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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Running title: *Modelling fin whale habitats*

Word Count (Abstract): 296

Word Count (Main Body): 5,110

References: 67

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 Generalised 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 inter-annual 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 to localised areas (n=16 for >30 days; n=4 for >6 months) was associated with warm, shallow, nearshore waters (>18°C, <500m); with cool waters (14-15°C) occurring over complex seafloor topographies and 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 localised areas. High-use habitats for fin whales are co-located 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 an endangered baleen whales in this globally significant biodiversity hotspot.

KEYWORDS (6-10)

satellite tracking, telemetry, LIMPET tag, cetacean, species distribution model, habitat model, remote sensing, ocean fronts, Finite-Size Lyapunov Exponent, upwelling

(A) INTRODUCTION

Understanding 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 and variability in habitat quality (Schick et al. 2008; Geijer et al. 2016). Many taxa are known to migrate between habitats suitable at different stages of the annual cycle owing to fluctuating resource availability (Drake & Dingle, 2007), a strategy observed in multiple baleen whale populations (Corkeron & Connor, 1999; Firestone et al. 2008, Horton et al. 2011, Ramp et al. 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 insights resulting from progressive techniques 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 (di Sciara et al. 2016; Geijer et al. 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 et al. 2014); Eastern Atlantic blue whales exhibit considerable intra-population variability in migratory movements with some individuals traveling north from central Africa following breeding while others migrate to the Southern Ocean (Rosenbaum et al. 2014); and blue and fin whales *Balaenoptera physalus* in the North Atlantic are known to suspend migration when biophysical conditions are conducive for foraging (Silva et al. 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; Barlow et al. 1994; Forney & Barlow, 1998) – a highly dynamic eastern boundary upwelling 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 over-exploitation (IUCN Red List of Threatened Species; Reilly et al. 2013), the fin whale is listed as a protected species under both the Marine Mammal Protection Act (1972) and 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 *et al.* 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 conservation and management strategies for baleen whales relies upon a more complete understanding of how environmental conditions influence the spatial ecology of different populations at ocean-basin scales and finer, and of 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 (e.g. Forney *et al.* 2015), for predicting how these habitats might shift with changing oceanographic dynamics (e.g. Hazen *et al.* 2013), and for identifying areas of overlap with anthropogenic threat (e.g. 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 co-exist 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 (e.g. 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 et al. 2016). Biophysical conditions in the CCS can be highly variable at (sub-)mesoscales (1-10 km) and over timescales of days-weeks-months, leading to heterogeneity in the manifestation of prey patches (Santora et al. 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 spatiotemporal distribution of important habitats (Croll et al. 2005).

Using a multi-year (2008-15) satellite telemetry dataset tracking the movements of 67 adult fin whales, we therefore aim to (i) model the relative influence of biophysical conditions on broad-scale patterns of occupancy in the CCS, (ii)predict seasonal habitat suitability for fin whales throughout the annual cycle; (iii) explore seasonal and inter-annual 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.

(A) MATERIALS AND METHODS

(B) 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 7-8m rigid hull inflatable boat with a modified bow pulpit, using a Dan-Inject pneumatic projector (Børkop, Denmark). Two types of tags were used: 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, 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 (15km h^{-1} for >1 h; Cotte 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 to 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).

(B) Environmental Data

The study area was defined by the extent of all filtered tracking data (130°W - 112°W; 20°N - 50°N ; Fig. 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 et al. 2015, Pierce et al. 2014).

Seasonal environmental data fields were created for each season (Spring: Mar – May; Summer: Jun – Aug; Autumn: Sept – Nov; Winter: Dec – Feb) 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 et al. 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 US) 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 timespan 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 sub-mesoscale 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.

(B) Habitat Modelling

A multi-scale approach was taken to habitat modelling. First, broad-scale 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; Fig. 2). Second, finer-scale models were used to investigate contemporaneous biophysical influences on individual residence times within high-use habitat.

(C) *Broad-scale seasonal presence-availability*

All filtered locations were plotted as individual tracks (Fig. 1a). Weighted locations were also summed within a 0.1° hexagonal grid as an indication of patterns of occupancy (Fig. 1b; ‘ggplot2’ package for R; Wickham 2009).

Broad-scale, seasonal presence-availability models were used to identify environmental conditions characterising high-use areas. First, areas used by whales in each season were identified using a kernel utilisation distribution (KUD) incorporating all tracking data, aggregated over all years to account for low and uneven sample sizes in individual years (Fig. 2). Utilisation 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 (Fig. 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 randomised background sampling from within the CCS domain (n=1500 for each iteration; Barbet-Massin *et al.* 2012).

Generalised 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). Generalised 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, 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 (Fig. 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. Inter-annual 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 (Fig. 5a).

(C) ***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 subset was 3.24 ± 4.4hrs (mean ± s.d.; range 0 – 61.2hrs). Residence time was calculated for all remaining location fixes, using a radius of 10km and a maximum time outside this radius of 12 hours (‘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 parameterisation 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).

(A) RESULTS

(B) Movements and Spatial Ecology

Telemetry data collected over timescales of days-weeks-months (Fig. 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 (Fig. 2b), and south into Mexican waters in the winter (Fig. 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; Fig1b; Fig. 2), though 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 (Fig. 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 localised 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 (Fig. 2).

(B) Broad-scale habitat suitability

Broad-scale models establish that relative habitat suitability over seasonal timescales were 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 (Fig. 3). Whale presence was associated with waters less than 3000m deep, particularly those shallower than 1500m (Fig. 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 (<500m) with warmer waters in the 16-20°C range - at the other extreme of thermal habitat availability in this domain (Fig. 3b). This was associated with utilisation of the SCB, a region into which the warm Southern California Countercurrent intrudes (Hickey, Dobbins & Allen 2003). Whales preferred intermediate chlorophyll-*a* concentrations (Fig. 3c), and areas of higher thermal front frequency (Fig. 3d). The influence of bathymetric rugosity (standard deviation in water depth; Fig. 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 (Fig. 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 US, but the most favourable conditions were in the SCB (Fig. 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 (Figs. 4b. 4c), 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 (Fig. 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).

Inter-annual 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.

(B) Biophysical influences on side fidelity

Residency in localised areas was initially revealed through mapping individual tracks, revealing a clustering of location fixes around bathymetric features in the SCB (Fig. 5, Fig. S3). Modelling individual residence times as a response to contemporaneous conditions generated further insight into (sub-)mesoscale biophysical influences on foraging decisions (Fig. 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; Fig. 6a) and shallow depths (Fig. 6b). Residence time was also elevated in the 14-16°C range, indicating associations with cooler water masses further offshore (Fig. 6a). The response curve for water depth peaks at 1500m – in concordance with the seasonal model. In terms of primary productivity, residence time was also highest at intermediate chlorophyll-*a* concentrations (Fig. 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 (Fig. 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 days^{-1} range (Fig. 6e). Similarly, spatial standard deviation in FSLE - a measure of the relative number and strength of convergent (sub-)mesoscale structures in the proximate environment – increased with residence time (Fig. 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.

