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Quantifying marine mammal hotspots in British Columbia, Canada

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Abstract. Global biodiversity is undergoing rapid decline due to direct and indirect anthropogenic impacts to species and ecosystems. Marine species, in particular, are experiencing accelerated population declines leading to many species being considered at risk by regional, national, and international standards. As one conservation approach, decisions made using spatially explicit information on marine wildlife populations have the potential to facilitate recovery and contribute to national and international commitments toward conservation targets. Delineating areas of intense use by species at risk can inform future marine spatial planning and conservation efforts, including the identification of marine protected areas. Methods for detecting hotspots (e.g., areas with high density and/or abundance) enable categorical mapping of the most intensely used areas. Yet, many of the current methods for delineating hotspots, such as the top 5% threshold, are subjective and fail to account for spatial patterns. Our goal was to map spatially continuous distributions of marine mammal densities and employ quantitative statistical methods to extract hotspot locations on the northern coast of British Columbia. We integrated systematically surveyed species information with environmental variables using generalized additive models to predict marine mammal distribution and density. Hotspots were identified from the density surfaces using two approaches: aspatial top 5% method and spatially local G_i^* statistic using three neighborhood definitions. Heterogeneous density patterns were observed for all species, and high-density regions were generally clustered in areas exhibiting oceanographic characteristics that may promote concentrated food resources. Combining species density surfaces and extracting hotspot locations identified regions important to multiple species and present candidate locations for future conservation efforts. Contributions from this research provide robust statistical methods to objectively map hotspot locations and generate GIS data products for informing coastal conservation decisions.

Key words: British Columbia, Canada; cetaceans; conservation prioritization; hotspots; marine conservation; marine mammals; pinnipeds; predictive modeling; species-habitat models.

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INTRODUCTION

On a global scale, ecosystems are experiencing biodiversity crises characterized by extirpations, rapid population declines, range contractions, and altered ecosystem functions (Butchart et al. 2010, Dirzo et al. 2014, McCauley et al. 2015). Ocean ecosystems are also exhibiting decreasing biodiversity due to increasing anthropogenic pressure, particularly in coastal areas (Lotze et al. 2006, Halpern et al. 2008). Consequently, many marine species are considered at risk, and despite conservation efforts, numerous species are failing to recover (e.g., Favaro et al. 2014, Kraus et al. 2016).

To address overwhelming evidence that human actions are directly, and indirectly, contributing to rapid marine species population declines, many national and regional agencies facilitate marine conservation initiatives through management frameworks, strategies, and tools. Many of these programs incorporate marine spatial planning (MSP), ecosystem-based management, systematic conservation planning (SCP), and marine protected areas (MPAs). As a key example, a number of countries, including Canada, pledged to meet biodiversity conservation targets (Aichi Targets) outlined at the Convention of Biological Diversity in 2010 in Nagoya, Japan. The 11th target designates a minimum of 10% of global marine and coastal waters as protected by 2020, which includes ecologically important habitats and regions of high conservation value (Convention on Biological Diversity 2013). To achieve conservation and management targets, it is essential to possess baseline information on marine species in order to identify where species occur in elevated densities and locate priority regions for conservation. In addition, baseline data on marine species help avoid the shifting baseline syndrome (Pauly 1995) and provide a foundational benchmark to measure and assess conservation effectiveness.

Ecological data on focal taxa, such as marine mammals, can be used as indicators to prioritize important marine regions (Zacharias and Roff 2001), as well as to delineate explicit boundaries for reserves, sanctuaries, and protected areas (Hooker and Gerber 2004). The generation of spatial data on marine species (e.g., distributions and densities) can offer valuable inputs for SCP tools, such as Marxan (e.g., Ball et al. 2009, Moore et al. 2016). As an example, systematic-line transect surveys of blue, fin, sei, and North Pacific right whales to estimate species abundance, distributions, and habitat associations in Canada's Pacific coast waters are identified as a high-priority action in support of species recovery objectives under the Species at Risk Act (SARA; Fisheries and Oceans Canada 2017). Further, incorporating species data with socioeconomic information and anthropogenic threats can formulate a more complete understanding of current scenarios so that area-based conservation measures, like MPAs, are more effective and successful in achieving set objectives (Boon and Beger 2016). However, due in part to logistical and financial challenges with data collection in ocean environments, marine mammal species are typically the focus of fewer scientific publications than terrestrial mammals (Schipper et al. 2008, Kovacs et al. 2012) and knowledge gaps are common. The IUCN red list indicates that over half of listed cetaceans are globally data deficient (IUCN 2016). Pinnipeds, on the other hand, have no data-deficient listings, yet 53% of species listed have declining or unknown population trends (IUCN 2016).

Predictive species-habitat models can be used to map species distributions and densities from survey data, and are often used to fill knowledge gaps. Species observations, which are discontinuous in nature, are related to environmental conditions through statistical models to predict species occurrence at unsampled locations (Franklin 2010). Models produce spatially continuous maps of species distribution and/or abundance, making regions where species aggregate more apparent. For example, marine mammals are sensitive to changes in environmental conditions and alterations in marine food webs, where species richness is often highly coupled with primary productivity and food availability (Schipper et al. 2008, Preikshot et al. 2013). Associations between environmental conditions and species distributions and densities allow species richness to be predicted at locations where surveys have not been completed. The patchy nature of species distributions within continuous space provides valuable insight into what environmental conditions may drive the observed spatial patterns while also identifying clustered regions of intense use by one, or more, species. Maps showing variation in species abundance contribute to the overall understanding of where organisms are located and which regions may exhibit elevated levels of species abundance or density (i.e., hotspots; see Reese and Brodeur 2006 [nekton organisms], Menza et al. 2016 [seabirds, pinnipeds, and cetaceans], and Nur et al. 2011 [seabirds]).

Quantifying the spatial patterns of marine species distributions in the form of hotspots can have important implications for the allocation of scarce conservation and planning resources at global and local scales, particularly when achieving conservation objectives such as the Aichi Targets or other site-specific conservation targets.

The term "hotspot" has many associated meanings and, in the strict sense, the definition is based on an estimate of endemic species and habitat loss or threat (Myers 1988, Myers et al. 2000, Mittermeier et al. 2011). In the broad sense, a hotspot refers to any area or region with exceptionally high biodiversity at the ecosystem, species, and genetic levels (Hoekstra et al. 2005). Mapped hotspots are prevalent in conservation prioritization literature and remain a common approach to identify regions of critical importance for marine conservation (Briscoe et al. 2016). A key criticism of the hotspot approach surrounds the static nature of hotspots and the tendency to assume that MPAs created based solely on hotspots would sufficiently protect species of interest. However, marine mammals have large migratory ranges and, as mobile marine predators, are highly influenced by environmental conditions and consequently, distributions are likely to change over time. For example, fin whales have recently expanded into regions of Caamano Sound, British Columbia, Canada, where they previously were not often found. Given limited monetary resources however, efficient targeting of protection efforts is imperative, whether creating an MPA or developing strategies to mitigate human impact within critical habitat. Identifying areas with a higher concentration of species than surrounding areas (i.e., hotspots) is useful when developing conservation policies (Hyrenbach et al. 2000), as these may be regions where current conservation resources could be most effectively allocated.

Hotspots with spatially explicit boundaries can be detected using methods that are both aspatial and spatial. In conservation biology, aspatial approaches to hotspot delineation are the most common and apply an arbitrary threshold, such as the top 2.5% (Orme et al. 2005, Ceballos and Ehrlich 2006), 5% (Parviainen et al. 2009, Tolimieri et al. 2015), or 10% (Tolimieri et al. 2015), to information, typically species richness measures, in order to partition hotspot locations. Some thresholds reach as high as 25% and 50% (e.g., Nur et al. 2011). However, movement in this discipline has shifted toward acknowledging spatial dependence in ecological datasets and incorporating spatially explicit methodology to understand spatial relationships (Liebhold and Gurevitch 2002, Wagner and Fortin 2005). Spatial methods for hotspot delineation enable thresholds to be statistically determined and account for the spatial patterns of species distributions (Nelson and Boots 2008). More specifically, using local measures of spatial autocorrelation, it is possible to map where species are most abundant and where the spatial patterns of species distributions are unlikely to have arisen from chance processes (Anselin 1995, Ord and Getis 2001, Boots 2002). While spatially local hotspot detection methods have been applied in terrestrial contexts (e.g., Nelson and Boots 2008, Zhihai et al. 2012), studies that apply spatially explicit hotspot detection have more recently expanded to include marine research (e.g., Nelson et al. 2011, Kuletz et al. 2015).

