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

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Abstract

Remote oceanic islands harbour unique biodiversity, especially of species that rely on the marine trophic resources around their breeding islands. Identifying marine areas used by such species is essential to manage and limit processes that threaten these species. The Tristan da Cunha territory 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 commercial activities. To inform marine management in the Tristan da Cunha Exclusive Economic Zone (EEZ), we identified statistically significant areas of concentrated activity by collating animal tracking data from nine seabirds and one marine mammal. We first calculated the time that breeding adults of the tracked species spent in 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 for each season we detected areas that are used more than expected by chance. Most of the activity hotspots were either within 100 km of breeding colonies or were associated with seamounts, being spatially constant across several seasons. Our simple and effective approach highlights important areas for pelagic biodiversity that will benefit conservation planning and marine management strategies.

Keywords: Seabird, Pinniped, Satellite tracking, Time-in-area, Marine Protected Area, Marine Conservation Planning.

Introduction

Remote oceanic islands provide breeding grounds for pelagic predators such as seabirds and pinnipeds, which 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 some of most important marine areas for many globally threatened pelagic species (Dias *et al.*, 2017; Heerah *et al.*, 2019; Kruger *et al.*, 2017). Protecting the pelagic areas on which these wide-ranging species depend can be challenging 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; Game *et al.*, 2010; Oppel *et al.*, 2018). 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 knowledge 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 pressures occur (Barr & Possingham, 2013; Barr *et al.*, 2016; Devillers *et al.*, 2015).

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). Among the most important islands for pelagic predators in the South Atlantic Ocean is the UK Overseas Territory of Tristan da Cunha, which constitutes 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 protected area in this marine province could, therefore, play a significant role in ensuring adequate representation of biodiversity in the global network of protected areas (Venter *et al.*, 2018).

The Tristan da Cunha islands support 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 this territory 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* (90%, Endangered), Sooty Albatross *Phoebetria 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 main threat to many seabird species (Caravaggi *et al.*, 2019; 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 bycatch, pollution or prey depletion (Dias *et al.*, 2019). 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 main 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 local economy. The 260 human 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 licensed some limited long-line and trawl fisheries on their offshore seamounts to raise revenue through license fees. However, these activities potentially threaten many of the globally important populations of marine vertebrates through bycatch or disruptions to local foodwebs (Dias *et al.*, 2019).

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 larger than 750,000 km^2, 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). Here we provide spatially explicit information on where globally important biodiversity concentrates within the Tristan da Cunha EEZ to inform the design of the marine protection regime and future fishing authorisations. We used 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 pelagic top predators can serve as an indicator of overall biological importance within the Tristan da Cunha EEZ and can be combined with economic assessments to ensure any proposed regime of protection meets conservation targets while permitting vital economic activity (Ban *et al.*, 2014; Carwardine *et al.*, 2008; Klein *et al.*, 2010).

