



Seasonal variation in marine bird distribution in the northeast Pacific Ocean

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ABSTRACT: Human activities have profound influences on marine ecosystems. Marine birds are particularly sensitive to these impacts and, given their ease of observation and diverse life histories, often represent good indicators of ecosystem health. Conserving marine birds and their ecosystems requires robust predictions of species distribution to help mitigate human disturbance in areas where large aggregations of diverse species occur. We modelled variation in marine bird species diversity (Shannon-Wiener Index) and taxonomic family level probability of occurrence to map the intensity and extent of highly diverse 'hotspots' in Canada's Pacific Exclusive Economic Zone. To do so, we paired 20 yr of survey data from the North Pacific Pelagic Seabird Database (1997–2017) and remote sensing data describing marine conditions and local geography (sea surface temperature, chlorophyll *a*, bathymetry, distance to shore, and benthic substrate type). These data were used to illustrate how seasonality within years and the El Niño–Southern Oscillation (ENSO) across years influenced spatial patterns in diversity. Hotspots were most persistent in Hecate Strait, off the west coast of Vancouver Island, and surrounding the Scott Islands in most seasons. Changes in hotspot locations and intensity were observed across seasons and within season under varying ENSO conditions. Our results provide a template for mapping marine species distribution for the purpose of identifying hotspots of diversity, and thereby facilitate planning to minimize harmful impacts in highly diverse and dynamic systems.

KEY WORDS: Marine bird occurrence · Species diversity · Ocean climate · Random forest · North Pacific Ocean · El Niño–Southern Oscillation

1. INTRODUCTION

Anthropogenic activities that degrade marine ecosystems are increasing globally. These effects are evident on Canada's Pacific coast (Clarke Murray et al. 2015) and are likely to interact with temporal and spatial variations in sea surface temperature (SST), wind, and air pressure to influence ecosystem productivity (Whitney 2015). Such factors have been linked to mass mortality in marine birds (Gibble et al. 2018, Jones et al. 2018), whales (Savage 2017), and pinnipeds (Menza et al. 2016). Given that SST anomalies

are predicted to increase in intensity, frequency, and duration via atmospheric forcing of the North Pacific Gyre Oscillation, Pacific Decadal Oscillation (PDO), and El Niño Southern Oscillation (ENSO; Di Lorenzo et al. 2008, Cai et al. 2014) as a result of climate change, identifying areas and processes likely to support highly diverse aggregations of marine species ('diversity hotspots') could help mitigate such threats.

Marine birds are important indicators of ecosystem state and change (e.g. Norris et al. 2007, Gutowsky et al. 2009) because their occurrence and abundance

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reflect productivity, trophic complexity, and energy transfer from low to high trophic levels across a range of spatial scales (Hunt & Schneider 1987, Parsons et al. 2008, Nur et al. 2011). In addition, areas that support multiple species of birds can further indicate habitats that provide multiple niches. Furthermore, 47% of all monitored marine bird species have declining population trends and 42% are considered 'Threatened' or 'Near Threatened' (BirdLife International 2018, Dias et al. 2019). Increasing knowledge of marine bird hotspot locations and how these vary across seasons could aid conservation planning and marine emergency preparedness for both marine birds as well as the ecosystems upon which they rely.

Biodiversity is a useful metric for protected area design, as the conservation of highly diverse areas can prevent declines of threatened species, maintain ecosystem services, and reduce habitat loss (Asaad et al. 2017). Diversity hotspots can be expected in areas supporting multiple niches, which rely on adequate primary production to support a complex food web (e.g. Chown & Gaston 1999). On an ocean-wide scale, high productivity is expected over the continental shelf where seasonal upwellings can occur (inside the 200 m isobath), intermediate productivity over the continental slope (represented by the 1000 m isobath), and low productivity in deep offshore waters (represented by the 3000 m isobath; Yen et al. 2005, Nur et al. 2011). At finer scales, highly productive areas are associated with nutrient-rich waters linked to vertical mixing at shallow bathymetric features, oceanic eddies, oceanic fronts, and proximity to river discharge (Crawford et al. 2005, Whitney et al. 2005, Jackson et al. 2015). Fine-scale water mixing can facilitate phytoplankton growth at high rates relative to other areas and lead to aggregations of secondary producers (i.e. zooplankton; Wiebe et al. 1976) and the predators (including marine birds) that rely on them.

The availability of prey for marine birds and other marine animals is influenced both directly and indirectly by zooplankton, which transfer energy from phytoplankton up to higher trophic levels. These relationships can be complex because the species composition and abundance of communities at higher trophic levels are also influenced by zooplankton biomass and community composition, factors that are both subject to interannual-to-decadal climate forcing through variations in the PDO and ENSO (Tanasichuk 2002, Mackas et al. 2007, Hipfner 2008, Bi et al. 2011). For example, shifts in communities dominated by large, lipid-rich zooplankton taxa to those dominated by smaller taxa are widely reported in response to SST anomalies in marine ecosystems (Chiba &

Saino 2003, Keister & Peterson 2003, Mackas et al. 2007, Bi et al. 2011). Such phenomena have been related to mass mortality of the piscivorous tufted puffin *Fratercula cirrhata* (Jones et al. 2019), zooplanktivorous Cassin's auklet *Ptychoramphus aleuticus* (Jones et al. 2018), and seasonally planktivorous short-tailed shearwater *Ardenna tenuirostris* (Kaler & Kuletz 2022). As climate anomalies are expected to increase in the coming years (Di Lorenzo & Mantua 2016), predicting areas that are most likely to support nutrient-rich zooplankton communities could contribute to conserving marine birds and hotspots of diversity.

Differences in breeding and migration timing along with variations in morphology, physiology, and foraging strategy may also influence how marine habitats are exploited by individual family groups or species (Table S1 in the Supplement at www.int-res.com/articles/suppl/m735p141_supp.pdf). During the Northern Hemisphere's spring and summer months, breeding marine birds are central place foragers, constrained spatially by their nest site but move more freely during nonbreeding months (Wakefield et al. 2009). Furthermore, many species undergo extensive seasonal migrations and as such are only present in the study area for part of the year (e.g. loons and sea ducks nest inland in the spring and summer, while shearwaters and albatrosses nest outside the study area in the Northern Hemisphere's winter and early spring). Within the same area, habitats might be partitioned by depth between surface foragers (e.g. albatrosses) and pursuit divers (e.g. cormorants), or by diet, such as between zooplanktivores (e.g. Cassin's auklet) and piscivores (e.g. common loon *Gavia immer*; Kaufman 2001).

