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Long-Range Movement of Humpback Whales and Their Overlap with Anthropogenic Activity in the South Atlantic Ocean

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Abstract: *Humpback whales* (Megaptera novaeangliae) *are managed by the International Whaling Commission as 7 primary populations that breed in the tropics and migrate to 6 feeding areas around the Antarctic. There is little information on individual movements within breeding areas or migratory connections to feeding grounds. We sought to better understand humpback whale habitat use and movements at breeding areas off West Africa, and during the annual migration to Antarctic feeding areas. We also assessed potential overlap between whale habitat and anthropogenic activities. We used Argos satellite-monitored radio tags to collect data on 13 animals off Gabon, a primary humpback whale breeding area. We quantified habitat use for 3 cohorts of whales and used a state-space model to determine transitions in the movement behavior of individuals. We developed a spatial metric of overlap between whale habitat and models of cumulative human activities, including oil platforms, toxicants, and shipping. We detected strong heterogeneity in movement behavior over time that is consistent with previous genetic evidence of multiple populations in the region. Breeding areas for humpback whales in the eastern Atlantic were extensive and extended north of Gabon late in the breeding season. We also observed, for the first time, direct migration between West Africa and sub-Antarctic feeding areas. Potential overlap of whale habitat with human activities was the highest in exclusive economic zones close to shore, particularly in areas used by both individual whales and the hydrocarbon industry. Whales potentially overlapped with different activities during each stage of their migration, which makes it difficult to implement mitigation measures over their entire range. Our results and existing population-level data may inform delimitation of populations and actions to mitigate potential threats to whales as part of local, regional, and international management of highly migratory marine species.*

Keywords: anthropogenic activity, Gulf of Guinea, habitat use, international management, migrations, population, satellite telemetry

Cuantificación de los Movimientos de Gran Amplitud y el Traslape Potencial con Actividad Antropogénica y las Ballenas Jorobadas en el Océano Atlántico Sur

Resumen: *Las ballenas jorobadas* (Megaptera novaengliae) *son manejadas por la Comisión Internacional de Ballenas como siete poblaciones primarias que se reproducen en los trópicos y migran a seis áreas de alimentación alrededor del Antártico. Hay poca información sobre los movimientos individuales dentro*

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de las áreas de reproducción o las conexiones migratorias hacia las zonas de alimentación. Buscamos un mejor entendimiento del uso de hábitat de la ballena jorobada y los movimientos en las áreas de reproducción cercanas a África Occidental durante la migración anual a las áreas de alimentación en el Antártico. También estudiamos el traslape potencial entre el hábitat de las ballenas y las actividades antropogénicas. Usamos radio-rastreadores Argos monitoreados por satélite para colectar información de 13 animales cerca de Gabón, un área de reproducción primaria. Cuantificamos el uso de hábitat para tres cohortes de ballenas y usamos un modelo de estado-espacio para determinar las transiciones en la conducta del movimiento de los individuos. Desarrollamos una métrica espacial de los traslapes entre el hábitat de las ballenas y los modelos acumulativos de actividades humanas, incluyendo plataformas petroleras, tóxicos y embarcaciones. Detectamos una heterogeneidad fuerte en la conducta del movimiento a lo largo del tiempo que es constante con evidencia genética previa de poblaciones múltiples en la región. Las áreas de reproducción de las ballenas jorobadas en el Atlántico oriental fueron extensas y se extendieron al norte de Gabón más tarde en la temporada de reproducción. También observamos, por primera vez, una migración directa entre las áreas de alimentación de África occidental y el subantártico. El traslape potencial del hábitat de las ballenas con las actividades humanas fue más alto en las zonas económicas exclusivas cercanas a la costa, particularmente en áreas usadas por ballenas individuales y la industria de hidrocarburos. Las ballenas se traslapan potencialmente con actividades diferentes durante cada fase de su migración, lo que dificulta la implementación de medidas de mitigación en toda su distribución. Nuestros resultados y los datos existentes de nivel de población pueden informar a las definiciones de poblaciones y a las acciones para mitigar amenazas potenciales para las ballenas como parte de un manejo local, regional e internaciones de especies marinas con migración alta.

Palabras Clave: Actividad antropogénica, Golfo de Guinea, manejo internacional, migraciones, población, telemetría satelital, uso de hábitat

Introduction

Satellite tracking studies provide detailed information about a variety of life history traits of migratory marine species, including range extent, site fidelity, and migratory patterns (Lagerquist et al. 2008; Hauser et al. 2010; Block et al. 2011). Knowledge of movement patterns and migratory routes can be instrumental in supporting many types of management decisions. For instance, satellite tracking has enabled insights on population delineation and structure (Lagerquist et al. 2008; Garrigue et al. 2010), which complement genetic studies to better inform management decisions. Such information can be used for mitigation of particular potential anthropogenic effects, such as those from shipping traffic (Mate et al. 1997), fisheries (Witt et al. 2011; Zydelis et al. 2011), and exploration for hydrocarbons (i.e., seismic surveys) (Findlay et al. 2006).

Large whales traverse vast stretches of ocean between breeding and feeding areas on a seasonal basis. Many sources illustrate migratory connections, including discovery tags (inserted into the blubber of individual whales and reported when the whale was killed) (Mackintosh 1942; Chittleborough 1965; Dawbin 1966), and noninvasive capture-recapture data based on photographs or genetic material (Valsecchi et al. 2010; Weller et al. 2012). Even with these methods, in most cases the specific movement routes, timing, speeds, and migratory cues related to whale migration and needed to inform conservation are still lacking (Zerbini et al. 2006; Lagerquist et al. 2008).