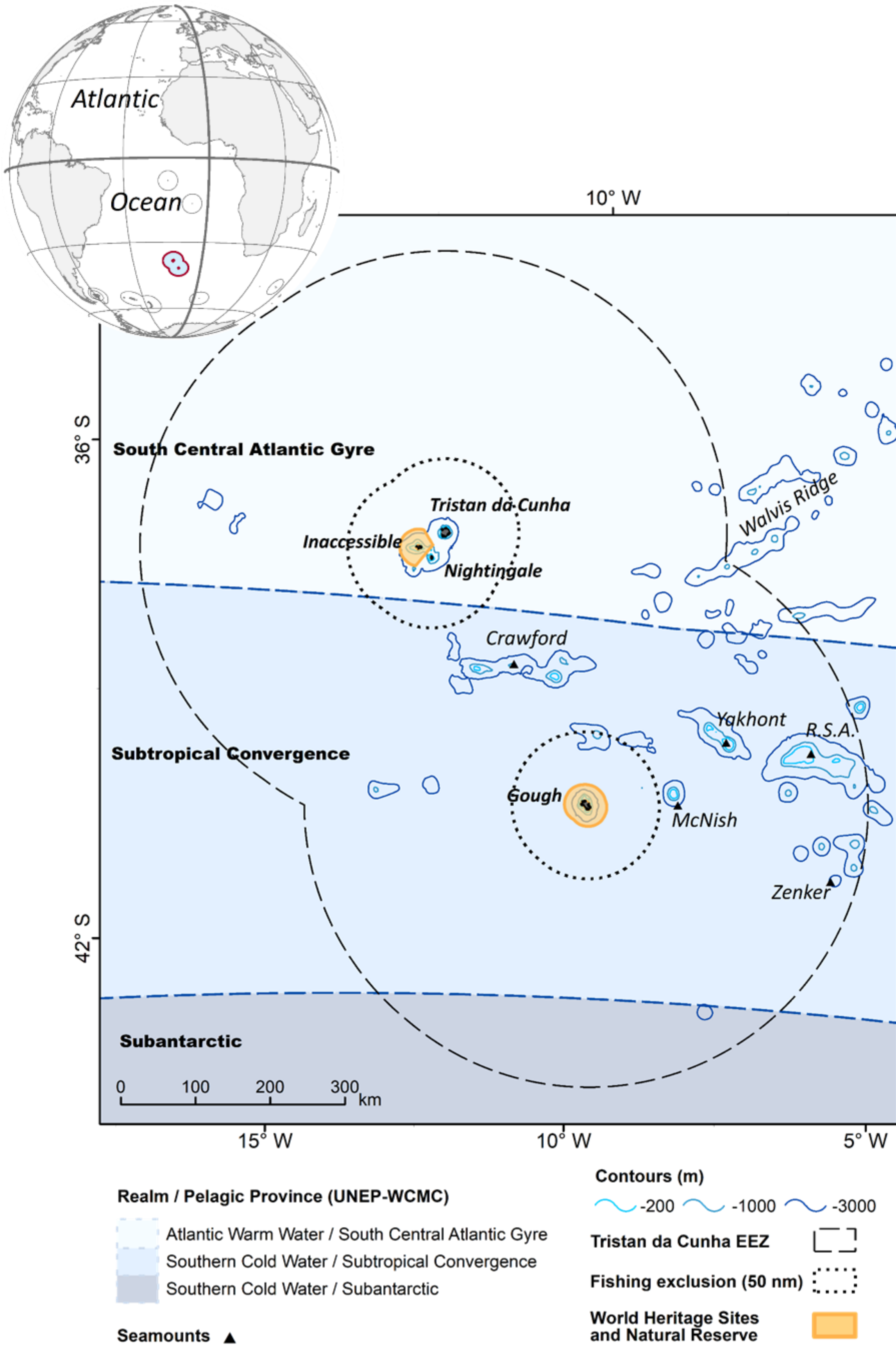
Methods

Study area

The Tristan da Cunha group in the central South Atlantic Ocean comprises four major islands: Tristan da Cunha, Inaccessible and Nightingale Islands in the north, and Gough Island some 380 km SE from Nightingale. The islands are the emergent 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 are proper seamounts, which create local upwelling of nutrient-rich waters and harbour significant biodiversity (Morato *et al.*, 2010) (Figures 1 and S1).

The two groups of islands belong to different oceanographic systems separated by the Subtropical Convergence Front (STC) (Smythe-Wright *et al.*, 1998). The northern islands lie in the warm temperate realm of the South Central Atlantic Gyre while Gough Island is in the Subtropical Convergence Zone (STCZ), with colder water all year round Spalding (Andrew *et al.*, 1995; Longhurst, 2007). 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). Together with surrounding waters, the EEZ is regarded as a single marine province and ecoregion because of its distinctive habitats and species assemblages (Longhurst, 2007; Spalding *et al.*, 2007).

The Tristan da Cunha EEZ extends up to 200 nautical miles (370 km) from the islands and covers an area of 758 770 km^2 (UNCLOS, 1982). The entire EEZ was declared a cetacean sanctuary in March 2001 (Hoyt, 2012). 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).



