First Description of Migratory Behavior of Humpback Whales From an Antarctic Feeding Ground to a Tropical Breeding Ground

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ABSTRACT

Background: Despite exhibiting one of the longest migrations in the world, half of the humpback whale migratory cycle has remained unexamined; until this point, no study has provided a continuous description of humpback whale migratory behavior from a feeding ground to a breeding ground. We present new information on the satellite derived offshore migratory movements of 16 humpback whales from Antarctic feeding grounds to South American breeding grounds. Satellite locations were used to demonstrate migratory corridors, while the impact of departure date on migration speed was assessed using a linear regression, and a Bayesian hierarchical state-space animal movement model was utilized to investigate the presence of feeding behavior en route.

Results: 35,642 Argos locations from 16 tagged whales from 2012-2017 were collected. The 16 whales were tracked for an average of 38.5 days of migration (range 10-151 days). The length of individually derived tracks ranged from 645–6,381 km. Humpbacks were widely dispersed geographically during the initial and middle stages of their migration but convened in two bottleneck regions near the southernmost point of Chile as well as Peru's Illescas Peninsula. The state space model found almost no instances of ARS, a proxy for feeding behavior, along the migratory route. The linear regression assessing whether departure date affected migration speed found suggestive but inconclusive support for a positive trend between the two variables. No clear stratification by sex or reproductive status, either in migration speed, departure date, or route choice, was found.

Conclusions: Southern hemisphere humpback whale populations are recovering quickly from intense commercial whaling and, around the Antarctic Peninsula, are doing so in the face of a rapidly changing environment. The current lack of scientific knowledge on marine mammal migration is a major barrier to cetacean conservation. This multi-year study sets a baseline against which the effects of climate change on humpback whales can be studied across years and

conditions and provides an excellent starting point for the investigation into humpback whale migration.

KEYWORDS

Humpback migration, animal movement models, HSSM, Animal Ecology, Conservation, Humpback whales, Antarctica

INTRODUCTION

Humpback whale (*Megaptera novaeangliae)* migrations, with recorded one-way distances of up to 8461km, are part of an annual cycle consisting of journeys between tropical calving grounds in winter and high latitude feeding grounds in summer (1,2). Baleen whale migrations are considered a response to the need to feed in cold waters and reproduce in warm waters (1,2). Currently, NOAA recognizes 14 distinct populations of humpback whales, based on breeding ground location, with seven in the Southern Hemisphere (3). These seven distinct population segments (DPS) are found distributed around lower latitude coastal regions in the Atlantic, Indian, and Pacific Ocean and rely on highly productive seasonal habitats in the Antarctic, with several populations utilizing the Western Antarctic Peninsula, one of the most rapidly warming areas in the world, as their foraging ground (4–6).

Humpback whales appear to generally remain loyal to their natal grounds and return for breeding and calving purposes year after year. In the foraging grounds, the whales disperse somewhat more broadly than in the breeding grounds, but with only limited overlap and intermingling between populations that breed in different geographic areas (7). The population breeding off the western coast of South America is the Southeastern Pacific DPS. Historically, these animals have been recorded crossing the equator into waters off Colombia, but in recent years, individuals from the Southeastern Pacific DPS have also been found further north off Panama and Costa Rica, in regions frequented by northern humpback populations (2,8). Breeding behavior has been observed as early as June, peaking between August and October. Specific calving sites have been documented in the nearshore waters off Colombia and Ecuador (9). A 2020 study noted that the average date of arrival for individuals of the Southeastern DPS in the breeding grounds in Gorgona National Park, Columbia, was the last week of May (10). As of 2011, abundance estimates for the Southeastern Pacific DPS were around 6,500 (11).

Migratory Behavior

Despite the humpback whale's status as one of the longest migrating species on the planet, little concrete information is known about their migration. As with most migratory species, the difficulty of consistently tracking migratory behaviors means that research on humpback whales has historically been biased toward the breeding and foraging areas. No published study has examined the day to day movements of humpback whales on their migration from foraging to breeding grounds — the only knowledge regarding this leg of migration inferred from historical whaling and sighting data. More information exists for the journey from breeding to foraging grounds, but most of this knowledge is from historical whaling data, with limited contributions from a handful of recent small-scale studies.

Estimation of rate of movement from whaling records indicated relatively constant mean southbound to northbound migratory speeds of 15° per month, and an approximate Southern Hemisphere migration duration of two to four months (7,12). Aerial observations of individuals found substantial individual variation in migration rates over short periods and recorded speeds ranging from 4.8 to 13 km h^{-1} over the course of a few hours (7). Recent satellite tag studies of longer duration have recorded mean migration rates of 4.21 ± 1.3 km·h^{-1} for North Atlantic humpback whales migrating from the Antillean Island chain to Canada, the Gulf of Maine, and the Eastern North Atlantic (13), 4.5 km·h^{-1} for humpback whales traveling from Hawaiʻi to Alaska (14), and 3.83 and 3.48 km·h^{-1} for humpbacks migrating from Brazil to Antarctica and South Georgia (15,16).

It is thought that migratory timing and route are heavily influenced by sex, reproductive status, and age of the animals (7,17–21). Felix and Guzman found that mothers with calves preferred a coastal route, while single adults tended more towards open waters (21). Historical whaling data for all southern hemisphere postwar land whaling stations indicates that females at the end of lactation are the earliest group to leave the Antarctic, followed by immature whales, mature males, resting females, and pregnant females (with start dates of twelve, twenty, twenty-three, and thirty-one days later, respectively). Migratory triggers are unknown but are thought to be environmental - such as daylight hours, sea ice formation, and prey abundance – or inherently biological – such as hormone or body condition-based (1,7). Dawbin hypothesized that the most likely environmental trigger was daylight and that the entire cycle depended on seasonal changes in Antarctic waters, as there is little fluctuation in daylight and temperature in the temperate breeding grounds (7). Since departure dates from foraging grounds and arrival into breeding grounds reported from whaling records and photo IDs (7,20) are segregated along sex, reproductive status, and age classes, it seems reasonable to hypothesize that marked differences in average migration speed among groups exist. However, to our knowledge, this has only been investigated in looking at females with calves vs single adults (13,21).

Humpback whales rarely feed on their migratory routes, instead subsisting on stored fat reserves accumulated in the foraging grounds (7,18). Dawbin (1966)'s investigation of thousands of historical whaling records indicated that whales caught in warm waters had empty stomachs. However, recent studies of humpback migration of various DPS's from breeding to foraging grounds have shown that some animals do feed along the migration route (13,21–28). The extent to which these feeding bouts occur is unclear.

