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ARTICLE

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Exploring habitat use and movement patterns of humpback whales in a reoccupation area off Brazil: A comparison with the Abrolhos Bank

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Abstract

After the worldwide moratorium on whaling, humpback whale populations began to recover, reoccupying former areas of use, as also observed on the Brazilian coast. Abrolhos Bank represents the area of greatest humpback whale concentration but the number of individuals to the north has increased, as has happened in the region of Serra Grande. To compare relative abundance, habitat use, and movement patterns between a well-established breeding and a reoccupation area, visual monitoring from land-based stations was performed: 160 days in the Abrolhos Archipelago located on the Abrolhos Bank and 133 days in Serra Grande in 2014, 2015, 2018, and 2019. While relative

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abundance varied annually in the Abrolhos Archipelago, it gradually increased in Serra Grande, surpassing the number registered in Abrolhos in 2019. Group composition frequency was similar between areas except for mother and calf accompanied by one or more escorts, which were more frequent in Abrolhos. Despite similar movement speed and linearity values, whales in Serra Grande had a higher reorientation rate. Monitoring different areas occupied by this population supports decisions about spatial management of the Brazilian coast in relation to the implementation of anthropogenic activities, especially in areas where whales have recently returned to occupy.

KEYWORDS
breeding area, depth, humpback whale, land-based survey, *Megaptera novaeangliae*, relative abundance, speed

1 | INTRODUCTION

Humpback whale (*Megaptera novaeangliae*) populations around the world were reduced almost to extinction due to the whaling industry (Zerbini et al., 2010). In this context, the humpback whales that migrated annually to Brazil to reproduce were exploited by whaling since the 17th century (Edmundson, 2014). At the beginning of the 20th century, this activity expanded to their feeding areas, around the South Georgia and South Sandwich Islands (Zerbini et al., 2011), when the Brazilian breeding stock A-BSA (International Whaling Commission, 1998, 2001) was impacted. As a result, this population was intensely affected (de Morais et al., 2016) and only 2.2% (between 440 and 616 whales) of the original stock was not captured (Zerbini et al., 2011).

In Brazil, after a moratorium on whaling (International Whaling Commission, 1998), the number of humpback whales is increasing (Andriolo et al., 2010; Pavanato et al., 2017; Wedekin et al., 2017), and this population was recently estimated at 93% (about 22,971 whales) of its preexploitation size (Zerbini et al., 2019). Along the Brazilian coast, the species is distributed across a broad range of latitudes (from 24°S to 5°S) and is typically found at depths <200 m (Zerbini et al., 2006). Nowadays, due to population growth, humpback whales are reoccupying historical areas of use (Gonçalves et al., 2018a; Rossi-Santos et al., 2008; Zerbini et al., 2004), extending their distribution to latitudes between 30°S–5°S (Andriolo et al., 2006; Ristau et al., 2019; Wedekin et al., 2010).

Annually, approximately 80% of humpback whales that migrate to the Brazilian coast are expected to be observed on the Abrolhos Bank (Andriolo et al., 2010; Wedekin et al., 2010). This large bank has approximately 46,000 km^2 (Ekau & Knoppers, 1999), extending up to 220 km east from the coastline (Leão & Kikuchi, 2001). The Abrolhos Bank is characterized by its calm and relatively shallow waters that provide optimal conditions for female humpback whales to give birth and nurse during the reproductive season (Martins et al., 2001; Morete et al., 2007). Only 0.913 km^2 of its area is protected by the Abrolhos Marine National Park located in the northern portion (19°S–16°S) of the Bank, where the Abrolhos Archipelago is located (ICMBIO, 1991; Figure 1).

To the north of the Abrolhos Bank, in the region of Serra Grande (14°S), the continental shelf is at its narrowest along the Brazilian coast (Prates et al., 2012). In this region, an increase in sightings of humpback whales has been

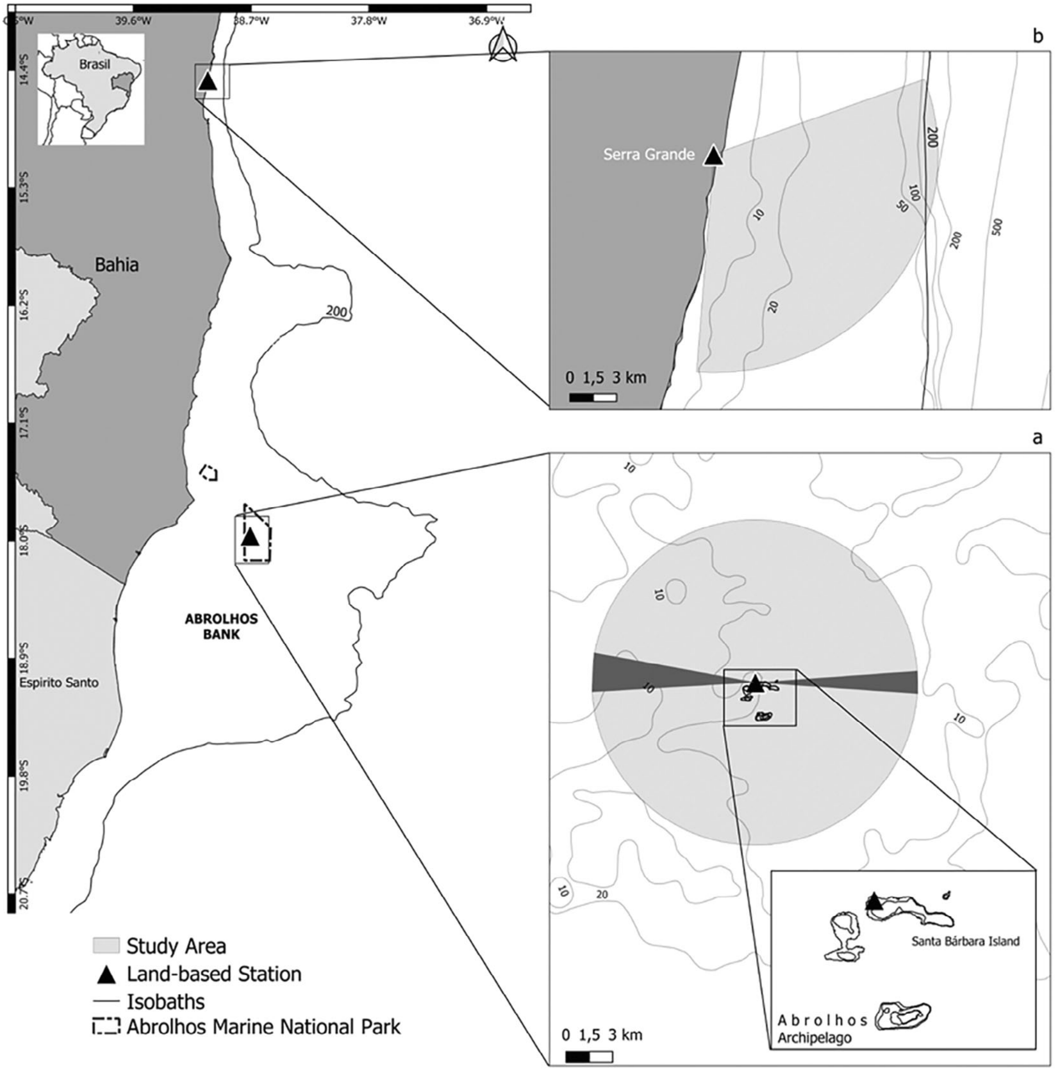

FIGURE 1 Study area located in Northeastern Brazil in the South of the state of Bahia. (a) The land-based observation station at Santa Bárbara Island, Abrolhos Archipelago, situated on the Abrolhos Bank, 38 m high, with a coverage of 250 km^2, with the exception of two sectors covered by islands: one to the east and the other to the west, covering arcs of 8° and 14°, respectively; and (b) the land-based observation station at Serra Grande, north from the Abrolhos Bank, at a height of 93 m, covering an area of 224.5 km^2.

observed between breeding seasons of 2014 and 2015 (Gonçalves et al., 2018a). This area is characterized by great depths right after the shelf break, leading the humpback whales to come closer to the coast (Gonçalves et al., 2018a).

