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It is the time for oceanic seabirds: Tracking year-round distribution of gadfly petrels across the Atlantic Ocean

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Abstract

Aim: Anthropogenic activities alter and constrain the structure of marine ecosystems with implications for wide-ranging marine vertebrates. In spite of the environmental importance of vast oceanic ecosystems, most conservation efforts mainly focus on neritic areas. To identify relevant oceanic areas for conservation, we assessed the year-round spatial distribution and spatio-temporal overlap of eight truly oceanic seabird species of gadfly petrels (*Pterodroma* spp.) inhabiting the Atlantic Ocean.

Location: Atlantic Ocean.

Methods: Using tracking data (mostly from geolocators), we examined year-round distributions, the timing of life-cycle events, and marine habitat overlap of eight gadfly petrel species that breed in the Atlantic Ocean.

Results: We compiled 125 year-round tracks. Movement strategies ranged from non-migratory to long-distance migrant species and from species sharing a common non-breeding area to species dispersing among multiple non-breeding sites. Gadfly petrels occurred throughout the Atlantic Ocean but tended to concentrate in subtropical regions. During the boreal summer, up to three species overlapped spatio-temporally over a large area around the Azores archipelago. During the austral summer, up to four species coincided in a core area in subtropical waters around Cape Verde, and three species shared habitat over two distinct areas off Brazil. The petrels used many

national Exclusive Economic Zones, although they also exploited offshore international waters.

Main conclusions: Tracking movements of highly mobile vertebrates such as gadfly petrels can provide a powerful tool to evaluate and assess the potential need for and location of protected oceanic areas. As more multispecies, year-round data sets are collected from wide-ranging vertebrates, researchers and managers will have greater insight into the location of biodiversity hotspots. These can subsequently inform and guide marine spatial planning efforts that account for both conservation and sustainable use of resources such as commercial fisheries.

1 | INTRODUCTION

Anthropogenic activities at sea, such as large-scale commercial fisheries, climate change and increasing concentrations of hazardous contaminants, are altering the structure and stability of marine ecosystems (Halpern et al., 2008; Hoegh-Guldberg & Bruno, 2010; McCauley et al., 2015). These processes are leading to the progressive deterioration of marine habitats. The identification of areas that retain high levels of biodiversity is important to inform conservation actions. The ratification of the Convention on Biological Diversity (CBD) by many countries seeks to identify biodiversity hotspots and establish networks of Marine Protected Areas (MPAs; Convention on Biological Diversity, 2012; Edgar et al., 2014). To identify MPAs, ecosystem-based approaches are more effective than single-species or single-taxon approaches (Agardy, 1994; Friedlander, Brown, & Monaco, 2007). In practice however, MPAs are often designed to protect far-ranging vertebrates of conservation concern, in part because our understanding of their ecology is greater than other components of marine ecosystems (Hooker, Whitehead, & Gowans, 1999; Maxwell et al., 2013). The abundance of top predators, such as seabirds, can be used as an ecological indicator of marine biodiversity (Karpouzi, Watson, & Pauly, 2007; Maxwell et al., 2013; Zacharias & Roff, 2001). Understanding the patterns of spatial and temporal variations of marine predators such as seabirds is therefore not only a fundamental question in animal ecology, but also a key foundation for their conservation.

Seabirds are increasingly threatened worldwide, and their populations are subjected to a variety of threats both at terrestrial breeding sites and at marine sites used for loafing and foraging (Butchart et al., 2010; Croxall et al., 2012). The extreme life history traits of many seabirds (Gaston, 2004; Lewison, Crowder, Read, & Freeman, 2004; Saether & Bakke, 2000) make them particularly sensitive to environmental perturbations which contribute, either directly or indirectly, to population declines. Because seabirds occupy extensive ranges and regularly cross eco-regional and geopolitical boundaries during both their breeding and non-breeding seasons (Jodice & Suryan, 2010), identification of preferred foraging habitats and locations can inform conservation and marine spatial planning. In this manner, seabird tracking studies can identify marine Important Bird Areas (IBAs), which can be used to help define MPAs (Delord et al., 2014; Lascelles, Langham, Ronconi, & Reid, 2012; Le Corre et al., 2012). Marine IBAs, as defined by BirdLife International (Lascelles et al., 2016), aim to identify significant marine regions that are critical for the long-term sustainability of seabird populations. Often IBAs in marine habitats include waters surrounding or adjacent to breeding sites of threatened seabirds or more distant foraging locations derived from tracks of a single species. However, identifying foraging areas that are shared in space and time by several species allows for an assessment of the extent to which different species are exposed to common threats. Therefore, multi-species approaches incorporating temporal variability are seen as the most relevant methods for defining marine IBAs or MPAs (Maxwell et al., 2013; Young, Maxwell, Conners, & Shaffer, 2015).

