OVERLAP OF PREDICTED COLD-WATER CORAL HABITAT AND BOTTOM-CONTACT FISHERIES IN BRITISH COLUMBIA

by

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ABSTRACT

Recently, there has been increased interest in studying impacts of bottom-contact fishing on cold-water corals (class Anthozoa) due to the role corals play in providing biogenic habitat as well as their limited capacity to recover from disturbance. Lack of information on the distribution of coral in British Columbia limits our ability to evaluate the extent and intensity of fishing activity in coral habitat. In this thesis, suitable habitat for four orders of coral (Alcyonacea, Antipatharia, Pennatulacea, and Scleractinia) was predicted using the species distribution modelling tool, Maxent. The extent of overlap between predicted coral habitat and footprints of three bottom-contact fisheries was determined. Depending on the type of coral, fishing has occurred in 30.4 to 46.5% of predicted habitat, with effort being disproportionately concentrated in areas of predicted coral habitat. Results strongly suggest that coral habitat in BC requires protection from fishing activity to guarantee long-term viability of coral populations.

Keywords: species distribution models; cold-water coral; bottom-contact fishing; Maxent; British Columbia

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1. INTRODUCTION

Declines in fish stocks around the world have caused governments and international bodies to begin to shift away from traditional single-species management towards ecosystem-based management frameworks (e.g. FAO 1995; FAO 2002). An essential component of ecosystem-based management that differentiates it from single-species management is that managers must take into account the impacts of fisheries on non-target species and habitats. This need to account for collateral effects has led to a growing interest in documenting and studying the impacts of trawling and other bottom-contact fisheries on benthic communities and non-target species (e.g. Sainsbury et al. 1997; Collie et al. 1997; Pitcher et al. 2000; Tillin et al. 2006).

The impacts of bottom-contact fishing on cold-water corals (class Anthozoa) have been of particular interest. Cold-water corals form complex, three-dimensional biogenic structures that provide habitat for several commercially important fish and invertebrate species (Roberts and Hirshfield 2004; Roberts et al. 2005). Cold-water corals support extensive biodiversity by providing fishes and invertebrates with protection from strong currents, refuge from predators, nurseries for juveniles, feeding areas, spawning areas, resting areas, and breeding areas (Roberts and Hirshfield 2004; Stone 2006; Jensen and Frederiksen 1992). However, cold-water corals are easily damaged by trawl, longline, and trap gear (Stone 2006; Hall-Spencer et al. 2002; Fosså et al. 2002; Koslow et al. 2001; Waller et al. 2007; Ardron and Jamieson 2006; Sinclair 2007). Heavy trawl gear can break coral or tip over the boulders or cobbles to which they are attached (Kreiger

2001; Freese et al. 1999). Traps can cause extensive damage if gear is dragged along the seafloor in areas with steep slopes or when gear is retrieved in strong winds or current (Stone 2006). Impacts from longline gear include shearing, entanglement, and disrupting substrate to which corals are attached (Stone 2006; Kreiger 2001).

Cold-water coral have a low capacity to recover from disturbance. They are very slow growing, have low recruitment rates, and live for tens to hundreds of years (Rogers et al. 2008). Surveys conducted in Alaska and the north-west Atlantic several years after trawling ceased show little evidence of coral recolonization and recovery (Kreiger 2001; Waller et al. 2007). In addition to physical damage, Waller and Tyler (2005) suggest that trawling activity at the Darwin Mounds off of Scotland may keep colonies of *Lophelia pertusa* (order Scleractinia) below the size of sexual maturity, making recovery impossible without gamete inputs from other sources.

The Atlantic and Pacific waters of Canada are home to a diversity of cold-water coral species. Canada is involved in domestic and international efforts to provide some protection for cold-water corals, though coral in British Columbia (BC) remain unprotected. Domestically, Fisheries and Oceans Canada (DFO) established a national Centre of Expertise in Cold-Water Corals and Sponge Reefs in 2008 (DFO 2009). The Center has a mandate to: (1) provide strategic advice to management; (2) support regional, national and international efforts for coral and sponge conservation; and (3) develop tools and approaches to improve coral and sponge conservation in Canada. The Newfoundland and Labrador and Pacific Regions of DFO are currently working on developing cold-water coral conservation strategies (DFO 2009). The Maritimes Region has a Coral Conservation Strategy integrated into a larger regional integrated

management plan (DFO 2006a). At the national level, DFO is preparing to release the Resource Management Sustainable Development Framework for managing fisheries resources in 2009. Included in this will be a policy and approach to manage impacts on sensitive benthic areas. The framework will include five steps: (1) data collection; (2) identification of sensitive areas; (3) impact assessment; (4) management; and (5) monitoring and evaluation.

In addition to domestic efforts, Canada is also a signatory to several international agreements that promote increased protection for cold-water coral and other sensitive benthic habitat, including the Convention on Biological Diversity (CBD) and several United Nations (UN) conventions. The 2006 Convention of the Parties to the CBD requested that Parties manage activities that may have significant adverse impacts on vulnerable marine ecosystems to ensure their conservation and sustainable use (CBD 2006). In that document, cold-water corals were specifically identified as vulnerable marine ecosystems requiring enhanced management and protection. A 2008 synthesis and review of the best available science again specifically identified cold-water corals as priority areas for biodiversity conservation in marine areas beyond the limits of national jurisdiction (CBD 2008). The United Nations General Assembly (UNGA) has also passed several resolutions urging member states to protect cold-water corals (UNGA 2004; UNGA 2006). These resolutions call on States and regional fisheries management organizations to identify vulnerable marine ecosystems and determine whether bottom fishing activities cause significant adverse impacts on those ecosystems. States and regional fisheries management organizations are urged to stop bottom trawling in areas where vulnerable marine ecosystems are known to occur and to ensure that destructive

fishing practices do not proceed unless conservation and management measures have been established (UNGA 2006). Concern was again expressed in 2008, and member States were urged to fulfil their commitments to reduce the rate of loss of biodiversity by 2010 (UNGA 2008).

In order to make informed decisions regarding the management and conservation of cold-water coral, managers require detailed information on the spatial distribution and habitat requirements of corals and threats they are facing. Unfortunately, the lack of basic information on distribution of cold-water corals in BC limits our ability to evaluate the extent and intensity of fishing activity in areas of coral habitat. Furthermore, almost all information on the presence of cold-water coral in BC is derived from research trawls and fisheries bycatch data. While useful, these data only provide information on the presence of damaged or destroyed coral aggregations, and are biased towards fishing locations (Ardron and Jamieson 2006). Research surveys have used multibeam echosounders and remotely operated vehicles (ROVs) to identify large cold-water coral reef complexes as well as smaller aggregations (Roberts et al. 2005; Conway et al. 2007). However, fishery-independent types of sampling in the deep-sea environment are prohibitively expensive and impractical for coast-wide surveys. Therefore, few areas have been surveyed and it is likely that many aggregations of cold-water corals remain undiscovered. This lack of basic distributional information on corals in BC presents a serious hindrance to managing and protecting corals and conserving the biodiversity associated with them.

Species distribution models (SDMs) can help meet science and management needs for conservation and planning by predicting areas of high habitat suitability for

species or other taxonomic groups of concern. SDMs use algorithms based on habitat or environmental conditions to predict the distribution of a species in as-yet-unsampled areas by relating occurrence data to background environmental data (Guisan and Zimmermann 2000; Guisan and Thuiller 2005). SDMs can thereby inform science and policy decisions by providing rapid and cost-effective methods for mapping and predicting suitable habitat for vulnerable species, even in data-limited situations. SDMs can also identify knowledge gaps, thereby focusing research and exploration to maximize the benefit of future effort and funding.

Several modelling approaches can be used to predict suitable habitat; however, many require both presence and absence information for the taxonomic group of interest. As with many marine organisms, extensive fishery-independent surveys have not been conducted for cold-water corals in BC. Therefore, there is a lack of reliable absence data, thus limiting the choice of SDMs to presence-only methods. One presence-only method, known as ecological niche factor analysis (ENFA) (Hirzel et al. 2002), has been used in several studies to predict the distribution of several taxa of cold-water corals on both regional and global scales. The first such studies used ENFA to predict the distribution of two families of alcyonacean corals, the Paragorgiidae and the Primnoidae, along the Atlantic and Pacific continental margins of North America (Leverette and Metaxas 2005, Bryan and Metaxas, 2007). Subsequent studies predicted the global distribution of scleractinian corals on seamounts (Clark et al. 2006), and the distribution of reef-forming *Lophelia pertusa* (order Scleractinia) at the regional and global scale (Davies et al. 2008).

ENFA, however, has poorer predictive performance than other presence-only methods (e.g. Tsoar et al. 2007; MacLeod et al. 2008). Maxent is a general purpose

machine-learning method for making predictions with only presence information (Phillips et al. 2006). Maxent has been shown to perform better than other presence-only techniques and some presence/absence methods (e.g. general linear models, generalized additive models) that have been modified for use with presence-only data (e.g. Elith et al. 2006; Phillips et al. 2006). A recent study by Tittensor et al. (2009) used both ENFA and maximum entropy modelling (Maxent) to predict the distribution of scleractinian corals on seamounts. They found that Maxent produced significantly better predictions than ENFA. Maxent's excellent performance even with small sample sizes (Pearson et al. 2007; Hernandez et al. 2006) and its previous use as a tool to assess threats and set conservation priorities for vulnerable and threatened primates in Indonesia (Thorn et al. 2009) make it an ideal SDM for the present analysis.

The objectives of this study are to (1) use Maxent to predict areas of suitable habitat for four orders of cold-water coral in BC (Alcyonacea, Antipatharia, Pennatulacea and Scleractinia); (2) determine the relative contribution of various environmental variables in determining the distribution of those corals; and (3) evaluate the spatial extent and intensity of three types of bottom-contact fishing (groundfish trawl, sablefish longline, and sablefish trap) relative to the predicted coral habitat. Areas of overlap between predicted coral habitat and fishing activity are identified, along with areas that may contain pristine coral aggregations that have not been disturbed by fishing activity. The results of this study can inform future ground-truthing and management decisions regarding the protection and conservation of cold-water corals in BC.

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2. METHODS

2.1. Study area

The study area was defined as the region within the Exclusive Economic Zone (EEZ) of Pacific Canada and less than 2450 m depth (Figure 1). The depth threshold was selected to include the deepest coral record while minimizing the overall size of the study area. The study area was divided into a grid of 500 m-by-500 m cells. There were a total of 666,010 grid cells in the study area.

2.2. Coral data

A database of 4,136 coral records was compiled using data obtained from several museums, online databases, Parks Canada, and Fisheries and Oceans Canada (Table 1). On-board observers in the groundfish trawl fishery in BC provide 100% coverage of the fishery and are required to report all bycatch, but their taxonomic identification of corals is generally not reliable (J. Boutillier, Pacific Biological Station, Nanaimo, BC, pers. comm.). Hence, these observer records were not used in this study. Records used in this study were originally obtained as part of research surveys, other scientific studies, and as bycatch in commercial fisheries that were sent to museums and identified by experts. Records were collected between 1882 and 2008, though the majority were collected in the past 20 years. The records represent 66 species from 28 families and 5 orders.

The cold-water coral records had varying levels of taxonomic and spatial resolution. Some records were identified to the species level while others were only

identified to order. All records were checked for consistent taxonomic classification (according to the Integrated Taxonomic Information System; http://www.itis.gov/) and were grouped so that the unique habitat requirements of each group could be identified. Limited data meant that records had to be grouped by order rather than species or family so that reasonable sample sizes could be obtained.

The recorded accuracy of spatial references ranged from several meters to several kilometres. Observations with a spatial resolution poorer than 500 m were excluded to ensure records were assigned to the correct grid cell. Multiple records of the same order that were located within the same grid cell were counted as a single observation. In total, 121 unique presence locations were used to construct the models for the order Alcyonacea, 49 for Antipatharia, 84 for Pennatulacea, and 32 for Scleractinia on the 500 m spatial scale (Table 2). At least 87% of the records used to build the model came from fishery-independent sources, thereby reducing the likelihood that the model is predicting the distribution of commercial fishing effort rather than the distribution of coral.

2.3. Environmental data

Decisions regarding which environmental variables to include were made based on ecological relevance and data availability. Data on depth, slope, spring surface chlorophyll *a* concentration, bottom tidal speed, and summer and winter values for bottom non-tidal current velocities, temperature, and salinity were collated to build a model of habitat suitability for cold-water corals. Factors that are likely to influence coral distribution but for which data were not available include bottom type, dissolved oxygen, phosphate, nitrate, silicate, inorganic carbon, per cent oxygen saturation, and

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aragonite saturation (Clark et al. 2006; Davies et al. 2008; Tittensor et al. 2009). The available data were imported into ArcMap 9.2 and interpolated to a 500 m-by-500 m raster using the natural neighbour technique (Watson 1992). The types and sources of environmental data used in this study are summarized in Table 3.

The depth layer was created using a mosaic of two rasters. A 75 m bathymetric dataset from Natural Resources Canada (derived from 1:250,000 bathymetric contours from the Canadian Hydrographic Service) was used for the majority of the area, while a 250 m digital elevation model from the US Geological Service was used for the southern section of the study area (E. Gregr, unpublished data, Scitech Environmental Consulting, Vancouver, BC, pers. comm.). Slope was calculated from the depth layer using the slope function in the Spatial Analyst extension of ArcMap. Slope was used as a proxy for bottom type. Steeper slopes are more likely to indicate rocky or hard bottom types (more suitable for alcyonaceans, antipatharians and scleractinians) while flatter areas are more likely to indicate sandy or muddy bottom types (more suitable for pennatulaceans) (Dunn and Halpin 2009; Hourigan et al. 2007).

Average spring (Julian days 80-171) surface concentrations of chlorophyll *a* were calculated from data obtained from the Ocean Color website (http://oceancolor.gsfc.nasa.gov/). Spring surface chlorophyll *a* concentration values were selected because the seasonality of phytodetrital food fall has been associated with the reproduction of at least two species of scleractinian corals in the Northeast Atlantic (Waller and Tyler 2005). Chlorophyll *a* data were interpolated from 4 km resolution data collected by the MODIS sensor from the years 2003-2006 (E. Gregr, unpublished data, pers. comm.). Land-based turbidity in near-shore waters can confound chlorophyll *a*

values. Therefore the data were restricted to values ranging from 0 to 40 mg/m^3 to limit the impact of turbidity (E. Gregr, unpublished data, pers. comm.).