(A) DISCUSSION

(B) Movement patterns and broad-scale 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 Mizroch et al. 2009; Geijer et al. 2016). 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 (Fiedler et al. 1998; Campbell et al. 2015), acoustic monitoring (Stafford et al. 2009; Širović et al. 2013), and photo-identification work (Falcone et al. 2011). For example, sightings surveys report fin whales as the most abundant baleen whale in the SCB (Moore & Barlow, 2011; Campbell et al. 2015); fin whale calls are acoustically detected throughout the annual cycle (Stafford et al. 2009; Širović et al. 2013; Stimpert et al. 2015); and individuals are repeatedly re-sighted 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 localised 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 et al. 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 et al. 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 sub-population 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.

(B) Biophysical drivers of residency

The tendency for individuals to remain for periods of weeks to months in localised 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 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 (Panigada et al. 2008; Cotté et al. 2009) 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 as calves are very seldom sighted (Falcone & Schorr 2014). It may be that these periods of residency to localised areas are associated with partial migration (Chapman et al. 2011), as observed in other baleen whale populations (Silva et al. 2013), or over-wintering of residents to the CCS.

(B) Implications for understanding population structure

Our findings suggest the possible presence of two sub-populations 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 sub-population (Archer et al. 2013). Non-migratory sub-populations have been observed elsewhere, albeit in geographically isolated seas (Gulf of California, Tershy et al. 1993; Mediterranean Sea, Bérubé et al. 2002; Castellote, Clark & Lammers 2012a; di Sciara et al. 2016; Geijer et al. 2016). Although these tracking data cannot provide incontrovertible evidence, it is arguable that the year-round residents of the SCB constitute a distinct sub-population and should be managed as such.

(B) 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; Forney et al. 2012; Redfern et al. 2013; Calambokidis et al. 2015). 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 (i.e. number of whales per unit area) are difficult to compare directly with habitat suitability

models (i.e. 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 anti-submarine 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 et al. 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. 2014). More recent abundance calculations estimate a population of approximately 8,500 (Barlow, 2016). However, these estimates do not incorporate potential population differentiation. A sub-population 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 (e.g. 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.

(A) ACKNOWLEDGEMENTS

We gratefully acknowledge the support of the US Navy, including the N45 and Living Marine Resources programs, which provided funding for fieldwork and tags. Additional funding was provided by NOAA's Southwest Fisheries Science Center and Alaska Regional Science Center, Washington Department of Fish and Wildlife Section 6, and the US Navy Pacific Fleet. We thank our collaborators from the Naval Undersea Warfare Center, in particular David J. Moretti and the Marine Mammal Monitoring on Naval Ranges group. Without the extensive logistic support of the Southern California Offshore Range staff, and San Clemente Island personnel, this work would not have been possible. We also wish to acknowledge the support of the Office of Naval Research, and Brad Hanson of the NOAA Northwest Fisheries Science Center for tag development. All appropriate ethics permissions were obtained prior to commencement of this work. Tagging was conducted under NOAA research permits 540-1811 and 16111, and conducted under the Cascadia Research Collective's Institutional Animal Care and Use

Committee.We thank Jeff Foster, John Calambokidis, and Cascadia Research Collective for assistance with tag deployments, and Elizabeth Becker of NOAA SWFSC for constructive comments on an earlier draft.

(A) SUPPLEMENTARY MATERIAL

Table S1 – Satellite tracking tag deployments summary.

Fig. S1 – Inter-annual variability in habitat suitability in the CCS.

Fig. S2 – Tracking duration by individual (days).

Fig. S3 –Movements of four individuals that remained resident to localised areas in the Southern California Bight for more than 30 days.

Fig. S4 – Smooth functions from broad-scale seasonal GAMM (overall, four seasonal datasets combined).

Fig. S5 – Smooth functions from broad-scale seasonal GAMM (spring, March - May).

Fig. S6 - Smooth functions from broad-scale seasonal GAMM (summer, June - August).

Fig. S7 - Smooth functions from broad-scale seasonal GAMM (autumn, September - November).

Fig. S8 - Smooth functions from broad-scale seasonal GAMM (winter, December - February).

(A) BIOSKETCH

Dr. Kylie Scales is a movement ecologist with broad interests in biogeography, quantitative ecology and conservation biology. Author contributions: GS, EF, AZ and RA conducted all satellite tagging work. KS carried out all analyses and drafted the manuscript; PM provided environmental data; EH and SB provided guidance on methods and edited the manuscript.

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(A) TABLES

See Supporting Information

(A) FIGURE LEGENDS

Fig. 1 (a) Filtered tracking data per individual (n=64), aggregated over all years (2008-15), with tag deployment locations as grey diamonds and track end-points as grey squares. (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.

Fig. 2 Seasonal kernel utilisation distribution (KUD) for (a) spring (Mar-May), (b) summer (Jun - Aug), (c) autumn (Sept - Nov), (d) winter (Dec - Feb), 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 (2") etopo2 bathymetry, showing water depth in metres. Extent of California Current System domain enclosed by dashed line and west coast of US.

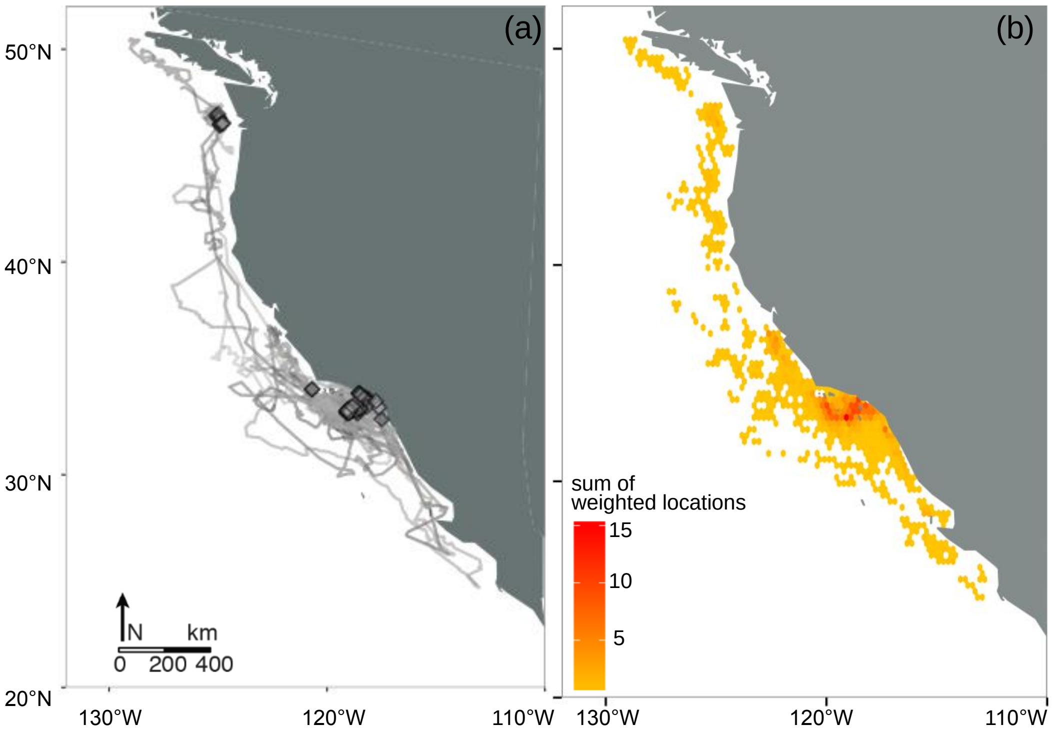
Fig. 3 Response curves of seasonal presence-availability GAMM, showing influence of (a) water depth (m), (b) sea surface temperature, SST (°C), (c) chlorophyll-a concentration, log(mg m^{-3}), (d) thermal front frequency (% time in which a thermal front ≥ 0.4°C present over that season), and (e) standard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

