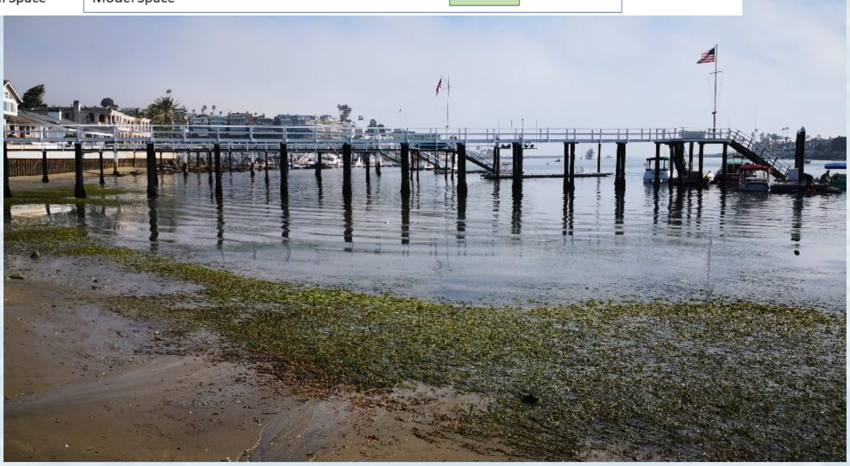
Options, Impediments, and Supports for the Development of an Eelgrass (*Zostera marina*) Habitat Occupancy Model in the Embayments of Southern California





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SOUTHERN CALIFORNIA COASTAL WATER RESEARCH PROJECT

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EXECUTIVE SUMMARY

Seagrasses are marine submerged aquatic angiosperms that form extensive beds or meadows in shallow coastal waters, and which influence the biological, biogeochemical, and hydrographic cycles of their local systems. Eelgrass, specifically *Zostera marina*, is the most common species of seagrass in the high salinity, shallow, soft-bottom sediments of Southern California's estuaries and embayments. Eelgrass is regulated at local, state, and federal levels in California because of its ecological, economic, and societal value, as well as its susceptibility to anthropogenic disturbance.

Despite the value and status afforded eelgrass within state and federal coastal management policy, there is no organized framework for assessing the condition of eelgrass beds in California. SCCWRP has recently developed a three-tiered assessment framework to assess both the biological resource and habitat aspects of eelgrass from the perspective of: 1. **Habitat extent** – How much eelgrass is in a location, relative to a reference-based expectation?; 2. **Condition of the organism** – How healthy is an individual eelgrass bed, relative to a reference-based expectation?; and 3. **Ecological functions** provided to the ecosystem – Is an individual bed providing expected ecological functions at a rate relative to a reference based expectation?

Focusing on Tier 1 of the assessment framework, the core functionality is the comparison of observed measures of eelgrass extent within sections of a water body to an estimate of what would be expected to be there under reference conditions. The health of the waterbody is then assessed as meeting management goals or not meeting those goals based upon the ratio of observed to expected eelgrass extent. The central impediment to developing this tool is how to define the reference expectation for specific locations. There are variety of ways one can define reference conditions, but for this scenario it has been determined that using a mathematical model to predict the location of eelgrass under minimally disturbed conditions is the preferred approach.

The goal of this report then was to provide a set of recommendations on the feasibility of and technical options for the development of a spatially explicit *Z. marina* habitat occupancy model applicable to estuaries and embayments of Southern California that could be used in the Tier 1 assessment tool. Via a survey of existing peer-reviewed literature and publicly available data sets, we endeavored to: 1. Determine if any of the pre-existing eelgrass models could be directly applied to Southern California; 2. Inventory the different modeling approaches used to predict seagrass habitats in other regions; 3. Compile a set of key physiological/rate process equations for *Z. marina* and key environmental predictors that could be used to parameterize a Southern California model; and 4. Inventory eelgrass and environmental data that could be used to parameterize a model.

From the recent (mostly post-2000) literature, we identified 35 different publications detailing predictive models of seagrass occurrence. We found a number of both statistical and mechanistic models covering 10 different species of seagrass with approximately 50% of these models focused on *Z. marina*. None of the publicly available models were developed or had been applied to the waters of Southern California.

We classified 16 publications as using statistical modeling approaches with mathematical underpinnings ranging from simpler generalized linear models to more complex non-linear and machine learning models. Water depth was included in all but one model, with measures of wave exposure and bottom slope as other frequently selected variables used to predict eelgrass habitat suitability. Water depth serves as a proxy measure of light availability, while also incorporating the likelihood of air exposure, desiccation, elevated temperature stress, etc. Conversely, wave exposure serves as a relatively direct measure of natural physical disturbance to the plant. The output of the models is the likelihood of observing or amount of seagrass at a given location based upon the predictor variables measured at the location.

We classified 19 publications as using mechanistic models for predicting the persistence, expansion, or decline of seagrass in a specific location over time. The basic structure of all the mechanistic models was weighing the gains (e.g., photosynthetic growth or import) of seagrass organic matter against the losses (e.g., respiration, mortality, or export), all of which are estimated from environmental forcing factors (water temperature, light, wave action, etc.), biological state variables (e.g., plant biomass, proximity to other plants, reproduction), and physiological rates of the species of eelgrass. Where or when organic matter gains were a net positive, seagrass would be expected to be present. Conversely, where or when organic matter gains were negative, the seagrass would be expected to be absent.

Our inventory of presently available data sources that could potentially be used for creation of statistical or mechanistic models of eelgrass habitat indicated that there are some amounts of nearly every data type needed to parametrize a model. However, the most of these data are only available for a handful of discrete locations in the region, mostly from larger systems like Newport, San Diego, and Mission bays. The region presently lacks data for key model parameters at a spatial resolution, spatial distribution, and temporal frequency needed to produce a statistical or mechanistic model applicable. Most acutely – based upon the ubiquity of their use in all types of eelgrass models – is the lack of high spatial-resolution water depth, clarity (e.g., turbidity, chlorophyll a), and quality (e.g., temperature, salinity) along the shallow fringes of the region's estuaries and embayments where eelgrass would be expected grow.

There are technical and conceptual advantages to either a statistical or mechanistic eelgrass habitat occupancy model. From the perspective of building a model for the Tier 1 habitat extent bioassessment tool, we are conceptually inclined toward pursuing a mechanistic model due to its relatively straightforward approach for making predictions under hypothetical (i.e., non-observed) conditions like minimally disturbed water quality or potential changes related to sea level rise and water temperature driven by climate change. Ultimately, however, the final approach to model creation and its parameterization in practice will be dependent upon a combination of utility of the model end products for management goals, as well as the personal preferences and expertise of the modelers.

None of the pre-existing *Z. marina* models available in the literature could be directly applied "out of the box" to Southern California. However, we are confident that the variety of examples in the literature can be used as a template or starting point in developing a model for the embayments of region. Furthermore, there are enough monitoring and data generation resources in the region that could be used for parameterizing draft models, albeit with limited spatial domains and predictive accuracy, to serve as a starting point for building a fully realized regional model.

Our recommendations for moving forward with the development of a regional-scale *Z. marina* habitat occupancy model are four-fold:

- **Collect high-resolution bathymetry data in the shallow portions of the region's coastal embayments** – Water depth at a scale relevant to eelgrass is a key variable used in every model we reviewed. These data can be collected in concert with ongoing eelgrass mapping surveys.

- **Develop a draft habitat occupancy model for *Zostera marina*** – For portions of the larger embayments in the region, there are likely enough data to build models for these locations. The practical experience gained from building these models will supplement the conceptual recommendations of this report to best inform the structure of a final, regional-scale model.

- **Support collaborations to investigate existing or produce new remotely sensed data for the region's coastal zone** – Many of the data types – temperature, water clarity, eelgrass presence – needed to parameterize models could be extracted from satellite and drone imagery. However, the algorithms and machine learning procedures used to produce these data need to be developed for the region.

- **Continue to support regional monitoring efforts of eelgrass and other SAV** – Monitoring programs like the Bight Regional Monitoring Program and individual permit-based monitoring efforts for eelgrass are the other major potential source of environmental predictor and eelgrass presence data that could be used to parameterize any future models that are developed.

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INTRODUCTION

Seagrasses are marine submerged aquatic angiosperms that provide a variety of ecological functions and ecosystem services in coastal ecosystems across the globe (Nordlund et al. 2016, 2017, Ruiz-Frau et al. 2017). They form extensive beds or meadows in shallow coastal waters that influence directly or indirectly the biological, biogeochemical, and hydrographic cycles of their local systems. As submerged marine flowering plants with underground root systems, seagrasses improve light conditions and water quality by reducing suspended sediment and nutrient concentrations and reduce hydrodynamic stress by attenuating waves (Gambi et al. 1990; Fonseca and Cahalan 1992). Via primary production and carbon fixation, seagrasses oxygenate the water column, increase local water column pH, and increase nutrient cycling relative to adjacent bare sediments (e.g., Nagel 2007; Cyronak et al. 2018; Ricart et al. 2021). The complex physical structure of seagrass beds serve as key habitat and nursery areas for a variety of epifauna, nekton, and infauna – including many commercially relevant and federally managed species (Connolly and Hindell 2006; Barnes and Ellwood 2012; Wong 2018; Olson et al. 2019; Barnes 2022). The grasses themselves can also be directly grazed upon by birds and turtles (Valentine and Heck 1999; MacDonald et al. 2013; Balsby et al. 2017).

Beyond the benefits and functions provided locally, seagrass beds are an important feature of the adjacent coastal ecosystems beyond the shallows where they grow. Beds grow throughout estuaries, embayments, and the shallow continental shelf – an important part of the coastal and estuarine mosaic, interspersed among emergent wetlands, biotic reefs, mudflats, and other intertidal habitats (Boström et al. 2006; Heck et al. 2008; Fulford et al. 2011).

