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Title	Assessing the distribution and vulnerability of a seabird community at sea to inform conservation and management
Authors	Critchley, Emma Jane
Publication date	2018
Original Citation	Critchley, E. J. 2018. Assessing the distribution and vulnerability of a seabird community at sea to inform conservation and management. PhD Thesis, University College Cork.
Type of publication	Doctoral thesis
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Download date	2026-10-30 11:44:52
Item downloaded from	https://hdl.handle.net/10468/7822



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Assessing the distribution and vulnerability of a seabird community at sea to inform conservation and management

Thesis presented by

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For the degree of

Doctor of Philosophy

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December 2018

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Declaration

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Emma Jane Critchley

Abstract

Seabirds are an apex predator in marine ecosystems and can be important bio-indicators for informing wider marine conservation and management. They face many threats from anthropogenic activities at sea but the interactions and subsequent impacts can often be difficult to monitor, particularly in pelagic regions. Ireland and Britain in the north-eastern Atlantic Ocean host internationally important numbers of many seabird species. However, there are challenges in assessing their distribution at sea, not least the time and costs involved in trying to do this at the community level. The large territorial waters of both countries also provide significant prospective marine fossil fuels and renewable energy. Therefore, there is the potential for detrimental impacts to seabird populations where hotspots of seabird density overlap with marine energy activity. In this thesis I demonstrate how existing data can be combined to assess the at-sea distribution, vulnerability, and gaps in conservation protection of seabird species at the national scale.

In Chapter 2, I use a distance-weighted, foraging radius approach to predict at-sea distributions (hereafter called foraging radius distributions) for all breeding seabirds in Britain and Ireland, identifying hotspots of highest density and species richness. Relatively simple foraging radius models have the potential to generate predictive distributions for a large number of species rapidly, thus providing a cost-effective alternative to large-scale surveys or complex modelling approaches. I calculate the percentage population coverage from current marine and coastal protected areas (MPAs) for all seabird species using foraging radius distributions. On average, 33% of coastal populations and 13% of pelagic populations overlap with MPAs, indicating that pelagic species, many of which are near threatened or endangered, have significantly less coverage from protected areas than coastal species. In Chapter 3, I test the effectiveness of the foraging-radius approach by comparing foraging radius distributions to empirical distribution data for multiple species taken from biotelemetry studies and aerial surveys. Foraging radius distributions correlate significantly with GPS tracking data for four species at the colony level. At the regional level, foraging radius distributions show mixed results when compared to aerial survey data, but correlate well with auks and terns in particular. In order to assess seabird vulnerability to oil pollution in European waters I develop a new Oil Vulnerability Index (OVI) that updates information on population size and conservation status, as well as accounting for the potential attraction/avoidance of seabirds to offshore infrastructure

(Chapter 4). The OVI scores are applied spatially and overlaid with current offshore petroleum activities to generate maps of seabird vulnerability to oil pollution in the Irish EEZ. Finally, I combine all of the information on seabird distributions, vulnerability to anthropogenic activities, and designated MPAs to carry out a spatial prioritisation analysis for conservation of seabirds in Irish waters (Chapter 5). The results reveal that those areas in the Irish EEZ that are most important for seabird populations and that should be prioritised for conservation, are also the areas that are experiencing the most pressure from anthropogenic activities.

Acknowledgements

Firstly, I would like to thank my supervisors John Quinn and Mark Jessopp for all of their knowledge, advice, and support over the last three and half years. I am extremely grateful for your belief in me, and for all of your efforts to ensure that I could turn what started as a research masters project in to this rather more extensive piece of work! Thank you also to my funders, the Irish Petroleum Infrastructure Programme for recognising the merit in continuing to fund this work beyond its original scope. I am grateful to James Grecian for his input and guidance at the start of this project, much of the initial work would have been a lot more difficult without his help and expertise.

None of the research in this thesis would have been possible without the extensive collection of data by hundreds of people over many decades. The Joint Nature Conservation Committee (JNCC), National Parks and Wildlife Service (NPWS) and Royal Society for the Protection of Birds (RSPB) all provided assistance in obtaining the up to date colony data that was essential for much of my analysis. Much of this data is collected by the generous contributions of many conservation organisations and volunteers across Britain and Ireland. I am also grateful to the NPWS for providing permission for the use of aerial survey data from the ObSERVE Programme, and to all of the observers who collected this. Most importantly, I'd like to thank the UCC seabird research group, Gavin Arneill, Adam Kane, Saskia Wischnewski and Ashley Bennison, for generously sharing their data and for allowing me to tag along on their research trips so I could pretend to be a field biologist for a short time. There's nothing like a week on an uninhabited island surrounded by hundreds of seabirds to remind you of the importance of our work.

To my friends and colleagues in the School of BEES, thank you for making the past few years so enjoyable. Particularly, Adam Kane, Amy Cooke, Darío Fernández-Bellon, Enrico Pirotta, Gavin Arneill, Iván de la Hera Fernández, Louise Archer, Maria Garagouni and Ronan O'Sullivan, long days in the office were never a chore with you lot around.

Finally, thank you to my family for your continued support and understanding as you watched me return to life as a student. Most especially to my Mum, who has proof-read nearly every single word I have ever written – I couldn't have done it without you.

Chapter 1

General Introduction

The first two decades of the 21st century have seen ever increasing awareness of the multitude of threats facing global biodiversity from anthropogenic pressures, as well as the urgent need to tackle them in order to prevent catastrophic losses (WWF, 2018). Extensive efforts have been made to catalogue threats facing terrestrial ecosystems (Hudson et al., 2014), with over-exploitation and habitat loss (mainly driven by human consumption) being the strongest drivers (Maxwell et al., 2016). The status of marine biodiversity, however, is more uncertain due to the difficulty of obtaining robust data in often remote and inaccessible regions. Even so, it is now clear that all areas of the world's oceans have been impacted by multiple, cumulative pressures from anthropogenic activities (Halpern, et al., 2008; Halpern et al., 2015).

Top predators in marine environments, as elsewhere, are disproportionately affected by anthropogenic threats (Maxwell et al., 2013; Sydeman et al., 2006). Seabirds, highly-mobile apex predators in marine ecosystems, are the most threatened of all avian groups globally and populations have declined significantly since the 1950s (Paleczny et al., 2015). The greatest drivers of population declines are mortality due to by-catch in fisheries, introduced mammalian predators and habitat destruction at breeding colonies (Croxall et al., 2012). However, the expansion of anthropogenic activities into ever more remote offshore regions in order to exploit food and energy resources introduces additional threats at sea (see Figure 1.1). The life-history and behaviour of seabirds at sea makes them particularly susceptible to these additional threats (Butchart et al., 2004).

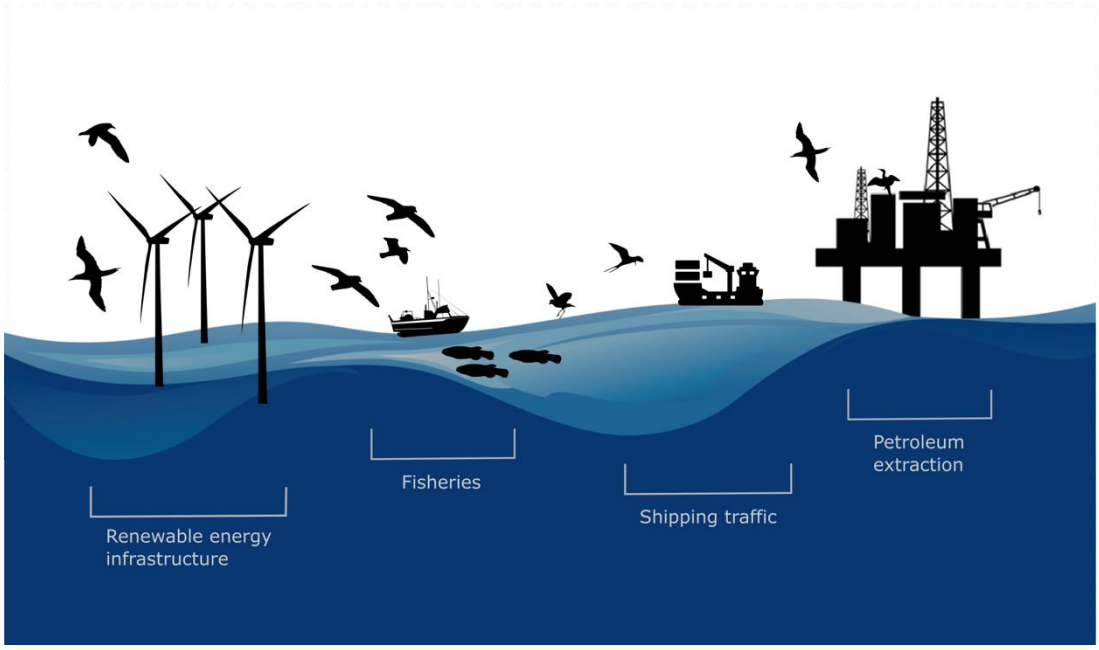


Figure 1.1 The main anthropogenic activities which threaten seabirds at sea.

1.1 Seabird ecology and vulnerability

Seabirds are generally long-lived species with delayed sexual maturity, high annual survival, and low fecundity rates, factors that make them vulnerable to any increases in adult mortality (Ashmole, 1971; Grémillet and Boulinier, 2009; Votier et al., 2005). A good understanding of their distribution at sea is essential to inform any assessments of population vulnerability to anthropogenic threats in the marine environment. All seabird species regularly return to their nest sites during the breeding season, where they become central place foragers living in often very large colonies. However, the distances covered on foraging trips from the colony can vary greatly depending on the species, from less than 1 km to over 12,000 km (Oppel et al., 2018).

Seabird species group into nine taxonomic orders (del Hoya et al., 2014; Furness, 2012; Nelson, 1980; Votier & Sherley, 2017) of which six are found in Britain and Ireland (the region of interest for this thesis). Chapters 2, 3, and 5 of this thesis focus on the core seabird orders of the procellariiforms, suliforms and charadriforms (See Table 2.1, Chapter 2 for a full list of species), whilst Chapter 4 additionally includes the anseriforms, gaviiforms and podicipediforms. The procellariiforms, which include fulmars, petrels, and shearwaters, are some of the furthest ranging species with many birds regularly traveling hundreds of kilometres on foraging trips during the breeding season (Guilford et al., 2008). They are predominantly surface feeders or surface divers and make use of their strong olfactory

senses and 'tube-nose' when foraging (Hutchison and Wenzel, 1980). Suliforms are mainly tropical species and only three species breed in Britain and Ireland. The Northern gannet is a long-ranging plunge diver, whereas the European shag and Great cormorant have shorter foraging ranges and are surface pursuit divers (Ashmole, 1971; Garthe et al. 2000). Multiple species of charadriiformes are found in our study region, with a wide variation in morphology and foraging modes. The seven gull species take advantage of a variety of habitats and are regular foragers on land (Rock et al., 2016). Skuas, the largest species in this group, are also opportunistic foragers and some individuals regularly engage in klepto-parasitism (Andersson, 1976). At the opposite end of the scale in terms of size, terns generally have a more marine lifestyle than gulls. However, whilst they are known to make the longest migration trip of any animal (over 80,000 km, (Egevang et al., 2010)), they have relatively short foraging ranges during the breeding season up to a maximum of about 50 km (Thaxter et al., 2012). Finally, the charadriiformes also includes the auks, of which there are four species breeding in Britain and Ireland. They are generally coastal foragers but have been known to travel distances up to 200 km (Thaxter et al., 2012). Their foraging mode of underwater pursuit, much like that of penguins, has led to reduced wingspan / wing area in comparison to body size for this group (Nelson, 1980). The anseriforms (ducks and geese), gaviiforms (divers or loons), and podicipidiforms (grebe) orders are generally inshore waterbirds whose presence in British and Irish waters increases in the winter months (Kirby et al., 1993; Lawson et al., 2015).

These variations in the foraging mode and patterns of habitat usage lead to different susceptibility to at-sea threats (Bicknell et al., 2013; Furness et al., 2012; Furness and Tasker, 2000; Votier et al., 2005; Wilcox et al., 2015). For example, time spent in contact with the water is dependent on whether species are surface feeders, shallow divers, or deep divers, and heavier-bodied, diving species are particularly susceptible to oil pollution (Camphuysen, 1989). Further differences are observed between short ranging species, such as cormorants and auks that utilise specific coastal features such as sand banks and tidal races (Soanes et al., 2014; Waggitt et al., 2017), and long-ranging species, such as procellariiforms, that are more likely to associate with shelf edges and frontal systems (Cox et al., 2016; Scales et al., 2014; Schneider, 1990), where they might face quite different threats such as by-catch in fisheries (Bradbury et al., 2017).

Outside of the breeding season seabirds are not constrained to return to the land, and as a consequence, species often have quite different distributions, which in turn may modify

their risk of interacting with anthropogenic threats (Wong et al., 2018). Many species either roam widely or undertake long migrations post-breeding (Egevang et al., 2010; Fayet et al., 2017). Large congregations of multiple species occur in important over-wintering areas such as the Mid-Atlantic Ridge and Canary Current Large Marine Ecosystem in the Atlantic Ocean, and along the California Current System in the Pacific Ocean, where birds are attracted to high productivity upwellings (Bennison and Jessopp, 2015; Grecian et al., 2016; Nur et al., 2011). During the non-breeding season seabirds may experience stress and mortality as a result of the energetic costs of migration, susceptibility to winter storms and wrecks, and interaction with fisheries and oil pollution in over-wintering areas (Harris and Wanless, 1996; Montevecchi et al., 2012). However, for the purpose of this thesis I will focus only on distributions during the breeding season. Constraints to return to the breeding colony and raise chicks mean that seabirds are likely to be most vulnerable to anthropogenic pressures during this time, with reduced ability to avoid them. Regularly returning to land exposes birds to interactions with predators and humans at the breeding colony; coastal waters surrounding the colony will have higher densities of fisheries and offshore energy infrastructure; and there is an increase in energetic demand for adults in order to incubate and provision a chick, sustain themselves and commute to and from foraging sites (Croxall et al., 2012; Markones et al., 2010).

1.2 Methods for assessing at-sea distributions

During the breeding season, seabird distribution at sea is influenced by location and abundance of prey, density-dependent competition, and associations with biotic and abiotic habitat features, as well as the location of breeding colonies (Sandvik et al., 2016). Large annual variation in both foraging area and range due to changes in prey availability have been observed for multiple species, indicating that distribution data collected for a single year is unlikely to be representative over a longer time period (Burke and Montevecchi, 2009; Davies et al., 2013; Elliott et al., 2009; Robertson et al., 2014). In order to reduce density-dependent competition around large or close neighbouring colonies, many seabird species are likely to exhibit some form of spatial segregation (Bolton et al., 2018; Sánchez et al., 2018; Wakefield et al., 2013). Once birds move further offshore, and densities decrease, less spatial segregation is observed but species from multiple colonies may still overlap at sites of high productivity (Bolton et al., 2018; Dean et al., 2015). The habitat features which drive this productivity, such as shelf edges and fronts, could provide important explanatory variables for seabird distributions, as some species will rely upon

them as predictable foraging sites (Weimerskirch, 2007). However, other environmental features which may be indicators of high productivity, such as chlorophyll or sea surface temperature, are more dynamic, and strong associations with seabird densities can be hard to find, particularly due to time lags between these proxies of primary productivity and actual foraging conditions (Wakefield et al., 2009).

Variation in the responses to these drivers of distribution, as well as the large distances covered by many seabird species, can make it challenging to assess at-sea distributions and potential interaction with threats, particularly at the community level. Increases in funding and development of technologies have greatly improved the resources available to researchers and conservation practitioners. However, even with recent methodological and analytical advances, biotelemetry and at-sea survey methods can still be extremely costly and time intensive, and can only sample a subset of the population. Furthermore, these methods may not be suitable for all regions, seasons or species - particularly smaller bodied species such as storm-petrels and terns which can be difficult to detect during surveys (Rogan et al., 2018). Here I will give a brief summary of the most commonly used methods for assessing seabird distributions at-sea, some of the potential limitations, and the alternative approach that I will use for this thesis.

Miniaturisation of tracking devices, along with innovations in analysis of tracking data, has greatly increased the collection of telemetry data for seabirds. A tool that was once only available for large bodied species such as albatrosses, has now been applied to some of the smallest seabird species, with tags weighing less than 1 g developed for storm-petrels. However, even with improvements in technology, the high costs of tracking devices still limit their utility. Often a significant amount of effort and resources are needed to capture a representative sample of a population or community over a long time period, especially for species with large ranges (Block et al., 2011; Grecian et al., 2016; Mason et al., 2018). Studies are now beginning to make use of tracking data collected from just a few colonies to model species distributions for an entire region. Recent work on four breeding species in Britain has shown how tracking data from multiple colonies can be utilised to assess habitat preference for a species in a region, which can then be included in a predictive model that also accounts for habitat accessibility for each individual colony (Wakefield et al., 2017). However, habitat associations can not necessarily be applied to other regions, and still provide limited explanation for the distribution patterns observed, with distance to coast

often emerging as the most important explanatory variable in predictive models (Wakefield et al., 2017; Warwick-Evans et al., 2018).

At-sea surveys (either aerial or ship based) have the scope to obtain data on all or most seabird species in a community whilst also covering much greater areas than tracking studies. The two approaches are often complementary (Lascelles et al., 2012), with recent ship surveys corroborating findings from tracking studies that suggested areas of high seabird species richness and abundance at the mid-Atlantic Ridge (Bennison and Jessopp, 2015). At-sea surveys are an established approach that have been widely used to inform marine spatial planning at multiple scales (Kober et al., 2010; Lambert et al., 2017; Smith et al., 2014). However, restrictions due to time, feasibility, and costs mean that data are generally collected at a coarser resolution than GPS tracking or over much longer time periods. Often this data is obtained from surveys conducted from vessels of opportunity and therefore tends to be spatially and temporally patchy, for example the European Seabirds at Sea database which spans over 40 years (Dunn, 2012). This leads to considerable challenges when combining data for distribution modelling, as populations may have experienced considerable change in the intervening period, and distribution varies seasonally and annually depending on environmental conditions (Burke and Montevecchi, 2009; Robertson et al., 2014).

Given these limitations, predictive distribution modelling is likely to be a more cost effective and realistic approach for assessing the distribution of multiple seabird species within a region, or indeed, an entire seabird community. However, multiple models can often predict different spatial hotspots whilst having relatively similar explanatory power, and therefore the use of ensemble models has been suggested as a more suitable approach (Lavers et al., 2014; Oppel et al., 2012). An alternative to more complex modelling approaches is the foraging radius method, which can allow for rapid assessment of species' distribution during the breeding season, and may be particularly useful in cases where empirical data is limited (BirdLife International, 2010a; Ronconi et al., 2012; Soanes et al., 2016; Thaxter et al., 2012). The method uses a foraging radius model to predict the occurrence of birds within the at-sea area surrounding a colony, up to a set colony-centred radius. Distributions are distance-weighted with a decay function so that areas closest to the colony are of highest importance. This approach is supported by results from multiple studies which have shown the importance of distance to colony as an explanatory factor for species presence or density at sea (Ford et al., 2007; Skov et al., 2008; Warwick-Evans et al.,

2018). The foraging radius method has been used to assess the distribution of a number of individual species including gannets and penguins (Grecian et al., 2012; Pichegru et al., 2010), and is now starting to be applied to entire seabird communities (Afán et al., 2018; Chapter 2). The continued publication of summary data from GPS tagging studies ensures that the best available data on species specific foraging ranges can be utilised in the foraging radius models (Jovani et al., 2015; Oppel et al., 2018; Thaxter et al., 2012). However, the basic method may require the addition of other habitat associations to make it applicable for some species e.g. those with very specific habitat associations such as shallow sand bars and tidal streams (Soanes et al., 2016).

1.3 Seabird vulnerability to oil pollution

Contamination due to oil pollution poses a serious threat to seabirds given their predominantly marine lifestyle, but is relatively understudied compared to other anthropogenic threats. Large spills, like the Deep Water Horizon disaster in 2010, have the capacity to devastate populations of vulnerable species in a matter of weeks or months (Haney et al., 2017). Although exact numbers can be hard to quantify, approximately 250,000 birds are estimated to have been killed by the Exxon Valdez spill (Piatt and Ford, 1996), and as many as 670,000 as a consequence of Deep Water Horizon (Haney et al., 2014). Although large tanker spills and well blow-outs can garner huge amounts of public and media attention, the remote location of many smaller spills means that seabird mortality often goes unnoticed. Furthermore, the dynamic nature of the marine environment makes predicting the potential impacts of future spills even more challenging, although increasingly powerful satellite technology and predictive models are becoming available.

Contact with oil is generally fatal for seabirds, and almost all oiled birds that are found alive will still subsequently die, even when brought to rehabilitation centres (Piatt and Ford, 1996; Sharp, 1996). Physiological impacts that lead to mortality include direct effects such as impairment of thermoregulation, flight, diving, and feeding behaviours (Helm et al., 2015; Jenssen, 1994; O'Hara and Morandin, 2010). Ingestion of oil when preening can also cause secondary effects, including immuno-suppression (Briggs et al., 1996) and disruption of endocrine function (Troisi et al., 2016). Even handling of birds during rescue and rehabilitation efforts causes additional stress which can add to overall mortality (Briggs et al., 1996). Rapid action is needed immediately following a spill to reduce the number of birds impacted, as most mortality occurs in the first two months (Piatt and Ford, 1996).

Given the severity of any contact with oil, even small scale discharges can cause significant mortality (Burger, 1993) and regular small spills have similar cumulative impacts to the less frequent large scale spills (Camphuysen, 1989; Fox et al., 2016).

Trends in oiling rates have been closely monitored in a few sites, and results from beached bird surveys in the North Sea suggest that rates of seabird mortality from oil pollution have dropped considerably in recent decades (Camphuysen, 2010). However, the transferability of these results to other regions is uncertain. It should be noted that the smallest declines in oiling rates were seen for offshore species, whose foraging ranges often overlap with intensively used shipping lanes. These areas pose considerable sources of oil pollution, and satellite data have revealed visible slicks around major shipping lanes in the North Sea (Camphuysen, 2010).

The expansion of petroleum exploration to more remote and unstable environments hugely increases the challenges involved in preventing spills and subsequently containing them, particularly in areas beyond national jurisdiction (Kark et al., 2015; Merrie et al., 2014). Oil and gas activities in the North East Atlantic are expanding into deeper waters in the wider Atlantic and northwards into the Arctic (OSPAR Commission, 2009). Most recently on the other side of the Atlantic, oil production in storm conditions resulted in a spill of an estimated 250,000 litres of oil off the coast of Newfoundland in Canada (The Guardian, 2018).

There is a need for consistent methodology to inform marine spatial planning prior to petroleum exploration licences being granted in regions important for seabird populations. Vulnerability indices can allow assessment of the species likely to be most at risk of contamination due to factors that influence habitat usage, individual behaviour, and population susceptibility to mortality. Whilst recent vulnerability indices have been compiled to assess risks to seabirds from marine renewables industries (Bradbury et al., 2014; Furness et al., 2013, 2012; Garthe and Hüppop, 2004; Kelsey et al., 2018; Wade et al., 2016), the only oil vulnerability index was developed in 1995 (Williams et al., 1995) and is in need of updating. These indices can be applied to seabird distributions to assess spatial vulnerability in a region, which can subsequently by overlaid with locations of marine energy infrastructure to assess exposure risk.

1.4 Marine protected areas for the conservation of seabirds

Protected areas are a vital conservation tool for protecting biodiversity from anthropogenic threats, and meeting international conservation targets. Globally, protected area coverage of the most important sites for some species has slowed increases in extinction risk over recent decades, and targeted expansion of these networks would help to improve biodiversity trends (Butchart et al., 2012). Whilst nearly 13% of the world's land surface has been designated as protected areas, progress towards the implementation of marine protected areas is much slower with global coverage reaching just over 4% (UNEP-WCMC and IUCN, 2016). The costs and challenges of identifying biodiversity hotspots are prohibitive for many marine regions, which is contributing to a delay in designating MPAs, particularly in the pelagic ocean (Game et al., 2009).

Ideally, selection of priority areas for seabird MPAs would follow a multi-species and multi-colony approach to identify areas of greatest importance (Ballard et al., 2012; Hooker et al., 2011; Nur et al., 2011; Ronconi et al., 2012). However, quantitative multi-species applications to identify priority landscapes (either marine or terrestrial) at the national scales have been limited due to insufficient species distribution or habitat data (Moilanen et al., 2005). In the case of avian communities, Important Bird Areas (IBAs) identified as part of the BirdLife International IBA programme provide a valuable resource for the initial scoping of protected areas. IBAs now form the basis of most protected area networks globally (BirdLife International, 2010b), and have proven to be effective in protecting other vertebrate species (Kukkala et al., 2016). IBAs are sites identified as important for the survival of a species or group of species based on a number of population threshold criteria (e.g. if a site holds > 1% of the global species population). The success of the approach in terrestrial ecosystems, particularly in Europe, has led to it being extended to inform the selection of MPAs, and 59% of marine IBAs in Europe are now protected (BirdLife International, 2014).

The identification of IBAs sometimes requires limited collection of empirical data as they can be identified based on existing knowledge of the foraging range and behaviour of a given species, using the foraging radius approach to generate foraging radius distributions. This is an approach recommended by BirdLife International to aid the subsequent implementation of MPAs for seabirds (BirdLife International, 2010a), and a number of recent reviews on seabird foraging ranges have greatly increased its feasibility (Jovani et al., 2015; Oppel et al., 2018; Thaxter et al., 2012).

It is essential that additional information beyond just species distributions is included in the identification of candidate MPAs. If we are to follow the principles of spatial conservation prioritisation MPA networks should be representative of all biodiversity in the region, adequate for the persistence of all species, and cost-efficient to meet conservation targets whist minimising socio-economic costs (Kukkala and Moilanen, 2013). The only way to achieve this is through the inclusion of data on anthropogenic activities, and knowledge of their potential impacts on biodiversity, in the spatial prioritisation assessment (Brown et al., 2015).

1.5 Study region

This thesis focuses on the seabird populations of Britain and Ireland, a region that supports breeding populations of 25 different species (See Chapter 2, Table 1 for full list) including some of international importance, such as the Manx shearwater (*Puffinus puffinus*) and European storm-petrel (*Hydrobates pelagicus*) (Mitchell et al., 2004).

The mainland of Britain and Ireland are surrounded by multiple smaller and often uninhabited islands that make ideal locations for seabird breeding colonies. This, coupled with vast coastal cliff habitat, ensures that seabird populations in the region are not constrained by availability of breeding sites. Furthermore, their position on the north east edge of the Atlantic Ocean provides a diverse array of foraging habitats from shallow estuaries and bays in the Irish Sea to the deep pelagic waters on the edge of the continental shelf. The breeding populations are relatively well studied compared to other regions of the globe, with national seabird censuses undertaken approximately every fifteen years as part of the Seabird Monitoring Programme (Mitchell et al., 2004), along with an extensive collection of biotelemetry and at sea survey data for many species (Dunn, 2012; Jessopp et al., 2018; Kober et al., 2010; Rogan et al., 2018; Wakefield et al., 2017). As a result, it provides an ideal region to test methods that may be readily utilised in more data poor regions of the globe, as I do here for the foraging radius method. This research is significant given that some of the most important global hotspots of seabird species richness are often those with poorest data coverage, particularly in the South East Atlantic and South West Pacific (Kot et al., 2010; Lascelles et al., 2016; Mott and Clarke, 2018).

