Delineating important killer whale foraging areas using a spatiotemporal logistic model

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ABSTRACT

Conservation management planning for highly mobile species requires an understanding of the distribution of areas that are biologically important to the species of concern. Collecting data on the locations of animal behaviors linked to biological characteristics, such as foraging, can be used to spatially describe biological important areas. However, spatial modeling of free-ranging animal behavior can be challenging, as behavioral observations of animals are often clustered, and sampling is commonly conducted at a higher frequency than changes in behavioral states, resulting in data that are usually highly autocorrelated in space and time. Here, we fit latent Gaussian process models to observational behavioral data to generate spatially-explicit predictions of foraging behavior within the critical habitat of an endangered population of fish-eating killer whales (*Orcinus orca*) in southern British Columbia, Canada, and northern Washington State, USA. We compare spatial models treating temporal autocorrelation in behavior in three ways: (1) ignoring temporal autocorrelation entirely; (2) traditional data-thinning to remove temporal autocorrelation, and; (3) using a temporal Gaussian process to account for temporal autocorrelation. Comparisons of autocorrelative structures for each model and visual comparison of broad spatial patterns demonstrate that our third approach yields more accurate results than when ignoring temporal autocorrelation entirely and higher precision results than when applying data-thinning methods. Within the identified areas of critical habitat, our models indicate two primary regions of intense killer whale foraging activity, and we delineate areas wherein the probability of foraging was particularly high as candidate locations for conservation management actions. This study underscores the value of refining our understanding of high-use areas for at-risk species by incorporating animal behavior data to inform area-based conservation measures.

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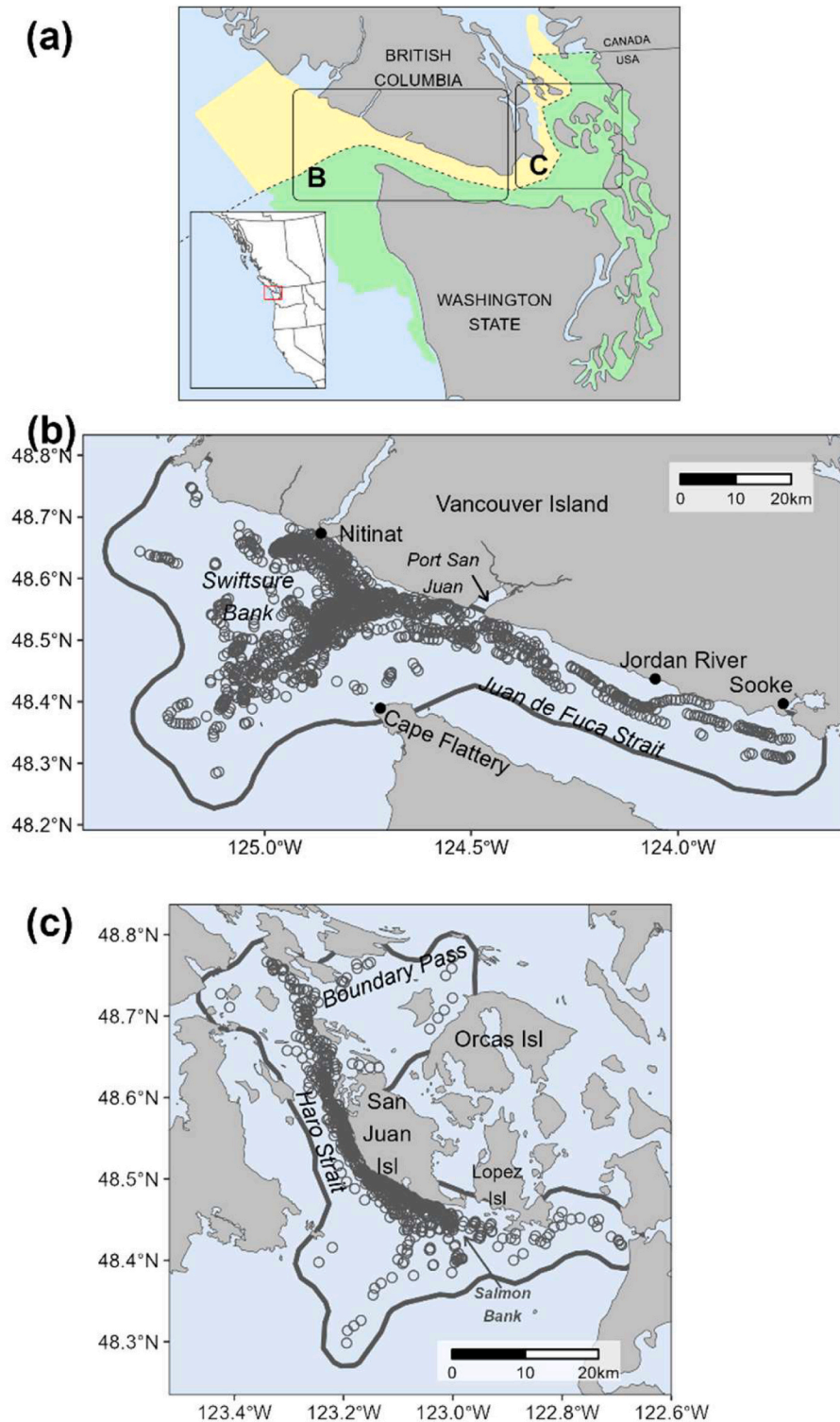
Fig. 1. Behavioral studies incorporated in this analysis primarily took place within (a) southern resident killer whale critical habitat in Canada (yellow) and the USA (green). Observations of traveling and foraging southern resident killer whales (grey circles) from (b) Thornton et al. (2022) in the Swiftsure Bank and Juan de Fuca region , and (c) from Noren et al. (2009) and Holt et al. (2013) in Haro Strait and adjacent waters. Polygons outlined in dark gray indicate the geographic extents of our models.

1. Introduction

Area-based management is a common strategy used in the conservation of at-risk species, ecosystem services and community biodiversity (Maxwell et al., 2020). Models of species distribution are often used to inform these spatial conservation efforts. However, while species distribution defines *where* the animals are, it provides little insight into *why* or *how* animals use their environment. Understanding how individuals interact with features within their habitat to improve their chances of survival and reproduction is one of the key pillars of the field of animal behavior (Tinbergen, 1963; Bateson and Laland, 2013). Incorporating animal behavior into these spatial descriptions is not common practice but is imperative for understanding the function that high-use areas provide a species (Caro, 1999; Camphuysen et al., 2012), and ultimately improves conservation outcomes (Johnson, 1980; Greggor et al., 2019; Hale et al., 2020). Including considerations of ecologically important animal behavior in spatial conservation measures is especially crucial for animals whose behaviors are differentially sensitive to disturbance by anthropogenic activities (Lusseau and Higham, 2004; Marty et al., 2019; Holzner et al., 2020). Spatial modeling of behavior not only provides a spatially explicit description of the functions of a species' habitat, but also allows investigation into what factors drive observed spatial patterns in behaviors and predictions of how those patterns may change under a variety of future scenarios (e.g., resource use, climate change).

