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Research article

Using spatial capture–recapture methods to estimate long-term spatiotemporal variation of a wide-ranging marine species

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Ecography
2025: e07878
doi: 10.1002/ecog.07878

Subject Editor: Nigel G. Yoccoz
Editor-in-Chief: Miguel Araújo
Accepted 27 May 2025

Determining population status to inform mitigation of anthropogenic threats requires statistical approaches that investigate spatial and temporal variation. In the face of climate change it is increasingly important to differentiate between changes in population size and redistributions of populations. This is especially true for wide-ranging species such as the blue whale. Abundance of eastern North Pacific blue whales has previously been estimated using (non-spatial) closed capture–recapture and distance sampling methods, but the estimates show opposite and diverging trends over the last 30 years. Evidence that the distribution has been expanding could explain the apparent disparity, due to the confounding effects of spatial variation in sampling and the changing distribution. To investigate this, we apply, for the first time, spatial capture–recapture (SCR) methods to blue whale photo-identification data from small boat surveys to estimate abundance. The study area was defined as the length of the continental USA coastline, extending approximately 100 km offshore. Average annual effort from 1991 to 2023 was 97 days, resulting in 7358 sightings of 1488 unique individuals. We find significant support for non-linear spatiotemporal variation. In all years, there were higher densities at lower latitudes but there were notable decadal cyclical fluctuations in the number of animals using the study area. This large variation in the numbers of animals using these waters motivates further study into the relationship with environmental changes. Our results are an important step in spatially explicit modelling of observational blue whale data, which highlight the value of including spatial and temporal data and are relevant to any marine mammal species monitored using photo-identification.

Keywords: abundance, blue whale, distribution, spatially explicit capture–recapture, spatiotemporal variation

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Introduction

Effective wildlife conservation requires reliable estimates of population size, but also an understanding of what influences the spatial and temporal distributions of populations (Sequeira et al. 2019, Grémillet et al. 2022, Tourani 2022). This information is critical to effectively implement conservation strategies and to manage impacting human activities which, in recent years, is more important than ever as we see increasing shifts driven by climate change (Hazen et al. 2013, Becker et al. 2019, Zhao et al. 2019). Monitoring to satisfy this dual focus in both space and time is logistically challenging and therefore rare, especially in populations with large and variable distributions (Stokes et al. 2010, Clare et al. 2019, Sequeira et al. 2019).

Baleen whales (*Mysticeti*) are one such taxonomic group, with ranges spanning thousands of kilometres and a variable distribution in feeding areas (Stone et al. 1990, Corkeron and Connor 1999, Grémillet et al. 2022). Accurately predicting spatiotemporal density is particularly important for these species as populations remain in variable states of recovery following severe depletion by commercial whaling up until the 20th century (Clapham et al. 1999), and recovery has often been limited by anthropogenic threats (Rockwood et al. 2018, Tackaberry et al. 2022, NOAA 2024). Management actions can reduce the impact of these threats but require a good understanding of the distribution of the populations so they can be deployed at the most impactful locations and times (Foley et al. 2010, Abrahms et al. 2019, Rockwood et al. 2020). Population abundance of these species has typically been estimated using capture–recapture methods applied to photo-identification data or distance sampling methods applied to visual line transect survey data, providing time-specific estimates of abundance in a specified area (Carretta et al. 2020). Most conventional capture–recapture methods do not include spatial information, so changes in estimates over time could be driven by actual population size change or population redistributions, which are not detected in non-spatial estimates (Amstrup et al. 2010, Tourani 2022). Distance sampling accommodates spatial variation within the defined surveyed area, but the scale of surveys required for large marine animals is logistically and financially challenging, and when surveys are conducted, they rarely have adequate statistical power to robustly estimate population trends (Taylor et al. 2007, Boyd and Punt 2021).

One of the most intensively studied baleen whale populations is the eastern North Pacific (ENP) blue whale population *Balaenoptera musculus* (Bailey et al. 2009, Barlow 2016, Calambokidis and Barlow 2020) but, despite this, abundance estimates have shown uncertain and conflicting trends since the first estimates in the early 1990s. Estimates using closed capture–recapture methods applied to photo-identification data over a rolling 4-year window show a stable to increasing population, but design-based estimates and estimates from species distribution models, both based on line transect data, suggest a stable or possibly decreasing trend (Barlow 2016, Becker et al. 2020, Calambokidis and Barlow 2020, Carretta et al. 2022). The limitations of each method mean it is challenging to make conclusive inferences about the population trend. The range of ENP blue whales extends from the Costa Rica Dome up to the Gulf of Alaska, but animals are encountered in their largest numbers off the United States west coast (USWC) (Bailey et al. 2009, Calambokidis et al. 2009a), which is an important summer and autumn feeding area for this population (Calambokidis et al. 1990, 2024). Most individuals then migrate south in winter (Bailey et al. 2009, Calambokidis et al. 2009a). An increase in photo-identification encounters off the west coast of Canada and in the Gulf of Alaska in the 2000s could reflect a return of the population to more northerly waters during the summer feeding months, as whales were known to be present in those areas pre-commercial whaling, although patterns are not well understood (Calambokidis et al. 2009a). The difference in abundance estimates from capture–recapture methods and those based on line transect data could be explained by a shifting distribution. The intermittent nature and uncertainty of abundance estimates using transect data make confirming a clear trend challenging, but capture–recapture methods lack spatial information to allow a shift in distribution to be assessed. There is thus a need to apply a modelling framework that can robustly estimate trends in abundance across both space and time (Tourani 2022).

One increasingly applied modelling framework that addresses these elements is spatial capture–recapture (SCR). SCR extends conventional capture–recapture models, explicitly modelling spatial variation in both the distribution and detectability of individuals that addresses the assumption from simple conventional capture–recapture models that animals have the same probability of being captured across the study area (Efford 2004, Royle et al. 2014). This assumption is commonly violated, thus SCR models should reduce bias in abundance estimates (Efford 2004, Royle et al. 2014, 2018). In addition, because SCR inherently accounts for individual variation in capture probabilities, we can explore how the population is distributed across the study area (Efford 2004, Royle et al. 2014). This provides a much richer picture of population abundance when compared to traditional capture–recapture models. SCR also offers benefits over distance sampling methods, through improved precision and accuracy and an enhanced ability to identify trends, as transect survey frequency is often limited by financial restrictions and photo-identification is collected more consistently (Taylor et al. 2007, Crum et al. 2021).

