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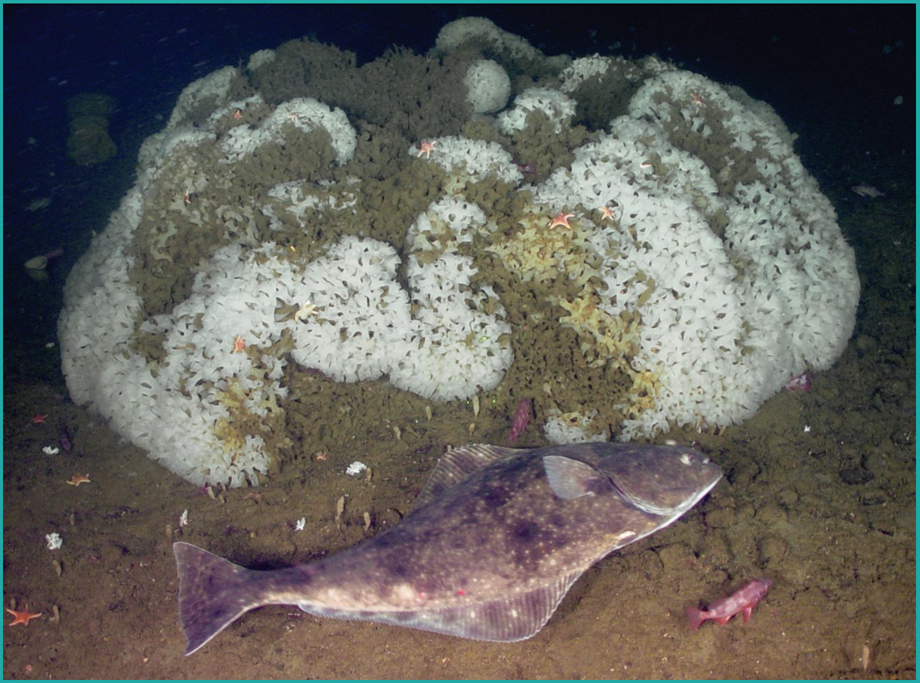

Report of Working Group 32 on Biodiversity of Biogenic Habitats

NORTH PACIFIC MARINE SCIENCE ORGANIZATION

PICES

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Report of Working Group 32 on Biodiversity of Biogenic Habitats

edited by
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Front cover:
The cold-water coral *Primnoa pacifica* (top) and sponge *Farrea occa* (bottom) are biogenic habitat-forming species found in the Northeast Pacific region of Canada (Photo credit: Jackson W.F. Chu/ CSSF-ROPOS).

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Acknowledgements

We thank all members of WG 32 for their insightful contributions, for their rich body of research on the biodiversity of biogenic habitats, and for diligently ensuring that WG 32 met its Terms of Reference. We are grateful to Anya Dunham (Canada) for making perceptive research contributions and for stepping in to serve as the interim co-chair from 2016 to 2018 while Janelle Curtis (Canada) was recovering from an accident when hiking in the mountains. We appreciate thoughtful guidance from the BIO Committee over the years. We also thank members of the PICES Secretariat for their support of WG 32, especially during Janelle Curtis' recovery. WG 32's contributions support the work of the North Pacific Fisheries Commission (NPFC), which now works closely with PICES through the joint PICES–NPFC Framework for Enhanced Scientific Collaboration in the North Pacific Ocean.

Janelle M.R. Curtis and Masashi Kiyota
Co-Chairs, Working Group 32

Executive Summary

PICES' Convention came into force in 1992 while the North Pacific Fisheries Commission's (NPFC) Convention on the Conservation and Management of High Seas Fisheries Resources in the North Pacific Ocean came into force in 2015. In 2019, the two organizations agreed on a joint PICES–NPFC Framework for Enhanced Scientific Collaboration in the North Pacific Ocean. This framework identified three broad areas of joint interest to PICES and NPFC including research on stock assessment for NPFC's priority species, an ecosystem approach to fisheries management, and vulnerable marine ecosystems (VMEs). NPFC identified four orders of corals – Alcyonacea, Antipatharia, Gorgonacea, and Scleractinia – as indicators of potential VMEs, but recognized that sponges and other invertebrates may also be identified as VME indicator taxa in the future. Although NPFC was formed a few years before the onset of the joint PICES–NPFC framework, WG 32's activities on the biodiversity of biogenic habitats support joint research activities related to VMEs.

One of the many motivations for developing a working group to focus on the biodiversity of biogenic habitat (WG 32) are the threats of bottom fishing and climate change to the distribution and abundance of corals, sponges, and other organisms that provide habitat for marine organisms, including commercially valuable species. Biogenic corals and sponges provide habitat for early life history stages of fishes and perform important functions in nutrient cycling and carbon sequestration. Catches of rockfishes and other commercially important species are higher where corals and sponges occur as bycatch. The goals of WG 32 centered on collating data on the distribution of corals, sponges, and associated fauna, using models to predict the distribution of these biogenic habitats, proposing indicators for assessing them, and reviewing their associations with commercially important species. WG 32 members collaborated effectively with each other and accomplished the overarching vision of contributing to a deeper understanding of the diversity and distribution of biogenic habitats in the North Pacific Ocean, and by doing so, enhancing the ability to engage in ecosystem-based fisheries management.

The distribution of fauna is difficult to monitor in marine environments, particularly in the deep sea. Yet, assessing the distributions of biogenic habitat is a precursor to understanding their role in the greater dynamics of the entire ecosystem (*e.g.*, biodiversity, ecosystem functioning, fisheries, *etc*.). Knowledge of the spatial distribution of species is valuable for understanding ecosystem structure and function. However, extensive sampling plans in logistically challenging environments are expensive, so data on biogenic habitats will continue to be sparse, particularly in the deep sea, in the immediate future. Hence WG 32 reviewed modeling approaches to predict the potential distributions of species and habitat suitability for corals and sponges and identified environmental and ecological predictors of patterns in the distribution and biodiversity of corals, sponges, and associated taxa.

Predictive modeling methods are often used to estimate the distribution of marine fauna using available data. Predictions of species' ranges from distribution models are also often used to inform marine management and conservation efforts, but few studies justify the model selected or quantify the uncertainty of the model predictions in a spatial manner.

One of the key activities of WG 32 was to review modeling approaches to predict the potential distributions of species and habitat suitability for biogenic habitats within national waters. Due to the now numerous species distribution modeling methods, there is some difficulty in selecting an appropriate algorithm. WG 32 members reviewed MaxEnt, generalized additive models (GAMs), and boosted regression trees. During PICES-2016, WG 32 convened a workshop on modeling approaches for corals and sponges and provided recommendations for data and modeling methods that should be considered for those biogenic habitats. Technical aspects of species distribution modeling, including the best practices for generating input data, creating models and evaluating the results, a data-driven approach to defining bioregions, a multi-scale assessment of species distribution models, and an assessment of model transferability were also examined during the workshop.

MaxEnt habitat models showed higher prediction accuracy at smaller grid cell sizes, and predicted high habitat suitability at such locations as ridges on upper slopes and terrace edges and surface undulation on seamount tops, suggesting the importance of sloped and/or irregular sea floor as habitat of large gorgonian corals. These results demonstrate that it is desirable to obtain bathymetric grid data at resolutions of 100 m or less for the purpose of predicting the distributions of corals at a local scale (*e.g.*, within a seamount). It is important to decide the optimum spatial resolution in consideration of the objectives, data availability, and geographical or biological characteristics.

WG 32 members recognized the value of producing multiple models for multiple areas because oceanic environments are subject to different currents and water masses, and different levels of topographical influence can vary drastically in their biogeochemistry. They also recognized the importance of spatially examining uncertainty in model predictions and how it varies over space.

Monitoring the status of biogenic habitats is difficult and costly, so WG 32 focused on developing effective indicators for assessing and monitoring diversity, and reviewing associations between biogenic habitats and commercial species. Indicators included trends in bycatch in commercial fisheries. WG 32 members proposed a structured, iterative approach to designing monitoring programs for marine biogenic habitats that allows for rigorous data collection to inform management strategies, even when data and resources are limited. Systematic monitoring approaches are needed to guide adaptive management strategies for data-limited marine biogenic habitats.

WG 32 members developed species distribution models (SDMs) for several major groupings of biogenic habitat-forming corals and sponges, in part, to assess the primary drivers of suitable habitat for these taxa and to identify potential areas of high diversity of biogenic habitats. Some members introduced a new method for assessing the validity of VME indicator taxa (Gorgonians, Alcyonacea, Antipatharia, and Scleractinia) and applied association analysis for identifying VME indicators on the basis of sea-floor visual imagery. Others reconstructed long-term, climate-driven range shifts in biogenic habitats and associated fishes in the western North Pacific Ocean from tropical to subarctic zones.

Another key outcome of WG 32's activities included the identification of large-scale environmental and ecological predictors for the distribution and biodiversity of coral, sponge, and associated taxa. Members assembled an exhaustive group of measured and derived predictor variables for the North Pacific Ocean on a 1 km^2 grid. These predictor variables were made available to all WG 32 members through a shared drive, which allowed them to use the layers in their own modeling efforts.

Overall, WG 32 members illustrated the value of SDMs for assessing potentially important environmental variables that could influence the distributions of biogenic habitat in areas with historically few observations (*e.g.*, offshore deep waters). By combining multi-model outputs into a single composite index for corals and sponges, potential areas of suitable habitat for multiple biogenic habitats were identified. Members showed how multi-models can also be used to empirically assess areas that have been identified as ecologically and biologically significant marine areas (EBSAs).

WG 32's models suggested that glass sponge reefs require a delicate balance of turbidity and suspended sediment concentration. Another study suggested that the thermal index, UV radiation, and water turbidity were important predictors for the occurrence of coral bleaching, which has affected coral reefs in Japan. That same study found that prediction models combining the effects of climate and ocean currents consistently explained observed community shifts significantly better than those relying on climate alone.

Data availability will likely remain poor in offshore areas. SDMs are one tool that can extrapolate modeled species–environment relationships into areas where species records are rare and provide an empirical foundation for hypothesis development. Members showed how applying a multi-model, multi-area approach can improve the interpretation of the modeled species–environment relationships and how which areas are predicted by the model to have high or low levels of uncertainty.

WG 32 members demonstrated that habitat-forming species are associated with many commercial fishes and invertebrates. Association analysis demonstrated that Gorgonians frequently co-existed with other benthic animals in the Emperor Seamounts area. One study proposed a new method to assess the characteristics of benthic communities and to screen for potential indicator taxa based on the analysis of co-occurrence tendencies among benthic taxa. Other analyses found that areas with more deep-sea corals and sponges had more rockfishes.

WG 32 members developed a biogeographical scheme for the Upper Bathyal zone (200–1000 m) using octocoral distributions. The main driver for twelve proposed biogeographical units seems to be temperature, which is a defining feature of water masses. Members also investigated how environmental variables influence the distribution of corals, including those changing as seas warm. Climate change is causing coral declines in southern Japan due to bleaching but range expansion in northern Japan.

The work of WG 32 has advanced our knowledge of deep-sea coral and sponge ecosystem distributions by providing tools for modeling presence, absence, and abundance of deep-sea corals and sponges. On that note, WG 32 recommends that PICES engage in further research on biodiversity in the North Pacific Ocean. Specifically, WG 32 recommends that PICES establish a new Working Group on Ecology of Seamounts, with a focus on understanding the distribution of benthic, demersal, and pelagic species that are associated with seamounts. A Working Group on Ecology of Seamounts would build on the contributions of WG 32 by mapping the distribution of seamount biodiversity and expanding research in some of the unique and abundant ecosystems of the North Pacific Ocean. The merits of a new Working Group on Ecology of Seamounts include: 1) the application of concepts developed by WG 32, 2) new data to better understand factors that influence the distribution and trends in seamount biodiversity and test key questions about the interactions among taxa that differ in life history (*e.g.*, plankton, filter feeders, fish, mammals), 3) identification of indicators to monitor change, 4) development of hypotheses to forecast responses to multiple stressors, which is aligned with the spirit of FUTURE, 5) maps of the distribution of benthic, demersal, and pelagic biodiversity and its indicators, 6) a new research avenue for PICES with clear linkages to other PICES activities, including the BIO Committee and the PICES–NPFC Framework for Enhanced Scientific Collaboration in the North Pacific Ocean.

Activities of Working Group Members and Colleagues

The following are ten contributions by members and colleagues of WG 32. Conclusions and Recommendations are then presented followed by five appendices that include the Working Group's Terms of Reference, membership, published literature related to WG 32 research, meeting reports and topic session/workshop summaries from PICES Annual Meetings, and article featured in PICES Press.

1. *MaxEnt modelling of biogenic habitat-forming cold-water corals and sponges in the Northeast Pacific region of Canada*

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Background and overview

This section summarizes the recent Canadian efforts in predictive modelling of the distributions of biogenic habitat-forming, cold-water corals and sponges (CWCS) in the Northeast Pacific region of Canada (NEPC). Biogenic habitat-forming CWCS are often the focal taxa when applying empirical frameworks designed to identify sensitive benthic areas or those that are vulnerable to significant adverse impacts as a result of fishing activities (Ardron *et al.*, 2014; Dunn *et al.*, 2014). These frameworks focus on criteria that can almost entirely be met by the presence of dense CWCS communities. Key ecosystem roles that CWCS have include habitat provisioning for early life history stages of rockfish and sharks (Baillon *et al.*, 2012; Henry *et al.*, 2013), nutrient cycling, and carbon sequestration (Henry and Roberts, 2007; Oevelen *et al.*, 2009; Chu and Leys, 2010; Chu *et al.*, 2011; Kahn *et al.*, 2015). Biological traits such as slow growth, low reproductive output and dispersal rates, and long life spans (Roark *et al.*, 2009; Jochum *et al.*, 2012) make CWCS especially vulnerable to destructive bottom contact fisheries. Thus, activities that remove or destroy CWCS directly results in the net loss of the aforementioned ecosystem functions and services.

Our NEPC case study area is the Pacific Exclusive Economic Zone (EEZ) of Canada. This region is notable for several globally unique biogenic habitat-forming CWCS communities (*e.g.*, glass sponge reefs, Krautter *et al.*, 2001) and is where the majority of Canadian seamounts are located (>80%, DFO, 2019). Seamount ecosystems are of noted interest to the scientific community because of their global biogeography patterns and high productivity. Dense populations of commercially important fish and communities of biogenic-habitat forming CWCS are frequently found at seamounts (Clark *et al.*, 2011; Guinotte and Davies, 2014). Historically, the majority of empirical knowledge on the distribution of habitat-forming CWCS in the NEPC has focused on the samples collected on the continental shelf and slope with only a sparse number of records coming from the offshore deep waters in the NEPC. Published knowledge of biogenic habitat-forming CWCS on NEPC seamounts has come from research mostly done at two outliers with summits occurring in <30 m depths (Bowie and Cobb seamounts); most seamounts in the NEPC do not have summits that extend into the epipelagic zone.

Species distribution models (SDMs) were developed for several major groupings of biogenic habitat-forming CWCS. The goals of these analyses were to assess the primary drivers of suitable habitat for CWCS in the NEPC, identify potential areas of high CWCS diversity (*i.e*., areas that were suitable habitat for multiple CWCS groups), and determine the extent of CWCS suitable habitat at seamounts in this region. To assess areas as suitable habitat for multiple biogenic habitat-forming CWCS, a ‘CWCS composite index’ was created from combining spatial predictions from the individual models developed for each CWCS group. Several environmental data layers (n = 32) were generated for SDM development; methods on how they were generated are described in detail. Additional details describe how historical CWCS occurrence records were queried and compiled from several regional databases and filtered before being used in SDM development. The CWCS composite index was applied to empirically assess seamounts that have been provisionally identified as ecologically significant habitats within the Canadian EEZ (Ban *et al.*, 2016).

Data compilation

Environmental data layers

SDMs require environmental data that cover the extent of the area of interest and are selected for their potential to influence the distribution of modelled taxa. Working Group 32 created an expansive set of 32, coarse-resolution (1 km^2), environmental data layers for use in CWCS SDM development for the PICES convention area. These data layers were created following the methodology first described by Davies and Guinotte (2011) and since expanded upon by others (Guinotte and Davies, 2014; Rowden *et al.*, 2017; Georgian *et al.*, 2019). Variables were obtained from a variety of sources (Table 1.1) and cover a range of bathymetry-derived variables, physico-chemical variables, and water column properties that are useful in predicting the potential distributions of benthic species in major ocean basins elsewhere. This case study focused on the area that covers the EEZ of the NEPC.

Bathymetry data and their derivatives are ubiquitous in benthic SDM studies. For this study, bathymetric data (https://topex.ucsd.edu/WWW_html/srtm30_plus.html) were obtained from the SRTM30+ layer at a native resolution of 0.0083° (~1 km) (Becker *et al.*, 2009; Sandwell *et al.*, 2014). The SRTM30+ layer (hereafter bathymetry) is derived from Sandwell *et al*. (2014), the Lamont-Doherty Earth Observatory Multibeam Synthesis Project, the JAMSTEC Data Site for Research Cruises, the National Center for Environmental Information (formerly the National Geophysical Data Center) Coastal Relief Model, and the International Bathymetric Chart of the Oceans.

Table 1.1 Environmental data layers generated by WG 32 with associated data or methods reference.

Variable name	Unit	Native resolution	Reference
Bathymetry-derived variables			
Bottom depth	metres	0.0083°	Becker *et al*., 2009; Sandwell *et al*., 2014
Aspect – east-facing [*eastness*]*		0.0083°	Jenness, 2013a
Aspect – north-facing [*northness*]		0.0083°	Jenness, 2013a
Curvature – General [*gencurve*]		0.0083°	Jenness, 2013a
Curvature – Cross-Sectional [*crosscurve*]		0.0083°	Jenness, 2013a
Curvature – Longitudinal [*longcurve*]		0.0083°	Jenness, 2013a
Slope	degrees	0.0083°	Jenness, 2013a
Roughness [*VRM*]		0.0083°	Sappington *et al*., 2007
Bathymetric Position Index [*bpi*] (1000m, 5000m, 10000m 20000m)		0.0083°	Jenness, 2013b
Seamounts polygon [*seamounts*]			Yesson *et al*., 2011
Chemical variables			
Alkalinity	μmol l^{-1}	3.6 × 0.8–1.8°	Steinacher *et al*., 2009
Dissolved inorganic carbon [*DIC*]	μmol l^{-1}	3.6 × 0.8–1.8°	Steinacher *et al*., 2009
Omega - aragonite (Ω_{ARAG}) [*arag*]		3.6 × 0.8–1.8°	Steinacher *et al*., 2009
Omega - calcite (Ω_{CALC}) [*calc*]		3.6 × 0.8–1.8°	Steinacher *et al*., 2009
Dissolved oxygen [*oxygen*]	ml l^{-1}	1°	Garcia *et al*., 2014a
Phosphate	μmol l^{-1}	1°	Garcia *et al*., 2014b
Silicic acid [*dSi*]	μmol l^{-1}	1°	Garcia *et al*., 2014b
Nitrate	μmol l^{-1}	1°	Garcia *et al*., 2014b
Particulate organic carbon [*POC*]	g C m^{-2} yr^{-1}	0.05°	Lutz *et al*., 2007
Physical variables			
Temperature	°C	0.25°	Locarnini *et al*., 2013
Salinity	pss	0.25°	Zweng *et al*., 2013
Current velocity – regional [*regfl*]	m s^{-1}	0.5°	Carton and Giese, 2008
Current velocity – vertical [*vertfl*]	m s^{-1}	0.5°	Carton and Giese, 2008
Current direction [*curdir*]	degrees	0.5°	Carton and Giese, 2008
Current direction – relative to aspect [*curapsect*]	degrees	0.5°	Rooper *et al*., 2014
3D current-surface angle [*curang*]	degrees	0.5°	This study
Surface-layer properties			
Chlorophyll-a [*chl-a*]	mg m^{-3}	4 km	Aqua MODIS (NOAA)
Photosynthetically active radiation [*PAR*]	W m^{-2}	4 km	Aqua MODIS (NOAA)
Sea Surface Temperature [*SST*]	°C	4 km	Aqua MODIS (NOAA)

* Shortened variable names are in square parentheses.

Several derivative variables were calculated from the bathymetry layer. Slope, aspect, and curvature were calculated using the toolkit ‘DEM Surface Tools v.2’ (Jenness, 2004, 2013a) for ArcGIS (v.10.4, ESRI). The slope of each grid cell (in degrees) was calculated using the four-cell method (Horn, 1981;

Jones, 1998). Aspect, or the maximum slope direction in degrees, is a circular variable (*i.e*., the difference between 0° and 359° is one unit) and thus was converted into two components: north-facing aspect (sin(aspect)) and east-facing aspect (cos(aspect)). Curvature generally describes the shape of the seafloor as a proxy to how the water column can interact with the substratum. Three types of curvature were calculated: general curvature, cross-sectional curvature, and longitudinal curvature. For general curvature, convex features have more positive values and concave features are more negative. For cross-sectional curvature, positive values are indicative of local features that may induce water divergence, and negative values are indicative of features that induce water convergence. Longitudinal curvature assigns positive values to features where water velocity is expected to decrease and negative values to features where velocity is expected to increase.

Bathymetry

Roughness is a measure of topographical complexity and was calculated using the vector ruggedness measure (VRM) index method (Sappington *et al.*, 2007). VRM generates a dimensionless index that incorporates the bathymetry, aspect and slope layers. This process uncouples the slope from the resulting roughness index calculated for a raster cell by measuring the dispersion of vectors orthogonal to the terrain surface for a user-defined neighbourhood of cells. Here, the VRM index layer was generated using a neighbourhood of the adjacent eight cells from the one km^2 bathymetry layer.

Bathymetric Position Index (BPI) quantifies the relative elevation of a feature relative to the surrounding seafloor, with positive values indicating features that are elevated and negative values indicating features that are depressed. BPI values close to zero indicate relatively flat surfaces or areas with constant slopes. As biological processes are scale-dependent, and because BPI is calculated at a user-defined scale, a range of BPI layers was generated: 1,000 m (the fine-scale limit of the method based on the bathymetry layer), 5,000 m, 10,000 m, and 20,000 m. BPI layers were generated using the toolkit 'Land Facet Corridor Designer v1.2' (Jenness, 2013b).

Oceanographic properties

Data layers for temperature, salinity, dissolved oxygen, and several dissolved nutrients were generated from data obtained from the World Ocean Atlas (WOA, v.2 2013). Carbonate chemistry (dissolved inorganic carbon, total alkalinity, $\Omega_{\text{ARAGONITE}}$, Ω_{CALCITE}) were obtained from Steinacher *et al.* (2009). Chlorophyll-a (chl-*a*), sea surface temperature (SST), and photosynthetically active radiation (PAR) data were generated using mission composites (average of 2002–2016 data) from the MODIS/Aqua NOAA program at a resolution of 4 km and resampled to match the extent and resolution of the bathymetry layer without interpolation.

Several layers that characterize current and flow patterns were generated because of the strong influence of water movement on sessile species distributions (Genin *et al.*, 1986; Leys *et al.*, 2011). A bottom current velocity layer was generated using data from the Simple Ocean Data Assimilation model (v.3.4.1, Carton and Giese, 2008) averaged as the composite of the years 1990–2007. Current velocities were calculated in both the horizontal and vertical dimensions, and current direction for each grid cell was calculated from zonal (*u*) and meridional (*v*) velocities according to the formula:

$$\text{Direction} = \frac{180}{\pi} \times \text{atan2}([u], [v]).$$

Current flows to the south when values are close to +180° and –180°, flows to the east at +90°, flows to the west at –90°, and flows to the north at 0°.

Two additional current layers were created to capture flow patterns relative to bathymetry. The first layer generated was a two-dimensional (2D) current layer that quantified current flow direction relative to seafloor aspect. In this 2D current layer, values of 0° indicate current flow is in the same direction as the direction of the steepest slope and values of 180° indicate current flows in the opposite direction of the steepest slope (*sensu* Rooper *et al.*, 2014). The second layer generated was a three-dimensional (3D) current layer that quantified the current direction relative to the seafloor plane. For this 3D current layer, the slope and aspect layers were used to define the 3D orientation of the seafloor for each raster cell, from which the direction normal to the plane was defined in Cartesian coordinates. The direction of the water current was then defined at the seafloor based on the velocities relative to the east-flowing (x), north-flowing (y), and vertical-flowing (z) directions, and the angle between the two vectors was calculated. 3D current layer values near 90° indicate the current is flowing near-parallel to the seafloor and values less than 90° indicate current is flowing into the seafloor (*e.g.*, northward flowing current into a south-facing seafloor slope).

WOA, carbonate chemistry, and current data layers were transformed to match the extent and resolution of the bathymetry layer using a variable up-scaling approach that approximates conditions at the seafloor (Davies and Guinotte, 2011). Each layer was first interpolated to a slightly higher resolution (0.5°) than its native resolution using inverse distance weighting, resampled to match the extent and resolution of the bathymetry data, and draped over the bathymetry data within its depth range. WOA data were available as 102 depth-binned layers from depths of 0–5500 m. Vertical resolution of WOA depth layers were 5 m (from 0–100 m), 25 m (100–500 m), 50 m (500–2000 m), and 100 m (2000–5500 m). Carbonate chemistry data (Steinacher *et al.*, 2009) were available in 25 depth-binned layers (6, 19, 38, 62, 93, 133, 183, 245, 322, 415, 527, 661, 818, 1001, 1211, 1449, 1717, 2014, 2340, 2693, 3072, 3473, 3894, 4329, and 4775 m). Simple Ocean Data Assimilation (SODA) current data were available in 50 depth bins (5.0, 15.1, 25.2, 35.4, 45.6, 55.9, 66.3, 76.8, 87.6, 98.6, 110.1, 122.1, 134.9, 148.7, 164.1, 181.3, 201.3, 224.8, 253.1, 287.6, 330.0, 382.4, 446.7, 525.0, 618.7, 728.7, 855.0, 996.7, 1152.4, 1320.0, 1497.6, 1683.1, 1874.8, 2071.3, 2271.3, 2474.0, 2678.8, 2884.9, 3092.1, 3300.1, 3508.6, 3717.6, 3926.8, 4136.3, 4345.9, 4555.566, 4765.4, 4975.2, 5185.1, and 5395.0 m). This up-scaling approach has repeatedly been shown to be effective for many global and regional scale variables (Davies and Guinotte, 2011; Yesson *et al.*, 2012).

All data layers were projected in the world equidistant conic PICES azimuthal equidistance projection (–180 central meridian, 1.0 km linear unit). The edges of data layers do not completely extend into the coastal fjords habitats in the NEPC. Thus this study could not capture this habitat type which is known to harbour dense populations of CWCS taxa (Leys *et al.*, 2004; Gasbarro *et al.*, 2018).

Species records

While CWCS communities have been studied extensively in the NEPC, a comprehensive dataset of georeferenced occurrence records had not been compiled prior to this study. The majority of the CWCS records came from Fisheries and Oceans Canada (DFO) research and commercial catch databases. CWCS are recorded as incidental catch in the commercial databases. DFO research records spanned 1963–2017 and include targeted surveys for stock assessments of commercial invertebrate and groundfish populations and synoptic research bottom trawl surveys used for monitoring biogeographic areas within the Canadian EEZ. DFO commercial groundfish catch records include fisher and observer logbooks and dockside validation data from trawl, trap, and longline fisheries throughout this region; only records from 1996–2017 were used in this study because of recording reliability (M. Surry, DFO pers. comm.). Queries of the DFO databases were done using internal, three-digit DFO codes (*n* = 581) that uniquely identify CWCS taxa to varying taxonomic levels (*e.g*., 2A0 = Porifera, 3S6 = *Paragorgia arborea*). Additional records up to 2014 were compiled from the Royal British Columbia Museum (RBCM) archives which are now available in open access (Wheeler, 2018).

Although over 17,900 individual CWCS records were compiled from the various data sources, additional data management and quality control and assurance steps were required before species data could be meaningfully used in SDMs. CWCS records spanned several decades and several levels of taxonomic resolution (*e.g*., identified down to only phylum level or down to species level). Up-to-date taxonomic names and a complete taxonomic hierarchy were manually appended to records and verified in the World Register of Marine Species (Worms Editorial Board, 2018). *A priori* expert-knowledge guided parsing of the records in order to filter out records that were inappropriate for use in SDMs focused on biogenic habitat-forming marine CWCS. For example, fresh-water sponges (*e.g*., *Spongila lacustris*) present in the museum records were filtered out based on expert-knowledge. Records of Calcarea class of sponges were excluded because no biogenic habitat-forming calcareous sponges occur in the NEPC. Because of the varying degrees of taxonomic resolution, only records with taxonomic resolution down to at least the class-level for sponges and order-level for corals were used in models. Records were pooled into six general biogenic habitat-forming CWCS groups. Four of these groups were orders of cold-water corals: Alcyonacea (soft corals), Scleractinia (stony corals), Antipatharia (black corals), and Pennatulacea (sea pens). We also modeled the distributions of two classes of sponges: Hexactinellida (glass sponges) and Demospongiae (demosponges) (Fig. 1.1).

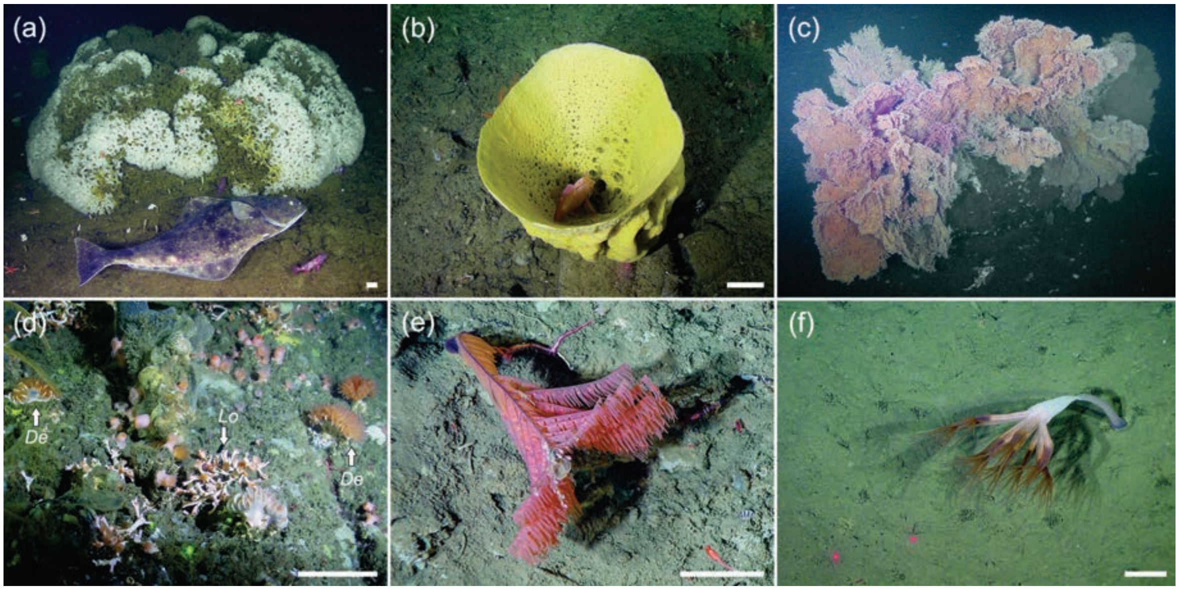

Fig. 1.1 *In situ* examples of the major, biogenic habitat-forming cold-water coral and sponges from the Northeast Pacific Region of Canada. (a) Glass sponge *Farrea occa* (class Hexactinellida), (b) demosponge *Mycale loveni* (class Demospongiae), (c) soft coral *Primnoa pacifica* (order Alcyonacea); also a gorgonian coral. (d) Stony corals *Desmophyllum* sp. (De) and *Lophelia pertusa* (Lo) (order Scleractinia), (e) black coral *Bathypathes* sp. (order Antipatharia), (f) sea pen *Umbellula* sp. (order Pennatulacea). Scale bars: (a,b,d) 10 cm, (e,f) 5 cm. No scale bar was available for (c).

Historically, several families of biogenic habitat-forming corals were associated with the now-defunct order Gorgonacea. However, since it is still common to refer to these corals (now in the order Alcyonacea) as ‘gorgonians’, we created a gorgonian model by using a subset of records (*n* = 428) in the ‘soft coral’ group that had at least a family-level of identification from the coral families: Anthothelidae, Paragorgiidae, Corallidae, Keroeididae, Acanthogorgiidae, Plexauridae, Gorgoniidae, Chrysogorgiidae, Primnoidae, and Isididae following the gorgonian grouping of Miyamoto *et al.* (2017). Sponge diversity and plasticity is problematic for species-level identification.

While the majority of glass sponges occurring in the NEPC are biogenic habitat-forming types, demosponges occupy niches that range from intertidal to deep-sea, with many species in this region being encrusting, non-habitat forming morphotypes. To prevent intertidal species from adding uncertainty to models developed for biogenic habitat-forming types, only demosponge records occurring in >100 m depths were used in the models which improved the performance of the final models (Chu *et al.*, 2019).

Following Davies and Guinotte (2011), coral and sponge data for each group were gridded to the 1 km^2 resolution of the environmental data layers and redundant records in each cell were removed (*i.e*., only one presence record per cell per group). Table 1.2 summarizes the final number of records in each of the CWCS groups used in this study.

Table 1.2 Number of records used in group-specific cold-water coral and sponge (CWCS) models.

CWCS group	Presence	Trawl-absences*	Depth-range** (m)
Glass sponges	1494	3248	28–3368
Demosponges	570	3465	100–2660
Soft corals	1960	4030	18–3624
Stony corals	717	4330	24–1388
Sea pens	3050	3678	8–2458
Black corals	51	4351	81–1985
Gorgonian corals	428	4447	41–3624

* Trawl-absences were generated from synoptic trawl surveys. The shallow extent of demosponge records was truncated at 100 m to remove non-biogenic habitat-forming types (*e.g*., encrusting intertidal spp.).
** Depth-range is the observed depth of the presence records.
Note that the gorgonian coral presence records are a subset of the soft coral records.

Species distribution modelling

Generating targeted absence data and depth masking

Individual MaxEnt species distribution models were developed for the seven CWCS groups. MaxEnt is often used in study areas where data are limited to only species presence data. However, the predictive power of SDMs is increased with the knowledge of absence locations (Phillips *et al.*, 2009). Therefore, targeted absence data were generated by taking advantage of the DFO synoptic research trawl surveys that occur in the study area (Nottingham *et al*., 2018) rather than using the random background sampling method that is the default setting in MaxEnt. Since 2003, DFO has followed a depth-stratified, random sampling trawl design over the area spanning the extent of the presence records in this study (Fig. 1.2 a,b). Trawl surveys identify all species caught in a trawl. Thus those without the occurrence of any of the model-specific CWCS species codes were considered a targeted absence record (Table 1.2). DFO synoptic research trawl surveys have been fairly reliable when used to generate absence data in SDMs that require presence–absence species data (*e.g*., Random Forest, Beazley *et al*., 2018).

The combined CWCS presence records occupied a depth range of 8–3600 m which reflects the depths of potential fishing activity in the NEPC. Seamount species are characteristically distributed within a preferred depth range (Clark *et al*., 2010). Therefore, the maximum modelled depth was limited to the depth range occupied by the presence records of each CWCS group (Table 1.2). MaxEnt (v.3.3.3e, Phillips *et al*., 2010) models were run with the default parameters for the convergent threshold (1025), maximum iteration value (500), and regularization multiplier (1) using the R package ‘dismo’ (Hijmans *et al*., 2017).

Environmental variable selection

Although MaxEnt is reasonably robust to multicollinearity among environmental variables used as predictors of species distributions (Elith *et al*., 2011), best SDM practices should always reduce the degree of correlation among model predictors. Using the R package ‘usdm’ (Naimi *et al*., 2014), variance inflation factors (VIFs) were examined among environmental variables. Values of the environmental variables were extracted at the location of the species data and VIFs were calculated starting with the complete set of environmental data layers. Variables with the highest VIF were iteratively removed until the final set of variables all had VIF values <10. Ecophysiologically relevant variables were preferentially retained (*e.g*., silicic acid for sponge groups, carbonate chemistry variables for corals) rather than variables with no direct influence on organism physiology (*e.g*., depth). This process of variable reduction was done separately using the species records belonging to each CWCS group. The final set of environmental variables used in each CWCS model is summarized in Table 1.3.

All models shared 18 variables: east-facing aspect, north-facing aspect, cross-sectional curvature, longitudinal curvature, slope, roughness, dissolved oxygen, regional current velocity, vertical current velocity, current direction, current direction relative to aspect, 3D current-surface angle, chlorophyll-a, photosynthetically active radiation, sea surface temperature, and topographic position index at three scales (1000 m, 5000 m, 20,000 m). The normalized relative importance for each variable used in their respective final CWCS models was assessed using a jack-knife procedure that compared models with and without the variable and the corresponding decrease in the area under the receiver operating characteristic curve (AUC, Phillips, 2005).

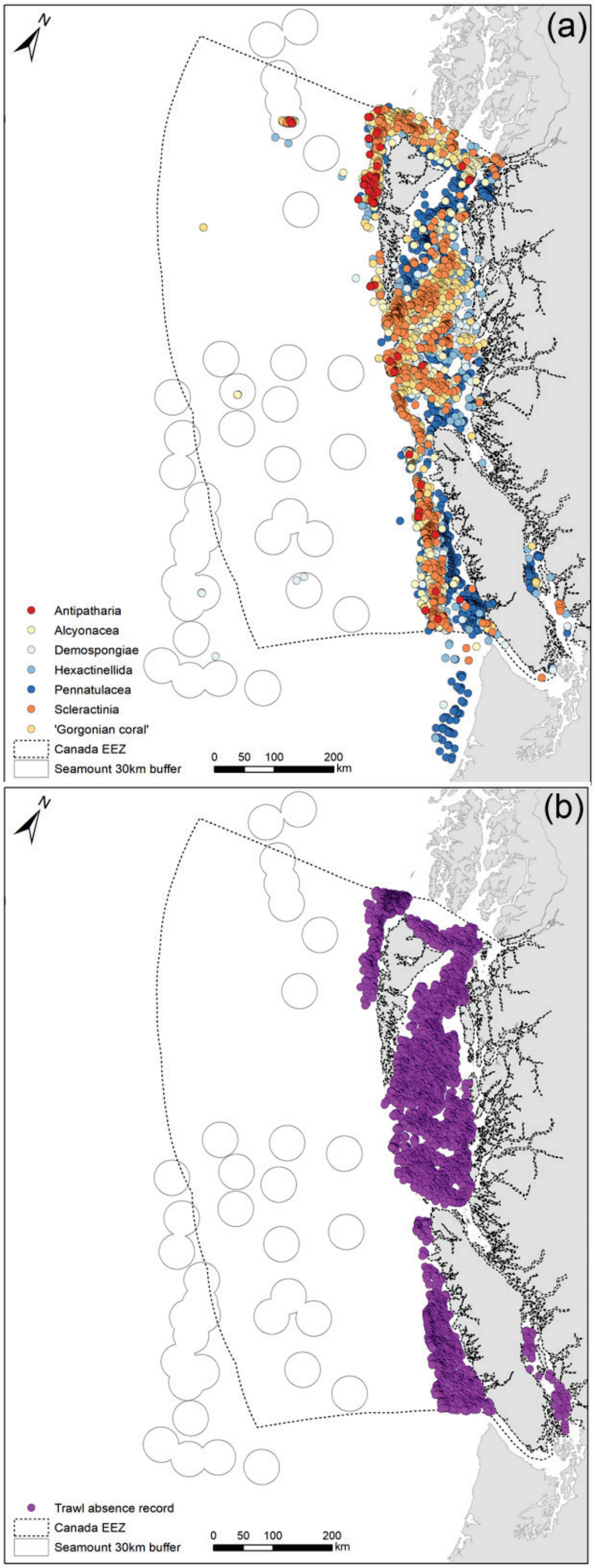

Fig. 1.2 Biogenic habitat-forming cold-water coral and sponge (CWCS) records used in this study. (a) Presence records for six CWCS groups and the gorgonian coral subgroup. (b) Trawl absence records used in this study. Location of named seamounts are delineated by a 30 km buffer zone around their respective summits.

Table 1.3 Final sets of environmental data layers used in models.

Variable	**Glass sponges**	**Demo-sponges**	**Soft corals**	**Stony corals**	**Black corals**	**Sea pens**	**Gorgonian corals**
eastness	X	X	X	X	X	X	X
northness	X	X	X	X	X	X	X
crosscurve	X	X	X	X	X	X	X
longcurve	X	X	X	X	X	X	X
Slope	X	X	X	X	X	X	X
VRM	X	X	X	X	X	X	X
oxygen	X	X	X	X	X	X	X
Regfl	X	X	X	X	X	X	X
Vertfl	X	X	X	X	X	X	X
curdir	X	X	X	X	X	X	X
curaspect	X	X	X	X	X	X	X
curang	X	X	X	X	X	X	X
chl-a	X	X	X	X	X	X	X
PAR	X	X	X	X	X	X	X
SST	X	X	X	X	X	X	X
BPI1000	X	X	X	X	X	X	X
BPI5000	X	X	X	X	X	X	X
BPI20000	X	X	X	X	X	X	X
BPI10000	X	X	X	X	X	X	–
dSi	X	X	–	X	X	–	–
Arag	–	X	–	X	X	–	–
Calc	–	–	X	–	–	X	X

Full name and units for each variable are summarized in Table 1.1.

Model validation

Model performance was assessed using five-fold cross-validation where occurrence data (presence and absences) were randomly sampled to create five equal data partitions that follow the same data ratio of presence–absence. Models were trained on four folds and tested with the remaining fold. Each iteration of this procedure ($n = 5$) rotated through the partitions always using a unique partition of records as the testing data. Mean and standard deviation of AUC, percentage correctly classified (PCC), correctly predicted presence (sensitivity), correctly predicted absence (specificity), and kappa was calculated to assess general model performance. Model thresholds were calculated by maximizing the sum and sensitivity using the R package 'PresenceAbsence' (Freeman and Moisen, 2008).

Model predictions of CWCS habitat suitability

A bootstrap resampling procedure ($n = 200$ iterations) was applied to each CWCS model to generate predictions of habitat suitability and spatially explicit measurements of uncertainty associated with the predictions at each raster cell (following Anderson *et al*., 2016; Rowden *et al*., 2017). Occurrence data and associated environmental predictors at those locations were randomly sampled with replacement to match the data ratio of presence and trawl-absences in Table 1.2. MaxEnt models were fit to each iteration, and logistic predictions of habitat suitability (0–1) were generated with values close to one indicating more suitable habitat. Mean and standard deviation (SD) were calculated from the 200 predictions; we use SD to quantify the uncertainty of the model predictions (*i.e*., predictions are more variable in areas with high SD).

In addition to generating predictions for each CWCS group, a 'CWCS composite index' was created that combined mean predictions among the four coral orders and two sponge class models. The gorgonian model outputs were excluded from the CWCS composite index because the species data were a subset of the Alyconacea model. Rasters of predicted habitat suitability for each CWCS group were reclassified into binary presence–absence layers using model-specific threshold (average of the five-folds) and then combined into a single, composite index (CI) layer where CI values of six would indicate suitable habitat for all six biogenic habitat-forming CWCS groups.

Results and application

Based on the multiple evaluation metrics, CWCS MaxEnt models performed reasonably well (*e.g*., AUC values ranged from 0.78–0.91, Table 1.4). *A priori* use of expert knowledge to parse the records was particularly effective as the Demospongiae model performance improved without shallow records (<100 m) when compared to a model that included shallow records (*e.g*., AUC increased by ~0.6 and sensitivity increased by 0.11). Water column properties were generally the most important predictors for CWCS occurring in the study area (Table 1.5). All CWCS models shared dissolved oxygen ([O2]) as a top-3 ranked predictor based on relative importance (10–47%). Examination of the marginal response curves for [O2] indicates the probability of CWCS occurrence is inversely related to [O2] levels in the study area with maximum probability occurring at the lower [O2] distribution, or ~0.3 ml L^{-1}. For both sponge groups, the top-ranked predictor was silicic acid (28–29%) with maximum probability occurring at the higher end of the silicic acid distribution or >100 μmol L^{-1}. All CWCS models predict areas of high habitat suitability (HSI mean ~1) to occur in the NEPC although to varying extents (Fig. 1.3). Relative extent and locations of prediction uncertainty also varied but was generally low in predicted areas of high habitat suitability (Fig. 1.4).

Table 1.4 Model performance statistics for cold-water coral and sponge MaxEnt models developed for this study.

CWCS group	AUC	Threshold	PCC	Sensitivity	Specificity	Kappa
Glass sponges	0.83 (0.01)	0.43 (0.02)	0.76 (0.02)	0.71 (0.05)	0.78 (0.05)	0.46 (0.03)
Demosponges	0.81 (0.02)	0.38 (0.06)	0.71 (0.06)	0.78 (0.11)	0.70 (0.09)	0.29 (0.05)
Soft corals	0.86 (0.01)	0.41 (0.04)	0.79 (0.02)	0.77 (0.06)	0.80 (0.05)	0.54 (0.02)
Stony corals	0.79 (0.01)	0.38 (0.05)	0.70 (0.05)	0.77 (0.08)	0.68 (0.07)	0.27 (0.04)
Black corals	0.91 (0.09)	0.31 (0.12)	0.97 (0.01)	0.84 (0.11)	0.97 (0.01)	0.39 (0.08)
Sea pens	0.78 (0.01)	0.57 (0.02)	0.71 (0.01)	0.70 (0.06)	0.71 (0.05)	0.41 (0.02)
Gorgonian corals	0.85 (0.01)	0.32 (0.06)	0.69 (0.03)	0.89 (0.04)	0.67 (0.04)	0.22 (0.03)

Values are mean (±1 SD) calculated from five cross-validation folds. AUC = Area Under the receiver operator characteristic Curve, PCC = percentage correctly classified.

Table 1.5 Ranked environmental predictors based on normalized, permuted importance for variables used in cold-water coral and sponge MaxEnt models.

Rank	**Glass sponges**		**Demosponges**		**Soft corals**		**Stony corals**		**Black corals**		**Sea pens**		**Gorgonian corals**	
	Variable	%	Variable	%	Variable	%	Variable	%	Variable	%	Variable	%	Variable	%
1	*dSi*	28.0	*dSi*	29.9	*oxygen*	36.0	*oxygen*	20.6	*oxygen*	39.0	*oxygen*	29.0	*oxygen*	47.4
2	*oxygen*	17.4	*chl-a*	14.2	*calcite*	16.4	*SST*	16.2	*chl-a*	14.1	*chl-a*	13.4	*PAR*	13.7
3	*PAR*	12.8	*oxygen*	10.2	*SST*	15.7	*aragonite*	15.3	*VRM*	11.5	*SST*	11.9	*SST*	8.5
4	*regfl*	11.6	*northness*	6.6	*PAR*	11.8	*PAR*	13.4	*calcite*	8.7	*regfl*	10.0	*bpi20000*	7.2
5	*slope*	4.9	*slope*	6.5	*chl-a*	9.6	*dSi*	9.2	*SST*	6.7	*bpi20000*	8.3	*eastness*	4.1
6	*northness*	4.8	*curdir*	6.2	*VRM*	3.1	*vertfl*	3.3	*eastness*	3.4	*slope*	5.8	*curdir*	3.6
7	*chl-a*	4.7	*curaspect*	5.6	*bpi20000*	2.1	*bpi5000*	3.2	*northness*	3.3	*calcite*	5.1	*regfl*	3.6
8	*VRM*	3.9	*PAR*	4.3	*eastness*	1.3	*curdir*	3.0	*dSi*	3.0	*PAR*	3.7	*northness*	2.9
9	*curdir*	3.7	*SST*	3.0	*northness*	1.1	*northness*	2.5	*slope*	2.4	*curaspect*	2.6	*chl-a*	2.7
10	*vertfl*	2.0	*bpi20000*	2.9	*regfl*	1.0	*slope*	2.3	*Curapsect*	1.8	*northness*	2.5	*VRM*	2.0
11	*curaspect*	1.6	*eastness*	2.6	*slope*	0.6	*regfl*	2.1	*bpi20000*	1.5	*vertfl*	2.4	*calcite*	1.8
12	*eastness*	1.3	*regfl*	2.3	*curaspect*	0.5	*eastness*	1.8	*curdir*	1.5	*eastness*	2.3	*slope*	0.8
13	*SST*	1.3	*bpi10000*	1.9	*vertfl*	0.3	*bpi10000*	1.6	*longcurve*	1.0	*curdir*	2.2	*vertfl*	0.6
14	*bpi20000*	1.2	*VRM*	1.3	*curdir*	0.3	*curaspect*	1.5	*regfl*	1.0	*bpi10000*	0.4	*curaspect*	0.4
15	*bpi10000*	0.7	*vertfl*	0.9	*longcurve*	0.04	*chl-a*	1.2	*salinity*	0.4	*bpi5000*	0.1	*bpi5000*	0.2
16	*bpi5000*	0.2	*arag*	0.7	*bpi10000*	0.03	*bpi20000*	1.0	*bpi10000*	0.3	*curang*	0.08	*bpi1000*	0.1
17	*crosscurve*	0.04	*bpi5000*	0.4	*crosscurve*	0.01	*VRM*	0.9	*PAR*	0.2	*VRM*	0	*crosscurve*	0.1
18	*curang*	0.02	*longcurve*	0.4	*bpi5000*	0.01	*longcurve*	0.5	*crosscurve*	0.1	*bpi1000*	0	*curang*	0.01
19	*longcurve*	0	*curang*	0.1	*curang*	0.001	*curang*	0.4	*vertfl*	0.1	*longcurve*	0	*longcurve*	0
20	*bpi1000*	0	*crosscurve*	0.05	*bpi1000*	0	*bpi1000*	0.2	*curang*	0.02	*crosscurve*	0	–	–
21	–	–	*bpi1000*	0.04	–	–	*crosscurve*	0.07	*bpi5000*	0.02	–	–	–	–
22	–	–	–	–	–	–	–	–	*bpi1000*	0	–	–	–	–

Full variable names are found in Table 1.1.

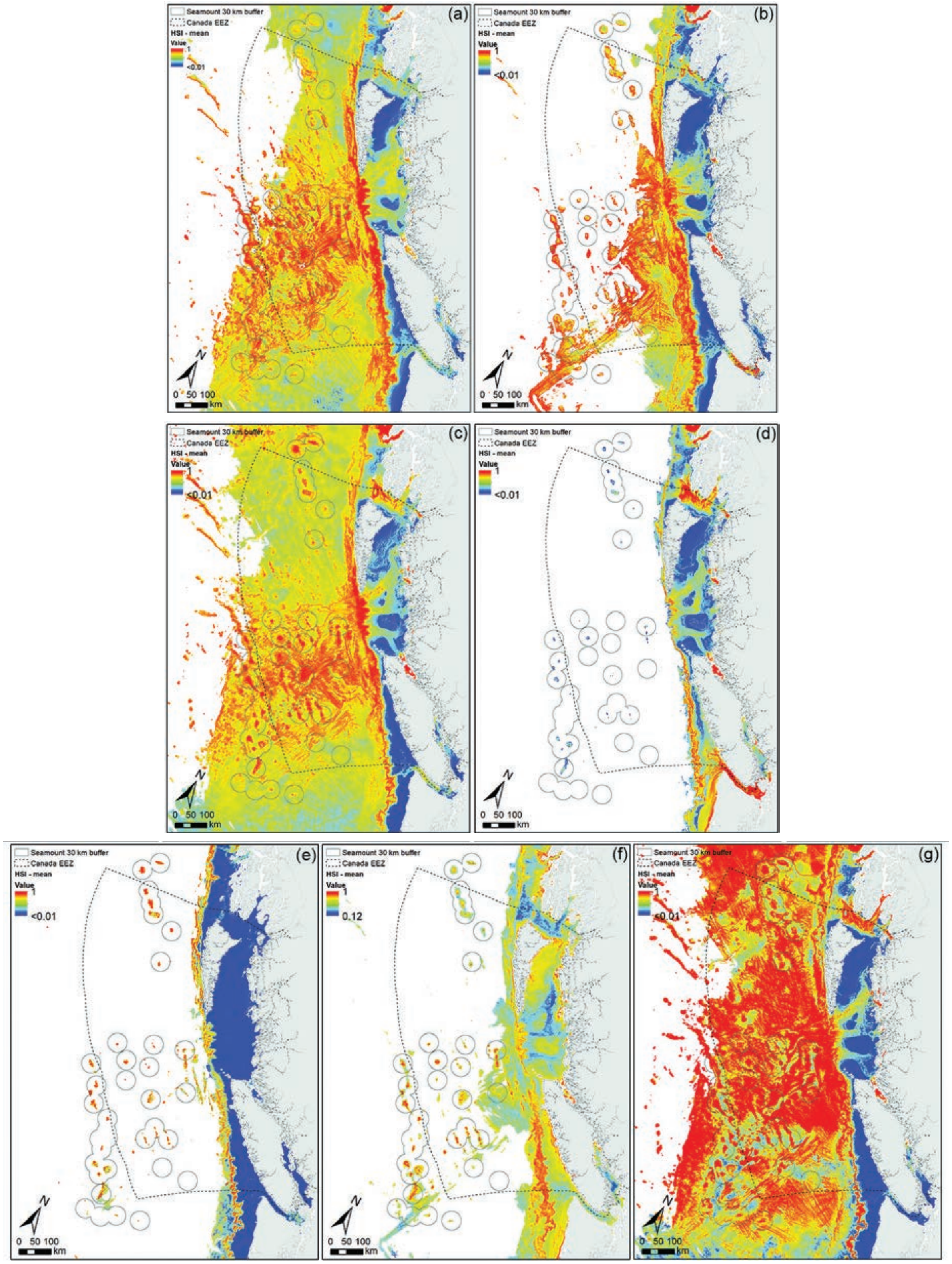

Fig. 1.3 Means of predictions of habitat suitability index (HSI) for (a) Hexactinellida sponges, (b) Demospongiae sponges, (c) Alcyonacea corals, (d) Scleractinia corals, (e) Antipatharia corals, (f) Pennatulacea corals, and (g) Gorgonian corals.