Fig. 4 Spatial predictions of seasonal presence-availability GAMM per 0.05° grid cell for (a) spring (Mar-May), (b) summer (Jun-Aug), (c) autumn (Sept-Nov), (d) winter (Dec-Feb), showing relative habitat suitability over California Current domain as Habitat Suitability Index (HSI) scaled from 0 to 1, where 1 represents greatest suitability.

Fig. 5 Fin whale use of the Southern California Bight (SCB). (a) Inter-annual variability in high-use areas. Black contours show kernel utilisation 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 inter-annual 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).

Fig. 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^{-1}), 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 10km radius of each relocation.

(A) FIGURES



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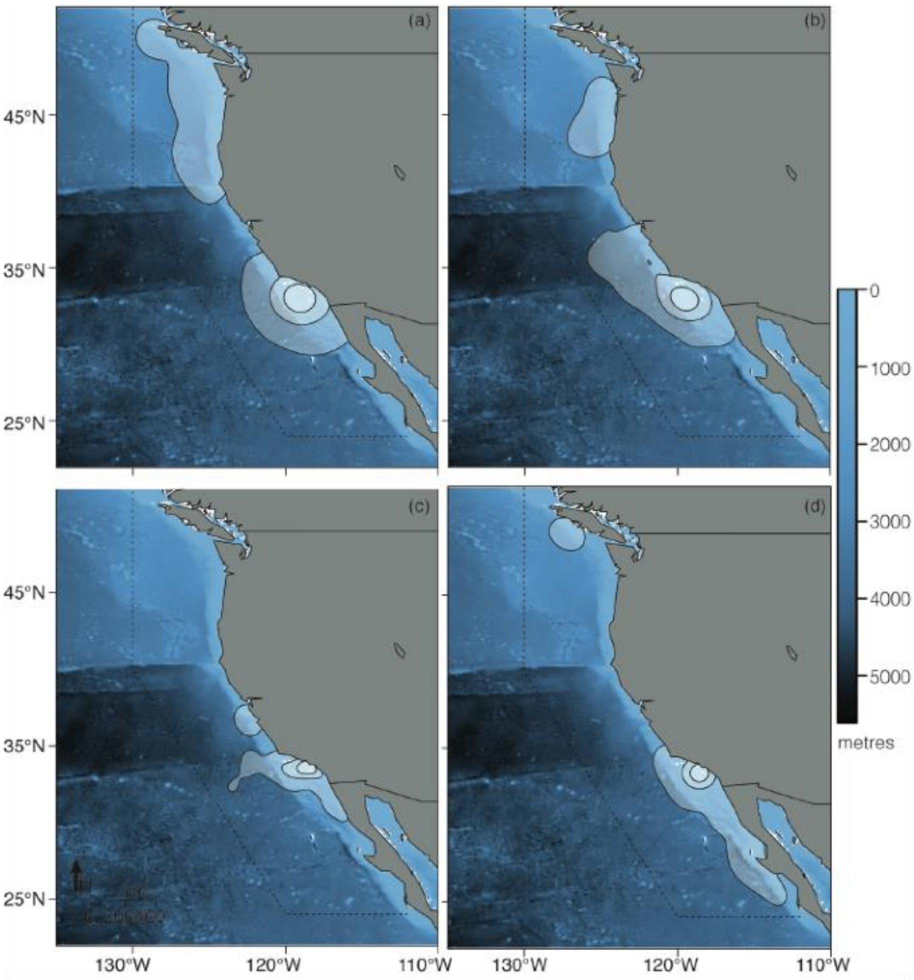

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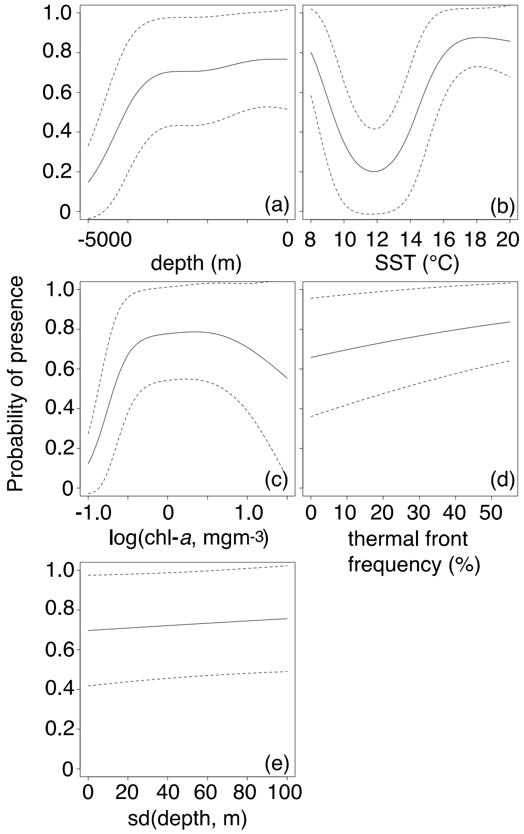