Gadfly petrels (genus *Pterodroma*) are among the most threatened and least studied species of oceanic seabirds, in part because they often breed in inaccessible places in small numbers (see Table 1) and forage in remote pelagic waters. Here, by compiling diverse tracking datasets, we investigate the year-round distribution of eight of the nine extant species of gadfly petrels that breed in the Atlantic Ocean. Observations at sea suggest that most of these species are migratory, dispersing over large areas of the central Atlantic Ocean (Enticott, 1991; Murphy & Mowbray, 1951; Simons, Lee, & Haney, 2013), although until recently there have been no tracking data for most of these species. A few recent studies have reported some information on the spatial distribution of four of the species considered here (Jodice, Ronconi, Rupp, Wallace, & Satgé, 2016; Ramos et al., 2016), but this is the first attempt to integrate the temporal-spatial pattern of habitat use across virtually all species in the genus breeding in the region (Table S1 in Appendix S1 summarizes the novelty of each data set). Our goal is to identify high-use areas for gadfly petrels within the Atlantic Ocean, by (1) explicitly linking breeding and non-breeding

TABLE 1 All gadfly petrel species (*Pterodroma* spp.) from the Atlantic Ocean. Geographical characteristics of sampled populations, minimum estimated breeding pairs, conservation status (according IUCN Red List of Threatened Species, version 3.1) and approximate breeding period of their main populations. The eight-sampled species included in the study are depicted in bold

Species	Breeding distribution	Longitude (°)	Latitude (°)	Estimated population (breeding pairs)	Conservation status (IUCN 3.1)	Breeding season	References
Zino's petrel (Madeira petrel) *Pterodroma madeira* (PMAD)	Madeira Island	−16.94	32.76	170	Endangered	Apr–Oct	Zino, Phillips, & Biscoito (2011)
Desertas petrel *Pterodroma deserta* (PDES)	Desertas Islands (Madeira Archipelago)	−16.40	32.48	360	Vulnerable	Jun–Dec	Oliveira, Menezes, & Ramírez (2008)
Bermuda petrel (Cahow) *Pterodroma cahow* (PCAH)	Bermuda Archipelago	−64.67	32.34	206	Endangered	Oct–Jun	Madeiros, Carlile, & Priddel (2012)
Black-capped petrel (Diablotin) *Pterodroma hasitata* (PHAS)	Hispaniola Island (Haiti and Dominican Republic)	−71.41	18.11	5,000	Endangered	Dec–May	Simons et al. (2013), Wingate (1964)
Jamaican petrel *Pterodroma caribbaea*	Jamaica			0	Possibly extinct	Nov–May	Carte (1866)
Cape Verde petrel (Gon-gon) *Pterodroma feae* (PFEA)	Cape Verde Archipelago	−24.34	14.95	620	Near threatened	Nov–Apr	Ratcliffe et al. (2000)
Saint Helena petrel *Pterodroma rupinarum*	Saint Helena Island			0	Extinct	Unknown	Welch et al. (2014)
Trindade petrel *Pterodroma arminjoniana* (PARM)	Trindade Islands	−29.33	−20.53	1,130	Vulnerable	Year-round[a]	Luigi, Bugoni, Fonseca-Neto, and Teixeira (2009)
Atlantic petrel *Pterodroma incerta* (PINC)	Gough Island, Tristan da Cunha	−9.94	−40.32	900,000	Endangered	Apr–Dec	Rexer-Huber, Parker, Ryan, & Cuthbert (2014)
Soft-plumaged petrel *Pterodroma mollis* (PMOL)	Several archipelagos in the Southern Ocean	−9.94	−40.32	400,000	Least Concern	Sep–Apr	Brooke (2004)
Great-winged petrel *Pterodroma macroptera*	Several archipelagos in the Southern Ocean			110,000	Least Concern	Mar–Nov	Brooke (2004)

[a]Feb–Aug analysed in the current study.

grounds of gadfly petrel species that breed across this ocean basin, and (2) evaluating the relative importance of these foraging areas by quantifying the spatio-temporal overlap among the species.

2 | METHODS

2.1 | Studied species and sampling design

Gadfly petrels are long-lived, colonial breeders that nest in rock crevices, burrows or on flat ground at remote islands and isolated places. Eight gadfly petrels that breed in the Atlantic Ocean included in this study are (from north to south within the basin, Table 1): Zino's petrel (*Pterodroma madeira*; hereafter PMAD) breeding on Madeira Island, Desertas petrel (*P. deserta*; PDES) on Bugio Island (in Desertas archipelago, 50 km from Madeira Island), Bermuda petrel (*P. cahow*; PCAH) on Bermuda archipelago, Black-capped petrel (*P. hasitata*; PHAS) on Hispaniola Island (Haiti and Dominican Republic), Cape Verde petrel (*P. feae*; PFEA) on the Cape Verde archipelago, Trindade petrel (*P. arminjoniana*; PARM) on Trindade Island, and Atlantic petrel (*P. incerta*; PINC) and Soft-plumaged petrel (*P. mollis*; PMOL) both on Tristan da Cunha and Gough Islands. The latter two island groups also support a population of Great-winged petrels (*P. macroptera*), but these have become rare due to introduced predators and none was available for this study. Two other gadfly petrel species are thought to have inhabited the Atlantic Ocean in the past, but both are considered extinct species nowadays: Jamaican petrel (*P. caribbaea*) and Saint Helena petrel (*P. rupinarum*; Table 1). All eight are medium-sized petrels, with PARM, PHAS and PINC the largest species (wingspans 895–1,040, 980–1,050 and 1,100–1,150 mm, respectively), and PMAD, PMOL, PDES, PFEA and PCAH smaller (wingspans 800–843, 830–950, 860–940, 880–943 and 880–945 mm). Six species are grey and white petrels, while PARM and PINC are mainly dark brown (Flood & Fisher, 2013). Breeding seasons are long (6–8 months in most cases), and differ among species; two North Atlantic (PMAD, PDES) and one South Atlantic species (PINC) breed primarily during the northern summer, three North Atlantic (PCAH, PFEA, PHAS) and one South Atlantic species (PMOL) breed during the northern winter, and the sole tropical-breeding species (PARM) breeds year-round with two distinct laying peaks (see Table 1 and Fig. S1 in Appendix S1). Little is known about their diet and foraging tactics, although it is assumed that most gadfly petrels are shallow divers, mainly feeding on small squid and pelagic fish (Flood & Fisher, 2013). Morphometric, behavioural and genetic studies concluded that PMAD, PDES, PFEA, PCAH and PMOL are more related among themselves than with PHAS and PINC (Bretagnolle, 1995; Imber, 1985; Welch, Olson, & Fleischer, 2014). These studies concluded that PARM belongs to a sister group, which includes gadfly petrel species from the Pacific and Indian Oceans. All species have restricted breeding ranges confined to a few islands, except PMOL, which also breeds in several sub-Antarctic archipelagos around the Southern Ocean. Most have small population sizes and are of high conservation concern (Table 1; http://www.iucnredlist.org/); PINC still has a large population, but is listed as Endangered due to predation of its chicks by introduced house mice