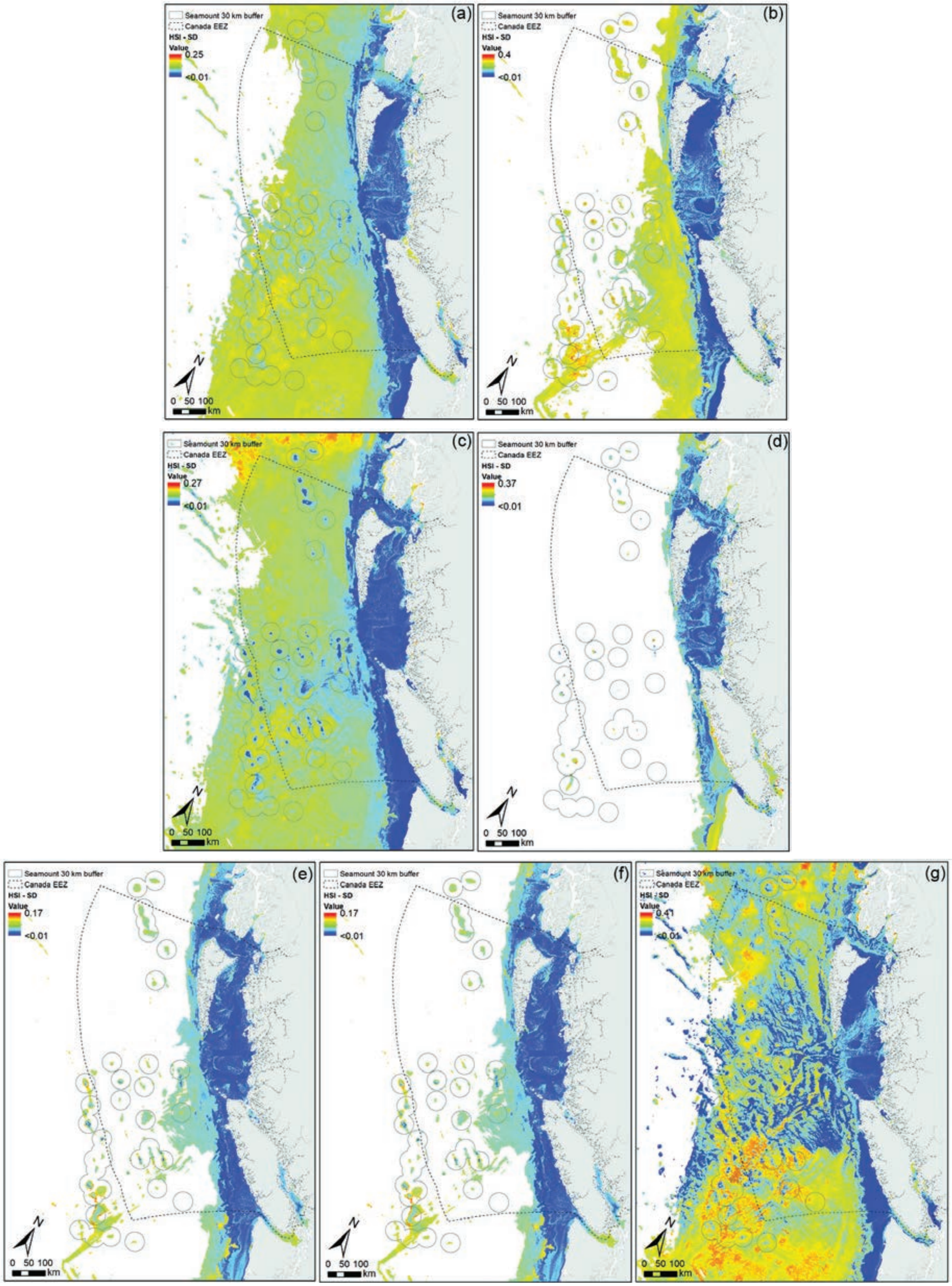

Fig. 1.4 Standard deviation of predictions of habitat suitability index (HSI) for (a) Hexactinellida sponges, (b) Demospongiae sponges, (c) Alcyonacea corals, (d) Scleractinia corals, (e) Antipatharia corals, (f) Pennatulacea corals, and (g) Gorgonian corals.

The CWCS composite index resolved extensive areas of suitable habitat on the continental shelf and slope, between 500 and 1400 m bottom depths, for all six biogenic habitat-forming CWCS groups (index score = 6, Fig. 1.5). Smaller isolated patches with a composite index = 6 also occur at five seamounts (Bowie, Hodgkins, Oshawa, Dellwood, and Union) within the Canadian EEZ boundaries. If we combine the total area with a composite index value of ≥ 5, 95% of the areas of potentially diverse biogenic habitat in the NEPC occurs on the continental shelf and slope of the study area (19,568 km^2) with the remainder occurring on seamount and seamount-like features occurring in offshore waters (1,084 km^2).

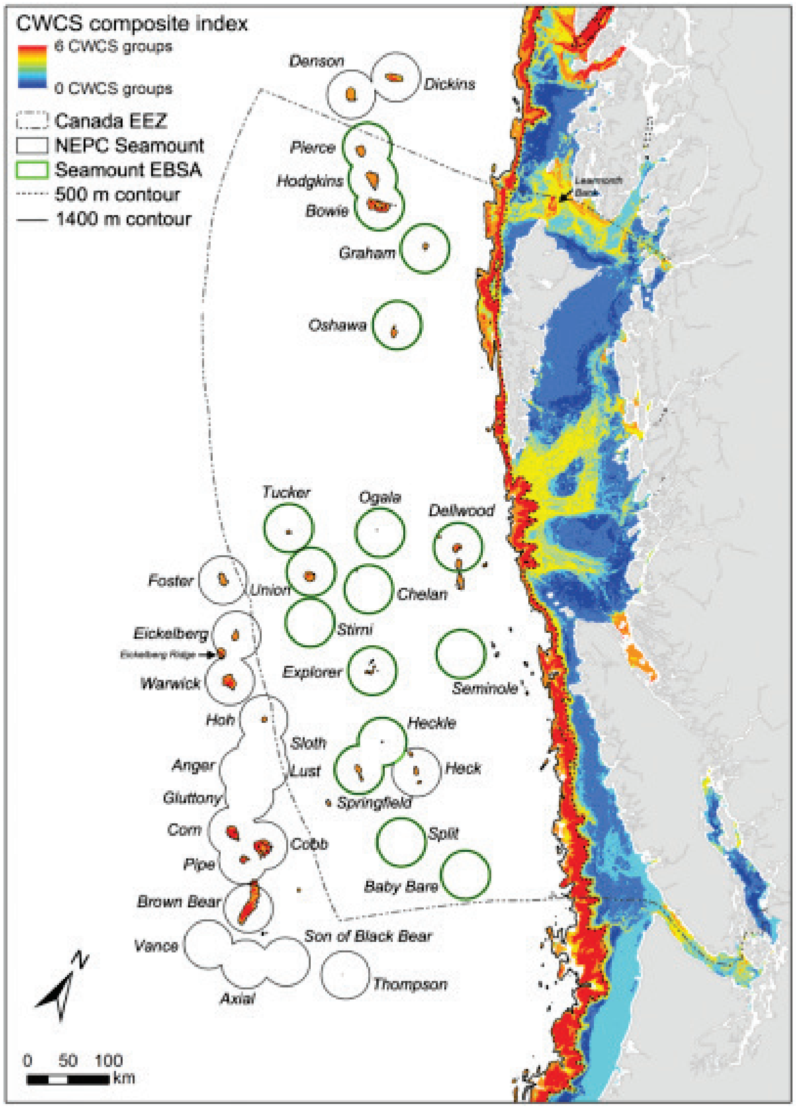

Fig. 1.5 Composite index of areas of suitable habitat for multiple groups of biogenic habitat-forming cold-water corals and sponges (CWCS). Colour indicates areas of suitable habitat for multiple CWCS groups modelled in this study. Circles outline a 30 km radius buffer around the summits of named seamounts in the Northeast Pacific region of Canada (NEPC). Green highlighted circles are seamounts identified by Ban *et al*. (2016) as ecologically and biologically significant areas (EBSA). Contours delineate 500 m and 1400 m bottom depths which covers the majority of the area that is highly suitable habitat for a diversity of habitat-forming CWCS.

Discussion and conclusions

This NEPC case study illustrates the value of species distribution models for assessing potentially important environmental variables that could influence the distributions of biogenic habitat-forming CWCS and generating habitat suitability predictions in areas with historically few observations (*e.g*., offshore deep waters). Although there is variation in the level of importance among individual predictor variables included in each CWCS model, severely low [O2] ([O2] < 0.5 ml L^{-1}) is an important predictor of habitat suitability for all CWCS groups in the NEPC (Chu *et al*., 2019). Preliminary assessment of model predictions has validated the model prediction of severely low [O2] being a strong predictor of biogenic habitat-forming CWCS in the NEPC. Using underwater vehicles to perform *post-hoc* visual surveys guided by the model predictions, dense communities of CWCS were discovered at Union and Dellwood seamounts in [O2] < 0.2 ml L^{-1} (Chu *et al*., 2019). By combining multi-model outputs into a single CWCS composite index to represent biogenic habitat diversity, areas of suitable habitat for multiple CWCS can also be used to empirically assess areas that have been provisionally identified as candidates of conservation interest (*e.g*., ecologically and biologically significant areas).

In addition to the importance of validating SDMs using *post-hoc* data collection, it is important to outline considerations when interpreting SDM outputs and how to apply them to facilitate future research directions. While oceanographic characteristics appeared to be the most important predictors in assessing CWCS habitat suitability, interpretations of results need to be constrained to scale, extent, and focal taxa of the study. Information on substratum type (*e.g*., most CWCS require hard substratum) can influence CWCS recruitment and are often important predictors of CWCS distributions (Krigsman *et al*., 2012; Masuda and Stone, 2015). However, these data were unavailable at the resolution and extent of the study area. Because most of the historical CWCS records in the NEPC have low taxonomic resolution, broad-scale models developed for this region require the available species data to be pooled into higher taxonomic groups. Although the regional models developed in this study still performed reasonably well, higher taxonomic resolution should generally improve model performance as this would account for species-specific niche differences which may spatially manifest in studies that focus on smaller scales.

In addition to improving overall data quality, applying different modelling approaches could also improve the degree of confidence ascribed to outputs and decrease the uncertainty associated with predictions generated using SDMs. Several different SDM approaches exist; aspects that differentiate models in their applied use include species input data requirements (*e.g*., presence-only, presence–absence, abundance) and model-specific assumptions and uncertainty. Therefore, ensemble modelling could be a future step that assesses model-specific uncertainty (Araújo and New, 2007) by 'averaging' uncertainty among models similar to the forecasting approaches used in climatology (Rooper *et al*., 2017). An additional modelling consideration could be to incorporate interspecific relationships into model assumptions (*e.g*., Joint SDMs, Harris, 2015), thus modelling community-level habitat patterns while accounting for interactions among co-occurring species.

Because extensive sampling plans in logistically challenging environments are expensive, data will continue to be sparse in the immediate future. Assessing the distributions of biogenic habitat-forming CWCS is a precursor to understanding their role in the greater dynamics of the entire ecosystem (*e.g*., biodiversity, ecosystem functioning, fisheries, *etc*.). In offshore areas where data are scant, data availability will likely remain poor given the remote setting and the complexities of international stakeholder dynamics. SDMs are one tool that can extrapolate modelled species–environment relationships into areas where species records are rare, thus providing an empirical foundation that can promote hypothesis development which can, in turn, concentrate limited science resources into targeted data collection in logistically challenging environments (*e.g*., Chu *et al*., 2019).

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2. *Predicting glass sponge (Porifera, Hexactinellida) distributions in the North Pacific Ocean and spatially quantifying model uncertainty*[1]

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Abstract

Predictions of species' ranges from distribution modeling are often used to inform marine management and conservation efforts, but few studies justify the model selected or quantify the uncertainty of the model predictions in a spatial manner. This thesis employs a multi-model, multi-area species distribution modeling (SDM) analysis to develop a higher certainty in the predictions where similarities exist across models and areas. Partial dependence plots and variable importance rankings were shown to be useful in producing further certainty in the results. The modeling indicated that glass sponges (*Hexactinellida*) are most likely to exist within the North Pacific Ocean where alkalinity is greater than 2.2 μmol l^{-1} and dissolved oxygen is lower than 2 ml l^{-1}. Silicate was also found to be an important environmental predictor. All areas, except Hecate Strait, indicated that high glass sponge probability of presence coincided with silicate values of 150 μmol l^{-1} and over, although lower values in Hecate Strait confirmed that sponges can exist in areas with silicate values of as low as 40 μmol l^{-1}. Three methods of showing spatial uncertainty of model predictions were presented: the standard error (SE) of a binomial generalized linear model (GLM), the standard deviation (SD) of predictions made from 200 bootstrapped GLMs, and the SD of eight commonly used SDM algorithms. Certain areas with few input data or extreme ranges of predictor variables were highlighted by these methods as having high uncertainty. Such areas should be treated cautiously regardless of the overall accuracy of the model as indicated by accuracy metrics (Area Under the receiver operator characteristic Curve (AUC), a threshold-independent model evaluation indicator and True Skill Statistic (TSS), a threshold-dependent measure of model accuracy), and such areas could be targeted for future data collection. The uncertainty metrics produced by the multi-model SE varied from the GLM SE and the bootstrapped GLM. The uncertainty was lowest where models predicted low probability of presence and highest where the models predicted high probability of presence and these predictions differed slightly, indicating high confidence in where the models predicted the sponges would not exist.

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Introduction

Biogeographical patterns for benthic marine taxa are poorly understood due to a lack of accessible geospatial information. Knowledge of the spatial distribution of species is a crucial prerequisite for the understanding of ecosystem functioning and processes as well as conservation management (Reiss *et al*., 2011). Fauna is more difficult to access and monitor in marine environments than in terrestrial environments. Due to the resulting limitation of data on marine taxa, predictive modeling methods are often employed in order to estimate their full distribution from the available data (Guisan and Zimmermann, 2000; Guisan and Thuiller, 2005). Species distribution models (SDMs) used for this purpose, also referred to as habitat suitability models or ecological niche models, estimate the relationship between species' coordinate data and the environment within which they exist (Franklin, 2010; Elith *et al*., 2011). While terrestrial SDM work is a fairly robust field, marine applications of SDM have been more recent in their developments (Reiss *et al*., 2011; Robinson *et al*., 2011). The field of marine SDM has been stimulated by increasingly available large-scale environmental data on ocean biogeochemistry and the need for prediction methods to quantify and estimate changes in species distribution in response to climatic changes (Reiss *et al*., 2011). However, a systematic review of 236 published papers on marine-based SDMs (Robinson *et al*., 2017) noted some shortcomings typical in the field. Only 9% of the reviewed studies tested their model results against independent data, which is generally accepted as an unbiased method of assessing model performance, and 94% of the reviewed studies failed to report the amount of uncertainty derived from data deficiencies and model parameters. When model predictions are evaluated against independent data, there is usually no spatial component to the summary statistics or visualization of patterns of uncertainty such as spatial clustering or links with specific predictor variables (Elith *et al*., 2002b). A popular method of interpreting and calculating prediction uncertainty involves measuring similarities between distribution predictions, where multiple taxa, models, areas and/or spatial resolution are tested and the resultant predictions are compared (Monk *et al*., 2012; Svensson *et al*., 2013; Pennino *et al*., 2016). Besides similarity calculations, measuring and quantifying prediction uncertainty is an underdeveloped aspect of marine SDM work and, along with testing several SDMs, will be explored in this contribution.

This contribution focuses on hexactinellid sponges in the North Pacific Ocean. The class Hexactinellida (kingdom Animalia, phylum Porifera), consists of between 400–500 species in two subclasses which contain five orders, 17 families, and 118 genera (Reiswig and Mackie, 1983). They are often referred to as glass sponges because their skeletons are composed of spicules of silica. Hexactinellid sponges are sessile, relying on filter-feeding to obtain the macroscopic detritus material they subsist on (Atwater and Fautin, 2001). After hatching, sponge larvae drift in the water column for a limited time before settling on the seafloor as juvenile sessile sponges (Maldonado, 2006). Observations of planktonic larval life in laboratories indicate that most larvae are anchiplanic, which means they generally remain in the water column for minutes to a few days, usually less than two weeks (Maldonado, 2006). Larvae are known to disperse under the influence of hydrodynamic processes that operate at a spatial scale of tens of meters to kilometers, and are not thought to be affected by active substratum selection, which operates at a smaller scale of centimeters to meters (Maldonado, 2006). Little is known about dispersion in hexactinellid sponges, and limited information about species within the hexactinellid class is available in the dataset used for this contribution. Therefore, it must be mentioned that this contribution operates under the assumption that glass sponges of different species react similarly to their environment, due to a lack of more specific data.

When the sponges die, their siliceous skeletons remain and future sponges grow directly on them, forming reefs. Their skeletons have left a fossil record as far back as the Cambrian/Pre-Cambrian, which would make them possibly the earliest living metazoans on earth (Leys, 2003). While they are found in every ocean in the world, they remain a rare taxon with a seemingly specific set of environmental conditions required to thrive. Research on deep-sea reef-forming benthic taxa is crucial as they are important indicators of the health of benthic ecosystems and often increase biodiversity where they are found (Beazley *et al*., 2013; Knudby *et al*., 2013). Their high diversity, large biomass, complex physiology and chemistry, and long evolutionary history lend sponges (and their endosymbionts) to play a key role in diverse ecological processes, including but not limited to predation, habitat provision, nutrient cycling, food chains, and bioerosion (Rützler, 2004). Unfortunately, benthic marine taxa are vulnerable to climate change as well as human activities such as fisheries, specifically deep-sea trawling (Rooper *et al*., 2017). Glass sponge reefs in the waters off the coast of British Columbia have recently been permanently protected from trawling and other human activities through the establishment of marine protected areas (MPAs). Since little is known about the distribution of this taxon outside British Columbia coastal waters, applying SDMs to glass sponges throughout the North Pacific Ocean will shed light on this otherwise difficult-to-research taxon.

The primary goals for this research were threefold:

1. To map hexactinellid (glass) sponge distribution for the entire North Pacific Ocean, as well as several smaller areas, by testing commonly used species distribution modeling methods;
2. To assess the model outputs both in terms of the relative importance of different environmental variables in making predictions about glass sponge presence/absence, as well as the specific dependence of glass sponge presence probability on these environmental variables;
3. To compare existing methods for mapping prediction uncertainty.

Species distribution modeling in marine environments

Species distribution modeling allows for the understanding of processes that create habitat distribution patterns and has become increasingly important in the face of threats such as habitat destruction, species invasions, pollution and climate change (Robinson *et al*., 2011). SDM algorithms require high-quality species presence/absence records as well as high-quality environmental information to infer the macroecological preferences of species (Tyberghein *et al*., 2012). By transferring SDMs from terrestrial to marine environments, the validity of the model and its predictive performance will be affected by the unique physical properties of marine habitats (Robinson *et al*., 2011). This is largely due to the fact that marine ecosystems have significantly less permanence than terrestrial ecosystems; for example, a treeline or grasslands may remain stable during a timeline of decades, while ecological and physical conditions in the water are in continual flux (Longhurst, 2007).

Existing guidance on model selection

Model complexity has increased greatly over time from environmental matching (*e.g*., BIOCLIM, DOMAIN) to more complex non-linear relationships between species and their environment (*e.g*., generalized additive models (GAMs), MaxEnt; Elith and Graham, 2009). BIOCLIM is an early SDM package which relates the bioclimatic environment species exist within to a number of environmental predictor variables, such as temperature or elevation (Booth *et al*., 2014). Due to the now numerous SDM methods, there is some difficulty in selecting an appropriate algorithm. The advice that would assist making an informed choice of method is currently scattered throughout literature (Elith and

Graham, 2009). It remains difficult to know which model is 'best' for the given data before comparing multiple models. This contribution therefore focuses on several commonly used SDMs.

Input data required for SDM work involves biological data: information about the species (single or multiple species) distribution, and environmental data: usually raster data describing the landscape the species is found within (Pearson, 2010). Biological data can be obtained in numerous ways: from surveys, museum collections, or personal collection and may be *presence-only* (PO, coordinates of where the species has been observed), or *presence/absence* (PA, coordinates of where the species has and has not been observed). Generally models are thought to have more ecological validity when fit with PA data as opposed to PO data; however, the quality of absence data is often questioned due to the possibility of 'false absences', which refers to instances when a species was present but not detected, or the environment was suitable but the species was absent (Pearson, 2010). Environmental data refer to predictor variables depicting climate, topography, land cover and vegetation, substrate, and other physical and chemical attributes of the area being modeled (Franklin and Miller, 2010). Spatial scale is often considered when collecting data and has two components: extent and resolution. Spatial extent refers to the size of the area being modeled and spatial resolution refers to the size of grid cells of the data. It is often common for datasets with large extents to have coarse resolution, and small extents to have high resolution (Pearson, 2010). As with other deep-sea species modeling efforts, due to the lack of information available concerning the niche environmental preferences of the relevant taxa, it is difficult to ascertain the importance of individual environmental variables prior to modeling. When working with taxa for which there are limited data, environmental input layers are by necessity often selected primarily based on their availability and presumed relevance, and less important variables can be identified and removed during the modeling process.

Statistical models

The linear model

Linear multiple regression models predict the response variable (Y) from a vector of multiple predictor variables, $X = (X_1, X_2,\ldots,X_p)$:

$$\hat{Y} = \hat{\beta}_o + \sum_{j=1}^{p} X_j\,\hat{\beta}_j + \varepsilon \qquad \text{(Eq. 1)}$$

where $\hat{\beta}$ is the vector of estimated coefficients and $\hat{\beta}_o$ is an estimated constant known as the intercept (Franklin and Miller, 2010). The error term, ε, is normally distributed with zero mean and constant variance, and the variance of Y is constant across observations (Franklin and Miller, 2010).

Generalized linear models

While Franklin and Miller (2010) note that ecological data often violate the assumptions of the linear model, generalized linear models (GLMs) are often used in modeling and can be described as extensions of the linear model that can cope with non-normal distributions of the response variable (Venables and Ripley, 1994). Distributions that are often used to characterize response variables in ecology include Gaussian, Poisson, binomial, negative binomial, and gamma (Franklin and Miller, 2010).

The linear model can be generalized using a link function that describes how the mean of Y depends on linear predictors, and a variance function that describes how the variance of Y depends on its mean (Chambers and Hastie, 1992). The equation for the GLM can be seen in Equation 2:

$$\delta\big(E(Y)\big) = LP = \hat{\beta}_o + \sum_{j=1}^{p} X_j\,\hat{\beta}_j + \varepsilon \qquad \text{(Eq. 2)}$$

where the predictor variables (far right side of the equation) are combined to produce a linear predictor, LP, and the expected value of Y, $E(Y)$, is related to the LP through the link function, $\delta()$ (Franklin and Miller, 2010). Formulating a GLM for SDM involves selecting the response distribution and the link function (collectively known as the family of the GLM), the variance function, and the predictors (Franklin and Miller, 2010). The link function describes how the mean of Y depends on the linear predictor. For a binary response variable, a binomial distribution and logit link function are used.

Generalized additive models

Generalized additive models (GAMs) differ from GLMs in their ability to identify and describe a non-linear relationship between response and predictor variables; they are non-parametric extensions of GLMs (Franklin and Miller, 2010).

$$\delta\big(E(Y)\big) = LP = \hat{\beta}_o + \sum_{j=1}^{p} X_j\, f_j + \varepsilon \qquad \text{(Eq. 3)}$$

where the coefficients of the GLM are replaced by a smoothing function, f (Franklin and Miller, 2010). The fit of a GAM model is generally evaluated by testing the non-linearity of a predictor versus the non-parametric fit (Franklin and Miller, 2010). GAMs are used for characterizing non-linear response curves of species because they can suggest the shape of the parametric response curve and are thus more flexible than GLMs (Franklin and Miller, 2010). GAMs are popular in SDM work because they tend to have high prediction accuracy, have been subjected to comparisons with other models and have proven to be useful (Franklin and Miller, 2010).

Machine learning models

Maximum Entropy (MaxEnt) distribution modeling

The MaxEnt model was created in order to make predictions and inferences from incomplete data (Phillips *et al*., 2006), for example, PO data. MaxEnt is one of the most common forms of SDM and "has been described as especially efficient to handle complex interactions between response and predictor variables" (Fourcade *et al*., 2014). MaxEnt is an acronym created for the concept of maximum entropy modeling (Guinotte and Davies, 2014), which extrapolates the likelihood a species has of existing in any specific geographic space. This can also be defined as a measure of dispersiveness. The underlying principle is that one should assume uniform distributions are preferred, given certain constraints (Nigam *et al*., 1999). Since becoming available in 2004, MaxEnt has been used to publish diverse projects including finding correlates of species occurrences, mapping current distributions, and other related tasks in ecological, evolutionary, conservation and biosecurity applications (Elith *et al*., 2011).

MaxEnt has often been explained as estimating a distribution across geographic space (Phillips *et al*., 2006). Elith *et al*. (2011) give an alternative view: a characterization that focuses on comparing probability densities in covariate space. Their research examines how MaxEnt can be understood by looking at Bayes' rule:

$$Pr(\gamma = 1|z) = f_1(z)Pr(\gamma = 1) \,/\, f(z) \qquad \text{(Eq. 4)}$$

where $\gamma = 1$ indicates presence, $\gamma = 0$ indicates absence, and z indicates a vector of environmental covariates. It must be assumed that all environmental variables z are available landscape-wide, and L is the extent of the landscape (not included in Eq. 4). $f(z)$ can be defined as the probability density of covariates across L, $f_1(z)$ can be defined as the probability density of covariates across locations within L where the species is present, and $f_0(z)$ can be defined as where the species is absent (Elith *et al.*, 2011). The quantity to be estimated is the probability of presence of the species, conditioned on the environment: $Pr(\gamma = 1|z)$.

Equation 4 can theoretically be explained by the following: that if the conditional density of the covariates at presence sites is known, $f_1(z)$, and if the unconditional density of covariates across the study area is known, $f(z)$, the prevalence $Pr(\gamma = 1)$ is the only remaining value necessary to calculate the probability of occurrence (Ward, 2007; Elith *et al.*, 2011). First, MaxEnt's core output involves estimating the ratio $f_1(z)/\,f(z)$. This gives insight about which features are important and how suitable one place is compared to another, which is the core of the MaxEnt model output. This explanation of MaxEnt's structure by ecologists rather than statisticians can be helpful in understanding the complicated processes that the data undergo.

Boosted regression trees

Boosted regression trees (BRT) is an ensemble method for fitting statistical models that differs from conventional techniques to fit a single parsimonious model; BRTs combine the strength of two algorithms: regression trees and boosting (Elith *et al.*, 2008). Regression trees are models that relate a response to their predictors by recursive binary splits, and boosting is an adaptive method which combines simple models to give improved prediction performance (Elith *et al.*, 2008).

The decision trees in BRT are tree-based models which partition the predictor space into rectangles, doing this using a series of rules to identify regions having homogeneous responses to predictors (Elith *et al.*, 2008). Then, a constant is fitted to each region, with regression trees fitting the mean response for observations in that region. Fitting a single decision tree is often done by growing a large tree and afterwards pruning it by collapsing the weakest links (identified through cross-validation) (Elith *et al.*, 2008). Decision trees are popular because they allow for information to be represented in an intuitive manner that is easy to visualize. Trees are insensitive to outliers and are able to accommodate missing data in predictor variables by using surrogates (Breiman *et al.*, 1984).

Study area

The Pacific Ocean, the largest and deepest of the earth's oceans, is about 15 times the size of the United States, and is almost equal in area to the total land area of the world. The ocean can be divided by the equator into two separate areas: the north and south. The study area for this project is contained by the boundaries of the North Pacific Ocean: bordered by the Arctic Ocean in the north, Asia in the west, the Americas in the east, and the equator in the south. It provides habitat for thousands of species, including cold-water sponges and corals. Due to the size of this study area, five sub-areas were delineated within the North Pacific Ocean to account for the likely varying physical and chemical environments across an area as large as the North Pacific Ocean. These sub-regions within the North Pacific Ocean include: a) the US Exclusive Economic Zone (EEZ) around Alaska, b) the Canadian EEZ around British Columbia, and c) the US EEZ around the Washington-Oregon-California coast, as well as d) two smaller areas within the Canadian EEZ which were manually delineated but roughly correspond to i) Hecate Strait and ii) the shelf waters west of Vancouver Island (Figs. 2.1–2.4). It is likely that there are varying environments within an area as large as the North Pacific Ocean, as well as varying groups of sponges. Using a multi-area analysis ensures a more comprehensive attempt at capturing these potentially different species–environment relations.

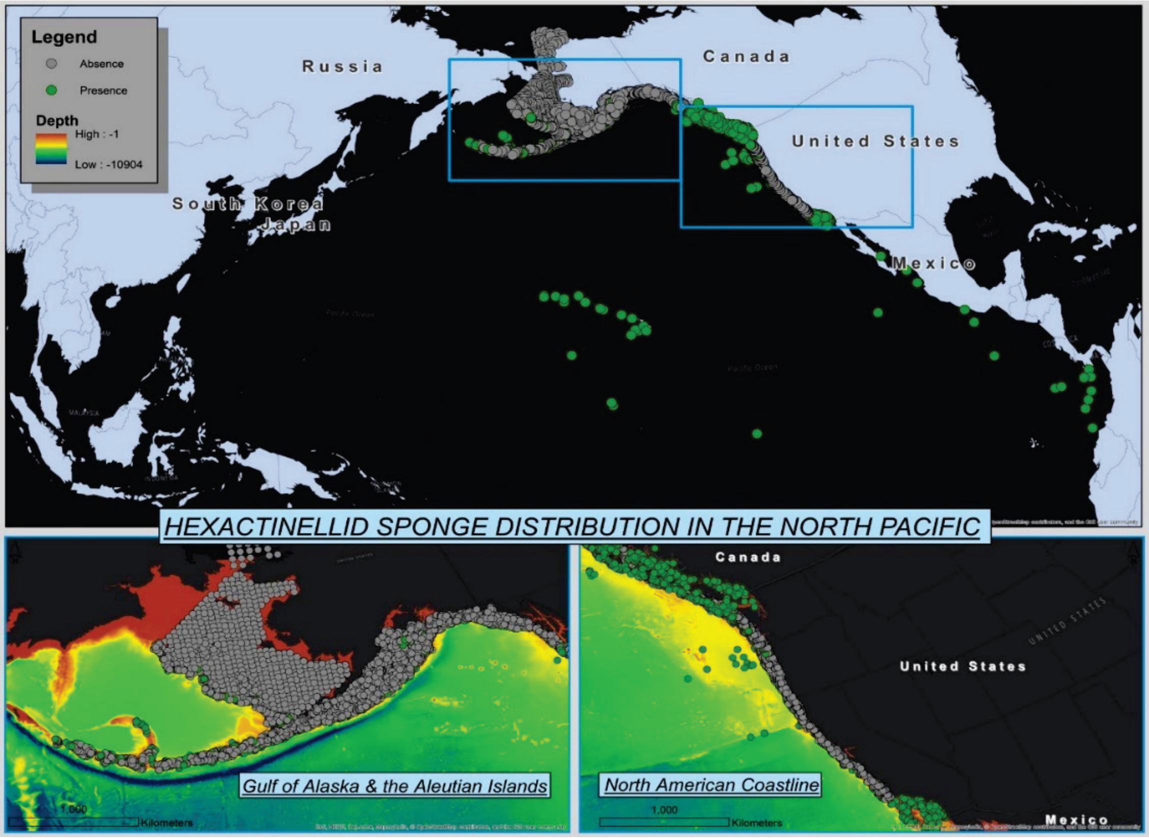


Fig. 2.1 Hexactinellid sponge distribution in the North Pacific Ocean with insets of the Gulf of Alaska and British Columbia coastline.

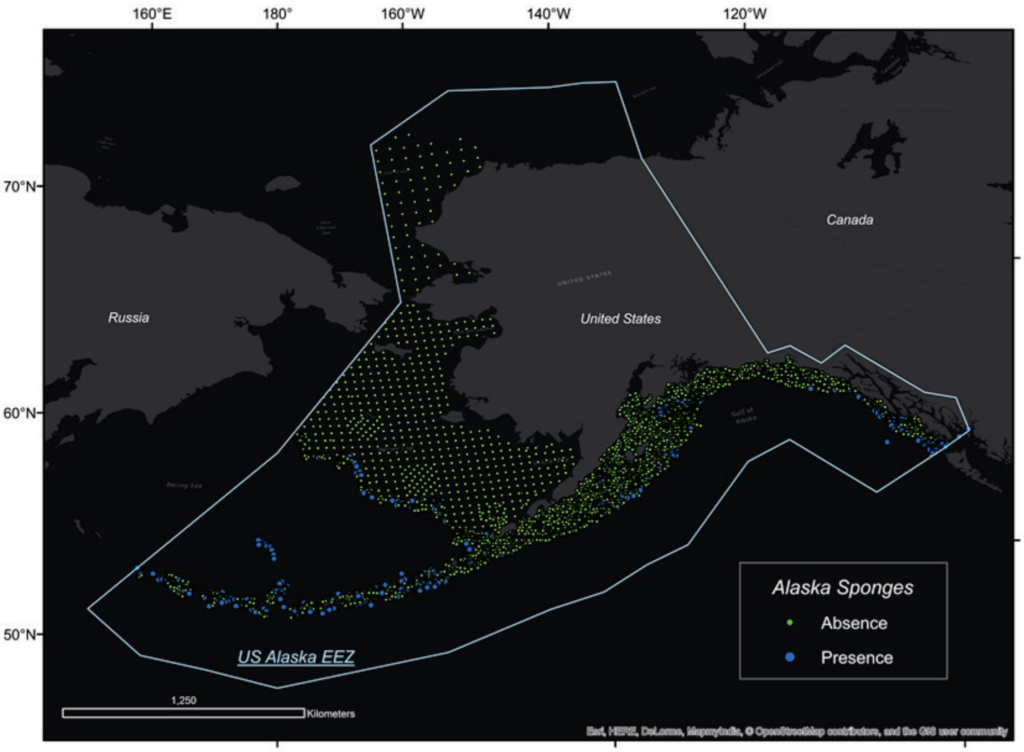


Fig. 2.2 Alaska sub-area with contained sponge presence/absence (PA) data.

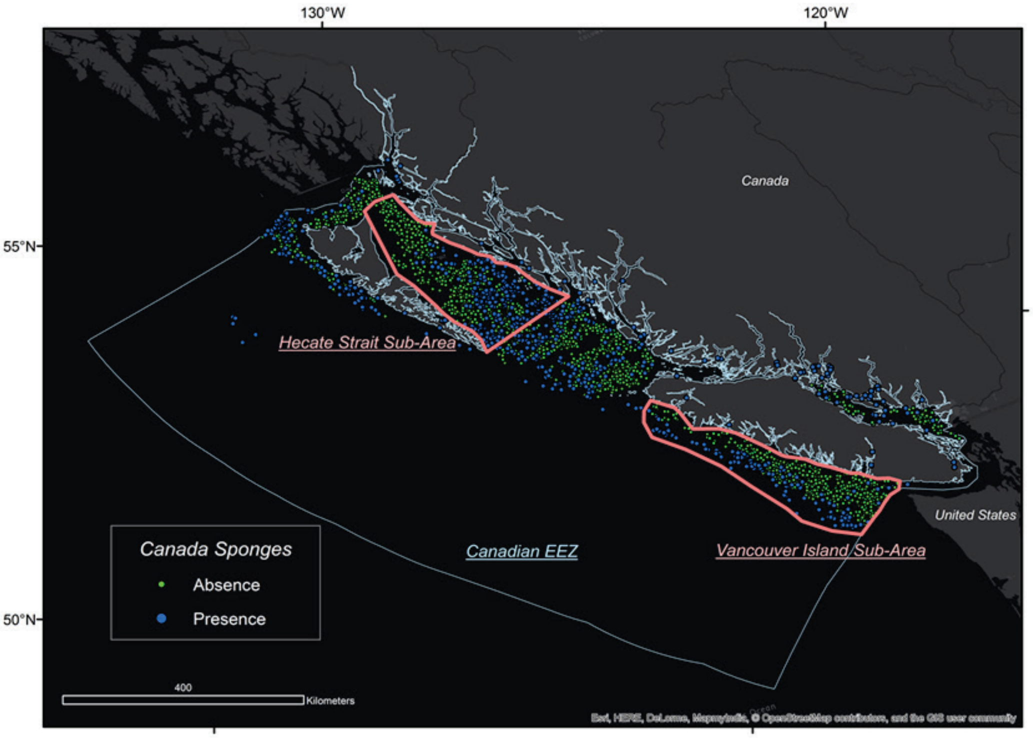


Fig. 2.3 British Columbia, Hecate Strait and Vancouver Island sub-areas with contained sponge PA data.

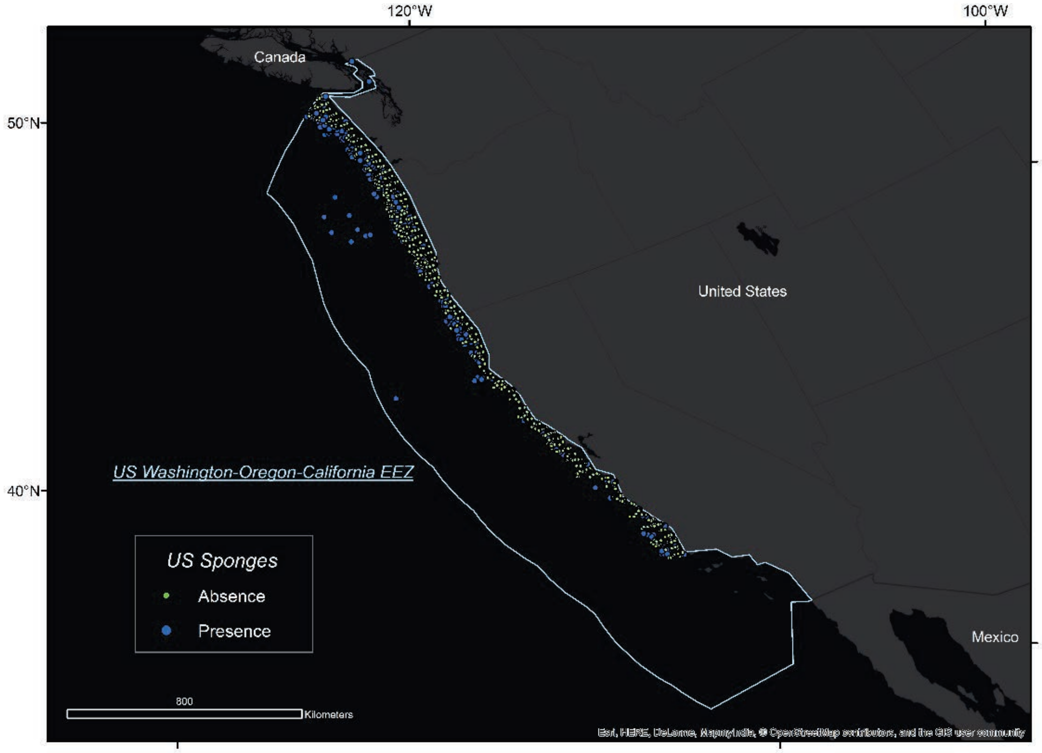


Fig. 2.4 United States Washington-Oregon-California sub-area with contained sponge PA data.

Biological data

Presence and absence glass sponge data were obtained from trawl surveys conducted by Fisheries and Oceans Canada (DFO) and the US Government. Data from several surveys were collected and merged to create a dataset containing both presence and absence information for 42,113 coordinate locations sampled between 1996 and 2016. The dataset contains 16,148 presence points and 25,684 absence points. As can be seen in Figures 2.1–2.4, and Table 2.1, the species presence/absence points are located largely in coastal waters along the coast of North America, and out along the Aleutian Islands, with a few data points from Hawaii. No data from the western North Pacific Ocean were used.

In an attempt to decrease sample bias, the original dataset of 42,113 coordinate points was thinned based on environmental variation (see Methods section for more detail). After the data were thinned based on local environmental variation of the predictor variables, the resultant dataset had 12,467 sponge PA points.

Table 2.1 Hexactinellid sponge data: location of data points and source.

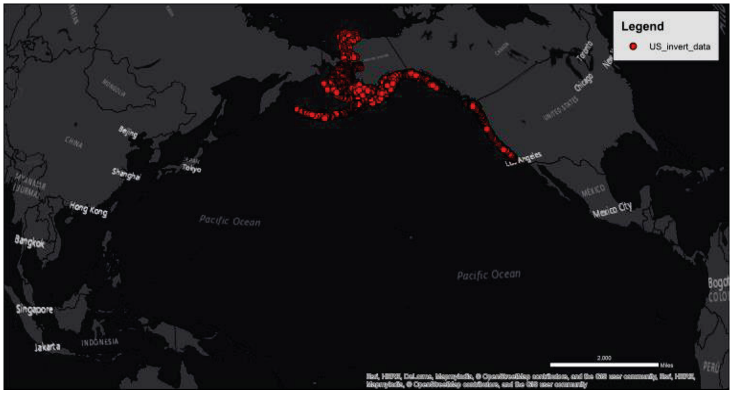
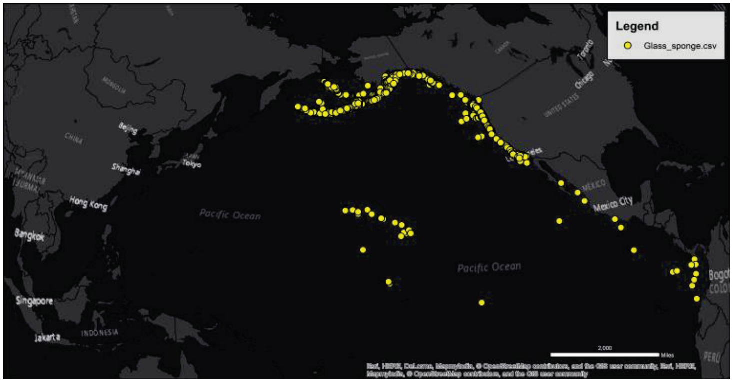
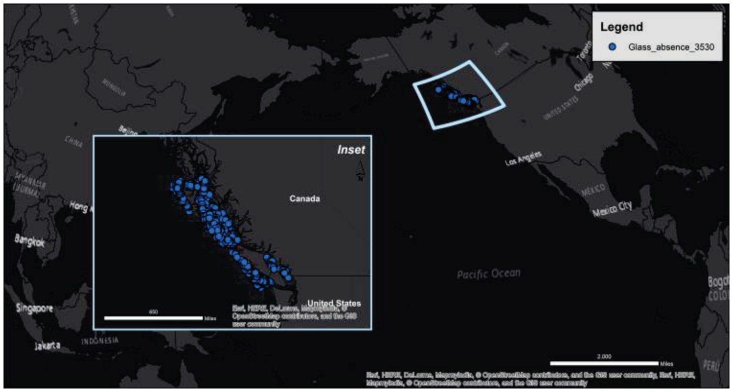
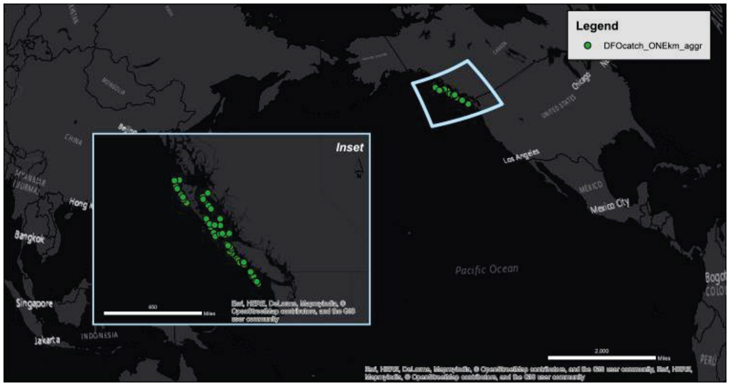
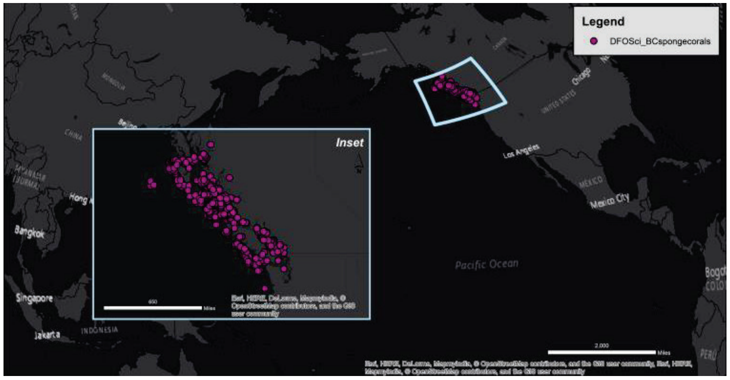
Data	Geographic extent	Number of presences	Number of absences
US bottom trawl surveys from Alaska (1996–2016) and US West Coast (1996–2004)		1008	22,322
Presence data from Working Group 32		14,134	0
DFO commercial bycatch logs		0	3530
DFO commercial catch records aggregated to 1km grid		251	0

Table 2.1 Continued.

Data	Geographic extent	Number of presences	Number of absences
DFO research databases and museum records		868	0
Total		42,113	

Environmental data

Environmental variables were selected based on availability and presumed likelihood of being relevant to the distribution of glass sponges. Potential environmental variables relevant to the distribution of glass sponges have been compiled from various sources through the North Pacific Marine Science Organization (PICES) Working Group 32 (Table 2.2). The environmental data layers are in a raster format, with a cell size of 1000 m by 1000 m, using an azimuthal equidistant projection with a central meridian of –180. The values reflect the near-sea floor part of the water column.

Table 2.2 Environmental variables, units and reference.

Variable name	Units	Reference
Alkalinity	μmol l^{-1}	Steinacher *et al.*, 2009
Aragonite saturation state	Ω_{ARAG}	Steinacher *et al.*, 2009
Aspect	degrees	Becker *et al.*, 2009
Calcite saturation state	Ω_{ARAG}	Steinacher *et al.*, 2009
Depth	m	Becker *et al.*, 2009
Dissolved inorganic carbon	μmol l^{-1}	Steinacher *et al.*, 2009
Eastness	degrees	Wilson *et al.*, 2007
Nitrate	μmol l^{-1}	Garcia *et al.*, 2014b
Northness	degrees	Wilson *et al.*, 2007
Oxygen	ml l^{-1}	Garcia *et al.*, 2014a
Phosphate	μmol l^{-1}	Garcia *et al.*, 2014b
Roughness	unitless	Wilson *et al.*, 2007
Rugosity	unitless	Becker *et al.*, 2009
Salinity	pss	Zweng *et al.*, 2013
Silicate	μmol l^{-1}	Garcia *et al.*, 2014b
Slope	degrees	Becker *et al.*, (2009)
Temperature	°C	Locarnini *et al.*, 2013
TPI (Topographic Position Index)	unitless	Wilson *et al.*, 2007
TRI (Terrain Ruggedness Index)	unitless	Wilson *et al.*, 2007

Methods

Many of the choices in the following methodology section were made in an effort to maximize reproducibility of this study. However, had other methods been selected, the results could have differed. Within the SDM field, reproducibility is a common problem. Advanced modeling techniques, data selection and processing require many choices to be made which decreases the replicability yet is nonetheless common and relatively unavoidable in SDM.

Data pre-processing

Spatial sampling bias, a common problem in marine and terrestrial SDM, decreases the accuracy and interpretability of SDM outputs. Spatial filtering is a common method of removing spatial bias as a data pre-processing step. For example, Boria *et al*. (2014) filtered clustered data to discard any data point within 10 miles of another point, and Varela *et al*. (2014) applied an environmental filter which discards presence points that are too clustered in environmental space. The following steps were taken to spatially thin the data in a manner which takes into account the differences in areas with high environmental variation and areas with low environmental variation. The principle at the basis of this method is that areas with low environmental variation across space require less geographically dense data to cover environmental variability than do areas with high environmental variation, and they can therefore be thinned more than areas with high variation in an effort to reduce bias in the dataset.

1. The local standard deviation (SD) of each predictor variable was calculated for a 9 × 9 km window centered on each cell, and then normalized to a 0–1 scale. The 19 normalized values were then added together to produce a single raster with a theoretical value range of 0–19, quantifying local environmental variation across the study area.
2. A histogram was plotted to view the frequency distribution of this local environmental variation (Fig. 2.5). If this histogram had been multimodal, spatial areas corresponding to each local maximum (*i.e*., clusters of low or high local environmental variation) could have been identified. However, the histogram was unimodal, so instead quintiles were calculated to separate the study area into five regions ranging from lowest to highest local environmental variation. The maximum value for each quintile can be seen in Table 2.3.
3. Five subsets of the presence/absence data were then generated, one for each quintile, and semi-variograms were generated based on the bathymetric values from each subset. Depth was chosen to be the predictor for which to produce semi-variograms for several reasons: 1) depth often is one of the most important variables in any SDM for hexactinellid sponges, and 2) it can be used as a proxy for many other variables in this study.
4. The semi-variograms all used 1000 m bins and a cut-off of 25,000 m to ensure standardization (Fig. 2.6). For each plot, the distance at which semi-variance increased to more than 500 was noted. For the first quintile (representing the area with lowest local environmental variation), this distance was ~15,000 m, for the second quintile it was ~7500 m, and for the third, fourth and fifth quintile it was ~2500 m. The semi-variance value of 500 was selected visually to provide a range of reasonable distances that were considered suitable to inform the scale of spatial thinning.

5. Based on these semi-variograms, block-based thinning was applied to the presence/absence data:

   i. A grid with 15,000 m cell sizes was overlaid on the study area, and the mean value of the local environmental variation raster was calculated for each cell. For those cells falling in the first quintile, *i.e.*, with mean local environmental variation <1.576 (see Table 2.3), the presence/absence data were aggregated according to the following rules:

      a) If no presence/absence observations were found in the cell, the output would be empty.

      b) If there were at least as many presence as absence observations in the cell, the output would be a presence point, located in the center of the cell.

      c) If there were more absence than presence observations in the cell, the output would be an absence point, located in the center of the cell.

   ii. This process was repeated with 7500 m cells applied to points in the second quintile, and with 2500 m cells applied to points in the third, fourth and fifth quintiles.

   iii. The outputs were combined to produce a single set of spatially thinned presence/absence observations. Out of the original 42,113 presence and absence points, 12,467 remained after thinning. A sample section from the Aleutian Arc can be seen in Figure 2.7, showing the difference between the original points and the thinned points.

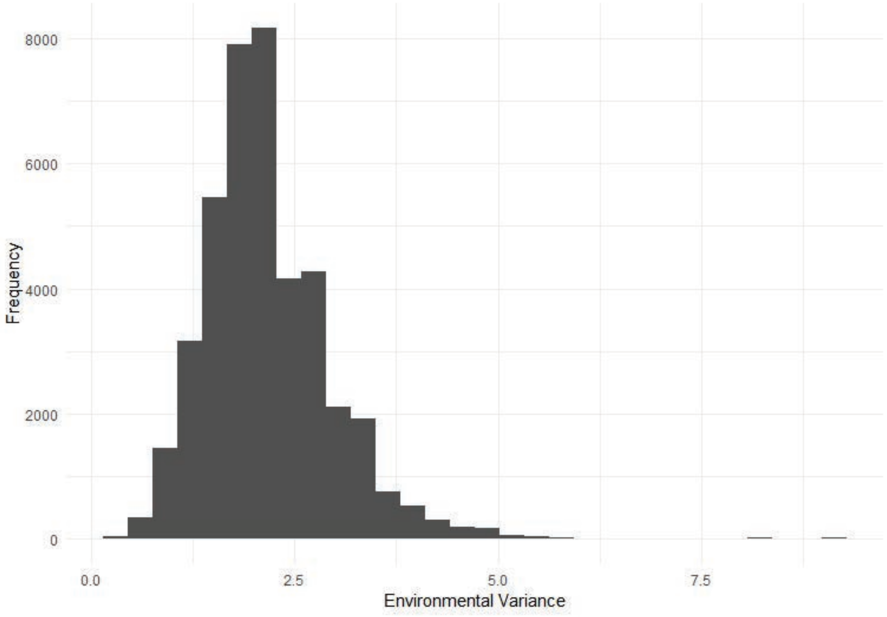


Fig. 2.5 Histogram showing environmental variance data distribution.

Table 2.3 Quintile breaks for the variance data (environmental variance values from Figure 2.5).