Only one study investigating humpback whale migration has looked specifically at the Southeastern Pacific DPS. Felix and Guzman (2014) compiled opportunistic sightings of humpback whales from 1994 to 2012 along the coast of Chile and Peru from the SIBIMAP database and deployed satellite tags on animals in waters off of Ecuador to track migration. The SIBIMAP database showed evidence of a coastal migration route, which Felix and Guzman suggested might be used by females with calves, while the satellite tags procured partial migration tracks for 6 animals on their southbound migration. Unfortunately, the majority of the tags ceased transmissions before departing Peru. While one animal was tracked relatively consistently to halfway down Chile, complete migration tracks were not available for any animals and partial migration tracks represented a very abbreviated portion of migration (21). Based on their average speed estimates (4.05 km h^{-1}) from these whales, Felix and Guzman suggested that migration of single whales in the Southeastern Pacific DPS would last on average 66.4 d (SD = 13.25) if using the offshore route and 70.8 d (SD = 14.12) along the coastal route (21).

Migratory Species Concerns

Generally, animals that exhibit long-distance migrations are vulnerable to climate change

(1,29), and gaps in scientific knowledge on marine mammal migration have been cited as a significant barrier to the conservation of cetacean populations (1,29,30). Without complete knowledge of the annual movements, including physical migratory routes and migratory connectivity amongst populations or management units, conservation measures may be deployed in wrong place, time, or for the wrong purpose (31). Indeed, addressing gaps in knowledge regarding migrations from feeding to breeding regions as climate-driven changes in feeding ground environments become more likely is crucial, as these changes can have significant effects on the timing of arrival of individuals in breeding areas and therefore their reproductive success (7,29). However, despite, or because of, having one of the longest migrations in the world, half of the humpback whale migratory cycle has remained unexamined; not a single study has investigated the behavior and route of whales during migration from foraging to breeding grounds.

The primary goal of this research is to use satellite telemetry and state-space animal movement models to explore gaps in our knowledge regarding the different parameters - speed, migratory triggers, migratory duration, migratory timing, migratory foraging behavior, and migratory sex and reproductive segregation- and geographic routes of the migratory pathways of the humpback whale by providing a first look at the Southeastern DPS’s migratory journey from the Antarctic foraging ground to a tropical breeding ground.

METHODS

Tag Deployment

In 2012, 2013, 2015, 2016, 2017, and 2018, we deployed 62 satellite-linked transmitting tags onto humpback whales in nearshore waters around the WAP from January to May. These animals were from the Southeastern Pacific DPS, which breeds off the Western coast of South and Central America (3). Wildlife Computers (Redmond, WA, USA) SPOT5, SPOT 6, and MARK 10 Platform Transmitting Terminals (PTTs) were utilized and tagging was limited to adult-sized animals (>12m). Each tag was contained in a sterilized housing and was anchored in the tissue beneath the blubber near the dorsal with stainless steel barbs, with the transmitting antenna remaining free outside of the animal (5). Tags were deployed from a range of 3-10 m from a Zodiac Mark V or a Solas ridged-hulled inflatable boat using an ARTS Whale Tagging PLT compressed air system (32).

Satellite transmissions were activated via a salt-water switch, and locations of the whales were obtained through the Argos System of polar-orbiting satellites (Argos, 1990). Tags were programmed to transmit during specific hours and days. Since the tags were also being utilized for other year specific projects, duty cycling varied across years. In 2012, tags were programmed to transmit between 00:00–04:00 and 12:00–16:00 GMT. In 2013, tags were programmed to duty cycle 3 hours on, 3 hours off, except for Sirtrack tags (identified by PTT IDs starting with 113), which duty-cycled at 6 hours on/6 hours off. The 2015 tags were programmed to transmit continuously, while in 2016 tags, some tags were programmed to transmit continuously, while three were programmed to duty cycle at 1 day on, 4 days off. Tags deployed in 2017 were programmed to duty cycle 12 hr on, 12 hr off.

Demographic Information

Skin and blubber biopsy samples were obtained from tagged whales whenever possible using standardized remote biopsy techniques (33). Samples were obtained from the upper flank below the dorsal fin (34). Blubber samples were used to provide life history and demographic information as covariates in models assessing migratory behavior. To determine the sex of biopsied whales, genomic DNA was extracted from these samples using a proteinase K digestion followed by a standard phenol-chloroform extraction method (35). To assign pregnancy within sampled females, progesterone, a lipophilic steroid hormone, was quantified from a sub-sample of blubber using a progesterone enzyme immunoassay (36). Pregnancy was then assigned by comparing the measured progesterone concentrations across a pre-validated binary logistic model developed from humpbacks of known pregnancy status sampled in the Gulf of Maine (36).

Data Processing

R (version 3.4.3, R Core Team, 2017) was used to filter raw observations from the satellite tags to remove points without location data, points with Argos error quality class Z (invalid location), and points with duplicate timestamps. In addition, clearly implausible points (e.g. on land or hundreds to thousands of kilometers from expected location) were visually inspected and removed. Maps of the animals' tracks were plotted using ggmap (37) in R (R Core Team, 2017).

Whales were determined to be migrating when they started a northward journey from the WAP without any significant or lasting return movements. The date of departure for each whale was determined visually by graphing latitude as a function of Julian day and assessing at which point the animal moved northward without any return movements. The static nature of the environmental data combined with the mobile nature of the humpback data's mobile nature precluded us from statistically evaluating the potential environmental trigger of light. Instead, we matched daylight hours in the WAP to tagging data and graphed this against the animals' latitudes in the same fashion that we determined departure dates.

To determine rates of migration, speeds on the migratory route were calculated with data corrected for location error with the simple default Hierarchical State Space Movement Model with a 12-hour timestep fitted in R using BSAM (Jonsen 2016, R Core Team 2017). Rate was the distance of the linear vector between 12-hour timestep locations. Distances between locations were calculated using the function distanceTrack from the Argosfilter package (Freitas 2012, R Core Team 2017). Average rates were calculated as the average of all 12-hour timestep rates for each animal.

As coastal nations have exclusive sovereign rights for the purpose of conserving and managing marine species within the bounds of their jurisdiction (38), the amount of time the migrators spent within EEZ boundaries was calculated by summing the number of regular timestep observations from the BSAM model within each country's national waters. While the satellite tags themselves did not collect data with great regularity, the BSAM model calculates true unobserved locations along regular time intervals from available data, and these intervals were utilized for EEZ analysis.

There were a number of locations where the tracks converged and allowed for a logical division of the migration corridor into three spatial sections, "*WAP-Cape Horn* (Drake passage)," "*Cape Horn* (Chile) – *Peninsula de Paracas* (Peru)," and *" Peninsula de Paracas* (Peru)- *Zona Reserverda Illescas* (Peru)." Since not all tags transmitted for the entire migratory journey, these 3 discrete spatial sections allowed for a more valid estimation and comparison of speeds in some sections along the journey. Average migratory speed was calculated for each section, as well as for the breeding area. As humpback whales leave the Antarctic peninsula at different times, a simple linear regression was performed using Julian day (predictor variable) and speed (response variable) to investigate whether the timing of migration affected the speed at which the animal migrates. Because very few tags transmitted to completion of migration, we chose to look at speed in the first migratory section from the WAP to Cape Horn (latitude = -55.9833). All data above -55.9833, as well as all animals that did not reach -55.9833, were filtered out, and the average speed over the section was calculated for each remaining individual. To correct for issues of heteroskedasticity, speed was transformed with a log function, and the residual plot was assessed for any obvious signs of nonlinearity and heteroskedasticity. A QQ plot was used to check for the normality of residuals, and the data were tested for influential data points. To determine whether sex and reproductive status had an impact on speed, two Welch's ANOVA tests were performed on the same speed data, using sex (male/female) as the predictor variable in the first test, and sex/reproductive status as the predictor variable in the second test (male, female-pregnant, female-not pregnant). For all tests, P-values <.01 indicated strong support, p-values between .01 and .1 offered suggestive, but inconclusive support, and p-values>.1 indicated no support (39,40).