Mus musculus (Wanless et al., 2012). Of the eight species studied, only PMOL is listed as Least Concern (Table 1).

2.2 | Tracking data: representativeness and spatio-temporal analysis

Tracking data for the eight gadfly petrel species were gathered from two kinds of tracking devices (see Tables S1 and S3 in Appendix S1 for device specifications and tracking periods, respectively). In most cases, geolocator tags were leg-mounted on breeding adults at the colony. The tags provide light data which are processed to produce raw spatial positions with an average accuracy of ~200 km (or ~2°; see Appendix S1; Phillips, Silk, Croxall, Afanasyev, & Briggs, 2004). Solar-powered Platform Terminal Transmitters (PTT) were fitted to the back of breeding PHAS. These devices have a duty cycle of 8 hr on then 24 hr off, with most positions measured accurate to within ca. 1,500 m. Raw spatial positions from geolocators and PTT were homogenized to two positions per day, filtered for unrealistic positions (Freitas, Lydersen, Fedak, & Kovacs, 2008; Phillips et al., 2004) and interpolated twice using bespoke codes written in R language (R Development Core Team, 2010). Specific data gathering, resampling, filtering and interpolating procedures on spatial data are described in Appendix S1.

When defining range distributions for a given population, an analysis of representativeness is strongly recommended when sample sizes are small or when high variability in distribution occurs within and between individuals (Delord et al., 2014). In such cases, a small number of tracked individuals may not be representative of the space usage of their whole population (Lascelles et al., 2016). Therefore, we conducted a representativeness analysis that allowed us to assess the robustness of our data sets. We used iterative and random track selection procedures (Table S2 in Appendix S1) to examine the extent to which core area distribution (i.e., 50% Utilization Distributions, hereafter UDs, see Appendix S1 for details) changed for each species and for each season (breeding/non-breeding) with increasing sample size. We excluded from this analysis those data sets for which we collected less than four tracks (i.e., PHAS and PMOL). A non-linear regression was then fitted to the modelled data to estimate the optimal sample size needed for a given data group to be considered adequately representative. Finally, representativeness indices were calculated on the basis of the estimated asymptote of each nonlinear regression (Lascelles et al., 2016).

We used 125 year-round tracks from 103 individuals to estimate five phenological and spatial parameters: (1) departure date from breeding site, (2) arrival date at breeding site, (3) duration of the non-breeding period (in days), (4) area exploited throughout the non-breeding period (as indicated by the 50% UDs; in 10^6 km^2), and (5) non-breeding range (orthometric distance between the breeding colony and the centroid of the 5% non-breeding UDs; in km). We evaluated the effect of species on the values for these non-breeding parameters by fitting a set of candidate Linear Mixed Models (LMMs). Here, each of the five parameters described above was a response variable, species was the main (fixed) explanatory variable and year a random effect (Table 2; see Appendix S1 for modelling specifications). High consistency in the species-specific migration patterns was observed in

those species with several years of sampling (see Table 2 for an overall estimation of the annual variability and Table S3 in Appendix S1 for detailed information). Therefore, species-specific data were pooled across years for subsequent analyses.

For the analysis of spatial distribution, we first estimated the importance of specific areas across the Atlantic Ocean for gadfly petrels, at the supra-specific level by enumerating the number of positions at which each species that were located within each 2 × 2° cell. These counts of positions were then weighed by considering the total numbers of positions in each species/data set (i.e., the sampling effort per colony site), and multiplied by the size of the population of origin (estimated as 2 × number of breeding pairs; Table 1) to obtain an absolute estimate of the intensity of use of areas by gadfly petrels across their supra-specific distribution (Figure 1).

