Presence-only species distribution modelling practices produce biased predictions for Alcyonacean corals on British Columbia's continental shelf and slope

by
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Abstract

Sedentary benthic species such as Alcyonacea corals form critical habitat for fishes and invertebrates, that are vulnerable to anthropogenic activities. Assessing risks to these organisms requires unbiased, quantitative species distribution models (SDMs); however, the accuracy of SDM methods is largely unknown. Here I investigated how data and model types affect SDM predictions of Alcyonacea probability of presence. I compared predictions from generalized additive models (GAMs) fitted to presence-absence observations over a stratified-random survey design with predictions from Maxent maximum entropy models fitted to presence-only bycatch records from commercial fisheries. I developed a simulation algorithm to evaluate the direction and magnitude of bias in each model type. I show that presence-only Maxent predictions are overly optimistic based on commonly used diagnostic measures calculated using cross-validation, and produce biased estimates of species distribution. This study demonstrates a need for robust presence-absence SDMs that will better inform management strategies to maximize conservation measures while minimizing economic losses.

Keywords: Presence-only; Bias; Species Distribution Models; Sensitive Benthic Habitats

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List of Acronyms

AICc	Akaike information criteria corrected for small sample size
ARC	Arc-cord ratio
AUC	Area under the receiver operating characteristic curve
BPI	Bathymetric position index
DEM	Digital elevation model
FC	Feature class
FOS	Fisheries Operating System
GAM	Generalized additive model
KDE	Kernel density estimate
Maxent	Maximum entropy model
MODIS	Moderate resolution imaging spectroradiometer
MPA	Marine protected area
MSPE	Mean squared prediction error
OECM	Effective area-based conservation measures
PacHarv	DFO’s Pacific Region
REML	Restricted maximum likelihood
RM	Regularization multiplier
ROMS	Regional Ocean Modelling System
ROR	Relative occurrence rate
ROV	Remotely operated vehicle
SBCV	Spatial block cross validation
SDM	Species distribution model
SEDI	Symmetric extremal dependence index
StRS	Stratified random survey
TSS	True skill statistic
VIF	Variance inflation factor

1. Introduction

Assessing risks to sedentary benthic species requires unbiased, quantitative species distribution models (SDMs) to infer species geographic and environmental range where direct observation is not possible (e.g., at inaccessible locations, over a wide spatial range, and where it is not financially feasible) and to predict the probability of occurrence in areas outside a particular study region. Sedentary benthic species such as cold-water corals and sponges exist throughout the world's oceans, and some are vulnerable to anthropogenic activities such as offshore industrial activity and commercial fishing (Lagasse et al., 2015; Rooper et al., 2014; Scanes et al., 2018; Williams et al., 2010). Bottom contact fishing with trawls, longlines, or traps occurs at depths of a few hundred to 1,500 m (Clarke et al., 2015) which makes observing the effects of fishing gear on sensitive benthic species expensive and logistically difficult. For many fisheries, the degree of risk posed by bottom contact remains uncertain because there is a great deal of uncertainty about the amount of overlap of fishing gear and sensitive benthic species.

Marine management strategies, such as marine protected areas (MPAs), can protect sensitive species from anthropogenic activities if placed in areas where sensitive species occur. MPAs are highly dependent on SDM predictions and accurate species distribution predictions depend on high quality data (Fei & Yu, 2016). Obtaining high quality data for sedentary benthic species that occur in the deep sea, however, often requires expensive equipment such as remotely operated vehicles (ROVs) and chartered ships, trained professionals to operate the equipment and many hours to collect and process the data. Although numerous SDM approaches exist depending on available data and modelling objectives, it is not always clear how data and model choices interact to affect the bias and precision of SDMs.

The type of data available is typically a limiting factor in SDM choices and, therefore, can limit the quality and relevance of conclusions. Presence-only data are more readily available because they can be obtained opportunistically at low expense and often cover large spatial extents (Vierod et al., 2014; Winship et al., 2020). In particular, presence-only bycatch data collected during commercial fishing activity often covers the large spatial and temporal scales needed for SDMs (Finney & Boutillier, 2010; Rooper et al., 2014, Welsford et al., 2013). On the other hand, presence-only data collected opportunistically lack robust survey sampling designs and typically involve sampling biases, which could lead to SDMs predicting patterns in the data collection methods rather than of habitat associations with species presence (Araújo et al. 2019). SDMs predicting fisheries bycatch is one example where fishing in areas of high habitat suitability where species density is high leads to the assumption that avoided areas represent true absences (Vignaux et al., 1998). Additionally, presence-only data collected opportunistically cannot be easily extrapolated to unsampled areas and, therefore, are not the preferred data type for species distribution modelling (Hastie & Fithian, 2013; Sit et al., 1998; Winship et al., 2020).

Presence and absence data collected following a robust survey sampling design represent the ideal data for species distribution modelling (Hastie & Fithian, 2013; Sit et al., 1998; Winship et al., 2020). Presence-absence data, however, are more difficult to obtain and typically require complex systems such as ROVs or autonomous cameras (Doherty et al., 2018). ROVs are highly maneuverable and collect high quality images of benthic species, but are also expensive, time consuming, require specialized professionals and support vessels to operate the vehicles, and ultimately cover only a small sample area which raises concerns about extrapolation to unsurveyed regions (Sit et al., 1998). Autonomous camera systems operate at a fraction of the cost and can cover a larger total spatial area than ROVs typically used in deep sea surveys. In addition, autonomous systems including cameras, accelerometers, and depth sensors can also be deployed in either opportunistic or systematic survey designs (Doherty et al., 2018). Autonomous systems sit stationary on the seafloor and therefore only collect images for a small area during each deployment; however, if deployed at a large enough number of locations following a statistically-robust survey design, SDMs can be applied to data to infer species presence in unsampled areas.

SDMs infer the probability that a species occurs in a particular location given local environmental conditions (e.g., bottom type, depth, slope, temperature). Functional relationships between the probability of presence and environmental variables that represent the core of SDMs are estimated via statistical models fitted to observations of presence or presence and absence for the species. The type of statistical model used depends on the available data. For example, presence-only SDMs are most commonly developed via Maxent maximum entropy methods (Phillips et al., 2006) that are designed to make predictions from presence-only data. Maximum entropy methods typically outperform other presence-only approaches based on predictive accuracy (Phillips et al., 2017). However, presence-only data can have large sampling bias that can, in turn, generate biases in SDM model estimates and predictions. For example, higher commercial fishing intensity occurs in areas where targeted species density is high, which can result in a higher probability of some members of the intended population being sampled than others (i.e., sampling bias). As a consequence of sampling bias, where more frequent sampling occurs in areas of observed presence, maximum entropy models may overestimate the probability of occurrence in highly sampled areas while underestimating presence in areas outside of the species' known extent of occurrence or in areas with less frequent sampling (Fitzpatrick et al., 2013). Additionally, the type of fishing gear can affect coral presence observations, for example, corals are more easily tangled in trawl gear than trap or longline gear. Other conditions can also affect presence observations, such as depth or current speed. Greater depths and current speeds increase gear retrieval distance and time, which decreases the chance of retaining corals. Finally, maximum entropy models estimate relative occurrence rate (ROR; Fithian & Hastie 2012) (i.e., the relative probability that a location is contained in a collection of presence samples) that can be difficult to interpret and validate (Merow et al., 2013). Maxent's raw ROR output can be transformed to predict probability of presence (known as Maxent's logistic output [Phillips and Dudik 2008]), however this transformation relies on the assumption that a parameter τ = 0.5 (more details in section 2.4) and has been criticized (Royle et al., 2012).

SDMs are more reliable when based on presence-absence data sampled in a statistically robust way (Hastie & Fithian, 2013, Winship et al., 2020). Some SDMs incorporate presence-absence data to address the sample bias and interpretability challenges of presence-only data (Hastie and Fithian, 2013; Lagasse et al., 2015). Generalized additive models (GAMs) are widely used in SDMs involving presence-absence data (Winship et al., 2020) because they can represent the usual non-linear and non-monotonic relationships between species presence/absence and environmental variables that are often observed in nature. GAMs can estimate probability of presence directly without relying on dubious transformation assumptions (Royle et al., 2012). Although presence-absence SDMs avoid some of the challenges that presence-only

SDMs encounter, obtaining quality absence data can be expensive and time consuming, leading to smaller sample sizes and lower model precision.

In this paper, I investigated how data type and model choice affects species distribution model predictions of cold-water coral (order Alcyonacea) probability of presence over the continental shelf and slope off British Columbia. Cold-water corals may support some commercially valuable fish and invertebrate species by providing critical 3-dimensional habitat (Stone et al., 2014; Krieger & Wing, 2002; Buhl-Mortensen et al., 2010). Additionally, these organisms are slow-growing, long-lived, and typically occur in isolated populations with limited larval dispersal and sporadic recruitment (Andrews et al., 2002, 2009; Mercier & Hamel 2011; Waller et al. 2014) which makes them vulnerable to contact by fishing gear (Auster et al., 1996; Bavestrello et al., 1998; Williams et al., 2010).

I compared predictions from GAMs fitted to presence-absence video observations collected via autonomous camera systems (Doherty et al., 2018) over a stratified-random survey design with predictions from maximum entropy models (Maxent) fitted to Alcyonacean presence-only bycatch records from large-scale commercial fisheries over the same area. I calculated Spearman's correlation coefficient and the "I" similarity statistic between predictions to compare the results of each data type. I then developed a simulation algorithm to evaluate the direction and magnitude of bias in each model type. I show that Maxent predictions from presence-only data were negatively correlated with predictions from GAMs based on presence-absence data, with Maxent predicting much lower probability of coral presence where the GAM presence-absence model predicted higher probability of presence and vice versa. Simulations show that such a negative correlation is expected because the Maxent model is biased and overestimates probability of presence in areas of observed presence (i.e., on the continental shelf) and underestimates probability of presence in areas with few or no observed presences (i.e., on the continental slope).

2. Methods

In this section I describe the study area and sampling design for presence-absence and presence-only data collection followed by a section describing the response variables, predictor variables, and how the predictor variables were converted into raster layers. I then present the generalized additive model (GAM) for the presence-absence data along with specific model choices such as the weighted effective degrees of freedom and model smoothing method followed by a similar section for Maxent maximum entropy models for the presence-only data and choices about the number of background sample points, feature classes, regularization, how I accounted for sample bias, and the output metrics. Finally, I present the model evaluation methods for both the GAM and Maxent models and the model comparisons.

2.1. Study area and sampling design

Fisheries and Oceans Canada annually conducts a stratified random survey (StRS; Lacko et al., 2020) that spans the continental shelf and slope along the west coast of Canada from the Alaskan border to Washington State in a southeast-northwest orientation (Figure 1). The StRS is a trap survey that targets sablefish to use as a fishery-independent index of abundance in their stock assessment. The survey is partitioned into 5 spatial and 3 depth strata (ranges are 183-457 m, 457-823 m, and 823-1372 m). Between 2013 and 2017, autonomous camera systems (Nyutco Ltd, North Vancouver, B.C.), accelerometers (HOBO Pendant G, Actilife wGT3x-BT monitors), and depth-temperature sensors (Sea-Bird SBE 39) were deployed on Korean conical traps aimed at surveying Sablefish (*Anoplopoma fimbria*) on bottom longline sets with 23-27 traps per set (Lacko et al., 2019).

Presence-absence data, used to fit GAMs in this study, was collected during the StRS. Autonomous camera systems described in Doherty et al. (2019) were programed to record 1-minute video clips every 2 hours when stationary on the seafloor and also when triggered (via the accelerometer) by gear movement along the bottom during retrieval. All epifauna observed was identified to the lowest distinguishable taxonomic rank possible, which was often the Order or Family level (see Doherty and Cox, 2017 and Doherty et al., 2018 for detailed species identification and images).