Despite the Abrolhos region being the area with the highest humpback whale concentration along the Brazilian coast (Andriolo et al., 2006, 2010), the period when the greatest number of whales is observed is similar to Serra Grande, between the end of August and the beginning of September (Gonçalves et al., 2018a; Morete et al., 2008). Previous studies show that the number of adult humpback whales observed per hour in the Abrolhos Archipelago reached 37 individuals and up to 11 calves (Morete et al., 2003, 2008). A study carried out in the last decade in Serra Grande shows a maximum number of adults of 14 individuals and up to 4 calves observed per hour

(Gonçalves et al., 2018a). Twenty years ago, 47.6% of groups in the Abrolhos Archipelago had calves (Morete et al., 2007), unlike the current reoccupation areas where this number is approximately 20% (Gonçalves et al., 2018a; Lunardi et al., 2008; Zerbini et al., 2004).

Humpback whales occupy shallow waters in Abrolhos Bank (Leão et al., 2003; Martins et al., 2001) but it is common to find spatial segregation of groups of mothers with calves in breeding areas, remaining closer to the coast in shallower waters than groups of adults (e.g., Betancourt et al., 2012; Craig et al., 2014; Gonçalves et al., 2018a; Smultea, 1994). In Serra Grande, Gonçalves et al. (2018a,b) observed that groups with calves escorted by adults remain in deeper waters, and that with the increase in the number of escorts, the distance to the coast where these groups were observed also increased.

Studies carried out using telemetry of humpback whales belonging to the BSA observed speed values (considering trajectories within periods of 24 hr) that varied between 1 km/hr and 4.2 km/hr during the migration to the feeding area, and between 0.75 and 1.80 km/hr in feeding grounds (Dalla-Rosa et al., 2008; Zerbini et al., 2006). In Serra Grande, land-based observations estimate the average speed value considering all groups to be 6.88 km/hr. Considering groups of only females with calves, lower speed values were registered, but their speed increases significantly in the presence of escorts, which has been also observed in the Abrolhos Archipelago (Bisi, 2006; Gonçalves et al., 2018b). Contrary to what has been observed in South Africa, humpback whales have more erratic trajectories along the Brazilian coast, presumably associated with breeding and nursing activities (Barendse et al., 2010; Gonçalves et al., 2018b).

Understanding the changes in habitat use requires consideration of population recovery and reoccupation processes that are associated with social and behavioral contexts, and habitat characteristics such as depth, distance from the coast, and marine geomorphology (Gonçalves et al., 2018a; Trudelle et al., 2016), which influence how humpback whales explore their breeding areas. Humpback whale movement patterns are related to their biological needs and habitat selection processes (Marcondes et al., 2021; Schick et al., 2008; Trudelle et al., 2016). In this study, we aim to compare the patterns of relative abundance, habitat use, and movement of humpback whales between the regions of Abrolhos Archipelago and Serra Grande.

2 | METHODS

2.1 | Study area

This study covered two distinct regions of occurrence of humpback whales within their range of distribution along the Brazilian coast, both in the South of Bahia state, northeastern Brazil: the Abrolhos Archipelago (17°S) located on the Abrolhos Bank, and Serra Grande (14°S), separated by approximately 420 km (Figure 1).

The size of the study areas was adjusted according to the elevation of each land-based observation station and the curvature of the Earth with an observation radius that maximizes the identification of the group composition and the presence of calves.

2.1.1 | Abrolhos Archipelago

Abrolhos Archipelago (AB) is in the northern region of the Abrolhos Bank and is composed of five volcanic islands (Leão et al., 2003). The archipelago stays between two coral reef arches, it is approximately 70 km from the coast and the depths rarely exceed 30 m (Leão et al., 2003). The average winter water temperature in the region is approximately 24.8°C (https://seatemperature.net/).

A land-based observation station was established (17°57′50″S, 38°42′30″W) at 38 m above sea level in the western portion of Santa Bárbara Island. The sampled area encompasses 9.3 km of observation radius around the station except for two sectors covered by the islands: one to the east and the other to the west, with cover arcs of 8° and 14°, respectively, totaling approximately 250 km^2 of the observed area (Figure 1a).

2.1.2 | Serra Grande

The Serra Grande (SG) region has a continental shelf about 10 km long (Prates et al., 2012) and reaches a depth of 90 m about only 15 km from the coast (Gonçalves et al., 2018a). The average winter water temperature is 25.9°C (https://seatemperature.net/).

A land-based observation station (14°28′30″S, 39°01′50″W) was established at 93 m above sea level and 315 m from inland to the shoreline. The study area encompassed a radius of 15 km from the land-based station, between azimuths 70° and 184°, totaling 224.5 km^2 (Figure 1b). It is not possible to observe the northeast portion of the area due to the vegetation and rocks that do not allow the monitoring.

2.2 | Data collection

The visual monitoring of humpback whales was performed between June and November in the Abrolhos Archipelago from 6:30 a.m. to 5:30 p.m. and between July and October in Serra Grande from 7:20 a.m. to 4:40 p.m., during the breeding seasons of 2014, 2015, 2018, and 2019. The sampling effort occurred on days with satisfactory visibility in both sites, with sea status less than or equal to Beaufort 4, according to the Beaufort Sea State Code (Gonçalves et al., 2018a). In the Abrolhos Archipelago data collection happened on every day that the Brazilian Navy authorized the team to stay on Santa Bárbara Island, and typically twice a week in Serra Grande.

The data collection was carried out by two to four observers who, with the naked eye, with the aid of 7 × 50 binoculars and a theodolite or a total station with 30X monocular magnification, searched for whales and followed them during the different methodologies applied. In the Abrolhos archipelago, the main observer who operated the theodolite or the total station was the same within each season, and in Serra Grande, it was the same throughout the study. Whales were located based on signs of presence, such as blows, splashes of water from aerial behaviors, or exposure of a body part (Morete et al., 2008).

In the Abrolhos Archipelago, a Sokkia DT5 Theodolite with 5′ precision was used. In Serra Grande, a TOPCON ES105 Total Station was used in 2014 and 2015, and a SPECTRA PRECISION FOCUS-2 Total Station in 2018 and 2019, both with 5′ precision. Both devices measure horizontal angles from a known reference point to the whale, and vertical angles between the observer and the whale (Bailey & Lusseau, 2004). The theodolite and the total stations differ only in that the total station has internal data storage capacity (Morete et al., 2018). In the Abrolhos Archipelago, the angles were manually recorded and then typed, while in Serra Grande, the angles were downloaded from the total station.