To evaluate the spatio-temporal overlap among the species, we also estimated the use of specific areas across the Atlantic Ocean by mapping the occurrence of different gadfly petrel species within every 2 × 2° cell, separately for each of four-three-month seasonal periods (i.e., December–February, March–May, June–August, September–November; Figure 2). Additionally, 50% UDs (in km^2) were calculated using the filtered, interpolated locations for each species, separately for each period. These steps resulted in a spatio-temporal estimate of diversity of gadfly petrel species across the Atlantic Ocean. We also calculated the spatial overlap between the areas used during these periods (95% UDs; Table S4 in Appendix S2) between species using the *kerneloverlap* function in the ADEHABITAT R package (Fieberg & Kochanny, 2005).

3 | RESULTS

3.1 | Spatio-temporal overlap of gadfly petrel species

We compiled 125 tracks that accounted for most of the annual cycles of the focal species (Table S3 in Appendix S1). After filtering and

interpolation, we obtained 58,420 locations, of which 45.0% were assigned to breeding season and 55.0% to the non-breeding period. Representativeness analysis (Lascelles et al., 2016) revealed that most datasets (split by species and season) adequately represent the spatial variability of the target population. Unfortunately, the non-breeding distributions of PCAH, and the distributions obtained from the few available tracks of PHAS and PMOL, failed to reach the threshold for representativeness established by Birdlife International. However, although the spatial assessments of these populations should be treated with caution, we included them because we believe that their inclusion contributes relevant data while their removal would hamper our understanding of areas used by gadfly petrels.
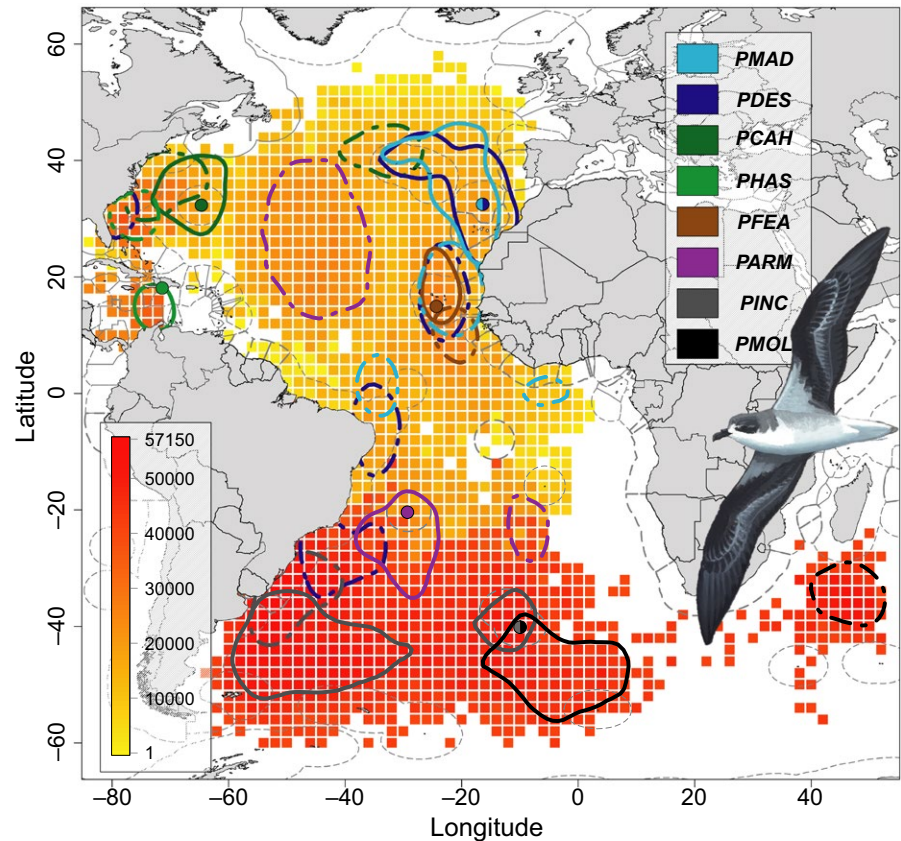
At the supra-specific level, gadfly petrels occur widely across the Atlantic Ocean, but they tend to concentrate in the subtropical regions and in temperate areas of the Southern Hemisphere (Figure 1). However, this result may be biased either by overestimates of the population sizes of PINC and PMOL (Table 1), or by an underestimate of the range of key taxa, such as PMOL, due to their limited tracking data (see Table S2 in Appendix S1 for representativeness analysis). Gadfly petrels use both offshore international waters and coastal national waters, either seasonally or year-round, leading to a complex pattern of spatio-temporal habitat use (Figure 1 and Table S5 in Appendix S2). Specifically, petrels used the Exclusive Economic Zones (EEZs) of 58 of the 97 countries bordering the Atlantic Ocean (Figure 1). However, the number of locations within EEZs varied considerably among species, ranging from 9% in PARM to 79% in PHAS (see Table S6 in Appendix S2 for details).