20%	40%	60%	80%	100%
1.576018	1.893480	2.200223	2.730262	9.180244

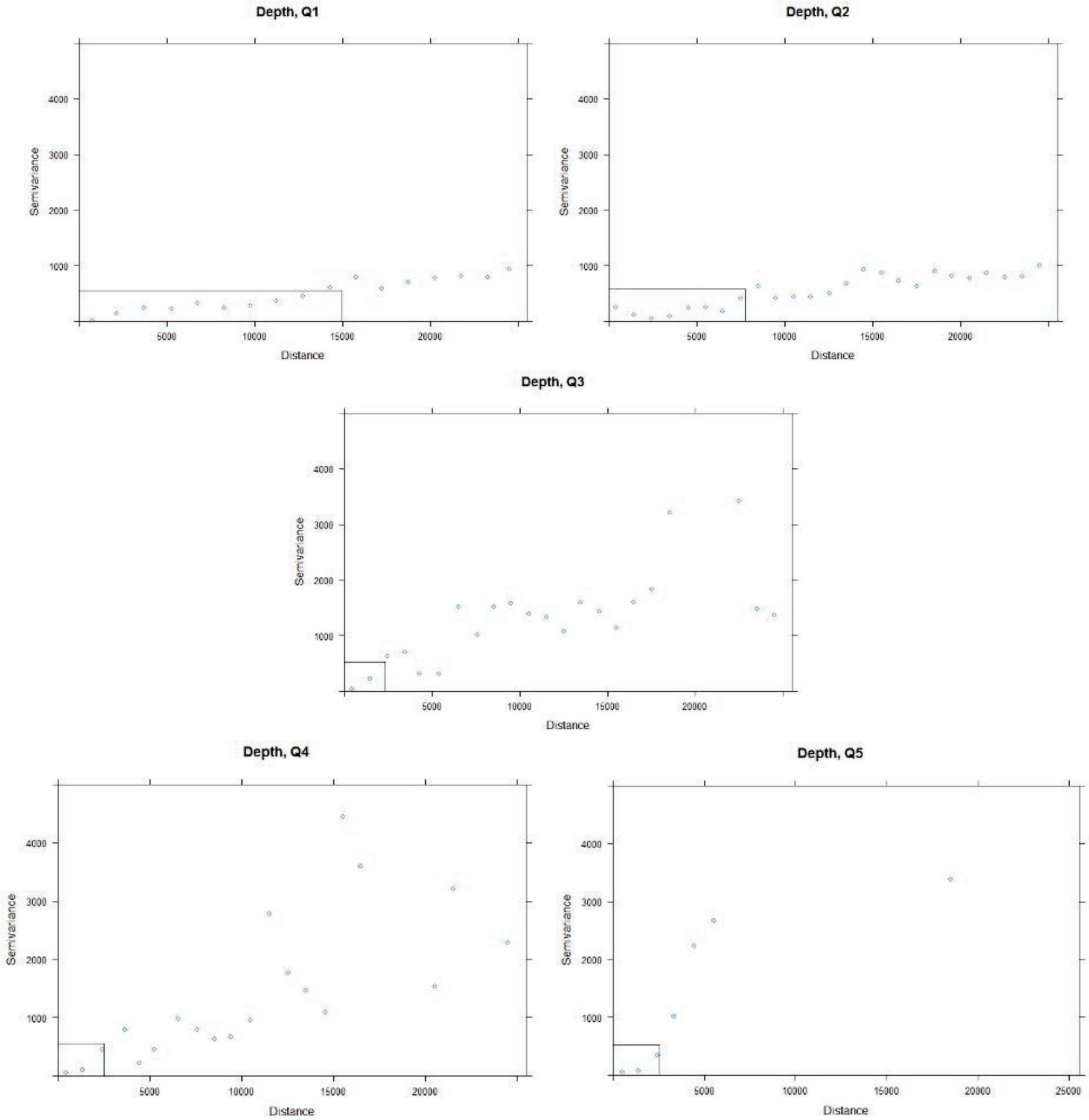


Fig. 2.6 Semi-variogram plots showing five quintiles, with semi-variance value of 500 indicated to show approximate calculation of range value.

Species distribution modeling

For each of the predefined areas, the following SDM types were tested using the ‘Biomod2’ (Thuiller *et al*., 2016) package in R (R Core Team, 2013): GAM, BRT and MaxEnt (resulting in 18 model-area combinations). The following parameters for modeling were used:

- ‘Number of Evaluation Runs: 3’: Running three evaluations means the calibration and evaluation are run 3 separate times independently, which allows for a more robust test of the models when independent data are not available.
- ‘Data Split: 80%’: this sets 80% of the data aside for calibration of models, with the remaining 20% used for validation.

- Model accuracy measures: Kappa, TSS, AUC; Kappa refers to Cohen's Kappa Coefficient, and TSS to True Skill Statistic (Zhang *et al*., 2015). Both Kappa and TSS are threshold-dependent measures of model accuracy. They range from −1 to +1, where +1 indicates perfect agreement between predictions and observations and values of 0 or less indicate agreement no better than random classification (Landis and Koch, 1977). The Area Under the receiver operator characteristic Curve (AUC) is an effective, threshold-independent model evaluation indicator and is also independent of prevalence (*i.e*., the frequency of occurrence) of the target species (Zhang *et al*., 2015). Ranges used to interpret accuracy metrics from these statistics can be found in Table 2.4.

Table 2.4 Model accuracy ranges for AUC, Kappa and TSS measures (Zhang *et al*., 2015).

	Poor	**Moderate**	**Good/Excellent**
AUC	< 0.7	0.7–0.9	> 0.9
Kappa and TSS	< 0.4	0.4–0.8	> 0.8

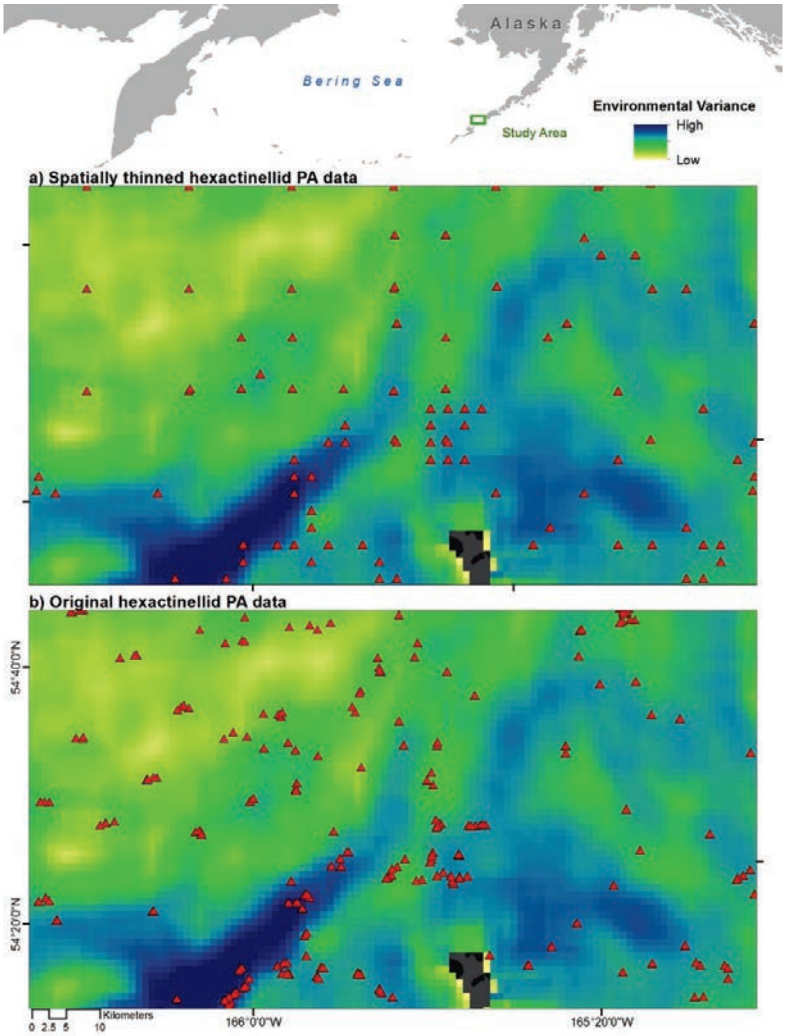


Fig. 2.7 Sample area showing spatially thinned data and original data on the Aleutian Arc.

Interpretation of model results

Model output can be classified into two types: aspatial and spatial. Aspatial outputs from models consist of variable importances and partial dependence plots depicting fitted functions relating probability of occurrence to each selected predictor, while spatial outputs consist of GIS (Geographic Information System) layers depicting the probability of presence across the study area (Ferrier *et al*., 2002).

Variable importance values were calculated for every model–area combination. These values quantify to what extent each predictor variable contributes to the predictions made by the model. The variable importance value is calculated as the result of one minus the correlation between the original prediction and the prediction with only the individual variable of interest. While the individual values are dependent on the algorithm used, they can still be used to provide relative information on predictor importances within the model.

Partial dependence plots provide a graphical representation of how likely the species is to be present, given a gradient of the specific environmental predictor. As with variable importance, these plots are calculated when the model is built, by averaging every other predictor variable except the one chosen predictor, and the change in model response is measured in relation to changes in the one variable. Partial dependence plots showing results from multiple algorithms can be used to visually compare species responses to environmental variable values. Partial dependence plots were generated for predictor variables that ranked in the top 25% in variable importance in several models and areas. The predictor variables chosen for closer analysis were alkalinity, oxygen, silicate, and phosphate. Additionally, frequency distribution plots were produced for alkalinity, oxygen, silicate, and phosphate in each area, showing the percentage of presence (as opposed to absence) data points across the range of environmental variable values. This information can shed light on which value ranges the species most commonly exists within. Partial dependence plots can be compared for similarities. Variable importance was also considered in an effort to find strong trends in how predictors contribute to different models/areas. It can be posited that if the response curves of a particular predictor variable are similar across multiple models/areas, the variable importance is likely to be high as well. When the response curves vary significantly, it is more likely those variables ranked toward the lower range of variable importance for the model.

Mapping prediction uncertainty

For the purpose of testing and comparing uncertainty metrics spatially, a binomial GLM was fit to the Hecate Strait boundary (Fig. 2.3), a subset of the original North Pacific-wide dataset; 1,255 presence/absence points were included within the area and three environmental predictors with high variable importance were selected and clipped to the same extent: alkalinity, oxygen and silicate. A GLM was selected because it can provide a model-based uncertainty measure that can be mapped in addition to the actual model predictions. The logit-link function was selected for the binomial GLM because it is appropriate for binary data and ensures the predicted values will be between 0 and 1 (Kindt *et al*., 2005). Three spatially explicit uncertainty metrics were compared using this GLM model: GLM prediction SE, bootstrapped GLM SD, and SD of multiple model predictions.

The first uncertainty metric involved producing partial dependence plots from the GLM outputs and adding confidence intervals to the partial dependence plots. In order to obtain the predicted values from the estimates of the coefficients, the inverse link function needs to be calculated. Using the inverse link function, the confidence interval was calculated as the fitted value plus/minus two times the standard error (SE) on the link scale. Confidence intervals (CIs) were calculated for alkalinity, oxygen and silicate. Adding CIs can provide information on why certain areas would have predictions with high or low confidence. Next (and separate from the CIs), the SE of the prediction was calculated. SE provides the absolute measure of the typical distance between the data points and the regression line, in the units of the dependent variable. The SE of the prediction was then written to a raster and thus the uncertainty of the model can be seen spatially.

The second uncertainty metric – bootstrapped GLM SD – was obtained by bootstrapping the GLM. Bootstrapping is an approach to statistical inference based on building a sampling distribution for a statistic by resampling repeatedly from the data. Two hundred bootstrap samples were created from the data. GLMs were then calibrated on the bootstrap samples, still using alkalinity, oxygen and silicate as predictors for the models. The calibrated models were then used to make predictions, and the SD was calculated for the predictions.

The third uncertainty metric – SD of multiple model predictions – aims to test if standard deviations are geographically comparable among a variety of models. By running eight models available in the Biomod2 package (GLM, BRT, GAM, FDA, MARS, RF, MAXENT.Phillips and MAXENT.Tsuruoka) on the Hecate Strait subset, the SD of all the predictions can be calculated, as for the GLM bootstrapping above. This provided a spatial view of where the models produced similar results and where they differed.

Results

Model performance

Model fit statistics and variable importance values from the GAM, BRT, and MaxEnt models run on the North Pacific basin-wide data, as well as the five sub-areas are presented in Table 2.5. Figures 2.8–2.11 present the outputs of these models in the form of partial dependence plots and show the data distribution for alkalinity, oxygen, phosphate and silicate for each model/area. Only these four variables were selected because they had consistently high variable importance values.

As can be seen in Table 2.5, AUC values for the majority of the models were between 0.7–0.9. These values are interpreted to indicate these models performed moderately well (See Table 2.4 for value ranges associated with model accuracy; Zhang *et al.*, 2015). Two MaxEnt models for the British Columbia (BC) and Alaska sub-areas performed poorly, with AUC values of 0.655 and 0.428 respectively, and the GAM and BRT models for the Vancouver Island sub-area performed especially well, with AUC values of 0.946 and 0.978, the highest of all the models and areas. The Kappa and TSS values reported similar results in terms of models in the North Pacific, BC, and Alaska generally performing poorly, and models in the Vancouver Island and Hecate Strait sub-areas performing well (more detailed results for all models and areas can be found in Table 2.5).

Variable importance

For each area and model type, the model assigns a variable importance value to each of the 19 environmental predictors which were used as input to the model. The variables are arranged by importance to the model on a scale of 0–1. Individual variables ranked among the top 25% within each specific model are highlighted in Table 2.5. Alkalinity is ranked within the top 25% of variables in 13 out of 18 models. Oxygen is the next variable of highest importance being ranked within the top 25% of variables in 9 out of 18 models. Variables which are ranked within the top 25% in at least 4 of the 18 models include phosphate, salinity, silicate, temperature, nitrate, depth, omega aragonite, and omega calcite. The remaining variables are ranked within the top 25% for less than four models.

Table 2.5 Model results, fit statistics and variable importance values (top 25% of variables in each model are bolded in blue) for the North Pacific and five sub-areas.

		North Pacific			BC EEZ			ALASKA EEZ			US WOC EEZ			BC Hecate Strait			BC Vancouver Island		
Model		GAM	BRT	MaxEnt	GAM	BRT	MaxEnt	GAM	BRT	MaxEnt	GAM	BRT	MaxEnt	GAM	BRT	MaxEnt	GAM	BRT	MaxEnt
Kappa		0.371	0.368	0.343	0.321	0.398	0.250	0.330	0.359	0.033	0.620	0.595	0.516	0.449	0.514	0.453	0.818	0.824	0.787
TSS		0.447	0.449	0.409	0.378	0.440	0.254	0.491	0.506	0.022	0.618	0.598	0.516	0.425	0.526	0.486	0.825	0.864	0.7
AUC Value		0.799	0.880	0.776	0.750	0.797	0.655	0.804	0.816	0.428	0.890	0.878	0.836	0.777	0.850	0.811	0.946	0.978	0.85
Variable Importance (Scale of 0–1)	Alkalinity	***1***	***0.410***	***0.071***	***1***	0.01	0.001	***1***	***0.163***	0.024	***1***	***0.22***	0.01	***1***	***0.136***	***0.137***	***1***	***0.013***	0.002
	Omega Aragonite	***0.973***	0.003	0.005	***0.703***	0.008	0	***0.837***	0.009	***0.05***	***0.679***	0.008	0.376	0.832	***0.048***	0.069	0.68	0.003	0
	Aspect	0.011	0.001	0	0.016	0.005	0	0.001	0.002	0.002	0	0	0.118	0.425	0.102	0.075	0.045	0.002	0
	Omega Calcite	***0.885***	0.009	0.015	***1***	0.021	0	***0.953***	0.014	0.023	***0.976***	0.011	0.219	***1***	0.005	0.046	***1***	0.001	0
	Depth	0.303	***0.025***	0.027	0.509	0.021	0.017	0.256	0.026	0.007	0.043	0.016	***0.7***	0.622	0.009	0.001	0.718	***0.101***	***0.166***
	Dissolved Inorganic Carbon	0.389	0.009	0	0.638	0.002	0.069	0.641	0.008	0.01	0.658	0.005	***0.629***	0.642	0.013	0.059	0.656	0.003	0.005
	Eastness	0.029	0.005	0.011	0.01	0.003	0.066	0.008	0.001	0	0.017	0.003	0.035	0.166	0.006	0	0.059	0	0
	Nitrate	0.367	***0.012***	***0.028***	0.559	***0.148***	***0.249***	0.35	0.021	***0.117***	0.2	0.027	0.322	0.099	***0.05***	***0.076***	0.609	0.003	***0.314***
	Northness	0.006	0.001	0	0.014	0.003	0	0.001	0	0	0.001	0	0	0.002	0.021	0.012	0.156	***0.016***	0.003
	Oxygen	***0.393***	***0.020***	***0.167***	0.48	0.007	0.111	0.113	***0.108***	***0.134***	0.405	***0.127***	0.239	***1***	0.011	0.074	***1***	0	***0.013***
	Phosphate	0.156	0.004	0.014	***1***	***0.121***	***0.13***	0.333	0.004	0.003	0.266	0.011	0.018	0.456	***0.048***	0.011	0.557	0	0
	Roughness	0.02	0.001	0.012	0.056	0.002	0.113	0.032	0.001	0	0.016	0.001	0.029	0.009	0.003	0	0.641	0.001	0.001
	Rugosity	0.003	0	0.004	0.05	***0.03***	***0.114***	0.025	0.001	***0.94***	0.015	0.003	0	0.029	0.006	0	0.443	0.001	0.001
	Salinity	0.021	0.008	0.014	0.633	0.018	***0.263***	0.116	***0.056***	0.021	0.017	***0.028***	***0.877***	0.589	0.011	0	0.562	0.002	0
	Silicate	0.241	0.002	***0.028***	0.482	0.002	0.071	***0.643***	***0.052***	0.003	0.504	***0.038***	0.001	***1***	0.008	0.028	0.821	0.001	0.009
	Slope	0.002	0.001	0.002	0.051	0.012	0.049	0.041	0.003	0.026	0.036	0.008	0	0.03	0.012	0	0.382	***0.053***	0
	Temperature	0.257	0.002	0.001	0.211	***0.034***	0.059	0.144	0.011	0.041	***0.818***	0.019	***0.411***	0.599	0.002	0.034	***0.897***	0.001	0
	TPI	0.024	0.008	0.001	0.012	0.01	0.046	0.028	0.027	0.002	0.031	0.007	0.064	0.003	0.006	0.066	0.31	0.006	***0.031***
	TRI	0.003	0	0	0.004	0.001	0.037	0.032	0.001	0	0.257	0.001	0.021	0.009	0.025	***0.087***	0.449	0.004	0.002

BC = British Columbia, EEZ = Exclusive Economic Zone, WOC = Washington, Oregon, California, GAM = generalized additive model, BRT = boosted regression tree, MaxEnt = Maximum Entropy model, Kappa = Cohen's Kappa Coefficient, TSS = True Skill Statistic, AUC = Area Under the receiver operator characteristic Curve, TPI = Topographic Position Index, TRI = Terrain Ruggedness Index

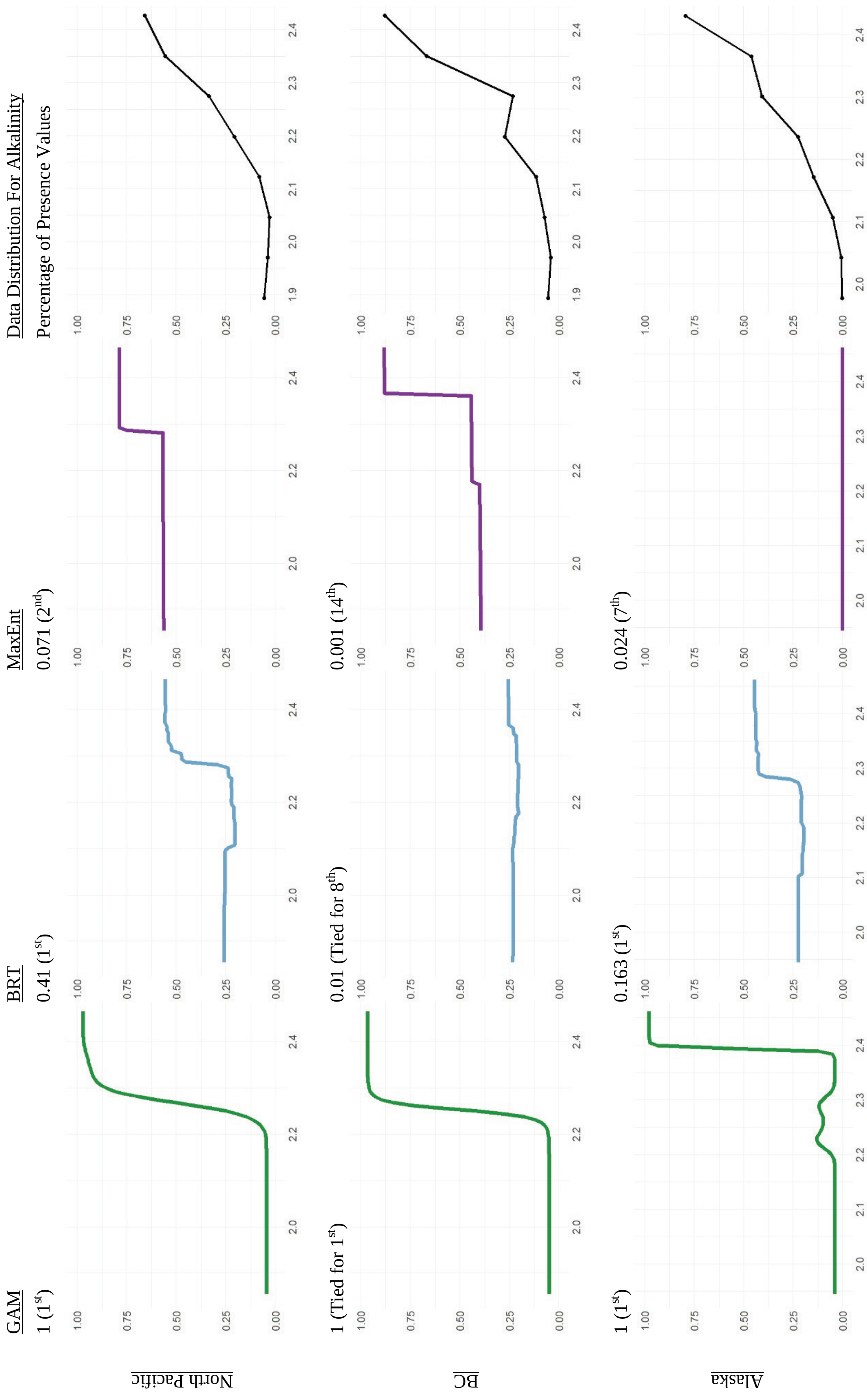


Fig. 2.8 Partial dependence plots for alkalinity (μmol l^{-1}) in all areas and models with ranked variable importance.

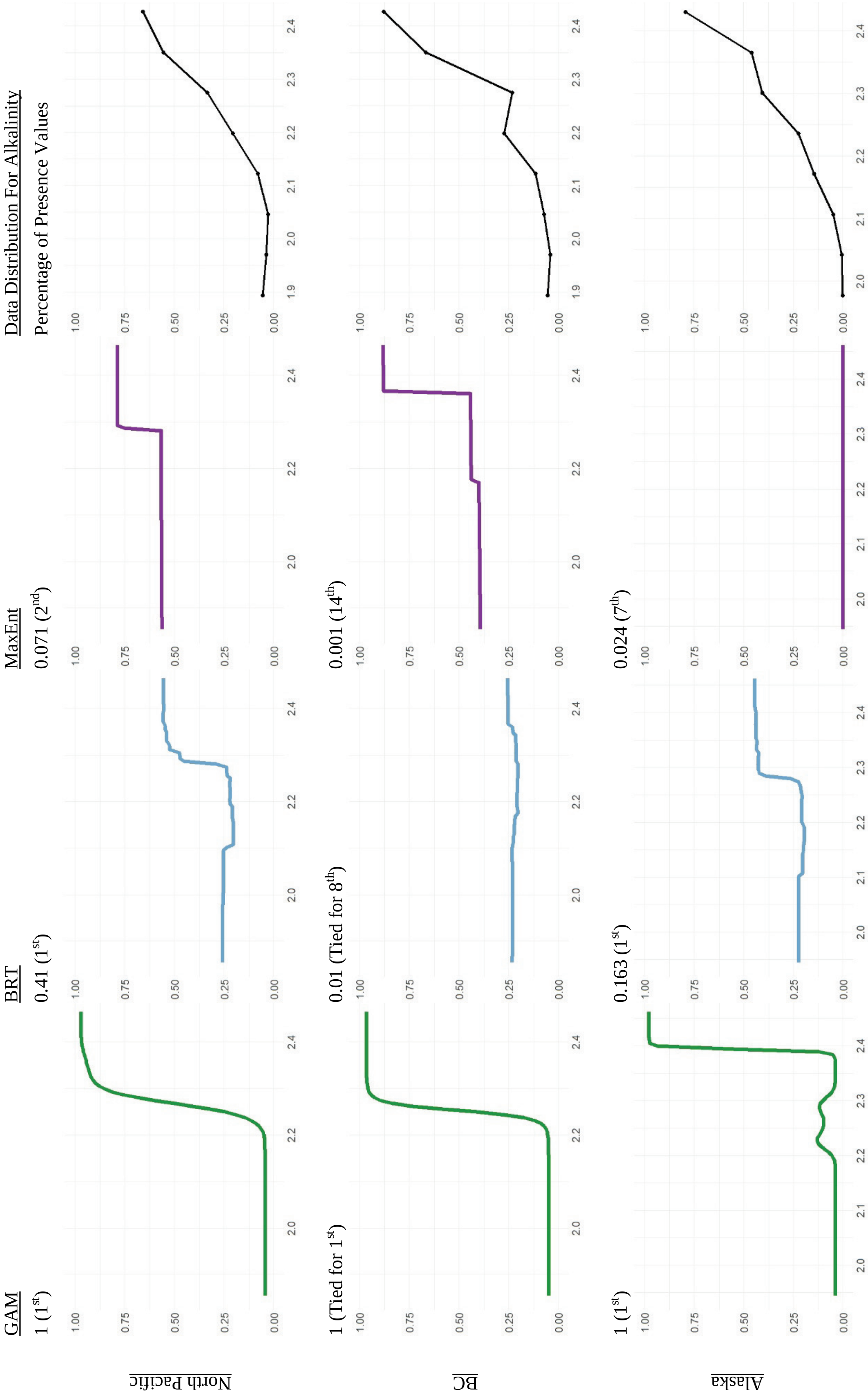


Fig. 2.11 Partial dependence plots for alkalinity, continued.

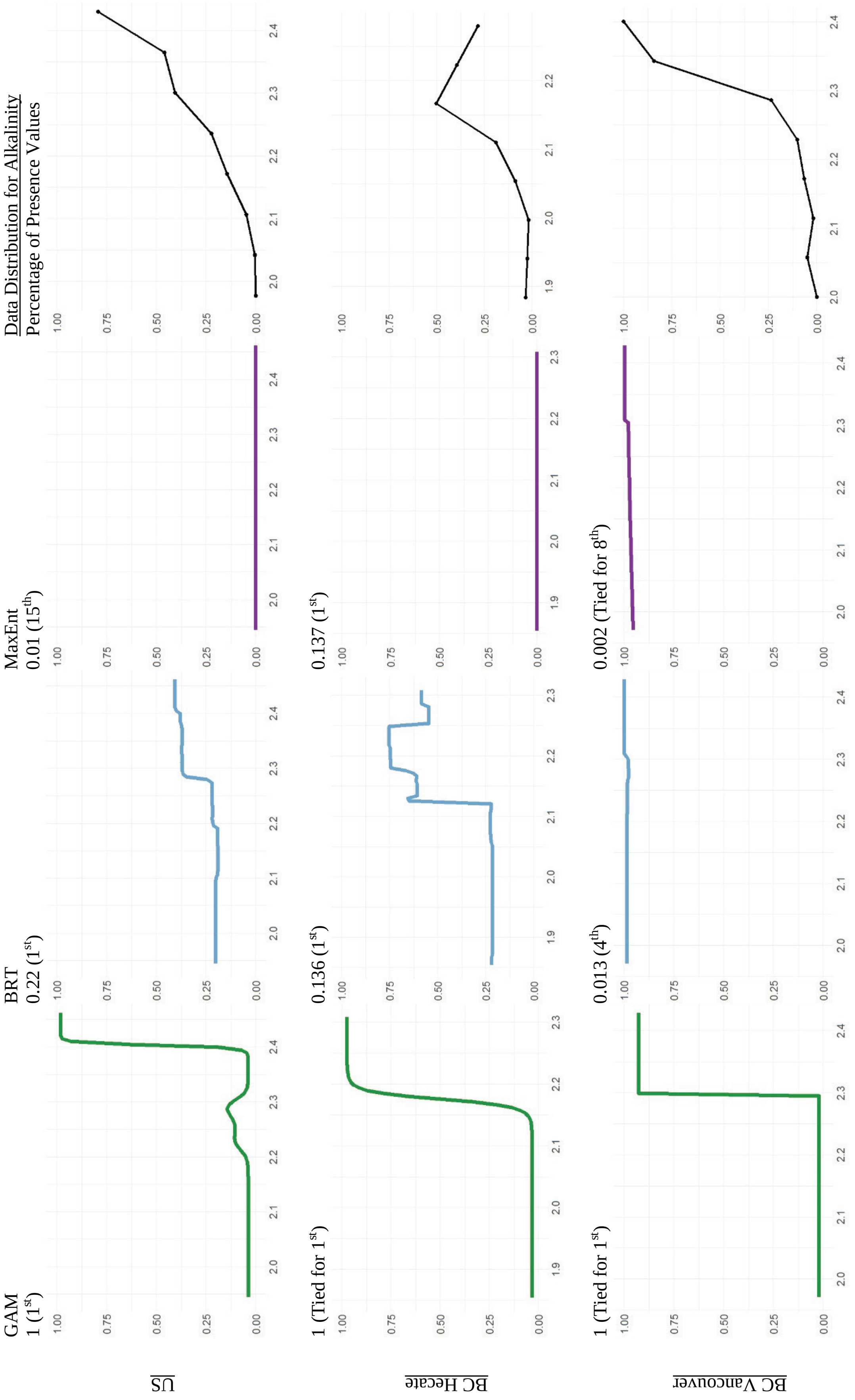


Fig. 2.12 Partial dependence plots for alkalinity, continued.

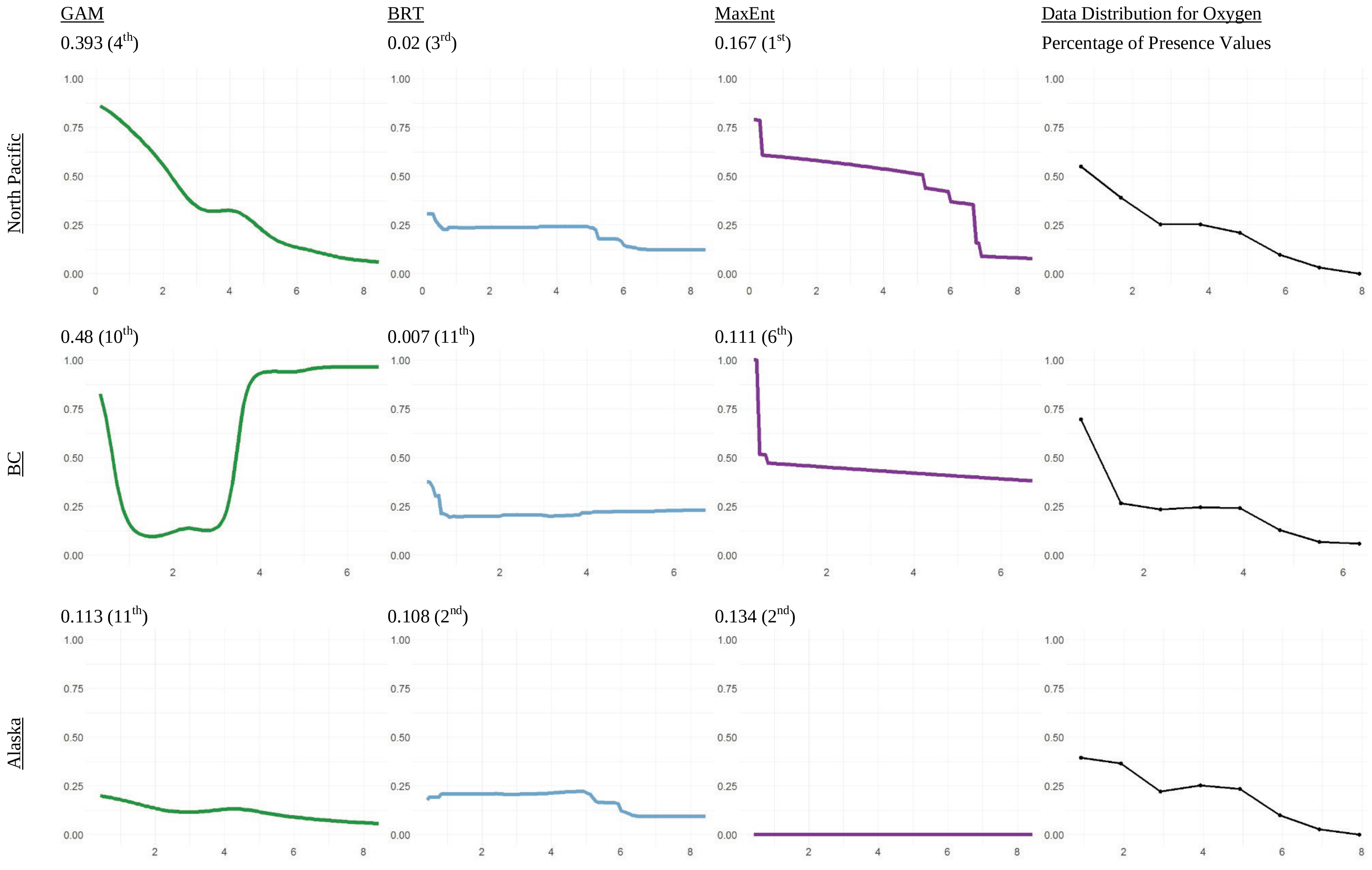


Fig. 2.13 Partial dependence plots for oxygen (ml l^{-1}) in all areas and models with ranked variable importance

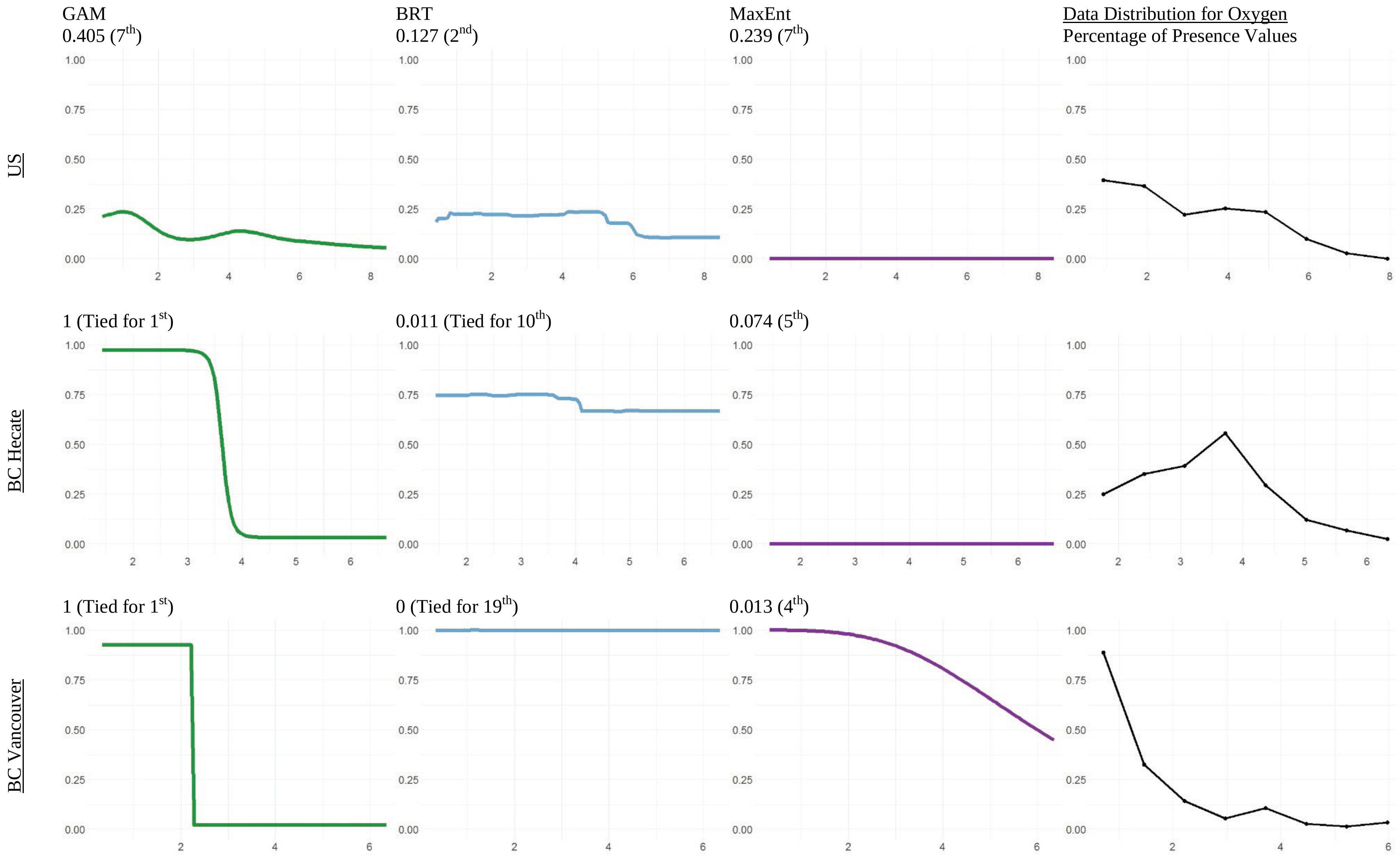


Fig. 2.14 Partial dependence plots for oxygen, continued.

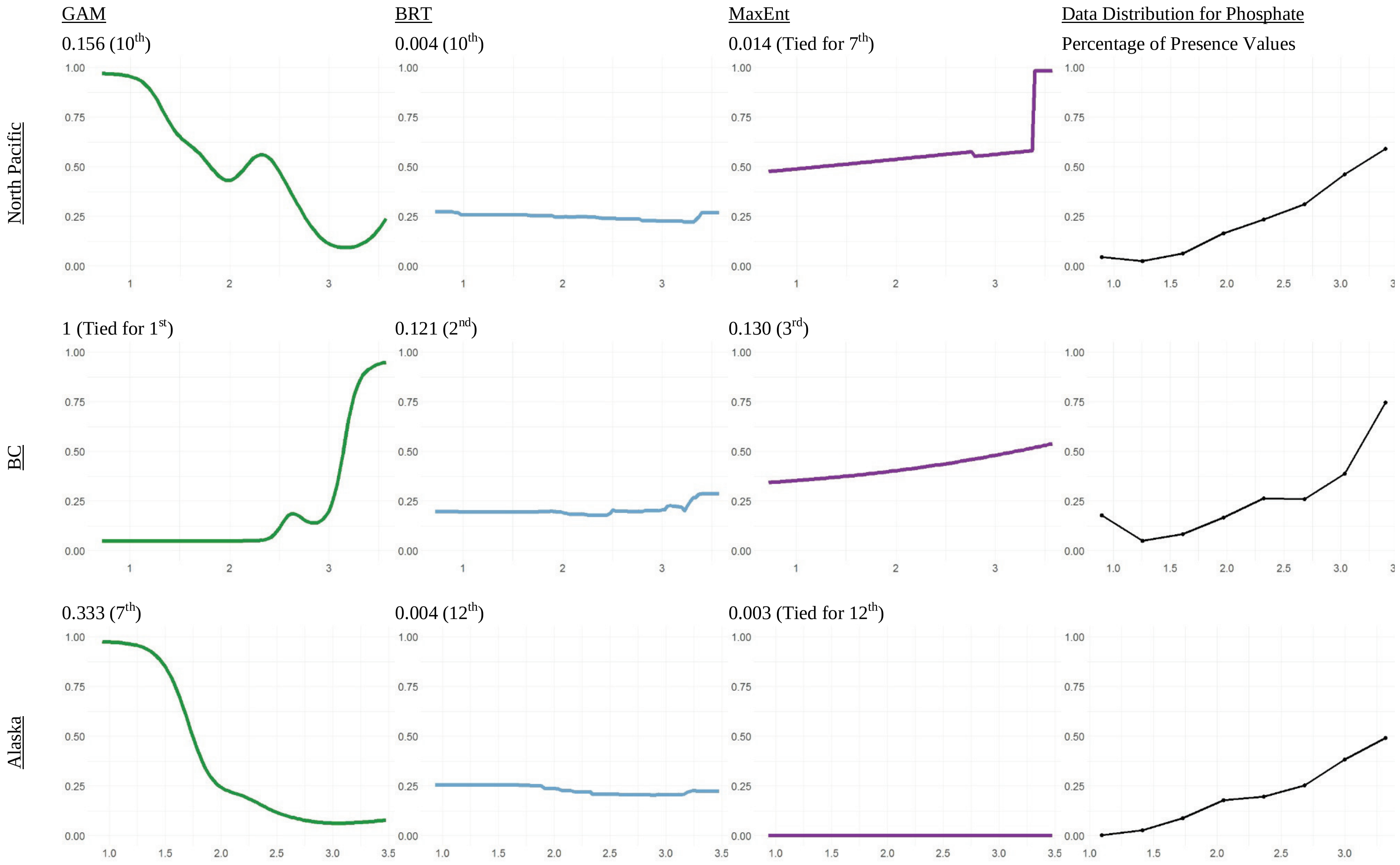


Fig. 2.15 Partial dependence plots for phosphate (μmol l^{-1}) in all areas and models with ranked variable importance.

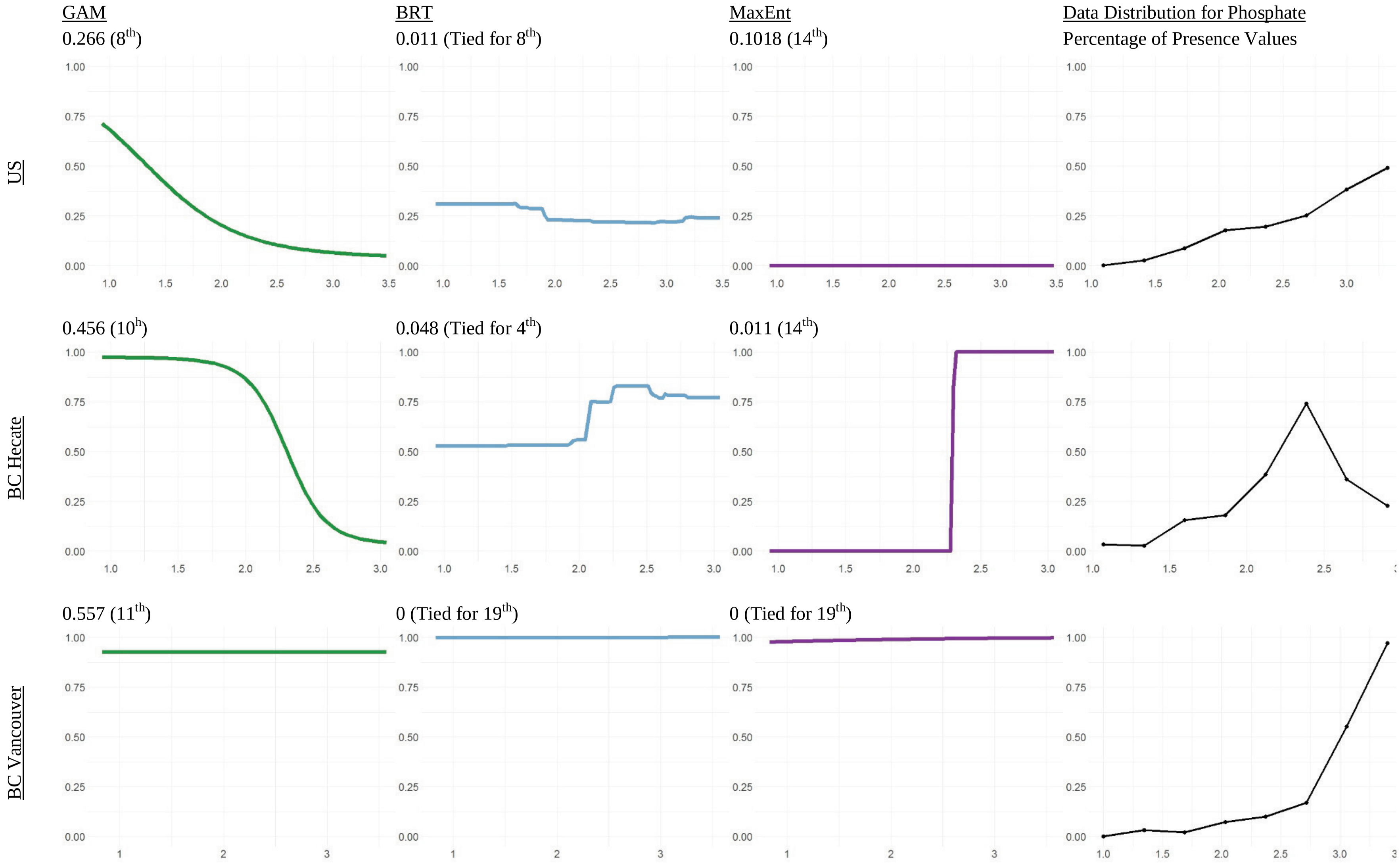


Fig. 2.16 Partial dependence plots for phosphate, continued.

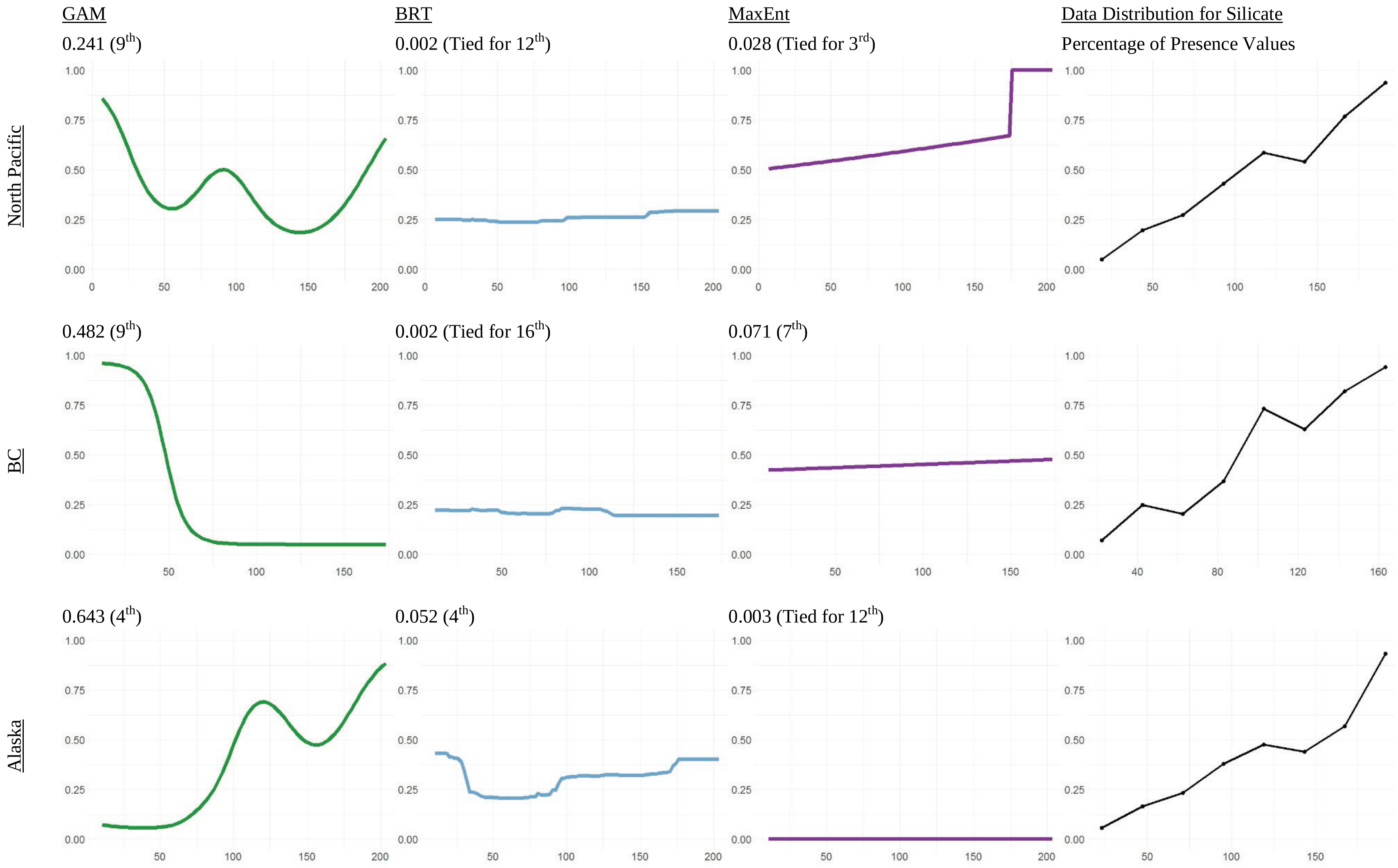


Fig. 2.17 Partial dependence plots for silicate (μmol l^{-1}) in all areas and models with ranked variable importance

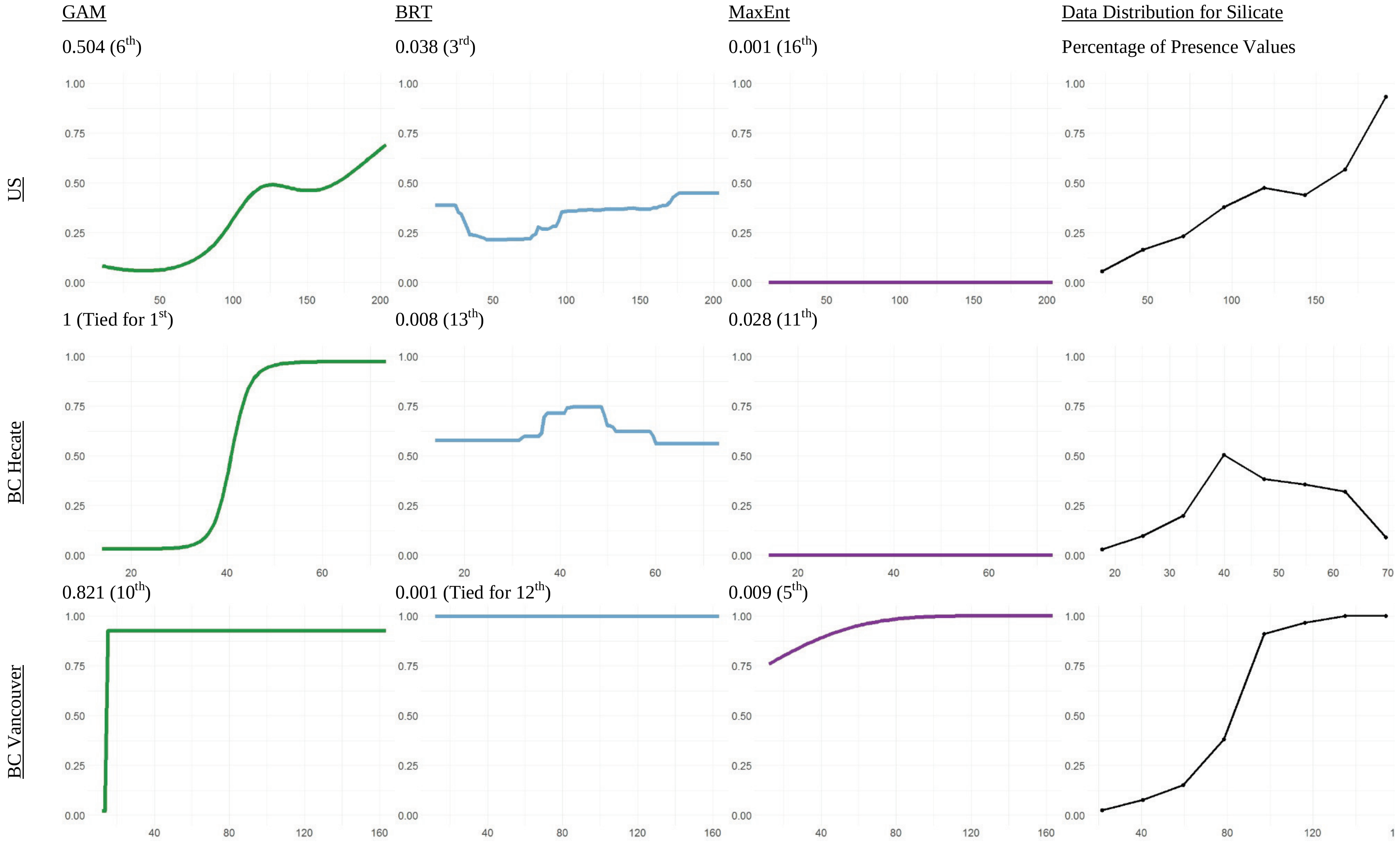


Fig. 2.18 Partial dependence plots for silicate, continued.

Partial dependence plots

Partial dependence plots generated for alkalinity, oxygen, phosphate and silicate can be seen in Figures 2.8–2.11. Table 2.5 presents depth as a frequently important variable in this analysis of glass sponges. Partial dependence plots from multiple models and areas show that as the taxon encounters depths shallower than 1000 m, the probability of presence decreases, confirming they are more likely to be found in deep waters (Fig. 2.12). Figure 2.13 shows the taxon data in the BC Vancouver Island sub-area. It can be easily noted here that the majority of the presence values are in the deeper waters. It is important to note that glass sponges also exist in shallow waters, as evidenced by the glass sponge reefs of coastal British Columbia (see Fig. 2.15).

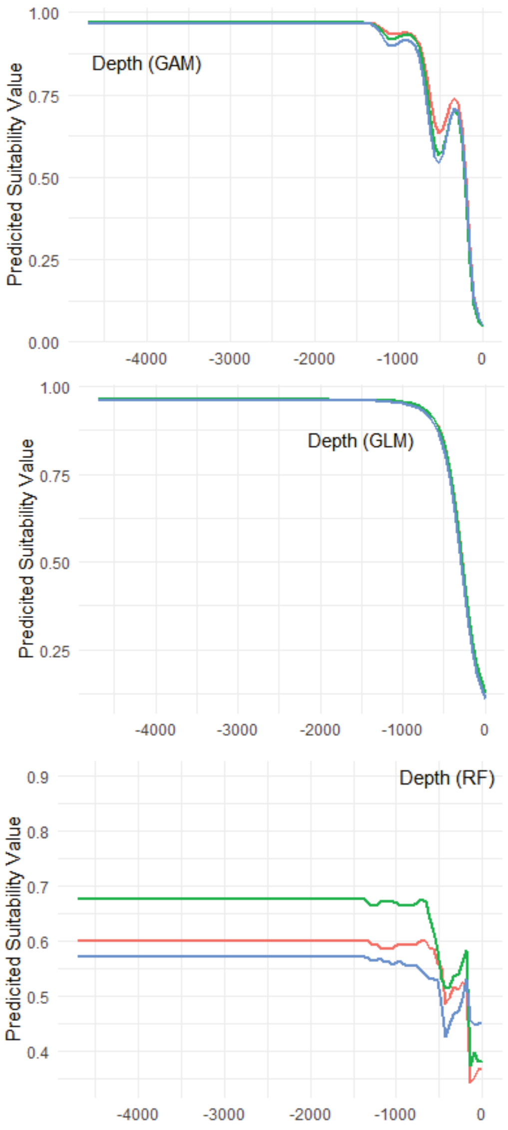


Fig. 2.19 Partial dependence plots for depth (m) from GAM, GLM, and random forest (RF) models. Each plot has three lines for each time the evaluation was run.

