www.nature.com/scientificreports

scientific reports

OPEN

Migratory behaviour of humpback whales in the southeastern Pacific under climate change

Virginie Millien[1], **Nicole Stafiej**[1], **Fernando Félix**[2,3] & **Hector M. Guzman**[4]✉

Humpback whales, a species of baleen whale occurring in all oceans globally, undergo seasonal migration between their breeding grounds in tropical warm waters and high latitude feeding grounds. Using multiple years of satellite tracking data, we modeled the effect of oceanic conditions on the movement behaviour of 42 humpback whales belonging to the Southeastern Pacific population (also known as Breeding Stock G) during their migration from breeding grounds in Costa Rica, Panama and Ecuador to feeding grounds in waters around the Antarctic Peninsula. We report evidence that during their migration, humpback whales engage in a movement behaviour frequently associated with feeding, and that this behaviour was more likely to occur in relatively more productive waters. We show that whales partly rely on cues they perceive in their immediate environment to initiate their southward migration, but also on their memory of oceanic conditions on their feeding grounds, timing their arrival with the complete melting of sea ice which triggers a bloom of krill in the Antarctic Ocean. Overall, our findings suggest that humpback whales integrate information they gather from their immediate environment to predict the oceanic conditions at distant locations and adjust the timing of their migration, maximizing their interaction with their preys. However, it is unclear if humpback whales will fully succeed in tracking their preys in a rapidly changing climate and ensure the long-term persistence of the species.

Keywords Humpback whales, Southward migration, Southeastern Pacific, Movement behaviour, Climate change

Seasonal migration has evolved independently among diverse animal groups as an adaptation for individuals to reduce predation or competition pressures, facilitate mate finding, or to fully take advantage of inter-annual seasonal peaks in food abundance[1,2]. Resource tracking, the process by which individuals adapt to phenological variation in fleeting resources across space, has been documented in a wide range of species. Most notable illustrations of resource tracking are observed in terrestrial mammals such as ungulates tracking changes in plant phenology, and marine mammals such as seals or whales tracking prey aggregation[3].

Under climate warming, seasonal cycles are rapidly shifting in both space and time[4], and changes in behaviour provide a mechanism for individuals to remain in phase with resource peaks. The efficacy of such response relies on the ability of an individual to detect changes in environmental cues determining its migratory behaviour. The decision for an individual to initiate migration may be guided by the environmental conditions experienced within its perceptual range, by its memory of long-term trends in resource availability at distant locations along the migratory route or at the destination site, or by some combination. Individuals undergoing long distance migration often display high site fidelity and a strong association with migration routes across years, suggesting that memory plays a significant role in determining their migration phenology and route (*sensu*[5]). With rapid global change, a high reliance on the memory of long-term climatic conditions in migratory species may result in a mismatch between the phenology of the migration and the seasonal resource peak[6].

Unless they adapt to climate change and associated changes in resource availability, species of baleen whales in the Southern Ocean are predicted to decline, bringing some to the brink of extinction by 2100[7]. One such species is the humpback whale (*Megaptera novaeangliae*), a species of baleen whale found in all oceans globally, ranging from tropical to temperate waters in the Northern Hemisphere, and from tropical to waters near the ice edge in the Southern Hemisphere. The Breeding Stock G (hereafter BSG), also known as the Southeastern Pacific population, breeds in the neotropical waters of the Southeastern Pacific in Costa Rica, Panama, Colombia,

[1]Department of Biology, McGill University, Montréal, QC H3A 1B1, Canada. [2]Museo de Ballenas, Av. Enríquez Gallo S/N, Salinas, Ecuador. [3]Pontificia Universidad Católica del Ecuador PUCE, Avenida 12 de Octubre 1076, Quito, Ecuador. [4]Smithsonian Tropical Research Institute, PO Box 0843-03092, Panama, Republic of Panama. ✉email: guzmanh@si.edu

Ecuador, and northern Peru (4 °S to 12 °N)[8]. Individuals from this subpopulation migrate to feeding grounds located mostly along the west side of the Antarctic Peninsula and to a lesser extent in southern Chile[9–11], where they spend the austral summer before returning to their breeding grounds. Humpback whales undergo one of the longest seasonal migrations of any mammal, with the longest recorded distance of 10,005 km between a breeding area in waters surrounding Nicaragua and a feeding area in the Antarctic, executed by a whale sighted in both locations in September and December 2017[12]. In feeding grounds, humpback whales build fat reserves to sustain energy for their long journey to their breeding grounds, during which they typically abstain from feeding[13]. There is evidence however that some humpback whale individuals engage in opportunistic feeding during their migration[14–22], but little is known about the frequency of such behaviour and its impact on the overall energetic budget.

It is also unclear what determines the decision of the whales to initiate their seasonal migration. In their review, Meynecke et al.[23] concluded that there is little known about the cues triggering seasonal departure from the breeding and feeding grounds in this species. Using 31 years of sighting records of data, Avila et al.[24], reported that a subpopulation of humpback whales from the BSG breeding in Colombia have shifted their arrival time to an earlier date by 1 month, although no environmental factor was clearly identified as a driver of this change in migration phenology. Ocean productivity combined with sea-surface temperature have been shown to be a key driver of the seasonal migration timing in a North Pacific populations of the blue whale and grey whale[25,26]. Previous studies have also linked arrival or departure times with oceanic conditions such as El Niño and upwelling indices in a humpback whale population of the Northeast Pacific[27,28]. However, while the movement behaviour and habitat utilization in its breeding and feeding grounds have been extensively studied[8,10,29–31], the southward migratory movement behaviour and phenology of the BSG population of humpback whales from the Southern Pacific is not well known (but see Felix & Guzman[32]).

Here, using satellite tag data, we modeled the migratory behaviour in BSG whales from three sites within the breeding areas, off the coast of Costa Rica, Panama, and Ecuador. The data spans a total of eight years, from 2009 to 2016, documenting the southward migration of the whales between September and December. We tested the hypothesis that humpback whales from the BSG population display distinct swimming behaviour depending on the route they use during their southward migration. We further evaluated whether whales using a coastal route engage in opportunistic feeding along their migration route, by displaying an Area Restricted Search (ARS) movement behaviour more frequently in relatively more productive waters along the South American continent coastline. We then tested the hypothesis that humpback whales rely on environmental cues they perceive in their immediate environment in their breeding ground to predict the oceanic conditions in their feeding ground and adjust the date of onset of their southward migration.

Results

Migratory pathways

An initial 4,763 locations for 47 whale individuals were transmitted by the satellite tags. After filtering the data and interpolating tracks (see Material and methods “Data processing” for details), the final dataset consisted in 6,098 locations from 42 whales (Fig. 1A, Supplementary Data S1), with an average number of locations per individual of 145 (Table S1). Only adult individuals were fitted with a satellite tag; 27 individuals out of the 42 whales tagged were females with a calf (Table S1), and the remaining 15 single individuals not accompanied by a calf were of unknown sex. The number of individuals tracked each year ranged from 4 to 15. On average, whales transmitted for 18 days (Table 1) over a cumulated distance of 1,070 km (104 to 5,536 km). Swimming speed ranged from 10.82 to 135.23 km per day. The total distance covered during tag deployment estimated from the latitudinal range varied from 12 km up to 4,445 km.

The initiation of migration was characterized by a change in swimming behaviour from ARS to transition movement behaviour observed below a threshold latitude south of the breeding ground. Out of the 42 whales, 16 whales (9 females with a calf and 7 adults of unknown sex) did not initiate their southward migration during the study (Table 1, Table S1, Figure S1). These whales were still transmitting from locations in their breeding grounds after some individuals had initiated their migration (e.g. individual tagged in Costa Rica in 2015 with tag ID 149462 still located in Golfo Dulce on September 26th, when its tag stopped transmitting; Fig. 1C, Figure S1). The remaining 26 tagged individuals (including 18 females with a calf) were transmitting while they were migrating. Two whales tagged in Ecuador in 2013 (IDs 131590 and 131591) only started transmitting well south of the tagging location, after they had initiated their migration. Of the 24 whale individuals that initiated migration during the study, six were tagged in Panama, 3 in Costa Rica, and 15 in Ecuador (Table 1; Fig. 1, B, C and D). In Panama and Costa Rica, the southward migration started at a latitude of 8.30°N to 8.42°N, and in Ecuador at a latitude between 2.09°S and 2.12°S (Fig. 2A). The date at which whales switched from an ARS to a transition movement behaviour was used as the date of the onset of migration. The migration was initiated between August 23rd and October 7th each year. The whales initiated migration later in the most recent years ($F = 43.15$, $p < 0.0001$, Fig. 2B) and when breeding at a higher latitude in Ecuador ($F = 4.93$, $p < 0.019$), but there was no difference in departure date between females and adults of unknown sex ($t = 1.17$, $p = 0.28$).