SCR models have been most widely used in terrestrial systems using structured data collected from fixed locations (e.g. camera traps or hair snares; Royle et al. 2018, Tourani 2022, Moqanaki et al. 2023). However, SCR can readily be applied in any system (e.g. freshwater: Raabe et al. 2014, Sutherland et al. 2018; marine: Marques et al. 2012, Pirotta et al. 2015, Bradley et al. 2017) using a variety of data sources. For example, SCR has been applied to unstructured data (data not collected from fixed locations), retrofitting structured 'traps' to data collected from a known location (Royle et al. 2011, Sutherland et al.

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2018, Broekhuis et al. 2021). To date, SCR studies using unstructured data in marine systems have been in relatively small study areas (Pirotta et al. 2015, Glennie et al. 2021, Winton et al. 2023), with the exception of Curtis et al. (2022) who developed a linear SCR model estimating the abundance of humpback whales *Megaptera novaeangliae* in their Central American wintering grounds. However, this model required adaptations due to a lack of effort data and was focused on generating a single estimate rather than a trend.

This study aims to apply SCR models to a large-scale marine system, modelling unstructured data with associated effort over a long time series to investigate spatiotemporal variation in density, which could be applicable for many wide-ranging marine species. We use SCR models applied to photo-identification data of ENP blue whales collected from small boat surveys along the continental USWC between 1991 and 2023 to:

1. explore spatiotemporal variation in density to determine if the spatial distribution of this population has changed;
2. estimate temporal changes in the population size of animals using the USWC;
3. explain inconsistencies between previous capture–recapture and distance sampling estimates; and
4. explore the potential to use SCR as a tool for informing management of human activities that might impact wide-ranging marine populations.

Material and methods

Data collection

Data used in this analysis were collected along the continental USWC between 1991 and 2023 by Cascadia Research Collective (CRC), a non-profit cetacean research organisation (Calambokidis and Barlow 2004, 2020, Calambokidis et al. 2009b). Data were collected every year, with most surveys conducted between June and November (Calambokidis and Barlow 2004, 2020, Calambokidis et al. 2009b). Surveys extended along the USWC from 32°N to 49°N, and generally did not extend further than 50 km offshore from the daily launch point (Fig. 1). Surveys were largely conducted in 5.3–5.9 m rigid-hull inflatable boats equipped with outboard engines (Calambokidis et al. 2009b). Surveys aimed to maximize humpback and blue whale encounters while attempting to maintain broad temporal and geographic coverage along the USWC. When blue whales were encountered, photos were taken of their flanks, aiming to get images of both sides if possible. Up to 2004, images were taken using 35 mm film cameras with 300-mm telephoto lenses (Calambokidis and Barlow 2004). Since then, digital images have been taken using digital SLR cameras primarily with 100–400 mm or 70–200 mm lenses.

Data processing and preparation

Image quality was assessed based on a three-tier quality criterion and only images of suitable quality were included in

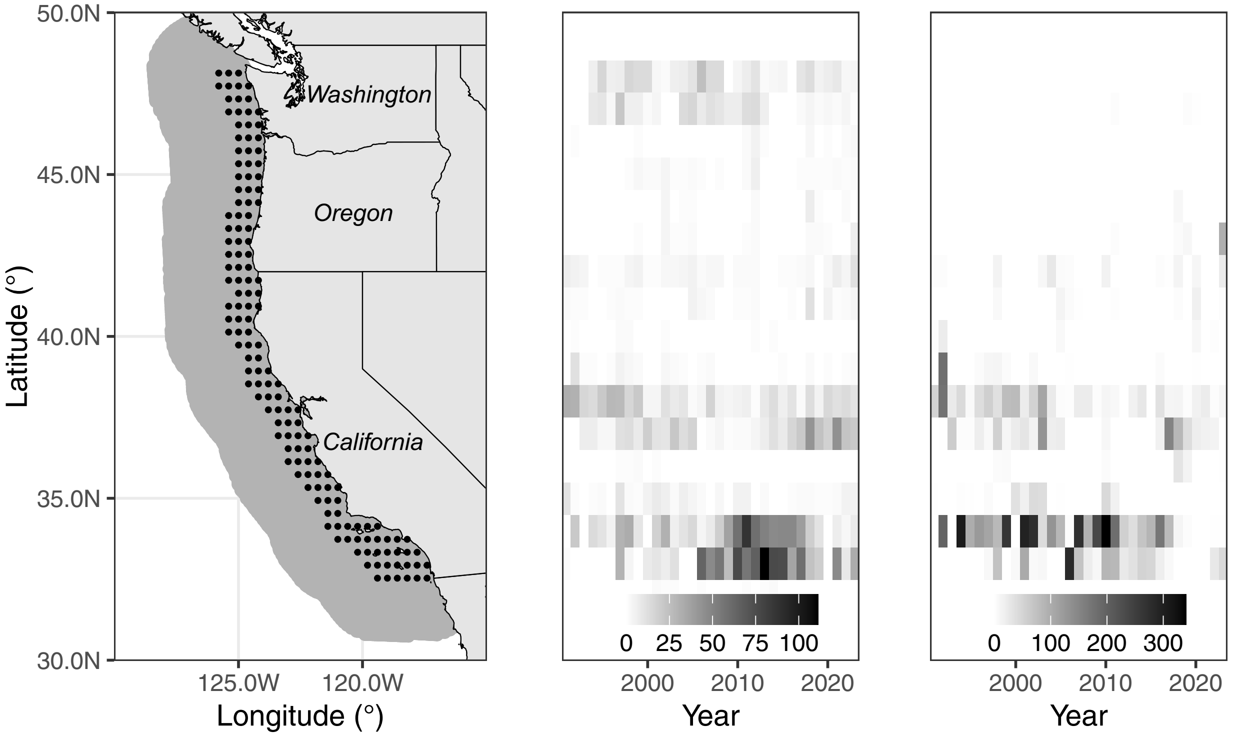

Figure 1. Left: map of study area. Darker grey area represents the state-space or mask (*S*) (see Model definition), trap locations are marked by black dots. Centre: effort summary by each degree of latitude; scale bar describes number of days of effort per year. Right: summary of encounters (captures) by each degree of latitude; scale bar describes number of encounters per year.

