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Multi-Taxon Predictions of Deep-Sea Corals and Sponges From Stacked Species Distribution Models in the United States West Coast Exclusive Economic Zone and Relation to Trawl Closure Zones

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ABSTRACT

Aim: Abundant species distribution models (SDMs) of deep-sea corals and sponges (DSCS) allow one to make community-level predictions about DSCS. Pairing that with the conservation information of Vulnerable Marine Ecosystems (VMEs) due to their sensitivity to seafloor trawling, one can assess the efficacy of established seafloor protections, known as Essential Fish Habitat and Conservation Areas (trawl closure areas), in the United States West Coast on a multi-taxon basis. From this, we seek to answer the following questions: (1) can accurate multi-taxon, trawl-sensitive DSCS distribution predictions be made for the US West Coast and (2) to what extent do current trawl protections overlap with multi-taxon distribution predictions and what are the conservation and management implications?

Location: United States West Coast marine waters.

Methods: A cluster analysis was run on 40 SDMs of DSCS, identifiable as VME indicators and assigned a VME indicator score based on criteria used by regional fisheries management organisations. SDMs of taxa in clusters were stacked and averaged to produce stacked SDM (S-SDM) prediction maps. All prediction maps were classified into five habitat suitability classes to facilitate interpretation. The total area within benthic ecoregion-bathymetric boundaries and the percentage overlap with the bottom trawl closure zone were computed for spatial contextualization and to determine protection coverage for S-SDMs, respectively.

Results: Cluster analysis identified 10 groups that represent unique S-SDMs for the region. Taxa clustered together have previously been documented together in surveys but some novel associations are reported. Geographically, the predicted occurrences can range along the entire western continental margin, be highly restricted, or constrained by recognised biogeographic boundaries. VME indicator metrics ranged from low to moderate. When trawl coverage was computed relative to the suitability's prevalence in the modelling domain, trawl protection was shown to be large for the highest suitability classes for most of the S-SDMs.

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Main Conclusions: Results indicate the clustering approach has some strengths in identifying known and documented associations between DSCS taxa but some are problematic and produce low to moderate VME indicator scores for S-SDMs, undercutting the conservation information the metric should convey. Coupled with the small predicted areas of the highest suitability classes, the wholesale recommendation for this approach for management purposes is difficult. We discuss avenues for methodological improvements.

1 | Introduction

Increasing anthropogenic threats to deep ocean ecosystems span several sources including resource extraction, waste dumping, fishery activities and climate change (reviewed in Ramirez-Llodra et al. 2011 and Harris 2020). Biogenic ecosystems, dominated by large epibenthic taxa, typify deep-sea regions most likely impacted by and slow to recover from anthropogenic activity. Bottom trawling in the fishing industry has historically been recognised as one of the most widespread and immediate threats to sensitive benthic species and habitats (Pusceddu et al. 2014; Clark et al. 2016), but other activities including pollution (Fisher et al. 2014; Cordes et al. 2016), deep-sea mining (Levin, Amon, and Lily 2020) and the impacts of climate change and ocean acidification (Levin and Le Bris 2015; IPCC 2019) are also expected to take a strong toll.

Deep-sea corals and sponges (DSCS) represent some of the archetypal fauna threatened by bottom trawling and serve as key indicator taxa in the identification of fishing-sensitive locations and habitats (CBD 2008; FAO 2009a). Multilateral efforts to address the impacts of deep-sea fisheries on the high seas resulted in the development of guidelines for the identification of vulnerable marine ecosystems (VMEs) and their protection from significant adverse impacts from fishing (FAO 2009a). Benthic species that are unique or rare, fragile, slow growing, slow to reproduce, provide functionally significant habitat, or contribute to structurally complex habitats or habitats that are fragile, are recognised as indicators of VMEs and the communities they create are afforded protection and management on the high seas by pertinent nation states and regional fishery management organisations (FAO 2009a, 2016). The concept and identification of VMEs to inform management is also increasingly applied at a national level, for example, in New Zealand (Stephenson et al. 2024) and Nordic countries (Buhl-Mortensen et al. 2023).

The United States (US) National Oceanic and Atmospheric Administration (NOAA) has recognised the ecological importance and vulnerability of DSCS communities and is committed to protect areas known to contain DSCS communities from fishing impacts and develop approaches to locate and further reduce interactions between fishing gear and DSCS (NOAA 2010). Within the United States (US) exclusive economic zone (EEZ), threat management from bottom fishing gear is authorised under the Magnuson-Stevens Fishery Conservation and Management Act (MSA, 16 U.S.C. 1801 et seq.). While the United States does not employ the VME terminology, NOAA and regional fishery management councils have used MSA authorities to protect important areas of biogenic habitats. These include protections from fishing of vulnerable essential fish habitat (EFH—defined as recognised environments necessary for fish spawning, breeding, feeding or growth), and more recently protection of deep-sea coral habitats in their own right. As with VME indicators, the question then often becomes: when should the abundance or combination of DSCS taxa in a particular area be considered a conservation priority (Hourigan 2014).

Identification of VMEs is usually determined by the abundance of indicator taxa (e.g. corals, sponges), but this is not the sole criterion. Quantitative identification of VMEs using autonomous and remotely operated vehicles (AUVs/ROVs) is ideal, but the spatial coverage of such surveys is far smaller than the practical size of fisheries management zones or offshore lease areas. The vastness of the deep ocean and the high financial and labour cost of vehicles serve as an impetus for complementary approaches to better target likely habitats.

Species distribution models (SDMs) are increasingly one such data-based complementary approach. SDMs (i.e. ecological niche or habitat suitability models) use statistical methodologies to estimate the distribution of suitable environmental regions for taxa in relation to available explanatory variable data (Guisan and Zimmermann 2000). The use of SDMs to predict the presence of VMEs is especially valuable due to the relatively unexplored and under-sampled nature of the deep ocean compared to the greater abundance of environmental data (Vierod, Guinotte, and Davies 2014). Predictive distribution models for VME indicator taxa have been recommended as a key step in identifying and protecting VMEs (e.g. Ardron et al. 2014). As SDMs for deep-sea taxa become more routine, multi-model approaches such as ensemble modelling (e.g. Robert et al. 2016; Winship et al. 2020) and model stacking (e.g. Wiltshire et al. 2018) have arisen and allow for community-level inference of predicted deep-sea faunal ranges and diversity. While most SDMs for deep-sea taxa initially focused on one or a few species (e.g. deep-sea reef-forming stony corals), the realisation that diverse VMEs may be formed by many different species has led to the development of new models. Extending the multi-taxon modelling approaches for predicting the presence of VMEs is on the rise and has been applied in the Atlantic (e.g. Burgos et al. (2020)) and the South Pacific (e.g. Anderson et al. 2016; Georgian, Anderson, and Rowden 2019; Stephenson et al. 2021) oceans.

Given the wide adoption of species distribution modelling, the opportunity to utilise a potential method of multi-taxon prediction in the deep sea is now present in the US EEZ off the west coast. This region includes the federally managed waters of the states of Washington, Oregon and California, and holds rich and diverse deep-sea coral and sponge communities (Clarke, Whitmire, and Yoklavich 2017). This large geographic region has been the focus of recent DSCS field research (e.g. Duncan et al. 2023), as well as the development of new presence-only SDM models for 46 taxa of DSCS (Poti et al. 2020). Therefore, the region and these SDMs may, therefore, serve as a useful test bed for applying multi-taxon predictive methodologies to corals and sponges and apply VME indicator concepts to marine protected areas in the United States.

Large portions of the US West Coast seabed were protected from bottom trawling in 2006, primarily to protect EFH (Clarke, Whitmire, and Yoklavich 2017). In 2020, based on new research, new areas were added or expanded to protect EFH and deep-sea corals, while others were reduced in size (PFMC 2019), yielding a net increase in protection of hard substrate and areas of known coral (excluding sea pens) and sponge records within fishable depths (Shester et al. 2021). Below 3500 m bottom trawling is completely closed as a precautionary measure, and provisions were recently adopted by the Pacific Fisheries Management Council that currently closed zones undergo routine study and monitoring (Shester et al. 2021).

In this paper, we apply a multi-taxon predictive model stacking methodology to the new, high-resolution species- and genus-level SDMs of DSCS in fishable depths off the US West Coast (Poti et al. 2020). This now affords the opportunity to combine them with VME indicator taxa information to answer the following questions: (1) can accurate multi-taxon, trawl-sensitive DSCS distribution predictions be made for the US WC EEZ and (2) to what extent do current areas protected from bottom trawling overlap with high-resolution multi-taxon distribution predictions and what are the conservation and management implications?

2 | Methods

2.1 | DSCS Models and Study Region

Habitat suitability models of DSCS along the US West Coast continental margin were commissioned by the Bureau of Ocean Energy Management (BOEM) to assess the potential benthic impact of offshore energy projects intended for the states of Oregon, Washington and California. Full details of the study and the modelling approach may be found in Poti et al. (2020). For the current study, we will briefly describe the modelling approach. Biological records at the genus and species level were retrieved from the NOAA Deep Sea Coral Research and Technology Program (NOAA 2016) for the US West Coast region that were identified from visual surveys such as ROV/AUV dives, manned submersibles and towed cameras for the greater lack in spatial bias. From an original 66 environmental factors (Table S2), a total of 22 depth and seafloor topography, seafloor substrate, ocean current and geographic parameters were used in the construction of models for 48 individual coral or sponge taxa (Table 1). Highly collinear variables (Spearman rank correlation coefficient $|\rho| > 0.7$) were removed (Figure S1). Models were built under the MaxEnt framework using an iterative model selection procedure and then bootstrapped 100 times, fitted with the subset of environmental predictors from the best model iteration, and then averaged across bootstraps to create spatial gridded predictions at a 200 × 200 m resolution for each individual taxon. Model performance was evaluated using a

TABLE 1 | Final list of environmental predictor variables used to fit models of DSCS occurrence, selected following pairwise correlation analysis.

Environmental predictor	Category	Unit
East–West (E-W) aspect	Depth & Seafloor Topography	Unitless
North–South (N-S) aspect	Depth & Seafloor Topography	Unitless
Depth	Depth & Seafloor Topography	Meters
General curvature	Depth & Seafloor Topography	Radians/100 m
Cross-sectional curvature	Depth & Seafloor Topography	Radians/100 m
Slope	Depth & Seafloor Topography	Degrees
Hard-soft	Seafloor Substrate	N/A
Percent gravel	Seafloor Substrate	Percent
Percent sand	Seafloor Substrate	Percent
Spring/Summer E-W bottom current velocity	Oceanography	m/s
Winter E-W BOTTOM CURRENT VELOCITY	Oceanography	m/s
Spring/Summer N-S bottom current velocity	Oceanography	m/s
Winter N-S bottom current velocity	Oceanography	m/s
Fall vertical bottom current velocity	Oceanography	m/s
Spring/Summer vertical bottom current velocity	Oceanography	m/s
Winter vertical bottom current velocity	Oceanography	m/s
Spring/Summer surface reflectance	Oceanography	sr-1
Winter surface reflectance	Oceanography	sr-1
Annual max wave power	Oceanography	Watts/m
Spring/Summer mean wave power	Oceanography	Watts/m
Distance to shore	Geography	meter
Latitude	Geography	degrees

set of four measures: the mean area under the receiver operating characteristic curve (AUC), the cross-validation AUC and two measures of model fit and stability due to the limitations of AUC for evaluating model performance using presence-only data (Lobo, Jiménez-Valverde, and Real 2008; Jiménez-Valverde 2012; Yackulic et al. 2013) (Table 2). For the present study, models of taxa that generally occurred more often at depths greater than the modelling domain (e.g. *Bathypathes* sp.) or taxa considered too sparsely distributed to be severely impacted by bottom trawls were excluded (e.g. *Asbestopluma* sp.). A total of 40 modelled taxa that were thus available for the present study's analysis. The list of modelled taxa and respective record counts are found in Table 3.