Discrete behavioral modes were determined by manually constructed hierarchical Bayesian state-space movement models. This was a departure from the simpler models use to assess true locations, as it allowed for differences in movement norms associated with behavioral states depending on whether the animals were in the foraging grounds, breeding grounds, or migratory route. This model associated spatial patterns of animal movement with predicted behavioral states while simultaneously accounting for and correcting the significant error inherent in Argos Satellite location data.

We used a discrete-time dynamic correlated random walk model following Jonsen et al. (2005) and Bestley et al. (2013), where each movement stemmed from either a 'traveling or 'area-restricted search' (ARS) state (41,42). When humpback whales encounter sufficient prey areas, they often engage in ARS by decreasing their travel speeds and increasing their turning angle radius and frequency; consequently ARS behavior is defined as shorter step lengths with larger and more variable turning angles. The terminology ARS is used instead of foraging, as whales may also be engaging in other behaviors such as resting and breeding in this state and our measurements are not based off of a direct measure of feeding but rather use movement metrics. In humpback whales this spatial signature may persist for up to several days in one location (43). The traveling state, which is thought to occur when the animals are either actively migrating or located in habitats unsuitable for foraging, is characterized by fast travel rates and infrequent and small turning angles; in a state-space model this behavior is recognized by the presence of long step lengths with small and infrequent turning angle radius.

The first component of the state space model was the process model, which estimates animal behavior with a first-difference correlated random walk (42). The process model took the form:

$$d_t \sim N_2[\gamma_{bt} T(\theta_{bt}) d_{t-1}, \Sigma]$$

where d_t is the difference between true unobserved locations and coordinate vectors x_t and xt_{-1} and N_2 is a bivariate normal distribution with covariance matrix Σ, where σ_{lon}^2 is the process variance in longitude, σ_{lat}^2 is the process variance in latitude, and ρ is the correlation coefficient. γ is the autocorrelation of direction and speed between consecutive locations, with a value of between 0 and 1 (γ=0 would signal a simple random walk). b_t is an index used to denote behavioral mode, e.g. ARS or traveling. T(θ) is the transition matrix with mean turning angle θ which provides the rotation required to move between d_t and d_{t-1}.

$$T(\theta) = \begin{pmatrix} cos\theta & -sin\theta \\ sin\theta & cos\theta \end{pmatrix}$$

$$\Sigma = \begin{pmatrix} \sigma_{lon}^2 & \rho\sigma_{lon}\sigma_{lat} \\ \rho\sigma_{lat}\sigma_{lon} & \sigma_{lat}^2 \end{pmatrix}$$

This model is considered a switching model in the vein of Jonsen, 2005, and a separate process model was run for each of the two behavioral states. As we are including two behavioral states, there were four possible transitions, two of which are calculated: α_1, the probability of remaining traveling at time t if traveling at time t-1, and α_2 , the probability of traveling at time t given foraging at time t-1.

The second component of the state space model was the measurement equation or observation model. This equation calculated the temporally regular unobservable "true" locations of the animals needed for the process equation from the error-prone and temporally irregular Argos location observations:

$$y_{t,i} = (1 - j_i)x_{t-1} + j_i\, x_t + \varepsilon_t$$

where i is an index for locations between times t and t+1, and j_i represents the proportion of the timestep at which the i^{th} observation is made. X_t is the unobserved true location of the animal at time t, $y_{t,i}$ is the i^{th} observed position during the regular time interval t-1 to t, and ε_t is a random variable representing the error in the Argos locations. The variance in Argos observations was fixed for each Argos class error as demonstrated in Jonsen et al. 2005. Various classes of Argos errors are strongly non-gaussian, and are thus traditionally calculated with t distributions (42). However, this can make the model so computationally complex that it cannot converge. This occurred with our models, and to counter this we removed any extreme and implausible locations from our data using the Argosfilter package in R (Freitas 2012, R Core Team 2017), and then ran the observation model with a multivariate normal distribution as done in Weinstein et al. (2017a, 2017b) (4,5). We used a timestep of 12 hours, which we deemed to be a conservative balance between taking into account gaps in the data as well as ensuring behaviors did not change between locations. Although only two behavioral states were modelled, the means of the MCMC samples provided continuous values from 1-2. A mean behavioral mode of <1.25 was considered traveling, whereas a value > 1.75 represented Area-Restricted Search. Estimations between 1.25 and 1.75 were treated as uncertain (44).

To help address the inconsistent transmitting nature and duty cycling of the tags as much as possible, a joint estimation, in which estimation of behavioral states is conducted jointly across multiple animal movement datasets rather than individuals, was done. This method assumes that movement parameters may differ among individuals but are drawn from the same set of distributions, and allows the model to estimate parameters and state variables with greater precision by assuming a general range in value for all animals to borrow strength across multiple datasets, thus filling in for any animals with suboptimal data (45).

Priors for γ and θ were set to reflect the assumptions that the travelling state would have greater autocorrelation and lower mean turning angles than the ARS state. To allow for variance in transition probability and behavioral state characteristics as the animals switched from feeding, to migratory, and then breeding areas, the variable Month was set as a random variable, allowing parameters for transition probability and autocorrelation to come from different probability distributions each month. This is different than a traditional BSAM model and important as it allowed for potential differences in spatial characteristics of behaviors - ARS in foraging and breeding grounds may present differently than ARS on the migratory route. This model was fitted in R using the software JAGS (Plummer, 2013) and the R rjags package (Plummer, 2016; R Core Team 2017). Where a gap of >1 day existed in the raw satellite transmission data the individual track was split and run as separate segments to avoid interpolating over long periods. Each model was run with two MCMC chains, consisting of 270,000 iterations each, the first 250,000 discarded as burn-in. The remaining 20,000 iterations were thinned, retaining every 8th sample to reduce autocorrelation and computational burden. The goodness of fit and chain convergence were assessed using the Gelman–Rubin statistic, and parameters with Gelman- Rubin (R) of less than 1.1 were considered converged as outlined by Gelman and Hill (2006) (46). Runs were conducted on the UCSC Hummingbird computational cluster with chains running in parallel.