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the database for analysis (Calambokidis et al. 2009b). Photo-identification images were used to match individual whales based on skin pigmentation patterns on the flank and back of both sides of the whale (Sears et al. 1990, 2013). Only animals with a right side identified were used in the analysis to avoid duplication (Vernazzani et al. 2017, Whittome et al. 2024). Matches were verified by at least two people and then included in the photo-identification catalogue with each whale being allocated a unique identification number (Calambokidis and Barlow 2004).

The study area was defined as the continental United States (US), and we used all sightings from surveys conducted between 32.3°N and 48.4°N latitude (Fig. 1). As the photo-identification data are unstructured, we created effective 'traps' (sensu Sutherland et al. 2018). A grid was applied to an area which spanned the extent of the encounters, and the centroid of each grid cell was considered the 'trap' (Fig. 1) with encounters allocated to the closest trap. We tested a range of grid cell sizes from 0.05° to 0.7° (equivalent to degrees latitude) and chose a resolution that maximised spatial captures while minimising computation (Supporting information). A cell size of 0.4° was selected which was equivalent to 0.4 degrees latitude or approximately 44 km.

To ensure temporal independence between observations, we thinned the data such that if an animal was seen in the same trap, in the same calendar week, only one record was retained – i.e. we assumed that observations separated by 1 week or more were independent. Each year was considered a 'session', numbered from 1 (1991) to 33 (2023), and we summarized the detection data (i.e. encounters of individuals) as the total number of independent detections in each year (where a year represented a single occasion).

A major benefit of SCR is the ability to summarise, and consider explicitly, the spatial sampling effort that gave rise to the data. Effort data were only available at the daily summary level for the full study period (Fig. 1). To create an approximate measure of effort, we took the starting point of each survey day and assumed that any traps within 50 km north or south of a straight line from the survey start point were 'operational' and thus able to record detections (see the Supporting information for encounters per unit effort). We also calculated the number of weeks each latitudinal band (and hence traps) was surveyed and used this metric as a measure of annual sampling effort.

Model definition

The spatial capture–recapture method is a hierarchical model with a process sub-model and a conditional observation sub-model (Efford 2004, Royle and Young 2008). The process model is a spatially explicit Poisson point process model that describes the spatial distribution of latent, or unobservable, individual activity centers (s). The observation model is a spatially explicit model for how the detection arises and is conditional on the underlying process model. The individual spatial encounter data, y, provide information about the location and number of activity centers (and hence the point process model) and how detection varies with distance from the (latent) activity center. Here we adopt a maximum likelihood approach to estimation (Borchers and Efford 2008), and because activity centers are latent, the model is an integrated likelihood where the integration is over the whole area where activity centers could be located (Borchers 2012). Below we describe the multi-session maximum likelihood SCR approach to estimate spatiotemporal variation in population density (Sutherland et al. 2019).

We treat each year as an independent and closed session, and the observation data are spatially referenced counts denoting the number of detections of an individual (i) at a trap (j). These counts were treated as Poisson random variables (Royle et al. 2014):

$$y_{ij} \sim \text{Poisson}\left(\lambda_{ij}\right)$$

We assumed each individual has an activity center (s_i), and that the rate of an individual being detected in a trap (λ_{ij}) was a function of the Euclidean distance between the individual's activity center (s_i) and the location of trap j (x_j). Activity centers were fixed within years and independent between years. Here we assumed the standard half-normal encounter model which conditional on its latent unknown activity center s_i:

$$\lambda_{ij} \mid s_i = \lambda_0 \exp\left(-\frac{d\left(x_j, s_i\right)^2}{2\sigma^2}\right),$$

where λ_0 is the baseline expected number of detections, σ is a spatial parameter that determines the distance over which encounter rates decline to 0, and $d(x_j,s_i)$ is the Euclidean distance between an individual's activity center and a trap.

In this formulation of the model, λ_0 and σ are parameters to be estimated and can be modelled as a function of covariates using standard GLM-like approaches. In this study, we were interested in accounting for interannual variation in detectability, which we did using a non-parametric smooth spline term for λ_0. We applied the standard $s()$ thin plate regression spline (Wood 2003). The temporal smooth allowed for variation in detectability and provided efficiency when compared to estimating λ_0 separately for each year. We were also interested in accounting for heterogeneity in detectability, which we did using a 2-class finite mixture model for both σ and λ_0 (Pledger 2000, Pledger and Phillpot 2008, Cubaynes et al. 2012). The data were collected largely within 50 km of the coast, but ENP blue whales also inhabit waters further offshore (albeit it in lower numbers; Barlow 2016). The 2-class mixture parameter allowed for variation in capture probability.

While individual activity centers were unobserved (a latent process), the spatial information contained within the detection data allowed the position of the activity centers to be inferred. This was formalized via a point process model used to describe the underlying spatial distribution of activity centers, and hence individuals, across the study

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area (Efford 2004, Royle et al. 2014, Sutherland et al. 2018). This required that the study area was explicitly defined, and was done by defining a state-space, or mask (*S*) (Fig. 1). The mask was defined as a buffer area around the trap array that contained all individuals which could have been sampled (Royle et al. 2014, Sollmann et al. 2016), and this area was gridded to generate points, where each point is the centroid of a pixel. Here we used a 200-km buffer around the traps with point spacing of 10 km, providing adequate space to reflect the distances blue whales can travel. The eastern edge of the buffer was clipped to remove points on land.

