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Should I stay or should I go? Modelling year-round habitat suitability and drivers of residency for fin whales in the California Current

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Abstract

Aim: Understanding the spatial ecology of endangered species is crucial to predicting habitat use at scales relevant to conservation and management. Here, we aim to model the influence of biophysical conditions on habitat suitability for endangered fin whales *Balaenoptera physalus*, with a view to informing management in a heavily impacted ocean region.

Location: We satellite-tracked the movements of 67 fin whales through the California Current System (CCS), a dynamic eastern boundary upwelling ecosystem in the Northeast Pacific.

Methods: We use a multi-scale modelling framework to elucidate biophysical influences on habitat suitability for fin whales in the CCS. Using generalized additive mixed models, we quantify the influence of a suite of remotely sensed variables on broad-scale patterns of occupancy and present the first year-round, high-resolution predictions of seasonal habitat suitability. Further, we model the influence of contemporaneous biophysical conditions on individual-level residence times in high-use habitat.

Results: We present evidence of year-round habitat suitability in the southern California Current System, robust to interannual variability, establishing that North Pacific fin whales do not follow the canonical baleen whale migration model. Within the high-use habitat in the Southern California Bight (SCB), individual-level residency in localized areas (*n* = 16 for >30 days; *n* = 4 for >6 months) was associated with warm, shallow, nearshore waters (>18°C, <500 m), with cool waters (14–15°C) occurring over complex seafloor topographies and with convergent (sub)mesoscale structures at the surface.

Main Conclusions: Biophysical conditions in the southern CCS generate productive foraging habitats that can support the fin whale population year-round and allow for extended periods of residency in localized areas. High-use habitats for fin whales are colocated with areas of intense human use, including international shipping routes and a major naval training range. Seasonal habitat suitability maps presented here could inform the management of anthropogenic threats to endangered baleen whales in this globally significant biodiversity hotspot.

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1 | INTRODUCTION

The spatial ecology of wide-ranging species is complex, as habitat selection is known to be driven by a range of inter-related intrinsic and extrinsic motivations, yet a comprehensive understanding of the dynamics of space use is essential for conservation and management. Wide-ranging species must make habitat selection decisions based upon the interplay between intrinsic motivations such as breeding cycles, inter- and intra-specific competition, predation risk and spatial memory, and extrinsic factors such as heterogeneity in habitat quality (Geijer, Notarbartolo di Sciara, & Panigada, 2016; Schick et al., 2008). Many taxa are known to migrate between habitats suitable at different stages of the annual cycle owing to fluctuating resource availability (Dingle & Drake, 2007), a strategy observed in multiple baleen whale populations (Corkeron & Connor, 1999; Firestone, Lyons, Wang, & Corbett, 2008; Horton et al., 2011; Ramp, Delarue, Palsbøll, Sears, & Hammond, 2015). Anticipating the broad-scale distribution of resources in this way confers a fitness advantage, but relies upon both predictability in the physical environment and prior knowledge of the system.

Recent developments in animal tracking and habitat modelling have vastly improved our understanding of the influence of the physical environment in habitat selection decisions across taxa (Block et al., 2011; Hays et al., 2016) and have challenged the canonical baleen whale migration model of predictable seasonal movements between low-latitude winter breeding grounds and high-latitude summer foraging grounds (Geijer et al., 2016). Multiple baleen whale populations are now known to contradict this rule. For example, the fin whale population of the Mediterranean Sea is known to remain resident to a sub-basin scale region throughout the annual cycle (Geijer et al., 2016; di Sciara, Castellote, Druon, & Panigada, 2016). The blue whale *Balaenoptera musculus* population of the Indian Ocean remain year-round in resource-rich regions associated with episodic upwelling off Sri Lanka (de Vos, Pattiaratchi, & Harcourt, 2014). Eastern Atlantic blue whales exhibit considerable intrapopulation variability in migratory movements with some individuals travelling north from central Africa following breeding, while others migrate to the Southern Ocean (Rosenbaum, Maxwell, Kershaw, & Mate, 2014). Blue and fin whales *Balaenoptera physalus* in the North Atlantic are known to suspend migration when biophysical conditions are conducive for foraging (Silva, Prieto, Jonsen, Baumgartner, & Santos, 2013). Similarly, humpback whales *Megaptera novaeangliae* are known to remain resident to particular areas for weeks to months to exploit super-aggregations of prey (Nowacek et al. 2011).

Fin whales are also thought to be present through the annual cycle in the California Current System (CCS; Forney & Barlow, 1998)—a major eastern boundary upwelling system that supports a diverse range of predatory marine vertebrates, both resident and migratory (Ainley et al., 2005; Block et al., 2011). Classified as *globally endangered* since 1996, following historical overexploitation (IUCN Red List of Threatened Species; Reilly et al., 2013), the fin whale is listed as a protected species under both the US Marine Mammal Protection Act (1972) and US Endangered Species Act (1973). Known as the "greyhound of the sea" for its speed of movement, this wide-ranging, long-lived, large-brained and social marine vertebrate is known to occur throughout the temperate zones of the global ocean (Edwards, Hall, Moore, Sheredy, & Redfern, 2015). However, our understanding of fin whale spatial ecology at (sub)ocean–basin scales, including population structure, migration patterns, preferred habitats, inter- and intra-population variability and plasticity in habitat selection decisions, is severely lacking, which complicates conservation (Geijer et al., 2016).

Developing effective management strategies for baleen whale populations relies upon a more complete understanding of how environmental conditions influence their spatial ecology at ocean-basin scales and finer scales, and the role of dynamic biophysical coupling in driving prey availability and, hence, space use decisions. Modelling habitat suitability for populations of conservation concern is useful for understanding animal–environment interactions, for locating high-use habitats and areas of residency (eg, Forney, Becker, Foley, Barlow, & Oleson, 2015), for predicting how these habitats might shift with changing oceanographic dynamics (eg, Hazen et al. 2013) and for identifying areas of overlap with anthropogenic threat (eg, Maxwell et al. 2013; Howell et al., 2015; Hazen et al., 2016)—all crucial aspects in developing effective strategies for protected species management.