Bottom tidal speed, as well as average summer and winter values for bottom salinity and bottom temperature were obtained from a well-validated tidal circulation model of the eastern North Pacific (Foreman et al. 2008). Summer and winter bottom non-tidal current values were also obtained directly from the senior author of that paper (M. Foreman, Institute of Ocean Sciences, Sydney, BC, pers. comm.). The non-tidal current speed values have not been validated, although the relative magnitudes should be reasonable (M. Foreman, pers. comm.). Current speed can influence the relative success of recruitment and colonization as well as feeding and growth rates of suspension feeders such as cold-water corals (Genin et al. 1986). All data from M. Foreman were provided in a finite element grid and have a variable resolution ranging from about 100 m in narrow coastal channels to 70 km in the deep ocean.

2.4. Maximum entropy

Maximum entropy (Maxent) is a general purpose machine-learning method for making predictions or inferences from incomplete information (Philips et al. 2006). Maxent estimates the most uniform distribution (maximum entropy) that defines a taxon's spatial distribution within a study area given the constraint that the expected value of each environmental variable for the predicted distribution matches the average values for the set of occurrence data (Philips et al. 2006). Each cell in the output map is assigned a probability of coral presence, which can be interpreted as the suitability of the habitat in that cell.

Maxent starts with a uniform probability distribution and iteratively calculates the probability of the species' presence at the sample locations until the increase in probability of occurrence from one step to the next falls below a given threshold (default $= 1 \times 10^{-5}$), or until the maximum number of iterations (default = 500) has been reached. The probability is displayed in terms of "gain", i.e. the log of the number of grid cells minus the log loss. Log loss equals the negative log likelihood of the test data and is the quantity that Maxent optimizes (Dudík et al. 2004). A uniform distribution over N sites achieves a log loss of ln N, with smaller values corresponding to a better prediction (Phillips and Dudík 2008).

Maximum entropy modelling was carried out using Maxent software version 3.2.19 (http://www.cs.princeton.edu/~schapire/maxent/). This program implements algorithms that are deterministic and guaranteed to converge to the maximum entropy distribution (Dudík et al. 2004). Maxent results are provided as a continuous gradient ranging from 0 (completely unsuitable) to 1 (perfectly suitable habitat).

2.5.   Model building

2.5.1.   *Sensitivity analyses*

A base case model was constructed for each order using all 10 environmental variables on the 500 m-by-500 m grid in the study area. The results of the models for each order were subjected to a set of sensitivity analyses to determine how dependent those results were on (1) the spatial resolution of data, (2) the depth cutoff of the study area, (3) the removal of correlated environmental layers, and (4) the removal of modelled data. The default parameter settings were tested with independent trials using the coral data. The Maxent defaults produced the best predictions (see Appendix 1 for details on

parameter optimization), therefore, in all cases, the default parameter settings were used. In addition to the 500 m-by-500 m grid resolution, models were also constructed using a 10 km by 10 km grid to determine whether the fine-scale information was significantly better. Coral records with coarser resolution (up to 10 km) were included in these models. The larger grid cells and additional records resulted in 118 unique locations for Alcyonacea, 44 for Antipatharia, 102 for Pennatulacea, and 45 for Scleractinia (Table 2). Models with a depth cutoff of 200 m, 500 m, 2000 m and 2800 m were created to test for the influence of the size of the study area on the results as well as the potential deterioration of environmental data quality further from shore. The number of coral records used in the models for each depth cutoff are listed in Table 2. The model's sensitivity to correlation among pairs of environmental variables was tested in two ways: first by removing environmental layers that were moderately correlated (Pearson's $r > 0.75$) and then by removing only those that were very highly correlated ($r > 0.90$) (see Figure A2.1 and Table A2.1 in Appendix 2 for results of correlation analyses and information on which layers were removed). The model's sensitivity to a possible influence of modelled data was tested by first removing all modelled environmental data (i.e., temperature, salinity, current, and tidal speeds) leaving only measured data, and then by removing only the ocean current and tidal data layers.

The Maxent models could not be tested for sensitivity to spatial autocorrelation in either the coral records or the environmental data. Spatial autocorrelation occurs when locations that are close to one another are more similar than those that are farther away. Standard statistical analyses assume that residuals are independent and identically distributed. If spatial autocorrelation is not accounted for, this assumption will be

violated, resulting in potentially biased parameter estimates and an increase in false positives (Type I error). Several methods exist to account for spatial autocorrelation when presence and absence data are available; however, no such methods exist when only presence data are available (Dormann et al. 2007), as is the case with this analysis.

2.5.2.   *Performance measures*

Many evaluation techniques for SDMs require continuous maps of probability of presence of a taxon to be converted into categorical maps indicating predicted presence or absence. In these situations, a threshold value must be selected as the cutoff between a location predicting the presence of the species and one predicting absence. Selecting an appropriate threshold can be difficult when only presence data are available. The area under the curve (AUC) of the receiver operating characteristic (ROC) is a commonly used threshold-independent measure of model accuracy (Fielding and Bell 1997) and was used here to evaluate results of sensitivity analyses. The ROC curve is obtained by plotting all sensitivity values (i.e., the proportion of observed occurrences that are correctly predicted, i.e., power, or the true positive fraction) on the *y* axis against their corresponding (1 - specificity) values (the proportion of absences incorrectly predicted as present, i.e., α, or the false positive fraction) for all available thresholds. The AUC thus provides a single number to evaluate the performance of a model that is independent of threshold selection (Phillips et al. 2006). The AUC is a measure of predictive accuracy and can have values ranging from 1.0 (indicating perfect distinction between presence and absence) to 0.5 (indicating a model that is no better than random). Though originally designed for presence and absence data, the AUC can be adapted for use with presence-only data by replacing absences with a random sample of background locations, or

pseudo-absences (Phillips et al. 2006). This changes the interpretation of the AUC so that it becomes the probability that the habitat suitability assigned to a randomly chosen presence site will be higher than that of randomly chosen background site (Phillips et al. 2006). For example, an AUC value of 0.75 indicates that 75% of the time a randomly selected presence location will have a higher habitat suitability score than a random background point. When used with presence-only data, the maximum achievable AUC is no longer 1, but is instead $1-a/2$, where a is the fraction of grid cells that the species' distribution covers (Wiley et al. 2003). Typically the value of a is unknown, so it is not possible to determine the optimal AUC score. Nevertheless, larger scores indicate better predictive performance. In addition to AUC, results of the sensitivity analyses were evaluated using log loss values.

When constructing base case models and models for the sensitivity analyses, the data for each order of coral were randomly partitioned 10 times with 60% of the data selected for training, and the remaining 40% reserved for testing. The data were partitioned 10 times rather than once to assess the average performance of each model (Phillips et al. 2008) and to allow for statistical testing of differences in the AUC and log loss using two-sided Wilcoxon rank-sum tests (Tittensor et al. 2009).

2.5.3. Final models

The final model for each coral order was constructed using the default parameter settings. All presence locations within the study area were included in the construction of the final model (as opposed to the 60% used to develop the models used in the sensitivity analyses) and thus contributed to estimating the corals' distribution. The contribution of each environmental variable to a model's fit to the data on presence of corals was

evaluated using Maxent's built-in heuristic estimate of variable contribution. However, due to the high level of correlation between many of the environmental variables, it was difficult to ascertain the relative importance of each variable in determining habitat suitability. Therefore, these results should be interpreted with caution.

The final predictive maps of habitat suitability for cold-water corals off the BC coast were divided into areas predicted to have a high probability of suitable coral habitat (predicted suitable habitat) and areas predicted to have a low probability of suitable coral habitat (predicted unsuitable habitat) to facilitate statistical analyses of the overlap with fishing effort. Maps were divided using the maximum sum of sensitivity-plus-specificity threshold value calculated for each order. The maximum sum of sensitivity-plus-specificity threshold is equivalent to finding the point on the ROC where the slope of the tangent line equals 1 (Cantor et al. 1999). This threshold was selected for its relative insensitivity to prevalence (i.e. the proportion of the study area with occurrence data) (Liu et al. 2005; Jiménez-Valverde and Lobo 2007), which is particularly important in this study due to the use of presence-only data. When building models with presence-only data, a large number of background points is required to capture the environmental variation in the study area. This results in extremely low prevalence values (Phillips et al. 2006). For example, the largest sample of coral for any order contains only 121 presence localities. This results in a prevalence of only 1.2% (when the default of 10,000 background points is used), making it important to select a threshold that is relatively insensitive to prevalence.

An error matrix derived from the binomial map for each order was used to calculate several test statistics to evaluate the predictive performance of the model. This

matrix or contingency table typically records the frequencies of each of the four types of prediction: (a) true positives; (b) false positives; (c) false negatives; and (d) true negatives. In the present study, only presence records are available, so it was not possible to determine the false positive and true negative values. However, the error matrix was used to calculate, for each order, the true positive rate (cases in which coral occurred and were predicted to occur) and the false negative rate (cases in which coral occurred but was not predicted to occur).

2.5.4.   *Significance testing*

Null models were used to test for significance of the Maxent models according to the method suggested by Raes and ter Steege (2007). To do this, 999 null models were constructed for each coral order using randomly selected locations (without replacement) from the study area. The number of random points used to construct the null models was equal to the actual number of presence points for each order of coral. The AUC values of the null models were then compared to that of the model constructed using all available coral presence data. The 95% confidence intervals were calculated by ranking the AUC scores of the 999 null models and selecting the 25th and 974th values (999 x 2.5% = 25; 999 x 97.5% = 974). Maxent models with higher AUC values than the upper confidence limit indicate that the correlations between localities where the order was present and the values of the environmental variables deviate from correlations that would have occurred by chance alone (Raes and ter Steege 2007). Models with lower AUC values than the lower confidence interval indicate that the relationships that the Maxent model is predicting between presence localities and environmental variables provides worse-than-random predictions of coral presence.

This method assumes that the original sampling design was randomly distributed over the entire study area and was not subject to any collection or environmental bias. This is unlikely to be the case with the cold-water coral data because surveyed areas will likely be concentrated close to shore, in areas of particular research interest (e.g. the shelf break), and in areas being fished. Raes and ter Steege (2007) and Dudík et al. (2005) propose a method for correcting for this bias when constructing the null models by estimating the sampling distribution of the original data. The randomly selected points for the null models are then only drawn from within that sampling distribution. Unfortunately, there is insufficient information to estimate the sampling distribution in this case and therefore the sampling bias cannot be accounted for in the construction of the null models. Nonetheless, the null models created still provide a better evaluation of species distribution model quality than simply using a subjective threshold, such as AUC ≥ 0.5 (Raes and ter Steege 2007).

2.6. Fishing data

Spatially explicit data on effort in the commercial groundfish trawl, sablefish trap, and sablefish longline fisheries between 1996 and 2004 were obtained from a database maintained by Fisheries and Oceans Canada (DFO 2006b). The trawl data include information on both bottom and mid-water trawls (excluding mid-water hake trawls). Mid-water trawls are most effective when conducted very close to the sea floor, so it is likely that the impacts of this fishery on benthic fauna are similar to those of bottom trawling (Rogers et al. 2008). Data on fishing effort were provided on a 4 km-by-4 km grid. To protect the privacy of fishermen, data were binned over all years, and at least three vessels had to record activity in a grid cell for it to be reported. Grid cells contained

information on cumulative fishing effort for each fleet (measured in hours trawled, traps set, or number of hooks). For ease of calculation, all 500 m-by-500 m cells falling within 4 km-by-4 km fishery grid cells were assigned the same values as larger cells. The values of the smaller cells should therefore be considered as rates per 16 km^2 rather than per 0.25 km^2. Potential overlap between bottom-contact fishing activities and coral habitat were evaluated by calculating the proportion of cells in areas of predicted habitat exposed to some level of fishing activity.

3. RESULTS

3.1. Distribution of coral

Records of alcyonacean corals were primarily concentrated along the continental slope, with approximately 40 records in the central and northern parts of Queen Charlotte Sound, and about 20 in the Strait of Georgia (Figure 2a). Records ranged in depth from 14 m to 2304 m and represented 8 families and 13 genera (Table 4). Records of antipatharian corals were nearly exclusively found along the continental slope (Figure 2b) and ranged in depth from 40 m to 2273 m. The Antipatharia records represented 3 families and 9 genera (Table 4). Records of pennatulaceans were also concentrated along the continental slope, with approximately 20 located in northeastern waters (Hecate Strait and Chatham Sound) (Figure 2c). Records ranged in depth from 22 m to 2158 m and represented 9 families and 9 genera (Table 4). Scleractinian coral records were dispersed throughout the study area, with records found along the continental slope, in Chatham Sound, Hecate Strait, Queen Charlotte Sound and the Strait of Georgia (Figure 2d). Records ranged in depth from 14 m to 2158 m and represented 3 families and 4 genera (Table 4).

3.2. Sensitivity analyses

While there was variation in results of the sensitivity analyses, models were generally insensitive to the spatial resolution of the data, depth cutoff, removal of layers of environmental variables that were correlated among themselves, and removal of modelled data. The main exceptions were for models built using a depth cutoff of

2800 m. When using the AUC as the evaluation metric, models with a depth threshold of 2800 m performed significantly better than the default case for all orders (2450 m) (Alcyonacea: $p < 0.00001$; Antipatharia: $p = 0.028$; Pennatulacea: $p = 0.007$; Scleractinia: $p = 0.007$). When using log loss as the evaluation metric, the models with the deeper cutoff performed significantly better than the default case for all orders except Antipatharia (Alcyonacea: $p < 0.00001$; Pennatulacea: $p = 0.002$; Scleractinia: $p = 0.043$).

These results, however, may be misleading. When used with presence-only data, the AUC is interpreted as the probability that habitat suitability assigned to a randomly selected cell containing an occurrence record is higher than that of a randomly selected background cell. When the study area is extended to include deeper waters where corals have not been found (the deepest coral record used in the analysis was found at 2302 m), there is a greater likelihood that the randomly drawn background cell used to construct the ROC will be drawn from those deeper waters where coral habitat suitability is low, thus artificially inflating the AUC value.

There were several other significant differences when log loss was used as the evaluation metric. The model built with a depth cutoff of 200 m was significantly better for Pennatulacea ($p = 0.023$), and models built with the data on a 10 km-by-10 km grid were significantly better for all orders except Scleractinia (Alcyonacea: $p < 0.0001$; Antipatharia: $p < 0.0001$; Pennatulacea: $p < 0.0001$). Note that due to the number of sensitivity analyses conducted (16 for each order), it is reasonable to expect there to be one or two significant differences by chance alone.