SCR models typically assume the point process model is homogenous, such that the activity centers are assumed to be uniformly distributed across *S*. Here our objective was to quantify temporal trends in population density, but also spatial variation in density. As such, we modelled density as a smooth function of both latitude (space) and year (time) (Efford 2024). In summary, our SCR model was defined as follows:

$$\log\left(\lambda_{0,i}\right) = \alpha_0 + \alpha_1 g_{\underline{i}} + s\left(\text{year}\right)$$

$$\log\left(\sigma_i\right) = \beta_0 + \beta_1 g_{\underline{i}}$$

$$\log\left(D_p\right) = \delta_0 + s\left(\text{latitude, year}\right)$$

where $\lambda_{0,i}$ represents the rate of detecting an individual at its activity center as a log-linear smooth function over time, where α_0 is the intercept, α_1 is the difference in detection between the latent groups (classes) 1 and 2, where $g=0$ for group 1 and $g=1$ for group 2, and *s*(*year*) represents the smooth function over time. We note that here λ_0 is the per week detection rate which allows us to account for between trap variation in effort (number of weeks ranged from 0 – i.e. traps with no effort in a year – to 14 – i.e. traps that had sampling in 14 different weeks). σ_i represents the rate at which detection declines with distance from the activity center based on a linear regression with intercept (β_0) and $\beta_1 g_{\underline{i}}$ indicates which of two groups the individual belongs to as described for λ. Density (*D*, whales per 10 km^2) at each state space pixel (*p*) is a log-linear function with intercept (δ_0) and a two-dimensional thin plate regression spline *s*() across latitude and year, to allow for flexibility in both dimensions in an interactive way. Note that the process model is a spatial point process model and therefore total abundance for the entire state-space can be derived by summing over all the pixels of the point process, and because the area is an explicit part of the model, this is the absolute abundance for that area.

A series of SCR models were run to estimate the optimal number of knots (*k*) or inflexion points for the smooth terms on density and baseline detection rate. Thin plate splines have a knot at each covariate value and then an eigen decomposition is used to select the first *k* eigen vectors which contain most of the variance (Wood 2003). Our objective was to quantify spatiotemporal variation in density while accounting for interannual variability in detectability. To offer the model maximal flexibility, we tested *k* values up to the point where the data no longer supported additional flexibility (i.e. the models no longer converged). For baseline detection, the maximum value at which the model converged was $k=3$ so this was selected for all models. For density, the maximum value at which the model converged was $k=10$, and model selection using Akaike's information criterion (AIC) supported $k=10$ over smaller numbers of knots (Supporting information; Sutherland et al. 2023). All analysis was carried out in R ver. 4.4.1 (www.r-project.org) using package 'secr' (Efford 2024).

There has been limited development of goodness-of-fit tests for maximum likelihood-based SCR models, and the available options only address a narrow range of types of lack-of-fit for simple SCR models (i.e. models without a combination of splines and finite mixture models; Choo et al. 2024). In SCR models, the activity centers can be clumped (overdispersed) relative to the Poisson distribution, which would cause the sampling variance of the density estimates to be underestimated (Borchers and Efford 2008, Efford 2024). In lieu of an appropriate goodness-of-fit test, we applied a variance inflation adjustment to each session based on Fletcher's c-hat (Fletcher 2012), which is a measure of overdispersion in the data (Efford 2024). It should be noted that this is a crude measure, and worst case scenario, as it ignores the complexity of the observation model, which was specifically adjusted to account for heterogeneity (Pledger 2000). The adjusted variance values demonstrate the maximum possible uncertainty so should be interpreted with caution, although the model point estimates are unaffected by the variance inflation. Encouragingly, though, investigations of whether this biases density estimates have shown that SCR is robust to such non-independence (Reich and Gardner 2014, Bischof et al. 2020).

Comparison of abundance estimates

As described above, some estimates of abundance have already been generated for the ENP blue whale population. These include line transect data modelled as design-based estimates and in species distribution models, and closed capture–recapture estimates over a rolling 4-year window modelled using Chao (M_{th}) and Darroch (M_{t}) models (Barlow 2016, Becker et al. 2020, Calambokidis and Barlow 2020). The line transect data represent a similar geographical extent to the mask definition (*S*) for the SCR model. However, the capture–recapture estimates use photo-identification data which span the full range of the population, expanding outside the USWC. In addition to the CRC small-boat survey data, these estimates also use other contributor data (e.g. other opportunistic sources including from whale watch platforms), which more than double the number of encounters used compared to the photo-identifications used in the SCR model. As these contributor data do not have effort associated, they were not included in the SCR model. To allow a more direct comparison to the abundance estimates generated from the SCR model, Chao and Darroch capture–recapture estimates were

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generated from the CRC survey data geographically limited to the continental USWC only (see Calambokidis and Barlow 2020 for method).

Results

SCR model results

Between 1991 and 2023 there was a total effort of 3191 days, averaging 97 days per year, ranging from 29 days in 1993 to 190 days in 2013. During this time there were 7358 encounters of 1488 individuals.

The 2-class mixture parameter on detection was included to account for unobserved heterogeneity. The mixture parameter indicated the probability of randomly selecting an individual from the first group was 0.429 (95% confidence intervals (CIs hereafter): 0.338–0.525), suggesting the two groups are split fairly equally in the population (Table 1). The detection model showed significant support for non-linear variation as all smooth terms had values different from 0 (Table 1). The difference in the baseline encounter rate (λ) between the two groups was significant (−4.181, CIs: −4.423 to −3.939; Table 1). Using the first year as a reference for illustration, this translates to an encounter rate of 0.120 (CIs: 0.101–0.143) for group 1 and 0.0018 (CIs: 0.0012–0.0028) for group 2. The difference in the space use parameter (σ) between the two groups was also significant (3.098, CIs: 2.995–3.201; Table 1), translating to smaller space use in the group 1 (19.516 km, CIs: 18.435–20.640 km; Table 1) compared to group 2 (432.35 km, CIs: 368.43–506.87 km; Table 1).

The density model had a two-dimensional smooth term with $k=10$ allowing density to vary over time and latitude. We found significant support for non-linear variation over space and time as nine out of 10 smooth coefficients had values different from zero (Table 1). The smooth terms suggest cycling of density over time where there are clear peaks and troughs (Fig. 2). In lieu of an appropriate goodness-of-fit test, we calculated Fletcher's c-hat values for each session, which ranged from 6.77 to 81.17 (Supporting information). Based on these values, we applied a variance inflation adjustment to the 95% confidence intervals around the density estimates to demonstrate the maximum possible uncertainty if the data are overdispersed relative to the Poisson distribution (Supporting information). We note again that this is a worst case scenario which ignores the complexity of our observation model, which was specifically adjusted to account for heterogeneity (Pledger 2000).