The whales that initiated migration swam further from the shore and faster than non-migrating individuals (Table 2). Migrating whales swam at a distance ranging from 7 up to 667 km off the coastline (Table S1), although most remained close to the coast (average distance of 66 km, Table 2). Female-calf pairs swam closer to the shore than adult whales of unknown sex ($t = 15.06$, $p < 0.0001$). Migrating individuals swam up to 135 km per day and traveled at a speed of 68 km/day on average (Table 2). The whales tagged in Panama all stopped transmitting once they reached a latitude of 5°S, and they used two distinct migration routes (Fig. 1D). Two whales (tag IDs 87740 and 138202) initially swam west towards Costa Rica, before changing direction and heading south towards Ecuador. The other four whales tagged in Panama initiated migration towards the east and remained close to the shore through the Gulf of Panama. The three whales that migrated from their breeding grounds in

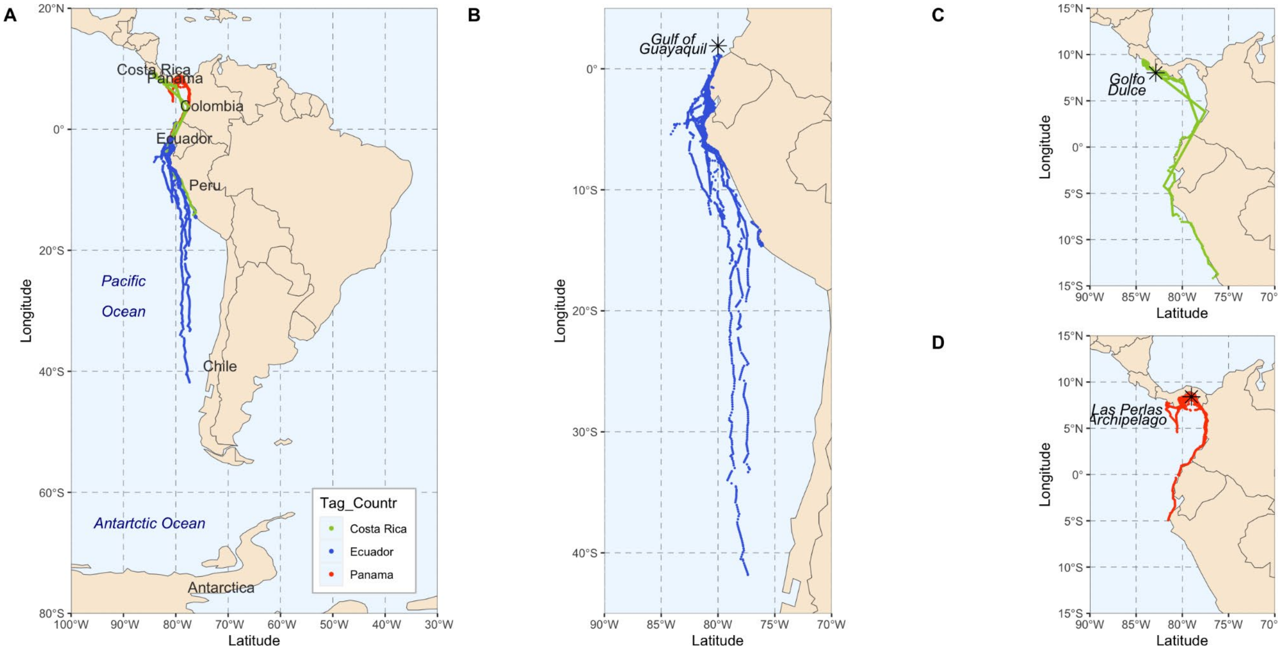

Fig. 1. **(A)** Study area and interpolated tracks of 42 humpback whales. The whales were tagged from 2009 to 2016 in three different areas (Tag_Countr): 2013 and 2016 in Ecuador **(B)**, 2015 in Costa Rica **(C)**, and 2009 in Panama **(D)**. The number of whales tagged were 22 in Ecuador, 4 in Costa Rica and 16 in Panama. The star symbol in panels A, B and C indicate the location of the tagging. Base maps were created in R[59], using the *sf*[64] and *rnaturalearth*[70] packages.

		n_whales		**tag_duration (days)**	
Tag_Countr	**Year**	**total**	**migrating**	**mean**	**range**
Panama	2009	13	4	22.0	17.3–24.6
Panama	2014	3	2	10.1	1.6–23.8
Ecuador	2013	15	8	12.5	2.0–26.3
Ecuador	2016	7	7	29.5	12.1–56.8
Costa Rica	2015	4	3	41.3	11.5–68.6
All Tagging Countries	All years	42	24	18.0	1.6–68.6

Table 1. Number of BSG whales tagged per breeding ground location and year, number of whales that initiated their southward migration during the study, and duration of transmission.

Costa Rica all used an identical route, initially in a south-east direction until they reached the shore in Colombia (Fig. 1C). A single whale tagged in Costa Rica (tag ID 149455) was detected at locations up to 15°S before it stopped transmission. All the whales that transmitted south of 15°S were tagged in Ecuador. These whales tended to travel in open waters along a nearly south azimuth once they crossed the 15°S latitude (Fig. 1B), even if they initially used distinct routes. A first group swam away from the Ecuadorian coastline, heading in a west-southwest direction for approximately 200 km before changing course to continue southward in the offshore migration corridor. The other group stayed closer to the shore until they reached 15°S latitude off the coast of Peru, when they changed direction and continued southward, away from the shore.

Movement behaviour

The stationary state-space model fit to the whole data set had a transition probability of 0.95 between the Area Restricted Search (hereafter ARS) behaviour and transiting states. The average step length was 0.11 (SD = 0.05) and 0.03 (SD = 0.02) km in the transiting and ARS behaviours, respectively (Figure S2). A total of 2,986 (49%) locations were assigned to an ARS movement behaviour, and 3,112 (51%) were assigned to a transiting movement behaviour. Besides in the breeding grounds prior to migrating, whales exhibited an ARS movement behaviour at locations all along the coastline of Colombia, Ecuador, and Peru, down to a latitude of 15°S (Fig. 3). The whales tended to exhibit more often an ARS movement behavior when closer to the coastline (t = -27.04, $p < 0.0001$), but in the most southern areas where whales displayed an ARS movement behaviour while migrating, they were located approximately 150 km away from the Peruvian coast (Fig. 3). Further south, none of the whales exhibited

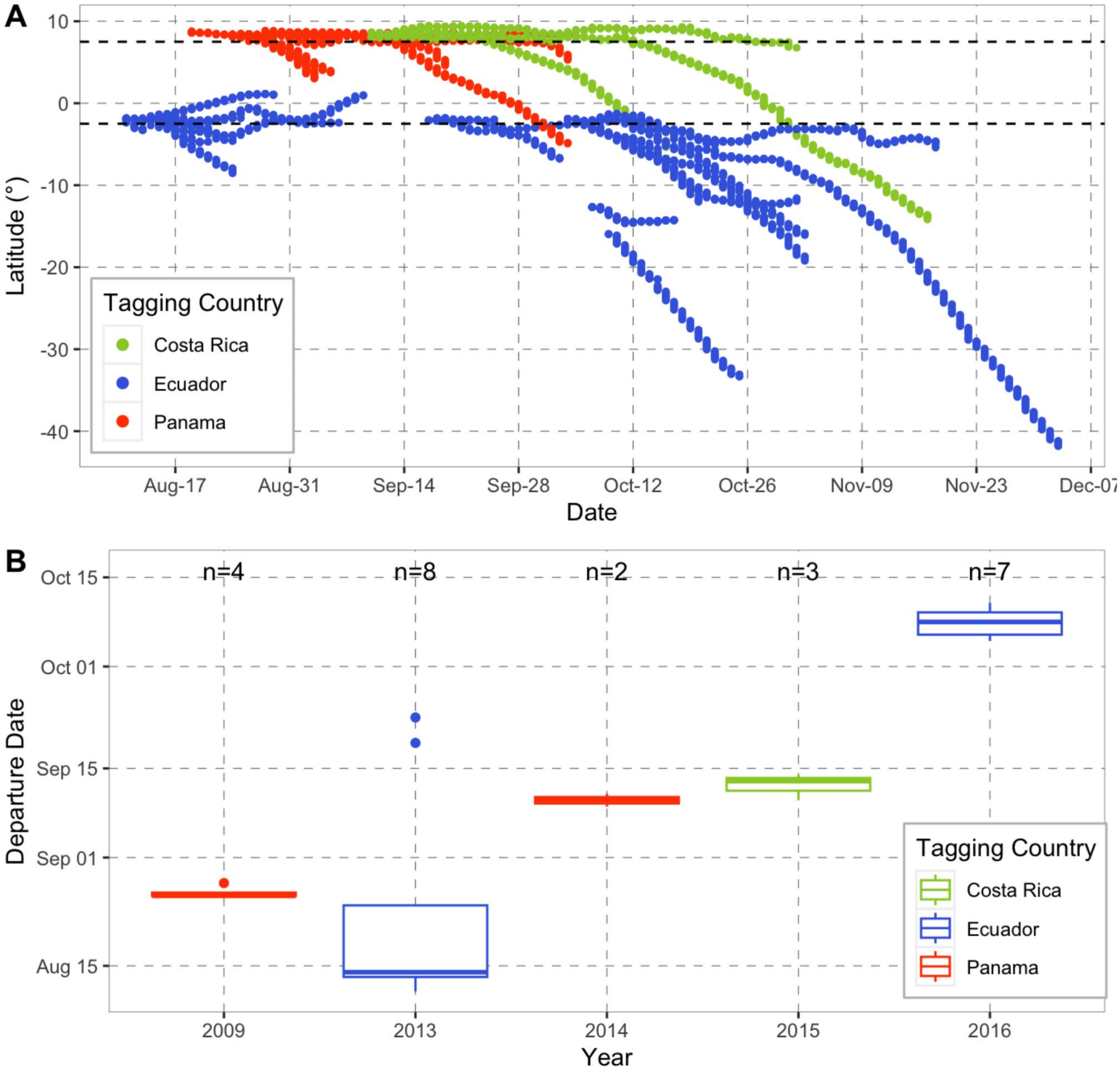

Fig. 2. **(A)** Latitude of locations as a function of the date of transmission for each whale in Panama (2009 and 2014), Costa Rica (2015), and Ecuador (2013 and 2016). The dotted line represents a latitudinal threshold at which a break in the slope occurs, marking the onset of the southward migration. This threshold is 8 °N in Panama and Costa Rica, and 2.5 °S in Ecuador. **(B)** Departure date of 24 migrating whales tagged in their breeding grounds in Costa Rica (2015), Panama (2009 and 2014), and Ecuador (2013 and 2016).

