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First description of migratory behavior of humpback whales from an Antarctic feeding ground to a tropical calving 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 now, no study has provided a continuous description of humpback whale migratory behavior from a feeding ground to a calving ground. We present new information on satellite-derived offshore migratory movements of 16 Breeding Stock G humpback whales from Antarctic feeding grounds to South American calving grounds. Satellite locations were used to demonstrate migratory corridors, while the impact of departure date on migration speed was assessed using a linear regression. A Bayesian hierarchical state–space animal movement model (HSSM) was utilized to investigate the presence of Area Restricted Search (ARS) en route.

Results: 35,642 Argos locations from 16 tagged whales from 2012 to 2017 were collected. The 16 whales were tracked for a mean of 38.5 days of migration (range 10–151 days). The length of individually derived tracks ranged from 645 to 6381 km. Humpbacks were widely dispersed geographically during the initial and middle stages of their migration, but convened in two convergence regions near the southernmost point of Chile as well as Peru's Illescas Peninsula. The state–space model showed almost no instances of ARS along the migratory route. The linear regression assessing whether departure date affected migration speed showed suggestive but inconclusive support for a positive trend between the two variables. Results suggestive of stratification by sex and reproductive status were found for departure date and route choice.

Conclusions: 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 8461 km, are part of an annual cycle consisting of journeys between

tropical calving grounds in winter and high-latitude feeding grounds in summer [1, 2]. Several theories exist as to what drives this behavior, and include the hypotheses that it is a response to the need to feed in cold waters and reproduce in warm waters for calf thermoregulation or killer whale predation evasion purposes [1, 2], a response to the need to undergo epidermal molt [3], or even a response to shifts in oceanographic conditions between glacial maxima [4]. Currently, the International Whaling

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Commission recognizes seven distinct breeding stocks of Southern hemisphere humpback whales based on calving ground location [5]. These breeding stocks are distributed around lower latitude coastal regions in the Atlantic, Indian, and Pacific Ocean and rely on highly productive seasonal habitats in the Antarctic. Breeding stock G, whose calving ground is associated with the western coast of South America, utilizes the Western Antarctic Peninsula (WAP), one of the most rapidly warming areas in the world, as its foraging ground [6–8].

Humpback whales appear to generally remain in their natal grounds and return year after year. In the foraging grounds, the whales disperse somewhat more broadly than in the calving grounds, but with only limited overlap and intermingling between populations that breed in different geographic areas [9]. The population calving off the western coast of South America is Breeding Stock G. In the nineteenth century, these animals were most frequently recorded crossing the equator into waters off Colombia, but in recent years, individuals in Breeding Stock G have also been sighted further north off Panama, Costa Rica, and Nicaragua in regions frequented by northern hemisphere humpback populations [2, 10, 11]. It is unclear whether these recent sightings constitute a behavior change or are simply a reflection of the paucity of research. Calving behavior has been observed as early as June, peaking between August and October [12]. Specific calving sites have been documented in the nearshore waters off Colombia and Ecuador [12]. A study spanning 31 years (1988–2018) noted that the average date of arrival for individuals of Breeding Stock G in the calving grounds in Gorgona National Park, Colombia, was the last week of May [13].

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 routes means that research on humpback whales has historically been biased toward calving and foraging areas. Research examining the day-to-day movements of humpback whales on their migration from foraging to calving grounds is exceedingly rare, with most of the knowledge regarding this leg of migration inferred from historical whaling and sighting data. More information exists for the journey from calving to foraging grounds [9, 14–26], but is still very scarce.

Estimation of rate of movement from whaling records in the Southern Hemisphere indicate relatively constant mean southbound to northbound migratory speeds of 15° per month, and an approximate Southern Hemisphere migration duration of two to four months [9, 27].

Aerial observations of individuals off the coast of Western Australia 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 [28]. 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 [25], 4.5 km·h⁻¹ for humpback whales traveling from Hawai'i to Alaska [29], and 3.83 and 3.48 km·h⁻¹ for humpbacks migrating from Brazil to Antarctica and South Georgia [30, 31].

It is thought that migratory timing and route are heavily influenced by sex, reproductive status, and age of the animals [9, 18, 19, 26, 28, 32]. Felix and Guzman's study of Breeding Stock G, which has the option of a coastal route up the Western side of South America, found that mothers with calves preferred a coastal route, while single adults tended more towards open waters [19]. Historical whaling data for all southern hemisphere postwar land whaling stations indicate 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 12, 20, 23, and 31 days later, respectively). Migratory triggers are unknown, but are hypothesized to be environmental—such as daylight hours, sea ice formation, and prey abundance—or inherently biological—such as hormone or body condition-based [1, 9]. 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 calving grounds [9]. Since departure dates from foraging grounds and arrival into calving grounds reported from whaling records and photo IDs [9, 26] are segregated along sex, reproductive status, and age classes, it seems reasonable to hypothesize that marked differences in mean migration speed among groups exist. However, to our knowledge, this has only been investigated in looking at females with calves vs single adults [19, 25].

Humpback whales are thought to rarely feed on their migratory routes, instead subsisting on stored fat reserves accumulated in the foraging grounds [9, 28]. Dawbin's [9] 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 Breeding Stocks have shown that some animals do feed along the migration route [15, 16, 21–23, 25, 33–37]. The extent to which these feeding bouts occur, and if they are opportunistic or annual, is unclear.

To our knowledge, only one study investigating humpback whale migration has looked specifically at Breeding

Stock G. Felix and Guzman (2014) compiled 241 opportunistic sightings of humpback whales from 1991 to 2004 along the coast of Chile and Peru from the SIBIMAP database and deployed satellite tags on animals in waters off 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 six animals on their southbound migration. Unfortunately, most 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 [19]. Based on their mean speed estimates (4.05 km h^{-1}) from these whales, Felix and Guzman suggested that migration of single whales in Breeding Stock G would last on average 66.4 days ($SD=13.25$) if using the offshore route and 70.8 days ($SD=14.12$) along the coastal route [19].