Improving our understanding of the spatial and foraging ecology of baleen whales is particularly important in the California Current System (CCS), where several populations of conservation concern coexist with intense anthropogenic pressure on the marine environment. Predicting habitat suitability for baleen whales in the CCS throughout the annual cycle and at sufficient spatial and temporal resolution is critical to anticipating overlaps with anthropogenic threats such as ship strike risk, underwater noise and fisheries (eg, Hazen et al., 2016). However, this is complicated by the inherent heterogeneity and variability in the physical environment in the CCS, a highly dynamic system subject to intense episodic upwelling events and a complex and variable flow field (Bograd, Leising, & Hazen, 2016). Biophysical conditions in the CCS can be highly variable at (sub)mesoscales (1–10 km) and over time-scales of days–weeks–months, leading to heterogeneity in the manifestation of prey patches (Santora, Sydeman, Schroeder, Wells, & Field, 2011). Baleen whales are known to exhibit threshold foraging responses, in that they will remain to feed on a particular prey patch until a prey density threshold is reached and energetic constraints prompt a behavioural switch to searching for other foraging opportunities (Piatt & Methven 1992; Hazen et al. 2009). Dynamic biophysical processes

determine the foraging seascape experienced by baleen whales in the CCS and, ultimately, the spatio-temporal distribution of important habitats (Croll, Marinovic, Benson, & Chavez, 2005).

Using a multi-year (2008–15) satellite telemetry dataset tracking the movements of 67 adult and sub-adult fin whales, we therefore aim to (i) model the relative influence of biophysical conditions on broadscale patterns of occupancy in the CCS, (ii) predict seasonal habitat suitability for fin whales throughout the annual cycle, (iii) explore seasonal and interannual variability in habitat suitability and (iv) elucidate the proximate environmental drivers of residency behaviour through modelling (sub)mesoscale biophysical influences on individual-level residence times in high-use habitat.

2 | MATERIALS AND METHODS

2.1 | Tagging and tracking

Fin whales were tagged off the coasts of Southern California (n = 58) and Washington State (n = 9). Argos-linked, Low Impact Minimally Percutaneous External-electronics Transmitter (LIMPET; Wildlife Computers, Redmond, WA, USA) tags were deployed from a 7–8 m rigid hull inflatable boat with a modified bow pulpit, using a Dan-Inject pneumatic projector (Børkop, Denmark). Two types of tags were used as follows: location-only SPOT5 tag (n = 49) and location and dive-reporting SPLASH10-A tag (n = 18). Duty cycling varied by tag type, to conserve battery power. SPOT5 tags were programmed to transmit daily for 50 days and then switch to every other day for 20 days, followed by every third day for 30 days, every fifth day for 50 days and then every 10th day thereafter. Programming for SPLASH10-A tags varied as new information was applied regarding battery and data transmission rates. Ten of the tags transmitted daily before they stopped, the remaining 8 transmitted for 20 (n = 1), 22 (n = 1), 23 (n = 4) and 28 (n = 2) days before switching to an every other day duty cycle (Table S1).

All location fixes were filtered using the Douglas algorithm (Douglas et al., 2012). We also ran an additional speed filter based on maximum feasible speed for fin whales (15 km/h for >1 h; Cotté et al., 2011). Tracks with fewer than three remaining locations (n = 3) were removed from the set used for further analysis (n = 64). All location fixes were reprojected to an equal-area projection system (EPSG:3410).

Location estimates were weighted according to tracking duration, to reduce bias associated with tagging location and uneven tracking durations. Low weights (increasing 0.1–1.0) were applied to the first 10 days of tracking. Each successive location was then weighted by the inverse of the number of individuals with locations on the same relative day, up to the 85% percentile of all track lengths (65d), beyond which all weights applied were equal to that threshold (following Irvine et al., 2014).

2.2 | Environmental data

The study area was defined by the extent of all filtered tracking data (130°W - 112°W; 20°N - 50°N; Figure 1). Static physiographic data were derived from the ETOPO2v2 2-minute gridded global relief dataset (NOAA National Centers for Environmental Information; http://www.ngdc.noaa.gov/mgg/global/etopo2.html). Standard deviation in water depth—a proxy for bathymetric rugosity—was determined using a 3x3 pixel moving window over this bathymetry field ("ncdf4" and "raster" packages for R; Hijmans, 2015; Pierce, 2014).

Seasonal environmental data fields were created for each season (Spring: March–May; Summer: June–August; Autumn: September–November; Winter: December–February) of each tracking year (2008–15). High-resolution monthly composites covering the entire tracking period were downloaded as NetCDF via NOAA's ERDDAP server (http://coastwatch.pfeg.noaa.gov/erddap/) and reprojected to an Equal-Area Scalable Earth projection (EPSG:3410, EASE-grid, http://spatialreference.org/ref/epsg/nsidc-ease-grid-global/) using the "raster" package for R (Hijmans, 2015).

Monthly SST composites were obtained using Local Area Coverage (LAC; 0.0125° resolution) of the Advanced Very-High Resolution Radiometer (AVHRR) sensor aboard NOAA's Polar Operational Environmental Satellites (POES). Monthly chlorophyll-*a* composites were obtained from Aqua-MODIS (West USA) at 0.0125° resolution. Seasonal medians were calculated for each year and for average seasonal conditions over the tracking period. Seasonal thermal front frequency (% time in which a front ≥0.4°C in gradient magnitude was present in each pixel) was derived using 8-day composite front maps processed from Pathfinder AVHRR SST data (Miller & Christodoulou, 2014).

Shorter time span composites were used as indicators of conditions contemporaneous to fin whale movements. These included time-matched daily Global High Resolution Sea Surface Temperature (GHRSST) data (Level 4, AVHRR, Blended) obtained via ERDDAP; 8-day chlorophyll-*a* composites from Aqua-MODIS via ERDDAP; Sea Surface Height (SSH) from AVISO Absolute Dynamic Topography (ADT; http://www.aviso.altimetry.fr/en/data/products/sea-surface-height-products/global/madt-h-uv.html); Eddy Kinetic Energy calculated from u and v fields of AVISO geostrophic velocities; and 4-day Finite-Size Lyapunov Exponent fields (FSLE; http://www.aviso.altimetry.fr/en/data/products/value-added-products/fsle-finite-size-lyapunov-exponents.html). The Finite-Size Lyapunov Exponent is a Lagrangian measure of submesoscale circulation (Cotté et al., 2011). Here, we use backward-in-time FSLE to identify convergent Lagrangian coherent structures such as fronts, eddies and upwelling filaments.