Direct behavioral observations in free-ranging animals has formed the cornerstone of the field of ethology (Hinde, 1966; Lorenz, 1970, 1981; Altmann, 1974) and, more recently, contributes to the fields of behavioral ecology and conservation behavior (Sutherland, 1998; Buchholz, 2007). While the use of direct behavioral observations has been instrumental in the conservation of a number of species and has led to substantial recovery efforts through a greater understanding of the function and subsequent protection of high use habitat areas (notable examples include Jane Goodall's seminal observations on chimpanzees (*Pan troglodytes*; van Lawick-Goodall, 1968) and Joyce Poole's influence on conservation and protection of African elephants (*Loxodonta* spp.; Poole and Moss, 2008, Poole and Granli, 2021)), the field of conservation behavior has been slow to emerge (Buchholz, 2007; Berger-Tal et al., 2011).

Due to the logistical difficulties of data collection, the resources required to collect sufficient observations to support advanced statistical methods, and the analytical challenges faced when examining data collected irregularly and/or using different sampling protocols, spatial modeling of free-ranging animal behavior more commonly occurs using biologging technology and behavioral inference from movement parameters (Wang et al., 2016; Wang, 2019; Jeantet et al., 2021). However, direct behavioral observations can provide many benefits, including the potential for less invasive and impactful data collection (Hawkins, 2004; e.g. Mulero-Pázmány et al., 2015), allowing for data collection from small at-risk populations where tagging operations may not yield sufficient data to offset the perceived risk to individuals. Direct behavioral observations also offer higher resolution sampling and more accurate classification of behaviors (e.g. Torres et al., 2018), the ability to collect individual and group behaviors concurrently (e.g., Ciuti et al., 2012; Noren and Hauser, 2016), the capacity to provide real-time contextual data for observations (e.g., group influence: Treherne and Foster, 1981; interspecific proximity or interactions: Creel and Winnie Jr, 2005; human activity in vicinity: Tarjuelo et al., 2015), and superior locational accuracy of observations (Rutz and Hays, 2009; Frair et al., 2010; e.g. Mulero-Pázmány et al., 2015).

Behavioral observations can be challenging to use in spatial analyses. Observations of animals are often opportunistic (particularly for rare or cryptic animals and/or challenging habitats) and clustered, where sampling is commonly conducted at a higher frequency than changes in behavioral states, resulting in data that are typically highly autocorrelated in space and time. In recent years, advancements in statistical approaches have allowed these challenging ecological data to be appropriately analyzed, such as through Hidden Markov modeling and similar state-space modeling (e.g., Macdonald and Raubenheimer, 1995; Schliehe-Diecks et al., 2012; Leos-Barajas et al., 2017). These approaches can generate spatially explicit predictions while accounting for spatial and temporal autocorrelation, and other complex structures and errors, and often rely on simulation-based Bayesian inference (e.g. Markov chain Monte Carlo, MCMC). As an alternative to this computationally expensive fitting method, integrated nested Laplace approximation (INLA) presents a fast approximate Bayesian method to fit latent Gaussian process models (Rue et al., 2009). INLA has been demonstrated to be an accurate and efficient approach to the spatial analysis of complex ecological data (Beguin et al., 2012; Yuan et al., 2017; Watson et al., 2021) that we now extend to mapping species behavior.

Here, we use behavioral data collected from an endangered population of killer whales (*Orcinus orca*) within their designated critical habitat to reveal the function of discrete areas within it. Southern resident killer whales (SRKW) comprise an endangered population of 73 animals (Center for Whale Research, 2022) that range from southeast Alaska to California, USA, in the northeast Pacific Ocean. The SRKW population are fish specialists, feeding predominantly on salmonids, and in the summer months, primarily on Chinook salmon (*Oncorhynchus tshawytscha*). This population is listed as Endangered under Canada's *Species At Risk Act* (SARA) and the USA's *Endangered Species Act* (ESA) (Species at Risk Act, 2002; National Oceanic and Atmospheric Administration NOAA, 2005), and critical habitat for the population has been designated in both countries (NOAA, 2006; Canada Gazette, 2009, 2018; NOAA, 2021) (Fig. 1a).

Our spatial analysis focuses on SRKW foraging behavior. We consider this behavior to be significantly important to the conservation of this population, as it is not only an essential life function but is directly affected by two of three primary threats to the survival and recovery of this population: reduced prey availability, and physical and acoustic disturbance from vessel traffic (Fisheries and Oceans Canada, 2018; NMFS, 2021). In particular, resident killer whales rely on sound for foraging, using echolocation for hunting and producing pulsed calls and whistles for communication among foraging group members (Ford, 1989). Additionally, foraging behavior has been shown to be disproportionately sensitive to human disturbance in resident killer whales (Williams et al., 2006; Lusseau et al., 2009).

2. Methods

2.1. Behavioral data

This analysis used boat-based observations of SRKW behavior that were collected within their core summertime habitat by three studies: Noren et al. (2009) in 2006 and Holt et al. (2013) from 2007 to 2009 in the Haro Strait region, and Thornton et al. (2022) from 2018 to 2021 in the Swiftsure Bank region (Fig. 1). These studies were conducted during the summer months, with some extension into the spring or fall (Noren et al., 2009: May-August; Holt et al., 2013: May-September; Thornton et al., 2022: June-August). While all observations from these studies were collected in serialized fashion, with individuals and/or groups surveyed over a period of time on a given day and their behavioral state assessed at distinct time intervals, the studies were conducted using different sampling protocols. Noren et al. (2009) and Holt et al. (2013) both documented behavioral states continuously every 10 min via instantaneous scan sampling (see Mann, 1999). However, where Noren et al. (2009) conducted individual focal follows, traveling parallel to and assessing the behavior of an individual focal animal (along with any individuals the focal animal was closely associated with in space), Holt et al. (2013) assessed the behavior of all individuals within 1 km of the research vessel, with the vessel shut down and positioned ahead of focal animals' path. Thornton et al. (2022) undertook two sampling methods: (1) individual focal follows, where the behavioral state of a focal animal was documented continuously via instantaneous scan sampling every 5 min as the research vessel traveled parallel to the path of the focal individual, and; (2) group behavioral surveys (GBS), where the research vessel transited among spatially discrete groups, travelling parallel to or following the path of a given focal group for a 5 min observation window and documenting its predominant activity (where the behavior must be exhibited by at least half the animals in the group for at least half the observation time; Mann, 1999) before transiting to the next focal group. For the purpose of our analysis, we consider data collected by these two methods in Thornton et al. (2022) as separate studies. Behavioral assessments in each of the four studies were terminated when the focal animal or group was lost to observers or when adverse conditions (e.g. inclement weather) precluded interpretation of behaviors. Were these conditions not previously met, Noren et al. (2009) suspended follows after 40 min of continuous sampling, Holt et al. (2013) ended behavioral sampling when the focal group moved beyond 1 km of the research vessel, Thornton et al. (2022) terminated follows after 60 min of continuous sampling or when active foraging activity ceased after 60 min, and Thornton et al. (2022) ended GBS sampling when no new groups were available for assessment. Herein we use the term "survey" generally, to refer to a bout of behavioral sampling resulting in a collection of observations, regardless of sampling method. We considered consecutive observations from a given study made more than two hours apart to belong to different, independent surveys.

