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Spatial scales of marine conservation management for breeding seabirds

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1. Introduction

Decision makers often have to select among different management actions that might benefit a given species, and management options can range from small-scale solutions that protect a local area from outside disturbance or destruction, to large-scale or global actions that regulate human activities which are considered detrimental. In the marine realm, the unambiguous delineation of important areas for the protection of biodiversity is complicated by the lack of obvious habitat boundaries [1-3], and in many cases the spatial scale of marine protected areas is inadequate to fully protect the species of interest [4, 5]. Selecting the most

appropriate conservation management option will therefore benefit from accurate knowledge about the spatial scale at which management is required to protect highly mobile species [6].

Seabirds are distributed across all of the world's oceans and adjacent coastlines and islands [7, 8]. They face multiple threats on land and at sea, and are more threatened than other groups of birds [9-11]. Because many seabirds feed on fish and are near the apex of the marine food chain, they are useful indicator species for the health of the marine environment and for marine spatial planning [12-14]. To protect seabirds at sea it is essential to understand their spatial distribution and potential exposure to anthropogenic threats. During the breeding season, seabirds are constrained to marine areas which they can reach from their nest while maintaining parental duties of incubating eggs or feeding chicks. The areas exploited during the breeding season are therefore important for the persistence of populations, and may be more feasible to manage than areas used during other life stages. However, some seabird species can travel thousands of kilometres even during the breeding season [e.g. 8, 15, 16], and the spatial scale of appropriate management may therefore vary.

Currently available approaches for seabird conservation at sea can be implemented across a range of spatial scales and within a variety of regulatory frameworks [5, 17]. Area-based management approaches such as marine protected areas can be based on a broad variety of management frameworks that range from complete protection from all extractive and destructive activities ('marine reserves') to multiple use areas that permit and regulate economic activity [18-20]. For seabirds, area-based measures range from the protection of breeding colonies at the very local scale, to marine foraging areas around colonies and further offshore where significant seabird concentrations occur [21-23]. At larger spatial scales, additional conservation management options exist for seabirds that are not based on the protection of a specific area [17]. For example, regulations that reduce or eliminate the incidental mortality (bycatch) of seabirds in industrial or artisanal fishing operations [11, 24, 25], or regulations that limit the extraction of food resources [26, 27], can be implemented across all spatial scales and may therefore mitigate key threats to widely dispersed species [28-30]. Deciding which of these policy instruments may be most appropriate for a given seabird species of conservation concern can be informed by a better understanding of the species' broad spatial distribution and aggregation patterns.

The distribution of seabird species was often inferred from observations at sea, until the development of small tracking devices in recent decades [31-33]. By 2017, more than 100

of the 360 species of seabirds had been equipped with tracking devices [34]; hence, sufficient seabird tracking data exist on the spatial scales of foraging to inform effective management at a broad taxonomic level [6, 35, 36]. To synthesize the existing information for management planning, two complementary aspects of seabird distribution patterns are particularly important, albeit not entirely independent: (1) the distance a species travels and the size of the marine area that birds of a given colony exploit; and (2) to what extent individuals of the same colony use the same areas at sea, which is referred to as 'spatial aggregation'. Even very mobile species can show high spatial aggregation at sea, and areas in which they congregate may be in national or international waters depending on the distance the birds travel from the colony [37, 38]. Here, seabird space-use with respect to these two aspects is quantified to indicate appropriate spatial scales for conservation management of breeding seabirds at the family level.

Existing tracking data from 52 species of ten different families collected in the Atlantic Ocean basin over the past two decades were used. These data were analysed with previously established methods [1, 39, 40] to quantify the broad space-use requirements and spatial aggregation patterns of adult seabirds during the breeding season, and variation among families was tested. This approach allowed an assessment of whether the patterns of taxonomically coherent groups of species are sufficiently consistent to provide guidance for the use of particular approaches to marine management.