2.3 | Habitat modelling

A multiscale approach was taken to habitat modelling. First, broadscale seasonal models were used to ascertain relative habitat suitability in the California Current System (CCS; enclosed by vertices at −112°W, −120°W, −130°W, 24°N, 40°N, 52°N; Figure 2). Second, finer-scale models were used to investigate contemporaneous biophysical influences on individual residence times within high-use habitat.

2.3.1 | Broadscale seasonal presence-availability

All filtered locations were plotted as individual tracks (Figure 1a). Weighted locations were also summed within a 0.1° hexagonal grid as

FIGURE 1 (a) Filtered tracking data per individual (*n* = 64), aggregated over all years (2008–15), with tag deployment locations as coloured diamonds (b) Sum of weighted locations per 0.1° hexagonal grid cell. Locations weighted to remove bias resulting from tag deployment location and by tracking duration per individual
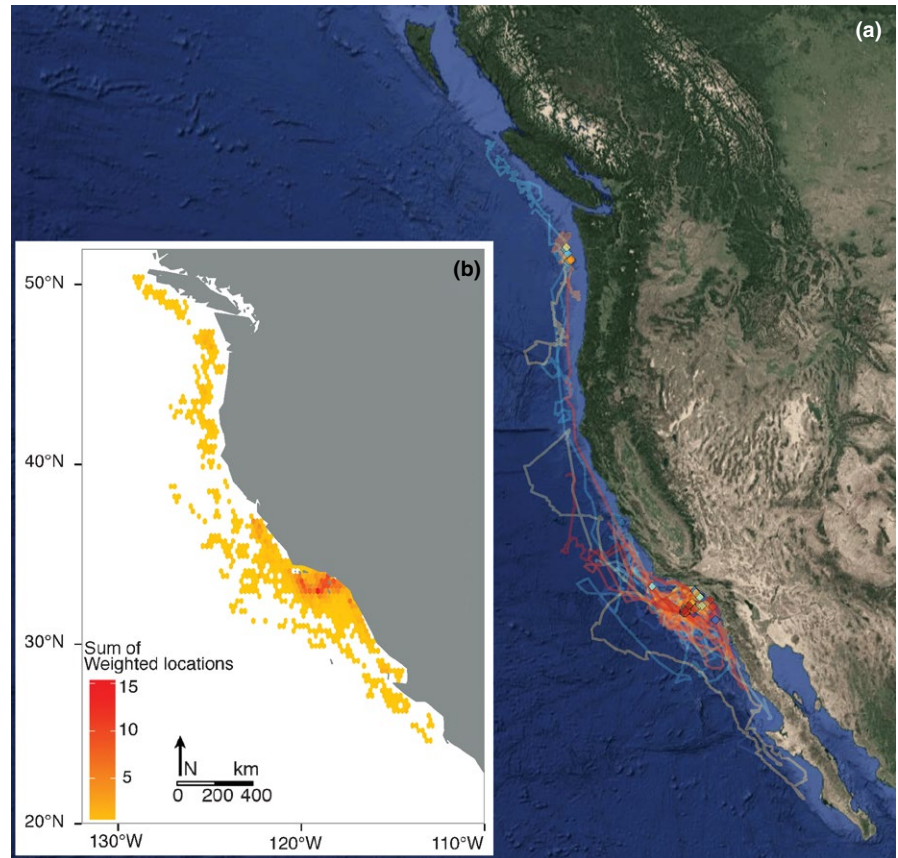
an indication of patterns of occupancy (Figure 1b; "ggplot2" package for R; Wickham, 2009).

Broad-scale, seasonal presence-availability models were used to identify environmental conditions characterizing high-use areas. First, areas used by whales in each season were identified using a kernel utilization distribution (KUD) incorporating all filtered tracking data, aggregated over all years to account for low and uneven sample sizes in individual years (Figure 2). Utilization distributions were generated using standard techniques in the *adehabitatHR* package for R (version 0.4.14; Calenge, 2006). A large bandwidth smoothing parameter was selected using the "h-ref" method (Figure 2). Presence locations (*n* = 200 for each iteration) were resampled at random from within the 95% seasonal KUD isopleths. Habitat availability during each season was quantified through randomized background sampling from within the CCS domain (*n* = 1500 for each iteration; Barbet-Massin, Jiguet, Albert, & Thuiller, 2012).

Generalized additive mixed models (GAMMs) with binomial errors were used to quantify seasonal habitat preferences ("gamm4" package for R; Wood & Scheipl, 2014). Environmental predictors were included on the basis of AIC corrected for sample size (AICc; "AICmodavg" package for R; Mazerolle, 2015). Generalized variance inflation factors (GVIFs) ensured predictor variables were not colinear. Season and tagging region were included as random effects. Initial models were constructed with unconstrained smooths, and then, smooths were constrained to five knots. Response curves were plotted by predicting over the range of each predictor while others were held constant at their mean (Figure 3).

Model diagnostics included k-fold cross-validation (CV), with a 75%/25% data split and random sampling of the presence-availability data frame over each of 5-folds, using area under the receiver operating curve (AUC) as a diagnostic measure (k-fold CV score, AUC = 0.76).

High-resolution spatial predictions (0.05°) of relative habitat suitability for fin whales (HSI, scaled 0-1) were generated through predicting from our GAMM response curves over multi-parameter physical datasets quantifying the average seasonal conditions in the CCS during the tracking period (2008–14), obtained via remote sensing. Interannual variability in seasonal habitat suitability was determined using a two-step process. Firstly, the standard deviation in our relative habitat suitability predictions for each 0.05° grid cell was calculated through prediction from model response curves over separate seasonal physical data fields for each year of the tracking study (Fig. S1). Secondly, 50% KUD isopleths for all animals tracked in each year were overlain to determine the extent of overlap in high-use habitat over the tracking period (Figure 5a).

