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Are marine protected areas and priority areas for conservation representative of humpback whale breeding habitats in the western South Atlantic?

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ABSTRACT

The establishment of marine protected areas (MPAs) is an important component of conservation strategies for large marine vertebrates. Thus, quantitative evaluations are necessary to assess whether their habitats are protected by these areas. In this study, the representativeness of government-established MPAs and identified priority areas for conservation (PACs) relative to the Brazilian wintering habitat of humpback whales was assessed using satellite telemetry data ($n = 74$ individuals). Argos-derived location data were filtered and modeled using a switching state space model (SSSM) and overlaid on shapefiles for MPAs and PACs. Humpback whales occurred in only 18.31% of the 71 MPAs observed within the species range. A lower frequency of locations was recorder inside rather than outside these areas. MPAs of Integral Protection used by humpback whales correspond to only 0.64% of the species wintering habitat. In contrast, a total of 40% of the 55 PACs observed within the same area was occupied by the whales, with a higher frequency of locations documented inside the PACs. Our results suggest that PACs encompass the species habitat in a more representative manner than MPAs. Because the former do not provide legal protection, they do not effectively contribute to the species conservation. We suggest PACs used by the species, especially Abrolhos Bank PAC, can be used as basis to refine conservation efforts of humpback whales in their breeding grounds in light of increased anthropogenic stressors. We also demonstrate that animal movement data obtained from satellite telemetry studies are useful for assessing the representativeness of MPAs and to improve management of whales.

1. Introduction

Establishing effective and representative systems of marine protected areas (MPAs) is part of a global strategy to conserve biodiversity (Convention on Biological Diversity – CBD, 2014; Kelleher, 1999; Prates, 2007). In the face of increasing threats, the use of MPAs is rising globally because these areas are viewed as an important management tool to prevent, reduce, or even reverse ongoing loss in marine biodiversity (Agardy, 1994; Agardy et al., 2003; Gormley et al., 2012; Hoyt, 2005; Spalding et al., 2008; Wood et al., 2008).

Because of their broad seasonal habitat, highly-mobile and migratory species typically offer a major challenge for spatial management (Game et al., 2009; Hyrenbach et al., 2000). Even though the usefulness of MPAs to protect these species is debatable (Notarbartolo di Sciara, 2007) because MPAs may only include a small portion of a species range, they may represent an effective measure for protecting part of their habitats (Game et al., 2009; Hoyt, 2005). However, the use of these areas as a management

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appliance depends on properly identifying and delineating spatial and temporal appropriate boundaries around important habitats (Ashe et al., 2010; Schofield et al., 2013; Silva et al., 2012; Williams et al., 2009).

The humpback whale (*Megaptera novaeangliae* Borowski, 1781) is a clear example of such migratory species, as it performs some of the longest migrations of any mammal (Rasmussen et al., 2007; Robbins et al., 2011; Stevick et al., 2011; Stone et al., 1990). Western South Atlantic humpback whales only occur off the eastern coast of Brazil during their wintering season (Martins et al., 2001) and typically occupy breeding habitats over continental shelf waters from 4°S to 24°S (Andriolo et al., 2010; Mamede, 2011; Zerbini et al., 2004). This population was nearly extirpated by commercial whaling in the beginning of the 20th century, but has been recovering since protection was afforded in the late 1960s (Ward et al., 2011; Zerbini et al., 2011a). Currently, this population is subject to other human stressors, including offshore development, fisheries and habitat degradation (e.g., Rocha-Campos and Câmara, 2011; Zappes et al., 2013; Zerbini and Kotas, 1998). Conflicts with such anthropogenic activities are expected to increase as these stressors expand and this population continues to grow and to re-occupy historical habitats (Andriolo et al., 2010; Zerbini et al., 2004).

Brazil signed and ratified the CBD in 1992. As such, the country has committed to improve conservation of biodiversity in the marine environment (CBD, 2014; Magris et al., 2013). Over the past 30 years, a series of protected areas have been established by the Brazilian government (e.g., Rylands and Brandon, 2005), yet only a small portion (1.87%) of the marine environment under Brazil's jurisdiction is currently under protection (Magris et al., 2013). Brazilian MPAs are unevenly distributed among the North, the East Coast and the South Brazilian continental shelves, with the largest protected extension corresponding to the North shelf and the largest number of MPA located in the East Coast shelf (Schiavetti et al., 2013). The Brazilian Ministry of Environment (MMA) has also identified a number of priority areas for conservation of the Brazilian biodiversity (hereafter referred to as PACs). These areas typically do not provide legal protection, but are proposed as useful approaches to guide future public policies (e.g., definition of areas for the creation of new MPAs) contributing to 'the conservation of biological resources, their sustainable use and sharing of benefits derived of this use' (MMA, 2002, 2007).