	Migrating		Non-Migrating		Mean comparison test	
	Mean	Range	Mean	Range	t	*p*
Distance (km)	65.99	(1–667)	11.19	(1–66)	32.99	< 0.0001
Speed (km/day)	67.99	(36.97–135.23)	33.04	(10.82–79.66)	69.98	< 0.0001

Table 2. Movement characteristics in BSG whales that initiated migration during the study (migrating, $n = 24$) and whales that did not initiate migration (Non-Migrating, $n = 18$). Distance: distance to the shoreline (km), speed: speed (km/day). Difference between groups were assessed with a t.test.

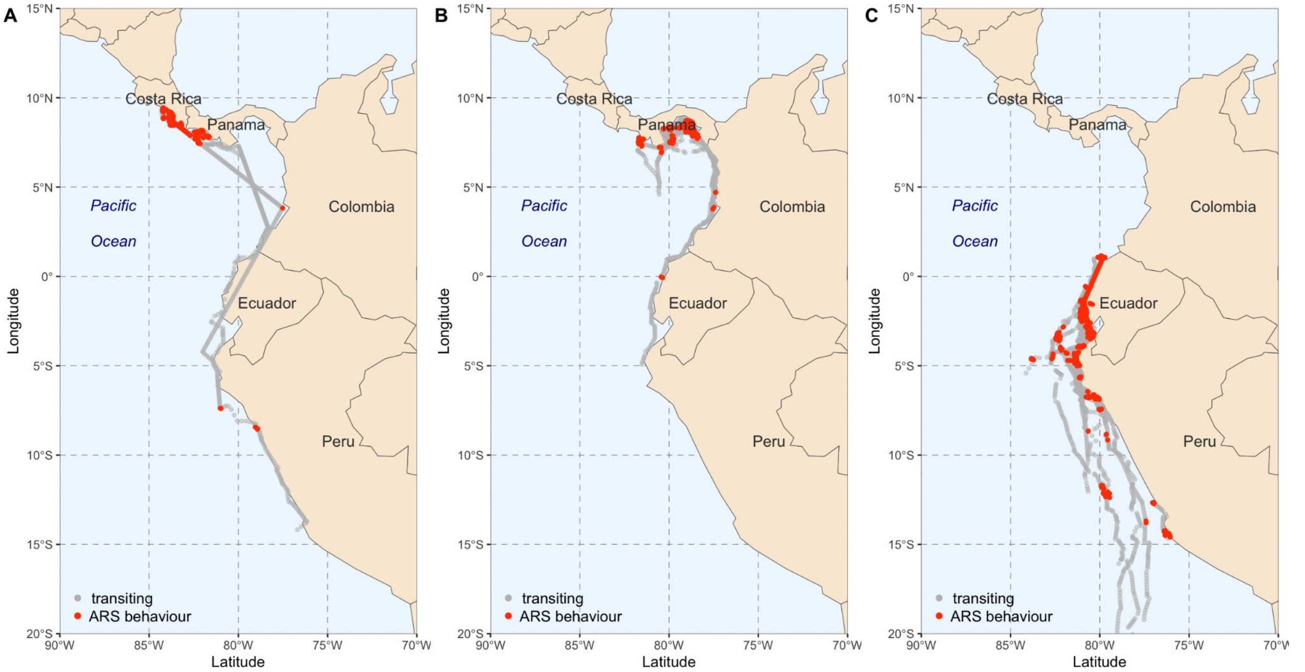

Fig. 3. Interpolated tracks of 42 studied humpback whales tagged in Costa Rica (**A**, *n* = 4), Panama (**B**, *n* = 16), and Ecuador (**C**, *n* = 22) classified into two states of movement behaviour: transiting (in grey) and Area Restricted Search (ARS) behaviour (in red). Base maps were created in R[59], using the *sf*[64] and *rnaturalearth*[70] packages.

an ARS movement behaviour, while swimming further away from the coast. One female individual tagged in Panama (tag ID 138203) migrated close to the coastline (less than 50 km) and exhibited an ARS movement behaviour along the coast of Colombia around 4°N, as well as off the coast of Ecuador, at about 0°N (Fig. 3B). A female tagged in Costa Rica (tag ID 149459) also exhibited an ARS movement behaviour at locations off the coast of Colombia at a latitude of 4°N, and another individual of unknown sex (tag ID 149455) exhibited an ARS movement behaviour close to the coast of Peru (approximately 50 km) at a latitude of 7 °S (Fig. 3A). Similarly, individuals tagged in Ecuador exhibited an ARS movement behaviour off the coast of Peru between 4°S and 5°S, and further south between 6.5°S and 7.5°S (Fig. 3C).

Oceanic conditions

The oceanic conditions in the breeding grounds from June to September of the year when whales were tagged varied significantly across years. Oceanic Niño Index (ONI) ranged from − 0.26 to + 1.31. Years 2009 and 2015 were categorized as El Niño years with an ONI value > + 0.5, while the remaining three years were normal (Figure S3A). A higher sea-surface temperature (SST) in the northern breeding grounds of Panama and Costa Rica was associated with a lower productivity or lower mean chlorophyll-a level (Figure S3B) as well as with a lower ONI ($t = 9.37$, $p < 0.0001$). Sea surface temperature decreased through the breeding season but was significantly lower and more variable in Ecuador than in Panama and Costa Rica (Figure S3B, Figure S3C). The input of cold waters off the coast of Ecuador lasted for a longer time in 2016 than in 2013, well into the breeding season of the whales, but the lowest average temperature during the upwelling regime was higher in 2016 (Figure S3C). The concentration in chlorophyll-a was generally lower in Panama and Costa Rica than in Ecuador (Figure S3B). Across all years, peaks of high concentration in chlorophyll-a occurred and were especially high in Panama in 2009 and in Ecuador in 2013 (Figure S3D), but occurred at different times (on July 8th 2009 in Panama, and June 6th 2013 in Ecuador). Overall, the maximum level of chlorophyll-a recorded in the breeding grounds during the breeding season decreased from 2009 to 2016, but the mean value did not change (Figure S3B).

During their migration, the whales experienced variation in chlorophyll-a concentration, with a peak in very high concentration at around 7.5°S latitude (Figure S4B). Smaller peaks also occurred at latitudes of approximately 5°N, 2.5°N and 14°S. The chlorophyll-a concentration dropped down to values close to zero at southern latitudes, below 15°S (Figure S4B). Sea surface temperature followed the expected pattern of decreasing values with increasing latitude, but with a sharp transition from warm to cold waters around 15°S, off the southern coast of Peru (Figure S4C).

One notable change in oceanic conditions in the feeding grounds has been a shift towards a delayed melting of the sea ice and a shorter duration of the melting, from 134 days in 2009 down to 60 days in 2016 (Figure S5A). More significantly, the first day of full melting of the sea ice (the earliest date at which sea ice concentration reached 0%) occurred later each year, from November 16th in 2008 to January 30th in 2016. The sea ice concentration seasonal average increased from 1.4% in 2009 to 16.5% in 2016, and the extent of sea ice (maximum sea ice concentration) also increased from 7.4% up to 57.1% (Figure S5A). The sea-surface temperature in the feeding grounds consistently reached its maximum each year by late February. However, the seasonal average of sea-surface temperature decreased over time, from 1.28 °C in 2009 down to 0.67 °C in 2016, (Figure S5B). The decrease in sea surface temperature was especially characterized by the seasonal maximums recorded, with a maximum of 2.77 °C in 2013, down to 1.58 °C in 2016.

Oceanic conditions and onset of migration

We modelled the effect of oceanic conditions in the breeding grounds on the date of the onset of the southward migration. The model with the departure date as a response variable revealed a significant effect of the second (Dim. 2, F = 56.702, $p < 0.0001$) and third (Dim. 3, F = 5.449, $p < 0.0307$) axes of the PCA run on the environmental variables (Table 3). Humpback whales initiated their southward migration earlier when levels of chlorophyll-a in the breeding grounds were lower (with higher Dim. 2, Fig. 4A, Figure S7A). Humpback whales also initiated their southward migration at an earlier date when the peak in sea surface temperature occurred earlier, in warmer waters, and in El- Niño years (higher Dim. 3, Fig. 4A, Figure S7B).

We then fit a model with the departure date as a response variable and the oceanic conditions (chlorophyll-a level and sea surface temperature) extracted at each location and time along the migration route of the 24 whales that initiated their migration during the study. The model revealed a significant effect of both Dim, 1 (F = 53.96 $p < 0.0001$) and Dim. 2 (F = 17.20, $p < 0.0005$) on the departure date of the whales (Table 3). Similarly to what was suggested with the breeding ground model, humpback whales left their breeding grounds at an earlier date when the waters they encountered during their migration route were less productive (lower Dim. 1) and warmer (lower Dim. 1 and higher Dim. 2, Fig. 4B, Figure S7C).

Finally, we modelled the effect of the oceanic conditions in the feeding ground of the Antarctic Peninsula waters on the date of the onset of the southward migration. The model revealed a significant effect of both Dim. 1 (F = 38.34, $p < 0.0001$) and Dim. 2 (F = 14.13, $p < 0.0002$) on the date of the onset of the southward migration (Table 3). Humpback whales initiated their migration later when sea ice concentration in the Southern Ocean was larger (higher Dim. 1) and when sea surface temperature was lower (lower Dim. 2) in the preceding feeding season (Fig. 4C, Figure S7D). Humpback whales also left their breeding grounds at a later date when the melting of sea ice in the Antarctic Ocean was delayed.

