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NOTE

Movement behavior of a blue whale between the Galapagos Archipelago and the Frontal System off Baja California Peninsula

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Abstract

The movement behavior of blue whales in the Eastern Tropical Pacific (ETP) is not well understood, especially regarding the migration of Northeast (NEP) and Southeast (SEP) Pacific populations. This study presents tracking data from a satellite-tagged blue whale recorded between the Galapagos Islands and the Baja California Frontal System. A Bayesian state-space model (BSAM) estimated the whale's movement trajectory, and a hidden Markov model (HMM) classified behavioral states. Environmental factors like sea surface temperature, chlorophyll-a concentration, primary productivity, and mesoscale eddies were analyzed to identify ecological drivers. The whale displayed foraging behavior in areas with lower temperatures, higher productivity, and elevated chlorophyll levels, with movements influenced by cyclonic and anticyclonic eddies. These findings improve understanding of blue whale migration and the potential overlap between NEP and SEP populations in key tropical regions. They suggest that areas like the Galapagos and Costa Rica Thermal Dome may serve as ecological corridors, influenced by eddies.

KEYWORDS

blue whales, eastern pacific, feeding/breeding areas, migratory routes, satellite tracking, thermal dome

The blue whale (*Balaenoptera musculus*) is not only the largest animal on Earth but also inhabits all the world's oceans. The northeast (NEP) and southeast (SEP) blue whale populations have been identified year-round in the Pacific Ocean. However, the migration patterns and behaviors of these populations may differ in their geographic and temporal segregation. Acoustic evidence suggests that SEP whales are heard more frequently in the southern portion of the Eastern Tropical Pacific (ETP) during the austral winter. Meanwhile, NEP whales are heard more frequently in the northern portion of the ETP during the boreal winter (Buchan et al., 2014, 2015; Stafford, 2016; Stafford et al., 1999a, 1999b). The northeast population migrates between wintering areas in the Frontal System off Baja California Peninsula (FTBCP) (sensu Etnoyer et al., 2004; Pardo et al., 2015) and the Costa Rica Thermal Dome (sensu Cromwell, 1958; Shi & Wang, 2024) in the ETP to feeding areas extending from California to as far north as the Gulf of Alaska (Busquets-Vass et al., 2021; Calambokidis et al., 2009; Mate et al., 1999). In contrast, the southeast population migrates toward the Chilean feeding grounds (Hucke-Gaete et al., 2004, 2018; Torres-Florez et al., 2015), and rarely to the Antarctic Peninsula, off the coast of South Georgia in the Southern Ocean (Calderan et al., 2020; LeDuc et al., 2017; Rojas-Cerda et al., 2022). However, the southeast population has a greater preference for the coasts of Peru and southern Ecuador, including the Galapagos Archipelago. Meanwhile, the NEP is more prevalent in Central America and Costa Rica Thermal Dome areas (Branch et al., 2007; Buchan et al., 2014, 2015; Busquets-Vass et al., 2021; Calambokidis et al., 2009; LeDuc et al., 2017; Stafford, 2016; Stafford et al., 1999a, 1999b). Studies have shown that SEP and NEP blue whales are genetically differentiated (LeDuc et al., 2017). Stable isotope analyses indicate that SEP whales do not commonly forage in the northeastern Pacific, consistent with the population structure in the eastern Pacific (Busquets-Vass et al., 2021).