We used environmental remote sensing techniques and a consolidated data set of marine bird observations from around the northeast Pacific (Drew & Piatt 2015, Fox et al. 2017) to examine temporal and spatial variation in marine bird diversity within Canada's Pacific exclusive economic zone (EEZ). Prior applications of a significant portion of these data have focused on marine bird distribution and density (e.g. Kenyon et al. 2009, Fox et al. 2017). In contrast, our main goal here was to estimate the seasonal distribution of marine bird family groups and species diversity over 2 decades by combining all available data for the region and incorporating permanent (e.g. bathymetry) and transient (e.g. SST) satellite data collected at broad spatial scales. We also aimed to predict how variation in ocean climate (e.g. Southern Oscillation Index, SOI), which is widely known to affect marine communities but challenging to estimate in short-term studies (Nur et al. 2011, Menza et al. 2016),

might affect the location and intensity of marine bird hotspots. By doing so, we aimed to identify high-quality habitat for marine birds across seasons and ENSO conditions. Our specific objectives were (1) to predict temporal and spatial variation in the diversity of marine birds and locate hotspots of species diversity by season and (2) in response to ENSO conditions, and (3) to describe how different marine birds grouped by family influenced seasonal patterns of marine bird diversity overall.

2. MATERIALS AND METHODS

2.1. Study area

Canada's Pacific EEZ (Fig. 1) contains a diverse array of habitats, sustains multiple fisheries, and currently hosts 51 designated Important Bird Areas (Clarke Murray et al. 2015, <https://www.ibacanada.com/mapviewer.jsp>). However, Ban & Alder (2008)

estimated that 27–29% of the Canadian EEZ is already subject to anthropogenic stress, particularly over the continental shelf and slope, due in part to fishing pressure and shipping traffic that could increase in the future (Nuka Research and Planning Group 2015). Within the EEZ, there is a bifurcation of the North Pacific Current and it is more strongly influenced by the Alaska Current in the winter and the California Current in the summer (Thomson 1981, Jackson et al. 2015). These seasonal shifts are associated with southerly, downwelling-favorable winds between October and March and northerly, upwelling-favorable winds between April and September (Jackson et al. 2015) as well as changes in wind speed and direction, which in turn can influence the flight trajectories of albatrosses, shearwaters, and petrels (Adams & Flora 2010).

The coast of British Columbia (BC) comprises a complex network of islands, inlets, and channels, which contribute to vertical mixing. The highest levels of productivity and the associated increase in marine

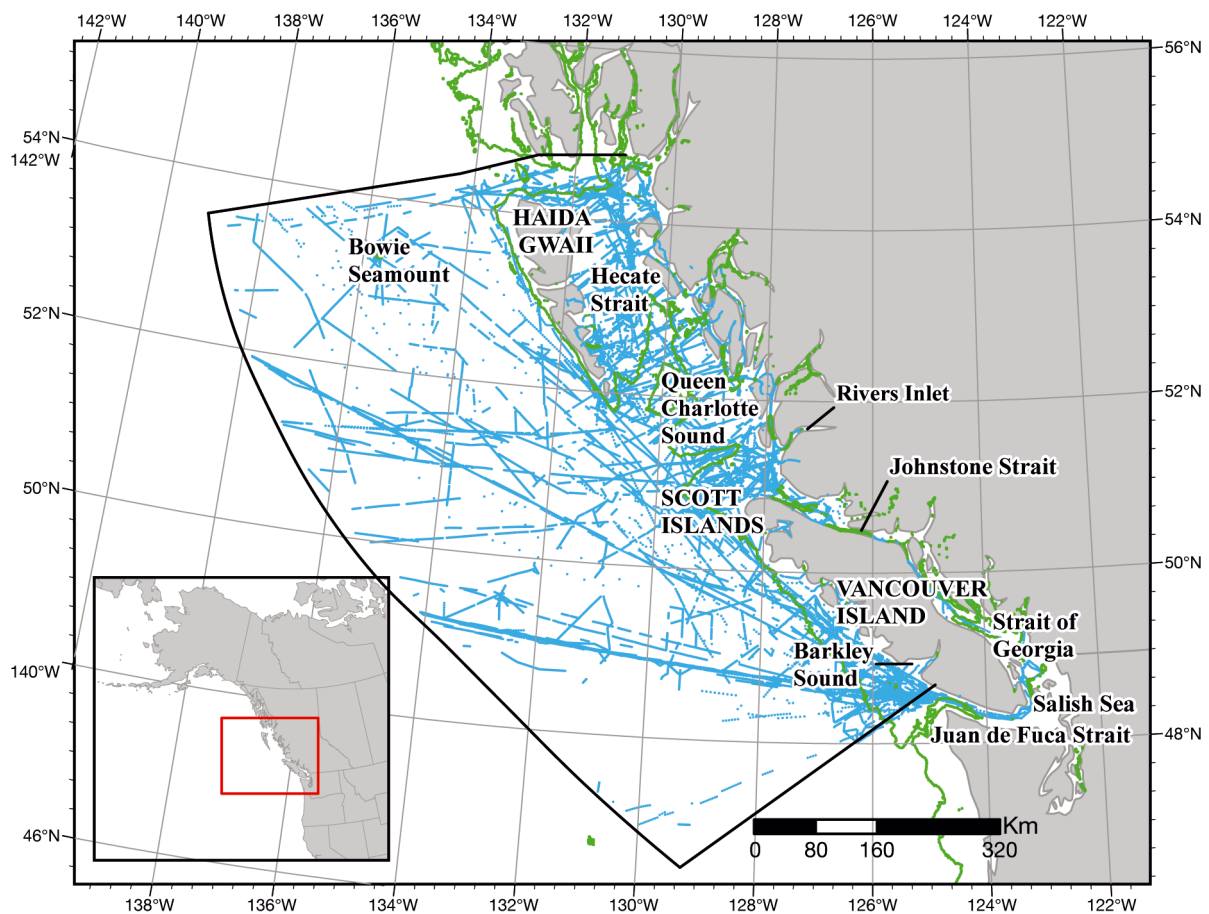


Fig. 1. Study area in Canada's Pacific Exclusive Economic Zone off the coast of British Columbia. Green line: the 200 m isobath; blue points: transect segments compiled from the North Pacific Pelagic Seabird Database for 1997–2017

bird abundance occur on the continental shelf and shelf break (Whitney et al. 2005). However, increased levels of productivity along the continental slope and deep offshore waters can be created through wind-driven mixing and the formation of mesoscale eddies transporting productive waters away from coastal areas (Crawford et al. 2005, Whitney et al. 2005).

2.2. Marine bird data

Marine bird occurrence and abundance data were acquired from the North Pacific Pelagic Seabird Database (NPPSD) version 3.0, a compilation of strip transect bird observations covering 270 259 km² (Drew & Piatt 2015, Fox et al. 2017). Data were acquired from opportunistic and directed ship transect surveys and standardized into discrete segments in the form of vector points. Surveys that were gathering data for only targeted bird species were not included in the analysis. Each segment included the names of species present, the number of individuals per species, and the location, date, and time each segment was surveyed. Coordinates were provided for either the centroid or point of origin for each survey segment.