Field observations of killer whale behavior for these studies were conducted under the authority of: US ESA NMFS permit no. 781–1824–00 and Canadian SARA permit no. 33 (MML 2006–07) (2006 observations; Noren et al., 2009); US ESA NMFS permit no. 781–1824–00 and Canadian SARA permits no. 68 A (MML 2007–08) and no. 85 (MML 2008 05) (2007–2009 observations; Holt et al., 2013), and; Canadian SARA permits no. XMMS 04 (MML-06) and no. 2018–001 (MML-01) and US ESA NMFS permit no. 21348 (2018–2021 observations; Thornton et al., 2022). Animal use protocols for 2018–2021 data collection by Thornton et al. (2022) were reviewed and approved by the DFO Pacific Region Animal Care Committee (Canadian Council on Animal Care certificate holder).

All four studies used established killer whale behavioral state categories: foraging, traveling, socializing, and resting (Ford, 1989). In addition to those four behavioral states, Holt et al. (2013) and Thornton et al. (2022) noted "travel-forage" or "search phase" behavior, respectively, where whales search for prey while transiting (Ford et al., 1994; Williams et al., 2006; Williams and Noren, 2009). Observations of this prey-searching behavior were reclassified as foraging for our analysis. For behavioral observations made in 2006 (Noren et al., 2009), prey-searching behavior was not differentiated from traveling and thus was unable to be reclassified. As foraging was our behavior of interest, and as exploratory variograms indicated strong spatial correlation of traveling and foraging behavior within both study regions but no such correlation for socializing and resting behaviors, data were filtered to only include observations of foraging and traveling. These two behavioral states formed the binary response variable for our models (Travel=0, Forage=1).

To ensure adequate spatial coverage of our data and avoid overextending our model predictions to areas with few data points, data records were filtered to exclude behavioral observations with geographic locations considered outliers. Outliers were defined as observations with latitudinal or longitudinal positions outside 1.5 times the interquartile range above the upper and below the lower quartile of locational positions in the dataset. Modeling extents were defined by a non-convex hull of observation locations within each region, extended by a 5% buffer, with simplified coastline removed.

To explore the temporal correlation of observations, we computed the proportion of pairwise observations that shared the same observed behavioral state at each time lag within a survey. Using the *Segmented* package in R, a segmented regression was then fitted to

Table 1

Summary of behavioral datasets used to inform models showing the number of southern resident killer whale observations by behavior, number of surveys conducted, and the mean, median, and maximum duration for the surveys.

Region	Dataset	No. observations			No. surveys	Survey duration (min)		
		Travel	*Forage*	*Total*		*Mean*	*Median*	*Max*
Haro	Complete	484	349	833	81	171	182	390
	Thinned	221	172	393	81	163	174	390
Swiftsure	Complete	937	854	1791	108	140	116	581
	Thinned	296	278	574	108	134	114	581

estimate the time lag at which the variability of observations became asymptotic (R Core Team, 2021; Muggeo, 2003, 2017). As sampling rates and the extent of temporal correlation of observations were relatively consistent among years and across studies within the same region, all observations from within each region (Haro and Swiftsure) were combined to inform our models (Table 1).

2.2. Spatial modeling

2.2.1. Approach

To estimate the probability of foraging within the two study regions, a spatiotemporal model with a Bernoulli error distribution was fit to each region's data using the Bayesian inference approach of integrated nested Laplace approximations (INLA; Rue et al., 2009), executed by the R package *inlabru* (Bachl et al., 2019):

$$\text{logit } p\,(i,s,t) = \text{beta}_0 + Z(s) + f(i,t) \tag{1}$$

where i is a given survey, s is the spatial location of a behavioral observation within a survey, and t is the number of minutes into the ith survey. The probability of foraging depended on both a spatial and a temporal Gaussian process, $Z(s)$ and $f(i,t)$ respectively, where the predicted probability of foraging at a given location was estimated as logit^{-1} ($\text{beta}_0 + Z(s)$). The spatial Gaussian process was approximated over a two-dimensional computational mesh of Delauney triangulations informed by the extent of the observations' spatial locations from the given region, with an outer extension of increasingly distant nodes serving to reduce edge effects. The maximum distance among interior nodes was bound between 4 and 20 km and the minimum triangle angle was limited to 21 degrees, following the advice of Righetto et al. (2018). The temporal Gaussian process was approximated over a one-dimensional mesh of a length equivalent to the maximum survey duration from the given region, with nodes located every 5 and 10 min, for the Swiftsure and Haro regions respectively, assuming the killer whale foraging behavioral state typically persisted for longer than this (Table 2). The spatial and temporal processes were modelled using Matérn stochastic partial differential equations (SPDE; Lindgren et al., 2011). Penalized complexity (PC) priors were applied to the SPDE model parameters to reduce the risk of the processes overfitting the data (Fuglstad et al., 2019) (Table 2). Further, to reduce the risk of spatial confounding, the temporal process was replicated by survey and a sum-to-zero constraint was applied to each replicate.