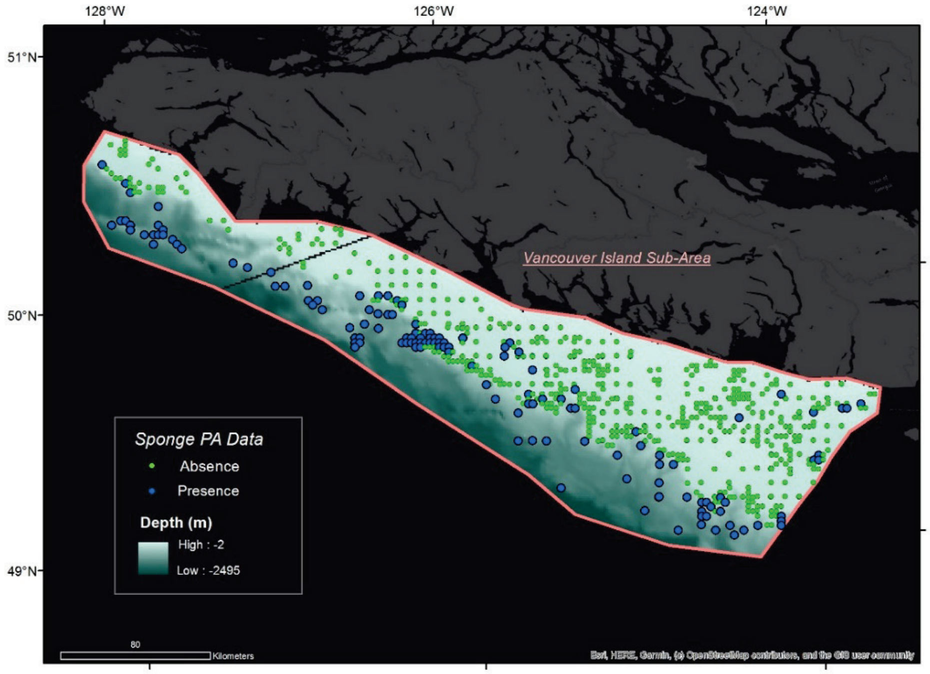


Fig. 2.20 Bathymetry and species data points within BC Vancouver Island sub-area (grey line is missing data).

Alkalinity

Figure 2.8 shows partial dependence plots and ranked variable importance for alkalinity, for each of the 18 model-area combinations. Within the North Pacific area, all three models suggest a high probability of glass sponge presence within highly alkaline waters. In the British Columbia area, the GAM model suggests an increase in glass sponge presence probability with alkalinity values higher than 2.2 μmol l^{-1}, a trend that is also present in each of the sub-areas. The BC Hecate Strait sub-area, in particular, suggests an increased probability of presence for glass sponges in alkalinity values of 2.2 μmol l^{-1} and higher. All three models produced comparable partial dependence plots for this area, where variable importance values for alkalinity rank 1st out of 19 variables for all three models. Finally, the data distribution plot for alkalinity values in the BC Hecate Strait sub-area shows a high percentage of presence values in alkalinity ranges of between 2.15 and 2.25 μmol l^{-1}. The BC Vancouver Island sub-area has a comparable GAM response curve as BC Hecate Strait; however, the BRT and MaxEnt models for BC Vancouver Island have lower variable importance ranks and do not show an increase in probability of presence with increased alkalinity values. The BC Hecate Strait sub-area has a range of alkalinity values of 1.855–2.308 μmol l^{-1}, while most other areas have a maximum of closer to 2.4 or 2.5 μmol l^{-1}.

Oxygen

Partial dependence plots for oxygen (Fig. 2.9) are interestingly varied as well; the general trend seen in GAM models from several of the areas suggests an increased probability of presence with lower oxygen values, except that the GAM model for the BC sub-area suggests the opposite. Oxygen was 10th in variable importance in the GAM model for the BC area, which means there is less indication in the model that glass sponges are strongly influenced by oxygen. The GAM plot for the BC area is interesting because it presents a pattern opposite to the oxygen plots for other areas, opposite to the plots for other models, and opposite to the data distribution itself. The variable importance values for oxygen in these models are not as consistently high as for alkalinity. The data distribution plots for all of the areas show a greater proportion of presence values in area with relatively low oxygen concentrations.

Phosphate

Response curves for phosphate can be seen in Figure 2.10 and present a wide variety of possible responses of probability of sponge presence in relation to phosphate content. Due to the lower variable importance values, it is more difficult to find strong environmental trends in the data. Phosphate was within the top three variables influencing the GAM, BRT and MaxEnt models within the BC sub-area. For the remaining areas, the variable importances range from 4th to last (19th). The plots from the BC sub-area indicate that probability of sponge presence increases with phosphate levels of roughly 3 μmol l^{-1} and higher. The next highest variable importance values are a result of the BRT and MaxEnt models for the BC Hecate Strait sub-area. Phosphate was 4th in variable importance for these two models and both indicate a slight increase in probability of presence between 2.0 and 2.5 μmol l^{-1}.

Silicate

Models which indicated that higher silicate content is more suitable for sponges included MaxEnt (North Pacific Ocean, BC Hecate Strait and BC Vancouver Island), and GAM (Alaska, US, BC Hecate Strait and BC Vancouver Island; Fig. 2.11). The data distribution plots largely indicate a greater proportion of presence values with increasing silicate value. The two partial dependence plots with the highest variable importance values (3rd) are the MaxEnt model in the North Pacific area and the BRT model in the US sub-area. While both these plots indicate a general increase in probability of presence in relation to an increase in silicate levels, the BRT model in the US also indicates an increased probability of presence with very low silicate contents. Generally, because silica plots have lower variable importance values than alkalinity or oxygen plots, less weight can be placed on their accuracy. The silicate GAM plot for the BC sub-area produced an opposite result to the remaining plots.

Spatial predictions

Figure 2.14 shows the predicted probability of glass sponge presence from the BRT, GAM and MaxEnt models for Alaska, in the form of a raster prediction probability of presence.

Alaska was selected for this section because it is a smaller area than the North Pacific (which is a large area, thus making predictions difficult to see in detail) but larger than the BC and US areas (which are quite small and have less variation in predictions of probability of presence). The AUC values for these three models respectively are 0.816, 0.804, and 0.428, meaning the BRT and GAM models performed very well and the MaxEnt model performed poorly. The MaxEnt model for the Alaska sub-area is the model that performed least well across all models and areas, and as can be seen in Figure 2.14c, the area is divided into red (high probability of presence) and blue (low probability of presence) without much variation between those two predictions. Figure 2.14a and b shows much more variation of probability of presence across the prediction.

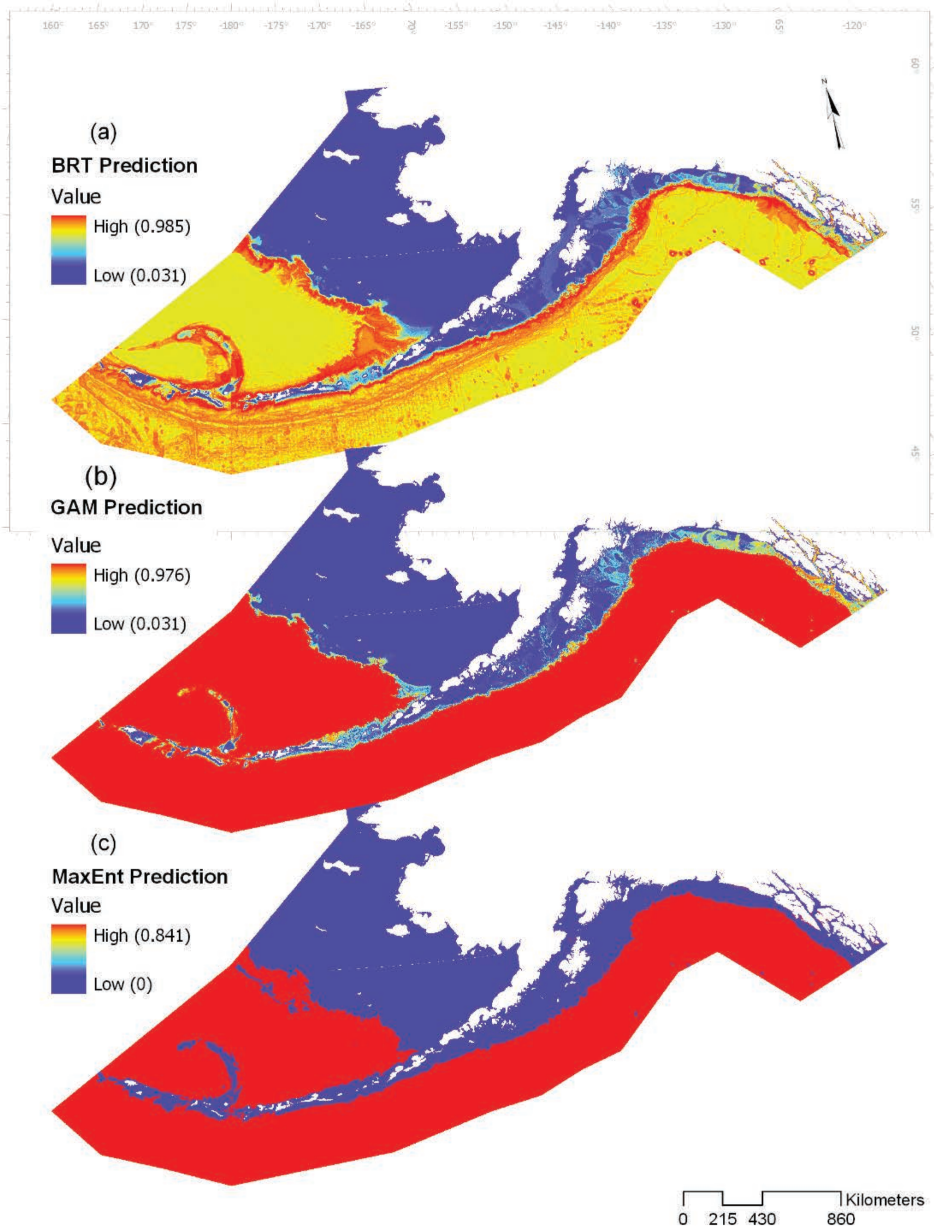


Fig. 2.21 Model predictions from BRT, GAM, and MaxEnt models for the Alaska sub-area.

Uncertainty metrics: BC Hecate Strait

Uncertainty refers to a lack of sureness or confidence about something (Elith *et al*., 2002b). Most outputs of SDM work are presented with confidence, with no indication of uncertainties, but it has been proposed that maps of uncertainty would help in the interpretation of these predictions (Elith *et al*., 2002b). The Hecate Strait sub-area in BC was used for the uncertainty metric analysis because of its high environmental variation and interesting patterns of alkalinity, oxygen and silicate distributions. The prediction from a GLM run on this area can be seen in Figure 2.15, along with the outlines of the Hecate Strait/Queen Charlotte Sound Glass Sponge Reefs Marine Protected Area (MPA).

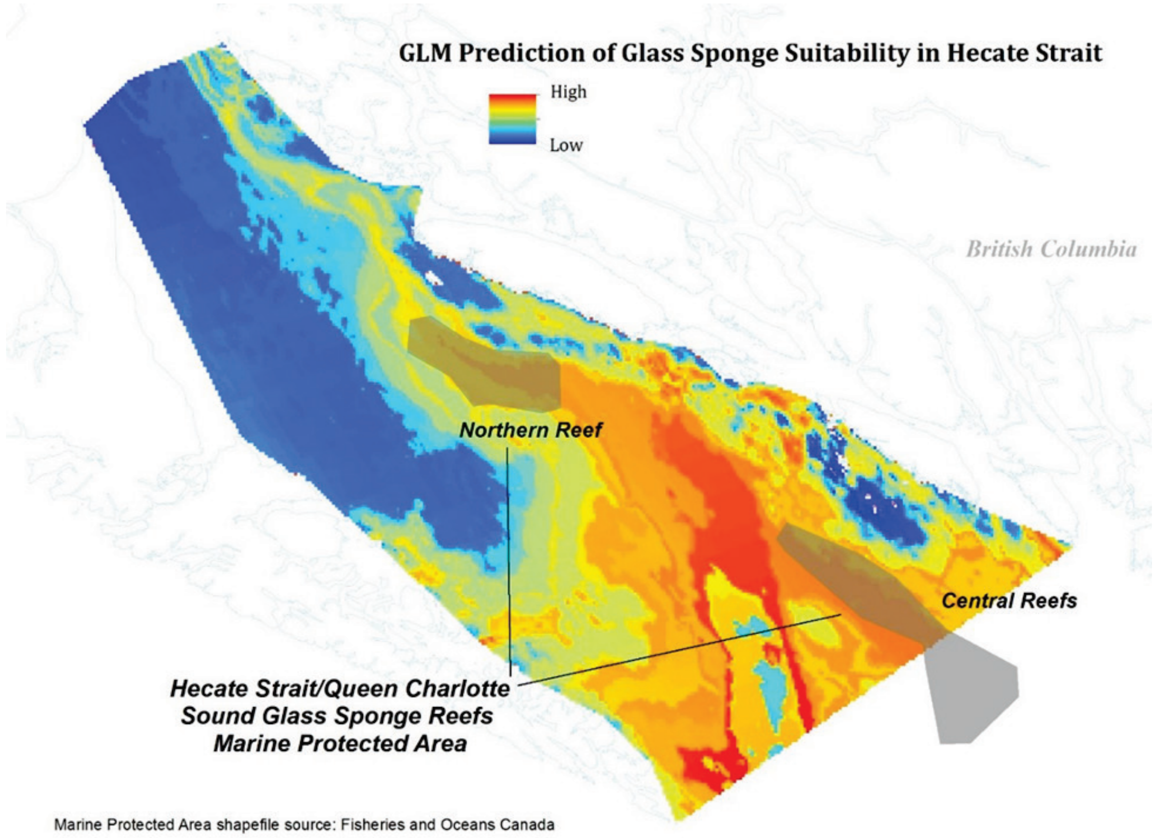


Fig. 2.15 GLM prediction of glass sponge probability of presence in Hecate Strait with Marine Protected Area (MPA) boundaries.

The Northern Reef and part of the Central Reef are contained within the Hecate Strait boundaries employed for this study. The MPA boundaries overlap with moderately high suitability for glass sponges, providing some confidence in the model predictions and their real-world accuracy, despite the MPA area boundaries not falling within the highest probability of presence areas (red areas).

Standard error of GLM predictions

Figure 2.16 shows the partial dependence plots for alkalinity, oxygen and silicate for the GLM model of the BC Hecate Strait sub-area, with model-based confidence intervals added. Generally, the confidence intervals are narrow, corresponding to a low expected error, for predictor value ranges with many data points, shown in the figure as a high density of red/blue lines. Value ranges with wider intervals have fewer data points. If the areas with wide confidence intervals overlap spatially, the relevant areas are likely to produce less certain predictions.

The SE of the GLM fit was written to a raster and can be seen in Figure 2.17a. Area 2 in the figure has high uncertainty.

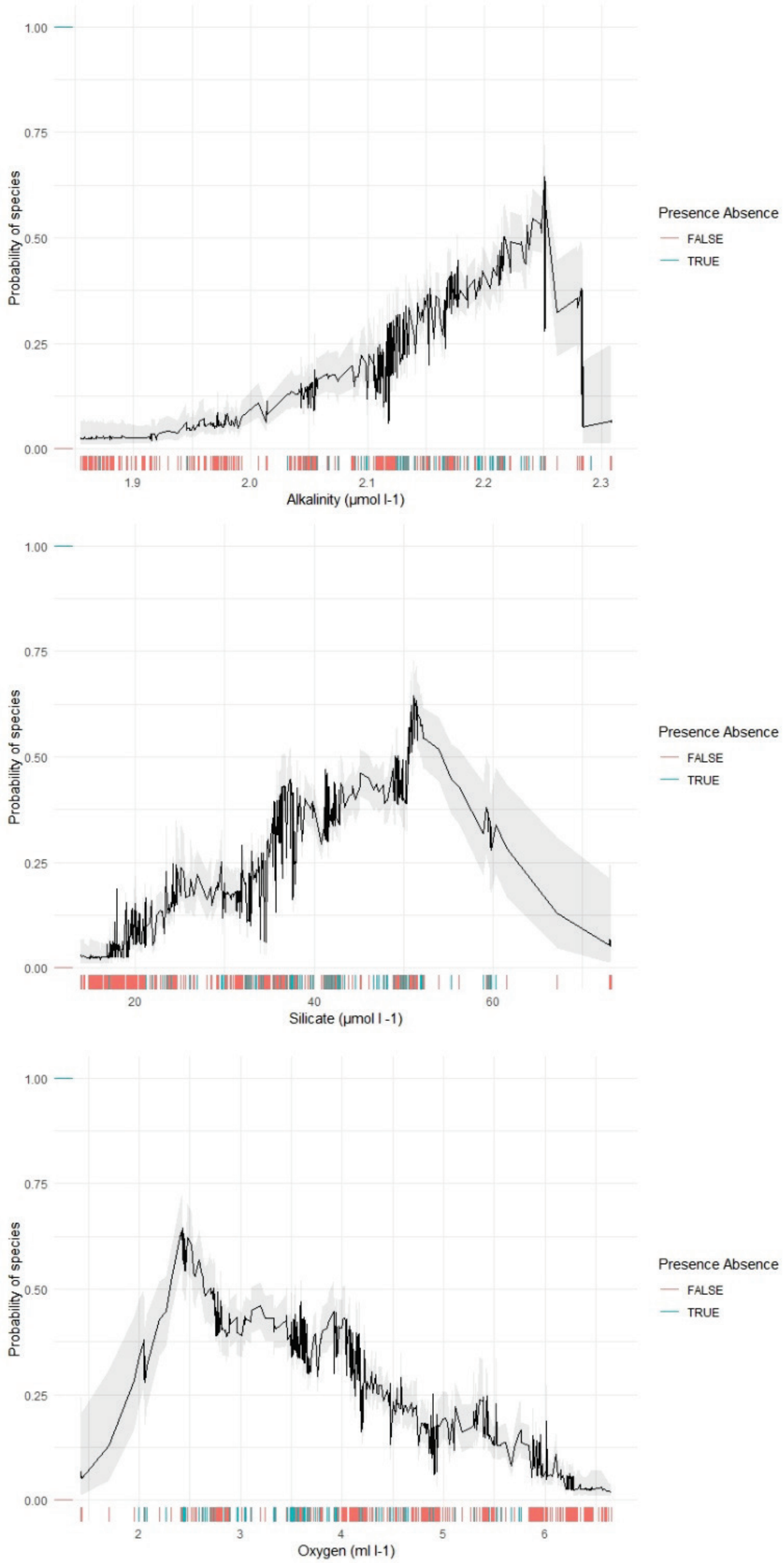


Fig. 2.22 Partial dependence plots for alkalinity, silicate, and oxygen with estimated confidence intervals.

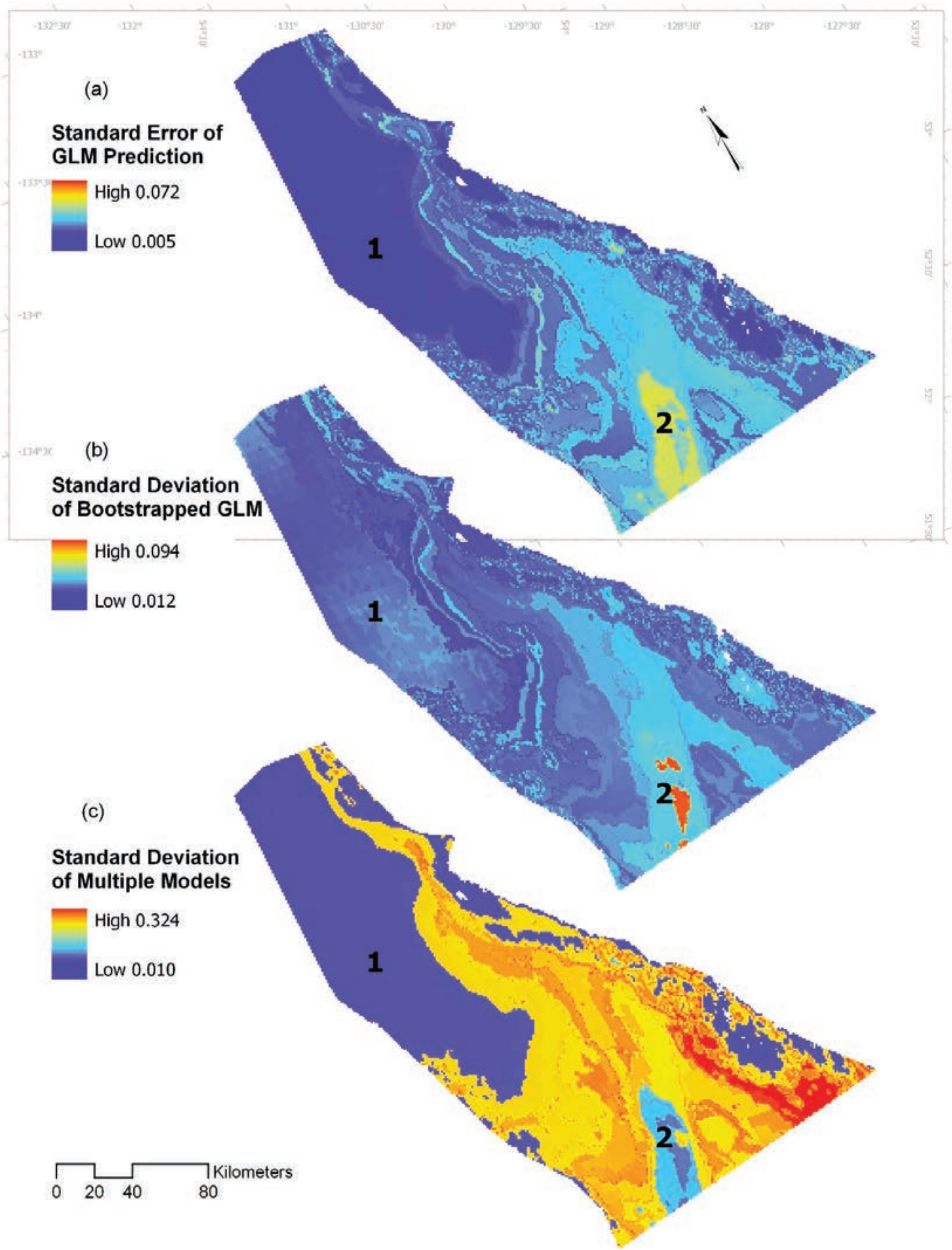


Fig. 2.17 Uncertainty metrics mapped to Hecate Strait: a) SE of GLM prediction, b) SD of bootstrapped GLM, and c) SD of multiple models.

There are very clear environmental gradients throughout Hecate Strait which can be visually confirmed to have an influence on the uncertainty metrics. Area 1 in Figure 2.17a has low alkalinity and silicate levels with high oxygen levels (Figs. 2.19–2.21). This combination of environmental values generally coincides with absence data for glass sponges, which the models interpret as unsuitable habitat. The SE in Fig. 2.17a is low, indicating high certainty in the prediction of low probability of sponge presence. Area 2 in Figure 2.17a has high uncertainty values. Area 2 corresponds with opposite niche environmental characteristics to Area 1; very high alkalinity levels, very high silica levels, and very low oxygen levels, all of which are value ranges that are poorly represented in the data. As can be seen in the partial dependence plots (Fig. 2.16), these value ranges are associated with low data density and high CIs. The GLM is forced to make predictions for these areas based on a combination of few data points with similar values and extrapolation from more data-dense value ranges, which leads to extreme predictions and higher uncertainty.

Standard deviation of bootstrapped GLMs

Figure 2.17b presents the result of bootstrapping the binomial GLM 200 times, calculating the SD for each cell and then writing this result to a raster. This method of spatially showing prediction uncertainty yields similar results to the initial method of calculating the SE from the GLM. It shares an area of high uncertainty with the first method (Area 2), which was noted as having extreme values of all three input predictors. This method, as well as the first method, does not show Area 1 to have high SE, indicating consistency across methods.

Standard deviation of multiple SDMs

Finally, Figure 2.17c presents the result of running multiple SDMs and mapping the SD of the model predictions. The models used and their individual predictions can be seen in Figure 2.18. This method shows the highest uncertainty to exist in the lower right corner of Hecate Strait, which corresponds to medium uncertainty in the first two methods. While taking a different approach from the first two methods, this final method is equally as important for determining spatial uncertainty from predictive models and yields interesting results that could aid policy makers in making informed decisions based on SDMs. Area 1 in Figure 2.17c has low SD because the majority of the SDMs produced a similar probability of presence for this area (Fig. 2.18). This is a consistent result from all three methods, indicating low uncertainty in environments considered unsuitable for the taxon in question. The areas that are yellow and orange yield higher error values because the models produced different results, despite having been calibrated with the same data. Each of the specific model outputs showed the highest probability of species to be in the area which has high standard deviation in Figure 2.17c. The resultant high SD is a result of this being the area of the model output that changes the most with different SDMs.

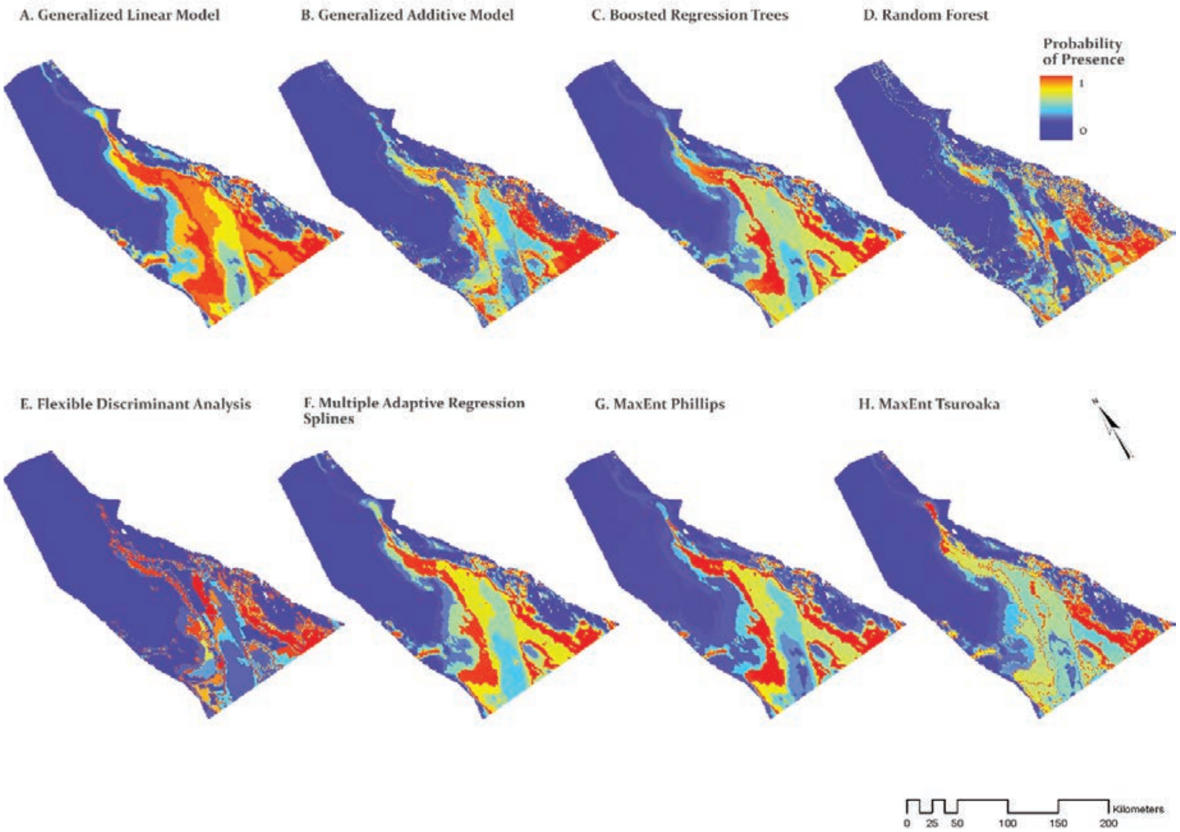


Fig. 2.23 Predictions of glass sponge probability of presence in Hecate Strait: a) GLM, b) GAM, c) BRT, d) RF, e) FDA, f) MARS, g) MaxEnt Phillips, and h) MaxEnt Tsuroaka.

Discussion

Aspatial model predictions: Partial dependence plots and variable importance

As a method of assessing the validity of models, partial dependence plots and variable importance rankings were presented and analyzed. The results presenting partial dependence plots and variable importance values from the GAM, BRT and MaxEnt models can provide information about 1) the ability of the model to describe the environment-species relationships, and therefore 2) the potential for using the model to make inferences about the ecology of glass sponges and characteristics of their habitats.

In addition to standard model performance metrics such as AUC, TSS and Kappa, ranked variable importance and partial dependence plots can inform how certain or uncertain an SDM-based prediction is. If a multi-model, multi-area approach has been used for the modeling, and a given environmental variable has high importance values across multiple model types and areas, a higher confidence can be placed in that variable having a non-spurious effect on the distribution of the response variable, *e.g.*, glass sponges in the present case. It is likely that the use of more models, and more environmentally distinct areas would serve to strengthen the multi-model, multi-area approach even more. The expected result from performing a multi-area, multi-model approach was that strong habitat preferences will be reflected similarly in partial dependence plots from different models and areas, while weak habitat preferences will not.

Using this approach, the partial dependence plots for alkalinity strongly suggest a causal relationship between alkalinity and glass sponge presence. According to the model results, glass sponge probability of presence increases in conjunction with higher alkalinity values, specifically at concentrations of 2.1 μmol l^{-1} or 2.2 μmol l^{-1} and higher. While several of the areas modeled produced this trend, the BC Hecate Strait sub-area displays arguably the most consistent result based on the fact that all of the three models for this area ranked alkalinity as first out of 19 other variables. Less confidence can be placed in certain areas and models where alkalinity is ranked lower and the associated response curves are inconsistent with those of high variable importance. For example, MaxEnt models in BC and US areas have alkalinity importance rankings of 14th and 15th respectively, and neither of the corresponding partial dependence plots provide any useful ecological information about how sponges respond to alkalinity levels. Although the models are too complex to provide a definitive explanation, it is likely that the BC and US areas have other environmental variables which are more influential for the model, and therefore the relationship between sponge presence and alkalinity is more difficult for the model to identify. Every highly ranked (top 25 percentile) partial dependence plot of alkalinity shows an increased probability of presence associated with high alkalinity values, generally above 2.2 μmol l^{-1}. Areas of Hecate Strait which meet these alkalinity values are relatively few and can be seen in Figure 2.19.

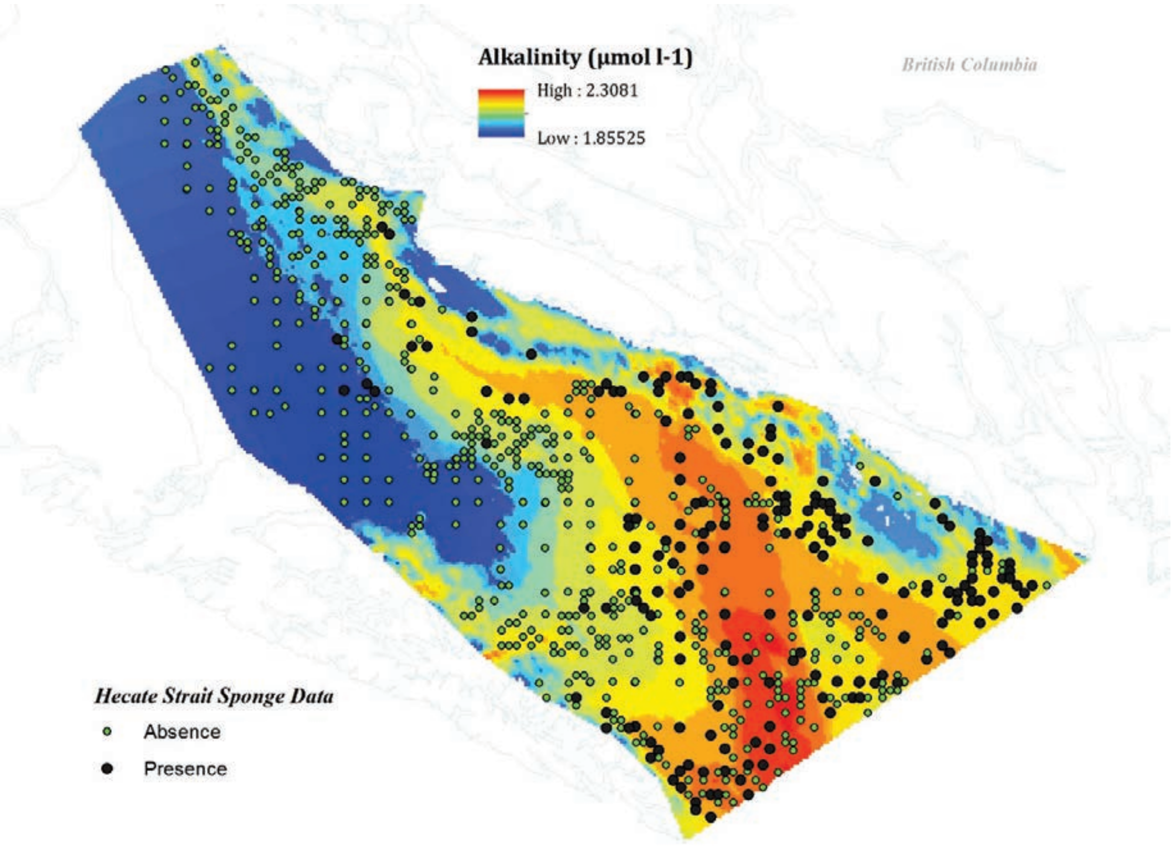


Fig. 2.24 Alkalinity values across Hecate Strait.

According to the partial dependence plots with high variable importance rankings, a high probability of glass sponge presence is associated with low oxygen values, generally below 2 ml l^{-1}. Deep-water sponges, and many other invertebrates, use little oxygen and have adapted to live in low-oxygen environments, *e.g.*, during low tide or in benthic sediments (Leys and Kahn, 2018). Leys and Kahn (2018) note that glass sponges tolerate long-term hypoxic conditions by reducing their filtration rate and feeding activity. Filtration, they concluded, is costly to glass sponges and attempting to slow their filtration has driven innovations in their morphology and physiology (Leys and Kahn, 2018). Chu *et al.* (2019) also found that dissolved oxygen was a highly ranked positive predictor of habitat for cold-water coral and sponge grounds in the Canadian Northeast Pacific Ocean. As a result of this finding, Chu *et al.* (2019) predicted that cold-water coral and sponge taxa would have lower oxygen requirements in comparison to highly mobile taxa such as fish. It was also found, in an attempt to validate the models predicting that cold-water corals and sponges are likely to occur in severely low oxygen environments, that these taxa exist in oxygen levels as low as 0.2 ml l^{-1} at the Union and Dellwood seamounts (both are southwest of the southern point of Haida Gwaii). Figure 2.20 shows the distribution of oxygen content across Hecate Strait. It is important to note how related oxygen and alkalinity are to each other in this area. With many sponges existing in high-alkalinity, low-oxygen waters, it is difficult to know whether this is because of the high alkalinity, the low oxygen, some combination of the two, or a third variable that is also correlated with both alkalinity and oxygen. This illustrates the benefit of using a multi-area approach, because these two variables may be less related in other areas which have also been modeled.

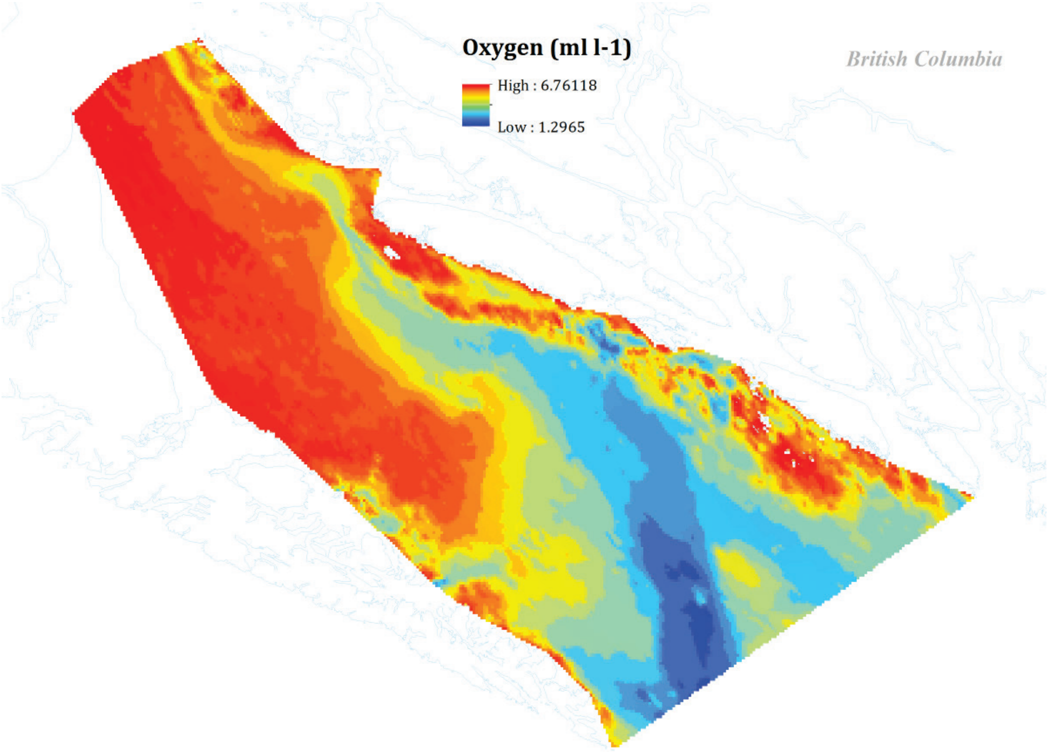


Fig. 2.20 Oxygen values across Hecate Strait.

Silicate was not often returned from the models as one of the top 25% of variables; however, certain models and areas did produce silicate as the most important variable. These included MaxEnt for the North Pacific area, GAM and BRT for the Alaska sub-area, BRT for the US sub-area, and GAM for the BC Hecate Strait sub-area. Out of these, most show an increased probability of glass sponge presence with high levels of silicate. High levels of silicate often overlap with high levels of alkalinity within Hecate Strait (compare Fig. 2.19 and Fig. 2.21).

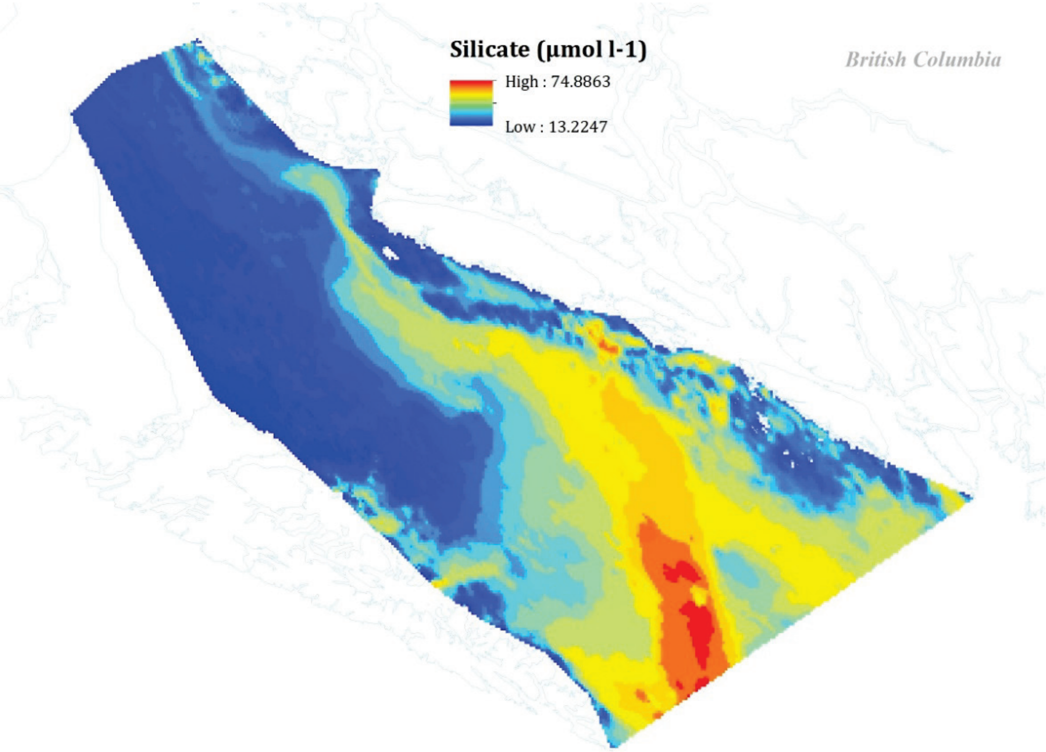


Fig. 2.25 Silicate values across Hecate Strait.

In published literature, it has been indicated that glass sponges need high levels of dissolved silica (Leys *et al*., 2004; Austin., 1984; Chu *et al*., 2019). Chu *et al*. (2019) found that silicic acid was a top predictor for sponge groups because biogenic silica (biogenic silica occurs when dissolved silicate transforms to particulate skeletal matter; Treguer *et al*., 1995) can constitute over 90% of the biomass of cold-water sponges. Silicate levels are high in both the Antarctic Ocean as well as the coastal Northeast Pacific Ocean, which are both regions of high glass sponge abundance (Treguer *et al*., 1995; Leys *et al*., 2004). Interestingly, the Hecate Strait area shows an increased probability of glass sponge presence at much lower levels of silicate than the remaining areas tested within this contribution. Many areas indicate high probability of glass sponge presence in areas with silicate values of 150 μmol l^{-1}; however, Hecate Strait indicates high probability of presence beginning where silicate values reach over 40 μmol l^{-1}. The highest level of silicate within the Hecate Strait sub-area is 74 μmol l^{-1}. Whitney *et al*. (2005) identified silicate levels of over 40 μmol l^{-1} around sponge reefs in Hecate Strait, thus confirming this result.

Evaluating partial dependence plots in addition to model accuracy metrics as an additional way to assess SDM outputs is a descriptive and largely qualitative exercise. The challenge is that there can be valuable information concerning ecological relationships, but also nonsensical and spurious relationships, presented in these plots. But there is value in producing multiple models for multiple areas because oceanic environments subject to different currents and water masses and different levels of terrestrial influence can vary drastically in their biogeochemistry. This contribution presented one approach to disentangling the two; by looking for species–environment relationships that are strong (as indicated by high variable importance), consistent between model types and consistent between different areas, it is possible to extract only those relationships most likely to be caused by ecological processes. The two anomalous plots mentioned in the results section, the oxygen and silicate plots from the GAM model for the BC sub-area, presented the opposite relationships of what the remaining models presented. These two plots are an excellent example of why it is important to not make inferences about ecological relationships based on single-model and single-area partial dependencies.

Using ranked variable importance values and selecting a threshold for a confidence cut-off can provide a quantitative measure of accuracy. Providing a measure of probable accuracy alongside model outputs can be helpful for environmental managers and stakeholders who require numerical models to estimate species distribution to design effective spatial management measures for conservation and protection.

Spatial model uncertainty predictions

Spatially examining the uncertainty of model predictions is not commonly done in SDM studies. However, it is important that potential users of SDM products have an understanding of the predictive accuracy of models and how this may vary across geographic space (Elith *et al*., 2005). Most evaluation metrics of predictive performance use a comparison of predictions against observations at a particular set of sites (Fielding *et al*., 1997). As also done in this contribution, statistics such as Kappa and AUC values are widely used to assess whether predictions are suitably accurate for their intended use. However, these statistics are somewhat restricted because they do not assess the predictions in geographic space and do not allow for exploration of spatial errors (Fielding *et al*., 1997; Elith and Burgman, 2002a; Elith *et al*., 2005).

Confidence intervals and standard error

It is suggested in SDM literature that plotting CIs around model predictions could be crucial to the interpretation of the models’ performance, particularly mapping CIs of these predictions (Elith *et al*., 2002b, 2005). CIs around plotted responses (such as partial dependence plots) help show where species–predictor variable relationships are most uncertain (Ferrier *et al*., 2002). Adding these error metrics is instrumental for producing models which can be understood as ecological realities (Elith *et al*., 2005). Figure 2.16 shows CIs added to partial dependence plots of alkalinity, oxygen and silicate. The largest CI on each plot correlates with the lowest density of data points in each variable. Sponge data where silicate values are greater than 55 μmol l^{-1} have the highest uncertainty, as there are fewer data points for silicate values over this threshold. As mentioned earlier, silicate levels in Hecate Strait have been documented to be lower than surrounding areas, yet glass sponges remain in great abundance in Hecate Strait.

According to Figure 2.15, the highest probability of glass sponge presence within Hecate Strait coincides with areas comprised of high alkalinity, very low oxygen, and medium-high silicate levels. Hecate Strait is a shallow asymmetric channel between Haida Gwaii and the northern mainland of British Columbia (Perry *et al*., 1994). It is a unique area due to its shape. It is roughly 140 km wide at its southern end and narrows to 48 km in the north, covering around 23,000 km^2 with depth values reaching down to 494 m. The shallowest part is the northwest area, which has low alkalinity levels, high oxygen levels and low silicate levels. This is also the area for which the lowest probability of presence for glass sponges was predicted (Fig. 2.15). This northwest area (labelled as Area 1 in Fig. 2.17) shows consistently low uncertainty with all three methods. All models used predicted low probability of sponge presence in this area, due to its physical characteristics mentioned previously, and all methods of quantifying uncertainty show low uncertainty in this area, indicating it is highly probably this area is unsuitable for sponges.

Using CIs as the only means of quantifying the uncertainty of SDM predictions is not a complete method, according to Elith *et al*. (2002b), who mention that uncertainty in model outputs is not explicitly accounted for in the CIs of GLMs. They suggest that bootstrapped CIs can better account for different sources of uncertainty rather than simply applying CIs to GLM predictions. This is an interesting avenue for further work on spatially quantifying model uncertainty, as only the SE of the GLM fit and SD of the bootstrapped GLMs were calculated in the work that underlies this contribution. Area 2 (Fig. 2.17) was identified as an area of highly uncertain predictions by both the SE of the GLM fit and the SD of the bootstrapped GLMs. The bootstrapped runs of the GLM produce very consistent predictions in the northwest part of Hecate Strait (Area 1). The third method of measuring uncertainty involved running eight SDMs on the same data used for the prior methods and then calculating SE of all eight predictions. Figure 2.17c presents high SE values around the southeast corner of Hecate Strait. This area has medium uncertainty in the first two methods, indicating slight differences in model predictions. The eight models produced consistent predictions for the northwest area of Hecate Strait, suggesting with a low level of uncertainty that sponge probability of presence in this area is low.

One method of comparing these three metrics of estimating uncertainty is by looking at the original biological input data. Area 1 mostly contains absence values and almost no presence values (Fig. 2.19). Therefore, it seems that when every model shows low probability of presence, one can assume with some confidence it is likely correct. Additionally, Area 1 is shallow, has high levels of oxygen and low levels of both silicate and alkalinity, which are environmental conditions that are the opposite of what models generally predict as suitable habitat for sponges. Figure 2.17a, b and c present Area 1 as having low uncertainty, indicating all assign low uncertainty to the prediction of low probability of presence in this area.

These results allow for the conclusion that if the model predicts low probability of presence, it has higher certainty in this prediction than in predictions of high probability of presence. The first two methods differ from the last method in what they show, but the first two methods show medium uncertainty in the same areas which are highly uncertain in the last method (the areas where the models all predict relatively high probability of presence, but of varying values and slightly different geographic spreads of this high probability of presence). This leads to the conclusion that uncertainty is generally lowest where the models predict the species not to be, and highest where the models predict the highest probability of species presence to be.

Both bootstrapping a model and running multiple SDMs are useful methods of calculating prediction uncertainty, and both these methods could be extremely useful for providing planners with information to consider when employing the predictions in conservation planning and decision making (Ferrier *et al*., 2002).

Limitations

Numerous limitations exist within SDM work; not all models are transposable to distinct environments, they are strongly dependent on the considered scale, they are difficult to implement in a management context, many models are not easily interpretable, and software is not always available to practitioners (Guisan and Thuiller, 2005). Alongside these limitations, a consistent limitation is the fact that any model will rely heavily on the quality of the input data. This study used a spatial data thinning method based on local environmental variation to eliminate the spatial sampling bias that was present in the original data set. Spatial bias is a common limitation in the SDM field because it may cause biased model results and it is difficult to tell if the species–environment relationships in the model are representative of the real world or if they are a function of how the data were sampled. When using biological data from another organization, such is the case here, it can be challenging to find sufficient details about the data to ensure its quality. There are also limitations in the interpretation of regression-based models and machine learning models. The two methods produce different results. For example, calculating uncertainty metrics is more easily done from regression models as opposed to machine learning models. This contribution compared a regression-based model with two machine learning models. A final limitation often overlooked in SDM studies is the spatial dependency of accuracy of the model outputs. Presenting the error spatially is an important aspect of SDM moving forward, as it will be easily understood by those in environmental management who are unfamiliar with the modeling methods. Spatially presented error metrics add value to the already used aspatial error metrics.

Conclusion

By analyzing a variety of commonly used SDMs and examining different spatial and aspatial metrics to quantify model accuracy and uncertainty, this contribution has shown how applying a multi-model, multi-area approach can improve the interpretation of the modeled species–environment relationships. It has also shown how different methods of uncertainty mapping can provide increased insight as to which areas are predicted by the model to have high/low levels of uncertainty.

Running three models on six areas showed that partial dependence plots can differ substantially between model types and adjacent geographical areas. It is therefore necessary to not overstate the ecological results presented in individual plots, and to be careful while interpreting them ecologically. One way to assess the ecological interpretability of partial dependence plots is to perform a multi-model, multi-area study, and compare plots across models and areas prior to drawing ecological inferences.

Based on the results presented in this contribution, it appears that glass sponges are most likely to be found in areas with alkalinity values greater than 2.2 μmol l^{-1} and oxygen values lower than 2 ml l^{-1}. While silicate was also an important environmental predictor, the results for the probability of sponge presence in relation to silicate are more variable. Every area except Hecate Strait indicated that glass sponges are more likely to exist in areas with silicate values of 150 μmol l^{-1} and over. However, lower values in Hecate Strait confirm sponges can exist in areas with silicate values of 40 μmol l^{-1} and over.

While model accuracy metrics like AUC and TSS contain important information about the ability of a model to produce good predictions, spatial uncertainty metrics can outline areas where predictions are more or less likely to be correct. There is a small area in the south of Hecate Strait (Area 2) that both the GLM and the bootstrapped GLM indicate as being subject to highly uncertain predictions. Such areas should be treated cautiously regardless of the overall accuracy of the model as indicated by the accuracy metrics, and such areas could be targeted for future data collection.

Finally, it was shown that different approaches to estimating prediction uncertainty can yield different but important results. This can be seen in Hecate Strait: predictions for the shallow, low-alkalinity area in the northwest part of Hecate Strait (Area 1) are consistent between models (all models give low probability of sponge presence), consistent between bootstrapped runs of the GLM models and the SE of the GLM model (which also all predict low probability of sponge presence), and are also consistent with the data points from that area. This indicates we are very confident in the model prediction of low probability of sponge presence in Area 1. The highest uncertainty corresponds to areas where models have presented high probability of presence; since these areas do not all overlap neatly, the uncertainty arises from these varying predictions.

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3. Mapping biogenic habitats: Distribution of glass sponge reefs and key variables likely to influence their condition

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Background

Glass sponge bioherms, or reefs, are unique biogenic habitats found along the coasts of western Canada and the United States. Sponge reefs were known only from fossil records until analogous live reefs were discovered in Hecate Strait and Queen Charlotte Sound in the 1980s (Conway *et al*., 1991). More recently, the reefs were found in Southeast Alaska (Stone *et al*., 2014) and in Chatham Sound near the border between Canada and Alaska (Shaw *et al*., 2018). A number of smaller reefs have also been discovered in the Strait of Georgia and Howe Sound (Conway *et al*., 2005, 2007; Cook *et al*., 2008; Chu and Leys, 2010; Clayton and Dennison, 2017; DFO, 2018; Dunham *et al*., 2018a,b), hereinafter referred to as the Salish Sea.

The reefs in the Salish Sea are built by the Dictyonine glass sponges *Aphrocallistes vastus* and *Heterochone calyx*. These sponges possess rigid three-dimensional skeletal frameworks that remain intact after the sponges' death (Leys *et al*., 2007). The reefs are formed when larval sponges settle onto exposed skeletons of dead sponges and fine sediments entrained in bottom currents are baffled and trapped by the dead reef matrix, solidifying reef structure (Leys *et al*., 2004; Krautter *et al*., 2006). The bulk of the reef thus consists of a dead sponge matrix cemented by sediments, with only the most recent generation growing 1 to 2 m above the reef surface (Conway *et al*., 2001).

Several studies have provided insight into the ecosystem function of the glass sponge reefs. The reefs contribute to the productivity of benthic ecosystems by forming habitat for diverse communities of invertebrates and fish (Cook *et al*., 2008; Marliave *et al*., 2009; Chu and Leys, 2010; Dunham *et al*., 2015), act as regionally important silica sinks (Chu *et al*., 2011; Tréguer and De La Rocha, 2013), and, being one of the densest known communities of deep-water filter feeders, link benthic and pelagic environments through carbon and nitrogen processing (Kahn *et al*., 2015). However, understanding of the reefs' overall role in the Salish Sea ecosystem was limited, as most of the empirical work to date has been constrained to a few well-studied areas.

Research summary

Members of Working Group 32 and collaborators undertook research to map glass sponge reefs in the Salish Sea, quantify their condition and ecosystem function, describe biodiversity associated with the reefs, and identify drivers behind live sponge cover variation (DFO, 2018; Dunham *et al*., 2018a,b; Conway *et al*., 2019). Standardized visual surveys using a Remotely Operated Vehicle (ROV) were undertaken and quantitative assessments of all known reef complexes in the Strait of Georgia (Dunham *et al*., 2018a), as well as the newly discovered and mapped reefs in Howe Sound (DFO, 2018) were completed. An information-theoretic approach was used to examine six seabed terrain characteristics (rugosity, slope, curvature, broad and fine bathymetric position indices [BBPI and FBPI, respectively], and minimum depth surveyed), bottom current estimates, and two measures of potential human impact (density of anthropogenic objects and past fishing pressure) as predictor variables for live reef-building sponge percent cover.