Migratory species concerns

Generally, animals that exhibit long-distance migrations are vulnerable to climate change [1, 38], and gaps in scientific knowledge on marine mammal migration have been cited as a barrier to the informed conservation of cetacean populations [1, 38, 39]. 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 the wrong place, time, or for the wrong purpose [40]. Indeed, addressing gaps in knowledge regarding migrations from feeding to calving 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 calving areas and possibly their reproductive success [9, 38].

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

Methods

Tag deployment

From February to May of 2012, 2013, 2016, and 2017, we deployed 16 satellite-linked transmitting tags onto humpback whales that commenced migration in

nearshore waters around the WAP. These animals were from Breeding Stock G, which breeds off the western coast of South and Central America [41]. Sirtrack tags and Wildlife Computers (Redmond, WA, USA) SPOT5, SPOT 6, and MARK 10 Platform Transmitting Terminals (PTTs) were utilized, and tagging was limited to animals $>12 \text{ m}$ in length. Each tag was contained in a sterilized housing prior to deployment and was anchored in the muscle near the dorsal with stainless steel barbs, with the transmitting antenna remaining free outside of the animal [7]. The tags were designed to implant up to a maximum of 290 mm into the back of the whale. 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 pneumatic line thrower compressed air system [42].

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 h on, 3 h off, except for Sirtrack tags (identified by PTT IDs starting with 113), which duty-cycled at 6 h on/6 h off. In 2016, some tags were programmed to transmit continuously and three were programmed to duty cycle at 1 day on, 4 days off. Tags deployed in 2017 were programmed to duty cycle 12 h on, 12 h off.

Demographic information

Skin and blubber biopsy samples were obtained from tagged whales whenever possible using standardized remote biopsy techniques [43]. Samples were obtained from the upper flank below the dorsal fin [44]. 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 [45]. To assign pregnancy within sampled females, progesterone, a lipophilic steroid hormone, was quantified from a sub-sample of blubber using a progesterone enzyme immunoassay [46]. 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 [46].

Data processing

The Argos data were Kalman processed. R (version 3.4.3, [64]) 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. Maps of the animals' tracks were plotted using ggmap [47] in R [64].

Whales were determined to be migrating when they started a northward journey from the WAP without any lasting return movements. The date of departure for each whale was determined visually by graphing latitude as a function of Julian day. Trends in departure date by sex and reproductive status were assessed by creating multiple graphs of date of departure grouped by year, sex, reproductive status, year and sex combined, and year and reproductive status combined.

To determine rates of migration, speeds on the migratory route were calculated with data corrected for location error with a simple default HSSM with a 12-h timestep fitted in R using BSAM [64, 65]. Rate was the distance of the linear vector between 12 h timestep locations. Distances between locations were calculated using the function distanceTrack from the Argosfilter package [64, 66]. Individual's mean speeds were calculated as the mean of all 12-h timestep rates for each animal. Great circle distance and speed were also calculated to allow comparison to more studies.

There were several 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 three discrete spatial sections allowed for a more valid estimation and comparison of speeds in some sections along the journey. Mean migratory speed was calculated for each section, as well as for the calving area. As humpback whales leave the Western Antarctic Peninsula at different times, a simple linear regression was performed using Julian day of the departure date (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 north of -55.9833, as well as all animals that did not reach the cape, were filtered out, and the mean 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, we report P values in the context of levels of support for the outcome rather than as a binary threshold of significance, with P -values < 0.01 indicating strong support, p -values between 0.01 and 0.1 offering suggestive, but inconclusive support, and p -values > 0.1 indicating no support [48, 49].

As coastal nations have exclusive sovereign rights for the purpose of conserving and managing marine species within the bounds of their jurisdiction [50], the amount of time the whales spent within Exclusive Economic Zone (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 provides unobserved estimated locations along regular time intervals from available data, and these intervals were utilized for EEZ analysis.

Discrete behavioral modes were determined with hierarchical Bayesian state-space movement models manually constructed in JAGS. This was a departure from the simpler models used to assess locations, as it allowed for differences in transition probabilities and movement norms associated with behavioral states depending on whether the animals were in the foraging grounds, calving grounds, or migratory route. This model-associated spatial patterns of animal movement with predicted behavioral states while accounting for the significant error inherent in Argos Satellite location data. Unlike the simpler BSAM HSSM, this model did not return the coordinates of calculated unobserved locations to the user, necessitating the creation of the BSAM model to determine the earlier mentioned variable of speed.

We used a discrete-time dynamic correlated random walk model following Jonsen et al. [52] and Bestley et al. [51], where each movement stemmed from either a 'traveling' or 'area-restricted search' (ARS) state [51, 52]. 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 calving in this state and

our measurements are not based off 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 [7, 53]. 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 [52]. 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 unobserved locations and coordinate vectors x_t and x_{t-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 ($\gamma=0$ would signal a simple random walk). b_t is an index used to denote behavioral mode, e.g. ARS or traveling. $T(\theta)$ 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 et al. [52], 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 unobserved locations of the animals needed for the process equation from the error-prone and temporally irregular Argos location observations:

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

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 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. [52]. Various classes of Argos errors are strongly non-gaussian, and are thus traditionally calculated with t distributions [52]. However, this can make the model so computationally complex that it cannot converge. This occurred with our model, and to counter this we ran the observation model with a multivariate normal distribution as done in Weinstein et al. [6, 7] and used the package Argosfilter in R [64, 66] to filter out implausible points that indicated speeds higher than ~ 20 km hr⁻¹ ($v_{max}=6$) [6, 7]. We used a timestep of 12 h, 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 modeled, the means of the Markov chain Monte Carlo chains 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 unknown [54].