Humpback whales (*Megaptera novaeangliae*) in the Southern Hemisphere have been the focus of considerable research efforts over the last few decades. Seven breeding populations are managed by the International Whaling Commission (IWC), an intergovernmental organization charged with the conservation of whales and the management of whaling (IWC 2007). These populations migrate between summer feeding areas in the nutrient-rich waters of the Southern Ocean and winter breeding areas in tropical waters (Townsend 1935; Mackintosh 1942). All populations of large whales in the Southern Hemisphere were severely depleted throughout the 18th, 19th, and 20th centuries; reductions in the population sizes of different species ranged from approximately 68% to more than 95% (Baker & Clapham 2004). The IWC afforded international protection to humpback whales in 1966; however, illegal whaling hampered initial recovery (Clapham et al. 2009; Ivashchenko et al. 2011).

West African whaling records suggest humpback whales undertake extensive movements between South Africa and the Gulf of Guinea between June and January (Townsend 1935). Results of genetic capture-recapture studies in waters off Gabon and the western coast of South Africa confirm these movements, at least for several mother and calf pairs (Pomilla 2005; Pomilla & Rosenbaum 2005; Carvalho et al. 2014). Boat-based and aerial surveys along the coast of Gabon show that large groups of animals congregate along the continental shelf and that this area serves as breeding habitat between June and October each year (Rosenbaum & Collins 2006). It has long been suggested that whales in this region move south during each austral summer to feed in Antarctic waters (Chittleborough 1965); however, these movements have not yet been confirmed. As is the case for many whale species, movements of humpback whale populations in the Southeast Atlantic region are not known, and very little is known about the localized or seasonal movements of individual whales. These data are particularly important given current offshore hydrocarbon exploration and the expectation that hydrocarbon production will greatly increase off the coast of West Africa by 2016 (Findlay et al. 2006) and globally by 2100 (Smith 2000). Hydrocarbon industry exploration and production activities, noise in the marine environment, and the potential for impacts at the individual and population level, are widely recognized and the focus of numerous research efforts (e.g., Schick & Urban 2000; Miller et al. 2009; Hatch et al. 2012). Moreover, as whale populations recover, accurate information on population dynamics, migratory connections between habitats, and other potential anthropogenic stressors or impacts are an essential part of the evaluative and management process related to any future considerations about whaling.

We deployed satellite tags on humpback whales along the coast of Gabon. Our goal was to better identify the whales' winter range by examining the localized movements of individuals throughout the Gulf of Guinea. We also aimed to characterize the timing, speed, and route of the spring migration, including the location of feeding areas during the austral summer. Additionally, we assessed the overlap of whale movements with exclusive economic zones (EEZs) and the potential overlap between whales and a range of anthropogenic uses, including offshore oil platforms, toxicants, and shipping lanes.

Methods

Satellite Tagging

We deployed Telonics ST-Argos transmitters (satellite tags) with an air-powered device at a range of 2–4 m from a raised-bow platform on the front of a 9-m rigid hull inflatable boat. Given limited tag transmission durations, we tagged whales toward the presumed end of the reproductive season to maximize data collection during the southbound migration (satellite tag specifications and deployment details in Supporting Information). Between 29 August and 12 September 2002, we tagged 13 humpback whales off Gabon (approximately 2°S, 9°E): 2 females with calves and 11 adults without calves. We tagged 2 other adults, but the tags were lost immediately. At the time of tag deployment, we digitally photographed and recorded video of individual whales (dorsal fins and flukes when possible) to document that tags were placed within 1m forward of the dorsal fin. We also used a modified crossbow to obtain a small sample of tissue for molecular sex identification.

Analysis of Movements

We fitted the behaviorally switching state-space model (SSM), originally developed by Jonsen et al. (2005) and refined by Breed et al. (2009), that estimates model parameters by Markov chain Monte Carlo (MCMC) to the locations of each humpback whale with the free software programs R v. 9.3 (R Core Team) and WinBUGS v. 1.4 (Bayesian inference Using Gibbs Sampling). The chronological sequencing of humpback whale locations connected by shortest distance between locations determined by SSM are typically called a *satellite track* (shown in Figs. 1 & 2). SSMs include 2 models that are solved simultaneously: a model of observation error and a mechanistic model of animal movement (Jonsen et al. 2005). Use of SSMs yields more accurate estimates of both the satellite locations and the uncertainty in those locations than raw tracking data. This is because the SSM draws on all of the data and the animal's behavior (e.g., speed and turning angles from the satellite track) to predict the probability of an animal being found at a certain location (Jonsen et al. 2003).

To apply the SSM, we first filtered Argos data to only include location classes (LC) A, B, 0, 1, 2, and 3. We removed locations with LC Z. We estimated locations and defined a regular time interval of 5 hours, which reflects the mean number of Argos locations per day for the animals in this study (Maxwell et al. 2011). We classified 2 states of behavior on the basis of 4 parameters: mean turning angle for localized ($\theta_{\text{localized}}$) and transiting behavior ($\theta_{\text{transiting}}$) and autocorrelation in both speed and direction for localized ($\gamma_{\text{localized}}$) and transiting behavior ($\gamma_{\text{transiting}}$). We ran 2 MCMC chains for 10,000 iterations after a burn-in of 5000 and further thinned the iterations by 5 to estimate the mean and variance for each location and behavioral parameter, retaining 5% of the total iterations. Posterior densities and trace plots of the 2 chains for each model parameter were examined to determine if the chains centered around the same mean (Supporting Information; Breed et al. 2009). For each MCMC iteration, 2 of the parameters (transiting or localized θ and γ) fit the displacement between 2 locations better, resulting in a natural separation between 2 of the 4 parameters. Based on this separation, each location was assigned to one of 2 behavioral states (0 or 1) (Breed et al. 2009). The 2 states showed differentiation in parameters: localized ($\gamma = 1.00$–1.50), slower movements with a high rate of acute turning angles (near 180°) within breeding or feeding habitats and transiting ($\gamma = 1.51$–2.00), faster, highly directional (turning angles near 0°), long-distance movements between patches of foraging or breeding habitat (details in Supporting Information).