The data were restricted to September 1997–September 2017 due to the temporal availability of the predictor variables and constrained to the boundaries of the Canadian EEZ. This resulted in 37 528 unique transect segments, with 60 850 unique bird observations and 691 survey days used in the final analysis. These counts included birds identified to species, genus, or family. Individual species had low rates of detection and absences accounted for 42% of the data set. Only boat surveys were included in the analysis. The sample areas ranged from 0.011–19.6 km². The data were truncated to include only segments with sample areas greater than 0.05 km² but smaller than 9 km² to remove potential outliers, as the goal of this study was to make predictions to 9 km² pixels. The average segment length was 1.57 km (median: 1.51 km) and the average segment width was 390 m (median: 400 m). The number of days transect surveys were conducted ranged from 5 in 2014 to 83 in 2007, with a median of 35 d surveyed yr⁻¹. No surveys were conducted in the study area in 2011 or 2013. Transects were concentrated in Hecate Strait, Queen Charlotte Sound, and off the west coast of Vancouver Island. Data were limited for the Salish Sea, several major inlets, and the southwest corner of the study area. The spatial boundaries of the data within the EEZ were -138.7 to -123.0 in longitude and 47.0 to 54.7 in latitude.

Bird observations were pooled regardless of recorded behaviour (water, flying, feeding, unknown) for 2 reasons: (1) to preserve sample size, as 34% of observations were of birds in flight, and (2) because all individuals were assumed to be using the site for foraging, resting, and/or travelling. With the latter reasoning, bird groups such as alcids, loons, and grebes, which forage from the water surface, could be assessed with known aerial foragers such as gulls, storm-petrels and albatrosses (Nur et al. 2011, Fox et al. 2017). Nevertheless, the inclusion of flying birds may have resulted in an overestimate of bird density and abundance from an increased encounter rate of birds and double-counting individuals (Spear et al. 1992) and potentially falsely inflated an individual's association with a specific geographic area. All bird abundance estimates should be interpreted as relative values.

To examine how marine bird distributions vary across the region over the annual cycle, bird observations were grouped into 5 seasons: early spring (March–April), late spring (May–June), summer (July–August), fall (September–October), and winter (November–February). Subsequent models were generated within those time constraints. These seasonal groupings were chosen in an attempt to capture important behavioural and biophysical phenomena, such as the arrival of locally northern breeding birds to colonies in early spring (Hipfner & Greenwood 2008, Sealy 2015), egg-laying in late spring (Hipfner & Greenwood 2008, 2009, Sealy 2015), or declines in primary productivity in the summer followed by phytoplankton blooms across the study area in the fall (Jackson et al. 2015). In addition, these seasonal definitions encompass the arrival of most shearwaters to waters off the BC coast on their migration to the Gulf of Alaska from late spring and their departure in fall as well as the seasonal migrations of jaegers and gulls breeding outside of the study area (e.g. Kenyon et al. 2009).

2.3. Predictor variables

Five environmental variables were selected to predict marine bird distribution based on predictors that proved generally important for model performance in previous studies (Huettmann & Diamond 2006, Yen et al. 2006, Louzao et al. 2009, Nur et al. 2011, Goyert et al. 2016, Menza et al. 2016, Fox et al. 2017). To measure ocean depth (m), a 30 arc-second (~1 × 1 km) bathymetry raster based on a satellite-gravity model calibrated by ship soundings was obtained from MARSPEC: ocean climate layers for marine spatial

ecology (Sbrocco & Barber 2013). A 0.0083° distance to shore raster was generated through a Euclidean distance calculation on a shoreline shapefile obtained from Freshwater Atlas Coastlines (British Columbia Data Catalogue 2008). A benthic features raster containing 16 eco-units that combined 4 depth, 4 terrain, and 4 substrate classes was obtained from BC Marine Conservation Analysis (British Columbia Marine Conservation Analysis Project Team 2011) and reclassified to the 4 substrate categories regardless of depth and terrain characteristics. These substrate classes were hard surface, mud, sand, and undefined (generally in deeper waters off the continental slope). To estimate photosynthesizing phytoplankton, monthly 4×4 km chlorophyll *a* (chl *a*; mg m^{-3}) raster files were acquired from the European Space Agency's Ocean Colour Climate Change Initiative (ESA OCCI; Sathyendranath et al. 2018). Seasonal chl *a* raster files were created by averaging the appropriate monthly chl *a* values. Daily 3×3 km SST ($^\circ\text{C}$) raster files were acquired from the European Space Agency's Sea Surface Temperature Climate Change Initiative (Good et al. 2019). Seasonal SST raster files were created by averaging daily SST raster files within the appropriate months. All predictor variables were resampled to 3×3 km to spatially align with the SST raster files. This resolution was chosen because it was sufficient to depict the mouths of some of the larger inlets (e.g. River's Inlet) and smaller straits (e.g. Johnstone Strait) that were missing in the chl *a* data set but coarse enough to make generalized estimates for those inlets. On average, 4% of the chl *a* pixels had no values and thus needed to be estimated using interpolation techniques. Two interpolation methods, kriging (Oliver & Webster 1990) and inverse distance weighted (IDW) interpolation (Watson & Philip 1985), were visually compared for their estimation of missing chl *a* values in areas with known chl *a* conditions (e.g. Johnstone Strait, which generally supports relatively low primary productivity due to intense vertical mixing; Thomson 1981). Kriging, with maximum 10 neighbours, resulted in fewer contradictory patterns of chl *a* distribution in well-known areas compared to IDW interpolation and was chosen as the most appropriate for interpolation in this region. Winter chl *a* values were especially patchy, particularly in the northernmost part of the study area and waters past the continental shelf. Due to the nature of visible wavelength remote sensing, this can be expected off the coast during prolonged periods of cloud cover and limited daylight hours in the winter. As a result, most of the season's pixel values came from the month of February. These 5 predictor vari-

ables as well as a lagged SST variable were assessed for collinearity using Pearson's correlation coefficient. The lagged SST variable was dropped because it was highly correlated ($>85\%$) with the current season's SST values in some seasons. While distance to shore and depth were also highly correlated, they represent different aspects of the marine environment (e.g. distance to freshwater input and colonies or the location of seamounts and fjords) and therefore could describe different habitats. This collinearity can be somewhat mitigated by the modelling approach described below. In addition to these 5 environmental variables, the sample area associated with each bird detection was also included as a predictor variable in the models to account for an expected increase in observations as the area covered by the surveys increased (Johnston et al. 2021).

All data were resampled to 9 km^2 pixels and spatially joined to the bird survey (NPPSD) data. To account for multiple surveys occurring within the same pixel, the sum of all sample areas provided for each transect segment that traversed through a single 9 km^2 pixel on the same survey day was calculated. Resampling the bird data to larger transect segments also serves to reduce the effects of spatial autocorrelation (Yen et al. 2004); however, this is not a major concern with this type of modelling (Diniz-Filho et al. 2003). To standardize model predictions, a sample area raster layer was created where all pixels were set to sample area = 9 km^2 (i.e. the spatial resolution of the output maps). This standardization procedure was based on Johnston et al.'s (2021) guidelines for modelling encounter rate using citizen science data, which is prone to variation in sampling effort. By accounting for the inconsistent sampling effort in the model-building phase and choosing a constant area at the prediction phase, the results should be interpreted as the expected value in each 9 km^2 pixel of the study area if the entire pixel was sampled. The remaining predictor raster values were extracted to the overlaying bird observations, matching the season in which an observation was recorded to the appropriate seasons in the dynamic variables of SST and chl *a*. In addition, the values of chl *a* from the season previous to the one being assessed were also extracted to account for any lag effects from the spatial and temporal distribution of phytoplankton. Models were trained on the extracted environmental variable values and then predicted across the entire study area using the full extent of the original environmental variables. All data processing was done in ArcGIS v.10.8.1 (ESRI 2020) and R v.4.0.2 (R Core Team 2020).