Nevertheless, the extensive knowledge of seabird populations and distributions in Britain and Ireland has not yet been translated into sufficient conservation actions. Under the European Union legislation (Council Directive 92/43/EEC on the conservation of natural

habitats and of wild fauna and flora, and Directive 2009/147/EC on the conservation of wild birds) both the UK and Ireland are required to designate networks of protected areas (e.g. Natura 2000 sites) for the conservation of birds. The most recent assessment on the progress of designation of marine IBAs as Natura 2000 sites in the EU found that both the UK and the Republic of Ireland were lagging behind many other countries in their protection of national seabird populations (BirdLife International, 2014). The Natura 2000 site implementation status for both Ireland and the UK were assessed as poor, with less than 1% of the marine area within each of the exclusive economic zones protected. This also falls very short of the Aichi Biodiversity Target 11 to protect 10% of the world's oceans by 2020 (Secretariat of the Convention on Biological Diversity, 2014). Although important breeding colonies are designated for a number of key species (e.g. Roseate tern (*Sterna dougallii*) on Rockabill Island) continued breeding failures and population declines demonstrate that land based conservation is not sufficient (Grémillet and Boulinier, 2009; Wanless et al., 2007).

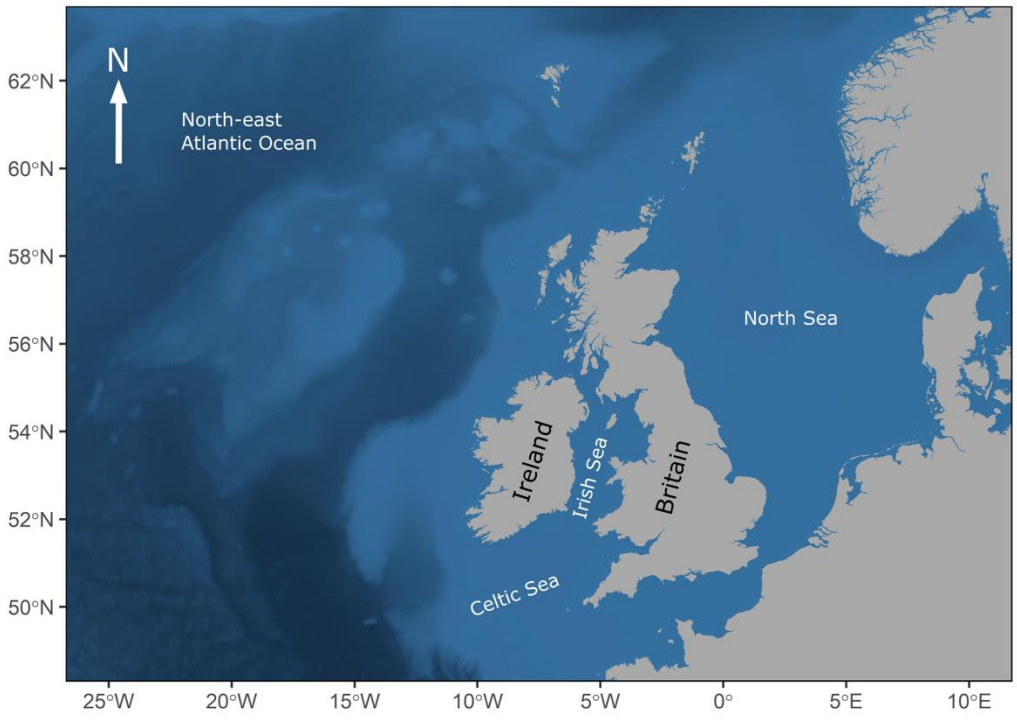


Figure 1.2 Map showing study region and location of key marine areas. The blue gradient shows bathymetry in the region, with darker blue indicating deeper waters, and lighter blue indicating shallower continental shelf waters.

1.6 Thesis aims and structure

This thesis aims to 1) develop a replicable foraging radius model to predict the distribution of a breeding seabird community at sea; 2) assess the suitability of the approach by comparing it to extensive GPS tracking and at-sea survey data; 3) develop a new oil vulnerability index which can be modified and applied to any breeding seabird population globally, and highlight areas of greatest risk to enable better decision making; and 4) utilise information on the distribution of a seabird community to assess its overlap with current protected areas, and identify priority areas for cost-effective conservation planning.

In **Chapter 2** I aim to apply the foraging radius method to predict the distribution of all seabird species breeding in Britain and Ireland, making use of readily available data on colony population sizes and species' foraging ranges. I will combine individual species distribution maps to identify hotspots of density and species richness in the region, and assess overlap of distributions with current marine protected areas at a species, family and foraging range group (coastal or pelagic foragers) level. This chapter aims to provide a replicable method suitable for assessing the distribution of seabirds in data-poor regions.

In **Chapter 3** I aim to assess the accuracy and utility of foraging radius distribution models by comparing foraging radius distributions to extensive empirical data from biotelemetry studies and aerial surveys. I will investigate agreement between foraging radius models and empirical distribution data at two scales; that of the species/colony level using GPS tracking data from species with short, medium and long foraging ranges; and at a community/regional level using aerial survey data.

In **Chapter 4** I aim to develop a new Oil Vulnerability Index (OVI) and apply it to breeding seabirds in Britain and Ireland. The OVI will utilise up to date information on population size and conservation status of seabirds in the region, as well as account for the potential attraction/avoidance of seabirds to offshore infrastructure. I will then assess the spatial distribution of oiling risk by applying OVI scores to distributions of seabirds and offshore petroleum activities.

In **Chapter 5** I will combine all of the information from the previous chapters to carry out a spatial prioritisation analysis for the conservation of seabirds in Irish waters. I will assess various scenarios, considering both existing MPAs, and intensity of anthropogenic activities in the region, and demonstrate how the inclusion of cost layers in spatial prioritisation assessments can change the areas selected for the most effective conservation planning.

In **Chapter 6** I will bring together the main findings of my thesis, discuss the implications for conservation of seabird populations both in Ireland and globally, and suggest areas for further study.

1.7 Additional Work

In addition to the chapters enclosed in this thesis, I have also been involved in the following research during my studies:

Jessopp, M., Mackey, M., Luck, C., Critchley, E., Bennison, A, and Rogan, E. (2018). The seasonal distribution and abundance of seabirds in the western Irish Sea. *Department of Communications, Climate Action and Environment, and National Parks & Wildlife Service, Department of Culture, Heritage & the Gaeltacht, Ireland.* 90pp

Arneill, G., Critchley, E.J., Wischnewski, S., Jessopp, M.J., and Quinn, J.L. (2018) Flight paths rather than nest density shape the biophonic component of a seabird colony soundscape. *IBIS* – In review.

Chapter 2

Marine Protected Areas show low overlap with foraging radius distributions of seabird populations in Britain and Ireland

Authors: Emma Jane Critchley, W. James Grecian, Adam Kane, Mark J. Jessopp & John L. Quinn

Author contributions: The study was designed by E.J.C., A.K., M.J.J, and J.L.Q.; E.J.C. carried out the data collection and analysis, with contribution from W.J.G. for the foraging radius method; E.J.C. led the writing of the chapter with contributions from all authors.

This chapter is published in Critchley, E.J., Grecian, W.J., Kane, A., Jessopp, M.J., Quinn, J.L., 2018. Marine protected areas show low overlap with projected distributions of seabird populations in Britain and Ireland. *Biological Conservation*. 224, 309–317.

2.1 Abstract

Marine Protected Areas (MPAs) are an important tool for the conservation of seabirds. However, mapping seabird distributions using at-sea surveys or tracking data to inform the designation of MPAs is costly and time-consuming, particularly for far-ranging pelagic species. Here we explore the potential for using predictive distribution models to examine the effectiveness of current MPAs for the conservation of seabirds, using Britain and Ireland as a case study. A distance-weighted foraging radius approach was used to project distributions at sea for an entire seabird community during the breeding season, identifying hotspots of highest density and species richness. The percentage overlap between distributions at sea and MPAs was calculated at the level of individual species, family group, foraging range group (coastal or pelagic foragers), and conservation status. On average, 32.5% of coastal populations and 13.2% of pelagic populations overlapped with MPAs, indicating that pelagic species (many of which are threatened) are likely to have significantly less coverage from protected areas. We suggest that a foraging radius approach provides a pragmatic and rapid method of assessing overlap with MPA networks for central place foragers. It can also act as an initial tool to identify important areas for potential designation. This would be particularly useful for regions throughout the world with limited data on seabird distributions at sea and limited resources to collect this data. Future assessment for marine conservation management should account for the disparity between coastal and pelagic foraging species to ensure that wider-ranging seabirds are afforded adequate levels of protection.

2.2 Introduction

Even though most of the world's oceans continue to be impacted by humans (Game et al., 2009; Halpern, et al., 2008), just over 4% of their area is currently protected (UNEP-WCMC and IUCN, 2016). There is an urgent need to speed up the identification and designation of Marine Protected Areas (MPAs) given that one of the Aichi Biodiversity Targets (11) is to protect 10% of the oceans by 2020 (Secretariat of the Convention on Biological Diversity, 2014; Watson et al., 2014). Seabirds provide an important focus for the development of protected areas. As is true for all marine top-predators, they are threatened by a suite of impacts, particularly from fisheries and pollution, and are in urgent need of protection in many parts of the world (Croxall et al., 2012). The use of Important Bird Areas (IBAs) to delineate candidate MPAs for the conservation of seabirds globally has been encouraged by conservation bodies (BirdLife International, 2010b; Lascelles et al., 2012). In the European Union (EU), as of 2014, 59% of areas identified as marine IBAs have been designated as either Special Protection Areas (SPAs) or Special Areas of Conservation (SACs) (BirdLife International, 2014). However, only 3.9% of the total EU marine area is designated for marine SPAs, similar to global levels of coverage, and much lower than the 12.5% designated for terrestrial SPAs (Ramirez et al., 2017). One of the reasons that designation of MPAs in Europe and elsewhere has been slow is that the costs and challenges of identifying biodiversity hotspots are prohibitive for many marine regions. In this paper we develop a simple modelling approach that can be used to quickly identify areas of importance for seabird communities, and assess coverage by existing protected areas.

Protected areas for seabirds usually focus on the locations of important breeding colonies, either at the nesting sites themselves or through seaward extensions in the waters immediately surrounding the colony (BirdLife International, 2010b). The use of IBAs based on short-range colony extensions works well for coastal foragers (McSorley et al., 2003; Wilson et al., 2009) – especially when individual colonies hold a high proportion of the total population – as the designated protected areas often encompass the majority of the colony's range. These coastal MPAs, however, are less effective for protecting pelagic species, whose ranges cover large areas, often crossing national boundaries (Game et al., 2009; Grémillet and Boulinier, 2009; Hyrenbach et al., 2000). At the same time, pelagic species are more threatened than coastal species, and many of the greatest threats, such as by-catch, occur in feeding grounds offshore (Croxall et al., 2012). Designation of MPAs in these areas, using a multi-species and multi-colony approach, can help ensure appropriate

conservation management practices are put in place (Ballard et al., 2012; Nur et al., 2011; Ronconi et al., 2012).

Ideally identifying important areas for seabirds should be done with empirical data since foraging areas are patchy and difficult to locate, especially for pelagic species. For example, recent work has identified multiple global hotspots for pelagic species using existing tracking data (Lascelles et al., 2016). In general, however, tagging studies rarely collect information from more than one or two colonies or species at a time (but see Dean et al., 2015 and Wakefield et al., 2017), and data is generally only collected for a limited time span within seasons, across seasons, and across years. Large-scale studies of multiple species from multiple colonies take a long time and enormous resources (Block et al., 2011; Grecian et al., 2016). Furthermore, although empirical data from aerial and ship surveys are highly valuable, even the European Seabirds at Sea database (amassing data from over 35 years) contains large gaps in coverage (Dunn, 2012; Stone, 1995). Replication within areas over time is limited and yet foraging areas can shift from year to year (Robertson et al., 2014), variability that is likely to increase with climate change (Grémillet and Boulinier, 2009). In many circumstances, therefore, predictive distribution modelling is likely to be a more cost effective and realistic approach for identifying biodiversity hotspots at an ecosystem level.

In recent years, an approach using colony census data together with foraging ranges of seabirds, who are central place foragers during the breeding season, has been used to identify hotspots for individual species (Grecian et al., 2012; Soanes et al., 2016; Thaxter et al., 2012). Predicted distributions from these models correlate well with GPS tracking and at-sea survey data for northern gannets (*Morus bassanus*) in Britain and Ireland (Grecian et al., 2012), and six other species globally (Soanes et al., 2016). Use of the method led to designation of the first MPA in Namibia for African penguins (*Spheniscus demersus*) (Ludynia et al., 2012). The foraging range approach is one of the recommended methods for identifying marine IBAs (BirdLife International, 2010a), and may be particularly useful in regions where distribution data is lacking and the cost of at-sea surveys would be prohibitive, such as the South East Atlantic or South West Pacific (Kot et al., 2010). This relatively simple method predicts a baseline distribution which can then be further refined using data on species specific foraging behaviours or other ecological factors to identify concentrated patches. However, it has yet to be applied on a large regional scale, for multiple colonies or for multiple species.

In this study we use the foraging range approach to produce foraging radius distributions for all seabird species breeding in Britain and Ireland, identifying potential hotspots of high abundance. We then assess overlap with marine protected areas at a species, family and foraging range group (coastal or pelagic foragers) level. The location of at-sea distribution hotspots will vary according to colony location and we hypothesise that the level of coverage by protected areas will be higher for coastal species, which would be better covered by seaward colony extensions than pelagic species. Finally, we discuss the validity and potential for using the foraging range approach globally.

2.3 Methods

Data collation

Open-access data for all seabird species breeding in Britain and Ireland were used to generate foraging radius distributions (see Table 2.1). Data on colony locations and population sizes were extracted from the Joint Nature Conservation Committee (JNCC) Seabird Monitoring Programme (SMP) Database [at www.jncc.gov.uk/smp] to create individual data sets for the 25 species that breed in Britain and Ireland. Most colonies have been counted at least as recently as the Seabird 2000 survey (Mitchell et al., 2004), however colony counts for some species were incomplete and were supplemented with information from BirdWatch Ireland and Royal Society for the Protection of Birds (RSPB) annual reports where available (Burke et al., 2012; Daly et al., 2015; Doyle et al., 2015). In the final dataset used for this study ~3% of colonies have not been censused in the last 30 years, these are all mainly colonies in remote regions. Additional colony data for locally threatened species (e.g. roseate tern) were provided with the permission of RSPB, however these distributions are not included here due to the sensitive nature of the data.

Maximum foraging range estimates were taken from reviews (Jovani et al., 2015; Thaxter et al., 2012), and more recent studies (Kane, A. Pers. Comm.; Thaxter et al., 2013; Wakefield et al., 2013) (see Table 2.1). The best available estimate was taken for each species, either from direct (e.g. GPS tracking), indirect (e.g. time-activity data loggers) or survey data (boat, aerial, or land-based). In general, values for foraging range obtained from direct and indirect estimates do not vary significantly (Camphuysen et al., 2007; Thaxter et al., 2012) suggesting that where tracking data is not available other methods can provide useful estimates of foraging ranges. Maximum foraging range was used to ensure that all potential usage areas were accounted for, even though densities of birds at the edge of the ranges would be very low. Whilst some studies using the foraging radius approach have used the mean of all maximum foraging ranges, maximum foraging ranges from multiple colonies are not available for all species in Britain and Ireland. In reality maximum distances are likely to vary quite a lot around the coasts and the use of the maximum recorded foraging range here is a conservative way to incorporate all of this variation. The validity of this approach is considered further in the discussion, including selected post hoc analyses using mean maximum foraging ranges.

Table 2.1

Summary for each species of the number of colonies in Britain and Ireland; total population size (individuals) from most recent colony counts; European conservation status; proportion of the European population contained in Britain and Ireland (%); maximum foraging range (km); and foraging range group (pelagic or coastal). European conservation status is taken from the IUCN Red List of Threatened Species (Choudhury et al., 2016). European population size was taken as the maximum estimate from the IUCN (Choudhury et al., 2016). The proportion estimated is therefore the minimum potential percentage of the biogeographical population contained in Britain and Ireland. Maximum foraging range was taken from a review by Thaxter et al., (2012) with a few exceptions, see table footnotes. Species with a maximum foraging range of less than 75 km were defined as coastal and those with a maximum foraging range of 75 km or greater were defined as pelagic.

Species	Number of colonies	Population size (individuals)	European conservation status	Proportion of European population	Maximum foraging range (km)	Foraging range group
Arctic skua *Stercorarius parasiticus*	643	4740	Least concern	4.23	75	Pelagic
Arctic tern *Sterna paradisaea*	959	116472	Least concern	6.43	30	Coastal
Atlantic puffin *Fratercula arctica*	405	869690	Endangered	7.50	200	Pelagic
Black guillemot *Cepphus grylle*	1323	38529	Least concern	5.19	15[c]	Coastal
Black-headed gull[a] *Larus ridibundus*	415	184240	Least concern	7.44	40	Coastal
Black-legged kittiwake *Rissa tridactyla*	538	704028	Vulnerable	15.96	120	Pelagic
Common guillemot *Uria aalge*	506	1271624	Near threatened	41.56	135	Pelagic
Common gull[a] *Larus canus*	1330	48110	Least concern	4.76	50	Coastal
Common tern[b] *Sterna hirundo*	376	35468	Least concern	3.11	30	Coastal
European shag *Phalacrocorax aristotelis*	1238	61798	Least concern	39.36	17	Coastal
European storm-petrel *Hydrobates pelagicus*	107	178138	Least concern	17.29	336[d]	Pelagic
Great black-backed gull *Larus marinus*	2010	36528	Least concern	13.73	60[c]	Coastal
Great cormorant[b] *Phalacrocorax carbo*	290	27084	Least concern	3.00	35	Coastal
Great skua *Stercorarius skua*	700	16016	Least concern	46.42	219	Pelagic

Herring gull[a] *Larus argentatus*	2633	278340	Near threatened	17.82	92	Pelagic
Leach's storm-petrel *Oceanodroma leucorhoa*	16	96714	Least concern	17.68	120	Pelagic
Lesser black-backed gull[a] *Larus fuscus*	907	180790	Least concern	26.79	181	Pelagic
Little tern *Sterna albifrons*	63	3424	Least concern	3.23	11	Coastal
Manx shearwater *Puffinus puffinus*	43	658798	Least concern	83.92	330	Pelagic
Mediterranean gull[a] *Larus melanocephalus*	16	1026	Least concern	0.16	20	Coastal
Northern fulmar *Fulmarus glacialis*	2643	1075514	Endangered	15.36	580	Pelagic
Northern gannet *Morus bassanus*	27	576088	Least concern	42.05	709[e]	Pelagic
Razorbill *Alca torda*	679	178773	Near threatened	17.53	95	Pelagic
Roseate tern *Sterna dougallii*	5	3060	Least concern	52.76	30	Coastal
Sandwich tern *Sterna sandvicensis*	64	34166	Least concern	11.58	54	Coastal

[a] Gull colonies that were located at a distance of greater than 5 km from the coast were classified as inland, following criteria set out by Mitchell et al. (2004) and excluded from analysis.

[b] For common tern and great cormorant a number of colonies were located at a distance inland greater than the maximum foraging range; these were excluded from analysis.

[c] Maximum foraging range taken from review by Jovani et al. (2015).

[d] Maximum foraging range taken from unpublished GPS tracking data from High Island, Co. Galway, Ireland (Kane, A., Pers. Comm.).

[e] Maximum foraging range taken from Wakefield et al. (2013).

Generating foraging radius distributions

Using the steps below, and as set out in Figure A.1 in the supplementary information, foraging radius distributions for individual colonies were generated following a similar process to Grecian et al. (2012). Maps of colony locations and population size can be seen in Figure 2.1a for sample coastal and pelagic species, and in the supplementary information for all species. The distribution maps are plotted on a 5 x 5 km grid and show the number of individuals predicted to occur in each grid square, if 50% of the colony is foraging at-sea at a given time. This accounts for the assumption that on average, one half of a breeding pair will remain at the nest at any one time (e.g. during incubation and early chick rearing). The proportion of the population at sea (and subsequent numbers of birds in each grid square) at any one time will vary with both time of day and season. However, the relative importance of each grid square will remain the same and the same hotspots will be identified.

Step 1: Create a grid surface (5 x 5 km grid) where values in each grid square represent the distance from the focal colony.

Step 2: Plot colony centred radii based on maximum foraging range for each species. Any land occurring within the foraging area is excluded to define the total available foraging area for the colony. Birds were assumed to only travel over sea, and therefore land was made too expensive to cross in the model. Maximum foraging range was used to ensure coverage of the majority of a colony's foraging area. However, it can be assumed that due to additional behaviours the individuals from a colony will not be spread evenly across this area, and steps 3 and 4 correct for this.

Step 3: Invert and normalise the grid square values, so that they all have a value of between 0 and 1 with the highest values being found closest to the colony. These values are now the probability of a bird occurring in a given grid square, with probability decreasing linearly as distance from colony increases.

Step 4: Weight values in each grid square by the inverse log distance from the colony. This weights the areas closer to the colony of higher importance to account for non-foraging behaviours such as washing/preening or rafting (Wilson et al., 2009).

Step 5: Normalise values so that the sum of all grid squares is equal to 1 i.e. 100 % of the at-sea population.

Step 6: Multiply proportions in each grid square by the total at-sea population (e.g. 50% of the breeding population). This generates the predicted number of individuals occurring per grid square.

These steps were repeated for each individual colony and the distributions were then summed to generate a foraging radius distribution map for the entire region (e.g. Britain and Ireland). A number of colonies in the dataset were located at a further distance inland than the reported maximum foraging range, therefore at-sea distributions were not created for these colonies. Most of these colonies were gulls (see Table 2.1 for specifics) and can be presumed to be mainly foraging over land (Rock et al., 2016). Table 2.1 contains details of all of the coastal colonies included in the analysis.

Distributions were summed across species to assess the overall distribution of all species collectively, as well as eight family groups (e.g. terns, gulls, see Appendix B for full list) and two foraging range groups (coastal vs. pelagic foragers). For the purpose of this study species with a maximum foraging range of less than 75 km were defined as coastal and those with a maximum foraging range of 75 km or greater were defined as pelagic. There is no clear bimodal distinction between the two groups, however a cut off of 75 km generates groups of comparable size (Coastal = 12; Pelagic = 13). The groupings also reflect the foraging ecology of the species, with terns, cormorants and most gulls in the coastal group and species such as gannet and Manx shearwater that are known to occur well off-shore in the pelagic group.

In order to assess species richness from the grouped distribution, the number of species occurring within each grid square was calculated.

Calculating protected area overlap

Coverage of protected areas for individual species was quantified by calculating the percentage of the at-sea population estimated to occur within the spatial boundaries of a protected area. Spatial data for the boundaries of all protected areas with marine components in Britain and Ireland were obtained from the World Database on Protected Areas (IUCN and UNEP-WCMC, 2016). These were then split into three types: (1) Special Protection Areas (SPAs); (2) OSPAR convention (Convention for the Protection of the Marine Environment of the Marine Environment of the North-East Atlantic) MPAs; and (3) all protected areas (PAs) combined (also including SPAs and OSPAR MPAs). This allowed a comparison between protected area types which often include seabirds as their

designation criteria to meet EU requirements (SPAs which are specifically for protection of birds and OSPAR MPAs which are designated for a wider range of taxa) and all other protected area types recognised in Britain and Ireland. All individual protected area polygons were merged to generate one polygon for each type (e.g. one polygon for all SPAs) to avoid double-counting birds that occurred in grid squares where protected areas overlap.

A Wilcoxon rank sum test was used to assess the difference in percentage overlap for (1) foraging group (coastal or pelagic) and (2) conservation status (Least Concern or Near Threatened and above). These comparisons were carried out for percentage overlap of SPAs, OSPAR MPAs and all PAs combined. All analyses were carried out in R version 3.2.1 (R Developement Core Team, 2016). Maps of the distributions were created using the R package 'ggplot2' version 2.00 (Wickham, 2016).

2.4 Results

Foraging radius distributions for all seabird species breeding in the UK and Ireland individually (Figure 2.1b for a sample of species, and supplementary information for all species) and in family groups (Figure 2.1c for a sample of family groups, and supplementary information for all family groups) were generated. The distributions generated show the average number of individuals per 5 x 5 km grid cell predicted to be at-sea during the breeding season.

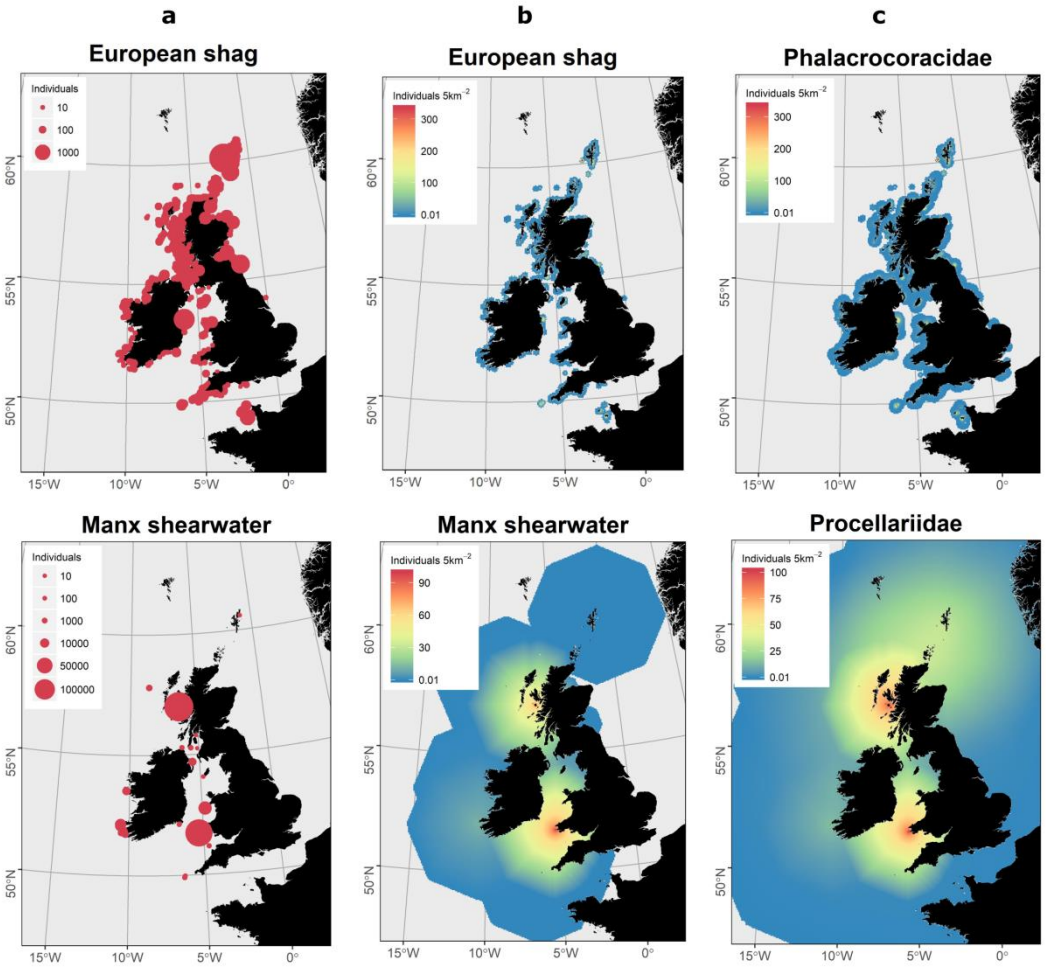


Figure 2.1 Maps for example coastal (Phalacrocoracidae) and pelagic (Procellariidae) family groups occurring in Britain and Ireland showing a) colony location and population size for a sample species, b) foraging radius distributions for a sample species, and c) foraging radius distribution for the family group. Maps for all species and groups can be found in Figures A.1, A.2 and A.3 in the appendix. Details of the species contained within each family group can be found in Table B.2.