To assess relative abundance, group composition, and the depth at their position, we scanned the entire area for an hour to record all groups sighted (Gonçalves et al. 2018a; Morete et al., 2007, 2008) twice a day, once in the morning and once in the afternoon, whenever environmental conditions allowed and the horizon line was sharp, allowing groups to be observed throughout the study area (Gonçalves et al., 2018a). The mean time interval between each 1 hr scan was 6.50 hr (SD = 1.71) in the Abrolhos Archipelago and 3.33 hr in Serra Grande (SD = 0.79), ensuring data independence (Gonçalves et al. 2018a).

During the remaining time of the sampling effort, the movement patterns of groups were studied using focal group sampling (Mann, 1999). The observer tracked one of the sighted whale groups using a total station or theodolite until the animals left the study area or until the visibility compromised the quality of the observation. When more than one group was present in the area, the group followed was selected based on shorter diving intervals, the occurrence of active behaviors by the individuals, and the proximity of the groups to the land-based station. These criteria optimized successful group observation and behavioral tracking, following previously established protocols in the same study areas (Gonçalves et al., 2018b). During a focal follow, the number of individuals, group composition, and position angles were continuously recorded whenever possible when the focal animal emerged. When the group consisted of more than one individual, the angle was with reference to the individual who directed the movement of the group, or to the calf, if present (Gonçalves et al., 2018b), since calves are more frequently found on the surface and more easily discriminated from other animals due to their smaller size.

2.3 | Definitions

A group was defined as one or more individuals moving in a coordinated manner, in the same direction, and with a distance estimated by eye between one animal and another that does not exceed 100 m (Morete et al., 2008; Whitehead, 1983). The groups with calves were classified as (1) mother with calf (MOC); and (2) mother and calf accompanied by one or more escorts (MOCE/+). In the absence of a calf, the definitions were based on the number of whales, which could be (3) solitary (1 AD), when one adult was observed; (4) two adults (DYAD), when two adults were sighted; (5) three or more adults (3 AD+), when more than two adults were sighted together; or (6) undetermined (UND), when it was not possible to determine the composition of the group. Due to the distance between the groups and the land-based station, it was not possible to discriminate between juveniles and adults: the whales were considered as adults or calves, the latter being considered as such when having up to 50% of the length of an adult (Chittleborough, 1965).

2.4 | Spatial analysis

To determine the UTM coordinates (E, N) of the groups, it was necessary to know the coordinates of the land-based stations and of reference points to calibrate the equipment. The UTM coordinates of the land-based stations and the reference points were determined using the same protocol mentioned in Gonçalves et al. (2018a) for both study areas.

Group UTM coordinates were calculated using trigonometric equations described by Gonçalves (2017). These equations relate the distance from the projection of the land-based station's location at sea level to the whale, which is equal to the height above sea level of the theodolite or the display of the total station, multiplied by the tangent of the vertical angle. For these calculations, the height of the theodolite or the total station installed, and the tidal variation were considered. The correction of errors due to the Earth's curvature (Vanicek & Krakiwsky, 1996) was done by transforming horizontal distances into spherical distances.

The depth at the estimated position of the recorded groups in the Abrolhos Archipelago was obtained from a bathymetric raster available on the MARSPEC website (http://www.marspec.org/). In Serra Grande, the depths of the observed groups were obtained through the vectorization of the Nautical Chart 1210 of the Brazilian Navy (Centro de Hidrografia da Marinha, 2018), followed by the interpolation of depth values using Kriging geostatistical analysis (Childs, 2004). By standardization, nautical charts and depth rasters use the lowest tides to calculate depth; therefore, differences in minimum depth values may occur in shallow areas. The difference in bathymetric accuracy between the two rasters did not exceed 2 m in depth; so, the bias of no standardization of depth rasters for the study areas was excluded. The depth of each sighting group was determined using the *Extraction* tool from the "Spatial Analyst Tools" package in ArcGIS 10.8.

2.5 | Movement patterns analysis

Trajectories were considered for the analyses when: (1) there were at least four positions recorded, (2) the group was monitored for at least 10 min, and (3) group composition was identified (Gonçalves et al., 2018b). From this, the following movement parameters were calculated:

Net speed (km/hr): calculated by dividing the linear distance between the first and last recorded point by the total time of the track (Barendse et al., 2010; Findlay et al., 2011; Gonçalves et al., 2018b).

$$\text{Net speed}\,(\text{km/hr}) = D/T$$

Leg speed (km/hr): obtained through the mean of speeds calculated by dividing the distance between two consecutive positions by the time taken to move between them (Barendse et al., 2010; Gonçalves et al., 2018b). We did not consider speeds above 30 km/hr because the maximum speeds recorded for humpback whales range from 18 km/hr (Findlay & Best 1996) to 27 km/hr (Zenkovich, 1937 in Winn & Reichley, 1985).

$$\text{Leg speed}(\text{km/hr}) = (d1/t1 + d2/t2 + \ldots dx/tx)/x$$

Linearity: calculated by dividing the total distance between the first and the last point of the trajectory by the sum of the distances between each consecutive point (Barendse et al., 2010; Gailey et al., 2007; Gonçalves et al., 2018b; Williams et al., 2002). The values obtained are an index that can range from 0 to 1, in which values closer to 0 represent more erratic movements, whereas values closer to 1 represent straighter paths (Burns, 2010; Gonçalves et al., 2018b; Schaffar et al., 2009).

$$\text{Linearity} = D/(d1 + d2 + \ldots dx)$$

Reorientation rate (°/min): obtained from the sum of all absolute values of change of direction between two consecutive points, divided by the total trajectory time (Gailey et al., 2007; Gonçalves et al., 2018b; Smultea & Würsig, 1995); higher values indicate more erratic trajectories (Burns, 2010).

$$\text{Reorientation rate}\left({}^{\circ}/\text{min}\right) = (\alpha 1 + \alpha 2 + \ldots \alpha x)/T$$

Net course (°): the direction in true degrees considering the first and last position of the trajectory (Barendse et al., 2010; Best et al., 1995; Findlay et al., 2011; Gonçalves et al., 2018b).

Where D = net distance, d = distance between each point, T = total time, t = time between each point, x = number of legs, and α = absolute value of change of direction between two consecutive points.

Values of net and leg speed, linearity, and reorientation rate of humpback whale groups were obtained using the "adehabitatLT" package R and the directions of the groups were obtained through the GPS TrackMaker program.

2.6 | Statistical analysis

The data collection period varied among seasons and between study locations. Thus, to avoid bias during comparative analyses between the two areas, we considered only the months of common observation (July–October) except for the estimate of the peak of the season. All statistical analyzes were performed in R Studio 2023.03.0 + 386 (R Core Team, 2023), using specific packages for each test.

2.6.1 | Relative abundance

We defined relative abundance as the number of humpback whales sighted in the study areas in each 1 hr scan. When it was not possible to determine group composition and the exact size of the group, we considered the number of whales that it was possible to count for undetermined groups (adults and calves, separately) without overestimating. Because of the fluctuation of relative abundance throughout the season (Morete et al., 2008), the peak of each breeding season was calculated using a segmented regression (Muggeo, 2008) of the total number of humpback whales observed per hour through the Julian Day. This analysis was obtained using the "Segmented" package in R, considering the entire data set of each area studied.