Oceanic conditions and movement behaviour during migration

We modelled the effect of oceanic conditions (sea surface temperature and chlorophyll-a level with and without a 30-day time lag) at each location and time along the track of each whale on their movement behaviour. The models explained between 26% and 27.5% of the deviance, and the model with the level of chlorophyll-a concentration as a covariate had the best fit with an AIC of 521.1 (Table 4). Humpback whales were more likely to be in a transiting state at southern location in colder (Fig. 5A), and in less productive waters (Fig. 5B and C).

	edf	Ref.df	F	*p*-value
Breeding Grounds Cue Model				
s(Dim. 1)	1.000	1.000	2.053	0.1681
s(Dim. 2)	1.000	1.000	56.702	**4.07e-07**
s(Dim. 3)	1.000	1.000	5.449	**0.0307**
Deviance explained = 79.3%; R-sq. (adj.) = 0.750; AIC = 189.763				
Migration Route Model				
s(Dim. 1)	1.000	1.000	53.958	**3.21e-07**
s(Dim. 2)	1.000	1.000	17.201	**0.0005**
Deviance explained = 77.2%; R-sq. (adj.) = 0.750; AIC = 188.097				
Feeding Ground Cue Model				
s(Dim. 1)	1.000	1.001	38.344	**4.24e-06**
s(Dim. 2)	1.536	1.785	14.125	**0.0002**
Deviance explained = 78.0%; R-sq. (adj.) = 0.753; AIC = 188.784				

Table 3. The effect of environmental cues on departure date in 24 humpback whales that initiated their southward migration during the study. Three distinct PCA were run for each dataset, and the PCA axes (Dim. 1, Dim.2 and Dim. 3) were used to characterize the oceanic conditions in the breeding grounds prior to their southward migration, along the migration route, and in the feeding ground of the Antarctic Ocean. Three General Additive models (GAMs) were fit with a gaussian family and departure day (Julian day) as a response variable. The first three, two and two axes were entered as covariates in the breeding grounds, migration route, and feeding grounds models, respectively. The tagging area was included in the breeding ground model as a parametric factor with two levels (North for Panama and Costa Rica, and South for Ecuador) to account for the differences in oceanic conditions between the two areas. Edf: effective degree of freedom, Ref.edf: reference degrees of freedom.

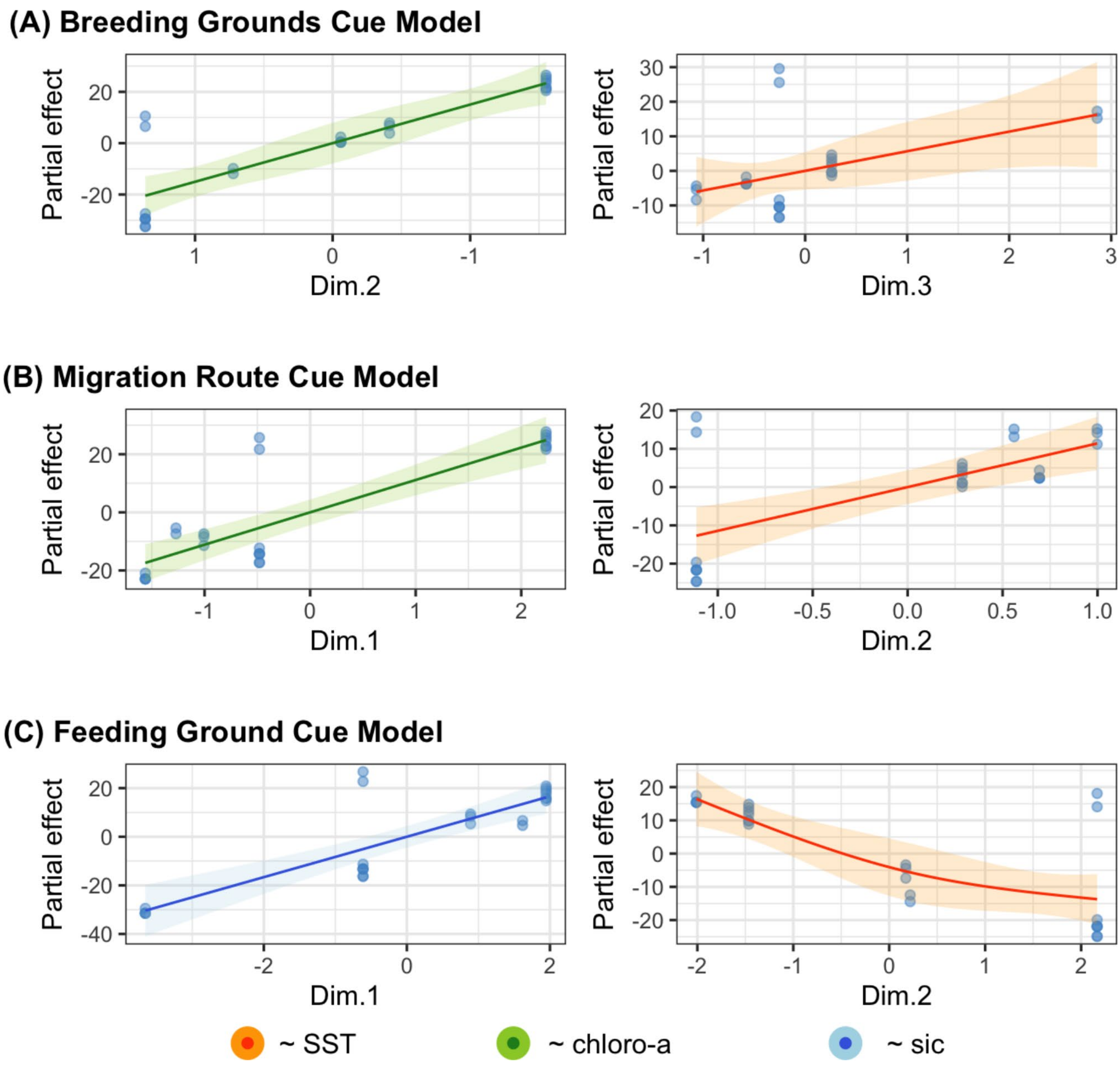

Fig. 4. The effect of the oceanic conditions on the departure date of 24 migrating humpback whales estimated by fitting three GAMs to the data. Model summaries are presented in Table 2. To facilitate visualization, the curves were colored by the environmental variable which correlated the most with each PCA axis, and the x-axis was reversed when this correlation was negative. **(A)** Whales initiated their migration at a later date when waters in their breeding grounds were less productive (Dim. 1) and when the peak in sea surface temperature occurred at a later date (Dim. 2). **(B)** Whales also left their breeding grounds at a later date when they encountered more productive (Dim. 1) and colder (Dim. 2) conditions during their migration. **(C)** The onset of the southward migration was delayed when sea ice concentration in the feeding ground in the year prior to the migration was higher (Dim. 1), melting was delayed (Dim. 2), and sea surface temperature was lower (Dim. 2).

Discussion

We described the migratory behaviour of the southward yearly migration of BSG humpback whales over multiple years, and how it relates to inter-annual changes in oceanic conditions. Migrating whales demonstrated a high fidelity to previously described migration routes for this population[32], with routes differing in their distance from the shore. Females with a calf tended to travel closer to the shore, preferring longer coastal routes, while adults travelling alone preferred the shorter oceanic routes, supporting the hypothesis that humpback whales migrate through coastal or oceanic routes depending on the individual and their reproductive status[8,32]. Nursing females may travel close to the shore to reduce predation risk on their calf from killer whales (*Orcinus orca*) that tend to forage in deeper waters offshore[33]. Because female humpback whales maintain constant communication

	edf	Ref.df	Chi-square	*p*-value
Sea surface temperature model				
s(sst, latitude)	24.36	29.00	529.7	< 2e-16
Deviance explained = 26.0%; R-sq. (adj.) = 0.29; AIC = 3892.96				
Chlorophyll-a model				
s(chloro-a, latitude)	25.44	29	521.1	< 2e-16
Deviance explained = 27.5%; R-sq. (adj.) = 0.31; AIC = 3323.47				
Chlorophyll-a (30-day time lag) model				
s(chloro-a (lag), latitude)	24.89	29	532.1	< 2e-16
Deviance explained = 26.3%; R-sq. (adj.) = 0.29; AIC = 3519.72				

Table 4. The effect of oceanic conditions on the movement behaviour of 24 humpback whales during their southward migration. Three General Additive models (GAMs) were fit with a binomial family and behavioural state (ARS versus transiting) as a response variable. Each covariate was modeled in interaction with latitude to account for the spatial structure in environmental variation. Edf: effective degree of freedom, Ref.edf: reference degrees of freedom.

