Marine hotspots of activity inform protection of a threatened community of pelagic species in a large oceanic jurisdiction in the South Atlantic

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Abstract

Remote oceanic islands harbour unique biodiversity, especially of species that rely on pelagic resources around their breeding islands. Identifying marine areas used by such species is important to reduce or limit threats that may put these species at risk. The Tristan da Cunha group of islands in the South Atlantic Ocean hosts several endemic and globally threatened seabirds and pinnipeds; how they use the waters surrounding the islands must be considered when planning industrial activities in the entire Exclusive Economic Zone (EEZ). We identified hotspots of activity by collating animal tracking data from nine breeding seabirds and one marine mammal to inform marine management in the Tristan da Cunha EEZ.

To detect statistically significant areas of concentrated activity, we calculated the time-spent-in-area that tracked individuals (breeding adults) of 10 focal species (mainly breeding adults of nine seabirds and adult female Subantarctic fur seals *Arctocephalus tropicalis*) invested in a grid of regular 10×10 km cells within the EEZ, for each of four seasons to account for temporal variability in space use. Applying a spatial aggregation statistic over these grids by each species we detected areas that are used more than expected by chance. Most of the activity hotspots were either within 100 km of the islands or were associated with seamounts being spatially constant across several seasons. Moreover, some species spend a large proportion of their time-at-sea inside the EEZ during certain breeding stages, rendering the sites we identified critical for their fitness. Our approach provides a simple and effective tool to highlight important areas for pelagic biodiversity that will benefit Tristan da Cunha's conservation planning and marine management strategies.

Keywords: Seabird, Pinniped, Tracking, Time-in-area, Getis-Ord G_i^* , Marine Protected Area, Marine Spatial Planning.

Resumen

Las islas oceánicas albergan una biodiversidad única y especialmente de especies pelágicas que dependen de los recursos oceánicos alrededor de sus colonias de cría. El territorio de Tristán de Acuña, en el Atlántico Sur, hospeda una comunidad de especies pelágicas rica en endemismos y en especies globalmente amenazadas que utilizan un amplio rango espacial del Océano Atlántico. Dada la enorme importancia de las aguas de este territorio es necesaria la aplicación urgente de medidas de protección y gestión de su Zona Económica Exclusiva (ZEE). Un primer paso para limitar y reducir las presiones que ponen a estas especies en peligro consiste en la identificación de las áreas que utilizan.

Hemos identificado las áreas que concentran una alta actividad estadísticamente significativa a escala de la ZEE ("hotspots" de actividad) a partir de la información obtenida con el seguimiento telemétrico de individuos (tracking). La muestra final se compuso de 397 individuos, en su mayoría adultos reproductores, de 10 de las especies que crían en las islas: nueve de aves marinas y una de pinnípedos (*Arctocephalus tropicalis*). Sobre el tiempo calculado que cada una de estas especies invierte localmente sobre una malla regular de celdas de 10 por 10 km y para cada una de las estaciones del año, aplicamos estadísticos de asociación espacial para detectar las áreas que registran una actividad superior a la esperable al azar y constatado la variabilidad estacional de la distribución espacial.

Los "hotspots" de actividad se localizaron alrededor de las islas y también asociados a montañas submarinas siendo espacialmente consistentes para diferentes estaciones del año. Además, hemos constatado que estas áreas tienen una importancia crítica en algunas de las fases de cría para ciertas especies, que pueden llegar a invertir gran parte del tiempo de búsqueda de recursos en el mar dentro de la ZEE. El enfoque que presentamos proporciona una herramienta simple y eficaz para detectar las áreas de importancia para las comunidades pelágicas en procesos de planificación para la conservación y la gestión de áreas protegidas como el de Tristán de Acuña.

Introduction

Remote oceanic islands provide breeding grounds for pelagic predators such as seabirds and pinnipeds that have to return to land to breed, and disperse widely across ocean basins to forage for marine resources (Block *et al.*, 2011; Dias *et al.*, 2017; Harrison *et al.*, 2018). Advances in animal telemetry have facilitated the identification of the most important marine areas for many globally threatened pelagic species (Dias *et al.*, 2017; Krüger *et al.*, 2017; Tancell *et al.*, 2013). Protecting the pelagic areas on which these wide-ranging species depend can be challenging (Oppel *et al.*, 2018) because many of these areas lie in waters beyond national jurisdiction where the establishment and enforcement of protection regimes is complex (Game *et al.*, 2009, 2010). Spatial planning of protection measures in waters that are under national jurisdiction is a useful first step towards protecting pelagic species, but requires a detailed analysis of the distribution of biodiversity and an understanding of the potential threats (Burger, 2018; Sala *et al.*, 2018) to avoid protecting opportunistic areas where no threats occur (Barr & Possingham, 2013; Barr *et al.*, 2016; Devillers *et al.*, 2015).