To help address the inconsistent transmitting nature 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 [55].

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 between ARS and Traveling, as well as variance in behavioral state parameters as the animals switched from feeding, to migratory, and then calving 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 was different than a traditional BSAM model and allowed for potential differences in spatial characteristics of behaviors—ARS in foraging and calving grounds may present differently than ARS on the migratory route if it encapsulates breeding or calving behaviors or if the parameters of feeding bouts differ during migration (e.g. smaller turning angles for migratory ARS than foraging ground ARS). The model was fitted in R using the software JAGS [67] and the R rjags package [64, 68]. 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 Markov chain Monte Carlo 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 [56]. Runs were conducted on the UCSC Hummingbird computational cluster with chains running in parallel.

Results

Tag deployment

Between 2012 and 2018, 16 of 62 animals tagged in the WAP commenced migration, transmitting a total of 35,642 locations, with five tags transmitting locations to the calving grounds. The transmission time of these tags ranged between 42 and 266 days (mean = 108 d, SD = 63.7). Migration start dates varied greatly, ranging from March 16th to July 15th (Table 1). Animals with tags that continued to transmit to the completion of migration reached the calving grounds (designated as Zona Reserverda Illescas, Peru) as early as June 19th and as late as August 1st (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 (Table 1). None of the animals were accompanied by calves at the time of tagging.

Individual data analyses and migratory route findings and patterns

A summary of each of the 16 animals' individual movements is provided in Table 1, and their routes can be

Table 1 Summary of northward migrations of 16 humpback whales (*Megaptera novaeangliae*) tagged off the Western Antarctic Peninsula in 2012–2017

PTT	Sex/pregnancy status	Start of N migration	End of N migration	Duration of migration tracked (days)	# of transmissions during migration	Great circle distance of tracked migration (km)	Completed migration?
112699	Unknown	15-Jun-12	1-Aug-12	47	342	6654	Yes
123236	Female (not pregnant)	16-Mar-13	NA	11	231	379	No
123232	Unknown	25-Apr-13	14-Jun-13	50	68	6640	Yes
121210	Male	30-Apr-13	23-Jun-13	54	906	6652	Yes
121207	Female (not pregnant)	7-May-13	NA	26	347	5113	No
123224	Female (pregnant)	23-May-13	NA	34	172	5411	No
131130	Female (not pregnant)	27-Apr-16	20-Jun-16	54	555	6714	Yes
131132	Male	9-May-16	NA	36	659	5195	No
131136	Unknown	30-Jun-16	NA	23	141	4244	No
131133	Male	5-Jul-16	NA	26	222	4117	No
131127	Unknown	15-Jul-16	NA	21	161	3296	No
166128	Female (pregnant)	18-May-17	NA	32	384	4354	No
166125	Female (pregnant)	5-Jun-17	NA	10	168	1508	No
166123	Male	14-Jun-17	25-Jul-17	41	548	6532	Yes
166122	Female (pregnant)	18-Jun-17	NA	14	190	1921	No
166126	Female (not pregnant–juvenile)	1-Jul-17	NA	19	204	3413	No

seen in Figs. 1 and 2. Of the 16 migrators, five (PTT ID=112699, 121210, 123232, 131130, and 166123) made it all the way to the calving grounds, representing the first complete migratory tracks of animals in Breeding Stock G. The animals all used routes with coastal and open water segments to migrate up the western side of South America (Figs. 1 and 2). The tag on 123232 ceased transmissions

during most of the northward migration along the Chilean coast, but then resumed and recorded the entire southward migration until October. By that time, the whale had returned to the Antarctic foraging grounds. Four whales (PTT IDs=131130, 123232, 121210, and 166123) crossed the equator and one ventured as far as 8.94 degrees north (PTT=131130). While there was no clear difference in

