

WhaleWatch: a dynamic management tool for predicting blue whale density in the California Current

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Summary

1. Management of highly migratory species is reliant on spatially and temporally explicit information on their distribution and abundance. Satellite telemetry provides time-series data on individual movements. However, these data are underutilized in management applications in part because they provide presence-only information rather than abundance information such as density.

2. Eastern North Pacific blue whales are listed as threatened, and ship strikes have been suggested as a key factor limiting their recovery. Here, we developed a satellite-telemetry-based habitat model in a case-control design for Eastern North Pacific blue whales *Balaenoptera musculus* that was combined with previously published abundance estimates to predict habitat preference and densities. Further, we operationalize an automated, near-real-time whale density prediction tool based on up-to-date environmental data for use by managers and other stakeholders.

3. A switching state-space movement model was applied to 104 blue whale satellite tracks from 1994 to 2008 to account for errors in the location estimates and provide daily positions (case points). We simulated positions using a correlated random walk model (control points) and sampled the environment at each case and control point. Generalized additive mixed models and boosted regression trees were applied to determine the probability of occurrence based on environmental covariates. Models were used to predict 8-day and monthly resolution, year-round density estimates scaled by population abundance estimates that provide a critical tool for understanding seasonal and interannual changes in habitat use.

4. The telemetry-based habitat model predicted known blue whale hot spots and had seasonal agreement with sightings data, highlighting the skill of the model for predicting blue whale habitat preference and density. We identified high interannual variability in occurrence emphasizing the benefit of dynamic models compared to multiyear averages.

5. *Synthesis and applications.* This near-real-time tool allows a more accurate examination of the year-round spatio-temporal overlap of blue whales with potentially harmful human activities, such as shipping. This approach should also be applicable to other species for which sufficient telemetry data are available. The dynamic predictive product developed here is an important tool that allows managers to consider finer-scale management areas that are more economically feasible and socially acceptable.

Key-words: *Balaenoptera musculus*, blue whales, California Current, dynamic ocean management, habitat use, satellite telemetry, ship strike risk, spatial ecology, species distribution model

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Introduction

Blue whales *Balaenoptera musculus* are the world's largest animal and make seasonal basin-scale migrations from foraging to presumed breeding areas (Rice 1974; Mate, Lagerquist & Calambokidis 1999; Branch *et al.* 2007; Bailey *et al.* 2009; Irvine *et al.* 2014). In the eastern North Pacific Ocean, they migrate between the California Current or the Gulf of Alaska and the eastern tropical Pacific coincident with periods of increased prey availability. North Pacific blue whales are believed to feed year round, in contrast to many other migratory whales (Reilly & Thayer 1990; Kenney, Mayo & Winn 2001). Blue whales in the California Current feed exclusively on krill (*Euphausia pacifica* and *Thysanoessa spinifera*; Fiedler *et al.* 1998), requiring incredible adaptation in lunge feeding, filtration and lipid storage to support their energy demands over their broad migrations (Goldbogen *et al.* 2011; Hazen, Friedlaender & Goldbogen 2015). Although krill are abundant in the California Current System, the dense patches blue whales require to forage successfully can be ephemeral, forcing them to adapt to periods of high and low energy gain over multiple spatial and temporal scales (Santora *et al.* 2011; Hazen *et al.* 2013b). In addition, the California Current is a highly dynamic eastern boundary upwelling system where seasonal pulses of wind-driven upwelling provide nutrient enrichment that serves as the building block for the pelagic food web (Bograd, Leising & Hazen 2016). Because blue whales make large movements seasonally and foraging habitats are dynamic, their foraging and migratory habitats may overlap with multiple anthropogenic threats at different times of the year.

Over the past century, human use of the ocean has expanded dramatically, resulting in increased exposure of top predators to anthropogenic activities (Maxwell *et al.* 2013; Redfern *et al.* 2013). Shipping lanes into two of the largest California ports, Los Angeles/Long Beach and San Francisco, directly overlap with important blue whale foraging hot spots, creating an area of high collision risk (Berman-Kowalewski *et al.* 2010; Maxwell *et al.* 2013; Redfern *et al.* 2013; Irvine *et al.* 2014). Estimated blue whale ship strike rates in the California Current average approximately 2 per year, although this is a conservative estimate given that many ship strikes go undetected (Berman-Kowalewski *et al.* 2010; Redfern *et al.* 2013). With ship strike mortality postulated as one of the major factors inhibiting recovery, there is an increased need for targeted management (Redfern *et al.* 2013). Most whales are unable to respond to the speed of vessels, requiring additional whale detection tools or mandatory speed restrictions (McKenna *et al.* 2015). A recent study estimated blue whales have returned to their carrying capacity before commercial exploitation in the eastern North Pacific, which would suggest ship strikes

are not severely limiting their population recovery (Monahan, Branch & Punt 2015). Nonetheless, improved year-round estimates of blue whale distribution and densities can be used to assess overlap with anthropogenic threats at finer temporal and spatial scales, for example weeks to months and tens of kilometres (Pendleton *et al.* 2012). These data could support near-real-time targeted management actions benefiting both ocean users and protected species (Maxwell *et al.* 2013, 2015; Lewison *et al.* 2015).

Highly migratory predators are difficult to manage using traditional techniques, such as static closures (Hooker *et al.* 2011), as they transit ocean basins using ocean features to find predictable foraging hot spots (Mate, Lagerquist & Calambokidis 1999; Bailey *et al.* 2009; Block *et al.* 2011; Maxwell *et al.* 2015). Shipboard line-transect surveys and mark–recapture studies have been used to estimate blue whale population abundance (Calambokidis & Barlow 2004; Barlow & Forney 2007) and have been used in the development of habitat-based density models (Forney *et al.* 2012; Redfern *et al.* 2013; Becker *et al.* 2016; Roberts *et al.* 2016). However, in marine systems, these approaches are often spatially and temporally constrained to a single season and navigable waters within a country's exclusive economic zone. In contrast, telemetry data provide a Lagrangian view of individuals moving through the environment and allow additional inference on their behaviour (Hazen *et al.* 2012; Yamamoto *et al.* 2015). These two approaches provide complementary data; however, telemetry data are generally underutilized in management because the data are presence-only, violate statistical assumptions including independence of observations (Maunder *et al.* 2006), require a large number of tags to adequately represent population patterns (Block *et al.* 2011; Wakefield *et al.* 2013) and in a worst case, can modify behaviour or fitness (Fossette *et al.* 2008). Nonetheless, mark–recapture approaches from tag data (e.g. acoustic and archival tags) have been used for population assessment (Block *et al.* 2011; Whitehead & Jonsen 2013; Allen & Singh 2016).

Prediction of habitat preference from telemetry data can be useful for management applications, yet density estimates are often necessary to estimate absolute risk. Here, we use satellite telemetry data for blue whales from 1997 to 2008 to develop a habitat preference model for blue whales in the California Current. Predictions were then scaled by the population abundance to estimate density (Aarts *et al.* 2008). We automated the predictive models to incorporate up-to-date environmental data, providing a year-round near-real-time tool for use by managers and other stakeholders, for example in ship strike risk models. The finer temporal scale of these models allows managers to assess trade-offs in strategies at the time-scales that are most informative for ship strike avoidance in the California Current.