Seagrasses, as with shallow coastal systems in general, are threatened by a range of anthropogenic stressors that have led to the decline across the globe (Short and Wyllie-Echeverria 1996; Short et al. 2014). Water clarity and shading are the most pervasive threats to seagrasses due to their dependence on light as photosynthesizers. Increased turbidity from point and nonpoint sources of eroded sediments, as well as nutrient-driven blooms of phytoplankton in the water column or micro- and macroalgae on the grass itself can also decrease light availability and negatively impact the health of the plants (Fitzpatrick and Kirkman 1995; Short et al. 1995; McGlathery 2001; Moore et al. 2014). In addition, physical disturbance from coastal modification (dredging, landfill activities, construction, etc.) and recreation (boating, fishing) physically destroy seagrasses and alter bathymetric profiles, which prevents sufficient light penetration to the sediment surface (Fonseca et al. 2004; Neckles et al. 2005; Sabol et al. 2005; Rehr et al. 2014). The variety and pervasiveness of these localized threats, alongside regional stressors (e.g., wasting disease, invasive species) (Ralph and Short 2002; Drouin et al. 2016; Groner et al. 2021) and global threats from climate change (e.g., sea level, increases in sea surface temperatures) (Duarte et al. 2018; Zimmerman 2021), make protecting seagrass systems and managing their multiple stressors vital to retaining their ecosystem functioning (Duarte 2002).

Within Southern California, the five major seagrass species that occur in marine and estuarine environments include *Zostera marina* (narrow-bladed eelgrass), *Zostera pacifica* (wide-bladed eelgrass), *Ruppia maritima* (widgeon grass), and *Phyllospadix torreyi* and *Phyllospadix scouleri* (surfgrass) (Green and Short 2003; Johnson et al. 2003; Coyer et al. 2008). These different species of seagrass all share a common need for light, water, and nutrients, but they each occupy different ecological niches and can therefore thrive under environmental settings that may be stressful to the other species (Johnson et al. 2003; Fernández-Torquemada and Sánchez-Lizaso 2011; Christiaen et al. 2016). Eelgrass, specifically *Z. marina*, is the most common species of seagrass in the high salinity, shallow, soft-bottom sediments of Southern California's estuaries and embayments. Extensive eelgrass beds have been documented in Mission Bay, San Diego Bay, Alamitos Bay, Newport Bay, the Lower Santa Ana River and Marsh, Batiquitos Lagoon, San Dieguito Lagoon, and more (Merkel & Associates 2014a; Coastal Resources Management Inc. 2017; Sherman and DeBruyckere 2018).

Due to the combination of high value to the ecosystem and susceptibility to anthropogenic disturbance, eelgrass is regulated at local, state, and federal levels in California (NOAA 1996; United States Environmental Protection Agency 2010; NOAA National Marine Fisheries Service 2014; California Regional Water Quality Control Board San Diego Region 2020). The California Eelgrass Mitigation Policy recommends no net loss of eelgrass habitat function and presents guidance on how to offset any direct human impacts to eelgrasses such as dredging and coastal construction (NOAA National Marine Fisheries Service 2014).

As an outgrowth of these different regulatory drivers and following on from recommendations from Bernstein et al. (2011), the number of local eelgrass mapping efforts in Southern California increased over the last 15-20 years (Merkel & Associates Inc. 2009, 2011, 2014b; Coastal Resources Management Inc. 2010, 2017). These efforts have largely focused on mapping current eelgrass extent in major embayments including Mission, San Diego, Newport, and Alamitos Bay. These works have provided an estimate of eelgrass distribution and extent through the major embayments. However, very little work has been done on assessing the condition or health of the region's eelgrass beds.

Condition assessment of eelgrass – and seagrasses in general – presents a unique challenge for bioassessment due to the dual nature of the organism as both a biological resource and as unique habitat other organisms are dependent upon (Jones et al. 1994; Wright and Jones 2006). Traditional bioassessment frameworks only consider the flora or fauna as a biological resource whose health or integrity is used to infer the condition of the habitat they occupy (Karr 1981; Weisberg et al. 1997; Neto et al. 2013). Conversely, biogenic habitat is typically evaluated using extent estimates and mapping to characterize the amount of habitat available (Bernstein et al. 2011; Sherman and DeBruyckere 2018; Finger et al. 2021). Neither of these approaches fully captures the complex role eelgrass plays in coastal ecosystems, so SCCWRP has developed a three-tiered assessment framework to assess both the biological resource and habitat aspects of eelgrass and other seagrass species throughout the region (McCune et al. 2020).

The SCCWRP SAV assessment framework has three tiers of assessment designed to evaluate eelgrass health from the perspective of: 1. **Habitat extent** – How much seagrass is in a location, relative to a reference-based expectation?; 2. **Condition of the organism** – How healthy is an individual seagrass bed, relative to a reference-based expectation?; and 3. **Ecological functions** provided to the ecosystem – Is an individual bed providing expected ecological functions at a rate relative to a reference based expectation? Reasonable progress has been made thus far on the developing and piloting of Tier 3 tools (McCune et al. 2020) and now focus has shifted toward developing the Tier 1 assessment tools.

The core concept of the Tier 1 assessment tool is the ability to compare observed measures of eelgrass extent (or other species of seagrass eventually) in a given water body to the extent that would be expected to be there under reference conditions. The health of the waterbody can then be assessed as meeting management goals or not meeting those goals based upon the ratio of observed eelgrass extent compared to expected eelgrass extent. The central problem in developing this tool is how to define the reference expectation for specific locations.

There are a variety of concepts in how reference condition can be defined (Stoddard et al. 2006), ranging from real-world minimally disturbed sites (Ode et al. 2016), real-world best available sites (Smith et al. 2001), to a conceptual model of what a community should be (Borja et al. 2000). Given the pervasive alterations of Southern California's estuaries and embayments, it is unlikely that there are sufficient data from the present or previous decades to provide a minimally disturbed estimate of eelgrass extent in the larger estuaries and embayments of the region, much less amongst the smaller estuaries and lagoons that dot the coastline. Consequently, we have chosen to pursue defining reference expectations of eelgrass presence via a predictive *Zostera marina* habitat occupancy model. Our rationale is that a spatially explicit habitat occupancy model would allow for the production of quantitative estimates of where eelgrass should occur within a given waterbody in the absence of, or at reduced levels of, human disturbance. These estimates would then serve as the reference expectations in a Tier 1 eelgrass assessment tool against which observed extent could be compared.

In addition to providing a reference expectation of where eelgrass could be for a Tier 1 eelgrass assessment tool, it is our hope that a predictive model could be used to help prioritize locations within a waterbody for eelgrass mitigation and restoration projects. If the final eelgrass habitat model can be linked to local climate change and sea level rise models, it could be used to predict suitable eelgrass habitat under present day and near future conditions. These types of data would be invaluable for the site selection of future mitigation and restoration projects.

Habitat occupancy models that are parameterized for specific species cannot typically be used to predict the distribution of other species "out of the box". However, as all seagrasses are photosynthetic angiosperms, the general structure of one seagrass model – incorporating light, environmental conditions, and nutrients – could broadly be applied to other species. That being said, the applicability of a given model across different species will likely be contingent upon the degree of phylogenetic and phenotypic similarities/differences between the species. For example, a *Z. marina* model could probably be used to predict distributions of *Z. pacifica* with some small changes to the magnitude or rates of model components to account for differences in morphology, growth rates, and salinity, temperature, light, etc. tolerances between the species, as they are congenerics. In contrast, a *Z*. *marina* model would likely need more significant re-tooling if it were to be used to predict *R*. *maritima* distributions, given the much greater morphological and physiological differences between the two conordinal seagrasses.

Report Goals

The overall goal of this report was to provide a set of recommendations on the feasibility and technical options for the development of a spatially explicit *Zostera marina* habitat occupancy model applicable to estuaries and embayments of Southern California. Via a survey of existing peer-reviewed literature and publicly available data sets, we endeavored to: 1. Determine if any of the pre-existing eelgrass models could be directly applied to Southern California; 2. Inventory the different modeling approaches used to predict seagrass habitats in other regions; 3. Compile a set of key physiological/rate process equations for *Z. marina* (e.g., photosynthesis, respiration, light attenuation) and key environmental predictors (e.g., light availability, water temperature, physical condition) that could be used to parameterize a Southern California model; and 4. Inventory eelgrass and environmental data that could be used to parameterize a model.

APPROACH

To understand what modeling approaches have been used to predict seagrass habitat in other regions, we surveyed the available white and grey literature for seagrass models, irrespective of model structure or target species. From these studies, we first determined if there were any *Z. marina*-specific models that could be used “off the shelf” in this region. There were not any, so we then broadened our scope to models that were focused on *Z. marina* in any location to identify the key physiological rates and environmental forcing factors that could be applicable to Southern California eelgrass. Lastly, based on the identified forcing factors, we searched local, state, and federal coastal monitoring programs for useful environmental data from Southern California estuaries and embayments, as well as data on eelgrass distribution.

There are two basic types of models that could be used to predict the suitability of a location for eelgrass – statistical and mechanistic models. We have classified statistical models as those that approach predicting habitat suitability based upon previous observations of the organism’s distribution along observed environmental gradients. Conversely, we have classified mechanistic models as those that rely on physiological/ecological rates of the organism to predict net growth or loss over time depending upon environmental data driving the rate equations. We used this statistical vs. mechanistic dichotomy to organize our literature review and data inventories, as well as frame our recommendations.

METHODS

We first focused on identifying ecological modeling studies that characterized seagrass spatial distributions. The bibliographic search was performed using Google Scholar and Science Direct databases. We included citations published from the year 2000 or later (to capture more modern modeling approaches with increasing computational capacity) and searched using the following list of terms alone and in combination (found in the title, abstract, or keywords).

eelgrass, Zostera marina, seagrass, mechanistic model, habitat occupancy, growth rates, spatial distribution, species distribution, species occurrence, model, spatial, habitat, predictive

During the search process, we screened the titles and abstracts of the results to prioritize papers that described specific models and applied to coastal marine environments. As such, reviews and other conceptual papers were deprioritized. Similarly, papers describing seagrass ecological studies, surveys, or assessments were not included unless the study also implemented predictive modeling approaches. In addition, we focused on papers that described model development, versus those that only documented application of a model. This systematic searching was not meant to be a definitive inventory on the subject, but rather an exercise to characterize different modeling approaches applied to seagrasses that would help us identify major data and knowledge sources/gaps for Southern California embayments and estuaries.