Blue whales migrate between high-latitude feeding areas, where they can find abundant euphausiids, and low-latitude breeding areas, likely used for mating and giving birth (Lockyer & Brown, 1981). However, no specific breeding areas have yet been identified. The Northeast and Southeast Pacific populations use the tropical water of the Eastern Pacific region widely for wintering and feeding. Reilly and Thayer (1990) showed evidence of the year-round presence of blue whales in the ETP. Indeed, the Galapagos Archipelago and the Costa Rica Thermal Dome are important feeding grounds for both blue whale populations (Palacios & Cantor, 2023; Reilly & Thayer, 1990). These areas also have high productivity and upwelling and serve as whale wintering and calving grounds (Busquets-Vass et al., 2021; Croll et al., 2005; LeDuc et al., 2017; Matteson, 2009; Pardo et al., 2015; Reilly & Thayer, 1990; Sears et al., 2013). Although relatively limited, there is circumstantial evidence of connections between the two populations in the Galapagos Archipelago and the Costa Rica Thermal Dome (Denkinger et al., 2023; Mate et al., 1999; Reilly & Thayer, 1990). Genetic studies (LeDuc et al., 2017) and photo identification (Denkinger et al., 2023) have shown that some of the blue whales in the Galapagos Archipelago are related to the NEP and SEP populations. Meanwhile, satellite tracking data (Mate et al., 1999) have shown that whales from NEP use the Costa Rica Thermal Dome. In the Costa Rica Thermal Dome, several cetacean species are supported by a standing stock of euphausiid prey, and a maximum chlorophyll concentration, which spans from May to September (Fiedler & Talley, 2006). Equatorial upwelling in the Galapagos Archipelago is most intense in the western region, where blue whales can find the euphausiid *Nictophanes simplex* (Palacios, 1999). Both tropical areas are likely breeding–feeding or calving grounds with potentially permanent or resident populations (Calambokidis & Barlow, 2004; Denkinger et al., 2023). However, there is insufficient research to determine how blue whales respond to environmental factors during migration.

Hence, studying blue whale population movement behavior is essential to understanding their ecological dynamics. In this study, we analyzed the trajectory of a satellite-tagged blue whale while feeding in the Galapagos Archipelago (Ecuador) during the shift from austral winter to summer. We analyzed the movement behavior in relation to various environmental variables.

A blue whale of unknown sex, approximately 18 m long, was tagged on October 3, 2021, between Cape Douglas and Espinoza Point on the northwest side of Fernandina Island, Galapagos Archipelago. A Wildlife Computers satellite transmitter model SPOT-372A was used (Wildlife Computers, Redmond, WA, USA). The tag model had a battery life of 540 days, assuming 250 Argos transmissions per day. The factory transmitters were a stainless-steel tube case that was 293 mm in length and 24 mm in diameter and weighed 390 g, coupled to a stainless-steel spear with a 3 cm triangular double-edged blade tip containing three pairs of 5 cm barbs placed at 90° to each other. The whale was tagged from a 5 m long fiberglass-hull inflatable boat at 2–4 m. Tags were deployed using an ARTS pneumatic line-thrower (Restech Inc., Bodø, Norway) coupled to a LK carrier developed by LKARTS-Norway. A detailed description of the tagging procedure is provided elsewhere (Guzman et al., 2013). The tag was attached to the whale approximately 2 m upfront of the dorsal fin on the left side. The tags were chemically sterilized, and plastic wrapped in the laboratory. In the field, the tag/spear was sprayed with Neomycin Sulfate–Clostebol Acetato (Neobol®) before deployment. The Animal Care and Use Committee of the Smithsonian Tropical Research Institute approved the procedure.

To maximize battery life, transmitters were programmed to limit transmissions to a time block from 01:00 to 22:00 h every 2 days and to slow the repetition rate after 10 consecutive dry transmissions. The tag-derived positions from Argos satellite location classes 3, 2, 1, 0, A, and B were used, with the range of errors in accuracy estimated at between 150 m and 5 km radius for plotting general filtered whale movements (Douglas et al., 2012; Guzman & Félix, 2017; Vincent et al., 2002). Raw data were plotted to evaluate transmission gaps (sensu Hearn et al., 2013) with a histogram of transmission quality and distribution of transmission time throughout the day. Raw transmissions were filtered to avoid data with unrealistic traveling speeds faster than 3 m s^{-1} (Hucke-Gaete et al., 2018), and transmissions occurring on land and with ARGOS quality "z."