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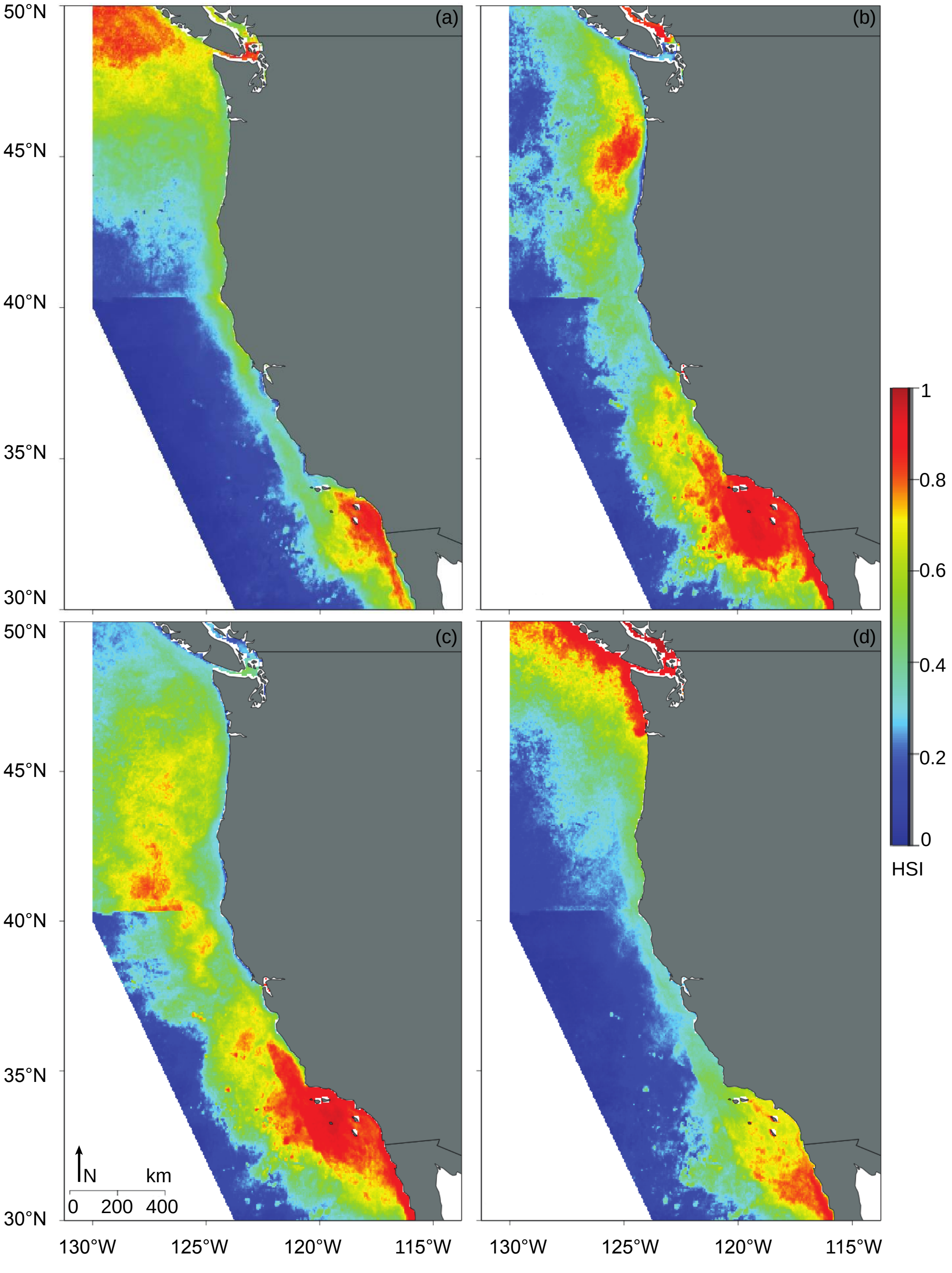

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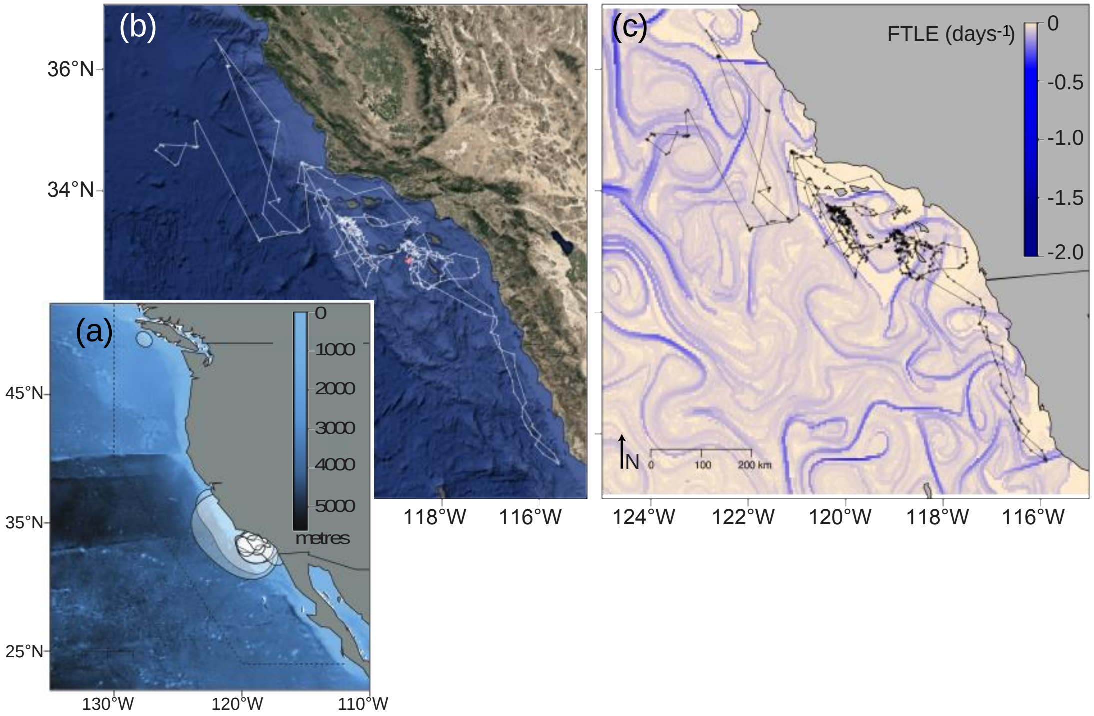

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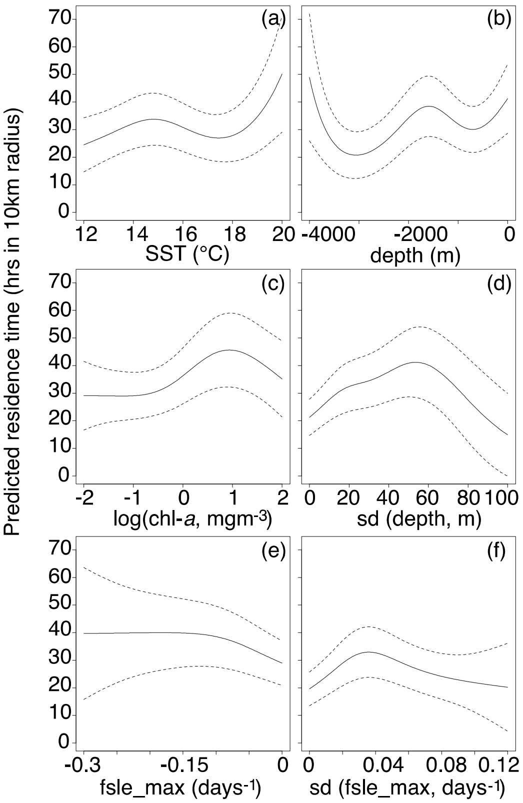

Fig. 6 Response curves of residence time GAMM for Southern California Bight, showing influence of (a) sea surface temperature, SST (°C), (b) water depth (m), (c) chlorophyll-a concentration, (d) standard deviation of water depth (m), a proxy for bathymetric rugosity, (e) Finite-Size Lyapunov Exponent, 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 10km radius of each relocation.