Literature Synthesis

To organize our resources and document details of their modeling approaches, we categorized the papers into a dichotomy based on the underlying modeling approach, either mechanistic modeling or statistical/correlative modeling. Key parameters and features of the sorted studies were recorded in an MS Excel workbook. We defined statistical approaches as ones that correlate the presence or abundance of seagrass with spatial environmental data to predict seagrass extent (sensu Robinson et al. 2017), while mechanistic approaches link seagrasses' environment and its fitness to predict resulting seagrass growth (Jarvis et al. 2014; Scalpone et al. 2020). Within a given category of modeling approach, we identified commonalities and differences in model structure and the different parameters used to drive the model.

Statistical modeling approaches generally require two types of inputs, species occurrence data and local environmental parameters. For each statistical seagrass model, we identified the final forcing factors for each model (e.g., water depth, sea surface temperature), the model response variable (e.g., probability of seagrass occurrence), and the type of model correlating those inputs (e.g., GAM [general additive model], RF [random forest], GLM [general linear model]), as well as the seagrass species and study location.

Mechanistic modeling approaches similarly need species occurrence and environmental data, but also require key biotic and abiotic process equations (e.g., photosynthetic rate, respiration rates, mortality rates) to relate those inputs and characterize seagrass growth. We collected details on what processes each model used to predict growth and environmental drivers, as well as seagrass species and study location information.

Available Data Inventory

Based upon the different environmental parameters used to drive the models reviewed in our literature search, we created an inventory of analogous data that could be available for Southern California. Our goal was to identify existing data and data gaps that might influence the overall approach and structuring of a predictive model of eelgrass occurrence.

We contacted local managers and SCCWRP collaborators associated with coastal and estuary monitoring efforts (e.g., Orange County Public Works, California Department of Fish and Wildlife) to identify environmental data sources that could accessed upon reasonable request. Additionally, we also searched for environmental data sources that were publicly available/accessible online (e.g., SCCOOS data, MODIS satellite data, etc.). Environmental data were cataloged with the data locations, spatial extent, temporal/spatial resolution, timespan, and how to access the data for future use. For eelgrass extent data, a recent inventory done for McCune et al. (2020) was used as a baseline inventory of available spatial data on eelgrass distribution in the large estuaries and embayments of Southern California. Eelgrass data were cataloged with the location of the data, spatial location, year of collection, types of eelgrass measurements collected (e.g., geospatial, bed perimeter, shoot density), and species identity. In addition, any ancillary environmental data collected concurrently with the eelgrass (e.g., stressors, habitat, associated biota) were also cataloged.

Results and Discussion

Literature Synthesis

Based upon our search criteria, we gathered 32 different publications detailing predictive models of seagrass occurrence (See the Holt and Gillett Annotated Literature Review files). We found a number of both statistical and mechanistic models that covered 10 different species of seagrass (including a species of *Posidonia*, and *R. maritima*), with one paper (Jayathilake and Costello 2018) focused on modeling the distribution of 37 species of seagrass concurrently at a global scale. Approximately 50% of these models included or were solely focused on *Z. marina*.

None of the publicly available models were developed or have been applied to the waters of Southern California. More broadly, none of the models were developed in or have been applied to the Pacific coast of North America. One statistical model of eelgrass habitat suitability (ELVS [Ecological Limits, Viability, and Sustainability]) has been used in identifying potential eelgrass restoration sites in Southern California and San Francisco Bay (Merkel 2011). However, details and components of the ELVS model are not readily available in the literature, which limits its utility for our purposes.

As detailed below, there were no unifying patterns in the motivations for creation or desired results that informed the approach with which a given model was created. Data availability and author personal preference/experience seemed to be the primary determining factors in how a given model was constructed. However, it is apparent that most of the mechanistic models were applied to smaller, discrete areas, while many of the statistical models were developed and applied to larger geographic areas. We suspect that this pattern was more reflective of the types and availability of data used to drive the models rather than one modeling approach being more appropriate at a given spatial scale versus another.

Statistical Models

We classified sixteen publications as using statistical modeling approaches, with study areas ranging from seagrass distributions in single coastal estuaries (Valle et al. 2013) to predicting distributions globally (Jayathilake and Costello 2018). Several of these studies had a direct management focus, demonstrating how predictive modeling can be used to investigate the effectiveness of alternative management scenarios for local (e.g., eutrophication) or regional (e.g., climate change) stressors. As in illustration, Bergström et al. (2013) evaluated different scenarios related to three potential eutrophication targets to be adopted across the Baltic Sea region and how they would impact eelgrass distribution. Similarly, Papaki et al. (2020) evaluated the impact of future climate change scenarios in the Mediterranean Sea, specifically changes in water depth and temperature, on the distribution of different families of seagrass across the region. Most closely related to our long term goals of using a habitat occupancy model to establish a reference baseline distributions for eelgrass, Vacchi et al. (2013) built a model for predicting the distribution of surfgrass (*Posidonia oceanica*) in the absence of anthropogenic disturbance.

The mathematical underpinnings of the statistical models we reviewed ranged from simpler generalized linear models (GLM) to more complex non-linear and machine learning models. Our inference was that the type of mathematical framework was chosen based largely on the form of the seagrass distribution data (e.g., presence only, presence/absence, continuous), the amount and spatial/temporal scale of environmental predictors, as well as the authors' perceptions on the nature of the predictor-response relationships (e.g., linear, quadratic, unknown). Where the form of the relationship between seagrass growth and predictors was known – either a priori or developed as part of the study – and there were a relatively limited number of predictor variables, more directed and structured models like GLMs (Van Der Heide et al. 2009; Crase et al. 2012; Vacchi et al. 2013; Detenbeck and Rego 2015) or general additive models (GAM) were most common (Bekkby et al. 2008; Bergström et al. 2013; Schubert et al. 2015). In scenarios where there were a larger number of potential predictors and the form of the response relationship was unknown, authors tended to use less structured, unsupervised modeling techniques like maximum entropy (MaxEnt) (Bergström et al. 2013; Downie et al. 2013; Jayathilake and Costello 2018), random forest (Bergström et al. 2013; Valle et al. 2014), or boosted regression trees (Valle et al. 2014). Less commonly applied approaches also include fuzzy logic and Bayesian modeling techniques (Grech and Coles 2010; March et al. 2013; Papaki et al. 2020).

The common response variable for nearly all of the statistical models was presence of the species of interest within a raster cell or pixel. These discrete spatial units of potential habitat ranged in resolution from 10s of meters to 30 arc seconds (~776 m at 33°N). Some studies worked with presence/absence as a binomial factor, while others were created from % cover within a cell. Most of the different model types can be adjusted to work with either a categorical or continuous format of the seagrass response data.

Conceptually, all of the predictor variables included in the different models were either direct measures or approximations of factors that positively or negatively influence the growth of the seagrass. The suites of predictors commonly included both continuous and categorial (binomial or ordinal) data. Water depth was included in all but one model, with measures of wave exposure and bottom slope as other frequently selected variables. In most instances, water depth serves as a proxy measure of light availability, while also incorporating the likelihood of air exposure, desiccation, elevated temperature stress, etc. Conversely, wave exposure serves as a relatively direct measure of natural physical disturbance that can remove the seagrass by breaking the blades or uprooting the whole plant. Overall, the types and scale of predictor data used in a given model seemed to depend upon the data availability and study area scale. Importantly, many of the studies were able to successfully use predictor data at differing spatial scales within a given model, even if they differed from the spatial scale of the seagrass data (Grech and Coles 2010; March et al. 2013; Detenbeck and Rego 2015).

Interacting with water depth, water clarity is another major component in approximating the light availability to seagrasses and, consequently, their growth. As such, many of the models included measures of secchi depth or turbidity, as well as water column chlorophyl a or biostimulatory compounds. When the completed models were used to hindcast or forecast different management scenarios related to eutrophication, these variables were often the ones manipulated to represent different scenarios and their consequences on seagrass distribution (Bergström et al. 2013; Vacchi et al. 2013; Valle et al. 2014; Detenbeck and Rego 2015). A number of models were also successful in incorporating measures of water temperature, salinity, sediment composition, and sediment nutrients.

Our best understanding of the ELVS eelgrass habitat model (Merkel 2011), which has been applied in California to assist in restoration planning, is that it uses sediment type, water depth, salinity, and light availability information. The model appears to create waterbody-specific distribution curves of eelgrass presence and cover across gradients of each predictor variable. The probability of eelgrass occurrence at a given location is then calculated from the composite of values extracted from those individual distribution curves using the habitat measurements observed at the location of interest (K. Merkel, pers comm).

Mechanistic Models

We classified nineteen publications as using mechanistic models for predicting seagrass growth, either for a single seagrass species or several depending on the study goals and applications. These studies generally parameterized the processes of growth and loss inherent to a given species of seagrass in order to capture how environmental conditions limit seagrass distribution

(Evans et al. 2015). In these studies, the persistence, expansion, or decline of seagrass in a specific location over time was predicted from a suite of environmental forcing factors (water temperature, light, wave action, etc.) and biological state variables (e.g., plant biomass, proximity to other plants, reproduction) modified by internal rates inherent to the species of interest (e.g., photosynthesis, respiration).

Most of the mechanistic models were created as stand-alone models that allow for investigation of the biology and ecology of a given species, as well as testing different climate change or eutrophication scenarios on seagrass health. Alternatively, some were constructed to be a part of larger ecosystem models of nutrients or carbon cycling (Erftemeijer and Middelburg 1995; Baird et al. 2016).