Atlantic
Ocean
10° W
36° S
42° S
South Central Atlantic Gyre
Tristan da Cunha
Inaccessible
Nightingale
Walvis Ridge
Crawford
Yakhont
R.S.A.
Subtropical Convergence
Gough
McNish
Zenker
Subantarctic
0 100 200 300 km
15° W
10° W
5° W
Realm / Pelagic Province (UNEP-WCMC)
Atlantic Warm Water / South Central Atlantic Gyre
Southern Cold Water / Subtropical Convergence
Southern Cold Water / Subantarctic
Seamounts
Contours (m)
-200 -1000 -3000
Tristan da Cunha EEZ
Fishing exclusion (50 nm)
World Heritage Sites and Natural Reserve

Figure 1. *The main geographic and oceanographic features surrounding the islands of Tristan da Cunha. 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 temporary licenses regulated through the Tristan da Cunha Fisheries Limits Ordinance (Tristan da Cunha Government, 1983). The fishery for the Tristan Rock Lobster is the only fishery permitted within 50 nautical miles (92 km) of all islands (Figure 1) and operates from April to December under a quota system using lobster pots that pose no threat to seabirds (Ryan and Glass 1991). 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 bluefin tuna *Thunnus maccoyii* in the South section of the EEZ. The occurrence of illegal, unreported and unregulated fishing is currently under study (OceanMind, 2018).

Collation and processing of tracking data

Several seabird species breeding on the 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) and Movebank (Wikelski & Kays, 2018) *(Table S1)*. We restricted the analysis to tracks acquired through 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 seven locations were recorded per foraging trip within the EEZ, and at least six trips of a given species in a given season (Soanes *et al.*, 2013; Tancell, Sutherland & Phillips, 2016).

We filtered locations for seabirds and seals to remove unrealistic locations using the speed filter within the R package "*argosfilter*" (Freitas, 2015), and applied a speed threshold of 3 $m \cdot s^{-1}$ for seals (Boyd, Staniland & Martin, 2002), 2.2 $m \cdot s^{-1}$ for penguins (Brown, 1987), and 23 $m \cdot s^{-1}$ for flying seabirds based on previously recorded movement speeds (Catry, Phillips & Croxall, 2004; Schoombie *et al.*, 2018). We used the "tripSplit" function to identify individual trips (Lascelles *et al.*, 2016). As our focal species do not breed simultaneously (Table S2) and the distribution of species and anthropogenic activities varies spatially across seasons, the trips were divided into quarterly periods to enable a seasonal analysis of space use (Dias *et al.*, 2017). We defined austral seasons as the four quarters of the year and applied 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, despite their asynchronous breeding. Because we aimed to identify areas within Tristan's EEZ that are most intensively used, we included all offshore tracking data regardless of behaviour. Although seabirds may use certain areas in some years but not in others (Paiva *et al.*, 2013), we calculated the overall intensity of use across all years as this is the most relevant metric for planning a supra-annual regime of protection.

To provide a scale of reference for the general importance of the EEZ in comparison to international waters (Figure S2), we quantified the proportion of time that tracked individuals spent within the EEZ. This analysis was performed for each breeding stage, as seabirds travel varying differences at different breeding stages (Oppel et al. 2018).

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) with complete tracks 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). The breeding season for each species is shown in Table S.2. Note that some individuals were tracked in more than one season.*

Name	Species	Ind	Years	Group		Device		Season			
				Tristan	Gough	PTT	GPS	Summer	Autumn	Winter	Spring
Northern Rockhopper Penguin	*Eudyptes moseleyi*	120	2012, 2016	90	30		120			27	116
Tristan Albatross	*Diomedea dabbenena*	86	2001, 2018		86	39	47	65	50	1	
Sooty Albatross	*Phoebetria fusca*	30	2006, 2015	11	19	14	16	13	9	14	30
Atlantic Yellow-nosed Albatross	*Thalassarche chlororhynchos*	65	2000, 2015	19	46	7	58	24	16	10	63
Atlantic Petrel	*Pterodroma incerta*	5	2014		5		5			5	
Soft-plumaged Petrel	*Pterodroma mollis*	8	2014		8		8	8			
Grey Petrel	*Procellaria cinerea*	15	2014		15		15		15		
Spectacled Petrel	*Procellaria conspicillata*	8	2009	8		8		8	8	8	8

Name	Species	Ind	Years	Group		Device		Season			
				Tristan	Gough	PTT	GPS	Summer	Autumn	Winter	Spring
Great Shearwater	*Ardenna gravis*	46	2009, 2016	20	26	21	25	35	6	2	42
Subantarctic Fur Seal	*Arctocephalus tropicalis*	14	2016, 2017	8	6	14		10	4	10	8
Total		**397**		**156**	**241**	**103**	**294**	**163**	**108**	**77**	**267**

While the data we used include most globally threatened species breeding on Tristan's islands, they do not comprehensively reflect the entire seabird breeding community of the territory: 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 at certain times of the year, hence our analysis does not characterise the spatial use of all Tristan's seabirds throughout the year. Besides, because fewer species are breeding in autumn and winter, and non-breeders at that time of year generally leave the EEZ (Dias *et al.*, 2017; Ronconi *et al.*, 2018), fewer data were available for autumn and winter than for spring and summer. Nonetheless, these data provide a representative sample of the pelagic megafauna and facilitate more informed management than could be designed without these data.

