# RESEARCH



# Ecological drivers of movement for two sympatric marine predators in the California current large marine ecosystem



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## Abstract

**Background** An animal's movement reflects behavioral decisions made to address ecological needs; specifically, that movement will become less directional in regions with high prey availability, indicating foraging behavior. In the marine realm, animal behavior occurs below the sea surface and is difficult to observe. We used an extensive satellite tagging dataset to explore how physical and biological habitat characteristics influence blue (*Balaenoptera musculus*) and fin (*B. physalus*) whale movement and foraging behavior in the California Current Ecosystem across four known bioregions.

**Methods** We fitted movement models to 14 years of blue whale satellite tracking data and 13 years of fin whale data to characterize their movement persistence, with higher move persistence values representing more directional movement and lower move persistence values representing less directional movement. Models were evaluated against a range of physical and biological environmental predictors to identify significant correlates of low move persistence (i.e., presumed intensified foraging behavior). We then used data from a subset of sensor-equipped tags that monitored vertical behavior (e.g., dive and feeding), in addition to movement, to test the relationship between vertical behavior and movement persistence.

**Results** Low move persistence was strongly correlated with shallower water depth and sea surface height for both species, with additional effects of chlorophyll-a concentration, vorticity and marine nekton biomass for blue whales. Data from sensor-equipped tags additionally showed that low move persistence occurred when whales made more numerous feeding dives. Temporal patterns of bioregion occupancy coincided with seasonal peaks in productivity. Most blue whale low-move-persistence movements occurred in the northern, nearshore bioregion with a late-season peak in productivity and were evenly distributed across all bioregions for fin whales.

**Conclusions** We demonstrated that low move persistence is indicative of increased feeding behavior for both blue and fin whales. The environmental drivers of low move persistence were similar to those previously identified for survey-based species distribution models, linking environmental metrics to subsurface behavior. Occupancy and movement behavior patterns across bioregions indicate both species moved to exploit seasonal and spatial variability

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in productivity, with blue whales especially focusing on the bioregion of highest productivity during late summer and fall.

**Keywords** Move persistence, Movement behavior, Feeding behavior, Blue Whale, Fin Whale, California current, Satellite tags, Biologging

## Background

Foundational ecological theory posits that an animal's movement reflects behavioral decisions made to address ecological needs like resource acquisition [1]. Patterns of local-scale behavior can influence broader trends of occurrence by driving the time spent in an area [2] or how individuals arrange themselves in relation to food patches [3]. Predictable patterns of available resources can influence broader trends of occurrence as individuals move to track changing resources to maximize foraging efficiency [4, 5]. In the marine realm, animal behavior occurs below the sea surface where observation is difficult, so correlative models using environmental data are often used to describe the distribution and/or movement behavior of animals and infer the drivers of such behavioral decisions, typically with the assumption that lessdirected movement is indicative of increased foraging effort [6, 7]. However, the interpretation of such models may be inaccurate without incorporating additional data on the subsurface behavior driving surface-level observations [8, 9].

As tracking technology has improved, researchers have been able to monitor the subsurface behavior of marine animals to better link fundamental behaviors like foraging effort to their more commonly observed surface expressions of occurrence and movement behavior [10-12]. This biologging technology has been applied to a variety of marine species to show that, in some cases, less-directed movement is indicative of foraging behavior [13-15], while other cases have shown more nuance, such as how ringed seals engaged in less directed movement in areas of higher prey biomass but foraged in areas with lower prey diversity and biomass [16]. However, technological limitations remain that have made identifying similar linkages between surface and subsurface behavior more challenging for large baleen whales.

Blue (*Balaenoptera musculus*) and fin (*B. physalus*) whales are the two largest animals that have ever lived [17–20]. Like other rorquals, they feed by engulfing large volumes of water and schooling prey and then expelling the water through fibrous baleen plates to retain the prey [21]. This engulfment, termed "lunge feeding," occurs during rapid acceleration through/into a prey swarm and can occur multiple times per dive. The evolution of this feeding behavior is closely tied to the large size of the animals, as it allows them to efficiently exploit highly concentrated prey patches [19, 22, 23]. As resource specialists, blue whales, and to a lesser extent, fin whales,

are limited in their foraging plasticity, with blue whales in particular needing to seek out the densest krill aggregations [24]. While individuals can vary their feeding tactics to exploit different concentrations of prey [25, 26], prey patch quality is related to a trade-off between the energetic content of available prey and the depth at which it is distributed, with individual decisions to move between patches being related to balancing energetic gains from feeding and the costs associated with diving to exploit them at different depths [27]. Thus, the dive and feeding behavior of an individual whale can offer a mechanistic link to that individual's movement decisions, which, in turn, inform population-level patterns of conservation and/or management interest like distribution and residence time [4].

Both blue and fin whales exploit the most productive environments of the California Current Ecosystem (CCE) off the west coast of North America. The ecosystem-scale (100-1000 s km) movements and occurrence of blue whales in the CCE are driven by seasonal aggregations of two euphausiid species (Thysanoessa spinifera and Euphausia pacifica; [28-30]), commonly called "krill", with whales arriving in the late spring-early summer and feeding until the late fall–early winter [31–33], when they migrate south to breeding areas off Mexico and near an offshore oceanographic feature called the Costa Rica Dome [34-36]. Although the seasonal movements of fin whales are less well understood, they appear to occur year-round off southern California, USA [37-39], and are predicted to occur most often off Oregon during the fall and winter months [40], suggesting they do not follow the typical baleen whale pattern of migrating to lower latitudes during the winter to breed and calve (see also [41-43]). In the CCE, fin whales primarily feed on the same species of krill as blue whales but can also feed on small fish and squid [44, 45].