The study area covers 136,336 km^2 of the US Pacific shelf and slope (from depths of 50–1200 m) from northern Washington to the United States–Mexico border. This depth range was selected because multibeam coverage beyond 1200 m was considerably lacking, fewer occurrences in the NOAA National Database for Deep-Sea Corals and Sponges in deeper waters were not identified to genus or species, and BOEM identified offshore waters to 1200 m as a high priority for its management needs (Poti et al. 2020). This depth range is also the most relevant for managing fishery impacts on vulnerable biogenic habitats as practically all commercial groundfish fishing occurs within this depth range and bottom trawling is prohibited deeper than 1280 m (Somers et al. 2022).

Much of the study region (Figure 1) shares similar oceanographic properties (Ware and McFarlane 1989; Hickey 1998; Mackas 2006): high biological production with widely distributed species. Strong gradients among water properties, current speed, and biological distributions cross the shoreline regions with frontal cutoffs aligned with alongshore currents, the shelf break and at times with upwelling cells. This region is highly influenced by wind-induced upwelling for at least part of the year. Narrow and strong, a subsurface current flowing north–south usually following the shelf break is present. This contributes to the strong bioregionalization demarcated by Spalding et al. (2007) along the west coast which includes three biogeographic ecoregions spanning named Oregon, Washington, Vancouver, Coast and Shelf; Northern California; and Southern California Bight and nestles within two recognised deep-sea coral biogeographic provinces: the Oregon Province spanning from the northern tip of Vancouver Island, Canada to Point Arguello/Point Conception, United States and the California Province which stretches south from there to about Magdalena Bay, Mexico (Briggs and Bowen 2012; Everett et al. 2022). The ecoregion boundaries of Spalding et al. (2007) have been retained but their nomenclature has been simplified. This leads to the formation of an Oregon region in the north, a central Northern California region and a Southern California region encompassing the Southern California Bight (SCB) (Figure 1A) akin to the ecoregion delineation adopted by NMFS (2013). By depth, the study region can be divided into three well-described depth zones: the shelf (0–200 m), the upper slope (200–600 m) and the Oxygen Minimum Zone (OMZ; generalised to 600–1200 m) as first described by Levin (2003) and Levin et al. (2010) (Figure 1A). The ecoregions and depth class boundaries form 9 ecoregion-depth polygons and were used to spatially contextualise subsequent analyses.

2.2 | VME Indicators and Model Stacking

2.2.1 | DSCS VME Indicator Score Calculation and Appropriateness as Indicators

The 40 individually-modelled taxa chosen to represent VME indicators include 28 corals (12 gorgonians, nine sea pens, two soft corals, three scleractinian corals, one black coral and one stylasterid coral) and 12 sponges (six glass sponges and six demosponges) (Table 3). While corals and sponges represent taxon groups designated internationally as VME indicators by most Regional Fisheries Management Organisations (RFMOs), the vulnerability of individual taxa and their contribution to creating VMEs will vary. The international VME criteria (FAO 2009b) have not previously been applied to most US West Coast DSCS species but may nevertheless provide a useful framework for considering vulnerability and conservation value.

To score individual taxa for their potential to contribute to VMEs, we adapted the scoring procedure of Morato et al. (2018), providing a score of 1 (low) to 5 (max) for the FAO (2009b) VME criteria of uniqueness or rarity, functional significance, fragility, life-history and structural complexity (Table S1). The category of 'functional significance' is comparable to the US definition of 'essential fish habitat' (EFH), the major authority that has been used to date to protect deepwater habitats in US waters. Scores given for this category were higher for those taxa that had demonstrated associations with fishes. The 'structural complexity' score was based on the size, extent of branching (for corals) and recorded occurrence in higher density patches. The scores, ranging from 1 (low) to 5 (high), indicate the level to which the indicator taxon fits the criteria outlined in FAO (2009b).

The gorgonians ranged from small species with few branches (e.g. *Callistephanus kofoidi and C. simplex*) to relatively large fan-shaped corals (> 30 cm in height and/or width) with many branches providing structure (*Acanthogorgia* spp., *Eugorgia rubens*, *Leptogorgia* cf. *chilensis*, *Isidella tentaculum*, *Paragorgia* spp. and *C. pacificus*). Watters, Laidig, and Yoklavich (2022) identified density hot spots that included several of these taxa: *Callistephanus* spp. (recorded as Plexauridae #1 and #3), *L. chilensis*, *E. rubens*, *L. chilensis*, *A. phyllosclera*, *P. longispina and C. pacifica*. Species of rockfishes (*Sebastes* spp.) showed significant associations in the SCB with *Acanthogorgia* spp., *A. phyllosclera* and *E. rubens*, while young rockfishes were also observed to be associated with *Plumarella williamsi*, a relatively small species (Henderson, Huff, and Yoklavich 2020).

Gorgonian corals are considered VME indicator taxa across RFMO regions while it is more mixed for soft corals (taxa without rigid skeletons) and sea pens (superfamily Pennatuloidea) corals (Baco et al. 2023). The soft mushroom coral, *Heteropolypus ritteri*, was among the most common coral species encountered between 200 and 1200 m on rocky substrata throughout the West Coast region. The stoloniferan soft corals in the genus *Clavularia* occur in the same depth range but have been reported much less frequently (Watters, Laidig, and Yoklavich 2022; NOAA 2016). Both these taxa are small and by themselves would seem to provide limited three-dimensional structure for other species.

TABLE 2 | Deep-sea coral and sponge record counts and model measures of performance, model fit and model stability.

Taxon	Training AUC	Cross-validation mean AUC	Model fit	Model stability
Acanthascus (R.) dawsoni	0.97	0.9	66.1	20.24
Acanthascus (S.) sp.	0.96	0.84	64.54	10.99
Acanthogorgia sp.	0.98	0.9	81.69	9.38
Acanthoptilum gracile	0.9	0.88	13.22	30.74
Adelogorgia phyllosclera	0.99	0.96	94.62	33.55
Anthoptilum grandiflorum	0.91	0.89	67.33	59.39
Antipathes dendrochristos	0.99	0.95	96.13	21.29
Aphrocallistes vastus	0.95	0.91	80.24	37.87
Balticina californica	0.92	0.84	76.34	30.53
Callistephanus kofoidi	0.95	0.8	76.02	9.05
Callistephanus pacificus	0.96	0.83	85.17	15.62
Callistephanus simplex	0.93	0.84	31.46	15.03
Chromoplexaura marki	0.89	0.78	37.61	0
Clavularia sp.	0.99	0.92	77.27	19.67
Coenocyathus bowersi	0.98	0.96	69.42	19.34
Craniella arb	0.98	0.97	50.5	8.66
Desmophyllum dianthus	0.98	0.92	83.87	20.99
Desmophyllum pertusum	0.97	0.94	67.1	5.6
Eugorgia rubens	0.98	0.96	78.46	46.31
Farrea occa	0.98	0.91	86.26	36.58
Funiculina sp.	0.97	0.93	95.87	31.54
Haliclona sp.	0.98	0.93	63.9	9.58
Heterochone calyx	0.97	0.8	83.55	13.07
Heteropolypus ritteri	0.93	0.9	94.71	36.58
Hyalonema sp.	0.98	0.97	89.12	38.52
Isidella tentaculum	0.96	0.91	39.26	4.94
Leptogorgia chilensis	0.96	0.91	18.69	44.17
Mycale sp.	0.97	0.84	95.05	22.42
Paragorgia sp.	0.94	0.87	91.49	23.14
Parastenella ramosa	0.99	0.93	80.62	11.87
Pennatula phosphorea	0.98	0.89	88.02	11.84
Plumarella williamsi	0.97	0.91	75.63	20.58
Polymastia sp.	0.98	0.86	80	19.39
Ptilosarcus gurneyi	0.93	0.87	65.37	40.29
Rhizaxinella gadus	0.99	0.94	76.86	17.02
Stylaster californicus	0.98	0.95	86.22	17.74
Stylatula sp.	0.85	0.8	25	39.04
Thenea sp.	0.98	0.91	92.66	37.6
Umbellula lindahli	0.98	0.95	98.03	42.06
Virgularia sp.	0.76	0.65	0	0

TABLE 3 | Record counts and taxonomy of VME indicator taxa used for modelling and the present analysis.

VME indicator	Order/ Superfamily	Family	Genus/Species	Record count	Grid cells with records
Black coral	Antipatharia	Antipathidae	*Antipathes dendrochristos*	2532	237
Gorgonian	Scleralcyonacea	Coralliidae (formerly Paragorgiidae)	*Paragorgia* sp.	5757	486
	Malacalcyonacea	Gorgoniidae	*Adelogorgia phyllosclera*	4130	194
	Malacalcyonacea	Gorgoniidae	*Eugorgia rubens*	2103	296
	Malacalcyonacea	Gorgoniidae	*Leptogorgia chilensis*	2242	211
	Malacalcyonacea	Gorgoniidae	*Callistephanus kofoidi*	1205	142
	Malacalcyonacea	Gorgoniidae	*Callistephanus pacificus*	3716	115
	Malacalcyonacea	Gorgoniidae	*Callistephanus simplex*	1659	186
	Malacalcyonacea	Gorgoniidae	*Chromoplexaura marki*	226	70
	Malacalcyonacea	Paramuriceidae	*Acanthogorgia* sp.	1469	105
	Scleralcyonacea	Keratoisididae	*Isidella tentaculum*	433	84
	Scleralcyonacea	Primnoidae	*Parastenella ramosa*	614	77
	Scleralcyonacea	Primnoidae	*Plumarella williamsi*	2942	207
Sea pen	Scleralcyonacea/ Pennatuloidea	Anthoptilidae	*Anthoptilum grandiflorum*	1509	868
	Scleralcyonacea/ Pennatuloidea	Balticinidae	*Balticina californica*	3951	393
	Scleralcyonacea/ Pennatuloidea	Funiculinidae	*Funiculina* sp.	10,895	346
	Scleralcyonacea/ Pennatuloidea	Pennatulidae	*Pennatula phosphorea*	1035	103
	Scleralcyonacea/ Pennatuloidea	Pennatulidae	*Ptilosarcus gurneyi*	667	380
	Scleralcyonacea/ Pennatuloidea	Umbellulidae	*Umbellula lindahli*	7730	585
	Scleralcyonacea/ Pennatuloidea	Virgulariidae	*Acanthoptilum gracile*	242	155
	Scleralcyonacea/ Pennatuloidea	Virgulariidae	*Stylatula* sp.	772	452
	Scleralcyonacea/ Pennatuloidea	Virgulariidae	*Virgularia* sp.	95	70
Soft coral	Malacalcyonacea	Clavulariidae	*Clavularia* sp.	264	98
	Scleralcyonacea	Coralliidae	*Heteropolypus ritteri*	13,040	1107
Stony coral	Scleractinia	Caryophylliidae	*Coenocyathus bowersi*	363	124
	Scleractinia	Caryophylliidae	*Desmophyllum dianthus*	651	183
	Scleractinia	Caryophylliidae	*Desmophyllum pertusum*	851	146
Stylasteridae	Anthoathecata/ Filifera	Stylasteridae	*Stylaster californicus*	1219	178