Materials and methods

TELEMETRY DATA

Blue whales were tagged off California, in the Gulf of the California, and in the eastern tropical Pacific (ETP) during 1993–2008 ($n = 182$); of these tracks, we examined those with available remotely sensed data and those that lasted longer than 7 days (1994–2008, $n = 104$; Fig. 1; Table 1). Over this time period, the tags consisted of a Telonics UHF transmitter with batteries housed in a stainless steel cylinder attached to the whale by either two subdermal attachments (surface-mounted style) or one-four-bladed attachment on the end of the housing (implantable style). Further tagging methodology and summaries of seasonal migration and hot spot use can be found in Mate, Mesecar & Lagerquist (2007); Bailey *et al.* (2009); Irvine *et al.* (2014). A Bayesian switching state-space model (SSSM) was applied to the raw, unfiltered locations from each track to account for satellite location errors based on the Argos location quality classes and to provide regularized tracks with one estimated location per day (Jonsen, Flemming & Myers 2005; Bailey *et al.* 2009; Irvine *et al.* 2014). After regularizing the presence data, we followed a series of steps outlined below and in Fig. 2.

ASSEMBLING CASE/CONTROL POINTS

As telemetry data provide information only on presence, we simulated tracks termed ‘pseudo-absences’ (Phillips *et al.* 2009) with daily positions (control points) for each true whale track (case points). These control points provide a measure of habitat

availability (Aarts, Fieberg & Matthiopoulos 2012) and were simulated using a correlated random walk (CRW) model (Kareiva & Shigesada 1983; Codling, Plank & Benhamou 2008). The CRW tracks had the same start and duration as the actual whale tracks with paired turning angles and step lengths randomly sampled from the telemetry-derived distributions (Zydalis *et al.* 2011; Willis-Norton *et al.* 2015). We created a series of 200 CRW tracks for each corresponding whale track (see Fig. S1, Supporting Information). Previous studies have demonstrated that model accuracy is heavily dependent on choosing appropriate control points that are in the same environmental space as the presence data. For example, overly similar control points can result in spurious projections, while those that are too broad can result in model overfitting (Thuiller *et al.* 2004; Phillips *et al.* 2009; Lobo, Jiménez-Valverde & Hortal 2010). To avoid overly broad control points, each CRW track was assigned a flag value based on correspondence with the actual whale track in terms of overall direction and distance (Willis-Norton *et al.* 2015). The flag value was calculated as the normalized difference between the actual whale and simulated CRW track length distance, d , summed with the normalized difference in net angular displacement, θ , of the whale and CRW track:

$$\text{Flag} = 2 \times (\text{distance}_{\text{whale}} - \text{distance}_{\text{sim}}) / \text{distance}_{\text{whale}} + (\text{angle}_{\text{whale}} - \text{angle}_{\text{sim}}) / 90.$$

The flag value ranged from 0 to 4, with 0 being the most similar and four the most dissimilar to the corresponding whale track. A CRW track travelling the same distance but opposite angle to the whale track would have a flag value of 2, an equivalent weighting to a CRW track travelling half the distance and at a 90° displacement. The CRW tracks in the upper quartile of flag

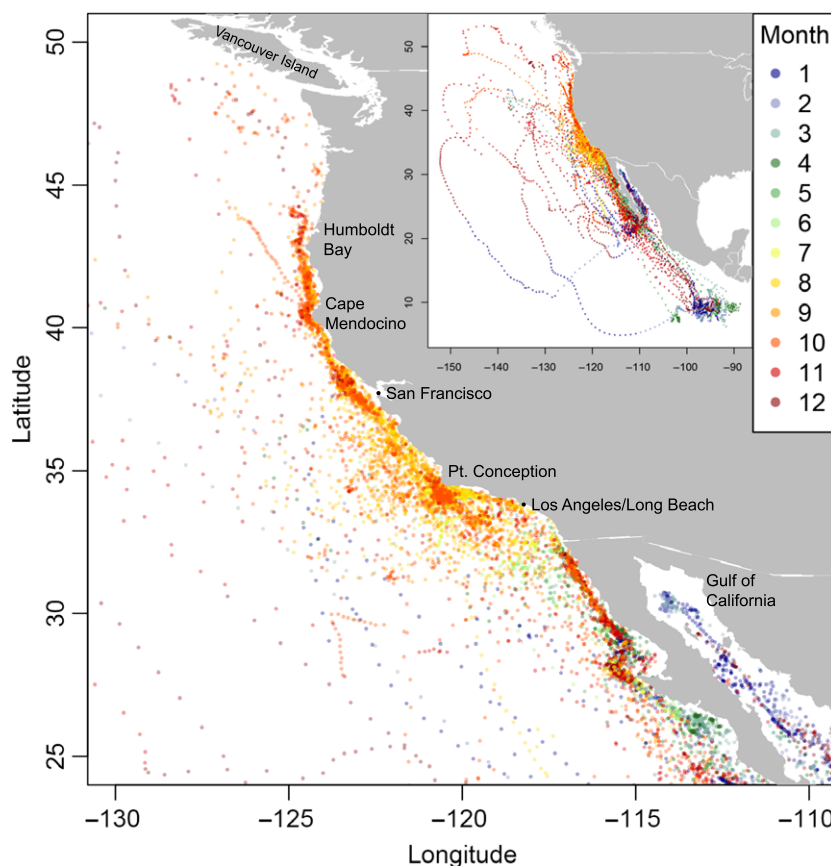


Fig. 1. Map of blue whale tag data set coloured by month highlighting seasonal migration in and out of the California Current.

Table 1. Tagging summary for blue whales and tag types used in this study. The number of tags and the number of state-space switching modelled (SSSM) tracks are included in columns 3 and 4

Year	# tags	# SSSM tracks	Primary tagging location	Notes
1993	10	0	Gulf of the Farallones	Tag type: surface-mounted
1994	17	2	Gulf of the Farallones	Delivery method: crossbow Mean duration = 7.6 days (± 15.1 days)
1995	26	8	Santa Barbara Channel	
1998	9	6	Cape Mendocino	Tag type: implantable
1999	23	16	Santa Barbara Channel	Delivery method: crossbow Mean duration = 68.9 days (± 78.1 days)
2000	13	6	Gulf of the Farallones	
2001	4	1	Gulf of California	
2002	2	2	Gulf of California	
2004	20	16	Gulf of the Farallones/ Santa Barbara Channel	Tag type: implantable Delivery method: ARTS Mean duration = 102.9 days (± 93.7 days)
2005	15	14	Gulf of the Farallones	
2006	12	7	Santa Barbara Channel	
2007	16	14	Santa Barbara Channel	
2008	15	12	Santa Barbara Channel	
Total	182	104		102.5 days (± 85.4 days)

values, and those that crossed land, were removed to ensure that the control points adequately represented the area potentially accessible to the whales.