MPAs and PACs include a portion of the habitat of humpback whales in their breeding grounds off Brazil, but the representativeness of these areas relative to the species distribution and movements is poorly known and the efficiency in providing proper habitat protection needs to be evaluated. Since 2001, satellite tagging has been conducted to assess this species' habitat use and migration (e.g. Zerbini et al., 2006, 2011b) in the western South Atlantic. This research method has proven to be effective in assessing animal movements and occurrence relative to the boundaries of protected areas (e.g., Maxwell et al., 2011; Tancell et al., 2013; Witt et al., 2008). In this study, we conduct the first quantitative assessment of the representativeness of protected and priority conservation areas for western South Atlantic humpback whales using Argos tracking data in order to evaluate whether these areas are consistent with the primary habitat used by this species. Representation of their habitat can be obtained by selecting protected areas where the species occurrence is more predominant (e.g., ANZECC, 1999; Harris and Whiteway, 2009), both on a spatial and temporal scale. Results of the analysis presented here can be used to improve conservation and management efforts for humpback whales and can serve as a model for assessing the representativeness of protected areas for whales in other parts of the world where satellite telemetry efforts have been implemented.

2. Methods

2.1. Study area and data collection

Tagging operations were conducted off Brazil during the humpback whale breeding season (August–November) from 2003 to 2009. Tags were deployed near coastal locations (Conceição da Barra, Espírito Santo State, and Nova Viçosa and Barra Grande, Bahia State) or during a tagging cruise conducted from Cabo Frio, Rio de Janeiro State to Natal, Rio Grande do Norte State (Fig. 1). Tagging operations were undertaken during good weather conditions (Beaufort sea state $\leqslant 4$) from a rigid hull inflatable boats ranging from 5.5 to 6.7 m in length.

SPOT 3, 4 and 5 satellite transmitters from Wildlife Computers were employed in multiple configurations, including mini-can and implantable transmitters ($n = 69$, Heide-Jørgensen et al., 2003, 2006; Zerbini et al., 2006, 2011b), and LIMPET tags ($n = 5$, Andrews et al., 2008). Tag deployment was carried out with (i) an 8 m-long fiberglass pole (for mini-can and implantable tags, Heide-Jørgensen et al., 2003), (ii) a pneumatic delivery system (ARTS, for implantable tags, Heide-Jørgensen et al., 2001) or (iii) a 150 lb crossbow (for LIMPET tags, Andrews et al., 2008).

2.2. Data filtering and modeling

Satellite locations were received from Service Argos, which classifies each location into different quality categories of decreasing accuracy: 3, 2, 1, 0, A, B (Argos, 1990). Argos-derived satellite location data were filtered to remove unrealistic locations using the SDA-filter based on swimming speed, distance between successive locations, and turning angles (Freitas et al., 2008). This study has considered only positions located in the breeding ground for the analysis, thus locations recorded after whales initiated their migration toward the feeding grounds were removed following the criteria adopted by Andriolo et al. (2006, 2010) and Mamede (2011).

A Bayesian switching state space model (SSSM) (Jonsen et al., 2007) was applied to the filtered data from each humpback whale track. Model predicted locations were computed at 6-h intervals (e.g. Andriolo et al., 2014) from the observed data (Argos locations) by accounting for errors caused by inaccurate observations (measurement equation) and the dynamics of the movement process (transition equation) (Patterson et al., 2008). The SSSM was implemented using the open source software packages R (R Core Team, 2012) and WinBugs (Lunn et al., 2000). Two Markov chains were run in parallel, producing a total of 50000 Markov Chain Monte Carlo (MCMC) samples for each chain. The first 20000 samples were discarded as burn-in, and every 15th remaining sample was retained to reduce autocorrelation. The posterior distribution of the model parameter estimates was computed with the remaining 2000 samples. The SSSM outputs include the estimation of behavioral states, which ranged in value between 1 and 2 (Jonsen et al., 2005). Jonsen et al. (2007) divided these states in three categories according to the direction and speed of movement: 'transiting' (state values between 1 and 1.25) was associated with more linear and faster movement, 'uncertain' (state values between 1.25 and 1.75) was associated with undefined movements, and 'area restricted search' (ARS) (state values ranging between 1.75 and 2) was associated to more convoluted and slower movements.