(Continues)

TABLE 3 | (Continued)

VME indicator	Order/ Superfamily	Family	Genus/Species	Record count	Grid cells with records
Glass sponge	Amphidiscosida	Hyalonematidae	*Hyalonema* sp.	331	235
	Lyssacinosida	Rosselidae	*Acanthascus (R.) dawsoni*	643	209
	Lyssacinosida	Rosselidae	*Acanthascus (rS.)* sp.	705	165
	Sceptrulophora	Aphrocallistidae	*Aphrocallistes vastus*	739	384
	Sceptrulophora	Aphrocallistidae	*Heterochone calyx*	1556	217
	Sceptrulophora	Farreidae	*Farrea occa*	844	176
Demosponge	Haplosclerida	Chalinidae	*Haliclona* sp.	615	102
	Poecilosclerida	Mycalidae	*Mycale* sp.	3173	165
	Polymastida	Polymastiidae	*Polymastia* sp.	465	93
	Suberitida	Suberitidae	*Rhizaxinella gadus*	242	57
	Tetractinellida	Tetillidae	*Craniella arb*	101	80
	Teractinellida	Theneidae	*Thenea* sp.	1363	184

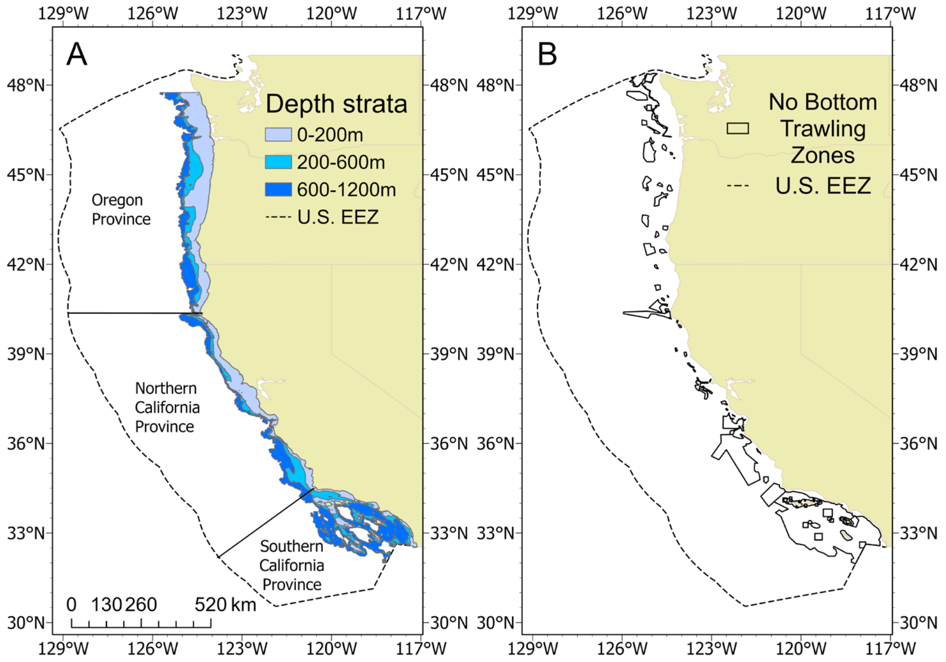

FIGURE 1 | (A) Modelling domain of the species distribution models within the boundaries of the US EEZ. It is divided into 3 depth strata (continental shelf, upper slope and oxygen minimum zone) and 3 ecoregions: The Oregon, N. California and S. California based on a merging of Spalding et al. (2007) and Everett et al. (2022). (B) Map of the Essential Fish Habitat and Closure zones off the US West Coast EEZ with year-round trawl bans.

Unlike most other modelled taxa, the nine sea pen taxa all occur on soft bottoms—a habitat that makes them more vulnerable to bottom trawl impacts. Sea pens are regularly recorded as bycatch in West Coast commercial bottom trawl fisheries (Clarke, Whitmire, and Yoklavich 2017), but there is limited information on the recovery potential of populations. *Anthoptilum grandiflorum*, *Stylatula* spp. and *Umbellula* spp. are among the most abundant coral taxa recorded from trawl surveys (Whitmire and Clarke 2007). Aggregations of sea pens in the Northeast Pacific may support higher densities of certain fish species (Brodeur 2001; Bosley et al. 2020). In the Northwest Atlantic, *A. grandiflorum* and sea pens in the genera *Balticina* (= *Halipteris*), *Funiculina*, *Pennatula* and *Umbellula* have been identified as VME indicator taxa in the NAFO convention area (Kenchington et al. 2015). *Virgularia* spp. have been identified as members of a biotope class of special concern in Norway (Gonzalez-Mirelis and Buhl-Mortensen 2015). *Funiculina quadrangularis* and *A. grandiflorum* in the Northwest Atlantic have been proposed as nursery habitat for larval redfish (Baillon et al. 2012), a congener to the west coast rockfishes.

The three scleractinian corals, *Desmophyllum pertusum* (= *Lophelia pertusa*), *D. dianthus* and *Coenocyathus bowersi* differ in their vulnerability and habitat roles. *D. pertusum* is a fragile, branching species that can form large colonies or groups of colonies. While these can provide important habitat structure, the species does not appear to form deep-water reefs or bioherms on the West Coast. *Sebastes rufus* and young-of-the-year rockfishes were more likely to be associated with patches of *D. pertusum* (Henderson, Huff, and Yoklavich 2020). The congener, *D. dianthus*, is a solitary cup coral that can occur in clumps but likely provides limited vertical structure. *Coenocyathus bowersi* is a colonial coral that forms small, low-lying colonies in shallower, rocky habitats. Like *D. dianthus*, it is likely less vulnerable to impacts from fishing gear than in *D. pertusum*.

The long-lived black coral, *A. dendrochristos*, is rare outside of Southern California. This species reaches among the largest sizes for a West Coast coral and its dense branching pattern appears to provide an important habitat for both fishes and invertebrates (Henderson, Huff, and Yoklavich 2020; Huff et al. 2013; Love et al. 2007). The lace coral, *Stylaster californicus*, was the only hydrozoan coral modelled. Colonies are branching and can reach high densities on shallow, rocky banks and outcrops in central and southern California (e.g. Love, Lenarz, and Snook 2010). Colony skeletons are fragile and easily broken and damage from recreational and commercial fishing nets has been reported (Engle and Coyer 1981; Odemar 1973).

Sponges are recognised as important components of VMEs. Like corals, they provide important three-dimensional structures and are vulnerable to impacts from fishing gears, especially trawling. The reported bycatch of sponges in commercial fisheries off the west coast between 2011 and 2014 was from 2400 to 12,900 kg per year; from 4 to 36 times the weight of coral bycatch (Benaka et al. 2019). However, most observations of sponges are not distinguished by genus, so the modelled taxa include only the most easily identified sponges; even their occurrence is likely missed in numerous surveys.

The six glass sponges, apart from *Hyalonema* sp., all reach large sizes and are major structure-forming species. *Heterochone calyx* and *Aphrocallistes vastus* form ecologically significant areas off the US WC, such as those found in Grey's Canyon, Washington where rockfishes were commonly observed sheltering in the sponges (Powell et al. 2018). In British Columbia, these two species, along with *Farrea occa*, are components of glass sponge reefs forming large mounds and creating significant amounts of habitat heterogeneity and framework for other fauna (Krautter et al. 2001; Maldonado et al. 2017; Du Preez and Tunnicliffe 2011). Glass sponge reefs in US West Coast waters have only been confirmed in the Southern California Bight, where only *F. occa* was the major component forming the bioherms (Duncan et al. 2023). The two *Acanthascus* subgenera also reach large sizes, are often abundant, and provide significant three-dimensional structure. Rooney (2016) reported a high proportion of individual *Acanthascus* spp. (59%) and *Heterochone calyx* sponges (29%) with one or more associated fishes off Oregon. Henderson, Huff, and Yoklavich (2020) reported significant associations of two rockfish species in Southern California with *Acanthascus (Rhabdocalyptus) dawsoni*. In the Gulf of Alaska, bigmouth sculpin deposit their eggs on *A. vastus* and *A. dawsoni* and the demosponge *Mycale loveni* (Busby et al. 2012). Off British Columbia, *Acanthascus* sponges are important components of sponge gardens, providing important habitat for rockfishes, as well as evidencing high vulnerability to trawling (Du Preez and Tunnicliffe 2011). Stalked glass sponges in the genus *Hyalonema* include species that occur in soft sediments as well as others on hard substrates. They reach smaller sizes and their role as habitat for fish has not been assessed, but along with *A. vastus* represent the most frequently encountered identifiable sponge taxa in NOAA West Coast groundfish trawl surveys (Bradburn, Keller, and Horness 2011).

The six demosponges represent a variety of abundant, mostly small sponges, with the exception of *Mycale* and *Thenea* sp. which reach sizes > 30–50 cm. Those with upright morphologies are expected to provide greater three-dimensional structure as well as greater vulnerability to damage from trawling. Increased abundance of *Haliclona* sp. in the Southern California bight was associated with increased abundance of three species of rockfishes (Henderson, Huff, and Yoklavich 2020). *Mycale* sp. are known to provide habitat for rockfishes in Alaska (Stone, Lehnert, and Reiswig 2011). Most of the other modelled demosponge taxa have not been assessed in relation to their contribution as habitat for fish.

2.2.2 | Habitat Similarity and Incorporation of Indicator Score

Habitat overlap between all modelled taxa was estimated using the 'I' similarity statistic (Warren, Glor, and Turelli 2008), a derivation of the Hellinger distance, computed using the 'dismo' (v 1.3.9) R package (Hijmans et al. 2017). The statistic ranges from 0 (no overlap) and 1 (complete habitat overlap). We used the reciprocal of the statistic (1—I) as a measure of dissimilarity so that groups found by the Ward-based cluster analysis identified groups of taxa with the most distinct distributions. Warren's 'I' was chosen as it was designed to measure habitat equivalency between the SDMs (e.g. model outputs) of two species without the assumptions Schoener's D (Schoener 1968) makes. Schoener's D assumes a degree of interaction between species in the same microhabitat and scales proportionally with species density (Warren, Glor, and Turelli 2008), assumptions made in the models of the current study. Clusters of similarly distributed DSCS taxa were determined from a dendrogram, with a cutoff of 0.80 depicted via the 'dendextend' (Galili 2015) R package.