Presence-only data, used to fit Maxent models in this study, were collected through at-sea observations by fishery observers during commercial trawl, trap, and longline fishing sets (DFO's Pacific Region PacHarv [1995-2007] and Fishery Operating System [FOS; 2007-2020]; Chris Rooper, personal communication, April 23, 2021). The At-Sea Observer Program provides third-party verification of harvesting activities, and scientific catch and sampling data. Presence-only data was provided on a 2 km by 2 km resolution for privacy reasons. Trawl sets had a 70-meter door width and averaged 6.42 km in length. Trap sets typically included 65 traps per set and averaged 2.9 km in length, with each trap estimated to laterally impact 0.0011 m of seafloor (Doherty et al. 2014). Longline sets laterally impacted 0.006-0.01 km of the sea floor (Welsford et al., 2014*b*) and averaged 2.9 km in length. I included presence observations from commercial bycatch collected from 1995 through 2020 within the stratified random survey area.

2.2. Response variable

Species distribution models, such as GAMs and Maxent maximum entropy models, relate a univariate response variable (presence or absence) to some predictor variables using a link function (e.g., logit, log, identity). I used observed presence or absence of Alcyonacea order corals because it was often not possible to distinguish corals to lower taxonomic levels. The Alcyonacea order was the second most abundant order of corals observed in both the StRS video and commercial bycatch records. Families within Alcyonacea observed include Alcyoniidae, Isididae, Nephtheidae, Paragorgiidae, Plexauridae and Primnoidae, most of which are known to provide habitat structure for marine organisms (Krieger & Wing 2002, Etnoyer 2008). The Alcyoniidae family, however, includes the *Heteropolypus* genus whose corals are smaller in size and commonly referred to as soft corals due to their non-rigid structure (Wing & Barnard 2004, Molodtsova 2013). Corals in the Alcyoniidae family are commonly found in close proximity to habitat structure forming corals (Doherty et al., 2021) and were therefore included in the response variable grouping.

2.3. Predictor variables

I considered 16 predictor variables based on data derived from two bathymetric digital elevation models (DEMs) for bathymetric predictor variables depth, bathymetric position index (BPI), rugosity, and slope, the MODIS moderate resolution imaging spectroradiometer (MODIS) for the chlorophyll predictor variable chlorophyll a concentration, the Regional Ocean Modelling System (ROMS; Masson and Fine 2012) for oceanographic predictor variables circulation current speed, tidal current speed, temperature, and salinity, output from a categorical substrate model for substrate predictor variables mixed, muddy, rocky, and sandy substrate, and historical fishing effort for fishing impact predictor variables trawl, trap, and longline to model coral distribution (Table 1). I visually inspected pairs plots of all predictor variables and calculated the variance inflation factor (VIF) to check for collinearity and multicollinearity between variables (Zuur et al. 2009). I removed predictor variables with high collinearity (VIF>10) and the remaining variables were converted to raster layers with a 100 m by 100 m resolution and were cropped to the extent of the study area using the raster package in R software version 4.0.5 (Hijmans, 2020, R core team, 2021). All environmental (i.e., bathymetric, chlorophyll, oceanographic, and substrate) predictor variable data, in the B.C. Albers projection (EPSG:3005), and fishing impact predictor variable data was provided by Fisheries and Oceans Canada (Cole Fields and Jessica Finney, personal communication, August 31, 2020; Chris Rooper, personal communication, April 23, 2021).

2.3.1. Depth and derivatives

Depth was derived from a British Columbia 3 arc-second DEM (Carignan et al. 2013) and a 100 m DEM (Gregr 2012; Table 1), resampled and mosaiced using ArcGIS 10.4 to produce a depth raster layer. I considered bathymetric derivatives, slope, rugosity and BPI, as predictors for coral distribution because they are sometimes associated with hard substrate and suitable coral habitat (Masuda & Stone 2015). Slope, the maximum rate of change of depth, was calculated in degrees. Rugosity, a measure of surface roughness used as an index of structural complexity, was calculated via the arc-cord ratio (ARC) rugosity method (Du Preez et al., 2015; Du Preez et al., 2016) because it decouples rugosity from slope. BPI can be positive (e.g., ridges or crests) or negative (e.g., valley bottoms) and was calculated using a neighbourhood distance of 2,500-25,000 m.

2.3.2. Chlorophyll

Mean surface chlorophyll-a concentration, which is a proxy for primary productivity, from MODIS L2 was calculated from reflectance using the OC4 and CI algorithms (Hu et al., 2012). Daily swath data between March and October from 2012-2015 were mosaiced by month and averaged over the 4-year period. Months with persistent cloud cover were excluded (i.e., November to February).

2.3.3. Oceanographic

Current speed was derived from ROMS (Masson and Fine 2012) and calculated from mean zonal (u) and meridional (v) velocities using a root mean square method after the velocities were spatially aligned by shifting them horizontally via linear interpolation. Circulation current speed, temperature, and salinity were calculated from a 15 day mean resolution, and tidal current speed was calculated from a 3 hour mean resolution, effectively distinguishing tidal from non-tidal ocean circulation current. I removed salinity because it was highly collinear with temperature and to lower the VIF values for all predictor variables to be below 10. Salinity was removed instead of temperature because corals tolerate a wide range of salinity and it is not a limiting factor for coral growth like temperature (Dullo et al., 2008).

2.3.4. Substrate

Substrate layers (rocky, mixed, sandy, muddy) were derived from a categorical substrate model that predicts four categories: rock, mixed, sand, and mud (Haggarty et al., 2018). Binary layers were created for each substrate category (where 1 = the substrate type for each layer). A focal sum was applied to each binary layer, taking the total number of cells classified as the substrate type (for each layer). These layers were then normalized to a 0-1 scale with 0 indicating no cells in the neighbourhood were the substrate type, and 1 indicating all surrounding cells were the substrate type. I only included rocky substrate here because muddy and sandy substrate layers were highly collinear and Alcyonacean corals are known to inhabit areas with rocky substrate (Masuda & Stone 2015).

2.3.5. Fishing

Finally, fishing impact on the sea floor was calculated for all bottom contact commercial fishing events within the study area to assess its potential effect on coral presence. Commercial fishing sets from 1995-2020 were used to calculate towlines following Welsford et al., (2014*b*) for longline, Doherty et al., (2018) for trap, and using a door width of 70 m for trawl (DFO’s Pacific Region PacHarv [1995-2007] and Fishery Operating System [FOS; 2007-2020]; Chris Rooper, personal communication, April 23, 2021). The study area was first divided into 100 m by 100 m grid cells and then further divided into 25 sub grids, each with sub-cells of 20 m by 20 m. Each towline was buffered by half its estimated impact width plus 10 m on each side to ensure that all tows passing through a grid cell would be counted as occurring in that cell. Overlap of towlines with grid cells was calculated using the fasterize function from the raster R packaged which only recognizes overlap between a polygon (e.g., a buffered towline) and grid cell if the polygon passes through the mid-point of the cell. The 20 m by 20 m sub-cells were then reclassified as 1 if any towline passed through them and aggregated to the 100 m by 100 m cells using the sum (i.e., how many 20 m by 20 m sub-cells were impacted) divided by 25. This created a raster layer for each gear type (i.e., trawl, trap, and longline) showing the cumulative proportion of impacted area in each 100 m by 100 m grid cell. For example, a 100 m by 100 m grid cell that had five 20 m by 20 m sub-cells impacted by trawl would have a value of 0.2 (5 sub-cells/25 total cells).

2.4. Model selection and performance

2.4.1. Generalized additive models for coral presence-absence – GAMs

I fit a generalized additive model (GAM) with a binomial distribution and logit link function to estimate the probability of coral presence in the study area (Doherty et al., 2021) i.e.,

$$logit(\pi_i) = \log\left(\frac{\pi_i}{1-\pi_i}\right) = \alpha + \sum_{j=1}^{p} s_j(x_{j,i}) + \epsilon_i \qquad (1)$$

where π_i is the probability of coral presence in each grid cell (i), α is an intercept, s_j is a thin plate regression spline smoothing function (Wood, 2003) for predictor variable $x_{j,i}$ for each grid cell (i), and the error ϵ_i is assumed to follow a normal distribution ($\epsilon_i \sim Normal(0, \sigma^2)$). Models were fit to presence-absence observations of Alcyonacean corals (n=209) using all possible combinations of predictor variables. I estimated bottom locations of presence and absence observations as the GPS coordinates for the middle of the set if cameras were mounted on trap numbers 13-15 and as the GPS coordinates for the end of the set if cameras were mounted on trap number 25. The majority of sets had 26 traps and the majority of cameras were mounted on trap number 13 to 15, except for 3 sets in which cameras were mounted on trap number 25. I used the mgcv R package (Wood, 2017) for GAM model fitting and the MuMIn R package (Bartón, 2020) for model selection. I weighted effective degrees of freedom by γ = 1.4 to correct for overfitting without compromising the model fit (Kim and Gu, 2004), used the restricted maximum likelihood (REML) model smoothing method, and limited degrees of freedom for the smoothing function ($k \leq 4$; Wilborn et al., 2018). I then ranked the models based on the Akaike information criteria value corrected for small sample size (AICc; Burnham & Anderson, 2002) and used the top model to predict Alcyonacea probability of presence for the entire study area. All model fitting was conducted in R software (R Core Team, 2021).

2.4.2. Maximum entropy model for coral presence-only – Maxent

I fit Maxent models using the maxent function in the dismo package in R (Hijmans et al., 2017) to estimate the probability of Alcyonacean coral presence in the study area. Maxent transforms the original predictor variables, called feature classes (FC), to linear, product, quadratic, hinge, threshold and categorical feature classes (Elith et al., 2011). I limited FC to linear, quadratic and a hybrid because the other relationships were not biologically plausible (Austin 2007; Merow et al., 2013). Maxent also uses a regularization multiplier (RM) to penalize feature classes that produce small improvements in the model and to avoid overfitting (Merow et al., 2013). Higher RM values reduce flexibility in the relationship between the species presence and predictor variables. Default Maxent values can create poor preforming models (Radosavljevic and

Anderson, 2014) especially when focusing on one or a few species (Phillips and Dudik 2008, Anderson and Gonzalez 2011). I used the ENMevaluate function in the R package ENMeval (Kass et al., 2021) to select the optimal values for FC and RM. Models were fitted using spatial block cross validation with 4 bins. In preliminary analyses I fit 3 Maxent models using presence observations from commercial fishing sets, research survey fishing sets, and both commercial and survey sets; however, here used commercial sets only because of sampling design differences between commercial and survey data and because the model predictions were dominated by the commercial data anyway due to the large difference in the number of data points (Figure A1). Finally, I removed all fishing impact predictor variables because the predicted probability of presence and the sampling method were confounded.

Sampling effort for commercial fishing sets within the study area was high in some areas and low or non-existent in others, which could indicate sampling bias. Sampling bias can cause SDMs to predict patterns in the sampling method rather than the relationship of species occurrence with predictor variables. One way to reduce the effect of potential sampling bias is to choose background data with the same bias as the sampling effort (Phillips et al., 2009; Fourcade et al., 2014). I used target-group sampling (Elith et al., 2011; Merow et al., 2013) to generate 10,000 background points with the same bias as the sampling effort. Target group sampling fits a kernel density estimate (KDE) to the locations of the occurrence data to estimate the density of samples in each cell.

I used the logistic output from Maxent to obtain predicted probabilities of presence; however, this option involves an arbitrary choice of 0.5 for the parameter τ, which is the implied probability of presence at sites with “typical” conditions for the species. The true value of τ is unknown, so this arbitrary value has been criticized for its effects on the predicted probabilities assigned to each location (Royle et al., 2012). To test the sensitivity of my Maxent model predictions to the value of τ, I varied τ values between 0.2 and 0.8 and, as a result, I was comfortable using Maxents logistic output as the probability of coral presence because predictive maps did not change with varying τ values (Figure A2).