(A) SUPPORTING INFORMATION

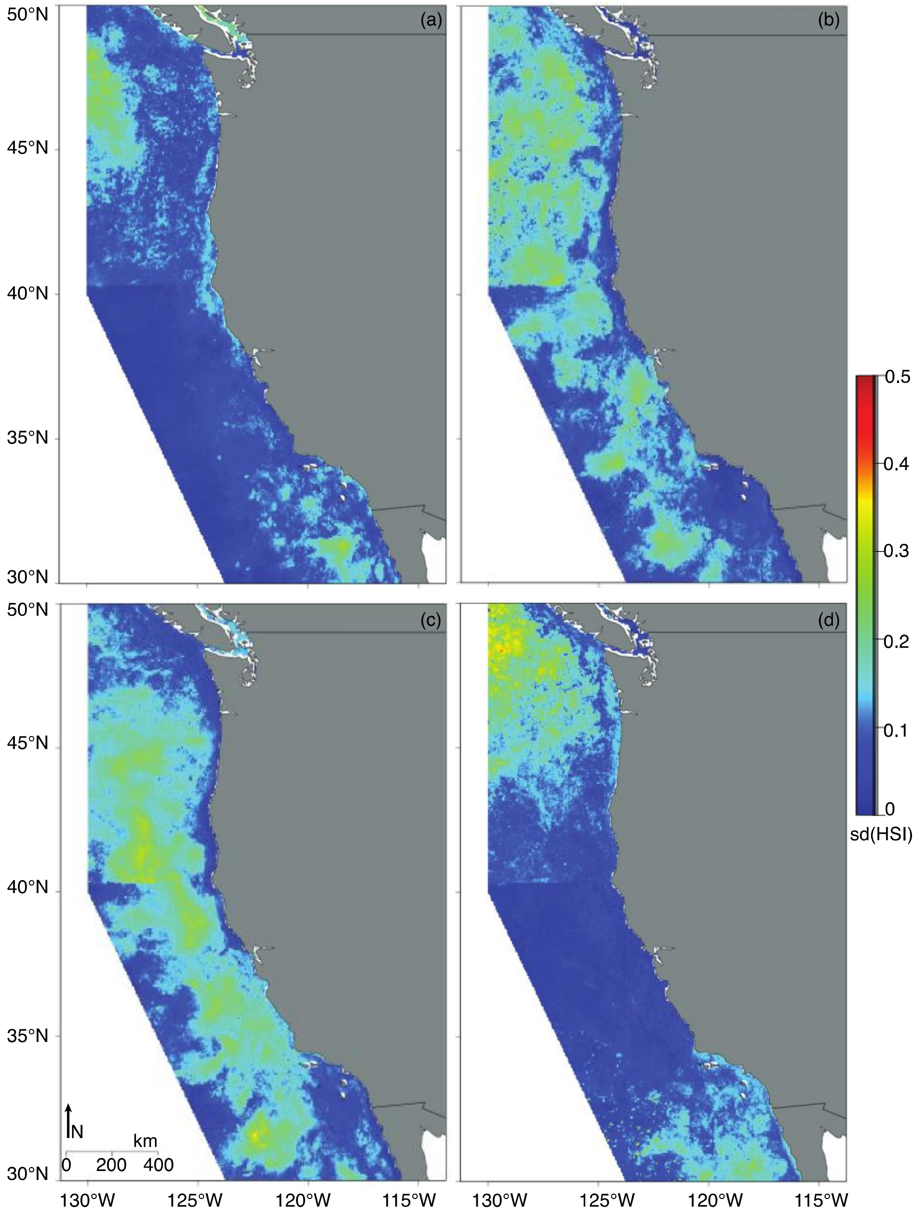

Fig. S1 Inter-annual variability in habitat suitability over California Current System (CCS) domain. Standard deviation in spatial predictions of seasonal presence-availability GAMM per 0.05° grid cell over all years of tracking study (2008-14), for (a) spring (Mar-May), (b) summer (Jun-Aug), (c) autumn (Sept-Nov), (d) winter (Dec-Feb), scaled as Habitat Suitability Index (HSI).

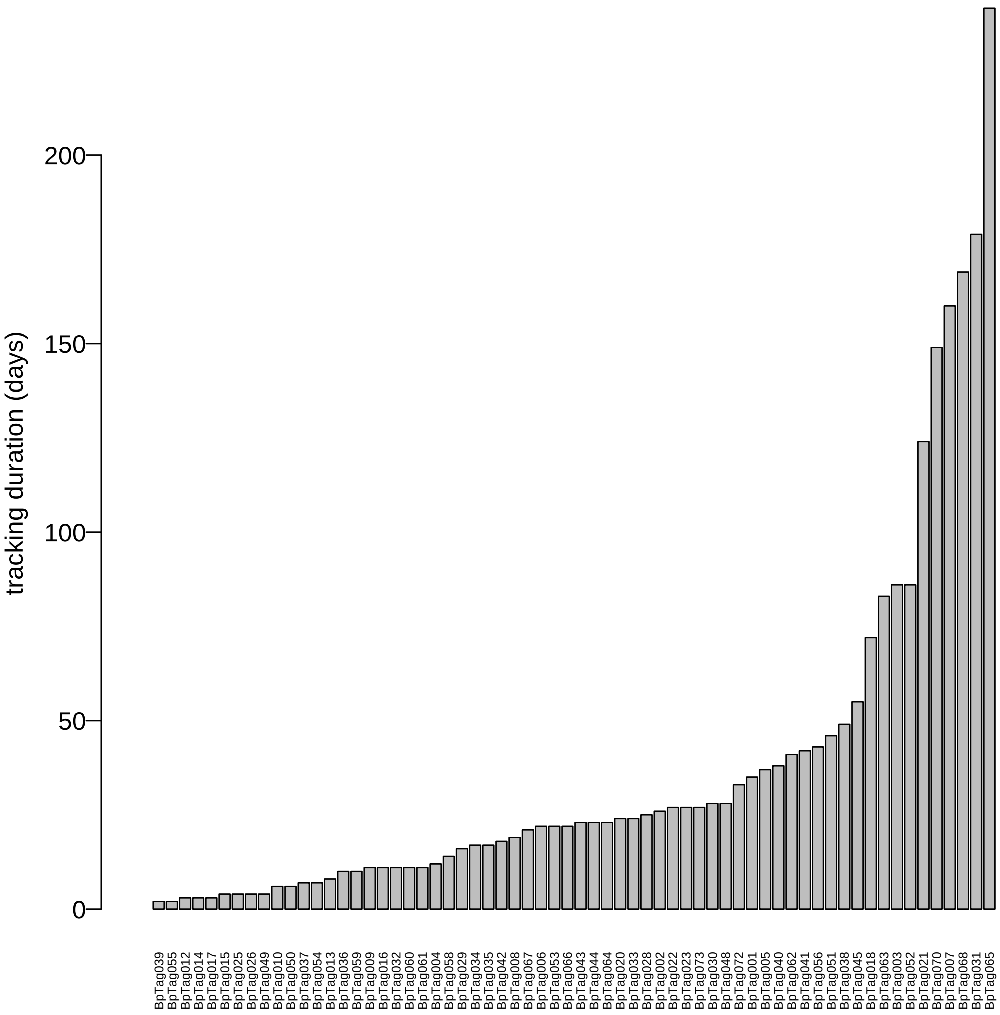

Fig. S2 Tracking duration by individual (days)