2.3. Representativeness analysis

In this study the Brazilian MPAs evaluated were the conservation units. These areas are divided in two classes according to the National System of Conservation Units (SNUC, 2000): (1) areas of Integral Protection (or no-take areas), and (2) areas of Sustainable

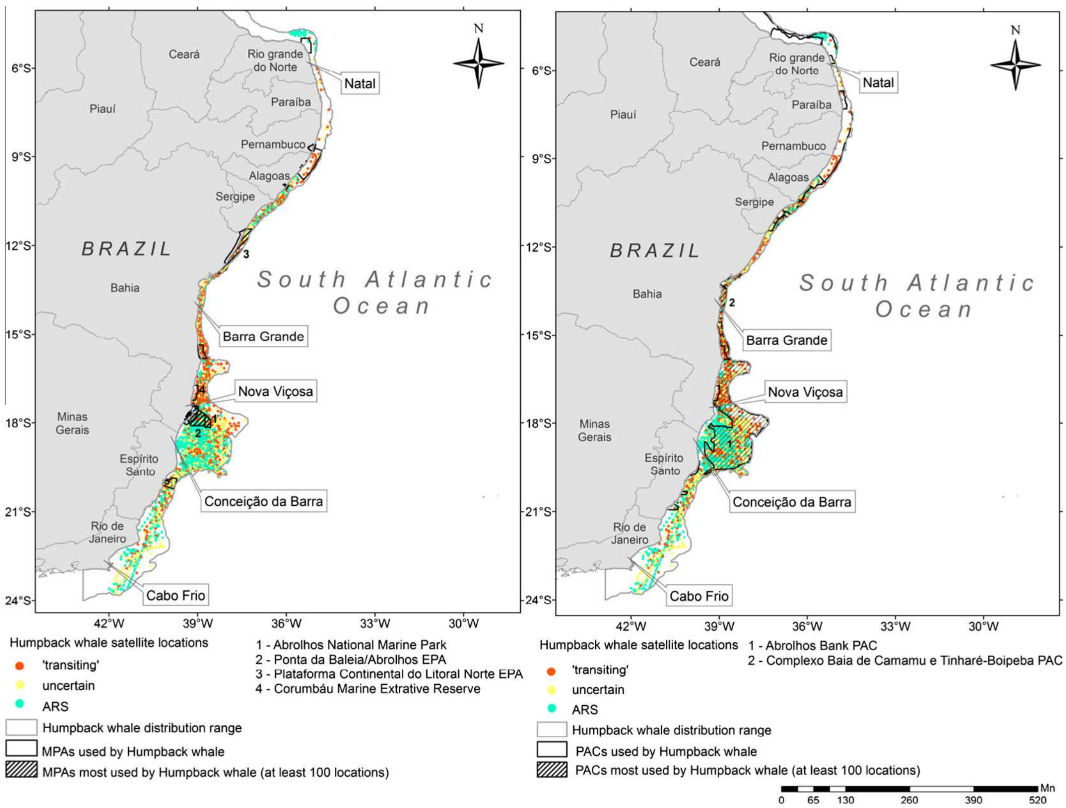

Fig. 1. Map of the study area showing the MPAs (left) and PACs (right) that were used and most used (areas with at least 100 locations) by humpback whales along the Brazilian coast, and humpback whale locations associated with each behavioral state (SSSM).

Use (or multiple-use areas). PACs are areas identified by the Brazilian government as 'priorities for conservation, sustainable use and sharing of the biodiversity benefits' (MMA, 2002, 2007). A more detail explanation of the definition of MPAs and PACs are included in the supplementary material.

Boundaries of MPAs and of PACs were obtained from databases provided by IBAMA ('Instituto Brasileiro do Meio Ambiente e dos Recursos Naturais Renováveis', 2011) and MMA (2011), respectively. The range of humpback whales in the wintering grounds was considered the area occupied by the whales within the 500 m isobaths from ~4°S (the northernmost satellite location) and ~24°S (the southernmost range of the species before they initiate their southbound migration) (Andriolo et al., 2010; Mamede, 2011), and the Brazilian coastline (based on a shapefile provided by SisCom/IBAMA ('Sistema Compartilhado de Informações Ambientais'), 2011). Only MPAs and PACs included within the range of the species were considered in this study. Among the PACs there were MPAs also classified as PACs by the local government (MMA, 2007) which were, therefore, removed from the PAC dataset as they represent areas already protected. In addition, the PAC dataset was further reduced to consider only PACs for which the main priority action consisted of creation/extension of MPAs. Thus, for the purpose of this study, PACs were defined as 'priority areas indicated mainly for the creation or extension of MPAs'.