2.4.3. Model evaluation

I evaluated model performance based on their ability to predict subsets of data that were withheld during model fitting (specifically, spatial block cross validation [SBCV], but referred to as cross validation hereafter) using four metrics: area under the receiver operating characteristic curve (AUC), mean squared prediction error (MSPE), true skill statistic (TSS), and symmetric extremal dependence index (SEDI; Ferro & Stephenson, 2011; Wunderlich et al., 2019). The AUC determines how well the model can distinguish between presence and absence or presence and background points. Higher AUC values indicate that the model is better at predicting true presences as presences and true absences/background points as absences/background points. An AUC value from 0.50-0.69 indicates poor discrimination or only marginally better than chance, from 0.70-0.79 indicates acceptable discrimination, from 0.80-0.89 indicates excellent discrimination and >= 0.90 indicates outstanding discrimination (Hosmer & Lemeshow 2000). Although AUC is a widely used metric to evaluate SDM performance, it does not measure goodness of fit (Lobo et al., 2008). I used MSPE to evaluate goodness of fit while minimizing spatial autocorrelation effects. Values of MSPE closer to 0 indicate better predictive performance. Spatial autocorrelation in the data can lead to autocorrelated model residuals that violate the assumption of error independence and result in biased model parameter estimates (Dormann 2007), confound model validation (Roberts et al., 2017), and overestimate model predictive power (Ploton et al., 2020). The SBCV I used separated the data into training and testing datasets using their spatial coordinates to ensure the datasets were far apart to reduce spatial autocorrelation, which was likely prevalent in this data because points close together have more similar characteristics. TSS compares the number of correct predictions, minus predictions attributable to random guessing, to a hypothetical set of perfect predictions. It is a reliable indicator of goodness-of-fit because it is insensitive to class imbalances of the magnitude I observed (i.e., a greater number of absences than presences), and is not dependent on prevalence, the proportion of sites where the species was present. TSS ranges from -1 to +1 with a score of +1 indicating perfect agreement and scores below 0 indicating performance no better than chance (Allouche et al., 2006). SEDI is a normalized version of the log odd ratio and ranges from -1 to 1 (Ferro & Stephenson, 2011). I calculated both TSS and SEDI values using a fixed threshold that maximized the sum of sensitivity and specificity (Cantor et al., 1999; Manel et al., 2001), which is equivalent to minimizing the sum of false absence/background and false presence misclassification likelihoods. SEDI values are analogous to TSS values but perform better with presence-only SDMs (Wunderlich et al., 2019).

2.5. Comparing GAM and Maxent model performance and predictions

2.5.1. Best-fitting model performance and predictions

I evaluated GAM and Maxent model performance based on AUC, MSPE, TSS and SEDI values. Additionally, I used the raster.overlap function from the ENMTools R package (Warren & Dinnage, 2021) to calculate Spearman’s rank correlation coefficient and the “I” similarity statistic and compare model predictions. Spearman’s rank correlation coefficient is a nonparametric approach that measures the monotonic association of two variables and ranges from -1 (perfect negative association of ranks) to +1 (perfect association of ranks). Benchmark values indicate zero (0), weak (0 to 0.4 and 0 to -0.4), moderate (0.4 to 0.7 and -0.4 to -0.7), strong (0.7 to 1 and -0.7 to -1) and perfect (1 and -1) association of ranks (Dancey & Reidy 2007). The “I” similarity statistic (Warren et al., 2008) is based on Hellinger Distances (Van der Vaart, 2000) and ranges from 0 (no overlap of predicted distributions) to 1 (the predicted distributions are identical). I used a difference map to show the degree of similarity between the model and data type predictions. Finally, I calculated the percent of suitable coral habitat in 2 proposed longline closures, the Cape St. James Site and the Offshore NW Dixon Site (DFO, personal communication, February 25, 2022), under each modelling scenario. The Cape St. James Site covers a 712 km^2 area, divided into two sections with 563 and 149 km^2 areas, at the Southern tip of Haida Gwaii, and the Offshore NW Dixon Site covers a 228 km^2 area at the Northern tip of Haida Gwaii.

2.5.2. Simulated model performance and predictions

Direct comparisons between GAM and Maxent model performance are invalid when each method uses different datasets. Assessing model performance using a common simulated dataset enables comparisons between modelling methods, therefore, I used the following simulation algorithm to evaluate the direction and magnitude of bias in each model type (i.e., GAM and Maxent model; Figure 2).

1. Generate a best estimate of the true underlying Alcyonacean probability of presence

    a. Fit a GAM to real presence-absence data (i.e., StRS video observations)

    b. Use the GAM from (a) to generate true probability of presence p_i at each grid location i

2. Generate 2 sets of 100 test data sets (i.e., one short and one long) to evaluate the performance of each model type in multiple scenarios

    a. Long data set: select a random sample of grid locations (n=5,000) from the true probability of presence from (1b). For each sampled grid location, draw a presence (1) or absence (0) Alcyonacea point from a Bernoulli distribution with probability p_i

    b. Short data set: select a random sample of grid locations (n=42) from the true probability of presence from (1b). For each sampled grid location, draw a presence (1) or absence (0) Alcyonacea point from a Bernoulli distribution with probability p_i

3. Simulate sample collection, presence-absence points, and estimation for GAM (hereafter referred to as GAM_0; Table 5)

    a. Select a stratified-random sample of grid locations (n=209) weighted by StRS sampling effort. For each sampled grid location, draw a presence (1) or absence (0) Alcyonacea point from a Bernoulli distribution with probability p_i

    b. Use the all-subsets GAM selection procedure (described above) to fit and select a top GAM for the sampled presence-absence points

    c. Compute diagnostics for the top GAM on a random test dataset generated from the procedure in step (2a; i.e., the long test dataset)

4. Simulate sample collection, presence-absence points, and estimation for GAM (hereafter referred to as GAM_noModSel; Table 5)

    a. Select a stratified-random sample of grid locations (n=209) weighted by StRS sampling effort. For each sampled grid location, draw a presence (1) or absence (0) Alcyonacea point from a Bernoulli distribution with probability p_i

    b. Use the same model structure as the best-fitting GAM to fit a GAM for the sampled presence-absence points

   c. Compute diagnostics for the fitted GAM on a random test dataset generated from the procedure in step (2a; i.e., the long test dataset)

5. Simulate sample collection, presence-absence points, and estimation for GAM (hereafter referred to as GAM_short; Table 5)

   a. Select a stratified-random sample of grid locations (n=209) weighted by StRS sampling effort. For each sampled grid location, draw a presence (1) or absence (0) Alcyonacea point from a Bernoulli distribution with probability p_i

   b. Use the all-subsets GAM selection procedure (described above) to fit and select a top GAM for the sampled presence-absence points

   c. Compute diagnostics for the top GAM on a random test dataset generated from the procedure in step (2b; i.e., the short test dataset)

6. Simulate sample collection, presence-only points, and estimation for Maxent model (hereafter referred to as Maxent_0; Table 5)

   a. Select a random sample of grid locations (n=11,917) weighted by commercial fishing effort. For each sampled grid location, draw a presence (1) or absence (0) Alcyonacea point from a Bernoulli distribution with probability p_i

   b. Keep the presence points (n~593) and discard the absence points

   c. Generate 10,000 background points weighted by commercial fishing effort

   d. Use a regularization multiplier of 3 and hybrid (linear, quadratic) feature class to fit a Maxent model for the sampled presence-background points

   e. Compute diagnostics for the Maxent model on a random test dataset generated from the procedure in step (2a; i.e., the long test dataset)

7. Repeat steps 3, 4, 5 and 6 for 100 trials

I used the predicted probability of presence from step (1) (i.e., from the best-fitting GAM) for comparisons because models using presence-absence data are expected to outperform those using presence-only data (Hastie and Fithian, 2012), the StRS video observations followed a standardized survey method that can be extrapolated to the entire study area (Sit et al., 1998), and, therefore, these results provided the most realistic representation of Alcyonacea probability of presence. I weighted presence observations by commercial fishing effort in step (6a) to ensure the randomly selected presence points would follow a similar distribution to the data used to fit the best-fitting Maxent model. The random sample of grid locations in step (6a) resulted in a different number of presence points for each trial of the simulation, but I accepted this level of variability because it was more computationally efficient. I did not run model tuning for the Maxent model because tuning on a subset of the simulation trials resulted in the same choice for FC values each time and all RM values had tying or similar AICc scores indicating there wasn't a benefit to choosing one RM value over another. I evaluated the simulated models using AUC because all the diagnostic metrics were highly correlated (Figure 3; Figure A3). The Maxent model diagnostics had weaker correlations, however, Maxent also had weaker "out-of-sample" predictive performance, which lead to higher variance in the diagnostic values and caused the weaker correlations. Additionally, AUC is the most frequently used diagnostic measure for SDMs and is used for both presence-absence and presence-only models (Allouche et al., 2006; Chu et al., 2019; Doherty et al., 2021; Liu et al., 2013; Warren et al., 2018). See table 5 for details of each model scenario.

3. Results

3.1. In situ observations of corals and sponges

Alcyonacean corals were the second most abundant taxonomic coral group I observed from the autonomous camera video within the study area, occurring in 31 (11%) of all camera sets (Table 2). They were also the most diverse with at least 7 distinct taxa, including Alcyoniidae, *Heteropolypus* sp., *Isidella* sp., *Paragorgia* spp., *Parastenella* sp., and *Swiftia simplex* (Table 3). Corals in the Unidentified Family group occurred at depths ranging from 517 m to 1,387 m and sometimes at high density with up to 24 distinct colonies observed at a single location (Table 3). I also observed Sponges (Phylum Porifera), Sea Whips (Order Pennatulacea), Hydrocorals (Order Anthoathecata), Black Corals (Order Antipatharia), Sea Lillies (Order Isocrinida) and Stony corals (Order Scleractinia) in the study area.

3.2. GAM and Maxent estimates of predictor importance

The best-fitting GAM from initial model fitting included circulation current speed, rocky substrate, rugosity, slope, and temperature as predictor variables, however, there was no clear relationship of rugosity or circulation on the probability of presence so they were removed from the analysis. The final best-fitting GAM included depth, BPI, tidal current speed, and slope as predictor variables. Depth, BPI, tidal current speed, and slope were the most important predictor variables and were retained in all of the best fitting models, with chlorophyll a concentration, longline impact and temperature occasionally included as well. Conditional relationships of the different predictors on the probability of Alcyonacean coral presence indicate that the probability of Alcyonacean coral presence was continuously increasing for all predictors in the best-fitting GAM (Figure 4).

The predictor variables with the greatest contribution to the best-fitting Maxent model were depth (68%), temperature (22%), rocky substrate (4%), and slope (4%). The predictor variables with the greatest permutation importance for the best-fitting Maxent model were depth (70%), temperature (23%), slope (3%), and rocky substrate (2%). Conditional relationships of the different predictors on the probability of Alcyonacean coral presence indicate that the probability of presence was continuously decreasing for depth, temperature and rocky substrate and followed a dome shaped response with high probabilities (>0.5) between 10-40% for slope (Figure 5).

3.3. Model performance

3.3.1. Generalized additive model

The best-fitting GAM had a mean AUC of 0.77, MSPE value of 0.07, TSS value of 0.31 and SEDI value of 0.44 (Table 4). The AUC value for the best-fitting GAM was within the range of acceptable discrimination (Hosmer & Lemeshow, 2000).

3.3.2. Maxent model

The best-fitting Maxent model had a mean AUC of 0.81, MSPE value of 0.13, TSS value of 0.53 and SEDI value of 0.71 (Table 4). The AUC value for the best-fitting Maxent model was within the range of excellent discrimination (Hosmer & Lemeshow, 2000).