3.3. Final models

The AUC values of the final models for the four taxonomic orders were all significantly higher than the median AUC of the null models (final model AUC > upper 95% CI of null model) (Table 5), thus the relationship between the orders' presence localities and environmental variables are not random (Raes and ter Steege 2007). The final models also all had high true positive and low false negative rates (Table 5), indicating that the Maxent models have good predictive capabilities.

3.3.1. *Alcyonacea*

Areas predicted by the final model as being suitable habitat for Alcyonacea were mostly concentrated along the shelf break, particularly in the northern and southern extents of the study area, and in the Goose Island, Moresby, and Mitchell's Gullies projecting into Queen Charlotte Sound (Figure 3a). Summer salinity contributed most to explaining the variation in location of Alcyonacea (27%), followed by spring chlorophyll *a* concentration (20%), winter salinity (14%), summer current speed (14%), summer temperature (12%), and depth (7%) (Figure 3a). Winter temperature, slope, tidal speed and winter current speed explained only a small proportion of variation in the data.

3.3.2. *Antipatharia*

Predicted suitable habitat for the order Antipatharia was identified primarily on the shelf break (Figure 3b). Depth explained the greatest proportion of variability in the model of habitat suitability (61%) followed by summer current speed (28%) (Figure 3b). The other environmental variables each explained less than 4% of the variation in the data.

3.3.3.   Pennatulacea

Predicted suitable habitat for pennatulacean corals was identified primarily along the shelf break, with patches located along the mainland and to the west of Vancouver Island (Figure 3c). The Maxent model for these corals was largely based on tidal speed (30%), and depth (22%) (Figure 3c). Other important environmental variables include summer salinity (10%), summer temperature (10%) and winter salinity (9%). The remaining variables each contributed less than 6% to the model.

3.3.4.   Scleractinia

For the order Scleractinia, predicted suitable habitat was identified along the shelf break in the southern extent of the study area, throughout the Strait of Georgia and Queen Charlotte Sound, around the Queen Charlotte Islands, Chatham Sound, and in the northwestern extent of the study area (Figure 3d). Spring chlorophyll *a* concentration contributed the most to the model (33%) (Figure 3d). Depth, tidal speed, and summer current speed all contributed similar amounts (21, 20, and 18%, respectively). Other variables each explained less than 4% of variability.

3.4.   Potential fishing overlap

Trawl fishing effort is distributed throughout the study area landward of the shelf break and occurs in 41,721 km^2 (25.1%) of the study area (Figure 4a). The cumulative trawling intensity over the nine year study period (1996-2004) ranges from 3 to 44,851 hours of trawling/16 km^2, with a median value of 769.6 hours of fishing/16 km^2 (Table 6). Median values are reported rather than means because the data are not normally distributed.

Trawl activity has occurred in 22.2 – 37.5% of predicted suitable habitat for the four orders of coral (Table 7). Trawl fishing has occurred in a disproportionately larger area of the predicted suitable habitat of three of the coral orders studied than it does in the total study area (Figure 5). For example, trawling has occurred in 25.1% of the total study area, yet it has occurred in 35.7% of the area in which the final Maxent model predicted suitable habitat for Alcyonacea (Figure 5). The exception to this disproportionally higher intensity of fishing in coral habitat is the order Antipatharia, which are more likely to occur in deeper parts of the shelf break where trawlers do not yet go.

The sablefish trap and longline fisheries cover substantially less area than the groundfish trawl fishery. The trap fishery occurs in 11,829 km^2 (7.1%) of the study area, while the longline fishery occupies 8,318 km^2 (5.0%) of the study area. The effort in both fisheries is concentrated along the shelf break (Figure 4b and 4c). Cumulative fishing effort over the nine year study period ranges from 125 to 63,531 traps/16 km^2 (median: 1,652 traps/16 km^2) for the trap fishery and from 800 to 763,675 hooks/16 km^2 (median: 16,900 hooks/16 km^2) for the longline fishery (Table 6).

The sablefish trap fishery occurs in 15.3 – 27.4% of predicted coral habitat, whereas the longline fishery occurs in 7.2 – 14.5% of predicted habitat (Table 7). As with the groundfish trawl fishery, effort in the trap and longline fisheries is disproportionately concentrated in areas of predicted suitable coral habitat (Figure 5).

Combined, the three fisheries cover 47,330 km^2 (28.4%) of the study area, and occur in 30.4 - 46.5% of predicted suitable coral habitat (Table 7). Thus, bottom-contact

fishing generally occurs with disproportionately greater frequency in areas of predicted suitable coral habitat than in the entire study area (Figure 5).

Areas of overlap between predicted suitable habitat and bottom-contact fishing activity as well as areas that may contain pristine coral aggregations are highlighted in Figure 6 for each of the four coral orders considered. For all orders of coral and types of fishing there is a significant, though weak, correlation between the intensity of fishing activity and the predicted suitability of habitat (Spearman's *rho*: -0.19 and 0.24, *p* < 0.001 in all cases).

4. DISCUSSION

This study represents the first attempt to use species distribution models (SDMs) to predict suitable habitat for several orders of cold-water corals and identify areas that may have been exposed to bottom-contact fishing. Even with limited data, distributions of coral in the orders Alcyonacea, Antipatharia, Pennatulacea, and Scleractinia along the coast of BC were predicted by Maxent and were robust to the spatial resolution of environmental variables, omission of correlated environmental variables, depth cutoff, and exclusion of modelled (as opposed to directly observed) variables. Depending on the taxonomic order, overlap of predicted suitable coral habitat and areas of all types of bottom-contact fishing was estimated to be between 30.4 and 46.5%. This study has demonstrated the utility of using SDMs to predict the distribution of cold-water corals and to identify areas of potential overlap between predicted suitable habitat and known threats. These results can guide future scientific research on locations of coral and help managers make more informed policy and conservation decisions both within Canada and internationally.

4.1. Predicted suitable habitat

In general, suitable habitat for the four coral orders examined here was predicted to occur primarily along the shelf break, and in the Malcolm Island, Goose, and Mitchell's Gullies. These results are supported by earlier findings by Bryan and Metaxas (2007) and Ardron and Jamieson (2006). Bryan and Metaxas (2007) used ENFA to predict the distribution of two families of alcyonacean coral, the Paragorgiidae and the

Primnoidae, in BC. The suitable habitat they identified was primarily found along the shelf break. Suitable habitat for the Primnoidae was also identified in Dixon Entrance and in the gullies projecting into Queen Charlotte Sound. The areas predicted for the Alcyonacea in the present study generally follow the same patterns of distribution as those predicted by Bryan and Metaxas (2007), although the current predictions encompass slightly more area along the continental shelf break and less area in Queen Charlotte Sound and Dixon Entrance. In methodological contrast, Ardron and Jamieson (2006) performed a density analysis on bycatch data from the BC groundfish trawl, which were not used in this study, to identify 12 areas of high coral and sponge concentration (Figure 7). Of those 12 areas, three are known to be locations of hexactinellid sponge reefs (areas 4, 6, and 8). Seven of the remaining nine areas identified in their analysis correspond to areas predicted by the current analysis as predicted suitable habitat for at least one order of coral (areas 3, 5, 7, 9, 10, 11, and 12 in Figure 7). The remaining two areas (areas 1 and 2 in Dixon Entrance and Chatham Sound) overlap with some areas identified as predicted suitable habitat, although the majority of the area was predicted as unsuitable. The discrepancy could be the result of areas 1 and 2 identifying concentrations of sponges rather than corals (as is the case with the sponge reef areas), or the Maxent models' failure to identify those areas as coral habitat.

4.2. Contribution of environmental variables

Strong correlation between pairs of environmental variables makes it difficult to determine the relative importance of each variable in contributing to the distribution of cold-water corals in BC. The variables used in this study were not only correlated with each other, but they may also be highly correlated with other variables that were not

included due to a lack of data. Some variables that were not included, such as bottom type, dissolved oxygen, nutrient concentrations, and aragonite saturation, may have a greater role in controlling the distribution of cold-water corals than variables that were considered. Nevertheless, Maxent's built-in heuristic estimate of the contribution of each variable provides an approximation of the relative importance of each environmental variable in explaining the distribution of each order of coral.

Of the environmental variables considered, depth and summer current speeds appeared most frequently among the most important variables explaining spatial distribution across all four orders of coral. Depth per se is likely to be of little direct ecological consequence. However, it is a correlate with a suite of environmental variables, such as temperature, salinity, dissolved oxygen, and aragonite saturation, which have been shown to have a direct effect on the distribution of corals (Clark et al. 2006; Bryan and Metaxas 2007; Davies et al. 2008; Tittensor et al. 2009). Unfortunately, some of these variables could not be considered here because of a lack of data. It is likely that the importance of depth in all the models is due to high levels of correlation with other biologically significant variables that may or may not have been considered in this study.

Summer current speed explained a relatively large amount of the variation in the location of cold-water corals in all four models. Earlier studies that used ENFA to describe the distribution of two families of alcyonacea corals (Bryan and Metaxas 2007) and a species of Scleractinia (Davies et al. 2008), as well as a study using ENFA and Maxent to model the distribution of Scleractinia on seamounts (Tittensor et al. 2009), also found that higher current speed is an important predictor of suitable cold-water coral habitat. Current strength is known to be important to cold-water corals because it affects

the rate at which food is supplied (Thiem et al. 2006) and can influence recruitment and colonization (Genin et al. 1986). Interestingly, winter current speed was a relatively unimportant predictor in all models, and tidal speed was only important for Scleractinia. In this study, the median summer current speed was lower than that of winter current speed (Figure A2.5 and Figure A2.6). Summer current speed may therefore have acted as a limiting factor for coral distribution (by restricting the food supply or larval dispersion, for example), thus making it more important in the models than winter current speed. Tidal speed decreases as depth increases. Tidal speed may therefore have been more influential in the model for Scleractinia due to the much shallower distribution of that order relative to the others (Figure A2.2).

Surface chlorophyll *a* concentration was a relatively important correlate of the distribution of the orders Alcyonacea and Scleractinia, but not of Antipatharia and Pennatulacea. Previous modelling studies of cold-water alcyonacean (Bryan and Metaxas 2007) and scleractinian distribution (Davies et al. 2008; Tittensor et al. 2009) also found chlorophyll *a* concentration to be an important determinant in the distribution of those types of coral. A stable isotope analysis conducted on several species of cold-water coral on the east coast of Canada found that different corals feed at a variety of trophic levels ranging from fresh phytodetritus to primarily carnivorous diets (Sherwood et al. 2008). Sherwood et al. (2008) speculate that substratum type likely exerts a large influence on the diet of cold-water corals by influencing the type and availability of suspended foods. For example, rocky substrata (preferred by Alcyonacea, Antipatharia and Scleractinia) can focus currents and provide an increased supply of fresh phytodetritus (Thiem et al. 2006), whereas areas with softer substrates (preferred by Pennatulacea) tend to have

slower currents and larger amounts of resuspended material. The deep distribution of Antipatharia in this study (median = 1128m; Figure A2.2) likely negates any linkages to surface chlorophyll *a* concentration. These differences in substratum preferences and depth distributions potentially account for the greater importance of chlorophyll *a* in predicting the distribution of Alcyonacea and Scleractinia, but not for Antipatharia and Pennatulacea.

Slope, used here as a proxy for bottom type, contributed relatively little information to the four models. At the scale used in this study, slope was probably able to capture some large-scale benthic features. However, the relatively low importance of this environmental variable in the four models probably indicates that the scale of measurement was too coarse to identify smaller-scale features such as ridges, boulders, and patches of soft sediment. As mentioned above, hard features are likely to be excellent predictors of suitable habitat for Alcyonacea, Antipatharia, and Scleractinia, while the Pennatulacea may be expected to be found in areas of softer substrata are (Hourigan et al. 2007; Chia and Crawford 1973). Future attempts to model coral habitat would benefit from the inclusion of more detailed bottom type information as it becomes available.

Effects of temperature and salinity on the distribution of cold-water corals are not clearly understood (Freiwald et al. 2004). In their analysis of the distribution of two families of alcyonacean coral, Bryan and Metaxas (2007) found lower than average temperature to be a relatively important predictor of the distribution of these corals in the Pacific. Conversely, Davies et al. (2008) and Tittensor et al. (2009) found that the Scleractinia they studied exhibited a preference for above-average annual mean

temperatures. Davies et al. (2008) found temperature to be good predictors of the distribution of *Lophelia pertusa*, while Tittensor et al. (2009) did not find temperature to be a strong predictor of the distribution of Scleractinia on seamounts. In the Maxent models developed here, it was found that winter temperature was relatively unimportant predictor for all orders, and summer temperature was important in the Alcyonacea and Pennatulacea models (as Bryan and Metaxas 2007 found), but not important in the Antipatharia and Scleractinia models (as Tittensor et al. 2009 found). As with previous studies, the Alcyonacea coral studied here seem to exhibit a preference for below average temperatures, while the Scleractinia seem to prefer above average temperatures (Figure A2.10 and Figure A2.11).

As with temperature, both Davies et al. (2008) and Tittensor et al. (2009) found that the scleractinian corals they studied exhibited a preference for higher than average annual mean values for salinity. Again, as with temperature, Davies et al. (2008) found salinity to be a good predictor of the distribution of *Lophelia pertusa*, while Tittensor et al. (2009) did not. Bryan and Metaxas (2007) did not include salinity in their analysis. This study found that summer and winter salinity were important in explaining the distribution of Alcyonacea and Pennatulacea, but were relatively unimportant for Antipatharia and Scleractinia (as Tittensor et al. 2009 found). In contrast to the previous studies, this study found that Scleractinia in BC seem to prefer slightly less saline waters than average (Figure A2.8 and Figure A2.9). This discrepancy could be due to species-specific habitat preferences. For example, Davies et al. (2008) examined *Lophelia pertusa*, which has not been found in BC, whereas the Scleractinia studied here were all shallow-water cup corals. In addition to their impact on coral physiology, temperature

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and salinity may have an indirect influence through their role in the stratification of water, or they may be correlated with other important variables that were not included.