ENVIRONMENTAL DATA

We extracted remotely sensed environmental data using the NOAA Coastwatch tool Xtractomatic (<http://coastwatch.pfel.noaa.gov/xtracto/>) at the time and location of each case and control positions. The predictor variables examined were identified based on hypothesized drivers of habitat and previously fit cetacean–habitat relationships (Redfern *et al.* 2006; Becker *et al.* 2012, 2016). The variables were sea surface temperature (SST), SST standard deviation, log-transformed chlorophyll-*a* concentration, sea surface height anomaly (SSHa), SSHa standard deviation, eddy kinetic energy, north wind speed, wind-driven Ekman upwelling, and the bottom variables bathymetry, standard deviation of depth (indicative of bottom rugosity), slope (gradient in depth) and aspect (dominant direction that the slope faces; see Table S1). Standard deviation in SST, SSHa and bathymetry were all calculated over a $100 \times 100 \text{ km}^2$ area at both case and control locations.

TELEMETRY-BASED HABITAT MODEL

Given that many cetacean–habitat relationships are nonlinear (Redfern *et al.* 2006; Becker *et al.* 2012), we fit both generalized additive mixed models (GAMMs) and boosted regression trees (BRTs) to predict blue whale habitat preference. The GAMMs were fit using a binomial family and a logit link function and residual maximum-likelihood estimator (MGLM version 1.8-7; Wood 2006) in R (version 3.10; R Core Team 2015), with individual nested as a random effect. Initial models incorporated unconstrained smooths, but smooths were restricted to five knots in final model selection to avoid overfitting. In addition, BRTs were explored because this method has fewer statistical assumptions and can predict when environmental layers are missing (GBM version 2.1.1; Elith & Leathwick 2009). We used a case–control design where the binary response variable for both modelling

approaches was a whale position (case point assigned a value of 1) or a control point representing available habitat (assigned a value of 0; Aarts, Fieberg & Matthiopoulos 2012). We explored year-round and separate seasonal models (winter–spring, December–June; summer–fall, July–November), as well.

Candidate models were generated based on hypothesized combinations of environmental covariates. Potential models were assessed based on weighted Akaike Information Criterion (AICw), in addition to area under the curve (AUC) cross-validation statistics. AUC statistics are calculated from receiver operating characteristic (ROC) curves that use the inflection point to maximize the true positive rate, while minimizing the false-positive rate (DeLong, DeLong & Clarke-Pearson 1988). We calculated ROC curves and AUC statistics using the ROCR package in R (1.0-7).

We explored the sensitivity of the models to selection of the control points. Two of the 200 CRW tracks per whale track were randomly selected and the models rerun. This process was repeated 40 times to examine whether the whale–environment relationships were robust to the selection of the simulated CRW tracks (see Fig. S1). For example, if an environmental variable was significant in only one of 40 GAMMs, it would indicate that control point selection was strongly influencing the final model, whereas a variable that was significant in the majority of the 40 models was more robust and independent of the control points selected.

NEAR-REAL-TIME PREDICTION OF HABITAT

Our GAMM and BRT models provided spatial predictions of habitat preference, which is proportional to density (Aarts, Fieberg & Matthiopoulos 2012). We compiled environmental data at 8-day and monthly temporal resolutions for 2005, 2008 and 2009 to create predictions of whale habitat preference. Predictions were then normalized such that the entire area summed to 1 and multiplied by the population abundance to obtain absolute density estimates (Aarts *et al.* 2008). The most recent mark–recapture population estimate for North Pacific blue whales is 1647 individuals (Calambokidis & Barlow 2013), which was used to scale our

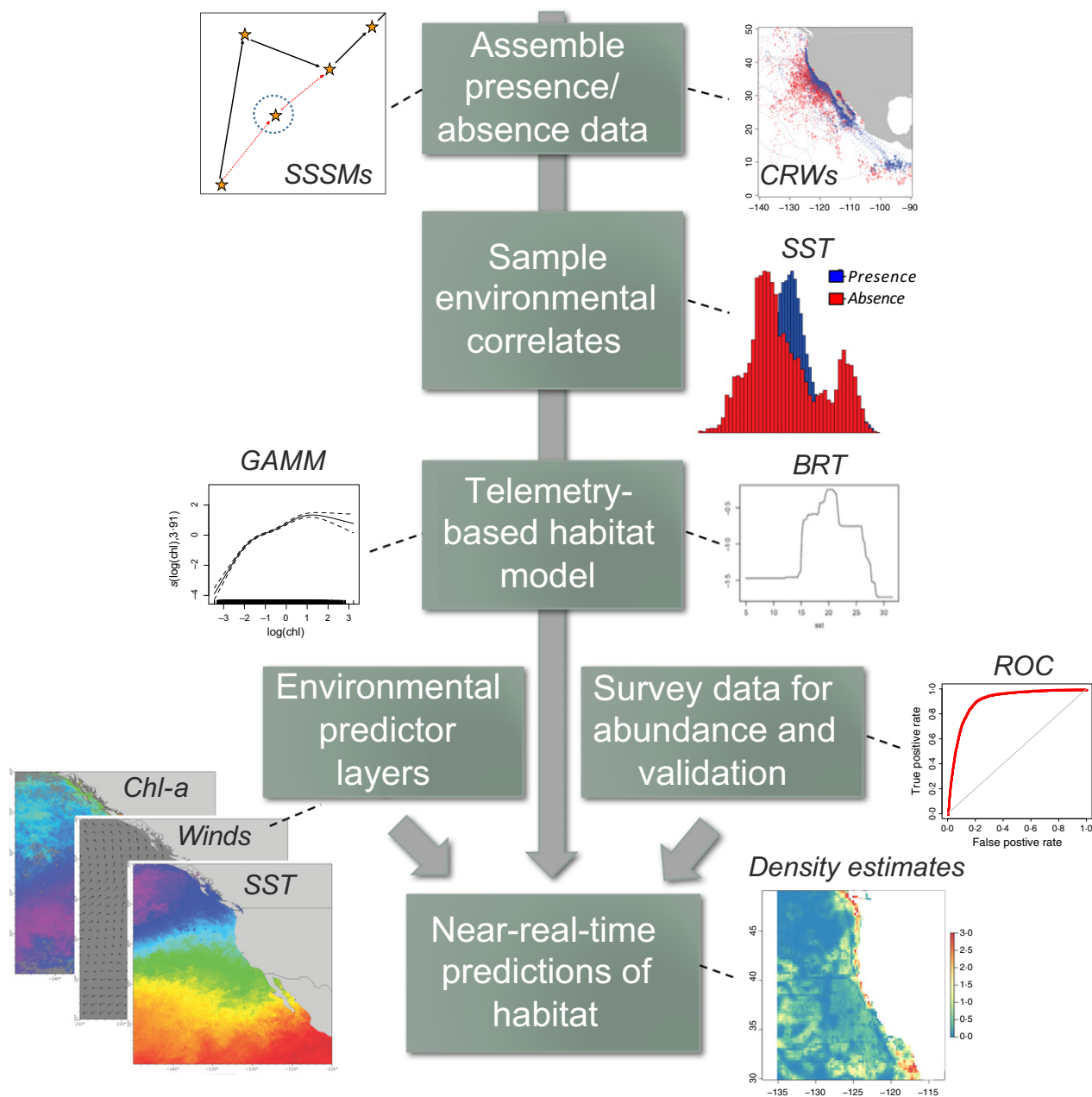


Fig. 2. Schematic highlighting the model fitting process. (1) Assembling the presence/absence data involves state-space switching models (SSSMs) to normalize whale (case) points and correlated random walks to simulating absence control points. Unrealistic tracks based on distance and direction of travel were flagged for removal. (2) Whale/control points spatio-temporally sample the environmental correlates for use in model fitting. (3) Generalized additive mixed models (GAMMs) and boosted regression trees (BRTs) were fit to case–control points to develop a predictive model. (4) Survey data were used to both convert habitat predictions to density and to validate the spatial and temporal component of model predictions. (5) Automated downloading of environmental predictor layers and prediction of habitat on the NOAA data server. (6) Near-real-time predictive maps are served via URL to the regional office website.