3.4. Predicted distribution of Alcyonacean corals

The best-fitting GAM and best-fitting Maxent model predicted different distributions for coral presence throughout the study area (Figure 6A & C). The best-fitting GAM predicted higher probability of presence at deeper depths along the continental slope with the greatest concentration in the northern region of the study area (Figure 6A), whereas the best-fitting Maxent model predicted lower probability of presence at deeper depths along the continental slope (Figure 6C). Additionally, the best-fitting Maxent model predicted higher probability of Alcyonacean coral presence at locations with higher concentrations of “true” presence observations and lower probability of presence at locations with fewer or no “true” presence observations (Figure 1A & 6C).

3.5. Degree of similarity between data types

There was a moderate negative correlation between the predictions from the best-fitting GAM and the best-fitting Maxent model ($rho=-0.56$, $p<0.001$). This means that as the predicted probability of presence from the best-fitting Maxent model increased the probability of presence from the best-fitting GAM decreased (Figure 7A). The predicted distributions for the best-fitting GAM and best-fitting Maxent model had an "I" similarity statistic value of 0.47, indicating moderate similarity between the distributions.

The Maxent model predicted 27.2% and 18.0% of the larger and smaller Cape St. James Site sections respectively contained suitable coral habitat (Figure 8B). The GAM predicted 20.8% and 16.5% of the larger and smaller Cape St. James Site sections respectively contained suitable coral habitat (Figure 8A). The Maxent model predicted 46.6% of the Offshore NW Dixon Site contained suitable coral habitat and the GAM predicted 1.6% of the site contained suitable coral habitat (Figure 8).

3.6. Simulated model performance and uncertainty in model selection

When I compared the simulated model's performance I found that simulated GAMs with model selection and a large test dataset (GAM_0) had a mean AUC value of 0.76 with a mode between 0.75 and 0.80 (Figure 9), while simulated GAMs without model selection and with a large test dataset (GAM_noModSel) had a mean AUC value of 0.82 with a mode between 0.80 and 0.85 (Figure 9). Additionally, GAM_noModSel had less uncertainty in predicted probability of presence compared to GAM_0 (Figure 10). Simulated GAMs with model selection and a small test dataset (GAM_small) had a mean AUC value of 0.77 with a mode between 0.80 and 0.90 (Figure 9). Finally, simulated Maxent models with a large test dataset (Maxent_0) had a mean AUC value of 0.65 with a mode between 0.64 and 0.66 (Figure 9). Maxent_0 had the narrowest distribution of AUC values, which didn't overlap with the best-fitting GAM or best-fitting Maxent model AUC values.

4. Discussion

Different data types provide varying degrees of information about the estimated spatial distribution of Alcyonacean corals. In this study, I compared the predictions of GAMs using presence-absence data and Maxent models using presence-only data, and simulation tested each method for bias. I found bias in the Maxent method, which resulted in overly optimistic diagnostic values. Additionally, the Maxent model predicted high probability of coral presence in areas where the GAM predicted low probability of coral presence and vice versa. Depth was an influential predictor variable in both the GAM and Maxent models; however, GAMs predicted increased probability of presence with increasing depths, while Maxent predicted decreasing probability of presence with increasing depth. The inverse relationships for depth may explain the large differences between each methods predictions.

4.1. Model performance

It is possible that evaluation scores for the best-fitting Maxent model in this study are artificially inflated. The best-fitting Maxent model performed well in all quantitative evaluations (i.e., AUC, TSS, SEDI, and MSPE); however, the validity of evaluating models based on cross validation (i.e., a model's ability to predict subsets of left out data) has been questioned (Jimenez-Valverde, Acevedo, Barbosa, Lobo, & Real, 2013; Reineking 2006). Presence-only models evaluated using cross validation could produce invalid results because they lack true absence data. Presence-only models use artificially generated background points chosen by the user based on a number of assumptions about the location and number of background points selected. Background point location and number choices are somewhat arbitrary and likely result in some background points being generated in areas of potential coral presence. Altering the number of background points can increase or decrease the contribution of various predictor variables to the model and, therefore, change the predicted probability of presence distribution (Acevedo et al., 2012). Altering the location of background points can affect some model evaluation metrics by assigning false negatives as true negatives and, therefore, erroneously improving the model evaluation scores (Acevedo et al, 2012; Hijmans, 2012; Jimenez-Valverde et al., 2013).

The results of the simulation procedure suggest that quantitative evaluations based on cross-validation are not valid measures of model performance for Maxent models, but are reasonable measures of model performance for GAMs, mainly because the presence-only data used for Maxent is biased in the first place. Maxent models performed poorly in the simulation procedure, which generated diagnostics by comparing model outputs to a random test dataset generated from the procedure in step (2) of section 2.5 and not using cross-validation. By simulating data from the "true" probability of presence and using this data to fit a model and make predictions I revealed a more realistic performance of the modelling method. Diagnostics for the Maxent method using cross-validation on the original data were substantially better (e.g., AUC=0.81) than to the average performance demonstrated in the simulation (e.g., mean AUC=0.65) suggesting that evaluating the Maxent model using cross-validation produced inflated values. In contrast, the GAM performed similarly in both quantitative evaluation methods (e.g., GAM using cross validation AUC=0.77 and mean simulated GAM AUC=0.76) suggesting that evaluating the GAM using cross-validation produced accurate values for this modelling method.

The Maxent modelling method not only provided an overly optimistic picture of model performance, it was also not a reliable predictor of the spatial distribution of Alcyonacean corals. For instance, compared to the GAM with presence-absence data, the Maxent approach misrepresented the distribution of Alcyonacean corals by producing biased estimates of probability of presence (i.e., poor functional accuracy), and predicted higher probability of presence around randomly selected presence points. Additionally, neither the diagnostic AUC value from the best-fitting GAM (i.e., the "true" value) or the best-fitting Maxent model overlapped with the distribution of AUC values produced by Maxent in the simulation. This complete separation of AUC values further suggests strong bias in the Maxent modelling method and diagnostics. Maxent is known to overestimate probability of occurrence in sampled areas, underestimate occurrence in unsampled areas, and predict patterns in the data collection method rather than that of species distribution (Araújo et al. 2019; Fitzpatrick et al., 2013), therefore, it is not surprising that the simulated Maxent model predicted, on average, much lower probability of coral presence in areas of true high probability of presence and vice versa. Depth had the greatest contribution to the best-fitting Maxent model (68%) and it's decreasing trend, compared to an increasing trend seen in the best-fitting GAM, is likely the reason for the large differences in model predictions.

In contrast to the Maxent method applied to presence-only data, the GAM approach with presence-absence data demonstrated acceptable functional accuracy. For instance, the simulated GAM, on average, predicted the true spatial distribution of Alcyonacean corals. GAM predictions resembled, on average, the true probability of presence distribution with weaker probability of presence values. These weaker values, however, are not an issue if functional accuracy is the goal as both the simulated GAM and the best-fitting GAM (i.e., the true GAM) predicted the highest probability of presence in the same areas. Additionally, the diagnostic AUC values from the best-fitting GAM (i.e., the "true" value) were within the distribution of AUC values produced by the simulated GAM, indicating that bias in not affecting this model type.

Most applications in generalized additive modelling involve some form of model selection; however, the uncertainty in this procedure is rarely represented. In this study, I found that model selection increased the uncertainty in probability of presence estimates. Overall, simulated GAMs without model selection produced higher AUC values because the model structure was the same as the "true" model (i.e., the same predictor variables were used each time), thus producing more similar predictions and decreasing uncertainty when applied to the test data set. In other words, model selection increased uncertainty by introducing more variability in the model structure through changing combinations of predictor variables.

The limited sample size of the presence-absence data (n=209) is one possible reason that the simulated GAM resulted in different model structures in each iteration. A larger sample size is more likely to reveal the true relationship between predictor variables and probability of presence, therefore decreasing model structure uncertainty by selecting the same predictor variables more frequently. This implies that the GAM can't consistently fit the underlying truth without a larger sample size. Additionally, the mean diagnostic values from the simulated GAM with a test dataset the same size as the best-fitting GAMs test dataset, was closer to the "true" value suggesting that the diagnostic values are sensitive to the size of the test dataset. Future research could estimate the sample size needed to consistently fit the underlying model structure and focus sampling efforts to achieve this number of samples.

Finally, my presence-absence data is not standardized by the area sampled by the cameras, which could be affected by, inter alia, camera angle or orientation, bottom complexity, and visibility. I controlled for the latter by discarding videos with obviously poor visibility; however, variation in visibility in the remaining videos could introduce sampling bias or additional sampling noise in the data. In such cases, coral presences are more likely to be counted as absences as visibility decreases, thereby under-estimating true coral presence.

4.2. Importance of accurate SDMs for conservation planning

Currently, the majority of SDMs for cold-water corals are fit using presence-only data (Guinotte & Davies, 2014; Lagasse et al., 2015; Rooper et al., 2014; Sundahl et al., 2020) and these SDM predictions are used to guide management practices such as MPA placement for sensitive benthic species. The results of this study show that management strategies informed by two different modelling scenarios (i.e., the best-fitting Maxent model predictions and the best-fitting GAM predictions) would result in different MPA location placement. Currently proposed closures in British Columbia intended to protect corals within the study area cover a 712 km^2 area, divided into two sections with 563 and 149 km^2 areas, at the Southern tip of Haida Gwaii (i.e., the Cape St. James Site) and a 228 km^2 area at the Northern tip of Haida Gwaii (i.e., the Offshore NW Dixon Site) (DFO, personal communication, February 25, 2022). Under the Maxent model scenario 27.2% and 18.0% of the larger and smaller Cape St. James Site sections respectively contained suitable coral habitat. Under the GAM scenario 20.8% and 16.5% of the larger and smaller Cape St. James Site sections respectively contained suitable coral habitat. The values for each model scenario at the Cape St. James Site were comparable, which demonstrates that not all areas are biased under the Maxent model scenario; however, part of the proposed closure was outside of the study area. In contrast, the Offshore NW Dixon Site was almost entirely contained in the study area, and 46.6% of the site contained suitable coral habitat under the Maxent model scenario while only 1.6% of the site contained suitable coral habitat under the GAM scenario. Both the Cape St. James Site and the Offshore NW Dixon Site locations were selected based on bycatch records of corals, however, the Offshore NW Dixon Site is located in a heavily fished area. The higher percentages of suitable coral habitat at the Offshore NW Dixon Site under the Maxent scenario are consistent with the expected bias in this modelling method. Maxent is likely predicting the distribution of samples, not coral habitat and, therefore, these sites may only be protecting a fraction of the coral habitat they were intended to.

As part of Canada's marine conservation target, commonly referred to as Aichi Target 11, Canada aims to protect 30% of marine and coastal areas by 2030 using MPAs and other effective area-based conservation measures (OECMs). Sedentary benthic species, such as cold-water corals, form 3-dimensional habitat (Stone et al., 2014; Krieger & Wing, 2002; Buhl-Mortensen et al., 2010), which supports various fish species, some commercially valuable. Misplaced MPAs can move fishing effort to more vulnerable locations, create unnecessary economic losses and increase fishing costs (Lagasse et al., 2015). Species distribution maps based on presence-only data can exacerbate these losses. Although this study used presence-absence video observations collected via autonomous camera systems (Doherty et al., 2018) over a stratified-random survey design, the survey was stratified for sablefish, not Alcyonacean corals. Although not ideal, the results of the models using this survey data are still applicable because model-estimated relationships are based on a randomized sampling design and, therefore, not specific to particular locations. Additionally, depth was an important predictor of coral presence and, therefore, the depth stratification of the StRS was likely appropriate. Depth is associated with other important environmental variables for corals such as oxygen and temperature (Georgian et al. 2014; Thresher et al. 2011; Woodby et al. 2009). The presence-only data collected opportunistically during commercial fishing occurred mostly in depths of 200-400 m and did not evenly sample the full range of depths in the study area. It is possible that this over representation of the 200-400 m depth range resulted in the Maxent model predicting higher probability of presence in areas occurring within this depth range. Additionally, corals are more likely to fall off of fishing gear with greater depths and retrieval times, which could cause Maxent to under-estimate coral presence at deeper depths.