4.3. Overlap with bottom-contact fishing

The overlap between predicted suitable coral habitat identified in this study and bottom-contact fisheries in BC is substantial. Depending on the coral, bottom-contact fisheries overlap with between 30.4 and 46.5% of predicted suitable habitat coral habitat. Fishing effort was disproportionately concentrated in areas of predicted suitable coral habitat relative to the entire study area, and there was a very small but significant correlation between the intensity of fishing and habitat suitability. These estimates of overlap are similar to those of other studies that have attempted to quantify the proportion of cold-water coral habitat impacted by fishing. In Norway, Fosså et al. (2002) estimated the extent of damage caused by bottom trawling on *Lophelia pertusa* reefs (order Scleractinia) using literature, fishermen's knowledge, and remotely operated vehicle (ROV) surveys. They estimated that 30 to 50% of the *Lophelia pertusa* reef areas have been damaged by trawling. Stone (2006) used a submersible to observe coral habitat in Alaska and found that 39% of the total area of the sea floor observed had been disturbed by bottom-contact fishing gear.

An important caveat must be borne in mind when considering the current estimates of overlap between predicted suitable coral habitat and bottom-contact fishing. As mentioned in the Methods section, a DFO privacy policy made it necessary to aggregate fishing data so that at least three vessels passed through the same grid cell during the study period (1996-2004). This restriction forced a trade-off between capturing more of the effort (i.e., being able to include more vessels) and overestimating

the area fished (i.e., larger grid cells). The data were provided on a 4 km-by-4 km grid. At this coarse resolution it is likely that the actual footprint of the fisheries is over-estimated. For example, using only bottom trawl records from 1996-2005 with no restrictions due to privacy concerns or the 2450 m depth cutoff used to define the study area in the present analysis, Sinclair (2007) determined that with a 5 km by 5 km grid, the estimated area impacted by trawling was 30,000 km^2. However, with a 1 km^2 grid, the estimated fished area was reduced by 37% to 19,000 km^2. The 4 km grid used in this study (which includes both bottom and mid-water trawls) results in an estimated fished area of approximately 43,000 km^2 when the study area depth restriction (i.e. the 2450 m depth cutoff) is removed. Thus, consideration of these large differences in the fishing footprint are particularly important when results are used to estimate the proportion of coral habitat impacted by fishing activity (Sinclair 2007).

Even if the estimates of spatial overlap between predicted suitable coral habitat and bottom-contact fishing generated here are overestimated, cold-water coral are intrinsically vulnerable to impacts from bottom-contact fishing when overlap occurs. There is much empirical evidence demonstrating that cold-water coral are substantially damaged by bottom-contact fishing. Substantial damage to, and removal of, these corals by fishing activities has been documented in BC (Ardron and Jamieson 2006), Alaska (Krieger 2001; Stone 2006), the north-east Atlantic (Waller et al. 2007), on seamounts in Australia (Koslow et al. 2001) and New Zealand (Probert et al. 1997), and off the coast of Norway (Fosså et al. 2002). In fact, FAO guidelines specifically identify Alcyonacea, Antipatharia, and Scleractinia as sensitive and potentially vulnerable to fishing activities (FAO 2008). The flexibility of most pennatulaceans may make them less vulnerable to

fishing gear, though there are still reports of them being damaged and physically removed by traps in BC (Troffe et al. 2005) and trawling in New Zealand (Probert et al. 1997). The capacity of cold-water corals to recover from damage is relatively low due to their long generation time (e.g. 15 - 25 years for a family of alcyonacean coral (Grigg 1976) and 10 - 31 years for some antipatharians (Parker et al. 1997; Grigg 1976)) and longevity (e.g. nearly 50 years for some pennatulaceans (Adkins et al. 2004) and more than 100 years for some scleractinians (Grigg 1976)). Surveys in areas where trawling has not occurred for several years reveal little evidence of coral recolonization and recovery (Kreiger 2001; Waller et al. 2007). If the extent of damage is great enough, and gametes from other sources cannot recolonize an impacted area, recovery may take decades, if it happens at all (Freiwald et al. 2004).

Cold-water corals in BC waters are currently unprotected. The World Conservation Union (IUCN) Red List Categories and Criteria assess the status of species at high risk of global extinction (IUCN 2001). The Committee on the Status of Endangered Wildlife in Canada (COSEWIC) has a complementary assessment process based on the IUCN criteria designed to provide advice regarding the status of Canadian species nationally at risk of extinction or extirpation (COSEWIC 2009). The absence of high-quality data should not deter attempts to apply the assessment criteria, and indeed methods involving estimation, inference and projection are emphasised as being acceptable (IUCN 2001). In fact, taxa that are poorly known can often be assigned a threat category on the basis of background information concerning the deterioration of their habitat (IUCN 2001).

This study is not intended to be a report on the status of cold-water coral in BC. A full evaluation using the IUCN or COSEWIC criteria needs to be completed before a recommendation can be made regarding the conservation status of corals. However, the IUCN and COSEWIC criteria can be used here to put the level of overlap between predicted suitable coral habitat and bottom-contact fishing into the context of internationally recognized and applied conservation status criteria.

According to the IUCN and COSEWIC criteria, a taxon can be listed as vulnerable (IUCN) or threatened (COSEWIC) if there is "an observed, estimated, inferred or suspected population size reduction of ≥ 30% over the last 10 years or 3 generations, whichever is the longer, where the reduction or its causes may not have ceased or may not be understood or may not be reversible, based on…a decline in index of area of occupancy, extent of occurrence and/or quality of habitat." (IUCN 2001). Bottom-contact fishing in BC has not ceased and will continue to occur, and perhaps expand, in the foreseeable future. Given the vulnerability of cold-water corals to bottom-contact fishing (e.g. Krieger 2001; Stone 2006; Waller et al. 2007; Koslow et al. 2001; Probert et al. 1997; Fosså et al. 2002; Troffe et al. 2005), it is reasonable to assume that contact with fishing gear will result in a reduction in population size and therefore a reduction in area of occupancy. Corals are not uniformly distributed throughout their area of occupancy, and the type and intensity of fishing activity will influence the extent of damage to and mortality of coral. It is therefore unlikely that the reduction in population size caused by bottom-contact fishing is linearly related to the area fished. Thus, estimates of overlap can only be used as a coarse proxy for reduction in population size at this time. In the nine-year period between 1996 and 2004, an estimated 30.4 to 46.5 % of predicted

suitable coral habitat potentially came into contact with bottom-contact fishing gear. For three of the orders examined, Alcyonacea, Pennatulacea, and Scleractinia, the estimate of potential overlap is over 40% (46.5, 46.2, and 41.9% respectively). Although an area being fished does not necessarily equal an area cleared of corals, the estimates of potential overlap, and by proxy, estimates of potential population reduction, are above the 30% metric used to list a taxon as vulnerable (IUCN) or threatened (COSEWIC), even if we allow error margins of ± 10%. This high degree of overlap strongly suggests that cold-water corals in BC are being put at risk by bottom-contact fishing, and precautionary measures, such as spatial gear restrictions, need to be considered to ensure they are protected.

4.4. Conclusions

This study demonstrates the utility of using species distribution models to predict suitable coral habitat and identify areas that overlap with known threats. The patterns of coral distribution predicted by the models are largely consistent with known distribution patterns in Pacific Canada as well as patterns predicted by other methods (Bryan and Metaxas 2007; Ardron and Jamieson 2006). Estimates of the extent of overlap between predicted suitable coral habitat and bottom-contact fishing are substantial. The results presented here strongly suggest that cold-water coral habitat in BC requires protection from fishing activity to guarantee the long-term viability of coral populations.

Although these models appear to provide good predictions of the location of coral on the BC coast, refinement of the models can be achieved by increasing coral sample sizes and including additional environmental variables. Small sample sizes, resulting in part from species identification issues, prevented species-level distribution modelling

because data had to be aggregated to the level of taxonomic order. Corals are encountered regularly during both research and fishing activities, but they are not always reported, correctly identified, geo-referenced, or entered into an accessible database. Improved reporting of coral sightings and bycatch on both research and commercial vessels would greatly increase the number of usable records of coral locations. The measurement and inclusion of additional environmental variables, most notably bottom type, dissolved oxygen, nutrient concentrations, and aragonite saturation, could provide additional information and improve model predictions.

Fishing data used in this study were rather coarse due to a DFO privacy policy. Finer-scale or exact locations of fishing effort would improve identification of areas that are vulnerable to impacts from bottom-contact fishing and more accurately inform an assessment of the conservation status of coral in BC.

Future research efforts need to focus on testing predictions of this study by ground-truthing with new surveys. As well, field comparisons should be made between areas that are predicted to have come into contact with bottom-contact fishing and those predicted to be untouched to evaluate the impact of fishing on coral.

Results presented here show a large overlap between predicted suitable coral habitat and bottom-contact fishing in BC, and suggest that the long-term viability of these coral populations may be threatened. Canada has national and international obligations to protect cold-water corals, but has yet to provide such protection in BC. The UN has called for a stop to bottom trawling in areas where vulnerable marine ecosystems are known to occur, and to ensure that destructive fishing does not continue until conservation and management measures have been established. A full status report on all

orders of cold-water coral in BC and Canada is needed to assess their conservation status so that appropriate protective measures can be taken. Until such assessments can be made, Canada should take a proactive and precautionary approach to cold-water coral conservation so that these important and vulnerable marine ecosystems are not irreparably damaged. In the absence of spatial or gear restrictions designed to protect coral, continued bottom-contact fishing in BC will result in continued damage to coral habitat.

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TABLES

Table 1 Data sources and number of coral records collected for this study. Note that some observations occur in more than one database.

Source	Number of records
California Academy of Sciences	142
Fisheries and Oceans Canada (DFO)	1,269
Parks Canada	653
Royal British Columbia Museum	97
Global Biodiversity Information Facility	1,762
Royal Ontario Museum	20
Canadian Museum of Nature	42
Smithsonian National Museum of Natural History	106
Marine Conservation and Biology Institute	45

Table 2 Number of distinct coral records used as a function of grid size and depth. The baseline case uses a 500 m-by-500 m grid size and 2450 m depth cutoff. Bold numbers indicate that models that could not be built due to small sample size.

Order	Baseline case (2450m)	10 x 10 km grid size	Depth cutoff			
			200 m	500 m	2000 m	2800 m
Alcyonacea	121	118	17	44	112	121
Antipatharia	49	44	**2**	**2**	44	49
Pennatulacea	84	102	25	25	83	84
Scleractinia	32	45	23	26	31	32

Table 3 The type and source of environmental data used in this study, showing range and median values for each environmental variable.

Environmental variable	Source	Original resolution	Minimum	Maximum	Median
Depth (m)	Canadian Hydrographic Service	75 m	1	2450	330
	US Geological Service	250 m			
Slope (degrees)	Derived from depth layer using Spatial Analyst Extention of ArcMap 9.2		0	70.73	0.79
Chlorophyll *a* concentration (µg/L)	Ocean Color http://oceancolor.gsfc.nasa.gov/	4 km	0.26	38.46	1.50
Summer current speed (m/s)	M. Foreman (Institute of Ocean Sciences, Sidney, BC, pers. comm.)	Variable	3×10^{-6}	1.03	0.015
Winter current speed (m/s)	M. Foreman	Variable	7×10^{-6}	1.27	0.021
Summer salinity (psu)	M. Foreman	Variable	17.63	34.68	33.95
Winter salinity (psu)	M. Foreman	Variable	25.56	34.68	33.91
Summer temperature (^{o}C)	M. Foreman	Variable	1.50	16.86	5.42
Winter temperature (^{o}C)	M. Foreman	Variable	1.53	9.38	6.13
Tidal speed (m/s)	M. Foreman	Variable	0.0052	0.92	0.046

Table 4 Families and genera represented in each taxonomic order used in this study.

Order	Families	Genera	
Alcyonacea	Acanthogorgiidae	*Acanthogorgia*	*Narella*
	Alcyoniidae	*Anthomastus*	*Paragorgia*
	Gorgoniidae	*Callagorgia*	*Parastenella*
	Isididae	*Eunephthya*	*Primnoa*
	Nephtheidae	*Gersemia*	*Swiftia*
	Paragorgiidae	*Isidella*	
	Plexauridae	*Keratosis*	
	Primnoidae	*Lepidisis*	
Antipatharia	Antipathidae	*Antipathes*	*Lillipathes*
	Cladopathidae	*Bathypathes*	*Parantipathes*
	Schizopathidae	*Chrysopathes*	*Trissopathes*
		Cladopathes	*Umbellapathes*
		Dendrobathypathes	
Pennatulacea	Anthoptilidae	*Anthoptilium*	*Ombellula*
	Funiculinidae	*Distichoptilum*	*Pennatula*
	Halipteridae	*Funiculina*	*Ptilosarcus*
	Kophobelemnidae	*Halipteris*	*Stylatula*
	Ombelluiidae	*Kophobelemnon*	
	Pennatulidae		
	Protoptilidae		
	Stachyptilidae		
	Virgulariidae		
Scleractinia	Caryophyllidae	*Caryophyllia*	*Balanophyllia*
	Dendrophyllidae	*Paracyathus*	*Javania*
	Flabellidae		

Table 5 Maximum sensitivity-plus-specificity threshold, area under the receiver-operator curve (AUC), null model median AUC, 95% confidence interval (CI) of the AUC, and the true positive rate (cases in which coral occurred and were predicted to occur) and false negative rate (cases in which coral occurred but was not predicted to occur) of the final model for each coral order.

Order	Maximum sensitivity-plus-specificity threshold	AUC	Null model median AUC	95% CI of null model AUC	True positive rate	False negative rate
Alcyonacea	0.331	0.908	0.743	0.701 - 0.790	0.88	0.12
Antipatharia	0.295	0.940	0.721	0.661 - 0.776	0.94	0.06
Pennatulacea	0.350	0.947	0.747	0.695 - 0.799	0.90	0.10
Scleractinia	0.352	0.864	0.754	0.681 - 0.816	0.84	0.16

Table 6 Cumulative minimum, maximum, and median values for fishing effort of the groundfish trawl (hours/16 km^2), sablefish trap (traps/16 km^2), and sablefish longline (hooks/16 km^2) fisheries over a nine-year period (1996-2004).