Overall, there was substantial variation in the timing of migration and in the spatial characteristics of non-breeding distributions among and within species (Table 2). In most cases, the year effect we observed accounted for a small proportion of the variability in use areas. All gadfly petrels spent 6–8 months on their breeding grounds (Fig. S1 in Appendix S1). PARM had the shortest breeding season (on average 169 ± 13 days), whereas PFEA at Cape Verde had the longest

TABLE 2   Linear mixed models (LMMs) evaluating the species effect on five migration characteristics of gadfly petrels that breed in the Atlantic. Parameter estimates (±standard error) from species-dependent LMMs included the year of sampling as random effect

	Colony departure date	Colony arrival date	Duration of the non-breeding period (days)	Area of the non-breeding period (10^6 km^2)	Distance from colony (km)
Fixed effects (estimate ± SE)					
PMAD	16 Oct ± 19.1	15 Mar ± 4.9	147.5 ± 6.0	1.1 ± 0.5	3,037 ± 402
PDES	27 Oct ± 10.8	02 Jun ± 2.9	182.1 ± 3.1	2.8 ± 0.3	5,136 ± 206
PCAH	04 May ± 28.3	21 Oct ± 7.3	163.9 ± 8.8	0.9 ± 0.7	1,705 ± 588
PHAS	13 Jun ± 42.6	15 Sep ± 10.8	95.7 ± 13.4	0.5 ± 1.0	1,591 ± 899
PFEA	30 Apr ± 19.6	07 Sep ± 5.0	128.3 ± 6.2	0.4 ± 0.5	682 ± 416
PARM	01 Aug ± 23.3	13 Feb ± 6.1	196.5 ± 7.0	6.9 ± 0.6	5,240 ± 469
PINC	30 Nov ± 20.8	27 Mar ± 5.4	120.2 ± 6.5	1.3 ± 0.5	3,406 ± 432
PMOL	06 May ± 41.7	11 Oct ± 10.5	159.7 ± 13.4	1.4 ± 1.0	5,030 ± 899
Random effects (variance ± SE)					
Year	206.8 ± 14.4	4.8 ± 2.2	12.3 ± 3.5	0.3 ± 0.5	114,819.0 ± 338.8
Residual	5395.5 ± 73.5	343.0 ± 18.5	643.2 ± 25.4	3.0 ± 1.7	2,498,349.0 ± 1,581.5

FIGURE 1 Habitat utilization by the eight species of gadfly petrels that breed in the Atlantic Ocean. Grid map shows the number of locations that fall in every 2 × 2° cell (units in birds/cell), corrected by the sampling effort on the population of origin (i.e., total number of positions from that colony site) and multiplied by the size of that population (see Table 1). Additionally, specific kernel density distributions (50% UDs) are depicted in continuous lines for the breeding season and in dashed lines for the non-breeding season for each of the species (in light blue, dark blue, dark green, light green, brown, purple, grey and black for PMAD, PDES, PCAH, PHAS, PFEA, PARM, PINC and PMOL, respectively). Exclusive Economic Zones (EEZs) are also shown in light grey dashed lines. Coloured circles show the location of the respective breeding colony. The bird silhouette represents PFEA (courtesy of Martí Franch). [Colour figure can be viewed at wileyonlinelibrary.com]

(237 ± 34 days; see Table S3 in Appendix S1). PARM, PDES, PINC and PMAD breed primarily during the boreal summer (at least from June to August), whereas PCAH, PFEA, PHAS and PMOL initiate breeding primarily during the austral summer (from December to February; Fig. S1 in Appendix S1). In general, the distributions of tracked birds were concentrated within 500–700 km around each colony during their breeding season, although several individual PMAD and PDES consistently exploited a large area around the Azores archipelago and most PINC foraged at the confluence of Malvinas/Falklands and Brazil Currents (Figure 1), both areas far from their breeding islands.

The distance from the breeding colony to the core non-breeding area (i.e., non-breeding range) was much larger in PARM, PDES, PINC, PMAD and PMOL than in PCAH, PFEA and PHAS (Table 2). Indeed, migratory strategies differed considerably among species: from almost non-migratory in PFEA or slightly dispersive in PHAS to long-distance, trans-equatorial migrations in PARM and PDES. In addition to this diversity in migration strategies, individuals of some species migrate to a common and unique wintering area (PARM, PHAS, PINC and PMOL), whereas individuals from other species disperse among various remote wintering sites (PCAH, PDES and PMAD).

In a few key areas, there was species overlap during specific periods of the year (Figure 2). In the boreal summer, there was large spatio-temporal overlap between breeding PMAD and PDES as well as non-breeding PCAH over a large area around the Azores (Figure 2c). Interestingly, several species, such as breeding PARM and non-breeding PFEA, PINC and PMOL, segregated spatially at that time

across the Central and South Atlantic (Figure 2c). During the austral summer, up to four species overlapped in a core area in subtropical waters around Cape Verde (i.e., non-breeding PARM, PDES and PMAD in addition to breeding PFEA; Figure 2a). At that time, several species also shared habitat over two distinct areas off Brazil: along the equatorial coast, where non-breeding PARM, PDES and PMAD concentrate, and in subtropical waters, where non-breeding PARM and PDES join breeding PINC at 20–40°S (Figure 2a).

4 | DISCUSSION

Until recently, few studies had investigated the individual-level distribution of related taxa inhabiting the same oceanic basin (Orben et al., 2015; Ramos et al., 2016; Young et al., 2015). Our study compares the year-round distributions, timing of life-cycle events, and marine habitat overlap of eight gadfly petrel species that breed across the Atlantic Ocean. By doing so, we provide relevant information for the conservation of such threatened species (McCauley et al., 2015).