4.3. Future research opportunities for benthic habitat management

Most existing coral datasets are from bycatch data collected during commercial fishing, which lack important information for species distribution modeling such as true absence data, and physical attributes of coral colonies and the surrounding environment (Doherty et al., 2018; Hastie and Fithian, 2013). Future studies could use the relationships estimated using presence-absence data in this study to design a specific presence-absence survey stratified by variation in expected coral habitat to inform species distribution with less bias. Presence-absence data can be analysed using well known statistical approaches and avoids models that rely on dubious transformation assumptions, such as those required by Maxent. Presence-absence data collection could be as simple and cost effective as deploying autonomous camera gear on any of Canada’s currently operating surveys, or could involve deploying ROVs as a more expensive option that may provide more detailed data.

Presence-only datasets collected during commercial fishing often suffer from sampling bias and other unknown biases, and this in turn creates biased species distribution model predictions, however, the relative influence of data and model structure on resulting species distribution has not been assessed (Fitzpatrick et al., 2013). Fitting each modeling method with different data types (e.g., presence-only and presence-absence) would allow us to identify whether bias exists in the data or the modeling method. Future modeling efforts could fit GAMs using the presence-only bycatch records and background data, and fit Maxent models using the StRS presence-absence data. This would remove any structural differences between the models and help to better understand the effects of generating background data.

4.4. Conclusions

In conclusion, this research confirms that inferences about species distributions from presence-only data can be overly optimistic based on commonly used diagnostic measures such as AUC calculated using cross-validation. Current species distribution modeling practices combining presence-only data with cross validation are of limited use for their intended applications in management (Bowden et al., 2021). The stark difference between the predicted probability of Alcyonacean coral presence produced from the best-fitting GAM and best-fitting Maxent model demonstrates a need for more robust presence-absence data to support Canada's strategy to protect sensitive benthic areas.

A survey designed specifically for corals, with an appropriately large sample size, would yield the best results, and would likely only need to be done once as corals are sedentary organisms. Additionally, information on coral density and size, and sea floor attributes is not available in presence-only data, and spatial clustering and colony size are important in conservation planning (Doherty et al., 2018). For example, fishing gear such as bottom longline hook and trap gear are more likely to impact larger free-standing corals in areas with steep bathymetry or high rugosity (Doherty et al., 2018). More robust SDMs created using presence-absence data could improve our understanding of coral distribution and, therefore, better inform management practices for coral protection, reduce economic losses from misplaced fishery closures, and ultimately improve coral and ocean health. Regardless of the desired objectives (e.g., informing management practices, coral conservation, minimizing economic losses, etc.) this research generates a more accurate and informative picture of Alcyonacean coral distribution and the limitations of data and model choices, which can be used to make better informed decisions.

5. Tables

Table 1. Predictor variables considered in modelling probability of presence and habitat suitability for Alcyonacean corals.

	Predictor layer(s)	Definition	Method	Native resolution(s)	Years	Source(s)
Bathymetry	Depth (m)	Distance from sea surface to the sea floor		3 arc seconds and 100 m		British Columbia 3 arc-second Bathymetric DEM (Carignan et al. 2013) and a 100 m DEM (Gregr 2012)
	BPI	Where a referenced location is relative to surrounding locations	Neighbourhood distance: 300-2,500 m			
	Rugosity	A measure of surface roughness	Calculated using arc-cord ratio (ACR) method (Du Preez et al., 2016)			
	Slope (degrees)	The maximum rate of change of depth	Maximum rate of change in depth between a cell and its neighbouring eight grid cells			
Chlorophyll	Mean chlorophyll a concentration (mg/m^3)	Milligrams of chlorophyll a per cubic meter	Calculated from reflectance using the OC4 and CI algorithms (Hu et al., 2012), mosaiced by month and averaged over years	1 km	2012-2015 (March to October)	MODIS L2 product

	Predictor layer(s)	Definition	Method	Native resolution(s)	Years	Source(s)
Oceanographic	Mean summer circulation current speed (m/s)	Continuous and directed movement of ocean water calculated using a 15 day mean resolution	Calculated from mean zonal (u) and meridional (v) velocities using a root mean square method after the velocities were spatially aligned by shifting them horizontally with linear interpolation	3 km	1998-2007 (April to September)	Regional Ocean Modelling System (ROMS) (Masson and Fine 2012)
	Mean summer tidal current speed (m/s)	Continuous and directed movement of ocean water calculated using a 3 hour mean resolution				
	Mean bottom temperature (°C)	Temperature at the sea floor averaged by year	Bottom layer was represented by the deepest of 30 sigma (a fractional vertical stretching coordinate) levels (followed bottom depth)			
	Mean summer bottom salinity (PSU)	Salt concentration at the sea floor in Practical Salinity Units averaged by year				
Substrate	Mixed substrate	A measure of mixed substrate density	Derived from a categorical substrate model that predicts 4 categories: rock, mixed, mud and sand	100 m	1984-2018	Categorical substrate model (Haggarty et al., 2018)
	Muddy substrate	A measure of muddy substrate density				
	Rocky substrate	A measure of rocky substrate density				
	Sandy substrate	A measure of sandy substrate density				

	Predictor layer(s)	Definition	Method	Native resolution(s)	Years	Source(s)
Commercial Fishing Impact	Trawl	Cumulative area of the seafloor impacted by trawl over the time period	Cumulative impacted area calculated using a door width of 70 m.	100 m	1995-2020	DFO's Pacific region PacHarv (1995-2007) and Fishery Operating system (FOS; 2007-2020) (Chris Rooper, personal communication, April 23, 2021)
	Trap	Cumulative area of the seafloor impacted by trap gear over the time period	Cumulative impacted area calculated following the methodology of Doherty et al., 2018			
	Longline	Cumulative area of the seafloor impacted by longline gear over the time period	Cumulative impacted area calculated following the methodology of Welsford et al., 2014*b*			

Table 2. **Presence (P) and absence (A) frequencies by sampling year and cumulative frequencies and percentages over 2013-2017 from 282 video samples obtained from sablefish stratified-random surveys.**

	2013	2014	2015	2016	2017	2013-2017		
	P-A	P-A	P-A	P-A	P-A	P-A	%P	%A
Gorgonian corals (Order Alcyonacea)	5-55	0-50	4-57	17-45	5-44	31-251	11%	89%
Sponges (Phylum Porifera)	17-43	3-47	16-45	23-39	5-44	64-218	23%	77%
Sea Whips (Order Pennatulacea)	5-55	11-39	17-44	12-50	7-42	52-230	18%	82%
Hydrocorals (Order Anthoathecata)	3-57	2-48	5-56	13-49	6-43	29-253	10%	90%
Black corals (Order Antipatharia)	0-60	0-50	0-61	0-62	6-43	6-276	2%	98%
Sea Lillies (Order Isocrinida)	0-60	0-50	1-60	0-62	0-49	1-281	0%	100%
Stony corals (Order Scleractinia)	0-60	0-50	0-61	1-61	0-49	1-281	0%	100%

Table 3. Summary of Alcyonacean corals (Order Alcyonacea) observed during sablefish stratified-random surveys from 2013 to 2017.

Family	Lowest Taxon Identified	Locations Observed	Distinct Colonies	Counts per video sample (range)	Depth range (m)
Alcyoniidae	Alcyoniidae	2	3	1 - 2	1067
	Heteropolypus sp.	1	1	1	567
Isididae	*Isidella* sp.	4	4	1	645 - 660
Paragorgiidae	*Paragorgia* spp.	4	7	1 - 3	219 - 707
Primnoidae	*Parastenella* sp.	1	5	1	1296
	Primnoidae	1	1	1	370
Plexauridae	*Swiftia simplex*	2	4	1 - 3	761 - 1133
Unidentified Family	Alcyonacea	16	40	1 - 24	517 - 1387

Table 4. Performance diagnostics for the best-fitting Maxent model, fitted with presence-only observations from commercial fishing, and the best-fitting GAM, fitted with presence-absence observations from a stratified random survey (StRS). AUC and MSPE were calculated using 5-fold cross-validation for the Maxent model and 5-fold spatial block cross-validation for the GAM.

Diagnostic measure	Maxent	GAM
Area under the receiver operating curve (AUC, [SD])	0.81 (0.015)	0.77 (0.162)
Feature classes	Linear, quadratic and hybrid	na
Predictor variables	Depth, temperature, rocky substrate, slope	Depth, BPI, tidal speed, slope
Regularization multiplier	3	na
Mean squared prediction error (SD)	0.13 (0.003)	0.07 (0.021)
True skill statistic (SD)	0.53 (0.017)	0.31 (0.178)
Symmetric extremal dependence index (SD)	0.71 (0.012)	0.44 (0.228)

Table 5. Details of 2 estimated model scenarios, the best-fitting Maxent model, fitted with presence-only observations from commercial fishing, and the best-fitting GAM, fitted with presence-absence observations from a stratified random survey (StRS), and 4 simulated model scenarios.

	Scenario	Model type	Model selection/ model tuning	Test dataset size	Sample size
Estimated	Best-fitting GAM	GAM	Yes	42	209
	Best-fitting Maxent	Maxent	Yes	119	593
Simulated	GAM_0	GAM	Yes	5,000	209
	GAM_noModSel	GAM	No	5,000	209
	GAM_short	GAM	Yes	42	209
	Maxent_0	Maxent	No	5,000	~593

Table 6. Closures intended to protect coral habitat and the percent of overlapping coral habitat predicted by the best-fitting GAM, fitted with presence-absence observations from a stratified random survey (StRS), and best-fitting Maxent model, fitted with presence-only observations from commercial fishing.

Closure type	Site name	Area (km^2)	Percent coral habitat (%)	
			GAM	Maxent
Longline closures	Cape St. James Site	563	20.8	27.2
	Cape St. James Site	149	16.5	18.0
	Offshore NW Dixon Site	228	1.6	46.6

6. Figures

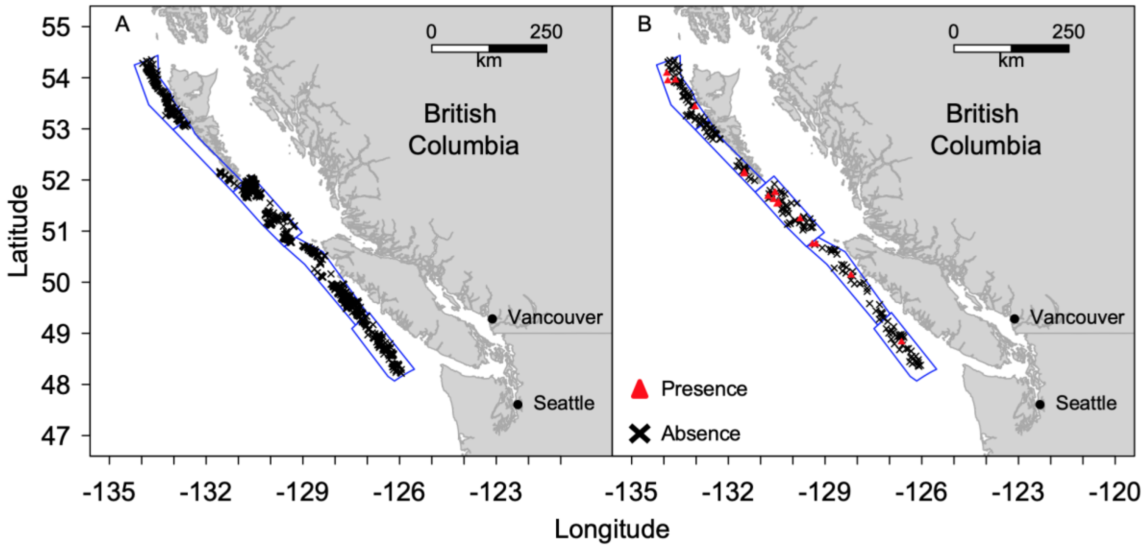

Figure 1. **Offshore stratified random survey areas (outlined in blue) off the coast of British Columbia, Canada. Depth strata, not shown, are 100–250 fathoms, 250–450 fathoms, 450–750 fathoms. Distribution of (A) opportunistic Alcyonacean coral occurrence observations from commercial fishing and (B) presence-absence observations from a stratified random survey (StRS).**