Type of fishing	Fishing effort (per 16 km^2)		
	Minimum	Maximum	Median
Trawl (hours)	3	44,851	770
Trap (traps)	125	63,531	1,652
Longline (hooks)	800	763,675	16,900

Table 7 Percentage of area of predicted suitable habitat for each order of coral and the entire study area that overlaps with three bottom-contact fisheries - trawl, trap, and longline (individually and cumulatively).

| | Area (km^2) | Percentage of area that overlaps with fishing activity | | | |
		Trawl	Trap	Longline	Cumulative
Alcyonacea	32,765	35.7	25.5	14.5	46.5
Antipatharia	23,669	22.2	21.3	7.2	30.4
Pennatulacea	18,496	37.5	27.4	11.0	46.2
Scleractinia	36,292	35.6	15.3	10.7	41.9
Study area	166,503	25.1	7.1	5.0	28.4

FIGURES
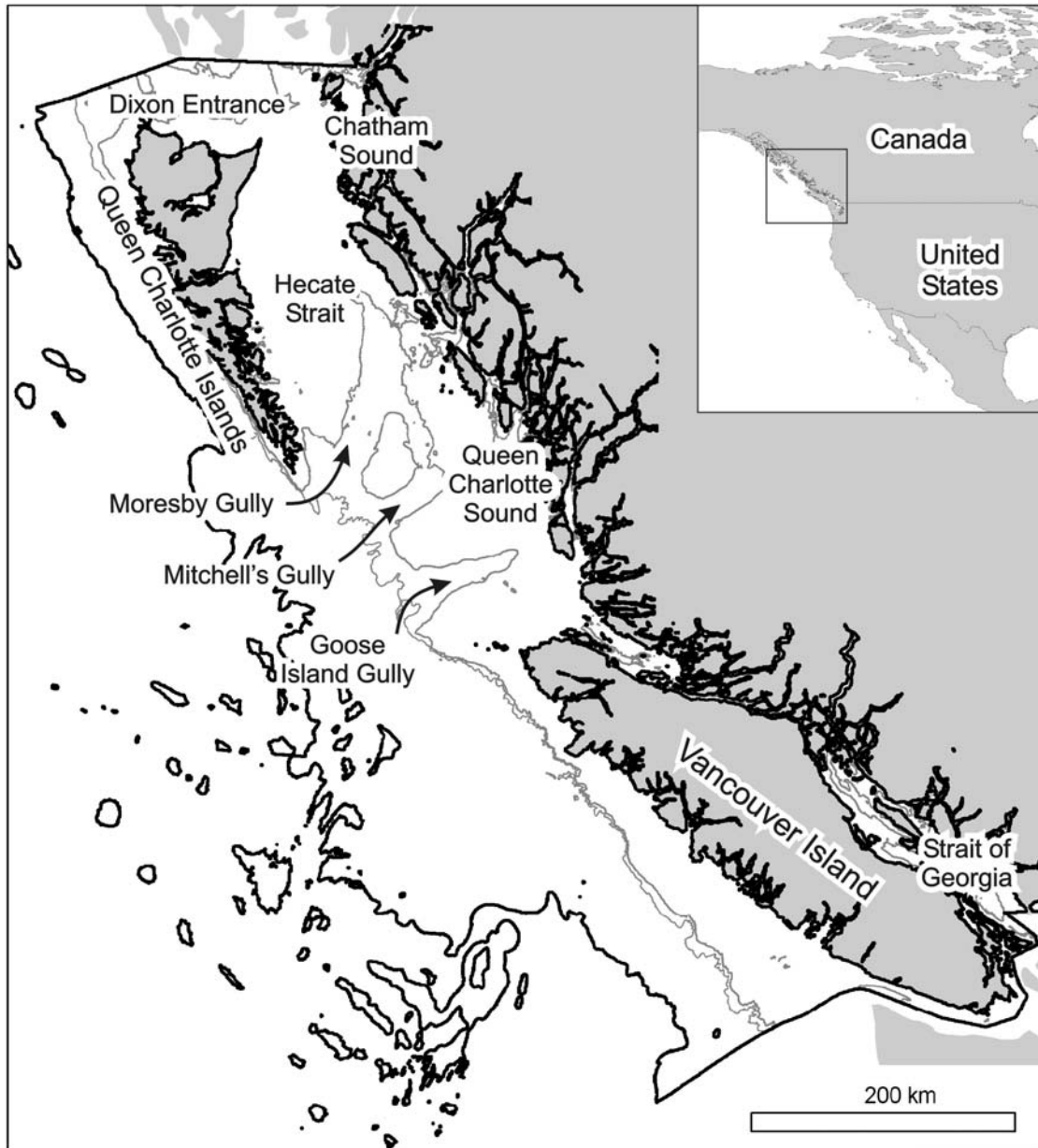
Figure 1 Map of the study area and places described. The thicker black line indicates the 2450 m depth cutoff of the study area, while the lighter grey lines indicate the 200 m and 500 m contours.
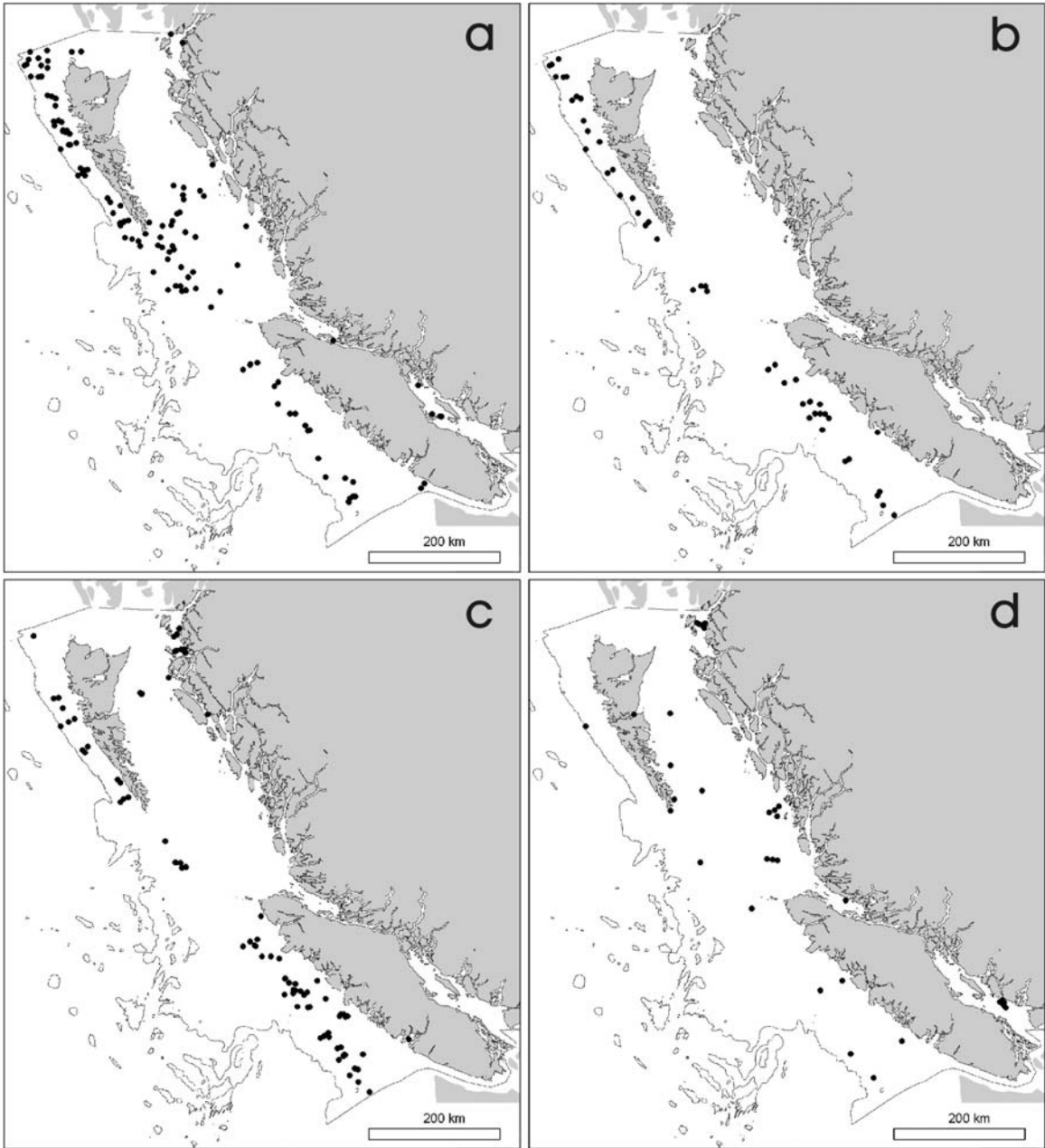
Figure 2 Distribution of coral observations used in the present study for (a) Alcyonacea
(*n* = 121); (b) Antipatharia (*n* = 49); (c) Pennatulacea (*n* = 84); and (d)
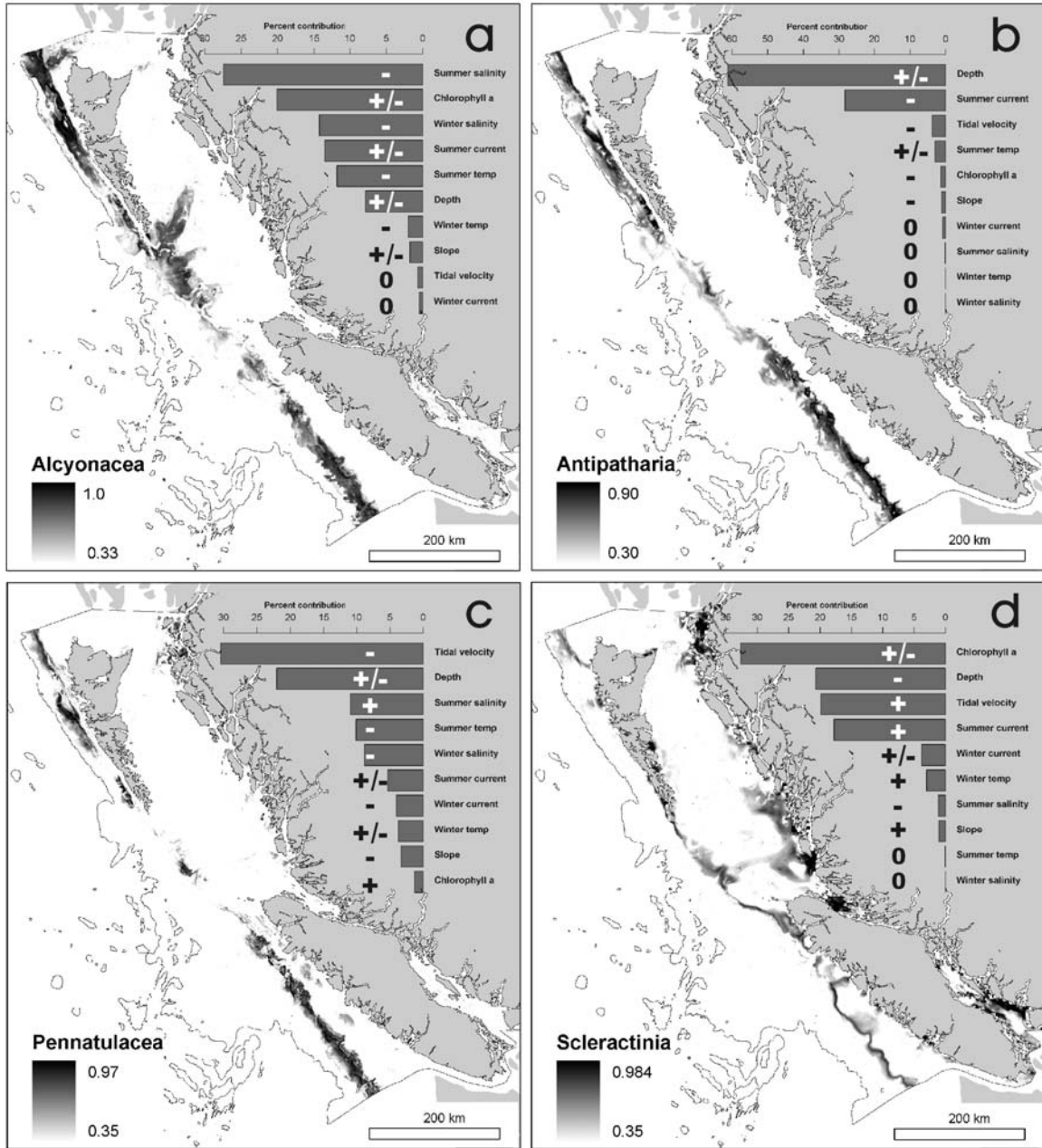Scleractinia (*n* = 32). The black lines represent the 2450 m depth contour
used to define the study area.

Figure 3 Distribution of suitable habitat predicted by the final Maxent model for each of the four orders of coral. Darker shades indicate higher suitability. White areas indicate less suitable habitat. Insets indicate the relative contribution of each environmental variable to explaining the variation in location of coral according to the Maxent model, while + and – signs indicate the direction of correlation between predicted habitat suitability and increasing values for the environmental variables. Zeros indicate a < 1% contribution to the model and +/- signs indicate an increasing and then decreasing suitability of habitat as the environmental variable increases (i.e., a nonlinear function).