2.4. Data analysis

Predictive models of species diversity and taxonomic family distributions were generated using random forest machine-learning methods (Breiman 2001) with the 'ranger' package in R (Wright & Ziegler 2017). Random forests are an ensemble learning method that can be used for regression and classification tasks (Breiman 2001). They construct multiple independent decision trees by bagging and bootstrapping samples and using a random subset of the top m predictors at each split in the tree to improve accuracy and reduce correlation among predictors (Breiman 2001, Segal & Xiao 2011, Kuhn & Johnson 2013). Random forest models are a computationally effective form of machine learning that demonstrate accuracy that is higher than or comparable to those of other species-predictive approaches (Oppel et al. 2012, Fox et al. 2017, Mi et al. 2017) and can operate with many types of predictors without the need to pre-process them or identify their relationships to the response variable (Kuhn & Johnson 2013). By randomizing the order in which predictor variables are incorporated into decision trees, random forest models are more robust to correlations between predictor variables than other models (Breiman 2001, Kuhn & Johnson 2013), making them an appropriate modelling choice for the inherently correlated ocean–climate predictors used in this study. Models were trained on 80% of the data and tested on the remaining 20% to assess accuracy before being predicted across the entire study area.

2.5. Species diversity model

To predict the spatial distribution of potential hotspots of marine bird diversity, a diversity index was used as the response variable in a regression random forest model using all segments identified to species. Species diversity measures the relationship between the number of species and the number of individuals within a species and is an important metric to consider when choosing potential sites for conservation measures, as it is a component of overall biodiversity (Hill 1973, Morris et al. 2014, Magurran 2021). The Shannon-Wiener Diversity Index (henceforth SDI) is the most commonly used diversity measure to compare species diversity between habitats (Clarke & Warwick 2001) and was chosen here because it is a metric that is equally sensitive to rare and abundant species and, as a compound index, has been shown to discriminate better between study sites than more

simple diversity measures such as species richness (Morris et al. 2014). The formula is as follows:

$$H' = - \sum_{i=1}^S p_i \cdot \ln(p_i) \quad (1)$$

where p_i is the proportion of the total count of the i^{th} species, and values of H' depend on both species abundance and evenness. Higher values of H' represent 9 km² pixels with higher species diversity. This formula, however, does not consider pixels where no birds were seen, as the log of 0 does not exist, and thus complete absences were inherently dropped from the model. The inability to account for total absences is an important shortcoming in many other popular diversity indices as well (e.g. Simpson's Diversity Index) but is problematic for our purpose because it results in the loss of all data from pixels in which birds were absent entirely, thus impeding the model's ability to minimize prediction error and produce reliable maps (Hazen et al. 2021). Therefore, the response variable was transformed by adding a constant of 0.1 to the predicted SDI value of each pixel. The pixels with no bird detections were forced to zero and added back into the model to allow for the differentiation between pixels where SDI = 0 because only one species was seen and pixels where SDI was forced to 0 because no species were seen. While this modification introduced some uncertainty about the influence of pixels with a total absence of birds versus a single species detected, the modified SDI values for all observations with at least a single species remained correlated with their original values (i.e. predicted SDI if true zeros are excluded; Pearson's $r = 1$).

Predicted SDI hotspots were identified as pixels with relatively high values of SDI in a given season (typically >2.4; orange to red where mapped), with moderate (0.8–2.4; light blue to orange pixels) and lower values (0.0–0.8; dark blue to light blue pixels) also noted. The performance of seasonal models was evaluated using R^2 , based on 'out-of-bag' data (excluded from the training set) to estimate variance accounted for by the model and the root mean square error. The absolute importance of each predictor variable to the models was assessed using the 'impurity measure' (variance of the responses) in 'ranger' (Wright & Ziegler 2017). The impurity measure is a tool used to decide the optimal split from a root node in the process of building decision trees within a random forest model (Nembrini et al. 2018). Relative importance was calculated by dividing the value of each predictor by the sum of all importance values for the model in question.

To make predictions for seasonal species diversity under different ENSO conditions, the SST and chl *a* raster data were grouped by seasons that overlapped with very high, very low, and moderate values in the SOI. The SOI measures the atmospheric changes associated with phase shifts in the ENSO and, when smoothed over time, is correlated with changes in meteorological and oceanic variables such as rainfall, SST, and wind in the eastern tropical Pacific Ocean and beyond (Chen 1982). SOI data from the National Centre for Environmental Information (NOAA 2020) included monthly values that were grouped and then averaged within the seasons defined here. We chose SOI over the Multivariate ENSO (MEI) or Oceanic Niño Index (ONI) because MEI estimates conditions in overlapping bimonthly periods, and ONI does so using overlapping trimonthly periods. In contrast, the SOI provided monthly estimates of ocean climate that could be precisely matched to the seasonal models we developed. Annual values of SOI were classed as a 'strong El Niño', 'neutral', or 'strong La Niña' season, where SOI was less than -1 , between -0.5 and $+0.5$, and greater than $+1$, respectively. By modelling hotspots of diversity in each case, we hoped to contrast the effects of the high SST and weak upwelling and mixing that characterize El Niño conditions and can reduce primary productivity (Jacox et al. 2015, Whitney 2015), with the cooler and more intense periods of upwelling and mixing that co-occur with La Niña conditions and can increase primary productivity. Our seasonal models of species diversity were used to predict SDI for strong La Niña, neutral, and strong El Niño conditions using raster layers that contained the newly grouped SST raster and the remaining predictor variables (in their original formats; see Section 3.2), with the exception of 'late spring', which only included SOI neutral conditions.

2.6. Estimating occurrence by taxonomic family

To estimate the spatial distribution of marine birds grouped by taxonomic family and better inform which bird groups might be contributing to areas of higher diversity predicted by our SDI approach, we also estimated and mapped probability of occurrence for albatrosses (Diomedidae), storm-petrels (Hydrobatidae), shearwaters (Procellariidae), gulls (Lariidae), alcids (Alcidae), loons (Gaviidae), and ducks (Anatidae) using a random forest classification model. Although foraging tactics and habitats vary in some of the families we studied, it was not

possible to estimate a probability of occurrence or density by species, given that 42% of the data recorded absences, 7% identified birds to family, and relatively few species were observed on >1000 transect segments. We therefore pooled observations of species by family to estimate their influence on our seasonal models of diversity. The 7 marine bird families were not equally represented across seasons, and a cut-off of at least 30 of the 9 km^2 pixels with presence records was used to create maps for a family in each season. Due to the low detection rates of most species, a significant class imbalance between bird presences and absences needed to be addressed to accurately predict bird occurrences. A substantially higher frequency of absence observations versus presence observations can overtrain the model, resulting in high specificity at the cost of low sensitivity (Kuhn & Johnson 2013). To remedy this issue, a down-sampling approach was used, which involves taking a random subset of the absence data equal to the number of presence data within the random forest building phase, thus resampling the absence data with the creation of each tree in the random forest. This approach is computationally effective and has the ability to retain important background information in larger study areas (Valavi et al. 2021). Furthermore, it has been demonstrated to improve model accuracy to a similar extent to those achieved by other popular class imbalance solutions in species distribution models (Valavi et al. 2021). We used area under the receiver operator curve (AUC) and Brier scores (overall out-of-bag prediction error) to evaluate model performance. The relative and absolute importance of each predictor variable to the models was assessed using the impurity measure (the Gini index) in 'ranger'.