The representativeness of the MPAs and the PACs to the humpback whale's wintering habitat were evaluated by overlaying the SSSM-predicted locations with polygons representing these areas in a GIS framework (ArcGIS Software, version 9.3, ESRI, 2008). The number of MPAs and PACs located within the species distribution range was determined using the 'Polygon in Polygon' analysis tool (Hawth's tools extension, Beyer, 2004). The humpback whale distribution area, the areas of the MPAs and the PACs, and the extent to which these areas overlapped was calculated using the 'Calculate Geometry' tool in ArcGIS. Finally, the 'Count Points in Polygons' tool (Hawth's tools extension) was used to identify the MPAs and PACs used by the monitored individuals and to calculate the number of positions recorded within each of these areas.

The representativeness of MPAs and PACs was inferred from the relative frequency of the occurrence of whale locations recorded in these areas. When a location was recorded in an area where there was overlap between two MPAs or PACs, the same location was computed for both areas. In evaluating, representativeness, MPAs and PACs used by humpback whales were considered both combined and individually. Because of the large number of areas available for this study, the results for individual areas presented here only include those for which at least 100 locations were observed.

2.4. Statistical analysis

The number of SSSM-predicted locations registered for each whale inside the MPAs or PACs was divided by the total number of locations for that individual in order to access their relative frequency inside these areas. The relative frequency of the three behavioral modes was also calculated. A non-parametric Wilcoxon test (U) was used to compare the relative frequencies of the locations recorded inside and outside the MPAs and PACs. A non-parametric Friedman test (Fr) was employed to compare the relative frequencies of locations recorded inside each MPA and PAC and to compare the differences among the relative frequencies associated with each of the three behavioral states registered inside the used MPAs and PACs. All statistical tests were conducted in software R (R Core Team, 2012) and p-values < 0.05 were considered significant.

3. Results

A total of 5026 predicted locations were generated with the SSSM. Behavioral states classified as transiting, uncertain or ARS corresponded to 966, 1197, and 2863 of the total number of predicted locations, respectively. The distribution of each behavioral state is illustrated in Fig. 1 (see also in Fig. A1 the distribution of each behavioral state separately). The total area of humpback whale breeding habitat off Brazil corresponded to 163 804 km^2.

3.1. Assessment of MPAs

3.1.1. MPAs combined

A total of 71 MPAs were fully or partially included within the humpback whale breeding habitat off Brazil, covering a total of 18 138 km^2. However, only thirteen (18.31%) MPAs were used by the individuals monitored, and their overlap to the species distribution range corresponded to 10.26% (16 809 km^2) of this area (Fig. 1, Table A1). Only two of these MPAs are areas of Integral Protection: Abrolhos National Marine Park and Santa Cruz Wildlife Refuge and they cover a total of 1056 km^2 or 0.64% of the species range.

A significant difference was observed between the relative frequency of humpback whale locations registered inside (16.61%) and outside (83.39%) ($U = 77.50$, $p < 0.001$) of MPAs. A similar pattern was observed for all behavioral states (transiting: $U = 145.50$, $p < 0.001$, uncertain: $U = 86$, $p < 0.001$, ARS behavior: $U = 61$, $p < 0.001$) (Fig. 2). ARS behavior was more frequent than transiting and uncertain behavioral states inside these areas. However, this difference was not statistically significant (Fr = 3.95, $p = 0.138$) (Figs. 1 and A1).

3.1.2. Individual MPAs

The MPAs frequency of use by humpback whales varied significantly among these areas (Fr = 306.74, $p < 0.001$). The MPAs where the highest relative frequencies of locations were observed are presented in Table 1. The extent of these areas (7437 km^2) corresponded to 4.54% of the distribution range of humpback whales off Brazil (see Table A1).

The relative frequency of locations registered inside these MPAs associated to each behavioral state was significantly lower than outside these areas (Table A3). Just inside Ponta da Baleia/Abrolhos Environmental Protected Area (EPA), ARS behavior was significantly more frequent than transiting and uncertain behavioral states. Inside the Plataforma Continental do Litoral Norte EPA, transiting was more frequent than uncertain and ARS behavior (see also Figs. 1 and A1).

3.2. Assessment of PACs

3.2.1. PACs combined

A total of 134 PACs were fully or partially included within the breeding range of humpback whales off Brazil. However, six of them were MPAs also classified as PACs by the local government, and 73 were PACs whose the main priority action indicated do not correspond to the creation/extension of MPAs. Thus, a total of 55 PACs (an overlap area of 69 949 km^2) were considered in this study. Whales were observed in 22 of these PACs (40%) which, together, corresponded to an overlap area of 65 798 km^2 and represented 40.17% of the distribution range of humpback whales (Fig. 1, Table A2). The relative frequency of humpback whale locations inside these PACs (60.80%) was significantly higher than outside (39.20%) ($U = 2158$, $p < 0.001$).