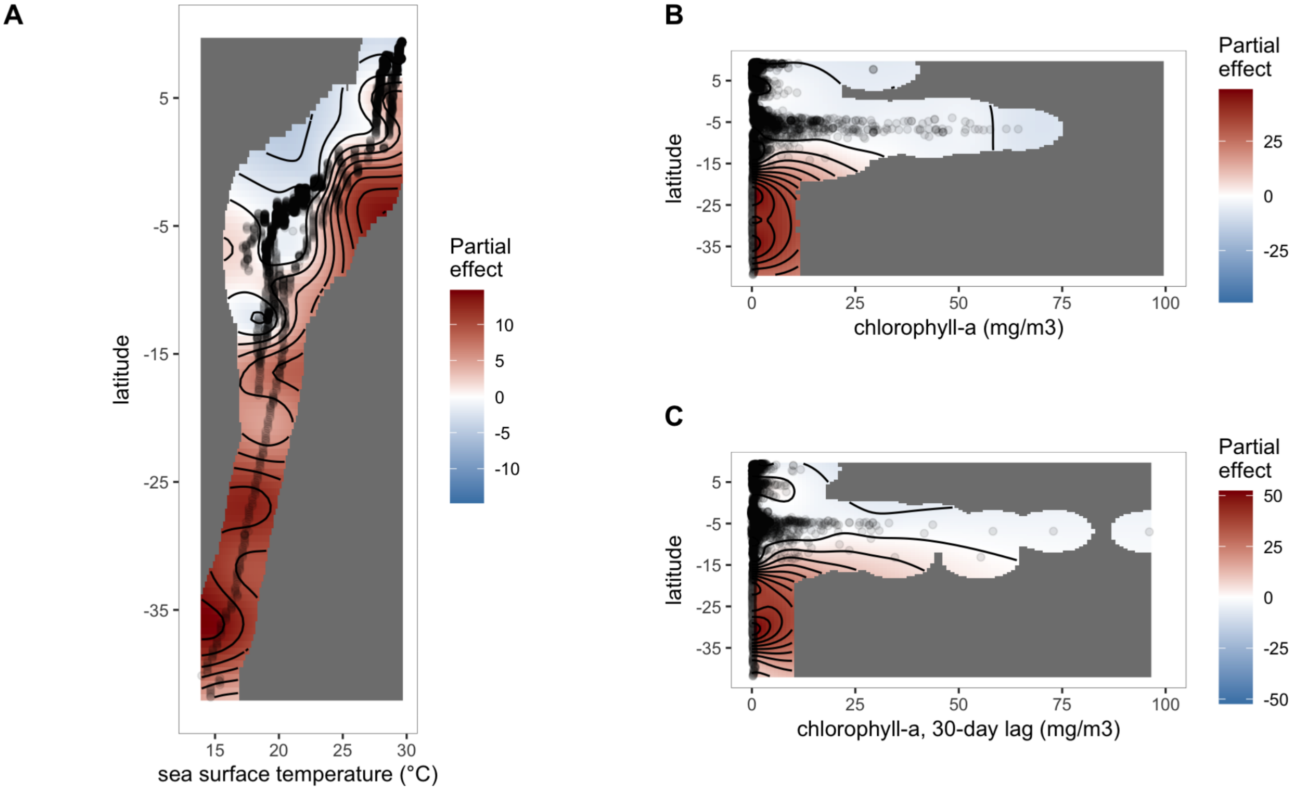

Fig. 5. The effect of the oceanic conditions on the movement behaviour of 24 migrating humpback whales during their southward migration. **(A)** Latitudinal variation in sea surface temperature extracted along the tracks of migrating whales, **(B)** Latitudinal variation in chlorophyll-a level extracted along the tracks of migrating whales, **(C)** Latitudinal variation in chlorophll-a level with a 30-day time lag extracted along the tracks of migrating whales. Partial effects indicate the effect of the covariate on the probability of a whale to be in an ARS (negative, colored in blue) or transiting (positive, colored in red) movement behavioural state. Whales were most likely to be in a transiting behavioural state at southern locations, in colder waters (**A**), and in less productive waters with lower levels in chlorophyll-a (**B** and **C**).

by calling their calf during migration, noise pollution close to the shoreline may also provide further protection to the mother-calf pair from nearby predators or from male escorts of humpback whales, by reducing their opportunity to detect the calls of the pair[34]. Whales travelling closer to the shore were also swimming at slower speeds, which has been associated with feeding behavior[10]. We also found that during their southward migration, female whales engaged more frequently in an ARS behavior than adults of unknown sex. Female whales travelling with a calf may engage in opportunistic feeding during their migration, because of their higher energetic requirement while still nursing[15,32], or to seek opportunities for their calf to rest during their first migration. Here, we found evidence for the first time of BSG humpback whales exhibiting an ARS swimming behaviour associated with waters with high productivity at several locations along the west coast of the South American continent in Colombia, Ecuador, and Peru, down to 15°S latitude. We identified two such areas off the coast of Peru that coincided with high levels of chlorophyll-a. Our results suggest that humpback whales, especially those swimming closer to the coastline, time their migration to coincide with strong seasonal wind-driven upwellings resulting in high productivity areas in two specific locations along the coast of Peru. Because waters with high levels of chlorophyll-a concentration are likely to host a larger amount of prey, these findings point to the possible occurrence of opportunistic feeding during migration and may help identify priority areas for habitat conservation (e.g[35]).

BSG whales frequent waters that are affected by El Niño Southern Oscillation (ENSO) conditions. In the Southern Pacific, El Niño is associated with a decrease in meridional trade winds and a westward displacement of the Pacific Subtropical Anticyclone that is tied to major oceanic current circulation in the region[36], resulting in unusually high sea surface temperature anomalies and a reduction of upwellings in El Niño years. While Felix and Haase[37] found no effect of El Niño on group size, structure or distribution of humpback whales breeding off the coast of Ecuador when comparing sightings in 1996, a normal year, with those in 1997, a strong El Niño year, a one-year lag response was found in this population with a significant reduction in birth rate[38]. Major oceanographic events such as El Niño may further impact the migratory behaviour of humpback whales, by delaying their southward migration in El Niño years, or as illustrated by a recently described unusual migration of a humpback whale between two oceanic basins[39].

We found a significant variability in the phenology of the southward migration of the BSG humpback whales, contrary to previous studies[25]. The timing of the onset of migration varied across individuals, being spread over several weeks across individuals that spend the winter in the same breeding ground. It has been found that in humpback whales spending the winter in warm tropical waters, female-calf pairs tended to leave their breeding ground later than male individuals, or females that did not birth in that year[14,25]. The peak of birthing in the region occurs in August[9], but some whales can extend their stay in their breeding ground until December[25]. Females that would have given birth at a later time would need to shift their departure date for the calf to be ready to achieve its first migration towards the feeding ground in Antarctica (e.g[25]). Here however, we did not find any evidence for such stratification of departure date.

Our results suggest that BSG whales may integrate environmental cues with other ecological or social components, and associate environmental conditions in the breeding grounds with those of the upcoming feeding season in the Southern Ocean to determine the date to initiate their migration. It appears that whales rely on environmental cues in their immediate surroundings, such as productivity and sea-surface temperature in their breeding grounds to make this decision. Moreover, the southern migration onset date of BSG whales was also correlated with the sea ice concentration in the feeding ground during the feeding season preceding the southward migration. BSG whales may thus integrate cues from the environmental conditions in the breeding grounds to predict the phenology of resource availability at their feeding ground in the upcoming feeding season. During the austral summer, BSG whales feed predominantly on krill (*Euphausia superba*), a resource they rely on to accumulate the fat reserves they need to return to their breeding grounds by the end of the summer of each year[40,41]. Larval juvenile krill overwinter under the sea ice, where they feed on phytoplankton that form clumps below the ice. Upon breaking-up of the sea ice in early summer, swarms of adult krill become available in the ice-free waters for marine mammals that will consume them in large quantity. The highest productivity levels in the Antarctic Ocean occurs at the onset of the breaking-up of the sea ice[42], which coincides with the arrival of migratory BSG whales to the area. A larger amount of sea ice during the winter in the Antarctic Ocean will result in delayed melting of the sea ice and later bloom in krill, creating a shift in the timing of maximum resources to which the whales are adapting by initiating their migration at a later date. BSG whales may thus also use environmental cues, likely based on previous experience, to determine the timing of their southern migration. It remains unclear if the cues come primarily from the breeding or from the feeding ground, or if both are complementary. Considering that accumulating sufficient energy for migration is crucial to reproductive success, it is likely that Antarctic conditions primarily dictate the onset of the northbound migration toward breeding areas. Conversely, once at the breeding grounds, whales may adjust the timing of their southbound migration based on environmental cues, optimizing their arrival at the feeding grounds. In line with these results, there is evidence for the reliance on long-term memory of oceanic conditions in the blue whale (*Balaenoptera musculus*) during its northward migration in the northern Pacific[6], in humpback whales (*Megaptera novaeangliae*) migrating off Brazil in the Southwest Atlantic Ocean[43], in north-eastern pacific grey whales (*Eschrichtius robustus*) summer migration[26], and in the narwhal (*Monodon monoceros*) which has delayed its autumn migration to the arctic over the past two decades[44].