Mechanistic models tend to be more mathematically complex than their statistical counterparts. As a consequence, many authors end up balancing the tradeoff between accuracy and model complexity in how they choose to parameterize their models (Baird et al. 2016). Increasing complexity provides greater control in the model when producing simulations, but it also creates greater data demands and requires greater computing power. As such, nearly all of the models we reviewed had chosen to focus the complexity of their calculations on a single aspect of seagrass physiology that they were most interested in exploring. A majority of the studies we considered were interested in the influence of light availability and capacity for light harvesting by the plants. Accordingly, we have many detailed examples of how one would build out the photosynthesis/growth components of a seagrass model (Cummings and Zimmerman 2003; Ralph et al. 2007; Kenworthy et al. 2014). As a contrast, Pedersen et al. (2016) and Zharova et al. (2001) focused on how to incorporate temperature effects and oxygen availability on the respiration and photosynthetic inhibition aspects of seagrass growth and loss. Another important aspect to consider and parameterize in a model, especially in the spatially explicit application of a seagrass model as we intend, is the interaction of seagrass beds with each other and on the sediment environment they live in (Wortmann et al. 1997; Newell and Koch 2004; Carr et al. 2010; Jarvis et al. 2014)

Though the model structure and relative complexity may have varied from study to study, all of the studies we classified as mechanistic models used seagrass organic matter as the predicted variable. The organic matter was represented as either total biomass (e.g., ash-free dry mass), carbon, or nitrogen, though all three forms are relatively interchangeable by application of ecological stoichiometric ratios (Fourqurean et al. 1997; Touchette et al. 2003). In most of the models, the accumulation of that organic matter was treated simply as a total value for the organism in a given space (e.g., 25 g of seagrass per model cell). However, some models did parse how the organic matter could be distributed among individual seagrass shoots (e.g., Carr et al. 2012) or into the above ground and below ground portions of the plants (Best et al. 2001; Burd and Dunton 2001; Baird et al. 2016).

The basic structure of all the mechanistic models was weighing the gains (e.g., photosynthetic growth or import) of seagrass organic matter against the losses (e.g., respiration, mortality, or export). Where or when organic matter gains were a net positive, seagrass would be expected to be present. Conversely, where or when organic matter gains were negative, the seagrass would be expected to be absent.

The positive gains in seagrass organic matter are a product of photosynthetic rates that fuels somatic growth of individual shoots and clonal expansion along the rhizomes, as well as import of seedlings from other beds (Ralph et al. 2007). The photosynthetic growth can be represented by species-specific light capture rates of the plant (*Z. marina*-specific rates presented in Zharova et al. 2001; Cummings and Zimmerman 2003; Straub et al. 2015; Zimmerman et al. 2015) applied to measured or modeled amounts of light. This growth is in turn mediated by water temperature in either asymptotic or unimodal functions, depending on the range of temperatures experienced (Zimmerman et al. 2015; Pedersen et al. 2016).

With these photosynthetic growth equations, accounting for the amount of light reaching the blades of seagrass at different depths is critical to "powering" the growth portion of the model. As such, this is typically one of the more complex parts of models to be parameterized. It begins with the amount of light at the air/water interface, which is typically estimated as a function of latitude and climate. The amount of photosynthetically active light available between the surface and the bottom of the water column must then be accounted for as a function of attenuation by the water itself, as well as shading from phytoplankton, CDOM, suspended sediments, epiphytic algae, and seagrass biomass before it can be used to calculate photosynthetic growth (Ralph et al. 2007). The initial amounts of light at the air-water interface (i.e., prior to any attenuation) is a location-specific type of data that will vary with latitude and climate (Best et al. 2001; Zharova et al. 2001; Straub et al. 2015). The rates and functions used to represent light attenuation processes are typically not treated as specific to any species of eelgrass nor any given location. However, the state variables used in those attenuation functions are treated as a mix of location specific measures (Burd and Dunton 2001; Straub et al. 2015) or as "best practice" values (Best et al. 2001; Carr et al. 2012; Pedersen et al. 2016), largely depending upon the available data and focus of the study for which the model was built.

Import of seedlings or encroachment of clonal adults from adjacent seagrass beds are positive contributions to seagrass organic matter that are external to the modeled bed but are important functions for spatially discrete models. Though it was not modeled in the majority of studies we reviewed, there were a few examples, including multiple models specific to *Z. marina*, (Wortmann et al. 1997; Jarvis et al. 2014; Straub et al. 2015; Scalpone et al. 2020) that considered the import of seedlings or the expansion of adjacent beds toward the net accumulation of seagrass organic matter.

Unlike many other primary producers, nitrogen and phosphorus are rarely used as limiting factors to growth in the seagrass models we reviewed. Most seagrasses, including *Z. marina*, obtain most of their nutrients from the sediment environment where the amounts of nitrogen and phosphorus are assumed to be in excess of what the plants need (though see Erftemeijer and Middelburg 1995; Scalpone et al. 2020). Where models did include measures of water column nitrogen, it was primarily used as a forcing factor for phytoplankton or epiphytic algal growth (Straub et al. 2015; Scalpone et al. 2020), which contribute to attenuation of available light to the seagrass.

To balance seagrass gains driven by light and import of biomass, seagrass mechanistic models characterize plant respiration (dark and light rates), mortality, and export (Ralph et al. 2007). Respiration was typically captured as a temperature-mediated function of total plant or above ground/below ground biomass (Burd and Dunton 2001; Baird et al. 2016), with Straub et al. (2015), Scalpone et al. (2020), and Zimmerman (2021) providing *Z. marina*-specific rate formulae. Some measures of standing stock biomass were needed to initialize the model and temperature measurements were taken from in situ (water) observations or modeled from air temperature (Scalpone et al. 2020). With respect to our broader goals for using an eelgrass habitat model, temperature profiles and their influence on respiration are where many studies have linked their seagrass models to climate change models (Zimmerman et al. 2015; Pedersen et al. 2016; Scalpone et al. 2020) to predict suitable condition for seagrass growth/persistence under different climate change scenarios.

Organic matter loss to mortality was almost uniformly treated as an emergent property of the seagrasses – incorporating true mortality, seasonal senescence, grazing, disease, and stochastic disturbances into one factor. Mortality was represented either as a constant rate (Burd and Dunton 2001; Zharova et al. 2001) or as a temperature-mediated function negatively impacting overall biomass (Baird et al. 2016). Some more complex models specifically included organic matter loss functions related to wave exposure (Zharova et al. 2001; Scalpone et al. 2020) both as a dynamic function or a constant rate. Wave exposure is a site-specific attribute that could be calculated for different parts of Southern California and applied to wave-based mortality functions. Seedling and flower production, as well as somatic expansion of the plants beyond discrete model cells/grids was the last major element of organic matter loss to consider in the models we inventoried. Flowering physiology and rate of seedling production are one of the less well-understood aspects of many species of seagrass, but Best et al. (2001), Jarvis et al. (2014), and Scalpone et al. (2020) did incorporate temperature-mediated seedling production functions for *Z. marina*.

Applicability to Southern California

None of the mechanistic or statistical models we reviewed could be directly applied "off the shelf" to predict habitat suitability of Southern California estuaries and embayments for *Z. marina*. It was our opinion that the lack of appropriate local data and the differences in environmental conditions in Southern California versus other parts of the world where models were developed would prevent direct application of other models. However, the general approach/structure of many of the statistical models or the *Z. marina*-specific rates of the mechanistic models should be relevant for creating a habitat occupancy model for the Southern California region.

Based upon the reviewed literature, a statistically driven model could resemble the concept illustrated in Box 1. There would be some manner of spatially discrete eelgrass response (e.g., probability of occurrence, % cover) and a series of predictor variables related to water column characteristics (clarity, quality), habitat characteristics (depth, currents, sediment composition), and spatial characteristics (connectivity to other beds, biogeography). The mathematical functions relating the response to the predictors can then be a variety of options noted above, ranging from regression-based approaches to machine learning-based approaches.

Conversely, a mechanistic-style model could resemble the concept illustrated in Box 2. The output of the model would be the net production of eelgrass organic matter (either growth or loss), which is the product of the increaser functions (e.g., photosynthesis, import) and the decreaser functions (e.g., mortality, respiration, export). Within this modeling approach, the increaser and decreaser functions are driven directly by external forcing factors (e.g., light, temperature) or by forcing functions altered by modifying functions (e.g., light attenuation, wave exposure).

The ELVS model applied in Merkel (2011) is likely not a viable option for developing a reference expectation for an eelgrass assessment tool, despite its previous usage in the region for restoration work. The actual underpinnings of the model are not publicly available and its utility and applicability to region-wide modeling could therefore not be fully appraised. Furthermore, the model is currently being updated for application in San Francisco Bay, a process which involves incorporating machine learning elements and a broader list of potential predictor variables into the original ELVS model (K. Merkel, pers. comm.). If future versions of this model become publicly available, it should be reevaluated as a potential option.

Ultimately, the final approach to model creation and its parameterization will be dependent upon a combination of utility of the end products for management goals, personal preferences and expertise of the modelers, the availability of the different types of forcing factor data for locations throughout the region, and the ability to create/obtain *Z. marina* physiological rates applicable to Southern California. While physiological rates, modifying equations, and stressor-response relationships specific to Southern California habitat and eelgrass populations would be ideal, our review of the literature would suggest that the many potential components of either modeling approach could be imported from other regions and their seagrass models as is, or with some small modifications.