The relative frequency of locations associated with each behavioral state was also greater inside than outside of the PACs (transiting: $U = 1403$, $p = 0.001$, uncertain: $U = 999$, $p = 0.027$ and ARS behavior: $U = 1190$, $p < 0.001$) (Fig. 2). ARS behavior was more frequent inside these PACs (32.90%) than locations with behavioral states classified as transiting or uncertain (Fr = 12.98, $p = 0.001$) (Figs. 1 and A1).

3.2.2. Individual PACs

When analyzed individually, the relative frequency of locations varied significantly among the PACs (Fr = 749.85, $p < 0.001$). The PACs with highest representativeness are listed in Table 1. The extension of these PACs (46 561 km^2) corresponded to 28.42% of the distribution range of humpback whales off Brazil (Table A2).

The Abrolhos Bank PAC was the largest and the one with greatest overlap with the range of humpback whales in their wintering grounds. This was the only PAC for which the frequency of whale locations was higher inside than outside, although this difference was not statistically significant (Table 1). Uncertain and ARS behavior were also more frequent inside than outside the Abrolhos Bank PAC but, again, this difference was also not significant. ARS behavior was significantly more frequent inside this PAC than transiting and uncertain behavioral states (Figs. 1 and A1, Table A3).

4. Discussion

The examination of presence/absence data and relative frequencies was demonstrated to be an efficient method to evaluate the representativeness of MPAs and PACs relative to the habitat of humpback whales in their wintering grounds off Brazil. When coupled with the estimation of behavioral modes (e.g. with an SSSM), results from such an analysis allow for improved assessment of representativeness as they allow distinguishing movements types and, thus, inferring about how these areas are used by the species. Behavioral modes classified as ARS have been associated with areas of feeding, resting or breeding in other marine vertebrates (Bailey et al., 2009; Jonsen et al., 2007). Because humpback whales do not typically feed in their wintering grounds (Clapham and Mead, 1999), it is more likely that this type of behavioral state represents mating/calving off Brazil and high density areas with greater frequency of ARS behavior may correspond to more important habitats that could perhaps be considered a priority for conservation (e.g., Hoyt, 2005). The SSSM can also be used to identify transit behavior, which could predominate in areas used by animals to transit across breeding regions. These may also be important for conservation on a broader perspective because of the potential importance of these areas to connect breeding sites.

4.1. Assessment of MPAs

In the Seventh Conference of Parties (COP 7) in 2004, it was agreed that 'at least 10% of each of the world's ecological regions should be effectively conserved' (CBD, 2014). As a signatory of the CBD, Brazil has recently committed to achieve the Aichi Biodiversity target 11 (COP 10) of encompassing at least 10% of coastal and marine areas within 'an effectively and equitably managed, ecologically representative and well connected system of protected areas' by 2020 (CBD, 2014). Currently, only a small portion (1.87%) of the marine waters under Brazilian jurisdiction is under legal protection, which demonstrates that Brazil is far from reaching this goal (Magris et al., 2013). However, some authors consider the setting of minimum percentage targets for conservation (e.g., the Aichi Biodiversity Target of 10%) a policy-driven target without evidence of considering biological requirement or conservation merit, which does not provide a basis for realistic assessments (Chape et al., 2005; Magris et al., 2013; Svancara et al., 2005).