2. Methods

2.1.Data collation and aggregation

Seabird tracking data were collated for adult birds during the breeding season, when individuals are most constrained in their space-use due to the need to return to the nesting site on land. This constraint to return to the nest will likely accentuate differences between families and therefore facilitate a greater contrast in the space-use across the taxonomic spectrum. While protecting juvenile, immature and adult life-stages outside the breeding season is equally important for the conservation of long-lived species [41, 42], the movement patterns of seabirds when they are not breeding may be more affected by their latitudinal distributions than by taxonomic differences [43, 44]. In addition, a broad taxonomic comparison of distribution patterns of juvenile, immature, and adult life stages outside the

breeding season is currently difficult due to the paucity of suitably high-resolution tracking data for these stages.

Seabird tracking data from the Atlantic Ocean basin were available from the BirdLife Seabird Tracking Database [34] or through institutional repositories or collaborators. The selection of data used for this analysis was opportunistic and taxonomically imbalanced because seabird tracking efforts have so far focused on species and families of larger body size. However, the data represent a broad taxonomic spectrum of seabird movements during the breeding season from a large geographical region and are therefore useful to inform spatial scales for management.

Only tracking data from Global Positioning System (GPS) loggers and Platform Terminal Transmitters (PTT) were used due to their high spatial accuracy, and only datasets with at least five individuals were included to minimise erroneous conclusions based on samples of insufficient size [1, 37, 40]. During the breeding season, adult seabirds can be constrained to forage within different distances from their nest depending on whether they are incubating eggs or feeding small or large chicks [16, 45-47]. All tracking data were therefore divided into two stages, distinguishing the incubation period from the chick-rearing period when adults regularly return to feed the chick and therefore may not travel as far. Tracking data were analysed separately for each combination of species, colony, and breeding stage, except for some species where the tracking period spanned different breeding stages that were not distinguished because of a lack of concurrent monitoring (classified as 'unspecified breeding', Table S1). Our analysis was based on 210 datasets of 52 species from ten seabird families (Tables 1 and S1).

2.2.Rationale for space-use quantification

The analysis to support the selection of appropriate spatial scales for conservation management was designed to quantify seabird space-use in terms of (1) the distance that birds travel from their colony and the extent of the overall area that was exploited, and (2) the spatial aggregation at sea and the size of areas where a significant proportion of the population concentrated.

Although tracking data were collated from a 20-year time period, and it is possible that seabirds may have shifted their distribution in response to environmental changes over that

time period [48, 49], the coarse metrics of space-use which are based on evolutionary differences among families are unlikely to have changed over two decades. Hence, the year in which data were collected was not considered in the analysis, and the analysis is based on the assumption that travel capabilities of the ten seabird families have not fundamentally changed between 1998 and 2017.

<<<< TABLE 1 here >>>>

Quantifying the travel distance and size of exploited area

First, unrealistic locations were removed based on a species-specific speed filter [50] and PTT data were linearly interpolated to a regular 1 hr interval to reduce differences between GPS and PTT data due to their different temporal sampling resolution [51]. Mean sampling schemes were one location every 17 ± 32 minutes (standard deviation, range 0.5 – 156) for GPS and one location every 65 ± 34 minutes (2.4 – 188) for PTT datasets. Tracking data were then divided into discrete foraging trips either manually or using species- and device-specific cut-off values for minimum distances and durations implemented with standard processing routines [1]. For each foraging trip the maximum distance from the colony (foraging range) and the total travel distance as the sum of all straight-line distances between all subsequent locations were calculated. The median (and range) of these trip characteristics are presented for each species, based on all foraging trips from all colonies and breeding stages, to provide a general overview of travel capabilities across seabird species [52-54]. These summaries were also calculated using just the first trip of any given individual to reduce pseudo-replication [55, 56], but this data reduction did not alter the broad taxonomic pattern (Table S2).

Because single-dimension trip characteristics do not capture the range of directionality across foraging trips from individuals in a colony, the area used by each species at each colony was also quantified. This area was calculated as the minimum convex polygon of 95% of all locations for each tracking dataset and is hereafter referred to as ‘exploited area'. A minimum convex polygon was chosen to encompass less frequently used areas, and 95% of locations were selected to avoid identifying an excessively large area due to some

erratic trips or low-quality location estimates; this approach is deemed appropriate for similarly large-scale taxonomic comparisons [57, 58].