We use a collection of blue and fin whale movement data spanning 20 years to examine the ecological correlates of their movement. We then use a smaller subset of dive and feeding behavior data to test the assumption that less directed movement is indicative of increased foraging behavior. As sympatric species that have evolved with the same lunge-feeding strategy, we hypothesize that the behavioral patterns associated with their movement will be similar for the two species at the CCE scale but that differences in their spatial and temporal distributions and the environmental correlates of movement will offer insight into how they partition similar resources.

## Methods

## Study area

The CCE is a highly productive, wind-driven eastern boundary current system off the west coast of North America. The high levels of productivity support a diverse food web with krill as one of the primary prey items [46, 47]. The upwelling generated from strong summer winds forms a southward coastal jet that broadly divides the region into three biogeographic domains [46]. Coastal waters are characterized by strong upwelling from wind-driven Ekman transport, producing locally intense regions of elevated productivity. Offshore waters are subject to spatially large but moderate rates of wind curl-driven upwelling that can cumulatively exceed the volume of upwelled water in coastal regions [46]. The coastal jet is deflected offshore at Pt. Conception, forming the boundary for southern California waters, where upwelling is less intense and biological assemblages differ from those of waters to the north [46]. Alongshore surface advection together with mesoscale oceanographic features like fronts and eddies shape krill distribution throughout the CCE, with the highest densities occurring along the continental slope, especially near steep bathymetric features like canyons [48–50]. The high levels of productivity across the region attract top predators like whales, which track the timing of the seasonal rise in productivity [31-33] while feeding on locally dense patches of prey [28, 29].

## Data collection

From 1998 to 2018, Oregon State University (OSU) and Marine Ecology and Telemetry research (MarEcoTel) deployed satellite-linked radio tags on 180 blue whales and 97 fin whales using the CCE, with the large majority of deployments (173 blue whales and 90 fin whales) occurring off southern and central California, USA (Fig. 1). Blue whale tags were deployed primarily during the summer and fall, while fin whale tags were deployed more evenly across seasons. Tag configuration evolved over the years but followed two implantable attachment designs, with consolidated-style (type-C; [51, 52]) tags deployed on 180 blue whales from 1998 to 2017 and 35 fin whales from 2004 to 2018 and anchored-style (type-A; [51]) tags deployed on 62 fin whales from 2008 to 2017. Tag configurations are defined in Andrews et al. (2019), where type-C tags have electronics and retention elements consolidated into a single implanted anchor, while type-A tags carry the electronics package external to the skin, attached by one or more anchors that puncture and terminate below the skin of the body or dorsal fin. All tags contained an Argos transmitter, batteries and a saltwater conductivity switch to limit satellite transmissions to periods when the tag was out of the water. A subset of type-C "RDW" tags (n = 22 deployed on blue whales in 2016 and 2017, and n = 9 deployed on fin whales in 2016) additionally incorporated a pressure sensor and tri-axial accelerometers to record dive depth, duration, and lunge-feeding events while attached to a whale [53]. Both types of tags were remotely deployed using an air-powered applicator [54] or a crossbow (in the case of older type-C tags) from a small boat at close range (2–20 m).

All tags produced locations through the Argos satellite system, operated by *Collecte Localisation Satellitales* (CLS) with transmissions to the satellite controlled by a saltwater conductivity switch. Argos locations were estimated by Doppler shift in the frequency of tag transmissions with error denoted by one of seven location classes (LC; 3, 2, 1, 0, A, B, Z in descending order of quality) or as an ellipse [55], although, for consistency across deployment years, ellipses were not used.

## Tag programming

Tags were programmed to transmit every 10 s only when out of the water during specified hours of the day. The specific duty cycles varied across field seasons and by species, but type-C tags were programmed to transmit during four or six 1-h periods per day, coinciding with times when satellites were most likely to be overhead. The tags were programmed with one of three duty cycles: (1) transmitting every day, (2) transmitting every other day, or (3) transmitting every day for the first 90 d and then transmitting every other day for the remainder of the tag life. type-A tags were scheduled to transmit daily for 50 d, after which they switched to every other day for 20 d, followed by every third day for 30 d, every fifth day for 50 d, and then every 10th day thereafter.

RDW tags generated Argos locations similar to other tags and were additionally able to report per-dive summaries of dive and feeding behavior while attached to a whale using an on-board event detection algorithm [53]. The tags recorded: dive depth every 5 s with 2 m vertical resolution up to a maximum of 511 m; dive duration at 1 s resolution up to a maximum of 4,095 s using the tag's SWS; and accelerometer readings every 0.25 s at 1/64th -G precision. The tag event detection algorithm was specifically developed to detect lunge-feeding behavior in rorqual whales (family Balaenopteridae), which produces strong stereotypical signatures in acceleration data [56-58]. Proxy validation of the event detection algorithm determined it correctly identified feeding dives with 74% accuracy [53]. Per-dive summaries of behavior were derived for dives>2 min in duration and 10 m in depth and consisted of dive start time, maximum dive depth, dive duration and number of feeding lunges (which was used to indicate a feeding/non-feeding dive). Each Argos transmission reported six to eight consecutive selected dive summaries and was randomly selected from a 10-message buffer [53].



Fig. 1 (A) Boundaries of four CCE bioregions based on spatial and temporal patterns in chlorophyll-a concentration from [74]. (B) The deployment locations for satellite tags attached to blue and fin whales off the U.S. West Coast and Mexico from 1998–2018. (C) The number of tags deployed during each month of the year by species

From the dive summary messages, we calculated dive end times as the sum of the dive start time and duration and then calculated post-dive intervals (PDIs) for consecutive dives within an Argos transmission as the difference between the dive start time and the end time of the previous dive. As only dives > 10 m in depth were recorded, the PDI represents the time spent shallower than 10 m between deeper dives. Complete recovery of all dive summary messages was not achieved, so the PDI for the last dive in a message was not calculated, as it might include dives that had not been received. To quantify the data recovery rate, we then calculated the percentage of the tracking period that was summarized by the received transmissions as the sum of all received dive durations and PDIs divided by the total duration of the time series.