The reefs varied widely in their estimated sponge cover: mean live reef-building sponge cover ranged from 0.2% to 17.5% (Fig. 3.1A) and dead sponge cover ranged from 0.1% to 42% (Fig. 3.1C). The frequency of occurrence of habitat categories also varied between reef complexes (Fig. 3.1D). Sponge rubble was observed in all reefs; rubble cover ranged from 0.1% to 14% (Fig. 3.1B).

The reefs were found to support diverse and abundant communities of invertebrates and fish, with 115 unique taxonomic groups observed (Dunham *et al.*, 2018a, online supplement S7). Expected species richness differed between reef complexes and ranged between 18 and 69.

For live reef-building sponge percent cover, the best fit model that explained 75% of the variation included the following explanatory variables: range of rugosity, curvature, minimum depth, and the interactions of range of rugosity with curvature and depth. In general, reefs with a broader range of rugosity had higher live sponge cover. However, for reefs located on strongly concave slopes (*i.e.*, negative profile curvature values), increased rugosity range led to lower live sponge cover. The deeper the reef was located the more concave the slope had to be before an increase in rugosity range switched from increasing to decreasing live sponge cover (Fig. 3.2). Overall, differences in live cover appeared to be largely driven by seabed terrain characteristics.

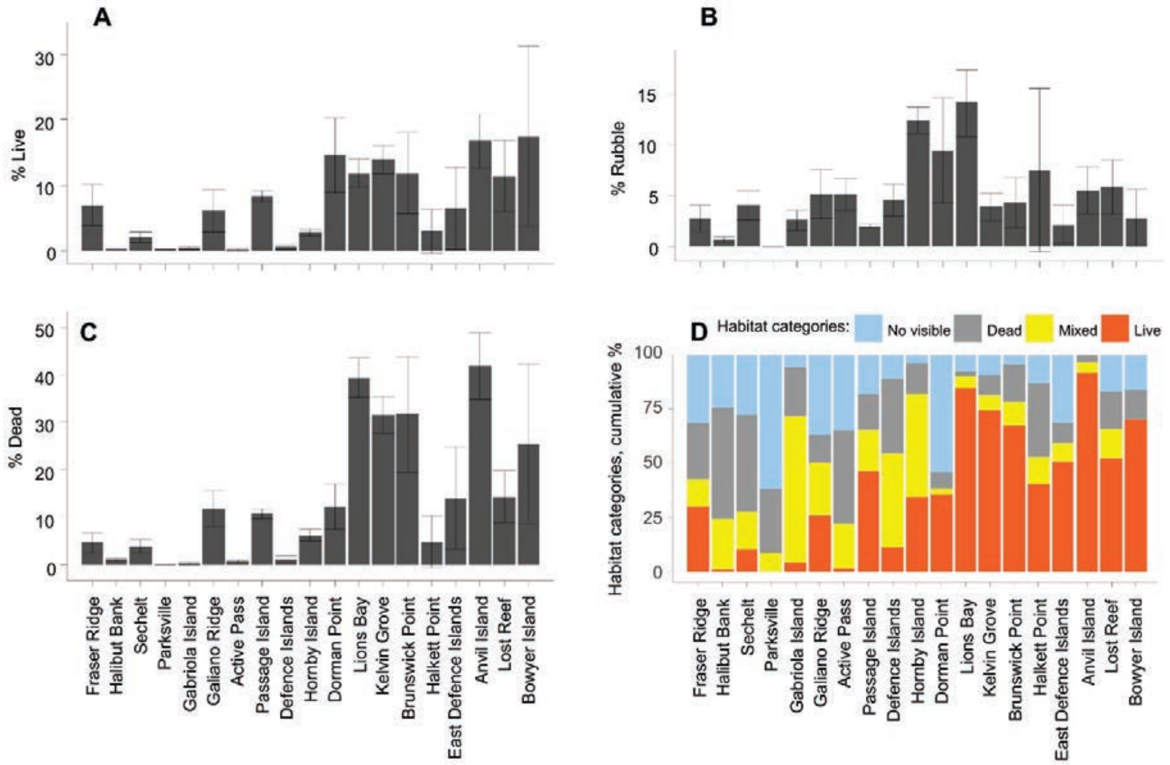

Fig. 3.1 Reef-building sponge cover and condition across 19 reefs: (A) live reef-building sponge percent cover per image, mean ± 95% Confidence Interval, (B) sponge rubble percent cover per image, mean ± 95% Confidence Interval, (C) dead reef-building sponge percent cover per image, mean ± 95% Confidence Interval, and (D) frequencies of occurrence of habitat categories per reef. Reproduced from Dunham *et al.* (2018a).

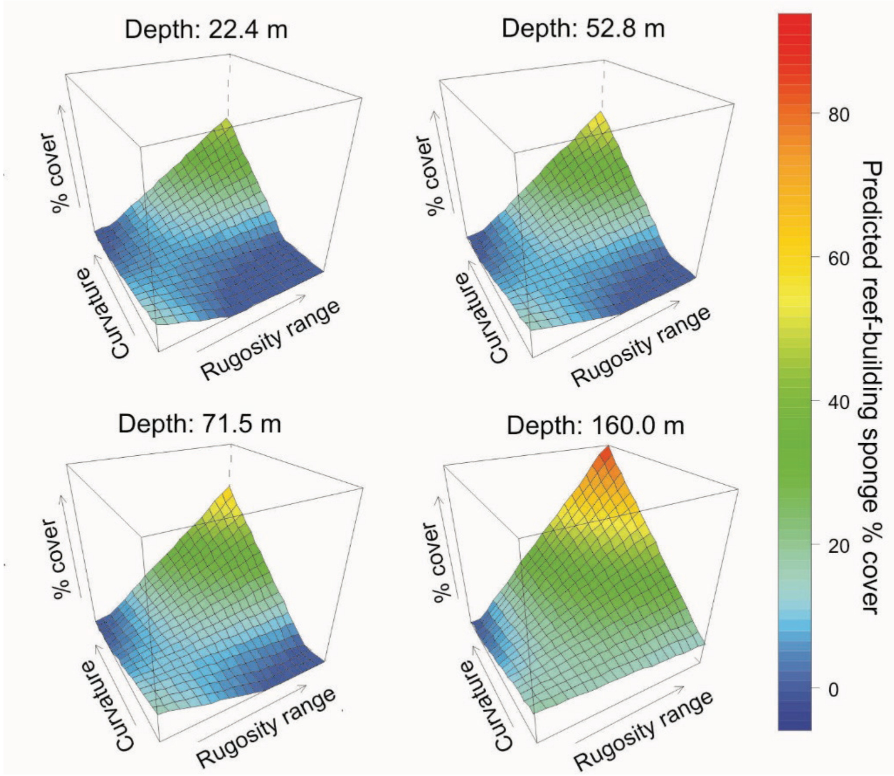

Fig. 3.2 Predicted live reef-building sponge cover from the model with seabed terrain variables that explained 75% of variation between reefs: % cover * rugosity-range + curvature + depth + rugosity-range * curvature + rugosity-range * depth. Predicted values less than 0 are displayed as 0% cover for clarity. Curvature gradient is from concave to convex. Reproduced from Dunham *et al*. (2018a).

In general, reefs with a broader range of rugosity exhibited higher live sponge cover. This may be explained by the more rugose seafloor generating local turbulence that may deliver nutrient-rich water to filter-feeding sponges. In addition, more rugose areas may promote infilling of the dead reef matrix with sediment which is crucial for supporting the reef mass and preventing sponge skeletons from dissolving in ambient seawater over time (Krautter *et al*., 2006), thus enabling reef existence and growth. However, for reefs located on strongly concave slopes, and especially those in relatively shallow waters, increased rugosity led to lower live sponge cover. These areas may be experiencing turbulence and suspended sediment concentrations that are too high to support reef-building glass sponges. Our results support the conclusion that glass sponge reefs require a delicate balance of turbidity and suspended sediment concentration.

Members of Working Group 32 and collaborators also reviewed glass sponge reef geological expressions (geomorphologies) across all known locations in the Pacific Ocean and combined these observations with available ecological datasets on sponge cover (Conway *et al*., 2019). The reef morphologies that develop over time are remarkably variable. We found a significant association between reef morphologies and the patch size of live reef habitat and live reef patch isolation. Ridge and bioherm reef morphologies support larger patches of live reef habitat surrounded by distinct areas of dead or dead and buried reef. Conversely, the small wave and thin biostrome reef morphologies typically have many small patches of live reef habitat surrounded by mixed live and dead reef. This supports the hypothesis that there is a link between the geologic reef morphology and the distribution of suitable habitat for live sponges within the reef. However, regardless of the reef morphology, live reefs occurred more commonly on the slopes up to the promontories of the reef form. Overall, the development of the diverse sponge reef morphologies and associated reef habitats appear to be driven by both physical and biological factors.

Reef-forming glass sponges are long-lived, but slow growing, exceptionally fragile, and thus slow to recover, especially from impacts that damage the reef's skeletal framework. Most reefs have been impacted by bottom-contact fishing activities. Using recent visual surveys conducted in Hecate Strait, Chatham Sound, and the Georgia Basin as reference baseline (2010–2017) and aggregating surveyed habitats at the geomorphic feature level (*i.e.*, all British Columbia sponge reefs), glass sponge reefs can be assigned a condition score of 4 (poor) following the classification of Ward (2011). It is important to note, however, that condition varies widely between reefs, and that the current level of glass sponge reef ecology and ecosystem function knowledge is not sufficient to confidently and comprehensively define and assess reef health. Therefore, this condition score should be interpreted with caution. The reef habitat trend over the last 5 years can be best characterized as stable. Because temporal data to support a trend in reef status requires a time frame of over 5 years (Dunham *et al.*, 2018b), this estimate is based on expert judgement, and associated confidence level is low. Integrated, comprehensive monitoring that employs relevant metrics of reef health at appropriate spatial and temporal scales and provides well-resolved time series is necessary to further understand sponge reef ecosystems, to assess the effectiveness of recently enacted protection measures (Marine Protected Areas, fishing closures), and to ensure adaptive management responsive to the state of the protected areas (Conway *et al.*, 2019).

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4. Potential indicators for assessing and monitoring diversity of biogenic habitats

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Background

Understanding the ecology and functioning of various biogenic habitats has shed light on their vital importance for the continued conservation of natural resources and associated ecosystem services. As resource management moves toward holistic, habitat-based approaches such as ecosystem-based fisheries management (Pikitch *et al*., 2004), there is a growing need for management actions that promote healthy biogenic habitats. These management actions require ecological monitoring with clear research questions, appropriate indicators, and a well-designed data collection process to produce robust data and useful outcomes (Underwood and Chapman, 2013). A recently developed framework for biological monitoring (Reynolds *et al*., 2016) offered an overarching view of the steps required for successful monitoring programs and emphasized the importance of linkages among various planning decisions. However, for data-limited biogenic habitats, designing monitoring programs can be challenging. The structure and functioning of such habitats and underlying ecosystem-level processes (*e.g.*, spatial extent, magnitude of natural variability in abundance and distribution of foundation species, species–habitat associations) are not well understood, often due to these habitats being remote and/or deep, limiting accessibility, and increasing monitoring costs. These limitations may jeopardize effective management and conservation of these habitats, many of which are threatened by human activities (Rossi *et al*., 2017). A clear road map for designing robust, efficient monitoring programs in the face of data and resource limitations was required.

Research summary

Members of Working Group 32 and collaborators reviewed recent publications (2012–2017) to obtain an overview of benthic assessment and monitoring approaches, methods, and indicators across a range of relatively well-studied marine biogenic habitats. Common themes relevant for all habitat types were identified and, drawing upon these themes, a systematic approach for establishing monitoring programs for data-limited biogenic habitats was developed (Loh *et al*., 2019).

Biogenic habitat monitoring efforts largely focus on the characteristics, distribution, and ecological function of foundation species, but may target other habitat-forming organisms, especially when community shifts are observed or expected, as well as proxies of habitat status, such as indicator species. Broad-scale methods cover large spatial areas and are typically used to examine the spatial configuration of habitats, whereas fine-scale methods tend to be laborious and thus restricted to small survey areas but provide high-resolution data. Recent emerging methods enhance the capabilities of surveying large areas at high spatial resolution and improve data processing efficiency, bridging the gap between broad- and fine-scale methods. Although sampling design selection may be limited by habitat characteristics and available resources, it is critically important to ensure appropriate matching of ecological, observational, and analytical scales.

Across biogenic habitat types, assessment and monitoring efforts share the following common themes: defining study objectives, assembling preliminary data, determining scale of interest, selecting indicators, determining study methods and sampling design, and full protocol review. Drawing on these common themes, we propose a structured, iterative approach to designing monitoring programs for marine biogenic habitats that allows for rigorous data collection to inform management strategies, even when data and resource limitations are present (Fig. 4.1).

As part of this project, members of Working Group 32 and collaborators also produced (1) an overview of the applicability, advantages, and disadvantages of broad- and fine-scale survey methods for biogenic habitats and (2) a summary of attributes, representative indicators, and associated metrics used for biogenic habitat assessments, with corresponding survey methods (Loh *et al*., 2019). These summaries can be used for developing monitoring programs for any type of biogenic habitat in the North Pacific and elsewhere in the world.

In oceans impacted by human pressures, biogenic habitat assessment and monitoring are crucial for attributing causes of decline and for providing solutions to mitigate habitat damage from anthropogenic impacts and monitoring environmental change (Downs *et al*., 2005). Systematic monitoring approaches, as laid out in Loh *et al*. (2019), are urgently required to implement science-based management, evaluate the success of protective measures, and guide adaptive management strategies for data-limited marine biogenic habitats.

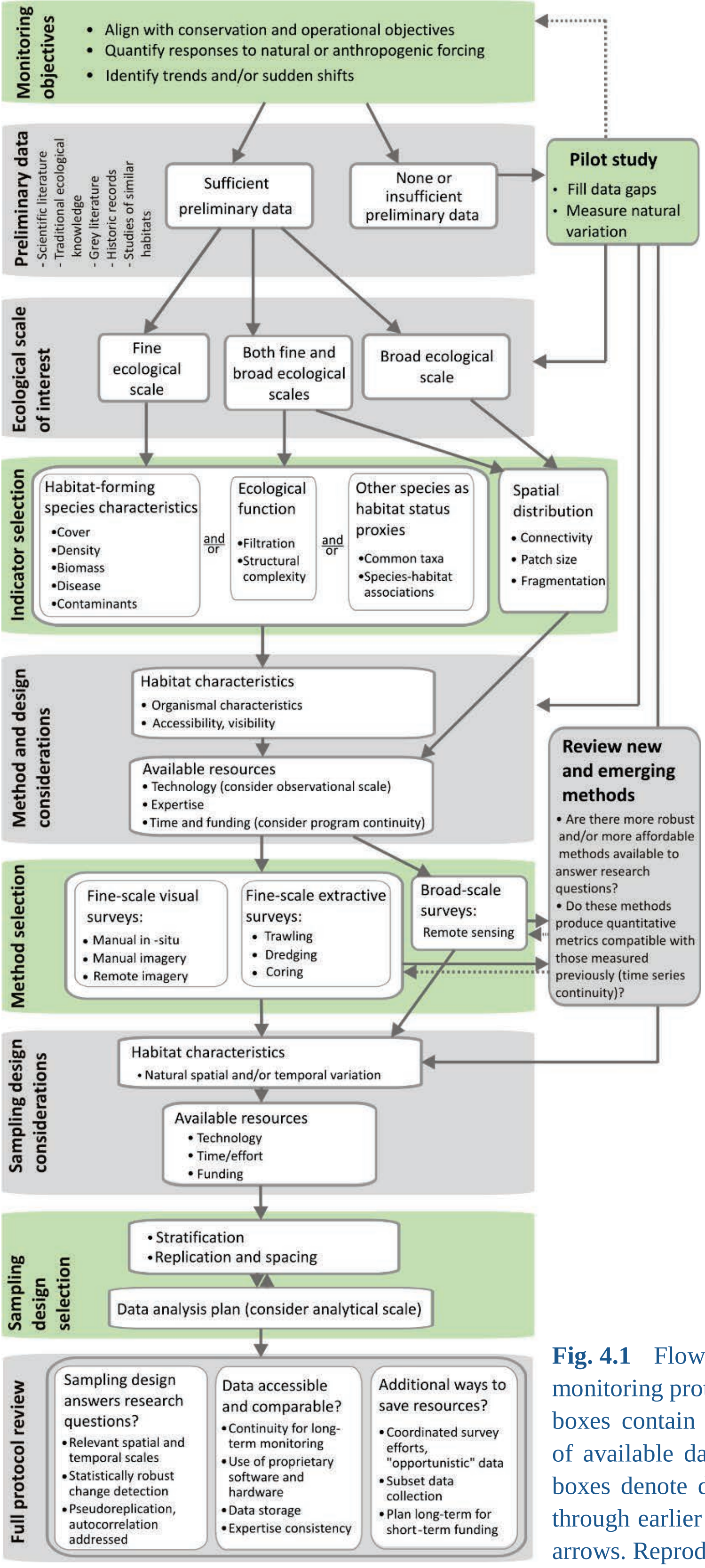

Fig. 4.1 Flowchart illustrating the development of a monitoring protocol for marine biogenic habitats. Gray boxes contain considerations (to facilitate evaluation of available data, methods, and protocols) and green boxes denote decisions. Key times for iteration back through earlier steps are denoted by the return dashed arrows. Reproduced from Loh *et al*. (2019).

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5. *Potential indicators for assessing and monitoring diversity of biogenic habitats*

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Background

Tropical and subtropical islands are associated with coral reefs, which provide ecosystem services, including fisheries, tourism, and coastal protection. This is especially true of reef islands that are composed fully of reef-derived materials. Global-scale environmental changes, including climate change, have been causing significant change on corals. Japan provides an ideal setting to examine these changes because it covers a wide latitudinal range, stretching from subtropical to temperate areas, and latitudinal limits of coral reefs and coral distributions are observed around the Japanese islands.

Seas around Japan have shown significant sea surface temperature (SST) rises (0.8°C–1.3°C/100 years in annual mean values; http://www.data.jma.go.jp/kaiyou/data/shindan/a_1/japan_warm/japan_warm.html), and the rising SSTs could have caused two consequences on Japanese corals: decline in the south due to anomalously high SSTs in summer that caused coral bleaching, and range expansion in the north due to rising winter SSTs that allowed the survival of warm-water corals in winter. The latter may be associated with a decline of macroalgae.

Research summary

Members of Working Group 32 and collaborators have worked on the detection and projection of the above issues as follows:

Bleaching in the south (Kumagai et al., 2018b)

Excessive SSTs can cause coral bleaching, resulting in coral death and decrease in coral cover. A SST threshold of 1°C over the climatological maximum is widely used to predict coral bleaching. In this study, we refined thermal indices predicting coral bleaching at high-spatial resolution (1 km) by statistically optimizing thermal thresholds, as well as considering other environmental influences on bleaching such as ultraviolet (UV) radiation, water turbidity, and cooling effects. We used a coral bleaching dataset derived from the web-based monitoring system Sango Map Project at scales appropriate for the local and regional conservation of Japanese coral reefs. We recorded coral bleaching events in the years 2004 to 2016 in Japan. We showed the influence of multiple factors on the ability to predict coral bleaching, including selection of thermal indices, statistical optimization of thermal thresholds, quantification of multiple environmental influences, and use of multiple modeling methods (generalized linear models and random forests). After optimization, differences in predictive ability among thermal indices were negligible. Thermal index, UV radiation, water turbidity, and cooling effects were important predictors of the occurrence of coral bleaching. Predictions based on the best model revealed that coral reefs in Japan have experienced recent and widespread bleaching.

Range shift in the north (Kumagai et al., 2018a)

Coral and macroalgal communities are threatened by global stressors. However, recently reported community shifts from temperate macroalgae to tropical corals offer conservation potential for corals at the expense of macroalgae under climate warming. Although such community shifts are expanding geographically, our understanding of the driving processes is still limited. Here, we reconstructed long-term climate-driven range shifts in 45 species of macroalgae, corals, and herbivorous fishes from over 60 years of records (mainly 1950–2015), stretching across 3,000 km of the Japanese archipelago from tropical to subarctic zones. Based on a revised coastal version of climate velocity trajectories, we found that prediction models combining the effects of climate and ocean currents consistently explained observed community shifts significantly better than those relying on climate alone. Corals and herbivorous fishes performed better at exploiting opportunities offered by this interaction. The contrasting range dynamics for these taxa suggest that ocean warming is promoting macroalgal-to-coral shifts both directly by increased competition from the expansion of tropical corals into the contracting temperate macroalgae, and indirectly via deforestation by the expansion of tropical herbivorous fish. Beyond the effects on individual species, our results provide evidence on the important role that the interaction between climate warming and external forces conditioning the dispersal of organisms, such as ocean currents, can have in shaping community level responses, with concomitant changes to ecosystem structure and functioning. Furthermore, we found that community shifts from macroalgae to corals might accelerate with future climate warming, highlighting the complexity of managing these evolving communities under future climate change.

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6. Selection of the proper spatial resolution for habitat modeling of cold-water corals

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Background

Cold-water corals are benthic cnidarians that generally inhabit deep-sea floors of the world ocean. Some deep-sea corals form complex, reef-like structures and provide habitats for other animals. Due to their slow growth, long life span, and slow recovery from physical damage, cold-water corals are claimed as important components of vulnerable marine ecosystems (VMEs). The assessment and management of impacts on VMEs are urgent tasks for deep sea bottom fisheries to fulfill the global requests for ecosystem-based fishery management. Habitat suitability modeling of cold-water corals has been used to estimate the priority areas of conservation interests. Habitat suitability modeling of cold-water corals are conducted at various spatial resolutions partly due to the limited availability of data from the deep-sea environment. Whereas coarse spatial resolutions, such as 1-degree grid cells, are helpful for broader strategic consideration of the selection of priority areas for conservation on regional and global scales, fine spatial resolutions are required for tactical management at local scales. Members of Working Group 32 and collaborators examined the effects of spatial resolution of bathymetric data on habitat suitability modeling of cold-water corals at a local scale, namely on seamounts. Large cold-water gorgonian corals on the southern Emperor Seamounts in the high seas of the central North Pacific Ocean were used as an example for planning the spatial management of the deep-sea habitat. The grid-cell size of the bottom bathymetry raster generated from the multi-beam echo sounder data was manipulated to investigate the effects of the spatial resolution of bathymetric data on terrain attributes and habitat suitability modeling of these corals.

Research summary

Working Group 32 members and collaborators have worked on spatial resolutions as follows (Miyamoto *et al*., 2017). Species occurrence data and high-resolution multi-beam bathymetry data were collected by ship-borne surveys in the Emperor Seamounts area from 2009 to 2013. Depth and terrain parameters were generated at six different grid-cell sizes from 25 × 25 m to 800 × 800 m and used as environmental variables for habitat analysis (Fig. 6.1). The values of terrain parameters showed different patterns at smaller (≤ 100 m) and larger (> 100 m) grid-cell sizes (Fig. 6.2). Accordingly, the topographic structures expressed by the raster maps changed with the grid-cell sizes. MaxEnt habitat models showed higher prediction accuracy at smaller grid-cell sizes, and predicted high habitat suitability at such locations as ridges on upper slopes and terrace edges and surface undulation on seamount tops, suggesting the importance of sloped and/or irregular sea floor as habitat for large gorgonian corals. Within the available data, the model of 25-m grid-cell resolution showed the best performance in habitat modeling of cold-water corals on the Emperor Seamounts. The sea floor structures predicted to be suitable for large gorgonians were consistent with the biological characteristics of large gorgonians. It was confirmed that MaxEnt models gave satisfactory performance at smaller grid-cell sizes (≤ 200 m). The variation in terrain attribute values also differed between smaller (≤ 100 m) and larger (≥ 200 m) grid-cell sizes. These results demonstrate that it is desirable to obtain bathymetric grid data at resolutions of 100 m or less for the purpose of predicting the distributions of corals at a local scale (*e.g.*, within a seamount). It is important to decide the optimum spatial resolution when considering the objective of analysis, data availability and geographical or biological characteristics.

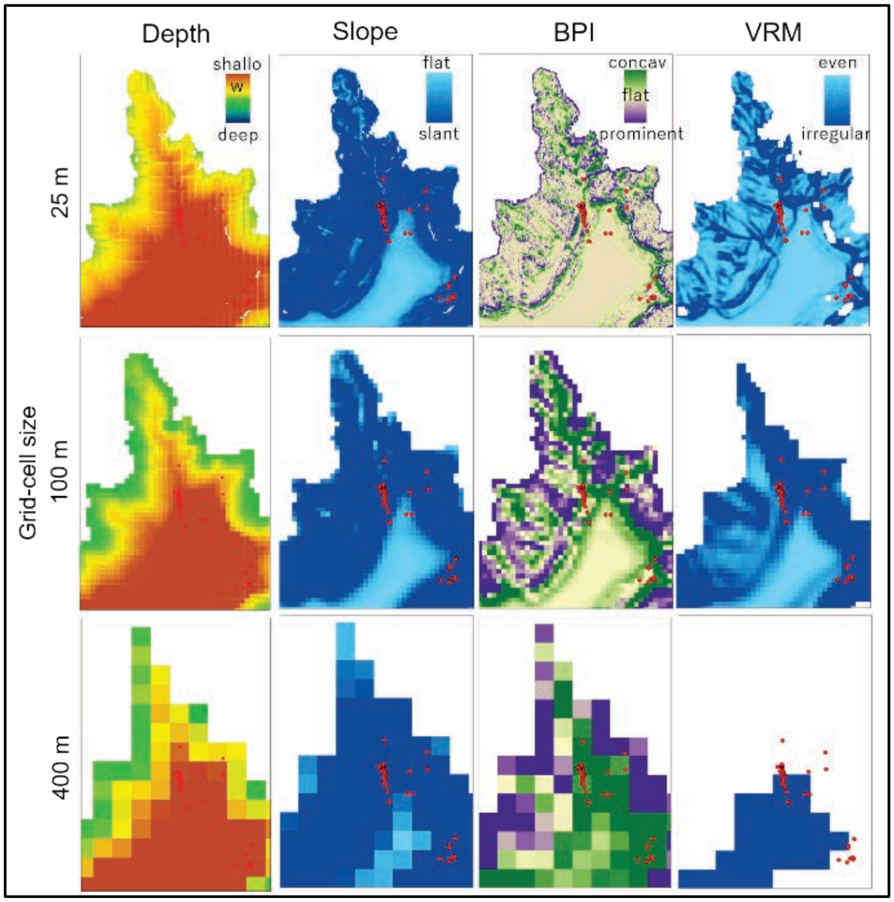

Fig. 6.1 Example of maps of depth and three terrain attributes [slope, bathymetric position index (BPI) and vector ruggedness measure (VRM)] at three grid-cell sizes for the Colahan seamount. Red dots represent location where large gorgonians were observed or collected. Reproduced from Miyamoto *et al*. (2017).

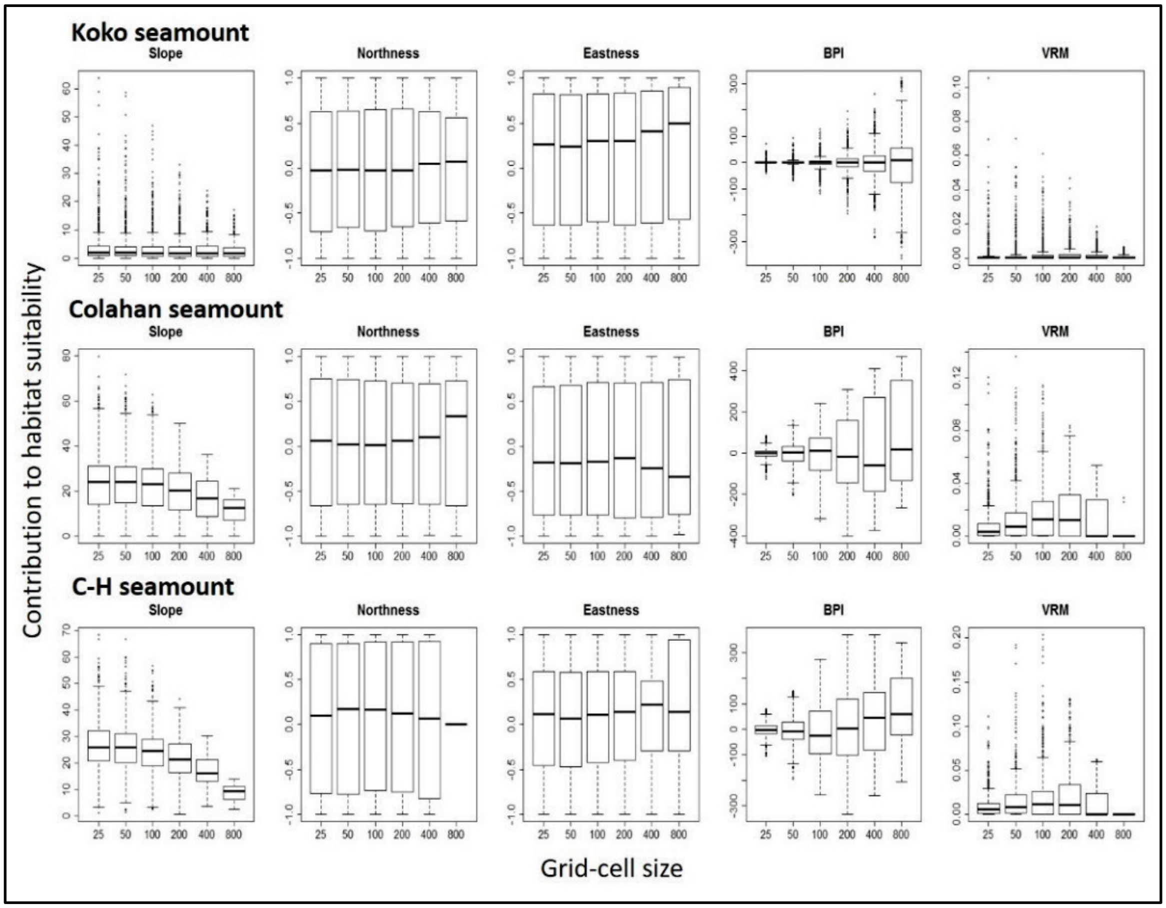

Fig. 6.2 Boxplots of terrain parameters as six grid-cell sizes on the three studied seamounts. Boxplots show median (thick black lines), range (dashed lines), upper and lower fifth and 95th percentiles (boxes), and outliers (points). *X*-axis indicates grid-cell sizes. BPI = bathymetric position index, VRM = vector ruggedness measure. Reproduced from Miyamoto *et al*. (2017).

Reference

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7. *Method for assessing the validity of the VME indicator taxa in the Emperor Seamounts area*

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Background

Some species of cold-water corals are known to provide biogenic habitats to other animals on the deep sea-floor in several areas of the world ocean. Due to their slow growth, long life span and slow recovery from physical damage, as well as their habitat forming property, cold-water corals are considered to be important components of vulnerable marine ecosystems (VMEs). In the Emperor Seamounts area of the North Pacific Ocean, four orders of cold-water corals: Gorgonians (Scleraxonia, Holaxonia and Calcaxonia), Alcyonacea (excluding Gorgonians), Antipatharia, and Scleractinia, were selected as VME indicator taxa by the North Pacific Fisheries Commission (NPFC), and the bycatch threshold was set at a tentative value similar to other Regional Fisheries Management Organizations (RFMOs). However, the appropriateness of these indicator species has not been examined scientifically. In this study, benthic samples collected through bottom surveys from 2009 to 2014 were identified and listed for delineating the characteristics of benthic fauna in the Emperor Seamounts area. Association analysis was applied to examine the validity of candidate VME indicator taxa as biodiversity indicators through examination of their co-occurrence with other benthic animals.

Research summary

Members of Working Group 32 and collaborators have introduced a new method for assessing the validity of VME indicator taxa as follows (Miyamoto and Kiyota, 2017). The benthos samples collected by the R/V *Kaiyo-maru* in the past six years were used to evaluate the effectiveness of four orders of cold-water corals (*i.e.*, Gorgonians, Alcyonacea, Antipatharia and Scleractinia) and other benthic animals as VME indicator taxa in the Emperor Seamounts area. The benthos samples were identified and listed, and their occurrence frequencies and total weights were calculated (Fig. 7.1).

Then association analysis, which is often used for discovering hidden relationships among purchased items in market transaction data (Blattberg *et al.*, 2008), was applied to the occurrence data per sampling haul to explore the co-occurring relationships of benthic animals. For example, an association rule which indicates that many customers purchasing item A also purchase item B is expressed in the form of {A} → {B} (Silverstein *et al.*, 1998, Hahsler *et al.*, 2005). In this expression, {A} is called the antecedent part and {B} is called the consequent part. In this study, such association rules were explored that indicate co-occurrence of benthic taxa such as “A habitat where benthos taxon A occurs is also inhabited by taxon B”. The haul-by-haul occurrence data were applied to the association analysis, and those rules that include one of the six candidate VME indicator taxa, *i.e.*, Gorgonians, Alcyonacea (sea fans), Antipatharia (black corals), Scleractinia (stone corals), Stylasterina (hydrocorals) or Porifera (sponges), in the consequent part were extracted. The effectiveness of an association rule is evaluated by the values of Support, Confidence and Lift. Gorgonians and Scleractinia showed high occurrence frequencies and large total wet weight (Fig. 7.2). The occurrence frequencies of Stylasterina, Alcyonacea, Antipatharia and Porifera were low, but the total wet weight of Porifera was relatively high because of the large water content. Many association rules that include Gorgonians or Scleractinia in the consequent part were extracted and showed high confidence and lift values. Only a small number of association rules were extracted for Porifera, and no rules were extracted for Alcyonacea, Antipatharia and Stylasterina. These results demonstrate that Gorgonians and Scleractinia frequently co-exist with other benthic animals and suggest their potential as VME indicator taxa in the Emperor Seamounts area. This study presents a new method to assess characteristics of benthic communities and to screen for potential indicator taxa based on the analysis of co-occurrence tendencies among benthic taxa.

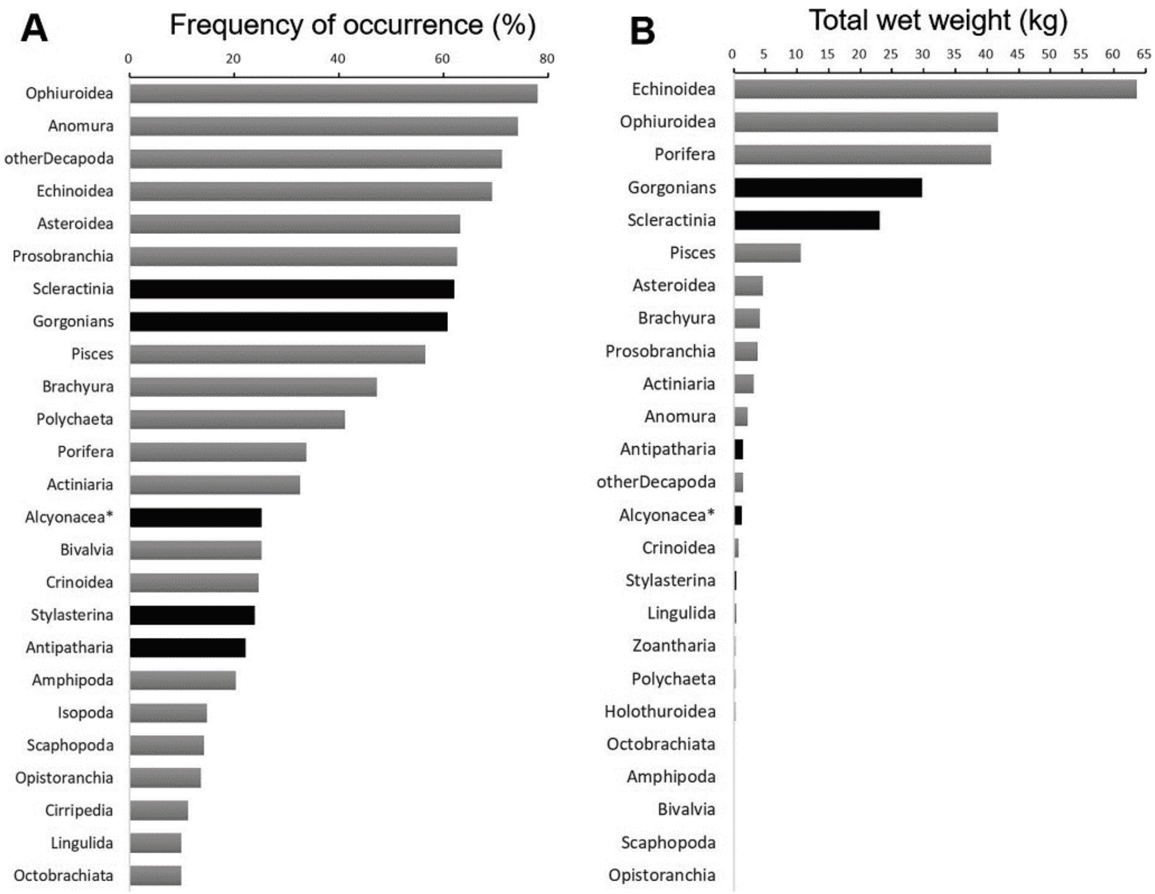
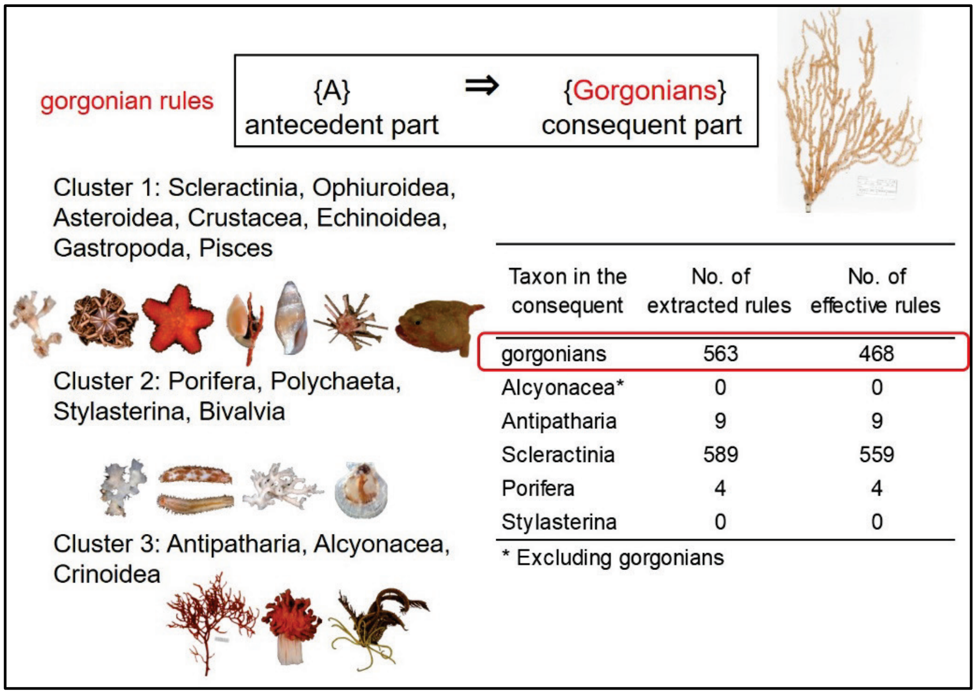


Fig. 7.1 Frequency of occurrence (A) and total wet weights (B) of benthic megafauna collected by surveys in the southern Emperor Seamounts area. Only the top 25 groups are shown in this figure. Alcyonacea* excluding Gorgonians (Scleraxonia, Holaxonia and Calcaxonia).



Taxon in the consequent	No. of extracted rules	No. of effective rules
gorgonians	563	468
Alcyonacea*	0	0
Antipatharia	9	9
Scleractinia	589	559
Porifera	4	4
Stylasterina	0	0

* Excluding gorgonians

Fig. 7.2 Example of results of Gorgonians association analysis. Most effective association rules had Gorgonians in the consequent part and other taxa in the antecedent parts.

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8. *Application of association analysis for identifying VME indicator taxa on the basis of sea-floor visual images*

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Research summary

Members of Working Group 32 and collaborators further explored another usage of the association analysis for identifying VME indicator taxa on the basis of visual seafloor surveys. Visual images of the sea floor were collected through observation surveys using the drop camera system operated by the R/V *Kaiyo-maru* in the Emperor Seamounts area. The benthic animals taken in each sea-floor footage were identified to family or order levels (Porifera, Stylasterina, Pennatulacea, Gorgonians, Alcyonacea (excluding Gorgonians), Antipatharia, Scleractinia, Actiniaria, Corallimorpharia, Zoantharia, jellyfish, Gastropoda, Cephalopoda, Polychaeta, Crustacea, Crinoidea, Asteroidea, Ophiuroidea, Echinoidea and Pisces), and their occurrence frequencies were calculated. Using the density of benthic taxa in sampling locations as multivariate distance data, the sea-floor photographing sites or benthic taxa were classified into clusters according to Ward's method. Canonical Correspondence Analysis (CCA) was applied to characterize the benthic community by environmental parameters (depth, flatness, softness and roughness). Cluster analysis indicated that the survey sites were classified into two large clusters such as hard bottom or soft bottom, and further classified into six clusters relevant to the variations of depth, flatness, softness and roughness. A CCA plot demonstrated the influence of sea-floor features on benthos occurrence (Fig. 8.1).

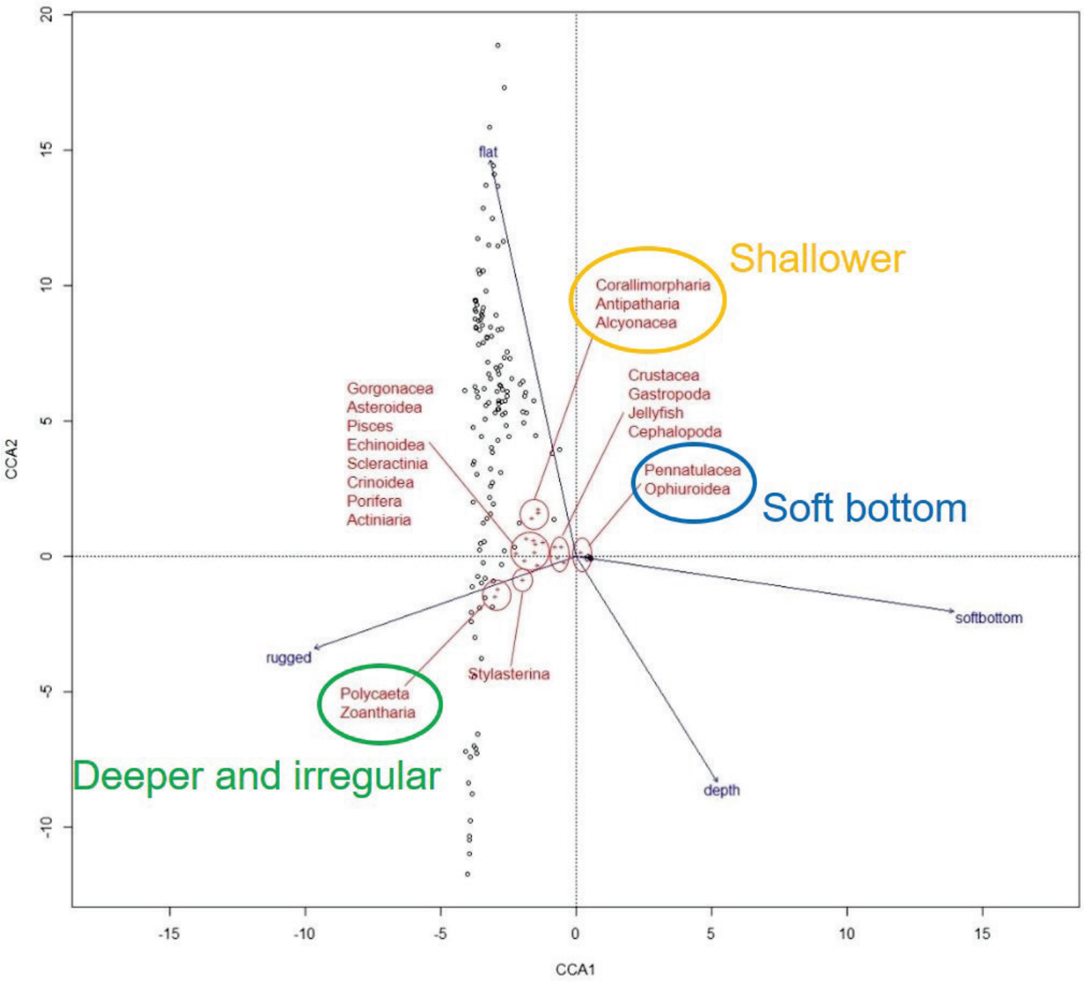

Fig. 8.1 Canonical Correspondence Analysis (CCA) plot characterizing the benthic community by four environmental parameters (*i.e*., depth, flatness, softness and roughness).

Then association analysis, which is commonly used for discovering hidden relationships among purchased items in market transaction data (Blattberg *et al*., 2008) and applied to assess the validity of benthic indicator taxa (Miyamoto and Kiyota, 2015), was applied to the occurrence data per sea-floor photographing site to explore the co-occurring relationships of benthic animals. Association rules that represent a strong relationship like A (condition part) →B (conclusion part) were extracted. The Gorgonians showed 27 effective association rules that included 10 taxa as antecedent (Table 8.1). Only a small number of effective rules were extracted when Scleractinia or Porifera were placed in the consequent. The extracted rules with Scleractinia or Porifera as the consequent included few taxa as antecedents. These results demonstrate that Scleractinia and Porifera are less effective as indicators of the benthic communities in the Emperor Seamounts area than Gorgonians.

Table 8.1 Number of effective association rules that include candidate vulnerable marine ecosystem indicator taxa as the consequent part.

Taxon in the consequent	No. of rules	Taxa in the antecedents
Gorgonacea	27	Alcyonacea, Antipatharia, Scleractinia, Porifera, Stylasterina, Crustacea, Crinoidea, Asteroidea, Echinoidea, Pisces
Alcyonacea	0	–
Antipatharia	0	–
Scleractinia	2	Antipatharia, Crustacea, Echinoidea, Pisces
Porifera	1	Gorgonacea, Echinoidea

In summary, the composition of the benthic community varied greatly depending on the bottom substratum, and Gorgonians were the dominant benthos on hard bottom that occupied many stations. Association analysis demonstrated co-occurrence of Gorgonians with many other benthic animals.

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Miyamoto, M., and Kiyota, M. 2017. Application of association analysis for identifing indicator taxa of vulnerable marine ecosystems in the Emperor Seamounts area, North Pacific Ocean. *Ecological Indicators* **78**: 301–310.

9. *Assessment of species diversity and dominance of shallow water corals using environmental DNA*

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Background

DNA that originated from various sources, such as mucus, metabolic waste, and damaged tissues from multicellular organisms exists in seawater and is called environmental DNA (eDNA). Recently eDNA has begun to be employed in aquatic environmental research, and it is also being used to monitor marine biodiversity. However, we are not aware of any reports that have attempted to use eDNA from seawater to monitor coral reefs. In this study, we performed tank experiments with running seawater as an initial proof of the concept.

Corals release massive amounts of soluble mucus, which transfers large amounts of energy and nutrients to the reef substrate. Due to the symbiont's natural rate of increase, corals steadily release *Symbiodinium* cells into the surrounding environment, suggesting that close to reefs, seawater should contain detectable quantities of DNA from both corals and *Symbiodinium*. Recently whole genome sequences of an *Acropora* coral and *Symbiodinium* have been published, and next-generation sequencing (NGS) technologies have been used to investigate coral reef biodiversity. For easier assessment of the species diversity of reef building corals, we developed a novel method for monitoring of *Acropora* corals from environmental DNA (eDNA) in seawater using NGS.

Research summary

We performed a tank experiment with running seawater using 19 *Acropora* species; *A. acuminata*, *A. austera*, *A. awi*, *A. cytherea*, *A. carduus*, *A. digitifera*, *A. echinata*, *A. florida*, *A. grandis*, *A. hyacinthus*, *A. intermedia*, *A.* sp1 aff. *echinata*, *A. microphthalma*, *A. muricata*, *A. nasuta*, *A. selago*, *A. tenuis* (Shinzato *et al*., 2018). Complete mitochondrial genomes of all the *Acropora* species were assembled to create a database and major types of their *Symbiodinium* symbionts were identified. Then eDNA was isolated by filtering inlet and outlet seawater from the tanks. We detected all of the tested *Acropora* types from eDNA samples. Proportions and numbers of DNA sequences were both positively correlated with masses of corals in the tanks. In this trial, we detected DNA sequences from as little as 0.04 kg of *Acropora* colony, suggesting that existence of at least one adult *Acropora* colony (~30 cm diameter = 1 kg) per m^2 at depths <10 m could be detected using eDNA in the field. Although this is the initial attempt to detect coral and *Symbiodinium* simultaneously from eDNA in seawater, this method may allow us to perform high-frequency, high-density coral reef monitoring of coral species composition and their health conditions without specialized skills to identify coral species using morphological traits.

Reference

Shinzato, C., Zayasu, Y., Kanda, M., Kawamitsu, M., Satoh, N., Yamashita, H. and Suzuki, G. 2018. Using seawater to document coral-zoothanthella diversity: A new approach to coral reef monitoring using environmental DNA. *Frontiers in Marine Science* **5**: 28. doi: 10.3389/fmars.2018.00028.

10. Studies of the distribution and diversity of biogenic habitat forming taxa in the USA

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[2] Present address: Fisheries and Oceans Canada, Pacific Biological Station, Nanaimo, British Columbia, Canada
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Background and overview

This report summarizes the recent contributions by the USA and its WG 32 members (Sam Georgian, John Guinotte, Chris Rooper and Les Watling) to assess the distribution, abundance and species associations of deep-sea corals and sponges within the US Exclusive Economic Zone (EEZ). It should be noted that the USA conducts extensive research on deep-sea coral and sponge within its EEZ and much of that research is summarized in reports by NOAA's Deep Sea Coral Research and Technology Program (https://www.fisheries.noaa.gov/national/habitat-conservation/deep-sea-coral-habitat). The most recent report on the state of deep-sea coral and sponge ecosystems was published in 2017 (Hourigan *et al*., 2017) and contains an expanded summary of the work on deep-sea corals and sponges in the USA. Here we focus on the research activities that were linked conceptually, temporally or directly to WG 32 activities and Terms of Reference.

Coral and sponge ecosystem data in the USA

Records of deep-sea coral and sponge presence and abundance in the North Pacific Ocean have been collected historically through a number of scientific activities by research organizations in the USA. These include data from the extensive fisheries-independent surveys of ecosystems on the US West Coast and Alaska (both longline and bottom trawl) where the relative abundance and species of corals and sponges are recorded. It also includes a number of other studies using visual survey methods, such as submersibles, remote operated vehicles, autonomous underwater vehicles and towed camera systems. Often these data have records of associated fish and invertebrate assemblages. In North Pacific Ocean waters a number of studies have documented associations of rockfishes (*Sebastes* sp.) and other demersal fish species with deep-sea corals and sponges, as well as identifying some key relationships between fish reproduction and these ecosystems.

Beginning about 2015 these historical data have been housed in a publicly accessible data portal (NOAA Deep Sea Coral and Sponge Portal, https://deepseacoraldata.noaa.gov/). From 2014 to 2019, members of WG 32 compiled data from studies in Alaska and the US West Coast and contributed these data ($n > 10{,}000$ observations) to the publicly accessible database making it available to the wider PICES community. The database follows the standards of OBIS-USA and is an extension of the international Darwin Core Standard. Key points for these aggregated data are:

- Most studies that collect data on coral and sponge distribution in the USA have records included in a publicly available database that is updated quarterly;
- Care in the use of these data is needed, as the quality can vary. A source listed for each data record can be used to check the validity and suitability for a given analysis.

Modeling approaches

One of the key activities of WG 32 was to review modeling approaches to predict the potential distributions of species and habitat suitability for corals and sponges (*e.g.*, MaxEnt, boosted regression trees, or high resolution bathymetry-based models) within national EEZs. During PICES-2016 (San Diego, USA), a 2-day workshop on "*Distributions of habitat-forming coral and sponge assemblages in the North Pacific Ocean and factors influencing their distributions*" was held on modeling approaches for deep-sea corals and sponges. It was co-convened by Drs. Kwang-Sik Choi (Korea), Janelle Curtis (Canada), Masashi Kiyota (Japan) and Chris Rooper (USA). The outcomes of the workshop were recommendations for data and modeling approaches that should be considered for deep-sea coral and sponge ecosystems. Technical aspects of the species distribution modeling, including the best practices for generating input data, creating models and evaluating the results, data-driven approaches to define bioregions, a multi-scale assessment of species distribution models, and an assessment of the model transferability were examined. The workshop also included a "hands-on" exercise of building some preliminary models of corals and sponges for data-limited taxa in the North Pacific Ocean. The goals of the modeling session were to: 1) evaluate existing environmental variables/mechanisms affecting basin-wide distribution of coral and sponge, 2) construct preliminary basin-wide habitat models for taxa, including glass sponges and corals in the North Pacific Ocean, and 3) provide model-based information for predicting potential changes in distributions of coral and sponge with climate change. An example of the model predictions for *Antipatharia* in the North Pacific Basin developed during the workshop is shown in Figure 10.1, with the important variables predicting the distribution shown in Table 10.1.

Table 10.1 Variables important in modeling the distribution of *Antipatharia* in the North Pacific Ocean for two alternative models, one without a bias grid correction for sampling distribution and one corrected for the sampling bias.

Variable	% Contribution without bias grid	% Contribution with bias grid
Calcite	58.6	65.5
Roughness	14.3	3.6
Temperature	7.8	11.2
Silicate	4.2	–
TPI 20,000 m	3.6	3.8
Dissolved oxygen	3.3	–
Dissolved inorganic carbon	3.2	–
Alkalinity	–	2.1
Regional currents	–	2.1
Vertical currents	–	2.0
AUC	0.945 (0.004)	0.925 (0.003)

TPI = Topographic Position Index
AUC = the area under the receiver-operator curve (an indication of overall model fit).