2.2.2. Temporal Gaussian process validation

To assess the validity of using a Gaussian process to account for temporal autocorrelation, we built spatial models without the temporal process fit to: (1) each region's complete dataset and (2) each region's dataset thinned to remove temporal autocorrelation (Table 1). The latter datasets were derived by filtering for observations that were at least 25 min apart in the Haro dataset and at least 20 min apart in the Swiftsure dataset. These temporal thresholds were informed by the segmented regression of our pairwise observations (previously described) as well as an autocorrelative assessment of the residuals of the space-only model using the complete datasets. Predictions from these two space-only models were visually compared to those of the spatiotemporal model to assess its accuracy; similar broad outcomes between the space-only, data-thinned model and the spatiotemporal model allowed us to infer accuracy of the latter model. Additionally, we computed functions of autocorrelation (ACF) and partial autocorrelation (PACF) (customized to incorporate uneven time steps and replicates) from the residuals of the three models to determine whether there was any evidence of temporal autocorrelation remaining.
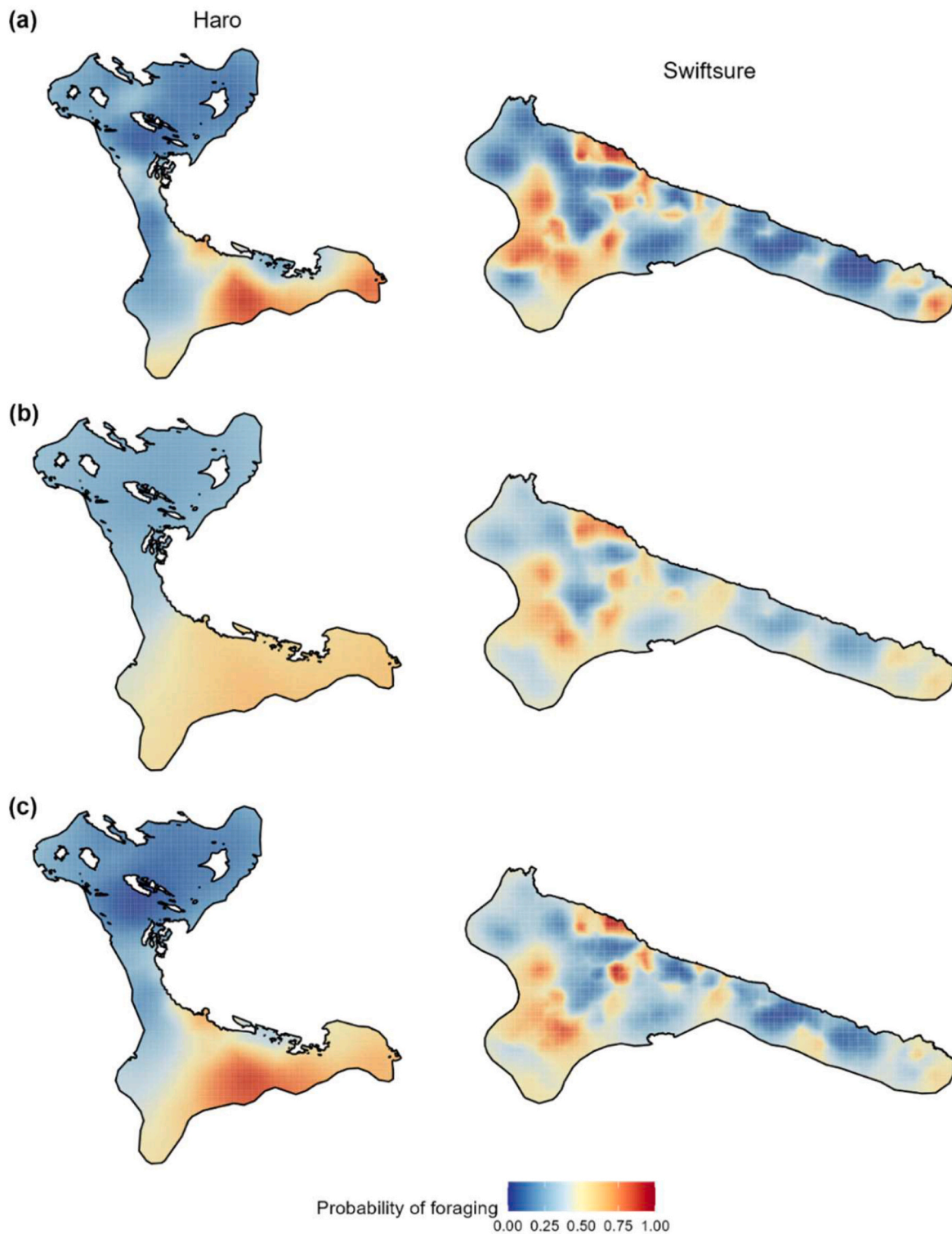
2.2.3. Model predictions

For each model, 1000 samples were generated from the approximated posterior distribution of the model parameter estimates over the spatial mesh, projected onto a 200 m x 200 m resolution pixel field. Posterior frequency statistics were then computed for each pixel.

To determine whether predictions derived from our spatiotemporal models could be interpreted as the probability of foraging at a given location conditioned on the event that they are either foraging or traveling at specific locations, we assessed several aspects of our temporal Gaussian process from our covariate-less spatiotemporal model. First, we computed the average time effect for each survey to confirm that our sum-to-zero constraint was appropriately applied to each replicate. This was done by generating 100 samples of the mean time effect for each survey extrapolated over the entire time mesh. Second, we examined whether average time effects showed any apparent spatial pattern (i.e. evidence of spatial confounding). To do this, we generated 100 samples of the mean time effect for each survey over our observations, then fit a generalized additive model (GAM) for a survey's mean time effect as a

Table 2

Description of Matérn SPDE model parameters informing the spatial and temporal Gaussian processes and the priors applied to them.

Process	Region	No. mesh nodes		Mesh interval	Mesh extent	PC prior settings			
		Complete dataset	*Thinned dataset*			*Range*		*Standard deviation*	
						Value	*Probability*	*Value*	*Probability*
Temporal	Haro	40	n/a	10 min	390 min	10 min	0.01	2	0.01
	Swiftsure	117	n/a	5 min	580 min	10 min	0.01	2	0.01
Spatial	Haro	649	629	n/a	n/a	2 km	0.01	2	0.01
	Swiftsure	1253	1243	n/a	n/a	2 km	0.01	2	0.01