Because initial headings after tagging varied between individual whales, we partitioned the tagged whales into 3 cohorts on the basis of the direction traveled immediately following tagging. Partitioning does not imply an

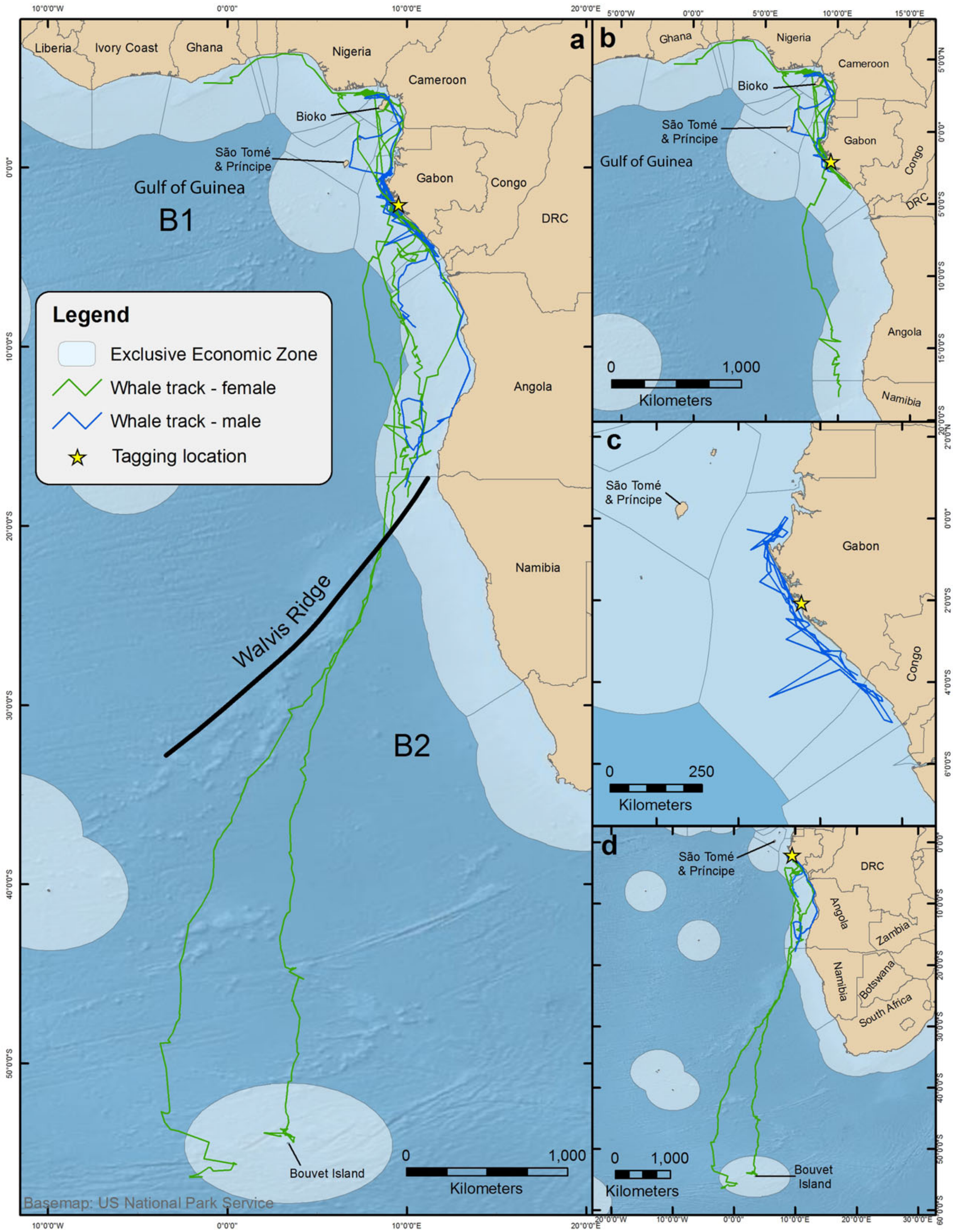

Figure 1. Satellite tracks for (a) all humpback whales, (b) north cohort, (c) central cohort, and (d) south cohort. The distribution of International Whaling Commission (IWC) Breeding Substock B1's breeding area off Gabon and Breeding Substock B2's migratory and feeding habitat off west South Africa, and the location of the Walvis Ridge, are also shown in (a).