Conditional effects plots also help to visualise the model results. Firstly, three points of latitude were selected at equal intervals to represent density over time (Fig. 3). The points of latitude were selected to span the study area at equal intervals. At all three latitudes we see the cyclical fluctuations in density, but with more prominence at lower latitudes and cyclical amplitudes that dampen from south to north. This could suggest a change over time and space of the distribution of the population as the density of animals at higher latitudes looks to be increasing in the peak years. We also selected specified time points to assess how density changed with latitude (Fig. 4). We selected the years with the lowest densities to remove the effect of the fluctuation. Overall, we see that densities are highest at lower latitudes and then decrease as latitude increases. We also find that density has decreased with each cycle, as 1998 has the highest, followed by 2013 and then 2023, signaling a possible decrease in density over time.

Table 1. Summary of spatial capture–recapture (SCR) model coefficients and associated variance. SE is the standard error, lower CI is the lower 95% confidence interval, and upper CI is upper 95% confidence interval. Parameters are density (*D*), baseline encounter rate (λ), and the encounter change rate (σ) a spatial parameter that determines the space over which encounter rates reduce towards 0. As λ and σ were modelled with a 2-class mixture parameter, there are two latent groups for each parameter, group 1 (g_1) and group 2 (g_2), for which pmix describes the logit scale probability that a randomly selected individual is in group 1. *D* and λ were fit using smooth terms so *k* values represent the coefficients and associated errors for each of the knots.

	Coefficients (β)	SE	Lower CI	Upper CI
Density (*D*)				
D intercept	−11.606	0.065	−11.732	−11.479
D smooth term ($k=2$)	0.651	0.166	0.324	0.977
D smooth term ($k=3$)	−0.715	0.165	−1.038	−0.392
D smooth term ($k=4$)	1.437	0.182	1.080	1.794
D smooth term ($k=5$)	−0.614	0.146	−0.901	−0.328
D smooth term ($k=6$)	0.061	0.045	−0.027	0.149
D smooth term ($k=7$)	−1.527	0.248	−2.013	−1.041
D smooth term ($k=8$)	3.871	0.759	2.384	5.359
D smooth term ($k=9$)	−1.036	0.044	−1.122	−0.949
D smooth term ($k=10$)	−0.348	0.086	−0.517	−0.179
Baseline encounter (λ)				
λ intercept	−2.122	0.089	−2.296	−1.947
λ (g_1) ($k=2$)	−0.421	0.164	−0.743	−0.099
λ (g_1) ($k=3$)	−0.542	0.046	−0.633	−0.451
Difference g_1 versus g_2	−4.181	0.124	−4.423	−3.939
Encounter change rate (σ)	9.879	0.029	9.822	9.935
Difference g_1 versus g_2	3.098	0.052	2.995	3.201
p_{mix}	−0.286	0.198	−0.674	0.101

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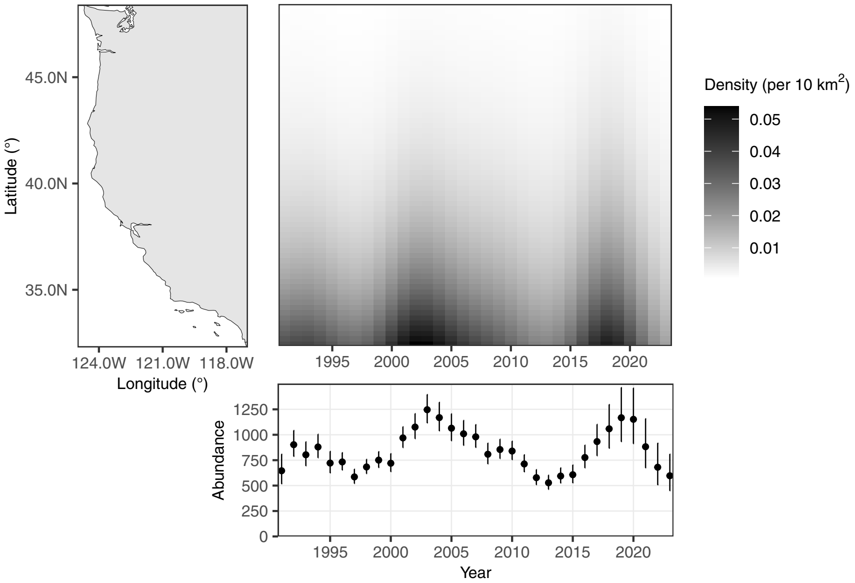

Figure 2. Summary of estimated density and abundance from spatial capture–recapture (SCR). Top right panel shows density surface in relation to the latitude of the coastline (top left). Bottom right panel shows estimates of abundance for the total population across the whole study area. Error bars represent 95% confidence intervals.

This is a model for density over time and space, and historically these results have been reported in terms of total population size. In SCR this means summing over time and space, so the population size represents the number of animals in the state space (*S*). Total abundance showed no overall trend across the study period, but also had cyclical fluctuations between around 500 and 1200 individuals (Fig. 2). This rate of change is not biologically possible for a long-lived species like blue whales (Ramp et al. 2006, Vernazzani et al. 2017), so suggests that in low abundance years the animals are spending time outside of the USWC study area.

Comparison of abundance estimates

When the abundance estimates from the SCR model were compared to estimates from other datasets and models (Fig. 5), the most similar were the Darroch estimates which had very similar values to the SCR estimates. The Chao estimates were also similar but diverged slightly in the late 1990s and mid–late 2010s. Design-based estimates and species distribution models showed larger differences in values and trends, although both sets of estimates had substantial uncertainty.