Fig. 2. Posterior mean predictions of covariate-less models showing the spatial distribution of SRKW foraging probability for the three modeling approaches: (a) space-only model using complete datasets (i.e. no attempt to deal with temporal autocorrelation), (b) space-only model using datasets thinned to remove temporal autocorrelation, and (c) spatiotemporal model using complete datasets, where a temporal Gaussian process is used to deal with autocorrelation.
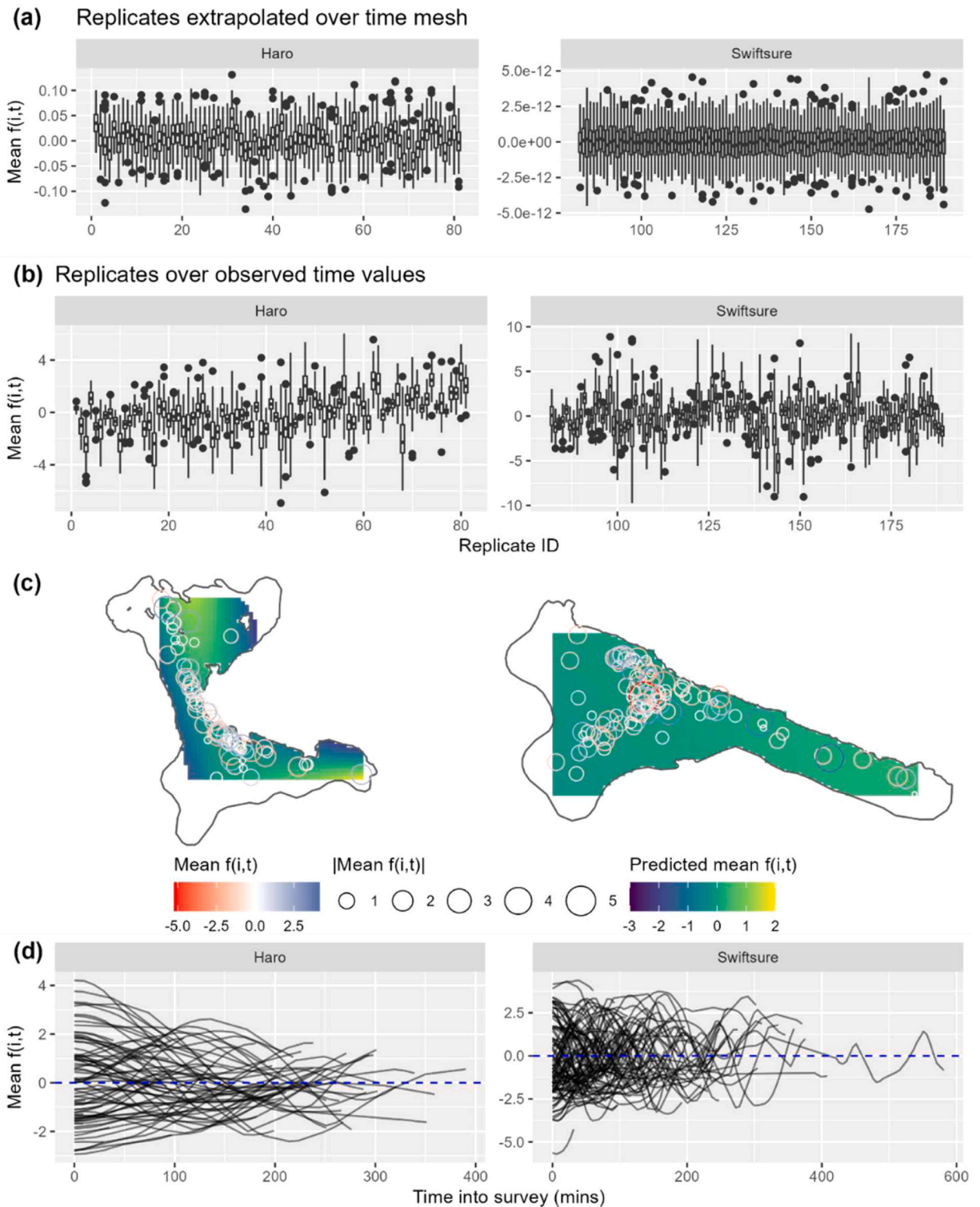
Fig. 3. Validation that temporal autocorrelation was accounted for within our covariate-less spatiotemporal model of SRKW foraging, for each study area. Temporal Gaussian process diagnostics for our covariate-less spatiotemporal model include:the average time effect of each survey (replicate) (a) extrapolated over the entire range of the time mesh, (b) within a survey's observed range, (c) at a survey's mean spatial location, and (d) over the duration of a survey.

function of its mean spatial location. And third, we assessed how the time effect changed over the course of a survey (i.e. whether the act of 'following' affected the observed behavior of the focal whale(s)). For this, we computed the mean time effect at each time step (averaged over 100 posterior samples) in a given survey and evaluated the overall trend of these time effects over the duration of surveys.

To assess the potential effect of the different sampling methods used among studies, as well as behavioral variability among study years, we compared our covariate-less spatiotemporal model to two others that included study and year as fixed effects, respectively. We compared this set of spatiotemporal models and selected the top-ranked models using Deviance information criterion (DIC; Spiegelhalter et al., 2002) and Widely Applicable or Watanabe-Akaike information criterion (WAIC; Watanabe, 2010) score comparisons. Models with score differences less than four (when compared to the score of the top-ranked model) were considered among the top model set.

We visualized "common foraging areas" (CFAs) and "frequent foraging areas" (FFAs) as predicted by our top-ranked spatiotemporal model, defined by pixels wherein the predicted probability of foraging exceeded 0.25 and 0.50, respectively. Pixels with predicted probabilities that met those criteria in more than 80% of the model's posterior samples were contoured to delineate the most probable foraging areas in each region.

3. Results

3.1. Model validation

Residuals of our space-only model informed by our complete datasets exhibited apparent temporal autocorrelation in ACF values and these models produced predictions of high confidence where probabilities of foraging were often close to 0 and 1 (Fig. 2a). This suggested an underestimation of uncertainty and a relatively uninformative model. Our space-only model informed by thinned data showed no indication of residual temporal autocorrelation in ACF or PACF values, and its predictions were of lower precision (and therefore of significantly lower spatial resolution, i.e. over-smoothed), where probabilities of foraging were of lower confidence, typically closer to 0.5 (Fig. 2b). Our spatiotemporal model (Fig. 2c) predicted similar broad outcomes to our space-only model using thinned data and the residuals of the spatiotemporal model did not show any evidence of temporal autocorrelation in ACF or PACF values, suggesting that the model provided accurate predictions and the temporal Gaussian process adequately accounted for temporal autocorrelation. The large gain in predictive precision using this spatiotemporal approach led to substantially increased spatial resolution of predictions (and therefore superior resolution of predicted foraging areas), compared to the data-thinning approach (Fig. 2).

The average time effect for each survey extrapolated over the full extent of our temporal mesh was near-zero, confirming that our sum-to-zero constraint was properly applied to each replicate (Fig. 3a). As survey durations varied, the average time effect over the actual observational range for each replicate was not necessarily near-zero (Fig. 3b). However, these time effects did not show any apparent spatial correlation; a survey's average spatial location was a statistically insignificant predictor of its mean time effect according to our GAMs (Haro: F=0.69, p = 0.63; Swiftsure: F=0.22, p = 0.88; Fig. 3c), with all areas in both regions having predicted mean time effects with confidence intervals that overlapped zero. This provided strong evidence that our spatial effect was being estimated free from any confounding by the temporal Gaussian process.

3.2. Model predictions

The average time effect over the course of surveys did not exhibit any change, with average time effects remaining symmetrical about zero over the duration of surveys (Fig. 3d). This suggested there was no apparent average effect of following animals on their observed behavior. Considering this and the lack of confounding by the temporal Gaussian process, we submit that the probability values predicted by our spatial Gaussian process represent the conditioned probability of SRKW foraging at a given location.

Table 3
Ranking of candidate models with the complete dataset and the thinned dataset, and respective model components according to WAIC and DIC scoring. The information criterion values for the space-only models are excluded from score comparisons as they are based on different assumptions than the spatiotemporal models (i.e. they ignore temporal autocorrelation altogether or are informed by a different dataset). Top-ranked model(s) for each region, according to score differences less than four, are indicated in bold.