2.2.1. Quantifying the spatial aggregation and size of area with concentrated use

Foraging areas may range from widely dispersed to highly concentrated in a relatively restricted area. First, the 'core area' for each individual was calculated as the 50% kernel utilization distribution, and the extent of overlap between core areas of all individuals of a given species at a colony in a given breeding stage was then quantified. To identify the core area, the scale of the area-restricted search derived from first-passage time analysis was used as the smoothing factor in the kernel density estimator [1, 59, 60]. Because the core area size is dependent on the smoothing factor, and area-restricted search may be difficult to detect for some species or data resolutions [61], an alternative approach was also used in which the smoothing factor was scaled to the median foraging range of a colony. Results from both approaches were highly correlated and did not affect our conclusions (Table S3), and only results from the former approach are presented. The overlap in core areas of individuals was quantified using Bhattacharyya's Affinity index (BA), a non-directional measure of home-range overlap that ranges between 0 (complete separation) and 1 (completely matching probability distributions), and is considered the most appropriate index for quantifying the similarity between utilisation distributions [39, 62]. Because the BA is calculated between pairs of individuals, the BA across all pairwise comparisons was averaged for a given dataset. Individuals for which <10 locations were available were excluded from the estimation of spatial aggregation.

In order to compare the size of the core areas of each population (hereafter 'area of concentrated use'), the 50% kernel utilisation distribution of each individual was delineated, and areas where the 50% kernels of at least 20% of tracked individuals of that population overlapped were identified [1].

To provide a scale of reference for the marine area requirements of seabirds, the sizes of existing marine protected areas were downloaded from the World Database on Protected Areas (www.protectedplanet.net, accessed 15 Aug 2017), and filtered to include only marine and coastal protected areas.

2.3.Assessing representativeness of datasets with varying sample size

Sample size can affect quantitative metrics of space-use based on tracking data [40, 51, 63]. Because datasets ranged from 5 to 119 individuals per colony and breeding stage, the representativeness of each dataset was quantified to characterise the distribution at the level of the colony. Following the approach of Lascelles et al. [1], each dataset was iteratively sub-sampled to randomly select tracking data from 3 to n-1 individuals, where n is the number of individuals tracked in that dataset. During each iteration, the 50% kernel utilisation distribution was calculated from the randomly selected data, and the proportion of the un-sampled locations that fell within the 50% isopleth was assessed. If the proportion of un-sampled locations contained within the 50% isopleth of the randomly selected individuals (hereafter referred to as the 'inclusion value') was ≥50%, then the dataset could be considered representative for the colony because the un-sampled individuals were already properly represented by the sampled individuals [1]. For each simulated sample size of every dataset 30 iterations were performed and the mean inclusion value across the 30 iterations was calculated for each sample size. A non-linear least-squares regression was then fitted to inclusion values to estimate the asymptote of each dataset based on the 30 iterations for each simulated sample size.

The representativeness of each dataset is reported as the proportion of the estimated asymptote that the mean inclusion value of a dataset achieved at the highest sample size. If this representativeness was >70%, a dataset was adequate to describe the space-use of the population [1, 40]. If the non-linear regression could not identify an asymptote due to a singular gradient (i.e. the area expansion had not levelled off with increasing sample size), the mean inclusion value for the largest sample size of that dataset was used. The level of representativeness was then tested for a positive correlation with the number of individuals that had been tracked by calculating the Pearson correlation coefficient. The proportion of datasets for each family where the tracking data were considered not representative for the spatial distribution of a given colony is presented (Table S4).