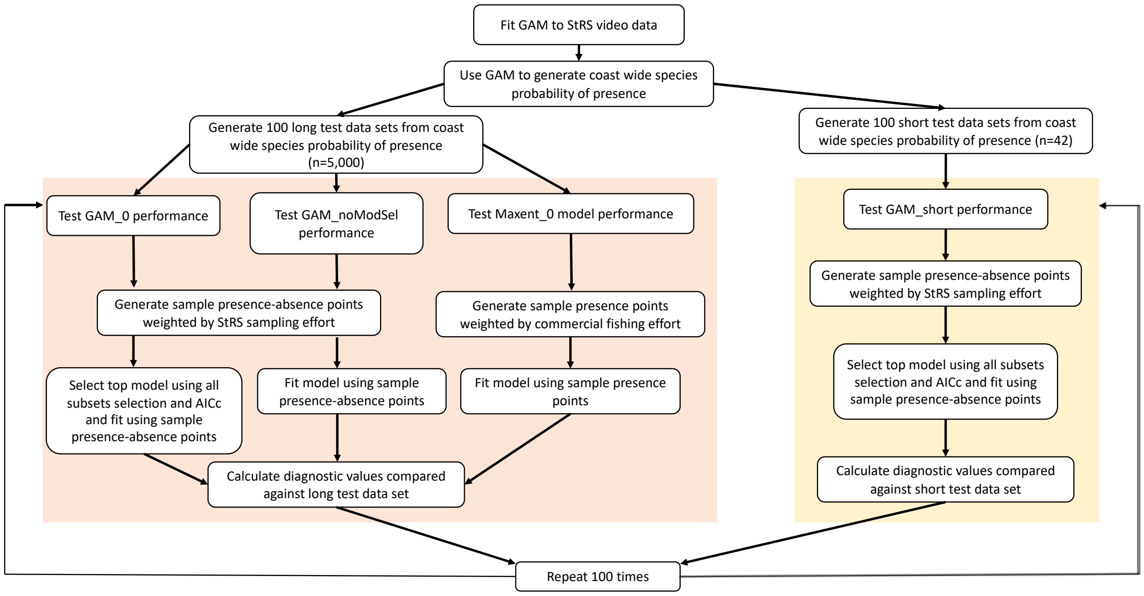

Figure 2. **Flow diagram of the simulation algorithm used to evaluate the direction and magnitude of bias in each model type (i.e., GAM and Maxent model). GAM_0 included model selection and a large test dataset (n=5,000), Maxent_0 excluded model selection and included a large test dataset (n=5,000), GAM_noModSel excluded model selection and included a large test dataset (N=5 000), and GAM_short included model selection and a small test dataset (n=42). All steps in the orange box were repeated 100 times using the long test dataset, and all steps in the yellow box were repeated 100 times using the short test dataset.**

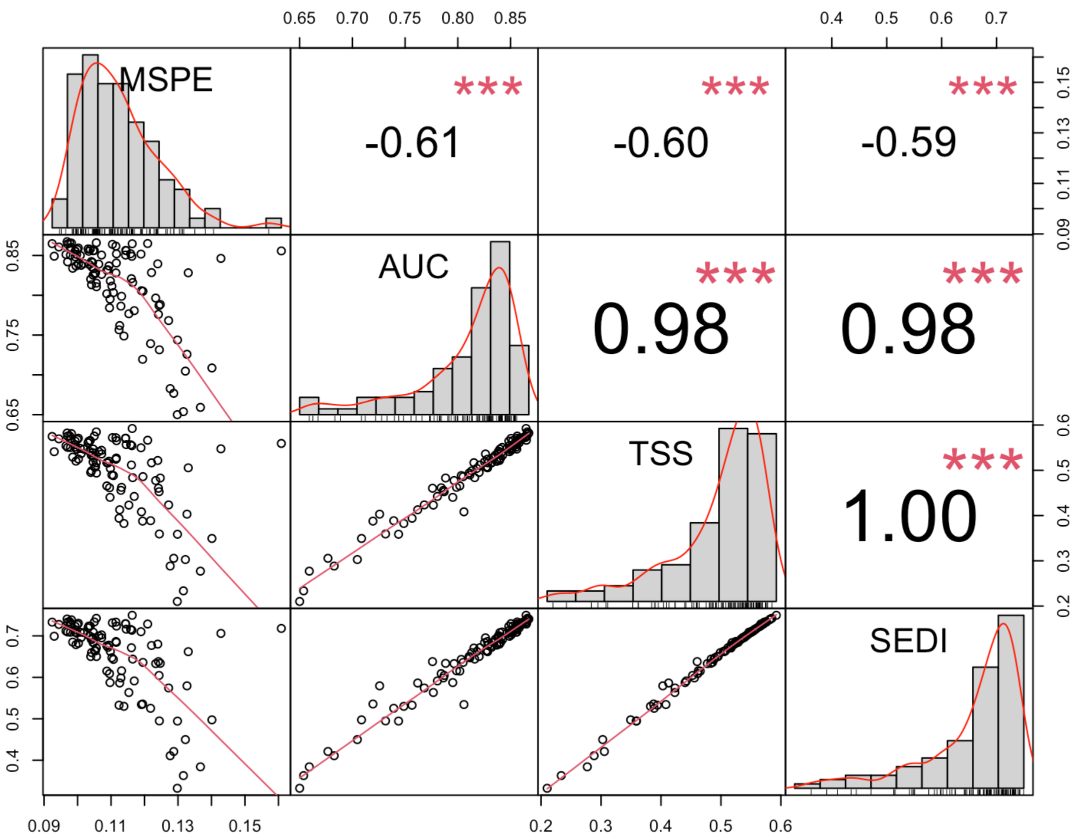

Figure 3. **Pearson correlation values, histograms, and scatterplots showing simulated diagnostic value distributions for a GAM without model selection and with a large test dataset (n=5,000).**

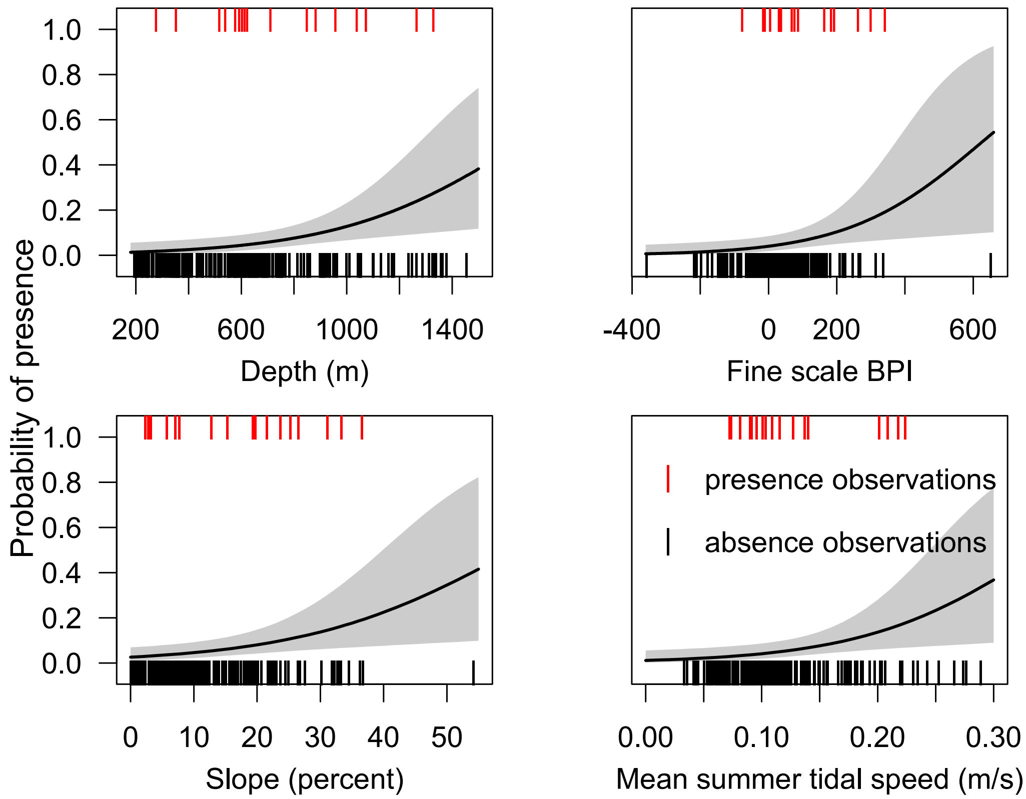

Figure 4. **Conditional relationships of predictor variables on the probability of Alcyonacean coral presence for the best fitting GAM, fitted with presence-absence observations from a stratified random survey (StRS), generated by varying the predictor variable of interest while keeping all other predictors at their average values. The thick black line shows the mean predictions and the grey polygons show the 95% confidence intervals.**

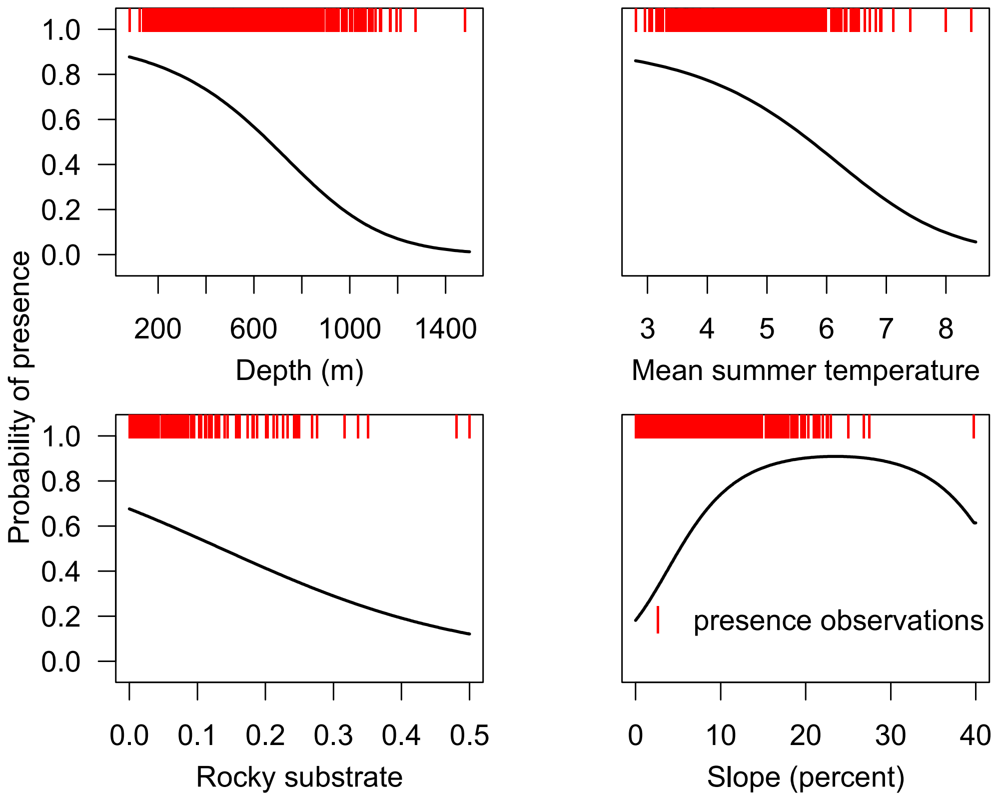

Figure 5. **Conditional relationships of the greatest contributing predictor variables on the probability of Alcyonacean coral presence for the best fitting Maxent model, fitted with presence-only observations from commercial fishing, by varying the predictor variable of interest while keeping all other predictors at their average values.**