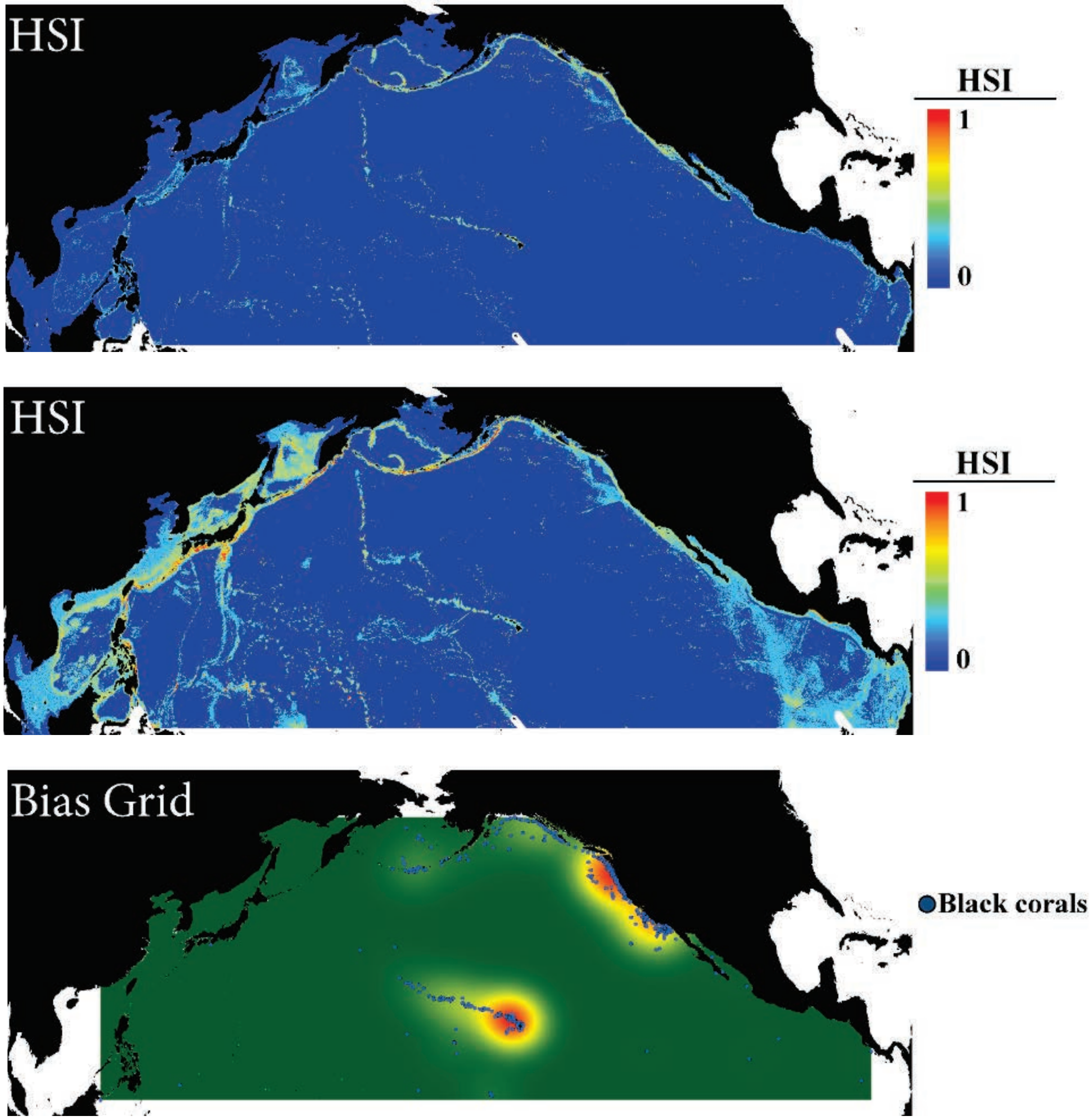


Fig. 10.1 Example models of the distribution for *Antipatharia* developed by WG 32 during the PICES-2016 modeling workshop. The predictions were developed from maximum entropy models without (top) and with (middle) a correction for sampling density (bottom). HSI = habitat suitability index.

In addition to the PICES workshop in 2016, a number of concurrent modeling efforts for Alaska and US West Coast were conducted by WG 32 members. A maximum entropy model was used to predict habitat suitability for deep-sea corals on the US West Coast (Guinotte and Davies, 2014) and a generalized additive modeling approach was used to predict the distribution, abundance and diversity of corals and sponges in the Aleutian Islands and eastern Bering Sea (Rooper *et al*., 2014, 2016). In the Gulf of Alaska, a suite of modeling methods (maximum entropy, general linear models, generalized additive models, boosted regression tree and random forest) were evaluated and used in an ensemble to predict the distribution of corals and sponges. In all, these efforts resulted in predictions of the distribution of coral taxa for the entire USA EEZ in the North Pacific. These models continue to be developed and improved (Guinotte *et al*., 2017) as new data and techniques become available. Key findings from this work are:

- Model validation using independently collected data is important to consider;
- Ensemble models can perform better across a range of species than individual models;
- The modeling method has less effect on the result than the quality of the underlying predictor and distribution data.

Environmental and ecological predictors

A key outcome in modeling the distribution of deep-sea coral and sponge ecosystems in the North Pacific Ocean that was advanced within WG 32 was the identification of large-scale environmental and ecological predictors for the distribution and biodiversity of coral, sponge and associated taxa. Dr. Samuel Georgian (USA) and colleagues put together an exhaustive group of measured and derived predictor variables for the North Pacific Ocean on a 1 km^2 grid (Table 10.2; Fig. 10.2). These included bathymetric and terrain variables as well as environmental variables thought to influence the distribution of deep-sea corals and sponges. A number of topographical variables were created, as complex seafloor features generally elevate local currents, which increase larval dispersal, food supply, sediment and waste removal, and dissolved oxygen flux (*e.g*., Dorschel *et al*., 2007). Since cold-water corals are filter feeders and therefore, reliant on the vertical transfer of surface productivity (Duineveld *et al*., 2007), the particulate organic carbon (POC) flux (mg C m^{-2} yr^{-1}) to the seafloor was also included as a proxy for food availability. The saturation state of the calcite polymorph of calcium carbonate, temperature (°C), salinity (psu), and dissolved oxygen (ml l^{-1}) were included due to their known biological relevance to cold-water octocorals (Mortensen and Buhl-Mortensen, 2004) and importance in previous habitat suitability models (Quattrini *et al*., 2013; Georgian *et al*., 2014; Etnoyer *et al*., 2017). Finally, the distribution of hard bottom substrates was included as the availability of hard substrata is essential for coral recruitment in a number of cold-water corals (*e.g*., Georgian *et al*., 2014) including Paramuricea (Mortensen *et al*., 2007).

Table 10.2 Geophysical and environmental variables available for modeling the distribution of deep-sea corals and sponges in the North Pacific Ocean.

Variable name	Filename	Unit	Native resolution	Reference
Bathymetry	srtm30	meters	0.0083°	Becker *et al*., 2009 Sandwell *et al*., 2014
Terrain variables				
Aspect	aspect	degrees	0.0083°	Jenness, 2013a
Aspect – Eastness	eastness		0.0083°	Jenness, 2013a
Aspect – Northness	northness		0.0083°	Jenness, 2013a
Curvature – General	gencurve		0.0083°	Jenness, 2013a
Curvature – Cross-sectional	crosscurve		0.0083°	Jenness, 2013a
Curvature – Longitudinal	longcurve		0.0083°	Jenness, 2013a
Roughness	roughness		0.0083°	Jenness, 2013a
Slope	slope	degrees	0.0083°	Jenness, 2013a
Topographic Position Index	tpi		0.0083°	Jenness, 2013b
Seamounts	seamounts			Yesson *et al*., 2011
Environmental variables				
Alkalinity	alk_stein	μmol l^{-1}	3.6 × 0.8–1.8°	Steinacher *et al*., 2009
Dissolved inorganic carbon	dic_stein	μmol l^{-1}	3.6 × 0.8–1.8°	Steinacher *et al*., 2009
Omega aragonite (Ω_{ARAG})	arag_stein		3.6 × 0.8–1.8°	Steinacher *et al*., 2009
Omega calcite (Ω_{CALC})	calc_stein		3.6 × 0.8–1.8°	Steinacher *et al*., 2009
Dissolved oxygen	dissox	ml l^{-1}	1°	Garcia *et al*., 2014a
Salinity	salinity	pss	0.25°	Zweng *et al*., 2013
Temperature	temp	°C	0.25°	Locarnini *et al*., 2013
Phosphate	phosphate	μmol l^{-1}	1°	Garcia *et al*., 2014b
Silicate	silicate	μmol l^{-1}	1°	Garcia *et al*., 2014b
Nitrate	nitrate	μmol l^{-1}	1°	Garcia *et al*., 2014b
Particulate organic carbon	POC	g C m^{-2} yr^{-1}	0.05°	Lutz *et al*., 2007
Regional current velocity	regfl	m s^{-1}	0.5°	Carton and Giese, 2008
Vertical current velocity	vertfl	m s^{-1}	0.5°	Carton and Giese, 2008
Current direction	curdir	degrees	0.5°	Carton and Giese, 2008
Current relative to aspect	curaspect	degrees	0.5°	Rooper *et al*., 2014
Chlorophyll a	chl-*a*	mg m^{-3}	4 km	Aqua MODIS, 2014
Photosynthetically available radiation	PAR	W m^{-2}	4 km	Aqua MODIS, 2014
Sea Surface Temperature	SST	°C	4 km	Aqua MODIS, 2014

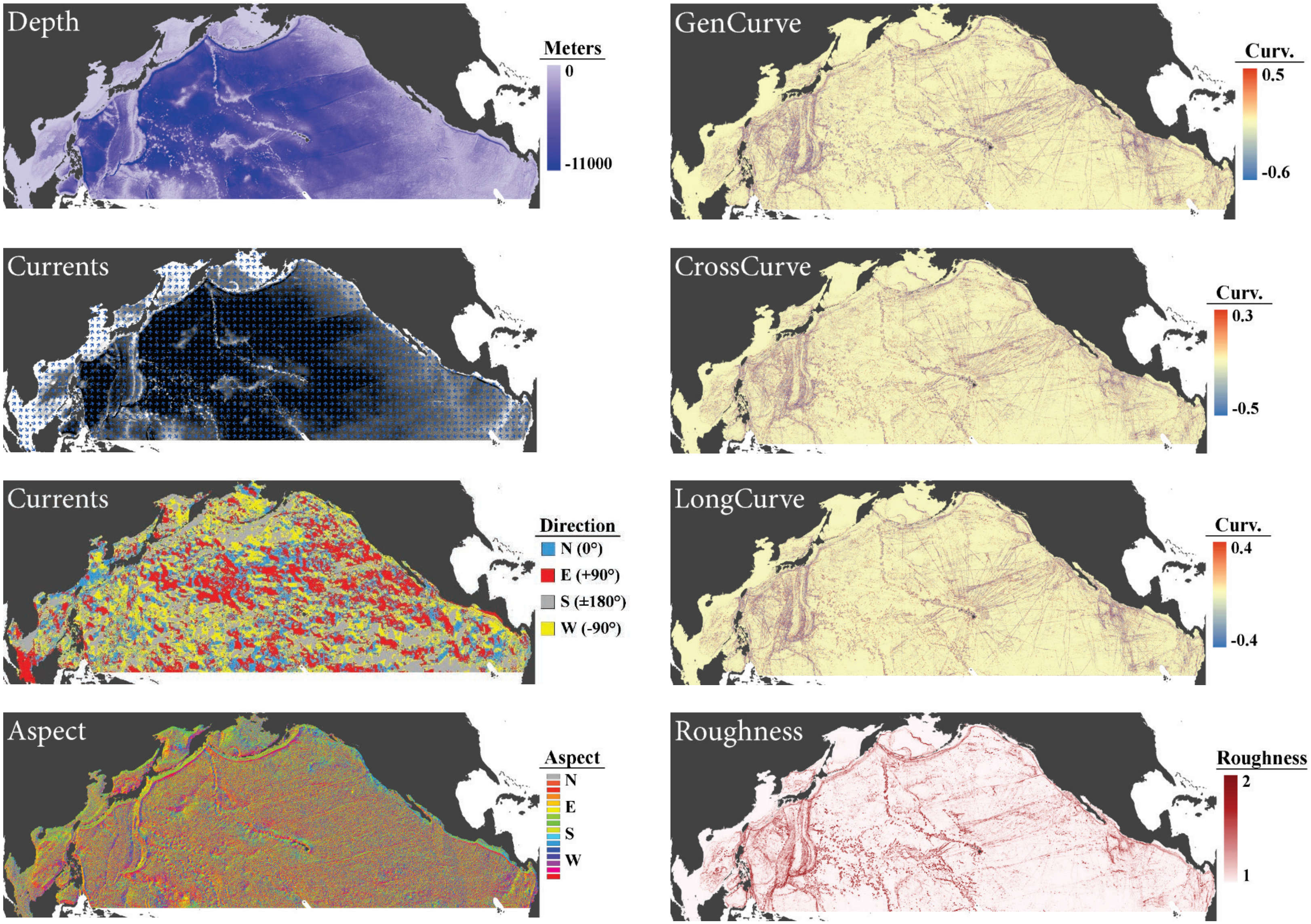


Fig. 10.2 Maps of individual variables available for modeling the distribution of deep-sea corals and sponges in the North Pacific Ocean.

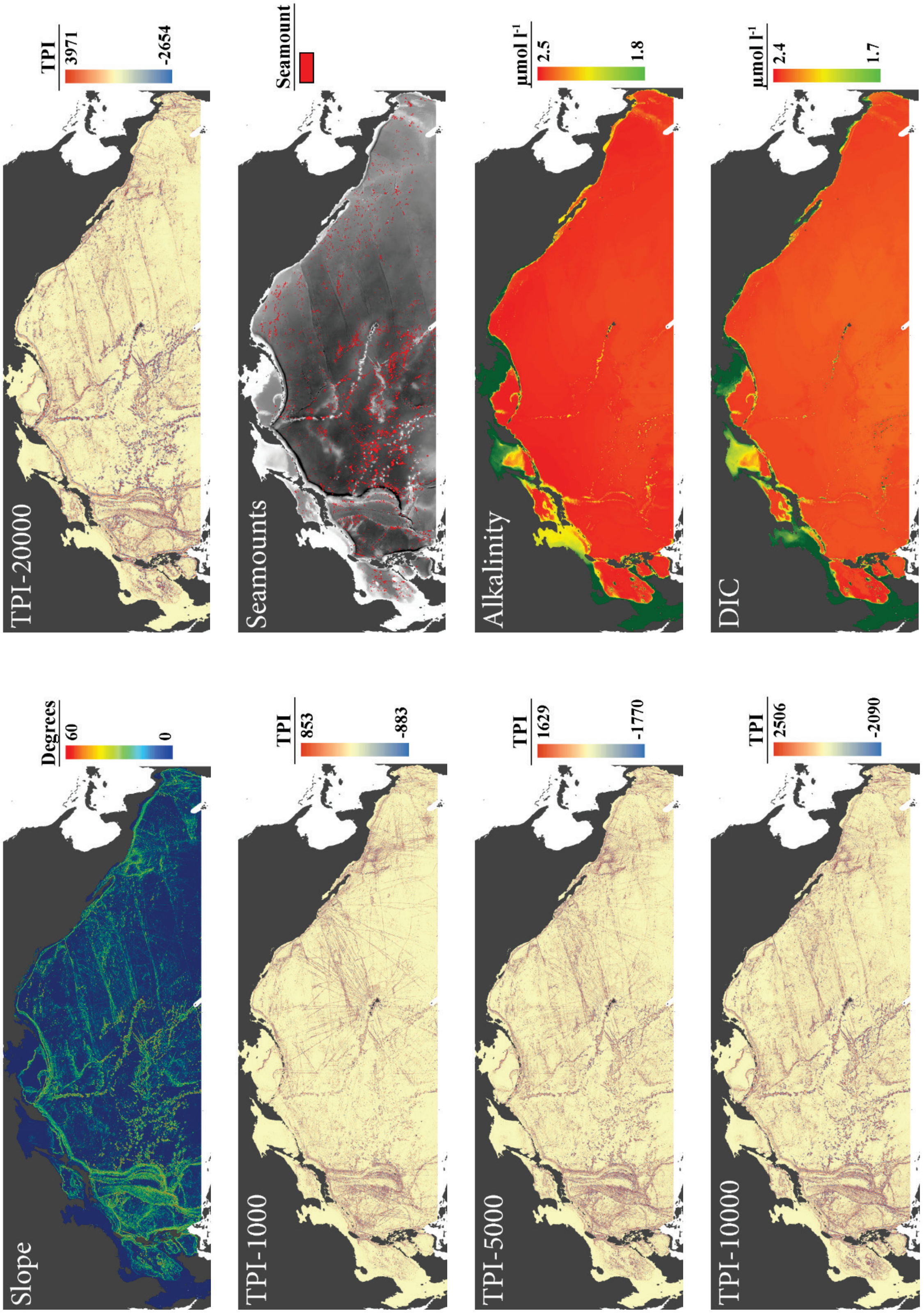


Fig. 10.2 Continued. TPI = topographic position index, DIC = dissolved inorganic carbon.

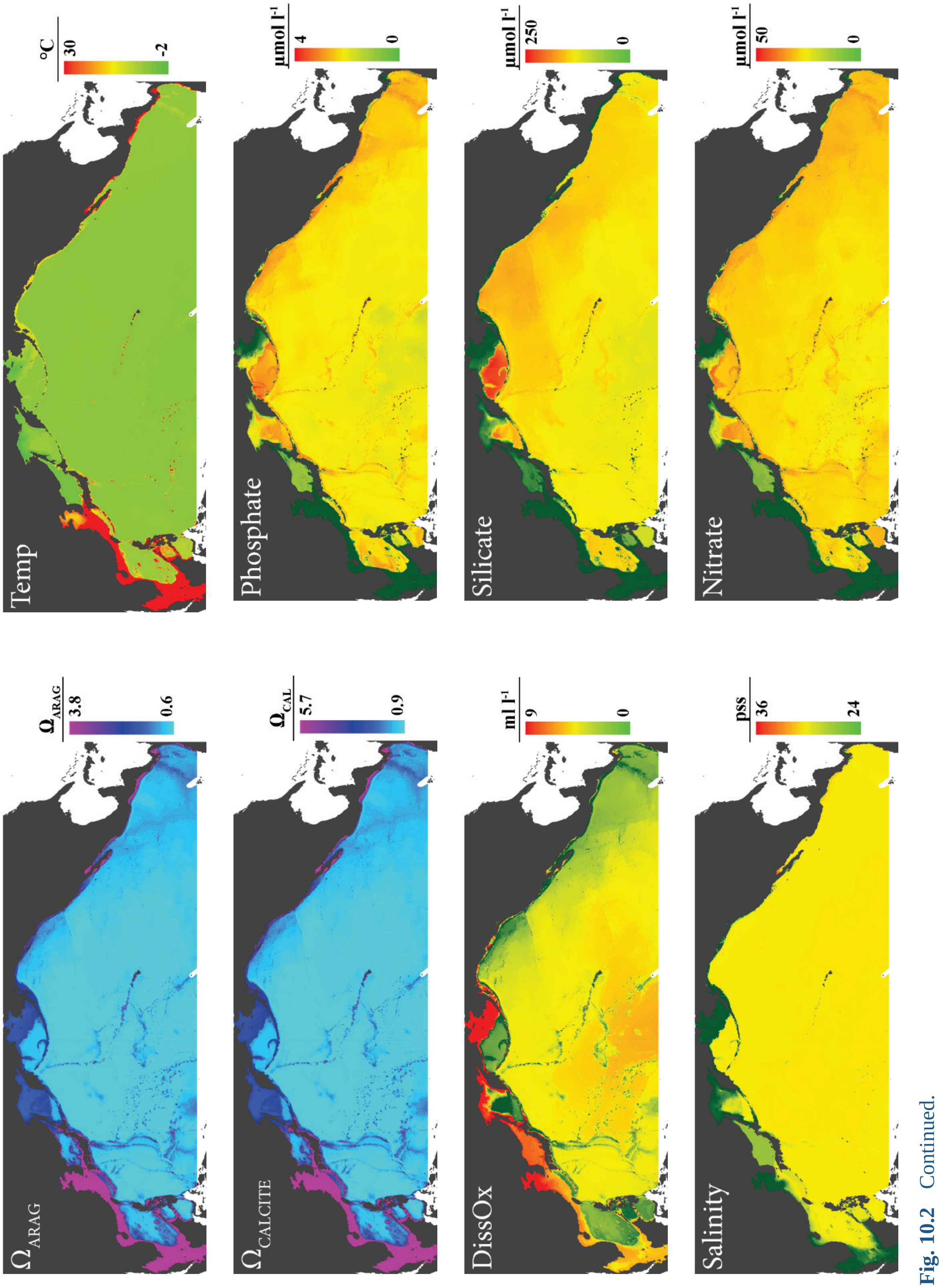


Fig. 10.2 Continued.

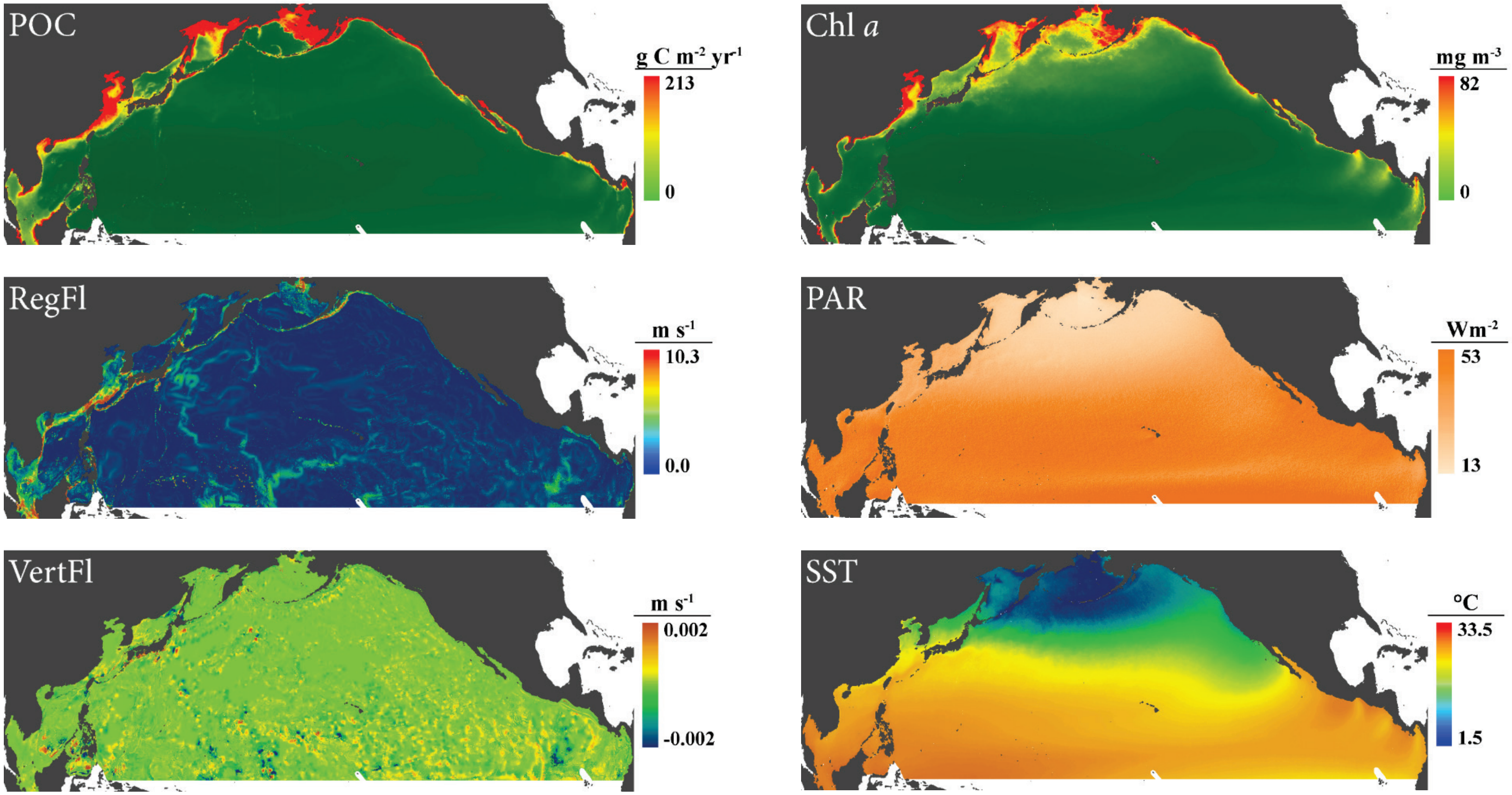


Fig. 10.2 Continued. POC = particulate organic carbon, RegFl = regional current flow, VertFl = vertical current flow, PAR = photosynthetically available radiation, SST = sea surface temperature.

Bathymetric data for the North Pacific were obtained from the SRTM30+ layer (Becker *et al*., 2009; Sandwell *et al*., 2014) downloaded from: topex.ucsd.edu/WWW_html/srtm30_plus.html. Ocean data in the SRTM30+ layer were derived from Sandwell *et al*. (2014), the LDEO Ridge Multibeam Synthesis Project, the JAMSTEC Data Site for Research Cruises, the NGDC Coastal Relief Model, and the International Bathymetric Chart of the Oceans. The native resolution of the SRTM30+ layer was 0.0083° or approximately one kilometer.

A suite of terrain variables was constructed using the SRTM30+ bathymetry layer. Slope, aspect, roughness, and curvature were calculated using the ArcGIS (v.10.4, ESRI) toolkit 'DEM Surface Tools' (v.2, Jenness, 2004, 2013a), and the topographic position index (TPI) was calculated using the toolkit 'Land Face Corridor Designer (v1.2, Jenness, 2013b). The slope of each grid was measured in degrees and calculated using the 4-cell method which has been shown to outperform other methods (Horn 1981; Jones 1998). Aspect represents the direction of the maximum slope and was converted to an index of 'eastness' using a sine transformation and an index of 'northness' using a cosine transformation. Curvature describes the shape of the seafloor to quantify how water should interact with the terrain. We calculated three types of curvature: general curvature, cross-sectional curvature, and longitudinal curvature. General curvature assigns more positive values to more convex features, and more negative values to more concave features. Cross-sectional curvature assigns positive values to features where water is expected to locally diverge, and negative values to features where water is expected to locally converge. Longitudinal curvature assigns positive values to features where water is expected to decelerate, and negative values to features where water is expected to accelerate. Roughness is a measure of topographical complexity and was calculated as the ratio of surface area to planimetric area. TPI quantifies the elevation of a feature relative to the surrounding seafloor, with positive values indicating features that are elevated and negative values indicating features that are depressed. Values close to zero may indicate either flat surfaces or areas with constant slopes. As TPI is heavily dependent on the analysis scale, and because benthic organisms may be simultaneously affected by both fine- and broad-scale features, we calculated TPI at multiple scales: 1,000 m (the finest resolution allowed by the bathymetry), 5,000 m, 10,000 m, and 20,000 m. Seamount locations were obtained from Yesson *et al*. (2011), and include all seafloor features greater than 1,000 m in height with a conical shape.

Environmental variables believed *a priori* to influence the distribution of benthic marine organisms were obtained from a variety of sources (Table 10.1). Dissolved oxygen, salinity, temperature, and nutrient data were obtained from the World Ocean Atlas (v.2 2013). Carbonate data (Ω_{ARAG}, Ω_{CAL}, dissolved inorganic carbon, and total alkalinity) were obtained from Steinacher *et al*. (2009). Chlorophyll a, sea surface temperature (SST), and photosynthetically available radiation (PAR) data were obtained as mission composites (average of 2002–2016 data) from NOAA's Aqua MODIS program at a resolution of 4 km, and were resampled to match the extent and resolution of the bathymetry data with no interpolation. Particulate organic carbon (POC) flux at the seafloor was obtained from Lutz *et al*. (2007). Bottom current velocity data were obtained from the Simple Ocean Data Assimilation (SODA v.3.4.1) model (Carton and Giese, 2008), with data averaged as the composite of the years 1990–2007. Current velocities were calculated as both horizontal and vertical velocities (m s^{-1}). Current direction for each grid cell was calculated from zonal (u) and meridional (v) velocities according to the formula:

$$\text{Direction} = 180/\pi \times \text{atan2}([u],[v])$$

with values of +180° and –180° indicating that the current flows to the south, +90° to the east, –90° to the west, and 0° to north. A current layer that quantifies the direction of current flow relative to the aspect of the seafloor was also calculated, with values of 0° indicating that the current flows in the same direction that the steepest slope is facing, and values of 180° indicating that the current flows opposite to the direction of the steepest slope (*sensu* Rooper *et al*., 2014).

Benthic variables (WOA data, carbonate data, and current data) were transformed to match the extent and resolution of the bathymetry layer using a variable up-scaling approach that approximates conditions at the seafloor (Davies and Guinotte, 2011). Briefly, each gridded layer was first interpolated to a slightly higher resolution (0.5°) than its native resolution using inverse distance weighting, resampled to match the extent and resolution of the bathymetry data, and draped over the bathymetry data within its depth range. This technique has been demonstrated to work effectively for many global and regional scale variables (Davies and Guinotte, 2011; Yesson *et al*., 2012). World Ocean Atlas data were available as 102 depth-binned layers from depths of 0–5500 m, with a vertical resolution of 5 m (from 0–100 m), 25 m (100–500 m), 50 m (500–2000 m), and 100 m (2000–5500 m). Carbonate data (Steinacher *et al*., 2009) were available in 25 depth-binned layers: 6, 19, 38, 62, 93, 133, 183, 245, 322, 415, 527, 661, 818, 1001, 1211, 1449, 1717, 2014, 2340, 2693, 3072, 3473, 3894, 4329, and 4775 m. SODA current data were available in 50 depth bins: 5.03355, 15.10065, 25.21935, 35.35845, 45.57635, 55.86325, 66.26175, 76.80285, 87.57695, 98.62325, 110.0962, 122.1067, 134.9086, 148.7466, 164.0538, 181.3125, 201.2630, 224.7773, 253.0681, 287.5508, 330.0078, 382.3651, 446.7263, 524.9824, 618.7031, 728.6921, 854.9935, 996.7153, 1152.376, 1319.997, 1497.562, 1683.057, 1874.788, 2071.252, 2271.323, 2474.043, 2678.757, 2884.898, 3092.117, 3300.086, 3508.633, 3717.567, 3926.813, 4136.251, 4345.864, 4555.566, 4765.369, 4975.209, 5185.111, and 5395.023 m.

These predictor variables were made available to all WG 32 members through a shared drive and allowed individuals and groups from the PICES community to utilize the layers in their own modeling efforts within their own EEZs. Key aspects of this predictor data set are:

- A wide variety of variables have been compiled into raster layers for use in modeling the distribution of deep-sea corals and sponges;
- The data captures long-term and large-scale patterns in variables for the North Pacific Ocean.

Preliminary North Pacific-wide deep-sea coral models

This suite of environmental data was used to construct preliminary habitat suitability models for a number of deep-sea coral taxa across the North Pacific Ocean. Models were constructed using a presence-only MaxEnt approach. The inclusion of correlated environmental variables may inhibit model performance and interpretation (*e.g.*, Huang *et al*., 2011). Therefore, highly correlated variables (Fig. 10.3) were removed based on their relationship with other variables and performance in preliminary MaxEnt models. The final variable set included the saturation state of calcium carbonate (either as calcite or aragonite depending on the biology of each taxon), seafloor roughness, temperature, silicate, TPI (20,000 m scale), dissolved oxygen, dissolved inorganic carbon, total alkalinity, regional current flow, and vertical current flow.

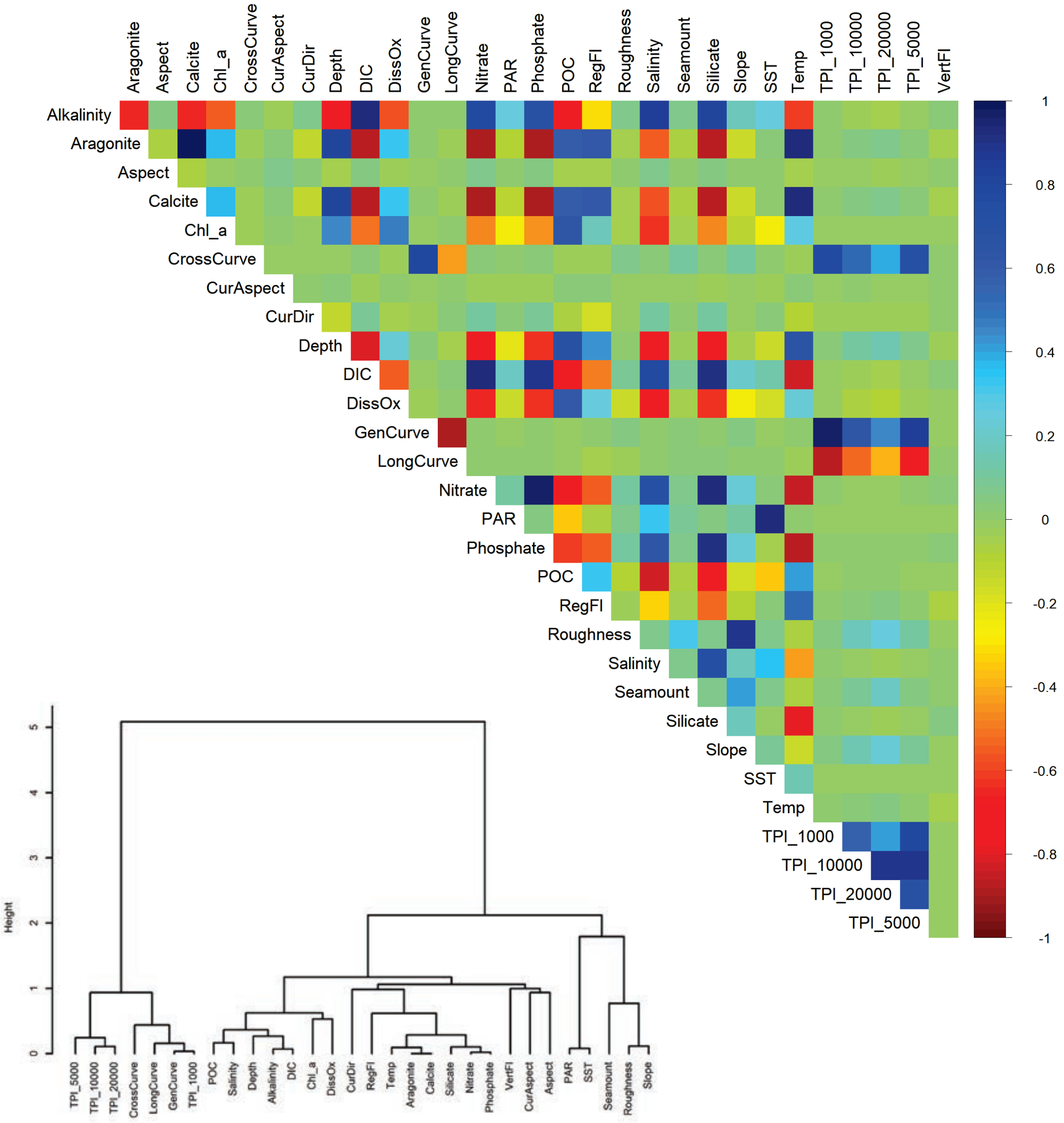


Fig. 10.3 Pearson correlations and cluster analysis of variables available for modeling the distribution of corals and sponges in the Pacific Ocean.

Georeferenced occurrence data were obtained for each taxon from the NOAA Deep Sea Coral Portal (DSCDP). While a common source of error in species distribution models, spatial bias in the sampling of occurrence data considerably weakens the performance and interpretability of models (Phillips *et al.*, 2009), and is often found in presence-only deep-sea species datasets due to the difficulties associated with sampling design in the deep-sea. However, it is possible to reduce the effects of sampling bias by selecting targeted background data that reflect the same bias as the occurrence data (Phillips *et al.*, 2009). Given the relatively high sampling bias observable in our field surveys, we generated a targeted set of background points in addition to a random set of points (see Fig. 10.1). To generate background points preferentially in areas that have been more extensively surveyed, we first created a two-dimensional kernel density estimate of sampling effort based on the presence locations for each taxon.

This created a probability grid from which 10,000 background points were sampled according to the probability grid weights. Previous studies using a similar approach to reduce the influence of sampling bias found that model performance was significantly improved (Fitzpatrick *et al*., 2013). Habitat suitability models were produced using this targeted-background approach in a MaxEnt environment run with default model parameters for the following taxa: Scleractinia (stony corals), Antipatharia (black corals), Pennatulacea (sea pens), and *Primnoa* (preliminary results in Fig. 10.4).

Proposed biogeography of the Upper Bathyal benthos in the Pacific Ocean based on octocoral distributions

One of the topics for discussion during WG 32 meetings was the global biogeography of benthic invertebrates and how invertebrates are taxonomically organized in the PICES area. Biogeographical classification schemes such as Briggs' biogeographic provinces (Briggs, 1974) and the Marine Ecoregions of the World (MEOW) (Spaulding *et al*., 2007) have been developed for continental shelf depths. However, the lack of faunal data in the deep sea has led to the development of biogeographical units based on oceanographic characteristics (Watling *et al*., 2013). During the lifetime of WG 32, Dr. Natalie Summers and Dr. Les Watling developed a biogeographical scheme for the Upper Bathyal (200–1000 m) in the Pacific Ocean using octocoral distributions.

They retrieved over 200,000 octocoral data records from the DSCDP, Ocean Biogeographic Information System (OBIS), Tropical Deep-Sea Benthos program (French National Museum of Natural History), Queensland Museum from the CIDARIS expeditions, and records retrieved from the Siboga expedition reports. They used cluster analysis to test octocoral distributions against four different biogeographical classification schemes used in the shallower and deeper zones of the ocean as well as one used for subdividing the mesopelagic region.

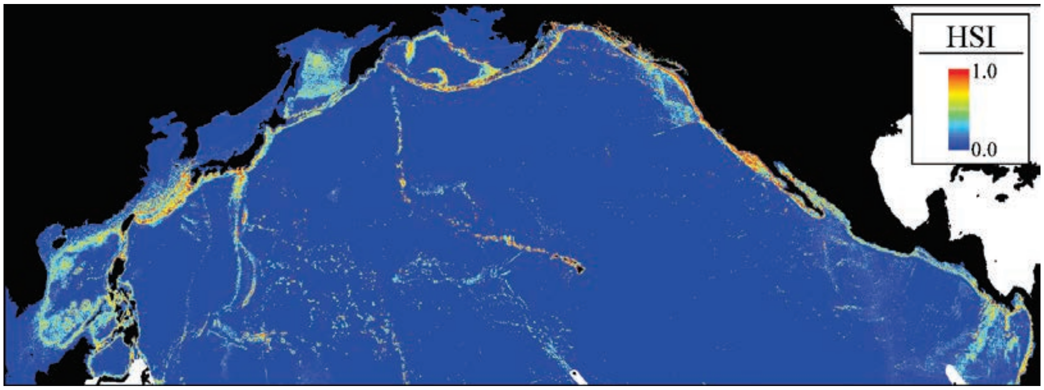
The four classifications used were based on: 1) The MEOW classification in the Pacific (Spalding *et al*., 2007) from the coast to 200 m depth (immediately above the Upper Bathyal), which consisted of 72 ecoregions containing at least one octocoral genus; 2) Watling *et al*. (2013) Lower Bathyal Provinces from 800 to 3,500 m in the Pacific; 3) Sutton *et al*. (2017) 14 Mesopelagic Provinces in the Pacific based on daytime mesopelagic faunal communities as well as environmental proxies derived from the MEOW ecoregions; 4) the three-dimensional Ecological Marine Unit (EMU) classification based on temperature, salinity, dissolved oxygen, nitrate, phosphate, and silicate data obtained from the 2013 World Ocean Atlas which, using cluster analysis, resulted in 9 EMUs in the Pacific Ocean. The latter is the only scheme that divides the Upper Bathyal into several depth zones (Sayre *et al*., 2017).

All classification schemes produced mostly concordant patterns with three major faunal distribution barriers: the North Pacific Current isolates the subarctic units by creating a steep temperature gradient; the Subantarctic Front separates the Subantarctic from the rest of the Pacific Ocean; and the East Pacific Barrier separates the East Pacific Ocean from the Central and West Pacific Ocean. Two other smaller but distinct provinces are the Indo-Pacific where Lower Bathyal genera are found in the Upper Bathyal, and Torres Strait/Coral Sea characterised by mesophotic genera. Dr. Summers and Dr. Watling proposed 12 Upper Bathyal provinces for the Pacific Ocean based on octocoral distributions (Fig. 10.4). The main driver for these units seems to be temperature, a defining feature of water masses. These units could potentially be subdivided into smaller regions based on habitat. Additionally, the clustering of EMUs provides evidence that the Upper Bathyal should in certain regions be divided vertically into two depth zones based on water masses. Key findings recommended to WG 32 members from this work include:

- There was consistency in results across multiple biogeographic classification schemes indicating strong trends in the data on octocorals;
- The biogeography of octocorals in the North Pacific is largely consistent with the oceanographic barriers created by temperature;
- There are four separate biogeographic provinces for octocoral (Fig. 10.5) found in the PICES region.

Scleractinia (Stony Corals)

Antipatharia (Black Corals)



Pennatulacea (Sea Pens)

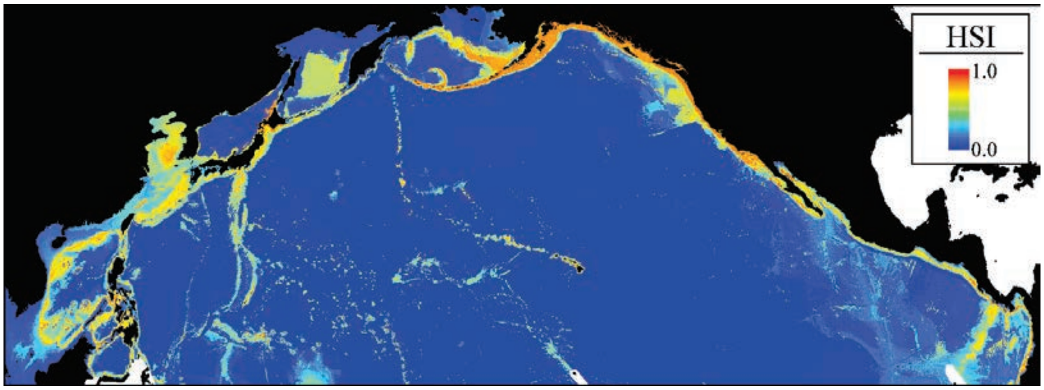


Fig. 10.4 Preliminary habitat suitability models for deep-sea coral taxa in the North Pacific Ocean.

Primnoa

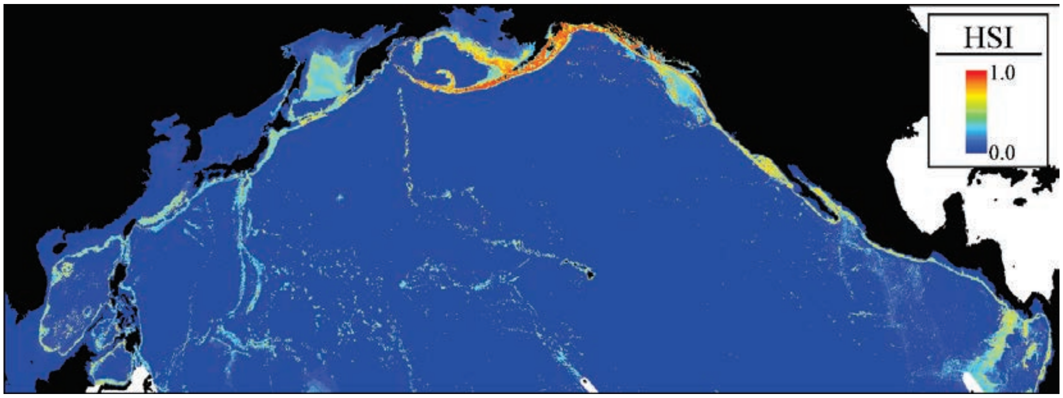


Fig. 10.4 Continued.

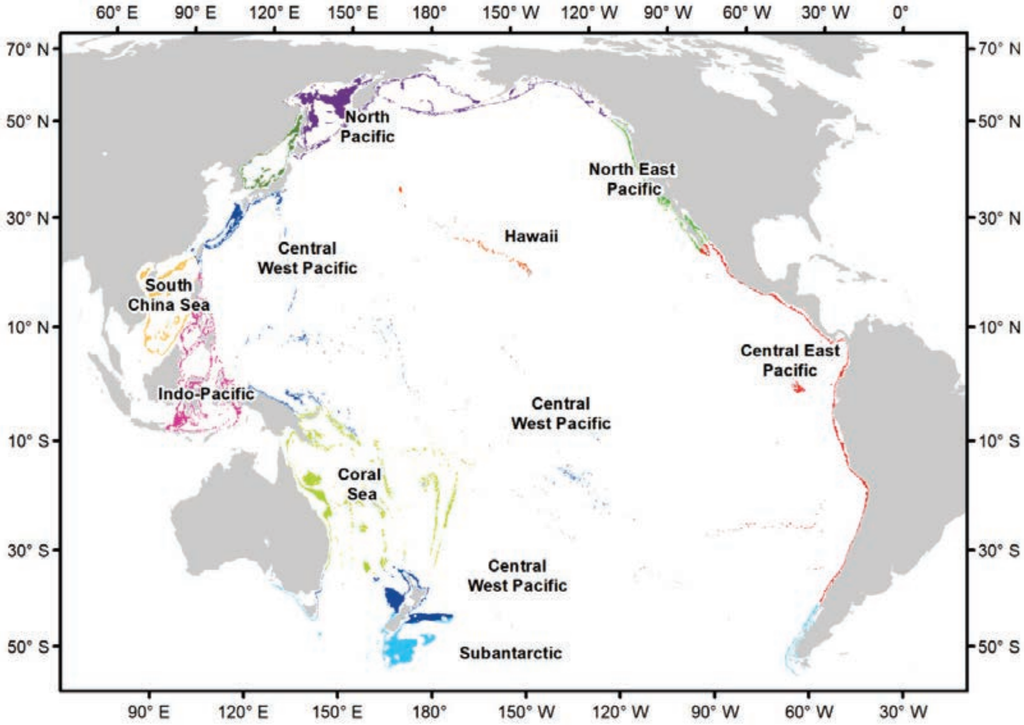


Fig. 10.5 Proposed Upper Bathyal Provinces for the Pacific Ocean based on analysis of 200,000 records of octocorals in the Pacific Ocean.

Indicators of diversity of biogenic habitats

Deep-sea coral and sponge ecosystems in the North Pacific Ocean are influenced by multiple climatological threats, such as rising sea temperature, harmful algal blooms, marine invasive species, hypoxia, and eutrophication. They are also affected by direct anthropogenic activities such as sea bed mining and bottom fishing. These multiple threats can act synergistically, but perhaps differently, from region to region to change ecosystem structure, function and dynamics. A goal of WG 32 was to advance the monitoring of deep-sea coral and sponge ecosystems.

In the US, the major threats to deep-sea corals and sponges are fishing and climate change. Monitoring the status of deep-sea corals and sponges is difficult and costly, so effective indicators of biogenic habitat health are needed. One group of indicators that has been developed in the US is trends in bycatch (Fig. 10.6) in commercial fisheries. Another indicator is the abundance of deep-sea corals and sponges estimated using multispecies geo-spatial modeling techniques (Thorson *et al*., 2015) applied to fishery-independent trawl survey data. Finally, the spatial extent and trend over time in bottom contacting fishing effort can be used as an indicator of potential fishing impacts on deep-sea corals and sponges. These data and indicators are currently updated and reported annually in the Ecosystem Status Reports of Stock Assessment and Fishery Evaluation documents for Alaska (Siddon and Zador, 2018). The data and trends over time are also available to be downloaded (https://access.afsc.noaa.gov/reem/ecoweb/index.php). These indicators do not necessarily capture the diversity of deep-sea corals and sponges, but they indicate instead what the population status might be and document the potential threats due to fishing activity. Further work is needed on this topic, especially work to integrate the spatially explicit fishing effort with the distribution models for deep-sea corals and sponges. Key recommendations to WG 32 members for this work include:

- There is a need to share relevant fisheries and environmental data that addresses trends and threats to biodiversity;
- There is a need for the development of marine spatial planning tools and tools to measure marine protected area performance.

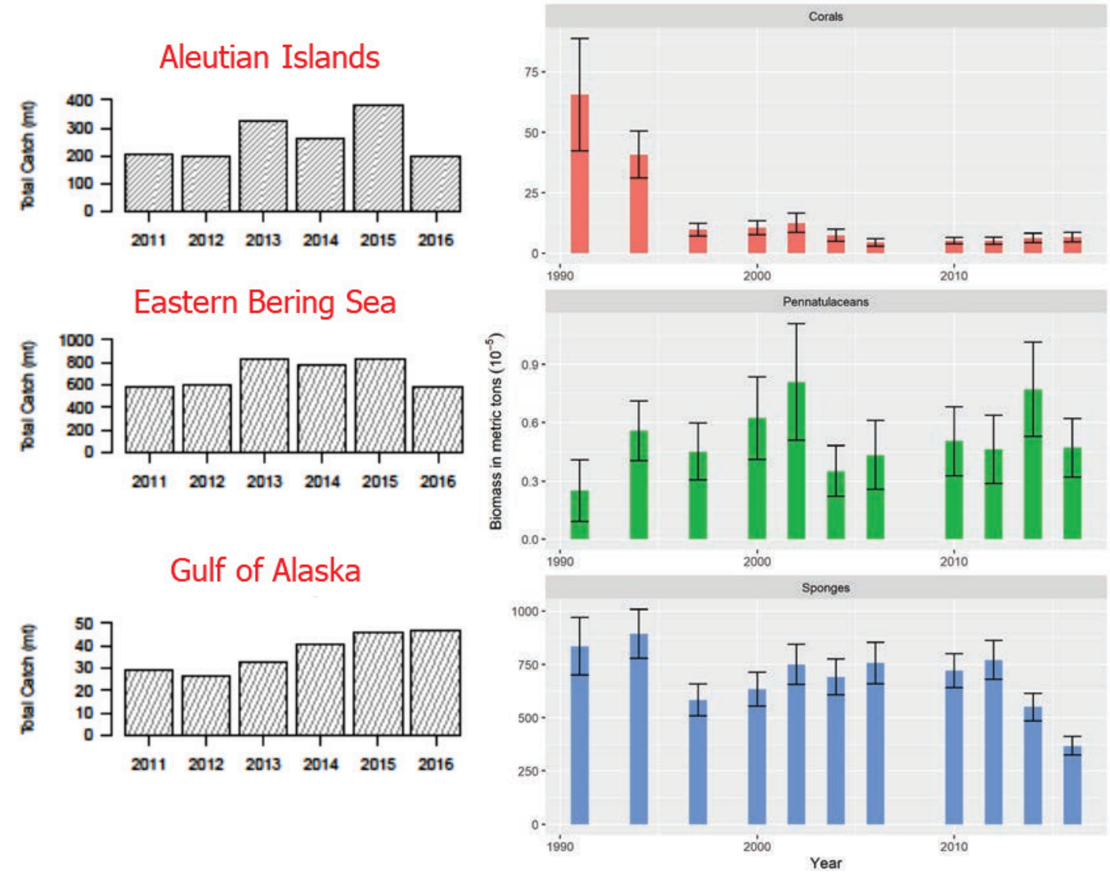


Fig. 10.6 Examples of indices used for monitoring biogenic habitats in Alaska. Total bycatch (left) in groundfish fisheries (A. Whitehouse, Alaska Fisheries Science Center, NMFS), time series of abundance of deep-sea corals and sponges in the Gulf of Alaska (right).

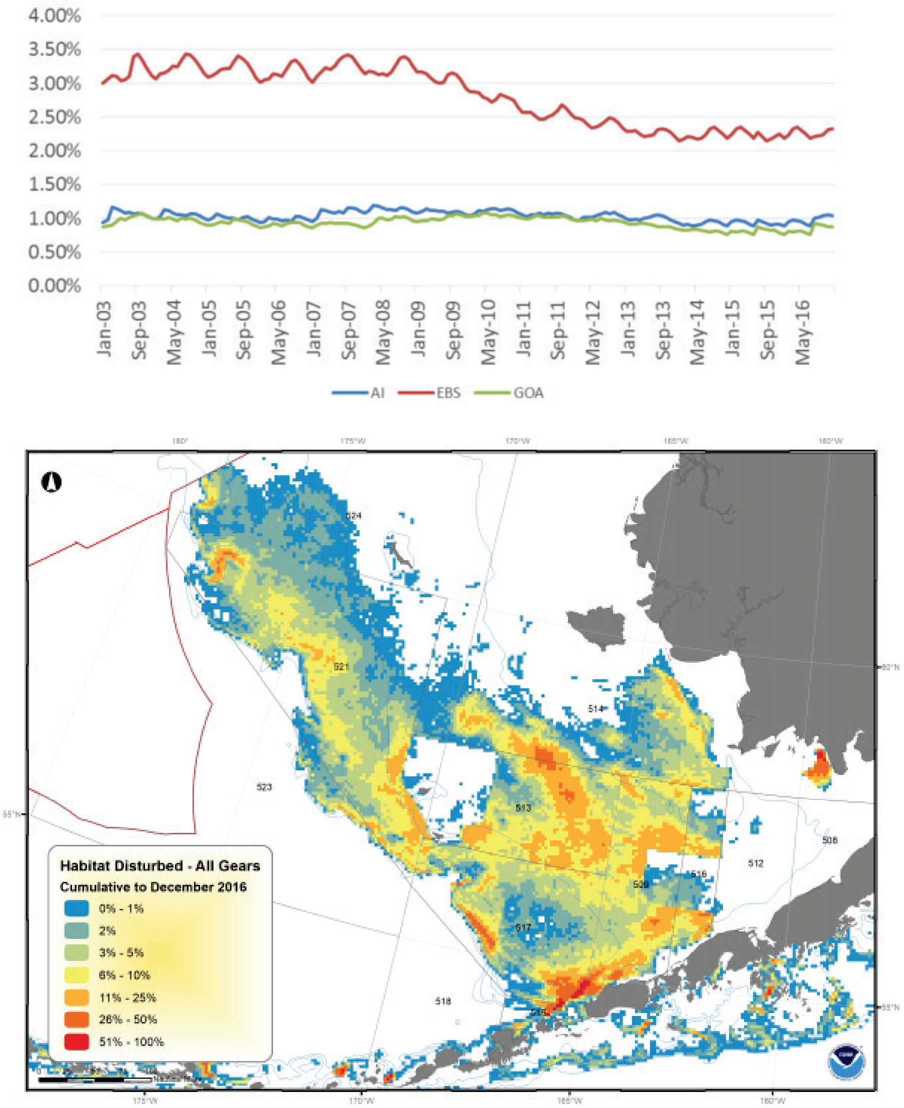


Fig. 10.6 Continued. Time series of area impacted by fishing gear in Alaska regions (top; Al = Alaska, EBS = eastern Bering Sea, GOA = Gulf of Alaska), cumulative spatial distribution of fishing effort (bottom). From J. Olson, Alaska Regional Office, NMFS.