Region	Dataset	Model components				WAIC	DIC	ΔDIC
		Spatial process	Temporal process	Study	Year			
Haro	**Complete**	x	x		x	**765**	**782**	**0**
	Complete	x	x	x		791	807	25
	Complete	x	x			830	849	67
	Complete	x				n/a	n/a	n/a
	Thinned	x				n/a	n/a	n/a
Swiftsure	**Complete**	x	x		x	**1628**	**1680**	**0**
	Complete	x	x			1637	1691	11
	Complete	x	x	x		1651	1699	19
	Complete	x				n/a	n/a	n/a
	Thinned	x				n/a	n/a	n/a

SRKW exhibited more persistent behavioral states in the Haro study area than in the Swiftsure study area, where in the latter animals switched between behavioral states more frequently within a given survey ($t_{df=187} = -3.24$, $p < 0.01$; Fig. 3d). In the Haro region, animals exhibited on average 0.69 behavioral state changes every survey hour (95% CI = 0.55–0.83; i.e. a change every 87 min, on average). Whereas in the Swiftsure region, animals switched between behavioral states more often, exhibiting on average 1.22 changes every survey hour (95% CI = 0.97–1.48; i.e. a change every 49 min, on average). This regional difference in behavioral state persistence was reflected in the ranges of each region's temporal Gaussian process: Haro's temporal process had a mean range ±mean SD of 217.9 ± 2.3 min, while Swiftsure's temporal process had a mean range of 65.2 ± 3.0 min.

For both regions, the top-ranked spatiotemporal model included year as a fixed effect (Table 3).

In the Haro region, the probability of foraging increased over the study years and in the Swiftsure region, the probability of foraging varied among study years as well (Fig. 4).

As data collected in the Haro region in 2006 did not consider prey-searching behavior to be 'foraging' and data collected in the region from 2007 to 2009 did, we consider the difference in predicted foraging probabilities between 2006 and subsequent years too confounded by the discrepancy in behavioral classifications to infer any biological reason for such a difference to exist. When controlling for the effect of year (as a fixed effect) and time (via the temporal Gaussian process), the spatial effect in the Haro region had a mean range±mean SD of 44.1 ± 1.2 km, while the Swiftsure model exhibited smaller spatial ranges, with a spatial Gaussian process mean range of 6.8 ± 2.2 km.

Notably, in the Swiftsure region, a study's data collection method had no significant effect on model outcomes, with our spatio-temporal model including study as a fixed effect ranking worse than our covariate-less spatiotemporal model (Table 3), demonstrating that individual focal follow and group behavioral survey sampling predicted similar spatial patterns of the examined behaviors. In the Haro region, because studies did not run concurrently and as Noren et al. (2009) only collected data for a single year, we were unable to distinguish the variability among the Haro region studies from potential interannual variability.

CFAs were identified in both regions. CFAs of the highest confidence were considered those where the pointwise probability of foraging exceeded 25% in more than 80% of our model's posterior samples. In the Haro region, a single, large highest-confidence CFA of 617 km^2 was delineated that encompassed the central and southern portions of the Haro model extent (Fig. 5). In the Swiftsure region, 12 highest-confidence CFAs greater than 1 km^2 were identified. Covering a total of 1081 km^2, these areas ranged in size from 1.05 km^2 to 608 km^2 (median = 24.5 km^2, mean = 90.1 km^2) and occurred in waters skirting Swiftsure Bank, north and south of the mouth of Port San Juan, and off Nitinat, Sooke and Jordan River (Fig. 5).

FFAs, where the pointwise probability of foraging exceeded 50%, were identified in both regions. Like CFAs, we considered FFAs of highest confidence when they met the FFA criterion in more than 80% of our model's posterior samples. In the Haro region, the highest-confidence FFAs were identified as an area of 338 km^2 along southwest San Juan Island, near the mouth of False Bay, and two areas of 13 and 3 km^2 east of Salmon Bank (Fig. 6). In the Swiftsure region, ten highest-confidence FFAs were identified, totaling 326 km^2 (mean = 32.6 km^2, median = 11.3, range = 5–122 km^2). These FFAs were located surrounding Swiftsure Bank, including off Nitinat, and within the Juan de Fuca Strait (Fig. 6).
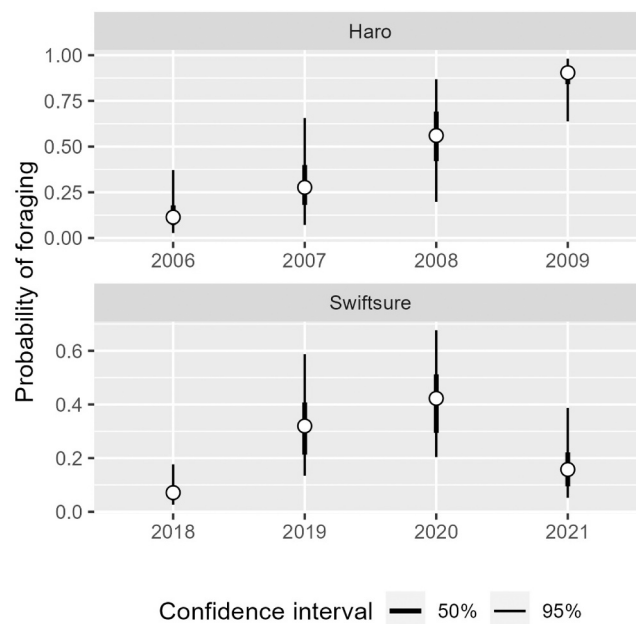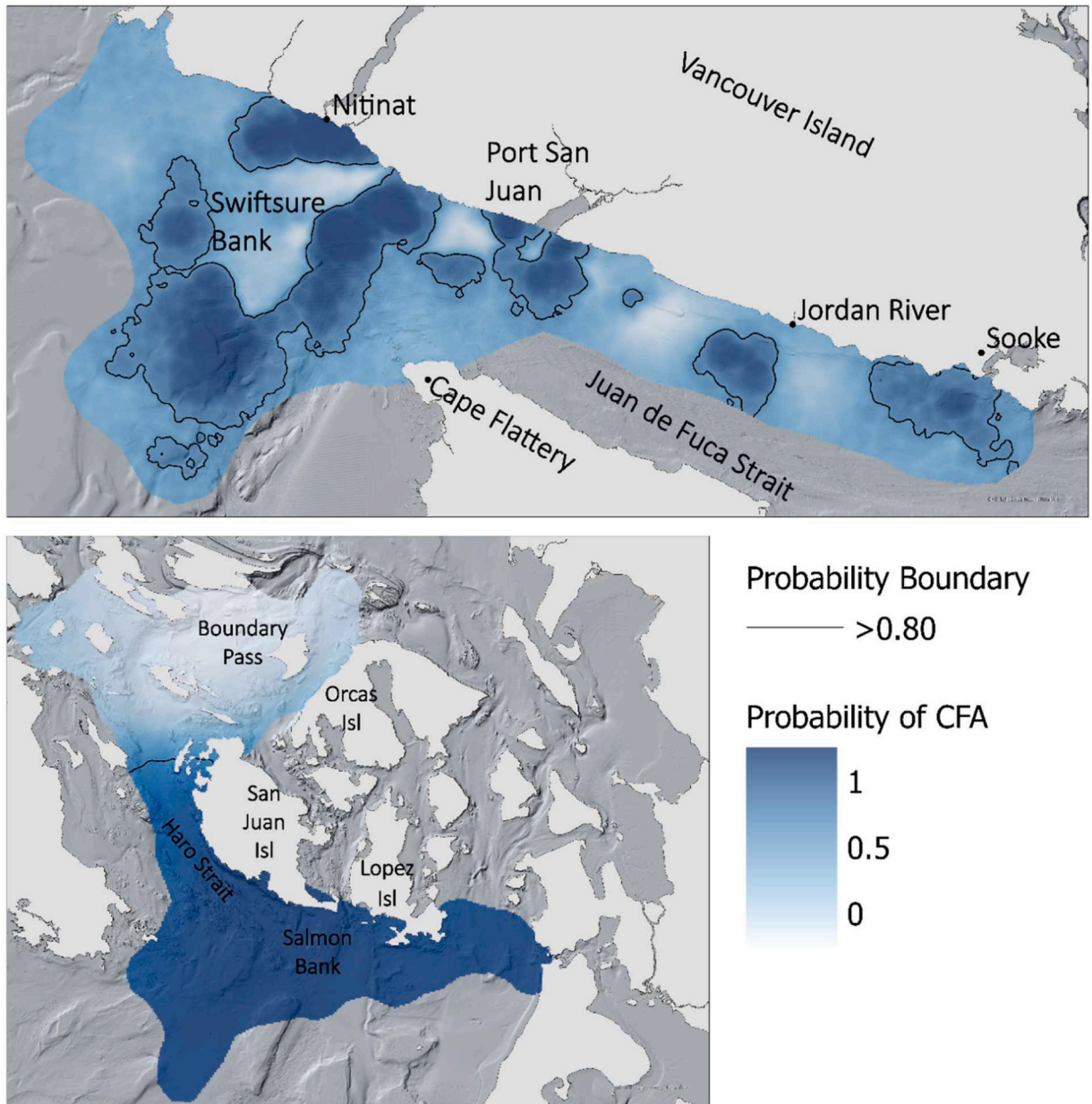