3. RESULTS

3.1. Seasonal variation in marine bird diversity

Modelled results of species diversity of marine birds varied strongly among seasons but was predicted as moderate to high ($\text{SDI} = 0.8\text{--}2.4$) across the continental shelf, shelf break, and continental slope in all seasons except for in winter, when SDI values were low to moderate ($0\text{--}0.8$) away from the coastlines (Fig. 2). In contrast, high SDI values (>2.4) were observed in a few spatially restricted areas in multiple seasons; most notably in northern Hecate Strait, west of Vancouver Island, west of Haida Gwaii, and near the Scott Islands. The percent of

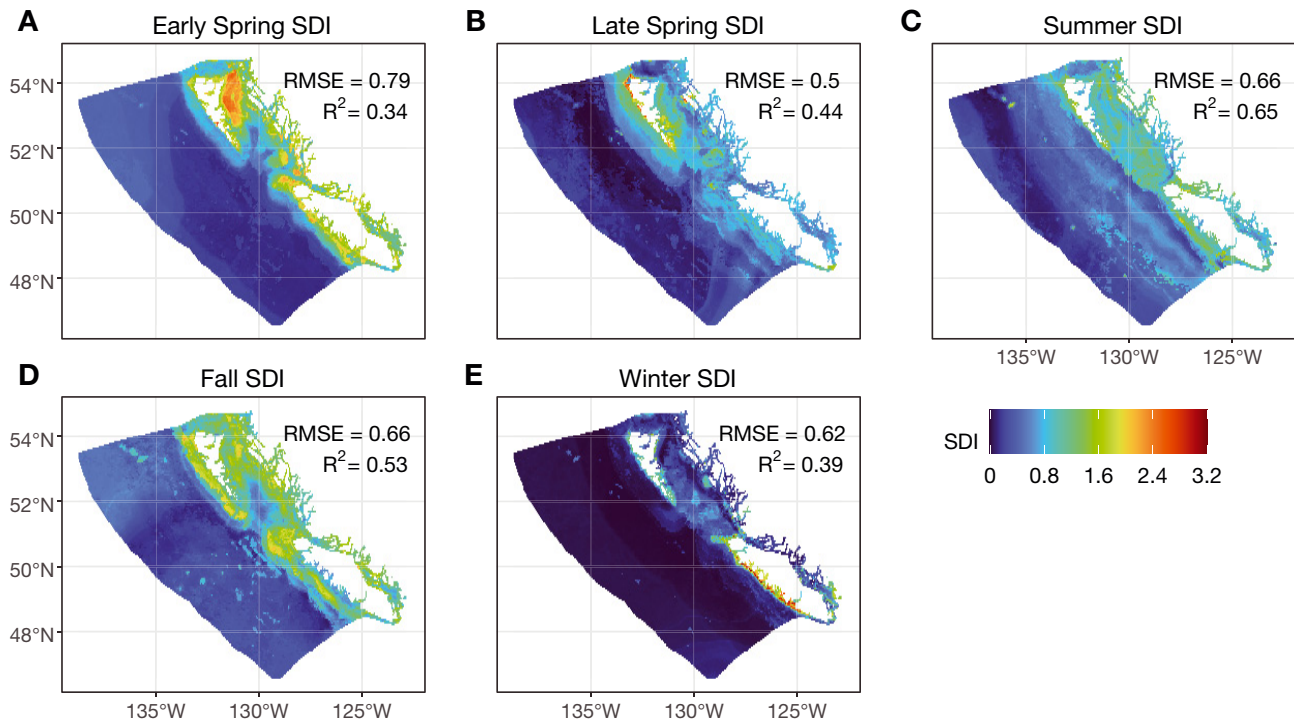


Fig. 2. Predicted diversity (Shannon-Wiener Diversity Index, SDI) of marine birds in (A) early spring (March and April), (B) late spring (May and June), (C) summer (July and August), (D) fall (September and October), and (E) winter (November, December, January, and February), in response to variation in chlorophyll *a*, sea surface temperature, bathymetry, distance to shore, and benthic substrate type. Hotspots of diversity were most prominent near the Scott Islands and off the west coast of Vancouver Island in most seasons. Seasonal models were created with regression random forests averaged over 1997–2017 for Canada's Exclusive Economic Zone off the British Columbia coast. Marine bird information was obtained from strip transect surveys compiled in the North Pacific Pelagic Seabird Database. RMSE: root mean square error

variation explained by the SDI model based on seasonal averages was 34% for early spring, 44% for late spring, 65% for summer, 53% for fall, and 39% for winter. Early spring showed distinct hotspots in northern and central Hecate Strait, the Scott Islands, western Vancouver Island, and in coastal waters of Queen Charlotte Sound. Late spring showed the highest SDI levels off the west coast of Haida Gwaii. Summer had the lowest overall SDI values, but showed slight peaks at Bowie Seamount, Queen Charlotte Strait, northern Hecate Strait, and off the west coast of Vancouver Island. Fall showed the highest SDI values in coastal waters and near the shelf break west of Haida Gwaii and Vancouver Island, in Hecate Strait, and surrounding the Scott Islands. Winter exhibited a strong predicted SDI hotspot on the west coast of Vancouver Island. Predictor importance varied by season, but generally depth, distance to shore, and SST were ranked as the most important variables (Fig. 3). Although correlated, distance to shore and depth differed in their importance across seasons, with depth generally ranking as more important except in late spring.