2.3.2 | Individual-level residence time

Finer-scale models explored the influence of contemporaneous biophysical conditions on residence times within the Southern California Bight (SCB), a high-use habitat identified in seasonal models. The SCB domain was restricted to south of 35°N and only the first 30 days of each track of whales frequenting the area were used, owing to irregularities in location fix frequency. Location fix interval in this data
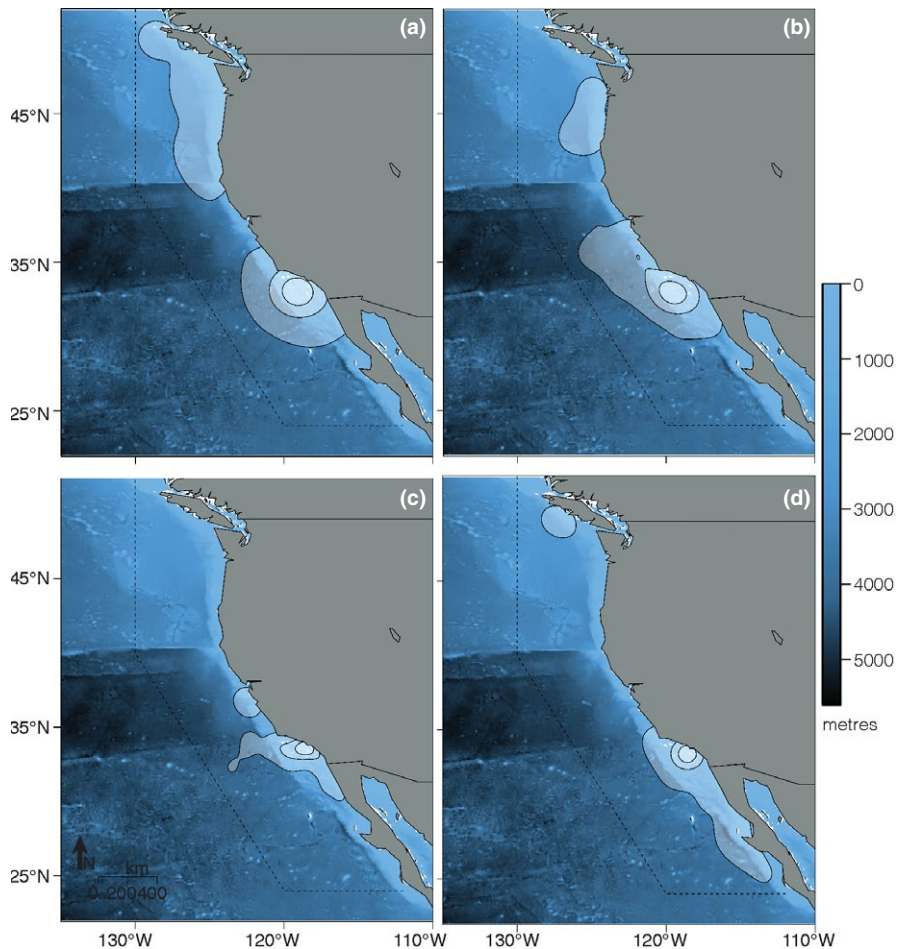
FIGURE 2 Seasonal kernel utilization distribution (KUD) for (a) spring (March–May), (b) summer (June–August), (c) autumn (September–November), (d) winter (December–February), aggregated over all years of study (2008–15). Black contours show 95%, 50% and 20% isopleths of all filtered tracking data from each season. KUD isopleths overlain on high-resolution ETOPOv2 bathymetry, showing water depth in metres. Extent of California Current System domain enclosed by dashed line and west coast of USA

subset was 3.24 ± 4.4 hrs (mean ± s.d.; range 0 – 61.2 hrs). Residence time was calculated for all remaining location fixes, using a radius of 10 km and a maximum time outside this radius of 12 hr ("adehabitatLT" package for R; Calenge, 2006).

Residence time in hours was used as a response variable in GAMMs, with a Tweedie distribution ("gamm4" and "tweedie" packages for R; Wood & Scheipl, 2014; Dunn, 2014) and an individual-level random effect. A sensitivity analysis was carried out to determine the optimal parameterization of the Tweedie distribution. All environmental covariates were checked for colinearity. Model selection involved AICc and proportion of deviance explained as indicators of relative variable importance. K-fold cross-validation was used, with five iterations of folds by individual (75% individuals in training subset; 25% in testing subset). Root-mean-squared error was used as a diagnostic, comparing model-predicted residence time to that observed (k-fold CV score, RMSE = 36.29; 0.16 of max. observed residence time).

3 | RESULTS

3.1 | Movements and Spatial Ecology

Telemetry data collected over time-scales of days–weeks–months (Figure 1a; Fig. S2; Table S1) has revealed complexity in habitat use

by fin whales in this dynamic marine ecoregion. A high degree of intra-population variability in space use was evident, as was the lack of a clear population-level seasonal migration between high-latitude foraging areas and low-latitude breeding areas, common to other baleen whales (Ramp et al., 2015). However, a general trend for increased use of areas in the central CCS between Point Arena (38.9°N, 123.7°W) and Point Conception (34.4°N, 120.5°W) during summer (Figure 2b), and south into Mexican waters in the winter (Figure 2d), is evidence of some seasonal movement within the CCS domain.

Tracking data clearly indicated a region of year-round residency in the Southern California Bight (SCB; Figure 1b; Figure 2), although it must be noted that 55 tag deployments (86%) took place within the SCB (Table S1). Fin whales were consistently present in the SCB during all seasons (Figure 2) and throughout all years of the tracking study. This year-round residency at the population-level was mirrored by extended residency at the individual level, with several whales tagged in different years exhibiting residency to localized areas for periods of 30 days or more (n = 16; Fig. S3; Table S1). Seasonal shifts in use of waters inside the SCB were also evident. Tracked whales tended to favour nearshore habitats along the mainland coast and in the northern Catalina basin in autumn and winter and then to disperse to the outer waters of the SCB, offshore and further north in spring and summer (Figure 2).