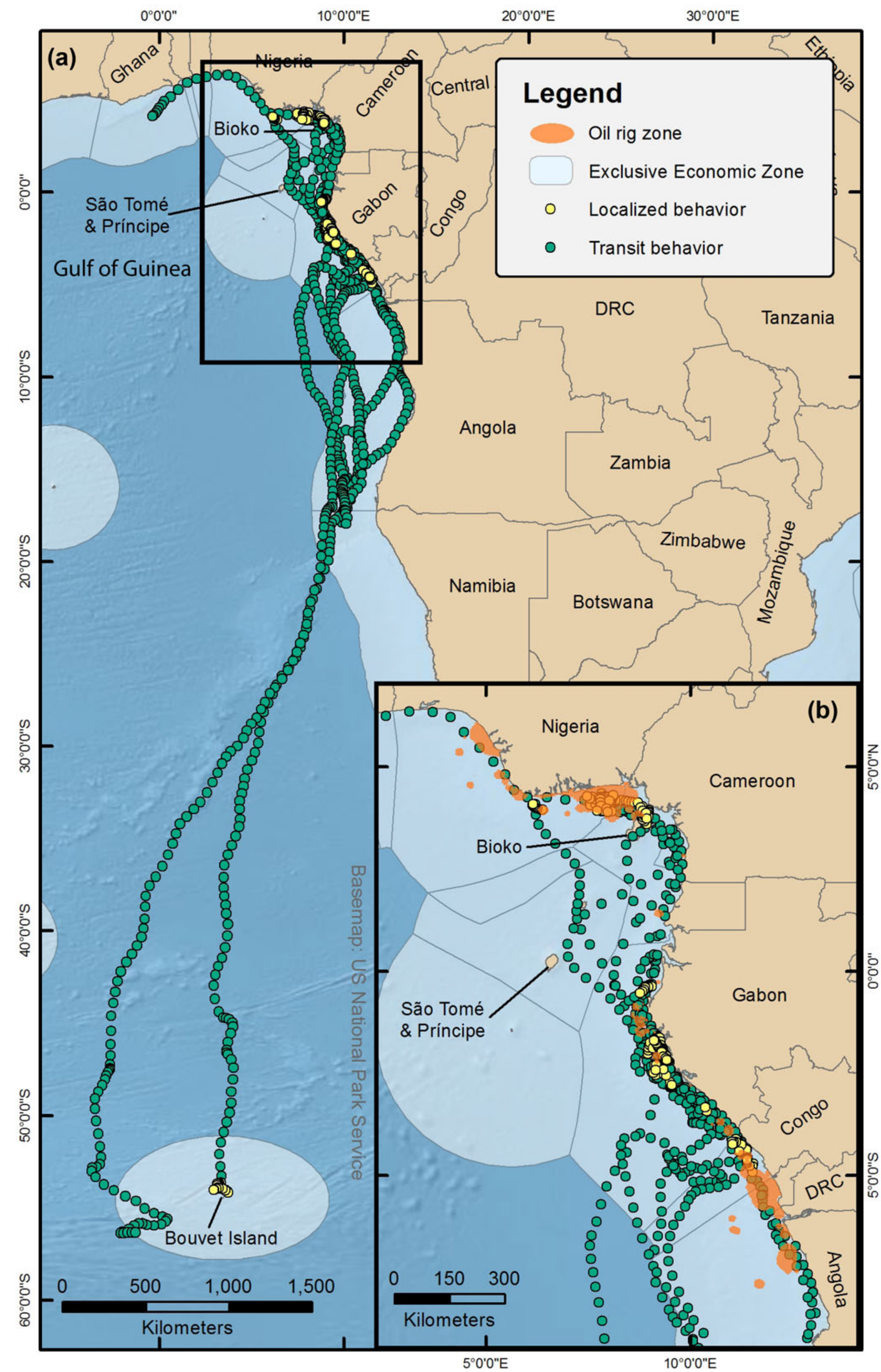

Figure 2. (a) Results of the state-space model for all whales (locations identified as localized and transit behavior) in relation to exclusive economic zones and (b) extent of potential overlap of whale locations with oil platform zones, taken from Halpern et al. (2008).

even contribution of data from individual animals within the cohort; the amount of data from a given tag is a function of individual whale behavior and tag longevity. We assigned whales that moved farther north into the Gulf of Guinea to the north cohort, whales that remained close to the Gabon coastline for the entirety of transmission to the central cohort, and those that traveled directly south beyond Gabon and Republic of Congo to the south cohort. We analyzed data from all tracks and from tracks within each cohort. Distances determined for tracks represented linear interpolation between locations.

To characterize how humpback whales used areas in EEZs and oceanic areas during their spring migration, we calculated the whale tracks' utilization distribution (UD), a type of home range that represents the probability an animal will occur in a given location within a defined period (Kernohan et al. 2001). We utilized the grid cell UD method detailed in Maxwell et al. (2011) for each 0.5° grid cell (Supporting Information); thus, each cell was assigned a value (between 0 and 1) reflective of the probability of an animal being found in that cell. To account for different durations of transmission among individuals, we weighted each location by the inverse of the number of individuals for which locations were recorded on that same day. The first 85% of locations were weighted in this manner; all locations after the 85% threshold received the same weight as the threshold day (Block et al. 2011). We created UDs with the weighted tracks.

Overlap between Whale Habitat and Anthropogenic Activities

We assessed the extent of potential overlap between humpback whale habitat using modeled global human activity with data from Halpern et al. (2008) using methods modified from Maxwell et al. (2013). We calculated the extent of overlap of humpback whale habitat with EEZs by determining the number of EEZs whales traveled through and the percentage of time spent within EEZs versus high seas (areas beyond EEZs). We further partitioned data to assess the percentage locations classified as localized or transiting within EEZs and oceanic areas.

To characterize overlap with human activities, we used the spatially explicit cumulative anthropogenic impacts model, representing an integration of 17 global data sets of human activities for 20 marine ecosystems (Halpern et al. 2008). We used 3 individual models, also from Halpern et al. (2008), to better identify areas where humpback movements overlap with anthropogenic activities: location and density of offshore oil platforms, ocean-based toxicants from ports and commercial ship activity (hereafter toxicants, modeled with dispersion of toxicants from ports and commercial ship activity), and density of vessel traffic in shipping lanes (hereafter shipping, modeled with known shipping lanes and density of vessels) (further model details are in Supporting Information and in Halpern et al. (2008)). The presence of oil platforms may not directly impact whales; however, we used them as a proxy for regions where current hydrocarbon activity occurs and future hydrocarbon activity may occur. Ocean-based toxicants represent the area and intensity of pollutants, largely oil, discharged from ports and commercial shipping activities. The effects of these toxicants have been characterized in whales (O'Shea & Brownell 1994). We used vessel traffic to represent the chance of ship strikes of whales or potential behavioral or migratory shifts by whales in response to shipping lanes or high densities of ships. Although incidence of ship strikes have not been studied in West Africa, incidence of strikes has been recorded elsewhere and is a widely held concern (Laist et al. 2001; Carretta et al. 2010). For each of these data sets, Halpern et al. (2008) modeled the underlying data to 1-km^2 resolution; however, no uncertainty estimates exist for this data set so caution should be taken in interpreting the results because potential impacts could be larger than those predicted by the model.