Shapiro–Wilk tests (*SW*) showed that relative abundance data were not normally distributed in either the Abrolhos Archipelago (SW = 0.93, $p < .001$) or the Serra Grande (*SW* = 0.92, $p < .001$). Thus, we applied Kruskal-Wallis tests (*K*) followed by post-hoc Pairwise Wilcoxon tests to assess if the number of adults and calves of humpback whales per hour observed in the same area varied between the breeding seasons, and Mann–Whitney Wilcoxon tests (*U*) to compare the relative abundance of humpback whales between the areas in each breeding season sampled.

2.6.2 | Group composition

The groups classified as UND observed during the one-hour scans were excluded from the analyses. The comparison of humpback whale group sizes across the areas was conducted through the Mann–Whitney Wilcoxon test (*U*). A contingency table with the absolute and relative frequencies of each group category was used to compare group composition between each area and apply the Pearson's chi-squared test (χ^2) to verify the association between the variables *group composition* and *study areas*, considering all the years together and separately by season.

2.6.3 | Depth

Only groups with a determined composition observed during the 1 hr scans were considered. Shapiro–Wilk (*SW*) tests showed that depth data were not distributed normally in either the Abrolhos Archipelago (*SW* = 0.95, $p < .001$) or Serra Grande (*SW* = 0.88, $p < .001$). We use the Mann–Whitney Wilcoxon test (*U*) to compare the depths between groups with and without calves in each area separately. The Kruskal-Wallis test (*K*) with a post-hoc pairwise Wilcoxon was used to evaluate differences in the depth of each group composition in each study area.

A multinomial logistic regression based on the linear combination of the predictor variable depth estimated the probability of sighting each group composition in both study areas using the "nnet" package in R. In the Abrolhos Archipelago, the model indicated probabilities of sightings in deeper areas (>30 m) than those registered in the study area monitored through visual monitoring, but which are found along the Abrolhos Bank.

2.6.4 | Movement patterns

Shapiro–Wilk tests (*SW*) did not demonstrate normal distribution of values of net speed (AB: *SW* = 0.88, $p < .001$; SG: *SW* = 0.98, $p = .03$), leg speed (AB: *SW* = 0.92, $p < .001$; SG: *SW* = 0.98, $p = .02$), linearity (AB: *SW* = 0.86, $p < .001$; SG: *SW* = 0.83, $p < .001$) nor reorientation rate (AB: *SW* = 0.91, $p < .001$; SG: *SW* = 0.88, $p < .001$) in any of the areas. For this reason, comparisons of each parameter between the areas were made using the Mann–Whitney Wilcoxon test (*U*). Due to the low number of focal groups sampled in the Abrolhos Archipelago, comparisons between categories of group composition between study areas were not feasible, but we compared each movement parameter considering the groups with and without calves separately between the areas.

The Rayleigh (*R*) test (Zar, 1974) was used to assess the circular uniformity of the data, which was only observed in the Abrolhos Archipelago $R = 0.28$, $p = .06$) and not in Serra Grande $R = 0.53$, $p = 0$). Consequently, we compared the direction of humpback whale groups between the areas using a nonparametric circular variance analysis known as the Watson Wheeler test (*W*), using the "circular" package R.

3 | RESULTS

3.1 | Sampling effort

During the 160 days of sampling in the Abrolhos Archipelago, 243 hr of scans and 33.59 hr of focal follows, including 35 focal groups, were carried out. In Serra Grande, during the 133 of sampling days, we conducted 168 hr of scans and 138.70 hr of focal follows with 264 focal groups (Table 1).

3.2 | Relative abundance

Throughout the 1 hr scans, 1,790 adults and 179 calves were registered in the Abrolhos Archipelago, and 858 adults and 65 calves in Serra Grande, totaling 2,892 observations of humpback whales in both areas during the four breeding seasons.

Segmented regressions showed a significant breakpoint in the total number of humpback whales in all breeding seasons in the Abrolhos Archipelago ($p < .001$) and Serra Grande ($p < .001$). The regression coefficients were positive for the first half of the season and negative after that (Figure 2). Except for Serra Grande in 2015, the peak of relative abundance occurred at the end of August (Table 2).

The relative abundance of adult whales in the Abrolhos Archipelago showed significant variation between years ($K = 12{,}619$, $df = 3$, $p = .006$), being significantly lower in 2019 than in 2014 ($p = .014$), 2015 ($p = .025$) and 2018

TABLE 1 Number of days of sampling effort, number of 1 hr scans, and number of groups tracked during the breeding season conducted from the land-based stations in the Abrolhos Archipelago and Serra Grande, in the south of Bahia state, Brazil, in 2014, 2015, 2018 and 2019.

		Abrolhos Archipelago	Serra Grande
2014	Sampling period	July to September	July to October
	Effort days	21	37
	Scans	32	52
	Focal groups	6	45
2015	Sampling period	July to November	July to October
	Effort days	61	30
	Scans	102	41
	Focal groups	14	76
2018	Sampling period	June to November, except July	August to October
	Effort days	34	29
	Scans	49	36
	Focal groups	7	59
2019	Sampling period	June to November	July to October
	Effort days	44	37
	Scans	60	39
	Focal groups	8	84
Total	Effort days	160	133
	Scans	243	168
	Focal groups	35	246