Fig. 4. Effect of year on the probability of southern resident killer whale foraging as predicted by the top-ranked spatiotemporal model for each region with 50% and 95% confidence intervals.

Fig. 5. Common foraging areas are defined as locations where the probability of foraging exceeded 0.25, as predicted by the top-ranked spatio-temporal models for (a) the Swiftsure Bank region and (b) the Haro Strait region. The probability of the area being a common foraging area is indicated by the blue gradient scale. Gray areas are outside the geographic extents of our model.

4. Discussion

The Haro Strait region and the Swiftsure Bank region represent two important areas for SRKW wherein foraging is a substantial seasonal use of the habitat. Through this analysis we have delineated areas of particularly intense foraging activity within both regions. In the Haro Strait region, there was an apparent north-south gradient in SRKW foraging behavior, where the probability of foraging was particularly high along the southwest shoreline of San Juan Island, as well as at and south of Salmon Bank. This is consistent with a previous spatial analysis of Noren et al.'s (2009) 2006 data (Noren and Hauser, 2016) as well as other SRKW behavioral and prey selection studies from the region (Heimlich-Boran, 1988; Hoelzel, 1993; Lusseau et al., 2009; Ashe et al., 2010; Hanson et al., 2010) that also indicate foraging as the predominant activity state southwest of San Juan Island and traveling behavior more probable further north in the region. Previous spatial modeling of SRKW behavior in the Haro Strait region from Ashe et al. (2010) does not deal with temporal autocorrelation, so direct comparison of foraging probabilities presented in that work and this study is not recommended, as
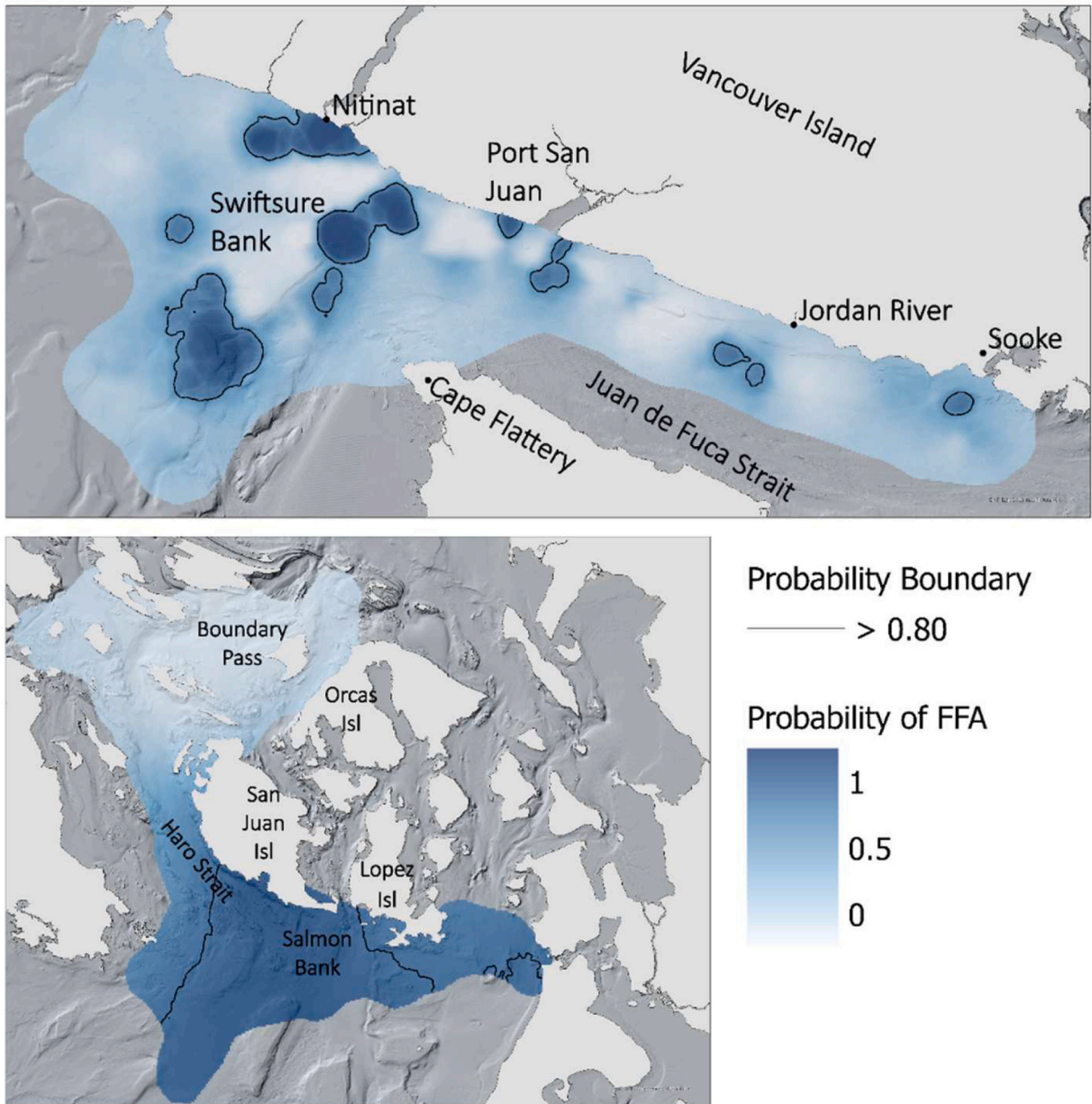
Fig. 6. Frequent foraging areas are defined as locations where the probability of foraging exceeded 0.5, as predicted by the top-ranked spatio-temporal models for (a) the Swiftsure Bank region and (b) the Haro Strait region. The probability of the area being a frequent foraging area is indicated by the blue gradient scale. Gray areas are outside the geographic extents of our model.