RESULTS

Tag Deployment

Between 2012 and 2018, 16 of the 62 animals tagged in the WAP commenced migration, transmitting a total of 35,642 locations, with 5 tags transmitting locations to the breeding grounds. The transmission time of these tags ranged between 42 and 266 days (mean=108 d, sd=63.7). Start dates varied greatly, with departure dates ranging from 3/16 to 7/15 (Table 1). Animals with tags that continued to transmit to the completion of migration reached the breeding grounds (designated as Zona Reserverda Illescas, Peru), as early as June 19th, and as late as August 8th (Table 1).

[INSERT TABLE 1]

Demographic information

Of the 16 animals that initiated migration, four were pregnant females, four were resting females (one juvenile), four were males, and four did not have biopsy samples and were thus of unknown sex. None of the animals were accompanied by calves at the time of tagging.

Individual data analyses

The start of migration, end of migration tracked, duration of migration tracked, number of transmissions during migration, and length of migration tracked were found for each animal (Table 1). The animals showed differences in regards to their migratory speeds, the start of migration, and geographic routes. A summary of each of the 16 animals' individual movements is provided in Table 1, and their routes can be seen in Figures 1 & 2.

Migratory Route findings and patterns

Of the 16 migrators, five (PTT ID= 112699, 121210, 123232, 131130, and 166123) made it all the way to the breeding grounds, representing the first complete migratory tracks of animals in the Southeastern Pacific DPS. The animals all used routes with coastal and open water segments to migrate up the Western side of South America (Figures 1-2). One animal had a particularly unusual trajectory – the tag on 123232 ceased transmissions entirely during a large part of the northward migration, but then resumed and recorded the entire southward migration until October. By that time, the whale had returned to the Antarctic foraging grounds. This represents the first satellite tagging of an animal on both legs of migration. Multiple whales (PTT IDs=131130, 123232, 121210, and 166123) crossed the equator and one ventured as far as 8.94 degrees north (PTT=131130). Interestingly, no clear stratification of route choice by sex or reproductive status was found (Figure 1C).

Whales left from numerous locations on the peninsula and remained relatively dispersed in the Drake Passage (Figures 1 and 2). Many of the animals then passed close to South America's western tip, resulting in a bottleneck that lasted from the tip of the continent until approximately -47 ° in the region of Chile's Parque Nacional Laguna San Rafael. The whales' trajectories then spread out again and ventured into deeper waters until hitting the coast near Peru's Peninsula de Paracas, at which point they migrated through a narrow corridor near the coast and up through the breeding area. Four whales, (PTT= 131136 -2016, sex unknown; PTT=166126 - 2017, juvenile resting female; PTT=166125 – 2017, pregnant female; PTT= 166122 – 2017, pregnant female), diverged from these trends, choosing deep water routes in areas where the rest of the whales stayed in coastal areas.

The average amount of time spent in national waters for the 5 animals with complete migration tracks (PTT ID= 112699, 121210, 123232, 131130, and 166123) was 72% of total migration time (Table 2).

The average speed for all the animals was 5.88 km hr^{-1} (SD=1.31). In general, average speeds followed a slow-fast-slow trajectory by track segment, with the average speed calculated for the animals highest during the middle section of migration from Cape Horn to Peninsula de Paracas, and lowest in the breeding area (Table 1, Figure 3). 15 migrators had tracks reaching to Cape Horn, and their average speeds over the distance can be seen in Table 1. The regression results showed suggestive but inconclusive support for the hypothesis that whales have faster migratory speeds the later they leave the peninsula ($F(1,13)= 4.117$, $p=.06346$). There was no relationship between speed and sex ($F(2, 3.11=0.003$, $p=.96)$) or speed and sex / reproductive status ($F(2, 4.8=.37$, $p=.71)$).

Table 2: Percentage of migratory time in national waters off the coast of South America by satellite tagged humpback whales. Only the 5 whales with complete migration tracks as generated by BSAM were included.

Animal ID	Chile (%)	Peru (%)	Ecuador (%)	Total Migratory Route in National Waters (%)	Migratory Route in International Waters (%)
112699	48%	28%	3%	79%	21%
121210	39%	21%	4%	64%	36%
123232	39%	25%	6%	70%	30%
131130	53%	17%	3%	73%	27%
166123	39%	30%	7%	75%	25%

The animals appeared to be almost exclusively traveling during their northward migration. Of the 4,230 behavioral points utilized by the model on the Northbound migratory route before Zona Reserverda Illescas, 3,875 were classified as Traveling, 294 as Unknown, and 61 (1%) as ARS. The 61 ARS locations all belonged to animal 123236 and occurred from March 23-26 around -66° W, -60° S in the Drake Passage. An additional 332 instances of ARS were observed in animal 123232 in the Drake passage on its southward return migration. From the movement patterns, it appears the animal may have already started its foraging season at this point but was kept further away from the peninsula as a result of sea ice extent (Figure 4). Unfortunately, not all the data were usable. The model required at least one transmission per timestep during three consecutive timesteps to create a track. This, combined with the varied nature of the duty cycling across the years as well as the inconsistent transmitting nature of the tags, resulted in a portion of the data being lost.

DISCUSSION

The results of our tracking analyses provide the first continuous description of humpback whale migratory behavior from a feeding to a breeding ground as well as the first complete migratory tracks of the Southeastern Pacific DPS. These humpback whales exhibited staggered departures from many locations along the WAP and embarked on northward migrations lasting between 41 and 54 days. The tagged individuals migrated at varying speeds, and a positive suggestive but inconclusive relationship between date of departure and speed indicates that animals leaving later may travel at faster speeds, potentially to make up for their later departure dates. Except for one animal in the Drake passage, ARS, which can be a proxy for foraging, did not occur on the northbound migratory route.

The telemetry data identified two previously undocumented geographic bottlenecks: the consolidation of the tracks starting at the coast of the Southern tip of Chile and stretching until the Parque Nacional Laguna San Rafael, as well as the portion of the annual cycle spanning the coastal areas from Peru's Peninsula de Paracas to the border between Columbia and Ecuador and into Panama (Figure 1B). Interestingly, the first bottleneck region lines up approximately with the Straits of Magellan and Northern Chilean Patagonia, two areas that have been suggested as alternative foraging grounds for animals in the Southeastern DPS; however, no instances of ARS were documented in these areas, nor did animals deviate from their northbound migration to enter the Straits of Magellan (47,48). It is worth noting that one individual recorded "Unknown" behavior near Northern Chilean Patagonia.

Our migratory tracks tentatively identify the area around Zona Reservada Illescas, Peru, as the start of the breeding area based on abrupt route change and the transition from transiting to ARS in animal PTT=123224. This delineation of the breeding ground is more in agreement with Guzman (21) than Rasmussen (2), which placed the border close to the equator in Salinas, Ecuador, more than 550 km away. Tagged whales in our study reached as far north as Panama, which was in agreement with Rasmussen's findings regarding the geographical extent of the breeding grounds.

One tagged whale, PTT 123232, provided information on the complete migratory cycle from the Antarctic to the tropical breeding ground and back to the Antarctic. While the tag stopped transmitting for a significant portion of the northward migration, this deployment represents the first tagged humpback to provide data for a continuous annual cycle. The southward route lined up closely with the northward route, indicating that humpbacks may use the same routes, regardless of migratory direction.