3.2 | Broad-scale habitat suitability

Broad-scale models establish that relative habitat suitability over seasonal time-scales was strongly influenced by water depth, thermal properties of water masses, primary productivity, the frequency of occurrence of thermal fronts and, to a lesser extent, bathymetric rugosity (Figure 3). Whale presence was associated with waters less than 3000 m deep, particularly those shallower than 1500 m (Figure 3a). A preference for cooler waters in the 8–10°C range likely reflects use of areas along the Washington coast in winter, although may also be associated with upwelling of cool waters further south. Fin whales also exhibited a preference for shallower depths (<500 m) with warmer waters in the 16–20°C range—at the other extreme of thermal habitat
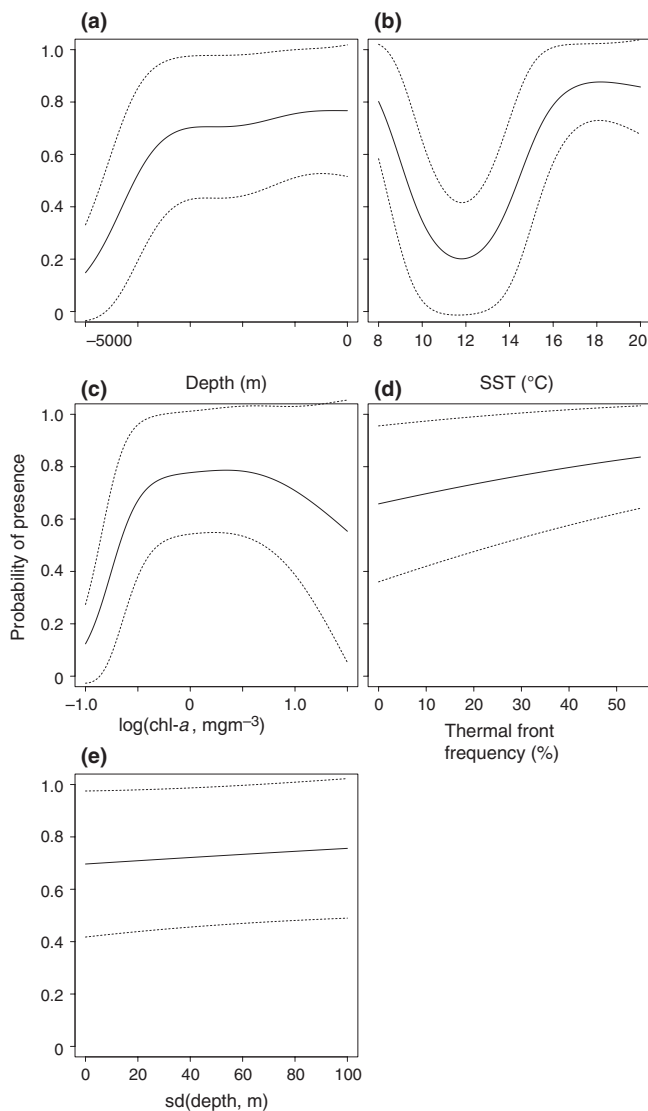

FIGURE 3 Response curves of seasonal presence-availability GAMM, showing influence of (a) water depth (m), (b) sea surface temperature, SST (°C), (c) chlorophyll *a* concentration, log(mg/m^3), (d) thermal front frequency (% time in which a thermal front ≥0.4°C present over that season) and (e) standard deviation of water depth (m), a proxy for bathymetric rugosity, on the probability of fin whale presence

availability in this domain (Figure 3b). This was associated with utilization of the SCB, a region into which the warm Southern California Countercurrent intrudes (Hickey, Dobbins, & Allen, 2003). Whales preferred intermediate chlorophyll-*a* concentrations (Figure 3c) and areas of higher thermal front frequency (Figure 3d). The influence of bathymetric rugosity (standard deviation in water depth; Figure 3e) is likely to reflect temporary associations with the shelf break in the northern CCS and with bathymetric features such as ridges and submarine basins in the central and southern CCS.

The combined influence of these biophysical parameters is evident in spatial predictions of seasonal presence-availability models (Figure 4). Habitat suitability was consistently high, year-round, in the SCB. In spring, suitable habitat was available to fin whales on the continental shelf along the entire western coast of the USA, but the most favourable conditions were in the SCB (Figure 4a). In summer and autumn, habitat suitability increased in the central CCS, including Monterey Bay and the region between Point Pinos (36.6°N, 121.9°W) and Point Conception (Figure 4b, c), presumably related to seasonal upwelling. In winter, suitable habitat again contracted to the southernmost region of the CCS, as fin whales moved south into warmer Mexican waters (Figure 4d). Here, we present a single model with seasonal environmental data for each of the four seasons informing overall predicted habitat suitability responses. Results of separate season-specific models are provided in Supporting Information (Figs S4–S8).

Interannual variability in habitat suitability was low across most of the CCS over the tracking period (2008–14; Fig. S1). Standard deviation in predicted habitat suitability among years was particularly low in the SCB.

3.3 | Biophysical influences on side fidelity

Residency in localized areas was initially revealed through mapping individual tracks, revealing a clustering of location fixes around bathymetric features in the SCB (Figure 5, Fig. S3). Modelling individual residence times as a response to contemporaneous conditions generated further insight into (sub)mesoscale biophysical influences on foraging decisions (Figure 6). Several individuals remained for extended periods in shallow, warm, nearshore areas, leading to highest predictions of residence time in warm contemporaneous SST (18–20°C; Figure 6a) and shallow depths (Figure 6b). Residence time was also elevated in the 14–16°C range, indicating associations with cooler water masses further offshore (Figure 6a). The response curve for water depth peaks at 1500 m—in concordance with the seasonal model. In terms of primary productivity, residence time was also highest at intermediate chlorophyll *a* concentrations (Figure 6c).