4.1 | Spatio-temporal distribution and overlap of gadfly petrels of the Atlantic

The eight species of gadfly petrel we studied are distributed widely across the Atlantic Ocean. Most species overlapped in their distribution though a few exploited particular and unique (i.e., unshared)
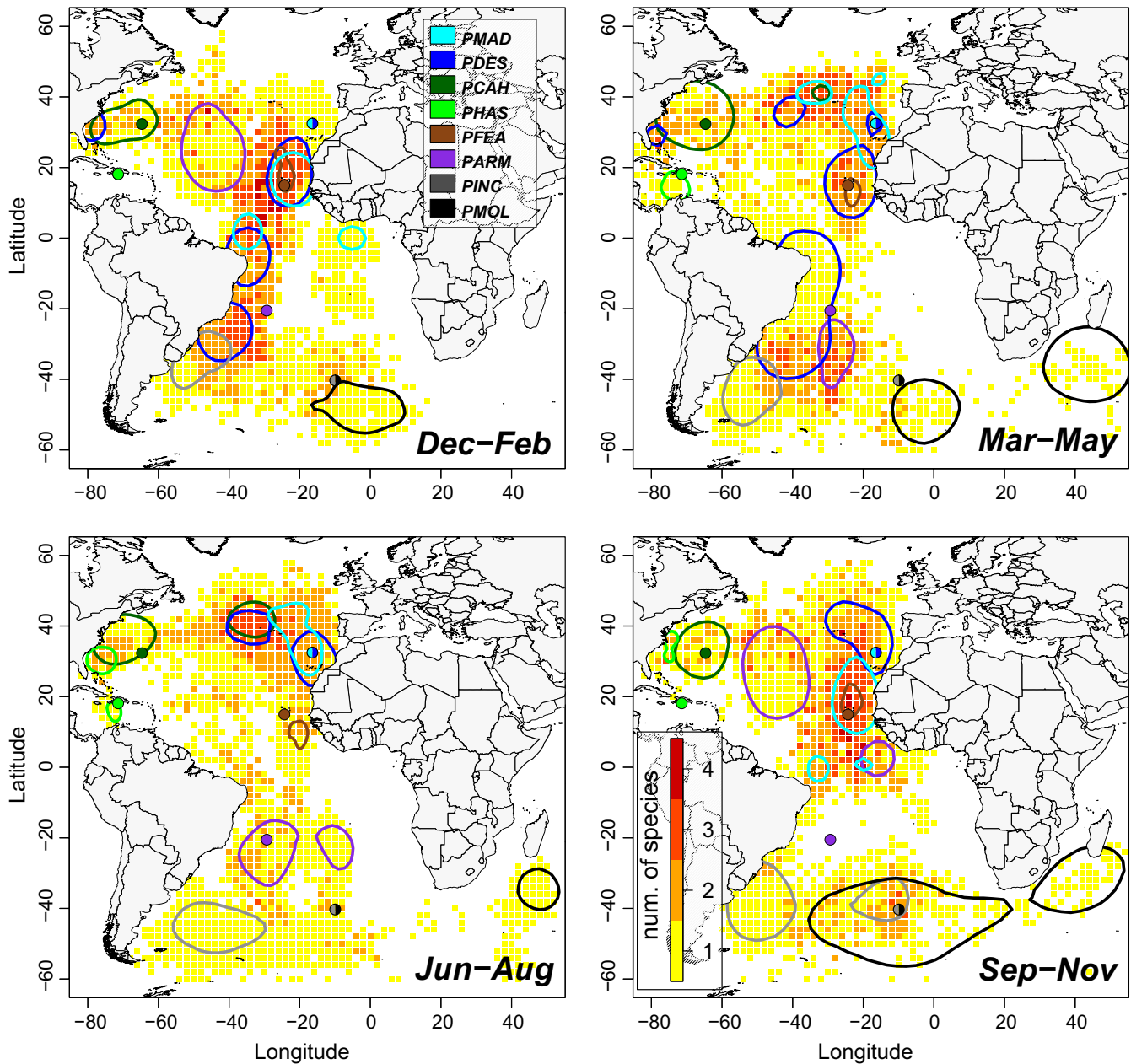
FIGURE 2 Spatio-temporal overlap among eight species of gadfly petrels that breed in the Atlantic Ocean (for December–February, March–May, June–August and September–November periods, separately). The number of species that overlap in every 2 × 2° cell is plotted as grid maps (yellow, orange, red, and dark red for one, two, three and four species, separately). Kernel density distributions (50% UDs) are also depicted on the respective grid map for each of the species (in light blue, dark blue, dark green, light green, brown, purple, grey and black for PMAD, PDES, PCAH, PHAS, PFEA, PARM, PINC and PMOL, respectively). Coloured circles show the location of the respective breeding colonies. [Colour figure can be viewed at wileyonlinelibrary.com]

areas. For instance, PARM exploited the oligotrophic waters of the Sargasso Sea, where no other gadfly petrel species seemed to forage. Interestingly, this species is the most distantly related of the petrels studied (Welch et al., 2014), which might account for its preference to forage on this vast and distinct area of the North Atlantic (Figure 1). By comparison, other gadfly petrel species concentrated in specific regions, with up to four species occurring simultaneously (see below). Species that overlapped spatially and temporally were often the closest related species, that is PCAH, PDES and PMAD south-east of

the Azores, or PDES, PFEA and PMAD around Cape Verde (Imber, 1985; Welch et al., 2014). These overlaps in the habitat exploitation of closely related species might suggest limited ecological segregation of these taxa (e.g., most are shallow divers that feed on similar pelagic prey of small size; Flood & Fisher, 2013; Ramos et al., 2016), which might be expected given their relatively recent evolutionary segregation (Welch et al., 2014).