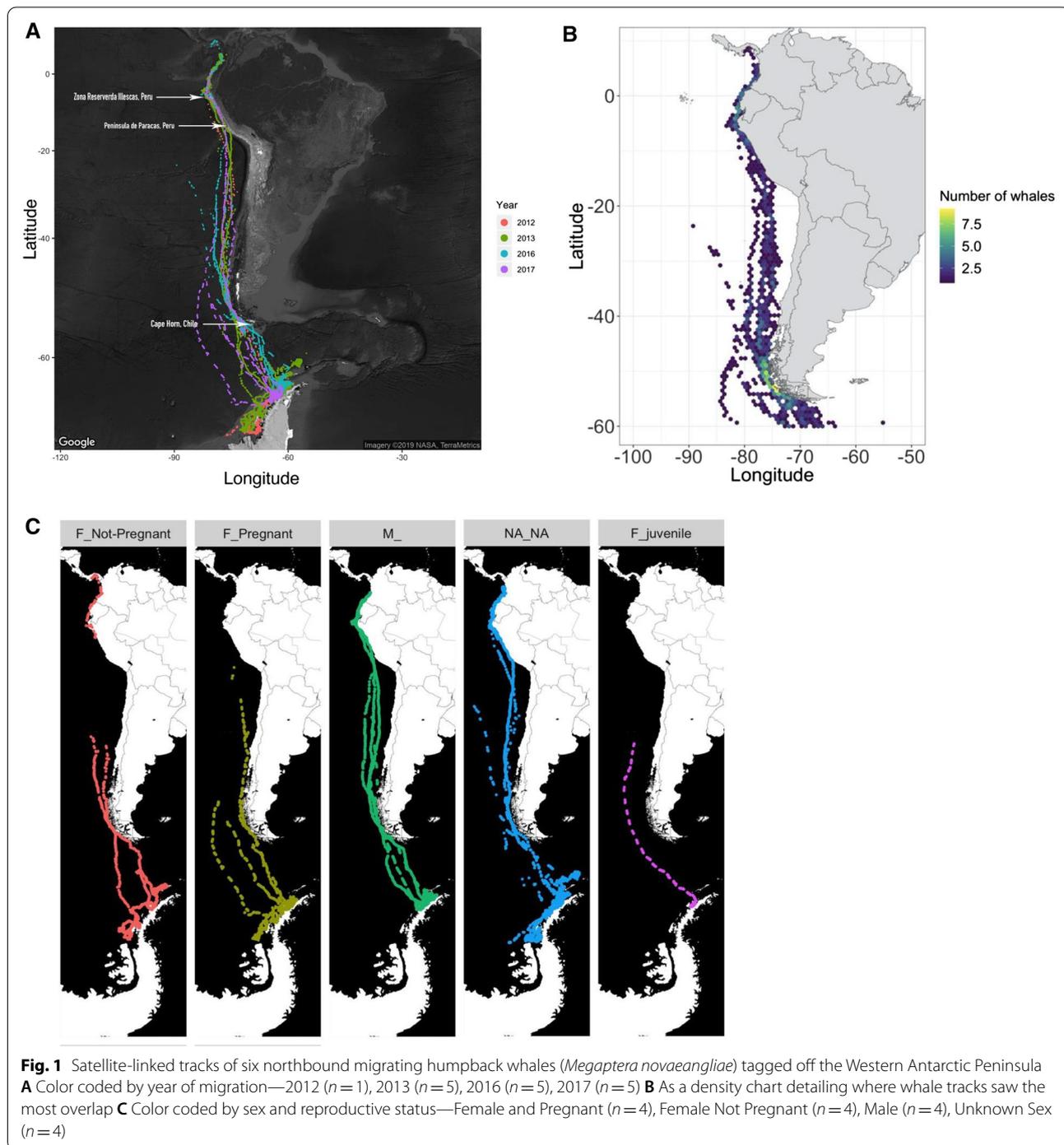


Fig. 1 Satellite-linked tracks of six northbound migrating humpback whales (*Megaptera novaeangliae*) tagged off the Western Antarctic Peninsula **A** Color coded by year of migration—2012 ($n = 1$), 2013 ($n = 5$), 2016 ($n = 5$), 2017 ($n = 5$) **B** As a density chart detailing where whale tracks saw the most overlap **C** Color coded by sex and reproductive status—Female and Pregnant ($n = 4$), Female Not Pregnant ($n = 4$), Male ($n = 4$), Unknown Sex ($n = 4$)

departure date between males and females, it did appear that resting non-pregnant females left the peninsula first, followed by pregnant females, and finally juveniles (Fig. 3A, B). Non-pregnant females and males all hugged the coast at Cape Horn, while more variability was seen with the pregnant females and juvenile, some of which took a more open water course (Fig. 1C). However, power to detect the effects of sex or reproductive status was low given the sample size in the three categories and the potential for interannual variability, and these trends may be rendered obsolete or become clearer with larger sample sizes.

Whales left from numerous locations on the peninsula and remained relatively dispersed in the Drake Passage (Figs. 1 and 2). Many of the animals then passed close to South America's southwestern tip, resulting in a convergence 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 calving 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 mean time spent in national waters (e.g. within EEZ boundaries) on the northward migration for the five animals that completed migration (PTT ID=112699, 121210, 123232, 131130, and 166123) was 72.2% (SD=5.63) of total migration time (Table 2).

The mean speed for all the animals calculated from the 12 h time steps was 5.88 km h^{-1} (SD=1.31), while the mean Great Circle speed for all animals was 5.53 km h^{-1} (SD=1.31). In general, mean speeds followed a slow–fast–slow trajectory by track segment, with the mean speed calculated for the animals highest during the middle section of migration from Cape Horn to Peninsula de Paracas, and lowest in the calving area (Table 3, Fig. 4). 15 whales had tracks reaching to Cape Horn, and their mean speeds over the distance can be seen in Table 3. The regression results showed suggestive but inconclusive support for the hypothesis that whales have faster migratory speeds the later they leave the peninsula ($F[1, 13]=4.117, p=0.06346$). There was no support for a relationship between speed and sex ($F(2, 3.11)=0.003, p=0.96$) or speed and sex/reproductive status ($F(2, 4.8)=0.37, p=0.71$).

23,526 (70%) of 33,643 filtered transmissions were utilized by the JAGS HSSM model, which required at least one transmission per timestep during three consecutive timesteps to create a track. Of these 23,526 points, 4230 belonging to 14 animals were located on the northbound migratory route before Zona Reserverda Illescas. The animals appeared to be almost exclusively in the Traveling state during their northward migration. Of the 4230 migratory behavioral points 3875 were classified as Traveling, 294 as Unknown, and 61 (1%) as ARS. The 61 ARS locations all belonged to animal 123,236 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 123,232 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 likely kept further away from the peninsula because of sea ice extent (Fig. 5).

Discussion

The results of our tracking analyses provide the first continuous description of humpback whale migratory behavior from a feeding to a calving ground as well as the first complete migratory tracks of Breeding Stock G. These humpback whales exhibited staggered departures from many locations along the WAP and embarked on northward migrations lasting between 41 and 54 days ($n=5$). The tagged individuals migrated at varying speeds, and suggestive but inconclusive support for a positive relationship between date of departure and speed suggests 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 was not detected on the northbound migratory route.

The telemetry data identified two previously undocumented geographic convergences: the consolidation of the tracks starting at the coast of the southwestern 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 (Fig. 1B). Interestingly, the first convergence 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

(See figure on next page.)