Bathymetric rugosity had a stronger influence on residence time than in seasonal models, presumably owing to associations with complex seafloor topographies in the SCB. The humped-shape response to standard deviation in water depth indicates a preference for seafloor features, but an apparent avoidance of the shelf break (Figure 6d). FSLE—which highlights Lagrangian coherent structures (LCS) such as mesoscale fronts, eddies and filaments—influenced individual residence times, particularly in the −0.05 to −0.01 per days range (Figure 6e). Similarly, spatial standard deviation in FSLE—a measure
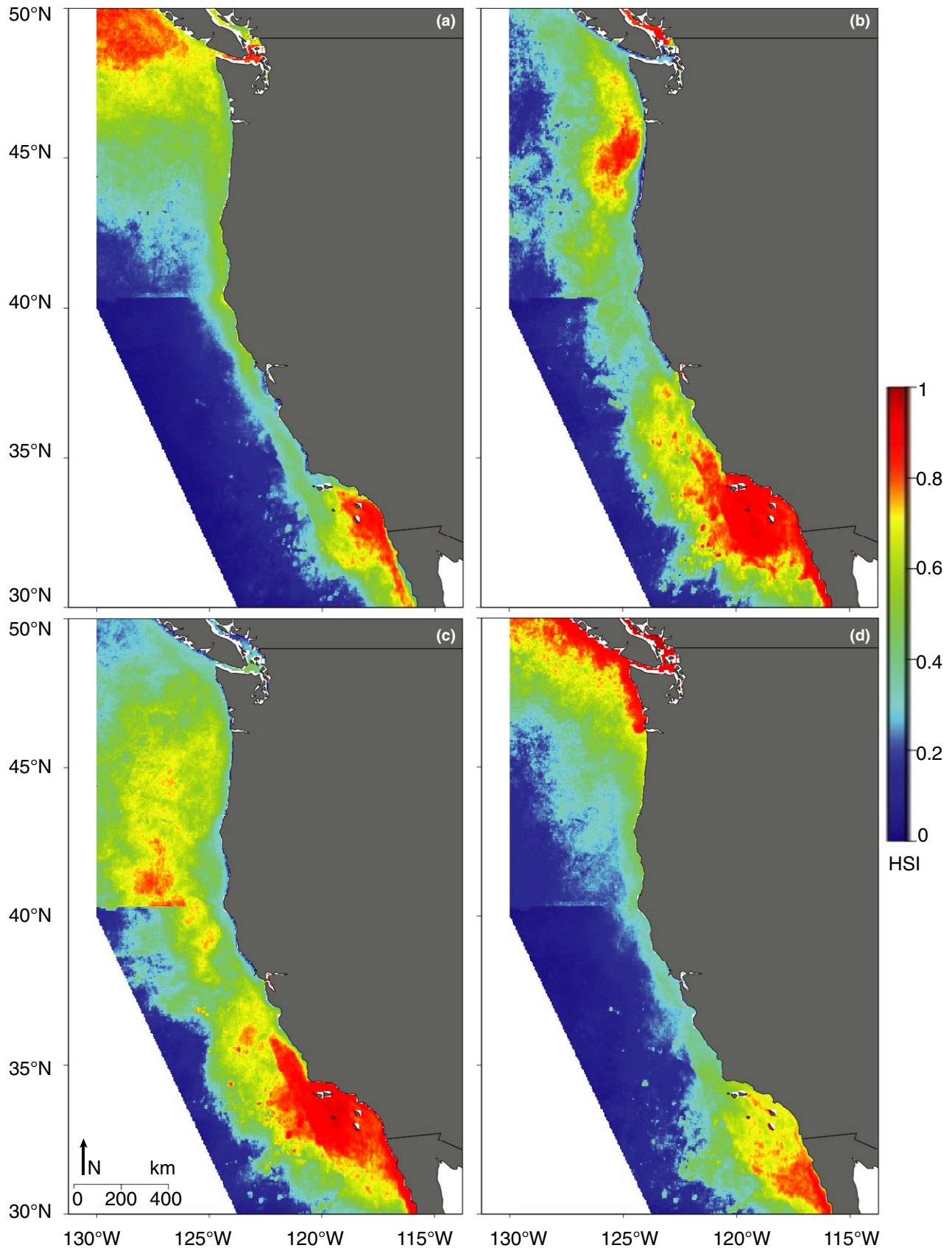
FIGURE 4 Spatial predictions of seasonal presence-availability GAMM per 0.05° grid cell for (a) spring (March–May), (b) summer (June–August), (c) autumn (September–November), (d) winter (December–February), showing relative habitat suitability over California Current domain as Habitat Suitability Index (HSI) scaled from 0 to 1, where 1 represents greatest suitability

of the relative number and strength of convergent (sub)mesoscale structures in the proximate environment—increased with residence time (Figure 6f). In summary, individual residence time appears to be strongly influenced by water depth and bathymetric features, and hence the interactions between complex seafloor topographies and Lagrangian coherent structures at the surface.

4 | DISCUSSION

4.1 | Movement patterns and broadscale habitat suitability

Satellite tracking the movements of fin whales in the California Current System has established that this population can be considered a clear exception to the canonical baleen whale migration model (see also Geijer et al., 2016; Mizroch, Rice, Zwiefelhofer, Waite, & Perryman, 2009). A clear hotspot of year-round habitat suitability for the CCS fin whale population, and of extended residency at the individual level, is evident in the Southern California Bight. This is corroborated by at-sea surveys (Campbell et al., 2015; Fiedler et al., 1998), acoustic monitoring (Širović, Williams, Kerosky, Wiggins, & Hildebrand, 2013; Stafford, Citta, Moore, Daher, & George, 2009) and photo-identification work (Falcone et al., 2011). For example, sightings surveys report fin whales as the most abundant baleen whale in the SCB (Campbell et al., 2015; Moore & Barlow, 2011); fin whale calls are acoustically detected throughout the annual cycle (Širović et al., 2013; Stafford et al., 2009; Stimpert et al., 2015); and individuals are repeatedly resighted in the SCB in photo-identification work (Falcone et al., 2011).

The observed variability in habitat use between individuals, lack of an extensive seasonal migration and extended residency in localized areas is likely tied to the comparatively broad foraging niche of fin whales. Fin whales feed on euphausiids, such as the krill species *Euphausia pacifica* and *Thysanoessa spinifera*, and small fish, such as northern anchovy *Engraulis mordax* and Pacific sardine *Sardinops sagax* (Pauly, Trites, Capuli, & Christensen, 1998), and have a propensity to prey-switch between krill and small pelagic fish. Fin whales can

therefore exploit a broader range of biophysical conditions when making foraging decisions than other baleen whales such as the blue whale, an obligate krill feeder (Mizroch, Rice, & Breiwick, 1984). Prey-switching may be a factor that enables fin whales to remain in the CCS year-round, although data limitations prevented direct testing of this hypothesis in this study.