Identification of multi-species hotspots of activity

To identify the most critical 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. Although birds and seals commute, forage and rest at sea, and these behaviours could be distinguished by tracking data

(Bennison *et al.*, 2018) we deliberately used all offshore tracking data because all areas where animals spend significant proportions of time are significant for management, regardless of the particular behaviour displayed in an area.

The time spent per grid cell has been used previously to show patterns of spatial use (Peron *et al.*, 2010; Pinaud, Cherel & Weimerskirch, 2005; Thiers *et al.*, 2017) and identifiying 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 core use. All locations on land and within the first buffer of grid cells around the islands (a 12 km buffer) were removed to avoid overrepresentation of inshore waters due to inaccuracy of locations when coastal breeding species are actually on land, near-shore rafting behaviour, and because near-shore waters are already legally protected (Fig. 1) and therefore of lower priority to be identified as hotspots.

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 estimating intensive use in cells when a long time gap separated two successive positions, we removed time gaps greater than six hours by cutting the tracking data into segments using the function “tripGap”. 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 (in hours) 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), which is a robust approach that has recently been used to identify other marine hotspots (Kuletz *et al.*, 2015; Queiroz *et al.*, 2016; Sussman *et al.*, 2019; Yurkowski *et al.*, 2019). This statistic compares the intensity of use of a given cell with the value of each adjacent cell within a given fixed radius – the cells in this radius are referred to as the spatial neighbourhood. The sum of values within the spatial neighbourhood is then compared with the sum of all values in a defined geographical area, in our case within the EEZ, to calculate the G_i* statistic (Ord & Getis, 1995). The G_i* statistic follows a Z-distribution and tests whether the sum of values across cells within the spatial neighbourhood 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 performed this analysis in ArcGIS 10.5 (ESRI, 2016) using the Hot Spot Analysis (Getis-Ord Gi*) tool from the Spatial Analyst extension and applying the False Discovery Rate (FDR) Correction (Caldas de Castro & Singer, 2006).

We defined the spatial neighbourhood for each season using a distance-based criterion (O'Sullivan & Unwin, 2010). To determine the appropriate distance threshold, we identified the radius at which spatial auto-correlation of relative time spent-in-area was most intense (Getis & Ord, 1996; Nelson & Boots, 2008) with the Incremental Spatial Autocorrelation tool (ESRI, 2016), measuring the spatial auto-correlation with the Global Moran's I at a Euclidean distance radii ranging from 10 to 100 km at 5 km intervals. We selected the distance at which Moran's *I* was highest as a reference to define the spatial neighbourhood for each season at the EEZ scale (Fu *et al.*, 2014; Overmars, de Koning & Veldkamp, 2003).

Results

Time spent 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 also varied by species and breeding stage (Table S3). All species spent at least 10% of their time at-sea within the EEZ, with generally less time during incubation (Grey Petrel 10% to Northern Rockhopper Penguin 83%) than during brood-guard when most species were confined to the EEZ (Tristan Albatross 82% to Northern

Rockhopper Penguin 100%, Table S3). Therefore, our analysis of hotspots within the EEZ captures a substantial proportion of these species' foraging periods at sea.

Hotspots detected

In spring and summer, spatial autocorrelation of relative time-spent-in-area showed a maximum at 48 km. Applying this distance as the spatial neighbourhood, we identified seven hotspots in spring ($P < 0.05$, Gi* z-score ≥ 2.84, Fig. 2a) and summer ($P < 0.05$, Gi* z-score ≥ 2.68, Fig. 2b).

Spring hotspots covered the 8% of the EEZ and accounted for 40% of the total time spent by the tracked species in EEZ waters (Fig. 2a). Spectacled Petrels (81%) and Great Shearwaters (63%) were the species that spent the largest proportion of time in these hotspots with the Northern Rockhopper Penguins (38%) and Subantarctic Fur Seals (32%).