For each model, except for oil platforms, we extracted the maximum value within a 0.5° grid cell from the underlying 1-km^2 resolution data from Halpern et al. (2008). To estimate overlap between whales and cumulative human activity, toxicants, and shipping, we normalized driver values to one and then multiplied the maximum value within each 0.5° grid cell by the UD value to create a relative potential impact (RPI) score following Maxwell et al. (2013). We used the RPI to determine the relative habitat use by animals and the amount of anthropogenic activity in each grid cell, resulting in a spatial metric reflecting the degree of potential interaction between whale habitat and anthropogenic activity throughout the study area. We determined the range of RPI values for all whales and for each cohort. For oil platforms, percent overlap of localized whale movements with oil platforms was calculated.

Results

Satellite Tagging

We obtained data from 13 of the 15 satellite tags. Two of the tags stopped transmitting <1 d after being deployed. The remaining 13 tags transmitted for 19–104 d each and recorded ≥ 40,545 km of travel (average 3116 km/whale at 2.8 km/h; Supporting Information). Six of the 13 tagged whales were males, and their tags transmitted for 19–45 d (mean 29 d [SD 11]). Males traveled 1146–3124 km (total track lengths: mean 1893 km [751]) at an average speed of 2.7 km/h (Supporting Information). The 7 tags on female whales transmitted for 25–104 d each (mean 57 d [31]) and recorded total distances (track lengths) of 1502–8195 km (mean 4163 km [2886]) at an average speed of 3.0 km/h.

Analysis of Movements

Movements of tagged whales were heterogeneous in terms of both direction and use of neritic (<200 nm from shore) and oceanic (>200 nm from shore) areas across the same period (Fig. 1). Six whales (4 females, including 2 with calves, and 2 males) traveled directly north following tagging (Fig. 1b). These whales traveled through EEZs north of Gabon in the Gulf of Guinea, including EEZs of the offshore islands of São Tomé and Principe (STP), Cameroon, Bioko Island, Nigeria, and as far north and west as the EEZs of Ghana (4.7°N, 1.4°W). Some individuals remained over the continental shelf for the duration of transmission, whereas others moved through oceanic areas to travel directly to neritic aggregation areas farther along the coast (Fig. 1b). The 2 males in the central cohort remained close to the coastline of Gabon or Republic of Congo for the duration of the transmission (Fig. 1c).

Five individuals (3 females, 2 males) traveled directly south into Angolan territorial waters toward feeding areas (Fig. 1d). These whales left the central Angolan coast and traveled south-southwest along the Walvis Ridge, a bathymetric feature running roughly southwest from the continental shelf to a point 2000 km west of South Africa. Three tags stopped functioning shortly after the whales started to travel along the ridge system. The 2 females with the tags that transmitted the longest (104 and 83 d) traveled the farthest (8195 and 7767 km, respectively, accounting for 39% of the total distance recorded by all tags). They covered nearly identical paths at similar speeds (averaging 4.8 km/h) as they traveled approximately 1200 km over the Walvis ridge; one whale passed over the ridge 16 d before the other (Fig. 1a). The 2 whales continued on the same general heading until they reached approximately 28°S, where they diverged and continued south. They reached the receding pack ice at 50°S and remained near Bouvet Island (20°W, 10°E; Fig. 1d) from late November until 20 December 2002.

Posterior densities (Supporting Information) and trace plots of the 2 MCMC chains for each parameter value constructed for the SSM indicated the chains converged upon a single mean for all parameters. Furthermore, the SSM demonstrated strong separation between the behavioral parameters (θ and γ), indicating that individual whales switched between localized movements and transiting movements. Three main areas of localized behavior were in known breeding areas off the coast of Gabon and Republic of Congo and farther north in the Gulf of Guinea within 30–40 km of Nigeria, Cameroon, and Bioko (Fig. 2b). This northernmost location had not yet been described as breeding habitat. Differences in individual behavior were also observed between whales traveling in neritic areas as opposed to oceanic areas. Two females (one with a calf) periodically switched between localized and transiting behaviors as they moved along the coast, whereas 3 individuals (2 females, one with a calf, and a male) moved rapidly through oceanic to neritic areas where they exhibited localized behavior on arrival. The SSM also demarcated localized movements for one of the females at the southernmost point of migration in the territorial waters surrounding Bouvet Island, which suggests this area is a feeding site (Fig. 2a).

Overlap between Whale Habitat and Anthropogenic Activities

The majority of transmissions occurred within EEZs (Table 1). The whales traversed 13 different EEZs; the north cohort moved through the greatest number ($N = 11$). The south and central cohorts moved through 5 and 2 EEZs, respectively. Across cohorts, animals spent the greatest amount of time in the EEZs of Gabon (43.54 d total), Angola (33.33 d total), and Nigeria (18.13 d total). Overall, whales spent 75.9% of their time within EEZs (north cohort, 92.1%; central cohort, 93.2%; south cohort, 62.9%). The entirety of localized behavior took place within EEZs for all cohorts (100%), whereas transiting behavior within EEZs (77.6% overall) was driven primarily by the north and central cohorts (91.6% and 92.9%, respectively) with the south cohort (67.8%) undertaking the long-distance, mainly oceanic, southern migration.