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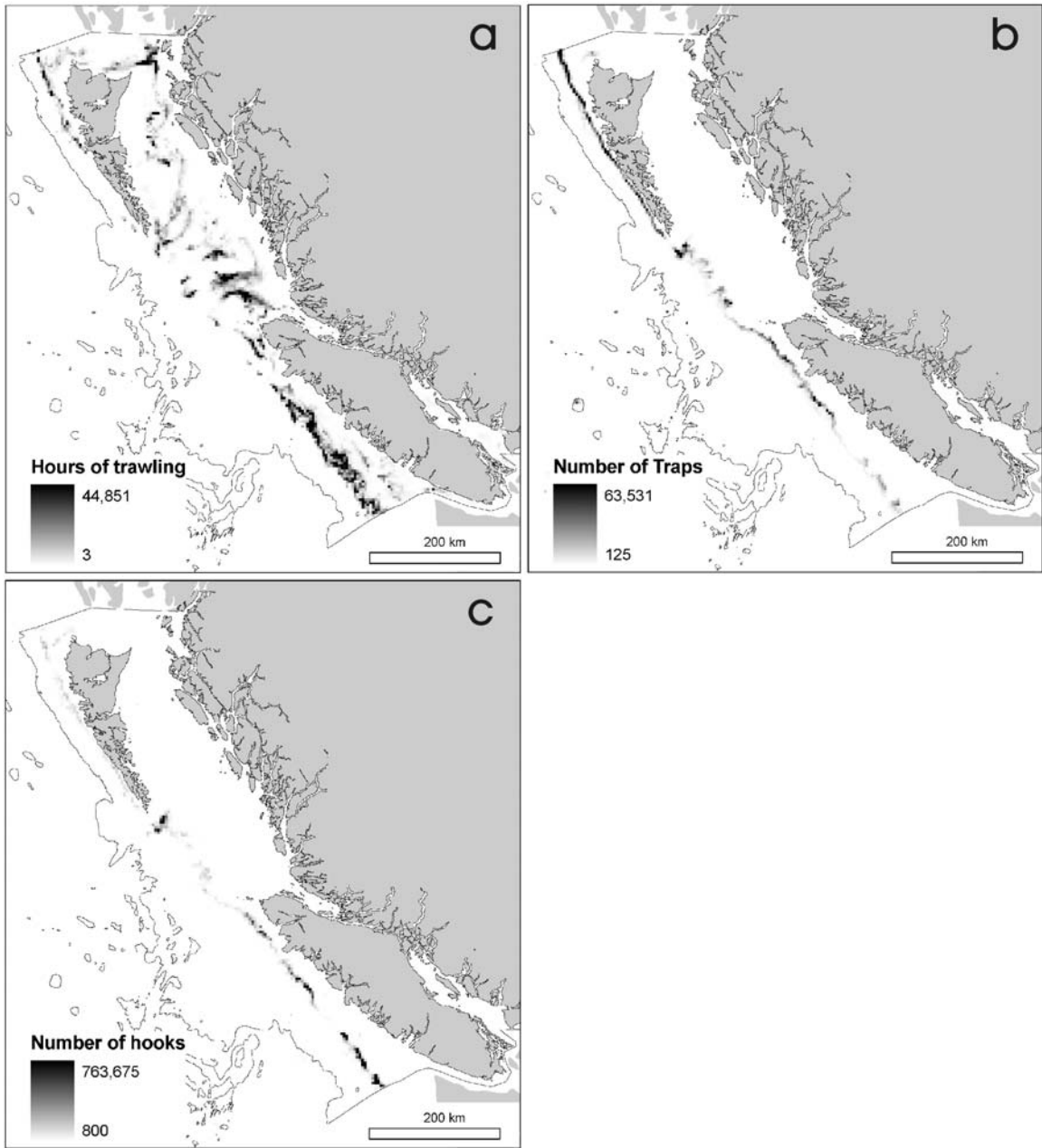
Figure 4 Spatial distribution and intensity of cumulative bottom-contact fishing effort over a nine-year period (1996-2004) for (a) groundfish trawl (trawl hours/16 km^2); (b) sablefish trap (traps/16 km^2); and (c) sablefish longline (hooks/16 km^2).
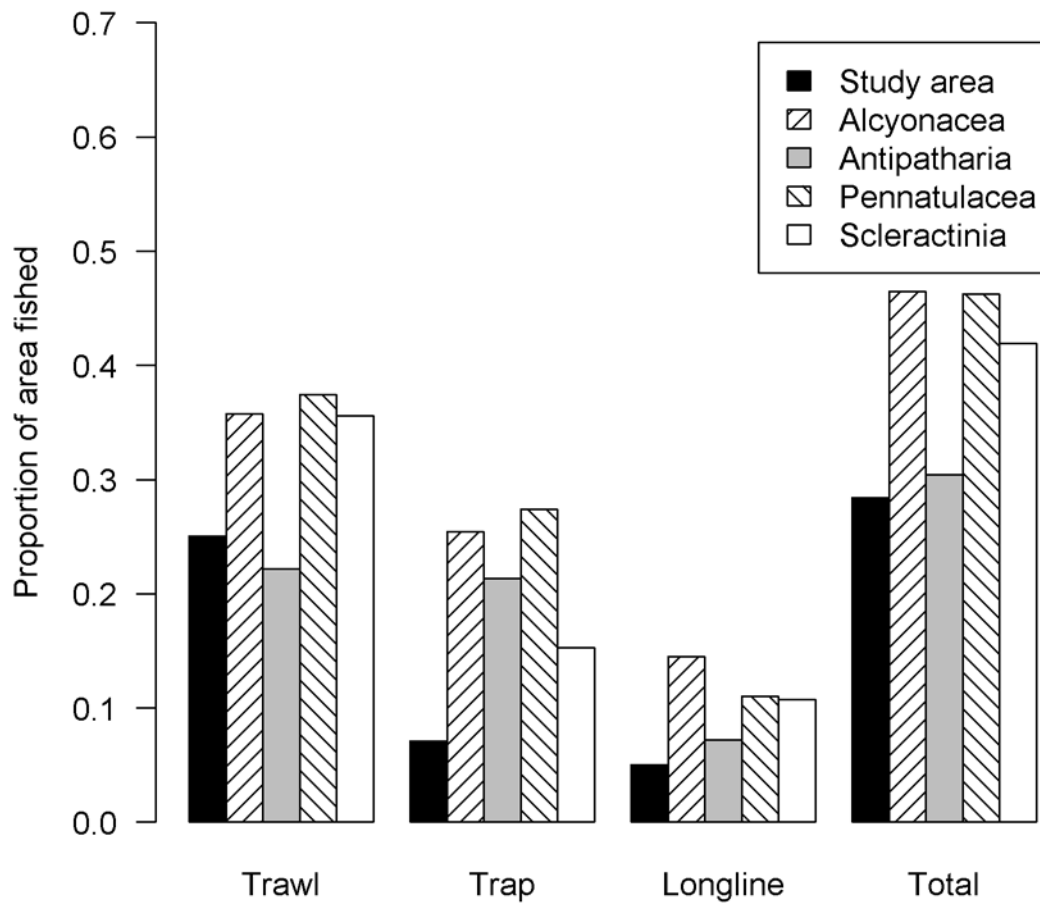
Figure 5 Proportion of area fished by the three bottom-contact fisheries in the entire study area (dark bars) and in areas of predicted suitable habitat for each order of coral. In nearly all cases, fishing effort is disproportionately concentrated in areas of predicted suitable habitat for corals.
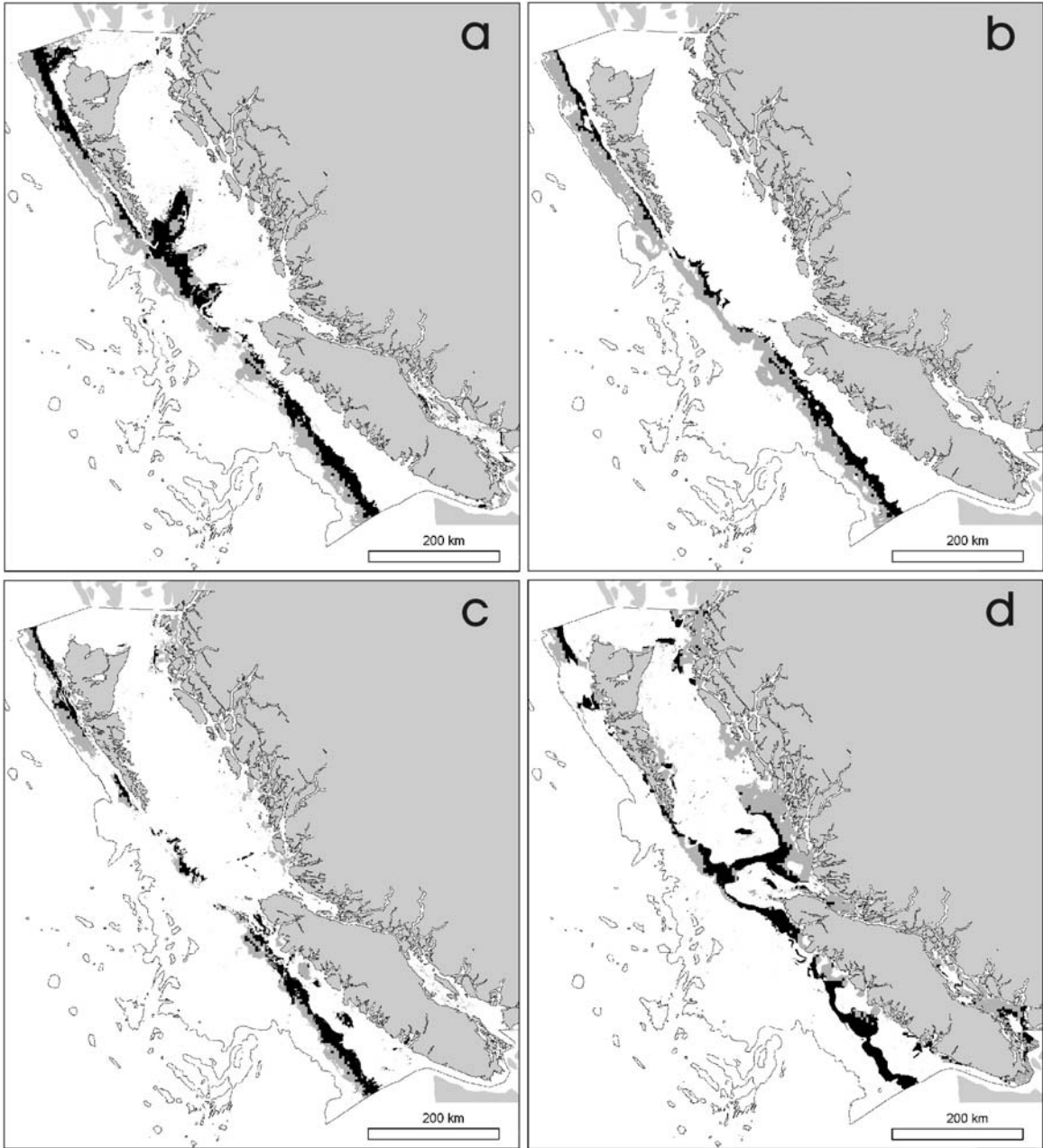
Figure 6 Areas of overlap (black) between predicted suitable habitat for corals and
bottom-contact fishing. Marine grey areas indicate predicted suitable habitat
that does not overlap with bottom-contact fishing. Maps are for (a)
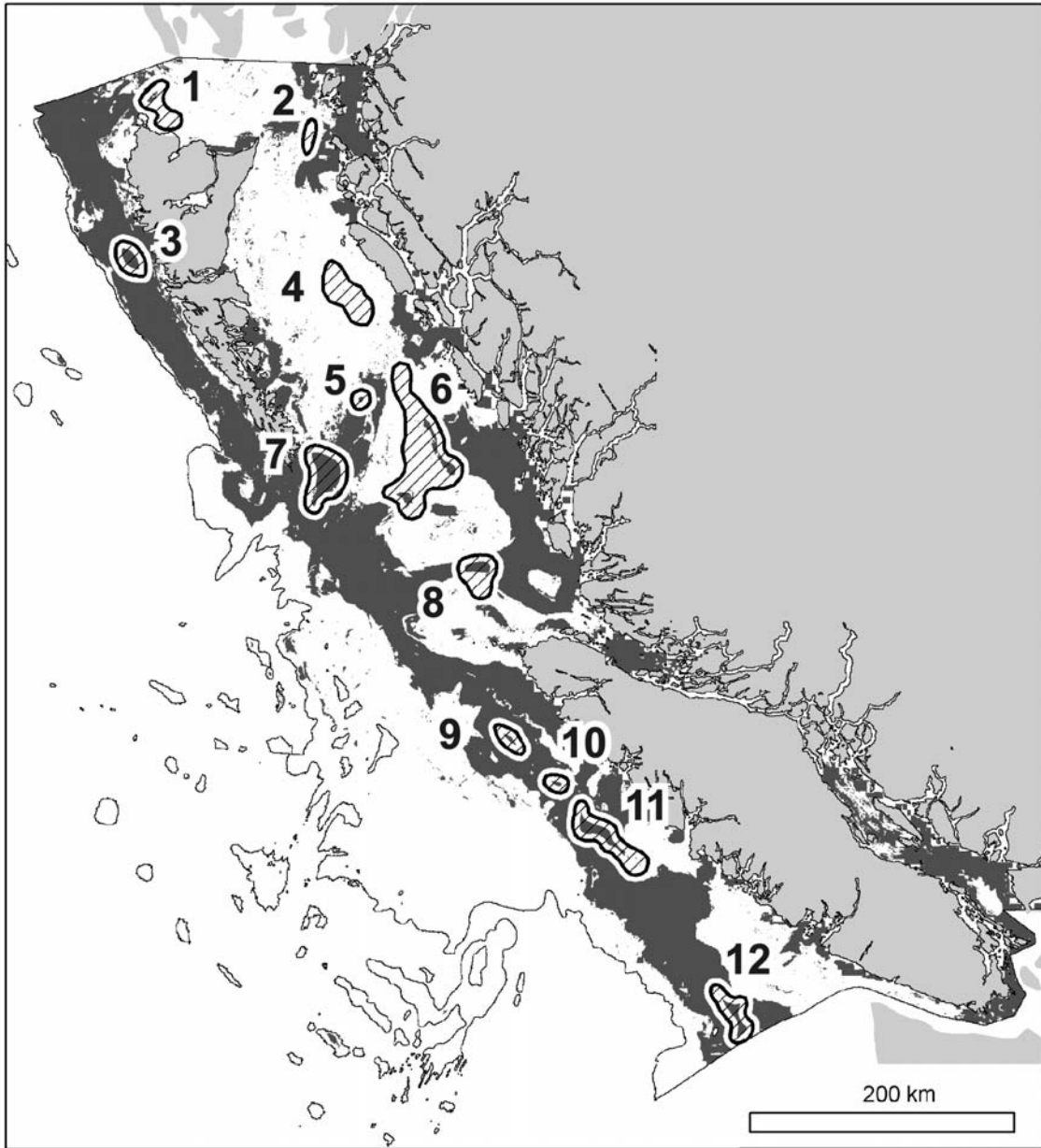Alcyonacea; (b) Antipatharia; (c) Pennatulacea; and (d) Scleractinia.

Figure 7 Comparison of areas of high coral and sponge bycatch as reported by Ardron and Jamieson (2006) (numbered polygons) and predicted suitable habitat for all coral from the present study (dark grey areas). Areas 4, 6, and 8 are known hexactinellid sponge reefs. Areas 3, 5, 7, 9, 10, 11, and 12 correspond with areas of predicted suitable coral habitat. Areas 1 and 2 correspond with some areas predicted as being suitable coral habitat, although the majority of the area was predicted to be unsuitable.

APPENDIX 1 – MAXENT PARAMETER OPTIMIZATION

Introduction

Maxent has several parameter settings that can influence the model's ability to correctly identify areas of presence and absence. Most notably these parameters are the number of background points used to represent environmental variables in the study area, the type and combination of feature classes used, the β values for those features, and the regularization multiplier (all explained below).

The Maxent spatial distribution is calculated over all cells in the study area for which there is a complete set of environmental data. When the number of cells is large, processing time can be very long. For this reason, Maxent uses a subsample (with a default of 10,000 cells) of the data to represent the range of environmental conditions available within the study area to reduce run time of the model without compromising predictive performance (Phillips and Dudík 2008).