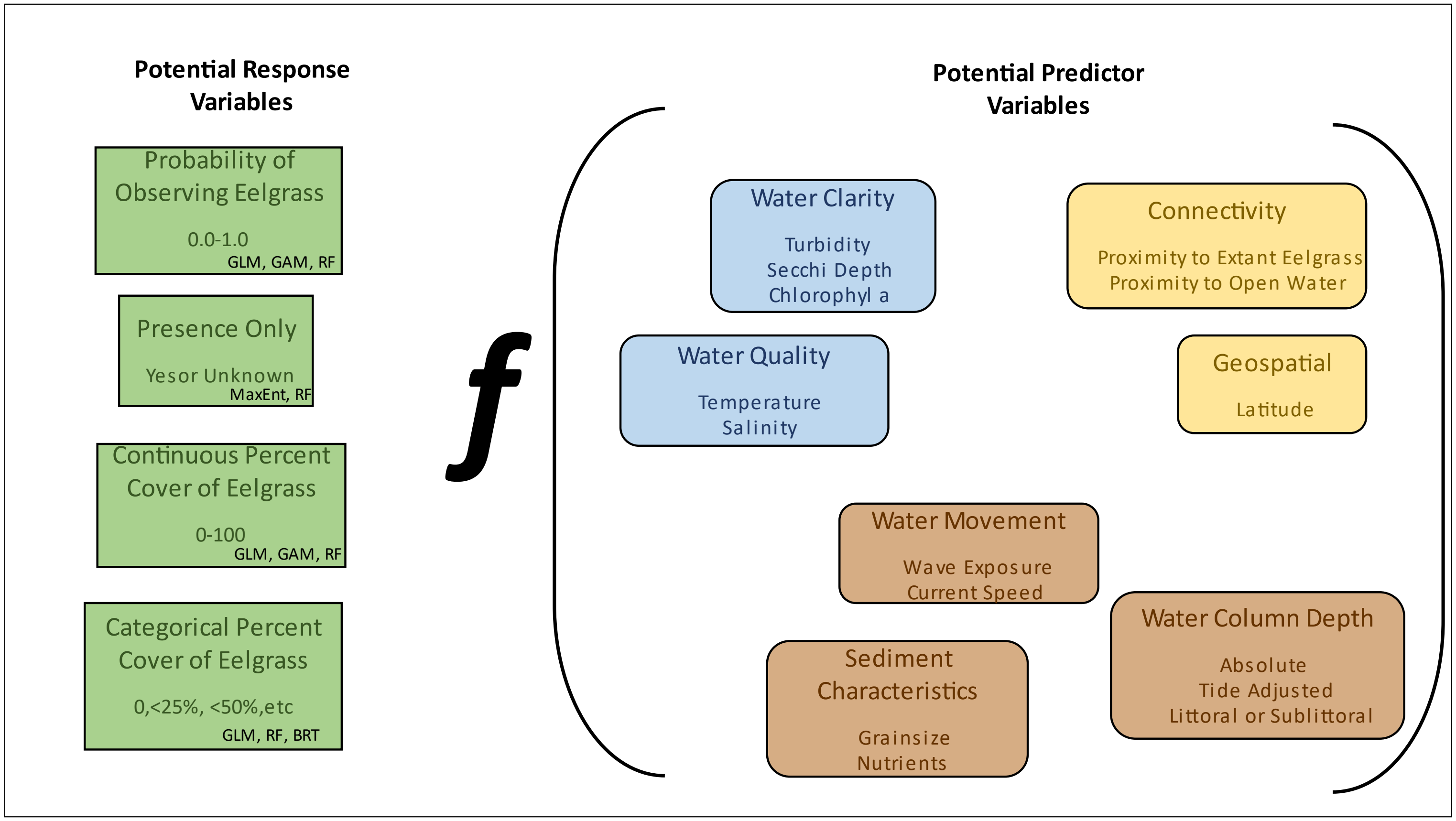

Figure 1. A conceptual diagram of the structure of a statistical habitat occupancy model for eelgrass (*Zostera marina*) based upon published models encountered during the literature review. Potential Response Variables are the different numerical forms of eelgrass "presence" that could be used in the model, including the numerical/categorical range of the variable and the type of mathematical framework that could be used to relate the response variables to the predictors. GLM=General Linear Model, GAM=General Additive Model, RF=Random Forest, MaxEnt=Maximum Entropy, BRT=Boosted Regression Tree. The Potential Predictor Variables are organized around the general classes of variables used in published *Z. marina* models, with some specific variables presented as an example. Blue rounded rectangles are water column variables, brown are habitat variables, and yellow are spatial variables.

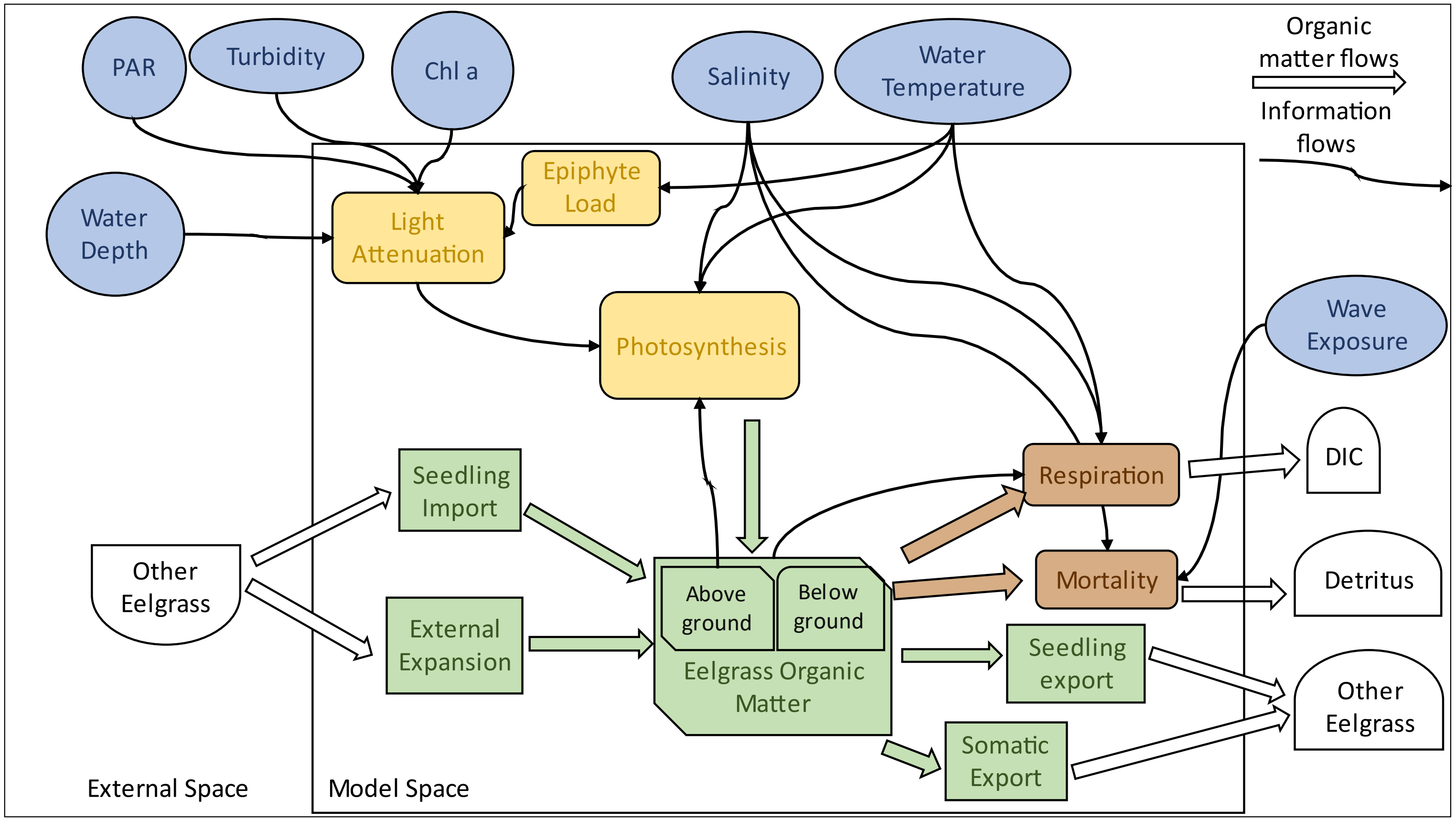

Figure 2. A conceptual diagram of the structure of a mechanistic habitat occupancy model for eelgrass (*Zostera marina*) based upon published models encountered during the literature review. The diagram is divided into two parts, the model itself (Model Space) and variables exterior to, but important to, the model (External Space). The thin arrows indicate the exchange of information (e.g., temperature, light, water depth) that are used by different rate equations. The block arrows represent the exchange of eelgrass organic matter (e.g., carbon, biomass) between different parts of the model. The ovals represent exterior forcing factors. The rounded rectangles represent rate equations related to eelgrass growth (yellow) or loss (brown). The regular rectangles represent constant variables of eelgrass growth or loss. The central polygon of Eelgrass Organic Matter represents the net accumulation or loss of biomass that would be the model's key output. The white rounded polygons represent external eelgrass organic matter sources (left) or sinks (right).

Data Inventory

As noted above, one of the elements that will influence the selection of a general modeling approach and the specific parameterization of that model will be the availability and coverage of both *Z. marina* occurrence data and predictor data, as well the forcing functions and constants that may be used in a mechanistic model. Based upon our review of publicly available data sources and conversations with scientists involved in environmental monitoring and modeling across the region, we were able to assemble an inventory of different data types that could be used in future model development. This data inventory was not meant to be exhaustive, but rather provide a high-level picture of the options available – the data sources, their spatial resolution, and their temporal extent – so as to best inform the planning of future modeling efforts.

The mapping of eelgrass extent in Southern California has largely occurred in the major embayments of the region, including Mission Bay, San Diego Bay, Newport Bay, and Alamitos Bay (Table 1). These studies used a combination of eelgrass observation methods, including diver eelgrass surveys and remote sensing techniques such as sonar, to document the presence or absence of eelgrass across survey regions. While all the surveys present a spatial estimate eelgrass extent, some of the efforts also documented eelgrass shoot density at stations across the survey areas. Less frequently, there have been survey efforts to map the extent of eelgrass in the smaller lagoons, estuaries, ports, and marinas along the coastline of the region. Older data collected under a mix of different surveys from 1994-2018 have been compiled by NOAA NMFS and are available online via EcoAtlas (https://www.sfei.org/data/eelgrass-survey-gis-data#sthash.oWB3xqG1.OHRaJ9BD.dpbs). Standalone regional reports encompassing the smaller waterbodies are also available (Table 1).

Table 1. Inventory of *Zostera marina* extent data from the Southern California Bight in publicly available reports or data files.

Survey Location	Survey Years	Source
Newport Bay	2003-2004; 2006-2008; 2009-2010; 2012-2014; 2016, 2018; 2020	Coastal Resources Management; Marine Taxonomic Services
San Diego Bay	1993; 1999; 2004; 2008; 2011; 2014	U.S. Navy; Merkel & Associates
Mission Bay	1988; 1992; 1997; 2000; 2007; 2013; 2016	Merkel & Associates
Alamitos Bay	2007-2009	Coastal Resources Management
Southern California Bight (Northern Santa Monica Bay, Point Dume to Los Angeles/Ventura County Line, Eastern Santa Cruz Island, Lower Santa Ana River, Santa Ana River Marsh, Huntington Beach Wetlands)	2013; 2015	Merkel & Associates

Much of these data are more than 5 years old and given the ephemerality of eelgrass beds waxing and waning with ocean conditions (Munsch et al. 2023), their exact boundaries probably should not be used to calibrate or validate any modern modeling predictions. However, if predictor data that were contemporaneous with the eelgrass data were available (from other sources), then the data would have more direct applicability to model building. At a minimum, these historical maps of eelgrass presence/extent could be used to guide modern data collection efforts oriented toward model development. Efforts are presently underway to more thoroughly map the presence of eelgrass beds in as many of the smaller embayments across the whole of Southern California (C. Loflen, pers. comm.; D. Gillett unpublished), data which may be of value to future modeling efforts.