Summer hotspots also covered 8% of the EEZ and accounted for 31% of the time that the tracked animals spent in this area (Fig. 2b). Spectacled Petrels spent almost all their time in these hotspots (97%), 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 to 26% of their time in hotspots.

In autumn, we found eight hotspots ($P < 0.05$, Gi* z score ≥ 2.51) with a spatial neighbourhood of 58 km. Autumn 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%), although given the small size of the sample (Table 1), some of these hotspots might be reflecting the individual behaviour of some birds. Atlantic Yellow-nosed Albatrosses (55%), Great Shearwaters (46%) and Tristan Albatross (36%) are also spending significant amounts of time in these areas.

We identified two hotspots in winter ($P < 0.05$, Gi* z score ≥ 2.94) (Fig. 2d), applying a spatial neighbourhood of 50 km, likely due to the sparse tracking data within the EEZ, and a third area partially in the southwest of the EEZ and crossed by the boundary. The two first 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. Atlantic Yellow-nosed (92%) and Sooty Albatrosses (89%) spent almost all their time in the EEZ in these hotspots, where the winter-breeding Atlantic Petrels and Northern Rockhopper Penguins spent 29% and 17% respectively.

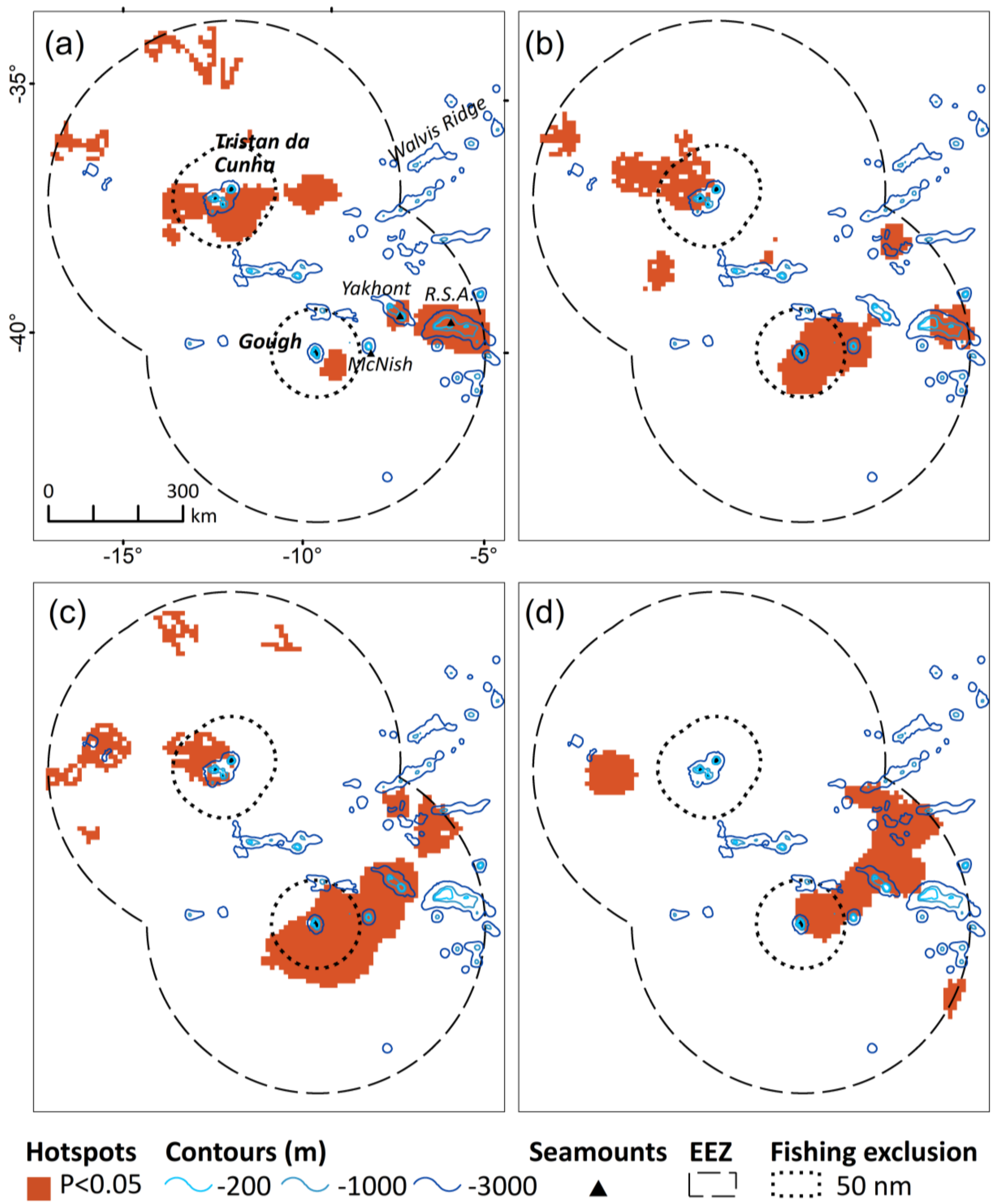


Figure 2. *Significant marine multi-species hotspots within the Exclusive Economic Zone (EEZ) of Tristan da Cunha identified from tracking data of nine seabird and one fur seal species collected between 2000 and 2018. Hotspots identify areas where tracked species spent more time than expected by chance. (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 (Fig. 3): areas around Gough and the northeast of Gough around the McNish, Yakhont and R.S.A. seamounts were identified as hotspots for several seasons; a continous area connects the eastern waters of Gough with the McNish and Yakhont seamounts in three seasons with some sectors within used all the year round. Some of the areas around and to the west of the northern islands were important in up to three seasons. For our 10 tracked species, 24.8% of the EEZ (188 797 km^2) were classified as a hotspot in any of the four seasons. The area of hotspots that were important in more than a single season was 70799 km^2 and therefore covered 9.3% of the EEZ.