One of the most important islands for these pelagic predators in the South Atlantic Ocean is Tristan da Cunha group of islands, whose Government has pledged to create a marine protection regime across its entire EEZ by 2020. This territory supports breeding populations of 25 seabird species and two pinnipeds (Ryan, 2007). Four seabird species are endemic to Tristan da Cunha and are listed as globally threatened (IUCN, 2018): Tristan Albatross *Diomedea dabbenena* (Critically Endangered), Atlantic Yellow-nosed Albatross *Thalassarche chlororhynchos* (Endangered), Atlantic Petrel *Pterodroma incerta* (Endangered), and Spectacled Petrel *Procellaria conspicillata* (Vulnerable). For five other species these islands supports the world's largest populations: Great Shearwater *Ardenna gravis* (99%, Least Concern), Macgillivray's Prion *Pachyptila macgillivrayi* (99%, Endangered), Northern Rockhopper Penguin *Eudyptes moseleyi* (87%, Endangered), Sooty Albatross *Phoebastria fusca* (57%, Endangered), and Subantarctic Fur Seal *Arctocephalus tropicalis* (63%, Least Concern).

All of these species are vulnerable to several pressures both on their breeding grounds and in the marine environment. On oceanic islands, invasive species are a key threat to many seabird species (Caravaggi *et al.*, 2018; Dilley *et al.*, 2015) and eradication of invasive species is an effective conservation tool (Holmes *et al.*, 2019; Jones *et al.*, 2016). However, even if land-based threats were removed, many species also face threats at sea, such as incidental bycatch, the capture of non-target marine species and/or individuals, in fisheries (Cuthbert *et al.*, 2005; Tuck *et al.*, 2011; Wanless *et al.*, 2009), or pollution (Burger, 2018; Croxall *et al.*, 2012). Therefore, the protection of marine foraging areas of seabird and pinniped species and the adequate

management of industrial activities is required to reduce threats that can adversely affect populations.

Tristan da Cunha's globally threatened seabird species disperse widely across the South Atlantic Ocean, and their most important foraging areas are off the coasts of South America, southern Africa and in Tristan's Exclusive Economic Zone (EEZ) (Dias *et al.*, 2017). The rich waters surrounding the islands are also important for the Tristan economy. The local population of some 260 inhabitants rely heavily on income from the fishery for Tristan Rock Lobster *Jasus tristani* (Glass, J. P, 2014), which provides 80% of government revenue and supports some basic services to the islanders. To diversify its sources of income, the Tristan Government has been investigating whether new pelagic long-line and trawl fisheries on their offshore seamounts could raise revenue through license fees. However, these activities potentially threaten many of the globally important populations of marine vertebrates through bycatch and/or disruptions to local foodwebs (Croxall *et al.*, 2012). Therefore, more spatially explicit information on where globally important biodiversity concentrates within the Tristan da Cunha EEZ is urgently needed before new fishing activities can be authorised for the long term. Information on biodiversity hotspots can then be incorporated with economic assessments to ensure a regime of protection that meets conservation targets required for a Marine Protected Area while permitting vital economic activity to persist (Ban *et al.*, 2014; Carwardine *et al.*, 2008; Klein *et al.*, 2010).

Here we identify priority areas across species to provide fundamental information for marine conservation planning within the EEZ of Tristan da Cunha. We use existing animal tracking data for nine seabirds and one pinniped that breed in the islands (Table 1) to detect multi-species clusters of activity by combining metrics of local use and spatial association (Getis & Ord, 1992). These seasonal hotspots of activity for the community of pelagic top predators can serve as an indicator of overall biological importance within the Tristan da Cunha EEZ and contribute to systematic conservation planning and sustainable management of the EEZ's marine resources.