Grouped distributions were produced for all coastal species (Figure 2.2a), all pelagic species (Figure 2.2b) and all species combined (Figure A.5). Hotspots of abundance for coastal species are spread around Britain and Ireland, with the east coast of Ireland, the south-east coast of England and the Shetland Islands shown as being particularly important. Conversely, for pelagic species, Scotland is of greatest importance. At the family level, considerable variation also occurs. For example, most tern hotspots are spread around the east coasts of Britain and Ireland whereas Procellariidae hotspots are clumped on the west coasts where they have easy access to distant foraging areas. A map of species richness was produced showing the potential number of species occurring within each grid square based on the foraging radius distribution for all species combined (Figure 2.3).

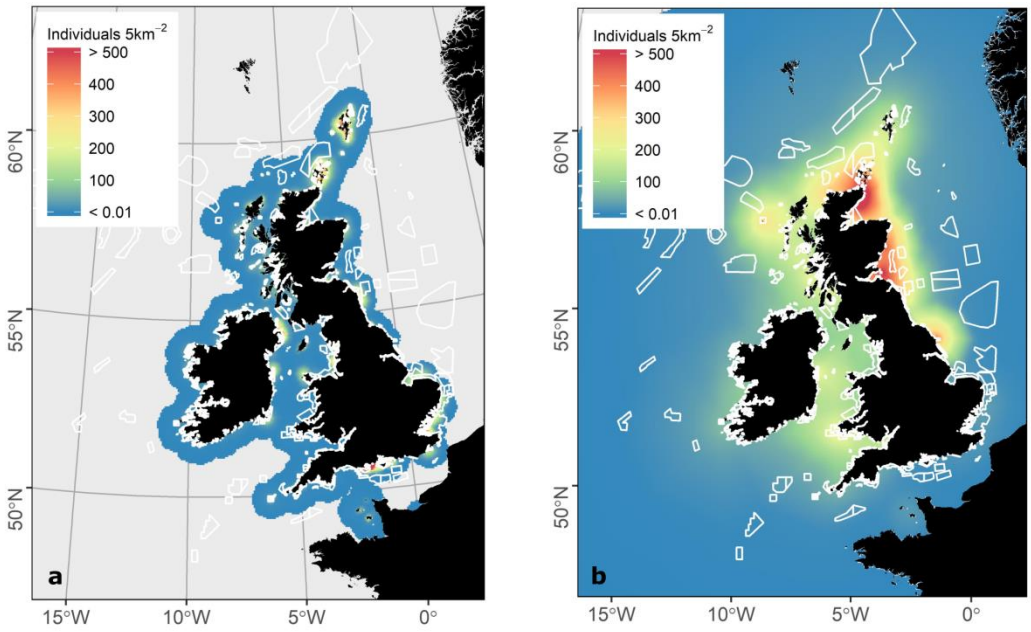


Figure 2.2 Maps showing the foraging radius distributions for a) all coastal species and b) all pelagic species, with protected areas overlaid (white polygons). The colour scale shows predicted density (individuals per 5 x 5 km square) if 50% of the colony is at-sea at a given time, and values are consistent across both maps. Grid squares with over 500 individuals are red and grid squares containing less than 0.01 are blue.

Overlap between foraging radius seabird distributions and currently designated protected areas (SPAs, OSPAR MPAs, and all PAs) ranged from under 7% of the at-sea population contained in all protected areas (European storm-petrel) to over 70% of the at-sea population (Mediterranean gull) (Figure 2.4). See Table B.1 in the supplementary material for a breakdown of overlap by species and family group. Values are likely to vary with the time of day, but remain representative for the time period when the majority of foraging takes place.

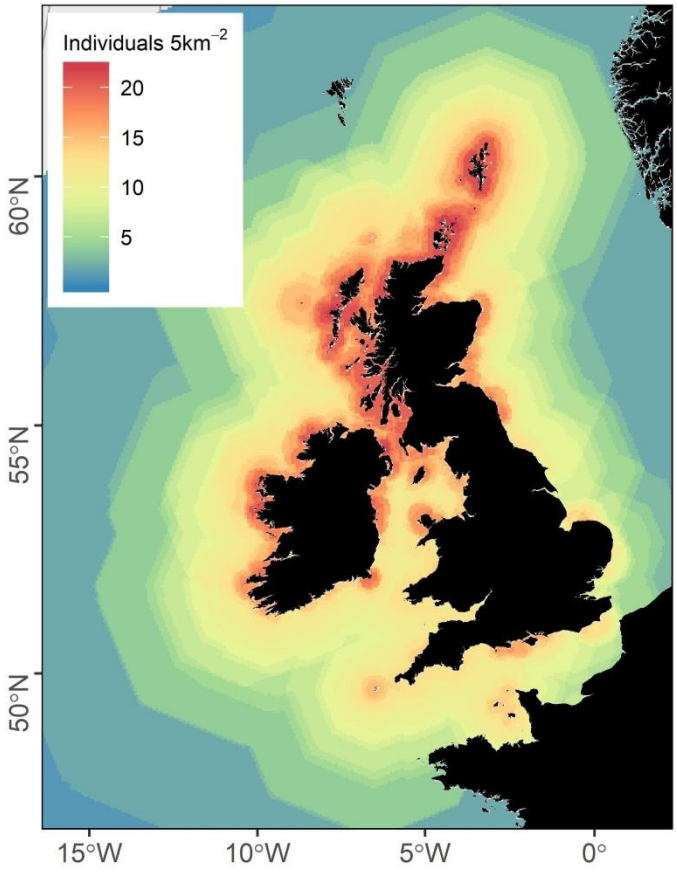


Figure 2.3 A map of species richness showing the potential number of species occurring within each 5 x 5 km grid square based on the foraging radius distribution for all species combined.

Overall, the percentage of a population covered by a protected area was significantly higher for coastal species (mean = 32.5%) than for pelagic species (mean = 13.2%) (p < 0.001, Table 2.2). This difference was also significant when considering SPAs (mean coastal = 18.1% and mean pelagic = 2.4%, p < 0.001), or OSPAR MPAs (mean coastal = 25.5% and mean pelagic = 11.9%, p = 0.001) individually. Non-threatened species had a higher coverage from protected areas than threatened species (mean non-threatened = 25.0% and mean threatened = 14.3%). This relationship was significant for overlap with SPAs (p = 0.01), but not for overlap with OSPAR MPAs (p = 0.09) or all PAs combined (p = 0.07) (Table 2.2).

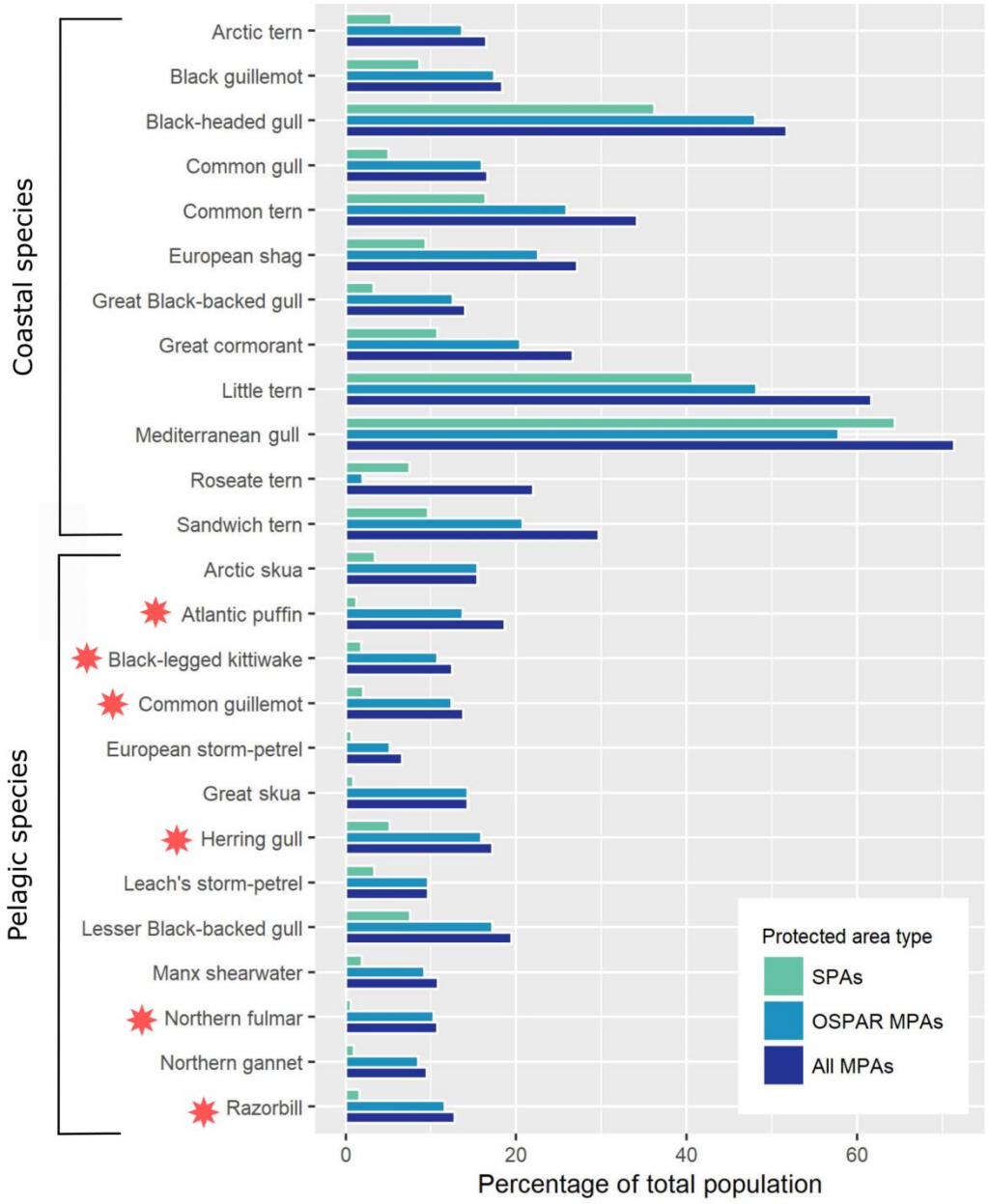


Figure 2.4 Percentage of predicted at-sea population contained within a currently designated protected area for: green = Special Protection Areas (SPAs); light blue = OSPAR Marine Protected Areas; and navy blue = All protected areas combined. Red stars indicate species that have a European Conservation status of 'Near threatened' or higher. Percentage values are not additive as there is spatial overlap between the different protected area types. See Table B.1 in the supplementary material for a complete list of the percentage values.

Table 2.2 Results of Wilcoxon rank sum tests to assess differences in percentage overlap for (1) foraging group (Coastal or Pelagic) and (2) conservation status (Least Concern or Near Threatened and above). Significant results are shown in **bold**. Mean percentage overlap contained within SPAs, OSPAR MPAs and all PAs combined is shown for each group.

Foraging group	**% overlap with predicted distributions**		
	SPAs	OSPAR MPAs	All PAs
Coastal	18.13%	25.45%	32.49%
Pelagic	2.43%	11.89%	13.21%
	Result of Wilcoxon Rank Sum test (p-value)		
coastal > pelagic	**<0.001**	**0.0012**	**<0.001**
Conservation status	**% overlap with predicted distributions**		
	SPAs	OSPAR MPAs	All PAs
Least Concern	12.45%	20.27%	25.04%
Threatened	2.11%	12.48%	14.29%
	Result of Wilcoxon Rank Sum test (p-value)		
least concern > threatened	**0.01**	0.09	0.07

2.5 Discussion

General patterns of distribution

Foraging radius based models using foraging ranges and colony sizes have previously been used to estimate and map densities of seabirds at sea for single or small numbers of species (Grecian et al., 2012; Ludynia et al., 2012; Soanes et al., 2016). Here we applied this approach for an entire seabird community in a major area for seabirds in Europe. Patterns of distribution varied remarkably between species. In particular a clear distinction is seen between hotspots for coastal versus pelagic species, which are reflected in the distribution of breeding colonies (Mitchell et al., 2004). Naturally the models show that abundance hotspots are located nearest the colonies or groups of colonies with the largest population sizes. Even though some seabirds will travel long distances away from the colony to forage, it should still follow that the largest colonies will be located where access to resources minimizes the cost of travel to reach resources (e.g. Sandvik et al., 2016), and where direct competition from other colonies is minimised (Furness and Birkhead, 1984). This basic principle of optimal foraging means that a foraging radius based model such as ours is well suited for capturing the majority of space use by central place foragers (Ashmole, 1963).

Protected area overlap

The analysis of overlap between protected areas and foraging radius distributions found large variation in coverage amongst species, ranging from 7% (European storm-petrel) to 70% (Mediterranean gull) of at-sea population contained in protected areas. In particular, we found a significantly higher proportion of coastal birds were covered by protected areas compared to pelagic birds, many of which are threatened globally, suggesting that they are afforded better protection from designated MPAs. This result is explained by the fact that most MPAs (particularly marine components of SPAs) are developed as extensions from the coast, often surrounding an important colony for a particular seabird species. This pattern occurred even though the foraging radius distributions are weighted so that proportionally more birds are found closer to the colony than at the edge of their foraging ranges, which will affect pelagic foragers more heavily. It is clear that due to the large foraging ranges of pelagic species, coastal colony-centred marine protected areas will not provide sufficient coverage to adequately protect them (see Game et al. (2009) on the lack of pelagic protected areas). While OSPAR MPAs seem to afford better protection to pelagic species than SPAs, the percentage overlap is still significantly lower than for coastal species.

Our analyses also suggest that current marine SPAs afford better protection to species with a conservation status of 'Least Concern' compared to those ranked as 'Near Threatened' or above. The level of coverage is also higher for 'Least Concern' species in OSPAR MPAs and all MPAs combined, but not significantly so. This reflects the fact that all species ranked 'Near Threatened' or above are also pelagic foragers, which have lower coverage by MPAs. For example, the Atlantic puffin is listed as a species of conservation priority in Europe (European Commission, 2010) and is categorised as Endangered on the European Red List (BirdLife International, 2015); however, our results show that it has less protection than many species of Least Concern. Less than 20% of the at-sea population is covered by protected areas, with only a small fraction of this contributed by SPAs. Thus, these analyses highlight the limitations of assuming that protected areas near colonies are necessarily going to serve the species that need most protection, particularly as the majority of foraging by pelagic species will occur in offshore areas (Game et al., 2009; McGowan et al., 2017). An important next step would be to assess which type of protected area (e.g. fixed or dynamic pelagic MPAs) would be more effective for these species, using additional information on foraging behaviour on a species by species basis and spatial prioritisation tools to inform future planning.

Predictive models of seabird biodiversity

A range of methods have been used to predict seabird distribution at sea, but all show that distance to colony is usually the most important factor (Chivers et al., 2013; Ford et al., 2007; Louzao et al., 2012; Skov et al., 2008). Some studies (see below) have explored how the use of different foraging ranges (e.g. maximum, mean maximum or mean) affects the potential accuracy of the predicted distributions. For gannets, Grecian et al. (2012) found that varying the foraging range used in models by ± 25% had no effect on how well the foraging radius distributions correlated with at-sea survey data, and elected to use maximum foraging range in the final model. Studies by Perrow et al. (2015) and Soanes et al. (2016) suggest that the use of the mean of all maximum foraging range estimates may be more appropriate to ensure that an area proposed for conservation is not unfeasibly large. This may be true when the foraging radius approach is used to delineate a home range area (km^2) for protection, whereas for this study the final foraging radius distributions are expressed in density of birds per grid square. The use of maximum foraging radius here allows the hotspots of highest abundance to be highlighted without completely discarding areas at the extremes of a species range where birds may still be foraging. Applying a log decay weighting to the distributions, as in step 4 of the methods,

results in low densities of birds at the edge of the distributions, approaching zero individuals. Furthermore, we conducted a posthoc analysis of MPA overlap using mean maximum foraging range for a short-, mid- and long-range forager, with values taken from Thaxter et al. (2012). The maximum and mean maximum overlaps were as follows: (northern gannet, 709 km range = 9.56% overlap and 229.4 km range = 12.55% overlap; black-legged kittiwake, 120 km range = 12.51% overlap and 60 km range = 13.86% overlap; common tern, 30 km range = 34.21% overlap and 15.2 km range = 27.55% overlap). Thus use of maximum versus mean maximum made little difference and use of maximum values in this approach is justified.

One limitation of foraging radius models is that they cannot account for all factors that explain where animals are found, and inevitably the predicted and true distributions will diverge. For example, density dependent segregation is likely to occur between colonies for all species (Furness and Birkhead, 1984; Wakefield et al. 2013), and within-colony segregation between breeders, non-breeders, and juveniles, or by sex may also occur (Fayet et al., 2015; Stauss et al., 2012; Votier et al., 2017). More importantly, however, spatio-temporal variation in oceanic, meteorological, and ecological factors leads to patchy resource distribution and variable prey availability (Gibb et al., 2017; Scales et al., 2014; Schneider, 1990). These factors are likely to be especially important since they can vary within (Grémillet et al., 2008) and across (Robertson et al., 2014) years, and over long periods of time (Behrenfeld et al., 2006); issues that will also confound empirical data. Despite these limitations, however, simple foraging radius models could be an important tool in seabird conservation for several reasons. First, dynamic oceanic and ecological factors cannot easily be included in a universal model of seabird distribution because such information is lacking for most species in most areas, even in our study area where seabirds have been studied relatively intensively. Moreover, in most cases it is unrealistic to expect these data to become available in the near future, because spatio-temporal variation is so difficult and costly to capture at any spatial scale, let alone at the scale of the marine environment for an entire community of species. Second, modifications to the model on a species-specific basis would need to greatly improve accuracy to be considered useful, at the cost of sacrificing general applicability for all species. Work to date suggests that model performance is not improved dramatically when additional data on resource abundance (Grecian et al., 2012) or bathymetric preference (Soanes et al., 2016) have been included. Third, the approach has already been shown to produce good correlations with distributions obtained from at-sea surveys or GPS tracking in a number of species in

different regions (Grecian et al., 2012; Ludynia et al., 2012). Although we are only just beginning to validate our model using a variety of different kinds of empirical data (see Chapter 3), visual comparison of our predictive distributions with the European Seabirds at Sea (ESAS) database outputs (Dunn, 2012; Stone, 1995) shows good agreement where there is sufficient coverage by ESAS. At the very least, this suggests that the foraging radius approach can be used to provide an important baseline distribution in poorly surveyed regions of the world, with the potential to include additional ecological factors where available to further refine distributions on a species by species basis. Finally, for a tool to be effective across multiple species and utilised by regulatory bodies, it should be simple to use and implement, which is true of the foraging radius model approach.

Conclusion

The foraging radius distribution maps generated in this study have identified both the species and areas that are currently lacking sufficient protection through establishment of protected areas during the breeding season, using a simple but universally applicable method. In particular, the combined species distributions allow us to see where hotspots with a large number of species are found, highlighting sites for further investigation. Although pelagic species are the most threatened group of seabirds globally, they were also the least well protected in our study area, where most MPAs are in coastal locations. Future assessment for marine conservation planning should account for at-sea distribution to ensure that wider-ranging seabirds are afforded sufficient levels of protection. Designation of MPAs does not per se confer protection, but appropriate management of activities within them, e.g. regulation of fisheries/petroleum exploration, can result in positive conservation outcomes at the broader ecosystem level (Costello, 2014; Yorio, 2009). Utilisation of distribution maps that show hotspots of both bird density and species richness in offshore waters should enable effective conservation measures to be put in place that benefit multiple species, either through fixed or dynamic MPAs (Game et al., 2009; Hays et al., 2016). Our approach relies on good abundance estimates for individual colonies, which themselves can be extremely challenging and costly to generate. However, these challenges are likely to be considerably less than those for collecting detailed tracking or at-sea survey data, though naturally both approaches are valuable and complementary. The foraging radius method used here is therefore likely to be particularly useful in regions around the world where little data on at-sea distributions currently exist.

Acknowledgements

Much of the colony data used in this study were extracted from the Seabird Monitoring Programme (SMP) Database [at www.jncc.gov.uk/smp]. Data have been provided to the SMP by the generous contributions of nature conservation and research organisations, and of many volunteers throughout the British Isles. We would like to thank Mark Bolton from RSPB, Ilka Win from JNCC and Alyn Walsh from NPWS for their assistance in obtaining up to date colony data for a number of species. We also thank Mark Bolton for helpful comments provided on previous versions of this manuscript, and two anonymous reviewers whose comments greatly improved this manuscript. We are grateful to the Irish Petroleum Infrastructure Programme for their continued support of this project, in particular Martin Davies and Nick O'Neill.

Chapter 3

Assessing the effectiveness of foraging radius models for seabird distributions using biotelemetry and survey data

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Author contributions: The study was designed by E.J.C., J.L.Q., and M.J.J.; E.J.C., A.B., A.K., S.W., D.T., J.L.Q. & M.J.J. carried out tracking and aerial survey data collection; E.J.C. carried out the analyses, with contributions from W.J.G. for the foraging radius method and A.C. who produced the GAMs; E.J.C. led the writing of the chapter with contributions from all authors.

3.1 Abstract

Many seabird species are threatened globally and face multiple risks when foraging. To adequately protect threatened populations, robust information on their distributions at sea is needed. Relatively simple foraging radius models have the potential to generate predictive distributions for a large number of species rapidly, thus providing a cheaper alternative to large-scale surveys or complex modelling approaches. Their effectiveness, however, remains largely untested. Here we compare foraging radius distribution models for multiple breeding seabird species to distributions from biotelemetry studies and aerial surveys. Foraging radius distributions were significantly correlated with tracking data for Atlantic puffin (*Fratercula arctica)*, European storm-petrel *(Hydrobates pelagicus)*, Manx shearwater *(Puffinus puffinus)* and razorbills *(Alca torda)* at the colony level. Correlations between foraging radius distributions and aerial survey data were also significant, but generally weaker for many species particularly for auks and terns. Correlations between foraging radius distributions and aerial survey data were benchmarked against more complex generalised additive models (GAMs) of the aerial survey data that included a range of environmental covariates. While GAM distributions had slightly higher correlation values with aerial survey data, both GAM and foraging radius models were poor at predicting distributions for gannets and fulmars in particular. Despite the limitations of foraging radius distribution modelling, we suggest that it is a pragmatic approach for assessing summer breeding distributions for many seabird species, and is likely to have acceptable utility in complex, temporally variable ecosystems, or when financial resources are limited.

3.2 Introduction

Determining the distributions of species for conservation planning can present many challenges. In particular, it is usually time-intensive and costly to capture a representative sample of the population, especially for species with large ranges. The challenges can be even greater for marine species, where the difficulties in accessing study sites can be limiting and the dynamic nature of the environment can cause high spatio-temporal variation in distributions. Consequently there is often insufficient data to inform conservation management in marine systems, leading to a difficulty in defining marine protected areas for many marine top predators (Dias et al., 2017; Game et al., 2009). This is especially true for seabirds, a taxonomic group for which there remains a major gap in the level of protection afforded at sea for even the most threatened species (Critchley et al., 2018; McGowan et al., 2017) and who face significant threats when foraging at sea (Croxall et al., 2012).

Predictive modelling has the potential to overcome these challenges, and is less costly and time-intensive than large-scale at-sea surveys or tracking studies. Techniques available for ecological modelling have expanded rapidly (Lascelles et al., 2016; Wakefield et al., 2009), giving conservation practitioners an array of choices. However, many predictive models are still reliant on the collection of extensive data to inform inputs, for example ecological niche models (Scales et al., 2015), and the spatial resolution and temporal averaging of environmental covariates can also influence the accuracy of predictive models significantly (Pearson et al., 2006; Péron et al., 2018; Scales et al., 2015). Some models avoid these uncertainties by taking a simpler and more mechanistic approach, modelling distribution based on a combination of telemetry and population data (Jones et al., 2015; Pikesley et al., 2018).

One simple method that can be applied to any central-place forager and requires little *a-priori* data on at-sea distribution is the foraging radius model approach (BirdLife International, 2010a; Critchley et al., 2018; Grecian et al., 2012). This approach projects distributions based on a set of foraging radii, a decay function from the central place or colony, and colony size, providing a rapid and cost-effective method for assessing at-sea distribution. While the use of simplified models is thought to sacrifice species-specific accuracy (e.g. due to habitat preferences) and fail to account for local variation (e.g. spatial partitioning), there is also evidence that for individual species it can be effective when compared to empirical data (Grecian et al., 2012; Ludynia et al., 2012; Soanes et al., 2016).

However, the effectiveness of foraging radius models has not yet been assessed at the community level across multiple species or colonies.

Empirical methods generate essential inputs for predictive distribution models. The best method to use is dependent on the species of interest, the area to be covered, accessibility, and the amount of resources available. At-sea surveys are an established approach to inform marine spatial planning at regional (Smith et al., 2014), national (Kober et al., 2012) and international (Lambert et al., 2017) scales. Aerial or ship-based surveys can target most seabird species in a community, often at large spatial scales, and if conducted following distance-based methodology, can also provide absolute abundance estimates (Embling et al., 2010). However, such data is often obtained from surveys conducted from vessels of opportunity, and tends to be spatially and temporally patchy (Dunn, 2012; Stone et al., 1995) with few repeated transects that would allow an examination of temporal variation. In contrast bio-logging studies provide detailed information on the fine-scale distribution of seabirds, usually during the breeding season (Dean et al., 2015; Soanes et al., 2016; Wakefield et al., 2013), and on broader scale movements during the non-breeding season (Frederiksen et al., 2012; Grecian et al., 2016; Jessopp et al., 2013). However, the individuals selected may not be representative of the wider colony, other colonies in the region, or other regions, given the inevitability of only ever being able to track a small proportion of a population (Soanes et al., 2013). The temporal scale of tracking is also usually heavily restricted by resources (Wakefield et al., 2009). Furthermore foraging areas can vary annually depending on environmental fluctuations (Robertson et al., 2014), a factor that is predicted to increase with climate change (Daunt and Mitchell, 2013; Grémillet and Boulinier, 2009). This source of variation is hard to capture by all empirical approaches. While foraging radius models do have limitations, the same is true for all empirical approaches, the robustness of which remains largely unknown.

Here we explore the accuracy and suitability of the foraging radius model approach for assessing distributions of seabirds at sea. We do this by comparing their output to empirical data from biotelemetry and at-sea aerial surveys. We apply the method at a national level in Irish waters, known to support diverse and internationally important numbers of breeding seabirds (Mitchell et al., 2004), comparing foraging radius distributions at a colony level to GPS tracking data obtained from four breeding species with short, medium and long foraging ranges, and at a regional and community level to extensive aerial surveys conducted over a two-year period. We also generate predicted distributions from the aerial

survey data using generalised additive models (GAMs), incorporating environmental predictors. Comparing these models to the empirical survey data serves as a benchmark for the correlation values between foraging radius distributions and empirical data, because GAMs are often considered to be the best method for modelling survey data (Booth and Hammond, 2014; Potts and Rose, 2018). We discuss the performance of the foraging radius model and the appropriateness of using this method for assessing seabird distributions under different scenarios.