The global rise in sea-surface temperature and changes in other oceanic characteristics associated with climate change will have significant impacts on marine ecosystems[45]. Climate warming may impact baleen whale distribution and their migration patterns, leading to spatio-temporal mismatches in interactions with preys[46–48]. In their breeding grounds of the tropical waters, the temperature is predicted to raise outside the suitable range of 21–28 °C by the end of the century for 35% of humpback whales globally[49], especially in El Niño years[29]. Whales breeding off the coast of Ecuador experience colder waters, especially in years with strong upwellings in this area[50,51]. However, with the warming of ocean waters, the upwelling regime and frequency are predicted to get weaker globally, thereby lowering productivity levels in the breeding grounds of these whales, as well as lessening opportunities for the whales breeding further north in Panama and Costa-Rica to encounter waters with high productivity along their migration route. The upwelling regime in the Southern Pacific is peculiar, in that it is wind-driven, with strong upwelling events triggered by changes in direction and intensity of the northeast Trade wind, as well as the seasonal migration of the Intertropical Convergence Zone. We found that humpback whales were exhibiting an ARS movement behaviour in three main regions along the coastline of Ecuador and Peru that all coincide with known areas of seasonal upwelling and associated high productivity. A change in the timing or location of these upwelling events may lead to a spatio-temporal mismatch between peaks in productivity and the whales. Similarly, the ability of migrating humpback whales to synchronize their arrival at their feeding grounds in Antarctica may be challenged with climate warming. Notably, studies have shown a reduction in krill availability with the increase in sea-surface temperature and decrease in sea ice duration, negatively impacting humpback whales in feeding grounds[6,41,52], leading some individuals to swim eastward of their known feeding area[53,54]. With such decrease in prey availability, humpback whales may need more time in feeding grounds or feeding during migration to attain their energy requirements. Migrating whales may also shift their diet as seen in humpback whales individuals feeding in the Magellan strait, southern Chile, that prey on squat lobsters (*Munida gregaria*) and Fuegian sprat (*Sprattus fuegensis*), in addition to krill (*Euphausia lucens*)[55]. A recent study also showed that humpback whales have shifted their arrival time at their breeding ground in Colombia earlier over the past three decades[25]. Because calf development in warm water is related to larger adult size[56], a later arrival at the breeding grounds may in turn contribute to the later onset of the southward migration we documented here. Together with previously published work, our study suggest that humpback whales may adapt to climate warming to reduce the spatio-temporal mismatch between their migration and their interaction with prey, along their migration route and in their feeding grounds.

Conclusion

Our study contributes to the understanding of the migration patterns of the Southeastern Pacific population of humpback whales, but it is also the first in the region to use satellite tagging data to examine the relationship between the onset of their southward migration and changing oceanic conditions. Developing our understanding of humpback whale migration and how it is affected by changing environmental conditions is valuable for predicting future threats to this species, as well as identifying the most critical areas and/or times for management and conservation. Here, we found that while humpback whales may engage in opportunistic foraging in areas of high productivity along their migration route to their feeding grounds, they time their migration to reach their feeding grounds with the time of the break-up of the sea-ice which triggers a bloom in krill in the Antarctic Ocean. This hypothesis is further supported by the fact that whales breeding in Ecuador, the most southern location in our study, initiated their migration later than whales breeding further north, in Panama and Costa Rica, resulting in all whales reaching the Antarctic Ocean around the same date. Overall, our findings suggest that humpback whales integrate information they gather from their immediate environment to predict the oceanic conditions at distant locations and adjust the timing of their migration, maximizing their interaction with their preys. However, it is unclear if humpback whales will fully succeed in tracking their prey in a rapidly changing climate and ensure the long-term persistence of the species.

Methods

Study area

The study area ranged from 9.47°N to 41.87°S latitude in the Southern Pacific (Fig. 1). Humpback whales were tagged in their breeding grounds at Golfo Dulce in southern Costa Rica (8.02°N, 82.88°W), in Las Perlas Archipelago in Panama (8.41°N, 79.02°W), and at the northern limit of the Gulf of Guayaquil, Salinas, in Ecuador (2.12°S, 80.54°W). These areas are all located in warm tropical waters, although both Las Perlas Archipelago in Panama and the Gulf of Guayaquil in Ecuador are subjected to strong seasonal wind-driven coastal upwelling[50,57].

Satellite tag data

Collection

Forty-seven humpback whales were tagged with real-time satellite transmitters from Wildlife Computers SPOT5 host version 5.02.1007, model AM-S193C. The tags were deployed using an ARTS pneumatic line-thrower (Restech Inc., Bodø, Norway) held 3 to 5 m from the whales. Only adult whales were tagged, and the transmitters were attached to the whales on either side of the dorsal fin, approximately 20 cm below and in front of the dorsal fin. The whales were tagged during five breeding seasons in Panama (2009, 2014), Costa Rica (2015) and Ecuador (2013, 2016, Table 1), with detailed tagging procedures described in Guzman & Felix[9] and Guzman et al.[58]. When accompanied by a calf at the time of tagging, the adult whale was classified as a female. All other adult whales tagged, whether they were solitary or in a group, were assigned as unknown sex.

Data processing

All satellite data were processed and analyzed in R version 4.2.2[59]. We used the *argosfilter* package[60] to filter out Z-class locations (10 locations), locations with duplicate time stamps within each individual whale, unrealistic locations based on speed with a threshold of 10 m/s (36 km/h) (45 locations), as well as short tracks with less than 10 locations (32 locations for 5 individuals with tag IDs 87731, 129272, 131592, 138206 and 138207). We then interpolated the tracks to estimate locations every 180 min (3 h) using the *move* package[61]. One whale (tag ID 131585) transmitted for 7 days, stopped emitting, then started transmitting 57 days later when it had reached its feeding ground in Antarctica (see[32]). As this individual had completed its southward migration, the final 179 locations were excluded from the dataset.

Movement modeling

We modeled the movement behaviour of each whale by fitting a stationary state space model with two behavioural states using the *moveHMM* package[62]. The first state was characterized by smaller step lengths (distance covered between two successive locations) and wider range of turning angles (change in movement direction) demonstrated during Area Restricted Search (ARS) behaviour, while the second state was characterized by larger step lengths and lower range in turning angle, characteristic of transiting behaviour (Figure S2). We set the initial parameters of the model by inspecting the distribution of the step length and turning angle values across the track data. The initial parameters of the model were set at a step length of 0.025 and 0.15 km and a turning angle of pi and 0 for states 1 and 2, respectively. We then ran the function viterbi in the *HMM* package[63] on the stationary state space model to assign each location to one of the two behavioural states.

Migration phenology

We visually inspected the tracks of each whale to identify individuals that initiated migration by plotting the latitude of their location as a function of date (Fig. 2A). The transition point from a near-zero to a steeper negative slope was interpreted as the point of onset of migration. We validated the identification of non-migrating whales by fitting a linear relationship between latitude and date, and extracting the slope value of this relationship to identify whales with a zero or positive slope value. We determined the date of the onset of migration for the remaining individuals, by extracting the earliest date at which an individual whale displayed a transiting behaviour south of a threshold latitude we determined visually (Fig. 2A). However, in Ecuador in 2013, one female whale (tag ID 131584) initiated a migratory movement behaviour southward, but eventually returned to its tagging location in its breeding ground and did not leave its breeding ground during tag deployment.

Environmental data

Collection

We extracted three distinct sets of environmental data and considered oceanic conditions (1) in the breeding ground during the breeding season up until the departure to the feeding grounds, from June 1st to September 30th, (2) during migration, and (3) in the feeding ground the year preceding the southward migration, between November 1st of the year preceding the tagging and March 31st of the year of the tagging. We used the same approach to characterize the oceanic conditions in the breeding and feeding grounds. For each two breeding grounds and the feeding ground, we built a polygon overlapping the study area and cropped out the land areas using the functions st_difference and st_intersection in the *sf* package[64]. We then drew 4,000 random locations within the resulting polygon using the st_sample function in the *sf* package[64] (Figure S6). We then assigned each location to one of 4,000 dates sampled in a regular sequence between June 1st and September 30th of the tagging year for the locations in the breeding grounds, and between November 1st and March 31st prior to the tagging for the feeding ground. Environmental data along the migratory routes were extracted for locations and times following the departure date of the whales that initiated their southward migration.

Extracted variables

We extracted the set of five 3-month sea-surface temperature anomalies of the Oceanic Niño Index (ONI) between May and October for each year of tracking data[65]. We also considered variables related to temperature (sea-surface temperature), productivity (chlorophyll-a) and sea-ice to characterize the oceanic conditions. We obtained the ONI data from the Climate Prediction Center of the NOAA National Weather Service[65], while chlorophyll-a, sea surface temperature, and sea ice data were downloaded from the ERDDAP data server, which provides open access to oceanographic datasets (Table S2). The chlorophyll-a concentration (mg.m-3), sea-surface temperature (°C), and sea ice concentration (%) data were downloaded using the *rerddap* package[66] and extracted using the *rerddapXtracto* package[67]. We calculated seven variables to characterize the oceanic conditions in the breeding grounds and in the feeding ground (Table S3), while we extracted three variables at each location along the migration route of each individual whale.

We calculated the daily average in chlorophyll-a for each sampling year in the breeding grounds, and used the following three variables:

- *mean_chloro*: the mean chlorophyll-a level observed across the entire breeding season for each sampling year in the two breeding grounds (2009, 2014 and 2015 in Panama/Costa Rica and 2013 and 2016 in Ecuador),
- *mean_chloro_lag*: same as *mean_chloro*, with a 30-day time lag,
- *mean_chloro_anomaly*: the anomaly in chlorophyll-a level, estimated as the difference between the average for each year and the historical average (mean daily chlorophyll-a observed across the entire breeding season between 2009 and 2016 in each breeding ground).

Next, we calculated the daily average in sea-surface temperature for each sampling year in the breeding and feeding grounds, and used the following four variables:

- *mean_SST*: the mean sea surface temperature observed across the entire breeding and feeding seasons for each sampling year in the two breeding grounds (2009, 2014 and 2015 in Panama/Costa Rica and 2013 and 2016 in Ecuador) and each sampling year in the feeding ground,
- *mean_SST_anomaly*: the anomaly in sea surface temperature, estimated as the difference between the average for each year and the historical average (mean daily STT observed across the entire breeding season between 2009 and 2016 in each breeding ground and across the feeding season between 2008 and 2016 in the feeding ground),
- *max_SST*: the maximum value of daily sea surface temperature observed during the breeding season in each breeding ground and during the feeding season in the feeding ground for each year,
- *day_maxSST*: the earliest date at which the mean daily sea surface temperature peaked to a maximum each year in each breeding ground and in the feeding ground.