Methods

Study area

The Tristan da Cunha group of islands in the central South Atlantic Ocean, consists of four major islands: Tristan da Cunha, Inaccessible and Nightingale islands in the north, and Gough Island some 390 km farther south. These two groups of islands belong to different oceanographic systems separated by the Subtropical Convergence Zone (Smythe-Wright *et al.*, 1998). The northern islands lie in the warm temperate realm of the South Central Atlantic Gyre while Gough

Island is on the Subtropical Convergence Zone, with cooler water all year round (Andrew *et al.*, 1995). The Sub-Antarctic Front, the northern boundary of the Antarctic Circumpolar Current carrying cold and highly productive waters (Spalding *et al.*, 2012), can also affect the southern portion of the EEZ (Fig. 1). The 200-nautical mile (370 km) EEZ surrounding both groups of islands covers an area of 758,770 km².

The emerged land of the main islands are the peaks of a system of volcanos at the western edge of the Walvis Ridge that lies east of the mid-Atlantic Ridge (Jokat & Reents, 2017; Peyve, 2011); other submerged peaks form seamounts, which create local upwelling of nutrient-rich waters and harbour significant biodiversity (Morato *et al.*, 2010) (Figure S1). The Tristan da Cunha EEZ and surrounding waters are regarded as a single marine province and ecoregion, given its distinctive habitats and species assemblages (Spalding *et al.*, 2007). The entire EEZ was declared a cetacean sanctuary in March 2001 (Hoyt, 2012), and Gough and Inaccessible Islands and their territorial waters out to 12 nautical miles (22.2 km) are World Heritage Sites (UNESCO, 2004) and Nature Reserves (Tristan da Cunha Government, 2006) (Fig. 1).

Figure 1. The main geographic and oceanographic features surrounding the Tristan da Cunha islands, the Tristan da Cunha archipelago main islands in the north and Gough island in the South. The bathymetric contours highlight the seamounts. The dotted line indicates the limits of the 50 nautical mile fishing exclusion area where the only commercial fishery allowed is for Tristan Rock Lobster.

Fisheries in the Tristan da Cunha EEZ are permitted under a system of temporal licenses regulated through the Tristan da Cunha Fisheries Limits Ordinance (Tristan da Cunha Government, 1983). The fishery for the Tristan Rock Lobster operates from April to December using lobster pots, is managed through a quota system, and is the only fishery permitted within 50 nautical miles (92 km) of all islands (Figure 1). A trawl and longline fishery for Antarctic Butterfish, also known as Bluenose Warehou *Hyperoglyphe antarctica*, has operated sporadically on four seamounts in the EEZ, with increased activity since 2015. In 2014, the Tristan da Cunha Government also licensed a Japanese vessel to fish for southern blue-fin tuna *Thunnus maccoyii* in the southern section of the EEZ. The occurrence of illegal, unreported and unregulated fishing is currently under study (OceanMind, 2018).

Collation and processing of tracking data

Selected species of seabirds (mainly the larger species) breeding on Tristan islands have been equipped with tracking devices since 2000, and Subantarctic Fur Seals since 2016. We compiled all available tracking data from these species to undertake a multispecies assessment of space use within Tristan's EEZ. Datasets were obtained from the BirdLife Seabird Tracking Database (BirdLife, 2017), Movebank (Wikelski & Kays, 2018). We restricted the analysis to tracks obtained using Global Positioning System (GPS) or Platform Transmitter Terminal (PTT) devices, as these have the necessary precision to allow a spatial analysis at the scale of the EEZ (Table 1). We used only tracking data where at least 6 locations were recorded per foraging trip within the EEZ, and at least 6 trips of a given species in a given season (Soanes *et al.*, 2013; Tancell, Sutherland & Phillips, 2016).

We filtered the locations for seabirds and seals to remove unrealistic locations using the speed filter within the R package "*argosfilter*" (Freitas, 2015), and applied a threshold of $10 \text{ m}\cdot\text{s}^{-1}$ for seals, $3 \text{ m}\cdot\text{s}^{-1}$ for penguins and $22 \text{ m}\cdot\text{s}^{-1}$ for the rest of the seabird species. As our focal species do not breed simultaneously and the distribution of species and anthropogenic activities varies spatially across seasons, the tracks were divided into quarterly periods to enable seasonal analysis of spatial use (Dias *et al.*, 2017). We defined austral seasons as the four quarters of the year and use the terms 'summer' (January - March), 'autumn' (April - June), 'winter' (July - September), and 'spring' (October - December) throughout. This approach allowed us to identify areas that are important for multiple species at the same time of year and facilitated the integration of the results in fisheries management plans that consider seasonal use.