The goal of this paper was to quantify hotspots and explore multiple techniques for hotspot identification using density surfaces (i.e., predicted abundance of individuals per unit area) in order to inform future policy on potential marine conservation areas. We have based our assessment on the broad meaning of a hotspot (i.e., an area with exceptionally high number of species) and further restrict this definition to a single taxonomic group of nine marine mammal species. In this study, we build upon existing baseline information for marine mammals in British Columbia (see Williams and Thomas 2007, Williams and O'Hara 2010, Williams et al. 2011, Best et al. 2015) by generating continuous density surfaces for nine species using the correlative modeling technique generalized additive models (GAMs). Our approach is distinguished from similar research (Best et al. 2015), who focused on generating estimates of species abundance using conventional distance sampling and GAMs, the latter of which included a limited number of predictor variables. Importantly, no subsequent analyses for quantifying spatial patterns generated from GAM predictions were undertaken by Best et al. (2015). Our approach builds upon the findings of Best et al. (2015) by incorporating dynamic and climatological variables in addition to static covariates. Moreover, predictive surfaces are combined for cetaceans and pinnipeds to demonstrate a comparative hotspot analysis approach for use in spatial prioritization. The resulting predicted surfaces from our generated GAMs are used to illustrate the utility of performing spatially specific methodology for extracting hotspot locations for spatial planning and conservation initiatives. Priority zones for conservation are identified by employing multiple approaches for hotspot identification. Comparison between aspatial and spatially local methodologies offers new perspectives on how various techniques for hotspot delineation influence both location and physical characteristics of hotspots when used in a marine context.

METHODS

Study region and species

Our research area is situated within the continental shelf of British Columbia, Canada, covering a region of 62,976 km^2 (Fig. 1). The northern coastal waters of British Columbia contain distinct spatial and temporal biophysical oceanographic characteristics (Thomson 1981) and a multitude of anthropogenic activities (Ban and Alder 2008, Murray et al. 2015). This region is highly productive, providing food resources and important foraging opportunities for migrating and resident marine mammals.

Of the 24 extant marine mammal species currently found in British Columbian waters (Ford 2014), this study focuses on nine species (seven cetaceans and two pinnipeds). Species were selected based on the number of presence observations within our survey data to maintain a sufficient quantity of non-zero samples for modeling. Cetaceans include common minke whale (MW; *Balaenoptera acutorostrata*), Dall's porpoise (DP; *Phocoenoides dalli*), fin whale (FW; *Balaenoptera physalus*), harbor porpoise (HP; *Phocoena phocoena*), humpback whale (HW; *Megaptera novaeangliae*), killer whale (KW, three ecotypes; *Orcinus orca*), and Pacific white-sided dolphin (PW; *Lagenorhynchus obliquidens*), whereas pinnipeds comprise harbor seal (HS; *Phoca vitulina*) and Steller sea lion (SSL; *Eumetopias jubatus*) species. Of the chosen study species, more than half are listed as provincially and nationally at risk (Table 1).

Species data

From 2004 to 2008, Raincoast Conservation Foundation conducted one of BC's largest systematic at-sea surveys. The stratified survey was specifically designed to promote effort efficiency and to maintain a random placement of transects (Thomas et al. 2007). Surveys over the five years were conducted via line transects and included six survey periods: Summer 2004 (June, July, and

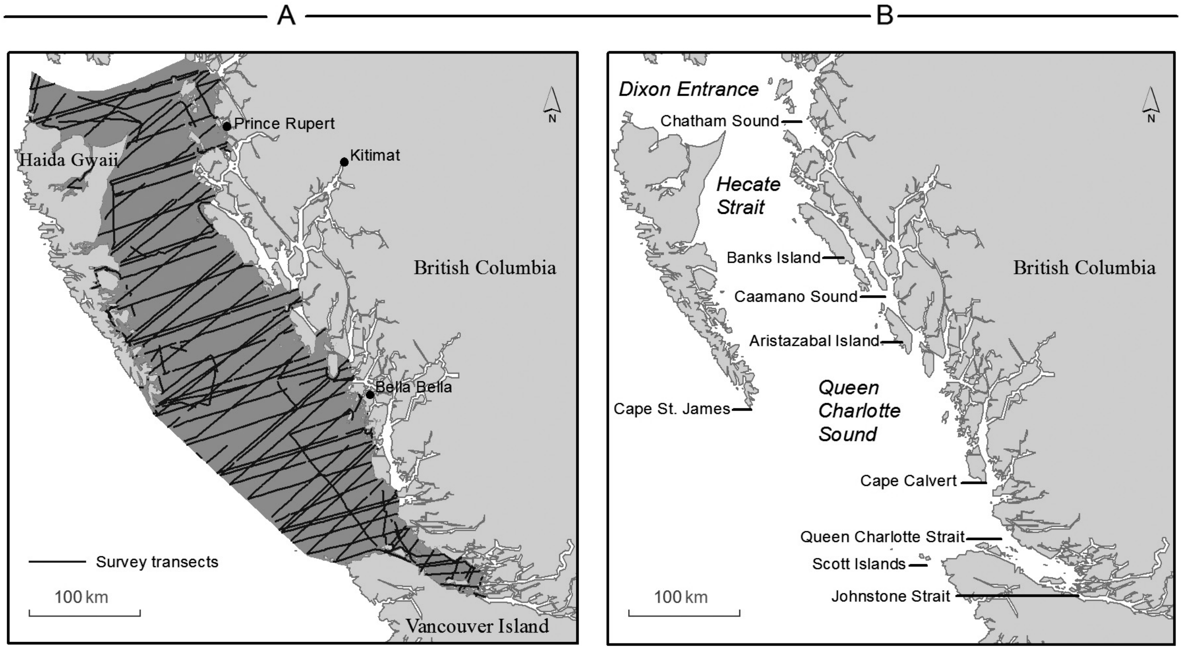

Fig. 1. Maps illustrating (A) study region that is indicated in dark gray with passage and on-effort survey transects (2004–2008) and (B) key oceanographic regions.

Table 1. Provincial, national, and global rankings of study species as of 1 September 2016.

Common name	Scientific name	BC list (BC)	COSEWIC (Canada)	Species at Risk Act (Canada)	IUCN (global)
Common minke whale	*Balaenoptera acutorostrata*	Yellow	NAR (2006)	N/A	LC (2008)
Dall's porpoise	*Phocoenoides dalli*	Yellow	NAR (1989)	N/A	LC (2008)
Fin whale	*Balaenoptera physalus*	Red	T (2005)	T (2006)	EN (2008)
Harbor porpoise	*Phocoena phocoena*	Blue	SC (2016)	SC (2005)	LC (2008)
Harbor seal	*Phoca vitulina*	Yellow	NAR (1999)	N/A	LC (2016)
Humpback whale	*Megaptera novaeangliae*	Blue	SC (2011)	T (2005)	LC (2008)
Killer whale	*Orcinus orca*				DD (2008)
Northeast Pacific offshore		Red	T (2008)	SC (2003)	
West Coast transient		Red	T (2008)	T (2003)	
Northeast Pacific northern resident		Red	T (2008)	T (2003)	
Pacific white-sided dolphin	*Lagenorhynchus obliquidens*	Yellow	NAR (1990)	N/A	LC (2008)
Steller sea lion	*Eumetopias jubatus*	Blue	SC (2013)	SC (2005)	NT (2016)

Note: Yellow, apparently secure; blue, special concern; red, extirpated, endangered, or threatened; NAR, not at risk; SC, special concern; T, threatened; LC, least concern; DD, data deficient; NT, near threatened; EN, endangered.