Maxent uses environmental layers to produce "features", which affect the type and complexities of relationships the model tries to fit. The Maxent software uses several feature classes, including linear, quadratic, product, threshold, and hinge features (Phillips et al. 2006; Phillips and Dudík 2008). There is also a categorical indicator feature, although this feature was not used in the current study because all environmental data were continuous. The linear, quadratic, and product features constrain the means, variances, and covariances of environmental variables, respectively, to match their empirical values (Phillips *et al*. 2006). Threshold features allow Maxent to fit binary

responses while hinge features allow a binary response to exist that is preceded or followed by a linear response to an environmental variable once a given threshold has been passed (Phillips and Dudík 2008). For example, a species may not be present in areas where the current speed is below a certain threshold. However, once that threshold has been passed, the probability of that species being present may then increase linearly as the current speed increases. The complexity of the model is controlled by the types of feature classes used and by settings called "regularization parameters", or β values, which control the error bounds on deviations of feature averages from their expected values (Dudík et al. 2004). These β values help prevent Maxent from overfitting the data by allowing the estimated probability distribution of a species' occurrence to fall within the empirical error bounds of the averages of the suite of features associated with each environmental variable rather than being exactly equal to it (Dudík et al. 2004; Phillips and Dudík 2008).

In addition to using β values, Maxent limits overfitting by using an additional regularization multiplier parameter. Values smaller than the default of 1.0 will result in a predicted distribution that fits the original input data more closely while larger values will result in a more diffuse, less localized distribution.

Phillips and Dudík (2008) determined the default set of feature classes, the β values for those features, and the number of background points using data on 226 terrestrial species, ranging from plants to mammals, from six regions in the world. The default values are well suited to a wide range of presence-only datasets as long as those data do not have characteristics that substantially deviate from the ones used by Phillips and Dudík (2008). To my knowledge, no other study has tested the applicability of these

default settings to other datasets, including marine organisms. I therefore decided to determine whether they were appropriate for the cold-water coral data used in this study.

Methods

When conducting the parameter optimization, data for each order of coral were randomly partitioned 10 times with 60% of the data selected for training, and the remaining 40% reserved for testing. Data were partitioned 10 times rather than once to assess the average performance of each model (Phillips et al. 2007) and to allow for statistical testing of differences in the AUC and log loss using two-sided Wilcoxon rank-sum tests (Tittensor et al. 2009).

Following the method used by Phillips and Dudík (2008), models were built for each order of coral for different feature class settings, i.e., (linear (L); linear and quadratic (LQ); linear, quadratic and product (LQP); threshold (T); hinge (H)). For the LQ and LQP settings a single β value was used, i.e. $\beta_L = \beta_Q$ and $\beta_L = \beta_Q = \beta_P$. The regularization parameter, β, was varied using the geometrically increasing sequence {0.02, 0.05, 0.10, 0.22, 0.46, 1.0, 2.2, 4.6} to bracket the range of suitable values suggested by theory (Dudík et al. 2004; Phillips and Dudík 2008). For each coral order and feature set, the average AUC and log loss values over the 10 random partitions were compared using two-sided Wilcoxon rank-sum tests to the AUC and log loss values obtained when using the default settings of the model.

The study area was composed of 666,010 500 m-by-500 m grid cells. For each coral order, models were built using 100, 1000, 10,000 (default) and 100,000 background grid cells to represent the range of environmental conditions available within the study

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area. Models were also constructed with regularization multiplier values of 0.1, 0.22, 0.46, 1.0 (default), 2.2, and 4.6. The resulting models were compared to results arising from the default settings using two-sided Wilcoxon rank-sum tests.

Results

In nearly all cases, the feature combinations and beta values tested did not produce AUC or log loss values that were significantly better than the default settings ($p > 0.05$) (Figure A1.1), though they were frequently significantly worse. Likewise, varying the number of background points and the regularization multiplier used to construct the model did not significantly improve the AUC or log loss scores ($p > 0.05$), and were occasionally significantly worse (results not shown).

Conclusion

The results of the parameter optimization analyses conducted for the four orders of cold-water coral in BC indicate that the default settings in Maxent are suitable for these data. It is therefore reasonable to use the default parameter settings for all subsequent analyses with these data.
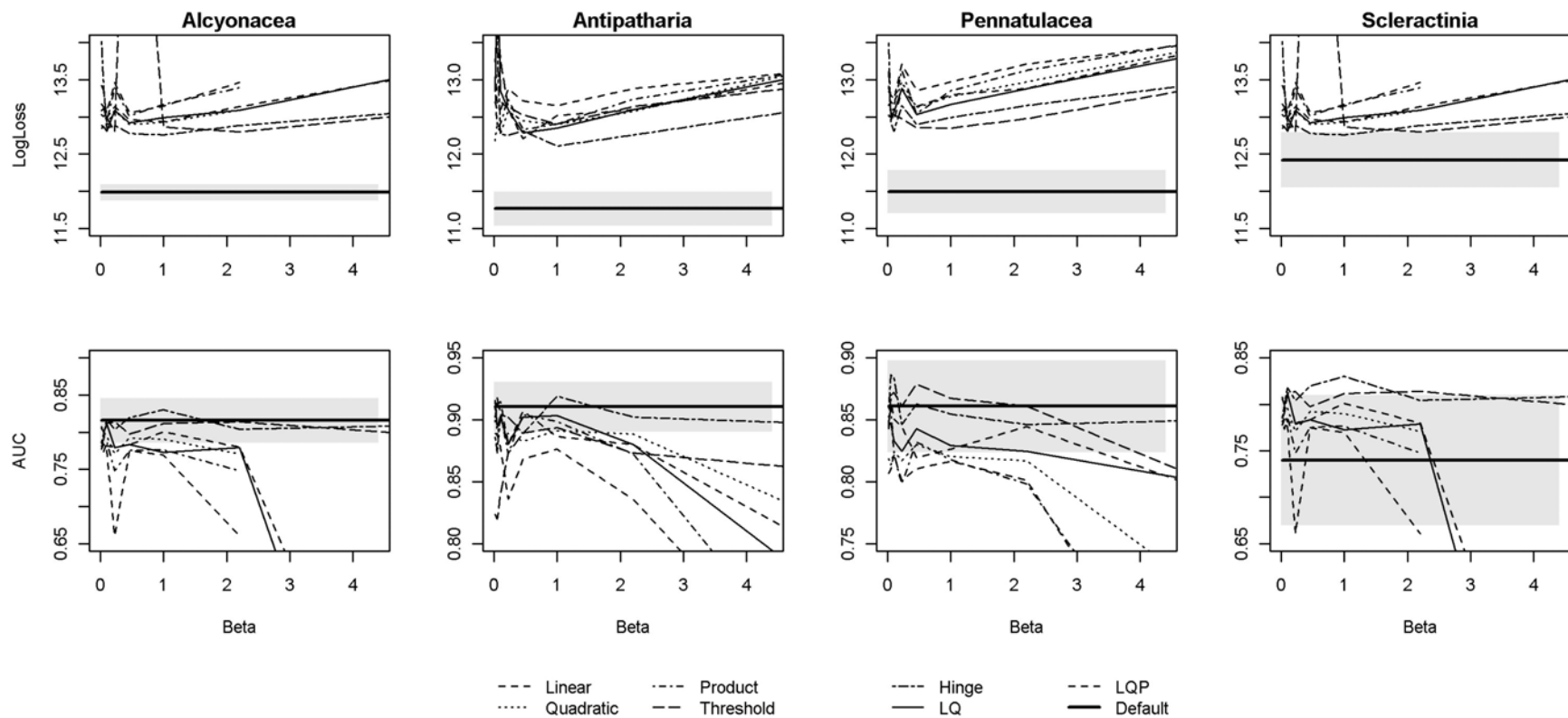
Figure A1.1 β- curves for the four orders of coral. Lines represent the average performance of Maxent in terms of log loss and AUC over 10 random partitions for each of the 7 features. The thick solid horizontal line indicates the average log loss and AUC scores obtained using the default settings. Grey areas indicate one standard deviation from the default averages.

APPENDIX 2 – ENVIRONMENTAL VARIABLES
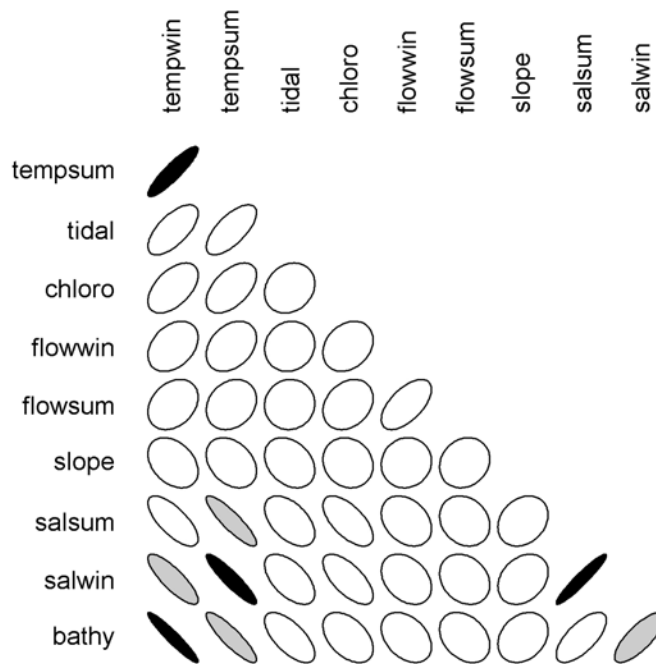
Correlation matrix of environmental variables

Figure A2.1 Ellipses with a positive slope indicate a positive correlation, while negative
slopes indicate a negative relationship. Thinner ellipses reflect higher
correlation. Grey ellipses indicate correlation r > 0.75 while black ellipses
indicate correlation r > 0.90. Tempwin = winter temperature; tempsum =
summer temperature; tidal = tidal speed; chloro = spring surface chlorophyll *a*
concentration; flowwin = winter current speed; flowsum = summer current
speed; slope = slope of seafloor; salsum = summer salinity; salwin = winter
salinity; bathy = depth.

Table A2.1 Environmental variables used for each sensitivity analysis run in which variables with a correlation of r > 0.75 or r > 0.90 were removed.

Run	Environmental variables used		
1	Depth	Summer current speed	Tidal speed
	Slope	Winter current speed	Summer salinity
	Chlorophyll *a* conc.		
2	Depth	Summer current speed	Summer salinity
	Slope	Winter current speed	Winter temperature
	Chlorophyll *a* conc.	Tidal speed	
3	Slope	Summer current speed	Tidal speed
	Chlorophyll *a* conc.	Winter current speed	Winter salinity
4	Slope	Summer current speed	Summer salinity
	Chlorophyll *a* conc.	Winter current speed	Summer temperature
		Tidal speed	
5	Slope	Summer current speed	Tidal speed
	Chlorophyll *a* conc.	Winter current speed	Summer temperature
6	Depth	Summer current speed	Summer salinity
	Slope	Winter current speed	Winter salinity
	Chlorophyll *a* conc.	Tidal speed	Summer temperature
7	Depth	Summer current speed	Summer salinity
	Slope	Winter current speed	Summer temperature
	Chlorophyll *a* conc.	Tidal speed	Winter temperature
8	Depth	Summer current speed	Winter salinity
	Slope	Winter current speed	Winter temperature
	Chlorophyll *a* conc.	Tidal speed	
9	Slope	Summer current speed	Summer salinity
	Chlorophyll *a* conc.	Winter current speed	Winter salinity
		Tidal speed	Winter temperature