For the predictor data necessary for developing a statistical model of eelgrass occurrence, we have organized potential data sources around the major variable classes depicted in Box 1 (Table 2). For each variable, many of which have multiple potential sources, we have characterized: 1) The nature of the data (directly measured, estimated from another data type, or output from a different model); 2) the approximate spatial scale and temporal resolution; 3) if there is regional coverage of the variable (i.e., data available for most of the embayments from Point Conception to the US-Mexico border) or if there is only data in the major embayments of the region (e.g., Newport or San Diego bays); and 4) the availability of those data and our opinion on the likelihood of obtaining those data.

All of the variable classes that could be used in a statistical model have some amount of available data, typically as point measures from the major embayments of the region. Unfortunately, true regional data coverage, within the large embayments and among the smaller systems is the major data gap that is apparent from Table 2. However, as noted in Table 2, obtaining regional-scale data at a relatively fine spatial scale within a given embayment can (conceptually) be achieved for nearly all the different data types.

Based upon the models available in the literature, accurate fine-scale measures of water depth and water clarity would most likely be the critical variables in a new statistical model of eelgrass habitat suitability. Water depth data can be obtained from NOAA navigation resources for the major embayments of the region, but the accuracy of those measures in the shallow fringes where most of the eelgrass should be growing is likely inaccurate and imprecise. At present, water clarity data that could be used in developing a model are only available at discrete eelgrass beds that have been previously studied or in other embayment locations that have some manner of permit-based monitoring (e.g., Newport Bay) associated with them. As such, obtaining measures or modeled estimates of water depth and water clarity is going to be critical to creating a regionally applicable statistical model of eelgrass habitat suitability.

Tables 3 summarizes the types of data needed to parameterize the forcing factors (3a), functional rates (3b) and constants (3c), that would be needed for developing a mechanistic model of eelgrass occurrence. The data types are organized around the different model components illustrated in Box 2. We have characterized each potential model parameter based upon: 1) the nature of component (measured or estimated values, modeled output, or a dynamic equation); 2) the spatial specificity (site, embayment, or region-scale); 3) the temporal scale; and 4) the availability of those data/equations and our opinion on the likelihood of obtaining them.

Like the predictor data for the statistical models, many of the forcing factors could presently be characterized at discrete points in the major embayments of the region, but the high resolution/frequency spatial and temporal measures of those data needed to drive a regional-scale mechanistic model are lacking. Conversely, many of the rate equations capturing *Z. marina* physiological processes (e.g., respiration, photosynthesis) and environmental intermediaries (e.g., light attenuation) that would likely comprise a mechanistic model are available from the literature. However, it would be prudent to validate at least some of key *Z. marina* rate equations to ensure that Southern California populations and genotypes have similar physiology to those from other regions from which the published equations were derived.

Table 2a. An inventory of potential sources for data that could be used as water clarity predictor variables in a statistical model of *Zostera marina* habitat occupancy. Each variable is characterized by the nature of the data (directly measured, estimated from another data type, or output from a different model), the approximate spatial scale and temporal resolution, whether there is regional coverage of the variable or if there is only data in the major embayments of the region, and our perception of the availability of those data and the likelihood of obtaining those data. Bight=Southern California Bight Regional Monitoring Program, CRM=Coastal Resource Managers, Inc., CSULB=California State University, Long Beach, EMPA=Estuarine Marine Protected Area monitoring program, JPL/NASA Jet Propulsion Laboratory / California Institute of Technology, MTS=Marine Taxonomic Services, Inc., NOAA=National Oceanographic and Atmospheric Administration, RESCQ=Regional Eelgrass Survey of Condition and Quality.

Variable	Turbidity			Secchi Depth		Chlorophyl a		
Data Type	Measured	Measured	Estimated	Measured	Measured	Measured	Measured	Estimated
Spatial Scale	Point	Point	100-m	Point	Point	Point	Point	100-m
Temporal Scale	Point	Point	Weekly	Point	Point	Point	Point	Weekly
Regional Coverage	No	Yes	Yes	No	Yes	Yes	Yes	Yes
Major Embayment Coverage	Yes	Yes	Yes	Yes	Yes	Yes	Yes	Yes
Status	Available	Aspirational	Aspirational	Available	Aspirational	Available	Aspirational	Aspirational
Likelihood of Achieving	100	25	75	100	75	100	75	50
Data Source	Stormwater agency monitoring	RESCQ Monitoring, Bight ‘23 Monitoring	JPL Satellite Data	CSULB, SONGS, CRM, MTS,	RESCQ Monitoring, Bight ‘23 Monitoring	Estuarine MPA Monitoring,	RESCQ Monitoring, Bight ‘23 Monitoring	JPL Satellite Data
Comment	Definitely in locations 303d listed for sediment, potentially in other systems	Unlikely to be collected by either program	Contingent upon successful DEVELOP project with SCCWRP & NASA/JPL	Collected at individual beds that have been studied previously	Probably will be collected by both programs	EMPA data not directly in beds but could be modeled. Less regional than Bight	Probably will be collected by both programs	Contingent upon successful DEVELOP project with SCCWRP & NASA/JPL

Table 2b. An inventory of potential sources for data that could be used as water quality and movement predictor variables in a statistical model of *Zostera* marina habitat occupancy. Each variable is characterized by the nature of the data (directly measured, estimated from another data type, or output from a different model), the approximate spatial scale and temporal resolution, whether there is regional coverage of the variable or if there is only data in the major embayments of the region, and our perception of the availability of those data and the likelihood of obtaining those data. Bight=Southern California Bight Regional Monitoring Program, CRM=Coastal Resource Managers, Inc., CSULB=California State University, Long Beach, EMPA=Estuarine Marine Protected Area monitoring program, JPL/NASA Jet Propulsion Laboratory / California Institute of Technology, MTS=Marine Taxonomic Services, Inc., NOAA=National Oceanographic and Atmospheric Administration, RESCQ=Regional Eelgrass Survey of Condition and Quality.

Variable	Water Temperature				Salinity		Wave Exposure	Current Speed
Data Type	Estimated	Modeled	Measured	Measured	Measured	Measured	Modeled	
Spatial Scale	100-m	500-m	Point	Point	Point	Point	100-m	
Temporal Scale	Weekly	Daily	Point	Point	Point	Point	Daily	
Regional Coverage	Yes	Yes	No	No	Yes	Yes	Yes	
Major Embayment Coverage	Yes	Yes	Yes	Yes	Yes	Yes	Yes	
Status	Aspirational (50 %)	Aspirational	Aspirational	Available	Available	Available	Aspirational	
Likelihood of Achieving	50	25	75	100	100	100	25	
Data Source	JPL Satellite Data	Prism Air Temperature Model	RESCQ Monitoring, Bight '23 Monitoring	CSULB, SONGS	Estuarine MPA Monitoring	Bight Program	NOAA	
Comment	Contingent upon successful DEVELOP project with SCCWRP & NASA/JPL	Model water temperature from air (sensu Scalpone et al. 2020)	Probably will be collected by both programs	Collected at individual beds that have been studied previously	EMPA data not directly in beds but could be modeled. Less regional than Bight	Bight data not directly in beds, but could be modeled	Apply NOAA models (sensu Detenbeck and Rego 2015)	

Table 2c. An inventory of potential sources for data that could be used as sediment characteristics and water depth variables in a statistical model of *Zostera marina* habitat occupancy. Each variable is characterized by the nature of the data (directly measured, estimated from another data type, or output from a different model), the approximate spatial scale and temporal resolution, whether there is regional coverage of the variable or if there is only data in the major embayments of the region, and our perception of the availability of those data and the likelihood of obtaining those data. Bight=Southern California Bight Regional Monitoring Program, CRM=Coastal Resource Managers, Inc., CSULB=California State University, Long Beach, EMPA=Estuarine Marine Protected Area monitoring program, JPL/NASA Jet Propulsion Laboratory / California Institute of Technology, MTS=Marine Taxonomic Services, Inc., NOAA=National Oceanographic and Atmospheric Administration, RESCQ=Regional Eelgrass Survey of Condition and Quality.

Variable	Sediment Grainsize		Sediment Nutrients		Water Depth		Littoral Gradient
Data Type	Measured	Measured	Measured	Measured	Measured	Estimated	Modeled
Spatial Scale	Point	Point	Point	Point	Point	Discrete	Point
Temporal Scale	Point	Point	Point	Point	Point	N/A	N/A
Regional Coverage	Yes	Yes	Yes	Yes	No	No	No
Major Embayment Coverage	Yes	Yes	Yes	Yes	Yes	Yes	Yes
Status	Available	Aspirational	Available	Aspirational	Available	Available	Aspirational
Likelihood of Achieving	100	75	100	75	100	100	90
Data Source	Bight Program, CSULB	RESCQ Monitoring, Bight '23 Monitoring	Bight Program, CSULB	RESCQ Monitoring, Bight '23 Monitoring	CRM, Merkel, MTS reports, CSULB	Bathymetry Maps/Models	Bathymetry Maps/Models, Tide Charts
Comment	Bight data not directly in beds, but could maybe be modeled	Probably will be collected by RESCQ, will be collected by Bight '23	Bight data not directly in beds, but could maybe be modeled	Probably will be collected by RESCQ, will be collected by Bight '23	Extract from published polygons for Newport, SD Bay, Mission, and others	NOAA Navigation resources, though shallow values are probably inaccurate	Calculated from bathymetry, depth measures, and tidal range models

Table 2d. An inventory of potential sources for data that could be used as connectivity and geospatial variables in a statistical model of *Zostera marina* habitat occupancy. Each variable is characterized by the nature of the data (directly measured, estimated from another data type, or output from a different model), the approximate spatial scale and temporal resolution, whether there is regional coverage of the variable or if there is only data in the major embayments of the region, and our perception of the availability of those data and the likelihood of obtaining those data. Bight=Southern California Bight Regional Monitoring Program, CRM=Coastal Resource Managers, Inc., CSULB=California State University, Long Beach, EMPA=Estuarine Marine Protected Area monitoring program, JPL/NASA Jet Propulsion Laboratory / California Institute of Technology, MTS=Marine Taxonomic Services, Inc., NOAA=National Oceanographic and Atmospheric Administration, RESCQ=Regional Eelgrass Survey of Condition and Quality.