August), Summer 2005 (August), Summer 2006 (August and September), Spring 2007 (April and May), Fall 2007 (October and November), and Summer 2008 (June and August). The Fall survey was not included due to the lack of sighting data. More than 16,000 km of trackline—over 5000 km within the study region—was surveyed to generate distance-corrected (Buckland et al. 2001, 2004) quantitative information for a number of marine mammal species using multiple covariate distance sampling (MCDS) techniques (Best et al. 2015). All transects were separated into one nautical mile segments and, for each segment, a density estimate (i.e., the number of individuals per km^2) was calculated (see Best et al. 2015). These estimates are particularly robust as they have been corrected for uncertain observer sightings along each segment using detection functions (Buckland et al. 2004, Hedley and Buckland 2004). For marine species, including those that dive underwater, uncertainty in observer sightings is unavoidable. Therefore, correcting for imperfect detection is vital to ensuring the most accurate assessment of species densities and to account for detection bias and missed observations. Although corrections are applied to adjust for detection errors, a key assumption of distance sampling is that detection is assumed perfect along the trackline ($g(0) = 1$), which is rarely the case in marine mammal surveys. For additional details on survey methods, see Thomas et al. (2007) and Williams and Thomas (2007), and for more information on MCDS and abundance estimates along transect segments, see Best et al. (2015) and Fox et al. (2017). To encourage information sharing and transparency, marine mammal sightings data will be openly available online (OBIS-SEAMAP, http://seamap.env.duke.edu/dataset/1485).

As marine mammal sightings were limited within the study region, all seasons and years (for both passage and on-effort transects) were combined to maximize the sample size for the modeling process. Pinniped observations both in water and hauled out on land were also collated. Vessel speeds remained relatively consistent at approximately 15 km/h throughout the survey extent; therefore, speeds ≤5 knots were removed from analysis to reduce bias.

Environmental covariates

Top predators, such as marine mammals, respond less strongly to short-term oceanographic conditions when assessed in transect-based habitat models, while proclivity for broader-scale and predictable oceanographic features has been shown (Mannocci et al. 2013). Therefore, temporally static and monthly averaged composites, as well as longer-term climatologies, were used in this analysis (Table 2). The 15 environmental covariates used to characterize marine mammal habitat were chosen based on data availability and spatial coverage for the study region. These can be classified into three categories: static, dynamic, and climatological. Static variables are those that are geographically fixed and/or temporally static. Dynamic and climatological variables are time-averaged

Table 2. Descriptions of the 15 original environmental covariates included in each generalized additive models.

Category	Variables	Summary	Resolution	Rationale
Static	Latitude and Longitude[1]	Derived from transect Global Positioning System data (m)	50 m	Spatial location shows strong influence on predictions using species distribution models (Best et al. 2015)
	Bathymetry[2]	Depth of ocean floor (m)	100 m	Top predators show response to bathymetric features; shallow topography may provide favorable foraging opportunities (Yen et al. 2004)
	Slope[2,3]	Slope (degrees) of the ocean floor derived from bathymetry data	100 m	Steep benthic relief promotes water movements, which increase and concentrate prey and/or primary production (Croll et al. 1998, Yen et al. 2004)
	Benthic terrain ruggedness[2,4]	Terrain ruggedness derived from bathymetry data (proportion)	100 m	Topographic complexity, such as rugosity, can create localized increases in productivity, aid in prey capture, and provide migration cues (Bouchet et al. 2015)
	Distance from coast[3,5]	Euclidean distance from nearest coastline feature (m)	50 m	Distance provides an indication of preference for near or offshore habitats, for example, distance to land used as covariate in humpback whale model (Dalla Rosa et al. 2012)
	Distance from continental shelf[3,6]	Euclidean distance (m) from continental shelf (200–1000 m depth and slope between 5% and 20%)	50 m	Continental shelf edge is characterized by upwelling and water column mixing promoting high productivity, prey, and overall biomass (Springer et al. 1996, Croll et al. 1998)
	Distance from high current areas[3,6]	Euclidean distance (m) from high current polygons (>3 knot current)	50 m	Productivity of areas (e.g., upwelling regions) driven by current strength or persistent eddy circulations (Smith and Whitehead 1993, Whitney et al. 2005)
Dynamic	Tidal current[7]	Root mean square average tidal speed (m/s)	500 m	Strong tidal currents influence ocean circulation leading to elevated nutrients and prey concentrations particularly in coastal ecosystems (Rogachev et al. 2008)
	Sea surface temperature (SST)[8]	Monthly averaged AquaMODIS daytime SST (°C)	0.05 degrees	Cold coastal surface waters may indicate upwelling regions (Jardine et al. 1993, Croll et al. 1998)
	Chlorophyll-*a* concentration[8]	Monthly averaged AquaMODIS chlorophyll-*a* concentrations (mg/m^3)	0.05 degrees	High chlorophyll-*a* concentrations indicate regions of high prey concentrations and are often used as a proxy for primary productivity (Ware and Thomson 2005)
	Wind[8]	Magnitude of monthly averaged QuikSCAT sea surface wind speed (m/s)	0.125 degrees	Wind induced water column mixing impacts eddy characteristics and strength, as well as the distribution and abundance of ocean productivity (Brodeur and Ware 1992, Stammer and Wunsch 1999)
	Sea height absolute[8]	Monthly averaged AVISO sea surface height (SSHA) deviation plus the long-term mean dynamic height (m)	0.25 degrees	Indicates areas of ocean movement, mixing, and variability, which may represent possible regions of enhanced ocean productivity (Rao et al. 2006)
	Sea height deviation (sea-level anomaly)[8]	Monthly averaged AVISO SSHA deviation from the mean geoid as measured from 1993 to 1995 (m)	0.25 degrees	Anomalies in sea level can be used to identify eddies, which create conditions that generate food-rich habitats (Crawford et al. 2007, Tosh et al. 2015)
Climatological	Temperature[9]	Long-term monthly averaged SST (°C) from 1955 to 2006	0.25 degrees	Distribution of top predators may be, in part, influenced by temperature as predators and/or their prey have varying thermal preferences (Block et al. 2011)
	Salinity[9]	Long-term monthly averaged sea surface salinity (ppm) from 1955 to 2006	0.25 degrees	Fresh water runoffs that are high in nutrients stratify the water and may affect the growth of algae (Campagna et al. 2008). Some marine mammals have been shown to avoid low-salinity areas (Tynan et al. 2005)

Notes: Rationales for each variable are included to justify the inclusion of each covariate specifically for marine mammal prediction. List of data sources: Raincoast Conservation Foundation (1); SciTech Consulting and Living Oceans Society; www.bcmca.ca (2); ArcGIS 10.0 tools (ESRI, Redlands, California, USA) (3); Benthic Terrain Modeler extension (Wright et al. 2012) (4); DataBC, Freshwater Atlas Coastlines, apps.gov.bc.ca (5); DataBC, Benthic Marine Ecounits—Coastal Resource Information Management System, apps.gov.bc.ca (6); Foreman et al. (2000), www.bcmca.ca (7); National Oceanic and Atmospheric Administration CoastWatch, www.coastwatch.pfeg.noaa.gov, accessed through Environmental Data Connector for ArcGIS (8); World Ocean Database, www.nodc.noaa.gov (9).

composites, monthly and yearly averaged multi-decadal periods, respectively.

Static variables include latitude, longitude, depth (m), slope (degrees), benthic terrain ruggedness (proportion), distance from the coast (m), distance from high current areas (m), and distance from the continental shelf (m). Latitude and longitude were recorded by a Global Positioning System (GPS) every 10 s during survey transiting and were collected using Logger 2000 software (International Fund for Animal Welfare, Washington, D.C., USA). Slope and benthic terrain ruggedness were calculated from a depth (bathymetry) 100 × 100 m resolution grid sourced from the BC Marine Conservation Atlas (SciTech Consulting and Living Oceans Society, www.bcmca.ca). Benthic terrain ruggedness was created using the Benthic Terrain Modeler extension from Geospatial Modeling Environment (Wright et al. 2012) using a 13-cell moving window. Euclidean distance to the coastline, high current regions (>3 knot current), and continental shelf were generated from layers from the British Columbian provincial government and calculated over a 50 × 50 m grid for the study extent (Freshwater Atlas Coastlines, Benthic Marine Ecounits, apps.gov.bc.ca). Continental shelf polygons were delineated by selecting regions with depth between 200 and 1000 m and a 5–20° slope.

Dynamic variables consist of the root mean square of average tidal speed (m/s), sea surface temperature (SST; °C), chlorophyll-*a* concentration (mg/m^3), wind speed (m/s), sea surface height (SSHA), and sea-level anomaly (SSHD). Dynamic predictors represent oceanographic conditions that are temporally variable, and therefore, remotely sensed imagery provides an averaged temporal composite for each. Monthly images, aside from the root mean square average tidal speed, were extracted for the study region from the National Oceanic and Atmospheric Administration (NOAA) CoastWatch program (www.coastwatch.pfeg.noaa.gov) for each month surveyed during the six selected survey periods. The root mean square average tidal speed was provided for the entire west coast of Canada and was generated though a 3D circulation model for coastal regions of the northeastern Pacific Ocean (Foreman et al. 2000, www.bcmca.ca).