3.2. SDI in response to ENSO

The intensity and extent of SDI hotspots varied when predicting how SDI may respond to variation in SST and chl *a* linked to ENSO conditions. Strong La Niña and neutral conditions in early spring were associated with more intense (higher SDI values) and extensive hotspots in Hecate Strait, near the Scott Islands, and off the west coast of Vancouver Island than observed under strong El Niño conditions (Fig. 4A). As summer SST increased from strong La Niña to neutral and strong El Niño conditions, SDI hotspots progressively decreased in intensity and extent in Hecate Strait and at the Scott Islands (Fig. 4B). However, the intensity of an offshore hotspot located above Bowie Seamount increased with El Niño conditions. Hotspots became smaller and less intense off the west coasts of Vancouver Island and Haida Gwaii and surrounding the Scott Islands under strong fall El Niño conditions (Fig. 4C). In contrast, hotspots in coastal Queen Charlotte Sound increased in intensity under the same conditions. Hotspots became progressively more intense in the coastal

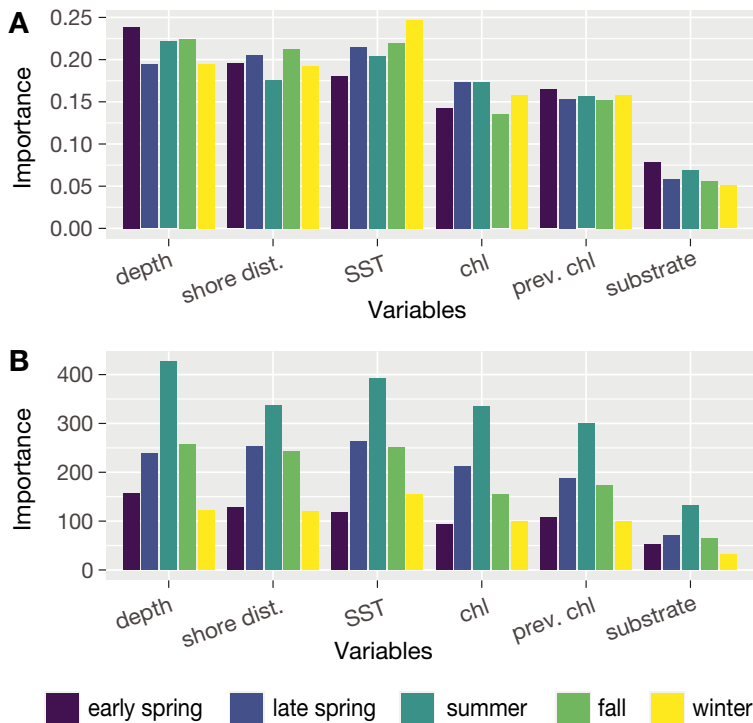


Fig. 3. (A) Relative and (B) absolute variable importance in predictive models of marine bird diversity (Shannon-Wiener Diversity Index) in 5 focal periods in the Northeast Pacific. Importance was assessed using the impurity measure (R package ‘ranger’; Wright & Ziegler 2017). Higher values indicate greater importance. shore dist.: distance to shore; prev. chl: chl a in the prior season; SST: sea surface temperature

waters of Vancouver Island under strong La Niña, neutral, and strong El Niño winter conditions, respectively (Fig. 4D).

3.3. Family level probability of occurrence

Probability of occurrence varied widely among families and seasons. Model AUC scores ranged from 0.74–0.98, indicating moderate to excellent performance, respectively. The median AUC was 0.87, with the best performance seen for loons and storm-petrels in late spring and shearwaters in winter, and worst for alcids and gulls in early spring and shearwaters in fall. Brier scores varied from 0.09 (high accuracy) to 0.20 (moderate accuracy). Notably, the Laridae were strongly associated with coastal and nearshore waters and were broadly distributed across the study area for most seasons (Fig. S1). The Alcidae had strong associations with coastal and nearshore waters across all seasons, with waters surrounding the Scott Islands consistently showing high probabilities of occurrence (Fig. S2). The Hydrobatidae were most likely to occur

over deep offshore waters in all seasons (Fig. S3). The Diomedidae and Procellariidae had high probabilities of occurrence near the shelf break off the coast of Vancouver Island and Haida Gwaii and within Queen Charlotte Sound for most seasons (Figs. S4 & S5). The Anatidae had the highest probability of occurrence in coastal waters, particularly near Vancouver Island and mainland BC (Fig. S6). The Gaviidae occurred near northern coastal waters in early spring but increased in Queen Charlotte Sound in late spring (Fig. S7). Predictor importance varied by family and by season, but generally depth, distance to shore, and SST were ranked as the most important variables (Fig. S8).

4. DISCUSSION

4.1. Predicted SDI hotspots and family contributions

Moderate to high levels of predicted SDI were consistently present on the continental shelf and slope across seasons, supporting earlier suggestions of high productivity in these oceanic areas compared to waters beyond the continental slope (e.g. Yen et al. 2005). Predicted marine bird distributions varied strongly between seasons. Early spring and winter showed the largest areal extent and most intense SDI hotspots, respectively, attributed to increases in the occurrence of several species of sea ducks, grebes, loons, jaegers, gulls, and alcids, many of which migrate outside of the study area to breed. However, model fit was highest in summer, which may indicate that marine birds responded more strongly to habitat features in summer than during migration in early spring or the winter non-breeding period.

Only a few predicted SDI hotspots persisted across multiple seasons. Off the west coast of Vancouver Island, including coastal waters, the continental shelf break and slope displayed high predicted SDI values in early spring, summer, fall, and winter. Similarly, off the west coast of Haida Gwaii, high values were predicted for late spring and fall. Waters off the west coast of Vancouver Island experience intermittent wind-driven upwelling in the warmer months (Thomson 1981) and high surface chl a concentrations from April to the beginning of November (Jackson et al.