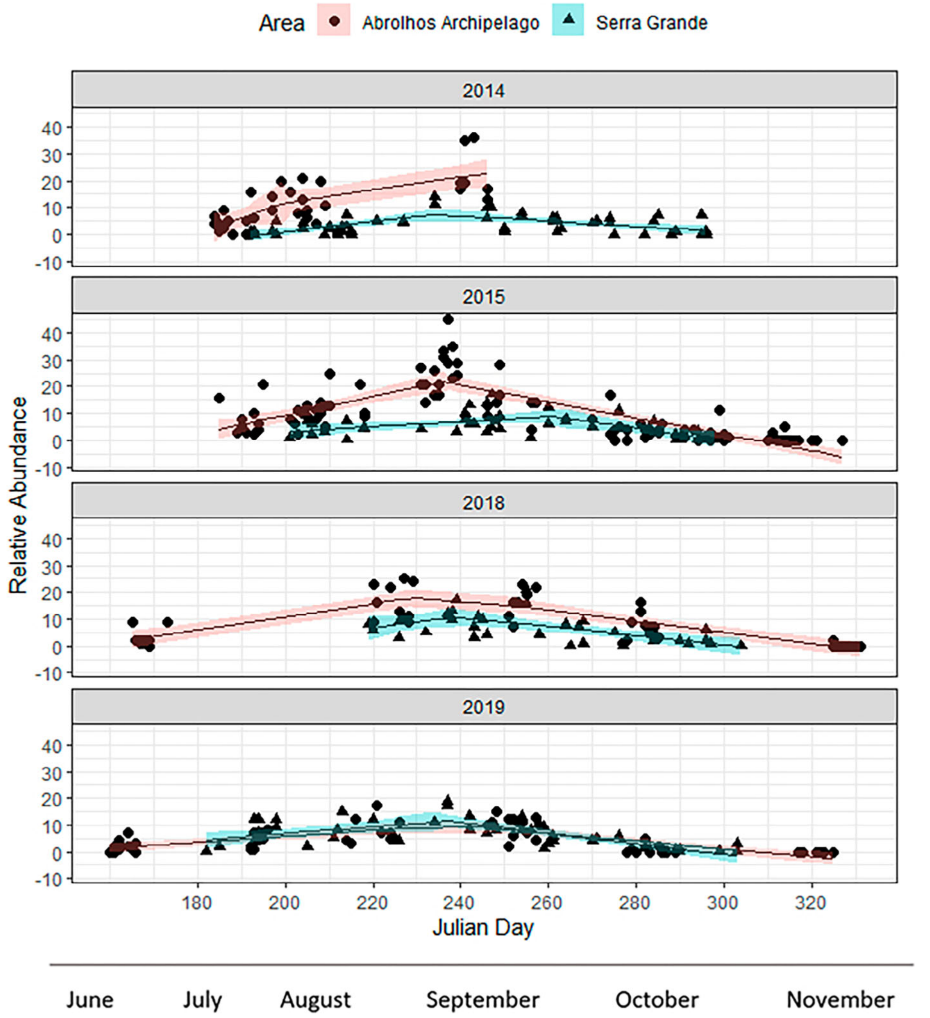

FIGURE 2 Number of humpback whales observed per hour considering adults and calves, along the Julian Days and months in the Abrolhos Archipelago (points) and in Serra Grande (triangles), in the South of Bahia state, Brazil, with the segmented regression model (the 95% confidence interval is shown in pink for Serra Grande and blue for Abrolhos Archipelago).

(p = .006). The variation in the number of adults was not observed in Serra Grande (K = 6,469, df = 3, p = .091). The comparison between areas showed that the relative abundance of adult whales at Abrolhos Archipelago was significantly higher than in Serra Grande in the breeding seasons of 2014 (U = 977, p < .001), 2015 (U = 2,304, p = .005), 2018 (U = 731, p = .005), but not in 2019 (U = 886, p = .75) (Table 3, Figure 3a). In summary, within the period studied, we observed a decrease in the number of adults in the last year in Abrolhos, while in Serra Grande, we observed a gradual increase, surpassing the number of adults observed in Abrolhos in 2019. In relation to the sightings of calves, their relative abundance was lower than that of adults in both areas (Table 3). The relative abundance of calves varied significantly among the years in Abrolhos Archipelago (K = 36,538, df = 3, p < .001) with the highest relative abundance of calves in 2018 compared to the other years (p < .001) and in 2015 it was significantly higher than 2019 (p = .046). In Serra Grande, the relative abundance of calves did not differ significantly among seasons (K = 5,096, df = 3, p = .164). The relative abundance of calves was significantly higher in the Abrolhos Archipelago than in Serra Grande only in the 2018 season (U = 888.5, p < .001) (Table 3, Figure 3b).

TABLE 2 The Julian Days and the respective dates (in parentheses) estimated through segmented regressions, representing the estimate of the days with the highest number of humpback whales (peak of the season) recorded in 2014, 2015, 2018 and 2019 in the Abrolhos Archipelago and Serra Grande, in the South of Bahia state, Brazil.

Year	Abrolhos Archipelago	Serra Grande
2014	238 (August 26)	234 (August 22)
2015	236 (August 24)	262 (September 19)
2018	234 (August 22)	238 (August 26)
2019	239 (August 27)	237 (August 25)

TABLE 3 Descriptive statistics (mean, standard deviation, minimum and maximum value) of relative abundance of adults, calves and total number of individuals of humpback whales observed between July and October by year and considering all the years (2014, 2015, 2018 and 2019) in the Abrolhos Archipelago and Serra Grande, in the South of the Bahia State, Brazil.

		Abrolhos Archipelago				Serra Grande			
		M	SD	Minimum	Maximum	M	SD	Minimum	Maximum
2014	Adults	10.75	8.14	0	32	3.59	3.27	0	14
	Calves	0.69	1.47	0	7	0.18	0.45	0	2
	Individuals	11.44	9.11	0	36	3.77	3.47	0	14
2015	Adults	9.88	8.90	0	39	4.83	3.68	0	13
	Calves	0.87	1.32	0	6	0.44	0.81	0	4
	Individuals	10.76	9.75	0	45	5.27	4.12	0	17
2018	Adults	10.68	6.60	1	24	6.22	5.08	0	20
	Calves	2.24	1.62	0	6	0.42	0.55	0	2
	Individuals	12.93	7.54	1	25	6.64	5.23	0	21
2019	Adults	5.51	4.70	0	16	5.80	4.83	0	17
	Calves	0.34	0.57	0	2	0.36	0.57	0	2
	Individuals	5.85	4.84	0	17	6.16	5.03	1	19
Total	Adults	9.20	7.89	1	39	5.11	4.35	0	20
	Calves	0.94	1.40	0	7	0.35	0.62	0	4
	Individuals	10.13	8.73	0	45	5.46	4.60	0	21

3.3 | Group composition

We excluded from the analyses 6.64% ($n = 52$) of the Abrolhos Archipelago groups and 33.89% ($n = 163$) of the Serra Grande groups because their composition was not identified. Group size ranged from one to nine individuals in the Abrolhos Archipelago (2.27 ± 1.11) and from 1 to 10 individuals in Serra Grande (2.21 ± 1.18). The average group size did not vary significantly between study areas ($U = 12{,}659$, $p = .22$).

DYADS and 1 AD represented the most observed groups in both areas, and MOC groups showed similar frequencies between the areas. (Table 4). Considering all years, an association between group composition and area was observed ($\chi^2 = 10.24$, $df = 4$, $p = .04$) probably due to the frequency of MOCE/+ in Abrolhos representing almost twice that of Serra Grande. However, using the same analysis but making comparisons by year, only in the 2018 season that a difference was observed in the frequencies of group composition by area ($\chi^2 = 17.90$, $df = 4$, $p = .001$), mainly with more MOCE/+ in Abrolhos and more 3 AD+ in Serra Grande (see Table S1).

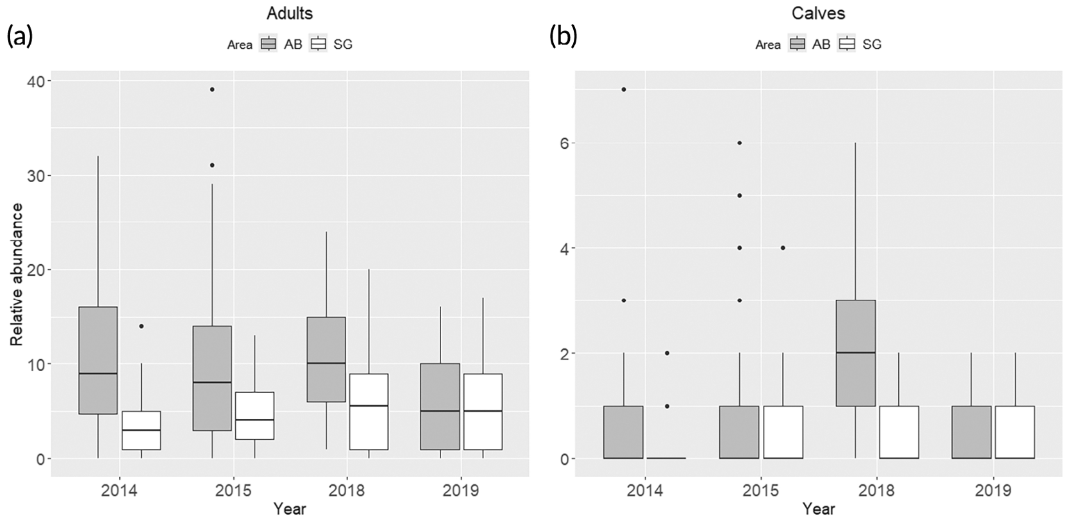

FIGURE 3 Boxplots of the relative abundance of humpback whale adults (a) and calves (b), observed per hour between July and October from land-based stations in the Abrolhos Archipelago (AB) and Serra Grande (SG), in the South of Bahia state, Brazil, along four breeding seasons.