Traditionally, the need to avoid conspecific competitors has been suggested as the most plausible explanation for spatio-temporal

segregation between related taxa breeding in close proximity to each other (Cairns, 1989; Wakefield et al., 2013). Either direct or indirect competition for limited resources implies a cost in terms of reduced foraging efficiency, which could promote segregation in habitat use by different populations in time (Friesen et al., 2007), space (González-Solís, Croxall, & Afanasyev, 2008) or diet (Wilson, 2010). However, in our case, the spatio-temporal overlap of PCAH, PDES, PFEA and PMAD, in addition to their small population sizes (Table 1), do not support the competition avoidance hypothesis that could explain the observed speciation processes (see above). Other causes such as local adaptations in breeding schedules (Friesen et al., 2007), and the high degree of philopatry of the species to remote and isolated oceanic islands (e.g., Ovenden, Wust-Saucy, Bywater, Brothers, & White, 1991), may have contributed to the differentiation of their ancestral populations while sharing similar resources and feeding grounds year-round to a great extent (Ramos et al., 2016).

4.2 | Key areas for Atlantic gadfly petrels and the implications for marine conservation

Our results suggest that gadfly petrel species dispersing from breeding colonies within the Atlantic Ocean aggregate in a few key areas at specific times. For example, the waters located off the east coast of North America, between Cape Hatteras (35°15′N, 75°31′W) and Cape Canaveral (28°27′N, 80°31′W; along the Gulf Stream) and east to Bermuda (32°20′N, 64°45′W), support endangered PHAS and PCAH and vulnerable PDES populations, especially throughout the boreal spring and summer (Mar–May and Jun–Aug). This area is likely inhabited by the entire wintering population of PHAS (Simons et al., 2013), by breeding and wintering PCAH and also by several non-breeding PDES. Many other endangered taxa of far-ranging oceanic vertebrates, such as sea turtles, predatory fish and many cetaceans, also exploit these waters (Best et al., 2012; Block et al., 2005; Curtis et al., 2014; Fossette et al., 2014; Kennedy et al., 2014). This adds relevance to the MPAs already identified in the Gulf Stream (Hare & Walsh, 2007; Selig et al., 2014), but also provides more evidence for reconsidering their geographic extent.

We also identified a high concentration of critically endangered gadfly petrels in the waters north-east of the Azores archipelago, where approximately half of the PCAH population winter and most breeding PMAD and PDES forage throughout the austral winter (Figure 2). The Convention for the Protection of the Marine Environment of the North-East Atlantic (OSPAR) has already delimited up to four restricted MPAs (O'Leary et al., 2012) that match relatively well the distribution of these three gadfly petrel species in the area, and it is currently evaluating a fifth which also overlaps with our study species (http://www.birdlife.org/europe-and-central-asia/news/ospar-wild-protect-ing-amazon-atlantic). BirdLife International has also proposed three restricted marine IBAs within that vast area, claiming specific protection for PMAD, Cory's shearwaters (*Calonectris borealis*) and wintering Sooty shearwaters (*Ardenna grisea*; Lascelles et al., 2016). Our study confirms the importance of a vast area northeast of the Azores for PMAD, but also for the conservation of PDES and PCAH. In addition,

a few studies have reported the presence of other endangered species of sea turtles in this area (Ferreira, Martins, Bolten, Santos, & Erzini, 2011; Fossette et al., 2014), both outside of two adjacent Portuguese EEZs (Azorean and Madeiran). Our data suggest that the area northeast of Corvo and Flores IBA (39°36′N, 31°10′W) warrant additional attention with respect to the conservation of North Atlantic gadfly petrels.

A third area that concentrates a large number of threatened gadfly petrels is located around the Cape Verde archipelago. Throughout several months of the austral winter, non-breeding PARM, PDES and PMAD, as well as PFEA year-round exploit these waters. Most of this area falls within the Cape Verde EEZ, although a significant portion of the range for these species may occur outside Cape Verdean waters (ca. 500 km north and south of the EEZ). The area is also inhabited by endangered sea turtles, predatory fish, rays and large cetaceans (Wenzel et al., 2009; Zeeberg, Corten, & de Graaf, 2006), although its conservation has not been considered until very recently (Lascelles et al., 2016).

Finally, our data identify two other areas off the Brazilian coast that appear to be important for the conservation of gadfly petrels in the Atlantic. The marine areas around the Brazilian archipelagos of Fernando de Noronha (3°51′S, 32°25′W), Atol das Rocas (3°51′S, 33°49′W) and Saint Peter and Saint Paul Rocks (0°55′N, 29°20′W) host important numbers of non-breeding PDES and PMAD, as well as breeding PARM. Although the waters of these Brazilian EEZs are protected, adjacent offshore areas used extensively by pelagic seabirds are largely unprotected. Furthermore, large numbers of breeding PARM, non-breeding PDES and PINC (year-round) also occur between the Brazilian coast and the archipelago of Trindade and Martin Vaz (20°31′S, 29°19′W). Both areas are designated as Ecologically or Biologically Significant marine Areas (EBSAs; Convention on Biological Diversity, 2012) as they host several key threatened species including sea turtles (Bellini, Santos, Grossman, Marcovaldi, & Barata, 2013; Silva et al., 2011), marine mammals (Groch, Palazzo, Flores, Adler, & Fabian, 2005; Siciliano, Moura, Filgueiras, Rodrigues, & Leite, 2012), predatory fish (Hazin, Vaske, Oliveira, Macena, & Carvalho, 2008; Hazin et al., 1994), as well as other seabirds (Dias, Granadeiro, Phillips, Alonso, & Catry, 2011; González-Solís et al., 2009; Ramos et al., 2015).