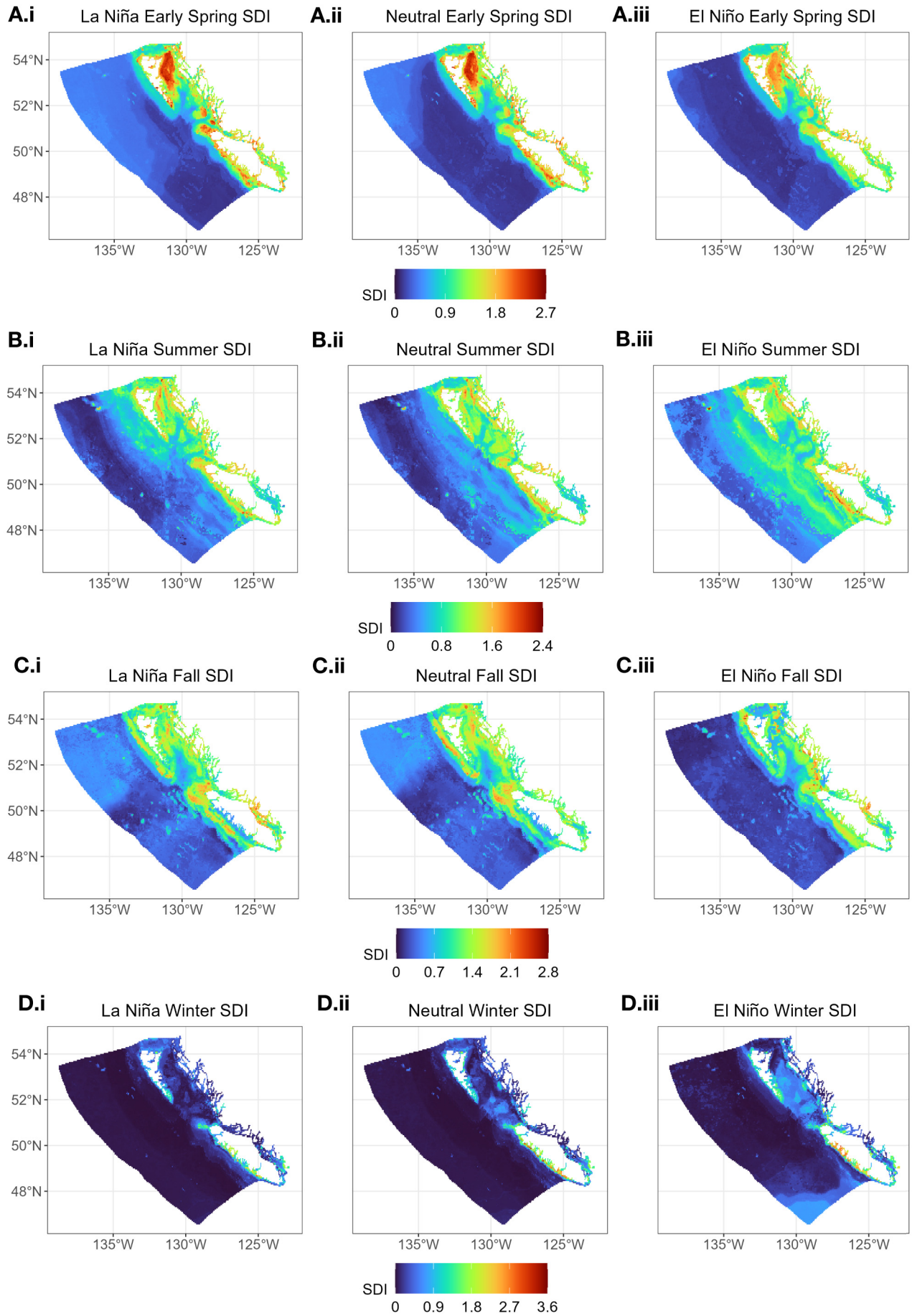


Fig. 4. Predicted spatial distribution of marine bird diversity (Shannon-Wiener Diversity Index, SDI) under changing sea surface temperature and chlorophyll *a* conditions during (i) strong La Niña, (ii) neutral, and (iii) strong El Niño phases of the Southern Oscillation Index in (A) early spring (March and April), (B) summer (July and August), (C) fall (September and August), and (D) winter (November, December, January, and February) in response to spatial variation in chlorophyll *a*, bathymetry, distance to shore, benthic substrate type, and sea surface temperature. Predictive models were created with regression random forests averaged over 1997–2017 for Canada's Exclusive Economic Zone off the coast of British Columbia. Marine bird information was obtained from strip transect surveys compiled in the North Pacific Pelagic Seabird Database

2015). In addition, the shelf break and continental slope off southwestern Vancouver Island is a common area for oceanic front and cyclonic mesoscale eddy formations, which can prolong and/or increase productivity in deeper waters (Hay 1992). The west coast of Haida Gwaii hosts multiple breeding colonies for several species, including Ancient murrelets *Synthliboramphus antiquus*, Cassin's auklets and rhinoceros auklets *Cerorhinca monocerata*, Leach's storm-petrels *Hydrobates leucorhous* and fork-tailed storm-petrels *H. furcatus*, and tufted puffins (Rodway et al. 2016). Marine bird diversity was predicted to be moderate to high along the continental shelf break and slope. Both the west coasts of Vancouver Island and Haida Gwaii in fall show moderate to high predicted diversity on the continental shelf break and slope, which may reflect the southwards migration route for multiple species. Indeed, the west coast of Vancouver Island is a known fall migration pathway for several species, including Sabine's gulls *Xema sabini*, California gulls *Larus californicus*, and Cassin's auklets (Vermeer et al. 1987). Furthermore, the fall family level probability of occurrence maps also showed high probabilities of occurrence for albatross and alcids off the west coast of Haida Gwaii and albatross and gull occurrence off the west coast of Vancouver Island.

The waters surrounding the Scott Islands had high predicted SDI values for both early spring and fall. This area experiences significant tidal mixing, with phytoplankton blooms occurring in late spring, episodically in the summer, and occasionally in the fall (Thomson 1981, Fort et al. 2006, Jackson et al. 2015). Moreover, it serves as an important source of *Neocalanus* copepods, euphausiid species, sand lance *Ammodytes personatus*, rockfish, Pacific cod *Gadus macrocephalus*, and Pacific herring *Clupea pallasii* during at least one of the 5 study seasons (Clarke & Jamieson 2006, Fort et al. 2006). The Scott Islands also host important breeding colonies for several species of marine birds, including pelagic cormorants *Urile pelagicus*, glaucous-winged gulls *Larus glaucescens*, common murre, tufted puffins, Cassin's and rhinoceros auklets, Leach's storm-petrels and fork-tailed storm-petrels (Rodway et al. 2016).

Northern Hecate Strait was predicted to have high SDI in early spring and fall, particularly northeast of Haida Gwaii, where a large shallow plain serves as an important rearing area for Pacific cod and invertebrates and where sea ducks are known to stage for migration (Clarke & Jamieson 2006). Family level occurrence maps for this region predicted high probabilities of occurrence for gulls and alcids in fall. Given that these families contain the highest number of individual species in the study area, they could be driving the high predicted species diversity in northern Hecate Strait during fall migration. By comparison, in early spring, family occurrences were predicted to be relatively low for ducks, loons, and alcids (50–75%) and other families (0–50%), suggesting migrants were more common in late than early spring. These differences may reflect sensitivity in the SDI to variation in species richness and evenness but not abundance, as the raw data indicate high species richness but low bird counts in early spring.

Aside from a slight increase in diversity at Bowie Seamount in summer (Fig. 2C), no prominent SDI hotspots were identified for offshore waters, which aligns with the probability of occurrence maps for known offshore families such as albatrosses. In contrast to the relatively shallow continental shelf, where ridges can cause currents to deflect nutrient-rich water upwards, productivity in the open ocean is much more dependent on wind patterns, which is less permanent and predictable than bathymetric features (Thomson 1981, Whitney et al. 2005). Foraging areas in these waters can also be created by wind pushing zooplankton offshore, which adds to the dynamic nature of this oceanic region (Thomson 1981). As offshore hotspots are likely to be ephemeral, their detection will require analyses conducted at finer temporal scales and increased survey effort in offshore waters.

Many SDI hotspots identified here are already recognized nationally and internationally as Important Bird Areas, particularly along the western coast of Vancouver Island, the eastern coast of Haida Gwaii, and around the Scott Islands (<https://www.ibacanada.com/mapviewer.jsp>). However, our models suggest that in some seasons, shelf-break habitats are as highly utilized as coastal habitats, and these are less

represented in IBA designations. Several SDI hotspots also overlap with proposed marine protected areas in the northern region, with the notable exception of the shallow plains off the northeast coast of Haida Gwaii (MPA Network BC Northern Shelf Initiative 2023).