TABLE 4 Contingency table of absolute and relative frequencies (in parentheses) of humpback whale group compositions observed during one-hour scans carried out from the land-based observation stations between July and October in the Abrolhos Archipelago and Serra Grande, in the South of Bahia state, Brazil in 2014, 2015, 2018 and 2019.

Group composition	Abrolhos Archipelago	Serra Grande
1 AD	174 (22.25%)	82 (26.45%)
DYAD	267 (34.14%)	100 (32.26%)
3 AD+	159 (20.33%)	72 (23.23%)
MOC	95 (12.15%)	39 (12.58%)
MOCE/+	87 (11.13%)	17 (5.48%)

3.4 | Depth

We estimated depth-at-site for the positions of 747 humpback whale groups around the Abrolhos Archipelago and 316 groups in Serra Grande. In the Abrolhos Archipelago, the groups were located at a mean depth of 6.97 ± 2.84 m and a maximum of 23 m, while in Serra Grande, the groups were located at a mean depth of 28.47 ± 10.02 m and a maximum of 90 m (Table 5).

Groups with calves were located at significantly lower depths than groups without calves both in the Abrolhos Archipelago ($U = 38{,}681$, $p < .001$) and Serra Grande ($U = 3{,}208.5$, $p < .001$). When comparing the depths for each category of group composition, a significant difference was observed between the depths where the groups were sighted in Abrolhos Archipelago ($K = 19.56$, $df = 4$, $p < .001$), with differences between MOC and DYAD ($p = .02$) and between MOC and 3 AD+ ($p = .04$). The variation in depths between the different groups was also observed in Serra Grande ($K = 66.88$, $df = 4$, $p < .001$) between MOC and 1 AD ($p < .001$) and between MOC and MOCE/+ ($p = .01$).

Multinomial logistic regression indicated a significant difference ($p < .001$) in the probability of sighting the different humpback whale group compositions in both study areas (see Table S2). From the land-based station in the

TABLE 5 Descriptive statistics (mean, standard deviation, minimum and maximum values) of depth (m) where the humpback whale groups were observed in 2014, 2015, 2018, and 2019, from land-based observation stations in the Abrolhos Archipelago and in Serra Grande, in the South of Bahia state, Brazil.

Group composition	Abrolhos Archipelago				Serra Grande			
	M	*SD*	Minimum[a]	Maximum	*M*	*SD*	Minimum	Maximum
1 AD	7.2	2.66	<5.00	16	28.33	6.53	10	43
DYAD	7.3	2.88	<5.00	23	30.04	9.21	7	78
3 AD+	7.1	2.91	<5.00	16	33.47	11	13	90
MOC	6.3	2.95	<5.00	16	18.24	8.32	6	36
MOCE/+	6.1	2.57	<5.00	13	24.85	9.01	12	48

[a]On the Abrolhos Bank, the mean tide is 1.7 m, with heights ranging from 0.47 m at the quadrature to 3.39 m at the syzygy (Leão & Kikuchi, 2001). Thus, in periods of high tides, whales can reach relatively shallow places and therefore, differences in minimum depth values can occur.

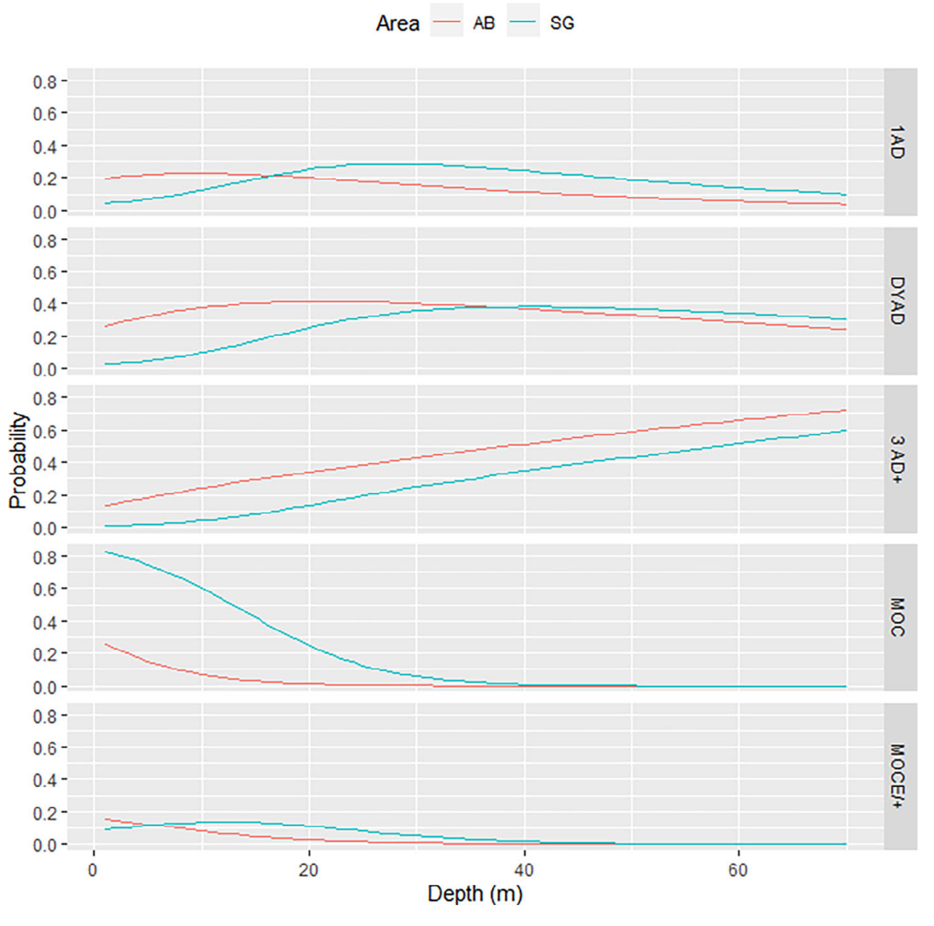

FIGURE 4 Probability of sighting a given humpback whale group composition according to depth (m) from the land-based observation stations in the Abrolhos Archipelago (AB) and Serra Grande (SG), in the South of Bahia state, Brazil, through a multinomial logistic regression.

Abrolhos Archipelago, the probability of finding groups without calves closer to the land is greater than from the land-based station in Serra Grande (Figure 4). However, the probability of sighting a MOC closer to the land is greater in Serra Grande than from the Abrolhos Archipelago (Figure 4). In both study areas, the probability of finding 3 AD+ increases directly with depth. Besides, in regions with up to 15 m, MOCE/+ groups showed an inversion in the probabilities of encounter between areas, being directly proportional in Serra Grande and inversely proportional in the Abrolhos Archipelago (Figure 4).