Although satellite tracking revealed no evidence of extensive seasonal migrations, predictions of relative habitat suitability within the CCS do reveal some regional seasonality in movements. The SCB appears to represent the southernmost extent of the summer range and northernmost extent of the winter range of the CCS population and may be an area in which a resident subpopulation remains year-round. Seasonality within the CCS is likely driven by processes of biophysical coupling associated with upwelling dynamics, including foraging opportunities induced by episodic wind-driven upwelling events that are most frequent in late spring and summer. In concordance with our results, at-sea surveys suggest that fin whales are present year-round but more abundant in the central and southern CCS during summer and autumn (Campbell et al., 2015). Known krill hotspots downstream of upwelling centres at Point Arena, Point Sur and Point Conception (Santora et al., 2011) are co-located with predicted high-suitability habitats for fin whales during summer and autumn. In particular, southward advection of nutrient-rich waters from the known upwelling centre at Point Conception (Fiedler et al., 1998) leads to enhanced prey availability in the SCB feeding grounds used year-round by fin whales.

4.2 | Biophysical drivers of residency

The tendency for individuals to remain for periods of weeks to months in localized areas within the SCB appears to be associated with foraging in productive habitats. Fin whales tended to remain for extended periods around bathymetric features such as seafloor ridges and escarpments, and within small-scale basins. Here, fin whales are likely to be exploiting prey aggregations resulting from (sub)mesoscale dynamics and trophic focusing, in which prey from immense volumes

FIGURE 5 Fin whale use of the Southern California Bight (SCB). (a) Interannual variability in high-use areas. Black contours show kernel utilization distribution (KUD) for each year of study (2008–14), as 50% KUD isopleth of filtered tracking data per year. Overlap between 50% KUD polygons per year (filled white) confirms low degree of interannual variability in high-use areas. (b),(c) Movements of one tagged whale (BpTag065) through the SCB, over complex seafloor topography (b) and in relation to Lagrangian coherent structures at the surface (c). White points show 555 Argos locations obtained over 239 days. Lines show interpolated movement path
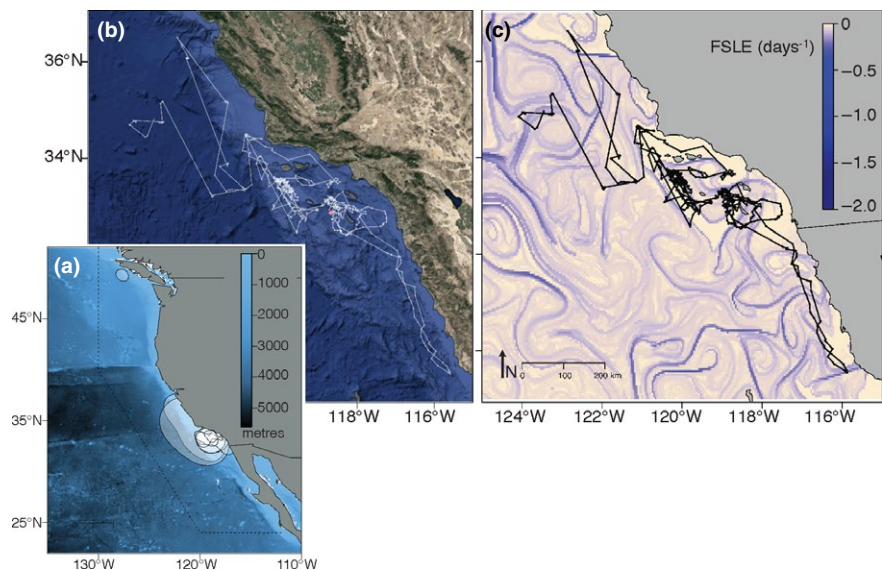
of water flowing around abrupt topographies is accumulated in confined layers (Genin, 2004). Bathymetric features and steep altimetric and temperature gradients have also been shown to be predictors of fin whale habitat suitability in the Mediterranean Sea (Cotté, Guinet, Taupier-Letage, Mate, & Petiau, 2009; Panigada et al., 2008) and along the east coast of the United States (Roberts et al., 2016).

Intense (sub)mesoscale dynamics in the SCB lead to complex spatial structuring in prey distributions and enhance foraging opportunities for fin whales. The SCB has an extremely dynamic flow field, owing to interactions between the mainland coast, the poleward-flowing Southern California Countercurrent, the equatorward main California Current offshore and the Channel Islands. Resultant (sub)mesoscale dynamics create an energetic field of Lagrangian Coherent Structures including multiple small-scale, cyclonic coastal eddies and transport fronts. Island wakes create strong surface vorticity (Dong 2007). These processes lead to the complex phytoplankton dynamics (Bialonski et al., 2016) and the circulation retention of potential prey in (sub)mesoscale structures (Fiedler et al., 1998; Logerwell, Lavaniegos, & Smith, 2001; Powell & Ohman, 2015). We contend that the fin whales in the Southern California Bight can exploit these rich foraging opportunities for extended periods year-round, explaining the patterns of residency we observed in this high-use habitat and the influence of FSLE in predicting high residence times.

Alongside seasonality in use of the wider CCS, finer-scale seasonal distribution shifts within the SCB were evident from this tracking work, and supported by photo-identification (Falcone et al., 2011). In winter, whales spent more time along the mainland coast and in the northern Catalina basin and then dispersed offshore and further north in spring and summer. Despite the evident preference for warm, nearshore waters, the SCB is unlikely to be a breeding ground in the sense of other migratory baleen whales, as young calves are very seldom sighted (Falcone & Schorr, 2014; Mizroch et al., 2009), although it is possible these predictable winter aggregations provide mating opportunities. It may be that these periods of residency to localized areas are associated with partial migration (Chapman, Brönmark, Nilsson, & Hansson, 2011), as observed in other baleen whale populations (Silva et al., 2013), or overwintering of residents to the CCS.