Fig. 2 Individual satellite-linked tracks of 16 northbound migrating humpback whales (*Megaptera novaeangliae*) tagged off the Western Antarctic Peninsula during Austral summer/fall 2012–2017. Several tags including PTT 123224, 123232, and 131130 experienced large gaps in transmissions on the northward migration. This is not immediately discernable for PTT 123232 because the southward migratory track lined up well with the northward track

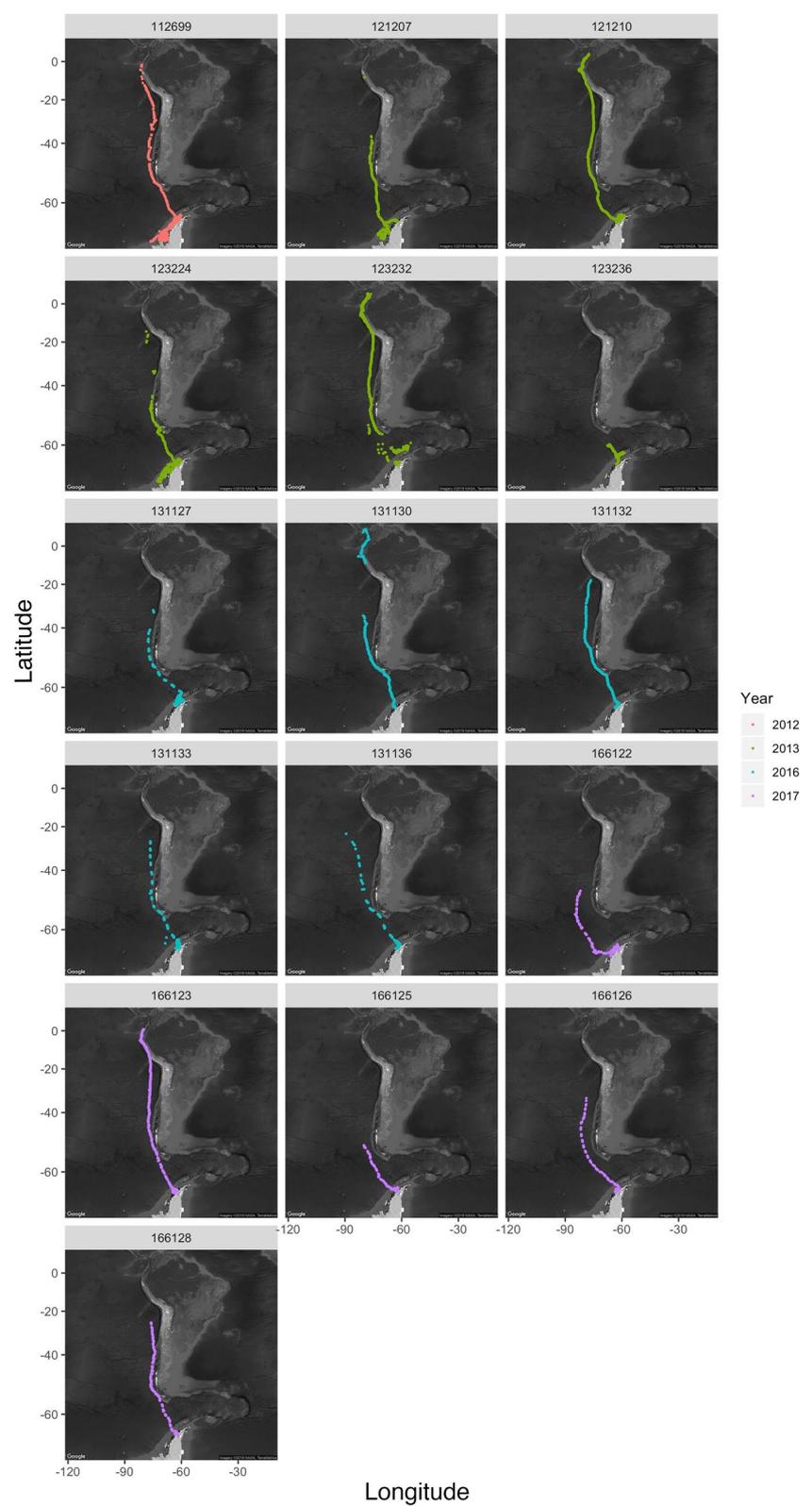


Fig. 2 (See legend on previous page.)