Sea surface temperature and salinity climatological variables are long-term multi-decadal monthly averages using data from 1955 to 2006, which represent general oceanographic trends. Both datasets were sourced from the World Ocean Database (http://www.nodc.noaa.gov).

Data preprocessing

Data were integrated using a hexagon grid, with a spatial resolution of 13.86 km^2 to allow integration with Environment and Climate Change Canada marine planning units (e.g., Fox et al. 2017). Hexagons have been extensively used in MSP as they allow for more efficient, compact (Nhancale and Smith 2011), and ecologically relevant configurations (Birch et al. 2007). Hexagons were attributed with mean covariate values; however, dynamic and climatological variables are monthly composites, thereby enabling the calculation of additional values by pooling across survey years. Calculations included the coefficient of variation (CV), minimum (min), and maximum (max) values. This resulted in an increase in environmental predictor variables used in modeling from 15 to 34. When data were missing from remotely sensed variables (within inlets, near shore, and due to cloud cover), values were interpolated using the nearest neighbor value. Season and year covariates were included in initial GAMs during preliminary model fitting, but the inclusion did not improve model fit, made no significant difference on prediction, and, in some cases, decreased the percent variance explained. For these reasons, seasonal and yearly covariates were removed.

Inclusion of correlated variables in models can result in reductions in model performance and overall model instability (Kuhn and Johnson 2013). We tested for correlation between the 34 covariates using the Spearman's rank correlation (rho) analysis by applying the rcorr function of the Hmisc package in R (R Development Core Team 2015, Harrell 2016). Relationships between variables were assessed in descending order of the absolute value of each correlation coefficient over a given threshold (Kuhn and Johnson 2013). Here, we chose a correlation coefficient threshold of $r_s > 0.70$ (Dormann et al. 2013) with a conservative statistical significance level of 0.01. The variable with the largest average correlation coefficient was removed. This process was repeated until all correlation coefficients fell below the set threshold. The remaining 22 covariates were as follows: longitude, latitude, bathymetry, terrain ruggedness, distance to coastline, distance to high current regions, distance to continental shelf, average tidal current, chlorophyll-*a* concentration (min, max, CV), SST (min, max, CV), SSHA (min), SSHD (avg, min, max), wind (avg, min, max), and salinity (max).

Modeling approach

Regression-based predictive models are a popular technique for modeling cetacean distributions (Redfern et al. 2006). We used a GAM to account for non-linear and non-monotonic trends, which are common in ecological studies (Hastie and Tibshirani 1990, Guisan et al. 2002, Wood 2006). A basic GAM can be expressed as:

$$g(\mu) = \alpha + \sum_{j=1}^{p} f_j(X_j) \tag{1}$$

where the intercept is represented by α and g (μ) is the "link" function that correlates the mean of the estimated response with the sum of all "smooth" functions (f_j) for each covariate value (X_j) (Hastie and Tibshirani 1990).

In this modeling approach, we use a GAM to relate the density (individuals per km^2) of each species to the 22 environmental variables selected from the correlation analysis. The GAM applies penalized regression splines using the mgcv package within R (Wood 2011, R Development Core Team 2015). We used a thin plate regression spline as the smooth function where the smoothing parameters used to control the degree of smoothness (wiggliness) of the fitted spline were estimated through generalized cross-validation (GCV). Generalized cross-validation was used rather than the unbiased risk estimator (UBRE) because the scale parameter was unknown (Wood 2006). To control for the tendency of GCV to overfit data, the degrees of freedom were modified from the default gamma value of 1–1.4 (Kim and Gu 2004) and basis functions were further penalized by reducing the k value (total allowable degrees of freedom for each spline) to 6 from the default 10. An additional penalty was added through the "select" function where covariates may be automatically removed from the model during fitting.

A weighting scheme was applied to compensate for zero-inflated species data, where the greater the weight value, the more emphasis that particular observation is given within the model (Wood 2016). Higher weights essentially increase the prominence of a given observation in the model fit. For example, with a weight value of five, an observation value can be said to have been observed five times, rather than once, effectively increasing the influence of certain observations over others. In this case, all non-zero observations were weighted and zero values were left unchanged. To select the optimal weight value, a comparison analysis was performed using a covariate saturated GAM for each species. Though the percent variance explained increased for higher weight values, the analysis demonstrated minimal improvements (<5% variance explained) beyond a weight of 10. As a result, a weight of 10 was applied to all non-zero observations.

To generate a parsimonious model, covariates were removed in a backwards selection procedure, beginning with variables with the highest P-value. Variables were removed until all were significant from a 0.05 significance level. Model performance was assessed by examining the percentage of explained deviance and the adjusted R^2, while the root mean square error (RMSE) of observed vs. predicted values was used to assess accuracy of model predictions.

Model predictions resulted in negative values for some species; however, for visualization purposes, all negative values were displayed as zero. Normalized species density maps were generated by dividing the predicted density values by the maximum predicted value for each species resulting in a range between 0 and 1 (similar to Nur et al. 2011 and Fox et al. 2017). Mapping relative densities in the form of a normalized numeric rather than absolute densities prevents one species from driving any hotspots identified when individual species maps are combined. Within-species normalized maps were collated together by summing the normalized values across cetaceans, pinnipeds, and all species for each hexagon. The three collated maps were subsequently used in hotspot analysis.

Hotspot analysis

To identify hotspots, we performed two types of analyses on the normalized density maps: the first, using an aspatial threshold approach and the second, applying a spatial statistical method

(Getis-Ord G_i^*) using three neighborhood definitions. Using one of the common aspatial approaches in biological conservation (e.g., Parviainen et al. 2009, Tolimieri et al. 2015), we identified the top 5% of data. A threshold set at the 95th percentile value defined hotspots as the highest 5% of the data. A second, but spatially explicit, approach to hotspot detection was applied next. Methods drawn from spatial statistics have additional advantages to the commonly applied top 5% approach—specifically, the use of statistical thresholds, incorporating spatially local autocorrelation, and the use of a test hypothesis where the null assumes patterns are generated from random process (Getis 2010). G_i^* detects spatial clustering of either high or low density (individuals per km^2), where clusters are greater than expected from spatial patterns generated from chance processes. G_i^* follows the basic form:

$$G_i^*(d) = \frac{\sum_j w_{ij}(d)x_j}{\sum_{j=1}^{n} x_j} \qquad (2)$$

where i is the pivot location, x is the attribute value of i—in this case, density—and w_{ij} is a spatial weights matrix created using a distance threshold (d) or the spatial configuration of adjacent cells to define neighbors of the ith observation (Getis and Ord 1992). Hotspots are identified when a pivot location and its surrounding neighborhood, defined by w_{ij}, include values of high density (individuals per km^2), relative to all density values within the study area. Permutation testing was used to determine whether the pattern of clustering is more or less than expected when compared to patterns generated from random process. The G_i^* statistic was performed using GeoDa software (v.1.6.6 October 2014, Anselin et al. 2010) with 999 permutations to determine significance at the 0.05 level.