Interestingly, none of our migratory parameters lined up with one of the most touted characteristics of migration – segregation along sex, reproductive, and age classes. While our sample size was not large (n=16), it was much larger than most similar cetacean telemetry studies of migration, and the lack of stratification is notable. It may be possible that segregation by sex and reproductive status has been overemphasized in past literature, that this pattern varies by DPS and is not adhered to in the Southeastern Pacific DPS, or that there are additional parameters that have not been accounted for. Our sample's nature can also explain some of the discrepancies – Felix and Guzman (2014) looked only at southbound migration and hypothesized that the coastal route vs oceanic route differed by whether the animal was a single adult or mother with calf. By the time of the northbound migration, calves had already been weaned and none of our tagged females were accompanied by offspring; therefore, the lack of observed coastal route does not contradict their findings.

It is also of note that our findings seemingly oppose those of Avila et al (2020), which states that whale arrival in the breeding grounds is becoming consistently earlier, with an average arrival date of the last week of May (10). Of our 16 animals, 8 had not even commenced migration by the last week of May, let alone made it to the breeding grounds.

Our study supported Dawbin's (1966) conclusions on migratory foraging, which stated that the animals did not forage on their northward migration. While telemetry data cannot conclusively rule out foraging behavior, only 1% of our recorded locations on the migratory route indicated ARS and all of these points belonged to one animal and occurred in the Drake Passage. Without more detailed data (e.g. dive parameters) it would not be possible to determine if this ARS included actual feeding behavior versus the myriad other reasons that an animal may cease transiting for a short period of time. A few cases of behavior were classified as unknown on the route, but the majority of points in this category were found in the breeding or foraging areas. As previously stated, certain instances of feeding bouts have been recognized on the migratory route in recent years (13,21,23,25,27,49). However, all of these recorded instances have occurred while individuals were migrating from breeding to feeding grounds. It is possible that supplementary feeding is a phenomenon relegated only to the route from breeding to feeding grounds – perhaps because there is less of a definitive date that whales need to reach their destination by, or because energy stores are running low while on the journey from foraging to breeding grounds whales have just replenished their food stores.

The average migratory rate for our animals was 5.88 $km \cdot h^{-1} \pm 1.31$ and 5.88 $km \cdot h^{-1} \pm .59$ for the complete tracks of the 5 animals that completed migration. Our animals completed the migration in 41-54 days and traveled between 33°-43° per month. These speeds were significantly faster than Dawbin (1966), who recorded south to north speeds of 15°per month, with approximate migration durations of 60-120 days. They were slightly higher than previously recorded telemetry speeds of 4.04± 1.08 km·h^{-1} (21), 4.3 ± 1.2 km· h^{-1} (13), 4.5 km·h^{-1} (14), and 3.83 and 3.48 km·h^{-1} (15,16). It is possible that the whales in our study utilized coastal currents, such as the Humboldt Current, along the west coast of South America, to increase their traveling speeds without incurring additional energetic costs. It is also possible that the Southeastern Pacific DPS experiences slightly higher migratory speeds than other populations or that, alternatively, migratory rates in the direction of the breeding ground are higher than that of the return route given that the whales are at their maximum energy storage and are motivated to establish themselves on breeding grounds.

The telemetry data also revealed that our humpback whale speeds, on average, were not constant and tended to be highest in the middle of migration. If this is a typical pattern, it could mean that many of the telemetry estimations in different studies of average migratory rates could be biased if calculations are based on only a short portion of the route.

We found no evidence that migration was triggered by daylight hours. There was no number of daylight hours at which all whales initiated migration. Instead, the whales departed from the Antarctic in conditions ranging from two to eight hours of sunlight. Suggestive support was offered for a positive relationship between migratory speed and departure date. This increase of speed with a later departure date could indicate that animals feel compelled to make up for lost time, presumably to arrive at the breeding ground in a coordinated manner.

Limitations

Due to the difficulty tagging marine animals, the sample size will always be an issue in marine mammal studies, and this should be kept in mind when viewing our results. In addition, while satellite telemetry makes it possible for us to obtain hitherto unheard-of levels of detail in our data, it is a relatively new technology, and limitations can present themselves. Many of our tags demonstrated variability in transmission performance. Failure to transmit may be caused by mechanical or electronic failure, poor implantation, or suboptimal position of tag deployment. A combination of variability in transmission performance and differences in duty cycling regimes across years meant that much of the data could not be incorporated into the HSSMs, and the lack of ARS may reflect data limitations stemming from a loss of transmission points. Future studies should be made to pick a duty cycling regime implemented consistently across years and specifically with state-space model timesteps in mind. In addition, the JAGS model should include the ability to fill in smaller gaps, as seen in BSAM and Jonsen (2007) (44).

Management Implications

The conservation of migratory species requires a knowledge of migratory routes' geographical locations, which can highlight areas of particular importance to a species (29,31). The humpback whales in this study spent the vast majority of their migratory time in territorial or exclusive economic zone waters of several nations, and knowledge of the jurisdictions in which the animals migrate can be taken into account when determining management policies as coastal nations have exclusive sovereign rights for conserving and managing marine species within the bounds of their jurisdiction (38).

To maximize conservation resources, the concept of site conservation, specifically focusing resources on sites particularly important to a species' life history, has been developed (50). Bottleneck sites, as well as breeding areas, are considered key areas (50). This study identifies two bottleneck regions off Chile's coast and from Peru's Peninsula de Paracas up into

Panama (Figure 1B). These two areas represent regions to concentrate conservation resources and pass legislation, and this information can be shared with the appropriate national organizations to advance efficient and effective conservation measures such as Marine Mammal Protected Areas (MMPA) (51). In addition, our data has been contributed to the Migratory Connectivity in the Ocean project (MiCO), which is currently developing a system to aggregates and generated actionable knowledge to support worldwide conservation efforts for numerous migratory species (52).

CONCLUSION

Understanding humpback whale migratory behavior and routes gives us a greater context to make effective and efficient conservation decisions in the face of the animals' changing environment. This study is a starting point for the long-term monitoring of the animals in an era of climate change. In the coming years, a significant challenge in the conservation of migratory species will be migrants' potential to shift routes in response to their changing environment. Long-term monitoring programs will allow conservationists and management specialists to monitor and anticipate these changing behaviors (29), identify conservation priorities, and provide baseline data against which the impacts of climate change on ecosystems and migratory species can be highlighted (19,29). Future studies should continue to grow the sample size and investigate routes, behaviors, sex, and reproductive segregation of migration. In particular, emphasis should be given to the bottleneck region between Magellan and Northern Patagonia's strait, to research whether or not our animals are feeding in this location on Antarctica's return route. The information presented here currently defines the behavior of humpback whale migratory behavior from feeding to breeding grounds and can serve as a baseline for future work on the species to compare and contrast how different environmental conditions and populations impact this behavior.