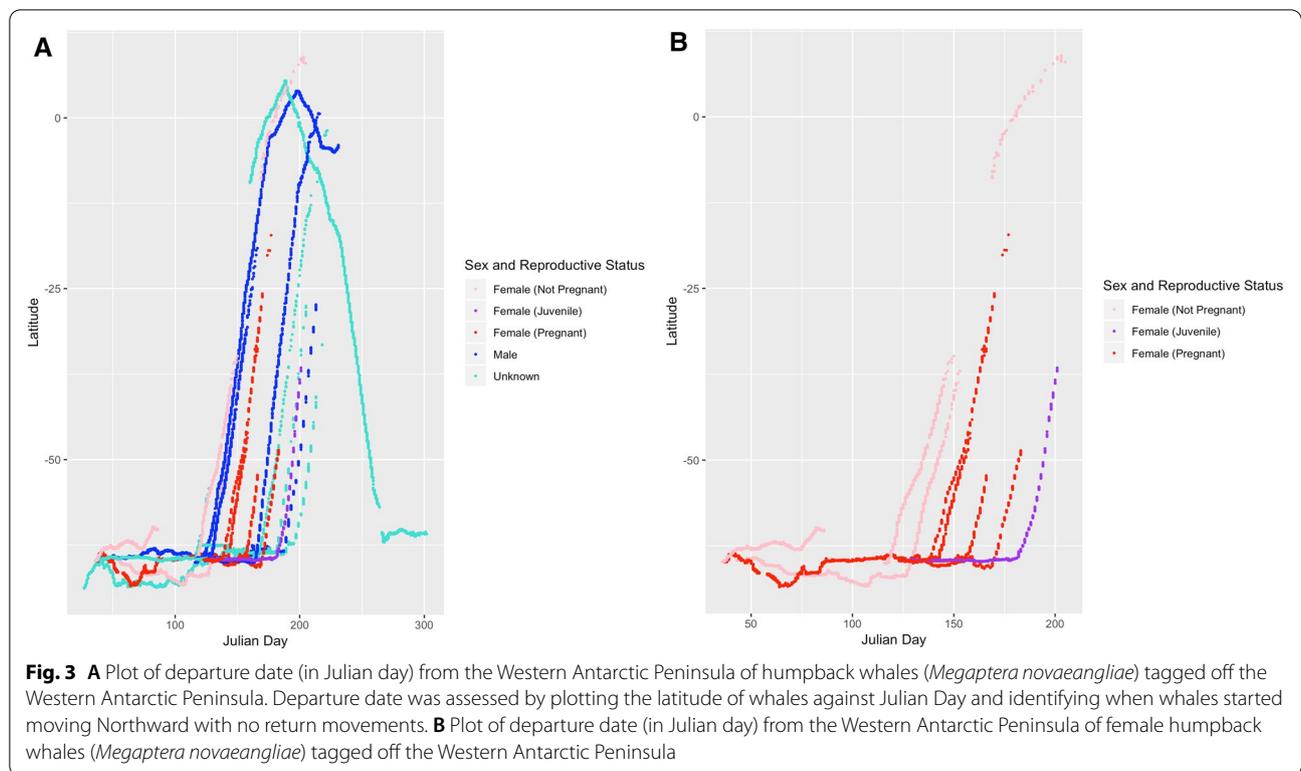


Table 2 The percentage of migratory time in national waters (Chile, Peru, Ecuador) off the coast of South America of five humpback whales (*Megaptera novaeangliae*) tagged off the Western Antarctic Peninsula

Ptt	Time in Chile (%)	Time in Peru (%)	Time in 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

Only the five whales with complete migration tracks as generated by the BSAM model were included. Only the portions of the route where the whales had the option to be in national waters (e.g. not the Drake Passage) were included

the documented feeding ground in the Straits of Magellan [34, 57, 58]. It is worth noting that one individual recorded “Unknown” behavior (e.g. values between 1.25 and 1.75) near northern Chilean Patagonia.

The migratory tracks tentatively identify the area around Zona Reservada Illescas, Peru, as the start of the calving area based on abrupt route change and the transition from transiting to ARS in animal PTT = 123224, a pregnant female. This delineation of the calving ground is more in agreement with Guzman [19] than Rasmussen [2], which placed the border close to the equator in Salinas, Ecuador, more than 550 km north. Tagged whales in our study reached as far north as Panama, which agreed

with Rasmussen’s findings regarding the geographical reaches of the calving grounds.

One tagged whale, PTT 123232, provided information on both the start and end of the migratory cycle from the Antarctic to the tropical calving ground and back to the Antarctic. While the tag stopped transmitting for the portion of the northward migration along the majority of Chile, to the best of our knowledge, this deployment represents the first tagged Southern Hemisphere humpback to provide data for both legs of migration. The southbound route lined up closely with the northbound route, indicating that humpbacks may use the same routes, regardless of migratory direction.

Table 3 The mean speed of northward migrations of 16 humpback whales (*Megaptera novaeangliae*) tagged off the Western Antarctic Peninsula (WAP) in 2012–2017

PTT	GC speed (km/hr)	Mean speed during migration (km/h)	Mean speed WAP—Cape Horn (km/hr)	Mean speed Cape Horn—Peninsula de Paracas (km/h)	Mean speed Peninsula de Paracas—Zona Reserverda Illescas (km/h)	Mean speed Zona Reserverda Illescas and above (km/h)
112699	5.5	5.8	4.9	6.4	4.4	3.4
12,236	1.2	1.7	1.7	NA	NA	NA
123232	5.5	5.8	4.7	6.2	3.8	3
121210	5.1	5.5	3.6	6	6.5	2
121207	4.6	4.7	5.9	4.4	NA	NA
123224	6.3	6.6	6.3	6.7	NA	NA
131130	5.1	5.4	5.4	5.2	7.2	2.5
131132	5.8	6.1	5.6	6.3	NA	NA
131136	6.6	6.8	7.2	6.7	NA	NA
131133	6.5	6.7	5.6	7.1	NA	NA
131127	6.2	6.9	6.1	7.2	NA	NA
166128	5.6	5.9	5.4	6	NA	NA
166125	6	6.3	6	7.3	NA	NA
166123	6.6	6.9	8	7.4	4.9	3.4
166122	5.2	5.7	5.6	5.8	NA	NA
166126	6.6	7.3	5.7	8.5	NA	NA

While our sample size was small ($n=12$), our data did appear to show some differences in leaving date and route choice among different sex and reproductive categories. Just like Dawbin [9], our data indicated that resting non-pregnant females left the peninsula before pregnant females. However, unlike in Dawbin's records, our Juvenile female ($n=1$) left after the other females, not before, and there was no identifiable difference between males ($n=4$) and females ($n=8$). Again, interannual variability and small sample size should be taken into account when considering these results.

Our findings do not align with those of Avila et al. [13], which states that whale arrival in the calving grounds is becoming consistently earlier, with an average arrival date of the last week of May [13]. Of the 16 migrating animals we tagged, 8 had not even commenced migration by the last week of May, let alone made it to the calving grounds.