There are multiple ways to define a spatial neighborhood (w_{ij}), and the selection of neighborhood type will influence which locations are included in the calculated hotspots. We employed contiguity and distance neighborhood definitions, which are commonly used with areal datasets (Dubin 2009). Contiguity matrices are typically employed when adjacency relationships between areal units are of interest. In ecological studies, equal area units, such as hexagons or grids, are generally used to represent continuous phenomena (Birch et al. 2007), providing natural definitions for contiguity. We implemented first- and second-order contiguity, meaning neighborhoods are defined by the shared boundaries of directly adjacent cells from pivot i for first order (lag 1) and those also directly adjacent to the first order (second order, lag 2; Nelson and Robertson 2012, Fig. 2). Adjacency is defined using terminology

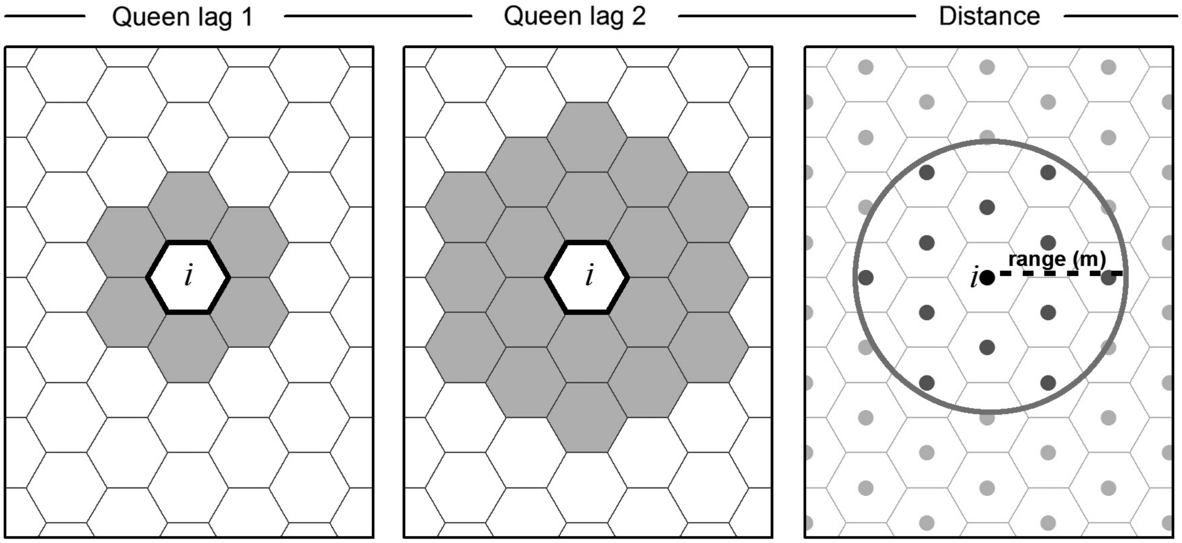

Fig. 2. Illustration of two different ways to define a spatial neighborhood: (1) queen contiguity defined as first order (lag 1) and second order (lag 2) and (2) distance-based radius (range value from semivariogram).

formulated around movements of chess pieces: rook, bishop, and queen (Dubin 2009). Rook contiguity considers neighbors to be cells adjacent to the immediate top, bottom, left, and right of pivot *i*, while the diagonal corners are not considered. Bishop contiguity is the opposite of rook, where only diagonal corners are included. In this case, we have chosen queen contiguity; it considers any neighbor that directly touches the cell border of *i*, regardless of direction (Fig. 2).

We also used a distance definition to demonstrate the sensitivity of G_i^* to various definitions of spatial neighborhoods. Distance-based definitions employ the use of a fixed distance threshold (radius), whereby all polygon centroids that fall within the defined distance are considered to be within the same spatial neighborhood (O'Sullivan and Unwin 2010). However, choosing the appropriate distance radius (i.e., threshold value) can be determined multiple ways. Here, the radius was determined by selecting the range value from an experimental semivariogram plot that was fit using an ordinary least-squares model (Cressie 1993, p. 94, Figs. 2, 3). Semivariograms are often applied in geostatistics (typically geology or earth sciences) to quantify spatial autocorrelation—or the strength of association—between observations as the distance between pairs of observations increases (Atkinson and Lloyd 2009). Semivariograms graph the semivariance of pairs of observations on the *y*-axis and the lag distance, which separates these observations on the *x*-axis. An empirical model is then used to fit a line to the plotted points from which certain numerical characteristics can be extracted. The *range* is a semivariogram characteristic that identified the distance at which spatial autocorrelation diminishes (scale of spatial variation) and provides an indication of when observations are no longer spatially related (O'Sullivan and Unwin 2010). It is logical to apply the range value as the distance threshold value as, by definition, hotspots are regions where greater-than-expected aggregations of highly similar values occur. When the semivariogram was run for the normalized density maps, the range value was similar between semivariograms, with a 28.1 km range value for cetaceans, 25.9 km for pinnipeds, and 23.8 km when all species were combined.

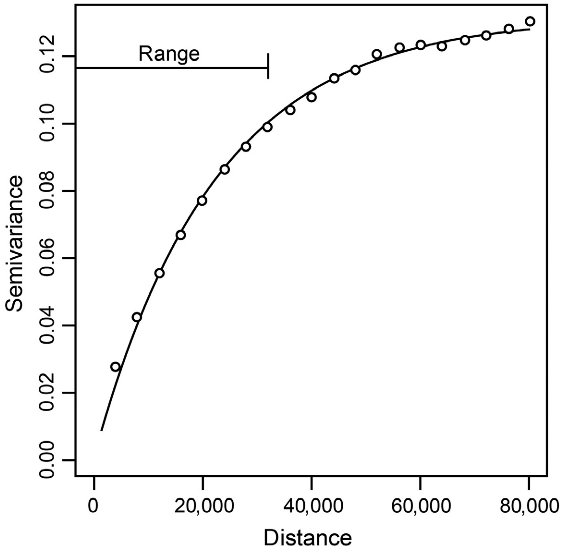

Fig. 3. A representative semivariogram from which the radius of a distance band-based spatial neighborhood can be determined by using the range value.

RESULTS

Species-specific density surfaces generated from GAMs showed that species densities were heterogeneously distributed across the study region (Fig. 4). The predictive performance of models, shown here using explained deviance and adjusted R^2 values, ranged between 25.50% and 9.44% and 0.2380 and 0.0838, respectively (Table 3). Visualization of each species map highlights clear regions where predicted species density is highest (Fig. 4). For example, DP shows high-density values in the most northern sections of the study region surrounding Dixon Entrance, whereas KWs show two regions of high values in sections of Chatham Sound and an area of coastal Queen Charlotte Sound between Calvert Island and Aristazabal Island. Interestingly, the density maps for FWs, HWs, and PWs all possess high values southeast of Haida Gwaii. Harbor porpoise and MW show spatially variable regions of high density distributed throughout the study region. Areas of high density for pinnipeds are situated in coastal areas; HS displays highest values in Caamano Sound, while SSLs have their highest densities in a more southern coastal region located off Cape Calvert.