#### Track regularization

Timeseries of Argos locations (tracks) are observed irregularly in time and with error, so we used a state space model to estimate locations at regular intervals with improved precision [59]. Prior to fitting the model, Argos tracks for both species were filtered to remove Z-class locations. Empirical error estimates of all non-Z location classes for free-ranging blue and fin whales were recently estimated at 650 m to 5500 km, depending on the location class [60]. Tracks often contained data gaps due to duty cycling and asynchrony between satellite passes and tagged whale surfacing intervals, so we split tracks at gaps > 3 d to avoid interpolating locations during periods with sparse observations. We retained segments > 6 d in duration and assigned each segment a unique identifier (ID). Following track splitting, there were 303 blue whale and 108 fin whale track segments with a mean of 4.4 and 7.5 (sd = 6.1 and 3.0) locations per day, respectively from 171 to 87 tagged blue and fin whales (Table 1). We then fitted the track segments to a continuous-time correlated random walk movement model using the R package aniMotum (v. 1.1-04; [61]) to predict locations at regular 12-h intervals (two locations per day) after filtering out locations requiring unrealistic swimming speeds (>15 km/h). A correlated random walk model was chosen over a standard random walk after reviewing the diagnostic output from both model fits. The time interval was chosen to balance the scale of resolved movement with the daily number of locations received. The same time interval was used for both blue and fin whales to facilitate comparisons. Tracks were then clipped to limit their extent to the CCE by removing locations south of 22°N and those occurring in the Gulf of California, Mexico.

## **Ecological predictors**

We extracted a suite of environmental predictors for each regularized location using custom code implemented in R (v. 4.2.1; [62]). We extracted water depth using the

SRTM 15+gridded bathymetry product [63] accessed from the NOAA ERDDAP server using the R package rerddapxtracto (v. 1.1.4; [64]). All other predictors were downloaded at a daily temporal resolution using the R package CopernicusMarine (v. 0.1.1) provided by the E.U. Copernicus Marine Service, which supports datasets of modeled physical and biological oceanographic processes at a global coverage. We selected sea surface temperature (SST), mixed-layer depth (MLD), and sea surface height (SSH) from the global physical reanalysis database [65]. Chlorophyll-a concentration (CHL) data were downloaded from the Global Ocean Biogeochemistry Hindcast [66], and zooplankton (Zoop) and epipelagic marine nekton biomass (Nekton) data were downloaded from the Global Ocean Low and Mid-Trophic Levels biomass content hindcast [67]. All covariates were accessed at a daily temporal resolution and 0.083-degree grid size, except for CHL, which was available at a 0.25-degree grid size. Zoop and Nekton data represented modeled biomass values integrated for the top 200 m of the water column, while we used model values from the surface layer for SST and CHL to facilitate comparisons to studies using remotely-sensed data. Whales feed on prey that exploits increased phytoplankton biomass (as measured by chlorophyll-a concentration), so using a lagged chlorophyll-a value is most relevant to account for the time needed for higher trophic levels to aggregate and exploit the initial rise in concentration. Therefore, we used 1-month lagged chlorophyll-a values based on the lag between peak chlorophyll-a concentration and blue whale occurrence identified in Abrahms et al. [32]. Dynamic oceanographic features like submesoscale eddies have been linked to zooplankton aggregations and foraging whales on a scale of hours to multiple days [68-70], so we also calculated surface vorticity values using daily grids of surface current velocities (u and v) in the eastward (x) and northward (y) directions, respectively, downloaded from the Copernicus Marine Service Global Physical Reanalysis Database [65]. Vorticity was calculated following Cade et al. (2022) as the difference in the derivative of  $\nu$  with respect to x and *u* with respect to y using the *focal* function in the R package Raster (v. 3.6-11). We extracted values for ecological predictors at each regularized track location and for the corresponding day and then examined their distributions for normality and assessed correlations to avoid multi-collinearity during model fitting (Additional file 1: Figs. A-1 and A-2).

## Move persistence modeling

We fitted blue and fin whale track segments to mixedeffects models estimating their move persistence using the R package *mpmm* [71]. Move persistence ( $\gamma_t$ ) is a continuous value ranging from 0 to 1, indicating the degree of autocorrelation in directionality and magnitude of an

Table 1	Tag deployment summary ta	able for blue and fin v	whales tagged in the	Northeast Pacific or	cean from 1998-2018	3. Data shown
are for tra	acks with at least one segme	nt>6 d (171 blue wh	hales and 97 fin whale	s)		