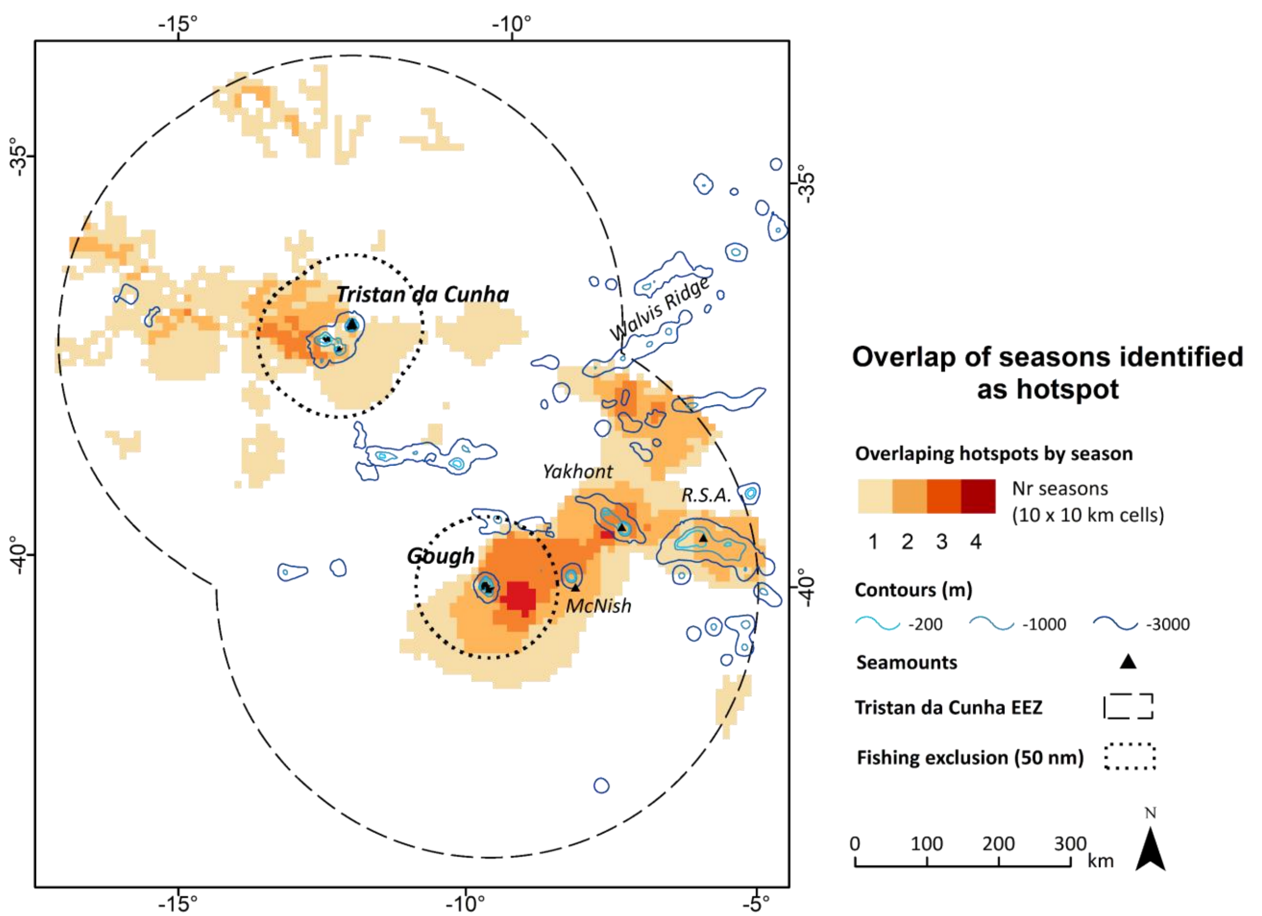


Figure 3. *Overlap of marine multi-species hotspots within the Exclusive Economic Zone (EEZ) of Tristan da Cunha identified from tracking data of nine seabird and one fur seal species collected between 2000 and 2018. Shading indicates in how many seasons an area was identified as a hotspot (Fig. 2).*

Discussion

The marine predators breeding on the islands of Tristan da Cunha Territory 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 by a subset of 10 marine predator species at different times of the year. These hotspots occurred primarily around breeding islands and submarine geographic features and covered only 25% of the EEZ, which should be considered of extraordinary value for marine conservation. Identifying hotspots is thus an effective approach to minimise the area required for protection and thus reduce the opportunity cost resulting from the protection of these areas of outstanding biodiversity value (Queiroz *et al.*, 2016; Sussman *et al.*, 2019; Yurkowski *et al.*, 2019).

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. Furthermore, 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 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). Our data, which are based on ten species representing different feeding niches and preferred prey species, therefore highlight that these areas are likely of broad significance across marine biodiversity, including for example sharks (Figure S3).

Seamounts are not only a productive foraging habitat for marine predators but also for fisheries targeting sizeable predatory fish. The Antarctic Butterfish fishery, exploiting a demersal fish species on the McNish, Yakhont and R.S.A. seamounts using either longlines or trawls, 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 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.*, 2019, *in press*) or the northeast waters of the Antarctic Peninsula (Waugh *et al.*, 2008) .

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 frequent (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, at present there is no apparent need for additional management measures to protect seabirds and marine mammals.