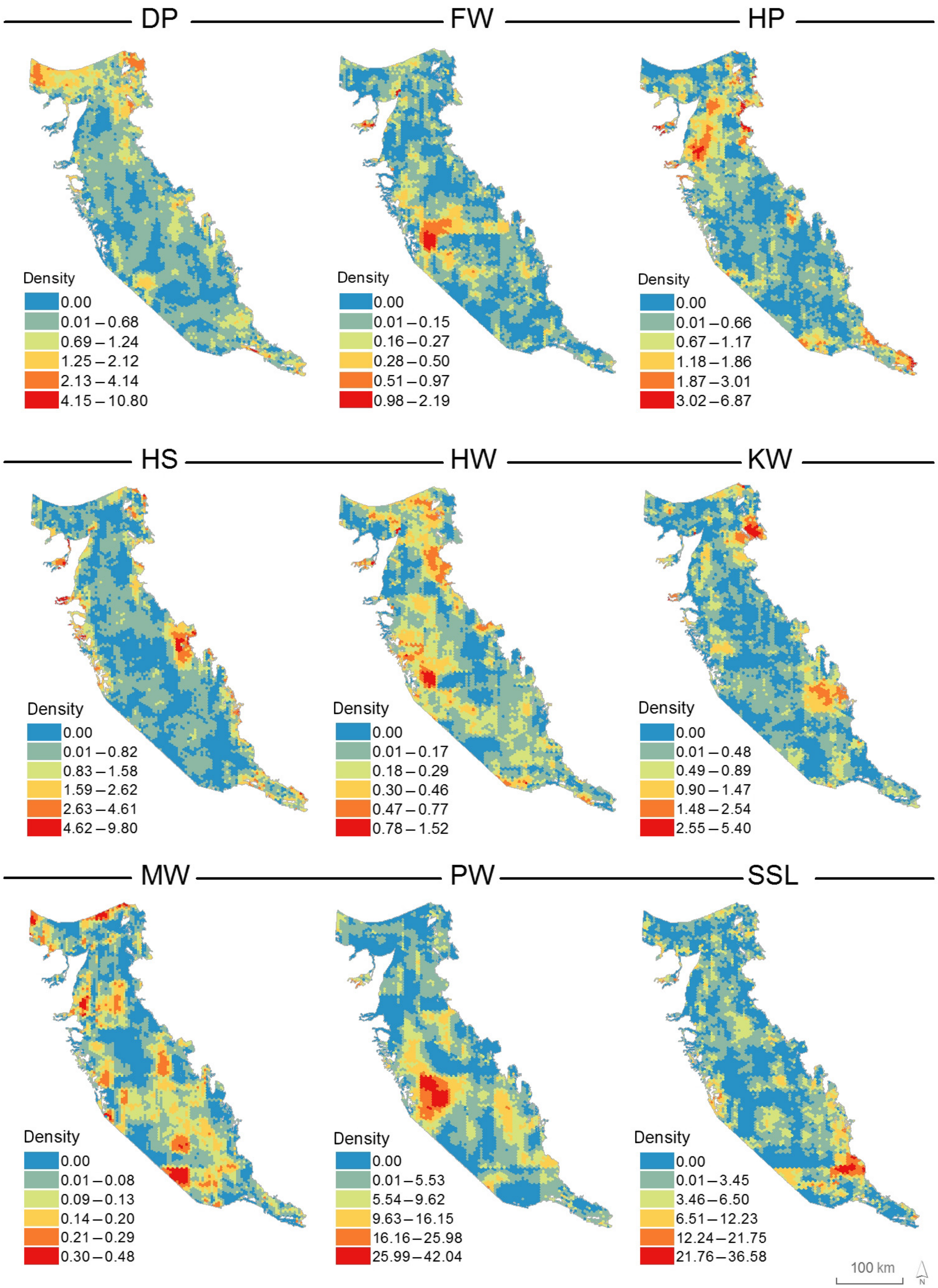

Fig. 4. Continuous density surfaces generated from species-specific generalized additive models. Density is

(Fig. 4. *Continued*)
defined as the number of individuals per km^2 and displayed on a hexagon grid (each hexagon is 13.86 km^2). Abbreviations include Dall's porpoise (DP), fin whale (FW), harbor porpoise (HP), harbor seal (HS), humpback whale (HW), killer whale (KW), common minke whale (MW), Pacific white-sided dolphin (PW), and Steller sea lion (SSL).

The normalized and summed species maps characterize the collective distributional patterns of cetaceans, pinnipeds, and all species combined (Fig. 5). Prominent regions of high density for cetaceans are identified southeast of Haida Gwaii near Cape St. James, a small area in outer Queen Charlotte Sound near the Scott Islands, and scattered areas in Chatham Sound and Dixon Entrance, which are in the northeast section of the study area and near the City of Prince Rupert. Highest predicted densities of pinnipeds are generally situated along coastal areas in the southern sections of the study area in regions featuring shallow banks and minimal ocean depths (Thomson 1981). Notable regions of high density are identified off Calvert Island (Cape Calvert) and another in Caamano Sound and adjacent to Aristazabal Island. When combined, regions that are shown to support elevated levels of species aggregations for both cetaceans and pinnipeds are clearly distinguished.

Hotspot analysis produced multiple spatial representations of potential candidate areas for conservation. The density threshold value calculated for the top 5% hotspots was similar between cetaceans (≥1.16) and all species (≥1.32); however, pinnipeds were different producing a threshold value of ≥0.41 (Fig. 5). The hotspot analysis showed that G_i^* hotspots coincide with areas identified from the top 5% approach, however covered a greater spatial extent, with smoother and more spatially complete borders. The G_i^* outputs showed fewer pockets of high-density regions but were larger in overall size compared with the top 5% method. These observations are apparent when the average size and the number of hotspots for each method are compared (Table 4). A clear trend is evident showing a decrease in the number of individual hotspots and an increase in average hotspot size for G_i^* methods over the aspatial top 5% technique. Furthermore, this observation is also exhibited when the spatial neighborhood definition changes. Configuration differences between outputs illustrate that the top 5% results are highly patchy, smaller, and display greater spatial heterogeneity than the G_i^* statistics, suggesting that aspatial approaches produce the most conservative hotspot estimates compared with spatial methodology. Hotspots are generally situated in coastal and nearshore regions and are consistently absent in central locations of the study area within Hecate Strait and Queen Charlotte Sound (Fig. 5). When cetacean and pinniped hotspots are compared, it appears that Caamano Sound and Cape Calvert hotspots are primarily driven by pinniped density, whereas cetacean density is responsible for the remaining hotspot regions.

DISCUSSION

Marine species distribution and density information is typically collected in the form of disjoint samples of sighting occurrences. For planning, mapping, and conservation directives, it is beneficial to convert samples of species occurrence to continuous surfaces that represent the possible distribution, abundance, or density of a population

Table 3. Generalized additive model performance summary statistics for each species.

Summary type	DP	FW	HP	HS	HW	KW	MW	PW	SSL
Number of non-zero observations	137	67	50	108	240	18	27	113	28
% deviance explained	24.50	13.10	25.50	23.30	14.50	9.44	11	9.94	13.30
Adjusted R^2	0.23	0.12	0.24	0.22	0.13	0.08	0.10	0.09	0.12
Root mean square error (predicted vs. actual values)	0.93	0.26	0.93	1.17	0.28	0.84	0.14	11.85	6.49

Note: Abbreviations include Dall's porpoise (DP), fin whale (FW), harbor porpoise (HP), harbor seal (HS), humpback whale (HW), killer whale (KW), common minke whale (MW), Pacific white-sided dolphin (PW), and Steller sea lion (SSL).

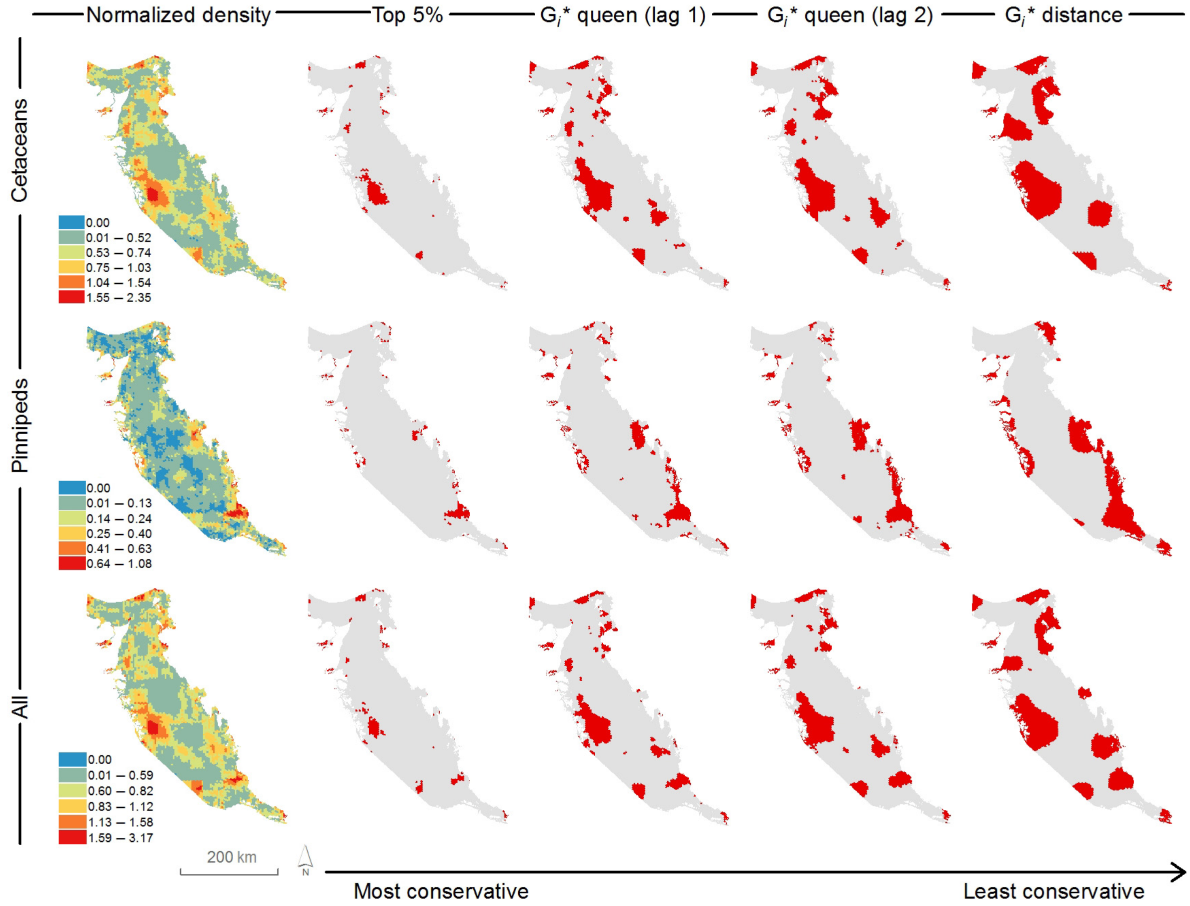

Fig. 5. Four hotspot outputs (top 5%, G_i^*queen [lag 1], G_i^* queen [lag 2], and G_i^*distance) generated from normalized and summed density maps (first column) for cetaceans, pinnipeds, and all species combined.