Species	Project ID	Tag type	#track segments	Mean seg- ment dura- tion (d)	SD seg- ment duration (d)	Mean locations/d	SD locations/d	# tracks	Mean track duration (d)	SD track dura- tion (d)
Blue	1998CA	Type-C	11	33.5	27.5	2.2	1.0	7	54.5	31.2
Blue	1999CA	Type-C	35	27.7	26.9	1.5	0.7	13	95.5	68.7
Blue	2000CA	Type-C	14	28.3	25.2	1.3	0.3	5	123.1	87.8
Blue	2001MX	Type-C	4	35.8	44.8	1.3	0.4	1	167.0	NA
Blue	2002MX	Type-C	3	86.8	92.2	1.5	0.4	2	137.8	78.3
Blue	2004CA	Type-C	21	50.0	35.4	2.0	0.7	16	71.5	50.1
Blue	2005CA	Type-C	23	32.1	28.2	1.6	0.7	14	72.5	59.8
Blue	2006CA	Type-C	26	22.9	18.3	1.3	0.4	8	127.8	97.9
Blue	2007CA	Type-C	38	33.1	28.5	1.6	0.4	14	107.0	85.3
Blue	2008CA	Type-C	23	38.5	32.1	1.7	0.6	12	96.0	59.8
Blue	2008CR	Type-C	8	32.5	34.3	1.6	0.8	2	158.6	52.7
Blue	2014CA	Type-C	23	54.7	65.1	20.0	42.4	20	64.6	70.3
Blue	2015CA	Type-C	28	52.7	42.7	17.8	38.2	20	78.0	49.2
Blue	2016CA	Type-C	18	64.4	56.3	5.6	1.1	15	79.2	56.9
Blue	2017CA	Type-C	28	57.7	36.2	5.2	1.2	22	76.8	41.9
		Mean	20.2	43.4		4.4		12.0	98.2	
Fin	2004CA	Type-C	1	9.3	NA	3.1	NA	1	9.3	NA
Fin	2006CA	Type-C	7	37.7	33.4	1.5	0.5	1	301.0	NA
Fin	2014CA	Type-C	9	27.4	21.3	7.0	6.7	6	45.5	43.5
Fin	2015CA	Type-C	16	35.9	37.5	12.6	31.6	12	50.7	64.1
Fin	2016CA	Type-C	14	25.3	23.2	5.6	2.0	13	29.8	29.3
Fin	2017CA	Type-C	1	38.6	NA	3.7	NA	1	42.3	NA
Fin	2018PNW	Type-C	1	14.5	NA	8.0	NA	1	35.9	NA
Fin	CenCal_2016	Type-A	1	6.7	NA	5.5	NA	1	6.7	NA
Fin	SoCal_2008	Type-A	4	32.2	19.5	6.6	3.0	3	44.0	24.2
Fin	SoCal_2009	Type-A	7	24.5	22.6	7.5	2.8	10	18.5	20.8
Fin	SoCal_2010	Type-A	3	38.6	26.4	8.8	1.5	3	38.6	26.4
Fin	SoCal_2011	Type-A	3	23.2	6.2	7.9	3.3	4	18.2	11.1
Fin	SoCal_2012	Type-A	13	29.1	19.5	7.5	2.5	13	29.1	19.5
Fin	SoCal_2013	Type-A	12	29.2	17.8	9.8	3.3	13	27.9	24.7
Fin	SoCal_2014	Type-A	2	45.1	33.6	7.9	1.1	2	45.1	33.6
Fin	SoCal_2015	Type-A	3	42.7	22.5	7.3	3.3	3	42.7	22.5
Fin	SoCal_2016	Type-A	2	13.0	9.3	5.3	1.2	1	30.0	NA
Fin	SoCal_2017	Type-A	2	39.3	39.3	8.8	4.3	2	39.3	39.3
Fin	WA_2010	Type-A	3	26.1	17.8	6.2	5.1	2	47.7	33.9
Fin	WA_2011	Type-A	1	27.0	NA	8.3	NA	2	15.5	16.3
Fin	WA_2012	Type-A	1	23.5	NA	14.3	NA	1	23.5	NA
Fin	WA_2013	Type-A	2	24.5	25.2	11.7	4.1	2	24.5	25.2
		Mean	4.9	27.9		7.5		4.4	43.9	

animal's movement, with high values indicating directional movement and low values indicating non-directional movement. The package uses a mixed-effects framework to model  $\gamma_t$  as a linear function of environmental/habitat predictors:

$$logit(\gamma_{t,k}) = (\beta_0 - b_{0,k}) + \beta_1 m_{t,1,k} + \dots + \beta_n m_{t,n,k} + \varepsilon_t \quad (1)$$

where  $\beta_0$  is the fixed intercept,  $\beta_1,...,\beta_n$  are the fixed regression coefficients,  $m_{t,1,k},...,m_{t,n,k}$  are the predictor

variables, *k* is the index for individual track segments, with  $b_{0,k}$  representing the random intercept of individual *k*, and  $\mathcal{E}_t$  is the error where  $\mathcal{E}_t \sim N(0, \sigma_{\gamma})$ .

Prior to model fitting, all covariates were scaled and centered. Due to the relatively large number of candidate predictors, we used a stepwise model selection approach to select the best performing model for each species. The model was first run with all predictor variables. Nonsignificant predictors were iteratively identified and removed based on their associated p values, and subsequent model performance was then checked using the change in Akaike's information criterion (AIC) from the previous model. Colinear predictors were tested singularly with the remaining predictors to determine which should be retained. If the top models were differentiated by <2 AIC, we followed the decision tree described in [72] to identify uninformative parameters and determine the final model. Finally, we fitted a null model with no predictors as a null hypothesis test of no ecological effects on blue and fin whale move persistence and then ranked all models based on their AIC values.

Once a final model was identified, we assessed its robustness using a 10-fold cross-validation method. We randomly split the track segments into 10 groups, then iteratively excluded one group, re-ran the model on the remaining data, and examined covariate estimates relative to the confidence intervals of covariates estimated from the model using all tracks. This is an adaptation of a more commonly used leave-one-out cross-validation method used for this framework (e.g., [16, 73]), which we implemented due to the relatively large number of track segments.