predictions. Monthly abundance estimates were not available for the entire year, so we multiplied the total abundance estimate by the proportion of tracking data within the California Current for each month. Predictions were made on a 25×25 km grid cell size (625 km^2) as it was the coarsest scale of environmental variables and was comparable to other habitat-based density estimates (Forney *et al.* 2012).

Ship-based line-transect surveys were conducted in July to November of 2005 and 2008 by the NOAA National Marine Fisheries Service (NMFS) Southwest Fisheries Science Center

(SWFSC; Barlow *et al.* 2009; Becker *et al.* 2016). We used monthly blue whale sightings as an independent data set to compare with our model predictions to assess their performance visually and using AUC statistics.

DEVELOPMENT OF A NEAR-REAL-TIME TOOL

The habitat preference models were incorporated into an automated process to create monthly predictions of whale occurrence and density (see Fig. S2). This approach required automating the

download and regriding of environmental data via the NOAA Coastwatch data server ERDDAP (<https://coastwatch.pfeg.noaa.gov/erddap/index.html>). We used 40 habitat models generated with different control points, which allowed us to calculate a spatial mean and standard deviation values. We also explored September predictions (a historically high-use month for blue whales) from two contrasting years, 2009 (an average year oceanographically) and 2015 (an anomalously warm year in the California Current; Bond *et al.* 2015). The resulting local monthly prediction data and maps are embedded in regional management websites for use in decision-making processes.

OVERLAP WITH HUMAN ACTIVITY

We summarized one year of commercial vessel density data as the number of vessels transiting a 1 km grid cell each day off the west coast of the United States to identify high-use shipping areas. The data were collected from the automatic identification system (AIS) ship-tracking data (NOAA Office of Coast Survey – <http://marinecadastre.gov/data/>) for vessels over 300 gross tons and all passenger ships. These shipping data were collected after the California Air Resources Board (CARB) rule in 2009, which resulted in more vessel traffic travelling south of the Channel Islands rather than in the channel-based traffic separation scheme (TSS; Redfern *et al.* 2013). To illustrate overlap with human activity, we compared our blue whale habitat preference predictions to shipping intensity to estimate the spatial and temporal overlap during 2009–2010.

Results

TELEMETRY-BASED HABITAT MODELS

The best-fit models relating the whales' distribution to the environment were seasonal GAMMs with separate models for winter–spring (December–June) and the other for summer–fall (July–November; Fig. 3; Table 2; see Fig. S3). Models selected using AICw alone resulted in anomalous prediction patterns, including high offshore densities compared to those selected via AUC primarily and AICw secondarily. The BRT models performed poorly as predictions did not agree with known blue whale habitat, and thus, results are presented in Figs S4–S6. The final seasonal GAMMs included the environmental variables SST, chlorophyll-*a* concentration, SSHa standard deviation, bathymetry and standard deviation of bathymetry, with four of five variables represented as nonlinear relationships (Table 2; Fig. 3). This also resulted in a final data set of 94 individual whales as chlorophyll-*a* was not available via the SeaWiFS satellite until late 1997. The 40 models we ran with different control points showed no change in which environmental variables were significant, highlighting that models were robust to control point selection (Table 2; see Fig. S3).

Generalized additive mixed model and BRT models showed similar contributions from environmental variables, with SSHa variability and bathymetry contributing the most in the summer–fall and SST contributing the

most explanatory power in the winter–spring (Figs S4–S6; Table 2). Our final summer–fall GAMMs showed a wide preference for SST values between 20 and 30 °C, increased chlorophyll-*a* concentrations (1–7.4 mg m⁻³), increased SSHa variability (>0.2 cm), shallower bathymetry (<2000 m) and both high and low rugosity (<200 m and >1200 m), representing the shelf-break and on or off shelf habitat, respectively (Fig. 3a–e). The winter–spring GAMMs had similar variable importance, with SST values >15 °C preferred, increasing chlorophyll-*a* concentration (>0.8 mg L⁻¹), increased SSHa variability (>0.2 cm), deeper bathymetry (1000–3000 m), and lower rugosities (<200 m) representing more offshore habitat (Fig. 3f–j).

NEAR-REAL-TIME PREDICTIONS OF HABITAT

Our monthly GAMM predictions captured the seasonal migration of blue whales and predicted similar California Current hot spots to those previously identified (Bailey *et al.* 2009; Irvine *et al.* 2014; Calambokidis *et al.* 2015; Fig. 4; see Fig. S7). Our predictions of the likelihood of whale occurrence ranged from 0 to 92%, and bootstrapped standard errors estimated from the control point selection were 5% on average across all months, although standard error per grid cell ranged from 0.1% to 18%. The average densities from our model predictions in the entire California Current were highest from August to October and ranged from 0 to 3.5 individuals per 25 × 25 km grid cell. Very few whales (<1 per grid cell) were predicted within the California Current between November and March. April through June showed increased predicted densities in the Southern California Bight (1–2 per grid cell). The greatest densities in summer and fall were predicted in the Southern California Bight (south of Pt. Conception, 34° N) and between Monterey Bay (~37° N) and Humboldt Bay (~44° N) within 300 km from shore. A few offshore hot spots were predicted at lower densities, particularly north of the Mendocino Escarpment (40.5° N).

Comparison with the NOAA/NMFS SWFSC line-transect survey sightings in 2005 and 2008 indicated fair agreement with our predictions (AUC values ranged from 0.55 to 0.66 across our model iterations; Fig. 6; see Fig. S7-video). Considerable survey effort occurred offshore, while the satellite tracks largely remained inshore, highlighting a difference in sampling effort between the two data sets. Sightings often overlapped with high predicted densities, while there were also cases where blue whales were observed in offshore areas with lower predicted density (e.g. Fig. 5).