3.5 | Movement patterns

In Abrolhos Archipelago, the distance and time ($M \pm SD$) during which groups were followed were 4.75 ± 5.07 km and 0.96 ± 0.98 hr, respectively. In Serra Grande, the groups were followed for 2.97 ± 2.35 km and 0.53 ± 0.38 hr. Groups with calves represented 65.71% in the Abrolhos Archipelago and 44.70% in Serra Grande. We did not find differences between the groups observed around the Abrolhos Archipelago and Serra Grande for net speed

TABLE 6 Descriptive statistics (mean, standard deviation, minimum and maximum value) of movement patterns of humpback whale groups according to focal group observations from the land-based observation stations between July and October in the Abrolhos Archipelago and in Serra Grande, in the South of Bahia state, Brazil, in 2014, 2015, 2018 and 2019.

	Abrolhos Archipelago				Serra Grande			
	M	*SD*	Minimum	Maximum	*M*	*SD*	Minimum	Maximum
Net speed (km/h)	5.06	4.23	0.32	13.45	4.93	2.35	0.20	11.48
Leg speed (km/h)	6.70	4.55	0.69	15.51	7.01	2.73	0.70	13.38
Linearity	0.77	0.21	0.17	0.98	0.80	0.20	0.18	1.00
Reorientation rate (°/min)	10.11	6.12	1.65	25.32	25.51	20.56	0.60	104.01
Net course (°)	113.08	92.2	1.32	355.4	176.9	76.96	2.09	359.59

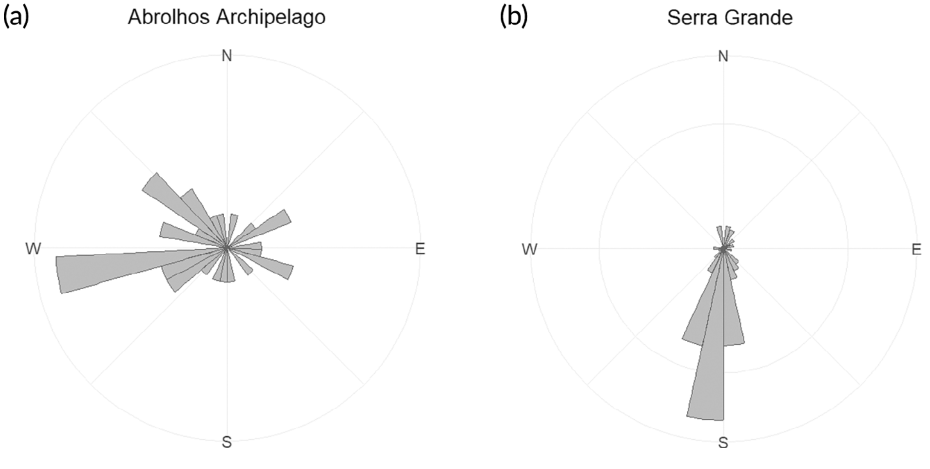

FIGURE 5 Relative frequencies (AB: $n = 35$; SG: $n = 264$) of the direction followed by groups of humpback whales monitored according to the focal group method between July and October during 2014, 2015, 2018, and 2019, carried out from land-based observation stations located in the Abrolhos Archipelago (a) and in Serra Grande (b), in the South of Bahia state, Brazil.

($U = 4{,}148$, $p = .326$), leg speed ($U = 4{,}062$, $p = .246$), or linearity ($U = 4{,}154$, $p = .33$) (Table 6). The mean reorientation rate of the groups observed around the Abrolhos Archipelago was significantly lower ($U = 2{,}238$, $p < .001$) than that of the groups observed in Serra Grande (Table 6). The circular mean value of net course of the groups differs significantly ($W = 34$, $df = 2$, $p < .001$) between the Abrolhos Archipelago and Serra Grande, with more trajectories heading west in the Abrolhos Archipelago and south in Serra Grande (Figure 5).

Comparing these same parameters in groups with calves between areas (AB: $n = 23$; SG: $n = 118$) and those without calves (AB: $n = 12$; SG: $n = 146$), the same patterns were observed, with higher reorientation rate observed in Serra Grande for both group types (with calves: $U = 719$, $p < .001$; without calves: $U = 340$, $p < .001$) and also a significant difference for the net course between these groups (with calves: $W = 24{,}65$, $df = 2$, $p < .001$; without calves: $W = 10{,}01$, $df = 2$, $p < .001$).

4 | DISCUSSION

To the best of our knowledge, this is the first paper that evaluates, on a fine-scale and simultaneously, the patterns of habitat use and movement of humpback whales for the same population including sites with different latitudes and environmental features as depth and extension of the continental shelf. Considering habitat differences between the Abrolhos Archipelago and Serra Grande, it was expected that some humpback whale patterns of use would also differ between sites. However, our results show overall similarity between habitat use in both sites, despite some differences in abundance and movement parameters.

As expected, the temporal occurrence of the whales was similar between the Abrolhos Archipelago and Serra Grande: the fluctuation in the number of humpback whales observed per hour showed the same pattern of increase followed by a decrease as the season progressed. The period of greatest relative abundance of whales in both study areas was at the end of August, corroborating previous studies (Gonçalves et al., 2018a; Morete et al., 2008).

The results show a higher relative abundance of adults around the Abrolhos Archipelago (about double) except for 2019, as this region is still known as the area with the highest concentration of humpback whales in Brazil (Andriolo et al., 2006, 2010). The lower number of adults observed in the Abrolhos Archipelago in 2019, which was surpassed by the number recorded in Serra Grande, may be attributed to interannual fluctuations previously documented in the Abrolhos Archipelago during other seasons (Morete et al., 2008). However, the maximum number of adults observed per hour in the Abrolhos Archipelago has decreased over the years and comparing with a previous study conducted nearly a decade ago (Morete et al., 2008). In contrast, Serra Grande has shown a gradual increase in the number of adults, which is consistent with the characteristics of a reoccupation area (Gonçalves et al., 2018a). The number of calves in the Abrolhos Archipelago follows a fluctuation pattern previously observed (Morete et al., 2007) that could reflect the 2–3 years reproductive cycle of the species (Chittleborough, 1953). In Serra Grande, the number of calves among the years of our study did not show significant differences and may be indicative of a progressive gradual process of reoccupation of that area.

The higher frequency of DYAD and solitary individuals observed in both study areas confirms the frequency patterns previously found in the Abrolhos Bank (Lunardi et al., 2008; Martins et al., 2001), as well as in lower latitudes where the species occurs in Brazil (Rossi-Santos et al., 2008; Zerbini et al., 2004). The observed frequencies of groups with calves in the Abrolhos Archipelago (23.28%) were close to the frequencies observed in Serra Grande (18.06%) and similar to proportions found in other breeding areas, such as the Gold Coast Bay in Australia (Valani et al., 2020) and Hawaii (Pack et al., 2017). Considering the four breeding seasons together, the 5% difference is due to the higher proportion of mothers and calves escorted by males in Abrolhos. However, it is important to highlight the drastic reduction in groups with calves in the Abrolhos Archipelago compared to the study carried out between 1998 and 2004 (Morete et al., 2007). This decrease associated with the increasing of abundance of BSA (e.g., Andriolo et al., 2010; Pavanato et al., 2017; Wedekin et al., 2017; Zerbini et al., 2019) suggests that females with calves select different sites (Morete et al., 2008), leading to the reoccupation of areas formerly used before whaling, since changes in habitat use could be a process influenced by population density (Crespo et al., 2019).