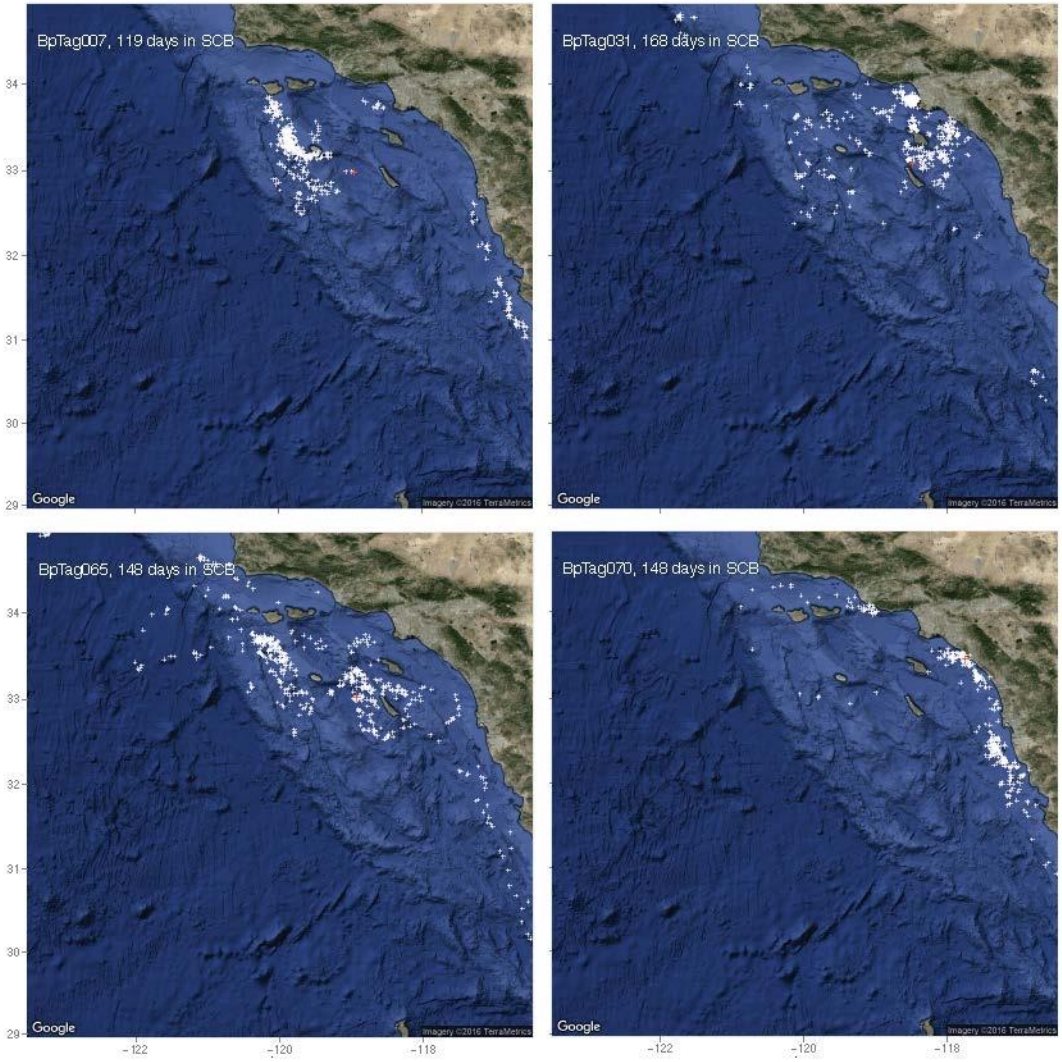

Fig. S3 Extended residency in Southern California Bight (SCB). Satellite tracking locations received from four individuals that spent over three months in the SCB.

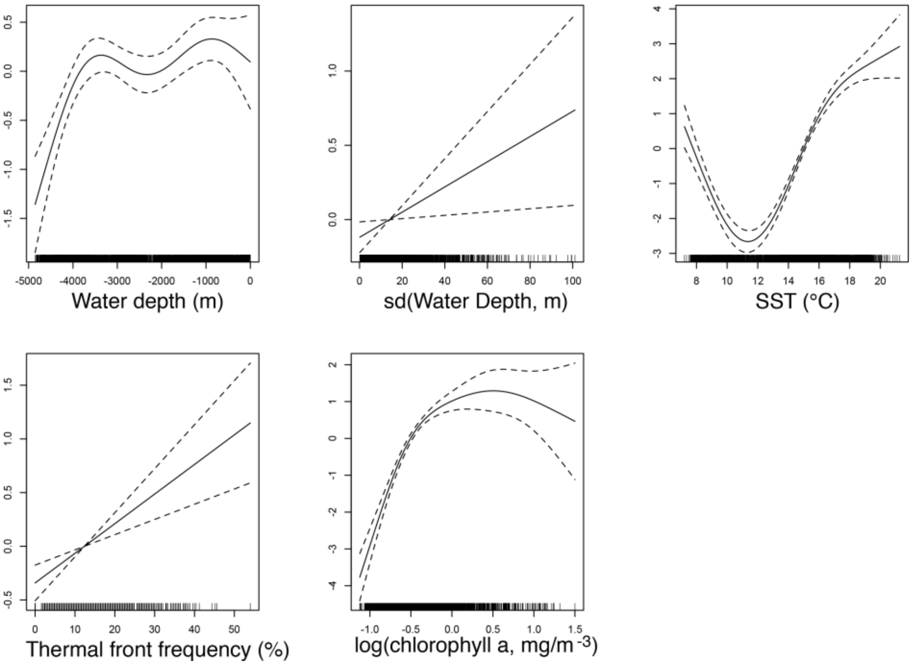

Fig. S4 Smooth functions from broad-scale seasonal GAMM (overall, four seasonal datasets combined).

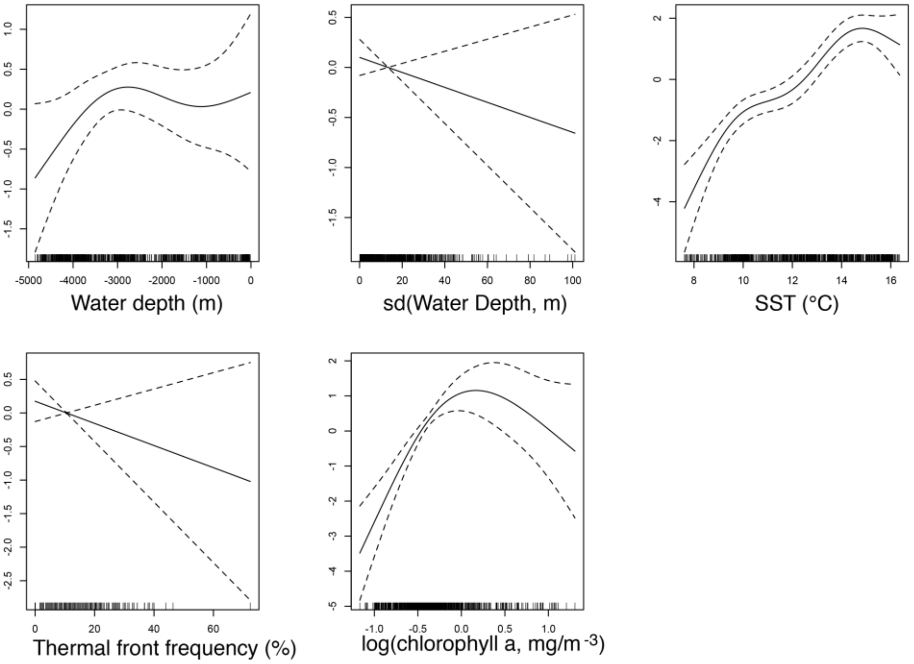

Fig. S5 Smooth functions from broad-scale seasonal GAMM (spring, March - May).