Associations between commercial species and biogenic habitats

In the USA EEZ of the North Pacific Ocean, there have been a number of recent studies that have examined the association of commercially important fish and invertebrate species and deep-sea coral and sponge ecosystems. On a larger scale (ecosystem) the studies have demonstrated a strong correlation between rockfishes (*Sebastes* sp.) and corals and sponges in bottom trawl survey catches (Sigler *et al*., 2015; Laman *et al*., 2015, 2018; Thorson and Barnett, 2017). In these studies, higher catches of rockfishes (and some other commercially important species) are higher where corals or sponges also occur in the catch. This indicates spatial correlation in density across large areas. The strength of these correlations is variable, with stronger associations in Alaska than on the US West Coast. However, functional relationships are difficult to resolve using bottom trawl survey data.

Two new studies conducted by members of WG 32 have examined the seasonal use of deep-sea coral and sponge habitat and cross-ecosystem associations at differing scales in Alaska. These studies found that the associations documented for rockfishes were consistent across seasons, indicating that rockfishes exhibit the same habitat associations during all times of the year (Conrath *et al*., 2019). Since most previous work in Alaska has focused on only summertime distributions, this is an important finding.

In a second study, comparisons of habitat associations for rockfishes were made for the same species group across two different ecosystems (the Aleutian Islands and eastern Bering Sea) at scales ranging from 1 m to 1000s of km. The study found that rockfishes, in particular, utilized habitat in the same way in both ecosystems (Rooper *et al*., 2019). This was in spite of the large differences in quantity and quality of habitat between the two ecosystems. In all, this study found that having more structured habitats (deep-sea coral and sponge) led to a greater abundance of rockfishes, regardless of the larger ecosystem characteristics. The key findings of these studies and others assessed by WG 32 were:

- Deep-sea corals and sponges serve as important habitats for commercially important rockfishes in the northeastern Pacific Ocean;
- The associations between rockfishes and habitat are constant over seasonal and annual time periods and over all spatial scales examined;
- A higher abundance of structured habitats, such as deep-sea corals and sponges, leads to an increased abundance of rockfishes.

Conclusions

Deep-sea coral and sponge ecosystems in the USA EEZ of the North Pacific Ocean are widely distributed. Data on deep-sea corals and sponges have been collated into a global database that is publicly available. The work of WG 32 has advanced our knowledge of deep-sea coral and sponge ecosystem distributions by providing a motivation and tools for modeling presence, absence and abundance of deep-sea corals and sponges. Variables developed in the workshop sponsored by WG 32 have also been crucial to moving the distribution modeling forward on a relevant scale (1 km^2) for management. Since the Working Group was formed, published models for all regions of the USA EEZ have been developed and used in management. In addition, some key work in the USA has documented the importance of deep-sea coral and sponge ecosystems to supporting productivity of commercially important fish stocks, particularly rockfishes. Current monitoring efforts relative to deep-sea corals and sponges in the USA EEZ focus primarily on time series of abundance, bycatch and fishing effort. The monitoring could be improved with more focused studies that address the biodiversity of biogenic habitats.

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Conclusions

The work of WG 32 has advanced our knowledge of deep-sea coral and sponge ecosystem distributions by providing tools for modeling presence, absence and abundance of deep-sea corals and sponges. Variables developed in a workshop sponsored by WG 32 have also been crucial to moving the distribution modeling forward on a relevant scale (*i.e.*, 1 km^2) for management. Since the Working Group was formed, published models for all regions of the USA EEZ have been developed and used in management. In addition, some key work in the US has documented the importance of deep-sea coral and sponge ecosystems to supporting productivity of commercially important fish stocks, particularly rockfishes. Current monitoring efforts relative to deep-sea corals and sponges focus primarily on time series of abundance, bycatch and fishing effort. The monitoring could be improved with more focused studies that address the biodiversity of biogenic habitats.

Species distribution models (SDMs) are one tool that can extrapolate modelled species–environment relationships into areas where species records are rare, thus providing an empirical foundation that can promote hypothesis development which can, in turn, concentrate limited science resources into targeted data collection in logistically challenging environments. Enhancing our community’s ability to better predict where diverse biogenic habitats occur is an important precursor to understanding how these habitats support other elements of the ecosystem, including commercially valuable species.

When it comes to applying and interpreting SDMs in marine ecosystems, WG 32 suggested keeping three points in mind:

- Ensemble models can perform better across a range of species than individual models;
- The modeling method has less effect on the result than the quality of the underlying predictor and distribution data;
- It is important to validate model predictions using independently collected data whenever possible.

Recommendation

WG 32 members recommend that PICES engage in further research on biodiversity in the North Pacific Ocean. Specifically, members recommend that PICES establish a new Working Group on Ecology of Seamounts, with a focus on understanding the distribution of benthic, demersal, and pelagic species that are associated with seamounts. Seamounts are unique habitats and are biodiversity hotspots with high rates of endemism. They can host diverse communities of benthic filter feeders, including corals and sponges. The biodiversity of fishes is also high; almost 800 species of fish have been recorded from seamounts, representing half of the orders of fishes. As such, seamounts are important sources of food. There are approximately 100,000 seamounts worldwide and their abundance is greatest in the North Pacific Ocean. The ecology of only a few seamounts has been studied, in part because of how deep and remote most are. The difficulty in studying the ecology of seamounts means that they are poorly understood habitats in terms of the benthic, demersal, and pelagic species that they support. A Working Group on Ecology of Seamounts would build on the contributions of WG 32 by mapping the distribution of seamount biodiversity and expanding research in some of the unique and abundant ecosystems of the North Pacific Ocean.

The merits of a new Working Group on Ecology of Seamounts include: 1) the application of concepts developed by WG 32, 2) new data to better understand factors that influence the distribution and trends in seamount biodiversity and test key questions about the interactions among taxa that differ in life history (*e.g.*, plankton, filter feeders, fish, mammals), 3) identification of indicators to monitor change, 4) development of hypotheses to forecast responses to multiple stressors, which is aligned with the spirit of FUTURE, 5) maps of the distribution of benthic, demersal, and pelagic biodiversity and its indicators, 6) a new research avenue for PICES with clear linkages to other PICES activities, including the BIO Committee and the PICES–NPFC Framework for Enhanced Scientific Collaboration in the North Pacific Ocean.

WG 32's focus on biogenic habitat has provided a proof of concept on how to undertake collaborative biodiversity research in the North Pacific Ocean. Major applications of the science products developed by a Working Group on Ecology of Seamounts would be the provision of further technical guidance on the application of SDMs, maps of known and predicted distributions of the benthic, demersal, and pelagic taxa associated with seamounts, and the development of seamount biodiversity indicators.

Appendix 1

WG 32 Terms of Reference

WG 32 term: 2015–2018
Extended 1 year to 2019
Parent Committee: BIO

Year 1:

- Compile data on the distribution of coral and sponge taxa, and associated fish and invertebrate assemblages in the North Pacific within National Exclusive Economic Zones (EEZs) and facilitate their submission to appropriate biodiversity databases (*e.g.*, Ocean Biogeographic Information System (OBIS));
- Compile data on key variables (temperature, velocity, ocean acidification, slope, aspect) hypothesized to influence coral and sponge distribution and diversity and catalogue sources of multibeam/swathe bathymetry data for distribution modeling within National EEZs;
- Hold a WG meeting, in conjunction with PICES Annual Meeting.

Year 2:

- Review modeling approaches to predict the potential distributions of species and habitat suitability for corals and sponges (*e.g.*, MaxEnt, Boosted Regression Trees, or high resolution bathymetry-based models) within National EEZs;
- Identify environmental and ecological predictors of patterns in the distribution and biodiversity of coral, sponge and associated taxa within National EEZs;
- Convene a session on biogenic habitat distribution and diversity at the PICES Annual Meeting;
- Hold a WG meeting, in conjunction with the PICES Annual Meeting.

Year 3:

- Review and propose potential indicators for assessing and monitoring diversity of biogenic habitats;
- Review and document associations between commercially important fish and invertebrate species and biogenic habitats;
- Prepare scientific reports for dissemination of results;
- Hold a WG meeting, in association with the PICES Annual Meeting.

Appendix 2

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Appendix 3

Publications related to WG 32 Research

Cairns, S.D., Stone, R.P., Moon, H.-W. and Lee, J.H. 2018. Primnoidae (Octocorallia: Calcaxonia) from the Emperor Seamounts, with Notes on *Callogorgia elegans* (Gray, 1870). *Pacific Science* **72**(1): 125–142, https://doi.org/10.2984/72.1.8.

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Appendix 4

Meeting Reports and Topic Session/Workshop Summaries from Past Annual Meetings

PICES-2015, Qingdao, China

PICES-2016, San Diego, USA

PICES-2017, Vladivostok, Russia

PICES-2018, Yokohama, Japan

PICES-2015
October 15–25, 2015, Qingdao, China

Report of Working Group on *Biodiversity of Biogenic Habitats*

The meeting of the Working Group on *Biodiversity of Biogenic Habitats* (WG 32) was held over two days at the 2015 PICES Annual Meeting in Qingdao, China from 9:00–18:00 h on October 15, 2015 and 9:00–18:00 h on October 17, 2015. Over the course of two days, 14 people participated in the meeting and represented all of the six PICES member countries (*WG 32 Endnote 1*). Dr. Oleg Katugin (Russia) and Dr. Ian Perry (Canada) participated as liaisons to the FUTURE program. The meeting was co-chaired by Dr. Janelle Curtis (Canada) and Dr. Masashi Kiyota (Japan). This report summarizes discussions at the meeting on some of the Agenda Items (*WG 32 Endnote 2*).

Thursday, October 15, 2015

AGENDA ITEM 2

WG 32 Terms of Reference

Dr. Curtis (Canada) presented an overview of the history of WG 32, the rationales for its establishment and the terms of reference. WG 32 members agreed to maintain an initial focus on corals and sponges and explore opportunities to expand the work to other structure-forming taxa (*e.g.*, seagrasses, kelps, reef-forming species) in the future. Key challenges identified by WG 32 members included: limited amount of data in deep and/or international waters; data sharing and management agreements; data standards; gaps in presence/absence data held by individual researchers that have not been submitted to OBIS; and differences in sampling design and survey methods. Opportunities identified were: greater availability of data within country EEZs; 2017 research survey on Emperor Seamounts with potential to groundtruth models; potential to develop coarse models that span the North Pacific Ocean as well as regional models developed with subsets of data; linkages to the FUTURE program and other expert groups; potential to predict responses to climate change; and potential to include data from the South Pacific Ocean and other neigbouring areas.

AGENDA ITEM 3

Review and discussion of coral and sponge distribution modelling in the North Pacific Ocean

Experiences with modelling sponges in the northwest Atlantic Ocean

Dr. Anders Knudby (Canada) summarized experiences developing species distribution models for sponges in the Northwest Atlantic Ocean. Key points from his presentation related to data quality and model extrapolation:

<u>Solid data foundation is paramount to model accuracy</u>

- Specific definition of the entity modeled is crucial for interpretation (what does a ‘presence’ mean in terms of ID, detectability, sampling method, and spatial and temporal scale?);
- More data is better, including data from neighbouring regions (in addition to the target region). They help establish tolerance limits;
- Absence records improve model performance;

- Data from varying regions help distinguish correlation from causality – primarily because they help detect spurious correlations;
- Additional sampling can be optimized from model results:
    - Targeting unsampled regions with high presence probability,
    - Targeting regions near hypothesized upper and lower tolerance limits.

Model extrapolation should be interpreted carefully

- Extrapolation (geographical and environmental) reduces model performance;
- Extrapolated predictions depend strongly on model structure (models 'assume' things about structure beyond sampled environmental space, *e.g.*, GLMs and GAMs extrapolate, RF does not);
- Variable importance differs by region, even within the relatively small area we worked in (small as compared to the PICES area);
- Oceanographic regions (water masses) are likely a good basis for modelling.

Key points from the Working Group discussion included:

- Environmental variables are often variations of a few sources of data (*e.g.*, min, mean, max values of temperature at different depths or from different seasons). Often we don't know exactly which variables influence distributions, so it can be difficult to decide which variables to include/exclude. Mean variable values often fell out of model when min and max variables were important.
- Relationships to environmental variables may not be stable over space or time. Quantifying variability over time requires multiple sampling events.
- Water masses are likely a good basis for modelling; variable importance differs by region.
- For sponge models, depth, slope, summer and fall sea surface Chl-*a* min and max, max bottom temp, min bottom salinity, and min and max bottom current were all influential of model performance. The distribution of other species may also correlate with sponge distributions (*e.g.*, pollock).
- Modelling of sponges suggests that transferability declines with distance.
- Calibration from larger region often improves model performance – *i.e.*, including data from neighbouring region may improve fit – but including data from whole area works not as well. In other words, including data from neighbouring regions can boost predictive accuracy of local models.
- Data from varying regions may help distinguish correlation from causality (*e.g.*, tolerance limits or empirical relationships within sampling area).
- Need to understand what a presence or absence observation means, *e.g.*, weight-based sponge ground threshold vs observed occurrence on ROV transect vs no bycatch in trawl survey.
- Absence records improve model performance.
- Use extrapolated predictions to target areas near hypothesized upper and lower tolerance limits; and to prioritize surveys (*e.g.*, on areas of high probability P).
- Model extrapolation should be interpreted carefully: reduces model performance, predictions depend on model structure (*e.g.*, tree-based model, assumes values that are beyond what are sampled are similar to values above or below threshold whereas Maxent will typically have pseudo-absences beyond range of values – less of an issue. Random Forest approach has interesting properties for extrapolation.
- Bias could be introduced by differences in sampling protocols/designs.
- Longevity of modelled species could be used to inform decisions on the use or exclusion of data from different time periods.

- Depth may be an important variable due to correlation with ecologically relevant variables, but also might be because it is measured more accurately. One might hypothesize that models that include depth may not extrapolate as well.

Overview of global and regional scale deep-sea modelling of corals

Dr. John Guinotte (USA) presented an overview of global and regional scale deep-sea habitat suitability efforts relevant to the North Pacific Ocean, specifically of global predictive habitat model results (derived from Maxent presence-only models) currently available for scleractinian reef-forming deep-sea corals (Davies and Guinotte 2011) and octocorals (Yesson *et al*. 2012) in the North Pacific Ocean. These model results were used to help guide the CBD EBSA identification/regional workshop process. He highlighted that significant improvements could be made in the region by incorporating new coral presence and absence information from PICES partner countries. The environmental, chemical, and physical database used to produce these models includes ~40 variables for the seafloor (global extent at 1 km × 1 km resolution). These data are publically available and could be used in any future modelling efforts for the North Pacific. Methods behind database development and accuracy assessment can be found in Davies and Guinotte (2011).

He also provided an overview of GAM (presence–absence) model results available from NOAA-NMFS for the Aleutian Islands (Rooper *et al*. 2014), Gulf of Alaska (Rooper *et al*., in prep.), and Eastern Bering Sea (Rooper, in prep). Taxa included in these analyses include sponges, corals, sea whips on a 100 m × 100 m grid. Probability of presence, density, and height were modeled for most taxa.

Dr. Guinotte presented an overview of Maxent modeling effort for deep-sea coral taxa conducted in 2013 that encompasses the entire U.S. EEZ around Alaska and the extent of Canada's EEZ off BC (Guinotte and Davies 2013). Spatial resolution of model results and seafloor database is 700 m × 700 m, derived from a custom bathymetry. Taxa are modeled to Suborder (Alcyoniina, Calcaxonia, Filifera, Holaxonia, Scleraxonia, Stonifera) and Order (Antipatharia and Scleractinia). He also presented an overview of Maxent modeling effort for deep-sea coral taxa conducted in 2014 that encompasses the entire U.S. EEZ around Washington, Oregon, and California (Guinotte and Davies 2014). Spatial resolution of model results and seafloor database is 500 m × 500 m, derived from a custom bathymetry. Taxa are modeled to Suborder (Alcyoniina, Calcaxonia, Holaxonia, Scleraxonia) and Order (Antipatharia and Scleractinia). These models did not include fisheries bycatch presence records. Due to a strong sampling bias issue regarding presence records in Monterey Canyon (MBARI), a cross validation/thresholding approach was used to identify high probability habitat in the region.

Drawing on experiences in the South Pacific Ocean, Dr. Guinotte presented an overview of 3-year joint project led by NIWA to predict VME habitat within New Zealand's EEZ and the SPRFMO Competence Area. Phase I of this project used Maxent (presence only) and Boosted Regression Trees (presence only) to predict habitat for 10 key VME taxa. SPRFMO has defined a number of benthic invertebrate taxa that are regarded as primary indicators of potential VME habitat.

1. Phylum Porifera - Sponges
2. Phylum Cnidaria, Order Actiniaria – Anemones
3. Phylum Cnidaria, Order Alcyonacea – Soft corals
4. Phylum Cnidaria, Order Gorgonacea – Sea fans
5. Phylum Cnidaria, Order Pennatulacea – Sea pens
6. Phylum Cnidaria, Order Scleractinia – Stony corals

7. Phylum Cnidaria, Order Antipatharia – Black corals
8. Phylum Cnidaria Family Stylasteridae – Hydrocorals
9. Phylum Echinodermata, Class Crinoidea – Sea lilies
10. Phylum Echinodermata, Order Brisingida – Armless stars

A field cruise was conducted in 2014 to the Louisville Ridge seamounts to assess model performance and to help determine which methods were superior. Deep-sea coral taxa were the focus. Details of model assessment, accuracy, and model/data limitations can be found in Anderson *et al*. (submitted). Key point: the accuracy of global bathymetry datasets (*e.g*., SRTM30) in areas where very few soundings exist can be highly inaccurate. Differences of > 1000 m were documented between actual depth (measured by multibeam) and SRTM30 depths (the depths upon which model results and seafloor database were based).

Finally, Dr. Guinotte presented an overview of integration of predictive deep sea coral model results (Davies and Guinotte 2011) with projected changes in seafloor temperature and carbonate chemistry (ocean acidification) for Southern Australia. Details can be found in Thresher *et al*. (2015). The combination of increasing temperature and decreasing saturation state will likely cause the demise of deep-sea reefs off southern Australia by 2100. Australian resource managers were convened in 2013 to discuss management options in light of this. All options were on the table, including genetic engineering, buffering with carbonates, translocation of corals and many others. The only realistic management option was determined to be to restrict benthic impacts and increase protection in the high seas/other EEZs where reefs will remain viable.

In his concluding remarks Dr. Guinotte stated that: 40 seafloor variables will be made publically available early 2016 (global, 1 km). They are available upon request now, but will be served via the web in early 2016. UNEP-WCMC is in the process of updating their global cold-water coral database. Guinotte is helping them with this update and requested coral records from PICES member countries. Dr. Les Watling may have records of 30 new coral species from the Hawaiian Ridge, in addition to all records documented in Watling *et al*. (2011) *Biology of Deep-Water Octocorals.* There will be a 2017 cruise on the R/V *Falkor* (SOI) to the Emperor seamounts to document bathyal biogeography and collect deep-sea corals. Dr. Watling is the PI and has agreed to help in field validation efforts of predictive habitat models that might be developed between now and 2017.

Partial list of available seafloor datasets for use in models (provided to WG 32 by John Guinotte)

Native Resolution

Variable name	Filename	Extent	Units	Reference
Terrain variables[1]				
Aspect	aspect	Full	Degree	Jenness (2012)
Aspect – Eastness[2,3]	eastness	Full		Wilson *et al*. (2007)
Aspect – Northness[2,4]	northness	Full		Wilson *et al*. (2007)
Bathymetry	srtm30	Full	m	Becker *et al*. (2009)
Curvature – Profile[5,6]	profilecurve	Full		Jenness (2012)
Curvature – Plan[5,7]	plancurve	Full		Jenness (2012)
Curvature – Tangential[5,8]	tangcurve	Full		Jenness (2012)
Roughness[9]	roughness	Full		Wilson *et al*. (2007)
Rugosity[5]	rugosity	Full		Jenness (2012)
Slope[5]	slope	Full	Degrees	Jenness (2012)
Terrain Ruggedness Index[9]	tpi	Full		Wilson *et al*. (2007)
Topographic Position	tpi	Full		Wilson *et al*. (2007)

Variable name	Filename	Extent	Units	Reference
Index[9]				
Environment variables				
Alkalinity[10]	alk_stein	Full	μmol l^{-1}	Steinacher *et al.* (2009)
Apparent oxygen utilisation[10]	woaaoxu	Full	mol O^2 m^{-3}	Garcia *et al.* (2006b)
Chlorophyll *a*[11]	modismin, modismean, modismax	Restricted	mg m^{-3}	NASA Ocean Color
Dissolved inorganic carbon[10]	dic_stein	Full	μmol l^{-1}	Steinacher *et al.* (2009)
Dissolved oxygen[10]	woadiso2	Full	ml l^{-1}	Garcia *et al.* (2006a)
Nitrate[10]	woanit	Full	μmol l^{-1}	Garcia *et al.* (2006b)
Omega aragonite[10,12]	arag_stein	Full	Ω_{ARAG}	Steinacher *et al.* (2009)
Omega aragonite[10,13]	oa	Restricted	Ω_{ARAG}	Orr *et al.* (2005)
Omega calcite[10,12]	calc_stein	Full	Ω_{ARAG}	Steinacher *et al.* (2009)
Omega calcite[10,13]	oc	Restricted	Ω_{ARAG}	Orr *et al.* (2005)
Percent oxygen saturation[10]	woapoxs	Full	% O_2^S	Garcia *et al.* (2006b)
Phosphate[10]	woaphos	Full	μmol l^{-1}	Garcia *et al.* (2006b)
Regional current velocity[14]	regfl	Restricted	m s^{-1}	Carton *et al.* (2005)
Salinity[10]	woasal	Full	pss	Boyer *et al.* (2005)
Silicate[10]	woasil	Full	μmol l^{-1}	Garcia *et al.* (2006b)
Seasonal variation index[15]	lutzsvi	Restricted		Lutz *et al.* (2007)
Temperature[10]	woatemp	Full	°C	Boyer *et al.* (2005)
Particulate organic carbon[16]	poc	Restricted	g C_{org} m^{-2} yr^{-1}	Lutz *et al.* (2007)
Vertical current velocity[17]	vertfl	Restricted	m s^{-1}	Carton *et al.* (2005)
Vertically generalized productivity model[18]	vgpmmin, vgpmmean, vgpmmax,	Restricted	mg C m^{-2} d^{-1}	Behrenfeld and Falkowski (1997)

Technical considerations for habitat modelling of sedentary benthic organisms:

Dr. Masashi Kiyota (Japan) made a presentation on technical challenges related to habitat modelling of marine benthic organisms. He explained that a habitat model (or species distribution model) is an empirical formulation of the static relationship between spatial occurrences of organisms with environmental variables. The model outputs may be affected by data properties (representativeness, independence, random sampling) and selection of study area, scale, resolution, and model types. These factors, as well as model validation and extrapolation should be considered during the modeling process in light of the purpose of model use. He also introduced a case study on the high-resolution modeling of large gorgonians in the southern Emperor Seamount area for fishery management, and indicated that the objectives and data requirements for fine scale local modeling are different from those for large scale global modeling.

Key discussion points following this presentation included:

- Empirical models based on a snap shot of distribution and environmental variables can be used to help understand the relationship between spatial use and niche; and to predict distributions in unsurveyed areas or under changing environment.
- May have quantitative data (counts, biomass); binomial data (presence or absence); or occurrence data (presence only data). Presence-absence data can be converted to presence-only data. In some cases, it’s not clear if an absence is true or not; presence-only modelling may be the second-best option, especially in data-deficient areas.
- Sources of data can include biological surveys, underwater visual survey methods (*e.g.*, drop camera, remotely operated vehicles), museum records, opportunistic records, integrated database (*e.g.*, OBIS)

- Metadata related to survey objectives, spatial extent, *etc*. may be poor leading to unknown biases and violations of assumptions, *i.e*., the data are representative, independent, and random (may be violated by repeated sampling and aggregated occurrence).
- Stitching data sources together is challenging when survey designs differ and there are concerns regarding matching resolution (*e.g*., in time, space).
- Ideally, sampling is random within the target study area. Realistically, sampling is typically biased to subareas.
- Envtal data are increasing with remote sensing, math modelling, online databases: oceanography, bathymetry, *etc*. But high-resolution deep-sea data are still insufficient in most places.
- Study area, resolution, variables, data type and model structure depend on objectives and data availability. Large-scale global/basin-wide models are useful for screening priority areas for conservation and survey (*e.g*., EBSA workshop in Moscow – predictions of deep-sea octocorals potential habitat – extrapolated from other ocean basins) but are inadequate for fine-scale management zoning. Fine-scale local models are more suited for ecological studies and conservation planning (*e.g*., zoning; MPA network design).
- Sensitivity analyses can be used to investigate influences of data quality and model structure (*e.g*., cell size). Data extrapolation; usually used in large-scale models and future predictions; may violate model assumption and cause problems in fine-scale local modelling.
- Model types include: regression (GLM, GAM, Maxent); Profile (ENFA), Classification (BRT, RF). Ensemble modelling is also an option, although ecological/biological interpretation is more challenging.
- Species distribution modelling is an iterative process that includes model development, prediction, groundtruthing, and refinement. Model validation: separation of training and test data may be difficult in data-poor situation and result in overfitting; what is the “best” model? – depends on practical utility as well as modeling philosophy.
- The influence of model structure/method is well-explored and documented in literature. Maps differ among methods, especially if data do not span the multidimensional variable space. Different model types portray the relationship between species and environmental data differently, but may have similar accuracy while differing in ecological appropriateness. Variable importance may differ among model types. Convergence lends credibility while divergence provides opportunities to better understand ecological relationships.

AGENDA ITEM 4
Review of available data

Canada

Dr. Curtis (Canada) presented an overview of the data, ongoing studies and research priorities from Canada’s perspective. Canada has diverse marine ecosystems that support >150 sponge taxa and tens of cold water coral taxa in fjord, bank, trough, canyon, ridge, slope, seamount, hydrothermal vent and plains habitats. Previous studies have developed predictions for four orders of corals (Alcyonacea; Antipatharia; Pennatulacea; Scleractinia) on the continental slope (*e.g*., Finney 2010). Models of coral and sponge taxa are presently being developed for two seamounts off the west coast of Canada (Cobb Seamount and Bowie Seamount). ROV/drop camera and other fishery-independent survey data are available to contribute to databases; however, fishery-related data will need to be manipulated to conform to Canada’s privacy policies. A better understanding of the distribution of habitat-forming corals and sponges would help support marine spatial planning initiatives (*e.g*., marine protected area network design within Canada's EEZ; conservation of vulnerable marine ecosystems in international waters). It was noted that Canada has museum records from provincial and national museums. Darlene Smith (Canada) offered to follow up with Canadian OBIS contact and the national museum.

China

Dr. Huang Hao (China) provided information from surveys undertaken from 1975 to 2014 on the species and distribution of reef-building shallow-water corals in China as listed below. He noted that most species, and thus data, were from southern China and that corals were less abundant and diverse in the North Pacific Ocean. Most research on corals has focused on shallow water ecosystems; there are few studies of deep-sea corals and these are usually associated with mineral exploration in the high seas of the Western Pacific Ocean. Forty-five coral genera occur in shallow waters; 26 are red-listed. Concerns regarding corals relate to the impacts of boat anchors, climate change, directed fisheries and typhoons. Data available on location of occurrences may be too coarse for developing SDMs. Also, China uses its own species coding system.

Number of species and distributions

Area	Species and genus
Guangdong and Guangxi provinces	21genus 45 species
FuJian province	8 genus 8 species
Hong Kong	21 genus 49 species
Tai Wan	58 genus 230 species
Hainan Island	34 genus 110 species
Paracel Islands	38 genus 127 species
Dongsha Islands	34 genus 101 species
Taiping Island	56 genus 163 species
Huangyan Island	19 genus 46 species
Spratly Islands	More than 50 genus 200 species

Species name and distribution

Species name	South China Sea	Hainan Island	Guangdong and Guangxi province	Hong Kong	Taiwan	Fujian
Acropora palifera	+				+	
Acropora illepora	+	+	+	+	+	
Acropora yacinthus	+	+				
Acropora corymbosa	+	+	+		+	
Acropora formosa	+	+	+			
Acropora humilis	+	+	+		+	+
Acropora abrotanoides	+	+				
Acropora valida	+	+			+	
Acropora pulchra	+	+	+			
Acropora lutkeni		+				
Acropora florida	+	+				
Acropora brueggemanni	+	+				
Acropora robusta	+	+				
Acropora nasuta	+	+				
Acropora cerealis	+	+				
Acropora selago	+	+				

Species name	South China Sea	Hainan Island	Guangdong and Guangxi province	Hong Kong	Taiwan	Fujian
Acropora haimei	+	+	+			
Acropora horrida	+					
Acropora echinata	+					
Acropora rosaria	+					
Acropora granulosa	+					
Acropora tenella	+					
Acropora aduncata	+					
Acropora cytherea	+	+	+	+		
Acropora tumida			+	+		
Acropora pruinosa			+	+		+
Montipora foliosa	+	+			+	
Montipora circumvallata		+				
Montipora efforescene	+	+				
Montipora truncata	+	+				
Montipora solanderi		+				
Montipora hispida	+	+	+			
Montipora stellata		+				
Montipora fragilis		+				
Montipora aenigmatica	+	+				
Montipora monasteriata	+	+	+			
Montipora turgescens	+	+				
Montipora venosa			+	+		
Montipora gaimardi		+				
Montipora foveaolata			+			
Montipora danae	+					
Pavona decussata	+	+	+	+		
Pavona frondifera	+	+	+		+	
Pavona cactus	+	+			+	
Pavona minuta	+				+	
Pavona varians	+	+	+			
Turbinaria undata		+	+			
Turbinaria peltata		+	+	+		+
Turbinaria stellulata			+			
Turbinaria elegans			+			
Turbinaria agaricia		+	+			
Turbinaria mesenterina			+	+		
盘状陀螺珊瑚 *Turbinaria mantonae*		+			+	
漏斗陀螺珊瑚 *Turbinaria crater*	+	+	+			
叶状陀螺珊瑚 *Turbinaria foliosa*			+		+	
绵琉蜂巢珊瑚 *Favia palauensis*	+	+				
标准蜂巢珊瑚 *Favia speciosa*	+	+	+	+	+	+
黄廯蜂巢珊瑚 *Favia favus*	+	+	+			
罗图马蜂巢珊瑚 *Favia rotumana*	+	+	+			
梳状菊花珊瑚 *Goniastrea pectinata*	+	+			+	

Species name	South China Sea	Hainan Island	Guangdong and Guangxi province	Hong Kong	Taiwan	Fujian
粗糙菊花珊瑚 *Goniastrea aspera*	+	+	+			
网状菊花珊瑚 *Goniastrea retiformis*	+	+				
少片菊花珊瑚 *Goniastrea yamanarii*		+				
深少片菊花珊瑚 *Goniastrea yamanarii profunda*	+	+				
顶枝珊瑚 *Acrhelia horrescens*	+	+			+	
圆饼珊瑚 *Cycloseris syslolites*	+					
碎双列珊瑚 *Diaseris fragilis*	+					
福石芝珊瑚 *Heliofungia actiniformis*	+					
刺石芝珊瑚 *Fungia echinata*	+	+			+	
楯形石芝珊瑚 *Fungia scutaria*	+					
石芝珊瑚 *Fungia sp.*	+	+			+	
波莫特石芝珊瑚 *Fungia paumotensis*		+			+	
弯石芝珊瑚 *Fungia repanda*	+				+	
圆结石芝珊瑚 *Fungia danai*	+					
弗利吉亚肠珊瑚 *Leptoria phrygia*	+	+				
交替扁脑珊瑚 *Platygyra crosslandi*		+	+			
精巧扁脑珊瑚 *Platygyra daedalea*	+	+	+	+	+	
中华扁脑珊瑚 *Platygyra sinensis*	+	+	+	+		
粗突小星珊瑚 *Leptastrea bottae*	+					
紫小星珊瑚 *Leptastrea purpurrea*	+	+	+	+		
横小星珊瑚 *Leptastrea transversa*	+					+
棘星珊瑚 *Acanthastrea echinata*	+	+				
赫氏叶状珊瑚 *Lobophyllia hemprichii*	+	+				
伞房叶状珊瑚 *Lobophyllia corymbosa*	+	+				
华贵合叶珊瑚 *Symphyllia nobilis*	+	+			+	
菌状合叶珊瑚 *Symphyllia agaricia*	+	+			+	
辐射合叶珊瑚 *Symphyllia radians*	+	+			+	
巨大合叶珊瑚 *Symphyllia gigantea*		+				
多形穴孔珊瑚 *Alveopora polyformis*	+					
高穴孔珊瑚 *Alveopora excelse*	+					
不规则穴孔珊瑚 *Alveopora irregularis*					+	
丛生盔形珊瑚 *Galaxea fascicoularis*	+	+	+		+	
稀杯盔形珊瑚 *Galaxea asteata*	+	+	+	+		
疣状杯形珊瑚 *Pocillopora verrucosa*	+	+				
多曲杯形珊瑚 *Pocillopora meandrina*	+				+	
埃氏杯形珊瑚 *Pocillopora eydouxi*	+	+				
鹿角杯形珊瑚 *Pocillopora damicornis*	+	+				
西沙珊瑚 *Coeloseris mayeri*	+				+	

Species name	South China Sea	Hainan Island	Guangdong and Guangxi province	Hong Kong	Taiwan	Fujian
澄黄滨珊瑚 *Porites lutea*	+	+	+	+		+
普哥滨珊瑚 *Porites pukoensis*	+	+				
火焰滨珊瑚 *Porites (Synaraea)rus*	+	+				
扁枝滨珊瑚 *Porites andrewsi*	+	+	+			
灰黑滨珊瑚 *Porites nigrescens*	+	+				
融板滨珊瑚 *Porites matthaii*	+	+				
地衣滨珊瑚 *Porites lichen*	+					
扁缩滨珊瑚 *Porites compressa*			+			
二异角孔珊瑚 *Goniopora duofaciata*		+	+			
斯氏角孔珊瑚 *Goniopora stutchburyi*			+	+		
细角孔珊瑚 *Goniopora gracilis*	+					
小角孔珊瑚 *Goniopora minor*	+					
深室沙珊瑚 *Psammocora profundacella*			+		+	
不等脊塍沙珊瑚 *Psammocora nierstraszi*	+					
毗邻沙珊瑚 *Psammocora contigua*	+	+	+			
血红沙珊瑚 *Psammocora haimeana*				+		
丑刺孔珊瑚 *Echinopora horrida*	+					
宝石刺孔珊瑚 *Echinopora gemmacea*	+					
薄片刺孔珊瑚 *Echinopora lamellose*	+	+				
粗糙刺叶珊瑚 *Echinophyllia aspera*		+	+	+	+	
奥芳刺叶珊瑚 *Echinophyllia orpheensis*	+				+	
撕裂尖孔珊瑚 *Oxypora lacera*	+					
滑真叶珊瑚 *Euphyllia glabrascens*	+	+				
缨真叶珊瑚 *Euphyllia fimbriata*	+	+				
壳形足柄珊瑚 *Podabacia crustacea*						
凹凸薄层珊瑚 *Leptoseris scabra*	+				+	
类菌薄层珊瑚 *Leptoseris mycetoseroides*	+					
纸薄层珊瑚 *Leptoseris papyracea*	+					
片薄层珊瑚 *Leptoseris gardineri*		+				
卷叶厚丝珊瑚 *Pachyseris involuta*	+					
标准厚丝珊瑚 *Pachyseris speciosa*	+	+			+	
皱纹厚丝珊瑚 *Pachyseris rugosa*	+	+				
泡囊珊瑚 *Plerogyra sinuosa*		+				
箭排孔珊瑚 *Seriatopora hystrix*						
吞蚀筛珊瑚 *Coscinaraea exesa*	+					
柱形筛珊瑚 *Coscinaraea columna*	+				+	

Species name	South China Sea	Hainan Island	Guangdong and Guangxi province	Hong Kong	Taiwan	Fujian
假铁星珊瑚 *Pseudosiderstrea tayamai*			+			
爱氏石珊瑚 *Lithophyllon edwardsi*			+	+	+	
壳形足柄珊瑚 *Podsbscis crustacea*		+			+	
小帽状珊瑚 *Halomitra pileus*	+					
健壮履形珊瑚 *Sandalitha robusta*	+	+			+	
多叶珊瑚 *Polyphyllia talpina*	+	+			+	
饶石珊瑚 *Herpolitha limax*	+				+	

Japan

Drs. Takeo Kurihara and Go Suzuki introduced WG 32 members to three monitoring programs of ecosystems in the Japanese EEZ:

1) Monitoring 1000 is organized by the Ministry of the Environment, Japan. This program has been monitoring about 1000 sites set in various habitats, which include coral reefs, kelp beds, and sea grass beds in shallow sea. In marine habitats quadrat samplings are mainly used. The program is to continue for 100 years but started only 10 years ago (so, needs additional 90 years). Some data of abundance of species will be downloadable together with location data.
2) Jalter (Japan Long Term Ecological Research Network). This is a framework of various monitoring programs organized by Japanese researchers/research groups, and is not as large as Monitoring 1000.
3) BISMaL (Biological Information System of Marine Life), a data system for biodiversity information, particularly in biogeographic data of marine organisms, constructed by Japan Agency for Marine Earth-Science and Technology (JAMSTEC). This dataset gives very useful information such as distribution ranges of deep-sea animals. This data set will become even more powerful if it is analyzed with J-DOSS, namely, Oceanographic Data and Information download service (Temperature, Current, Depth, Biology, Marine information around Japan). The URL is: http://www.jodc.go.jp/index.html.

Key discussion points following this presentation included:

- The Fishery Agency of Japan has conducted surveys on deep-sea corals within and beyond Japanese EEZ, but sharing of the survey data is difficult due to sensitive issues such as poaching of precious corals that occurred extensively from late 2014 to early 2015.
- Even with limited coral or sponge data, WG 32 could use environmental data to develop predictions with models extrapolated from elsewhere (*e.g.*, Hawaii); these predictions could be groundtruthed in the future.
- How do shallow, meso-photic, and deepwater corals differ in their adaptations to different environments and how are these likely to respond to climate change? These questions have important implications in terms of climate change refugia.
- Efforts to identify EBSAs within Japanese waters included analyses of deep-sea coral data.
- Some previous surveys since thr 1970s employed quadrat sampling along the Japanese coastal islands. Data include mollusks, shallow sea sponges; and environmental variables.

WG 32 recognized that it would be difficult to develop a habitat modelling project for coral reefs and there would be a need to bring a collaborator on board, such as Dr. Hiroya Yamano (Japan), who is conducting future projection modelling for coral reef distribution, and is collaborating with Korean scientists. Dr. Kwang-Sik Albert Choi (Korea) agreed to contact Dr. Yamano about the potential for collaboration on WG 32 activities.

Some considerations regarding modelling of shallow water corals were discussed. A good bathymetry layer and information on xooxanthellae, light extinction, temperature, salinity, depth penetration of blue wavelength (from satellites), and water clarity data would be ideal. Models developed for shallow water corals in Australia were able to predict 90% of known reefs and identified many meso-photic populations that were not previously known. Mesophotic populations may play an important role as refugia.

Korea

Dr. Kwang-Sik Albert Choi (Korea) provided an overview of research undertaken in Korea on corals and sponges, dating back to the 1960s when species were identified and distribution information was collected. Monitoring and collection of sponges and corals is managed by the Ministry of Oceans and Fisheries, with a focus on biodiversity (museum specimen collection). Of the universities in Korea having information on species identifications, depth distributions, and ranges of corals and sponges, these may be available to WG 32 members. Dr. Choi is interested in monitoring climate change using coral as indicator species. The northern limit of coral reefs is in Okinawa. Korea has warmer species due to the Kurishio Current. Korea also has the highest range of temperature increase (*e.g.*, a 10 degree increase recently), which is linked to the spread of invasive/non-indigenous species including *Alveopora japonica* (Scleractinia, shallow water species, like snowflake coral in Hawaii, with long polyps that look like anemones. While red-listed by the IUCN, it is establishing/spreading very quickly and affecting local kelp and algae. Dr. Choi's research in part focuses on understanding the spread of this species. Regular sampling stations are monitored in southern Japan and Jeju. No deepwater corals have been identified yet (only corals in < 20 m). He is examining the relationships between corals and benthic organisms. The corals have slow growth and a 15-year lifespan. Benthic gastropods and bivalves are associated with coral carpets. The switch from kelp bed to *A. japonica* likely has implications for fisheries, but these are not well-studied. The important question about *A. japonica* is about expansion, so scale is important as well as resolution of environmental data.

Russia

No report was available on the types of data, ongoing studies and research priorities from a Russian perspective.

USA

Dr. Chris Rooper presented information on coral and sponge data and studies in the U.S. Northeast Pacific Ocean. The National Marine Fisheries Service has been conducting research on coral and sponges on the U.S. west coast (2010–2013) and Alaska (2012–2014) to document the presence, distribution, biology and ecology of coral and sponge communities. Importantly, records of coral and sponge presence for the NE Pacific have been compiled into a centralized database available from the Deep Sea Coral Research and Technology Program (NOAA). These records include recent camera surveys throughout Alaska, as well as historical records from bottom trawl, longline, ROV and submersibles throughout the NE Pacific. Bycatch data recorded from the commercial fisheries is available, but of limited use. Environmental data available include outputs from Regional Ocean Models (ROMS), tidal current predictions and observations, satellite observations of primary productivity and bathymetry from a number of sources. There have also been some small-scale intensive studies that produced multibeam maps. Models of coral and sponge distribution have been produced and validated for all regions in Alaska. Some models of coral and sponge distribution are also available for areas of the U.S. West Coast. Ancillary data on species associations with deep-sea corals and sponges are also available for all regions.

Key discussion points following this presentation included:

- Several surveys are standardized according to grid or strata, which makes them suitable for habitat modelling studies.
- Standardized surveys provide reasonably good species ID, often to family level, as well as good density estimates and size information from camera surveys. Sponge species identification is fairly poor. Other data include CPUE for trawl surveys.
- Non-standardized data include commercial fisheries bycatch information, which tends to be less reliable in terms of taxonomy. Where observer data are used, may need to use higher level classifications to reduce uncertainties/errors associated with misidentifications. Some non-standard submersible surveys cover small areas or collect data on a few species (*e.g.*, *Primnoa*).
- NOAA maintains a Deep Sea Coral and Sponge Database. Most data come from U.S. waters and the database will be available online. People will be able to submit data with some measures to capture level of data quality/uncertainties.
- Little is known of the reproduction or dispersal patterns
- Substrate type is available on the west coast of USA but not in Alaska.
- Some seamounts occur within the U.S. EEZ, but are not fished and so they have not received the same attention in terms of standardized surveys. Some surveys have been carried out on seamounts in the Gulf of Alaska.
- NWFSC does some genetic analyses for species identification, but no efforts to ID sponges with genetic analysis.
- Puget Sound has one of best environmental datasets.
- Developing models for a full basin, with estimates of error associated with them, should be considered; within basin, regional models should be developed where there are areas with better data.
- Understanding where you don’t have great performance could be valuable outcome – in terms of prioritizing future surveys.
- Image data puts you in a strong position to look at species-habitat associations (as opposed to trawl data) *i.e.*, ToR 3 (see WG 32 webpage, http://www.pices.int/members/working_groups/wg32.aspx).

Members noted that there may be additional U.S. records from state agencies that are not already in NOAA’s database. Dr. Rooper offered to look into this. Dr. Guinotte noted that MBARI also has records and will follow up on their availability.

AGENDA ITEMS 5 AND 6

Identify scientific research questions of mutual interest for WG 32 members and linkages to FUTURE

WG 32 members discussed a number of scientific questions that would address its terms of reference and link WG 32 activities to FUTURE themes, while focusing the group’s activities on one or more research questions of mutual interest that span the broad range of ecosystems and life histories characteristic of coral and sponge taxa in the North Pacific Ocean.

The activities of WG 32 could be linked to all three of the FUTURE themes, which were presented by Dr. Ian Perry (Canada):

1. What determines an ecosystem's intrinsic resilience and vulnerability to natural and anthropogenic forcing?
2. How do ecosystems respond to natural and anthropogenic forcing, and how might they change in the future?
3. How do human activities affect coastal ecosystems and how are societies affected by changes in these ecosystems?

General research interests common to multiple PICES member countries included:

- Development of general tools for spatial management that could be applied to a broad range of structure-forming species, including seagrasses, kelps, corals and sponges (*e.g.*, linking SDM to planning software like Zonation or Marxan);
- Development of usable species distribution models for coral and sponge taxa that could be applied in management contexts, *e.g.*, maps of known or hypothesized vulnerable areas;
- Refinement of existing models with improved data: over-prediction of SDM models can be improved with better species and environmental data;
- Comparison of factors that influence the distributions of shallow, meso-photic, and deep-sea assemblages.
- Identification of tolerance thresholds for a range of environmental variables (*e.g.*, temperature, aragonite saturation), which are fundamental to understanding/predicting climate change impacts; potentially link to research on coral invasion in northwestern Pacific Ocean (*A. japonica*) or vulnerability of *Lophelia pertusa* to ocean acidification in the northeastern Pacific Ocean, and empirical studies of threshold responses. This information could provide insight into vulnerability/resilience of these biogenic habitats. Within the Pacific Ocean, there is a north–south gradient in effects of ocean acidification for stony corals, but there is little evidence of this being an issue for soft or black corals. Indeed, little information exists about temperature or other tolerances for soft or black corals. One question might be to undertake an east–west comparison of gradient in carbonate chemistry for stony corals. Tolerances are better known for shallow-water species;
- Development of models of coral and sponge diversity indices (richness, evenness, taxonomic diversity, *etc*.); refer to work by Dr. Charles Veron who is compiling distribution data for corals;
- Linkage of information on genetic structure, connectivity and distributions to improve predictions for species responses to climate change, *etc*. In the Northeast Pacific Ocean, NOAA's Deep Sea Coral Research and Technology Program is analysing genetic samples of *Primnoa pacifica*, while in the Northwest Pacific Ocean, there is a long-term monitoring program of *A. japonica*;
- Improvement of understanding of the factors that influence recruitment/recovery; fragmentation *vs* broadcast spawning; what is dispersal potential and suitable conditions for settlement? No signs of recolonization after 15-year closures despite nearby potential source populations. Similarly, no recovery was observed among sponges subjected to trawling in in late 1990s (research by Linc Freese);
- Linkage of research to a shallow coral reef recovery program in south China led by local governments, the program, funded through the State Oceanic Administration (SOA), involves planting/seeding over large areas in southern China;
- Measurement/documentation of coral recruitment rates. Recruitment is episodic and rare. USA has tried to measure recruitment for deep-water corals with settlement plates (Robert Stone, PI), but found no evidence of recruitment. Some data from Japan are available on recruitment of deep-sea

precious corals, where recruitment is continuous (Nozomu Iwasaki). Data are available from Japan on coral recruitment on settlement plates dating back to 1970;

- Documentation of coral losses due to eutrophication, damage, *etc*. Develop an understanding of coastal stressors – status/indicator monitoring (*e.g.*, water clarity/turbidity);
- Evaluation of the effects of fishing on distribution patterns: What is the influence of the relative amount of effort? Are there thresholds related to disturbance?

Dr. Knudby (Canada) formulated five goals related to development and application of species distribution models:

1. Developing ‘basin-wide’ (within EEZ is fine) models, and
2. Interpreting their ecological meaningfulness both in terms of predictions and model structure and what it says about species (or order/family/genera) tolerance limits, then
3. For those species/genera we feel we have identified tolerance limits well for, develop some climate projections with a range of assumptions about dispersal, and
4. For those species we have not identified tolerance limits for, suggest data sets that could be accessed or sampling that needs to be done in order to do so.
5. Finally, a test of the use of SDM for definition of biogeographic regions may have potential. The idea would be to use model performance to assess the optimal location of a boundary (*e.g.*, along the U.S./ Canada coast, where can we subdivide the coast to achieve optimal model performance on both sides of a boundary?) And does that correspond with expert opinions on biogeographic provinces as well as knowledge of current systems/water masses?

WG 32 members noted that the development of a basin-wide glass sponge model could be novel contribution to the scientific literature.

AGENDA ITEMS 7 AND 8
Review agenda for WG 32 for Day 2 meeting

Dr. Curtis reviewed the agenda with WG 32 members for the next day’s meeting before adjourning.

AGENDA ITEMS 9 AND 10
Compilation of data and models of coral and sponge distributions

Dr. Guinotte agreed to coordinate the compilation of deep-water coral record data *i.e.*, >50 m depth. Dr. Rooper agreed to take the lead on compiling shallow water coral species <50 m depth. Dr. Knudby will take the lead on compiling data on glass sponges in the North Pacific Ocean. All three will draft templates for data submission/collation and circulate them to members. The data submission template should include absence and presence of data. OBIS contacted the WG 32 Co-Chairs to offer support with development of templates and submission to their online database. They may be potentially linking environmental data to occurrence data. UNEP is also updating its global coldwater database and there is a Millenium Coral Reef Mapping Project being run by the United Nations Environmental Programme World Conservation Monitoring Center (UNEP-WCMC). NOWPAP may be a source of data in the Northwest Pacific Ocean. Key questions relate to:

- Which environmental data are available to model future scenarios (*i.e.*, responses to climate change)? Minimum and maximum values for environmental variables could be more informative and mean values, especially for shallow-water species. Landsat, MODIS, K490, and other data are available. Obtaining high resolution bathymetry (250 m–1 km) data will be challenging.

- Which coral taxa will be modelled? This will be informed by the availability of data and confidence in taxonomic identification, however, members discussed this question. USA prioritizes reef-forming species, including branching gorgonian corals (Alcyonacea), including *Primnoa pacifica* and *Paragorgia* sp., Isididae, while Canada is developing models for indicators of vulnerable marine ecosystems identified by NPFC and NAFO. The main framework-forming species in the southern portion of the PICES area include *Lophelia pertusa*; *Madrepora oculata*; *Enallopsammia rostrata*. One option identified was to focus first on deep-sea coral and sponge distributions, and then initiate activities on shallow-water species following the PICES-2016 workshop proposed for WG 32.
- How to manage data-sharing agreements? *e.g.*, UNEP may have ownership of data; a Sharepoint site is also used by ICES, *etc*.
- What resolution should the data be in? USA compiles its data to a 5 km grid, while some of Canada's data are on a 1 km grid.
- What spatial scope should be assumed for PICES area? Focus should be northward of 30°N.
    - Does fishing effort influence distribution patterns? There is an effort to compile fishing data led by Dr. Ray Hilborn (USA). Dr. Rooper will follow up on availability of this dataset.
    - How do we standardize species codes (*e.g.*, those used by JAMSTEC, WoRMs OBIS, DFO, *etc*.)? The TCODE Committee may be able to provide guidance on how to address this issue.

Some members suggested that data be submitted to OBIS in Year 3 to give researchers a chance to publish papers related to the data. One potentially fruitful alternative to developing new species distribution models would be to undertake a meta-analysis of existing studies to identify trends common to papers, or differences between western and eastern Pacific ecosystems (or shallow, meso-photic, and deep).

AGENDA ITEM 11

Workshop on biogenic habitat distribution and diversity

WG 32 members developed a proposal to convene a workshop at the 2016 PICES Annual Meeting in San Diego, USA (*WG 32 Endnote 3*). The aims of this workshop are to improve our understanding of factors influencing the distributions of corals and sponges in the North Pacific Ocean, improve habitat models predicting their distribution, and predict how their distributions are likely to shift in response to natural and anthropogenic forcing, including climate change. In preparation for the workshop, members and collaborations will synthesize data, develop models, undertake sensitivity analyses and prepare inputs/outputs for further analysis and interpretation. Sensitivity analyses could examine the effects of model structure/method, data inputs, resolution, taxonomic level, transferability, scalability.

WG 32 members recognized this would require a considerable investment of time and that opportunities to secure funding for research/technical support would help alleviate workloads. Potential sources of funding include NOAA's deep-sea coral program and DFO's International Governance Strategy program.

Members also recognized the potential for participation at the 6th International Symposium on Deep-Sea Corals that will be held in Boston, USA in September 2016.

AGENDA ITEM 12
Biodiversity indicators

Development of biodiversity indicators will follow work on species distribution models. Some discussion points on this topic related to:

- Methodology for collecting data to inform monitoring that is comparable across the North Pacific Ocean;
- Some indicators of threats to biodiversity have been identified (*e.g*., VME indicator species are indicators themselves).

AGENDA ITEM 13
Associations with fish and invertebrates

There is a need to understand the functional relationship between biogenic habitat that underpins associations with fish/invertebrates (*e.g*., shelter, feeding), but WG 32 members recognized this is difficult to do. Research led by Dr. Rooper and collaborators indicates a higher abundance of rockfish in areas with greater coral density. Members agreed that this term of reference could be addressed through a review of existing literature. This could turn into a primary publication.