NEAR-REAL-TIME TOOL

The near-real-time tool termed 'WhaleWatch' was automated to provide monthly estimates of likelihood of occurrence, uncertainty estimates and density of blue whales

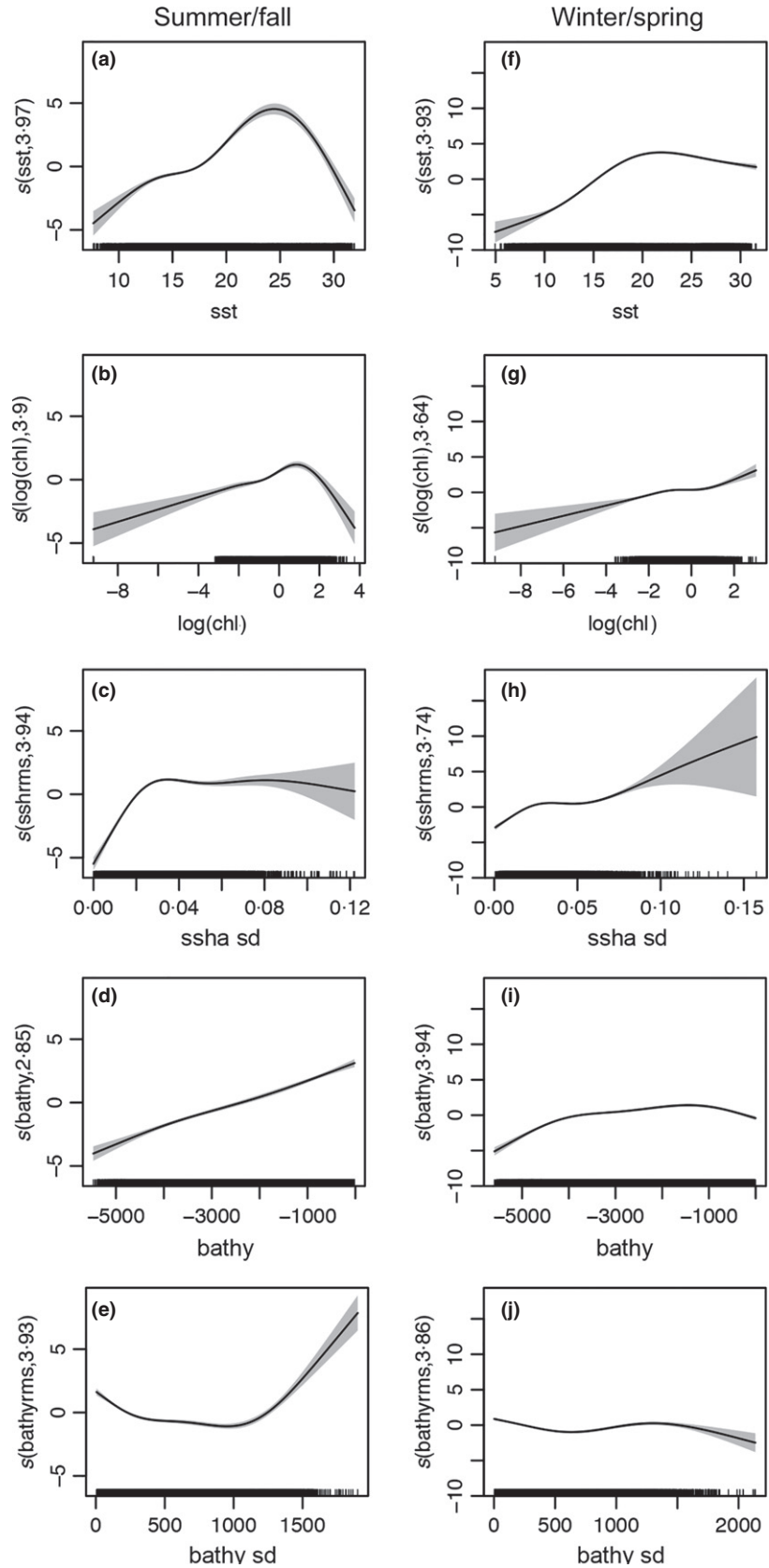


Fig. 3. Generalized additive mixed model partial plots for blue whale presence/absence variables in winter/spring (December–June; a–e) and summer/fall (July–November; f–j). Partial response is on the y-axis with standard error shown in grey. The range of the environmental variable is on the x-axis.

(0–3.5 individuals per 625 km²; <http://oceanview.pfeg.noaa.gov/WhaleWatch/>; see Fig. S8). Because the images are hosted via restful URLs (http://oceanview.pfeg.noaa.gov/WhaleWatch/images/WhaleWatch_current.png), the image is

automatically updated monthly on the NOAA/NMFS West Coast Region website when new predictions are made (<http://www.westcoast.fisheries.noaa.gov/whalewatch/>; see Fig. S9).

Table 2. Four candidate generalized additive mixed model summaries for seasonal, annual full and annual reduced models including Akaike Information Criterion (AIC) and area under the curve (AUC) statistics

	edf	F	n-significant
<i>Summer</i>			
sst	3-967	134-724	40
log(chl)	3-899	33-564	40
ssh sd	3-939	162-419	40
Bathy	2-847	185-528	40
Bathy sd	3-926	85-774	40
	$R^2 = 0.417$	AIC = 109 934-320	
		AUC = 0-861	
<i>Winter</i>			
sst	3-932	520-662	40
log(chl)	3-640	22-089	40
ssh sd	3-738	108-896	40
Bathy	3-938	107-749	40
Bathy sd	3-862	47-362	40
	$R^2 = 0.280$	AIC = 81 018-105	
		AUC = 0-855	
<i>Full</i>			
sst	3-984	552-051	40
log(chl)	3-901	29-235	38
ssh sd	3-979	316-054	40
Bathy	3-844	343-527	40
Bathy sd	3-860	125-023	40
	$R^2 = 0.334$	AIC = 177 822-723	
		AUC = 0-845	
<i>Reduced</i>			
sst	3-989	955-522	40
Bathy	3-911	849-284	40
Bathy sd	3-910	241-537	40
	$R^2 = 0.226$	AIC = 157 116-585	
		AUC = 0-802	

In the models presented, all variables were significant with P values less than 0.001.

The web-based predictions showed much higher densities off the U.S. West Coast in September 2009 compared to 2015 reflecting interannual variability in blue whale distribution as a result of changing environmental conditions (Fig. 6). In the California Current, 2009 has been described as an 'average' year in terms of the sea surface temperature and other variables in the model, while 2015 was a year of reduced ocean mixing and warmer surface temperatures (Bond *et al.* 2015).

OVERLAP WITH HUMAN ACTIVITY

Measurements of shipping traffic and predicted blue whale density showed high overlap (see Figs S10 and S11). Compared to shipping intensity from October 2009 to October 2010, blue whales were predicted in high densities in the TSS into Long Beach and Los Angeles largely from April to November and in the TSS into San Francisco Bay from August to October (Figs S10 and S11). The blue whale densities from our model predictions suggest that overlap between blue whales and shipping traffic in the California Current is greatest between August and October.