Model rasters of DSCS taxa grouped in the same cluster were stacked and averaged to produce multi-taxon distribution maps. In contrast to the distributional patterns of clustered groups, we also stacked the full set of models and averaged them. When averaging ecological models, it is often recommended to weight them to reduce prediction error (Dormann et al. 2018) but no clear guidance is present in the scientific literature as the best weighting method when stacking SDMs (though some arguments have been made for weighting when stacking models of rare taxa (Rosner-Katz, McCune, and Bennett 2020)) and so we opted for a more exploratory approach and did not employ a weight when combining models. Model stacking follows the 'predict first, assemble later' approach where the individual taxa are modelled first, then predictions are combined (i.e. stacked) to produce a community-level prediction (Calabrese et al. 2014; D'Amen et al. 2017). The advantage of this approach is it permits one to combine predictions from a multitude of different, individually modelled taxa. The multi-taxon predicted distributions produced from this analysis are not assemblages or communities in the textbook sense, in that direct observation was not made of species living in close proximity. For the sake of terminology simplification, hereinafter, we use the term stacked species distribution model (S-SDM) to refer to groups of modelled taxa in the same cluster that have been averaged together. The VME indicator score for each stack's constituent taxa was also averaged, via the root mean square similar to how Morato et al. (2018) compute the scores for individual taxa, to produce a single index to the whole S-SDM's sensitivity to trawling.

In an effort to facilitate interpretation, habitat suitability values in resultant S-SDM prediction maps were classified into 5 levels of suitability: very low (0–0.2), low (0.21–0.40), moderate (0.41–0.60), high (0.61–0.80) and very high (0.81–1.00).

2.3 | Overlap Analysis of S-SDMs With Ecoregion-Depth Polygons and With Areas Closed to Bottom Trawl Fishing

All model raster pixels from each S-SDM that fell into an ecoregion-depth polygon or within the bounds of a trawl closure area shapefile polygon were extracted using the mask and crop functions of the 'raster' (v. 3.16-14) R package (Hijmans et al. 2015). The area was computed from pixel value densities within ecoregion-depth polygons.

To analyse the amount of overlap the S-SDMs have with existing trawl closures, a shapefile of 74 seafloor areas closed year-round to bottom trawling (demersal seines sometimes excepted) that fell into the modelling domain was constructed using those established in the Pacific Fishery Management Council's Groundfish FMP Amendments 19 and 28, and the Closed Area designations established in CFR 50 Part 660.70. Since the modelling effort was limited to 1200 m, all seafloor-protected areas in deeper waters were removed using the erase tool in ArcGIS Pro (ESRI, v 2.6) (Figure 1B). A table of all 74 bottom trawl closure areas with respective enforcing authorities is listed in Table S3.

To determine how much of each predicted suitability class is protected by established trawl closure zones, pixel densities within trawl closure polygons were used to compute the percentage of area of S-SDM suitability class that falls within established seafloor bottom trawl protections by dividing pixel densities in the polygons by the total density of the suitability class in the modelling domain.

All overlap analyses were conducted in the WGS 1984 Hotine Oblique Mercator Azimuth Center projected coordinate system to ensure consistency and comparability in the area measurements.

3 | Results

3.1 | Predicted S-SDM Distributions, Habitat Comparisons and VME Indicator Score

Values of the 'I' dissimilarity index ranged widely from 0.11 to 0.95, where values closer to 0 represent no overlap and those closer to 1 represent total overlap. Cluster analysis identified seven groups at a cutoff of 0.8, three of which can each be further divided into 2 smaller sub-groups (Figure 2). Generally, S-SDMs were predicted to most likely occur in highly localised patches off the west coast of the United States, save for two extending across the entire coastline and largely composed of sea pens occupying the largely dominant soft substrate type.

S-SDM 1 comprises the stylasterid and gorgonian corals, *Stylaster californicus* and *L. chilensis* and the demosponge *C. arb* (Figure 3A) with an average VME Indicator Score of 3.35. High and very high suitability classes occupied a total of 51.8 km^2 of the modelled area and were limited to the 0–200 m depth range, the bulk of which was centred in the N. California ecoregion (Table 4).

The second group, S-SDM 2 (VME Indicator Score: 3.39), was formed by stony coral *C. bowersi*, and the gorgonian corals *E. rubens* and *A. phyllosclera* (Figure 3B). Localised high and very high suitability take up a combined 223 km^2 (Table 4). It is entirely found in the S. California ecoregion between 0 and 200 m (Table 4), especially around the Santa Rosa and San Clemente islands of the Channel Islands archipelago.

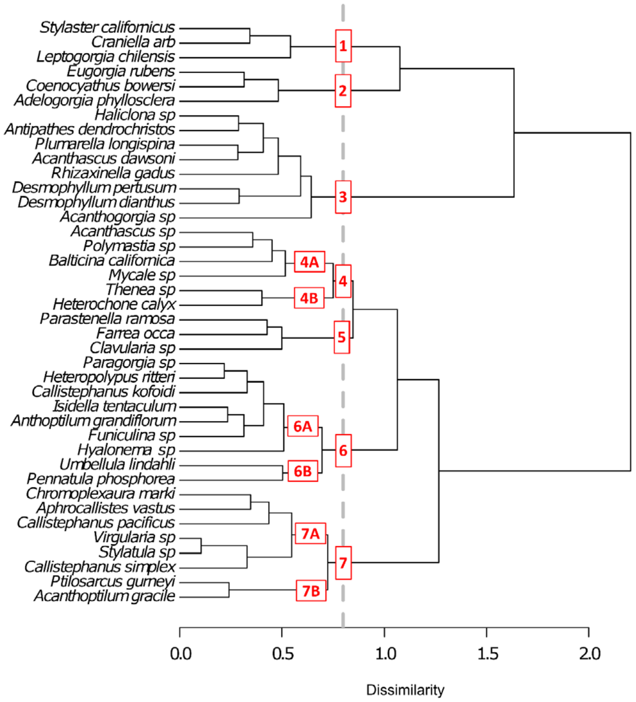

FIGURE 2 | Dendrogram of the modelled distributions of deep-sea coral and sponge taxa off the US west coast. Cluster analysis was conducted using the reciprocal of the Warren's 'I' similarity statistic. Red labels signify the 7 S-SDMs at the 0.80 dissimilarity level and the 6 subgroups observed through review of the distribution patterns of taxa in each group.

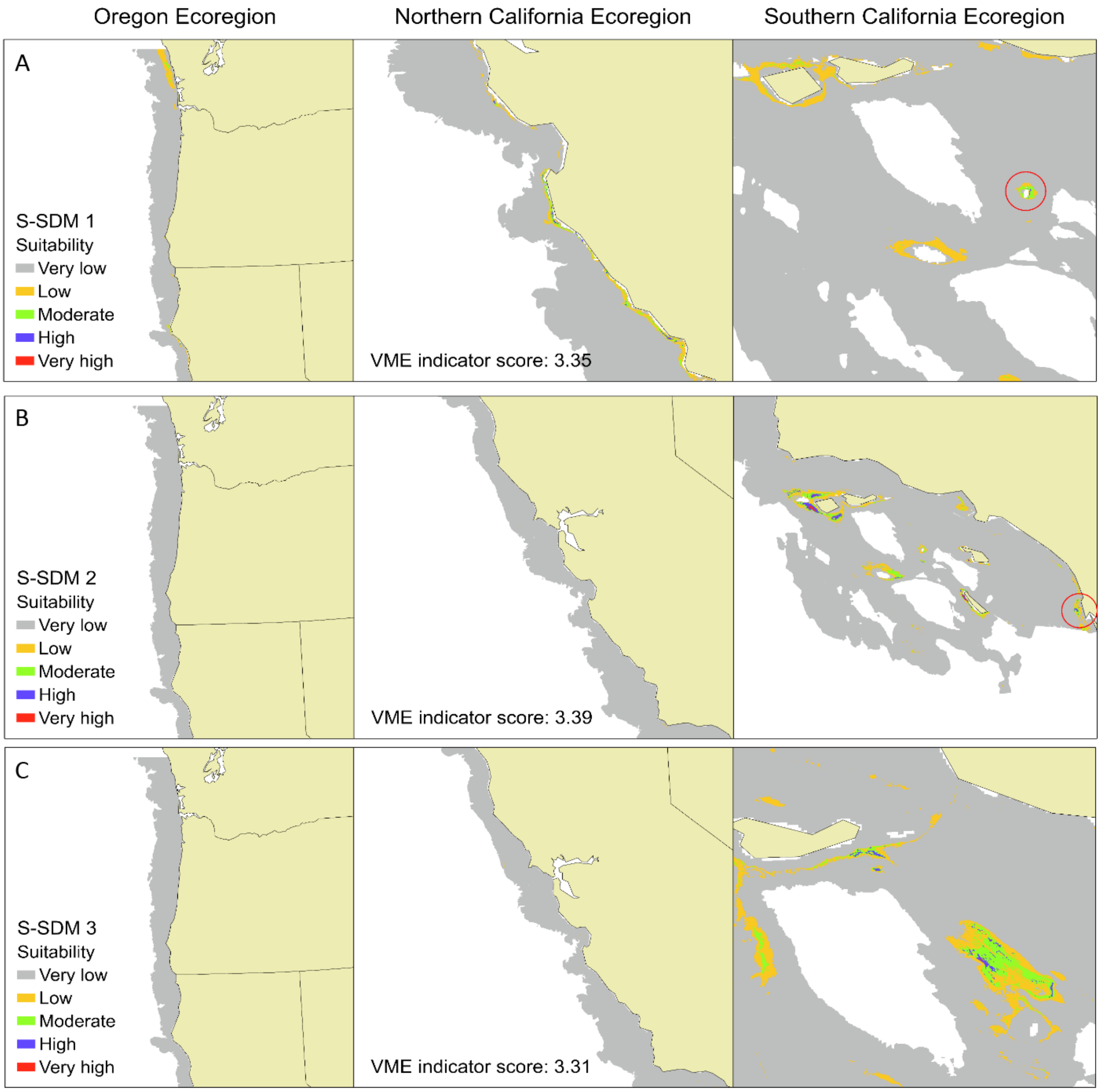

FIGURE 3 | (A) Prediction map of VME S-SDM 1 containing the stylasterid and gorgonian corals *Stylaster californicus* and *Leptogorgia chilensis*, respectively, along with the demosponge *Craniella arb*. (B) Prediction map of VME S-SDM 2 containing the stony coral *Coenocyathus bowersi* and the gorgonian corals *Eugorgia rubens* and *Adelogorgia phyllosclera*. (C) Prediction map of VME S-SDM 3 containing the stony corals *Desmophyllum pertusum*, *D. dianthus*, the black coral *Antipathes dendrochristos*, the gorgonian corals *Plumarella williamsi* and *Acanthogorgia* sp., the demosponges *Rhizaxinella gadus* and *Haliclona* sp. and the glass sponge *Acanthascus dawsoni*. High and Very High suitability are indicated in red circles when not visible in the map panel.

S-SDM 3 (VME Indicator Score: 3.31), composed of *D. pertusum*, *D. dianthus*, the black coral *A. dendrochristos*, the gorgonian corals *P. longispina* and *Acanthogorgia* sp., the demosponges *R. gadus* and *Haliclona* sp. and the glass sponge *A. dawsoni* (Figure 3C). Primarily observed in the S. California ecoregion, the bulk of the 21.08 km^2 of the high and very high suitability for this S-SDM is predicted to occur south of Santa Cruz Islands and north of Santa Barbara Island, between 200 and 600 m (Table 4).