Table 1. Tracking data used to identify hotspots of pelagic megafauna activity in the Tristan da Cunha Exclusive Economic Zone. The numbers indicate the number of adult individuals (Ind) tracked per group of islands (Group) with either Platform Terminal Transmitter (PTT) or Global Positioning System (GPS) devices between 2000 and 2018. Austral seasons are: Summer (January to March), Autumn (April to June), Winter (July to September), Spring (October to December). Note that some individuals were tracked in more than 1 season.

Name	Species	Ind	Date From To	Group		Device		Season			
				Tristan	Gough	PTT	GPS	Summer	Autumn	Winter	Spring
Northern Rockhopper Penguin	<i>Eudyptes moseleyi</i>	120	15/09/2012 30/11/2016	90	30		120			27	116
Tristan Albatross	<i>Diomedea dabbenena</i>	86	07/02/2001 03/05/2018		86	39	47	65	50	1	
Sooty Albatross	<i>Phoebastria fusca</i>	30	17/09/2006 18/12/2015	11	19	14	16	13	9	14	30
Atlantic Yellow-nosed Albatross	<i>Thalassarche chlororhynchos</i>	65	12/01/2000 30/11/2015	19	46	7	58	24	16	10	63
Atlantic Petrel	<i>Pterodroma incerta</i>	5	12/07/2014 14/08/2014		5		5			5	
Soft-plumaged Petrel	<i>Pterodroma mollis</i>	8	04/01/2014 08/03/2014		8		8	8			
Grey Petrel	<i>Procellaria cinerea</i>	15	04/04/2014 08/05/2014		15		15		15		
Spectacled Petrel	<i>Procellaria conspicillata</i>	8	11/01/2009 03/12/2010	8		8		8	8	8	8
Great Shearwater	<i>Ardenna gravis</i>	46	30/09/2009 23/12/2016	20	26	21	25	35	6	2	42
Subantarctic Fur Seal	<i>Arctocephalus tropicalis</i>	14	22/07/2016 16/06/2017	8	6	14		10	4	10	8
Total		397		156	241	103	294	163	108	77	267

While the data we used cover most globally threatened species breeding on the islands, they do not comprehensively reflect the entire seabird breeding community of this territory: 25 seabird species breed in the islands, of which especially the smaller species (terns, storm-petrels, diving petrels and other small petrels) have not been tracked with high-resolution devices. The tracking data for larger species have often been obtained from only a subset of known breeding colonies

and at certain moments of the year, hence our analysis does not characterise the spatial use of all Tristan's seabirds throughout the year. Nonetheless, these data provide a representative sample of the pelagic megafauna and will therefore facilitate more informative management than could be designed without these data.

Identification of multi-species hotspots of activity

To identify the most important areas within the EEZ, we first calculated the proportion of time that each species spent in a unit area in each given season and used these species-level metrics of the intensity of space use to estimate patterns of spatial association.

The time spent per grid cell has been used to show patterns of spatial use (Peron *et al.*, 2010; Pinaud, Cherel & Weimerskirch, 2005; Thiers *et al.*, 2017) and to identify core foraging areas (Casper *et al.*, 2010; Soanes *et al.*, 2013; Warwick-Evans *et al.*, 2015), and is a useful proxy to quantify the relative importance of marine areas. We used a regular grid with cells of 10×10 km within the EEZ (7931 cells) in an equal-area projection to analyse patterns of spatial use. All locations on land and within 12 km of colonies were removed to avoid errors associated with low quality locations provided by Argos Satellite Telemetry (Douglas *et al.*, 2012), which could inflate estimates of the time-at-sea around breeding colonies (if positions ashore are erroneously considered as at-sea).

We calculated the time spent per grid cell for each species in each season from all the tracking data using the function "tripGrid" in R package "trip" (Sumner, 2016). To avoid cells accounting for long periods when two successive positions were separated by a long time gap, we removed time gaps >3 hours. Because different species had different tracking effort across seasons and we aimed to obtain a multi-species metric of the intensity of use of all grid cells within the EEZ, we scaled the amount of time spent by each species in each grid cell to the total tracking effort for that species in each quarter. This approach ensured that areas of intensive use were not biased towards species with more intensive tracking effort in a given season. We added the relative amount of time spent per species across all species in a season, which yielded one grid per season with the relative amount of time spent per grid cell.