Time series data are available for corals and fish in shallow waters within China and may be useful datasets to examine in terms of interactions between fish and corals. Other studies focus on: reproduction of commercial fish, white-streaked grouper (*Epinephelus ongus*) in southern Japan where spawning is associated with branching corals; trends in coral or coral bleaching in relation to grouper dynamics; and interactions between coral reef, groupers, and fishers. In this example, groupers aggregate around coral reefs and provide fishing opportunities, but fishers agree to close areas during the breeding season to ensure sustainability. This is potentially an interesting example to explore in terms of the changes in coral distribution.

AGENDA ITEM 14
Review of proposed WG 32 workshop for PICES-2016

Dr. Curtis reviewed the proposal for 2-day Workshop on "*Distributions of habitat-forming coral and sponge assemblages in the North Pacific Ocean and factors influencing their distributions*" (*WG 32 Endnote 5*) with WG 32 members before adjourning the meeting.

WG 32 Endnote 1

WG 32 participation list*

Members

Kwang-Sik Albert Choi (Korea)
Janelle Curtis (Co-Chair, Canada)
John Guinotte (USA, on behalf of Les Watling)
Masashi Kiyota (Co-Chair, Japan)
Anders Knudby (Canada)
Takeo Kurihara (Japan)
Chris Rooper (USA)
Go Suzuki (Japan)

Observers

Malcolm Clark (New Zealand)
Huang Huo (China)
Oleg Katugin (Russia)
Ian Perry (Canada)
Darlene Smith (Canada)
Thomas Therriault (Science Board Chair)

* Dr. Jianming Chen (China) met independently with WG 32 Co-Chairs in Qingdao, China, on October 18, 2015 to discuss mutual research interests.

WG 32 Endnote 2

WG 32 meeting agenda

Thursday, October 15, 2015; 9:00 – 18:00

1. Welcome, sign-in, and introductions

Meeting objectives:
To review the terms of reference (ToR), exchange information about data availability, and identify opportunities and challenges. WG 32 ToR and members are posted on the WG 32 web page at https://www.pices.int/members/working_groups/wg32.aspx.

2. Terms of Reference

Review the Terms of Reference, and identify key opportunities and challenges. Develop a shared vision on how we carry forward with tasks in eastern, central and western North Pacific Ocean.

3. Review and discussion of coral and sponge distribution modelling in the North Pacific Ocean
    a) Technical issues related to habitat modelling (Kiyota)
    b) Experience with SDM in Atlantic Ocean (Knudby)
    c) Basin wide predictions in Pacific Ocean (Guinotte)

4. Review of available data
    a) Summarize previous studies, ongoing research, and the sources of species and environmental data available in the northeast Pacific Ocean to develop species distribution models for corals and sponges (Canada, USA to prepare short presentations).
    b) Summarize previous studies, ongoing research, and the sources of species and environmental data available in the northwest and central Pacific Ocean to develop species distribution models for corals and sponges (China, Japan, Korea, Russia, USA to prepare short presentations).

5. Identify scientific research questions of mutual interest for PICES WG 32 members

Given discussions of available data, opportunities and challenges, discuss potential research avenues linked to the ToR that could be developed into a PICES Report and primary publication(s) of mutual interest.

6. Linkages with FUTURE (Ian Perry)

Review FUTURE plans and discuss opportunities for WG 32 to link with FUTURE activities.

7. Review Agenda for WG 32 Meeting, Day 2 (October 17, 2015) and other matters

8. Meeting Adjourned; WG 32 Dinner

Saturday, October 17, 2015, 9:00 – 18:00

Meeting objective:

Develop the workplan to achieve the Terms of Reference (ToR) and produce scientific publications of mutual interest. The ToR are posted on the WG 32 web page.

Welcome, sign-in, and introductions

9. Compilation of data
    a) Develop a plan to compile data on the distribution of corals, sponges, and associated biota, and facilitate their submission to appropriate databases.
    b) Develop a plan to compile data on key variables (temperature, velocity, ocean acidification, slope, aspect) hypothesized to influence coral and sponge distribution and diversity and catalogue sources of multibeam/swathe bathymetry data for distribution modeling.

10. Models of coral and sponge distributions
    a) Develop a plan to review modeling approaches to predict the potential distributions of species and habitat suitability for corals and sponges (*e.g*., Maxent, Boosted Regression Trees, or high resolution bathymetry-based models).
    b) Develop a plan to identify environmental and ecological predictors of patterns in the distribution and biodiversity of coral, sponge and associated taxa.

11. Workshop on biogenic habitat distribution and diversity

Review the draft proposal to convene a workshop on biogenic habitat distribution and diversity at the 2016 PICES Annual Meeting in San Diego, USA.

12. Biodiversity indicators

Develop a plan to develop indicators for assessing and monitoring diversity of biogenic habitats.

13. Associations with fish and invertebrates

Develop a plan to study associations between fish and invertebrate species and biogenic habitats

14. Proposed WG 32 workshop at 2016 PICES Annual Meeting

Review WG 32 proposal to convene a session on distribution and biodiversity of biogenic habitat for the 2016 PICES Annual Meeting in San Diego

15. Meeting Adjourned; Evening WG 32 Dinner

WG 32 Endnote 3

Proposal for a 2-day Workshop on *"Distributions of habitat-forming coral and sponge assemblages in the North Pacific Ocean and factors influencing their distributions"* at PICES-2016

Convenors:
Shallow water corals – Dr. Kwang-Sik Choi (Korea)
Benthic habitat modeling – Dr. Chris Rooper (USA)
Western Pacific Ocean – Dr. Masashi Kiyota (Japan, corresponding convenor)
Eastern Pacific Ocean – Dr. Janelle Curtis (Canada, corresponding convenor)
Deep-sea corals – Dr. Les Watling (USA)

Invited speakers:
Shallow water corals: Dr. Hiroya Yamano (Japan)
Management applications: Dr. Malcolm Clark (NIWA, New Zealand)
Hexactinellida: Dr. Henry Reiswig (Canada)

Changes in the marine environment influence global and regional distribution patterns of marine organisms including corals and sponges in shallow, mesophotic, and deepwater ecosystems. The biogenic habitats formed by these organisms support a broad range of biodiversity, and provide critical habitats for some socio-economically important fishes and invertebrates that attract commercial fishing and other anthropogenic activities. The aim of this workshop is to improve our understanding of factors influencing the distributions of corals and sponges in the North Pacific Ocean, improve habitat models predicting their distribution, and predict how their distributions are likely to shift in response to natural and anthropogenic forcing, including climate change. In preparation for the workshop, WG 32 members and collaborators will compile new data on corals and glass sponges in the North Pacific Ocean as well as existing environmental data to improve model prediction and interpretation based on a multi-model approach. Specifically, deep-sea coral habitat suitability models developed using records from all ocean basins will be improved with the addition of coral location data from the North Pacific Ocean. New habitat suitability models will be developed for deep-sea sponges and multi-model comparisons will be made for both coral and sponge taxa. Workshop participants will be invited to discuss, compare, and evaluate the influence of predictor variable data, and different modelling approaches on results. This process will help identify potential ecological and physiological mechanisms influencing their distributions and provide insight into the potential for changes in their distribution under different climate change scenarios. A novel contribution anticipated from this workshop will be the first habitat predictions for glass sponges (Hexactinellida) at a basin-wide scale in the North Pacific Ocean. Workshop participants will synthesize lessons to be learned from the modelling exercise, future tasks to further improve predictive accuracy, and possible applications for supporting marine spatial planning processes.

Co-sponsoring organization: Marine Conservation Biology Institute; Benthic habitat modeling – Dr. John Guinotte (USA)

PICES-2016

November 2–13, 2016, San Diego, USA

Excerpted from:

Summary of Scientific Sessions and Workshops at PICES-2016

BIO Workshop (W3)

Distributions of habitat-forming coral and sponge assemblages in the North Pacific Ocean and factors influencing their distributions

Co-convenors: *Kwang-Sik Choi (Korea), Janelle Curtis (Canada), Masashi Kiyota (Japan), Chris Rooper (USA)*

Invited Speaker:
Hiroya Yamano (Center for Environmental Biology and Ecosystem Studies, NIES, Japan)

Background

Changes in the marine environment influence global and regional distribution patterns of marine organisms including corals and sponges in shallow, mesophotic, and deepwater ecosystems. The biogenic habitats formed by these organisms support a broad range of biodiversity, and provide critical habitats for some socio-economically important fishes and invertebrates that attract commercial fishing and other anthropogenic activities. The aim of this workshop was to improve understanding of factors influencing the distributions of corals and sponges in the North Pacific Ocean, improve habitat models predicting their distribution, and predict how their distributions are likely to shift in response to natural and anthropogenic forcing, including climate change.

Summary of presentations

The 2-day workshop was held on November 2 and 3, 2016. It was co-convened by Drs. Kwang-Sik Choi (Korea), Masashi Kiyota (Japan) and Chris Rooper (USA). The invited speaker was Dr. Hiroya Yamano (Japan). The workshop comprised three sessions of oral presentations in the morning and early afternoon of the first day, with a total of 9 papers presented. It was followed by species distribution modelling session during the rest of the first day and throughout the second day. The workshop was attended by more than 20 researchers.

The oral session 1 covered recent topics in habitat-forming shallow-water corals including direct and indirect impacts of environmental changes, case studies of future projection modeling, and field monitoring of annual reproductive cycles of coral species expanding their geographical ranges to higher latitudes. H. Yamano highlighted that the current level of CO_2 emission enhances seawater temperature warming, ocean acidification and sea level rise in global scale and increases precipitation and sediment discharge from land to sea in regional scale, and these processes affect the distribution and condition of shallow-water corals in a complex manner.

In session 2, deep water coral and sponge distributions were summarized in three talks. A significant difference in water mass characteristics in the North Pacific was considered important to predict the presence of deep water octocorals, and the existence of three bathyal biogeographic provinces in the North Pacific was suggested. Understanding the factors that contribute to the distribution of corals and sponges in deep water may be elucidated using a modeling approach. The major glass sponge habitats confirmed were those forming reefs along the British Columbia coast.

Session 3 focused on technical aspects of the species distribution modeling, including the best-practices for generating input data, creating models and evaluating the results, data driven approach to define bioregions, a multi-scale assessment of species distribution models, and an assessment of the model transferability. In addition to the research focus of each presentation, these talks elicited excellent discussions concerning the selection of informative variables, the most appropriate methods for evaluating models, and lessons learned from currently unpublished work in progress.

Building on the information presented during the oral presentation sessions, the late afternoon and second day of the workshop were devoted to the exercise of building some preliminary models of corals and sponges for data limited taxa. The goals of the modeling session were: 1) to evaluate existing environmental variables/mechanisms affecting basin-wide distribution of coral and sponge, 2) to construct preliminary basin-wide habitat models for taxa including glass sponges and corals in the North Pacific Ocean and 3) to provide model-based information for predicting potential changes in distributions of coral and sponge with climate change.

Currently available environmental layers and species distributional data were presented, and subsequent fruitful discussion suggested avenues for improving these datasets, including the addition of new data (*e.g.*, PAR, SST, current direction, storm surge, and new terrain metrics). In addition, workshop participants evaluated the appropriate taxonomic resolution to use in modeling efforts, and generated a preliminary list of taxa to model (shallow-water corals, glass sponges, stony corals, gorgonian corals and sea pens). After the habitat variables and response data were compiled, cleaned and discussed, the initial models were developed for shallow-water corals and glass sponges.

It was particularly beneficial to have the combined experience of both modelers and biologists in order to be able to standardize and refine the modeling approach based on the expert understanding of species taxonomy, biology, and ecology. Preliminary models and data sets were shared among the WG 32 members and will provide a common basis to iteratively discuss and develop the best methods inter-sessionally for overcoming issues that arose during the modeling process.

List of papers

Oral presentations

Environmental factors affecting the distribution of habitat-forming shallow-water corals (Invited)
Hiroya Yamano

First report on the annual gametogenesis of high-latitude corals *Alveopora japonica* (Eguchi, 1968) and *Oulastrea crispta* (Lamarck, 1816) on Jeju Island, Korea
Jin-Soo Park, Sang-Yul Park, Shashank Keshavmurthy, Chang-Keun Kang and Kwang-Sik Choi

Biogeographic patterns and hypotheses relating deep-sea coral distributions to water masses
Les Watling

Factors affecting the large scale distribution of deep sea corals and sponges in the Alaskan ecosystems of the North Pacific Ocean
Christopher N. Rooper, Rachel Wilborn and Pamela Goddard

Seascape ecology of glass sponge reefs: Fine scale measurements of habitat heterogeneity and its relationship to community structure
Stephanie K. Archer, Jannet Mossman and Anya Dunham

Resolving biogeographic patterns in the deep sea using species distribution modeling
Samuel E. Georgian and Erik E. Cordes

Data-driven bioregions for local ecosystem context in species distribution models
Andrew McMillan and Anders Knudby

Selection of the proper spatial resolution for habitat modeling of cold-water corals
Mai Miyamoto, Masashi Kiyota, Hiroto Murase, Takeshi Nakamura and Takeshi Hayashibara

Testing the transferability of species distribution models between shallow seamounts in the North Pacific Ocean
Dana Haggarty, Janelle Curtis and Cherisse Du Preez

Report of Working Group 32 on *Biodiversity of Biogenic Habitats*

The second business meeting of the Working Group on *Biodiversity of Biogenic Habitats* (WG 32) was held on 4 November 2016 in San Diego, USA, under the chairmanship of Dr. Masashi Kiyota (Japan). Fifteen people participated in the meeting and represented five PICES member countries (***WG 32 Endnote 1***). Dr. Kiyota welcomed all participants, including new member from China, Dr. Shufang Liu, to the meeting before conducting business (***WG 32 Endnote 2***).

AGENDA ITEM 2
Summary and follow-up of the workshop W3

WG 32 reviewed the progress made through the 2-day BIO Workshop (W3) on "*Distributions of habitat-forming coral and sponge assemblages in the North Pacific Ocean and factors influencing their distributions*" which was held on November 2 and 3, 2016 antecedent to the WG meeting:

- Potential factors influencing the distribution of deep/shallow water coral species were reviewed, and available data sets relevant to these factors were compiled;
- Species distribution models (SDMs) for deep-water glass sponges and shallow-water corals were developed;
- Impacts of global warming and ocean acidification and regional changes in precipitation and soil flux on shallow-water corals were summarized;
- Future projection modeling of the impacts of climate change and ocean acidification on shallow-water coral species were presented;
- Participants confirmed that the following future projection data would also be applicable to SDMs of deep-water species:
  - sea water temperature,
  - aragonite/calcite concentration related to ocean acidification,
  - water currents and their relation to bottom topography.

The progress on the above items fulfills the terms of reference (TORs) of the WG 32 for Year 2.

Dr. Chris Rooper (USA) presented additional outputs of species distribution models developed for shallow-water corals and deep-water glass sponges. Results of the glass sponge model prompted discussion regarding how future iterations of the model might be improved. A number of good suggestions were offered and will be incorporated into future collaborative modeling that WG 32 will conduct during the inter-sessional period.

Dr. Hye-Won Moon (Korea) made a presentation entitled "*Distribution and diversity of corals in Korea*" that demonstrated changes in coral species composition and distribution in Korean waters and summarized their conservation and monitoring status. Participants noted that such information would fit into the Year 3 TORs of the WG, especially for the purpose of establishing indicators for monitoring the biogenic habitats.

AGENDA ITEM 3
Possible inter-sessional works

Further development and improvement of SDMs and data sets:

- Program code and input data of the SDMs developed during the workshop were shared among the participants. WG 32 will continue the following works during the inter-sessional period:
  - Data treatment (addition of environmental data, data cleaning, variable selection, trial of data thinning and other techniques);
  - Application to other species (*e.g*., stony corals, gorgonian corals and sea pens);
  - Expansion of the target area to include the entire PICES region of the North Pacific;
  - Application and comparison of multiple models, including models that can handle presence/absence type distribution data;
  - Application of future projection data.

Dissemination of the results:

- WG 32 discussed the publication of workshop results as original scientific papers. Participants agreed to continue the discussion while checking the progress accomplished through the inter-sessional works.

AGENDA ITEM 4
WG 32 work plan for 2017

Participants recalled that the TORs of WG 32 for Year 3 included following items:

- Review and propose potential indicators for assessing and monitoring diversity of biogenic habitat;
- Review and document commercially important species that are associated with biogenic habitats;
- Prepare scientific reports for dissemination of results.

To accomplish these tasks, Dr. Anya Dunham (Canada) proposed to convene a 1-day Topic Session at PICES-2017 (***WG 32 Endnote 3***). Participants discussed that the Workshop/Topic session should cover both indicators of biogenic habitats and association of commercially important species with these habitats.

AGENDA ITEM 5
Other issues

Nomination of an acting Co-Chair

WG 32 discussed how to supplement the immediate absence of Co-Chair, Dr. Janelle Curtis. Dr. Dunham was nominated by the WG to act as co-chair until Dr. Curtis returns to work.

Membership and participation

WG members asked Dr. Oleg Katugin (observer, Russia) about future participation of Russian scientists in WG 32. He will continue to encourage Russian specialists on cold-water corals to participate at the next meeting of the WG.

WG 32 Endnote 1

WG 32 participation list

Members

Kwang-Sik Choi (Korea)
Anya Dunham (Canada)
Masashi Kiyota (Co-Chair, Japan)
Anders Knudby (Canada)
Shufang Liu (China)
Hye-Won Moon (Korea)
Chris Rooper (USA)
Les Watling (USA)

Observers

Samuel Georgian (USA)
Oleg Katugin (Russia)
Naoki H. Kumagai (Japan)
Qiufen Li (China)
Mai Miyamoto (Japan)
Hiroaki Saito (Japan)
Go Suzuki (Japan)

Members unable to attend

Canada: Janelle Curtis (Co-Chair)
China: Jianming Chen, Hui Huang, Keji Jiang, Zhuojun Ma, Shu Wang, Feng Zhao
Japan: Takeo Kurihara
Korea: Seonock Woo
Russia: Tatyana Dautova
USA: John Guinotte

WG 32 Endnote 2

WG 32 meeting agenda

1. Welcome
2. Summary and follow-up of the workshop W3
3. Possible intersessional works
4. WG 32 work plan for 2017
4. Other issues

WG 32 Endnote 3

Proposal for a 1-day Topic Session on *"Indicators for assessing and monitoring biodiversity of biogenic habitats"* at PICES-2017

Duration: 1 day

Co-Convenors: Anya Dunham (Canada), Hye-Won Moon (Korea)

Suggested Invited Speakers: Peter Mumby (University of Queensland, Australia), Mary Yoklavich (NOAA, USA).

Session Description

Biogenic habitats formed by corals, sponges, and other structure-forming taxa support a broad range of biodiversity, including socio-economically important fishes and invertebrates, and are known to be vulnerable to disturbances. Predicting, assessing, and monitoring shifts in habitat-forming species and associated communities in response to natural and anthropogenic forcing require suites of measurable indicators. The goal of this session is to improve our understanding of ecologically relevant, sensitive, observation-based indicators for assessing and monitoring biogenic habitats. We invite presentations on indicators encompassing single or compound metrics of the marine biota in a broad sense (from physiological to species, community and habitat levels) which could be measured to indicate the state of, or monitor impact to, biogenic habitats and communities they support. Empirical studies and literature reviews on indicator development, assessment, and/or application are invited. WG 32 members and collaborators will present a literature review of documented functional associations between commercially important fish and invertebrate species and biogenic habitats and potential ways to incorporate these associations into indicator development. In line with the PICES-2017 theme, this session will help improve our understanding and ability to identify and characterize changes in biogenic habitats, as well as their recovery potential. It will help inform management and policy decisions and marine spatial planning processes to maintain ecosystem biodiversity, structure, and function.

PICES-2017

September 22–October 1, 2017, Vladivostok, Russia

Report of Working Group 32 on *Biodiversity of Biogenic Habitats*

The third business meeting of the Working Group on *Biodiversity of Biogenic Habitats* (WG 32) was held on September 23, 2017 in Vladivostok, Russia, under the chairmanship of Dr. Masashi Kiyota (Japan). Five people participated in the meeting and represented two PICES member countries (***WG 32 Endnote 1***). Several members who could not attend the meeting reported progress on their inter-sessional activities (see ***WG 32 Endnote 2***) and/or provided comments through the E-mail communication.

AGENDA ITEM 1

Progress in species distribution modeling of corals and sponges

A progress report by Drs. Chris Rooper (USA), Anders Knudby (Canada) and Samuel Georgian (USA) was provided for the meeting that demonstrated on-going activity in constructing species distribution models for corals and sponges in the North Pacific Ocean. Three lines of research are:

1) Compilation of basin-wide environmental variables used in the modeling;
2) Procurement of additional records of presence and absence for benthic invertebrate taxa from sources in the North Pacific Ocean;
3) Construction of preliminary models for benthic invertebrates.

Work is also proceeding on developing and testing new techniques for species distribution modeling. For example, the modeling team has generated new environmental variables that reflect processes important to biogenic habitats (*e.g.*, angle between sea floor surface and current direction) and has developed a spatial bias grid which can account for and accommodate the spatial biases in species records caused by the prevalence of biological sampling in the eastern North Pacific.

In 2018 WG 32 expects to construct draft models for 5 groups of benthic invertebrates: 1) glass sponges, 2) gorgonian corals, 3) stony corals, 4) sea pens, and 5) shallow-water corals. The environmental variables, models and methodologies will be presented in talks at the proposed Topic Session on "*Indicators for assessing and monitoring biodiversity of biogenic habitats*" at PICES-2018 (see ***WG 32 Endnote 3***). These analyses will also form the basis of peer-reviewed manuscripts and reports anticipated at completion of WG 32's term, proposed for 2018.

AGENDA ITEM 2

Preparation for a topic session and paper submission

Preparation for a topic session

A report on the preparation for the Topic Session on "*Indicators for assessing and monitoring biodiversity of biogenic habitats*" was provided by Dr. Anya Dunham, one of the Co-Convenors. At PICES-2016, WG 32 proposed the Topic Session for the PICES 2017 Annual Meeting which was recommended by Science Board and accepted by Governing Council. Due to operational issues, WG 32 withdrew this Topic Session prior to PICES-2017. Therefore, WG 32 requested:

1) A one-year extension to complete WG 32's terms of reference;
2) A Topic Session at PICES-2018 (see resubmitted proposal in ***WG 32 Endnote 3***).

Participants discussed possible topics for the Topic Session. There was a question about the definition of the indicators, and participants confirmed that the indicators can include broad categories from physiological to species, community and habitat levels.

Dr. Mai Miyamoto presented her study to evaluate the effectiveness of cold-water corals as community diversity indicator taxa in the Emperor Seamounts region of the western North Pacific. She presented a new method to assess characteristics of benthic communities and to screen for potential indicator taxa based on the analysis of co-occurrence tendencies among benthic animals. Using this technique, she demonstrated the effectiveness of gorgonians and stony corals as indicator taxa that can represent the existence of various benthic taxa.

Dr. Tatiana Dautova presented results of surveys and researches in the northwestern Pacific that indicate high diversity of octocorals in the deep-sea zones of the Russian waters. She pointed out the importance of the Kurile Islands as pathway of cold-water coral diversity and suggested further research on taxonomy, biology and ecology of the cold-water corals in Russian waters.

Dr. Go Suzuki presented the on-going studies of his colleague on the use of environmental DNA (eDNA) as a species diversity indicator for shallow water corals. Laboratory studies and field experiments are in progress to examine the practicability of eDNA for biogenic habitat such as coral reefs.

Participants agreed that these topics will provide good materials for the anticipated Topic Session in 2018.

Paper submission

Dr. Dunham reported the progress of her team on the preparation of two papers addressing indicators for assessing and monitoring biogenic habitats:

1) Methods of benthic cover assessment in biogenic habitats;
2) Visual survey design for deep water biogenic habitats.

These papers will be presented in the anticipated Topic Session at PICES-2018, and may be refined using input received during the topic session. They will also form the basis of peer-reviewed manuscripts and reports anticipated for completion in 2018.

AGENDA ITEM 3

Collaboration with NPFC on a VME Workshop 2018

The North Pacific Fisheries Commission (NPFC) requested PICES to participate in and co-sponsor an NPFC/FAO Workshop on "*Protection of Vulnerable Marine Ecosystems in the North Pacific Fisheries Commission Area: Applying global experiences to regional assessments*" to be held in Tokyo, Japan in

March 2018. WG 32's parent committee, BIO, will bring this request to the Science Board for further consideration.

Dr. Alexander Zavolokin, Science Manager of the NPFC Secretariat, presented the scope and outline of the VME Workshop. Two PICES experts, Drs. Janelle Curtis and Chris Rooper, will tentatively attend the VME Workshop. Participants discussed the possible collaboration between PICES and NPFC. PICES experts have ample scientific knowledge on the taxonomy, biology, biodiversity of corals, sponges and other associated organisms as well as the analyses and management of environmental and anthropogenic factors affecting their biodiversity mainly in the area within the national jurisdiction. NPFC scientists are engaged in the management of fisheries and conservation of marine ecosystems in the areas beyond national jurisdictions in the North Pacific. Participants recognized that the collaboration between PICES and NPFC on this issue will be beneficial to both organizations, and endorsed the collaboration of PICES on the NPFC/FAO VME Workshop.

AGENDA ITEM 4
Other issues

Participation from member countries
A new participant from Russia, Dr. Tatiana A. Dautova was welcomed by the WG members.

Related activities
A report was provided by Dr. H.W. Moon that introduces the Korea–U.S. joint agreement on Vulnerable Marine Ecosystems for examining fisheries bycatch in the Emperor Seamounts region and constructing an identification guide. The program was to fulfil the requirements of UNGA Resolution 61/105, NPRFMO (inter-governmental agreement prior to the establishment of NPFC) and NPFC.

WG 32 Endnote 1

WG 32 participation list

Members	Observers
Masashi Kiyota (Co-Chair, Japan)	Mai Miyamoto (Japan)
Go Suzuki (Japan)	Alexander Zavolokin (NPFC)
Tatiana N. Dautova (Russia)	

Members unable to attend

Canada: Janelle Curtis, Anya Dunham, Anders Knudby
China: Jianming Chen, Hui Huang, Keji Jiang, Shufang Liu, Zhuojun Ma, Shu Wang, Feng Zhao
Korea: Kwang-Sik Albert Choi, Hye-Won Moon, Seonock Woo
USA: John M. Guinotte, Chris Rooper, Les Watling

WG 32 Endnote 2

WG 32 meeting agenda

1. Progress in species distribution modeling of corals and sponges
2. Preparation for a topic session and paper submission on indicators for assessing and monitoring biogenic habitats
3. Collaboration with NPFC on VME Workshop 2018
4. Other issues

WG 32 Endnote 3

Proposal for a Topic Session on “*Indicators for assessing and monitoring biodiversity of biogenic habitats*” at PICES-2018

Duration: 1 day

Convenors: Anya Dunham (Canada), Hye-Won Moon (Korea)

Suggested Invited Speakers: Mary Yoklavich (NOAA, USA); Peter Mumby (University of Queensland, Australia); Peter Houk (University of Guam)

Biogenic habitats formed by corals, sponges, and other structure-forming taxa support high species abundance and biodiversity, including socio-economically important fishes and invertebrates. These habitats are also known to be vulnerable to disturbances from human impacts and climate change. Predicting, assessing, and monitoring shifts in habitat-forming species and associated communities in response to natural and anthropogenic forcing require suites of measurable indicators. The goal of this session is to improve our understanding of ecologically relevant, sensitive, observation-based indicators for assessing and monitoring biogenic habitats. We invite presentations on indicators encompassing single or compound metrics of the marine biota in a broad sense (from physiological to species, community and habitat levels) which could be measured to indicate the condition of biogenic habitats and monitor changes to the habitats and communities they support. Empirical studies and literature reviews on indicator development, assessment, and/or application are invited. WG 32 members and collaborators will present a literature review of documented functional associations between commercially important fish and invertebrate species and biogenic habitats and address methods to incorporate these associations into indicator development. This session will help improve our understanding and ability to identify and characterize changes in biogenic habitats, as well as their recovery potential. The results of this session will help inform management and policy decisions and marine spatial planning processes that can maintain ecosystem biodiversity, structure, and function.

PICES-2018
October 25–November 4, 2018, Yokohama, Japan

Excerpted from:

Summary of Scientific Sessions and Workshops at PICES-2018

BIO Topic Session (S4)
Indicators for assessing and monitoring biodiversity of biogenic habitats

Convenors: *Anya Dunham (Canada) corresponding, Hye-Won Moon (Korea)*

Invited Speaker:
Yves-Marie Bozec (The University of Queensland, Australia)

Background

Biogenic habitats formed by corals, sponges, and other structure-forming taxa support high species abundance and biodiversity, including socio-economically important fishes and invertebrates. These habitats are also known to be vulnerable to disturbances from human impacts and climate change. Predicting, assessing, and monitoring shifts in habitat-forming species and associated communities in response to natural and anthropogenic forcing require suites of measurable indicators. The goal of this session was to improve our understanding of ecologically relevant, sensitive, observation-based indicators for assessing and monitoring biogenic habitats. Presentations on indicators encompassing single or compound metrics of the marine biota in a broad sense (from physiological to species, community and habitat levels) which could be measured to indicate the condition of biogenic habitats and monitor changes to the habitats and communities they support were invited. Empirical studies and literature reviews on indicator development, assessment, and/or application were invited. WG 32 members and collaborators also presented a literature review of documented functional associations between commercially important fish and invertebrate species and biogenic habitats and addressed methods to incorporate these associations into indicator development. This session was intended to help improve our understanding and ability to identify and characterize changes in biogenic habitats, as well as their recovery potential. The results of this session will help inform management and policy decisions and marine spatial planning processes that can maintain ecosystem biodiversity, structure, and function.

Summary of presentations

The session consisted of 9 oral presentations (three of which were cancelled) and 3 posters that covered a wide variety of biogenic habitat indicators. Oral presentations were given during a half-day session on October 30 and included three presentations by early career scientists. The Session's invited speaker, Yves-Marie Bozec, presented his research on mechanistic indicator of dynamics in coral reef habitats under multiple disturbances such as overfishing and global warming. He showed implications for reef monitoring and indicators and forecasting structural complexity through simulation modelling. Go Suzuki suggested a new method to assess species diversity and dominance of shallow water corals using environmental DNA; he presented the results of an experimental study to detect of eDNA in coral tanks that showed promise and suggested further testing of the technique in the open water. Mai Miyamoto presented a novel application of association analysis for identifying VME indicator taxa using sea floor visual images from the Emperor Seamount (method that minimizes the impacts on the sea floor via examining visual images without sampling). Composition of benthic community varied depending on the bottom substratum; gorgonians were dominant taxa. Anya Dunham showed the results of a review paper on the methods for assessing habitat-forming species and associated biodiversity, outlined a systematic assessment and monitoring survey protocol, and walked the audience through an application of this protocol to a case study of glass sponge reefs, a new biogenic habitat type not previously assessed in a quantitative way. Jackson Chu reported on the environmental niche space and distributions of cold-water corals and sponges in the northeast Pacific Ocean, highlighting the correlation of cold-water corals and sponge distribution with low oxygen zones. Finally, Hyeong-Gi Kim discussed his findings on the differences in nematode assemblages associated with *Sargassum muticum* in its native range in South Korea and as an invasive species in the English Channel. Discussion centered on the broad range of indicator approaches developed (from eDNA to visual survey techniques to modelled distributions) and on the challenges and progress made on developing quantitative approaches. Based on high quality of oral presentations and posters, diversity of indicator approaches, and level of attendance (~85 participants), the Topic Session "*Indicators for assessing biodiversity of biogenic habitats*" at PICES-2018 was deemed to be a success.

List of papers

Oral presentations

Identifying mechanistic indicators of coral reef resilience (Invited)
Yves-Marie Bozec

Assessment of species diversity and dominance of shallow water corals using environmental DNA
Go Suzuki, Hiroshi Yamashita, Yuna Zayasu and Chuya Shinzato

Application of association analysis for identifying VME indicator taxa based on sea-floor visual images
Mai Miyamoto and Masashi Kiyota

Marine biogenic habitats: assessing benthic cover and species-habitat associations
Tse-Lynn Loh, Stephanie K. Archer, Anya Dunham

Modelling the environmental niche space and distributions of cold-water corals and sponges in the northeast Pacific Ocean
Jackson W.F. Chu, Jessica Nephin, Samuel Georgian, Anders Knudby, Chris Rooper and Katie S.P. Gale

Comparison of nematode assemblages associated with *Sargassum muticum* in its native range in South Korea and as an invasive species in the English Channel
Hyeong-Gi Kim, Lawrence E. Hawkins, Jasmin A. Godbold, Chul-Woong OH, Hyun Soo Rho and Stephen J. Hawkins

Poster presentations

Transcriptome study of scleractinian coral *Alveopora japonica*
Seonock Woo, Sung-Jin Hwang, In-Young Cho and Min-Sup Kim

Predictive modeling methods for deep-sea sponges in the North Pacific Ocean
Fiona Davidson, Anders Knudby

Changes in the fish community in seagrass bed on the Pacific coast of northeastern Japan before and after (2009-2017) the tsunami following the 2011 off the Pacific coast of Tohoku Earthquake
Kentaro Yoshikawa, Hikaru Nakano and Jun Shoji

Appendix 5

PICES Press Articles related to WG 32

Applying global experiences to regional assessments: A workshop on the Protection of Vulnerable Marine Ecosystems in the North Pacific Fisheries Commission Area

by Chris Rooper and Masashi Kiyota

Vulnerable marine ecosystems (VMEs) are benthic habitats comprised of taxa that are typically long-lived and slow growing, and that become reproductively mature at advanced ages. These life history characteristics make them very susceptible to impacts from disturbances, such as deep-sea fishing and seafloor mining activities. VMEs are may also be impacted by the effects of climate change and ocean acidification, since these ecosystems occur in generally stable deep-water environments and can require calcium carbonate or other minerals for their skeletons. In the North Pacific Ocean VMEs are generally comprised of taxonomic groups such as Gorgonians and Scleractinians (for corals) and Hexactinellids and Demosponges (for sponges). In the North Pacific Ocean, the existing VMEs are vulnerable to damage from both the ongoing bottom contacting fishing gear (bottom trawls, longlines, pots, gillnets) and the effects of climate change (warming and acidification). These ecosystems are of particular concern in the North Pacific Ocean because of their role as habitat for fishes, their trophic role in the ecosystem and their life history characteristics which make them slow to recover.

The North Pacific Fisheries Commission (NPFC) is the Regional Fisheries Management Organization (RFMO) for international waters (exclusive of nations' EEZs) of the northern Pacific Ocean. This includes the PICES region of interest (north of 30 degrees latitude), where it occurs in international waters. The objective of the NPFC is to "ensure long-term and sustainable use of the fisheries resources in the Convention Area while protecting the marine ecosystems of the North Pacific Ocean in which these resources occur".

Bottom fishing in the North Pacific Fisheries Commission Convention Area is limited to a subset of seamounts south of 45 degrees and north of the northern Hawaiian Islands (USA EEZ) in the Emperor Seamount chain in the western North Pacific Ocean and about 8 seamounts in four aggregations in the eastern North Pacific Ocean. Canada, Korea, Japan and Russia are convention members that currently participate in these fisheries, with Canadian fishing vessels operating exclusively on the eastern seamounts and Korea, Japan and Russia operating in the Emperor Seamount Chain. The Korean, Japanese and Russian fisheries utilize bottom trawls, gillnets and longlines and in recent times only a small number of vessels from each country have participated in the fishery (1, 4 and 1, respectively). The trawl and gillnet fisheries target the North Pacific armorhead (*Pentaceros wheeleri*) and the splendid alfonsino (*Beryx splendens*), and bottom longlines target skillfish (*Elirepis zonifer*). Historically, there has been a more extensive footprint of the fishery which included seamounts that are now part of the United States EEZ. The Canadian fishery is limited to a maximum of about 6 vessels fishing in a given year, with only a single vessel fishing at a time, and the vessels use longlined pots to capture sablefish (*Anoplopoma fimbria*).

Participants of the NPFC/FAO VME Workshop in Yokohama, Japan.

The goals of the four day workshop were to increase understanding of the interactions between fishing and VME's in the NPFC convention area and to draw on the experiences of other Regional Fisheries Management Organizations (RFMOs) and experts to make recommendations on how the NPFC can put in place appropriate measures to protect and assess impacts on VME's. The meeting was chaired by Drs. Masashi Kiyota (Japan) and Loh-Lee Low (USA). The workshop was held at the National Research Institute of Fisheries Science, Japan Fisheries Research and Education Agency in Yokohama, Japan, from March 12–15, 2018, and was sponsored by the NPFC, FAO and PICES. Representatives from Japan, Canada, China, the Republic of Korea, Russia and the United States attended the meeting. In addition, invited experts from two other RFMO's (the Convention for the Conservation on Antarctic Marine Living Resources and the South Pacific Regional Fisheries Management Organization) and representatives of PICES, FAO and the Deep Sea Conservation Coalition were also in attendance.

The workshop began with presentations by representatives of FAO and RFMOs on the role of these organizations in management of impacts on VMEs and deep-sea fisheries. These presentations provided a good introduction to the issues around VMEs, particularly with regards to United Nations General Assembly Resolution 61/105 that seeks document and mitigate significant adverse impacts of fishing activities on VMEs and implement a precautionary approach to VME management. Dr. Hassan Moustahfid highlighted a recently published document from FAO that reports on the global efforts to manage and protect VMEs and Dr. Tony Thompson presented the legal framework for international obligations for VME management. Dr. Odd Aksel Bergstad provided historical background on seamount bottom fisheries across multiple Atlantic Ocean RMFOs (presented by Dr. Ellen Kenchington) and the nations currently participating in NPFC fisheries each presented information on their current fishing activities in the region.

Invited experts examined VMEs from a number of perspectives, with many interesting presentations on current and historical research. These presentations fell into a number of sub-themes and each provided background and a summary of lessons learned. The workshop organizers drew from a wide variety of experts in order to provide examples of successful research and management of VMEs in other RFMOs and individual countries. Drawing on the presentations and discussions from both invited experts and representatives from NPFC member states, the interesting points and highlights of the workshop are given organized by sub-topic below.

Species characteristics and VME identification

One of the more informative topics brought out by presentations and general discussions was the definition and identification of VME taxa. Dr. Tatiana Dautova (Russia) provided an overview of her research on the taxonomy and connectivity of coral populations in the North Pacific. This presentation highlighted the connectivity of coral populations, not only in the North Pacific, but potentially on a broader scale (globally) for some taxonomic groups including *Paragorgia* corals. Potential mechanisms for connectivity among populations was discussed broadly by the group as well as the potential "source" in an evolutionary sense of the corals that occur in the North Pacific. Clearly more research is required on this research topic.

One of the key points of the discussions of species characteristics and identification was the relatively high level of taxonomic uncertainty for a number of VME groups in the North Pacific Ocean. Drs. Eunjung Kim (Korea), Bob Stone (USA) and Cherisse Du Preez (Canada) all spoke about their respective efforts to produce reference materials for VME identification. In particular, Dr. Kim's presentation provided an example of a taxonomic guide that was being developed by collaborators from Korea and the USA that could be easily used by fisheries observers to identify VME indicator species. It was clear from these discussions that a uniform approach to taxonomic identification and training observers was needed for the NPFC region.

Finally, a wide ranging discussion of VME characteristics brought out the important point that there are unique differences between VMEs in the eastern and western NPFC area. Although sponges and corals occur on both sides of the North Pacific Ocean, the discussion indicated that sponges tend to make up a larger portion of the VME taxa in the east than in the west. Gorgonian and Scleractinian corals appear to be more prevalent in the Emperor Seamounts than the seamounts in the eastern North Pacific.

Fisheries characteristics and potential impacts

Presentations describing the existing bottom contact fisheries in the North Pacific Ocean indicated that they appear to be fairly limited in terms of number of vessels participating (although concerns with unreported fishing activity that may be occurring was also referenced during discussions). However, there is limited life history information for the two species fished in the Emperor Seamounts (North Pacific armorhead and splendid alfonsino) and the occurrence of fishable abundance is determined by entry of new recruits to the adult population. The sablefish population that is fished on eastern North Pacific seamounts appears to be connected to populations within the EEZ of Canada and the USA and because of this, more is known about the population dynamics and status. The gear types used by the countries participating in the seamount fisheries; longlined pots (Canada), bottom gillnets (Japan) and bottom trawls (Japan and Korea) are all known to have impacts on VMEs.

Dr. Ellen Kenchington (Canada) presented an assessment of actions that have been implemented in other RFMOs in the Atlantic Ocean and the eastern Canadian EEZ to address significant adverse impacts on VME taxa. One of the highlights of this presentation was the discussion of the role of VMEs in ecosystems and benthic ecosystem functions. Studies examining sponges in the Atlantic revealed that they can filter 95% of the particulate matter from about 25,000 litres of water per day. The role of VME taxa in communities can thus be very important to the functioning of the ecosystem and Dr. Kenchington's presentation demonstrated the need and current methods used for identifying and surveying VMEs and assessing impacts on these communities.

Assessment of impacts of fishing on VME taxa is often difficult to document. Dr. Chris Rooper (USA/PICES) presented information on the rates of damaged VME taxa from the eastern Bering Sea in Alaska, where sea whips, corals and sponges have all been impacted by bottom fishing gear, with sea whips being the most commonly impacted due to their occurrence in an area with intensive fishing. Dr. Rooper also presented a summary of efforts in the Alaska region to account for bycatch of VME indicator species using fisheries observers and bottom trawl survey collections as well as changes in fishing gear implemented in Alaska that have led to reduced VME impacts.

An invited expert, Dr. Amy Baco-Taylor (USA), presented an overview of a recent research cruise to the Emperor Seamounts and northern Hawaiian Ridge. This presentation was broadly discussed throughout the workshop, as Dr. Baco-Taylor found evidence of the impacts of fishing on VME taxa at actively fished seamounts. Dr. Baco-Taylor also found evidence for recovery and potentially new recruitment of Scleractinian and Gorgonian corals in areas where fishing had stopped when the USA extended its EEZ. This is a relatively unique finding and prompted much discussion on the implications of recovery on management strategies (e.g. should management focus on "freezing the footprint" of existing fisheries or recovering previously impacted areas where VME taxa were likely to occur).

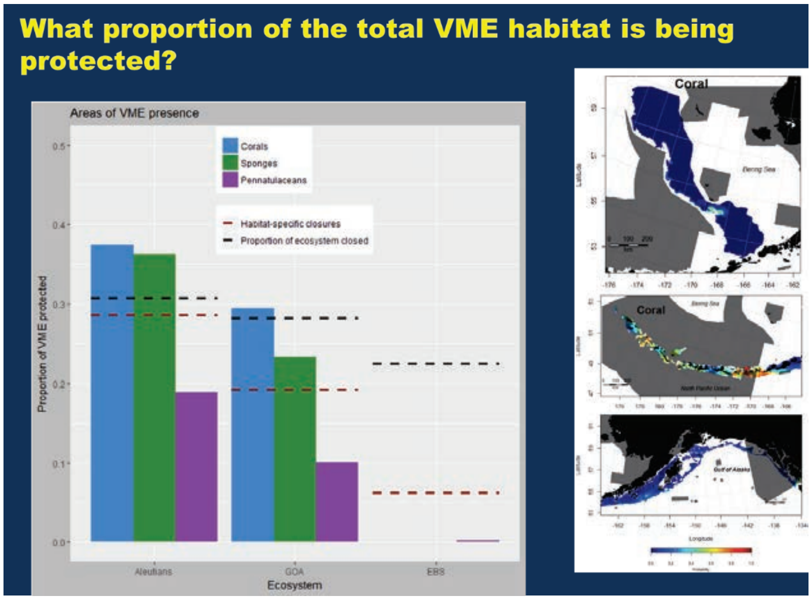
Another important conversation centered around the rules for what fishing vessels should do when they encounter VME taxa as bycatch. Dr. Masashi Kiyota (Japan) led a wide ranging discussion of these VME encounter protocols and their implications. Much of the focus of these discussions was guided by the experiences of other RFMOs in implementing encounter protocols (especially in the CCAMLR region). It was generally concluded that the existing encounter protocols were too generic and broadly applied across taxonomic groups and regions. For example, the absence of Scleractinian corals from bycatch in areas where they were known to exist creates some concern about whether encounter protocols are effective in addressing concerns for these taxa. Additionally, there was a large amount of discussion on whether move-on rules, temporary closures and communication of temporary closures as currently implemented were effective at reducing encounters with VME taxa.

Exploratory fishing was a somewhat related topic addressed by Dr. Dirk Welsford (Australia/CCAMLAR). Exploratory fishing protocols can rely on the same encounter protocols as for non-exploratory fishing activity, so the participants raised some similar concerns for this topic with regards to move-on rules, temporary closures and regional and taxa-specific encounters. Another consideration for exploratory fishing is the importance of data sharing from these activities among member nations and fisheries and making distinctions (and potentially different rules) for research activity versus fishing activity. The experiences of Dr. Welsford and the different RFMOs were very helpful in guiding this discussion, as exploratory fishing is a topic that has been approached differently in the different regions.

Spatial management techniques

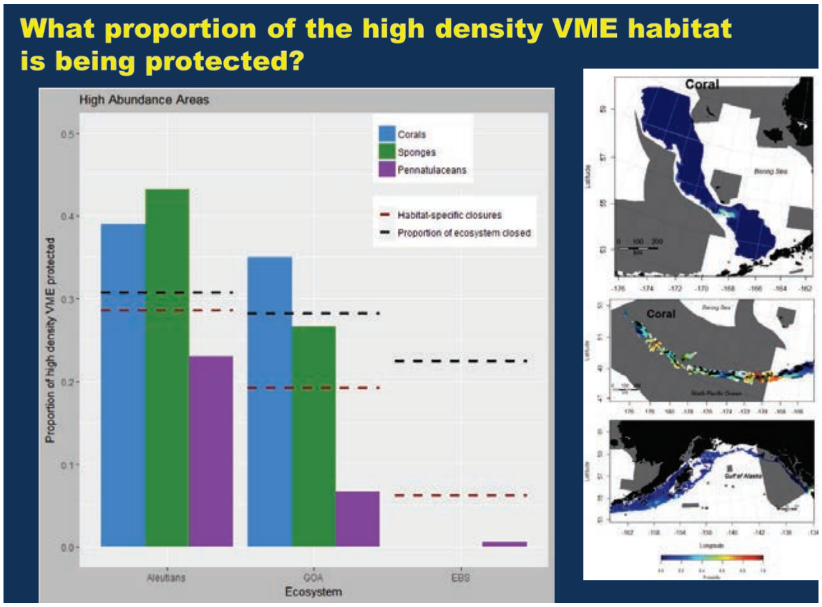
One of the approaches that can be used to evaluate and mitigate impacts of fishing activity on VMEs is by using spatial management techniques. Highlights of talks describing spatial management methods included the descriptions of experiences and approaches from other regions (SPRFMO, CCAMLR, and NAFO) and presentations on North Pacific seamount VMEs. The basis for many of the approaches from RFMOs outside the North Pacific and within member nations' EEZs is formulating maps or species distribution models that identify potential areas of VMEs.

Dr. Chris Rooper (PICES/USA) presented research on how fishing closures have been implemented and evaluated in Alaska. The research began with building spatially explicit models of the distribution of coral and sponge ecosystems in Alaska and validation of these models using independent surveys. This work allowed evaluation of the proportion of VME habitat that was closed to fishing in each of Alaska's large marine ecosystems, as well as the proportion of high value, high density and high diversity areas that were currently in closed areas. This evaluation showed some interesting results for VMEs in Alaska, in that even though ~50% of the coral and sponge habitat was open to fishing in the Aleutian Islands, only ~15.4% of the open area was observed to be fished (estimated from vessel monitoring data). It also showed that for some regions, significant portions of closed areas were devoid of VME taxa. The major lesson learned from these studies was that careful evaluation of fishing patterns relative to the distribution of VMEs can provide important data for ecosystem management.



What proportion of the total VME habitat is being protected?

Estimated proportions of total area of coral and sponge (VME) presence protected from mobile bottom fishing gear in Alaska ecosystems using species distribution models and existing area closures (data courtesy of Chris Rooper Alaska Fisheries Science Center, USA, PICES WG 32 member and John V. Olson, NMFS - Alaska Regional Office, USA).

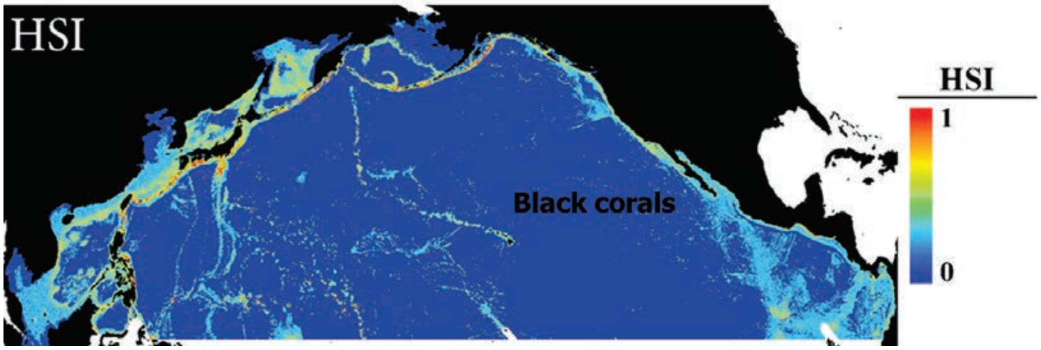


What proportion of the high density VME habitat is being protected?

Estimated proportions of high density coral and sponge (VME) habitat protected from mobile bottom fishing gear in Alaska ecosystems using species distribution models and existing area closures (data courtesy of Chris Rooper Alaska Fisheries Science Center, USA, PICES WG 32 member and John V. Olson, NMFS - Alaska Regional Office, USA).

Dr. Ashley Rowden (New Zealand/SPRFMO) and Dr. Martin Cryer (New Zealand/SPRFMO) presented a summary of the SPRFMO experience in managing VMEs and fishing. This summary, in particular stood out as a very well developed example of the use of spatial management measures to protect and conserve VMEs. In this example, member nations developed distribution models for VMEs, tested and validated these models using field observations, brought in fisheries participants to map where fishing was occurring and was most profitable and then combined these in a spatial decision making software program (Zonation) to provide a tool with which management decisions could be made in a spatially explicit framework. The tool allowed stakeholders to consider trade-offs among objectives (such as maximizing fish production vs. maximizing VME protections) when evaluating management decisions. The example from SPRFMO would serve as an excellent guide for development of VME management for other RFMOs including the NPFC.

Within the NPFC, there have also been some initial steps to begin mapping and modeling VME distributions. Dr. Masashi Kiyota (Japan) presented the results of an impact assessment study for the Emperor Seamounts. The presentation included information from research that examined the overlap of fishing activity and benthic taxa on a small scale (using underwater cameras). As part of these analyses, Dr. Kiyota presented the results of association analysis developed by Dr. Mai Miyamoto to evaluate the representativeness of VME indicator taxa. These analyses were useful in identifying two actual VMEs occurring on the outer margins of main fishing grounds on the Emperor Seamounts.



Predicted probability of habitat suitability (HSI) for black corals (Antipatharians) for the North Pacific Ocean based on maximum entropy modeling of presence records. Map courtesy of Samuel Georgian (Marine Conservation Institute, USA, PICES WG 32 member).

Also in the North Pacific Ocean PICES Working Group 32 (Biodiversity of Biogenic Habitats) has been working on VME distribution models for the North Pacific Ocean. In 2016 this working group sponsored a workshop (W3, Distributions of habitat-forming coral and sponge assemblages in the North Pacific Ocean and factors influencing their distributions). A number of workshop participants (predominantly from Canada and the USA) have been developing a suite of environmental indicators and species distribution models for VME taxa in the broader North Pacific Ocean. These efforts were summarized by Dr. Rooper, with reference to the upcoming PICES Topic Session titled "Indicators for assessing and monitoring biodiversity of biogenic habitats to be held at PICES-2018 Annual Meeting.

Recommendations

Each of the presentations were followed by wide ranging and interesting discussions. Breakout groups were also used to address specific topics. Many of these discussions and breakout groups resulted in recommendations that were assembled on the final day of the workshop. There were a number of recommendations for managing VME's (~30 in total) in the final report, covering topics such as data collection and management, encounter protocols, significant adverse impact assessments, fishing footprints, exploratory fishing protocols, and spatial management measures. The recommendations of particular interest to the PICES community were:

- The need to put in place a data sharing agreement among member nations;
- Standardization of data collection protocols (including taxonomic guides) among member nations;
- Development of area specific indicators and taxon encounter thresholds instead of generic indicators and thresholds;
- Development of measurable objectives for assessing impacts of fishing on VME's;
- Consideration of fisheries closures for both "pristine" and "recovering" VME sites;
- Development of tools for spatial management measures (SDM and maps, Zonation tools) that can assist in decision-making;
- Periodic reviews and updates of VME management with new information as it becomes available.

These and the other recommendations generally reflected the desire to put into place a framework that will allow for the input of additional relevant scientific data that can contribute to the decision-making processes within the NPFC. Finally, there was quite a bit of discussion of potential collaboration with other organizations (such as PICES) to provide expertise, scientific advice and assistance with some of the scientific analyses. This recommendation will likely be a topic of discussion for the Joint PICES-NPFC Study Group for *Scientific Cooperation in the North Pacific Ocean*.

Dr. Chris Rooper (chris.rooper@noaa.gov) is a research fisheries biologist with the National Marine Fisheries Service, Alaska Fisheries Science Center in Seattle, Washington. His research interests are in the function of habitats for fishes, particularly rockfishes and deep-sea corals and sponges, using a combination of in situ studies with underwater cameras and regional scale modeling. In PICES, he is a member of the Working Group (WG 32) on Biodiversity of Biogenic Habitats.

Dr. Masashi Kiyota (m.kiyota@nagasaki-u.ac.jp) is a professor at the Graduate School of Fishery and Environmental Sciences, Nagasaki University, Japan. His Ph.D. study was on breeding systems and foraging ecology of northern fur seals and their relation to population dynamics and management. He worked at the Japan Fisheries Research and Education Agency for many years and conducted scientific research on large marine animals such as marine mammals, seabirds, and sea turtles to understand their ecology and mitigate their interactions with commercial fisheries. His recent studies focus on the assessment of fishery impacts on marine ecosystems, including bottom fisheries and VMEs. In PICES, he is Co-Chair of the Working Group (WG 32) on Biodiversity of Biogenic Habitats.