For the feeding ground, we calculated three additional variables related to sea ice concentration in the Antarctic Ocean:

- *mean_sic*: the mean value of daily sea ice concentration observed across the feeding season in each sampling year,
- *max_sic*: the maximum in daily sea ice concentration observed across the feeding season in each sampling year,
- *day_start_melting*: the earliest date at which the daily sea ice concentration reached 0, marking the first day of complete melting of sea ice.

Finally, we extracted the sea surface temperature and chlorophyll-a level values with and without a 30-day time lag at each location of the whales during their migration.

Environmental data processing
Because most of these variables were highly correlated (e.g. high levels of chlorophyll-a are associated with colder waters), we ran a Principal Component Analysis (PCA) on each three sets (breeding grounds, migratory routes and feeding ground) of environmental variables, using the function prcomp from the *stats* package in R[59]. The variables were scaled for all three PCAs, and we used the package *factoextra*[68] to extract and visualize the results of the PCA. The first three axes of the PCA run on seven variables from the breeding grounds explained 98.8% of the variation (Figure S7A). The first axis was negatively correlated with variables of sea surface temperature (mean, maximum and anomaly) and positively correlated with chlorophyll-a levels (mean and anomaly). Levels in chlorophyll-a were also negatively correlated with the second axis, and variation along the third axis was mostly explained by the date of the peak in sea surface temperature. The mean value of sea surface temperature along the migration route was negatively correlated with the first axis of the second PCA, which explained 76.6% of the variation, and positively correlated with the second axis (23.2% of the variation, Figure S7B). Variation along the second axis was positively correlated with levels in chlorophyll-a (both the mean value and mean value with a 30-day time lag). Finally, the first two axes of the PCA run on the variables in the feeding ground explained 99.1% of the variation (Figure S7C), the first axis being negatively correlated with sea surface temperature (mean, maximum and anomaly) and positively correlated with sea ice concentration (mean and maximum). The date of the peak in sea surface temperature was positively associated with the second axis, while the earliest day of complete melting (sea ice concentration of 0%) was negatively correlated with the second axis (Figure S7C).

Environmental conditions and onset of migration

We ran three distinct models (breeding, migrating and feeding) to test for the effects of the oceanic conditions at the breeding grounds, during migration and at the feeding ground on the date of the onset of the southward migration of humpback whales off their breeding grounds. For each three model, a Generalized Additive Model (GAM) was fitted using the *mgcv* package in R[69] with a gaussian family, departure date (Julian day) as the response variable, and axes of the PCA that cumulatively explained more than 98% of the variance as covariates (first three axes for the breeding ground model, first two axes for the migration model and first two axes for the feeding model), As sea-surface temperature and chlorophyll-a levels differed across breeding grounds in Ecuador and breeding grounds in the tropical waters of Panama and Costa Rica, we included in the breeding model the tagging area as a two factor (North vs. South) covariate. Model formula were as follow for the breeding ground model: *Julian day ~ Tag_area + s(Dim.1) + s(Dim.2) + s(Dim.3)*, migration model: *Julian day ~ s(Dim.1) + s(Dim.2)*, and feeding ground model: *Julian day ~ s(Dim.1) + s(Dim.2)*.

Environmental conditions and movement behaviour during migration

To test for the effect of oceanic conditions on the movement behaviour of humpback whales during their southward migration, we fit a GAM model with a binomial family and the movement behavioural state (ARS versus transiting) as a response variable using the *mgcv* package in R[69]. For each 24 whales that initiated their migration during the study, we used the subset of the data including only locations recorded after their departure date. We included in the model three covariates: the sea surface temperature and the chlorophyll-a levels with and without a 30-day time lag, each term in interaction with latitude. Due to high correlations between the covariates (i.e. colder waters typically are more productive), we fit three distinct models, one for each of the covariate.

Data availability

All data used for this study are included in this article as Supplementary Information files.

Received: 12 March 2024; Accepted: 20 January 2025

References

1. Avgar, T., Street, G. & Fryxell, J. M. On the adaptive benefits of mammal migration. *Can. J. Zool.* **92** (6), 481–490 (2014).
2. Corkeron, P. J. & Connor, R. C. Why do baleen whales migrate? *Mar. Mamm. Sci.* **15**, 1228–1245 (1999).
3. Abrahms, B. et al. Emerging perspectives on resource tracking and animal movement ecology. *Trends Ecol. Evol.* **36**, 308–320 (2021).
4. Wang, J. et al. Changing lengths of the four seasons by global warming. *Geophys. Res. Lett.* **48** (6), e2020GL091753–e2020GL092021 (2021).

5. Bracis, C. & Mueller, T. Memory, not just perception, plays an important role in terrestrial mammalian migration. *Proc. R. Soc. Lond. B Biol. Sci.* **284**, 20170449 (2017).
6. Abrahms, B. et al. Memory and resource tracking drive blue whale migrations. *Proc. Natl. Acad. Sci.* **116**, 5582–5587 (2019).
7. Tulloch, V. J. et al. Future recovery of baleen whales is imperiled by climate change. *Glob. Change Biol.* **25**, 1263–1281 (2019).
8. Guzmán, H. M. & Félix, F. Movements and habitat use by Southeast Pacific humpback whales (*Megaptera novaeangliae*) satellite tracked at two breeding sites. *Aquatic Mammals* 43(2), 139–155 (2017). (2017).
9. Acevedo, J. et al. Migratory preferences of humpback whales between feeding and breeding grounds in the eastern South Pacific. *Mar. Mamm. Sci.* **33** (4), 1035–1052 (2017).
10. Dalla Rosa, L. et al. Movements of satellite-monitored humpback whales on their feeding ground along the Antarctic Peninsula. *Polar Biol.* **31**, 771–781 (2008).
11. Hucke-Gaete, R. et al. A historical feeding ground for humpback whales in the eastern South Pacific revisited: The case of northern Patagonia, Chile. *Aquat. Conserv. Mar. Freshw. Ecosyst.* **23** (6), 858–867 (2013).
12. De Weerdt, J., Ramos, E. A. & Cheeseman, T. Northernmost records of Southern Hemisphere humpback whales (*Megaptera novaeangliae*) migrating from the Antarctic Peninsula to the Pacific coast of Nicaragua. *Mar. Mamm. Sci.* **36** (3), 1015–1021 (2020).
13. Dawbin, W. H. The seasonal migratory cycle of humpback whales. In *Whales, Dolphins and Porpoises* (Norris, K. S. ed.). 145–170 (1966).
14. Findlay, K. P. et al. Humpback whale super-groups–A novel low-latitude feeding behaviour of southern hemisphere humpback whales (*Megaptera novaeangliae*) in the Benguela upwelling system. *PloS One*. **12** (3), e0172002 (2017).
15. De Weerdt, J. & Ramos, E. A. Feeding of humpback whales (*Megaptera novaeangliae*) on the Pacific coast of Nicaragua. *Mar. Mamm. Sci.* **36** (1), 285–292 (2020).
16. Gendron, D. Evidence of feeding by humpback whales (*Megaptera novaeangliae*) in the Baja California breeding ground, Mexico. *Mar. Mamm. Sci.* **9** (1), 76–81 (1993).
17. Gales, N. I. et al. Satellite tracking of southbound East Australian humpback whales (*Megaptera novaeangliae*): Challenging the feast or famine model for migrating whales. *Int. Whal. Comm. Sci. Comm. Doc.* **SC61/SH17** (2009).
18. García Cegarra, A. M., Castro, C. & Van Waerebeek, K. Feeding of humpback whales in low latitudes of the Southeast Pacific Ocean. *Neotrop. Biodivers.* **7** (1), 421–430 (2021).
19. Owen, K. Potential energy gain by whales outside of the Antarctic: prey preferences and consumption rates of migrating humpback whales (*Megaptera novaeangliae*). *Polar Biol.* **40**, 277–289 (2017).
20. Pinto & Alves, L. C. *Record of Feeding by Humpback Whales (Megaptera novaeangliae) in Tropical Waters off Brazil*. 45 (Publications, Agencies and Staff of the US Department of Commerce, 2009).
21. Reinke, J., Lemckert, C. & Meynecke, J. O. Coastal fronts utilized by migrating humpback whales, *Megaptera novaeangliae*, on the Gold Coast, Australia. *J. Coastal Res.* **75** (10075), 552–556 (2016).
22. Van Waerebeek, K., Alfaro-Shigueto, J. & Arias-Schreiber, M. Humpback whales off Peru: new records and a rationale for renewed research. In *International Whaling Commission Scientific Committee Document* SC/48/SH1, Aberdeen (1996).
23. Meynecke, J. O. et al. The role of environmental drivers in humpback whale distribution, movement and behavior: A review. *Front. Mar. Sci.* **8**, 720774 (2021).
24. Avila, I. C. et al. Humpback whales extend their stay in a breeding ground in the Tropical Eastern Pacific. *ICES J. Mar. Sci.* **77**, 109–118 (2020).
25. Szesciorka, A. R. et al. Timing is everything: Drivers of interannual variability in blue whale migration. *Sci. Rep.* **10**, 7710 (2020).
26. Joyce, T. W. et al. The role of sea ice in the distribution, habitat use, and phenology of eastern North Pacific gray whales. *Mar. Ecol. Prog. Ser.* **709**, 141–158 (2023).
27. Ingman, K. et al. Modeling changes in baleen whale seasonal abundance, timing of migration, and environmental variables to explain the sudden rise in entanglements in California. *PLoS One*, **16**(4), e0248557 (2021).
28. Pelayo-González, L. et al. Decreases in encounter rate of endangered Northeast Pacific humpback whales in Southern Costa Rica: Possible changes in migration pattern due to warming events. *Front. Mar. Sci.* **9**, 927276 (2022).
29. Denkinger, J. et al. Humpback whale (*Megaptera novaeangliae*) winter distribution and core habitats in relation to El Ninõ Southern Oscillation and depth in coastal and oceanic waters off Ecuador. *Mar. Mamm. Sci.* **39** (3), 876–892 (2023).
30. Guzman, H. M., Condit, R. & Pérez Ortega, B. Population size and migratory connectivity of humpback whales wintering in Las Perlas Archipelago, Panama. *Mar. Mamm. Sci.* **31** (1), 90–105 (2015).
31. Pelayo-González, L. et al. Habitat use of south-eastern Pacific humpback whales (*Megaptera novaeangliae*; Borowski 1781) in Golfo Dulce, Costa Rica. *Mar. Freshw. Res.* **73** (12), 1465–1474 (2022).
32. Félix, F. & Guzmán, H. M. Satellite tracking and sighting data analyses of Southeast Pacific humpback whales (*Megaptera novaeangliae*): Is the migratory route coastal or oceanic? *Aquat. Mamm.* **40** (4), 329–340 (2014).
33. Capella, J. J. et al. Spatiotemporal differences in killer whale (*Orcinus orca*) predation on humpback whales (*Megaptera novaeangliae*) along the eastern South Pacific. *Endanger. Species Res.* **37**, 207–281 (2018).
34. Videsen, S. K. A., Bejder, L., Johnson, M. & Madsen, P. T. High suckling rates and acoustic crypsis of humpback whale neonates maximise potential for mother–calf energy transfer. *Funct. Ecol.* **31**, 1561–1573 (2017).
35. Guzman, H. M., Hinojosa, N. & Kaiser, S. Ship's compliance with a traffic separation scheme and speed limit in the Gulf of Panama and implications for the risk to humpback whales. *Mar. Policy*. **120**, 104113 (2020).
36. Zou, Y. & Xi, X. An ongoing cooling in the eastern Pacific linked to eastward migrations of the Southeast Pacific Subtropical Anticyclone. *Environ. Res. Lett.* **16** (3), 034020 (2021).
37. Félix, F. & Haase, B. A note on humpback whales off the coast of Ecuador during the 1997 'El Niño'event. *J. Cetacean Res. Manag.* **3** (1), 59–64 (2001).
38. Seyboth, E. et al. Influence of krill (*Euphausia superba*) availability on humpback whale (*Megaptera novaeangliae*) reproductive rate. *Mar. Mamm. Sci.* **37** (4), 1498–1506 (2021).
39. Felix, F. et al. A new case of interoceanic movement of a humpback whale in the Southern hemisphere: The El Niño link. *Aquat. Mamm.* **46** (6), 578–584 (2020).
40. Johnston, D. W. et al. Initial density estimates of humpback whales *Megaptera novaeangliae* in the inshore waters of the western Antarctic Peninsula during the late autumn. *Endanger. Species Res.* **18** (1), 63–71 (2012).
41. Friedlaender, A. S. et al. The effects of prey demography on humpback whale (*Megaptera novaeangliae*) abundance around Anvers Island, Antarctica. *Polar Biol.* **31**, 1217–1224 (2008).
42. Swadling, K. M. et al. Biological responses to change in Antarctic Sea ice habitats. *Front. Ecol. Evol.* **10**, 1073823 (2023).
43. Horton, T. W. Multi-decadal humpback whale migratory route fidelity despite oceanographic and geomagnetic change. *Front. Mar. Sci.* **7**, 414 (2020).
44. Shuert, C. R. et al. Decadal migration phenology of a long-lived Arctic icon keeps pace with climate change. *Proc. Natl. Acad. Sci.* **119**(45), e2121092119 (2022).
45. IPCC. *Climate Change 2022: Impacts, Adaptation, and Vulnerability. Contribution of Working Group II to the Sixth Assessment Report of the Intergovernmental Panel on Climate Change [H]*. 3056 (eds. Pörtner, O.) (Cambridge University Press, 2022).
46. Cushing, D. H. Plankton production and year-class strength in fish populations: An update of the match/mismatch hypothesis. *Adv. Mar. Biol.* **26**, 249–293 (1990).
47. Anderson, J. J. et al. Modeling climate change impacts on phenology and population dynamics of migratory marine species. *Ecol. Model.* **264**, 83–97 (2013).