To identify statistically significant clusters of cells with relatively high intensity of use by the study species within the Tristan EEZ, we used an indicator of spatial association, the Getis-Ord G_i^* (Anselin, 1995; Getis & Ord, 1992). This statistic compares the intensity of use of a given cell with the value of each neighbouring cell within a given fixed radius and contrasts this variation with the values from all cells within the EEZ to calculate the G_i^* statistic. The G_i^* statistic follows a Z-

distribution and tests whether the sum of values across cells within a fixed radius deviates from what could be expected by chance if a similarly sized random sample was drawn from all the values in the entire EEZ. If cells with a relatively high intensity of use are surrounded by further high-value cells, the cluster is recognised as a statistically significant hotspot within the EEZ.

We defined the spatial neighbourhood for each season using a distance-based criterion (O'Sullivan & Unwin, 2010) and determined the appropriate distance threshold by identifying the radius at which spatial auto-correlation was most intense (Getis & Ord, 1996; Nelson & Boots, 2008). We calculated Moran's I , a statistic that quantifies spatial autocorrelation, at distances ranging from the average distance that ensures at least eight neighbours to 100 km at 5 km intervals. Then we selected the distance at which Moran's I was highest to define the spatial neighbourhood for each season at the EEZ scale.

Results

Time invested in the EEZ

We used tracking data from 397 individuals of 10 species, resulting in a total of 39,312 hours (equivalent to 1,638 days) of tracking data between 2000 and 2018. Tracking efforts were not equally distributed across seasons, with greater tracking effort during spring (28,944 hours) and summer (8,971 hours) than in autumn (5,256 hours) or winter (5,097 hours). The extent of the EEZ used by tracked animals also varied among seasons, with 75% of the EEZ used in spring, 68% in summer, 66% in autumn and 17% in winter, when many species migrate away from the islands.

The proportion of time spent within and outside the EEZ varied by species and breeding stage. All species spent at least the 10% of their time at-sea within the EEZ, with generally less time during incubation (Grey Petrel 10% to Northern Rockhopper Penguin 83%, Table S1) than during brood-guard when most species were confined to the EEZ (Tristan Albatross 82% to Northern Rockhopper Penguin 100%, Table S1). Thus, our analysis of hotspots within the EEZ captures a substantial proportion of these species' foraging period at sea.

Detected hotspots

In spring and summer, spatial autocorrelation of relative time-spent-in-area shown a maximum at 48 km. Applying this distance as the spatial neighbourhood, we identified seven hotspots ($P < 0.05$, G_i^* z-score ≥ 2.84) in spring (Fig. 2a). These hotspots accounted for 40% of the total time spent by the tracked animals in an area that covered only 8% of the total EEZ area. Spectacled

Petrels (81%) and Great Shearwaters (63%) were the species that spent the greatest amount of time in these hotspots, the next group is led by Northern Rockhopper Penguin (38%) and Subantarctic Fur Seal (32%).

For summer (Fig. 2b), we also detected seven hotspots ($P < 0.05$, G_i^* z-score ≥ 2.68) that covered 8% of the EEZ area but accounted for 31% of the total time spent by the tracked species in EEZ waters. Spectacled Petrels spent almost all their time in a given hotspot (97%), followed by Great Shearwaters (52%), Atlantic Yellow-nosed (37%) and Tristan Albatrosses (30%). The remaining species (Subantarctic Fur Seal, Sooty Albatross and Soft-plumaged Petrel) spent 21-26% of their time in hotspots.

In autumn, we found eight hotspots ($P < 0.05$, G_i^* z score ≥ 2.51) with a spatial neighbourhood of 58 km. These hotspots accounted for 38% of the total time in the EEZ and covered 12% of the EEZ area (Fig. 2c). Sooty Albatrosses spent most of their time in these hotspots (69%), with Atlantic Yellow-nosed Albatrosses (55%), Great Shearwaters (46%) and Tristan Albatross (36%) also spending significant amounts of time in these areas.

We only identified two hotspots in winter ($P < 0.05$, G_i^* z score ≥ 2.94) with a spatial neighbourhood of 50 km, likely due to the sparse tracking data available. These two hotspots covered 7% of the EEZ and accounted for 17% of the time spent by all the tracked species in the EEZ for this season (Fig. 2d). Atlantic Yellow-nosed (92%) and Sooty Albatrosses (89%) spent almost all their time in the EEZ in these hotspots, while winter-breeding Atlantic Petrels (29%) and Northern Rockhopper Penguins (17%) showed less clustered behaviour in the EEZ.