Due to the extensive continental shelf where the Abrolhos Archipelago is located, depths are shallow, explaining the significantly lower depths where humpback whale groups were found compared to Serra Grande. In both study areas, the spatial distribution of the different categories of group composition was evident, with groups with calves occupying significantly shallower areas than groups without calves as is common for humpback whales off the Brazilian coast (Gonçalves et al., 2018a; Martins et al., 2001) and in other populations (e.g. Craig et al., 2014; Félix et al. 2001; Trudelle et al., 2018). In addition, the difference between the depths where MOC and MOCE/+ groups were sighted only significant in Serra Grande, where there is an increase in the presence of MOCE/+ groups proportional to the increase in the depth (e.g., Betancourt et al., 2012; Félix & Botero-Acosta 2011; MacKay et al., 2016). This may be related to the greater range in bathymetric characteristics of the region, where mothers and calves are observed to be more segregated from other groups (Gonçalves et al., 2018a). The concentration of mother and calf in shallower waters is known to be a strategy to prevent male harassment, maternal care disruptions, and calf injuries during male courtship behaviors (Craig et al., 2014; Ersts & Rosenbaum, 2003; Smultea, 1994). Still, the higher proportion of MOCE/+ in the Abrolhos Archipelago is likely due to the lower variation in depth compared to Serra Grande, allowing mother and calves groups to be more accessible to males (Gonçalves et al., 2018a).

Consequently, the higher probability of sighting MOC groups from the land-based station in Serra Grande is related to the steep bathymetric slope of the region, causing groups to cluster closer to the coast and to be easily detected (Gonçalves et al., 2018a). In this way, the lower probability of observing MOC groups from the land-based station in the Abrolhos Archipelago is possibly because of the low bathymetric variation of the Abrolhos Archipelago, with shallow and calm waters found throughout the Bank, with the animals spreading out instead of being concentrated just around the archipelago.

Movement patterns of humpback whales can be influenced by group size (Tyack & Whitehead, 1983), the presence of calves and escorts (Bisi, 2006; Félix & Botero-Acosta, 2011; Gonçalves et al., 2018b; Kennedy et al., 2014), behavioral states (Dalla Rosa et al., 2008), choice of migratory routes (Riekkola et al., 2020), and social (Noad & Cato, 2007) and environmental characteristics (Findlay et al., 2011; Kavanagh et al., 2016; Trudelle et al., 2016). Gonçalves et al. (2018b) suggested that the higher speeds observed in Serra Grande compared to other breeding areas could be due to greater ocean currents characteristic of the region, which is in an unprotected open ocean area, when compared to the shallow and reef-protected waters, such as the Abrolhos Archipelago. Despite that, we observed a similarity in net and leg speeds of the groups between both study areas, which indicates the same behavioral pattern of the species on the breeding area off the Brazilian coast. This also can be observed for linearity, with groups presenting trajectories with values below those considered for migration (Barendse et al., 2010) indicating that the BSA is using Serra Grande and Abrolhos Archipelago in the same way, looking for whales to mate or giving birth and nursing. Nevertheless, reorientation rates differed significantly between the study areas. Humpback whales showed higher reorientation rates in Serra Grande ($25.51^\circ \pm 50.56^\circ$/min) than around the Abrolhos Archipelago ($10.11^\circ \pm 6.12^\circ$/min) and in other areas with calmer waters, such as in New Caledonia, where the average group reorientation rate was $11.09^\circ \pm 10.69^\circ$/min (Schaffar et al., 2009). The higher reorientation rate in Serra Grande could be a consequence of the large bathymetric variation in this area, where whales need to change direction more often to actively search for shallower and more appropriate depths (Gonçalves et al. 2018a), while around Abrolhos, the whales can follow linear paths for longer periods and stay in the same suitable habitat.

Additionally, humpback whales showed variability in the direction taken around the Abrolhos Archipelago while most groups moved to the south in Serra Grande, as previously observed in this region throughout the season (Gonçalves et al., 2018b). As also observed in Western Australia (Jenner et al., 2001), the migratory route of humpback whales from feeding to calving areas seems to be farther from the coast but when returning to feeding grounds, humpbacks use more coastal waters (Gonçalves et al., 2018b). It also seems that the spatial limitation of the sampling area from the land-based station in Serra Grande may have influenced the observation of groups moving north using more distant waters and outside our study area (Gonçalves et al., 2018b).

Between 2003 and 2009, humpback whales were monitored off the Brazilian coast using satellite transmitters and their movement pattern was compatible with whales in transit in Serra Grande region (de Castro et al., 2014). However, the whales have been tagged closer to the end of the breeding season when humpback whales show higher linearity values associated with the beginning of migration (Gonçalves et al., 2018b), and a large gap of time passed between studies, when an increase in population was registered and possibly changes in their strategies for using the area. Our results show that in more recent years, the similar speed and linearity values of the whales between the different study areas suggest that the whales explore and move in a similar way in the northeast of Brazil.

The trend in the number of recorded whales at the two sites, and the decrease in the frequency of groups with calves observed in recent years in the Abrolhos Archipelago, suggests that the Abrolhos Archipelago region has reached carrying capacity. From the moment that the Abrolhos Bank, considered an optimum habitat for the population, becomes saturated (indicated by stabilization or decrease in the number of whales present), whales tend to begin using areas less populated, where their presence becomes more frequent, as has been observed for the southern right whale population (Crespo et al., 2019). At the same time as the BSA reoccupation process takes place, anthropogenic activities are planned throughout Brazilian coastal waters (e.g., Bezamat et al., 2014; Bortolotto et al. 2016). Understanding baseline occurrence and habitat use of wild populations becomes fundamental for determining whether management measures are required to prevent negative impacts on the population (Pavanato et al., 2017), especially in recently reoccupied areas. Thus, comparative studies about habitat use and movement patterns of humpback whales, such as those presented here, in different areas of the coast under different conservation challenges, can help spatial planning and management of areas of economic interest, while identifying suitable habitats for the expansion of protected areas.

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AUTHOR CONTRIBUTIONS

Bianca M. Righi: Conceptualization; formal analysis; funding acquisition; investigation; validation; visualization; writing – original draft. **Julio E. Baumgarten:** Conceptualization; funding acquisition; investigation; project administration; resources; supervision; validation; writing – review and editing. **Maria Emilia Morete:** Conceptualization; funding acquisition; investigation; methodology; resources; writing – review and editing. **Rafaela C. F. Souza:** Data curation; investigation; writing – review and editing. **Milton C. C. Marcondes:** Funding acquisition; project administration; writing – review and editing. **Renata S. Sousa-Lima:** Conceptualization; funding acquisition; investigation; writing – review and editing. **Niel N. Teixeira:** Formal analysis; methodology; resources; software; writing – review and editing. **Fernanda A. S. Tonolli:** Data curation; investigation. **Maria Isabel C. Gonçalves:** Conceptualization; data curation; formal analysis; funding acquisition; investigation; methodology; project administration; resources; supervision; validation; visualization; writing – original draft.

DEDICATION

We want to dedicate this paper to Julio E. Baumgarten for all his generous ideas and teachings that led us during the development of this study. His legacy will be carried on forever.

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