Another remarkable 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), leading to increasing pollution (Ryan *et al.*, 2019). 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 an effective traffic separation scheme in the EEZ; an "area to be avoided" around the islands, protecting at least the 50 nm Fishing Exclusion zone thus reducing the risks of damage by international shipping activities. Given the outstanding international importance of the entire EEZ, seamounts included, the measures implemented should be equivalent to Particularly Sensitive Sea Areas (PSSA). These areas are promoted by the International Maritime Organization (IMO) as a specific conservation measure where special protection is needed given 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. Some breeding species such as Brown Skua *Catharacta antarctica*, Broad-billed Prion *Pachyptila vittata* or MacGillivray's Prion *Pachyptila macgillivrayi* were not included in our hotspot assessment because these species have only been tracked with Global Location Sensing (GLS) loggers, which have too large uncertainty for our analysis (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 away from their breeding grounds (Hedd *et al.*, 2018; Oppel *et al.*, 2018). The absence of data for smaller species may result in an overemphasis of existing data, such as the hotspots identified from Sooty Albatross tracking data in autumn, which may be due to the preference of a small number of individuals and treated with caution. 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 pledged in 2016 to create a community-driven and science-led marine protection regime across its entire EEZ by 2020 (CEFAS, 2018). We have now provided scientific evidence from a broad range of marine species showing which areas of these territorial waters should be given priority for protection. The process of marine spatial planning has started in Tristan da Cunha, and our approach will allow the easy incorporation and updating of existing hotspot areas when new information becomes available.

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