Two other modelling studies largely corroborate our results. Fox et al. (2017) previously identified the outer Queen Charlotte Sound and several small areas adjacent to eastern Haida Gwaii and northeastern Vancouver Island as being consistently important to bird diversity (defined by the authors as marine bird species/group normalized density and richness), as predicted in an ensemble model. Fox et al. (2017) also identified central Hecate Strait as relatively important, but only in April–June. Of note, Fox et al. (2017) contributed the majority of the 2005–2008 marine bird data for Hecate Strait, Queen Charlotte Sound, and Queen Charlotte Strait used in this study. A second study by Nur et al. (2011) used the same 1997–2008 observation data as our study for waters off the west coast of Vancouver Island. Using a bagged decision tree model for the California Current System, they identified the Scott Islands, western Vancouver Island (particularly near Barkley Sound), and Juan de Fuca Strait as multispecies hotspots. Comparing these predictions with our marine bird SDI hotspot predictions indicates agreement on the importance of the Scott Islands area and the coast of northwest Vancouver Island in most seasons, Hecate Strait in spring, and Juan de Fuca Strait, albeit only in late spring. In contrast with Fox et al.'s (2017) predictions of Queen Charlotte Strait and outer Queen Charlotte Sound's importance in all seasons, our study only predicted these areas to be important in summer. In contrast to Nur et al.'s (2011) predictions of predominantly coastal important bird areas, our models emphasized areas along the shelf break as being similarly or more important SDI hotspots.

Discrepancies between our SDI model results and the hotspot analyses of Fox et al. (2017) and Nur et al. (2011) might have arisen via the modelling methods employed, temporal coverage, areas considered, and survey data or predictor variables used. Although all predictive layers used here were also used by Fox et al. (2017) and Nur et al. (2011), those studies included 23 predictors that were not available over the 20 yr period modelled here or were omitted to reduce collinearity. The temporal and spatial resolutions of these studies also differed, as did the species modelled. For example, Nur et al. (2011) relied on 16 species, including 7 larids, a family that we found to be most diverse in coastal waters. The metrics used to

identify important areas for marine birds can also influence greatly the mapped predictions, with models of marine bird density perhaps emphasizing areas of relatively high abundance, whereas SDI reflects species richness and evenness. Using a compound species diversity index, such as SDI, can complement conventional density-based hotspot analyses and simple diversity measures, such as species richness. Identifying conservation targets and performance metrics are thus important next steps in selecting hotspots most likely to benefit from the mitigation of anthropogenic influence.

4.2. Hotspot responses to ENSO events

Seasonal variation in SDI varied dramatically between strong La Niña, neutral, and strong El Niño seasonal SST conditions. Warmer conditions associated with strong El Niño events resulted in less intense hotspots in Hecate Strait during early spring and summer and off the western coast of Vancouver Island during early spring (Fig. 4A,B), which could potentially indicate that breeding planktivorous and piscivorous birds dispersed more widely and/or travelled further from their colonies in response to rising SST. Increases in SST have been linked to reduced upwelling, increased stratification, shifts in the composition and food quality of zooplankton communities, reductions in the body mass of forage fish, abundance of spawning adults, and survival of eggs and larvae, all of which may influence the persistence of hotspots over decadal scales (Thomson 1981, Chiba & Saino 2003, Keister & Peterson 2003, Mackas et al. 2007, Tommasi et al. 2013, von Biela et al. 2019, Laurel & Rogers 2020). In contrast, SDI hotspots in fall can be seen shifting in intensity, size, and location under changing ENSO conditions, while higher levels of SDI can be seen moving further into inlets of western Vancouver Island during winter (Fig. 4C,D). This trend may reflect a 'thermal foraging niche' for marine birds, particularly during seasons when they are not constrained to nest sites or colonies and are able to travel further to source temperature-sensitive prey.

Many studies have shown species range and density shifts during marine heatwave events, including northward movements of multiple species of marine birds (Veit et al. 1996), as well as increased dispersal from breeding colonies and avoidance of high SST areas in Cassin's Auklets in the winter (Johns et al. 2020) and decreased marine bird density (Hyrenbach & Veit 2003). The simulated responses of bird SDI to

variability in the ENSO presented here further highlight the need for a dynamic approach to conservation measures in complex marine ecosystems, as planning for average conditions could potentially miss important changes in bird distributions, as suggested by the changing spatial patterns of diversity hotspots. This is of particular relevance today, as marine spatial planning to reach Canada's conservation targets of protecting 25 and 30% of marine and coastal areas by 2025 and 2030, respectively, is actively underway but is largely uninformed with regard to future climate change scenarios and focuses instead on creating resiliency and representative habitat replication (e.g. MPA Network BC Northern Shelf Initiative 2023).

4.3. Caveats

Vessel-based at-sea survey data on marine birds are often challenging to collect due to the costly nature of at-sea surveys and dependence on suitable environmental conditions and ships of opportunity. While the compiled data provided by the NPPSD greatly improved the spatial and temporal coverage of this study, marine bird data were still absent for a large portion of Canada's Pacific EEZ from 1997–2017, particularly in the southwestern region, the Salish Sea, and most inlets. As such, model predictions for these areas could be biased by data collected from regions with more survey coverage. In addition, the surveys included in this study were collected from multiple boats of varying sizes and speeds under variable weather conditions, but as information on these important factors was not always available, these could not be accounted for in the models. In addition, our estimates of chl *a* were often patchy and required interpolation in coastal inlets, Johnstone Strait, and large areas offshore, especially in winter. Indeed, winter models are largely influenced by chl *a* levels occurring in February, given that much of the data were missing due to cloud cover and reduced daylight hours in the previous winter months.

The use of the SDI to model potentially important areas for birds allowed us to keep a large amount of data in the study that on a species level would not have been sufficient to model species richness or density. While this method allowed us to maintain information on the spatial distribution of less common birds, it is likely biased towards bird families with a greater number of species. For example, while alcids had 12 species observed within the EEZ for the study duration, albatrosses had only 3.

4.4. Conservation implications

Marine birds in BC face numerous threats, including bycatch in commercial fisheries, oil pollution, and the effects of climate change on ocean productivity (Ban & Alder 2008, Di Lorenzo & Mantua 2016). With the projected increase in shipping traffic (e.g. Trans Mountain Pipeline expansion project predicted 7-fold increase in vessel traffic; Nuka Research and Planning Group 2015), an accurate understanding of marine bird distributions is critical for their protection from further disturbance. Our maps illustrate some of the pelagic and coastal areas used more or less often by marine birds in the Canadian Northeastern Pacific and highlight hotspots of species diversity. Such hotspots reflect conditions where resources are sufficiently abundant to facilitate the co-existence of multiple marine bird species. Furthermore, by targeting areas of high biodiversity for protected area planning, ecosystem functions and services can be maintained (Asaad et al. 2017). Such maps have the potential to inform decisions aimed at minimizing anthropogenic impacts in diversity hotspots and helping Canada achieve its targets for the protection of 25 and 30% of marine and coastal areas by 2025 and 2030, respectively (<https://www.dfo-mpo.gc.ca/oceans/conservation/plan/index-eng.html>). The seasonality of these models, paired with the predictions for how bird distributions could change between strong El Niño, La Niña, and neutral periods, offer an opportunity for a dynamic and adaptive approach to marine spatial planning. Given the predicted increase in frequency and intensity of climate anomalies, understanding the spatial patterns of marine bird diversity in response to rising sea temperatures could play a role in conserving these species, as well as the environment they and other organisms rely upon.

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