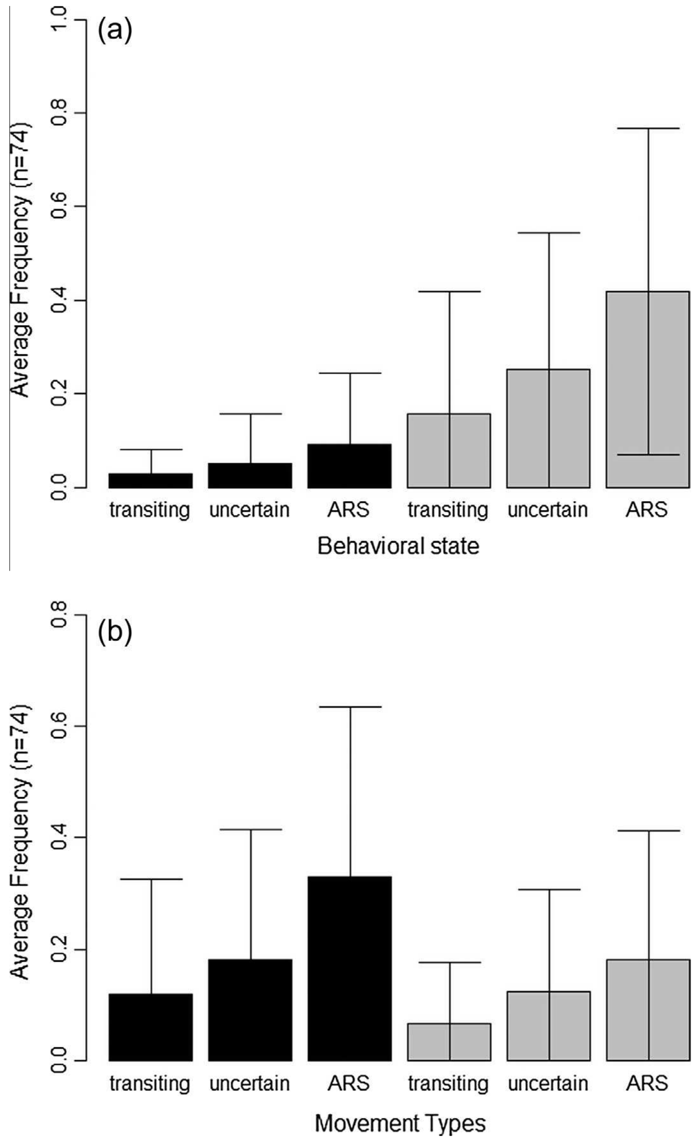

Fig. 2. Average relative frequency of humpback whale locations related to each behavioral state registered inside (black) and outside (gray) of Brazilian MPAs (graphic 1) and PACs (graphic 2).

Table 1
The MPAs and PACs that were most used (areas with at least 100 locations) by humpback whales along the Brazilian coast.

	Average relative frequency of locations		*U* test[a]
	Inside	Outside	
MPA			
Ponta da Baleia/Abrolhos Environmental Protection Area (EPA)	0.102	0.898	$U = 21$, $p < 0.001$
Abrolhos Nacional Marine Park	0.024	0.976	$U = 0$, $p < 0.001$
Plataforma Continental do Litoral Norte EPA	0.018	0.982	$U = 0$, $p < 0.001$
PAC			
Abrolhos Bank	0.535	0.465	$U = 1617.50$, $p = 0.216$
Complexo Baia de Camamu Tinharé-Boipeba	0.040	0.960	$U = 3$, $p < 0.001$

[a] Comparison of the frequency inside and outside each MPA and PAC.

Although the existing MPAs represented 11.07% of the humpback whale habitat in their breeding ground, protection afforded by those areas used by the species is relatively limited. It could be argued that this may be a consequence of the conservation goals of these MPAs because in many cases they were not designed to protect such highly mobile species. A low coverage of breeding habitats have been observed even for MPAs designed and/or managed to protect the humpback whale habitat (MPAs #1, 2, 3 and 4 in Fig. 1) (CNUC, 2014; ICMBio, 2014; SEMA-Bahia, 2014). If only these MPAs are considered in a representativeness analysis, they would correspond to just 5.09% of the species habitat.

At least three of these areas (MPAs #1, 2, and 4 in Fig. 1) are located inside the Abrolhos Bank, a region considered the most important breeding site for humpback whales in the western South

Atlantic (e.g. Andriolo et al., 2006, 2010; Martins et al., 2001; Morete et al., 2003). Yet, they do not encompass the southern portion of the Bank where many anthropogenic activities are currently under development (Martins et al., 2013). In addition, recent data show that relatively high-density areas are also found outside the Bank providing evidence that historical habitats are being reoccupied (Andriolo et al., 2010; Zerbini et al., 2004). This is relevant because anthropogenic activities in these regions are possibly as or more developed than in Abrolhos Bank and development started when populations were still depleted (Andriolo et al., 2010). These areas require protection, which could be achieved by the establishment of MPAs, especially if they can be planned as part of a spatially continuous network that would include existing protected habitats.

Another important point to consider is the management class for the MPAs in which humpback whales were observed. Only two out of 13 areas correspond to MPAs of 'Integral Protection'. The others fall in the less restrictive 'Sustainable Use' class. The latter allows for a series of human activities, many of which are known as potential to impact humpback whales (Johnson et al., 2005; Marcondes and Engel, 2009; Rocha-Campos and Câmara, 2011; Sousa-Lima and Clark, 2008; Wiley et al., 2011; Williams and O'Hara, 2010). Therefore, MPAs of 'Integral Protection' protect the animals and their habitats from potential sources of impact in a more effective manner. However, because of their relatively small size (the two areas together correspond to only 0.64% of the range of the species) they provide little protection to the humpback whale breeding habitat off Brazil. In addition, only five MPAs have an established management and/or zoning plan, which could potentially regulate some of the known humpback whale stressors (CNUC, 2014; ICMBio, 2014; SEMA-Bahia, 2014) (Table A1) including boat traffic, whale watching, fishing, and seismic and/or oil and gas activities. Because management plans define the management objectives for protected areas and because they provide a basis for decision making (Bertzky et al., 2012; Gabrié et al., 2012; Lee and Middleton, 2003; SNUC, 2000), the lack of such a plan for the remainder eight MPAs indicate there is still a potential for the development of activities harmful to humpback whales within their boundaries.