3.3 Methods

Foraging radius model

Foraging radius seabird distributions were generated for individual colonies of all seabirds across the UK and Ireland during the breeding season using the foraging radius model approach as described in Critchley et al. (2018). The model predicts the occurrence of birds within the at-sea area surrounding a colony, up to a set colony-centred radius. The mean of all maximum foraging ranges (mean maximum foraging range) reported for each species was taken from the literature (Thaxter et al., 2012 and more recent studies, see Table D.1 for a list of foraging ranges and sources). A 5 x 5 km grid was generated across the study area, and the probability of occurrence within each grid square was first calculated by taking the normalised inverse distance from the grid square to the colony, so that all squares had a value of between 0 and 1 with the highest values being found closest to the colony. Distributions were then distance-weighted using a logarithmic decay function so that areas closer to the colony were of higher importance per unit area, accounting for non-foraging behaviours such as washing/preening or rafting (Wilson et al., 2009). Values were again normalised so that all grid squares summed to 100% and then multiplied by estimates of the breeding population, taken from the JNCC Seabird Monitoring Programme (SMP) Database [at www.jncc.gov.uk/smp] and additional colony surveys from National Parks and Wildlife Service and BirdWatch Ireland annual reports (Burke et al., 2015; Daly et al., 2015; Doyle et al., 2015), to estimate abundance per grid square.

The distribution maps were plotted on a 5 x 5 km grid and show the number of individuals predicted to occur in each grid square, assuming 50% of the colony is foraging at-sea at a given time. This accounts for the assumption that on average, one half of a breeding pair will remain at the nest at any one time (e.g. during incubation and early chick rearing). These steps were repeated for each individual colony and the distributions were then summed to generate a foraging radius distribution map for each species over the entire region. To test the sensitivity of varying foraging range on comparisons with other methods of assessing at-sea distribution, foraging radius distributions were also generated using the maximum of all recorded foraging ranges for each species (see Table D.1).

GPS tracking

GPS tracking data were collected from Manx shearwaters (*Puffinus puffinus)* breeding on two Islands off the west coast of Ireland, Great Blasket, Co. Kerry (2014-2015; 52.10 N,

10.52 W, n=24), and High Island, Co. Galway (2014-2016; 53.55 N, 10.26 W, n=65); from Razorbills (*Alca torda)* breeding on the southeast coast of Ireland on Great Saltee, Co. Wexford (2014; 52.12 N, -6.61 W, n=11); from European storm-petrels (*Hydrobates pelagicus)* breeding on the west coast on High Island, Co. Galway (2016; 53.55 N, 10.26 W, n=8), Ireland; and from Atlantic puffins (*Fratercula arctica)* breeding on the southeast coast on Little Saltee, Co. Wexford (2017; 52.13 N, -6.62 W, n=9) (see Figure 3.1). All data were collected during chick rearing, apart from for Manx shearwater for which data was also collected during the incubation stage.

All tracked birds were caught at their nest or burrow by hand, crook or purse nets. Manx shearwaters and Razorbills were fitted with GPS loggers (i-gotU GT-120, Mobile Action Technology, Taiwan) attached dorsally to contour feathers using strips of waterproof Tesa tape (4651, Tesa GmbH, Germany). European storm-petrels were tracked using 0.95g Pathtrack GPS tags attached to the tail feathers using Tesa tape (4651, Tesa GmbH, Germany). Atlantic puffins were tracked using Ecotone Uria GPS loggers attached ventrally to the lower back using Tesa tape (4651, Tesa GmbH, Germany). Deployment weight was kept below 3% (puffins, razorbills, storm-petrels) or 4% of body mass (Manx shearwater). On return to the colony, tags were recovered and downloaded from all species except puffins, where data was obtained by remote download. The use of Tesa tape as a temporary attachment method in all cases allowed for any tags not retrieved to drop off. Licenses for capture and deployment of devices were granted by National Parks and Wildlife Service, and British Trust for Ornithology.

Tags were programmed to record locations every 2-30 minutes depending on the tag used and the species tracked. All location fixes were included in analyses, except those generated whilst birds were within a 2 km buffer of the centre of the colony, or where recorded over land (see Figure 3.1 for a map of colony locations and tracks). All track processing was carried out in ArcMap 10.3.1. Bivariate kernel utilisation distributions were generated for each species using the adehabitatHR package (Calenge, 2015) in R. For Manx shearwaters, utilisation distributions were estimated for the two colonies separately and data for multiple years were combined. All utilisation distributions were generated using the reference smoothing factor from the package on a 2 km x 2 km grid, apart from Manx shearwater distributions which were created at a resolution of 5 km x 5 km due to computational issues with processing the large numbers of relocation data points at a higher resolution.

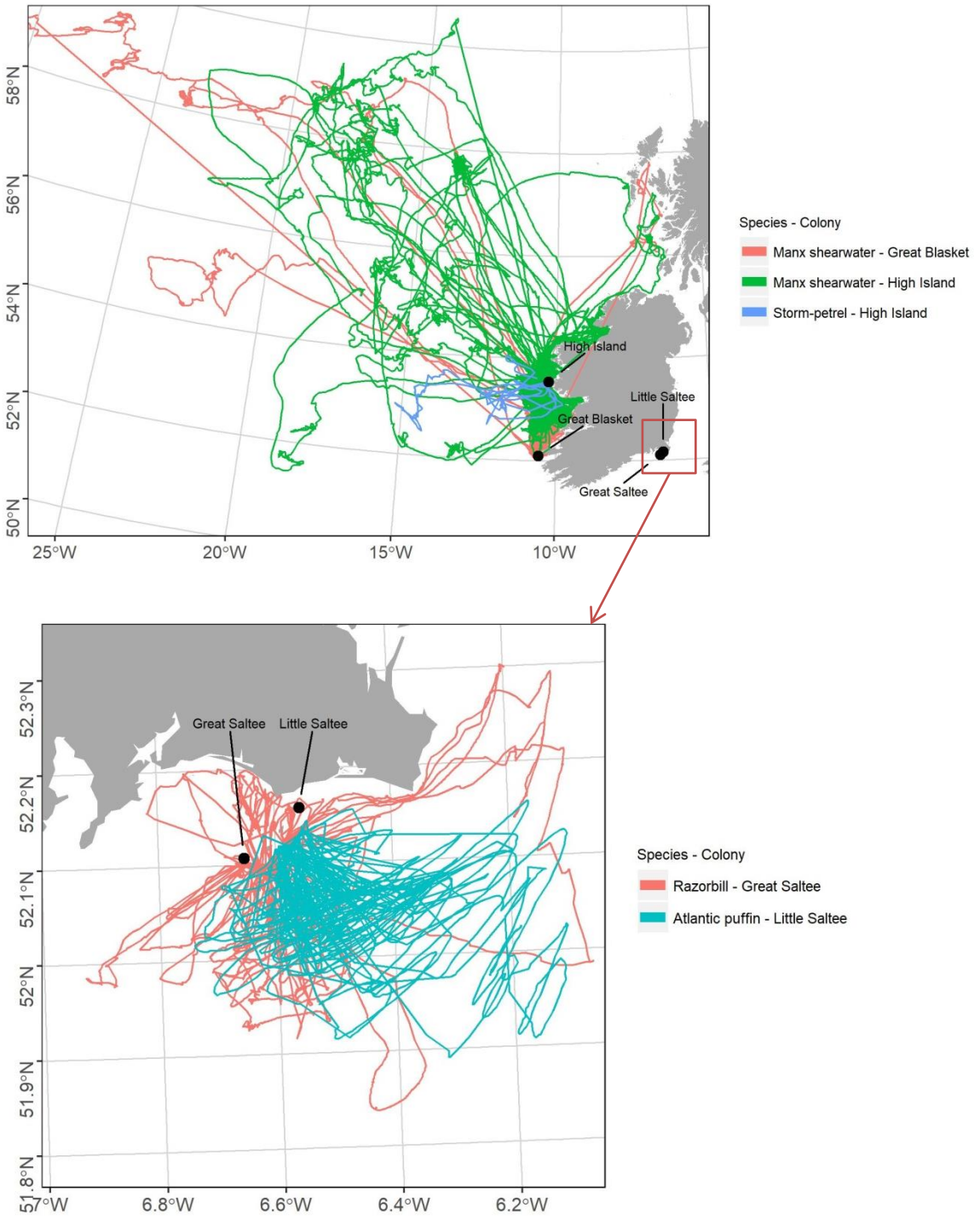


Figure 3.1 GPS tracks and colony locations for Manx shearwater and European storm-petrel on the west coast of Ireland and inset for razorbill and Atlantic puffin on the south east coast of Ireland.

Aerial surveys

Aerial survey data was obtained from the ObSERVE aerial survey programme (Jessopp et al., 2018; Rogan et al., 2018), conducted over the 2015 and 2016 breeding seasons. Two

sets of surveys were flown, a broad-scale survey covering predominantly offshore waters, and a fine-scale survey covering the western Irish Sea, including inshore coastal waters. Broad scale survey transects were designed to provide equal coverage for the survey area, and consisted of equally spaced randomly placed zig-zag lines (Figure 3.2) that were positioned differently in 2015 and 2016 to allow for a more representative coverage of the study area. The fine scale survey transects consisted of 55 parallel lines spaced approximately 3.7 km (2 nautical miles) apart, and between 20-30 nautical miles in length, and were only surveyed in 2016. The parallel line design sought to cover all the shallower sand banks on the Irish east coast which broadly run in a north-south direction, while also taking in aquatic habitat adjacent to the banks (Figure 3.2).

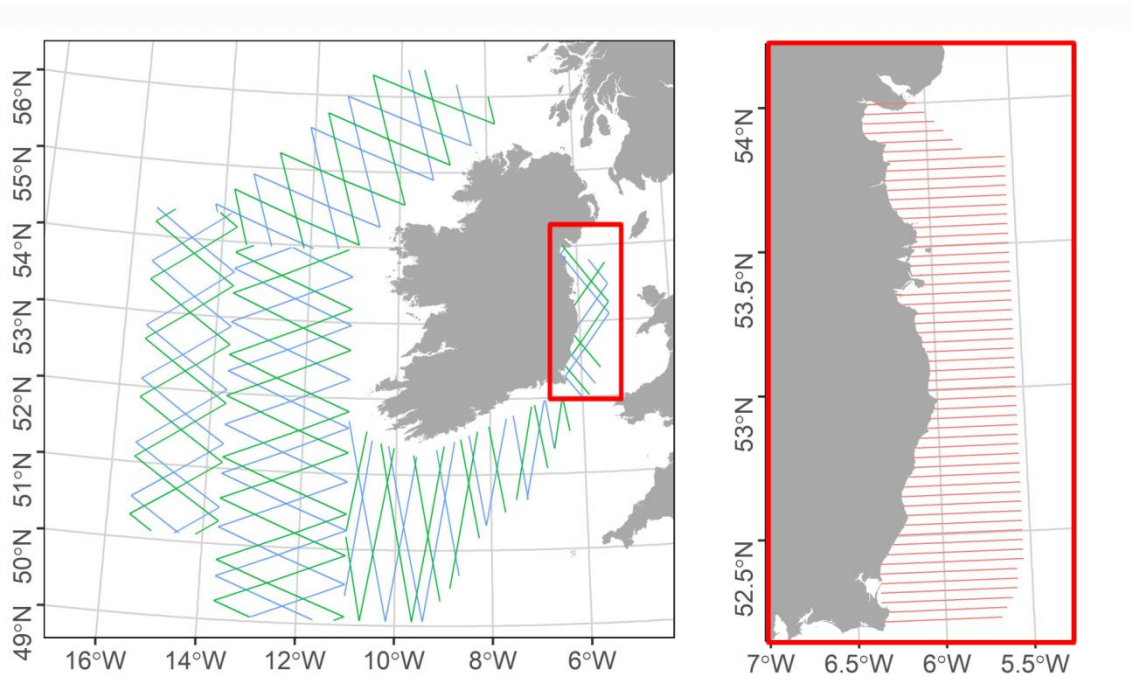


Figure 3.2 Broad-scale aerial transect lines flown in summer 2015 (blue) and 2016 (green) and inset, fine-scale aerial transects in the Irish Sea flown in summer 2016 (red).

Surveys used a fixed high-wing, twin-engine Britten-Norman (BN-2) Islander fitted with bubble-windows to afford observers unrestricted views of the transect area beneath the aircraft. Flying speed was 90 knots (167 km/hr) at an altitude of 183 m on broad scale surveys, and 76 m on fine-scale surveys under target weather conditions of Beaufort Force 3 or less, with good visibility (1 km or more). The plane's geographic position was recorded every two seconds using an on-board GPS linked to a data logging computer. Two fully trained observers, one either side of the plane, employed a strip transect methodology, recording all seabirds within a 200 m distance band either side of the aircraft, determined

by use of inclinometers (Camphuysen et al., 2004). When seabirds came abeam of the aircraft, a date/time stamped record was produced consisting of location (latitude, longitude), species ID, and group size. Species were identified to the lowest taxonomic level whenever possible. When individuals could not be identified to species level, they were grouped into higher taxa categories.

Density of seabirds from both the fine scale and broad scale survey data was determined by dividing the number of individuals sighted by survey effort (distance travelled multiplied by strip width and corrected for observer effort), to give density per km^2 for each strip segment. The centre point for each segment was taken as the spatial point for comparison with foraging radius distributions.

In the broad scale surveys, summer seabird abundance and distribution was also modelled using Generalized Additive Models (GAM) with a logarithmic link function, and a Tweedie error distribution following Cañadas and Hammond (2008). Distributions were predicted at a resolution 0.10 x 0.06 degrees (latitude x longitude) as a function of a wide range of environmental covariates. See supplementary materials (D.3, Tables D.4 and D.5) for further details of methods and environmental covariates used.

Distribution comparisons

Densities of seabirds per grid cell were compared across distributions using a Dutilleul modified *t*-test of correlation (Dutilleul et al., 1993), which accounts for spatial autocorrelation within the data. Individual Dutilleul's modified *t*-tests for each species/family group were conducted using the *SpatialPack* package (Vallejos et al., 2018) in R. At the individual colony scale, kernel densities from GPS tracking data were compared to foraging radius distributions for the same colonies (Figure 3.3). At the regional scale, aerial survey outputs for fine-scale surveys in the Irish Sea and broader offshore waters (two summer surveys combined to include any inter-annual variability in distributions) were compared to the regional foraging radius distributions for each species/family group (Figure 3.3). A benchmark for the foraging radius model correlations was provided by comparing aerial survey data to modelled GAM distributions incorporating a range of environmental variables (see supplementary material D.3, Tables D.4 and D.5). All analysis was carried out in R version 3.4.3 (R Development Core Team, 2016).

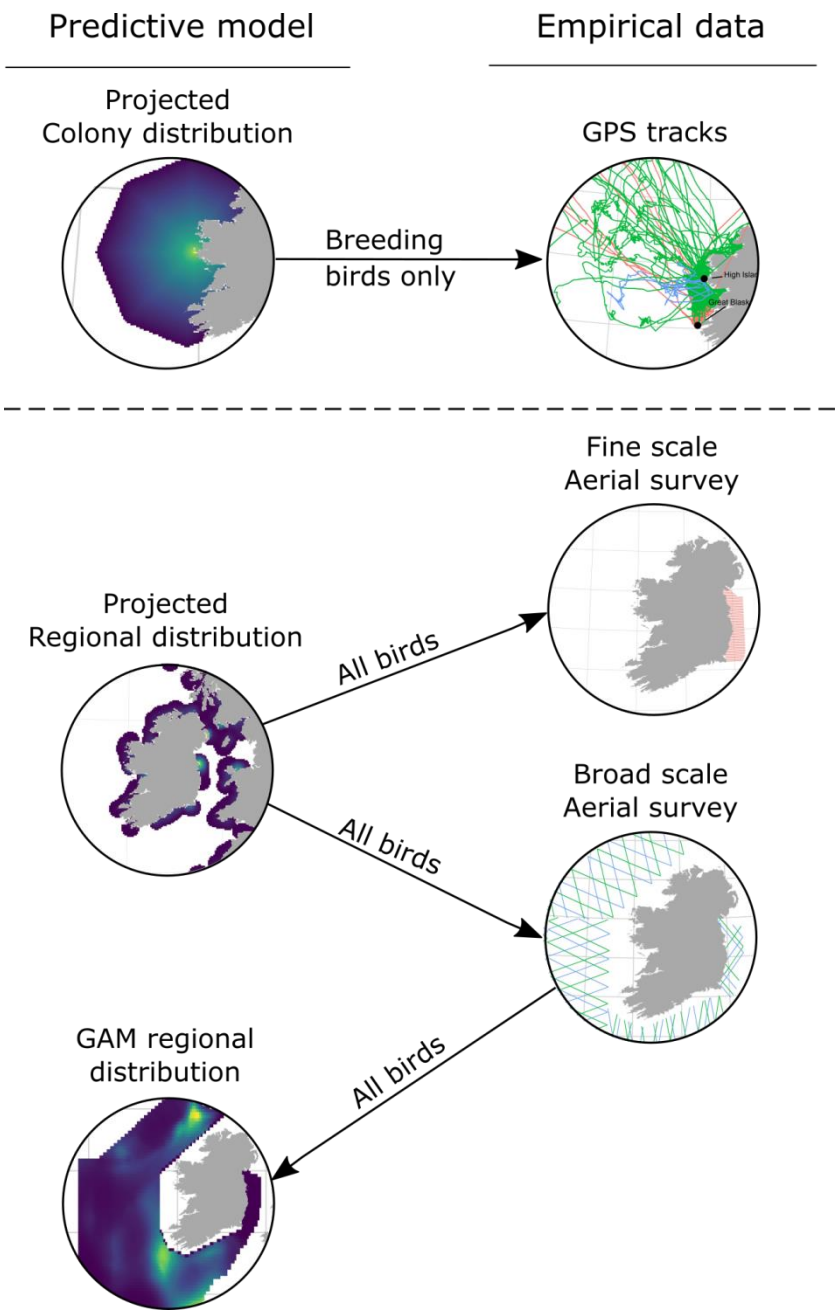


Figure 3.3 Schematic of comparisons for colony level and regional distributions

3.4 Results

Example colony level and regional distribution maps, both foraging radius and empirical, are shown for Manx shearwater (Figure 3.4) and razorbill / auks (Figure 3.5).

Comparison of foraging radius distributions with GPS tracking data

Correlations of colony-level foraging radius distributions with kernel estimated utilisation distributions from GPS tracking data ranged from 0.2 to 0.645; all $p < 0.05$, (see Figure 3.6 and Table D.6). For all species, the use of mean maximum foraging range in the foraging radius model resulted in stronger correlations than using maximum foraging range. For far-ranging pelagic species, correlations increased only marginally with the use of mean maximum foraging range; from 0.532 ($p < 0.05$) to 0.574 ($p < 0.005$) in European storm-petrel, and from 0.211 ($p = 0.002$) to 0.344 ($p < 0.001$) at High Island, and 0.2 ($p = 0.01$) to 0.282 ($p < 0.001$) at Great Blasket for Manx shearwater. For short-ranging coastal species, the difference was greater; from 0.473 ($p < 0.001$) to 0.641 ($p < 0.001$) for razorbill, and from 0.225 ($p < 0.001$) to 0.557 ($p < 0.001$) for Atlantic puffin.

Comparison of foraging radius distributions with fine-scale Irish Sea aerial survey data

There were few significant correlations between foraging radius distributions and empirical data from fine-scale surveys, with the notable exceptions of terns (0.335 - 0.392, $p < 0.001$) and Manx shearwater (0.112, $p < 0.05$) although these correlation values were low, see Figure 3.6 and Table D.7. At the species level, significant positive correlations were found for arctic and common tern (0.166 - 0.339, $p < 0.05$), roseate tern (0.3133 - 0.391, $p < 0.001$) and sandwich tern (0.194 - 0.209, $p < 0.05$). No significant correlation was noted for all species combined, Atlantic puffin, auks, black guillemot, black-legged kittiwake, cormorant/shag, gulls, little tern, Manx shearwater, northern gannet, northern fulmar, petrels, and razorbill/guillemot.

Comparison of foraging radius distributions with broad-scale offshore aerial survey data

When comparing regional foraging radius distributions to broad-scale survey data the best correlations were found for auks (0.389 – 0.426, $p < 0.001$) and terns (0.424 – 0.439, $p < 0.001$), see Figure 3.6 and Table D.8. Significant correlations were also found for all species combined (0.151 – 0.167, $p < 0.01$), gulls (0.141 – 0.161, $p < 0.005$) and black-legged kittiwake (0.129 – 0.155, $p < 0.005$). There was no significant correlation between foraging radius distributions and broad-scale aerial survey data for petrels, Manx shearwater, northern gannet or northern fulmar. Marginal differences in correlation values were found

with the use of mean maximum vs. maximum foraging range for foraging radius distributions.

Benchmarking correlations

To provide a benchmark for correlations between foraging radius distributions and aerial survey data, we compare GAM modelled distributions with empirical aerial survey data. Not surprisingly GAM correlations with aerial survey data were stronger than for foraging radius distributions, but still low values (see Figure 3.6 and Table D.8). Significant correlations were detected for petrels, Manx shearwater, northern fulmar, and northern gannet, whereas correlations between foraging radius distributions and aerial survey data were not significant for these species.

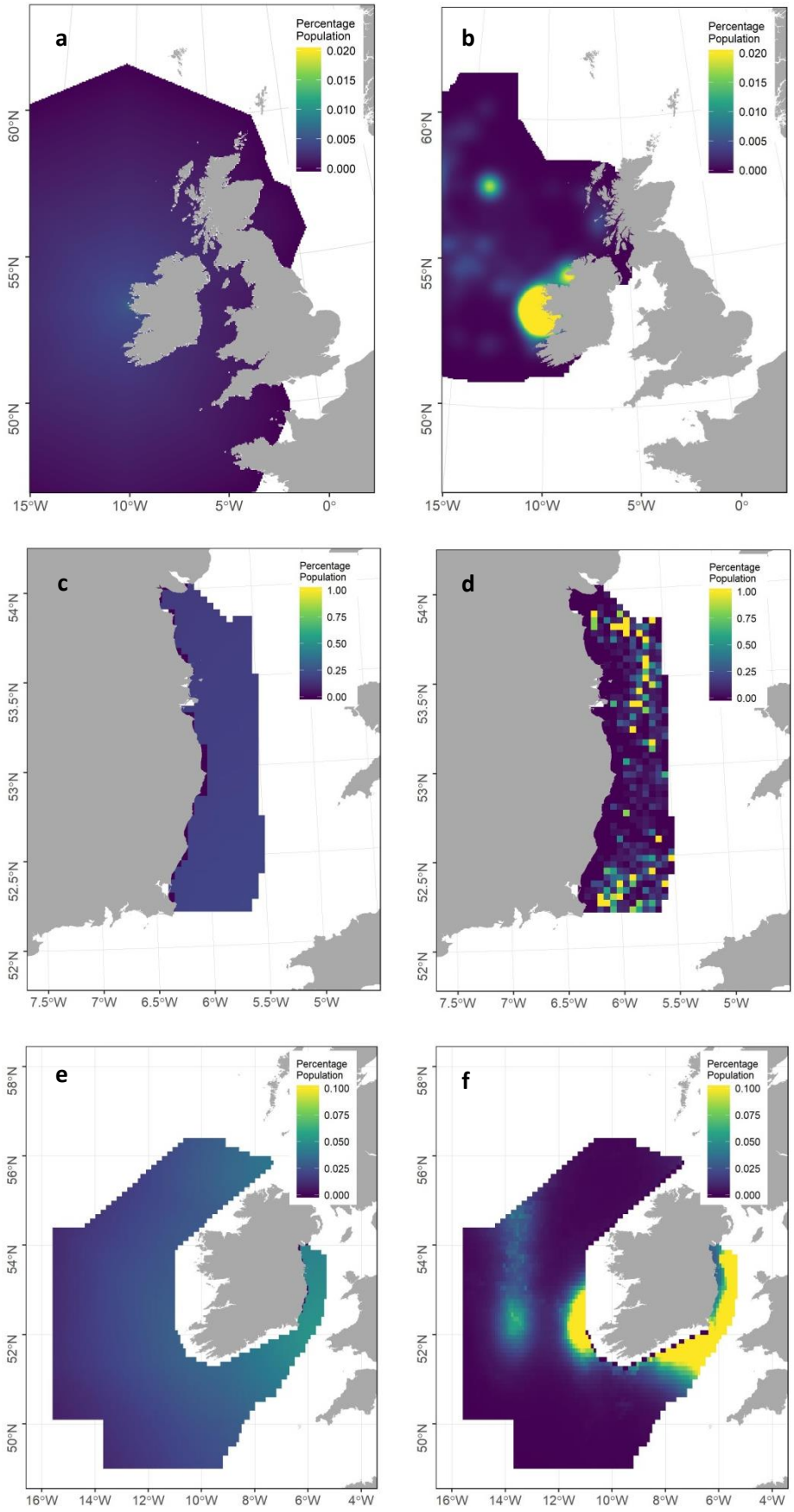


Figure 3.4 Maps showing a) foraging radius distribution of Manx shearwaters from High Island colony only, generated using the mean maximum foraging radius (population

estimate from Seabird 2000 census; Mitchell et al., 2004); b) kernel density at-sea distribution for Manx shearwaters breeding on High Island, Co. Galway, generated from three years of summer breeding season GPS tracking data (2014-16); c) foraging radius distributions of Manx shearwaters in the Irish Sea generated using the mean maximum foraging radius; d) empirical density values of Manx shearwaters in the Irish Sea from fine-scale aerial surveys (2016); e) foraging radius distribution for all Manx shearwater colonies in Ireland and the UK generated using the mean maximum foraging radius (population estimate from Seabird 2000 census; Mitchell et al., 2004): and f) GAM modelled density for Manx shearwaters in Irish waters, generated from two years of summer ObSERVE aerial survey data (2015-16). Densities for all maps were normalised to percentage at-sea population per 5 km grid square, i.e. all grid squares in each map sum to 100%.