The fourth S-SDM can be further divided into 2 smaller groups S-SDM 4A and 4B. The demosponges *Mycale* sp., *Polymastia* sp., the glass sponge *Acanthascus (Staurocalyptus)* sp. and the lone cnidarian, the sea pen *B. californica* (= *Halipteris californica*), constitute S-SDM 4A (VME Indicator Score: 2.98) (Figure 4A). This S-SDM only reached moderate suitability and occupied a total of 55.8 km^2 (Table 4) scattered around the Northern and Southern California ecoregions between, mostly 600 and 1200 m in depth. S-SDM 4B (VME Indicator Score: 3.33), was only composed of sponges, the hexactinellid *Heterochone calyx* and the demosponge *Thenea* sp. (Figure 4B), and had high and very high suitability totalling 497 km^2. It was largely was predicted to be found in the S. California ecoregion at depths 600–1200 m (Table 4) southeast of Anacapa and Santa Cruz Islands, and southeast and east of Santa Catalina and Santa Clemente islands.

The soft coral *Clavularia* sp. and the gorgonian *P. ramosa*, along with the hexactinellid sponge *F. occa*, formed S-SDM 5 (VME Indicator Score: 3.20) (Figure 4C). High and very high suitability

TABLE 4 | Total area of vulnerable marine ecosystem S-SDM habitat suitability classes within each ecoregion-depth polygon.

	Oregon 0–200 m (km^2)	Oregon 200–600 m (km^2)	Oregon 600–1200 m (km^2)	N. California 0–200 m (km^2)	N. California 200–600 m (km^2)	N. California 600–1200 m (km^2)	S. California 0–200 m (km^2)	S. California 200–600 m (km^2)	S. California 600–1200 m (km^2)
S-SDM 1									
Very low	26,842.92	11,171.12	14,285.08	13,395.96	8491.68	13,211.56	7918.6	11,122.6	24,321.32
Low	2048.72	0	0	1348.8	0	0	1070.76	0.76	0
Moderate	186.08	0	0	238.96	0	0	77.24	0	0
High	1.48	0	0	44.56	0	0	5.04	0	0
Very high	0	0	0	0.64	0	0	0.08	0	0
S-SDM 2									
Very low	29,076.6	11,171.12	14,285.08	15,026.56	8491.68	13,211.56	7078.32	11,119.96	24,319.88
Low	2.6	0	0	2.36	0	0	1246.96	3.04	1.44
Moderate	0	0	0	0	0	0	523.44	0.36	0
High	0	0	0	0	0	0	189.92	0	0
Very high	0	0	0	0	0	0	33.08	0	0
S-SDM 3									
Very low	29,079.2	11,171.12	14,285.08	15,012.52	8485.28	13,211.4	8565.36	10,333.64	24,320.08
Low	0	0	0	16.4	6.4	0.16	392.36	679.2	1.24
Moderate	0	0	0	0	0	0	105.72	97.72	0
Very high	0	0	0	0	0	0	8.08	12.32	0
High	0	0	0	0	0	0	0.2	0.48	0
S-SDM 4A									
Very low	26,680.76	11,122.68	13,918.96	13,637.44	7981.76	12,992.96	8915.24	10,328.04	23,042.16
Low	2398.44	48.44	366.12	1391.48	509.36	197.52	156.48	795.12	1245.2
Moderate	0	0	0	0	0.56	21.08	0	0.2	33.96
High	0	0	0	0	0	0	0	0	0
Very high	0	0	0	0	0	0	0	0	0
S-SDM 4B									

(Continues)

TABLE 4 | (Continued)

	Oregon 0–200 m (km^2)	Oregon 200–600 m (km^2)	Oregon 600–1200 m (km^2)	N. California 0–200 m (km^2)	N. California 200–600 m (km^2)	N. California 600–1200 m (km^2)	S. California 0–200 m (km^2)	S. California 200–600 m (km^2)	S. California 600–1200 m (km^2)
Very low	28,886.8	10,972.2	14,249.52	14,943.32	8393.44	13,141.36	8665.48	10,546.04	22,954.76
Low	152.04	171.68	33.4	85.08	95.04	55.6	330.36	388.52	589.08
Moderate	40.36	27.24	2.16	0.52	3.12	13.92	72.2	104.24	369.48
High	0	0	0	0	0.08	0.68	3.52	45	250.96
Very high	0	0	0	0	0	0	0.16	39.56	157.04
S-SDM 5									
Very low	29,079.2	11,148.92	12,338.24	15,026.96	8319.12	12,715.6	9014.12	10,015.72	23,697.64
Low	0	22.2	1306.52	1.96	154.68	384.68	57.6	1024.64	571.12
Moderate	0	0	479.48	0	17.84	106.96	0	67.08	48.68
High	0	0	125.36	0	0.04	4.32	0	15.12	3.84
Very high	0	0	35.48	0	0	0	0	0.8	0.04
S-SDM 6A									
Very low	29,079.2	10,671.56	9227.12	15,027.96	8141.96	8495.04	9070.52	10,448.72	11,889.36
Low	0	499.52	4876.24	0.96	345.96	4487.84	1.2	667.2	11,798.64
Moderate	0	0.04	181.72	0	3.76	212.8	0	7.44	630.64
High	0	0	0	0	0	15.88	0	0	2.68
Very high	0	0	0	0	0	0	0	0	0
S-SDM 6B									
Very low	29,079.2	11,171.12	14,091.4	15,028.92	8216.92	10,545.96	9070.36	10,674	22,354.68
Low	0	0	193.68	0	257.76	1815.88	1.36	414	1481.88
Moderate	0	0	0	0	13.6	584.92	0	35.36	484.64
High	0	0	0	0	3.4	193.72	0	0	0.12
Very high	0	0	0	0	0	71.08	0	0	0
S-SDM 7A									
Very low	7337.28	350.28	1718.92	14,349.84	5365.72	5482.2	7515.92	10,212.84	23,652.12

(Continues)

TABLE 4 | (Continued)

	Oregon 0–200 m (km^2)	Oregon 200–600 m (km^2)	Oregon 600–1200 m (km^2)	N. California 0–200 m (km^2)	N. California 200–600 m (km^2)	N. California 600–1200 m (km^2)	S. California 0–200 m (km^2)	S. California 200–600 m (km^2)	S. California 600–1200 m (km^2)
Low	21,474.44	10,089.96	12,269.68	679.08	3118.2	7657.96	1540.68	910	668.76
Moderate	267.48	730.8	296.44	0	7.76	71.4	15.12	0.52	0.44
High	0	0.08	0.04	0	0	0	0	0	0
Very high	0	0	0	0	0	0	0	0	0
S-SDM 7B									
Very low	12,114.12	10,909.52	14,285.08	4920.16	6775.04	12,642.32	5246.32	9089.32	22,585
Low	8185.56	261.52	0	3549.4	1126.52	488.92	1974.08	1490.48	1718.24
Moderate	5158.6	0.08	0	4831.12	513.44	80.32	1167.24	298.28	18.08
High	1981.04	0	0	1686.84	76.68	0	623.04	209.64	0
Very high	1639.88	0	0	41.4	0	0	61.04	35.64	0

were predicted to occur for a total of 184.96 km^2 (Table 4) in all three ecoregions, but principally in the Oregon ecoregion from 600 to 1200 m (Table 4).

Similar to the fourth cluster, S-SDM 6 can be subdivided into S-SDMs 6A and 6B. S-SDM 6A (VME Indicator Score: 2.78) spanned a large number of taxa, including the gorgonian corals *Paragorgia* sp., *C. kofoidi* and *I. tentaculum*, the soft coral *Heteropolypus ritteri*; the sea pens *Anthoptilum grandiflorum* and *Funiculina* sp.; and the glass sponge *Hyalonema* sp. (Figure 5A). The locations of the greatest predictability classes were very geographically narrow since there was no observation of the very high suitability class (Table 4), leaving only the high suitability to total 18.56 km^2 in the N. California ecoregion off Monterrey and a smaller 2.68 km^2 around 57 km from San Miguel Island, both at depths 600–1200 m (Table 4). S-SDM 6B (VME Indicator Score: 2.21), was composed exclusively of two sea pens *U. lindahli* and *P. phosphorea* (Figure 5B). High and very high suitability combined for a total of 268.32 km^2 (Table 4) primarily located in the N. California ecoregion at depths 600–1200 m in waters off the city of Monterrey, California.

S-SDM 7 can also be divided into a further two groups, S-SDM 7A and 7B. With a large taxonomic composition, S-SDM 7A (VME Indicator Score: 2.96) features the gorgonian corals *C. pacificus*, *C. simplex* and *C. marki*; the sea pens *Stylatula* sp. and *Virgularia* sp.; and the glass sponge *A. vastus* (Figure 6A). Very high suitability was not observed, leaving high suitability to total an extremely low 0.12 km^2 (Table 4) in the Oregon ecoregion at depths of 200–1200 m (Table 4) in waters west of North Bay, Washington. Only three of the component taxa, *C. marki*, *A. vastus* and the sea pen *Virgularia* sp. (Table S4). S-SDM 7B (VME Indicator Score: 2.10) was a two-species cluster of two sea pens *P. gurneyi* and *A. gracile* (Figure 6B). High and very high suitability were quite widespread along the western US coast, totalling 6355.20 km^2, found in each ecoregion and primarily at depths from 0 to 600 m (Table 4).

3.2 | Overlap of Predicted S-SDMs With Areas Protected From Bottom Trawling

The current EEZ areas shallower than 1200 m (i.e. within the model domain) where bottom trawl fishing gear is prohibited (Table S2) cover an area of 49,190 km^2, or about 36.08% of the study area. A visual depiction of the trawl closures overlaying the S-SDMs is illustrated in Figures S2–S5. When the coverage by trawl closure area is broken down by suitability class relative to the total area occupied in the overall modelled region, protection by trawl closure area can be considerably high. The 'very low' and 'low' suitability class coverage could be low but was more frequently > 26% at a minimum (Figure 7A–J). 'Moderate' suitability and up could have notably high overlap, however. S-SDM 3, 4A and 4B routinely had > 80% for the predicted suitability class and often nearing or equaling 100% (Figure 7C–E). The percentage of predicted high and very high suitability classes protected in no-trawl zones ranged from 0 (e.g. S-SDM 7A) to 100% (e.g. S-SDM 3, 4B and 6A) depending on the particular S-SDM. For the highest suitability classes, whether the coverage is high or low, some