The analysis presented here clearly shows that ARS behavior and transiting are still mostly under no legal protection because their frequency is greater outside the MPAs. ARS was the behavioral state most frequent within the Ponta da Baleia/Abrolhos EPA (MPA #2 in Fig. 1), which could be explained by the location of this MPA in the main breeding habitat of the species in the region (Andriolo et al., 2010). Transiting was the behavioral state most frequent within the Plataforma Continental do Litoral Norte EPA (MPA #3 in Fig. 1), where risk of collision with vessels is described as a possible conflict (SEMA-Bahia, 2014). Both of these MPAs are of 'Sustainable use' areas and they have no management plan. Therefore, the adoption of management measures for them is timely to improve the protection of the whales that use these areas as breeding and transiting areas, respectively. Additionally, as Ponta da Baleia/Abrolhos EPA covers an area where the ARS behavior is most frequently observed, we suggest that it could be changed from 'Sustainable Use' to 'Integral Protection'.

4.2. Assessment of PACs

Usage of the combined PACs areas by the humpback whales overlapped with (and thus were more representative of) the species habitat to a much greater extent than the MPAs. This was already expected since these areas covered 40.17% of the species breeding range and accounted for 60.80% of the humpback whale locations. Consequently all the behavioral states were encompassed in a more representative way, highlighting the importance of these PACs as a possible tool for species management. Individually, the Abrolhos Bank PAC was the one where the presence of the species was more frequent. ARS behavior predominated inside this area, confirming that the area covered by this PAC constitutes the main breeding site for humpback whales off the coast of Brazil.

Although the concepts and tools of systematic conservation planning (e.g., Margules and Pressey, 2000; Pressey et al., 2007) were incorporated in the process for PACs identification (MMA, 2007), these areas are not legally recognized as protected areas and therefore, they still do not effectively contribute to biodiversity conservation along the coast of Brazil. Because of their greater representativeness, results presented here demonstrate that the PACs used by humpback whales represent a useful network of areas that could be used as a basis to refine existing or design new MPAs in order to increase species habitat protection. One example is the Abrolhos Bank PAC, which corresponds to 27.37% of the species distribution range and covers over half of the humpback whale locations, being located in a region that corresponds to the main breeding aggregations of the species off Brazil. However, if the protection of areas outside Abrolhos Bank is planned for the future, identifying of portions of high concentration of ARS behavior among the PACs used by the species could be an effective way to delineate areas for their protection.

4.3. MPAs and conservation of humpback whales

Humpback whales may be a useful surrogate for multispecies conservation. They occupy large habitats, have high socioeconomic significance (e.g., sustain profitable whale watching activities; Caro, 2010), and are regarded as a charismatic species. Thus, they can be considered as umbrella and flagships species (see Simberloff, 1998) and efforts toward their conservation may enhance biodiversity protection and garner strong support from local communities (Olds et al., 2014).

Whaling reduced most whale populations to near extinction (Clapham et al., 1999) but many, including western South Atlantic humpback whales, have been recovering since protection (Best, 1993; Noad et al., 2011; Zerbini et al., 2011a). Because many anthropogenic activities started to be developed in the wintering grounds off Brazil during a period of low population density, recovery and reoccupation of historical habitats should increase risk of conflict with such activities (Andriolo et al., 2010). Therefore, expanding conservation efforts (e.g. by improving marine protected areas) is critical to ensure this recovering population remains healthy.

The refinement of protected areas for humpback whales should account for other ecological criteria and for economic and social aspects (e.g., human activities, the local knowledge and stakeholders involvement in the planning procedure) (Airame et al., 2003; Gerhardinger et al., 2009; Giakoumi et al., 2012; Green et al., 2009; IUCN-WCPA, 2008; Maxwell et al., 2013; Schofield et al., 2013; Teh et al., 2013). Knowledge of the distribution, seasonality and intensity of human-related stressors, many of which are known to occur in important humpback whale habitats (Marcondes and Engel, 2009; Martins et al., 2013; Sousa-Lima and Clark, 2008; Zappes et al., 2013), is important to maintain areas relevant for human development open while minimizing harmful impacts and needs for enforcement (Dunn et al., 2011; Hobday et al., 2011; Maxwell et al., 2013). An example of areas accounting for all these aspects are the seasonal and dynamic management areas implemented on the western North Atlantic to reduce threats from driftnet fishing artifacts and vessel collisions to right whales (*Eubalaena glacialis*) (Asaro, 2012; Merrick, 2005).