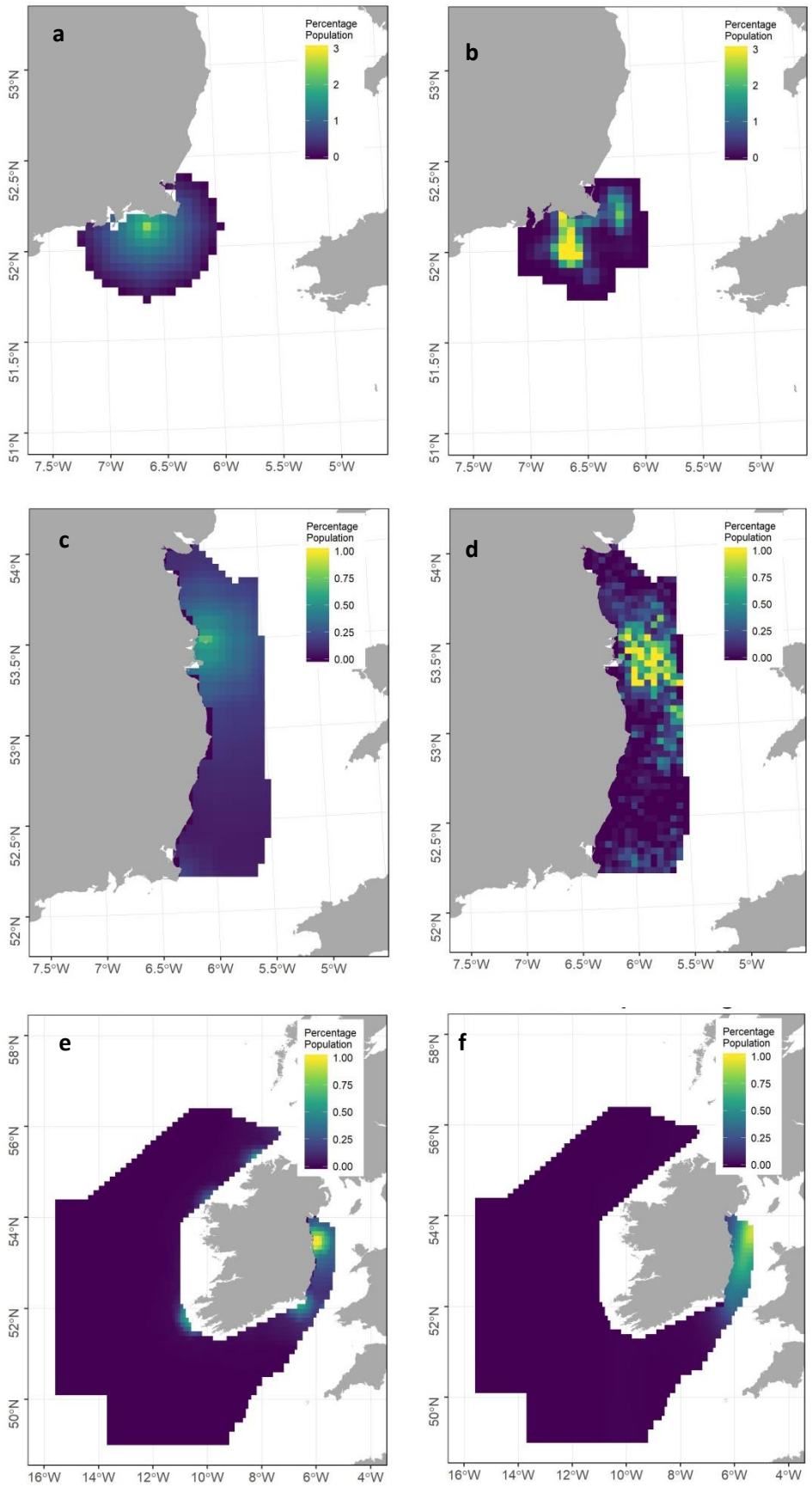


Figure 3.5 Maps showing a) foraging radius distribution for razorbill from the Great Saltee colony only generated using the mean maximum foraging radius (population estimate from

Seabird 2000 census; Mitchell et al., 2004); b) kernel density for razorbill breeding on Great Saltee, generated from summer breeding season GPS tracking data (2014); c) foraging radius distributions in the Irish Sea generated using the mean maximum foraging radius for all auk species; d) empirical density values in the Irish Sea from fine-scale aerial surveys (2016) for all auk species; e) foraging radius distribution for all auk colonies in Ireland and the UK generated using the mean maximum foraging radius (population estimate from Seabird 2000 census; Mitchell et al., 2004); and f) GAM modelled density for auks in Irish waters, generated from two years of summer ObSERVE aerial survey data (2015-16). Densities for all maps were normalised to percentage at-sea population per 5 km grid square, i.e. all grid squares in each map sum to 100%.

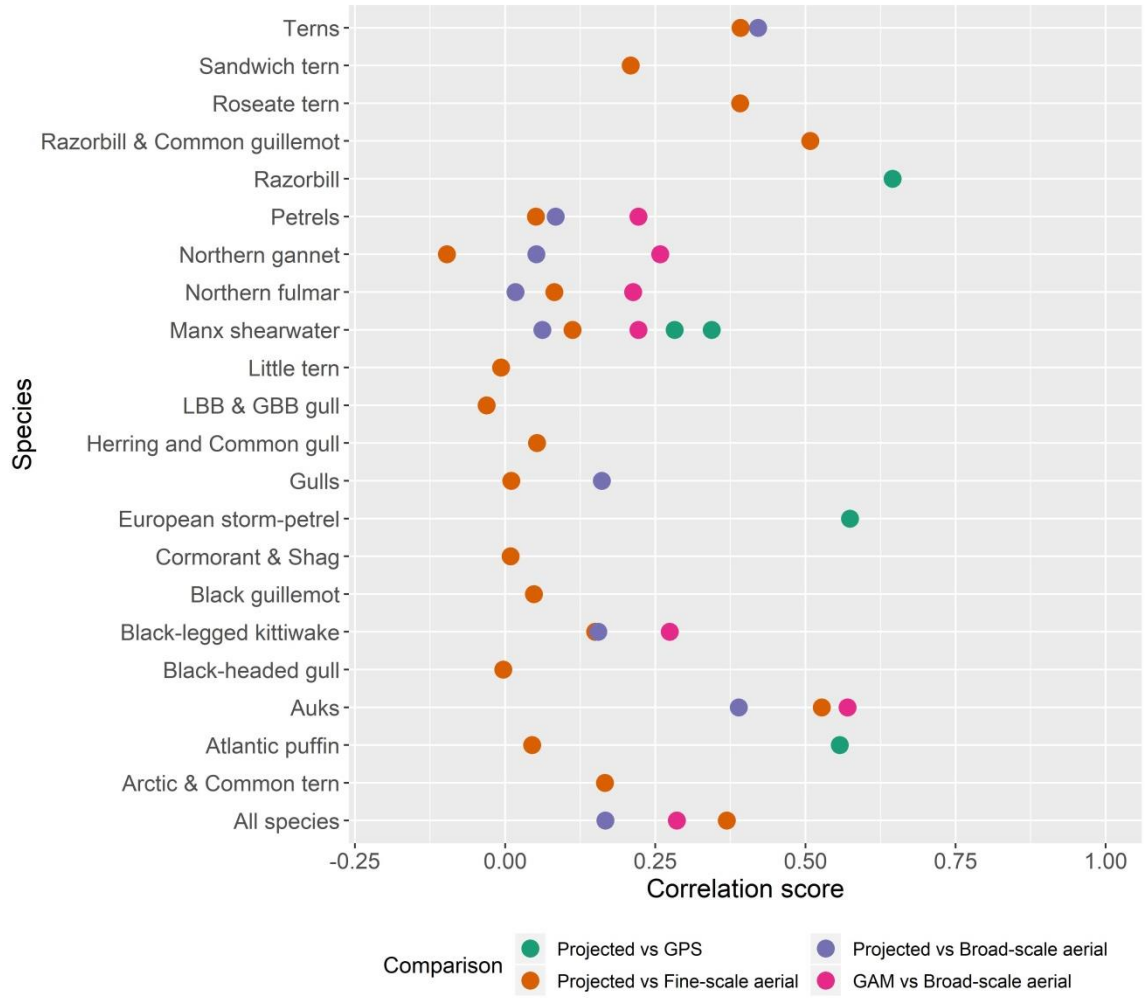


Figure 3.6 Pearson correlation coefficients for comparisons between a) individual colony kernel densities (from GPS tracking data) and foraging radius distributions for that colony using mean maximum foraging range - two correlation values are shown for Manx shearwater as tracking data was collected from two colonies; b) empirical survey data (fine-scale Irish Sea) and foraging radius distributions using mean maximum foraging range; c) empirical survey data (broad-scale offshore) and foraging radius distributions using mean maximum foraging range; and d) empirical survey data and predicted GAM distributions. In all cases *p* values were calculated after accounting for spatial autocorrelation using Dutilleul's (1993) method.

3.5 Discussion

Our results show reasonable agreement (i.e. a value of 0.55 or above) between a simplified foraging radius foraging radius model and empirical data from GPS tracking studies across three seabird species in this study, for both short and long range foragers. For comparisons with aerial survey data highest correlations were found between foraging radius distributions and broad scale aerial survey data at the family group level for both auks and terns. Other correlations between foraging radius distributions and aerial survey data were either low, although benchmark correlations against a more complex GAM approach were also low, or not significant for a number of species and family groups.

Comparison of foraging radius distributions with GPS tracking data

The correlations found between foraging radius distributions from single colonies and GPS tracking data are promising, particularly as it holds true for both short ranging and long ranging foragers. Correlation values for Atlantic puffin, European storm-petrel and razorbill were higher than was previously found for gannets by Grecian et al. (2012), even with relatively small sample sizes for the GPS tracking data (n = 9; 8; 11). Given how expensive it can be to track some of these species either due to their size, e.g. European storm-petrels, or difficulty of accessing their colonies, foraging radius models provide a valuable alternative to collecting additional empirical data. The lower values found for Manx shearwaters could be explained by the variation in behaviour seen due to their dual foraging strategy of frequent chick-provisioning trips and longer self-maintenance trips, which can produce a bi-modal distribution for the species (Shoji et al., 2015). Thus a foraging radius model based on mean maximum foraging range is unlikely to be representative of their foraging distributions. The difference between the foraging radius distributions and GPS tracking is also notable when visually comparing Figure 3.4a to Figure 3.4b. In contrast, a visual comparison of the Razorbill foraging radius distribution (Figure 3.5a) to the GPS tracking data (Figure 3.5b) reflects the higher correlation value that was found for this species. Despite these promising results, it should be noted that both methods compared here only capture the distribution of breeding birds and do not account for juveniles, immature birds, and non-breeding adults.

Comparison of foraging radius distributions with aerial survey data

At a regional level, correlations were low overall between foraging radius distributions and empirical data from both broad scale offshore surveys and fine scale coastal surveys. This

discrepancy can be explained by a number of factors that are not accounted for in the basic foraging radius model, as well as limitations of survey data, both of which we discuss in detail below. In particular, variability in density-dependent competition (Wakefield et al., 2013) across multiple colonies and movement of non-breeders can have significant effects on regional distributions. Whereas both the foraging radius distributions and GPS distributions only account for breeding birds, survey data captures all birds observed, regardless of breeding stage. Seabird populations are composed of a significant number of juveniles, immature birds, and non-breeders, which can display very different foraging behaviour compared to the colony constrained breeders (Fayet et al., 2015; Grecian et al., 2018).

Highest correlations were found for auks and terns, at both the family group and individual species level, and across both the fine scale coastal and the broad scale offshore surveys, suggesting that the foraging radius model is a suitable method for assessing their distribution. This is likely to reflect the foraging behaviour of these groups, which are restricted to smaller home ranges due to their high flight costs, in contrast with pelagic species. Terns have a high level of variability in foraging modes (Eglington et al., 2013) both within and across years, and appear to rely on trophic level segregation rather than spatial segregation to avoid competition (Robertson et al., 2014). Auk distribution has previously been shown to be closely linked to distance to colony (Johnston et al., 2015) and sympatric species also rely on niche segregation rather than spatial segregation during the breeding season (Linnebjerg et al., 2013; Shoji et al., 2015). These factors probably explain why a foraging radius distribution with a uniform decay from the colony appears to be a reasonable representation of their distribution.

The foraging behaviour of many of the species showing poor correlations is more strongly associated with specific habitat cues or environmental conditions, which are often patchily distributed (Wakefield et al., 2009). Many gull species forage inland during the breeding season (Rock et al., 2016), while pelagic foragers, including the Manx shearwater and northern gannet, will cue to specific environmental features, such as frontal systems (Grecian et al., 2018; Scales et al., 2014) or fishing vessels (Bodey et al., 2014). Shorter ranging benthic foragers such as cormorants, shags and divers are known to have strong foraging associations with shallow sand bars and tidal streams (Waggitt et al., 2017), which will not be captured by a general foraging radius method. Modifying the foraging radius model for each species to account for known environmental features should improve the

match with empirical data, as has previously been shown for gannets (Grecian et al., 2012), though doing so is likely challenging for at least two reasons. First, although primary productivity and sea surface temperature are often touted as being one of the most important, readily accessible environmental features, there is still considerable uncertainty about their utility for predicting foraging locations due to spatiotemporal lags (Grémillet et al., 2008; Oppel et al., 2012; Wakefield et al., 2009). Second, the influence of environmental features will in many cases be colony specific, and for example dependent on both the location of the colony and intra- and inter-specific competition, leading to unaccounted for spatial variation (Huettmann and Diamond, 2001).

The lower correlations seen between the foraging radius distributions and aerial survey data, compared to GPS tracking data, may also be due to the resolution of the underlying data. This is unlikely to be the case for spatial resolution since the Dutilleul's test groups all similar value cells into larger blocks for comparisons. Temporal resolution may be more important. Survey data is a snapshot of the distribution in a given area at a given time and will be very much dependent on the seascape (e.g. sandbanks (Fijn et al., 2016)) and the environmental conditions (e.g. wind strength/direction (Gibb et al., 2017)) on that day or at that time. Foraging radius models are unaffected by such variation, and may represent average distributions over longer periods of time. GPS data is collected over a period of days to weeks, and therefore also likely to include more environmental variability. In cases where multi-year survey data is not available it may be more appropriate to utilise foraging radius distributions (based on robust colony data) to inform spatial management (e.g. MPAs) as these will better reflect spatio-temporal variability in the distribution of breeding individuals. Furthermore, survey data may be less reliable for some species due to misidentification or low detectability. European storm-petrels in particular can be difficult to pick out given their small size and dark colour. Other closely related species, such as cormorants and shags, may be difficult to separate, and additionally spend much of their time underwater whilst at sea.

When benchmarking correlations between foraging radius distributions and aerial survey data against a more complex GAM approach, we noted higher correlation values for GAM outputs. This is unsurprising given that aerial survey data was also included in the GAMs along with environmental variables. However two points are notable. The first is that correlation patterns across species for the foraging radius model/aerial survey and the GAM/aerial survey comparisons were similar. Similarly both modelling approaches

(foraging radius and GAM) performed better for auks and terns compared to the longer ranging procellariiformes and northern gannet. Correlation values higher than 0.3 were found only for auks using the GAM model, and for auks and terns using the foraging radius model; there was insufficient empirical survey data on tern observations for use in a GAM model. The lack of a major improvement in the use of GAM models could be explained by the fact that most of the environmental variables were dropped during the model selection process, with distance to coast, latitude, longitude and an interaction between latitude and longitude often the only explanatory variables retained. Indeed, for many centrally-placed species it appears that distance to the coast or colony is one of the strongest drivers of seabird occurrence and abundance (Johnston et al., 2015; Warwick-Evans et al., 2018), emphasising further why foraging radius models may be an effective, pragmatic approach.

Finally, we found that correlation values generally increased marginally with the use of mean maximum foraging range in the foraging radius model as opposed to maximum foraging range, although not in all cases. As estimates for maximum foraging range often come from a single study, it may be more appropriate to take a conservative approach and use mean maximum foraging range, particularly if the distribution is to be used for site designation purposes. MPA designations are usually based on core foraging areas, which is often taken as the 50% utilisation distribution (Arcos et al., 2012; Lascelles et al., 2016). It should also be noted that maximum foraging range is likely to vary with colony size (Jovani et al., 2015) and where the relationship is clear, e.g. for gannets (Lewis et al., 2001), this should be accounted for in the foraging radius model.

Conclusions

Overall the foraging radius method showed a reasonable match with empirical GPS data at the colony level, and only slightly underperformed at the regional level compared to a much more complex model requiring extensive empirical survey data. Our findings support the suggestion that foraging radius models may be a viable alternative for assessing at sea distributions rather than collecting additional empirical data (Afán et al., 2018; BirdLife International, 2010a; Critchley et al., 2018; Grecian et al., 2012), particularly when resources are limited. The foraging radius method is a far quicker and more cost-effective method for assessing at-sea distribution over a large area compared to GPS tracking studies or at-sea surveys. We suggest that further empirical research is needed over a larger number of species, colonies and regions, focusing on the ability of foraging radius models to capture average distributions over longer time periods.

Acknowledgements

We are grateful to the land owners for providing access to colonies for the GPS tracking studies: Feichin Mulkerrin at High Island, Pat and Liezel Bellue at Little Saltee, and the Neale Family at Great Saltee. The design and funding for aerial surveys were provided by Ireland's Department of Communication, Climate Action and Environment and the Department of Culture, Heritage and the Gaeltacht, under the ObSERVE Programme established in 2014. We are grateful for the support and assistance of both Departments in undertaking this work. We would particularly like to thank the Aerosotravia pilots Romain Fert, Paul Rameau and Laurent Pellicer, the plane's engineer Noel Barr, and observers Mick Mackey, William Hunt, Ciaran Cronin, Steve Geelhoed, Nicole Janinhoff, Hans Verdaat, Nick Richardson, Milaja Nykanen, and Patricia Breen for their collective efforts and contribution to the aerial surveys. Funding for development of foraging radius distributions was provided by the Petroleum Infrastructure Program (IS013/08), and funding for telemetry work was provided by the Zoological Society of London (Good gifts programme), Petroleum Infrastructure Programme (IS013/08), and the Irish Research Council (GOIPD/2015/81).

Chapter 4

An updated oil vulnerability index for seabirds: a European case study

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Author contributions: The study was designed by E.J.C., A.K., M.J.J, and J.L.Q.; E.J.C. carried out the data collection and analysis, with contribution from A.K.; E.J.C. led the writing of the chapter with contributions from all authors.

4.1 Abstract

Seabird vulnerability to oil pollution, and subsequent mortality, has been highlighted during a number of high profile disasters in recent decades. Understanding the spatial distribution of risk posed by marine infrastructure is crucial for effective mitigation and management of current and potential risks. Vulnerability indices can be used to assess risk to seabirds from offshore energy infrastructure by combining factors relating to behaviour, movement and conservation status. We develop a new Oil Vulnerability Index (OVI) that accounts for the potential attraction of seabirds to, or their avoidance from, offshore infrastructure, with updated information on population sizes and conservation status. The new index highlights Procellariiformes such as the northern fulmar *(Fulmarus glacialis)* and European storm-petrel *(Hydrobates pelagicus)* as more vulnerable to risks from petroleum industry than previously considered, largely because of a high reliance on the marine environment and attraction to offshore infrastructure. Conversely, previously high vulnerability species such as divers *(Gaviidae)* and skuas *(Stercorariidae)* are now considered lower risk because of limited amounts of time spent on the water in offshore areas. To account for indirect impacts to seabirds actively avoiding oil infrastructure and service vessels we develop a separate index to calculate vulnerability to displacement (DVI) from habitats of importance. The DVI shows that divers and auks are particularly susceptible to displacement. Applied to at-sea distributions of seabirds, the new indices provide a valuable tool for assessing risk and informing mitigation.

4.2 Introduction

Seabird populations are in decline globally (Paleczny et al., 2015), and while there are a number of readily observable causes such as nesting habitat destruction and introduced predators (Croxall et al., 2012), there are likely to be numerous additional 'hidden' losses at sea due to anthropogenic impacts. By-catch in fisheries is estimated to kill at least 160,000 seabirds annually (Anderson et al., 2011), and oiling incidents, whilst better mitigated than by-catch, are still likely to cause thousands of seabird mortalities per year (Wiese and Robertson, 2004; Wilhelm et al., 2007). Contact with oil is generally fatal for seabirds due to multiple physiological impacts such as impairment of thermoregulation, flight, diving, and feeding behaviours, and internal regulatory functions (Briggs et al., 1996; Helm et al., 2015; Jenssen, 1994; O'Hara and Morandin, 2010; Troisi et al., 2016). Given the severity of any contact with oil, even small scale discharges can cause significant mortality (Burger, 1993) and regular small spills have similar cumulative impacts to the less frequent large scale spills (Camphuysen, 1989; Fox et al., 2016).

Whilst accidental oil tanker spills both in Europe and globally have declined in number and volume in the last two decades, the offshore location of spills that do occur can make their impact hard to measure (Wilhelm et al., 2007), and large spills (i.e. more than 7 tonnes) still arise (EEA, 2008). Regular oil spills still occur in the English Channel and Bay of Biscay which are important over-wintering areas for auks. For example the Erika spill in 1999 killed up to 130,000 auks (Le Rest et al., 2016). Furthermore, although tanker spills are declining, a number of large oil well blowouts in recent years have contributed significantly to seabird mortality due to oil pollution (Haney et al., 2017). Predicting the potential impacts of future spills is even more challenging given the dynamic nature of the marine environment. Oil and gas activities in the North East Atlantic are expanding into deeper waters in the wider Atlantic and northwards into the Arctic (OSPAR Commission, 2009). Lack of knowledge of the distribution of seabirds in these regions and their potential vulnerability to oil pollution limits our ability to predict the risks to seabird populations from proposed and existing petroleum exploration sites.

Vulnerability indices are an essential tool for assessing potential impacts from anthropogenic activities (Certain et al., 2015; Furness and Tasker, 2000; Garthe and Hüppop, 2004). For example, the increasing development of marine renewable energy infrastructure has led to considerable efforts to assess their potential impacts to seabird populations using vulnerability indices. In contrast, the Oil Vulnerability Index (OVI) has not

been updated since it was first developed by Williams et al. (1995), and there is scope to refine it based on more recent methods used for renewable energy indices. These indices generally combine multiple risk factors to generate an overall vulnerability score for individual species, and subsequent vulnerability ranking in relation to other species (Garthe and Hüppop, 2004; Furness et al. 2012). Factors such as the proportion of time spent on the water and the potential rate of population recovery are scored on a scale of low to high vulnerability, and weighted according to their estimated influence on overall risk. Vulnerability factors are grouped into three main components: the likelihood of an individual being in an area with marine energy devices (hereafter called habitat overlap); the risk of interaction when they are in that area (e.g. collision or oiling risk); and conservation status. The likelihood of entering an area, and the risk to a bird when there, are both components that predict risk to the individual bird. The conservation status component predicts the sensitivity of a population to mortality (e.g. caused by oiling or collision with infrastructure). Combining all three components gives a score for the population level vulnerability of each species to marine energy infrastructure.

Most renewable vulnerability indices build on an initial wind farm vulnerability index developed by Garthe and Hüppop (2004), which averages risk factors of a similar nature, including conservation status, before combining them. Subsequent indices have modified the approach by changing the weighting of factors to account for variation in importance of factors, as well as including factors that measure attraction to, or avoidance of, marine energy infrastructure (Furness et al., 2013; Wade et al., 2016). Many of the risk factors used for renewable vulnerability indices are also likely to be relevant for assessing impacts from petroleum activities. In particular, given that birds will only suffer from collision if they actually enter an area with marine energy infrastructure this is a factor that will have a significant influence on overall vulnerability.

As well as ranking species to highlight those most at risk from potential impacts, vulnerability indices can be used for a spatial risk assessment by combining them with species' distributions and known or future risks (Tulloch et al., 2015). These maps can help to inform marine spatial planning for future offshore energy developments, guide mitigation measures following an oil spill, and inform follow-up assessment on population impacts. Previous spills (e.g. Deep Water Horizon in the Gulf of Mexico) have shown how the lack of information on species distributions can significantly limit the ability to assess the overall population impact from a spill (Haney et al., 2014). Collecting sufficient

empirical data on seabird distributions can be extremely challenging given the large ranges that many species cover. However, foraging radius distribution models based on foraging radii and breeding population size provide a useful alternative for quickly predicting at-sea distributions for spatial assessments (Afán et al., 2018; Critchley et al., 2018; Grecian et al., 2012).

Given the age of the most recent oil vulnerability index (Williams et al., 1995), and improvement in our knowledge of seabird behaviour and conservation status in Britain and Ireland, it is timely to update the assessment of seabird vulnerability to oil spills and infrastructure. Here we develop a new Oil Vulnerability Index for seabirds in British and Irish waters, following recent methods used for marine renewables indices. All of the relevant vulnerability factors required for an OVI are reviewed and updated with the most recent available data. We also develop a Displacement Index for assessing seabird vulnerability to being displaced due to disturbance by offshore petroleum infrastructure and transport vessels. We apply both indices to foraging radius distributions of seabirds in Ireland and the UK, based on current population estimates, to produce maps of seabird sensitivity to oil pollution and offshore petroleum activity.

4.3 Methods

Updating the Oil Vulnerability Index (OVI)

Generating the OVI involved six steps: 1) Identifying factors that could influence individual risk and population level vulnerability to offshore petroleum industry (see Table 4.1); 2) Updating factors with most recent data; 3) Grouping factors into one of three components: a) Habitat overlap, b) Risk of oiling, and c) Conservation status; 4) Identifying possible formulae from the literature for combining the vulnerability factors from previous studies; 5) Calculating vulnerability scores and species rankings using each formula; and 6) Choosing the most suitable new index based on the flexibility it allows in the weighting of risk factors. We then assessed differences in rankings between the chosen OVI and all other OVI formulae using a correlation analysis to inform our understanding of how the risk factors and their combination influence vulnerability scores.

A: Habitat overlap factors

Factors related to disturbance of birds due to offshore petroleum infrastructure were updated following Wade et al., (2016) (Table 4.1, A1-A2). There have been limited systematic studies on disturbance and attraction of seabirds to offshore petroleum infrastructure, such as oil rig platforms and tankers (but see Wiese et al., 2001 and Ronconi et al., 2015 for a summary of potential interactions), and similar data for offshore wind farms (Wade et al., 2016) were used instead. Fixed infrastructure and transport vessels were treated as separate factors. Disturbance can have both positive and negative effects on populations; a high level of disturbance/avoidance of offshore petroleum infrastructure will result in low oiling risk, whereas attraction to infrastructure, due to bright lights or fish aggregation for example (Wiese et al., 2001), will result in increased oiling risk. Attraction may also cause additional mortality due to direct collision with platforms or incineration in gas flares (Ronconi et al., 2015). Previous offshore energy vulnerability indices either did not include disturbance or accounted for it as a negative factor that increased individual risk. To correct for this, Wade et al. (2016) modified the wind vulnerability index from Furness et al. (2013) to incorporate disturbance as a positive effect, which lowered overall risk of collision.

Conversely, high levels of disturbance could lead to some species being displaced from valuable foraging habitats, leading to more indirect impacts. To account for the negative effect of disturbance to populations, a separate index of vulnerability to displacement (DVI)

by offshore petroleum infrastructure (both fixed platforms and vessels) was calculated, following Furness et al. (2013), Certain et al. (2015), and Wade et al. (2016).

As species that spend a significant amount of time at sea are considered to be at greater risk than those that forage close to shore or over land, a factor accounting for reliance on the marine environment was used following Williams et al. (1995) (Table 4.1, A3). In contrast, when assessing vulnerability due to displacement, species which have limited foraging ranges and strong habitat specialisations are likely to be more greatly affected by any level of disturbance. Therefore a factor relating to habitat use flexibility (Table 4.1, A4) was included in the DVI to account for this.

B: Oiling risk factors

The original OVI (Williams et al. 1995) incorporated data on species oiling rates taken from North Sea beached bird surveys (Camphuysen, 1989, 2010). However, due to concerns about the robustness and transferability of results from beached bird surveys this factor was not included in any of the new indices. Instead the primary risk factor identified as being specific to oiling risk was percentage of time spent on the water (Table 4.1, B1). Values for this were taken from the inverse of reported values for percentage time flying in Furness et al. (2012).