Our data demonstrate that the five areas within the Atlantic Ocean we identified as frequently occupied by this suite of threatened and endangered gadfly petrels warrant conservation attention. Further, other seabird species, including Northern gannets (*Morus bassanus*; Fort et al., 2012; Montevecchi et al., 2012), *Calonectris* shearwaters (Dias et al., 2011; González-Solís et al., 2009), and Bulwer's petrels (*Bulweria bulwerii*; Ramos et al., 2015) all frequent at least some of these oceanic hotspots at various stages of their annual cycle. Other threatened apex predators, such as several species of cetaceans, sea turtles, tunas and sharks (Block et al., 2005; Fossette et al., 2014; Kennedy et al., 2014; Skomal et al., 2009; Wenzel et al., 2009) also occur here. Most of these regions support commercial fisheries, including purse seiners, longliners and pelagic trawlers from various nations that target tuna, small pelagic fish and cephalopods (Pauly & Zeller, 2015). Although there is no evidence of bycatch of gadfly petrels in any of these areas

(Anderson et al., 2011; Bugoni et al., 2008; Huang, Chang, & Tai, 2009), many other threatened species are unintentionally caught there (Lewison et al., 2014; Zeeberg et al., 2006). The lack of bycatch reports for gadfly petrels may be because they are not caught, or because they are overlooked due to their often small population sizes. As a result, bycatch of gadfly petrels needs further study before being considered as a major threat (Table 1). Our analyses identify several marine areas within which the assessment of bycatch risk to non-target or declining species, such as gadfly petrels, may be warranted. In addition to direct mortality through bycatch, seabirds may also experience negative effects on their populations due to the depletion of food resources by fisheries, particularly those that target small pelagic fish (Cury et al., 2011). Therefore, our analyses also identify areas within which an assessment of the interaction between seabirds and commercial fisheries may be warranted, as well as a reassessment of the current policies that govern such fisheries. Indeed, an integrated sustainable harvest management of pelagic fisheries not only serves to protect areas for the conservation of marine biodiversity but also supports sustainability for the fishing industry in and around these areas (Coll et al., 2012; Davies, Martin, Mees, Chassot, & Kaplan, 2012; Roberts, Hawkins, & Gell, 2005).

Our study provides unique insights into the year-round spatial distribution of these secretive and threatened petrel species that breed across the Atlantic Ocean. Such detailed information related to the spatio-temporal distribution of threatened gadfly petrels can be used to inform pelagic MPAs or marine IBAs as well as other aspects of marine spatial planning. Several of these areas already benefit from protection measures due to the biodiversity they support; however, many others remain unprotected. In this regard, tracking the movement of highly mobile vertebrates, such as oceanic seabirds, can provide new insights allowing the evaluation of the location and function of protected areas. Some of the areas we identified as frequently used by gadfly petrels occur within national EEZs, and hence may be more easily designated as MPAs by a responsible national authority. Many other areas are located in international waters, which complicates the collaboration and coordination needed to identify and enact MPAs or other conservation measures (Game et al., 2009). Currently, Regional Fisheries Management Organisations (RFMOs) have a central role in encouraging commercial fishing fleets operating in the high seas to implement management measures that minimize impacts on non-targeted predators (Cullis-Suzuki & Pauly, 2010). Analyses on the spatio-temporal distributions of key marine species, like the multispecies data set we provided in this study, represents a fundamental component for developing efficient management strategies by RFMOs across marine ecosystems.

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AUTHOR CONTRIBUTIONS

R.R. and J.G-S. designed the study; R.R., N.C., J.M., I.R., V.H.P., H.D., F.Z., M.B., G.R.L., L.B., P.G.R.J., P.G.R. and J.G.-S. conducted the fieldwork; R.R. analysed the data; R.R. and J.G-S. wrote the first complete version of the manuscript; N.C., V.H.P., F.Z., L.B., P.G.R.J., and P.G.R. read and commented on the manuscript.

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BIOSKETCH

Raül Ramos is currently interested in the spatial ecology of highly mobile vertebrates. During his PhD thesis, he focussed on the ecological application of intrinsic biogeochemical markers on various fields such as the trophic ecology of seabirds and their long-distance migrations. During several postdoctoral studies, he went on to study the biogeography of many seabird species from a poorly studied habitat (the pelagic ecosystem) and how the environment and long-distance movements affect population dynamics of those species. The knowledge and the technical skills he acquired throughout these studies, led him into the present question of how individual fitness influences the migratory decisions taken by long-distance migrants (i.e., carryover effects).

SUPPORTING INFORMATION

Additional Supporting Information may be found online in the supporting information tab for this article.