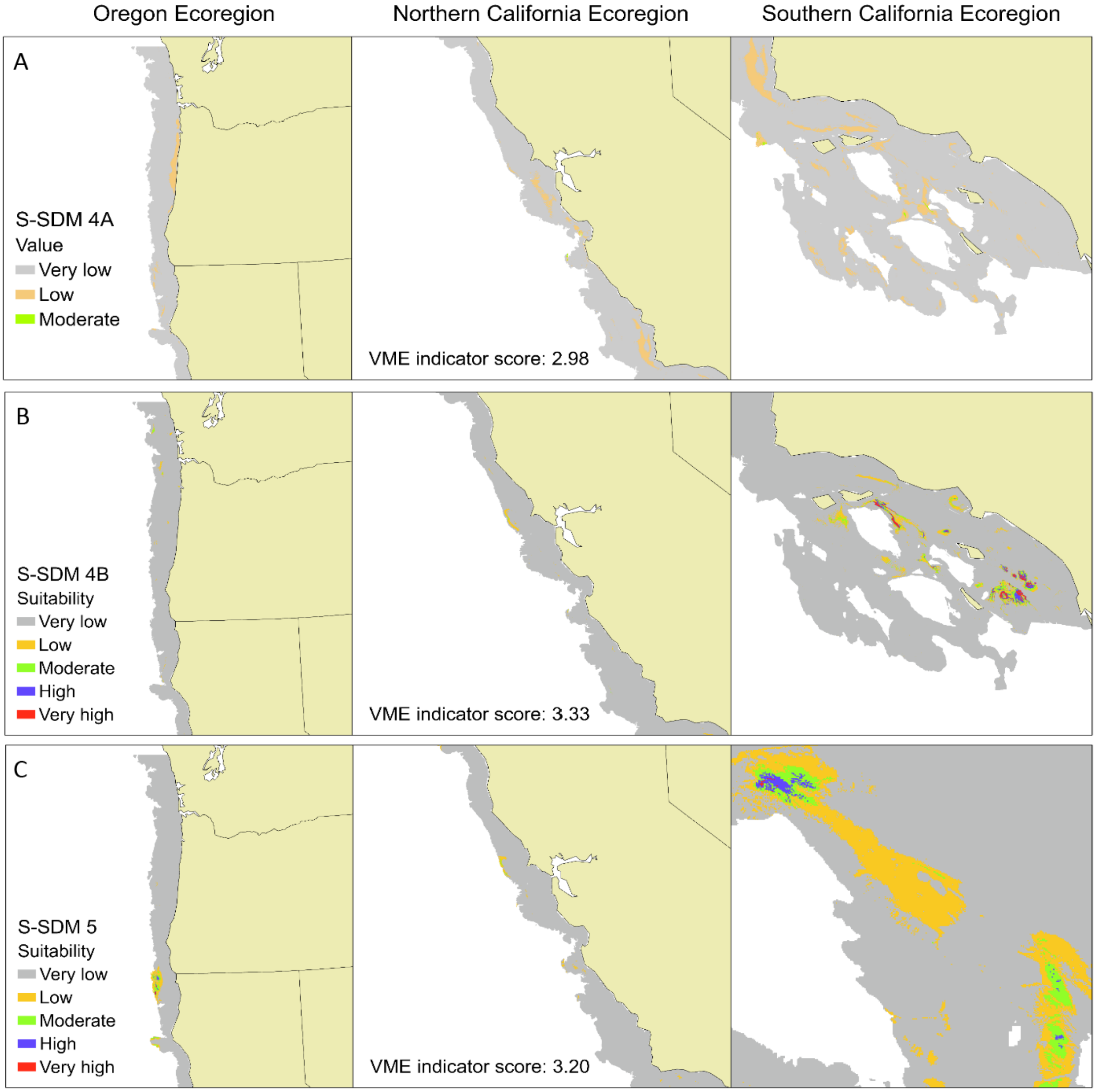

FIGURE 4 | (A) Prediction map of VME S-SDM 4A containing the demosponge *Mycale* sp., the glass sponges *Acanthascus (R.) dawsoni* and *Acanthascus (S.)* sp. and the sea pen *Balticina californica*. (B) Prediction map of VME S-SDM 4B containing the glass sponge *Heterochone calyx* and the demosponge *Thenea* sp. (C) Prediction map of VME S-SDM 5 containing the gorgonian coral *Parastenella ramosa*, the soft coral *Clavularia* sp. and the glass sponge *Farrea occa*.

taxonomic patterns also emerge. The S-SDMs with the most protection at the highest predicted suitability, S-SDMs 3, 4A and 4B, composed almost exclusively of hexacoral, and octocorals, or sponges (Figure 7C–E). S-SDMs that contained sea pens usually had the least coverage from trawl closure areas at the highest predicted suitability (Figure 7G–J). S-SDM 6A, however, did display total coverage for the 'high' suitability class (Figure 7G).

4 | Discussion

4.1 | S-SDM Composition, Distribution and Relation to Field Observations of DSCS Taxa

In this examination of multi-taxon DSCS distribution prediction, the coral and sponge VME indicator taxa in each of the 10 clustered S-SDMs are considered to have relatively similar predicted distributions off the US West Coast and measures of average predicted suitability from the resulting stacks and since the probabilities are categorised, they are not considered proper analogues of species richness (Guillera-Arroita et al. 2015). Suitability may be related to DSCS species richness but is not directly proportional (Aranda and Lobo 2011; Guillera-Arroita et al. 2015) and is more similar to predicted co-occurrence of some combination of the species in a particular cluster. The clustering approach used approximates the VME community concept put forward by Watling and Auster (2021) and leverages SDMs to make community composition predictions of DSCS communities in ways akin to those advocated by Gros et al. (2022). Generally, our results show that moderate, high and very high suitability were quite localised, leaving large swathes of space to contain very low to moderate predicted suitability, however, a few patterns emerge. Most of the S-SDMs are not predicted to occur in all ecoregions. Southern California often contained the highest suitability

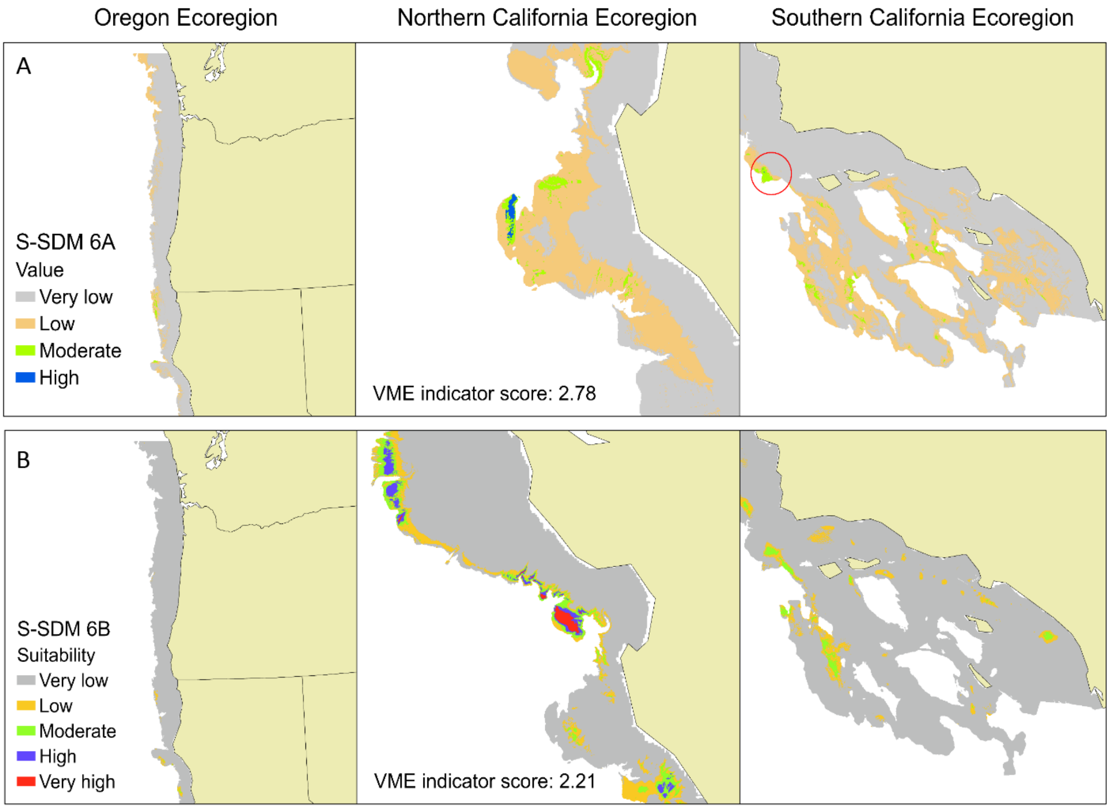

FIGURE 5 | (A) Prediction map of VME S-SDM 6A containing the gorgonian corals *Paragorgia* sp., *Callistephanus kofoidi*, *Isidella tentaculum*, the soft coral *Heteropolypus ritteri*, the sea pens *Anthoptilum grandiflorum* and *Funiculina* sp. and the glass sponge *Hyalonema* sp. (B) Prediction map of VME S-SDM 6B containing the sea pens *Umbellula lindahli* and *Pennatula phosphorea*. High and Very High suitability are indicated in red circles when not visible in the map panel.

for many of the S-SDMs and reinforced its designation as an important biogeographic area for deep-sea corals (Everett et al. 2022) but also reflects a degree of bias as one of the most well-sampled areas of the West Coast US. Bathymetrically, the depth zone with the highest suitability varied with S-SDM. S-SDMs with a greater predicted presence in the 0–200 m depth zone presumably are more structured by the California Undercurrent whose core operates at 250 m (Summers and Watling 2021). Those S-SDMs with greater predicted suitability for the 600–1200 m depth zone may be reflective of a diversity boost around the transitional boundaries around the OMZ between 400 and 600 and 1000 and 1200 m as has been seen with demersal fish off the northeast Pacific (Anderson, Tolimieri, and Millar 2013).

The taxa belonging to S-SDM 1 are a reasonable grouping as most of these species are known to occur in shallow depths and have been observed in partial combination (specifically *C. arb* and *S. californicus*) in the Channel Islands (Miller et al. 2014). While *C. arb* has a large known geographic distribution along the entire North American Pacific continental margin, the structure-forming *S. californicus* rarely has been observed north of California and *L. chilensis* has not been reported north beyond southern British Columbia (NOAA 2016). *S. californicus* and *L. chilensis* are among the most abundant habitat-formers at depths between 30 and 100 m off central and southern California and have been observed together in coral density 'hot spots' offering benthic complexity and refuge to various benthic fauna (Watters, Laidig, and Yoklavich 2022; Etnoyer and Morgan 2003).

The stony and gorgonian corals of S-SDM 2 and the finding of the spatial distribution restricted to S. California and depths of 200 m show strong accord with what has been reported. *E. rubens* and *A. phyllosclera* tend to occupy depths between 50 and 100 m (Salgado, Nehasil, and Etnoyer 2018) and have been observed frequently associated in situ (Etnoyer et al. 2020; Everett and Park 2018; Salgado, Nehasil, and Etnoyer 2018; Watters, Laidig, and Yoklavich 2022). The full set of all three taxa has been observed on the same transects in the Channel Islands (NOAA 2016).

Most of the constituent taxa of S-SDM 3, excepting *D. dianthus*, *A. dawsoni and Haliclona* sp., have been observed in the same study among three offshore banks in the SCB region (Yoklavich et al. 2013) and many of the taxa have been noted to be co-located on the same transect records in the NOAA National Database for Deep-Sea Corals and Sponges (NOAA 2016). The predicted distributions of the component taxa tend to display strong correspondence but in comparison to the known distributions of surveyed locations, some disagreement is noted (NOAA 2016). *A. dendrochristos*, for instance, is entirely restricted to the SCB while the other taxa are more widely distributed coastwide. The highest suitabilities falling in the SCB likely is a byproduct of most of this taxon's records occurring in this region.