#### Variation in movement behavior across bioregions

The CCE can be characterized in terms of four bioregions based on the timing and intensity of chlorophyll-a production (Fig. 1A; [74]). The four bioregions include (1) SummerMin, which represents predominantly offshore regions of the U.S. West Coast with elevated chlorophylla levels in winter, spring and late fall; (2) LatePeak, which represents nearshore waters ranging from southern California to the northern extent of the CCE, with a spring peak in chlorophyll-a during April and May, followed by a longer, late summer elevated period from July through October; (3) Flat, which is characterized by offshore waters across the entire extent of the CCE with weak seasonality; and (4) EarlyPeak, which describes southern nearshore CCE waters where chlorophyll-a increases from November through May and decreases from its peak in early June to a minimum in late October. We investigated the timing of occurrence in each of the bioregions by examining the day of the year for regularized locations that fell in each region and assessed patterns of movement behavior in each bioregion by examining how move persistence values varied across the regions.

#### Dive data processing and behavioral drivers of movement

To examine the behavioral drivers of movement, we linked RDW tag dive and feeding data to regularized locations by generating 12-h summaries of received dive behavior to match the time step of regularized track locations. These summaries included median maximum dive depth and number of feeding dives (dives with at least one lunge-feeding event). Data recovery rates were typically less than 100%, so we also calculated the percentage of the time step summarized (percent summarized), which was calculated as the sum of all dive durations and PDIs that occurred during the interval divided by the interval duration (12 h). In some cases, PDIs spanned two 12-h periods. In those instances, the time between the end of the last dive in a period (the start of the last PDI) and the end of the period was included in the calculation of the first period's percent summarized, and the remainder was added to the following period's PDI values. To mitigate potential biases associated with variable data recovery rates, we created a 'feeding dive rate' metric for each time step that relativized the number of feeding dives by dividing it by the sum of dive durations and PDIs occurring within the time interval (i.e., the duration of data available for that time step). The result was a metric representing the hourly rate of feeding dives that occurred during the data available for each time step. We then tested the relationship between move persistence values at each location and the corresponding feeding dive rate and median maximum dive depth that occurred during each time interval using beta regression implemented in the R package betareg (v. 3.1-4; [75]). We used beta regression because it is better suited to response variables that range between 0 and 1. We also tested how prey concentration (in the form of zooplankton biomass) was related to dive and feeding behavior, by fitting a generalized linear regression with a gamma distribution and log link with Zoop as the response variable and the corresponding feeding dive rate and median maximum dive depth values as the explanatory variables. Feeding dive rate, and median maximum dive depth values were scaled and centered to improve interpretability. Models were fitted using the R package *lmer4* (v. 1.1–32; [76]). In both cases, we included a "species" indicator term to account for potential differences between blue and fin whales.

## Results

The geographic distributions of blue and fin whale tracks were similar, with the fin whale range extending further north to Haida Gwaii, Canada, compared to that of the blue whales, which had greater occupancy of the southern portion of the CCE off the Baja California Peninsula (Fig. 2). The majority of blue whale locations occurred across all four CCE bioregions from mid-summer until early winter (~August to December, Fig. 3B). During winter and spring, more locations occurred in the EarlyPeak bioregion off southern California, USA, and Baja California, Mexico, compared to the other three bioregions. Temporal occurrence of fin whales in the CCE bioregions followed a bimodal distribution, with most locations occurring in the more southerly SummerMin and EarlyPeak bioregions during winter and spring and a progression of occupancy occurring from mid-summer



Fig. 2 Spatial distribution of mean move persistence values for satellite-tagged blue (left) and fin (right) whales tracked in the eastern north Pacific Ocean from 1998–2018. Values are presented on a 0.25-degree grid. Low movement persistence indicates less-directional movement while higher values indicate directional movement

to late-fall with high occupancy in the EarlyPeak bioregion, followed by the Flat bioregion and finally the Late-Peak bioregion (Fig. 3D).

Lower move persistence values were widely distributed for both species but generally occurred near the continental shelf and slope (Fig. 2). Both blue and fin whales exhibited the full range of move persistence values (0.01– 0.99), although blue whale values were generally higher than those of fin whales (Fig. 3, Additional file 1: Fig. A-3). Move persistence values were equivalently distributed across all four bioregions for fin whales, but for blue whales, lower values primarily occurred in the LatePeak bioregion, with slightly lower values also occurring in the EarlyPeak region (Fig. 3A).

For blue whales, all models out-performed the null model, and the best performing model for predicting move persistence included water depth, CHL, SSH, vorticity, and Nekton, (Table 2). Move persistence increased with increasing water depth, SSH, and vorticity and it decreased with increasing CHL and Nekton (Fig. 4).

The best performing model for fin whales included water depth, SSH, CHL, and Zoop, although the was only suggestive evidence of an effect for CHL and Zoop (p = 0.033 and 0.078 respectively; Table 2). All fin whale

models also out-performed the null model. Fin whale predictors of move persistence had weaker effects than blue whale predictors, with move persistence increasing with increasing water depth and SSH and decreasing with increasing CHL and Zoop (Fig. 5). Despite the difference in significance level and effect size for ecological covariates between blue and fin whales, the range of values utilized by both species were very similar, although fin whales occupied somewhat deeper waters (Additional file 1: Fig. A-4).

Cross-validation of the best performing model for each species indicated that the models were robust to perturbations in the data. All parameter estimates when one group of track segments was excluded fell within the confidence intervals for the corresponding parameters estimated from the model with all track segments (Additional file 1: Fig A-5).

Out of 2291 regularized RDW tag locations, dive data were reported during at least part of the time interval for 1930 locations, representing a total of 49,320 dives from blue whales and 14,158 from fin whales. The percentage of a location interval summarized ranged from 0 to 100%, with a mean of 46% (SD = 25%) for blue whales and 45% (SD = 30%) for fin whales (Additional file 1: Fig. A-6).