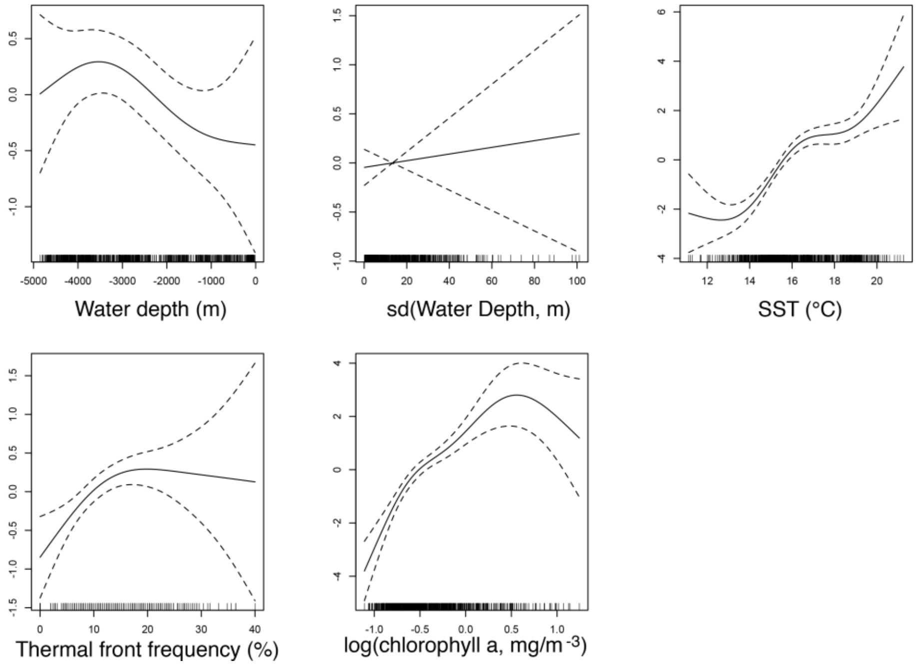

Fig. S6 Smooth functions from broad-scale seasonal GAMM (summer, June - August).

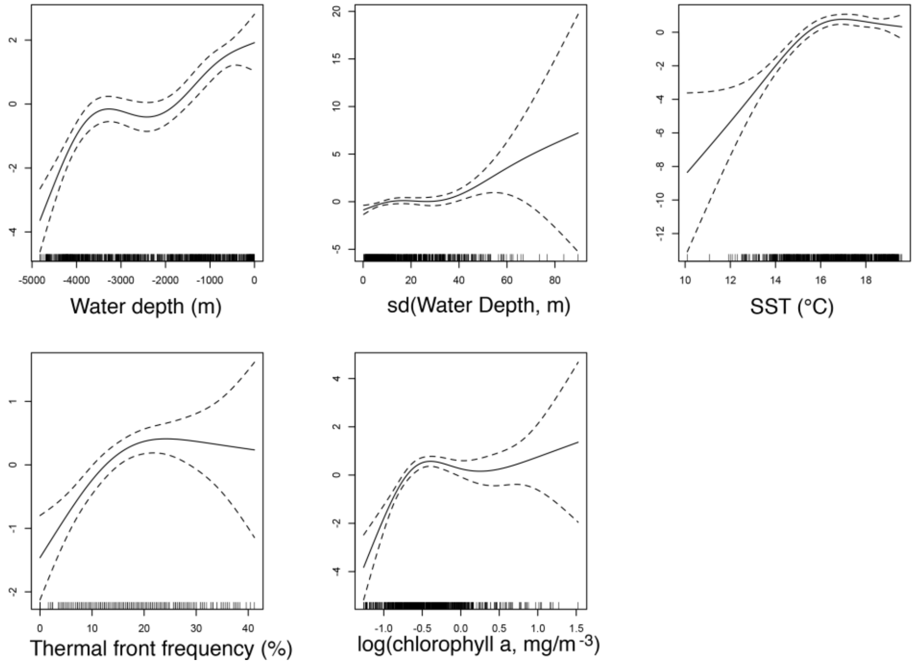

Fig. S7 Smooth functions from broad-scale seasonal GAMM (autumn, September - November).

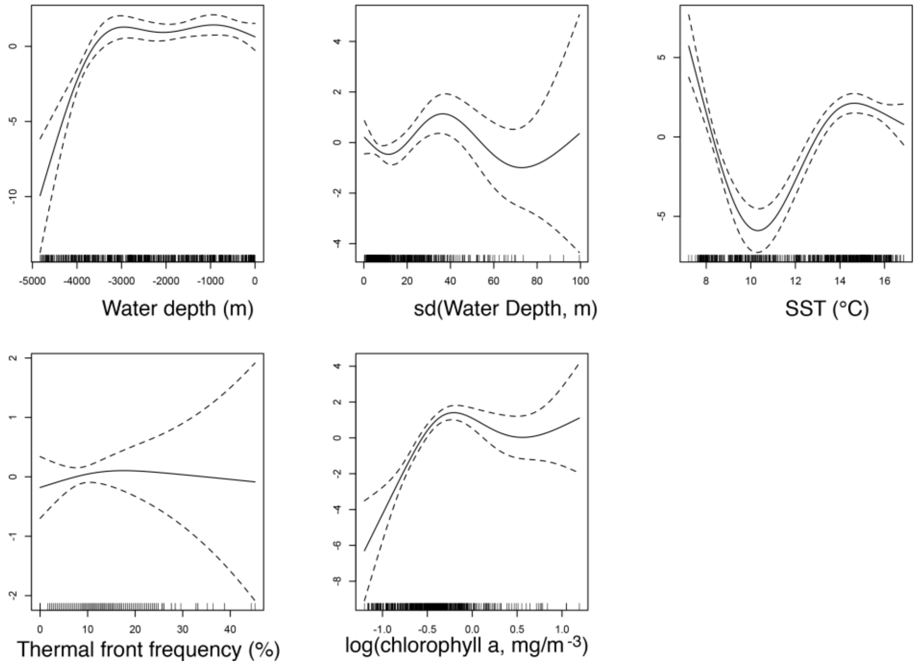

Fig. S8 Smooth functions from broad-scale seasonal GAMM (winter, December - February).