The range of RPI scores for all tagged whales was 0.00–0.59 (median 0.02) (Table 1, Fig. 3). The greatest RPI scores occurred in EEZs and near coastlines across all cohorts (Fig. 4). The central cohort, which was found exclusively in EEZs, had the highest median RPI score (0.07; Table 1; Figs. 3 & 4b–c). Notably, the north cohort represented the widest range of RPI values and the highest absolute value (Fig. 3). The north and south cohorts showed comparable potential overlap with shipping and ocean toxicants (Table 1, Fig. 3). These variables were spatially correlated due to toxicants representing, in part, discharge from the commercial vessels. North and central animals were in close proximity to oil platforms off the coasts of countries bordering the Gulf of Guinea and 41.4% of localized behavior potentially overlapped with the presence of oil platforms in this region (Fig. 2b). The south cohort animals showed the highest overlap in neritic areas off Gabon, Republic of Congo, and Angola, prior to their oceanic southern migration (Fig. 4d). A number of high value shipping RPI cells for this group occurred where migrating individuals crossed major shipping lanes when moving along the Walvis Ridge (Table 1, Fig. 3).

Discussion

Supporting Evidence for Multiple Populations

The humpback whale populations that inhabit the western coast of Africa are managed by the IWC as 2 breeding substocks (B1 and B2) within Breeding Stock B. Whales in the Gabon and Congo breeding area (B1) are genetically distinct from the relatively small number of whales

Table 1. Habitat-use and movement behavior of humpback whale cohorts within exclusive economic zones (EEZs), and the relative potential impact of anthropogenic activities on each cohort throughout their range.

		Transmission		*Time in EEZs*[a]		*Behavior in EEZ (%)*[b]		*Median relative potential impact score*[c] *(range)*		
Cohort	*N*	*days*	*period*	*N*	*%*	*localized*	*transit*	*cumulative*	*shipping*	*toxins*
All	13	111	29 Aug–21 Dec	13	75.90	100.00	77.60	0.02 (0.00–0.59)	0.04 (0.00–0.27)	0.02 (0.00–0.35)
North	6	51	1 Sep–21 Oct	11	92.10	100.00	91.60	0.02 (0.00–0.55)	0.03 (0.00–0.27)	0.03 (0.0–0.35)
Central	2	40	9 Sep–18 Oct	2	93.20	100.00	92.90	0.07 (0.00–0.26)	0.04 (0.00–0.13)	0.05 (0.00–0.23)
South	5	111	29 Aug–21 Dec	5	62.90	100.00	67.80	0.03 (0.00–0.40)	0.03 (0.00–0.22)	0.03 (0.00–0.27)

[a]*Number of EEZs traveled through by all tagged whales and by each cohort (N). Percent time indicates the percentage of transmission positions within EEZs.*
[b]*Percentage of time spent in EEZs during localized or transit behaviors.*
[c]*Relative potential impact (RPI) score is the utilization distribution value multiplied by the normalized and transformed anthropogenic impacts from Halpern et al. (2008). Values are across all cells used by humpback whales within groupings.*

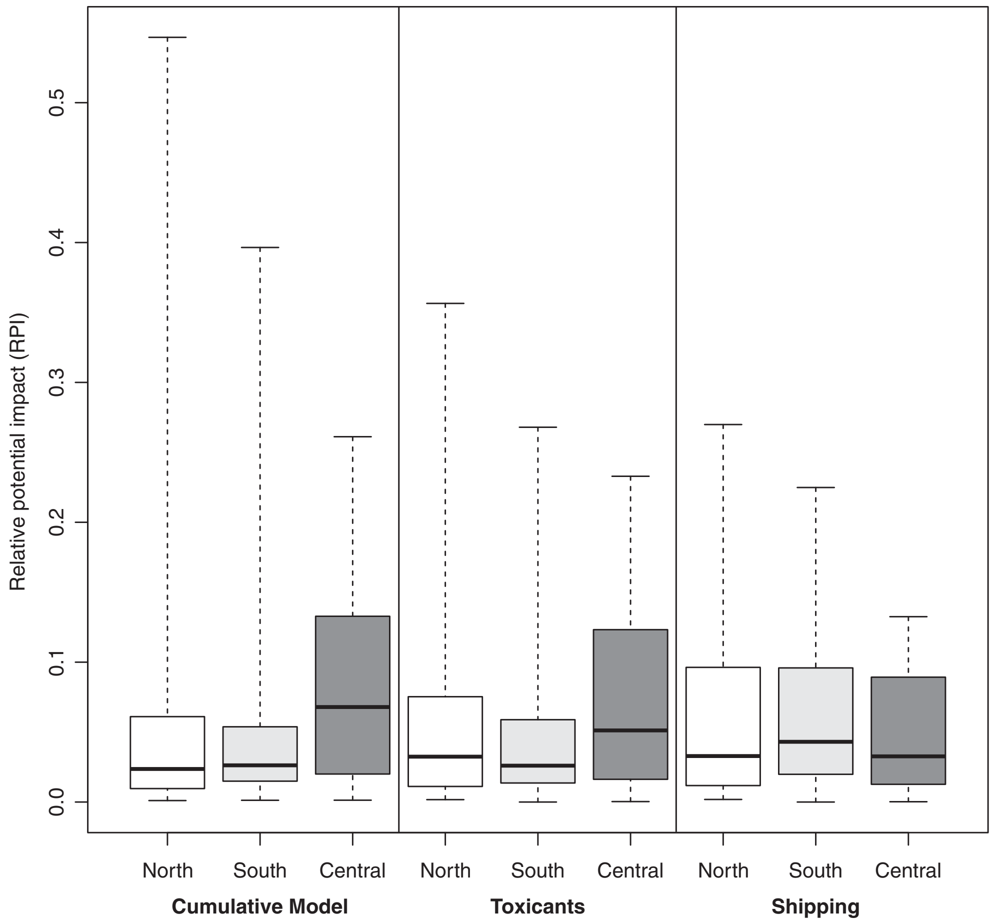

Figure 3. Range of relative potential impact (RPI) scores for each humpback whale cohort (whiskers, maximum and minimum values; dark center line, median value; outer box lines, first and third quartile values for each cohort). The RPI score is the utilization distribution value (i.e., relative habitat use) for humpback whales multiplied by the normalized and transformed values of human activities from Halpern et al. (2008).