**Fig. 3** Distribution of blue (top) and fin (bottom) whale move persistence values and timing of occurrence in four biogeographic regions in the California Current Ecosystem described by [74]. The four regions were derived based on spatial and temporal patterns in chlorophyll-a concentration: SummerMin represents regions with elevated chlorophyll-a levels in winter, spring and late fall; LatePeak represents a spring peak in chlorophyll-a during April and May, then a longer, late summer elevated period from July through October; Flat is characterized by weak seasonality, and EarlyPeak describes where chlorophyll-a increases from November through May and decreases from its peak in early June to a minimum in late October

Maximum dive depths were deeper during the day for both blue and fin whales, although fin whale dives were shallower (mean = 89.9 m vs. 106.0 m, SD = 52.6 vs. 87.2 respectively; Fig. 6).

Move persistence significantly decreased with increasing rate of feeding dives and increasing median maximum dive depth (p < 0.0001 and p = 0.00022 respectively; beta regression), leading us to reject the null hypothesis of no effect, although the effect size was much smaller for dive depth (Fig. 7). The species indicator term in the model was also significant (p < 0.0001), although the difference in predicted move persistence values between species was small for both covariates (Fig. 7).

Zoop was not significantly associated with either the feeding dive rate nor the median maximum dive depth,

so we did not reject the null hypothesis of no effect (p = 0.19 and p = 0.79, respectively; gamma GLMM).

## Discussion

For the first time, we link ecosystem-scale baleen whale movement directly to subsurface dive and feeding behavior to demonstrate that non-directed movement is indicative of increased feeding behavior for both blue and fin whales in the CCE. Occupancy and movement behavior patterns across CCE bioregions indicate both species moved to exploit seasonal and spatial variability in productivity, with blue whales especially focusing on the LatePeak region, which has the highest productivity during late-summer and fall. Species differences in the ecological drivers of move persistence suggest that, while both generally select continental slope waters,

Species	Model	df	AICc	log_lik
Blue	~ Water depth + SSH + Vort + CHL + Nekton + (1 $ tagID $	11	-56294.9	28158.45
Blue	~ Water depth + MLD + SSH + Vort + CHL + Nekton + Zoop + (1 tagID)	13	-56292.4	28159.2
Blue	$\sim$ Water depth + MLD + SSH + Vort + CHL + Nekton + (1 tagID)	12	-56292.4	28158.19
Blue	$\sim$ Water depth + MLD + SST + SSH + Vort + CHL + Nekton + Zoop + (1 tagID)	14	-56292.2	28160.1
Blue	$\sim$ Water depth + SSH + CHL + Nekton + (1 tagID)	10	-56284.8	28152.41
Blue	~ Water depth + MLD + SST + Vort + CHL + Nekton + Zoop + (1 tagID)	13	-56283.5	28154.77
Blue	$\sim$ Water depth + SSH + Vort + CHL + (1 tagID)	10	-56283.2	28151.59
Blue	~ Water depth + MLD + SSH + Vort + CHL + Zoop + (1 tagID)	12	-56282.4	28153.2
Blue	~ (1 tagID)	6	-55890.8	27951.41
Fin	$\sim$ Water depth + SSH + CHL + Zoop + (1 tagID)	10	-8010.08	4015.057
Fin	~ Water depth + SSH + CHL + (1 $ $ tagID)	9	-8009.79	4013.909
Fin	$\sim$ Water depth + SSH + Vort + CHL + Zoop + (1 tagID)	11	-8009.09	4015.568
Fin	~ Water depth + SSH + Vort + CHL + Nekton + Zoop + (1 tagID)	12	-8007.85	4015.952
Fin	~ Water depth + MLD + SSH + Vort + CHL + Nekton + Zoop + (1 tagID)	13	-8005.86	4015.956
Fin	$\sim$ Water depth + SSH + (1 tagID)	8	-8004.85	4010.435
Fin	$\sim$ Water depth + MLD + SST + Vort + CHL + Nekton + Zoop + (1 tagID)	13	-7994.14	4010.098
Fin	~ Water depth + MLD + SST + SSH + Vort + CHL + Nekton + Zoop + (1 tagID)	14	-7991.84	4009.955
Fin	~ (1 tagID)	6	-7944.08	3978.048

**Table 2** Candidate move-persistence models of blue and fin whales tracked in the Eastern North Pacific ocean, ranked by Akaike information criterion (AIC)

additional habitat selection decisions may serve to partition resources between the two.

The relative move persistence of tagged blue and fin whales represented different levels of feeding intensity well, as feeding dives were more prevalent during periods of low move persistence. While such patterns have been demonstrated in other species [13, 15, 77], this study confirms that horizontal movement characteristics can be used as a proxy for regional-scale foraging behavior (e.g. over multiple days and 10s to 100s of km) in blue and fin whales. The continuum of move persistence values likely reflects exploratory movements as whales searched for, sampled, and evaluated prey patches while selecting a feeding site. The observed relationship between deeper median dive depth and lower move persistence values indicates that tagged whales further modified their behavior to remain near deeper, denser, prey patches; such behavior has been shown to enable fin whales to maximize energy intake by targeting densely aggregated prey [27]. However, the full extent of considerations driving these movement decisions are poorly understood and may involve additional factors like memory [32] or potentially unrelated social behavior, as tagged male blue and fin whales off southern California, USA, passed actively feeding conspecifics without stopping, indicating that prey availability is not the only driver of their movement [78].