Discussion

Our findings show that there are cyclical fluctuations in the numbers of ENP blue whales in the USWC area between 1991 and 2023 (Fig. 2). As blue whales are a long-lived species (Ramp et al. 2006, Vernazzani et al. 2017), these cannot feasibly reflect changes in actual population size. Therefore, it is most likely that the number of animals visiting the USWC follows a cyclical pattern, and that in the trough years, animals are elsewhere. The USWC is a summer and autumn feeding area for this population, but its range extends both north and south of the USWC (Bailey et al. 2009, Calambokidis et al. 2009a). Generally, as animals arrive at the USWC they are migrating north from wintering areas, such as the Gulf of California in Mexico and the Costa Rica Dome off Central America (Bailey et al. 2009, Irvine et al. 2014, Ugalde De La Cruz 2015). The troughs in our results could correspond to periods when animals may be spending minimal time in USWC waters, possibly remaining further south, such as in the waters off the Baja California peninsula, moving offshore or transiting the USWC, rapidly reducing the likelihood of being captured. The population size of another large whale species, the eastern North Pacific gray whale *Eschrichtius robustus* has shown to be sensitive to changing environmental conditions, with cyclical reduction between 15 and 25%

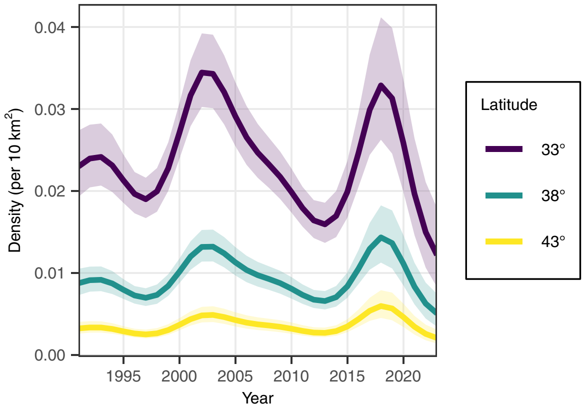

Figure 3. Conditional effects plot of density over time at three latitude points. Shaded areas represent 95% confidence intervals.

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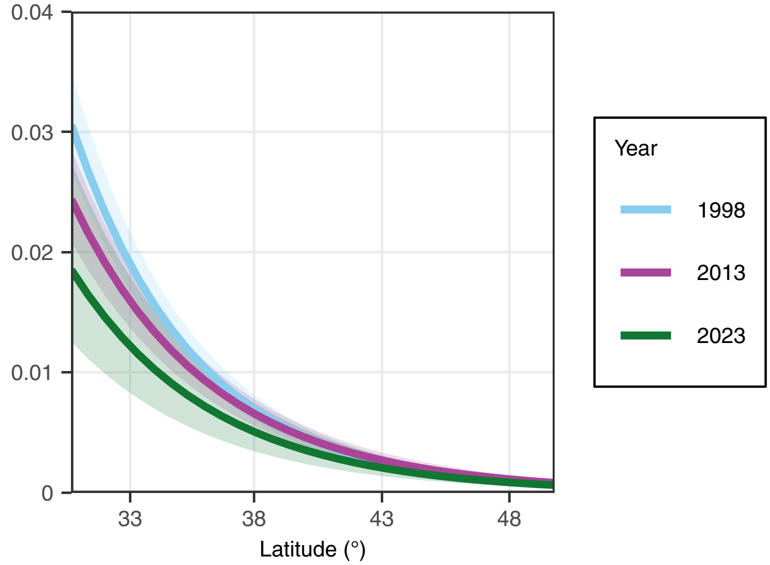

Figure 4. Conditional effects plots of density by latitude in three lowest density years. Shaded areas represent 95% confidence intervals.

(Stewart et al. 2023). Environmental change could also be a contributing factor to fluctuations in blue whale abundance in USWC waters, which should be explored further in future research.

The variable spatial distribution is most likely related to prey concentration. Globally, blue whale movements are closely related to high productivity areas throughout the year (Reilly and Thayer 1990, Branch et al. 2007). They target