(Franklin 2010, Becker et al. 2014, Menza et al. 2016). Predictive species-habitat modeling techniques offer methods to extract meaningful spatial information from limited species observations by relating environmental conditions to abundance or density estimates. The resulting continuous surfaces fill gaps in survey data and provide baseline information valuable for MSP and conservation ventures. One example of a recent initiative is the Marine Plan Partnership for the North Pacific

Table 4. Hotspot summary table illustrating the total number and average size of hotspots generated from aspatial (top 5%) and spatial (Gi^*) techniques.

Category	Summary type	Top 5%	G_i^* queen (lag 1)	G_i^* queen (lag 2)	G_i^* distance
Cetaceans	Number of hotspots (n)	44	42	32	23
	Average size (km^2)	65.26	230.89	378.50	779.52
Pinnipeds	Number of hotspots (n)	81	70	67	19
	Average size (km^2)	27.30	87.57	111.82	718.38
All	Number of hotspots (n)	62	60	44	22
	Average size (km^2)	40.60	149.08	259.13	823.32

Notes: The G_i^*queen (lag 1 and lag 2) labels represent the contiguity neighborhood approach, where spatial lag 1 includes all adjacent neighboring cells to the pivot location, while lag 2 additionally includes all adjacent neighbors to lag 1 cells. The G_i^*distance metric incorporates a distance threshold for the neighborhood, where distance was based on the range value from a calculated semivariogram plot of 28.1 km for cetaceans, 25.9 km for pinnipeds, and 23.8 km for all species combined.

Coast (MaPP) located within the Pacific North Coast Integrated Management Area (PNCIMA). Marine spatial planning projects, such as MaPP, typically aim to generate strategic directives for regional zones that balance the needs of multiple stakeholders (including biological communities) considering both present and future conditions and needs. Therefore, species distribution and density maps, like those generated in this study, enhance marine plans by providing a continuous surface that indicates current species patterns, identifies candidate areas for conservation prioritization, and supplies a baseline from which future change can be detected. Where available, capacity for informed decision-making may be further improved by combining numerous prediction maps from multiple regions along the northeast Pacific coast (e.g., Menza et al. 2016 [Washington coast] and Becker et al. 2014 [California coast]) to increase understanding of basin-wide distributional patterns and to form a holistic picture of species patterns.

Despite the value of distribution and density maps for planning and conservation, spatial data for marine species are often incomplete. The challenges of distribution and density mapping for marine species revolve around the complexities of conducting analyses using sparse survey sightings for ocean regions that are difficult to sample consistently and completely. Furthermore, the prohibitive cost of at-sea research and the extreme weather conditions common for northern coastal latitudes hinder the ability to collect species information. Consequently, studies of marine species often rely on zero-inflated sightings data (e.g., Oppel et al. 2012, Menza et al. 2016), include coarse resolution environmental predictors (Redfern et al. 2006), and produce solely spatial predictions rather than seasonal estimates (e.g., Winiarski et al. 2014). These factors likely contribute to lower model performance than may be standard in terrestrial studies, yet often represent the best available information for many marine species. In this study, explained deviance values from our GAMs are consistent with other prediction surfaces for marine mammals. For example, Mannocci et al. (2014) produced explained deviances for cetaceans in the South Pacific gyre between 5% and 30% and Best et al. (2015) generated values between 11% and 51% for marine mammals in coastal British Columbia. The limited number of non-zero observations in this study required the aggregation of sighting observations across seasons and years but nevertheless, represents the most up-to-date distributions for many marine mammals in British Columbia.

Placing hotspots in context

Prediction surfaces as standalone map products supply a wealth of valuable information, particularly for combating the shifting baseline syndrome (Pauly 1995) and acting to fill knowledge gaps in species distributions and densities. However, these maps can also be used to identify spatially explicit hotspots outlining potential candidate areas for future protection. Geographic areas showing consistent hotspots of intense use by marine species may indicate areas of persistent concentrations of productivity that attract elevated numbers of marine mammals and result in spatial aggregations of one, or more, species (Bouchet et al. 2015). Predictable hotspots may be driven by oceanographic conditions, which promote ocean mixing and elevated primary productivity, such as eddies, high current regions, or upwelling zones (Bakun 2006). In the northeast Pacific Ocean, trophic interactions are influenced from bottom-up processes, where concentrations of chlorophyll-*a* are highly correlated with elevated numbers of higher trophic-level organisms, including zooplankton and fish (Ware and Thomson 2005), and, in turn, attract mobile, high trophic-level predators. Regions supporting dense aggregations of species (i.e., hotspots) often represent favorable habitat and, given suitable protections (e.g., MPA status), provide an effective strategy to protect biodiversity (Hyrenbach et al. 2000).

Hotspots have long been used to guide spatial planning and conservation efforts to areas that will provide the greatest benefit given limited conservation resources (Myers 1988, 1990, 2003, Myers et al. 2000, Worm et al. 2003, Selig et al. 2014). Generally, hotspots for conservation purposes are identified with threshold cut-offs chosen in varying ways to separate extreme values that are considered "hot" from all other non-hot regions. Typically, thresholds are arbitrarily selected based on study context and data type (Cañadas et al. 2014). The threshold values vary among studies, often ranging somewhere between the top 2.5% and 10% of data values. For example, Ceballos and Ehrlich (2006) used distributions of land mammals to identify hotspots that represented the top 2.5% of species richness, endemism, and threatened species indices. Tolimieri et al. (2015), on the other hand, incorporated both 5% and 10% thresholds when extracting hotspots of demersal fish biodiversity. Although the top percentage approach provides data required to develop conservation plans, it does not account for potential bias that likely occurs when determining threshold values based on user opinion. Variability in threshold choices indicates a lack of consensus on the most appropriate strategy. Recognizing the limitations of subjective thresholds, we have applied methods from spatial statistics to quantify hotspots. The main differences between top percentage thresholds and spatial techniques are the ability to account for spatial patterns in the data and objectively identify hotspots.

Identifying hotspots

This study illustrates multiple approaches for detecting spatially explicit hotspots in marine mammal data. Our analysis demonstrated that the aspatial top 5% threshold produced the most conservative (smallest) hotspot outputs. In a changing climate with increasing anthropogenic pressures, conservative methods may not allow for sufficient uncertainty given that the spatial patterns of species distributions will likely change through time. Specifically, Hazen et al. (2013) suggest that by 2100, some marine predators in the northeast Pacific Ocean will exhibit up to a 35% change in highly used habitat, due to shifts in environmental conditions. Hotspots with highly patchy, complex, and convoluted geometry present highly precise hotspot borders. If MPAs are created based on these precise regions, they may not adequately protect core habitat regions should species distributions shift over time. Criticisms of incorporating hotspots into conservation planning often stem from the knowledge that marine species are mobile and, as predators, may shift their distributions if prey availability and environmental conditions change. Furthermore, survey areas do not include the entirety of the study species migratory range and will increase uncertainty in population trends because only a sample of the total population is recorded (Forney 2000). As a result, overly conservative estimates depicting very small hotspots may fail to identify regions large enough—typically larger than similar land-based reserves—to account for extensive migratory ranges and the dynamic processes that influence marine species and systems (Gerber et al. 2003, Hooker and Gerber 2004).