C: Conservation factors

Finally, conservation factors were updated to be geographically relevant for the area of study - Europe, Britain and Ireland - and to include more recent data on population sizes (Table 4.1, C1-C6). Conservation status was based on both national assessments from the Irish and UK Birds of Conservation Concern reports (Colhoun and Cummins, 2013; Eaton et al., 2015) and European IUCN red list status (BirdLife International, 2015). Recent population estimates were sourced from the JNCC for regional populations (JNCC SMP, 2018) and IUCN for European populations (Choudhury at al., 2016). Factor scores for potential rate of recovery of a population (Table 4.1, C6) were taken from Williams et al. (1995).

Table 4.1 Vulnerability factors included in calculating risk and vulnerability scores

Notation	Factor	Source
	Habitat overlap	
A1	Disturbance by structures	Wade et al. (2016)
A2	Disturbance by vessels & helicopters	Wade et al. (2016)
A3	Reliance on the marine environment	Williams et al. (1995)
A4	Habitat use flexibility	Wade et al. (2016)
A5	Attraction to structures	Inverse of A1
A6	Attraction to vessels & helicopters	Inverse of A2
	Risk of oiling	
B1	Percentage of time on water	Inverse of time in flight from Furness et al. (2012)
	Conservation status	
C1	EU birds directive status	European Commission (European Commission, 2010a)
C2	UK conservation status	BOCC4 (Eaton et al., 2015)
C3	Irish conservation status	BOCCI 2014-2019 (Colhoun and Cummins, 2013)
C4	IUCN conservation status	IUCN European Red List - (BirdLife International, 2015)
C5	Percentage of the biogeographical population	IUCN (Choudhury et al., 2016) & JNCC (JNCC, 2018)
C6	Potential rate of recovery of a population	Williams et al. (1995)

Vulnerability index combinations

There are multiple ways of combining factors in a vulnerability index, with no agreed formula that holds true for all possible risks. We calculated vulnerability scores using a number of different factor combinations to assess how this affected the overall risk rankings for species. The combinations follow those used to calculate vulnerability scores for other marine energy risks: wind (Certain et al., 2015; Furness et al., 2013; Garthe and Hüppop, 2004; Wade et al., 2016); wave (Furness et al., 2012); and tidal (Furness et al., 2012). All indices used the updated factors listed in Table 4.1 (see Table E.1 for factor scores for all species). The scores calculated were then used to generate ranks for each species for each new OVI. Ranks within each index were absolute from 1 to 34.

All OVIs firstly combine habitat usage and oiling risk factors (A; B) to give an oiling/collision risk score for individuals of each species. The conservation factors (C) are combined together for each species to give a score for population level sensitivity (in the specified region) to any impacts on individuals (i.e. mortality) within the species' populations. The oiling/collision risk score is then multiplied by the conservation score to calculate overall population level vulnerability to interactions with offshore petroleum infrastructure.

Most OVI formulae are a linear combination of factors, either multiplicative or additive, with some weighting of factors considered higher importance (OVIs 1, 7, 8), while some do not distinguish importance and take the average of all factors within a component (OVI 3). OVI 9 treats factors as either primary factors (the base), or aggravating factors (the exponent) which mediate the influence of related primary factors, according to the method suggested by Certain et al. (2015). A weighting added to the aggravating factor (0.5 in this case, as recommended by Certain et al. (2015)) adjusts their influence over the primary factors. Weighting values close to 1 result in little difference between the primary and aggravating factors, whereas values close to 0.1 give the aggravating factors a much higher contribution to the final score.

A correlation matrix was calculated using the corrplot package (Wei and Simko, 2017) in R to assess whether changes in the formula for combining factors resulted in changes in the rankings of species across indices. Subsequent analysis used OVI 9, which allows for more flexibility in weighting factors according to their influence on oiling/collision risk.

$$OVI\ 1 = A3 + (2\ \times B1) + (2 \times C5) + C6$$

- *follows Williams et al. (1995)*

$$OVI\ 2\ = A3 \times (B1/A1) \times \sum_{i=1}^{6} C_i$$

- *follows Wade et al. (2016)*

$$OVI\ 3 = (A1 + A2 + A3)/2 \times B1\ \times \sum_{i=1}^{6} C_i\ /6$$

- *follows Garthe & Hüppop (2004)*

$$OVI\ 4 = A3\ \times B1\ \times \sum_{i=1}^{6} C_i$$

- *follows Furness et al. (2013)*

$$OVI\ 5 = ((A1 + A2 + A3) \times B1 \times \sum_{i=1}^{6} C_i)/100$$

- *follows Furness et al. (2012)*

$$OVI\ 6 = (A1 + A2 + A3 + B1) \times \sum_{i=1}^{6} C_i$$

- *follows Furness et al. (2012)*

Weightings for the indices that follow: x = 2; y = 3; z = 1.

$$OVI\ 7 = x((A1 + A2 + A3)/3) \times y(B1) \times z(\sum_{i=1}^{6} C_i\ /6)$$

$$OVI\ 8 = x((A1 + A2 + A3)/3) + y(B1) + z(\sum_{i=1}^{6} C_i\ /6)$$

For the following index all factors were divided by 5 to give scores of between 0 and 1

$$OVI\ 9 = (B1 \times (A5 + A6)/2)^{(1-A3/(A3+0.5))} \times ((C1 + C2 + C3 + C4 + C5)/5)^{(1-C6/(C6+0.5))}$$

- *follows Certain et al. (2015)*

Displacement vulnerability index (DVI)

To account for the negative effect of disturbance by structures, service vessels, and helicopters a displacement score was also calculated for each species following Certain et al. (2015). The formula used to calculate the scores was:

$$DVI = (((A1 + A2)/2)^{(1-A4/(A4+0.5))}) \times ((C1 + C2 + C3 + C4 + C5)/5)^{(1-C6/(C6+0.5))}$$

Cluster analysis

To see if similar species (e.g. family groups) have similar levels of vulnerability to oiling/collision and displacement, we carried out a cluster analysis in R using Wards D method (Ward, 1963). Clustering was based on similarity in Euclidean distance between species rankings for both the OVI and DVI.

Vulnerability maps

To assess the vulnerability of seabirds spatially, the vulnerability indices (OVI & DVI) were applied to distributions of all breeding seabirds at a national level, using Ireland as a case study. Ireland hosts important numbers of breeding seabirds and has seen a recent increase in interest for exploration of offshore oil and gas resources. Oil vulnerability maps were produced by multiplying the log of seabird density per 5 x 5km grid square, generated using a foraging radius model approach (Chapter 2), by the species' OVI score. This follows suggestions by other vulnerability studies, where the use of log density ensures that areas of extremely high seabird density do not skew the distributions (Williams et al. 1995 and Bradbury et al., 2014). To give greater distinction between high and low risk species, vulnerability scores were normalised to between 1 and 0.01 prior to multiplying by log density, inflating the scores for high risk species and reducing the scores for low risk species, e.g. the highest score of 0.8 was up-weighted to 1 and the lowest score of 0.38 was down-weighted to 0.01. Individual maps were produced for each species and then summed together to assess overall oiling/collision risk to all seabirds in the region. This method was repeated using the DVI scores to produce separate maps of displacement vulnerability. For plotting purposes, values in each grid square were again normalised to between zero and one to allow comparisons across areas and between maps.

Spatial exposure risk

The vulnerability maps essentially only show potential risk and need to be combined with maps of existing infrastructure to assess actual exposure risk (Pirotta et al., 2018). Both the

oil and displacement vulnerability maps were overlaid with polygons of a) petroleum option and licence blocks to account for risk from exploration activities, and b) major European shipping lanes which are likely to have higher density of oil tankers than surrounding waters. Data for petroleum licence blocks and their associated authorisations were obtained from the Irish Petroleum Affairs Division (DCENR, 2017). Data for European shipping lanes were taken from the European Commission's 'motorways of the sea' project which designates specific marine corridors for freight movement in the European Union (European Commission, 2010b). Additional polygons of ferry routes (Marine Institute, 2017) were used for the displacement maps. Risk will not be uniform across all areas and therefore grid squares were scored from 1 (low risk) to 4 (high risk) as follows: blocks with a petroleum licence option = 1; ferry routes = 2 (for DVI only); blocks with a granted exploration licence = 2; shipping lanes = 3; blocks with a lease undertaking = 3; and blocks with a petroleum lease granted = 4. The sum of risk scores in each grid square was calculated to generate an overall risk layer. Vulnerability values within the risk activities polygons were extracted and weighted by the associated risk score. Resulting exposure risk values were normalised to between zero and one to allow comparisons across different maps and areas.

4.4 Results

Oil vulnerability indices correlations

Figure 4.1 shows correlation values between all OVIs. All indices had low correlation with rankings from the original OVI reported in Williams et al. (1995), which did not include any updated factors. We next compared correlations of all other indices with OVI 1, which follows the same formula as the old OVI but was calculated using updated data, and removes the factor that relies on data from beached bird surveys. OVI 2 and OVI 9, which both include disturbance as a positive factor (other OVIs treat disturbance as a negative factor) correlate more strongly with OVI 1 than with any of the other OVIs. Not much difference is seen between OVIs 3-8 as they all correlate strongly with each other. OVI 9 was developed as the most suitable Oil Vulnerability Index as the formula allows more flexibility in weighting factors according to their influence on oiling risk, by changing the weighting added to the aggravating factors. This OVI, which builds on the method recommended by Certain et al. (2015), also distinguishes between factors that are conditional to each other and should be multiplied and those that are of a similar nature and should be averaged. Whilst the argument could be made for using the simplest formula (OVI 1 or 2), OVI 9 clearly defines the mathematical relationship between factors and follows rules that can be applied to any vulnerability assessment, therefore making scores more comparable across indices.

Vulnerability scores and rankings

Table 4.2 shows the updated scores and rankings for all seabird species for both the new OVI (OVI 9) and the DVI. The scores and rankings for OVI 9 (Table 4.2, e) vary greatly from those calculated according to the original OVI (Williams et al., 1995) (Table 4.2, a). OVI 9 shows that most procellariiforms, such as the northern fulmar and European storm-petrel, are now considered more vulnerable to the risks associated with offshore petroleum industry, while previously high vulnerability species such as divers and skuas are considered lower risk. The DVI scores show divers and auks are particularly susceptible to displacement due to offshore activities, whilst all gull species show low vulnerability to displacement.

Relationship between OVI 9 and DVI

Following a cluster analysis across both OVI 9 and DVI rankings (Figure 4.2), it was found that species generally grouped taxonomically, e.g., most procellariiforms, auks (Alcidae),

divers (Gaviidae), and gulls (Laridae) are clustered close together. The scatterplot in Figure 4.3 shows the relationship between OVI 9 and DVI for all taxonomic groups, also highlighting the distinct clusters. The alcidae group show highest combined vulnerability for both OVI 9 and DVI, and a positive correlation across the two indices. Gulls appear to have a negative correlation between OVI 9 and DVI, with a decreasing OVI score as DVI increases. No other relationships are visible for the other seabird family groups, but in general they still form distinct clusters on the scatterplot (Figure 4.3). Procellariiforms have high OVI 9 scores and very low DVI scores, whereas many of the diver and sea-duck species conversely have high DVI scores and lower OVI 9 scores.

Spatial distribution of vulnerability and risk

Spatial vulnerability to oil infrastructure risks and displacement risks in the Irish EEZ for all species combined can be seen in Figure 4.4. For both risks, high vulnerability is observed in the Irish Sea, particularly north of Dublin Bay. The south west coast of Ireland appears to have higher vulnerability scores for oiling/collision compared to displacement, and in general high displacement vulnerability is concentrated closer to the shore than oil infrastructure vulnerability. Spatial vulnerability to oiling/collision for representative high vulnerability order/family groups (procellariiforms and auks) and a low vulnerability family group (terns) can be seen in Figure 4.5.

The exposure risk maps for oil infrastructure vulnerability and displacement (Figure 4.6) again show that the highest vulnerability occurs along the east coast where high seabird density overlaps with a major European shipping lane, and a licenced petroleum exploration block south of Dublin Bay. High levels of displacement vulnerability are also seen in spatially restricted areas on the west and south west coasts due to overlap with ferry routes (Figure 4.6b).

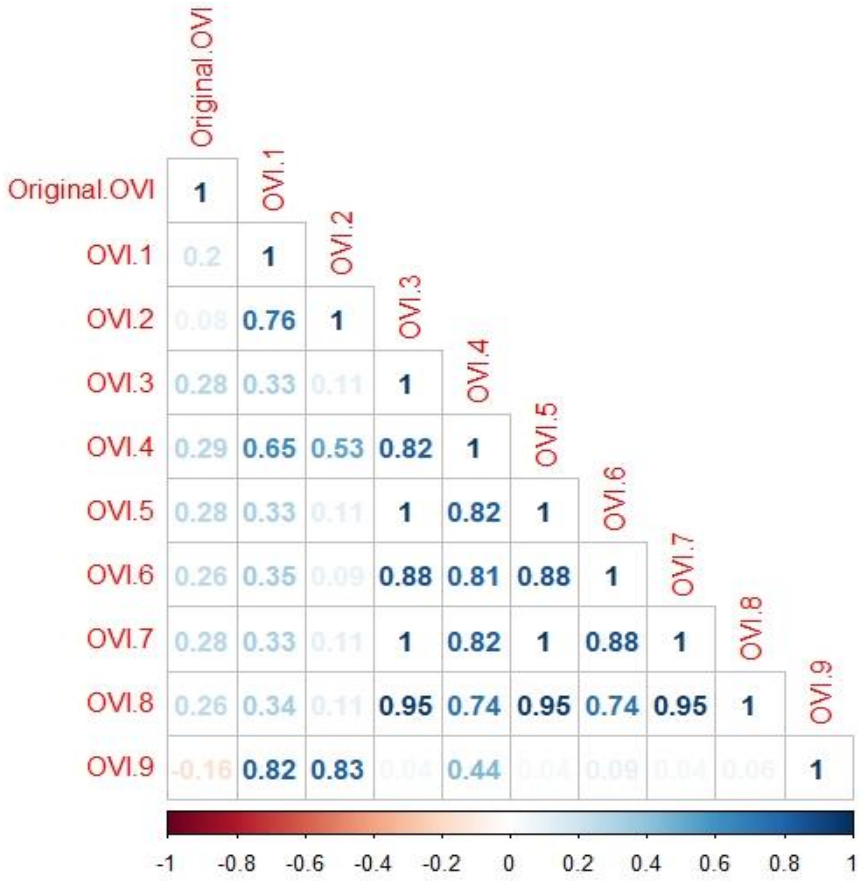


Figure 4.1 Correlation plot for all OVIs generated using the corrplot package (Wei & Simko 2017) in R. High values, in dark blue, indicate a strong similarity in species rankings between two indices.

Table 4.2 Scores and ranks for a) OVI from Williams et al., 1995, b) population oil infrastructure vulnerability (OVI 9 = Oiling/collision risk * Population sensitivity), c) population displacement vulnerability (DVI = Displacement risk * Population sensitivity). Rankings are colour coded as follows: ranks 1-9 = red; ranks 10-17 = orange; ranks 19-25 = yellow; and ranks 26-34 = green. See Table E.2 for Oiling/collision risk, Displacement risk, and Population sensitivity scores and rankings.

	Original OVI		OVI 9		DVI	
Species	**Score**	**Rank**	**Score**	**Rank**	**Score**	**Rank**
Arctic skua *Stercorarius parasiticus*	24	6	0.48	23	0.34	30
Arctic tern *Sterna paradisaea*	16	29	0.47	26	0.57	17
Atlantic puffin *Fratercula arctica*	21	14	0.77	3	0.72	7
Black guillemot *Cepphus grylle*	29	1	0.66	15	0.64	10
Black-headed gull *Larus ridibundus*	11	34	0.72	8	0.49	24
Black-legged kittiwake *Rissa tridactyla*	17	27	0.70	11	0.54	19
Black-throated diver *Gavia arctica*	29	2	0.41	31	0.82	1
Common eider *Somateria mollissima*	16	30	0.54	21	0.57	16
Common goldeneye *Bucephala clangula*	16	31	0.39	32	0.61	12
Common guillemot *Uria aalge*	22	11	0.71	9	0.76	4
Common gull *Larus canus*	13	33	0.62	17	0.48	25
Common scoter *Melanitta nigra*	19	21	0.38	34	0.69	8
Common tern *Sterna hirundo*	20	17	0.46	27	0.56	18
European shag *Phalacrocorax aristotelis*	24	7	0.71	10	0.63	11
European storm-petrel *Hydrobates pelagicus*	18	25	0.76	4	0.28	31
Great black-backed gull *Larus marinus*	21	15	0.74	6	0.43	26

Great cormorant *Phalacrocorax carbo*	20	18	0.57	18	0.52	21
Great northern diver *Gavia immer*	29	3	0.51	22	0.78	2
Great skua *Stercorarius skua*	25	5	0.64	16	0.35	29
Great-crested grebe *Podiceps cristatus*	23	9	0.38	33	0.49	22
Greater scaup *Aythya marila*	20	19	0.45	29	0.61	13
Herring gull *Larus argentatus*	15	32	0.78	2	0.38	27
Lesser black-backed gull *Larus fuscus*	19	22	0.74	5	0.36	28
Little auk *Alle alle*	22	12	0.55	20	0.49	23
Little tern *Sterna albifrons*	19	23	0.46	28	0.59	14
Long-tailed duck *Clangula hyemalis*	17	28	0.56	19	0.66	9
Manx shearwater *Puffinus puffinus*	23	10	0.74	7	0.28	32
Northern fulmar *Fulmarus glacialis*	18	26	0.80	1	0.27	33
Northern gannet *Morus bassanus*	22	13	0.66	14	0.54	20
Razorbill *Alca torda*	24	8	0.70	12	0.75	5
Red-throated diver *Gavia stellata*	29	4	0.42	30	0.78	3
Sandwich tern *Sterna sandvicensis*	20	20	0.48	24	0.58	15
Sooty shearwater *Ardenna grisea*	19	24	0.70	13	0.26	34
Velvet scoter *Melanitta fusca*	21	16	0.47	25	0.72	6

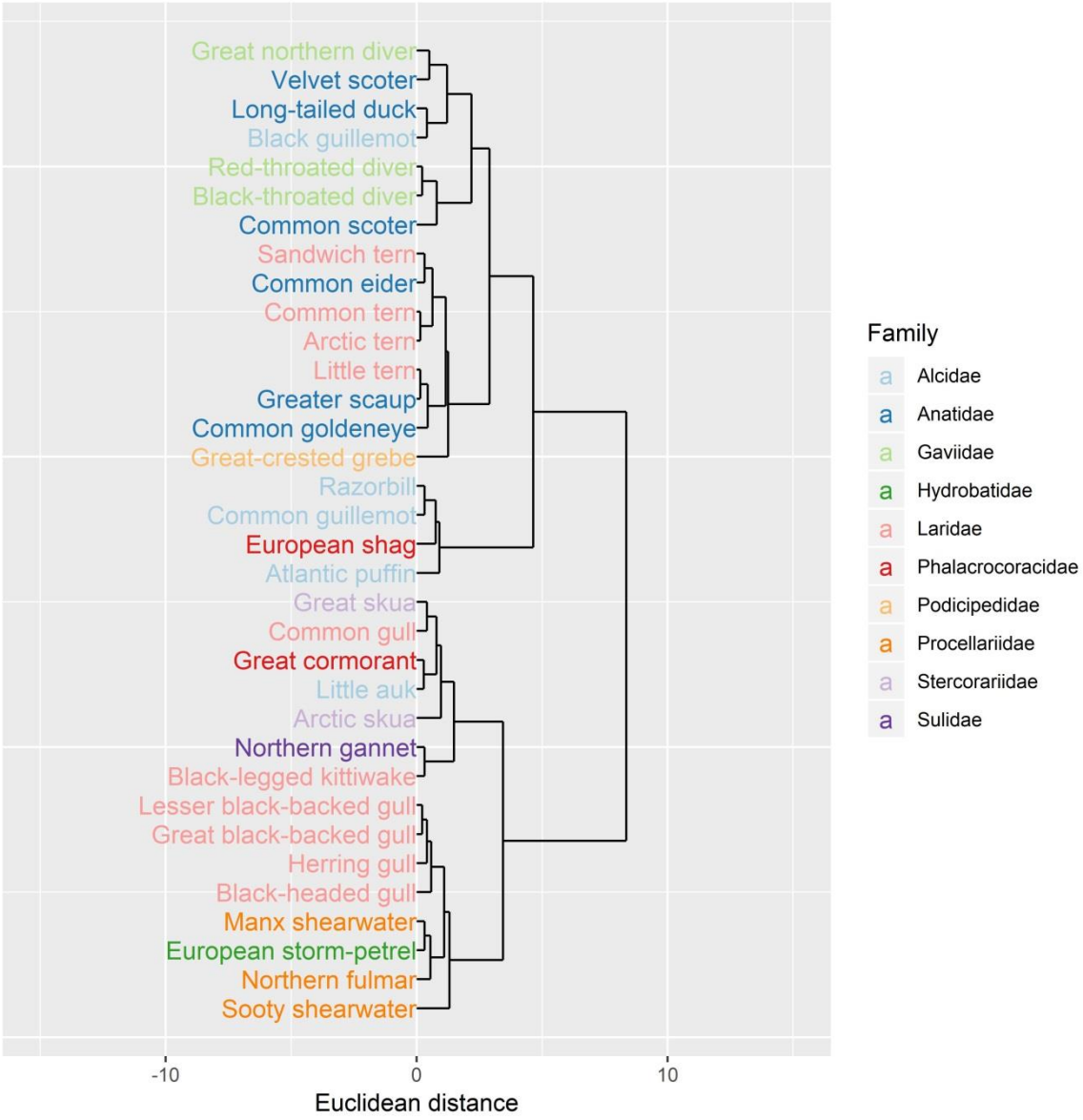


Figure 4.2 Dendogram showing clustering of species according to dissimilarities in OVI and Displacement rankings. Larger Euclidean distances represent greater dissimilarity between groups. Colour coding relates to taxonomic family group, see legend.

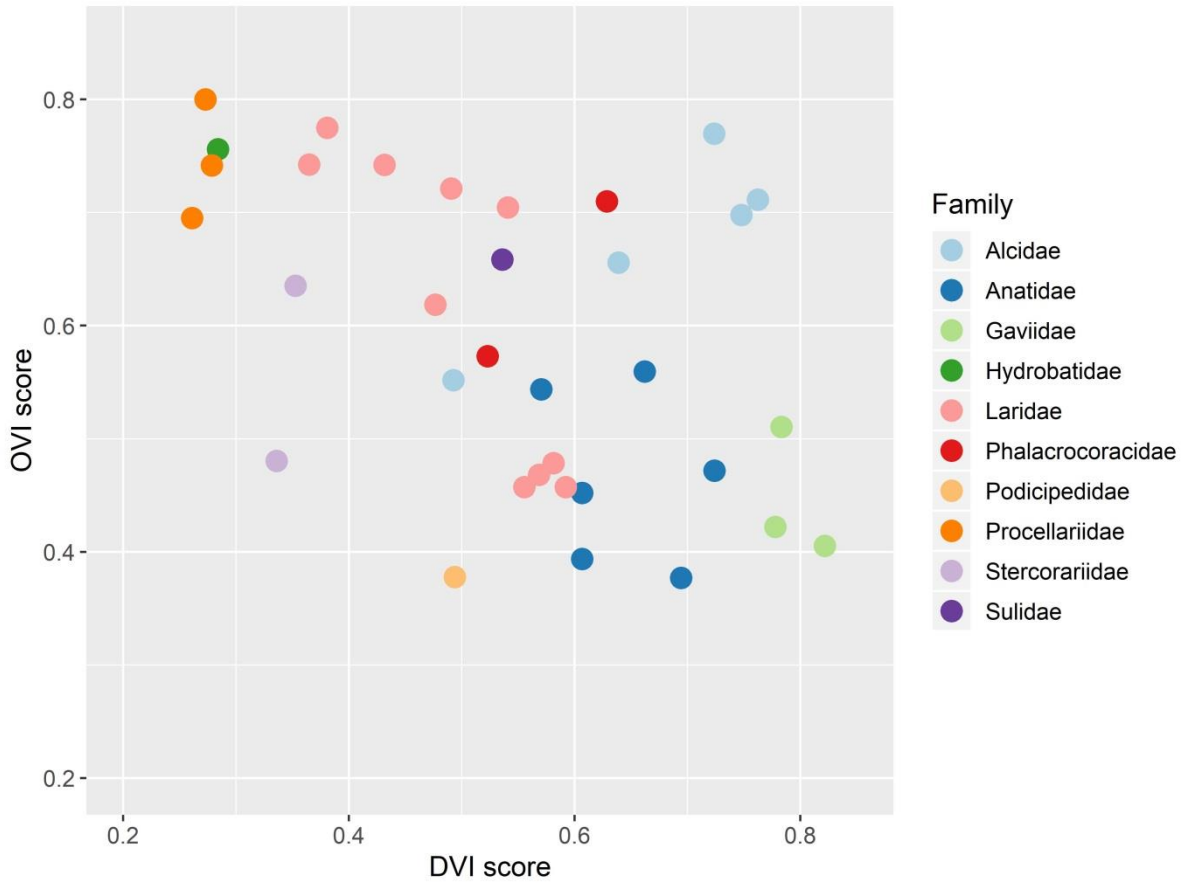


Figure 4.3 Scatterplot showing relationship between OVI 9 and DVI scores for all species. Colour coding relates to taxonomic family group, see legend.

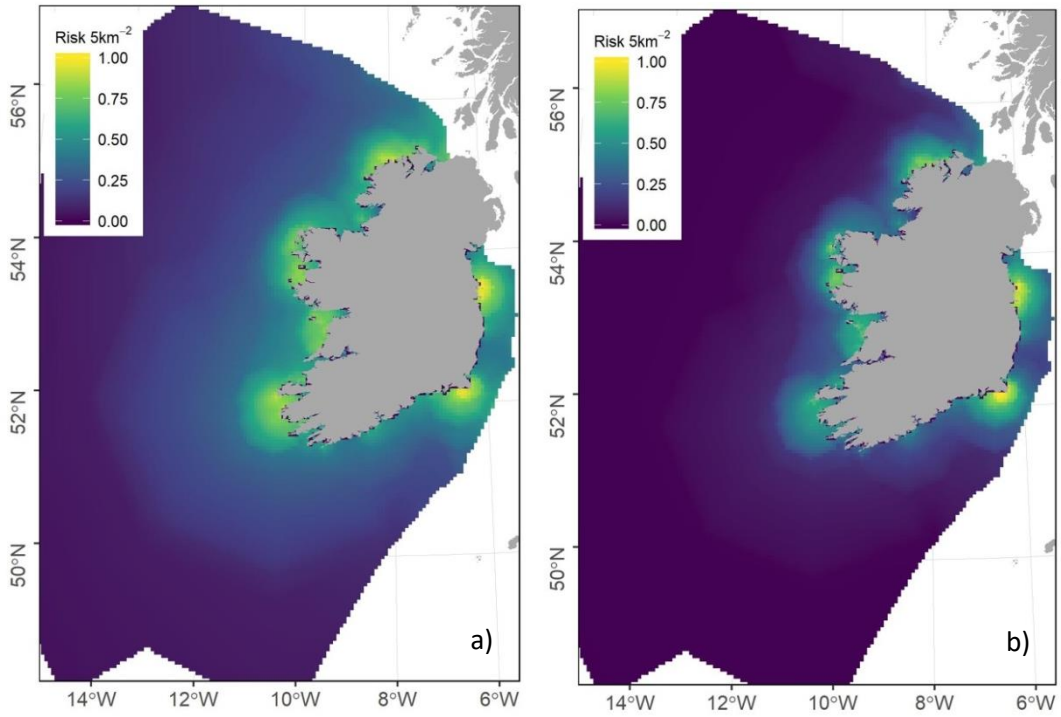


Figure 4.4 Vulnerability of all species to a) oiling/collision risks and b) displacement risks in Irish waters. Vulnerability is normalised to between 0.01 and 1 to allow comparisons across the two maps.