Discussion

Previous blue whale studies have used satellite tracks to create kernel densities and home ranges (Irvine *et al.* 2014) or have used survey-based sightings and oceanographic variables to predict habitat-based densities (Forney *et al.* 2012; Redfern *et al.* 2013; Becker *et al.* 2016). Each of these approaches has particular advantages, with survey data providing instantaneous snapshots of blue whale abundances but only for surveyed years and seasons (e.g. July–November, in this case). Combining our large satellite telemetry data set with oceanographic correlates provided a year-round prediction of potential habitat. Tracking data typically sample a small portion of the population and often from only one or a few tagging locations, potentially limiting their inference for the entire population. However, our telemetry data set spanned more than a decade, including twelve months of the year and animals tagged at multiple locations (Table 1; Bailey *et al.* 2009; Irvine *et al.* 2014). Both visual comparison and AUC calculations between sightings data and our model predictions indicated fair agreement as surveys had greater offshore effort, while the whales were tagged predominantly in coastal waters (within 100 km from shore in the California Current). Because of the coastal focus of tagging locations (Table 1), site fidelity could result in an undersampling of offshore foraging habitat (Calambokidis & Barlow 2004), potentially causing our blue whale densities to be underestimated offshore. Using year-round telemetry data and ocean habitat proxies, we provide spatially explicit density predictions for all seasons, which is critical when managing highly migratory species.

Long-term telemetry data have greatly improved our understanding of blue whale annual migrations from the eastern tropical Pacific in winter and spring to the eastern North Pacific in the summer and fall (Mate, Lagerquist & Calambokidis 1999; Bailey *et al.* 2009; Irvine *et al.* 2014). The exact temporal cues and triggers of these migrations remain unknown; however, they are likely driven by recurrent krill patches, given the whales' reliance on this single prey resource. Studies modelling krill distribution in the California Current have found a strong association with the shelf-break and eddy kinetic energy (Santora *et al.* 2011); thus, physical variables likely serve as proxies for prey density in our blue whale models. In the absence of year-round krill density measurements, we must rely on oceanographic covariates to predict likely habitat.

We found our models were able to capture habitat-use characteristics of blue whales and to provide year-round density estimates for blue whales in the California Current. Our range-wide models showed that blue whales used more inshore, high rugosity (measured by standard deviation of bathymetry), and 20–30 °C surface temperature habitat in the summer, while there was a preference for offshore, low rugosity, warmer temperatures and higher chlorophyll-*a* concentration habitat in the winter.

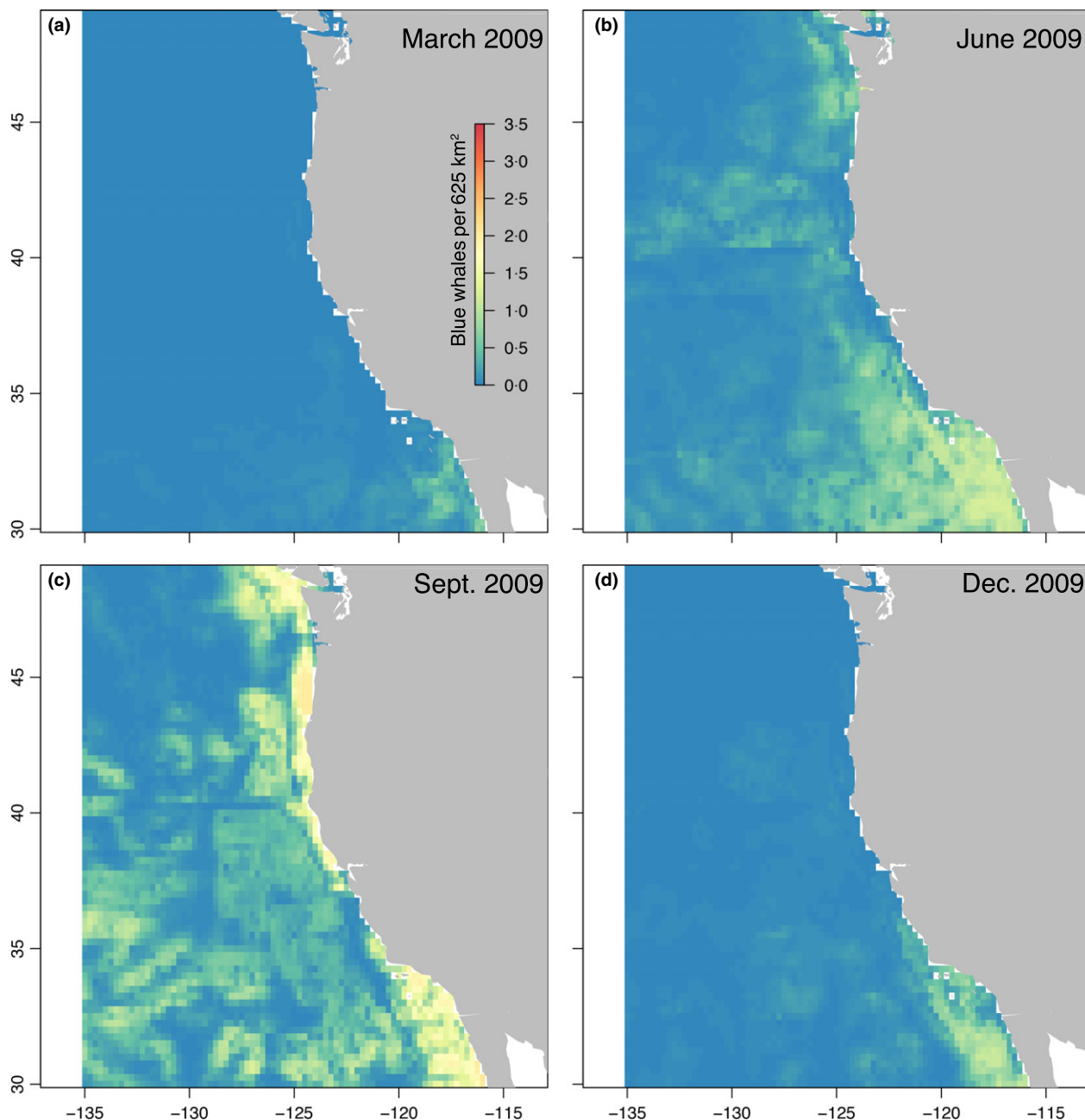


Fig. 4. (a–d) Blue whale habitat predictions from seasonal GAMMs for March, June, September and December of 2009. Density is included as number of whales per 625 km².

While these SST preferences are higher than California Current-only studies (Becker *et al.* 2016), our models include the migratory use of offshore waters and the tropical Pacific (Bailey *et al.* 2009). Blue whales showed a positive relationship with the standard deviation of SSHa, a metric of mesoscale activity, year-round. While wind forcing drives much of the upwelling dynamics in the California Current, it was less useful in these models likely because of a lag between upwelled nutrients and a change in krill density (Croll *et al.* 2005) and because of the importance of stratification in modulating the effects of upwelling on the ecosystem (Jacox *et al.* 2015).