The filtered transmissions were modeled with a Bayesian state–space random walk model (BSAM). This model estimated the animal movement track based on ARGOS satellite data error and was designed for transmissions that occur irregularly in time (Jonsen et al., 2005). The BSAM was run using the "fit_ssm" function from the bsam R software package (Jonsen, 2016). The model was set to two-time steps per day (tstep = 0.50), a thinning of 10 to minimize within-chain sample autocorrelation, and a span of 0.2 for the degree of smoothing. The estimated locations based on BSAM results were modeled with a hidden Markov model (HMM) to identify different behavioral states and correlate them to environmental variables. The HMM model was run using the function "fitHMM" available in the R package "moveHMM" (Michelot et al., 2016). The initial values were set to 60 ± 10 km for migratory behavior, 20 ± 10 km for foraging behavior, and π to 0 for the turning angle. The daily sea surface temperature, 8-day composite chlorophyll-a concentration, and 14-day composite productivity were used as model covariates. They were

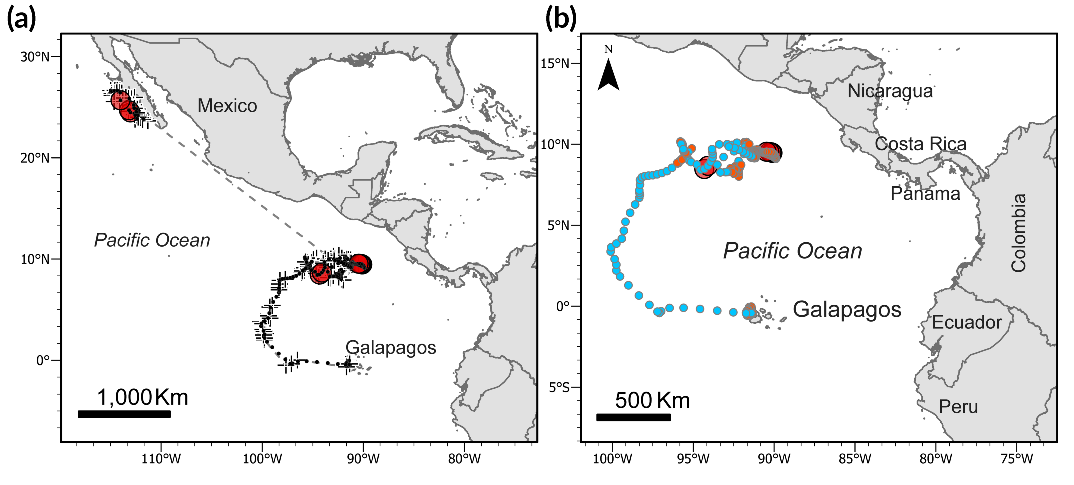

FIGURE 1 (a) Original transmitted blue whale locations (crosses), Bayesian state–space random walk model (BSAM) estimated locations (black dots), and locations that occurred within an eddy (red circles). (b) Hidden Markov model (HMM) behavioral state (blue = migration, orange = foraging) and location that occurred within an eddy (red circles).

obtained from NOAA's Environmental Research Division ERDDAP server (NOAA ERDDAP, 2023). Temporal and spatial pairing between estimated locations and environmental data was performed using the R software "xtracto" function in the "xtractomatic" package (Mendelssohn, 2018). The estimated locations were superimposed in time and space with the occurrence of eddies obtained from Mesoscale Eddy Trajectories Atlas (SSALTO/DUACS, 2023). All analyses were conducted using R software version 3.4.4 (R Core Team R, 2018), and the data were visualized in ArcGIS Pro V10.

A total of 683 transmissions with 354 Argos locations were used to model the blue whale track (Table S1). Transmission quality varied and was distributed throughout the day (Figures S1 and S2). A substantial transmission gap of nearly 6 months (January 14 to July 2, 2022) occurred between the Costa Rica Thermal Dome and the FTBCP. This cannot be explained as detachment or "floating tag transmissions" (sensu Hearn et al., 2013) due to the approximately 400 g weight of the tag steel case. The blue whale's lack of satellite location records during the gap segment may be attributed to the sea conditions, such as waves and winds interfering with the transmissions.