While varying between species, patterns identified by ecological predictors from the move persistence final models are directly related to ocean productivity and its drivers. In the CCE, alongshore winds and ocean currents interact with steep bathymetric features like submarine canyons incising the continental shelf to form and aggregate zooplankton patches [49, 50]. The strong correlation between shallower water depth and lower move persistence indicates that blue and fin whales changed their movement behavior to remain in these areas longer and corresponds well with results of sightings-based models [7, 40, 79]. Blue whale move persistence was lower in areas with high lagged chlorophyll-a concentration, indicating they further selected more biologically productive areas within the CCE, as expected for their massive size [24]. The significant effects of SSH and vorticity indicate these areas were driven by coastal upwelling dynamics of the CCE as SSH is lower nearshore when water is advected away from land [46, 80], and sub-mesoscale oceanographic features (measured by vorticity) can aggregate and retain prey, which are then exploited by blue whales [69, 70]. The observed positive relationship between move persistence and vorticity was unexpected based on other observed relationships with feeding rates [69, 70]. However, these features and associated prey concentrations evolve over periods of hours to multiple days, so the temporal scale of our vorticity analysis and/or the movement track segments may have been too coarse to resolve their effect.

In contrast to blue whales, fin whale movement was correlated with fewer ecological predictors, and showed smaller effect sizes, suggesting they modified their movement behavior in relation to different drivers of prey aggregation compared to blue whales. This may, in part, be due to many fin whale tracks occurring during winter months, when the CCE shifts to a pattern of more moderate, regional productivity, or even downwelling [46]



Fig. 4 Ecological drivers of blue whale movement behavior. Results from the top move-persistence mixed model for fixed (thick blue line) and random (individual whales; thin yellow lines) effects. Low move-persistence is indicative of less directed movement while high values indicate directed move-ment. Predictors were scaled and centered prior to model fitting



Fig. 5 Ecological drivers of fin whale movement behavior. Results from the top move-persistence mixed model for fixed (thick blue line) and random (individual whales; thin yellow lines) effects. Low move-persistence is indicative of less directed movement while high values indicate directed movement. Predictors were scaled and centered prior to model fitting

and year-round residents [81] may engage in reproductive activities. Tagged blue and fin whales occupied similar geographic and oceanographic spaces within the CCE (e.g., Additional file 1; Fig. S4), but the observed differences in significant covariate effects on their movement indicate they responded differently to these similar features, suggesting how they may partition their habitat.

As obligate krill feeders, we expected blue whale movement to be strongly influenced by modeled zooplankton biomass, while drivers of fin whale movement might be



Fig. 6 Diel variability of maximum dive depth recorded from RDW-tagged blue and fin whales tracked in the CCE during summer - fall 2016 and 2017

more variable due to their ability to feed on both zooplankton and nekton [44, 45]. Thus, the significant contribution of marine nekton to blue whale movement behavior, and only suggestive evidence for an effect of zooplankton for fin whales was unexpected. Most significant covariates were measures of productivity that can be measured directly (e.g., chlorophyll-a and SSH) and then extrapolated for the modeled data layer. However, they represent correlative links in the physical and biological processes leading to zooplankton production, while zooplankton biomass should have offered a more mechanistic link to the driver of blue and fin whale movement on their feeding grounds. Tagged blue and fin whales both made deeper daytime dives, indicating that they were foraging on vertically migrating zooplankton (Fig. 6; [56, 82]); however, there was no observed relationship between the dive depth or feeding dive rate and modeled zooplankton biomass. The epipelagic marine nekton data layer used in this analysis has been shown to improve a species distribution model for fin whales in the CCE, but not blue whales [83], and zooplankton were not considered. In addition to their spatial and temporal resolution, we selected these data layers for their global extent to facilitate potential comparisons to other study areas. However, it is possible the modeled linkages between physical and biological processes in this dataset do not adequately represent zooplankton biomass in the CCE.

Blue whales predominantly occupied the CCE during the summer to late fall seasons, migrating from their wintering grounds to forage on productivity generated by the CCE wind-driven coastal upwelling system [29, 32, 35]. While much of their wintering grounds are outside the CCE [35], tagged blue whales did occupy the EarlyPeak bioregion in the nearshore waters off western Baja California, Mexico and southern California during late-winter and spring, where the seasonal chlorophyll-a maximum would generate the greatest opportunities for foraging during that time of year [74]. Low move persistence values predominantly occurred in the LatePeak bioregion, indicating tagged whales focused their foraging efforts in this central and more northerly CCE region,



**Fig. 7** (Top) Relationship between move persistence and feeding dive rate, (bottom) relationship between move persistence and dive depth. Lower move-persistence values indicate less directional movement. Data are derived from satellite tags attached to blue and fin whales off California during summer and fall 2016 and 2017. Shaded regions indicate the 95% confidence intervals. Feeding dives rate is a metric representing the hourly rate of feeding dives that occurred during the data available for each time step

which is driven by nearshore, wind-driven upwelling similar to what has been described in more localized areas like Monterey Bay, California [29, 84] and Pt. Conception, California [28]. This highly productive bioregion is likely to produce dense zooplankton aggregations, allowing tagged whales to exploit the foraging efficiencies related to their size [24] while also maximizing energy intake during a limited temporal window before migrating south for the winter.

Fin whales occupy the CCE year-round [39, 40], and their occupancy of different bioregions reflected a pattern of selecting the bioregion with the highest productivity for the time it was occupied. During winter and spring, bioregions off southern California with higher productivity had the highest occupancy, while summer and fall showed a progression, with the whales moving from regions with earlier peaks in chlorophyll-a concentration off southern California to those with later and more intense peaks further north (Fig. 3). Move persistence values were approximately evenly distributed across all bioregions, indicating that the whales foraged as they moved throughout the CCE.