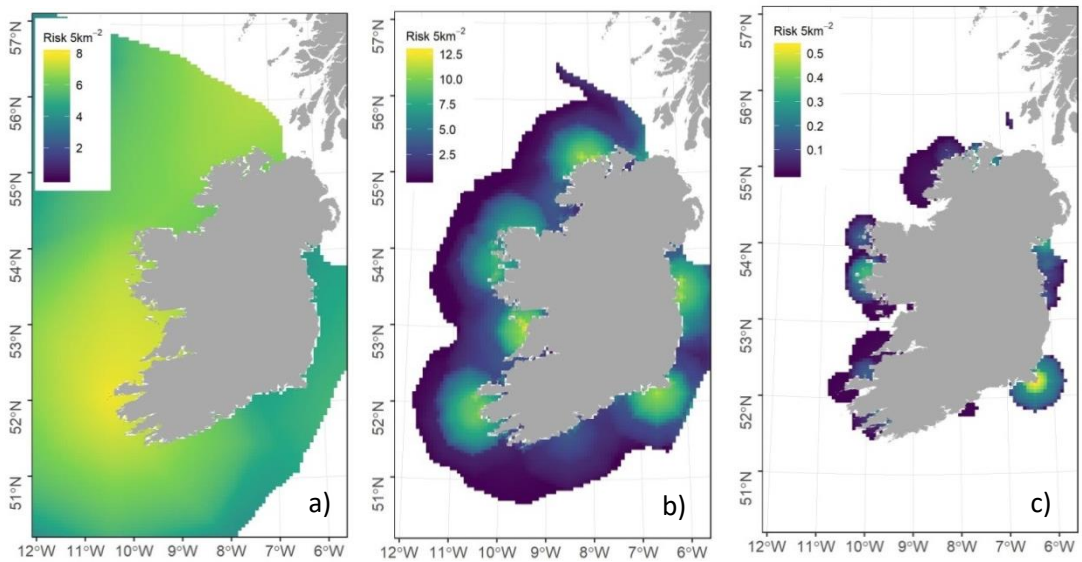


Figure 4.5 Vulnerability to oiling/collision risks in Irish waters of a) procellariiforms; b) auks; and c) terns. Note difference in scale for risk values across maps.

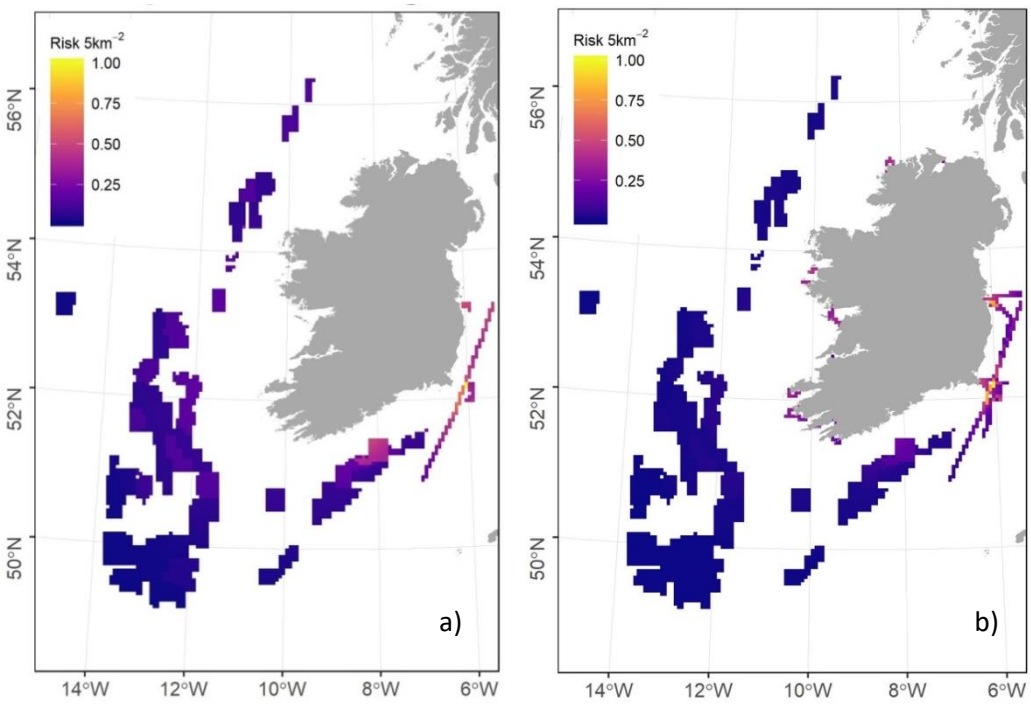


Figure 4.6 Risk of exposure of all species to a) oiling/collision and b) displacement in Irish waters. Polygons represent areas containing petroleum option and licence blocks (DCENR, 2017) and major European shipping lanes (European Commission, 2010b) in 6a, plus ferry routes Marine Institute, 2017) in 6b. Risk is normalised between 0.01 and 1 within risk areas.

4.5 Discussion

Seabird vulnerability to petroleum infrastructure is dependent on a species' movement ecology, behaviour at sea and conservation status. We found that the use of a new OVI formula accounting for all of these factors considerably changed species' vulnerability scores and overall rankings from the original OVI (Williams et al., 1995). Most species with high OVI scores had low DVI scores and vice versa, apart from auks which are relatively high risk for both. There was also a clear taxonomic trend when looking at similarities across the two vulnerability rankings, with family groups clustering together.

Oiling/Collision Vulnerability (OVI)

The greatest increase in oiling/collision vulnerability ranking was seen for gulls and procellariiforms, groups that both show high levels of attraction to offshore platforms and transport vessels. This suggests that the inclusion of factors accounting for attraction to petroleum offshore infrastructure is a key driver for changes to the oiling/collision ranking. For the most vulnerable species, high levels of attraction were coupled with either a large percentage of time spent on water (e.g. for gulls) or a high reliance on the marine environment (e.g. for procellariiforms). Additionally, procellariiforms, particularly storm-petrels and shearwaters, are attracted to the lights and flares on offshore platforms and are also known to take advantage of the concentration of prey in the waters immediately surrounding platforms (Wiese et al., 2001). Although gulls might overlap less with offshore platforms due to their shorter foraging ranges, they show strong co-occurrence with fishing vessels at sea (Wahl and Heinemann, 1979), which would increase their vulnerability. Whilst auks show only a medium level of attraction to offshore infrastructure, their foraging behaviour, spending a large percentage of time on the water with a high reliance on the marine environment, gives them a high score overall for individual oiling/collision risk. The addition of conservation factors to individual oiling/collision risk to generate population level vulnerability to petroleum infrastructure slightly changes the overall rankings. In particular, Atlantic puffin and European storm-petrel have a higher level of vulnerability when accounting for conservation factors (see Table 4.2 and Table E.2), most likely due to their status as birds of conservation concern in Ireland and the UK (Colhoun and Cummins, 2013; Eaton et al., 2015).

Conversely, species that were judged to be most vulnerable to petroleum infrastructure in the original OVI, such as divers and skuas, now rank the lowest using the updated OVI. The

original OVI is strongly influenced by the factors that account for reliance on the marine environment and potential rate of population recovery, which divers and skuas both score highly for. Their subsequent low ranking in the updated OVI can be attributed to either low attraction to offshore infrastructure and vessels (e.g. divers and grebes) or limited amounts of time spent on the water (e.g. skuas and terns).

The removal of an oiling rate factor based on beached bird surveys (Camphuysen, 1989, 2010) also influenced changes in species' scores and rankings. Whilst observational data on species specific susceptibility to oiling would be useful to include in an OVI, there is too much uncertainty around the representativeness of current data to warrant their inclusion. The recovery rate of seabird carcasses is often very low compared to overall mortality, as many carcasses will sink to the sea or be scavenged – for example a 15% recovery rate was estimated for the Exxon Valdez spill. Recovery rates will also be highly dependent on sea conditions, as well as geographic area (e.g. confined seas vs. open oceans) and species foraging range (e.g. recovery rates for coastal birds are likely to be far higher), so are not reliable as an accurate estimate of general susceptibility for a species (Piatt and Ford, 1996).

Displacement vulnerability (DVI)

An almost inverse pattern of rankings was found for seabird vulnerability to displacement due to offshore petroleum activity. Most species with high OVI scores had low DVI scores and vice versa, apart from auks which scored highly for both – most likely due to their poor conservation status (see Figure 4.3). Divers also have a high level of susceptibility to displacement due to offshore activities, which is not surprising given that they show significant levels of disturbance in combination with high reliance on the marine environment. This is supported by recent work in the UK that found divers, grebes and seaducks to have the greatest levels of displacement due to all anthropogenic activities (Cook et al., 2018). High DVI values for auks and divers are a cause for concern given that both of these groups are usually mid- to short- range foragers (Oppel et al., 2018). Even a small amount of displacement could preclude them from accessing important foraging habitats locally. The contrast in rankings between oiling/collision and displacement vulnerability highlights the importance of calculating vulnerability to these two risks separately. Combining both risks in to one ranking is likely to erroneously diminish estimates of the impact of either risk.

Spatial patterns of vulnerability and exposure risk

A difference in intensity of oiling/collision vulnerability and displacement vulnerability was also observed spatially, with oiling/collision vulnerability extending further offshore. Vulnerability to both risks is high in coastal waters, particularly in the Irish Sea and North Celtic Sea, as spatial vulnerability at the community level is primarily driven by the abundance of birds. However, displacement vulnerability maps show higher concentrations of values closer to near shore, most likely because species with higher vulnerability to displacement are generally coastal foragers with short foraging ranges, e.g. auks, divers and shags. Near-shore areas have also been highlighted as the areas of greatest risk for oil pollution in Irish waters by OSPAR, particularly in the winter months (OSPAR Commission, 2009). In contrast, values on the oiling/collision vulnerability map are spread out more diffusely due to pelagic species generally having higher OVI scores. Note that the foraging radius distributions used for this study are based on available population data from Seabird 2000 colony counts (Mitchell et al., 2004). The use of more recent population data would improve the robustness of density estimates and subsequent spatial vulnerability.

Whilst the vulnerability distribution maps can be utilised to inform future marine spatial planning, they do not reveal anything about the risks posed by current offshore petroleum activities. Therefore redistributing vulnerability within existing petroleum and shipping areas and weighting values according to activity type allows us to assess the areas of highest risk of exposure to oiling/collision or displacement. Unsurprisingly the highest exposure risk for both OVI and DVI is seen in coastal waters, particularly along the east coast, mainly due to the overlap of a major European shipping lane with areas of high seabird density. There are also medium levels of OVI risk in areas of active petroleum exploration on the south coast, and medium levels of DVI on the west coast where ferry routes cross areas of high seabird densities. Where other offshore activities (e.g. wind farms) are located in the same areas, the overall risk to seabird populations in the region would increase substantially. Spatial exposure risk is also likely to increase with further petroleum development; future-exploration blocks in European coastal waters appear to have significantly higher species richness than current license blocks, and greater proportional overlap with marine protected areas (Harfoot et al., 2018).

While we provide an updated vulnerability Index for oil, useful refinements to the approach could include using seasonal seabird distributions based on empirical data from at-sea surveys along with seasonal data on shipping intensity or oil extraction intensity within

licence blocks. Oil exposure risk will also be heavily influenced by local sea conditions and currents following a spill. The nature of currents in Irish waters indicate that many offshore spills, particularly on the west coast are more likely to spread northwards rather than directly inshore towards areas of high seabird density, apart from a gyre in the western Irish Sea (Hill et al., 1994). Oceanographic models along with historic oil spill data can be used to produce oil flow models, as has recently been done in British Columbia (Fox et al., 2016).

Conclusion

The updated OVI significantly changes our understanding of risks to seabirds from offshore petroleum infrastructure. By incorporating disturbance/displacement from petroleum infrastructure, we highlight the increased risk to procellariiforms in particular that will be essential when responding to oiling/collision incidents and subsequent monitoring of population impacts. Applying the indices spatially to identify risk provides a valuable tool that can be used to inform future spatial planning, identify where the most vulnerable species are concentrated in the event of a spill, and assess how current petroleum activities may be impacting populations. Our results show that the species in some seabird families are consistently highly vulnerable to risks associated with petroleum infrastructure and therefore, their at-sea distributions should be taken in to consideration when planning petroleum activities.

Chapter 5

Spatial prioritisation for seabird conservation in Irish waters during the breeding season

Authors: Emma Jane Critchley, John L. Quinn & Mark J. Jessopp

Author contributions: The study was designed by E.J.C., J.L.Q., and M.J.J.; E.J.C. carried out the data collection and analysis; E.J.C. led the writing of the chapter with contributions from all authors.

5.1 Abstract

Effective conservation of seabird populations is often reliant on designation of appropriate Marine Protected Areas. However, progress on their implementation to meet international conservation targets is slow. In the European Union (EU), legally binding directives require the designation of protected areas, yet many member states have so far failed to meet these obligations. Ireland is one such country, where less than 1% of the marine area is currently protected, even though it is an important breeding location for many of Europe's seabird populations. Seabirds in this region face multiple threats from a range of anthropogenic activities, and it is vital that these are accounted for in any conservation planning. In this study we demonstrate the utility of a spatial prioritisation approach for generating conservation planning solutions for an entire seabird community. Using the spatial prioritisation tool Marxan we optimize seabird conservation areas within Irish waters, with the aim of meeting the EU habitats directive requirements. We assess various scenarios, considering both existing Marine Protected Areas, and intensity of anthropogenic activities. Our results show that there is high overlap between the areas of greatest importance for seabird populations and those containing the highest intensities of anthropogenic activities, suggesting that more effective management of these areas is required to ensure favourable conservation status of populations.

5.2 Introduction

Protected areas are a key tool for the conservation of biodiversity. In the European Union (EU), the Birds Directive (2009/147/EC) and Habitats Directive (92/43/EEC) require each member state to designate networks of protected areas (e.g. Natura 2000 sites) for the conservation of birds. Specifically, these networks must allow populations to remain at a viable level within natural habitat and are only considered 'adequate' if at least 20% of a species national population is contained within the network (European Commission, 2010a, 2007; European Environment Agency, 2016). Despite on-going efforts to implement and expand these networks of protected areas, meeting EU and international obligations remains challenging, particularly for avian groups such as seabirds that utilise both terrestrial and marine habitats (Grémillet and Boulinier, 2009). Designated areas for the protection of seabird hotspots are limited, with recent assessments of marine protected areas (MPAs) showing low coverage of at-sea distributions, particularly for pelagic species (Critchley et al., 2018; McGowan et al., 2017). This is a major issue for many seabird populations as expanding offshore anthropogenic activities result in increased exposure to threats such as by-catch and oiling at-sea (Croxall et al., 2012).

Ireland and its surrounding waters are of particular importance to many seabird populations, supporting breeding populations of 24 species including internationally important numbers of European storm-petrels (*Hydrobates pelagicus*), Manx shearwaters (*Puffinus puffinus*), and a number of important tern colonies (Mitchell et al., 2004). Many of these seabird populations are thought to be in decline due to the impacts of multiple stressors, often caused by anthropogenic activities in the marine environment (Lynas, 2007). With a diverse array of methods and target species, fisheries occur around the entirety of the Irish coast, with particularly high concentrations in the Celtic Sea and Irish Sea where potential conflict with seabirds could occur (BirdWatch Ireland, 2016). Fisheries can cause direct impacts from by-catch, which is one of the leading causes of mortality in seabirds (Croxall et al., 2012), as well as indirectly through competition for resources (Bertrand et al., 2012; Cury et al., 2011). For example, a study on Black-legged kittiwakes (*Rissa tridactyla)* in the Irish Sea found that populations were vulnerable to local food shortages (Chivers et al., 2012); however, the overall impacts of fisheries can be difficult to assess given that some species benefit greatly from discards (Bicknell et al., 2013). High densities of shipping also pose significant threats due to risks of pollution and potential oil spills (Halpern et al., 2008), particularly given that any contact with oil is generally fatal for seabirds (Briggs et al., 1996; Fox et al., 2016). The Celtic and Irish Seas experience high

densities of commercial shipping, with a major route through the Irish Sea designated as an EU 'Motorway of the Sea' (European Commission, 2010b). Additional risks are arising from Ireland's nascent marine energy industry. Petroleum exploration is increasing in many offshore areas, with extraction at a number of sites (DCENR, 2017). Given the vulnerability of many seabird species to oil pollution (see Chapter 3) this is a threat which needs to be monitored carefully. Offshore wind farms are also in the early stages of development, mainly on the east coast (4coffshore.com/offshorewind) but their coverage is likely to increase due to recent investments and policy support (Lange et al., 2018). Considering all of these potential conflicts and threats, a robust network of MPAs and conservation planning is required for Ireland's seabird populations.

A recent progress assessment for the identification and protection of marine Important Bird Areas (IBAs) in Europe found that many countries are lagging behind EU requirements, with the majority of countries protecting 3% or less of their marine area (BirdLife International, 2014; Ramirez et al., 2017). Eight countries, including Ireland and the neighbouring UK, were identified as having 'poor' progress. The lack of Natura 2000 sites in Ireland has already resulted in the imposition of significant fines (Department of Arts, Heritage and the Gaeltacht, 2015). Although there is now 50% overlap of MPAs with marine IBAs many of Ireland's breeding seabird populations, particularly pelagic species, are still significantly under-protected (Chapter 2). Within Ireland, requirements for the designation of MPAs are recognised in the National Biodiversity Action Plan and more specifically in the Group Action Plan for Marine and Sea Cliff Birds in Ireland (BirdWatch Ireland, 2011; Buckley et al., 2017). However, progress towards implementation has been slow (Birdlife International, 2010b; BirdWatch Ireland, 2011; Ramirez et al., 2017). Thus there is an urgent need for further designation of MPAs in Irish waters to ensure better protection of both its resident and migratory seabird species, and to meet EU and International obligations.

The EU's Marine Strategy Framework Directive was recently developed to ensure that the use of marine resources is conducted at sustainable levels and that a good environmental status is maintained in all EU member states. Actions to meet the requirements of this directive should take into account the wide array of users, activities and biodiversity in territorial waters. One such approach is the use of a systematic conservation planning in the designation of new protected areas to ensure that conservation objectives can be met efficiently (Margules and Pressey, 2000). A key component of this approach is spatial

prioritisation, identifying the most important areas for conservation of biodiversity, whilst also taking account of all other activities in the area (Kukkala and Moilanen, 2013). This method requires collation of data on i) the distribution of species or habitats to be protected and for which conservation targets should be set; ii) the planning units that can be used to meet the targets and their status (e.g. existing MPAs); and iii) the costs of each planning unit (e.g. intensity of anthropogenic activities). This information is then combined to formulate a conservation problem that can be solved by a spatial prioritisation algorithm, using a number of dedicated programmes. Marxan is one such programme that has been used widely for systematic conservation planning, with results frequently used to guide conservation decisions (McIntosh et al., 2017; Sinclair et al., 2018), including for seabird communities in California and Patagonia (Afán et al., 2018; McGowan et al., 2013). Marxan uses a minimum-set algorithm to identify close to optimum solutions to a conservation problem, meeting conservation targets whilst minimising costs (Possingham et al., 2000), as opposed to other tools such as Zonation which aim to maximise conservation benefits within a fixed cost (Moilanen et al., 2005).

In this study we conduct a spatial prioritisation exercise using Marxan to optimize seabird conservation areas within Irish waters, with the aim of meeting the EU habitats directive requirements. We assess a number of different scenarios for a marine protected area network, both including and excluding current MPAs, and both with and without considering impacts of anthropogenic activities. The solutions for these scenarios are compared to identify key locations that are always prioritised for protection, as well as areas where conflicts between biodiversity conservation and anthropogenic activities may arise.

5.3 Methods

Spatial data

At-sea distribution data for all 24 seabird species breeding in Ireland were obtained from foraging radius distributions (Critchley et al., 2018) and aerial survey data collected over 2016-2018 (Rogan et al., 2018), representing the best available data for seabirds in this region during the breeding season. Foraging radius distributions data were available for all breeding seabirds in the Irish EEZ (see Figure 5.1) with values of abundance per grid square at a 5 km^2 resolution. Aerial survey data were available for Black-legged kittiwake, Manx shearwater, Northern Fulmar (*Fulmarus glacialis*) and Northern gannet (*Morus bassanus*) individually. Aerial survey data for auks, petrels and terns were available at the family group level as they could not be identified to species level during aerial surveys. Aerial survey sightings were modelled within survey strata using a range of environmental covariates (see Rogan et al., 2018 for detailed methods) to provide a density distribution, and interpolated using inverse distance weighting to extend distributions coastally, covering inshore areas not surveyed. Resulting distributions were then transformed to match the resolution (5 km^2) and coordinate system of the foraging radius distributions (Universal Transverse Mercator zone 29N). Interpolation was carried out using the 'gstat' package in R (Gräler et al., 2016; Pebesma, 2004).

The inclusion of two different distribution layers (foraging radius and survey data) builds on recent work which found that the inclusion of distribution layers for both marine IBAs and important habitat features was required in a spatial prioritisation analysis to ensure sufficient protection of seabird populations (McGowan et al., 2017). Foraging radius distributions will not capture important areas offshore that are driven by habitat associations and that are more likely to be identified from survey data. However, as the aerial surveys only covered a small portion of coastal waters in the Irish EEZ this limits our confidence in the accuracy of the modelled distributions inshore. Therefore, the inclusion of two complementary distribution layers should ensure that important areas both inshore and offshore are sufficiently captured in the spatial prioritisation. Survey data also captures distributions of non-breeders and juveniles which make up a significant portion of seabird populations but cannot be accounted for in a foraging radius distribution model. Each distribution was assigned as a feature layer for which a conservation target must be met in the spatial prioritisation solution.

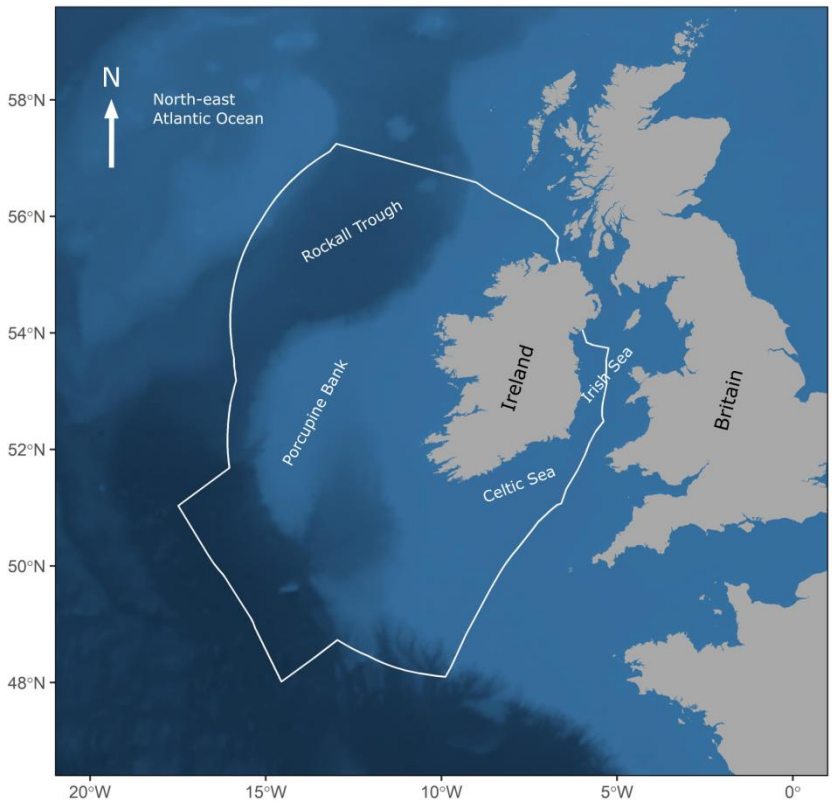


Figure 5.1 Location of the study area and outline of the Irish Exclusive Economic Zone (EEZ).

Spatial data for the boundaries of all current protected areas with marine components in Britain and Ireland were obtained from the World Database on Protected Areas (IUCN and UNEP-WCMC, 2016). The main protected areas for seabirds in Ireland are SPAs and SACs (designated as Natura 2000 sites to meet EU requirements) and OSPAR convention (Convention for the Protection of the Marine Environment of the North-East Atlantic) MPAs, which generally cover offshore areas.

Anthropogenic activities data for cost layers were composed of polygons delimiting a) the spatial extent of all petroleum licence blocks in Irish waters; b) proposed areas for wind farm developments in Irish Waters; c) major European shipping lanes; d) Irish ferry routes; and e) fishing intensity in Irish waters. Data for petroleum licence blocks and their associated authorisations were obtained from the Irish Petroleum Affairs Division (DCENR, 2017). Data for proposed wind farm developments were replicated from https://www.4coffshore.com/offshorewind/ [Nov 2018]. Data for European shipping lanes were taken from the European Commission's 'motorways of the sea' project which designates specific marine corridors for freight movement in the European Union

(European Commission, 2010b). Date for ferry routes were taken from the "Ferry routes" theme accessed through Ireland's Marine Atlas at http://atlas.marine.ie/ [Nov 2018]. Data for fishing intensity were taken from "Fishing Method All Gears" theme accessed through Ireland's Marine Atlas at http://atlas.marine.ie/ [Nov 2018].

Preparation of all data inputs was carried out in R version 3.4.3 (R Developement Core Team, 2016).

Spatial prioritisation

A 5 x 5 km grid was chosen for use as a planning unit layer for the spatial prioritisation exercise, matching the resolution of the underlying species distribution data. The suitability of this grid for policy planning purposes in the region cannot be assessed here, but it provides a good intermediate resolution for coastal planning units which may be smaller, and offshore planning units which would likely be much larger.

The objective of the spatial prioritisation exercise was to reach a target of protecting 20% of the population of each species, meeting EU Habitats Directive requirements (European Environment Agency, 2016), whilst minimising the total relative cost. Costs were calculated as the total value of planning units contained within a solution. Planning units with high cost values are given less priority for inclusion in a solution than planning units with a low cost. Cost values for anthropogenic activities were scored from 1 (low cost) to 5 (high cost) according to the intensity of the activity, and likely impact to seabirds, following expert advice in McGowan et al. (2013), see Table 5.1. The sum of activity costs in each grid square was calculated to generate an overall costs layer.