2.4. Statistical analysis

To examine whether there was evidence for variation in space-use patterns at a higher taxonomic level [64, 65], the effect of seabird family on maximum travel distance from the colony, spatial aggregation (BA), the size of an area of concentrated use, and the size of the exploited area was tested. Generalised linear mixed models that included colony size and the

stage of the breeding cycle as fixed effects were used. These two factors affect the space-use patterns of seabirds [66-68], but the analysis did not aim to investigate the relative importance of these factors and no inference was drawn from those parameters. The sampling rate of the tracking device was also included as a fixed effect because it can affect the extent and shape of home-range areas [51]. In addition, variation at the species and colony level was accounted for by including these two variables as random intercepts to avoid pseudoreplication [69]. Because some datasets had small sample sizes, each dataset was weighted based on the level of representativeness that was attained in the sensitivity analysis to reduce the influence of small and possibly unrepresentative datasets on the overall conclusions.

The data collation of all individual foraging trips was used to test the effect of seabird family on maximum travel distance from the colony. The effect of seabird family on spatial aggregation, the size of an area of concentrated use, and the size of the exploited area was tested at a population level because the latter three measures were calculated for each unique combination of species, colony, and breeding stage.

For each of these four response variables, two models were fitted that differed only by the inclusion of seabird family as a fixed factor in one of the pair of models, while all other fixed and random factors were identical. A likelihood-ratio test was used to infer whether seabird family explained a significant amount of variation in space-use variables that was not already accounted for by other fixed or random effects [70]. All analytical steps were conducted in R 3.4.2 [71], and code to replicate the analyses is provided at https://github.com/steffenoppel/seabirds.

3. Results

Seabird tracking data from 52 species across ten families were collected between 1998 and 2017 in 210 unique combinations of species, colony, and breeding stage (Table S1). The data contained a total of 12,039 distinct foraging trips from 5419 individual birds, with a mean of 21 tracked individuals (range 5 - 119) per dataset, and included >10% of the species in each family that breed in the Atlantic Ocean basin (Table 1).

As expected, seabird species varied enormously in foraging trip characteristics, with single foraging trips ranging from <1 km to >12,000 km (Table 2). There was considerable variation

within species and families in the foraging range, and some of this variation was explained by the breeding stage (Fig. 1). Despite substantial variation among breeding stages, species and colonies, there was clear evidence that foraging range varied at the family level (LR-Test χ^2_9 = 55.57, p < 0.001), with cormorants having the shortest ranges, and albatrosses the largest (Table 2, Fig. 1). This pattern remained equally strong if only a single trip per individual was used in the analysis (Table S2).

<<<< FIGURE 1 here >>>>

Seabirds also varied markedly in the extent to which they congregated at sea. The average Bhattacharyya's Affinity index for a given dataset ranged from virtually no overlap (BA < 0.001 for four datasets; Adélie Penguin *Pygoscelis adeliae*, European Shag *Phalacrocorax aristotelis*, Common Guillemot *Uria aalge*, Tristan Albatross *Diomedea dabbenena*) to very high overlap (BA = 0.91; Magellanic Penguin *Spheniscus magellanicus*). Due to the high variation in overlap among species and between breeding stages, there was no significant variation among families (LR-Test χ^2_9 = 12.22, p = 0.20). For most families there was higher overlap during chick-rearing than during incubation (Fig. 2). Cormorants, gulls and auks had consistently high overlap in both breeding stages, while albatrosses and frigatebirds showed consistently low overlap (Fig. 2).

Owing to variability in travel distance and aggregation, the size of the marine area exploited by seabird populations during the breeding season varied by six orders of magnitude among families (Table 2; LR-Test χ^2_9 = 57.91, p < 0.001), with cormorants and penguins having generally the smallest exploited areas and albatrosses and Great Shearwaters (*Ardenna gravis*) the largest (Table 2).

<<<< FIGURE 2 here >>>>

Low overlap of individual core ranges can frequently lead to unrepresentative tracking data, as the foraging behaviour of untracked individuals is poorly captured by those already tracked. There were 101 (48%) datasets that did not meet the criteria for representativeness

that would be required to designate marine important bird areas following Lascelles et al. (2016), with 100% of the frigatebird datasets (n = 3) and 80% of albatross datasets (n = 20) not representative at the population level. For gulls, penguins and gannets, >60% of datasets were representative (Table S3). There was a positive correlation between the number of individuals tracked and the level of representativeness (r_s = 0.332, p < 0.01, n = 210), and of the datasets that included >50 individuals only three were not representative (all from albatrosses, Fig. S1).