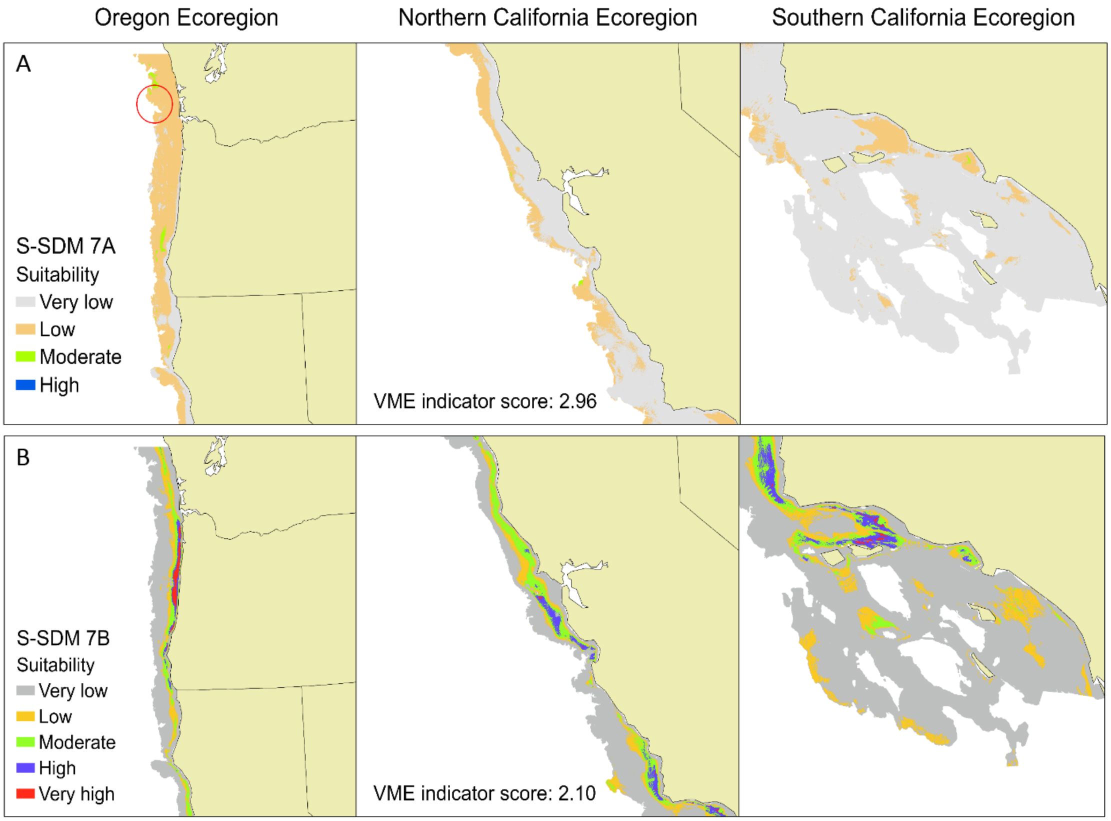

FIGURE 6 | (A) Prediction map of VME S-SDM 7A containing the gorgonian corals *Callistephanus pacifica*, *C. simplex*, *Chromoplexaura marki*, the sea pens *Stylatula* sp. and *Virgularia* sp. and the glass sponge *Aphrocallistes vastus*. Inset: Bar plot of the total area occupied by each suitability class. (B) Prediction map of S-SDM 7B containing the sea pens *Ptilosarcus gurneyi* and *Acanthoptilum gracile*. High and Very High suitability are indicated in red circles when not visible in the map panel.

S-SDM 4A and 4B are either dominated by or exclusively contain poriferans, and similar to S-SDM 2 and 3, have the greatest amounts of the highest suitability classes primarily located in the SCB. However, with these S-SDMs, we start to observe some of the first problematic associations from the cluster analysis. The taxa from 4A have been observed in previous ROV surveys in the SCB region (e.g. Piggy Bank Seamount (Fruh, Clarke, and Whitmire 2010; Yoklavich et al. 2011)). However, as a sea pen, *B. californica* prefers soft substrate in strong contrast to the poriferans that make up the rest of the group. Mixed substrate topography might explain the inclusion of sea pens in this grouping but this substrate type is hardly present in the SCB (Poti et al. 2020). If it is present, it perhaps occurs at a scale not captured at the resolution of the current models. Grouping taxa with strongly different ecological preferences could also point to a problem with the clustering approach and could also explain the lack of high suitability predicted for this S-SDM.

The grouping of taxa in S-SDM 4B is less problematic, often observed together on the same transects, on Piggy Bank (Yoklavich et al. 2011), for example. Both taxa, however, have been observed in the eastern Pacific from Canada to Mexico (NOAA 2016). Thus, the S. California predictions for this S-SDM likely do not capture the full range of the component taxa.

The highest suitability for S-SDM 5 has been predicted in each ecoregion at depths from 200 to 1200 m but the three component species can generally be deeper than the 1200 m cutoff. At least a quarter of *P. ramosa* records and about half of *F. occa* observations are deeper (NOAA 2016). Their inclusion in the current study is warranted because they are well-represented in the modelling domain. In situ encounters of the component taxa include the full set at Greater Farallones National Marine Sanctuary (Graiff et al. 2021) and in part at Piggy Bank (Fruh, Clarke, and Whitmire 2010) in the SCB. Researchers in the N. California and Oregon ecoregions observed the full combination in waters off the Oregon-California border to Mendocino Ridge (Yoklavich et al. 2016). In general, though, *Clavularia* and *P. ramosa* are rarely reported to occur on the same dive or transect (NOAA 2016). Also, it should be noted that *Clavularia* may be less easy to distinguish visually and should be a point to reconcile if this taxon is modelled again.

S-SDMs 6A presents another potentially problematic, yet interesting, combination of taxa with the inclusion of predominantly soft substrate-inhabiting sea pens, *A. grandiflorum* and *Funiculina* and hard substrate-inhabiting gorgonians, a soft mushroom coral and glass sponges in the genus *Hyalonema* (which includes species that occur in soft sediments as well as others on hard substrates). The pockets of high and very high suitability do not show strong correspondence with areas of mixed substrate depicted in Poti et al. (2020). Sea pens have been observed to attach to rocky outcroppings (e.g. Williams and Alderslade (2011)), namely a few congeners to *A. grandiflorum*, these two sea pens have exclusively been observed in

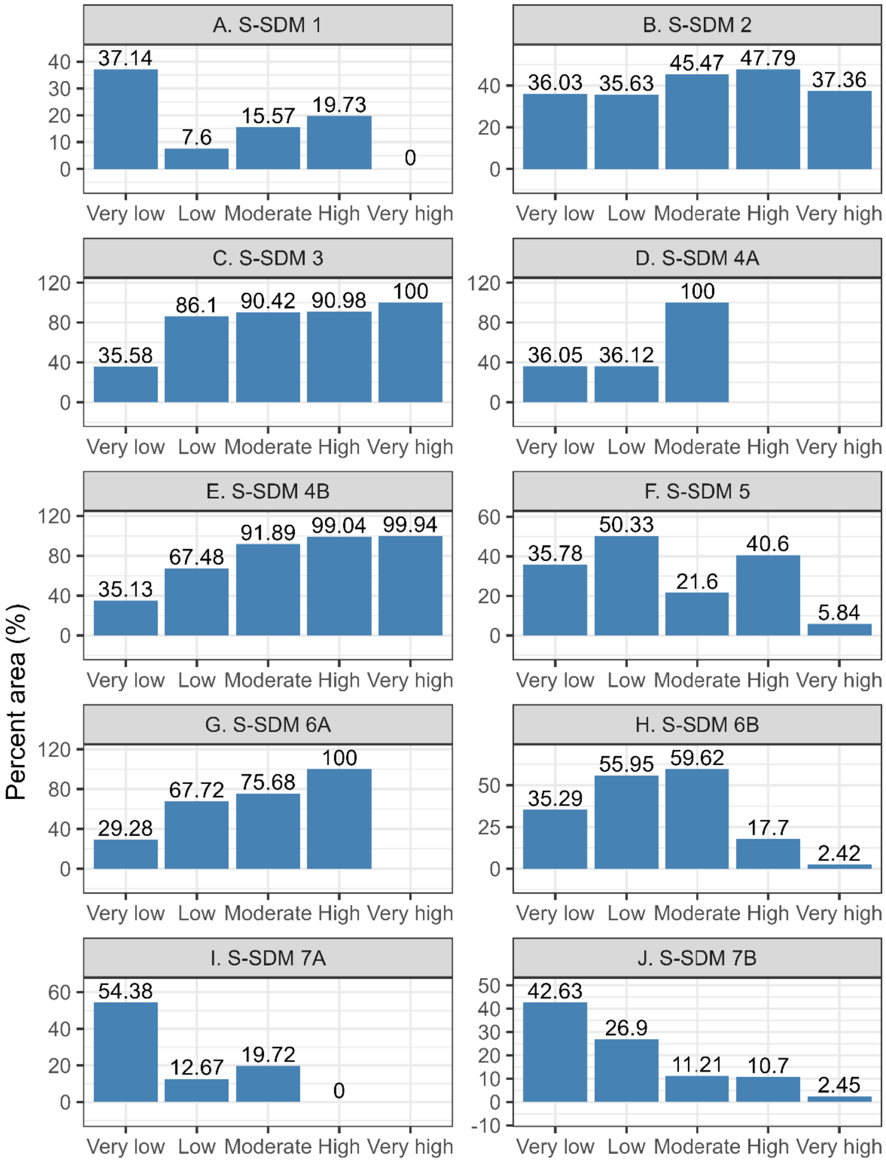

FIGURE 7 | Bar plots depicting the percentage area of each S-SDM suitability class that overlaps bottom trawl closure zones relative to the total area of each suitability class (very low, low, moderate, high and very high), off the US West Coast.

soft substrate. Nonetheless, subsets of the predicted combination have been observed in past surveys in the N. and S. California ecoregions where it is most predicted to occur (Yoklavich et al. 2016, 2011) and is not surprising as many Alcyonacean corals like *Paragorgia* sp., *H. ritteri* and *Isidella* congeners are commonly observed together on the North American Pacific margin (Doherty et al. 2021). S-SDM 6B, is entirely composed of two other sea pens, *Umbellula lindahli* and *Pennatula phosphorea*. These species have been observed together in the S. California ecoregion on Piggy Bank (Yoklavich et al. 2011) and on multiple transects in the National Database (NOAA 2016).

The six taxa that form S-SDM 7A are a mix of hard-bottom gorgonians, soft-bottom pennatulaceans and a large glass sponge. There is very little predicted high suitability habitat, and moderate suitability areas are mostly in the Oregon ecoregion at depths from 200 to 1200 m. All six taxa are abundant and widely distributed across the region with the exception of *A. vastus*, which has not been reported in the SCB (NOAA 2016). The full combination of taxa predicted in this S-SDM is one of the hardest to confirm in situ from past surveys of the region. The subset of *A. vastus*, *Virgularia* sp. and various *Callistephanus* (formerly *Swiftia*) sp. have been observed in the Olympic Coast National Marine Sanctuary (NMS) (Brancato et al. 2007). Another subset (*Virgularia* sp. and *Stylatula* sp. on soft substrata and *C. marki* on neighbouring hard substrata) has been documented in surveys of the Rittenburg Bank in the Greater Farallones NMS (Etnoyer et al. 2014).

Similar to S-SDM 6B, S-SDM 7B, contains sea pens exclusively, but differs in that the highest suitability occurs in all ecoregions and particularly on the shelf (50-200 m) where much of the bottom trawl fishing occurs. The highest suitability classes of this S-SDM are predicted to occur in especially large areas (> 1000 km^2) in the Oregon ecoregion but there are considerable pockets of the highest suitability in the other ecoregions. While the size of the patches of highest suitability is among the largest of the S-SDMs, these taxa commonly are encountered together in NMFS and other surveys coastwide (NOAA 2016), suggesting that this association may be more widespread.