The tag transmitted for 250 days, and the track was divided into two segments. The first segment was from the tagging site at Galapagos Archipelago on October 4, 2021, to the end of the long migration to the Costa Rica Thermal Dome on January 13, 2022. The second segment was from the start of the second long migration from the Costa Rica Thermal Dome on January 14, 2022 to the FTBCP (July 2, 2022), until its last transmission on July 12, 2022. Two BSAM models were run, one for each track segment, estimating 227 locations with a maximum of two locations per day (Figure 1a).

The HMM model was only run for the first segment of the track from the tagging location at Galapagos Archipelago to the start of the long migration in the Costa Rica Thermal Dome. During this time, the HMM model identified 80 locations (39%) where the whale was recorded in a migratory behavioral state (step length 45.0 ± 25), and 124 (61%) locations where the whale was recorded in a foraging behavioral state (step length 13.3 ± 1.2) maximum log-likelihood: −1059.77 (Figure 1b).

Foraging behavior was identified in Galapagos Archipelago, the Costa Rica Thermal Dome, and when the whale arrived in the FTBCP. It occurred in environmental conditions with significantly lower temperatures ($p < .05$), higher productivity ($p < .05$), and chlorophyll concentration levels ($p < .05$) (Table 1, Figure 2).

Nine locations were estimated within an eddy (Figure 1). When the whale was foraging at the Costa Rica Thermal Dome, it stayed inside a cyclonic eddy for at least 2 days (November 20 and 21, 2021). It then remained in an anticyclonic eddy for at least 2 days (December 28 and 29, 2021). At the end of the long migration to the FTBCP, the whale encountered a cyclonic and an anticyclonic eddy (Figure 1).

Our study provides behavioral insights into a single blue whale traveling from the Galapagos Archipelago to the FTBCP. Previous research has documented this migratory route (Calambokidis & Barlow, 2004; Denkinger et al., 2023; Reilly & Thayer, 1990). However, genetic studies indicated limited genetic exchange between the two populations (LeDuc et al., 2017; Torres-Florez et al., 2015). Nonetheless, blue whales have been sighted in the Galapagos Archipelago during the austral summer and winter, with one individual appearing in both the Galapagos Archipelago and the Costa Rica Thermal Dome in different years and months (Denkinger et al., 2023).

TABLE 1 Mean ± SE of environmental variables for each behavioral state.

Environmental variable	Foraging 1 Galapagos Archipelago	Foraging 2 Costa Rica thermal dome	Foraging 3 FTBCP	Foraging All	Migrating and transmitting
Sea surface temperature	20.8 ± 0.1	26.4 ± 0.1	20.6 ± 0.27	24.6 ± 0.23	26.3 ± 0.2
Chlorophyll	0.5 ± 0.03	0.42 ± 0.02	0.81 ± 0.3	0.49 ± 0.055	0.283 ± 0.01
Productivity	945.6 ± 26.7	646.6 ± 15.79	11,228 ± 184	777.3 ± 32.9	530.2 ± 21.29