48. Van Weelden, C., Towers, J. R. & Bosker, T. Impacts of climate change on cetacean distribution, habitat and migration. *Clim. Change Ecol.* **1**, 100009 (2021).
49. Von Hammerstein, H. et al. High-resolution projections of global sea surface temperatures reveal critical warming in humpback whale breeding grounds. *Front. Mar. Sci.* **9**, 837772 (2022).
50. Cucalón, E. Oceanographic characteristics off the coast of Ecuador. In *A Sustainable Shrimp Mariculture Industry for Ecuador* (eds. Olsen, S. & Arriaga, L.). 185–194 (Coastal Resources Center, University of Rhode Island, 1989).
51. Chinacalle-Martínez, N. et al. Oceanic primary production trend patterns along coast of Ecuador. *Neotrop. Biodivers.* **7** (1), 379–391 (2021).
52. Hill, S. L. et al. Modelling southern ocean ecosystems: Krill, the food-web, and the impacts of harvesting. *Biol. Rev.* **81** (4), 581–608 (2006).
53. Dalla Rosa, L. et al. Feeding grounds of the eastern South Pacific humpback whale population include the South Orkney Islands. *Polar Res.* **31** (1), 17324 (2012).
54. Castro, C., Engel, M. H. & Martin, A. R. first humpback whale movement between Ecuador and the South Sandwich Islands. *Aquat. Mamm.* **49** (4), 382–387 (2023).
55. Haro, D. et al. Ontogenetic and seasonal analysis of the diet and isotopic niche of humpback whales in the Magellan Strait, Chile. *Mar. Ecol. Prog. Ser.* **669**, 213–226 (2021).
56. Rasmussen, K. et al. Southern Hemisphere humpback whales wintering off Central America: Insights from water temperature into the longest mammalian migration. *Biol. Lett.* **3** (3), 302–305 (2007).
57. D'Croz, L. & O'Dea, A. Variability in upwelling along the Pacific shelf of Panama and implications for the distribution of nutrients and chlorophyll. *Estuar. Coast. Shelf Sci.* **73** (1–2), 325–340 (2007).
58. Guzman, H. M., Gómez, C. G. & Guevara, C. A. Potential vessel collisions with Southern Hemisphere humpback whales wintering off Pacific Panama. *Mar. Mamm. Sci.* **29** (4), 629–642 (2013).
59. R Core Team. *R: A Language and Environment for Statistical Computing* (R Foundation for Statistical Computing, 2022).
60. Freitas, C. *Argos Locations Filter. R Package Version 0.70* (2022).
61. Kranstauber, B., Smolla, M. & Scharf, A. *move: Visualizing and Analyzing Animal Track Data. R Package Version 4.1.12* (2023).
62. Michelot, T., Langrock, R. & Patterson, T. A. moveHMM: An R package for the statistical modelling of animal movement data using hidden Markov models. *Methods Ecol. Evol.* **7** (11), 1308–1315 (2016).
63. Himmelmann, S. S. D. L. *HMM: Hidden Markov Models. R Package Version 1.0.1* (2022).
64. Pebesma, E. Simple features for R: Standardized support for spatial Vector Data. *R J.* **10** (1), 439–446 (2018).
65. NOAA. National Centers for Environmental Information. El Niño/Southern Oscillation (ENSO). (2023). https://www.ncei.noaa.gov/access/monitoring/enso/sst. Accessed 5 June 2023 (2023).
66. Chamberlain, S. *General Purpose Client for 'ERDDAP' Servers. R Package Version 1.0.2* (2023).
67. Mendelssohn, R. *rerddapXtracto Extracts Environmental Data from 'ERDDAP' Web Services. R Package Version 1.1.4* (2022).
68. Kassambara, A. & Mundt, F. *Extract and Visualize the Results of Multivariate Data Analyses. R Package Version 1.0.7* (2020).
69. Wood, S. N. *Generalized Additive Models: An Introduction with R*. 2nd Ed. (Chapman and Hall/CRC, 2017).
70. Massicotte, P. & South, A. *rnaturalearth World Map Data from Natural Earth. R Package Version 1.0.1* (2023).

Acknowledgements

This study was partially financed by the NSERC discovery grants #2017-03839 and #2024-04374 to V.M., the Smithsonian Tropical Research Institute, Secretaría Nacional de Ciencia y Tecnología de Panamá (SENACYT), the Candeo Fund at the International Community Foundation to H.M.G., and a private charitable trust as part of the Whales & Climate Research Program to F.F. We thank the governments of Ecuador, Panama and Costa Rica for providing the research permits.

Author contributions

V.M., H.M.G. designed the study; F.F., H.M.G. collected the data; V.M., N.S. conducted the analyses; V.M. wrote the manuscript with contributions from N.S., F.F., and H.M.G. All authors reviewed the manuscript.

Declarations

Competing interests

The authors declare no competing interests.

Additional information

Supplementary Information The online version contains supplementary material available at https://doi.org/10.1038/s41598-025-87489-4.

Correspondence and requests for materials should be addressed to H.M.G.