4.2 | Predicted S-SDM Overlap With Areas Protected From Bottom Trawling and the Relevance of the VME Indicator Scores

Area-based fishing gear restrictions in federal waters off the West Coast now protect large areas of the seafloor from bottom trawling. These protections cover approximately 36.08% of the area modelled. This allows analysis of the extent to which the higher suitability predicted habitat for the proposed 10 taxon clusters (S-SDMs) are protected. When analysed by suitability class, trawl closures appear to provide moderate to complete protection for areas of high and very high predicted suitability for the majority of the S-SDMs identified from the cluster analysis. Protection coverage for the highest suitability classes ranged from 37% to 100%, S-SDMs 2—4B & 6A receive much of this from the establishment ban on bottom trawling in the new Southern California Bight trawl closure area (PFMC 2019). However, it must be noted that the geographic extent of the highest suitability classes for all of these S-SDMs is a tiny fraction of the whole modelling domain, not reaching more than a few dozen kilometres at most. This undercuts the notion of high coverage for the highest predicted suitability for multiple combinations of taxa and may not provide useful findings for regional managers. It should also be noted that with the complete ban on trawl fishing in the SCB, one might expect protection for S-SDMs primarily predicted to occur there (e.g. S-SDM 1–3) to be near 100%, especially for the small areas, the highest suitability classes occupy. However, this was not observed due to the jurisdiction of the federal organisation that enforces the trawl closures, the Pacific Regional Fisheries Management Council does not apply in waters less than 3 miles from shore (NOAA 2022) and where much of the highest predicted occurrence for some of the S-SDMs are observed.

The highest suitability classes of the two S-SDMs composed exclusively of sea pens, 6B and 7B, are largely unprotected from trawling, a product of trawl closure areas preferentially targeting rocky habitats that are both better habitat for many other corals and sponges, as well as less suited for bottom trawl gear. Given the vulnerability of sea pens to bottom trawling, further investigation into their ecological role and value as habitat for other species is warranted.

The most direct comparison for the results of the present study is with the findings from Shester et al. (2021) who estimated overall coverage of highly suitable coral habitat by trawl closures for the US WC EEZ was 63% and could be as high as 96% for some ecoregions like the SCB. The difference in protection coverage between these estimates and the current study likely stems from the advancement in data availability between the models used in each study and the narrower modelling domain used in Poti et al. (2020). On the difference in modelling approaches, Shester et al. (2021) employed the best models available at the time, generated by Guinotte and Davies (2014) and used only areas categorised as the highest predicted coral habitat suitability (Level 4) to calculate the overlap with fishery protections. These models were limited by the 500 × 500 m spatial resolution of the bathymetry present at the time, the low taxonomic resolution (left at the order and suborder level) of the biological data, did not include sea pens and sponges, the low count of biological records (2120) and the low number of environmental predictors available. In contrast, the models used in the present study, detailed in Poti et al. (2020), modelled DSCS taxa at a 200 × 200 m spatial resolution with over 250,000 DSCS taxa records at the genus and species level, and using 22 environmental predictors. Increasing spatial resolution is generally thought to be important to distinguish areas that could be protected from human activities that harm sensitive DSCS taxa (Gullage, Devillers, and Edinger 2017; Rengstorf et al. 2013; Sundahl, Buhl-Mortensen, and Buhl-Mortensen 2020). Coupling this with the cluster analysis approach, one can understand why the protection available for multi-taxon predictions can be so different.

Increased spatial and taxonomic resolution means smaller suitable areas are identified for each taxon. Looking only at those areas with a specific combination of these taxa will mean even smaller areas and some of these might be missed by small MPAs. Alternatively, however, this might mean that a greater percentage would be captured by larger MPAs (at a cost to fishers). This overall denotes the need to revisit the use and approach in aggregating SDMs in evaluating the effectiveness of MPA design.

Previous attempts to incorporate the VME indicator scores tend to be more spatially explicit (e.g. Stephenson et al. (2024) and Burgos et al. (2020)) by identifying areas where VMEs are likely to be found. However, as the VME is not a conservation unit employed in US waters, we looked to more broadly apply the VME indicator scores for the conservation information they provide by simply taking the root mean square of the individual taxa in an S-SDM. Taking the quadratic mean of the scores of all the individuals generated S-SDM VME indicator scores that signified each was of low to moderate vulnerability to trawling. Even though the benefit of using the quadratic mean gives greater weight to larger values in the cluster, the practical effect still seems to be that one less vulnerable taxon can bring down the cluster mean. This will have a much bigger impact on the perceived vulnerability of a community than the mean/quadratic mean difference. Thus, managers should determine the degree of vulnerability of the community by the quadratic mean and the taxon in the S-SDM with the greatest VME indicator score.

4.3 | Caveats of the Modelling and Stacking Approach

Multiple articles list recommendations on best practices for improving predictions of deep-sea taxa distributions (e.g. Kenchington et al. (2019a), Winship et al. (2020)) and for those of VME indicator taxa (e.g. Bowden et al. (2021), Stephenson et al. (2021)). For multi-taxon predictions off the WC EEZ, improvement may come in a few ways: improvement and expansion in the biological and environmental data underlying the models, the method of SDM construction and the method of leveraging the models to make multi-taxon predictions. Additionally, although the modelling focus on depths no deeper than 1200 m addresses the depth range most relevant to offshore wind and trawl fishing, many DSCS taxa that occur in deeper waters were excluded. Indeed, a few modelled taxa for Poti et al. (2020) were omitted due to their overall preference for greater depths and whose inclusion could have biased clustering, for example, *Bathypathes* sp. Given the increase in predicted suitability with depth for some of the S-SDMs, increasing the depth coverage of the models would enhance the utility of these predictions in spatial management planning for issues beyond trawling. However, it should be noted that the 1200 m limit was also imposed due to gaps in the environmental data and bottom trawling is prohibited beyond 1280 m.

Environmental predictors used in the models of this study could be augmented through refinement of the sources that were used and expanding the number of biologically pertinent variables. Multibeam bathymetry used in the models of Poti et al. (2020) was sometimes missing or of coarse resolution, forcing interpolation and resampling from other sources to fill the gaps. Ocean productivity and circulation parameters came from low-resolution sources and that required resampling to the 200 × 200 m grid for use in the distribution model construction. Further, some biologically relevant parameters were missing and could have enhanced the predictive power of models and, thereby, the predictive power of the resulting stacks. Variables such as silicate, aragonite saturation and dissolved oxygen levels, have all been shown to be important for models of DSCS in northeastern Pacific waters (Chu et al. 2019) and should be incorporated into future models once their spatial coverage has improved.

The MaxEnt approach is the most popular method of modelling the distribution of DSCS and while it remains useful for many use cases, other modelling frameworks are increasingly employed (Winship et al. 2020). Stacking the subsequent models, as in the current study, ignores some important macroecological considerations such as interspecific interactions, dispersal and abiotic filtering. Some are advocating the use of a joint-species distribution framework (Kenchington et al. 2019a; Winship et al. 2020; Gros et al. 2022) for a more community-driven approach to modelling and the ability to explicitly incorporate interspecies interactions, which the present study's clustering approach does not capture well (Ferrier and Guisan 2006). In contrast, D'Amen et al. (2017) advocate a framework for community reconstruction with a designed species pool, applying an abiotic filter based on a species' niche, implementing macroecological constraints to set the limit of coexisting species number, and employing the biotic rules for choosing among the potential species in the pool. This has the advantage of incorporating the joint effects of biogeographical and community-level processes, a central tenet of seascape ecology to the deep sea (Swanborn et al. 2022), and could enhance the resulting cluster solutions and even have implications for MPAs. One potential implementation of this concept is the use of archetypes wherein predictive models are generated based on species grouped together by their responses to environmental gradients (e.g. Dunstan, Foster, and Darnell (2011)). Similarly, one could also attempt a multi-taxon prediction approach that utilises the Regions of Common Profiles modelling framework (Foster et al. 2013) that treats the environment as a collection of regions where the set of probabilities of observing a number of species remains approximately constant within regions and distinct from other regions. These alternative methods potentially address the problems we observed in some S-SDMs that grouped taxa with strongly differing niche preferences (i.e. hard substrate with soft substrate taxa) or better pair taxa that have been known to strongly associate, e.g. *A. vastus* and *H. calyx* are dominant sponges found in Grey's Canyon off Washington state (Powell et al. 2018) but did not pair together in the cluster analysis. Indeed, this study highlights a major limitation in the 'predict first, assemble later' approach–not enforcing congruence with known communities (Ferrier and Guisan 2006). Future WC EEZ DSCS models should also explicitly factor the biogeographical boundary between Point Conception and Los Angeles, California (Clarke, Whitmire, and Yoklavich 2017). Incorporating its effect on larval dispersal could enhance the effectiveness of existing trawl closure areas, even push it towards a network-based strategy for protecting DSCS. Such considerations have been useful for developing SDMs for DSCS in MPAs in the Northwest Atlantic (Kenchington et al. 2019b).

5 | Conclusions

Presented in the current study is a relatively novel approach to identifying regions of high suitability for multiple disturbance-sensitive deep-sea taxa. These predictions should be viewed as preliminary and open to refinement. Based on the NOAA Deep Sea Coral and Research Technology Program National Database, the prediction of the S-SDMs used one of the most extensive collections of DSCS records available for any large ocean area, focusing on species and genera recognised as the most important and vulnerable 'habitat-forming' deep-sea taxa in the US West Coast region. The clustering approach identified 10 predicted assemblages of coral and sponge taxa that were mostly well aligned with field observations of co-occurring species with noted caveats. The clustering approach can also infer some known associations in situ and offers a possible alternative method of aggregating models other than simply stacking all the models. Nevertheless, the approach as tested at the West Coast regional level resulted in very small areas identified as high suitability for all but one assemblage dominated by sea pens, indicating that the geographic extent to which it can predict high suitability may be limited in the current implementation. Therefore, it may have drawbacks for region-wide conservation assessment and planning for managers that want to aggregate SDMs to understand and protect assemblages of vulnerable species. Managers attempting mult-taxon prediction in the future must do so judiciously and consider an approach that meets their requirements well.

Author Contributions

Conceptualisation: A.S. and M.P. Data curation: A.S. and T.H. Data analyses and methodology: A.S., Y.L., R.M., T.H., D.W., H.C. and R.E. Funding acquisition: J.C. Project administration: A.S. Supervision: A.S. Validation: A.S. and T.H. Visualisation: A.S. Writing original draft: A.S. Writing – review and editing: A.S., M.P., A.W., Y.L., H.C., J.C. and T.H.

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Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

The data and respective documentation used in the present study can be found in the publicly available NOAA repository: https://coastalscience.noaa.gov/project/predictive-benthic-habitat-suitability-modeling-of-deep-sea-biota-on-the-us-pacific-outer-continental-shelf/. Result files supporting the present study are available on this public NCEI web-accessible folder (https://www.ncei.noaa.gov/waf/dsc-data/supplementary/) and consist of (i) the code and shapefiles used to generate the outputs for the study, (ii) the GeoTIFF rasters of the S-SDMs produced from the stacking method and (iii) the dissimilarity matrix from the cluster analysis.

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Supporting Information

Additional supporting information can be found online in the Supporting Information section.