The eastern North Pacific population of blue whales had approximately 3000 individuals taken by whalers over 30 years from Mexican to Canadian waters in the early to mid-20th century (Clapham *et al.* 1997). Blue whales in the eastern North Pacific are listed as threatened under the endangered species act with ship strikes identified as a source of annual mortality (Calambokidis & Barlow 2013; Redfern *et al.* 2013). Recent population estimates have remained steady in the California Current across mark-recapture data sets between ~1600 and 2000 individuals (Calambokidis & Barlow 2013), while shipboard surveys have documented a distributional shift in the number of

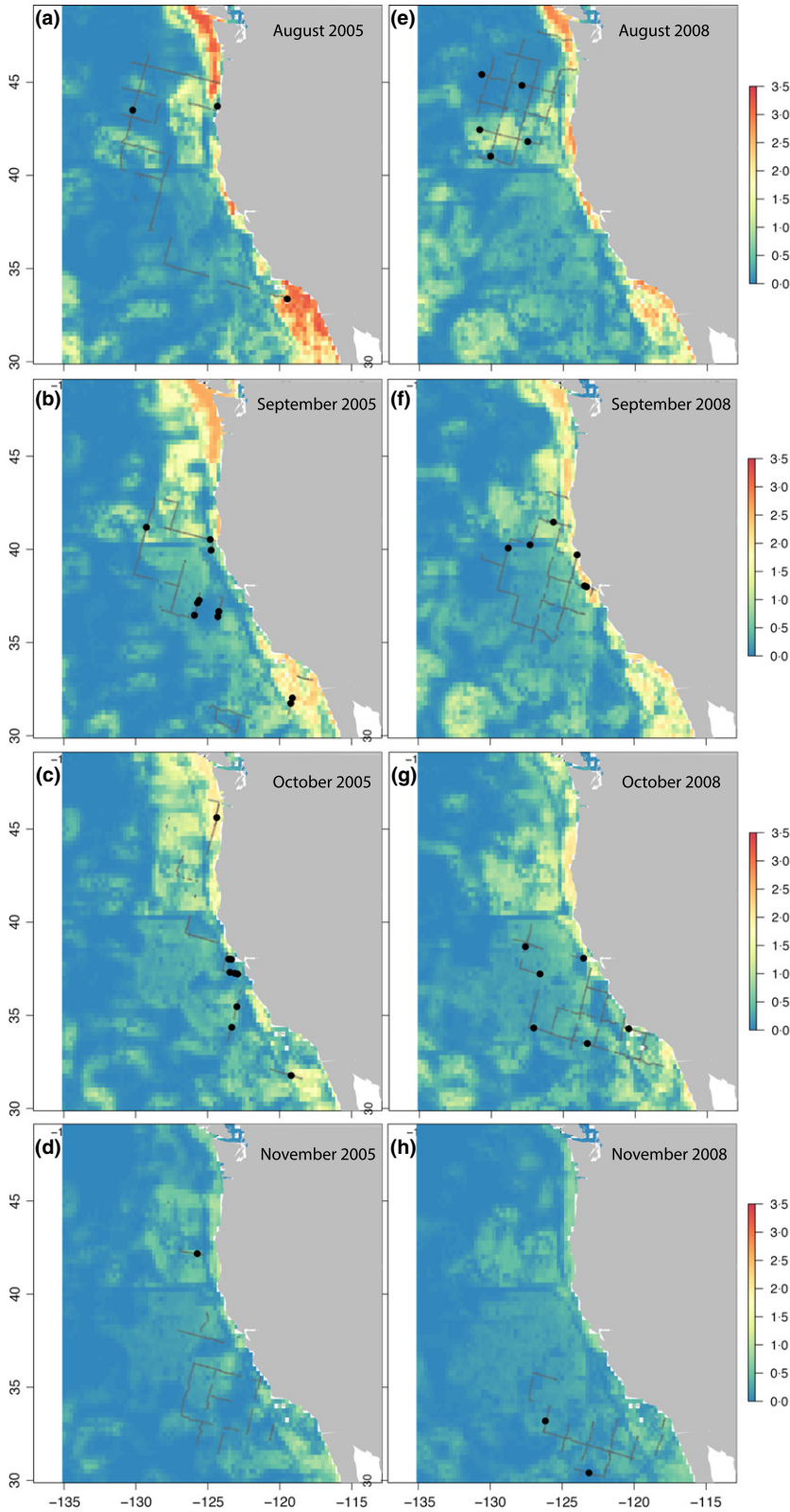


Fig. 5. (a–h) Comparison of blue whale habitat predictions for fall 2008 in US EEZ with SWFSC sightings data shown as black points. Survey track lines (on effort) are shown as grey lines. Density is included as number of whales per 25×25 km grid cell.

whales found off California, Oregon and Washington since 1998 (Barlow & Forney 2007; Barlow *et al.* 2009). A recent modelling study suggested that blue whales have recovered to c. 97% of their carrying capacity offering a positive message for recovery (Monnahan, Branch & Punt

2015). Nonetheless, efforts to reduce ship strikes are important for both continued recovery and adherence with management regulations (Calambokidis & Barlow 2004; Redfern *et al.* 2013; Irvine *et al.* 2014). Global trends towards rebuilding and recovery of exploited and

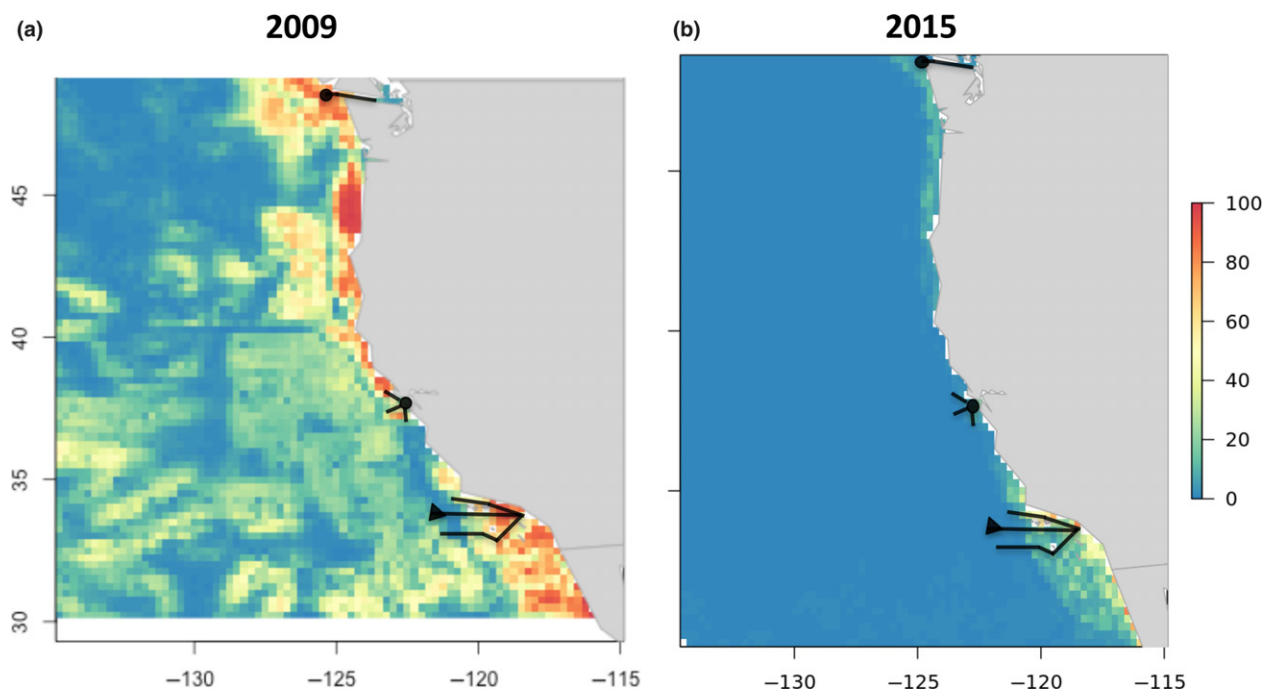


Fig. 6. Predicted habitat preference from the web-based tool (<http://oceanview.pfeg.noaa.gov/WhaleWatch/>) for (a) September of 2009 and (b) 2015. The year 2009 was an average year in the California Current, while 2015 was a period of unusual warming. The current locations of shipping lanes are overlaid in black. This output highlights the interannual variability in blue whale use of the California Current.