Our findings suggest that spatial techniques for identifying hotspots (based on detecting spatial patterns) may avoid the stated limitations of aspatial approaches (e.g., the top 5% threshold). Local measures of spatial association, such as G_i^*, provide robust and objective definitions of hotspots, when compared with aspatial methodology. Aspatial methods produce spatially patchy hotspots with more precise borders than may be warranted by the quality of the input data. In assessing methodological approaches, the G_i^* statistic has many advantages over the top percentage threshold. First, the G_i^* method is based on an arithmetic framework where thresholds to delineate a hotspot are derived from statistical values calculated by incorporating spatial patterns in the data. Second, spatial statistics account for spatial autocorrelation and form results that quantify the level of similarity between values as distance between them increases (Fortin and Dale 2009). Lastly, unlike aspatial approaches, G_i^* method employs a test hypothesis. Hypothesis testing differentiates spatial patterns generated from random process from those processes that generate clusters of species. The metric allows the inclusion of statistical significance measures to convey levels of uncertainty, which is important for making informed policy decisions. Using a statistical test to determine where realized processes are different than expected, based on null hypotheses of randomness, provides a mechanism to monitor a seascape for unexpected change in a variety of phenomena.

As our results indicate, different neighborhood definitions for G_i^* affect the number and size characteristics of defined hotspots. Queen contiguity definitions (lag 1 and lag 2) produce hotspots with smaller areas than those generated by the distance definition; however conversely, contiguity neighborhoods generate greater overall numbers of hotspots compared to the distance metric. These differences are to be expected, as the distance neighborhood is not confined to the boundaries of the hexagon grids. In this case, the spatial weights matrix can include observations further from the pivot point than lag 1 and lag 2 contiguity-based metrics. As a result, the distance-based parameters were far greater (up to 25.9 km) than those of contiguity, which extended only as far as two hexagon cells (~10 km). The distance-based technique thus produced larger hotspots. It is also pertinent to note that the areal unit (grid size) of the species distribution maps will influence hotspots generated by neighborhood metrics, as increasing grid sizes may generate larger and less numerous hotspots.

Hotspot comparison

We compared hotspots identified in this study with previous research conducted in the Queen Charlotte Basin to identify areas of consensus and divergence. Previous marine mammal research has highlighted regions where elevated occurrence of marine mammals is likely to occur. The high-density region along southeastern Haida Gwaii identified as a key hotspot for cetaceans aligns with notable areas for HWs distinguished by Dalla Rosa et al. (2012) using data from a similar period (2004–2006). The Kitimat Fjord System, adjacent to our study region, has been identified as a region frequented by rorqual whales (Keen 2017, Keen et al. 2017). Similarly, our GAMs show elevated densities of HWs and MWs in Caamano Sound, next to the Kitimat Fjord. However, this area did not produce significant hotspots for cetaceans, but instead, hotspots are present for pinnipeds. Additionally, archived locations where commercial whaling kills were greatest indicate regions where historical distributions and abundance were potentially high. Fin whale kills, mapped by Gregr and Trites (2001), were particularly prominent in Caamano Sound; however, our FW GAM did not indicate this as a high-density region. Recent observations of FW presence in Caamano Sound may suggest that recovery of this species in the region could be occurring and the survey data from this study were not recent enough to detect this use.

Most, but not all, hotspots identified by all four techniques in this study coincide with ecologically and biologically significant marine areas (EBSAs) that were classified based on expert opinion (Clarke and Jamieson 2006, Jamieson and Levesque 2014). EBSA zones identified as hotspots include Learmouth Bank, Chatham Sound, Caamano Sound, Dogfish Banks, Cape St. James, Scott Islands, and North Island Straits. Many EBSAs identified by Clarke and Jamieson (2006) are incorporated into three additional important nearshore regions listed by Jamieson and Levesque (2014). These include the nearshore region along the lower southeast tip of Haida Gwaii (Haida Gwaii/Queen Charlotte Nearshore), the island regions surrounding the community of Bella Bella (Bella Bella Nearshore), and from the north tip of Banks Island to the southern tip of Aristazabal Island (Central Mainland Nearshore). Congruence between hotspot maps, both within our hotspot methodological approaches and within previous research, emphasizes the validity of the results produced in this study.

The majority of hotspots show agreement with EBSAs; however, our study identifies additional important areas: areas adjacent to Cape Calvert in the Central Coast and the most southern area of Queen Charlotte Strait. The Cape Calvert hotspots are likely attributed to the high density of SSLs and DPs in this region, in addition to moderate densities of HWs, KWs, and PWs. Our results indicate that all marine mammals are present in the southern Queen Charlotte Strait; however, we note that only the most southern region was identified as a hotspot in our study, while the North Islands Straits EBSA include the entire strait region. In addition, our study identifies prominent hotspots located in the northernmost section of eastern and western Dixon Entrance, which appears to be driven by the occurrence of DP.

Management and conservation implications

Site-based conservation, which is often situated around extremely important areas for individual species, has been suggested as an effective measure for identifying regions of conservation prioritization for wildlife (Skov et al. 2007, Hinch and De Santo 2011). Yet, conservation efforts are limited without detailed information on species distributions and densities. Spatial locations where multiple species concentrate in predictable habitats can reveal important biological hotspots vital to further our understanding of distributional patterns and movements (Block et al. 2011) and to facilitate recovery strategies. However, species density maps provide snapshots of spatial patterns and should not be expected to remain constant, particularly for mobile species.

Since 2008, when the survey data were last collected, notable shifts in FW distributions have been recorded in Caamano Sound and changes in other species distributions are expected and likely to occur, particularly in populations recovering from significant depletion during the whaling era. In addition, rorqual whales have been recorded to frequent inlets and areas of the Kitimat Fjord System (Keen 2017, Keen et al. 2017), while portions of our study region near fjords did not show significant hotspot clusters for cetaceans. Consequently, the hotspots we have identified do not reflect recent distributional shifts, nor do they capture other potential discrepancies due to the age of survey dataset or possible edge effects due to the location of the study region. These points only reiterate and reinforce the importance of repeating surveys and call for additional caution when using hotspot information for planning purposes. This does not negate the usefulness of these data however, but instead, highlights the need to use these data in conjunction with other sources of information. Nearly a decade later, for many species, these survey data remain the best available information for distributions and abundance for marine mammals in BC and as a result, highlight the need for survey data to be repeatedly updated for conservation actions to be effective.

Predictions of marine mammal distributions and densities, as well as the quantification of hotspots, have immense potential for contributing to marine mammal conservation goals and objectives despite the stated limitations and cautionary recommendations. In Canada, several marine mammal species are listed under SARA and critical habitat designations have yet to be identified for the majority of listed species. Given that Canada's Pacific coastal ecosystems are subject to often intense anthropogenic pressures (e.g., Ban and Alder 2008), with a number of significant industrial projects being proposed (i.e., Pacific NorthWest LNG Project) in addition to experiencing the consequences of climate change, the identification of areas important to marine mammals is an important contribution to conservation and management efforts.

We found that the identification of geographic hotspots using spatial statistical methodology offers robust techniques for quantifying important habitat and locating species aggregations crucial to future planning efforts. Importantly, the delineation of regions of intense use is highly influenced by the method used to extract hotspots. Our findings suggest that hotspots identified based on spatial neighborhood characteristics, rather than arbitrarily determined threshold criteria, produce more objective and quantitatively defensible outputs. Further, hotspot regions we have identified coincide with previously identified important habitats for marine mammals. Agreement between studies suggests increased confidence in the effective application of spatial statistical methodology for hotspot identification and conservation prioritization.

Considering that the distribution and density patterns of marine mammals in north coastal regions of British Columbia are poorly understood, our study builds upon previous research of distributions and densities (Best et al. 2015) and provides assessments and comparison between various techniques for hotspot delineation. The results of this study can be applied within the broader framework of conservation planning (Margules and Pressey 2000, Pressey and Bottrill 2009) and incorporated into spatial planning software such as MARXAN and C-Plan. It is recognized that effective conservation strategies must be based on more than just the number of species in a region, and comprehensive conservation strategies cannot be centered exclusively on the number of species of a particular taxon present in an ecosystem. Nevertheless, hotspot information, as we have defined it, is important for setting conservation priorities and is increasingly important in decision-making for cost-effective strategies to preserve biodiversity. Hotspots can be dynamic and often ephemeral, but that does not diminish their ecological importance. Rather, it compels conservationists to continually monitor and adapt management strategies to environmental changes. As the field of conservation planning continues to evolve, the methodology used to derive spatial inputs for future planning initiatives should also be further refined. This research provides alternative approaches for quantifying hotspots of species distributions in the marine environment and provides further development in the application of spatial pattern-based methods supporting future marine conservation.

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