the probability values cannot be interpreted in the same way. Notably, Ashe et al.'s (2010) model predictions closely resemble the predictions from our first model approach that ignores temporal autocorrelation (Fig. 2a). No previous studies on SRKW behavior have been conducted in the Swiftsure area, and so these results represent the first comprehensive analysis of the functions the region provides to the SRKW population. Previous research has suggested that the Swiftsure Bank region is a significant SRKW foraging area (Ford, 2006; Ford et al., 2010, 2017; Hanson et al., 2010).

Foraging areas are commonly defined as areas wherein foraging is the predominant behavior exhibited (e.g., Noren and Hauser, 2016; McComb-Turbitt et al., 2021). Here we do the same in describing frequent foraging areas (FFAs), wherein the pointwise probability of foraging is greater than 50%. However, in addition to FFAs, we also present common foraging areas (CFAs) wherein SRKW forage regularly, though not predominantly. Given the endangered status of SRKW and the threats they face including reduced prey availability, we consider it prudent to present these broader foraging areas for conservation consideration. CFAs capture areas adjacent to FFAs where SRKW foraging may be more opportunistic or where they may forage while in transit. Protection of the foraging

environment in these areas could support greater overall foraging success and therefore should be considered when evaluating options for mitigation and recovery actions. Selection of management areas must often consider the balance between their ecological value and the economic and social costs of their management, both of which increase with the size of the area; areas should be large enough to be effective, but small enough in size and/or number to feasibly allow for monitoring and enforcement (Halpern, 2003; Ashe et al., 2010; Slooten, 2013). In presenting a suite of foraging areas of varying scales, we offer several options that might satisfy both practical and ecological requirements for effective and successful management of important SRKW habitat.

We caution against making regional comparisons between our model results from the Haro and Swiftsure study areas. Behavioral data from these two regions were collected nearly one decade apart and the characteristics of the datasets (e.g., sampling rates, sample sizes) differ significantly. For example, while there was a significant difference in the persistence of behavioral activity states between the Haro and Swiftsure study regions, where in the latter animals typically switched between behavioral states more frequently within a given survey, we consider this difference too confounded by the discrepancy in the regions' sampling protocols and the disparity in the timing of the regions' studies to speak to any potential biological reason that such a difference in behavioral persistence between the regions might suggest. We reiterate that in this study we refer to "behavioral (state) persistence" as the continuity of a given behavioral state exhibited by an individual or group *within a behavioral survey*, as opposed to the use of the term in previous discussions on SRKW foraging, referring to the longevity of an important foraging site (e.g. Noren and Hauser, 2016).

Through this analysis, we demonstrate three approaches to constructing spatially explicit models of animal behavior. The first does not attempt to mitigate autocorrelation of the observational data, the second incorporates data-thinning, a traditional and effective method for mitigating autocorrelation in behavioral data (e.g. Karniski et al., 2015), and the third uses a temporal Gaussian process to account for autocorrelation. The first approach is a cautionary demonstration of the peril of ignoring inherent autocorrelation. This approach suffers from autocorrelation bias and produces over-confident predictions (i.e. with greatly underestimated levels of uncertainty). Comparing the outcomes of this model to our other approaches highlights foraging areas that are likely artifacts of sampling bias. The data-thinning approach is expected to be the most accurate of our approaches, as it requires little-to-no assumptions about the autocorrelative structure in the data. However, while thinning data may be effective at removing temporal autocorrelation, the predictions from these models suffer from low precision due to the low sample size retained after thinning, leading to predictions of low spatial resolution (e.g. De Solla et al., 1999). Our third, spatiotemporal approach is expected to be less accurate than data-thinning as it relies on strong assumptions of the autocorrelation in killer whale behavior—in that it follows a Matérn process with the same degree of persistence for each survey, as well as throughout the study region. However, it offers much greater precision as significantly more data are retained and used, which is particularly beneficial for studies of low sample size. Using the data-thinned model predictions as reference, we have demonstrated that we can be confident in the accuracy of our spatiotemporal model predictions *and* have the added benefit of the improved precision of this approach that provides sharper spatial resolution of predicted foraging areas. As such, we consider this spatiotemporal approach preferable for inference to a space-only model using data thinned to remove temporal autocorrelation.

Our analysis serves as an additional example of INLA proving a flexible and efficient tool to implement complex hierarchical models. INLA has been shown to work well with systematically collected data series (e.g. Yuan et al., 2017), as well as opportunistically collected point data, and combinations of the two (e.g. Watson et al., 2021). This flexibility serves observational ecological data well, in that such data may come from opportunistic or systematic sampling, often from historical and contemporary sources respectively, using a variety of sampling protocols. INLA's computational performance (i.e. speed of fitting) is significantly faster for fitting latent Gaussian process models than competing Bayesian approaches (e.g. MCMC), which typically require a lot of computing power. Further, INLA's ability to incorporate stochastic partial differential equation models, which allow spatial patterns unaccounted for by explanatory variables to be defined, provides an additional advantage to its use in the spatial modeling of ecological datasets.

This study corroborates observed spatial patterns in SRKW foraging behavior in the Haro Strait region described over the last few decades and presents the first comprehensive analysis of SRKW foraging behavior in the Swiftsure Bank area. As the foraging areas we identified in these regions are near shipping lanes and considering the importance of sound use by SRKW for foraging, these data highlight areas where noise mitigation efforts could be beneficial and provide guidance for the development of effective management strategies in support of SRKW survival and recovery. In delineating areas of importance within SRKW critical habitat defined by critical ecological functions for the population, we present crucial direction for conservation measures for this population, with implications for area-based management of at-risk species in general.

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Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data Availability

Data will be made available on request. Analyses reported in this article can be reproduced using the data provided by Stredulinsky et al. (2023). This repository also contains the final products of the article's analyses.

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