Accounting for the level of representativeness of each dataset, and simulating the size of an area of concentrated use across a range of sample sizes, there was a strong effect of family on the size of areas of concentrated use (LR-Test χ^2_8 = 57.91, p < 0.001). The largest areas of concentrated use were found in albatrosses and gannets, and the smallest in cormorants and gulls, but within each family, the size of the area of concentrated use varied by two to four orders between different species and breeding stages (Fig. 3).

<<<< FIGURE 3 here >>>>

There was a negative correlation between the level of spatial aggregation at sea and the size of the area exploited during the breeding season (r_s = -0.285, p < 0.001, n = 210), resulting in a gradient of space-use that can inform the relevant scales for conservation management (Fig. 4). Species with large ranges generally had low spatial aggregation (bottom right in Fig. 4), and were mostly albatrosses, petrels, shearwaters, storm petrels, frigatebirds and tropicbirds. Short-ranging species were mostly cormorants, auks and gulls, and tended to show higher aggregation at sea (top left in Fig. 4). For most species, tracked birds had smaller ranges and showed greater aggregation during the chick-rearing than during the incubation stage.

<<<< FIGURE 4 here >>>>

4. Discussion

Seabird species range from those that congregate at sea and can be efficiently protected within a small area, to those that disperse widely and range over areas that can encompass

millions of square kilometres. For the study species in the Atlantic Ocean basin, there were consistent differences among families in both maximum foraging range and the size of areas used at sea. Within this spectrum, albatrosses, petrels, storm petrels, frigatebirds, and tropicbirds travelled on average farther and dispersed more widely at sea during the breeding season than cormorants, penguins, auks, and gulls, although there was considerable variation within each family. Although some species may have recently shifted or expanded their foraging ranges due to climate-induced changes in the marine environment [48, 72], these shifts in spatial location are unlikely to be a result of fundamental changes to the species' travel capabilities, and our broad conclusions are therefore robust to climatic changes in the near future.

Our synthesis can be used to identify the management approaches likely to be most effective given the geographic scale over which the threats to a certain species need to be addressed. For some species, this broad-scale information at the family level may be sufficient to implement certain conservation actions without the need for further detailed data on individual movements from a given colony [6, 35, 73]. Some of the widely dispersing species use areas at sea that may be considered too large for the establishment and enforcement of strict marine reserves that ban all economic activity that negatively affect birds and other biodiversity [4, 19, 20]. However, other management approaches that reduce threats such as bycatch in fishing gear or depletion of prey resources can be implemented across very large spatial scales – either within appropriately managed protected areas that regulate rather than ban economic activities, or in the framework of other effective area-based management measures or sustainable-use regulations that apply to large marine regions without the designation of protected areas [74-77]. All management approaches should also consider that not only seabirds, but also their threats may disperse at sea and occur only in certain areas or at certain times. Static structures such as wind turbines or gillnets will affect seabirds only at one location, whereas oil, plastics and other pollutants disperse freely with currents and therefore need to be managed at different spatial scales [5]. Threats from fisheries will only occur where a particular fishery operates, and regulation of such fisheries is most important where fisheries and species vulnerable to interactions co-occur [30]. Hence, multiple management mechanisms addressing various threats in time and space may be required to safeguard particular species.

Our data represent some families better than others, and our results may not be fully representative of species-rich families such as gulls and terns, or storm petrels. For some

families there may also be significant intra-family variation, which our data collation may not capture appropriately: penguins, for example, include both migrant and resident species, but our tracking data encompassed mostly migrant species, which have greater foraging ranges even during the breeding season [78]. Nonetheless, for families that encompass few species, such as the tropicbirds and the frigatebirds, the information provided here is likely more accurate and transferrable than for the gull family which encompasses >40 species in the Atlantic Ocean basin with a diverse range of body sizes and travel capabilities [79, 80]. Because high-resolution GPS tracking devices have only recently become small enough to track small seabirds [81], our data are biased towards larger-bodied species, with many storm petrels, small auks, and diving petrels not yet represented in tracking databases. Hence, while our study is a useful first step towards synthesizing seabird tracking data, there are some knowledge gaps where strategic tracking of certain families and species groups will advance our understanding of the space-use of smaller seabirds in the future.