The bimodal distribution of fin whale occupancy throughout the year was due in part to the seasonality of tag deployments, while the pattern of blue whale deployments reflected the whales' well-established seasonal occurrence in the CCE (Fig. 1; [31, 35]). This, as well as other characteristics inherent to tracking data, like variable tracking duration and deployment location, should be considered when making population-level inferences, as there may be under-sampled regions or time periods [85]. Tags in our study were primarily deployed off southern and central California and exhibited different dispersal patterns between species [86]. Further, tracking segments were shorter in duration for fin whales (Table 1), leaving less time for them to disperse throughout their range and there is evidence that not all fin whales disperse throughout the entire CCE [81]. Thus, additional work may be needed to confirm if our results extend to less-sampled regions and times of year, like the waters off Oregon where fin whales are predicted to occur during winter and spring [40], or to early-season blue whale movements as they arrive on the feeding grounds in late spring at the onset of coastal upwelling.

As sympatric species, blue and fin whales are expected to partition resources. The results of our study indicate that both species use similar foraging strategies, modifying their movement behavior when feeding, but may vary tactics. Blue whales must maximize their energy intake during their seasonal stay in the CCE [35], and this was reflected in how they modified their movement in relation to elevated chlorophyll-a concentrations and physical features that serve to generate and aggregate prey (in the form of continental shelf and slope waters). In contrast, fin whales occur year-round in the CCE [39, 40], and the lack of a migration-related energy expenditure may allow them to forage in regions of more moderate productivity. This year-round residency may result in consistently better body condition than a migratory strategy, as has been suggested in a study comparing migratory blue whale populations to a population resident to the moderately productive waters off New Zealand [87]. A year-round presence may also allow fin whales to partition resources spatially, temporally, and possibly by trophic level, as has been observed with sympatric humpback and blue whales in Monterey Bay, California, USA, where humpback whales make early-season arrivals to feed on krill, then incorporate schooling fish in other parts of the bay when blue whales arrive [88]. The timing of fin whale occupancy of different bioregions in our study suggests they may track seasonal peaks in productivity across the CCE, similar to how blue whales track the mean timing of chlorophyll-a blooms during northward migration [32]. The significance of SSH, and modest effect of CHL on fin whale movement behavior compared to that of blue whales may represent a focus on different oceanographic productivity regimes, with fin whales exploiting wind-stress-curl driven productivity, which can occur year-round and produces broader regions of elevated densities of small phytoplankton and schooling fish [89], while blue whales track the timing of seasonal coastal upwelling [29, 32]. A continuing question is what, if any, role the ability to forage on non-zooplankton prey further contributes to patterns of fin whale occupancy in the CCE [44, 45].

## Conclusions

Both blue and fin whales conformed to ecological theory by modifying their movement behavior to remain in areas of profitable foraging [90]. This linkage of subsurface behavior to more readily observable horizontal movement behavior offers additional important context for existing and future research on blue and fin whale distributions and related conservation questions [91, 92]. Tagged whales moved among CCE bioregions to exploit the varying timing of productivity throughout the region; however, the physical and ecological processes driving that productivity are subject to inter-annual variability and may collapse under extreme scenarios [74]. Indeed, there is evidence of an apparent trophic decoupling in the CCE [93], in which case the connections we observed and those identified in other studies of blue and fin whale distributions [40, 91, 92] may no longer hold for some future climate scenarios. In such cases, the ability to mechanistically link horizontal movement to one of its primary drivers (e.g., feeding) may aid in the identification of new trophic pathways compared to standard correlative methods.

#### Abbreviations

CCE	California Current Ecosystem
CHL	Chlorophyll-a concentration
MLD	Mixed-layer depth
Nekton	Epipelagic marine nekton biomass
PDI	Post-dive interval
SSH	Sea surface height
SST	Sea surface temperature
SWS	Salt-water switch

## **Supplementary Information**

The online version contains supplementary material available at https://doi.or g/10.1186/s40462-025-00542-9.

Supplementary Material 1

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#### Author contributions

LI led and assisted with data collection, conducted the analysis, and drafted the manuscript. DP assisted with securing funding for the project and tagging, led and assisted with data collection, and supervised the analyses. BL led and assisted with data collection. GS and EF secured funding for fin whale tagging and led and assisted with data collection. BM secured funding for the project and tagging and led data collection. All co-authors reviewed and provided input on the draft manuscript.

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#### Data availability

Some of the datasets supporting the conclusions of this article are available in Movebank repositories:

Mate BR, Palacios DM, Irvine LM, Follett TM. 2019. Data from: Behavioural
 estimation of blue whale movements in the Northeast Pacific from state-space

model analysis of satellite tracks. Movebank Data Repository. https://doi.org/1 0.5441/001/1.5ph88fk2.

• Palacios, D.M. and B.R. Mate. 2020. Blue and Fin Whale Movements from Tags Deployed in California (2014-2017) and in Oregon (2018). Research Workspace. https://doi.org/10.24431/rw1k463.

The remainder of the datasets will be uploaded to Movebank at the time of publication.

## Declarations

#### Ethics approval and consent to participate

The activities reported in this study involving the deployment of implantable tags on large whales were carried out under the authorization of the U.S. National Marine Fisheries Service Marine Mammal Protection Act and Endangered Species Act scientific research permits and further reviewed and approved by the Institutional Animal Care and Use Committees. For all blue whale tagging and OSU fin whale tagging, the relevant permits were NMFS permit #841 (1998), #369–1440 (1999–2004), #369–1757 (2005–2013), and #14856 (2014–2018) and Oregon State University Institutional Animal Care and Use Committee permit #4495 and #4884. Fin whale tagging by MarEcoTel was conducted under NOAA research permits 540–1811 and 16111 and approved by Cascadia Research Collective's Institutional Animal Care and Use Committee.

#### **Consent for publication**

Not applicable.

#### **Competing interests**

The authors declare no competing interests.

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