Abbreviations

ARS: Area-Restricted Search

EEZ: Exclusive Economic Zone

LTER: Long Term Ecological Research Project

WAP: Western Antarctic Peninsula

MiCO: Migratory Connectivity in the Ocean project

MMPA: Marine Mammal Protected Area

UAS: Unmanned Aerial System

Ethics approval and consent to participate

All animals were handled by experienced professionals under permits: NMFS 14907, 14,809, and 14,856, ACA Permits 2009–013 and 2015–011, Duke University IACUC A049-122-01, Ucsc Iacuc friea1706, and OSU ACU 4513

Consent for publication

Not applicable

Availability of data and materials

The humpback whale datasets generated and or analysed during the current study are available in the WhalePhys repository, https://github.com/bw4sz/WhalePhys/tree/master/Data/Humpback

The Palmer Station datasets analyzed during the current study are available in the Palmer Station Weather – Daily Averages repository, https://oceaninformatics.ucsd.edu/datazoo/catalogs/pallter/datasets/28

Competing interests

The authors declare that they have no competing interests

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Authors' contributions

ASF, LI, RTM and LP collected the data. LP led laboratory/tissue analysis. ASF and MM conceived the analysis. MM performed the analysis and wrote the text. WG provided energetics support. All authors commented on text and figures. All authors read and approved the final manuscript.

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Figure Titles and Legends

Table 1: Summary of northward migrations for 16 whales fitted with satellite-linked telemetry tags

Table 2: Percentage of migratory time in national waters off the coast of South America by satellite tagged humpback whales

Figure 1: Satellite-linked tracks of humpback whales satellite tagged off of the WAP by A) Year B) Density C) Sex & Reproductive Status

Figure 2: Migratory movements of individual humpback whales satellite-tagged off the Western Antarctic Peninsula during austral summer/fall 2012-2017

Figure 3: Average speeds of humpback whales by segment of migratory route

Figure 4: ARS, traveling, and unknown behavior exhibited by satellite tagged humpback whales on their northward migration from Antarctica

Table 1: Summary of northward migrations for 16 whales fitted with satellite-linked telemetry tags

Ptt	Sex/ Pregnancy Status	Start of N Migration	End of N Migration	Duration of Migration Tracked (days)
121210	Male	4/30/13	6/23/13	54
131130	Female (not pregnant) resting	4/27/16	6/20/16	54
123232	Unknown	4/25/13	6/14/13	50
112699	Unknown	6/15/12	8/1/12	47
166123	Male	6/14/17	7/25/17	41
131132	Male	5/9/16	NA	36
123224	Female (pregnant-NL)	5/23/13	NA	34
166128	Female (Pregnant-NL)	5/18/17	NA	32
121207	Female (not pregnant - resting)	5/7/13	NA	26
131133	Male	7/5/16	NA	26
131136	Unknown	6/30/16	NA	23
131127	Unknown	7/15/16	NA	21
166126	Female (NP – juvenile-resting)	7/1/17	NA	19
166122	Female (Pregnant -NL)	6/18/17	NA	14
123236	Female (not pregnant-resting)	3/16/13	NA	11

166125	Female (Pregnant-NL)	6/5/17	NA	10

Table 1 continued

Ptt	# of transmissions during migration	Great Circle (GC) Distance of tracked migration (km)	GC speed (km/hr)	Average Speed during migration (km/hr)
121210	906	6652	5.1	5.5
131130	555	6714	5.1	5.4
123232	68	6640	5.5	5.8
112699	342	6654	5.5	5.8
166123	548	6532	6.6	6.9
131132	659	5195	5.8	6.1
123224	172	5411	6.3	6.6
166128	384	4354	5.6	5.9
121207	347	5113	4.6	4.7
131133	222	4117	6.5	6.7
131136	141	4244	6.6	6.8
131127	161	3296	6.2	6.9
166126	204	3413	6.6	7.3
166122	190	1921	5.2	5.7
123236	231	379	1.2	1.7
166125	168	1508	6	6.3

Table 1 continued

Ptt	Average Speed WAP-Cape Horn (km/hr)	Average Speed Cape Horn – Peninsula de Paracas (km/hr)	Average Speed Peninsula de Paracas- Zona Reserverda Illescas (km/hr)	Average Speed Zona Reserverda Illescas & above (km/hr)	Completed Migration?
121210	3.6	6	6.5	2	Yes

131130	5.4	5.2	7.2	2.5	Yes
123232	4.7	6.2	3.8	3	Yes
112699	4.9	6.4	4.4	3.4	Yes
166123	8	7.4	4.9	3.4	Yes
131132	5.6	6.3	NA	NA	No
123224	6.3	6.7	NA	NA	No
166128	5.4	6	NA	NA	No
121207	5.9	4.4	NA	NA	No
131133	5.6	7.1	NA	NA	No
131136	7.2	6.7	NA	NA	No
131127	6.1	7.2	NA	NA	No
166126	5.7	8.5	NA	NA	No
166122	5.6	5.8	NA	NA	No
123236	1.7	NA	NA	NA	No
166125	6	7.3	NA	NA	No