4.3 | Implications for understanding population structure

Our findings suggest the possible presence of two subpopulations of fin whales using the CCS—one that remains resident in the SCB year-round, aggregating nearshore in autumn and winter and dispersing into deeper waters during spring and summer, and one that ranges further offshore. Whether these are separate populations or subsets of one is difficult to determine, but genetic data do indicate the presence of a Southern California subpopulation (Archer et al., 2013). Non-migratory subpopulations have been observed elsewhere, albeit in geographically isolated seas (Gulf of California, Tershy et al 1993; Mediterranean Sea, Bérubé et al. 2002; Castellote et al. 2012a; di Sciara et al., 2016; Geijer et al., 2016). Although these tracking data cannot provide incontrovertible evidence, it is arguable that the
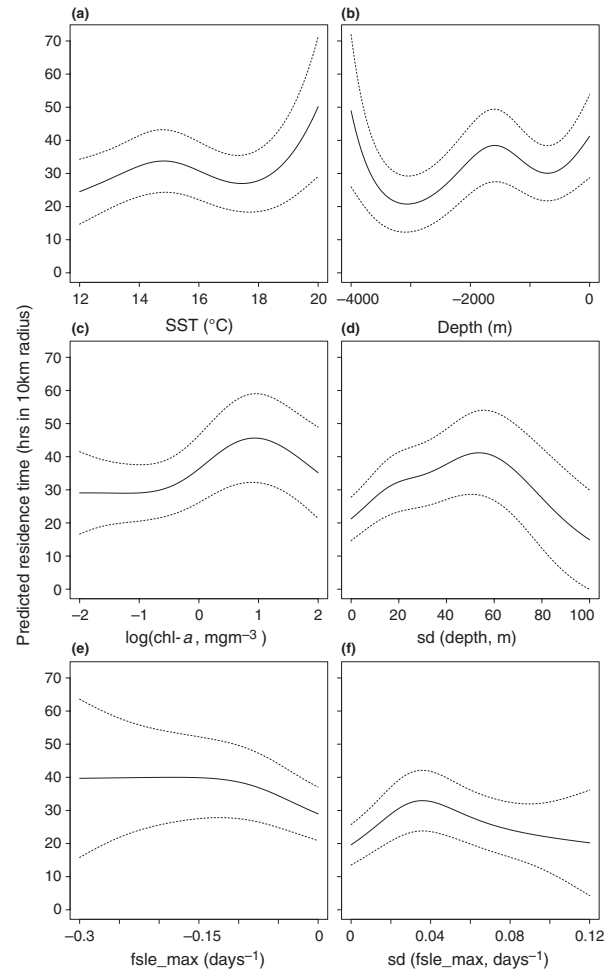

FIGURE 6 Response curves of residence time GAMM for Southern California Bight, showing influence of (a) sea surface temperature, SST (°C), (b) water depth (m), (c) chlorophyll *a* concentration, (d) standard deviation of water depth (m), a proxy for bathymetric rugosity, (e) Finite-Size Lyapunov Exponent, FSLE (days), which identifies Lagrangian coherent structures (LCS) and (f) standard deviation of FSLE over a 3-grid cell radius, a proxy for mesoscale oceanographic dynamics. Influence of all predictors plotted on response scale, residence time within a 10 km radius of each relocation

year-round residents of the SCB constitute a distinct subpopulation and should be managed as such.

4.4 | Implications for protected species management

The importance of the Southern California Bight for fin whales appears to have been underestimated in previous models of relative habitat suitability based on ship survey datasets (Becker et al., 2012; Calambokidis et al., 2015; Forney et al., 2012; Redfern et al., 2013). This has potentially significant implications for conservation and management. The SCB is under intense anthropogenic pressure, fringed by the human population centres of Los Angeles and San Diego. Major international shipping routes pass through the Southern California Bight; thus, the risk of ship strike and increased underwater noise

are legitimate threats to this population. Fin whales are known to be highly sensitive to underwater noise resulting from shipping and seismic surveys (Castellote, Clark, & Lammers, 2012b), and 8 of 10 fin whale mortalities attributed to ship strike off California during 2009–15 occurred in the SCB (NOAA, unpublished data).

Previous habitat suitability predictions for baleen whales have been used as evidence supporting a change in the position of the major shipping lane through the Santa Barbara channel—an area intensively used by blue whales during summer (Fiedler et al., 1998)—to reduce the risk of ship strike (Redfern et al., 2013). However, our results suggest that the proposed change in shipping routes could increase this risk for fin whales.

While predicting absolute densities remains a major challenge, and density models (ie, number of whales per unit area) are difficult to compare directly with habitat suitability models (ie, relative habitat suitability per unit area), satellite tracking has generated valuable new insights into habitat suitability for fin whales in the CCS and the resulting risk of ship strike in areas in which fin whales are semi-resident.

In addition to risks from shipping, the US Navy's Southern California (SoCal) Range Complex and Point Mugu Sea Range are located in the SCB. Training activities within the Range Complex include live fire exercises, surface and underwater explosions, and antisubmarine warfare (including MFA sonar), while activities within the Point Mugu Sea Range include live fire exercises and a limited number of surface explosions. A total of 88% of location fixes were received from within the SoCal Range Complex (50%) or Pt. Mugu Sea Range (38%). Overlap between naval activities and high-use habitat could entail deleterious consequences for the fin whale population, through exposure to these training activities and collisions with military vessels.

Alongside displacement from preferred habitats, potential impacts of exposure to anthropogenic noise include the masking of communications, and changing vocal behaviour (Williams, Clark, Ponirakis, & Ashe, 2014). The importance of the SCB for this population suggests that these activities could entail population-level consequences for this protected species in the CCS.

The fin whale population of the California Current may require more careful management to adequately mitigate these threats. The Northeast Pacific fin whale population is currently managed as a single stock estimated to number 3,000 individuals (Carretta et al., 2015). More recent abundance calculations estimate a population of approximately 8,500 (Barlow, 2016). However, these estimates do not incorporate potential population differentiation. A subpopulation resident to the SCB year-round will experience intensification of anthropogenic threat and so require more targeted management strategies than a diffuse migratory population. Ultimately, accurate space use predictions informed by a detailed understanding of population size and structure, spatial ecology and habitat preferences of populations of conservation concern (eg, Hazen et al., 2016) are likely to be instrumental in designing management solutions that can accommodate both human users and the conservation of protected species as we move further into the Anthropocene.

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BIOSKETCH

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SUPPORTING INFORMATION

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