(<500) observed feeding and migrating off west South Africa (part of the B2 Substock) (Fig. 1a; Pomilla & Rosenbaum 2005; Rosenbaum et al. 2009; Barendse et al. 2011). Within Substock B1, fine-scale differences in measures of genetic population substructure across time have been detected (Carvalho et al. 2014), which is consistent with previous observations of temporal segregation of migrating humpback whales on the basis of age, sex, and reproductive status (Ersts & Rosenbaum 2003). The exact location of the breeding area for B2 remains unknown, but it is thought to be north of Gabon in the Gulf of Guinea (IWC 2010).

Our finding that groups of whales moved in different directions is consistent with these genetic data and is the strongest evidence to date that movements, seasonality, and habitat use may differ within and among breeding

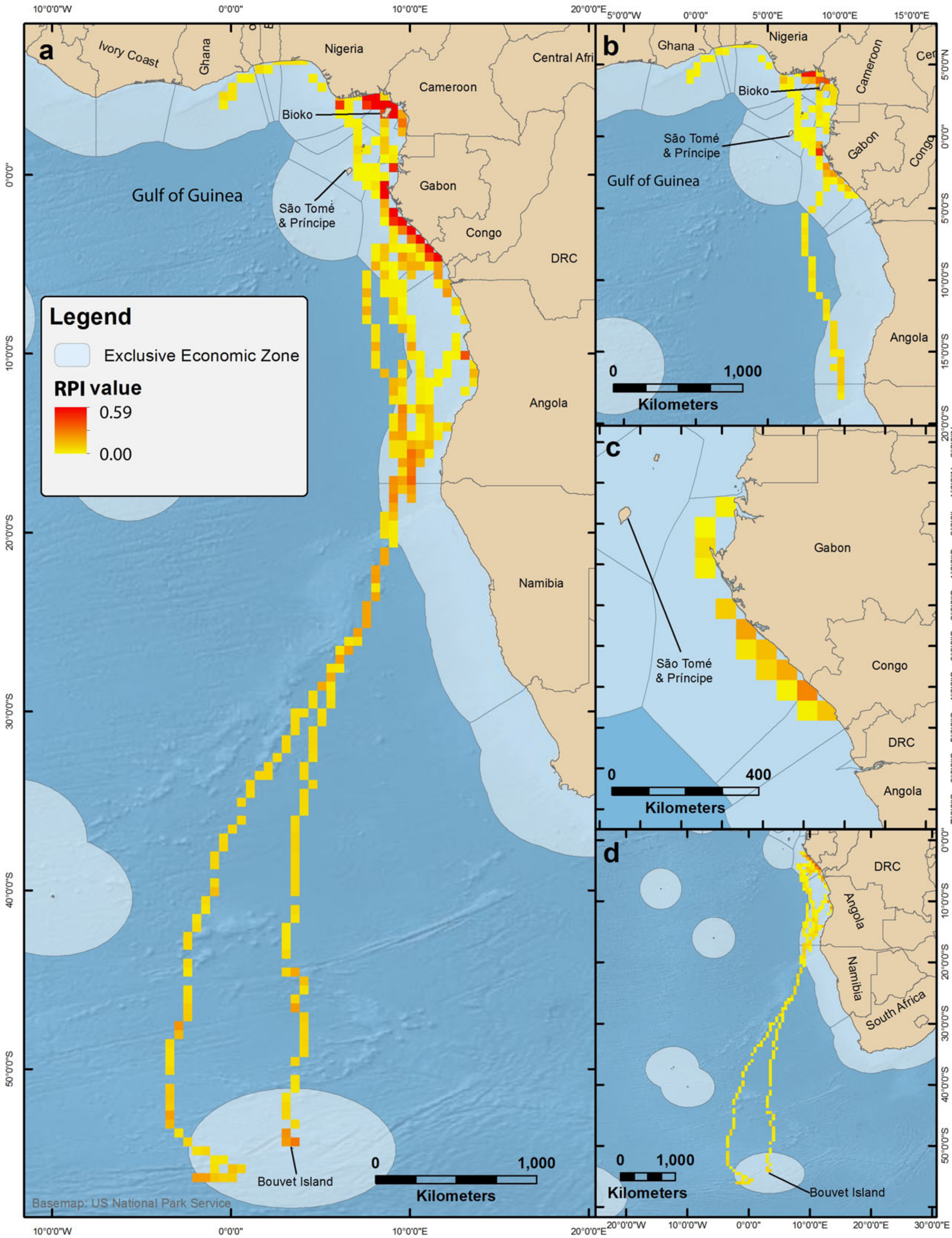

Figure 4. Relative potential impact (RPI) scores, which represent the relative use of the study area by animals and potential range overlap with the intensity of cumulative anthropogenic activities for (a) all humpback whales, (b) north cohort (c) central cohort, and (d) south cohort. The RPI ranges from low risk of potential impact (0.00) to high risk of potential impact (0.59). Size of grid cells is 0.5°.

stocks in the region (Rosenbaum et al. 2009; Barendse et al. 2010; Carvahlo et al. 2014) That some whales, including the 2 females with calves, were still traveling northward during September and October (Fig. 1b) suggests these individuals may have left the summer feeding areas later in the season (or feed in waters farther north, possibly as part of the B2 feeding aggregation off west South Africa) and were still in the process of migrating to a breeding area north of the Equator. These individuals appeared to have been transiting through the breeding ground off Gabon when tagged. This was unexpected because September to December is considered late in the breeding season for this population, and the majority of tagged individuals are expected to travel south (Chittleborough 1965; Best et al. 1995). We presumed another cohort that had completed the annual breeding cycle was commencing its southbound migration to Antarctic waters at the same time (Fig. 1d). Our results therefore showed that potential breeding areas for humpback whales in the eastern Atlantic are extensive and include the entire coast of Gabon (range: 500 km) and the territorial waters of Equatorial Guinea, São Tomé, Principe, Cameroon, and Nigeria (Fig 1b) and extend farther north (to 4.7°N) late in the breeding season.