Figure 2. Significant marine multi-species hotspots within the Exclusive Economic Zone (EEZ) of Tristan da Cunha identified from tracking data of nine seabird and one fur seal species collected between 2000 and 2018. Hotspots identify areas where tracked species spent more time than expected by chance. (a) Spring (October to December, $n = 7$ spp.), (b) Summer (January to March, 7 spp.), (c) Autumn (April to June, 8 spp.), (d) Winter (July to September, 6 spp.).

Several hotspots were broadly similar across all seasons: the areas around Gough and to the northeast of Gough around the McNish, Yakhont and R.S.A. seamounts were identified as hotspots in all seasons, while the areas around and to the west of the northern islands were important in at least three seasons (Fig. 3). Throughout the year, about 25% of the EEZ can be classified as part of a hotspot (188 797 km²) for these 10 tracked species, and the 37.5% of this area (7 0799 km²) is part of a hotspot in more than one season.

Figure 3. Overlap of marine multi-species hotspots within the Exclusive Economic Zone (EEZ) of Tristan da Cunha identified from tracking data of nine seabird and one fur seal species collected between 2000 and 2018. Shading indicates in how many seasons an area was identified as a hotspot (Fig. 2).

Discussion

The marine predators breeding on the islands of Tristan da Cunha disperse widely across the South Atlantic Ocean and the entire EEZ of Tristan da Cunha is one of the most important marine areas in the South Atlantic Ocean for these species (Dias *et al.*, 2017; Ronconi *et al.*, 2018; Schoombie *et al.*, 2017). Our analysis highlights that these mobile marine predators are not uniformly distributed throughout the EEZ. We identified significant hotspots of activity that were consistently used at different times of the year. These hotspots occurred primarily around breeding islands and submarine geographic features and should be considered of extraordinary value for marine conservation.

The hotspots we identified confirmed the scientific justification for the Tristan Government's long-standing community-led closure of the 50-nautical mile (93 km) buffer around all four islands to all commercial non-lobster fishing, and this closure should be retained in any marine protection regime as marine areas near breeding colonies are of high value for seabirds and pinnipeds during the breeding season (Oppel *et al.*, 2018; Soanes *et al.*, 2016; Williams *et al.*, 2014).

We also identified hotspots around different seamounts in all seasons (Yakhont Seamount) and during spring and summer (R.S.A. and McNish seamounts). Seamounts are recognised to be diversity hotspots (Worm, Lotze & Myers, 2003) and important feeding grounds for marine predators at various scales (Bost *et al.*, 2009; Weimerskirch, 2007; Yen, Sydeman & Hyrenbach, 2004), likely because local upwelling of cold and nutrient-rich waters provides a reliable supply of prey (Morato *et al.*, 2010). Seamounts are not only a productive foraging habitat for marine predators but also for fisheries targeting large predatory fish. The Antarctic Butterfish fishery occurring on the McNish, Yakhont and R.S.A. seamounts therefore overlaps with the hotspots for Tristan, Atlantic Yellow-nosed, and Sooty Albatrosses and Great Shearwaters - four species that are susceptible to long-line bycatch in the South Atlantic Ocean (Glass, N *et al.*, 2000; Jiménez *et al.*, 2014). Although these wide-ranging species also use vast areas of the South Atlantic beyond the EEZ, they spent almost all their time-at-sea during the early chick-rearing stage in Tristan waters and then rely almost exclusively on the productive waters around Tristan's seamounts. Hence, we recommend that any fishery in this area require temporal and spatial closures, and the mandatory adoption of all available mitigation measures to minimise the risk of bycatch, as has been implemented around South Georgia (Handley *et al.*).

The only commercial fishery currently operating within the 50 nm buffer around the four islands catches Tristan Rock Lobster and Common Octopus *Octopus vulgaris* using traps deployed on the

seafloor up to a depth of 200 m. There is no seabird or seal bycatch reported for this fishery, and nocturnal collisions with vessels are the main threat when small nocturnal petrels are disorientated by ship lights (Ryan, 1991). However, since artificial deck illumination at night was reduced, fatal collisions have become less common (Glass, J. P & Ryan, 2013) and currently do not pose a significant risk to Tristan's seabird or seal populations. Although this fishery overlaps spatially with the hotspots we identified around breeding islands, currently there is no apparent need for additional management measures to protect seabirds and marine mammals.