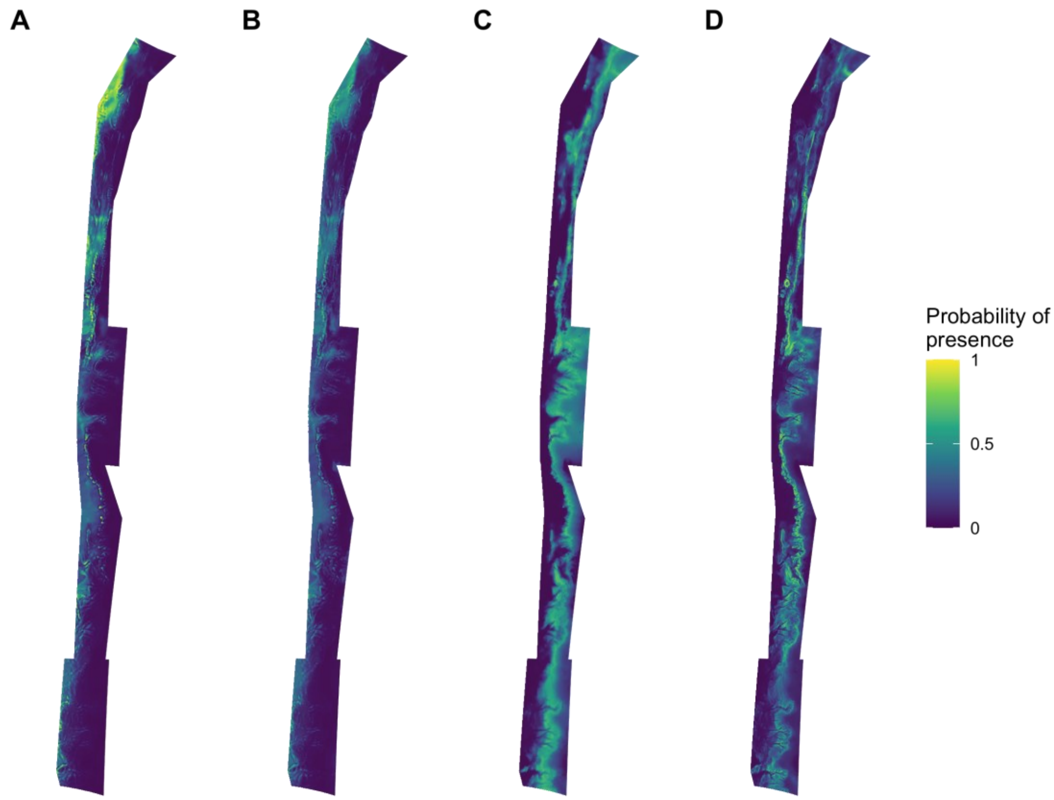

Figure 6. **Predicted probability of Alcyonacean coral presence for the (A) best-fitting GAM, fitted with presence-absence observations from a stratified random survey (StRS), (B) mean of the simulated GAMs (i.e., GAM_0), (C) best-fitting Maxent model, fitted with presence-only observations from commercial fishing, and (D) mean of the simulated Maxent models (i.e., Maxent_0).**

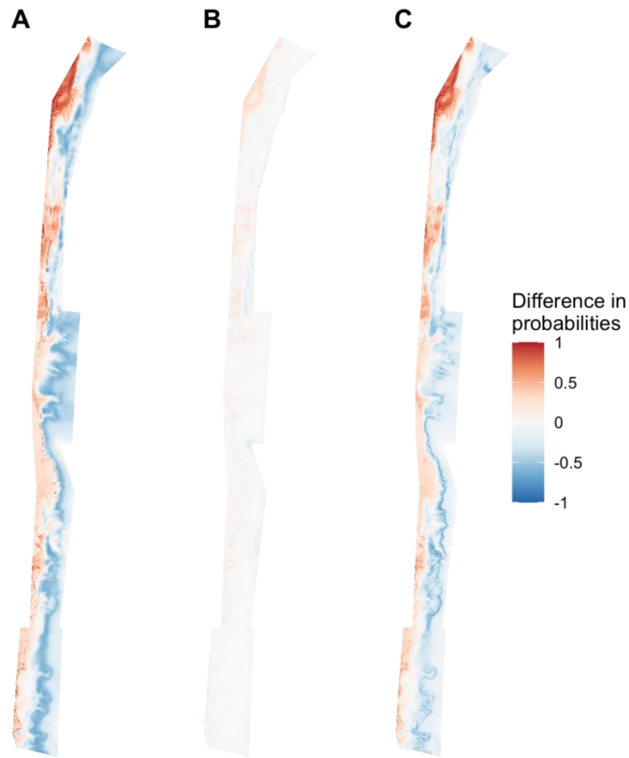

Figure 7. **Difference in Alcyonacean coral predicted probability of presence between (A) the best-fitting GAM, fitted with presence-absence observations from a stratified random survey (StRS), and best-fitting Maxent model, fitted with presence-only observations from commercial fishing, (B) the best-fitting GAM and mean of the simulated GAMs (i.e., GAM_0), and (C) the best-fitting GAM and mean of the simulated Maxent models (i.e., Maxent_0). Red coloring indicates areas where the best-fitting GAM predicted higher probability of presence than the model(s) it was compared against and blue coloring indicates areas where the comparison model(s) predicted higher probability of presence than the best-fitting GAM.**

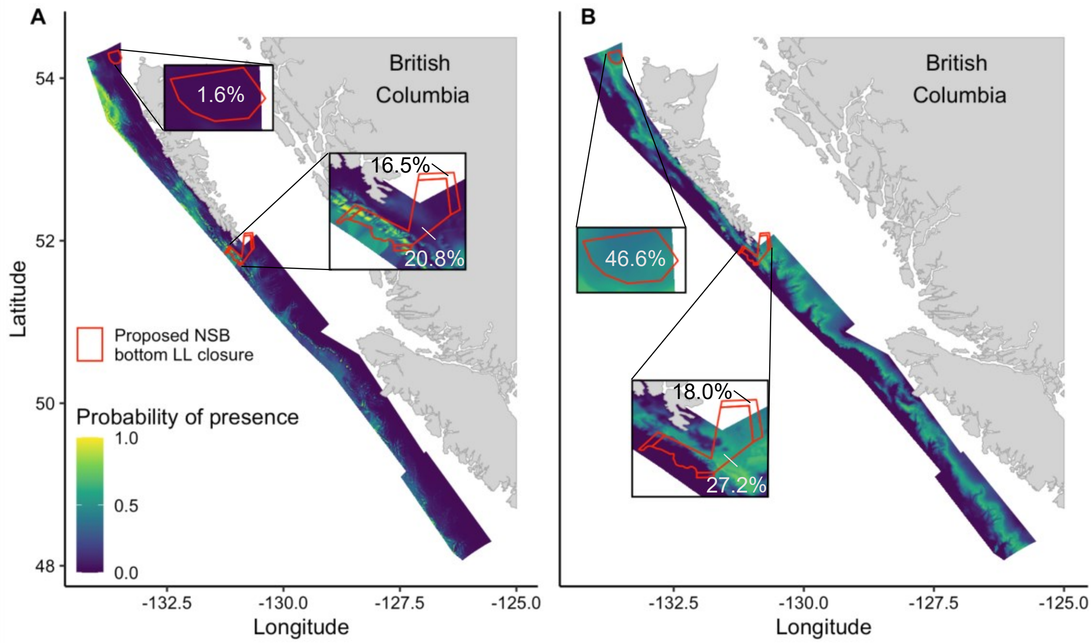

Figure 8. **Predicted probability of Alcyonacean coral presence for the (A) best-fitting GAM, fitted with presence-absence observations from a stratified random survey (StRS), and (B) best-fitting Maxent model, fitted with presence-only observations from commercial fishing. Polygons show areas closed to longline fishing to protect bottom habitat in the Northern Shelf Bioregion with the percent of suitable coral habitat labeled.**

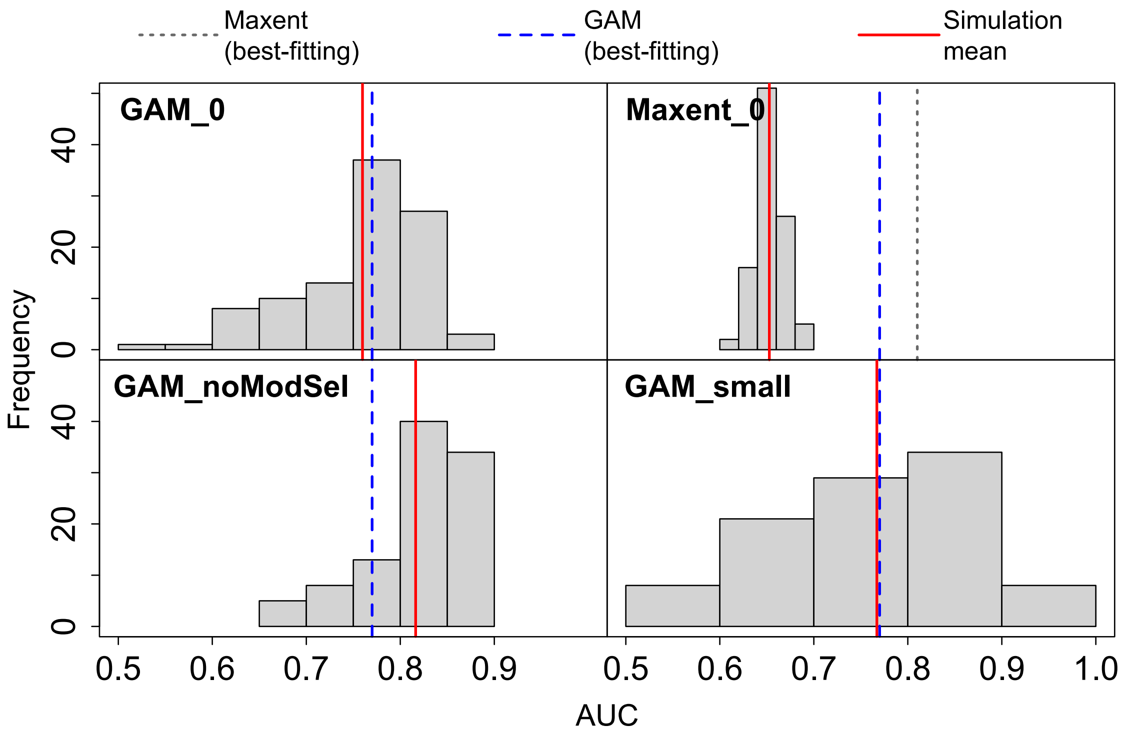

Figure 9. **Distribution of AUC values from a simulated (A) GAM that included model selection and a large test dataset (n=5,000), (B) Maxent model with a large test dataset (n=5,000), (C) GAM without model selection and a large test dataset (N=5 000), and (D) GAM that included model selection and a small test dataset (n=42).Vertical lines display AUC values based on cross validation for the best-fitting Maxent model (grey, dotted) and best-fitting GAM (blue, dashed), and mean AUC values of each simulated model (red, solid).**