Besides the incomplete coverage of all species within each family, there was large variation in the number of colonies from which tracking data for a given species were available. Seabird foraging ranges are known to vary within species, with respect to colony size and environmental factors such as ocean productivity and the foraging habitat available within a given radius [56, 66, 82-84]. The inclusion of tracking data from either a very small or a very large colony may therefore have misrepresented the typical space-use of particular species [85]. While such differences need to be considered for the implementation of specific protection measures, our broad scale analysis indicated that the differences in space-use between families were generally larger than differences within species, and our overall conclusions are unlikely to be affected by a few atypical datasets.

Our results also highlight that for some families the space-use patterns vary substantially between incubation and the chick-rearing stage (Figs 1 and 2, Table 2), which may be relevant for seasonal site protection or other dynamic area-based management measures that aim to regulate certain activities during discrete periods [86]. However, some of the apparent variation between breeding stages might be a consequence of varying data coverage and inter-specific differences. For example, among gannets and boobies our results seem to indicate that birds have extremely low spatial aggregation during incubation compared to brood-guard (Fig. 2). This pattern is potentially because the largest gannet in our dataset, the Northern Gannet (*Morus bassanus*), which forages in temperate and productive waters, has mostly been tracked while feeding chicks [87-89], whereas the available data

during incubation were from the smaller, tropical boobies, which forage in less productive waters and may therefore disperse more widely at sea [90-92]. Nonetheless, our data clearly indicate that most seabirds have smaller foraging ranges and show greater aggregation at sea during the chick-rearing than the incubation period, which could be used to inform appropriate management approaches at different times of the breeding cycle.

The dataset and space-use metrics that was collated could also be used with various explanatory variables to understand the causes of variation and predict the likely movement scales of other species of seabirds for which no tracking data exist. Such extrapolations have been applied successfully to different colonies within species [83], but if space-use requirements can also be predicted across species then some conservation management may proceed on that basis rather than await species-specific local tracking data [93, 94]. The generality of the differences found among families could be tested with data from additional species, regions and marine systems, or life-history stages. Nonetheless, researchers considering which seabirds to track for the purpose of improving conservation management are encouraged to first critically examine the value that the collected data will add to existing knowledge [35, 36, 95].

Our review focussed on adult birds during the breeding season to facilitate a broad taxonomic comparison. However, in long-lived seabirds, immature or adult birds not actively breeding may comprise a larger proportion of the total population, and may have fundamentally different space-use patterns and distributions than breeding adults [96-98]. Seabird conservation therefore requires not only the protection of breeding adults, but also of other life stages, which may not occur in the same spatial area. The broad scales of space-use that are summarised here for breeding adults will not be sufficient to evaluate all potential spatial overlaps with threats that may lead to population declines, and further tracking of highly threatened species or different life stages may be required to facilitate effective management [35].

In summary, seabirds are well-known indicators for the health of the marine environment [12-14], and may therefore constitute a useful tool for marine spatial planning. Many seabirds, especially cormorants, penguins, auks, and gulls congregate in certain areas at sea which are useful candidates for area-based management approaches such as marine protected areas. Marine protected areas can be managed in a variety of ways that may permit and regulate certain economic activities, and for marine protected areas of very large size, the

complete exclusion of all economic activities may neither be practical nor desirable [18, 19, 99]. Our results show that some families, especially albatrosses, petrels, storm petrels and highly pelagic tropical species such as frigatebirds and tropicbirds, disperse widely at sea, and require management approaches that are implemented at large scales such as bycatch regulations, compliance monitoring and other fisheries observer programmes, or large-scale spatial and temporal fishing closures.

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