Distribution of environmental variables

Figures A2.2 – A2.11 illustrate the relative frequency density distribution of each environmental variable within the entire study area and for each order of coral. These figures visually demonstrate that the coral are selective in terms of habitat and that each order has unique habitat preferences that differentiate them from each others. For example, Antipatharia and Pennatulacea are distributed unevenly with respect to depth. They are found disproportionately more frequently in the 500 – 1500 m depth range than they are at other depths.
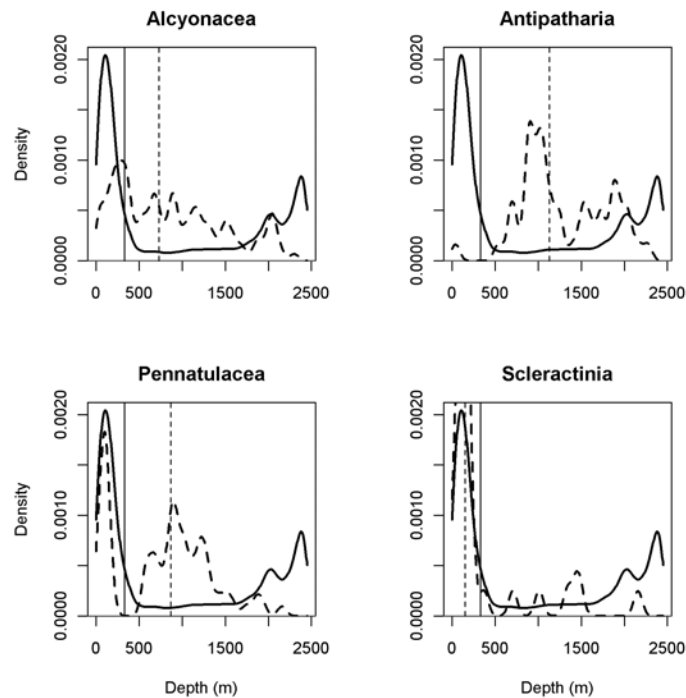
Figure A2.2 Relative frequency density plot of **depth (m)** for the entire study area (solid lines) and for each order (dotted lines). Vertical lines indicate median values.
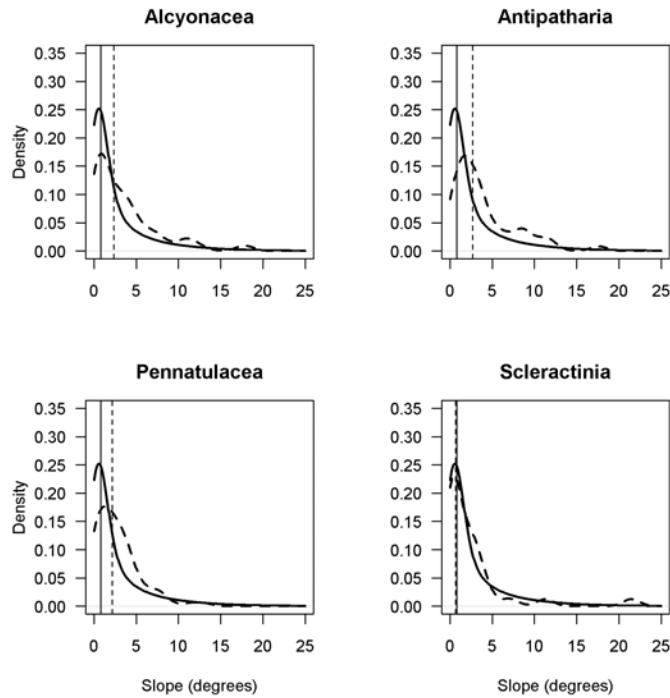
Figure A2.3 Relative frequency density plot of **slope (degrees)** for the entire study area (solid lines) and for each order (dotted lines). Vertical lines indicate median values.
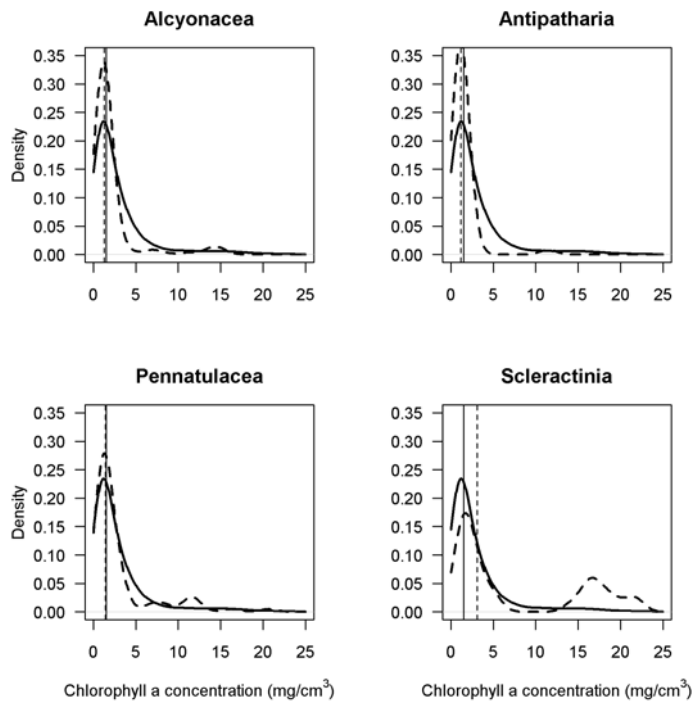
Figure A2.4 Relative frequency density plot of **spring chlorophyll *a* concentration (mg/cm³)** for the entire study area (solid lines) and for each order (dotted lines). Vertical lines indicate median values.
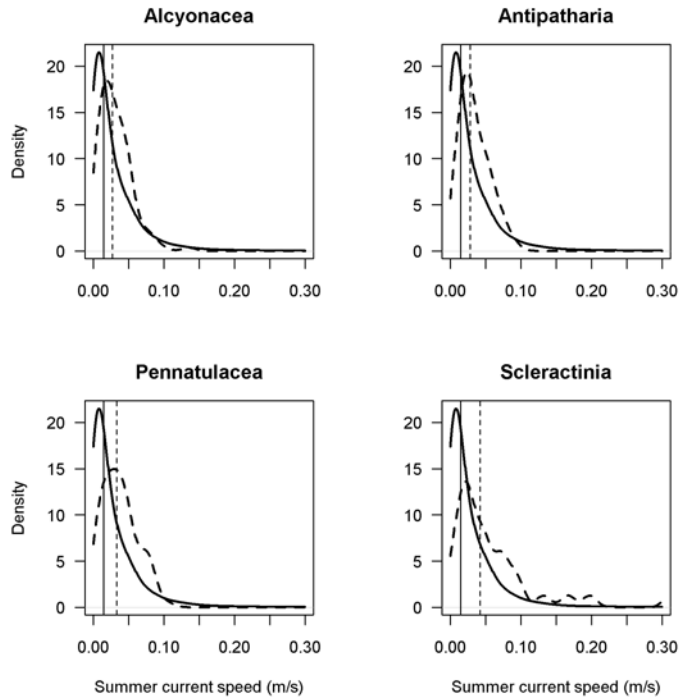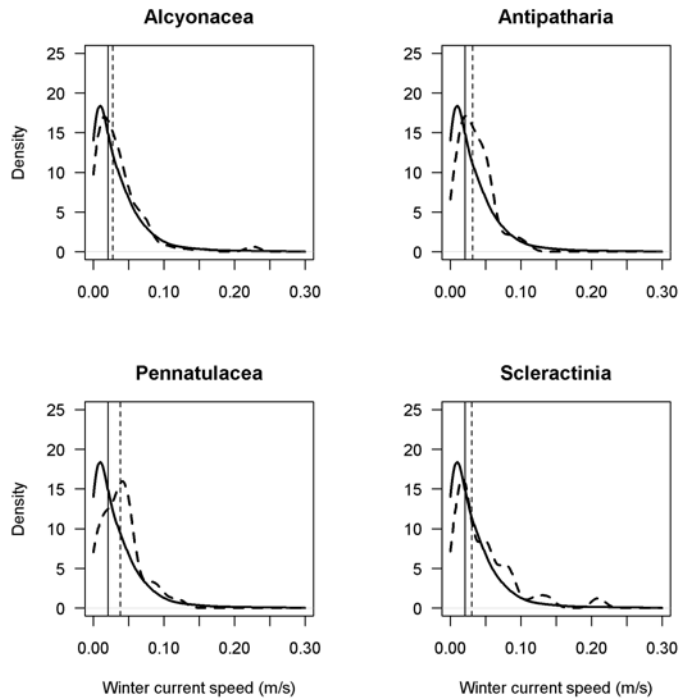
Figure A2.5 Relative frequency density plot of **summer current speed (m/s)** for the entire study area (solid lines) and for each order (dotted lines). Vertical lines indicate median values.

Figure A2.6 Relative frequency density plot of **winter current speed (m/s)** for the entire study area (solid lines) and for each order (dotted lines). Vertical lines indicate median values.
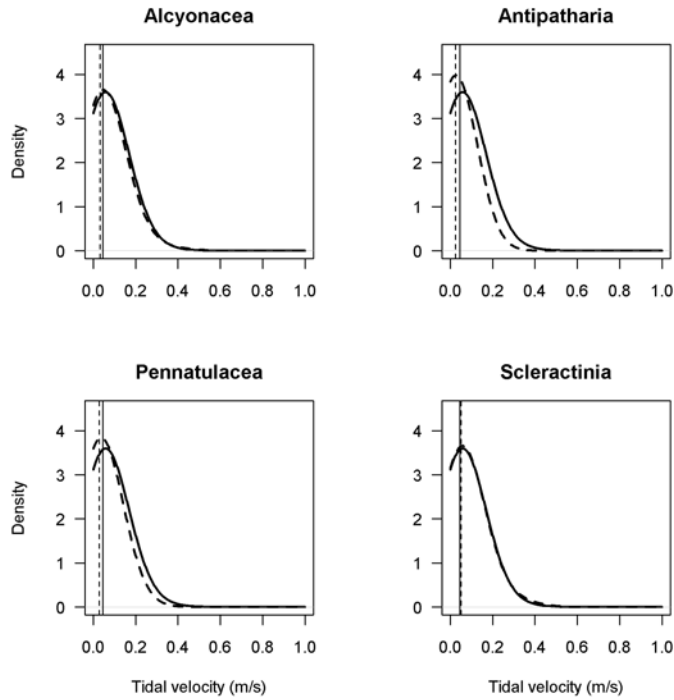
Figure A2.7 Relative frequency density plot of **tidal speed (m/s)** for the entire study area (solid lines) and for each order (dotted lines). Vertical lines indicate median values.
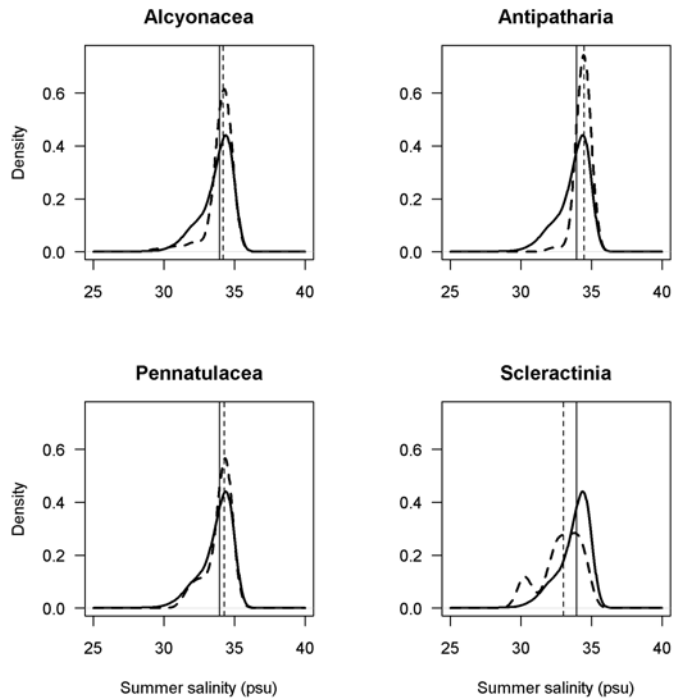

Figure A2.8 Relative frequency density plot of **summer salinity (psu)** for the entire study area (solid lines) and for each order (dotted lines). Vertical lines indicate median values.
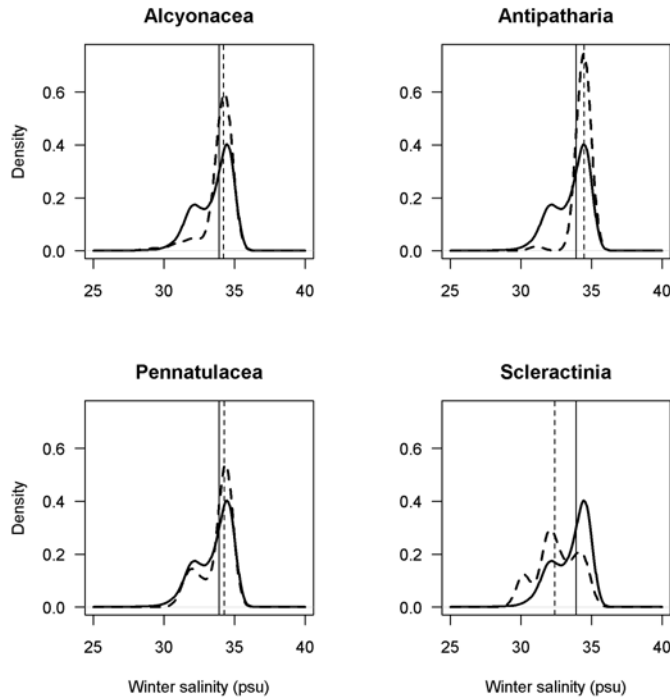
Figure A2.9 Relative frequency density plot of **winter salinity (psu)** for the entire study
    area (solid lines) and for each order (dotted lines). Vertical lines indicate
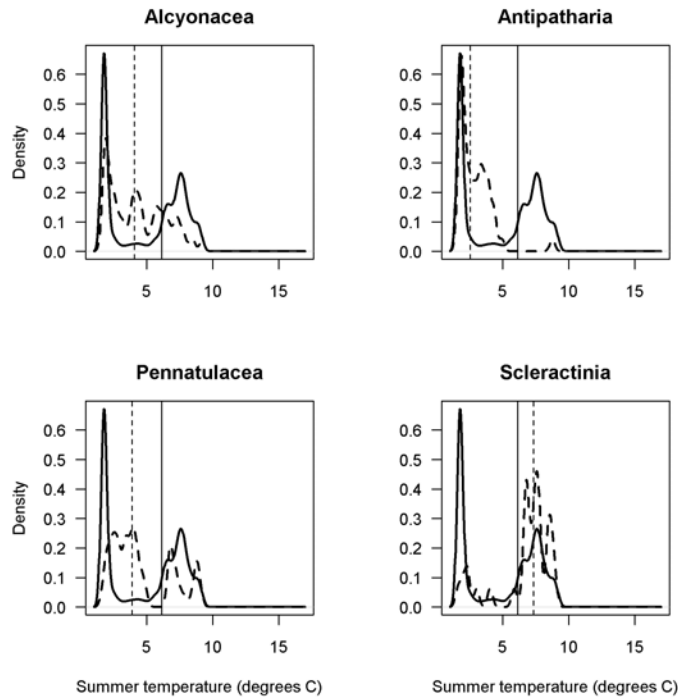   median values.

Figure A2.10 Relative frequency density plot of **summer temperature (^{o} C)** for the
    entire study area (solid lines) and for each order (dotted lines). Vertical lines
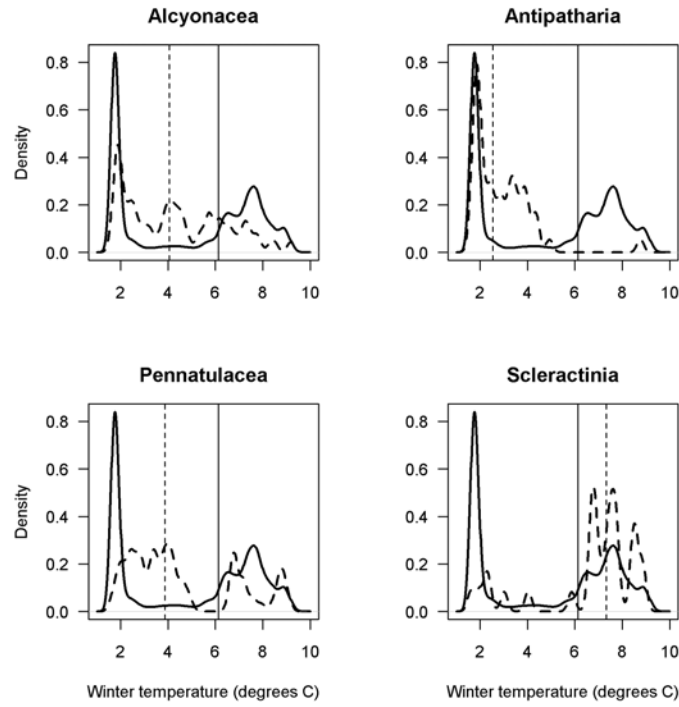   indicate median values.

Figure A2.11 Relative frequency density plot of **winter temperature ($^\circ$ C)** for the entire study area (solid lines) and for each order (dotted lines). Vertical lines indicate median values.