protected species stocks are continuing (Worm *et al.* 2009; Monnahan, Branch & Punt 2015; Roman *et al.* 2015), yet there remain additional opportunities to align fisheries and conservation goals using a suite of management tools (e.g. ecosystem-based and dynamic ocean management) instead of relying on a single approach (Worm *et al.* 2009).

Telemetry data combined with species distribution models (SDMs) offer a novel approach towards examining management scenarios (Carvalho *et al.* 2011; Guisan *et al.* 2013; McShea 2014; Allen & Singh 2016), yet SDMs are infrequently used in marine management (Marshall, Glegg & Howell 2014). This is in contrast to terrestrial systems, where SDMs have been used to examine overlap between species such as the migratory saiga antelope *Saiga tatarica* or caribou *Rangifer tarandus* and risk (e.g. human development and climate-induced changes), dynamically (Singh & Milner-Gulland 2011; Taillon, Festa-Bianchet & Côté 2012; Bull *et al.* 2013). SDMs can be used to identify potentially undiscovered habitat, but also to look at distributional metrics such as residency time, migration cues and foraging effort that ultimately can inform dynamic management approaches (Bailey *et al.* 2009; Carvalho *et al.* 2011; Hooker *et al.* 2011). In addition, ensemble approaches combine multiple models and even data types to improve predictions (Araújo & New 2007; Scales *et al.* 2015; Yamamoto *et al.* 2015). Running SDMs in a predictive mode allows for habitat estimates at finer temporal scales (days to months) limited by environmental data availability. Such dynamic approaches provide an

opportunity to minimize management actions (e.g. area closures) and enforcement need, while maximizing management effectiveness (Lewison *et al.* 2015; Maxwell *et al.* 2015).

Here, we have developed a dynamic management tool that uses remotely sensed variables to predict blue whale density in the California Current at 8-day and monthly time-scales (<http://www.westcoast.fisheries.noaa.gov/whalewatch>). Our habitat model provides a valuable approach for understanding blue whale distribution that can be combined with shipping data (see Fig. S11) or other potential threats to look for spatio-temporal opportunities for targeted management. Both dynamic and seasonal management areas (DMAs and SMAs) have been implemented to reduce ship strike risk for North Atlantic right whales *Eubalaena glacialis*, yet voluntary dynamic speed restrictions (in DMAs) were less successful than mandatory seasonal speed restrictions (SMAs; van der Hoop *et al.* 2015). Similarly, voluntary strategies were found to be inadequate to mitigate ship strike risk for blue whales on the west coast as shipping vessels did not significantly alter their speed (McKenna *et al.* 2012). However, we have several reasons to believe that mandatory dynamic management approaches could be successful for blue whales in the California Current. First, the obligate prey (krill) of blue whales are more strongly tied to dynamic features (Croll *et al.* 2005; Santora *et al.* 2011) than the prey (diapausing copepods) of North Atlantic right whales (Baumgartner *et al.* 2003). Secondly, the managers and the shipping industry using the ports of

Long Beach and San Francisco have been engaged in the development of ship strike risk tools since the problem was identified (Redfern *et al.* 2013). Finally, there are multiple options available to implement these predictions in a risk-limiting approach. Specifically, shipping traffic could be adjusted to alternate shipping lanes or could have mandatory speed restrictions implemented only in high-risk scenarios providing a dynamic approach. Also, periods of high risk could trigger additional marine mammal monitoring to validate the occurrence of whales and enforce any speed restriction rules. The predictive model presented here provides a critical step towards developing seasonal and dynamic management approaches to help reduce the risk of ship strikes for blue whales in the California Current.

Our models will require ongoing validation to ensure the species–environment relationships identified here persist in the future, particularly if the climate changes beyond the conditions experienced during our study. Static management approaches that are sufficient now may become less effective in the future, such that dynamic ocean management inherently provides an opportunity to be proactive for climate-induced distribution shifts in marine species (Hazen *et al.* 2013a). Increased technological capacity from animal telemetry, environmental data from satellite remote sensing and computationally intensive models offer opportunities for targeted management applications to protect critical pelagic habitat and respond to environmentally driven changes in species distributions.

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Data accessibility

The data used in this manuscript are available via the Integrated Ocean Observing System's Animal Telemetry Network website (<http://oceanview.pfeg.noaa.gov/ATN/>).

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Supporting Information

Additional Supporting Information may be found in the online version of this article.

Fig. S1. Entire dataset of blue whale tracks (blue) and correlated random walk simulated pseudo-absences (red) used in the modelling framework. Inset: Actual track (black) and correlated random walk simulated pseudo-absences (red) for a single tagged blue whale.

Fig. S2. Automated data processing flowchart identifying the steps once models have been fit and best environmental predictors have been identified.

Fig. S3. Receiver operating curves for seasonal (black), full (blue), reduced (red), boosted regression tree (green) models with false positive on the *x*-axis plotted against the true positive on the *y*-axis. A perfect receiver operating curve would have a true positive rate of 1 and a false positive rate of 0 (hollow circle).

Fig. S4. BRT variable influence for summer/fall and winter/spring models. Relative contribution is represented on the *x*-axis.

Fig. S5. BRT response curves for winter/spring and summer/fall models.

Fig. S6. Blue whale habitat predictions from seasonal BRTs for March, June, September, and December of 2009.

Fig. S7. Animated blue whale habitat predictions from GAMMs for January to December of 2009. Density is the number of whales per 25×25 km grid cell.

Fig. S8. Southwest Fisheries Science Center hosted tool predicting blue whale likelihood of occurrence and density at a monthly time step (<http://oceanview.pfeg.noaa.gov/WhaleWatch/>).

Fig. S9. Regional office project description serving the real-time predictive maps and describing the tool for use by managers and shippers (<http://www.westcoast.fisheries.noaa.gov/whalewatch/index.html>).

Fig. S10. Blue whale predicted habitat climatologies (1997–2009) for (a) summer-fall and (b) winter-spring modelled periods. Density is the number of whales per 25×25 km grid cell.

Fig. S11. Commercial vessel density data from October 2009–2010 showing areas of low (blue) to high (red) shipping intensity.

Table S1. Satellite products, resolution, time periods covered and source of data used in our modelling approach (fitting and prediction).