An assessment of stressors potentially affecting the western South Atlantic humpback whale population and some of the MPAs where the species occur been done for the eastern coast of Brazil (coastal waters of Bahia and Espírito Santo States), in order to identify priority areas for the species conservation (Martins et al., 2013). However, because of the wider habitat used by this species and the diversity of anthropogenic activities throughout its range, a more thorough evaluation is recommended. Results from such analysis should then be integrated with those provided here in order to further refine protection areas for humpback whales.

It is important to recognize that identifying important areas for conservation of migratory and mobile species as cetaceans is not a simple task, and that the variation in these species space-use patterns presents enormous challenges in MPA design (Silva et al., 2012). Hintz and Garvey (2012) indicate that migratory or dispersing organisms may be subjected to different degrees or types of protection depending on where they occur and how they are legally and biologically perceived. These points are important to consider here because the seasonal migratory nature of humpback whales typically leads them outside of the Brazilian jurisdictional waters and therefore their full protection is a matter of international discussion. In the case of the western South Atlantic whales, however, conservation efforts in the coastal breeding habitats are likely to provide significant protection to the habitats in which this population is more vulnerable to human activities because the migratory routes and destinations of Brazilian humpback whales are located in relatively remote areas with little access to humans (Zerbini et al., 2006, 2011b).

Hoyt (2005) indicates that there is not a single ideal protected area for cetaceans, because their needs vary by species, population, and location, must be evaluated in an ecosystem context, and must consider possible future human development. Stationary protection may only represent small windows of their life history (Game et al., 2009; Maxwell et al., 2011, 2013). As a migratory species, humpback whales likely require seasonal rather than year-round protection (Schofield et al., 2013). Hence, adopting mobile areas for protection (areas temporally and spatially variable to reflecting the dynamic behavior and distribution of them) may be a more effective alternative (see Annual Meeting of the American Association for the Advancement of Science, 2012 about mobile marine reserves). Although this approach has not yet been adopted as a measure to protect the breeding habitat of humpback whales by Brazilian government, it may be valuable to consider mobile MPAs as a strategy in planning future MPAs for humpback whales off Brazil.

Systematic conservation planning has been proposed as a valuable framework for MPA network design (Giakoumi et al., 2012; Magris et al., 2013; Pressey et al., 2007). In addition to the biodiversity representation this type planning considers the persistence of biodiversity processes, their dynamics in time and space and the dynamics of their threats (Grantham et al., 2011; Pressey et al., 2007). These features should also be considered in reviewing or further developing conservation areas for humpback whales off Brazil. The analysis of the representativeness of MPAs and PACs presented here are important to better inform this process because it allows identifying the portion of the humpback whale's habitats covered by these areas as well as how these areas are potentially used by the whales through the estimate of their behavioral states.

5. Conclusion

This study constitutes the first comprehensive and quantitative evaluation of the representativeness of MPAs and or other areas of conservation relevance to the wintering habitat of humpback whales in the western South Atlantic using satellite telemetry data.

The assessment performed here demonstrated that current MPAs provided limited protection to the wintering habitat of humpback whales along the eastern coast of South America. Even though PACs do not offer legal protection, they include a much greater proportion of the species' habitat and are, therefore, more representative of their breeding range. Therefore, PACs could be used as a basis for the refinement of a network of MPAs in order to enhance protection of the humpback whale habitat. Because the Abrolhos Bank PAC was the PAC most used by the species it could be prioritized to guide conservation efforts to protect humpback whales. However, given the large extent, notably of this PAC, information on the humpback whale behavioral state, and other topics not addressed in this study such as the habitat use by the species and the spatial and temporal distribution of anthropogenic activities in this area should be considered to define the most efficient way to manage it. Based on our results PACs could be refined considering areas of high concentration of ARS humpback whale behavior.

In light of increasing anthropogenic stressors along the humpback whale breeding habitat and of their grow rate, an expansion in the proportion of the habitat protected is desirable and a review of the current areas is strongly recommended. Such a review should consider an adequacy or the establishment of management plans for existing MAPs, it should assess the feasibility of implementing stationary or mobile protected areas, or even the adoption of control and mitigation measures of human activities that could potentially impact humpback whales. Additionally, an extension of the monitoring effort especially through the areas of recent reoccupations is also suggested.

The approach presented here can inform this process by evaluating the representativeness of MPAs used by mobile species with wide, seasonally dynamic distributional ranges.

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Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.biocon.2014.09.013.

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