Variable	Eelgrass Proximity			Open Water Proximity			Latitude	
Data Type	Measured	Measured	Measured	Measured	Measured	Measured	Measured	Measured
Spatial Scale	Discrete	Discrete	Discrete	Discrete	Discrete	Discrete	Point	Point
Temporal Scale	Point	Point	Point	Point	Point	Point	Point	Point
Regional Coverage	No	Yes	Yes	No	Yes	Yes	No	Yes
Major Embayment Coverage	Yes	Yes	Yes	Yes	Yes	Yes	Yes	Yes
Status	Available	Aspirational	Aspirational	Available	Aspirational	Aspirational	Available	Aspirational
Likelihood of Achieving	100	75	50	100	75	50	100	50
Data Source	CRM, Merkel, MTS reports, CSULB	RESCQ Monitoring, Bight '23 Monitoring	JPL Satellite Data	CRM, Merkel, MTS reports, CSULB	RESCQ Monitoring, Bight '23 Monitoring	JPL Satellite Data	CRM, Merkel, MTS reports, CSULB	JPL Satellite Data
Comment	Extract from published polygons for Newport, SD Bay, Mission, and others	Probably will be collected by RESCQ, may be collected by Bight '23	Contingent upon successful DEVELOP project with SCCWRP & NASA/JPL	Extract from published polygons for Newport, SD Bay, Mission, and others	Probably will be collected by RESCQ, may be collected by Bight '23	Contingent upon successful DEVELOP project with SCCWRP & NASA/JPL	Extract from published polygons for Newport, SD Bay, Mission, and others	Contingent upon successful DEVELOP project with SCCWRP & NASA/JPL

Table 3a. Inventory of data sources for potential external forcing factors that could be used as input data for a mechanistic model of *Zostera marina* growth. Each parameter is characterized by their type (measured, estimated, or output of another model), their spatial specificity (site, embayment, or region-scale), their temporal scale, the availability of those data, and our opinion on the likelihood of obtaining them.

Data Characteristics	Water Depth		Photosynthetically Active Radiation	Turbidity		Chlorophyl a		
Data Type	Measured	Estimated	Modeled	Measured	Estimated	Measured	Measured	Estimated
Site Specific	Yes	Yes	No	Yes	Yes	Yes	Yes	Yes
Embayment Specific	No	No	No	Maybe	Maybe	Maybe	Maybe	Maybe
Region Specific	No		Yes	No	No	No	No	No
Spatial Scale	Discrete	Discrete		Point	100-m	Point	Point	100-m
Temporal Scale	Point	N/A	Daily	Point	Weekly	Point	Point	Weekly
Status	Available	Available	Available	Aspirational	Aspirational	Available	Aspirational	Aspirational
Likelihood of Achieving	100	100	100	25	75	100	75	50
Data Source	Side Scan Eelgrass Surveys	Bathymetry Maps/Models	NOAA, MODIS	RESCQ Monitoring, Bight '23 Monitoring	JPL Satellite Data	Estuarine MPA Monitoring	RESCQ Monitoring, Bight '23 Monitoring	JPL Satellite Data
Comment	Some eelgrass restoration studies did general bathymetry mapping	NOAA Navigation resources, though shallow values are probably inaccurate	Spatial resolution unclear	Unlikely to be collected by either program	Contingent upon successful DEVELOP project with SCCWRP & NASA/JPL	EMPA data not directly in beds but could be modeled. Less regional than Bight	Probably will be collected by both programs	Contingent upon successful DEVELOP project with SCCWRP & NASA/JPL

Table 3a (continued).

Data Characteristics	Water Temperature				Wave Exposure	Salinity	
Data Type	Estimated	Modeled	Measured	Measured	Modeled	Measured	Measured
Site Specific	Yes	Yes	Yes	Yes	Yes	Yes	Yes
Embayment Specific	Maybe	Maybe	Maybe	Maybe	Maybe	No	No
Region Specific	No	No	No	No	No	No	No
Spatial Scale	100-m	500-m	Point	Point	100-m	Point	Point
Temporal Scale	Weekly	Daily	Point	Point	Daily	Point	Point
Status	Aspirational	Aspirational	Aspirational	Available	Aspirational	Available	Available
Likelihood of Achieving	50	25	75	100	25	100	100
Data Source	JPL Satellite Data	Prism Air Temperature model	RESCQ Monitoring, Bight '23 Monitoring	CSULB, SONGS	NOAA	Estuarine MPA Monitoring,	Bight Program
Comment	Contingent upon successful DEVELOP project with SCCWRP & NASA/JPL	Model water temperature from air (sensu Scalpone et al. 2020)	Probably will be collected by both programs	Collected at individual beds that have been studied previously	Apply NOAA models (sensu Detenbeck and Rego 2015)	EMPA data not directly in beds but could be modeled. Less regional than Bight	Bight data not directly in beds, but could be modeled

Table 3b. Inventory of data sources for potential dynamic rate equations that could be used as internal functions for a mechanistic model of *Zostera marina* growth. Each parameter is characterized by their type, spatial specificity, the availability of those data, and our opinion on the likelihood of obtaining them.

Data Characteristics	Light Attenuation	Epiphyte Loading	Photosynthesis Rate	Biomass Translocation	Respiration Rate	Mortality Rate
Data Type	Equations	Equations/Measured	Equation	Equation	Equation	Equation
Site Specific	No	No	No	No	No	No
Embayment Specific	No	No	No	No	No	No
Region Specific	No	Maybe	Maybe	Maybe	Maybe	No
Status	Available	Aspirational	Aspirational	Available	Aspirational	Available
Likelihood of Achieving	100	50	75	100	75	100
Data Source	Manuscripts 1,2,3,4,5,6,7,8, 10, 11	Manuscripts 1,5,8	Manuscripts 2,4,5,6,7,8,10,11	Manuscripts 2, 5,7,8,10, 11	Manuscripts 2,4,5,6,7,8,10,11	Manuscripts 1,2,5,7,8,10,11
Comment	Mechanistic relationship, modified by inputs of other parameters	Most likely need to be modified for Southern California conditions	May need to account for Southern California populations	May need to account for Southern California populations	May need to account for Southern California populations	Most use a simple linear equation, not region-specific

Manuscript #	**Citation**	**Species**
1	Baird et al. 2016	*Z. muelleri*
2	Best et al. 2001	*Z. marina*
3	Burd and Dunton 2001	*Halodule wrightii*
4	Cummings and Zimmerman 2003	*Z. marina*
5	Jarvis et al. 2014	*Z. marina*
6	Kenworthy et al. 2014	*Z. marina*
7	Scalpone et al. 2020	*Z. marina*
8	Straub et al. 2015	*Z. marina*
9	Wortmann et al. 1997	*Zostera spp.*
10	Zharova et al. 2001	*Z. marina*
11	Zimmerman et al. 2015	*Z. marina*

Table 3c. Inventory of data sources for potential rate equations that could be used as constants for a mechanistic model of Zostera marina growth. Each parameter is characterized by their type, spatial specificity, the availability of those data and our opinion on the likelihood of obtaining them.

Data Characteristics	Seedling Import	External Expansion (In)	Seedling Export	Somatic Export (Out)
Data Type	Estimated	Estimated	Estimated	Estimated
Site Specific	No	No	No	No
Embayment Specific	Maybe	No	Maybe	No
Region Specific	Maybe	No	Maybe	No
Status	Aspirational	Available	Aspirational	Available
Likelihood of Achieving	75	100	75	100
Data Source	Manuscripts 2,5,7,8	Manuscripts 2,5,8,9	Manuscripts 2,5,7,8	Manuscripts 2,5,8,9
Comment	May need to account for Southern California populations, but little data available outside Chesapeake Bay	Most use a non-region specific equation	May need to account for Southern California populations, but little data available outside Chesapeake Bay	Most use a non-region specific equation

Manuscript #	Citation	Species
1	Baird et al. 2016	*Z. muelleri*
2	Best et al. 2001	*Z. marina*
3	Burd and Dunton 2001	*Halodule wrightii*
4	Cummings and Zimmerman 2003	*Z. marina*
5	Jarvis et al. 2014	*Z. marina*
6	Kenworthy et al. 2014	*Z. marina*
7	Scalpone et al. 2020	*Z. marina*
8	Straub et al. 2015	*Z. marina*
9	Wortmann et al. 1997	*Zostera spp.*
10	Zharova et al. 2001	*Z. marina*
11	Zimmerman et al. 2015	*Z. marina*

Supports and Impediments to a *Zostera marina* Model

Our review of the literature has illustrated that there are several different model structures that could be used to build a habitat occupancy model of *Z. marina* in Southern California. As with nearly all modeling exercises, however, the nature, quantity, and quality of the data used to drive the model will be the limiting factors on its usefulness. Large-scale, waterbody-to-waterbody spatial coverage and small-scale, within-waterbody coverage of the key modeling variables is critical to developing a regionally applicable and locally specific model of where eelgrass should be growing.

Based upon our understanding of the scope of coastal monitoring data in Southern California, there is good representation of the required data types that could be used to build basic models of eelgrass habitat suitability. Table 1 indicates that there is a reasonable amount of response data (i.e., presence and distribution of eelgrass) in the major embayments of the region. Tables 2 and 3 indicate that there is some amount of data available for many of the predictors or forcing factors that would most likely be used in modeling habitat suitability, albeit primarily from small portions of the major embayments. These two pieces of information suggest that it would be reasonable for one to begin developing a *Z. marina* habitat occupancy model. Analysis of this model – what are the most important variables, where in the region is the model performing most poorly – could be used to prioritize the types of data to collect and where to collect it from.