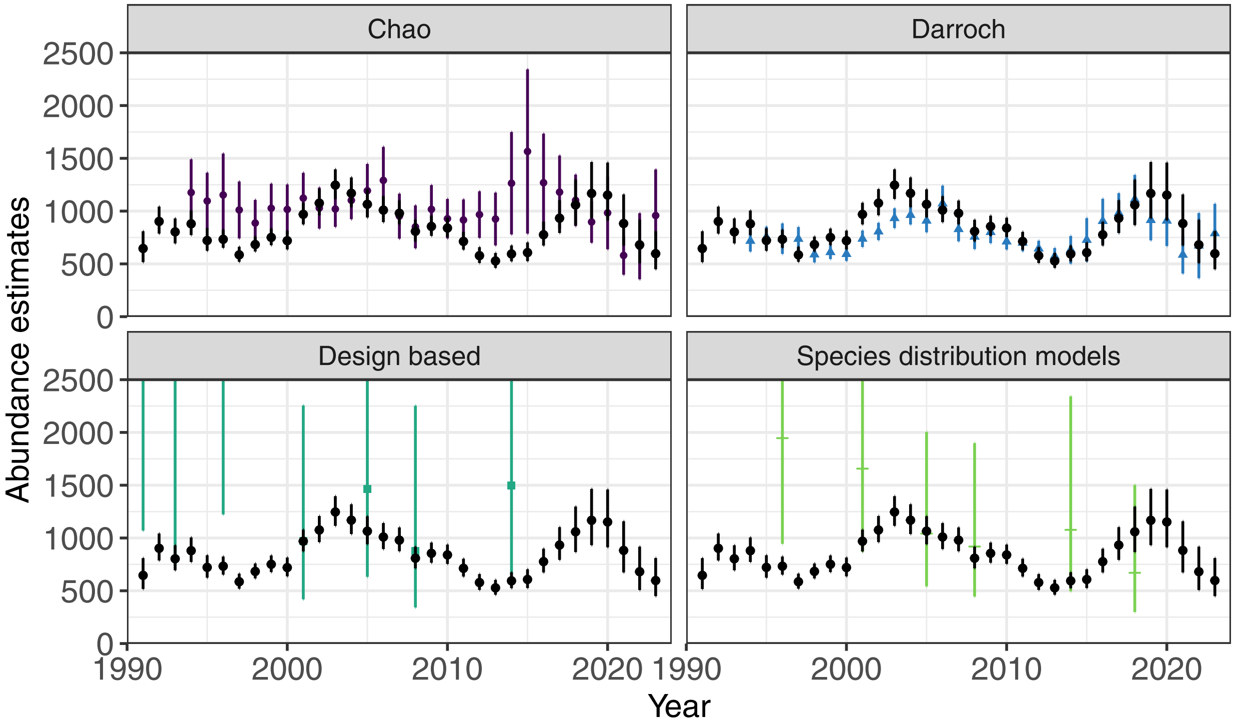

Figure 5. Comparison of spatial capture–recapture (SCR) abundance estimates (black points on all plots) to estimates generated by other methods based on photo-identification and line transect data. Error bars represent 2 standard errors for Chao and Darroch estimates and 95% confidence intervals for all others. The y-axis has been truncated to better show variability in the estimates; the design-based estimates were 2569, 2641, and 2936 in 1991, 1993, and 1996, respectively, with the upper 95% CIs of 6167, 9508, and 7048, respectively (Barlow 2016, see the Supporting information for plot with extended y-axis). The upper 95% CI for the species distribution model in 1996 is 4009 (Becker et al. 2020). For Chao and Darroch capture–recapture estimates data were limited to the CRC survey data from the continental USWC only. Chao and Darroch estimates are 4-year rolling estimates (Calambokidis and Barlow 2020).

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specific species of krill, feeding on high-density aggregations (Croll et al. 2005, Goldbogen et al. 2011). Krill are sensitive to ocean temperatures, favoring cooler ocean conditions (Cimino et al. 2020, Phillips et al. 2022). The distribution of *Thysanoessa spinifera,* the preferred species of krill for ENP blue whales (Fiedler et al. 1998, Croll et al. 2005, Nickels et al. 2018), has been shown to shift north in warmer years (Lilly and Ohman 2021). If there were ample krill resources as the whales migrated north in spring (e.g. off the west coast of Baja California), there may not be a motivation to continue north and reach the USWC. Conversely, if krill resources shifted north due to warmer waters further south, this could explain the higher densities of whales in the USWC area in other years. This is also supported by the general trend of density declining with increasing latitude (Fig. 4). If whales were finding ample food, there would be no motivation to continue moving north and expend resources travelling. Over the study period, there was dampened amplitude cycling as you move northward (Fig. 3). However, in peak years, there is some evidence that the density at lower latitudes declines slightly over time while the peak density at higher latitudes appears to be increasing, suggesting more animals are moving further north. This type of shift in distribution could be driven by climate change warming the oceans, as generally waters are cooler at higher latitudes and krill is known to shift north in warmer years (Lilly and Ohman 2021).

Overall abundance of the ENP blue whale population showed no overall trend between 1991 and 2023, though overall density fluctuated (Fig. 2). Abundance estimates from the SCR model show good concurrence with the Chao and Darroch 4-year rolling closed capture–recapture estimates generated from an equivalent dataset, especially with the Darroch estimates. The Chao estimates diverge at two points, both of which are peak periods in the SCR model. The SCR model found that there is increased density which spreads further north in these periods. The Chao model accounts for individual heterogeneity in capture probabilities, so, if some individuals were shifting their distribution and subsequently less likely to be recaptured, it would explain why estimates are higher. These results highlight the value of SCR when compared to traditional capture–recapture models. While similar information about the overall population trend is provided by traditional capture–recapture and SCR models, SCR informs on the distribution of the population and can explain variation in abundance. SCR estimates were also compared to the two sets of estimates based on the USWC line transect data. In the 1990s the estimates from transect data are much higher but from the 2000s onwards showed better concurrence, especially with the estimates from species distribution models. The fluctuations in abundance detected by the SCR model are somewhat reflected in the design-based and species distribution model estimates, but the latter lack the resolution to make conclusive inferences about trends. This reinforces the need for approaches that can detect both spatial and temporal variation in populations, as exemplified by this case where the irregular line transect sampling years happened to miss the years in peak abundance estimated by the SCR model. Wide-scale line transect surveys are commonly used to monitor cetacean populations and, while they have benefits, our results reinforce caution when interpreting results from these surveys, especially where they have irregular temporal and broad spatial resolution.

From all these results, we infer that, by assessing density in both space and time, the abundance estimates generated by the SCR models do more robustly represent blue whale numbers off the USWC, and also explain the divergence seen in trends from other estimates. The cyclical fluctuations found by the SCR model suggest that a varying portion of the population is using the USWC and that this continues to shift over time. Notably, a line transect survey off the west coast of Baja California in 2018 estimated much higher abundance of blue whales than the equivalent estimates for the USWC, supporting the possibility that, in some years, some individuals never reach the USWC (Becker et al. 2020, 2022).

As this is a relatively novel modelling approach for these types of data, ensuring we accurately represented all facets of the data was an important consideration. One such major consideration was accounting for individual heterogeneity, which is common in baleen whale photo-identification datasets (Hammond and Sears 1990, Ramp et al. 2006, Hammond et al. 2021). ENP blue whales show site fidelity (Busquets-Vass et al. 2017, 2021) so accounting for individual variation in space use is important. While spatial capture–recapture inherently accounts for this individual variation in space use, the sampling in this study was coastally focused which could have introduced bias. If some individuals were differentially using inshore and offshore waters, the inshore animals would be more likely to be recaptured (Calambokidis and Barlow 2020). The introduction of the 2-class mixture parameter allowed capture probability and likelihood of detection to be modelled as two separate classes, accounting for any possible bias created in abundance estimates by heterogeneity in capture probabilities (Pledger 2000). While there could be residual individual heterogeneity in detection rate, e.g. involving additional classes, there is no biological evidence for selecting more classes and other diagnostics would not be a reliable way to select a different mixture (Dorazio and Andrew Royle 2003, Pledger and Phillpot 2008). Additionally, 2-class mixtures have been shown to be sufficient to substantially correct for any bias in abundance estimates caused by heterogeneity (Pledger 2000, Cubaynes et al. 2012). The mixture parameter, which is the proportion of the population expected to be in the first group, suggested the two groups of whales represented 43 and 57% of the population. There was a notable difference in baseline detection rate supporting the inclusion of the mixture parameter. The difference in the σ parameter (rate at which likelihood of detection declines as animals move away from the activity center) also showed a sizeable difference between the groups (19.516 km versus 432.35 km), suggesting two very different movement behaviors in the population with group two moving far greater distances within the season than group one. This is likely the result of compensatory heterogeneity, which reinforces the application of the