The boundary between the breeding area of B1 and the feeding area of B2 off South Africa is also unknown, but it may be in the vicinity of the Walvis Ridge, close to the Angola-Benguela Front where it meets the African coast near 18°S (Fig. 1a; Rosenbaum et al. 2009; IWC 2011). Given the long distance movement of whales observed north and west from Gabon, such boundaries among populations may be temporal or ephemeral.

Our limited sample size greatly constrains the degree to which we can extrapolate our results to the population level. The number of humpback whales in the neritic waters of Gabon is approximately 1200 during this period of the breeding season (Strindberg et al. 2011). The 13 whales in our sample, however, were representative of similar satellite telemetry studies for this species (e.g., $n = 8$: Hauser et al. 2010; $n = 11$: Zerbini et al. 2006; Lagerquist et al. 2008; $n = 12$: Garrigue et al. 2010; $n = 26$: Horton et al. 2011). Furthermore, overall results are consistent and have been verified from more extensive tagging efforts (A. Zerbini, personal communication). More data will be essential for elucidating whether 2 breeding substocks overlap during migration or whether a single breeding stock has an extensive breeding range.

Confirmation of sub-Antarctic Feeding Areas

The migration of 2 females to the feeding areas around Bouvet Island is the first demonstration of direct movement and connectivity between low-latitude breeding regions of West Africa and sub-Antarctic feeding areas (Fig. 2). Highly directional southbound migrations have also been observed in humpback whales tagged off Brazil (Horton et al. 2011), indicating that such behavior may be common among populations. Our findings suggest that the underlying bathymetric feature of the Walvis Ridge may be important in determining the location of at least part of the long-distance migratory path (Fig. 1a). Further satellite telemetry studies hold considerable promise for increasing understanding of these long-distance, oceanic movements that remain inaccessible to direct observation.

Extent of Potential Overlap with Anthropogenic Activities

There is little empirical data on whale residence times in the South Atlantic Ocean. Our tagging data support assessments of potential range overlap of these animals with anthropogenic activities over time. Due to the high level of heterogeneity in habitat use and movement among individuals, humpback whales in the southeast Atlantic move through areas with variable anthropogenic activities, resulting in differing levels of RPI (Table 1; Figs. 2 & 4). This variability poses challenges for mitigation measures aimed at reducing the overlap between whale presence and human activities because different subsets of the populations are potentially in contact with different stressors, both in neritic and oceanic areas, at any given time during the breeding and migration periods (July–February). The switching between localized and transit behaviors identified by the SSM also indicates that breeding areas are not entirely spatially or temporally discrete, presenting additional challenges for spatially explicit management strategies throughout large parts of their range (Fig. 2).

During September and October a majority of transmitted positions were within EEZs of countries bordering the Gulf of Guinea (Table 1). Although the location of positions is driven by the location of the original tagging site in Gabon, the use of EEZs near the Gulf of Guinea is more extensive than previously thought; there were transmitted positions from 13 different EEZs. The highest degree of range overlap with anthropogenic activities was within the EEZs of Cameroon, Gabon, and Nigeria (Fig. 4). Within these neritic areas, whales may be particularly vulnerable to potential impacts associated with shipping and associated toxicants. At higher latitudes, whales had lower levels of RPI, the greatest of which coincided with shipping activity (Table 1, Fig. 4). Direct mortality of humpback whales from vessel strikes is low (Laist et al. 2001); however, a major shipping lane overlaps with what increasingly appears to be a migration route for these animals.

All whales passed oil platforms that have been or are associated with exploration (existing oil and gas leases and seismic surveys), development (construction), and production activities (Fig. 2). This means the majority of breeding habitat is likely to fall within areas where hydrocarbon industry activity is present. Exploration, development, and production are expected to expand, and existing exploration and production areas may be in place for at least the next 30 years. Thus the potential overlap we have identified is a minimum and likely an underestimate. The scale of humpback whale breeding habitat and migratory movements and potential overlap with anthropogenic activities we identified highlights the potential spatially extensive, long-term cumulative exposures and potential impacts for individuals in this population (Hatch et al. 2012; Maxwell et al. 2013).

Our findings emphasize the need for nationally-relevant and transboundary management measures for these whales and similar migratory marine species (Maxwell et al. 2011; Witt et al. 2011). Ours was a conservative assessment of potential overlap with anthropogenic activities, given our small but informative sample size of tagged whales and that the northernmost extent of the breeding range has not been fully identified. The already sizable challenges of designing and implementing nationally-relevant and transboundary management measures will be particularly complex given the different institutional capacities of the countries in this region. Where management resources are limited, satellite telemetry studies can assist in prioritizing areas of key concern, for example the habitat off Nigeria, Cameroon, Bioko, and Gabon we identified.

Further research into the potential anthropogenic effects of industrial activities will better inform environmental impact assessments associated with hydrocarbon exploration and production and garner private and public sector support for nationally and regionally relevant policies and targeted mitigation for whales and other cetaceans.

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Supporting Information

Additional methodological information (Appendices S1–S5) is available online. The authors are solely responsible for the content and functionality of these materials. Queries (other than absence of the material) should be directed to the corresponding author.

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