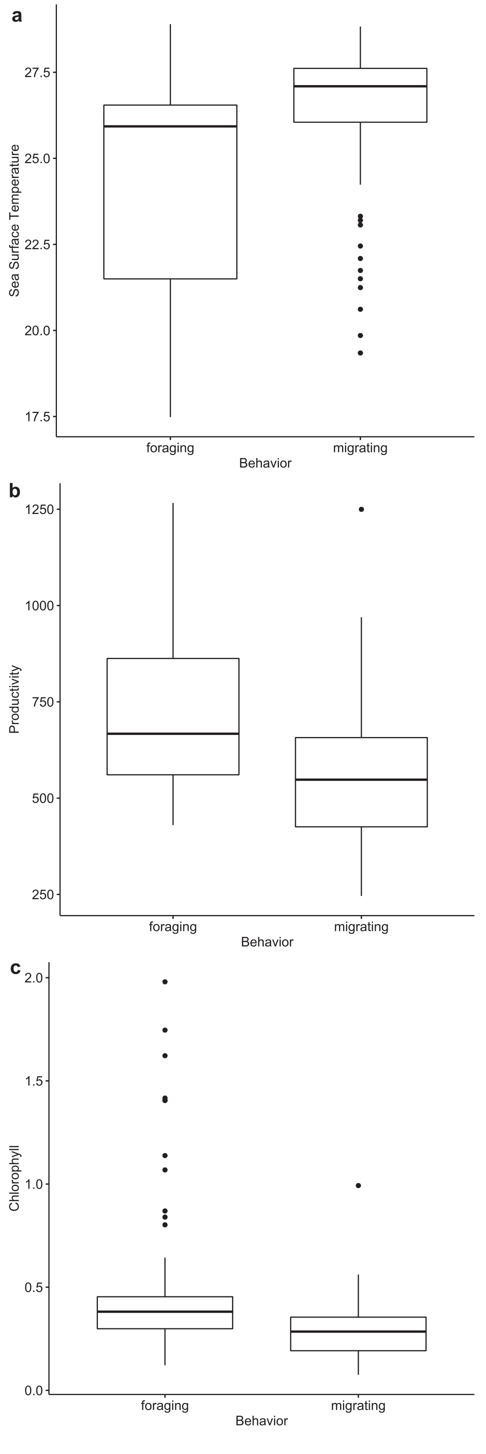

FIGURE 2 Measures of (a) sea surface temperature, (b) productivity, and (c) chlorophyll concentration levels for each behavior state.

Our findings indicate that blue whales engage in foraging behavior in areas with higher productivity, higher chlorophyll concentration levels, and lower temperatures. This has reinforced the importance of these oceanographic features for the species' regional home range. These findings align with those of previous research studies, which established a correlation between the foraging behavior of blue whales and specific oceanographic features (Abrahms et al., 2019; Matteson, 2009). Blue whales prefer areas with elevated chlorophyll concentrations, which is critical to their foraging success. Consequently, the Galapagos Archipelago and the Costa Rica Thermal Dome are crucial for the species since both these areas are feeding and calving locations (Blevins et al., 2022).

Eddies significantly influence the movements of whales. Humpback whales preferred foraging within and around eddies (Bedriñana-Romano et al., 2022). Eddies can affect the concentration of krill, the primary food source of blue whales, and primary productivity in areas where these whales feed. In the North Pacific, where blue whales feed during summer, the eddies positively impact krill concentration because the currents surrounding them tend to be colder and richer in nutrients. This supports the growth of phytoplankton and zooplankton at the base of the food chain (Scales et al., 2014).

Moreover, blue whales primarily aggregate in areas of high primary productivity, coinciding with the presence of euphausiid biomass as their preferred prey (Burtenshaw et al., 2004). Acoustic and satellite records have shown that NEP whales migrate northward along the Oregon and Washington coasts to a secondary feeding area with high primary productivity off Vancouver Island in the autumn. Marine eddies, particularly those generated by convergent coastal currents, contribute to the increase in nutrient load and primary productivity in the region (DiGiacoma & Holt, 2001). Our findings support the relationship between blue whales and the presence of marine eddies as key habitats for their feeding behavior and seasonal displacement in the Northeast Pacific.

Eddies formed in the Costa Rica Thermal Dome and the FTBCP area are important feeding grounds for these whales. The study findings suggest that eddies significantly impact blue whale populations' feeding habits and provide valuable insights into how these cetaceans interact with their environment.

Overall, our research findings highlight that conservation efforts for blue whales should consider the importance of feeding and potential breeding grounds in the Galapagos Archipelago and the Costa Rica Thermal Dome. Palacios and Cantor (2023) emphasized the imperative to enhance our understanding of blue whale's migration routes, home ranges, and local and regional movements through satellite tagging in the Galapagos Archipelago. Our study addresses this need and provides preliminary migratory information to support their protection. However, we recognize that conclusions about population connectivity cannot be drawn from the movement of a single tagged individual.

AUTHOR CONTRIBUTIONS

Hector M. Guman: Conceptualization; investigation; methodology; project administration; resources; writing – original draft; writing – review and editing. **Rocío M. Estévez:** Investigation; methodology; writing – original draft; writing – review and editing.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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