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2-class mixture parameter on both the σ and λ_0 parameters (Efford and Mowat 2014). While using a 2-class mixture parameter is a good way to account for heterogeneity in detection, it does not explicitly account for heterogeneity in any spatial structure, which could be present in the population. However, SCR methods have been found to be robust even to complete transience (Royle et al. 2016). In addition, a simulation study found capture–recapture data increased accuracy and precision when estimating population trends and an improved ability to distinguish whether trends were driven by actual changes in population abundance or distribution shifts, which supports the use of these data to answer such biological questions (Boyd and Punt 2021).

Other aspects of the population's life history also create potential sources of bias not explicitly accounted for in this modelling approach. SCR models assume animals have a static activity center (Efford 2004, Royle et al. 2014). ENP blue whales are a migratory population, with animals moving between lower latitudes in winter and higher latitudes in summer, although there are examples of animals diverging from these patterns (Mate et al. 1999, Bailey et al. 2009, Busquets-Vass et al. 2021). There can also be variation in location and timing of migration; movements may be based on food availability as opposed to being driven by other life history events (e.g. calving or mating) (Szesciorka et al. 2020, Oestreich et al. 2022). Blue whales off the USWC predominantly demonstrate feeding behavior (Palacios et al. 2019, Fahlbusch et al. 2022) so are less likely to be making large movements relative to other times in the year. However, animals are more likely to be moving north in spring and early summer, and south in late summer and autumn.

The SCR model developed here provides an initial approach to integrating spatial data into a capture–recapture framework for a wide-ranging marine species. However, other steps can be taken to improve inferences from the model, offering an opportunity to continue developing this work further. While the small boat surveys provide a good representation of the USWC coastal waters, they do have limitations. These surveys miss offshore waters, and therefore a considerable part of the range, and this may limit the number of recaptures and lead to abundance estimates that are biased low relative to the whole population. Future studies could explore the addition of other datasets which could increase the number of recaptures across their range including waters further offshore (e.g. opportunistic photo-identification data). They could also include biotelemetry data to provide information on the movement patterns of individuals.

Another interesting development would be to explore how well environmental covariates explain the spatiotemporal variation, helping us to understand not only the movements, but what drives them (Santora et al. 2017, Fahlbusch et al. 2024). The clear cyclical nature of the density fluctuations points to a cyclical environmental event such as the Pacific Decadal Oscillation (Fiedler 2002), which has previously been linked to body condition in ENP blue whales (Wachtendonk et al. 2022). If we can understand how blue whale abundance off the USWC fluctuates with environmental change, it improves our ability to predict their distribution and, where necessary, manage human activities that threaten the population. This is particularly relevant in the face of a changing climate which will likely continue to impact the distribution of the populations, making the need for robust spatiotemporal estimates and appropriate methods to generate them increasingly important. Furthermore, for species that are subject to anthropogenic pressures, knowing where animals are is crucial to implementing mitigation measures in the most effective way. For example, baleen whales are subject to entanglement in fishing gear and ship strikes (Rockwood et al. 2018, Saez et al. 2021). Mitigation to reduce impacts, such as fisheries closures and speed limits for ships, rely heavily on up-to-date information on distribution and abundance (Wiley et al. 2011, Abrahms et al. 2019, Hausner et al. 2021). We believe SCR is an interesting and valuable approach to modelling data for wide-ranging marine species to answer these questions. However, while SCR models are robust to a wide range of assumption violations (Choo et al. 2024), there is a need for further work on appropriate goodness-of fit-testing to validate these methods in this setting.

To provide robust information for conservation and to effectively manage human activities that may impact a population, knowledge of spatiotemporal variation is critical. SCR is a useful tool for modelling spatiotemporal abundance of wide-ranging marine populations, which offers particular value as populations undergo redistributions in the face of climate change.

Acknowledgements – We thank everyone from the Cascadia Research Collective involved in the collection, processing, and matching of the blue whale photo-identification images. We are grateful for the trust in our use of data from such an extraordinary long-term database. We would like to specifically thank Kiirsten Flynn for her guidance in navigating and using the data. Thank you to Jay Barlow for sharing his code for running the Chao and Darroch closed capture–recapture models. Applying these models to our more limited west coast only dataset allowed us to make a direct comparison, which was an important step to put our SCR results in context. We are particularly grateful to Jeff Moore and Alex Curtis (NOAA SWFSC) who also provided valuable scientific input into the project. We also thank two reviewers for their insightful comments which greatly improved this manuscript.

Funding – Funding support was provided by NOAA under multiple grants and contracts for both the work that generated the data and the analysis.

Permits – Data were collected under National Marine Fisheries Service permit (latest permit no. 21678).

Author contributions

Georgina Whittome: Conceptualization (lead); Data curation (lead); Formal analysis (lead); Funding acquisition (supporting); Methodology (equal); Visualization (lead); Writing – original draft (lead); Writing – review and editing (lead). **John Calambokidis**: Conceptualization (supporting); Data

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curation (supporting); Funding acquisition (lead); Project administration (lead); Supervision (supporting); Writing – review and editing (supporting). **Philip S. Hammond**: Conceptualization (supporting); Supervision (supporting); Writing – review and editing (supporting). **Sophie Smout**: Conceptualization (supporting); Methodology (supporting); Supervision (supporting); Writing – review and editing (supporting). **Chris Sutherland**: Conceptualization (supporting); Data curation (supporting); Formal analysis (supporting); Methodology (equal); Supervision (lead); Visualization (supporting); Writing – review and editing (supporting).

Transparent peer review

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Data availability statement

Data are available from the Dryad Digital Repository: https://doi.org/10.5061/dryad.wh70rxx13 (Whittome et al. 2025).

Supporting information

The Supporting information associated with this article is available with the online version.

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