Table S1 – Satellite tracking summary

TagID	Tag deployment longitude	Tag deployment latitude	Deployment date	Deployment time	Tracking duration (days)	Total number location fixes	Total distance travelled (km)	Maximum displacement from tag deployment (km)	Minimum water depth (m)	Maximum water depth (m)
BpTag001	-118.604	32.868	2008-08-08	11:18 PM	35	85	781	142	-422	-1556
BpTag002	-119.114	32.966	2008-10-22	4:41 AM	26	133	1964	421	-64	-1556
BpTag003	-118.995	33.005	2008-10-23	4:14 AM	86	564	5482	297	-87	-1952
BpTag004	-119.092	32.895	2009-07-24	9:14 PM	12	8	197	74	-435	-1556
BpTag005	-118.974	32.965	2009-07-25	7:27 PM	36	85	1564	213	-389	-3669
BpTag006	-118.967	32.976	2009-07-25	8:12 PM	22	168	1157	142	-435	-1704
BpTag007	-118.958	32.977	2009-07-25	8:34 PM	160	489	4973	861	-46	-3764
BpTag008	-118.963	32.964	2009-07-25	9:48 PM	19	126	1307	414	-435	-4303
BpTag009	-118.104	33.569	2009-11-12	8:43 PM	11	49	276	24	-494	-517
BpTag010	-118.283	33.666	2009-11-13	9:39 PM	6	27	182	50	-494	-797
BpTag012	-117.497	32.603	2009-11-16	7:32 PM	3	22	108	49	-108	-1342
BpTag013	-118.211	33.549	2009-11-21	10:37 PM	8	62	282	31	-494	-680
BpTag014	-118.525	33.839	2009-11-22	9:28 PM	3	26	281	65	-87	-880
BpTag015	-118.521	33.819	2009-11-23	12:06 AM	4	28	249	30	-494	-797
BpTag016	-118.540	33.830	2009-11-24	6:38 PM	11	17	131	37	-494	-680
BpTag017	-125.089	46.880	2010-05-06	6:15 PM	3	26	128	40	-625	-1901
BpTag018	-124.970	46.808	2010-05-06	8:53 PM	72	190	5247	1969	-185	-4514
BpTag020	-124.915	46.407	2010-05-09	7:28 PM	24	224	1726	646	-572	-3120
BpTag021	-118.692	33.073	2010-06-28	2:15 PM	124	586	3861	568	-110	-4066
BpTag022	-118.692	33.073	2010-06-28	2:49 PM	27	211	1769	326	-389	-3752
BpTag023	-124.871	46.475	2011-02-10	7:52 PM	27	145	1624	540	-112	-2450
BpTag025	-124.927	46.724	2011-02-10	9:50 PM	4	9	243	207	-625	-2484
BpTag026	-118.979	32.995	2011-05-04	5:07 PM	3	42	304	143	-679	-1556
BpTag028	-119.067	33.048	2011-05-06	5:25 PM	23	107	896	174	-435	-1704
BpTag029	-120.688	34.017	2011-06-22	10:31 AM	16	79	996	405	-507	-1886
BpTag030	-120.688	34.017	2011-06-22	6:43 AM	28	235	1739	283	-347	-4118
BpTag031	-118.483	33.081	2012-01-20	6:24 PM	174	469	5710	639	-84	-3730
BpTag032	-118.281	33.597	2012-01-20	8:34 PM	10	60	353	27	-494	-517
BpTag033	-118.278	33.600	2012-01-20	11:04 PM	24	123	598	55	-87	-680
BpTag034	-118.288	33.592	2012-01-21	12:20 AM	17	87	458	49	-87	-680
BpTag035	-118.281	33.584	2012-01-21	12:51 AM	17	113	635	55	-87	-680
BpTag036	-118.175	33.204	2012-03-14	8:53 PM	10	47	258	34	-782	-1138
BpTag037	-118.505	33.108	2012-03-15	8:56 PM	7	37	224	61	-978	-1556
BpTag038	-118.511	33.111	2012-03-16	7:01 PM	49	360	2406	194	-422	-1556
BpTag039	-118.446	33.104	2012-03-16	9:11 PM	2	19	103	32	-782	-978
BpTag040	-118.959	33.066	2012-03-20	4:42 PM	38	126	2853	978	-449	-4482
BpTag041	-119.038	32.996	2012-03-20	6:45 PM	41	142	1799	310	-108	-1940
BpTag042	-119.052	32.991	2012-03-20	8:43 PM	17	122	611	109	-749	-1556
BpTag043	-119.125	33.140	2012-03-21	7:14 PM	23	244	1438	84	-389	-1556
BpTag044	-124.993	46.950	2012-07-20	1:10 AM	23	242	1759	486	-185	-3062
BpTag045	-119.070	32.960	2012-11-17	9:18 PM	55	341	4276	1087	-64	-4249
BpTag048	-118.869	33.036	2013-01-05	8:14 PM	28	293	1732	112	-552	-1556
BpTag049	-118.842	33.004	2013-01-05	9:06 PM	3	31	135	35	-1138	-1219
BpTag050	-118.875	32.982	2013-01-05	10:06 PM	6	68	253	36	-1038	-1556
BpTag051	-118.648	33.189	2013-01-08	6:40 PM	46	375	2342	127	-248	-1556
BpTag052	-118.692	33.338	2013-01-13	8:35 PM	86	461	3350	178	-248	-1556
BpTag053	-118.468	33.747	2013-01-16	9:51 PM	22	184	1281	142	-85	-880
BpTag054	-124.778	46.544	2013-03-09	8:34 PM	7	73	481	162	-143	-1412
BpTag055	-124.851	46.489	2013-03-09	9:34 PM	2	15	82	25	-749	-1847
BpTag056	-124.779	46.502	2013-03-09	10:44 PM	43	257	2117	108	-98	-1942
BpTag058	-118.969	32.928	2013-03-23	6:40 PM	14	144	586	74	-679	-1556
BpTag059	-119.038	32.983	2013-03-29	4:15 PM	10	84	481	29	-1117	-1556
BpTag060	-119.050	32.948	2013-03-29	6:59 PM	10	94	566	93	-880	-1556
BpTag061	-119.014	32.985	2013-03-29	9:55 PM	11	75	416	28	-1107	-1556
BpTag062	-119.033	32.898	2013-03-30	5:39 PM	41	205	1985	142	-389	-1556
BpTag063	-118.866	33.157	2013-05-19	1:01 PM	81	273	2997	291	-389	-3752
BpTag064	-118.657	33.014	2013-07-08	9:52 AM	23	188	2188	308	-389	-3171
BpTag065	-118.932	33.025	2014-01-10	4:55 PM	239	555	7026	537	-85	-4334
BpTag066	-118.947	33.007	2014-01-10	5:36 PM	21	146	1121	132	-679	-1658
BpTag067	-117.622	33.164	2010-08-26	4:06 PM	20	98	1191	318	-385	-3390
BpTag068	-118.996	32.906	2015-01-03	4:42 PM	129	31	3296	1277	-419	-4242
BpTag070	-117.756	33.454	2015-01-11	11:24 PM	149	355	3925	309	-85	-2010
BpTag072	-119.068	33.027	2015-06-30	5:11 PM	33	257	2246	809	-389	-4525
BpTag073	-118.831	33.217	2015-08-24	7:24 PM	27	129	999	131	-87	-1178