Figures

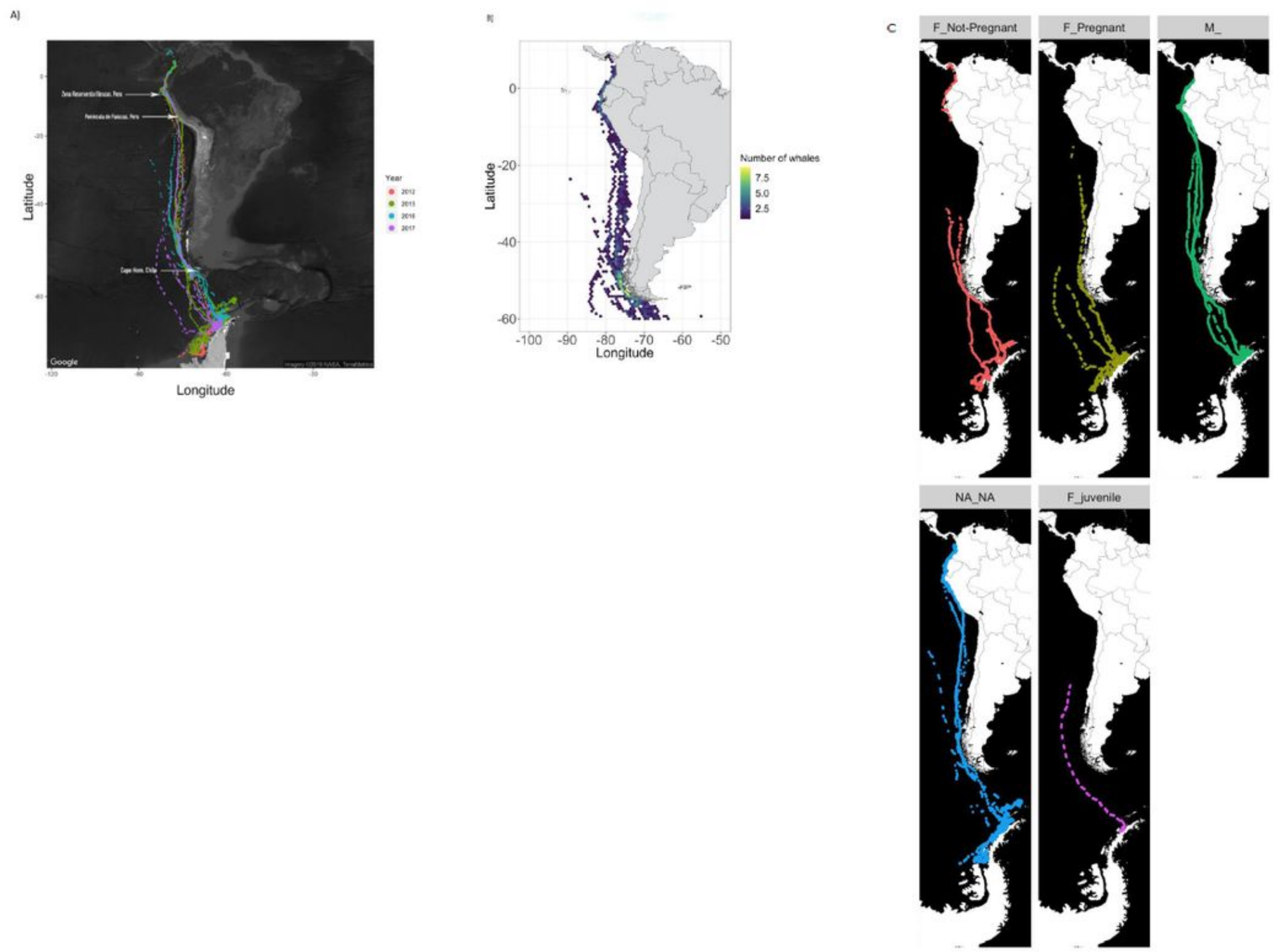

Figure 1

Satellite-linked tracks of humpback whales satellite tagged off of the WAP by A) Year B) Density C) Sex & Reproductive Status

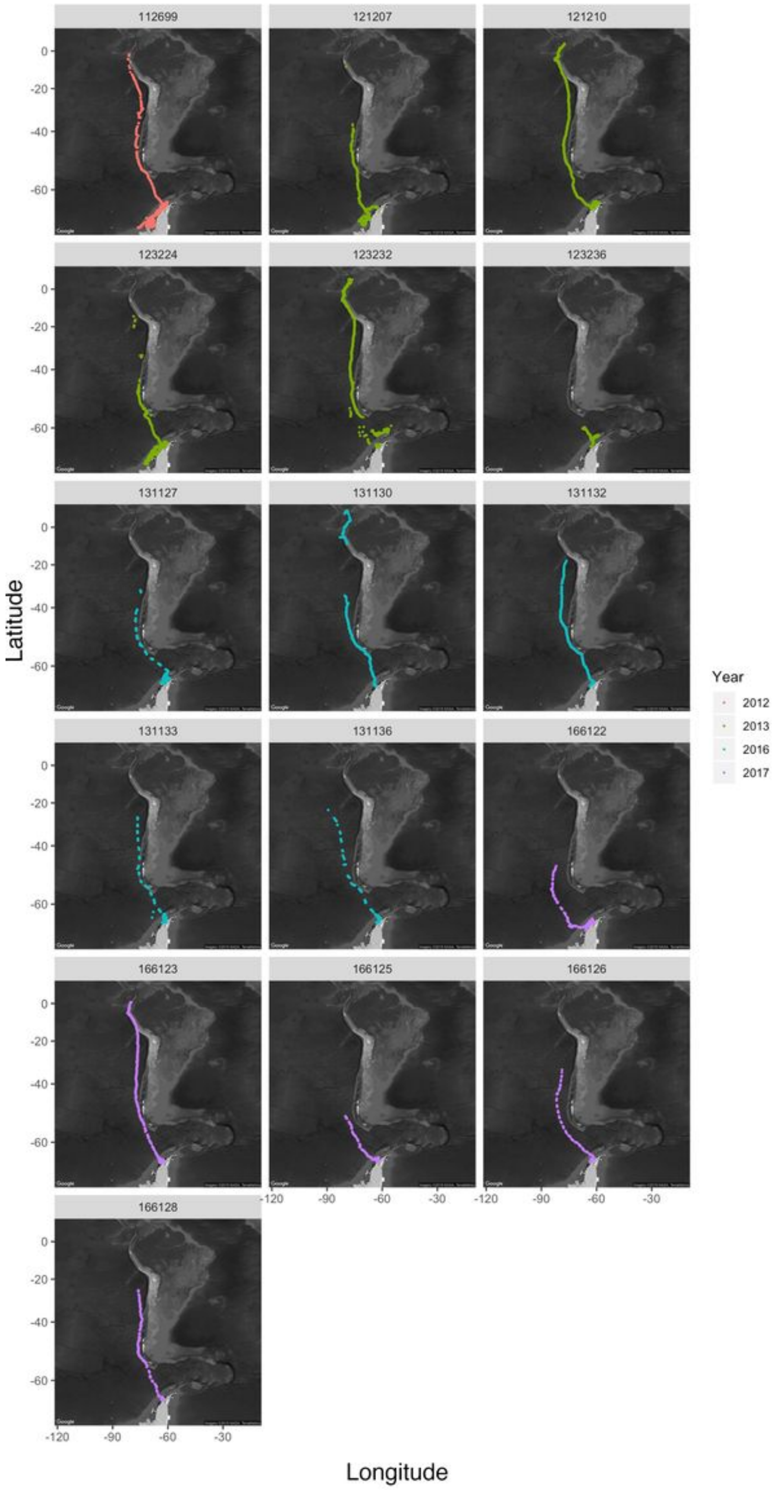

Figure 2

Migratory movements of individual humpback whales satellite-tagged off the Western Antarctic Peninsula during austral summer/fall 2012-2017