Our study indicated no ARS bouts on the northward migration, which may support Dawbin's [9] conclusions on migratory foraging, which stated that the animals did not forage on their northward migration. While the model did indicate that there were no common hitherto unknown feeding stopover sites used by the whales on the migratory route, it could not rule out opportunistic feeding of the whales en route, which would likely transpire over shorter time periods than the 12-h timestep and may not involve the characteristic multi-day prey searching signature that is recognized as ARS in our

model. Additionally, as foraging occurs on vertical and horizontal planes and satellite data operates only on a horizontal plane, not all foraging behavior will be captured as ARS [59]. While telemetry data cannot conclusively rule out foraging behavior, only 1% of our recorded locations on the migratory route indicated ARS and all these points belonged to one animal and occurred in the Drake Passage. Without more detailed data (e.g. accelerometer data) 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 most points in this category were found in the calving or foraging areas. As previously stated, certain instances of feeding bouts have been recorded on the migratory route in recent years with most [19, 21–23, 25, 60] but not all [35–37] taking place on the journey to the foraging grounds. It is possible that supplementary feeding is a phenomenon more common on the route from calving 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 calving grounds whales have just replenished their food stores. In addition, the foraging ground bound migration may better align with the spring bloom and increased prey availability on the migratory route.

The mean migratory rate for all the animals regardless of track length was $5.88 \text{ km}\cdot\text{h}^{-1} \pm 1.31$. For the

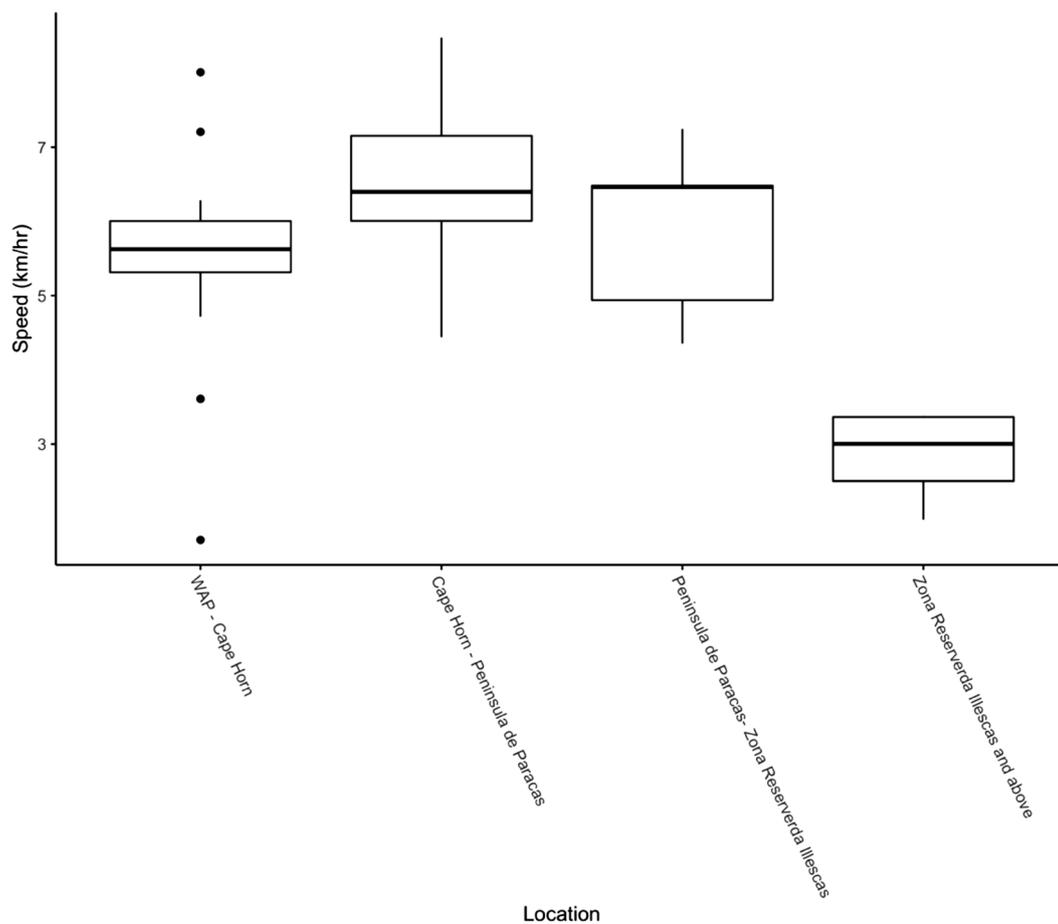


Fig. 4 Boxplot of mean speeds by segment of migratory route of humpback whales (*Megaptera novaeangliae*) tagged off the Western Antarctic Peninsula. Speeds were calculated through the BSAM generation of 12-h time step locations

five animals that completed migration, the mean migratory rate $5.88 \text{ km} \cdot \text{h}^{-1} \pm 0.59$. The animals completed the migration in 41–54 days and traveled between 33° – 43° per month. These speeds were significantly faster than Dawbin [9], who recorded south to north speeds of 15° per month, with approximate migration durations of 60–120 days. They were slightly higher than the aforementioned previously recorded telemetry speeds of humpback whale migrations of $4.04 \pm 1.08 \text{ km} \cdot \text{h}^{-1}$ [19], $4.3 \pm 1.2 \text{ km} \cdot \text{h}^{-1}$ [25], $4.5 \text{ km} \cdot \text{h}^{-1}$ [29], and 3.83 and $3.48 \text{ km} \cdot \text{h}^{-1}$ [30, 31]. It is possible that the whales in our study utilized coastal currents, such as the Humboldt Current, along the western coast of South America to increase their traveling speeds without incurring additional energetic costs. It is also possible that Breeding Stock G experiences slightly higher migratory speeds than other populations or that, alternatively, migratory rates in the direction of the calving 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 calving grounds. Another potential cause of the differences is a result of different calculation methods. Our speeds were calculated from HSSMs and the aforementioned papers do not elaborate on methodology used to determine speed. Our method used BSAM, which should correct for location error and thus give more accurate speed results, but it should be noted that the BSAM model needed to fill in a significant gap for PTT 131130 which could have affected the results for that animal. The telemetry data also revealed that the 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 mean migratory rates could be biased if calculations are based on only a short portion of the route.