CONCLUSIONS

One of the goals of Southern California's bourgeoning eelgrass monitoring and assessment program, as described in McCune et al. (2020), is to develop a *Z. marina* habitat suitability model that can be used to make reference condition predictions of where the seagrass would be expected to grow in any Southern California waterbody in the absence of or with minimized local anthropogenic disturbance. As such, it is not sufficient to be able to model present-day eelgrass distributions, but rather make predictions of where it could be. To achieve these goals, a model will need to be applicable across the region and produce predictions at a practical scale (i.e., 100 m^2, not 1,000m^2) to allow for intra-waterbody assessments. There are a variety of examples in the literature for *Z. marina* models that can be used as a template or starting point in developing a model for the embayments of Southern California. Furthermore, there are enough monitoring and data generation resources in the region to serve as a starting point for parameterizing a model. Unfortunately, it must be noted that the region presently lacks data for key model parameters at a spatial resolution, spatial distribution, and temporal frequency to produce a statistical or mechanistic model to make predictions across all of the region's different waterbodies.

A lack of data is the biggest impediment to developing a regional-scale eelgrass habitat model with sufficient resolution and coverage. The question though is what types of data should be collected and from where. To inform that decision process, our literature and data review would suggest a two-pronged strategy. First, collect the most commonly used environmental data used as predictors in other *Z. marina* models – water depth, water column turbidity, water column chl a, salinity, and water temperature – with good resolution within and between waterbodies, especially in waterbodies other than Newport, San Diego, and Mission bays. Secondly, build draft models using presently available data, which will most likely resemble any final model structurally, but will be spatially limited in their domain. Analysis of these draft models will then enable us to determine what are the most influential variables, which can then be compared to the literature survey and subsequently prioritized for collection across the region.

A mechanistic model of *Z. marina* habitat suitability would be centered around making spatially explicit predictions of net eelgrass growth based upon dynamic estimates of photosynthesis, respiration, mortality, etc. In an assessment framework, this would take the form where those locations with conditions that would predict an accumulation of *Z. marina* biomass would be expected to support eelgrass beds, while those with conditions that would predict a loss of *Z. marina* biomass would not be expected to support eelgrass beds. The assessment tool would then make comparisons of where eelgrass is observed to where the model predicts it "should be". The benefits of a mechanistic modeling approach would include:

+ The model structure makes it easier to create predictions outside of currently observable conditions, which would provide a clearly defined version of a minimally disturbed reference condition against which waterbodies can be evaluated.

+ The model structure can be built to easily interface with sea level rise and climate change models, where they are available.

+ There are several published equations and datasets representing the interactions of biotic and abiotic parameters for *Z. marina* that can be used in building out the model.

The drawbacks of the mechanistic approach would include:

– Using eelgrass growth as an endpoint necessitates including timeseries for many of the data types (e.g., temperature, light), running the model across a long enough period of time to allow for an accumulation or loss of biomass.

– The endpoints of net accumulation or loss are less directly interpretable in a habitat suitability bioassessment context than the outcomes of statistical models.

– Many of the data types likely needed as forcing factors in the model are themselves model outputs or need to be quantified from remotely sensed imagery. While these can be generated, to date they have not been.

– None of the *Z. marina*-related rate equations available in the literature have been developed from Southern California populations. Eelgrass from this region may have slightly different physiology than populations from other regions, which may require modification of literature-based equations.

A statistical model of *Z. marina* habitat suitability would be centered on making spatially explicit predictions of eelgrass presence (or percent cover) based upon empirical relationships established between eelgrass and environmental variables like water depth, sediment composition, or proximity to other eelgrass beds. In an assessment framework, locations with conditions predictive of a high probability of observing eelgrass would be expected to support eelgrass beds, while those locations with conditions predictive of a low probability of observing eelgrass would be expected to not support eelgrass beds. The benefits of statistical model approach would include:

+ The model output of predicted probabilities of occurrence or of percent cover is directly interpretable in a habitat suitability bioassessment context.

+ The model can be constructed empirically (i.e., only the variables with the most explanatory power are retained), which does not rely on a priori insight into the population dynamics of eelgrass to construct the model.

+ While the model accuracy would most likely be improved by incorporating temporal variability, it is not reliant upon the inclusion of time series data.

The drawbacks of a statistical approach would include:

– The model structure makes it difficult to make predictions outside of the domain of the data used to establish the empirical relationships, which makes obtaining a minimally disturbed reference expectation more difficult.

– The model may be spatially constrained by the data used to develop it if the interactions of the predictor variables change across the region. If so, this would limit the domain across which the model could be applied.

– Traditional statistical models require large amounts of observational measures of predictor and response variables for both calibration and validation of the model. Acquiring these data at the scale and resolution needed to make a regional model may be impractical.

From the perspective of building an occupancy model that would be used to set expectations for a Tier 1 habitat extent bioassessment tool, we are inclined toward pursuing a mechanistic model of habitat occupancy. As noted above, the choice of underlying model structure is as much related to preference and experience of the person doing the work, as it is to the technical tradeoffs associated with each type of model. Consequently, we would ultimately defer to modeling experts who would be doing this work. Our preference toward the mechanistic models for regional bioassessment purposes is born out of the relatively straightforward approach to using a mechanistic model to make predictions under hypothetical (i.e., non-observed) conditions like minimally disturbed water quality or potential changes related to sea level rise and water temperature. However, if a statistical approach was pursued, we are confident that we would determine a way to apply it within a Tier 1 bioassessment tool. If there is capacity and interest, creating draft versions of both statistical and mechanistic models using existing data and then comparing their performance and utility to bioassessment tool development would be a useful exercise in ultimately determining what manner of model should be developed at the regional scale.

RECOMMENDATIONS

To further advance the interests of the Southern California community of SAV researchers, managers, and regulators toward the development of an eelgrass modeling framework that could identify the portions of our coastal embayments that can and should support eelgrass now and in the near future, we would recommend the following courses of action:

- **Begin collecting high-resolution bathymetry data in the shallow portions of the region's coastal embayments:** Water depth is a critical variable in modeling eelgrass included that was in every published model we were able to review and is therefore likely to be included in any new models built for Southern California. As such, water depth also represents the most critical data gap in our regional data sets. While there are bathymetry data for most coastal waterbodies in the region, the measurements lack accuracy and precision (0.25 – 0.5 m resolution) along the shallow fringes of the embayments where eelgrass is likely to grow. A concerted effort to collect detailed bathymetry data for vegetated and unvegetated sediments across the region is needed to enable the creation of any eelgrass habitat models. While a full, region-wide bathymetric mapping effort covering every potential waterbody where eelgrass may grow is daunting, it needs to be done. A strategy to move forward might be to ensure the collection of bathymetry data in concert with any new eelgrass mapping efforts, as well as expanding those efforts beyond the major embayments they typically take place in. To make the bathymetric mapping efforts more efficient, the surveys could be limited to or begin with the shallow (< 7 m) fringes of systems where eelgrass would have sufficient light, as well as prioritizing key embayments (e.g., those with historical eelgrass beds, but infrequent eelgrass mapping efforts (e.g., Seal Beach wetlands, Bolsa Chica wetlands)). There is also the possibility to use high-resolution depth data collected at a limited spatial scope to model shallow depths at broader spatial scales using the more widespread NOAA data or possibly from remotely sensed areal images.
- **Begin developing a draft regional-scale habitat occupancy model for *Zostera marina***: Though the lack of regional-scale data is a significant impediment to developing a regional eelgrass model that could be used for our proposed bioassessment framework, enough data are available to begin building a draft model (mechanistic or statistical) for a select part of the region. A draft model will have a limited domain and limited

accuracy, but the exercise of building a draft should provide specific practical insight into the best structure for a future regional model. The process would also refine what are the most influential/important data types to parameterize a model beyond the conceptual recommendations of this report. This experience could then be used to guide future eelgrass data collection efforts beyond the data types like water depth and water clarity that can be assumed a priori to be important in eelgrass modeling and which we have already highlighted.

- **Support collaborations to investigate existing or produce new remotely sensed data for the region's coastal zone:** Based upon the literature review, one of the approaches other environmental modelers have used to obtain data of sufficient spatial coverage and temporal frequency is to take advantage of data that can be extracted from remote sensing platforms. These include satellite imagery, manned and unmanned aerial photography, and submersible sensors. Modern satellite imagery (e.g., www.sentinel-hub.com) represent an untapped resource of coastal data among the Southern California management community. Recent collaborations between SCCWRP and the NASA JPL research group have shown great promise for obtaining useful environmental data for estuaries and embayments from satellite imagery. High resolution spatial and temporal patterns of turbidity, chlorophyl a, and possibly the location and species composition of SAV beds could also be produced from this imagery. However, algorithms need to be developed to extract these data from remote imagery and the estimates need to be ground-truthed. Supporting these types of collaborations with JPL, NOAA, and other agencies collecting remotely sensed data would be extremely valuable in filling the data gaps in parameters needed to predict presence and growth of eelgrass.

- **Continue to support regional monitoring efforts of eelgrass and other SAV:** The collection of biotic and abiotic data by one or two agencies for the purposes of developing a habitat model is not an efficient way to eliminate gaps in the data needed for modeling. Regional monitoring programs like the Southern California Bight Regional Monitoring Survey provide an ideal platform to collect priority eelgrass and environmental data from multiple waterbodies beyond the larger ones that are monitored more regularly. Furthermore, outside of the years when the Bight Program is collecting data, there are a myriad of local eelgrass monitoring efforts related to discharge permits, mitigation, and restoration activities. Encouraging collaboration among these different groups to facilitate the development of standardized eelgrass monitoring methodologies, a set of standardized of non-SAV environmental parameters (e.g., water clarity, chlorophyll a, grainsize), and centralized data repositories would help to generate data needed for calibration and eventual validation of a *Z. marina* habitat occupancy model. Organizations like MARINe (https://marine.ucsc.edu/overview/index.html) or the Southern California Kelp Consortium (http://kelp.sccwrp.org/) could provide a template for encouraging cooperation among the different parties monitoring eelgrass across Southern California. Continued participation in these types of monitoring efforts by regional and state water board staff will help to ensure an alignment between the evolving science of seagrass monitoring and its potential use in management and regulatory environments.

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