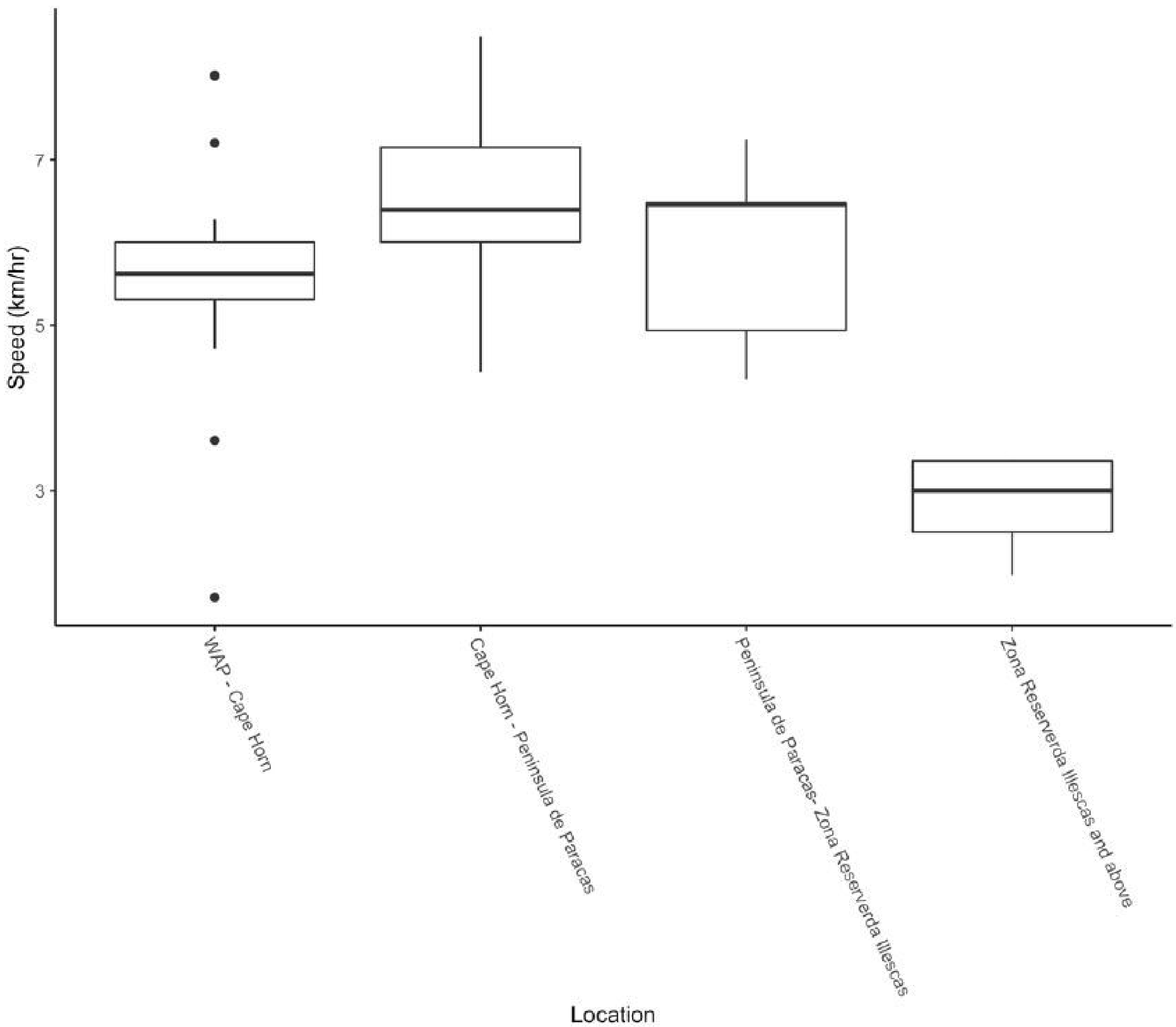

Figure 3

Average speeds of humpback whales by segment of migratory route

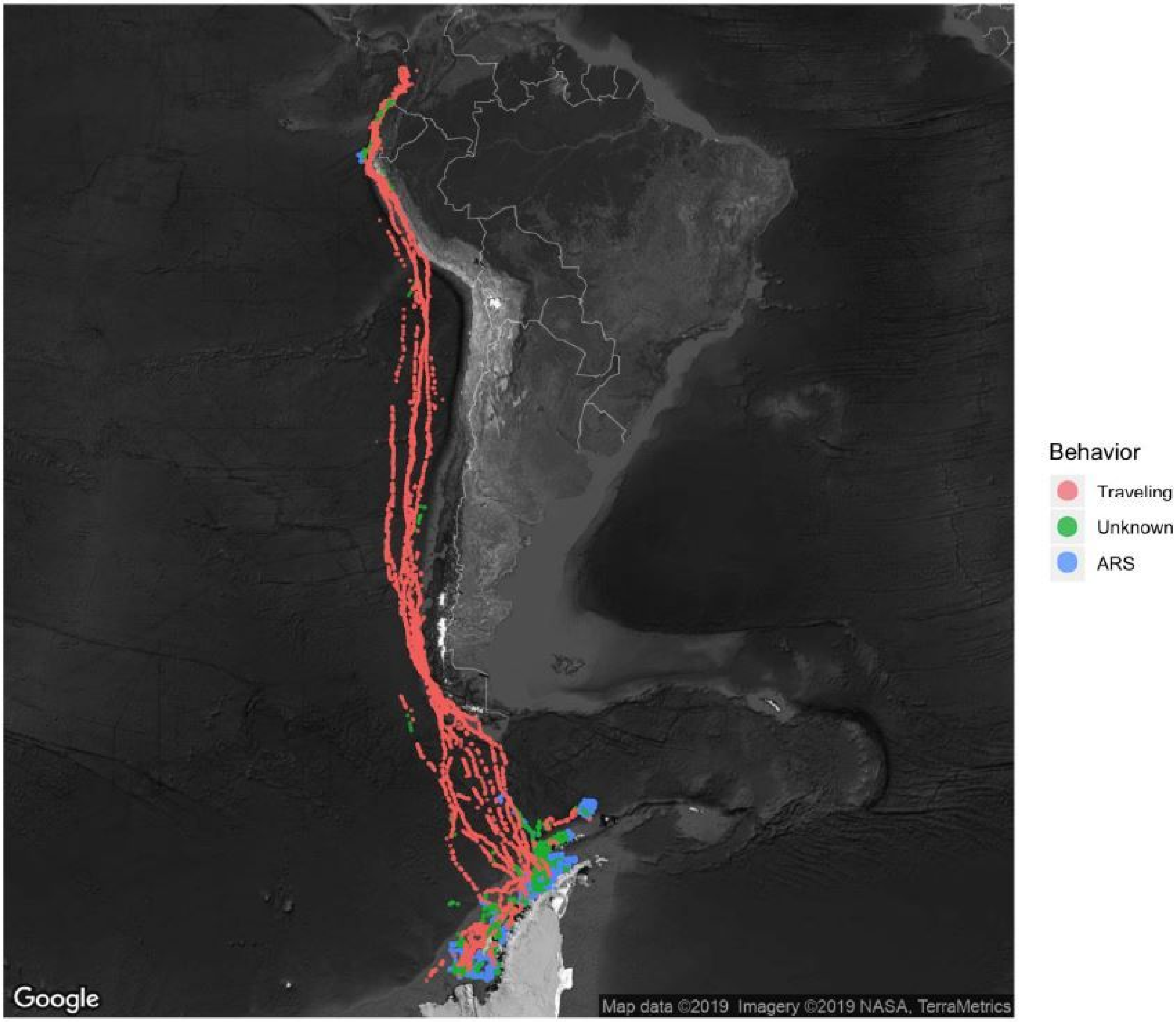

Figure 4

ARS, traveling, and unknown behavior exhibited by satellite tagged humpback whales on their northward migration from Antarctica