Suggestive, but inconclusive 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

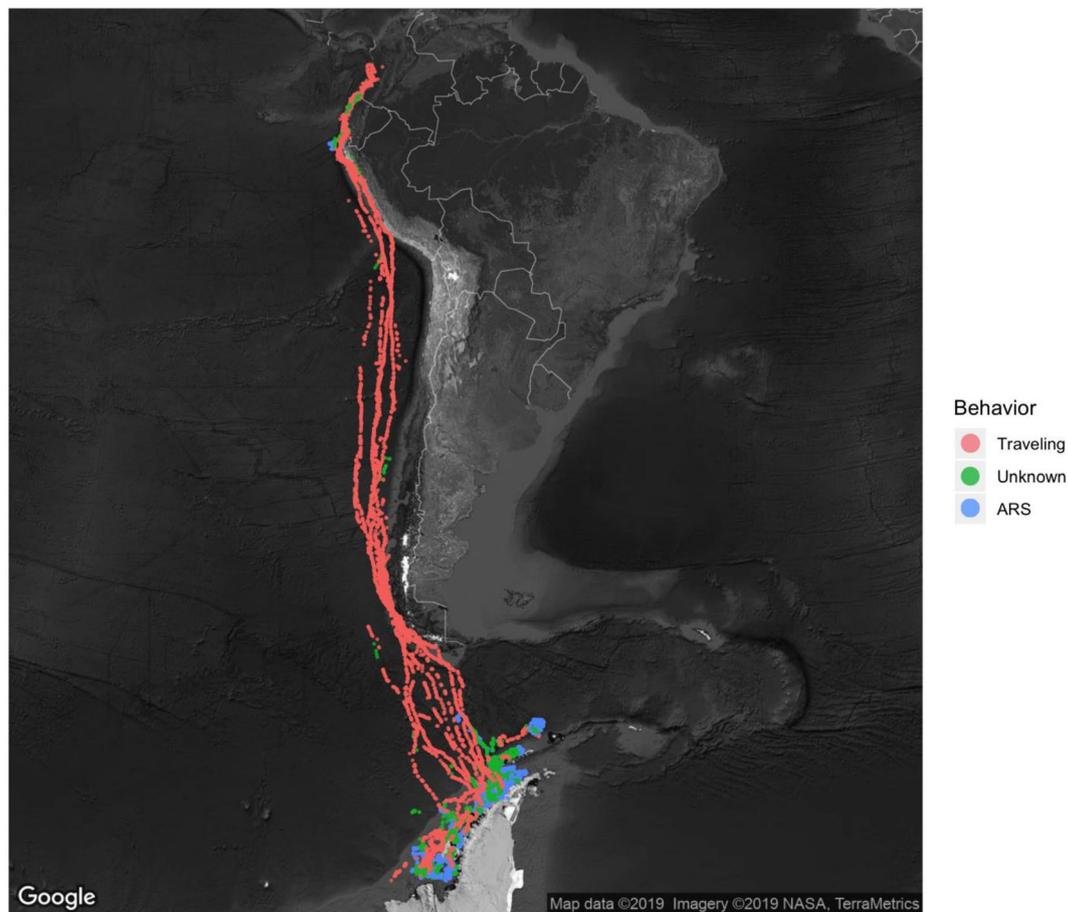


Fig. 5 Behavioral states of 14 humpback whales (*Megaptera novaeangliae*) generated using an HSSM created in JAGS. States including Area Restricted Search, Traveling, and Unknown behavior were assigned to the satellite transmissions of 14 northbound migrating humpbacks tagged off the Western Antarctic Peninsula

make up for lost time, presumably to arrive at the calving ground in a coordinated manner.

Management implications

The conservation of migratory species requires a knowledge of migratory routes' locations, which can highlight areas of particular importance to a species [38, 40]. The humpback whales in this study spent the vast majority (72.2%) of their migratory time in territorial or exclusive economic zone waters of several nations (Table 2). 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 [50].

To maximize conservation resources, the concept of site conservation, specifically focusing resources on sites particularly important to a species' life history,

has been developed [61]. Convergence sites, as well as calving areas, are considered key areas [61]. This study identifies two convergence regions off Chile's coast and from Peru's Peninsula de Paracas up into Panama (Fig. 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 [62]. In addition, our data have been contributed to the Migratory Connectivity in the Ocean project (MiCO), which is currently developing a system to aggregate and generate actionable knowledge to support worldwide conservation efforts for numerous migratory species [63].

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 [38], identify conservation priorities, and provide baseline data against which the impacts of climate change on ecosystems and migratory species can be highlighted (18, 38). 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 convergence region between the Straits of Magellan and Isla Grande de Chiloé, to research whether the animals are feeding in this location on the return route to Antarctica.

Abbreviations

ARS: Area-restricted search; EEZ: Exclusive Economic Zone; HSSM: Hierarchical State–Space Model; LTER: Long-Term Ecological Research Project; WAP: Western Antarctic Peninsula; MiCO: Migratory Connectivity in the Ocean project; MMPA: Marine Mammal Protected Area; PTT: Platform Transmitting Terminals; UAS: Unmanned Aerial System.

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Authors' contributions

ASF, LI, RTM, AR, DJ, DN and LP collected the data. ASF and AR contributed to study genesis. LP led laboratory/tissue analysis. VAG helped with tag acquisition. ASF and MM conceived the analysis. MM performed the analysis and wrote the text. WG contributed energetics analysis. ASF, LI, RTM, DJ, DN, WG, and LP commented on text and figures. All authors read and approved the final manuscript.

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Availability of data and materials

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

Declarations

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, Uccs lacu friea1706, and OSU ACU 4513.

Consent for publication

Not applicable.

Competing interests

The authors declare that they have no competing interests.

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