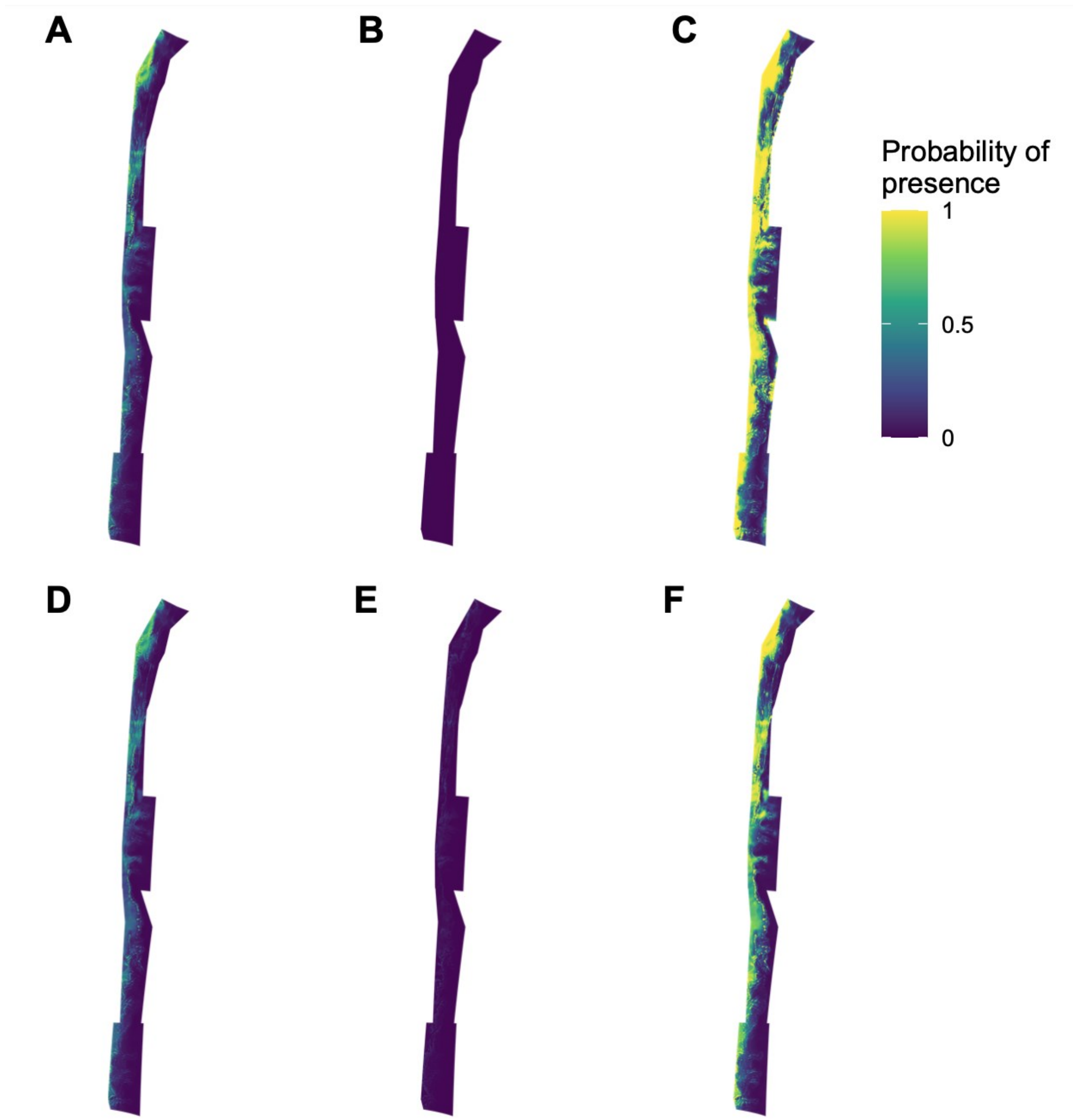

Figure 10. (A) Mean predicted probability of Alcyonacea coral presence, (B) lower and (C) upper 95% confidence intervals for a simulated GAM (i.e., GAM_0) with model selection and a large test dataset (n=5,000) and mean (D) predicted probability of Alcyonacea coral presence, (E) lower and (F) upper 95% confidence intervals for a simulated GAM (i.e., GAM_noModSel) without model selection and a large test dataset (n=5,000).

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Appendix: Supplemental Figures

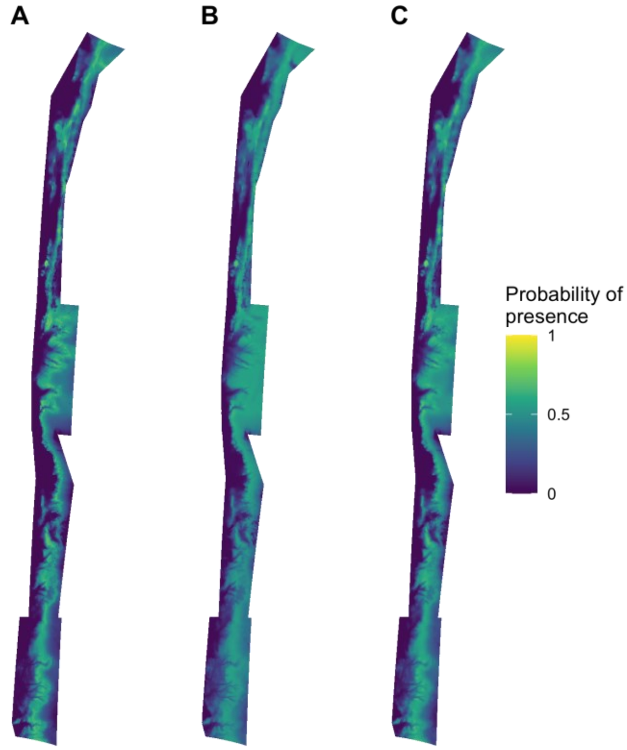

Figure A1. Predicted probability of Alcyonacea presence for Maxent models fitted using (A) commercial bycatch records, (B) survey bycatch records, and (C) both commercial and survey bycatch records.

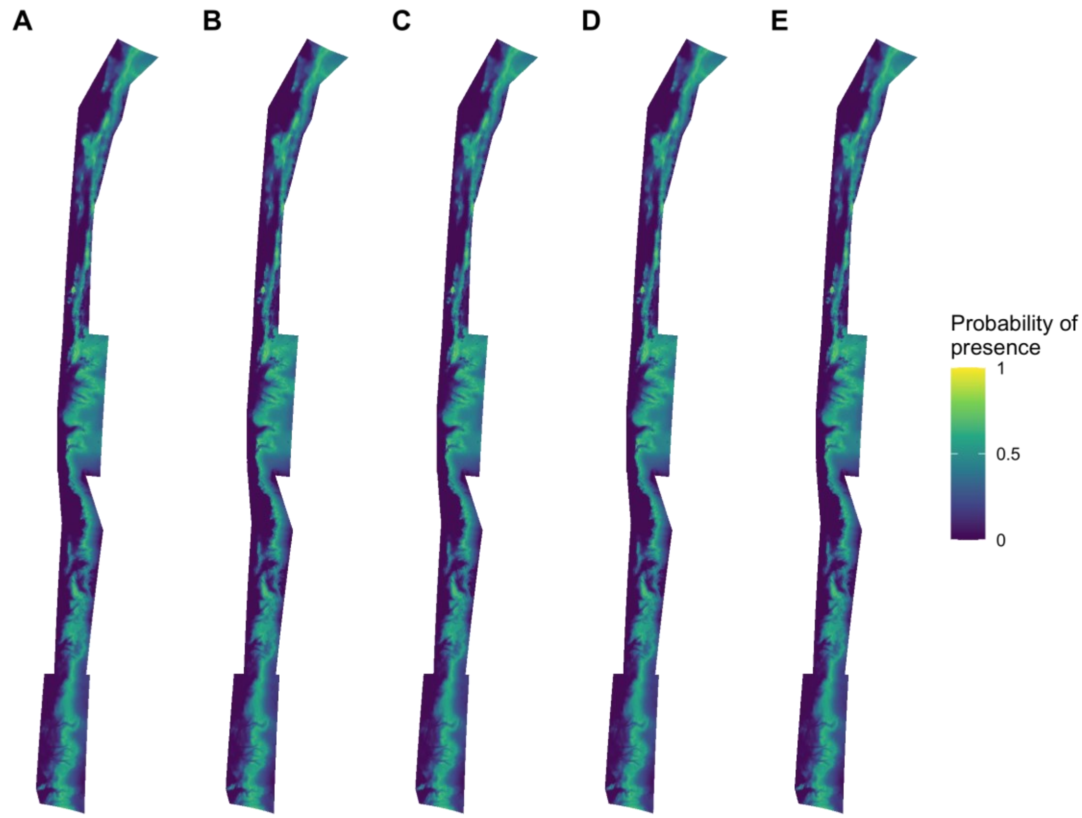

Figure A2. **Maxent predicted Alcyonacean coral probability of presence, fitted with presence-only observations from commercial fishing, with tau values of (A) 0.2, (B) 0.4, (C) 0.5, (D) 0.6, and (E) 0.8.**

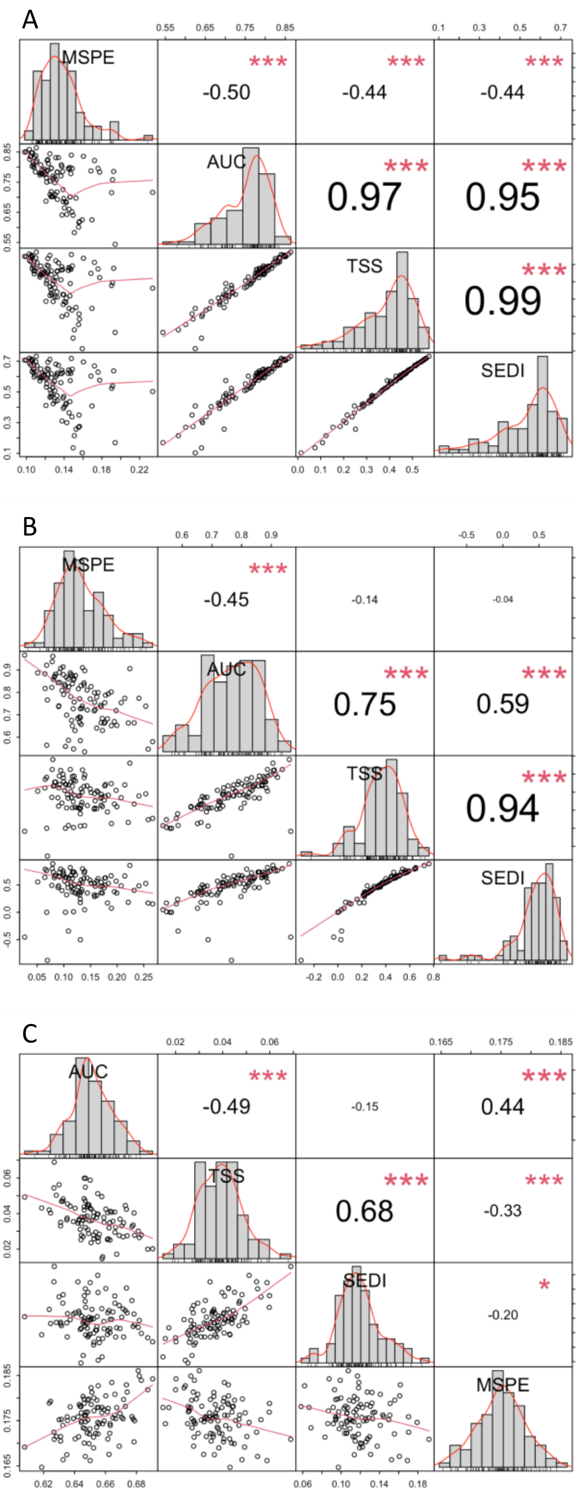

Figure A3. **Pearson correlation values, histograms, and scatterplots showing simulated diagnostic value distributions for (A) a GAM with model selection and a large test dataset (n=5,000), (B) a GAM with model selection and a small test dataset (n=42), and (C) a Maxent model without model selection and a large test dataset (n=5,000).**