Another major pressure on the EEZ is the presence of an increasingly busy shipping lane in the northern EEZ that transects hotspots identified in spring and autumn. In 2016 more than 2400 cargo vessels traversed these waters (OceanMind, 2018). The risk of accidents was highlighted in 2011 by the grounding of the bulk carrier *MS Oliva* on Nightingale Island, which resulted in a spill of 1,500 tonnes of fuel oil and the death of thousands of endangered seabirds, mainly Northern Rockhopper Penguins. Our results justify and provide evidence for the establishment of a traffic separation scheme in the northern EEZ to reduce the risks of further damage by international shipping activities and the designation of a Particularly Sensitive Sea Area (PSSA). This designation is a specific conservation measure promoted by the International Maritime Organization (IMO) for areas that need special protection because of their significance for recognised ecological, socio-economic, or scientific attributes that may be vulnerable to damage by international shipping activities (IMO, 2006).

Our results indicate that hotspots are used more than expected by chance in several seasons (Fig. 2). There may be further use of these important areas at other times of the year that we were not able to capture in our analyses because tracking effort is concentrated in spring (October to December) and early summer (beginning of January) when most species breed. In addition, these areas may also be used by other species and taxonomic groups including sharks (Figure S2). Besides, some breeding species such as Brown Skuas *Catharacta antarctica*, Broad-billed Prions *Pachyptila vittata* or the near-endemic MacGillivray's Prions *P. macgillivrayi* were not included in our hotspot assessment because we lack high-resolution tracking data. These species have been tracked with Global Location Sensing (GLS) loggers, but the positional error associated with these devices (~150 km) renders these data unsuitable for our analysis within the local EEZ (Dias *et al.*, 2017; Phillips *et al.*, 2004). Other small seabird species, notably storm-petrels, diving petrels, and terns, have not been tracked so far, and while terns likely remain within the EEZ during the breeding season, storm-petrels are very mobile and may utilise areas far from their breeding grounds (Oppel *et al.*, 2018; Pollet *et al.*, 2014). Nonetheless, our analysis suggests that marine activity hotspots do exist for the marine vertebrates breeding in Tristan da Cunha at the spatial

scale of the EEZ and this information could be used to improve marine conservation planning (Osmond *et al.*, 2010).

The Tristan da Cunha Government is in the process of establishing a marine protection regime for its entire EEZ by 2020 (CEFAS, 2018). With an EEZ of more than 750,000 km², the Tristan da Cunha Government has a unique opportunity to contribute to the protection of one of the last marine wilderness regions on earth (Watson *et al.*, 2018) and to the representativeness of marine protection globally. The Convention on Biological Diversity aims to ensure the creation of "ecologically representative" systems of protected areas (CBD, 2010), but this condition is frequently ignored when protected areas are established (Devillers *et al.*, 2015; Venter *et al.*, 2018). The Tristan da Cunha EEZ is one of 62 global marine provinces (Spalding *et al.*, 2012), but its biodiversity is currently not adequately represented in marine protected areas. An effectively managed Marine Protected Area in the Tristan EEZ could, therefore, play an important role in ensuring adequate representation of biodiversity in the global network of protected areas (Venter *et al.*, 2018).

Acknowledgements

This analysis was greatly facilitated by the Global Seabird Tracking database (www.seabirdtracking.org) hosted by BirdLife International and the Movebank (www.movebank.org) hosted by the Max Planck Institute for Ornithology. We appreciate the support of R. Phillips (British Antarctic Survey), A. Carneiro and M. Dias (BirdLife International), BirdLife South Africa, L. Welch (United States Fish and Wildlife Service), K. Powers and D. Wiley (NOAA/NMS Stellwagen Bank National Marine Sanctuary), Jennifer Caselle (University of California Santa Barbara), and G. Buchanan, J. Mallord, S. Wischniewski and J. Vickery (RSPB). We also acknowledge a large number of fieldworkers involved with the collection of tracking data, funding institutions and the Government of Tristan da Cunha who approved this research.

Funding information: Darwin Plus Programme Project Pinnamin (DPLUS059), United Kingdom Department for Environment, Food, and Rural Affairs. RSPB, the UK partner in BirdLife International. BirdLife South Africa. South African National Antarctic Programme (SANAP), through the National Research Foundation.

Data accessibility: All data are available on either the BirdLife Seabird Tracking database (www.seabirdtracking.org), or Movebank (www.movebank.org).

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