Table 5.1 Cost values assigned to anthropogenic activities in planning units

Activity	Cost
No activity	1
Petroleum exploration	
Petroleum licence option	2
Granted exploration licence	3
Lease undertaking	4
Petroleum lease	5
Renewables	
Proposed wind farm sites	2
Vessels	
Ferry routes	2
Shipping lanes	4
Fishing intensity	
< 50 hrs	1
50 – 2000 hrs	2
2000 – 3000 hrs	3
3000 – 5000 hrs	4
5000 – 7000 hrs	5

Four scenarios were chosen to assess the spatial solutions for meeting these targets under varying constraints:

- Scenario 1 identified priority areas for seabirds based solely on species abundances per grid square with no additional constraints. All planning units had a cost of 1.
- In scenario 2 all existing MPAs were 'locked-in' ensuring that they were always selected for inclusion in the spatial solution. Therefore, any planning unit which overlapped with a MPA polygon was allocated as 'locked-in' within the planning units layer. All additional planning units had a cost of 1.
- Scenario 3 did not include MPAs as locked-in, but accounted for relative cost values of planning units due to intensity of anthropogenic activities within each unit (Table 5.1).
- Scenario 4 considered costs due to anthropogenic activities (Table 5.1) whilst also retaining all 'locked-in' MPAs in the solution.

All scenario prioritisation problems were solved using the 'prioritzr' package in R (Hanson et al., 2018). The package utilises integer linear programming techniques and the commercial problem solver 'guirobi' to find the optimal solution to Marxan style problems more efficiently than the original Marxan software (Beyer et al., 2016). For each scenario a spatial solution map was produced showing the planning units included in the optimal solution, and a table of the percentage population of each species contained within those planning units.

Scenarios 1 - 4 were first run for populations of all seabirds within the Irish EEZ, and then just within the Irish Sea, an area known to be of high importance for seabirds (Jessopp et al., 2018; Mitchell et al., 2004; Rogan et al., 2018). To then compare priority areas across different spatial scales, scenarios 1 and 2 were also run for all seabird populations in Ireland and the UK combined using just foraging radius distributions as aerial survey data does not cover the entire region.

Difference maps

A difference map was generated for scenarios 1 and 4 in the Irish EEZ, to highlight changes in prioritisation areas between scenario 1, which acts as a baseline, and scenario 4, which has the most constraints. This shows the planning units that are (a) always selected in both scenarios, (b) only selected in scenario 1 but not in scenario 4, and (c) only selected in scenario 4 but not in scenario 1.

5.4 Results

The combined anthropogenic activities layer (Figure 5.2) highlights that the highest intensity of activities occurs in the north Celtic Sea basin, the Irish Sea and along the edges of the Irish continental shelf.

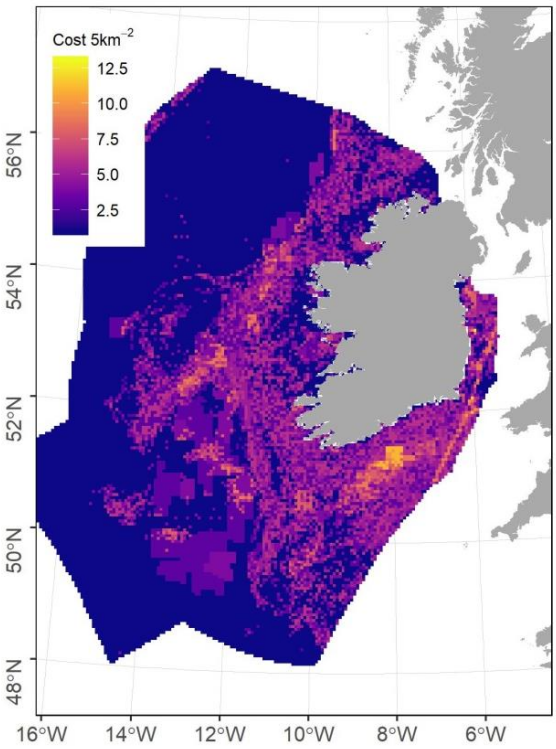


Figure 5.2 Anthropogenic activities costs based on the distribution of all activities and sum of costs per 5 km grid square. Higher values indicate higher intensity of anthropogenic activities.

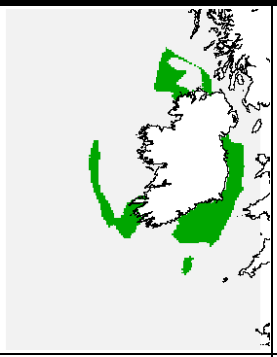
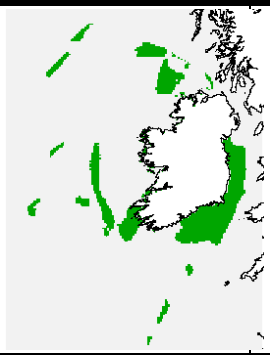
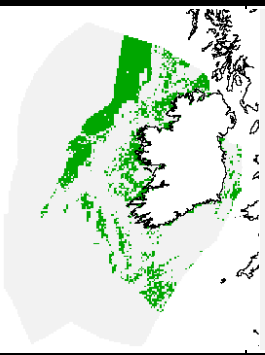
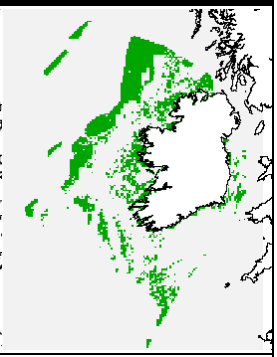
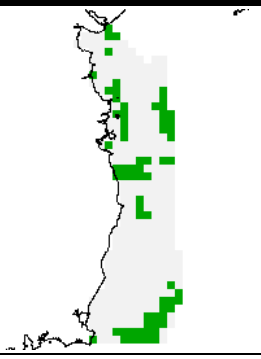
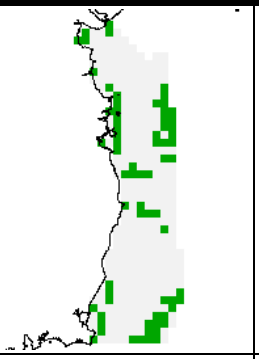
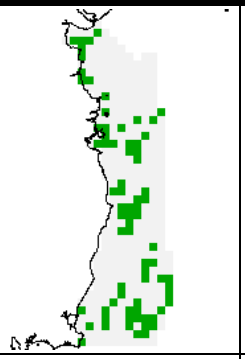
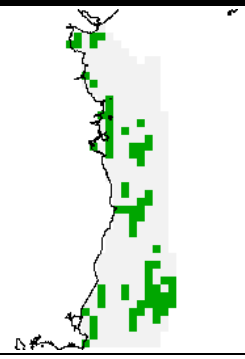
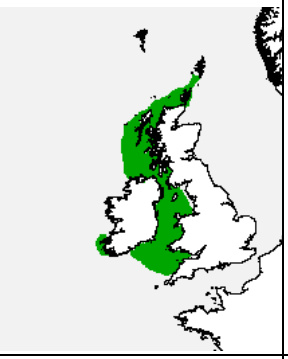
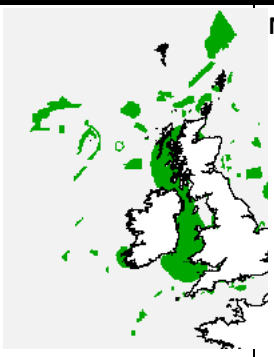
Spatial prioritisation solutions

There was general agreement across all scenarios that the Irish Sea and areas offshore from the west coast of Ireland were necessary for inclusion to meet the 20% conservation target for all species (Table 5.2, A). Scenarios 1 and 2, which did not account for activity costs, both met conservation targets for all species by including all of the Irish Sea and Celtic Sea, areas extending out from the south-west coast, the north-west coast and along the Porcupine bank. The inclusion of MPAs in scenario 2, however, expanded the selection of planning units to additional areas further offshore (mainly OSPAR MPAs). Once anthropogenic activity layers were included in scenarios 3 and 4 the spatial solutions became considerably patchier and much of the Irish and Celtic Seas were excluded, see Figure 5.3 for a more detailed map of scenario 4. Instead, large areas along the north-west

shelf edge were included in the two solutions, at a higher overall cost to the solutions not accounting for anthropogenic activities. The difference map for scenarios 1 and 4 (Figure 5.4) shows limited overlap in the areas included for each solution, mainly in the Irish Sea, south-west and north-west coasts. A large amount of variation in the percentage population coverage for each species was seen when comparing scenarios 1 and 4 (Figure 5.5). For example, whilst roseate tern (*Sterna dougallii*) populations have 100% population coverage in scenario 1 this drops to 36% in scenario 4. In contrast, little tern (*Sterna albifrons*) population coverage increases from 28% in scenario 1 to 100% in scenario 4. However, there is no clear pattern of one scenario consistently providing higher coverage than the other.

In the scenarios focused on just the Irish Sea (Table 5.2, B) an increase in patchiness can be seen when anthropogenic activities are accounted for. However, planning units are included in roughly the same areas (e.g. Dublin Bay) in the spatial solutions for all four scenarios. Scenarios looking at the wider region of Ireland and the UK (Table 5.2, C) included the majority of the Irish Sea and north Celtic Sea in both solutions, along with a smaller area extended out from the south-west coast. The inclusion of existing MPAs (scenario 2) did not considerably reduce the planning unit coverage in these areas.

Table 5.2 Spatial solutions for scenarios 1 – 4 in the Irish EEZ and Irish Sea, and for scenarios 1-2 in Ireland and the UK. Areas coloured in green are planning units selected to meet the 20% target for all species. Solution cost is the sum of the costs of all planning units retained in the solution. These are relative costs based on the likely impacts of activities to seabirds rather than economic costs.

	Scenario 1 No constraints	**Scenario 2** MPAs locked-in	**Scenario 3** Anthropogenic activity costs	**Scenario 4** Anthropogenic activity costs + MPAs
A) Irish EEZ				
Solution map				
Solution cost	2223	2415	3084	3783
B) Irish Sea				
Solution map				
Solution cost	69	69	98	138
C) Ireland and the UK				
Solution map			**NA**	**NA**
Solution cost	6908	7105		

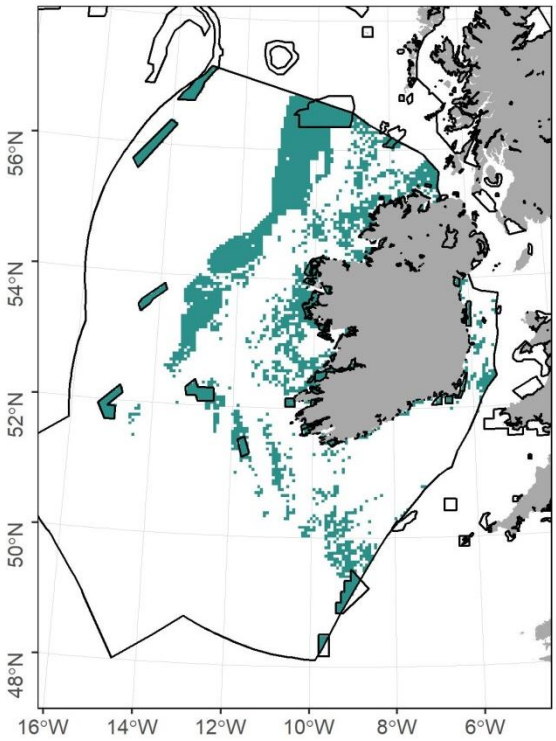


Figure 5.3 Spatial solution for scenario 4 (including MPAs and anthropogenic activity costs). Areas in green are planning units selected to ensure coverage of 20% of the populations of all species. Lines in black delineate current MPAs and the Irish EEZ.

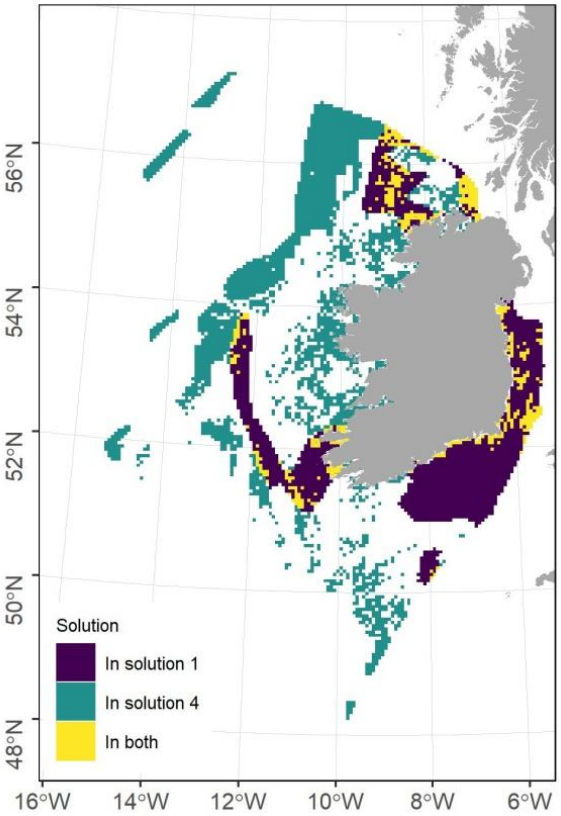


Figure 5.4 Map showing difference in planning unit selection between scenario 1 and scenario 4 in the Irish EEZ. Areas in purple were only selected in the solution map for scenario 1 (no constraints) and not in the solution map for scenario 4 (activity costs + existing MPAs); areas in green were selected only for the solution map in scenario 4 and not in the solution map for scenario 1; and areas in yellow were selected in the solution maps for both scenarios.

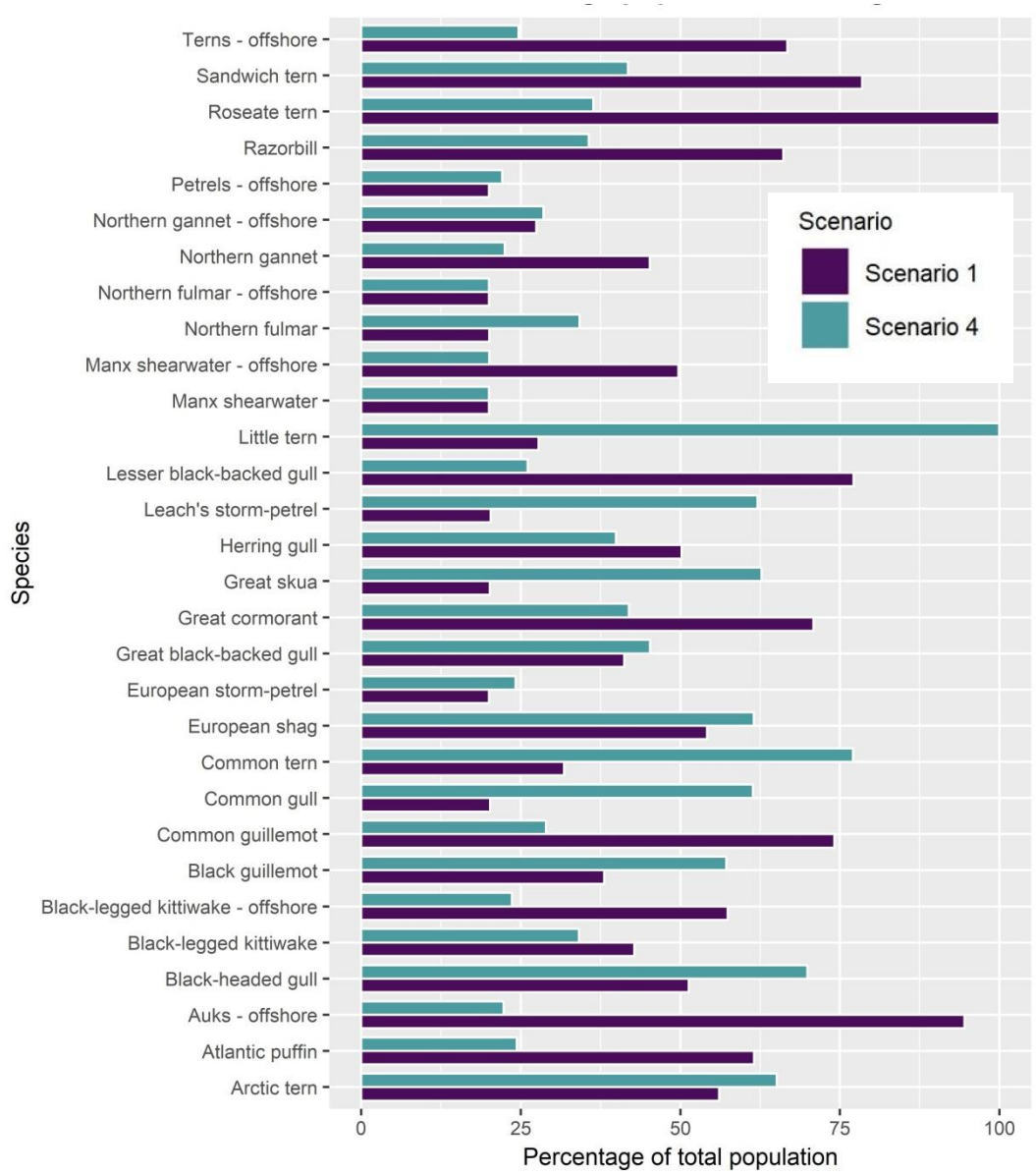


Figure 5.5 Percentage of the population of each species contained within the spatial solutions for scenario 1 (purple) and scenario 4 (green). See Table F.1 in the supplementary material for a complete list of the percentage values for all scenarios.

5.5 Discussion

Our results show that the potential for conflict between seabird populations and anthropogenic activities is high within a number of key areas in the Irish EEZ, particularly the Irish Sea. The addition of MPAs to our scenarios (scenarios 2 and 4) did not have much of an impact on the areas selected for prioritisation, apart from further offshore, suggesting that coastal MPAs are already located in areas of high priority. In contrast, the inclusion of the anthropogenic cost layer (scenarios 3 and 4) greatly changed the selection of priority areas, with much greater patchiness in the planning units selected and higher solution costs.

The solutions for our initial scenario (1), considering spatial prioritisation based on species distributions only, identified the Irish Sea and Celtic Sea as the areas of highest importance for Irish seabird populations. The importance of these areas was further emphasised when we looked at spatial prioritisation across the wider region of Ireland and the UK. This is unsurprising given that the Irish and Celtic Seas are utilised by seabird populations from both Ireland and the UK, and host many, often large, colonies of multiple species. However, the scale of their importance is striking as the entire Irish Sea and North Celtic Sea are included in solutions for both scenario 1 and 2. The south-west coast of Ireland was also highlighted as an area of importance across both scales. Offshore islands in this region host internationally important breeding colonies of European storm-petrels and Manx shearwaters (Arneill, 2018; BirdLife International, 2018; Mitchell et al., 2004). The importance of the north-west coast of Ireland in the Irish EEZ prioritisation scenarios is likely due to the influx of birds from larger colonies on the west coast of Scotland, particularly Manx shearwater, Northern fulmar, and Northern gannet.

The addition of existing MPAs in scenario 2 did not greatly change the planning units included in the prioritisation solution compared to scenario 1. Additional areas were selected offshore, mainly where existing OSPAR MPAs are in place. However, OSPAR sites are designated for a wide range of species and habitat features, not just seabirds, and the analysis shows that these are unlikely to provide much additional conservation benefit to seabird populations. Similarly, a recent study in Patagonia found that offshore IBAs did not contribute as much to conservation targets as colony focused solutions closer to shore (Afán et al., 2018).

The greatest changes in the spatial prioritisation solutions were seen for scenarios 3 and 4, with the addition of a cost layer accounting for the intensity of anthropogenic activities,

compared to scenarios 1 and 2. This is most likely due to the amount of overlap between seabird hotspots and human usage hotspots in the region, particularly in the Irish and Celtic Seas. In the Celtic Sea a combination of high intensity of fishing along with active petroleum extraction contributes to very high combined cost values in planning units. High concentrations of fishing activity and petroleum licence blocks overlap along the edge of the continental shelf, and shipping lanes leading up through the Irish Sea also contribute to higher cost values. The increase in costs of planning units in these areas greatly reduced their likelihood of being included in an optimal solution, even given the high densities of multiple species of seabirds. Previous studies have also shown how the type of costs used for prioritisation (e.g. just area costs vs. all activities) is a key driver for the selection of priority areas (Delavenne et al., 2012; Klein et al., 2008).

However, seabirds may continue to use areas regardless of activity intensity and therefore conservation plans should not be devised solely to avoid perceived/potential conflict (McGowan et al., 2013). Indeed, our results show that the areas of highest importance for seabird populations overlap considerably with the areas of highest intensity of anthropogenic activities; therefore these areas could still be incorporated in to an MPA network. There is an important balance to be found between meeting biodiversity conservation goals whilst accounting for multiple stakeholder interests (Klein et al., 2008) This aspect should be carefully considered for any future conservation planning in the region.

The spatial patchiness seen in the intensity of anthropogenic activities (Figure 5.2) leads to considerable patchiness in the solution for scenarios 3 and 4, particularly in coastal waters. It should be noted that the scale of the planning units (5 km^2) may also have contributed to the patchiness, as individual, isolated planning units can be selected for prioritisation. The Marxan method does allow users to specify the amount of clumping that should be observed, via a boundary length modifier function. However, we felt it was not appropriate to set values for the boundary length in this study as decisions on the overall size and connectivity of protected areas should be made in conjunction with policy makers.

Whilst the inclusion of anthropogenic activities, as well as a thorough understanding of their impacts, is important for conservation planning, the prioritisation solutions presented here are not prescriptive. Firstly, it should be noted that area-based conservation may not be appropriate for all seabird species – e.g. wide range foragers with diffuse distributions where ocean basin level management measures or dynamic MPAs may be more

appropriate (BirdLife International, 2010a; Game et al., 2009; Hyrenbach et al., 2000). In contrast, for short-range foragers with vulnerable populations (e.g. roseate tern, Atlantic puffin) it may be necessary to protect their entire foraging range to ensure adequate conservation measures. These decisions would need to be made with expert advice and input from policy makers to ensure that any recommendations are viable and cost-effective. Finally, the solutions proposed here are based on information from breeding distributions only, and may not be appropriate as conservation measures outside of the breeding season.

It is also important to consider the scale of conservation planning, particularly in a marine environment where species may cross trans-national boundaries on a daily basis. Our results show the Irish Sea, which sits within both the Irish and UK EEZs, is hugely important for seabird populations in the region, suggesting that multi-lateral conservation agreements would be required for their protection. The issue of trans-boundary cooperation has recently been highlighted by the European Commission's DG MARE and is being addressed by a joint roadmap with UNESCO to accelerate Marine Spatial Planning processes worldwide (IOC-UNESCO, 2017).

Conclusion

In this study we have illustrated how the approach of systematic conservation planning can be utilised to identify priority areas for a seabird community. Considering all conservation features, existing MPAs and anthropogenic activities at the same time allows an efficient assessment of how targets can be met, whilst minimising costs for the solution. The results of our spatial prioritisation exercise demonstrate how the inclusion of additional knowledge, beyond just species distributions, can significantly change priority areas for conservation planning in a region, as well as highlighting where potential conflicts may arise.

Chapter 6

General Discussion

Seabirds are the most threatened avian group and populations are in decline globally (Croxall et al., 2012; Paleczny et al., 2015). Impacts from anthropogenic activities, including over-fishing, habitat destruction and marine pollution, are expanding in to more remote offshore regions of the already heavily impacted oceans (Maxwell et al., 2013; Halpern et al., 2015; Grémillet et al., 2018; Wilcox et al., 2015). There is an urgent need to implement conservation measures for the protection of vulnerable species.

Understanding where species are distributed and their potential overlap with anthropogenic activities is an essential first step in developing appropriate conservation plans. In place of costly, long-term, and large-scale studies, predictive methods can make use of already collected data and basic ecological understanding of a species' behaviour to rapidly assess their distribution. The results of this thesis have 1) demonstrated the utility of the foraging radius method for assessing the at-sea distribution of a seabird community at national and biogeographic scales, 2) updated the methodology for assessing the vulnerability of seabirds to oil pollution, and 3) highlighted the areas of greatest importance, and greatest risk, for breeding seabirds in Ireland, as well as gaps in the current level of conservation protection for seabirds in both Britain and Ireland.

6.1 Utility of the foraging radius method for assessing the distribution of a seabird community

As central-place foragers, the distribution and abundance of seabirds at sea is primarily driven by a few key measures: the location of breeding colonies; the population size of colonies; and the maximum distance that can be covered by a species based on their behaviour, physiology, and constraints to return regularly to the nest to feed chicks (Wakefield et al., 2017; Warwick-Evans et al., 2018; Weimerskirch et al., 2001). The foraging radius method takes advantage of these ecological features to produce predicted distributions that are not reliant on complex modelling of empirical data from remote tracking or at-sea surveys.

In this thesis I have applied the foraging radius approach to an entire breeding seabird community at the biogeographic level, incorporating populations of 25 species from two

countries. The results of Chapters 2 and 3 demonstrate the utility of this method and are particularly promising for a rapid assessment of community distribution in data poor regions.

The results of the distribution comparisons in Chapter 3 show that the foraging radius method works well when assessing distributions at the colony level, showing reasonable correlations with GPS tracking data for multiple birds. Indeed, multiple studies have found that even when using much more complex modelling approaches, distance to the coast or colony remains the strongest driver of seabird occurrence and abundance (Warwick-Evans et al., 2018; Skov et al., 2008; Ford et al., 2007; Johnston et al., 2015). A foraging radius approach is effective at capturing the high densities of birds that will occur in the waters immediately surrounding a colony, making the distributions a particularly good match for short-ranging species (e.g. Atlantic puffin and razorbill as seen in Chapter 3). It has also proven to be a good match for a long ranging species as well, the European storm-petrel, with only a small number of individuals traveling to the furthest edges of a foraging area. Within a certain distance from the colony, birds are likely to spread out as much as possible to reduce density dependent competition, particularly at large colonies where resources in the immediately surrounding waters will be depleted (Ashmole 1963; Gaston et al., 2007). This results in a diffuse distribution of birds around the central colony, similar to the inverse log density decay rate used for our foraging radius model.

However, when birds move further offshore, distributions will be much sparser and instead of distance to colony, habitat or productivity cues may be more important determinates of density, as seabirds aggregate at resource patches such as shelf edges, upwellings, oceanic fronts and sand bars depending on their foraging mode (Scales et al., 2014; Waggitt et al., 2017; Cox et al., 2018; Weimerskirch 2007).

These stronger habitat associations offshore may partly explain why correlations between foraging radius distributions and aerial survey data were lower compared to correlations with GPS tracking data. Birds from multiple colonies aggregating in offshore patches are likely to be captured by survey data, whereas the basic foraging radius model will not predict any offshore aggregations. It's likely that the foraging radius distributions will correlate well with survey data up to a certain distance from the coast, at which point the correlations break down as density dependent competition becomes less important. One way to test this would be to clip both distributions to set distances from the coast (e.g.

bands of 10, 20 km etc.) and examine how the correlation values vary with distance to coast. Figure 6.1 provides a conceptual diagram illustrating the approach.

Even so, this does not necessarily mean that the inclusion of habitat data will improve the correlation of foraging radius distributions with aerial survey data. Given the dynamic and heterogeneous nature of the marine environment it is often very difficult to find strong relationships between environmental covariates and abundance (Wakefield et al., 2009). For example, extensive tracking data from the large-scale FAME project (four species and over 1,300 birds from 29 colonies) still resulted in distributions where distance to colony provided the greatest explanation for abundance (Wakefield et al., 2017). Even the GAM distribution models for the empirical ObSERVE survey data (Chapter 3) did not retain most of the included habitat variables, with distance to the colony or coast remaining the only explanatory variables. Furthermore, Grecian et al. (2012) found that the inclusion of habitat association data (Chlorophyll A concentration) in a foraging radius model for northern gannets did not significantly improve the correlation with at-sea survey data.

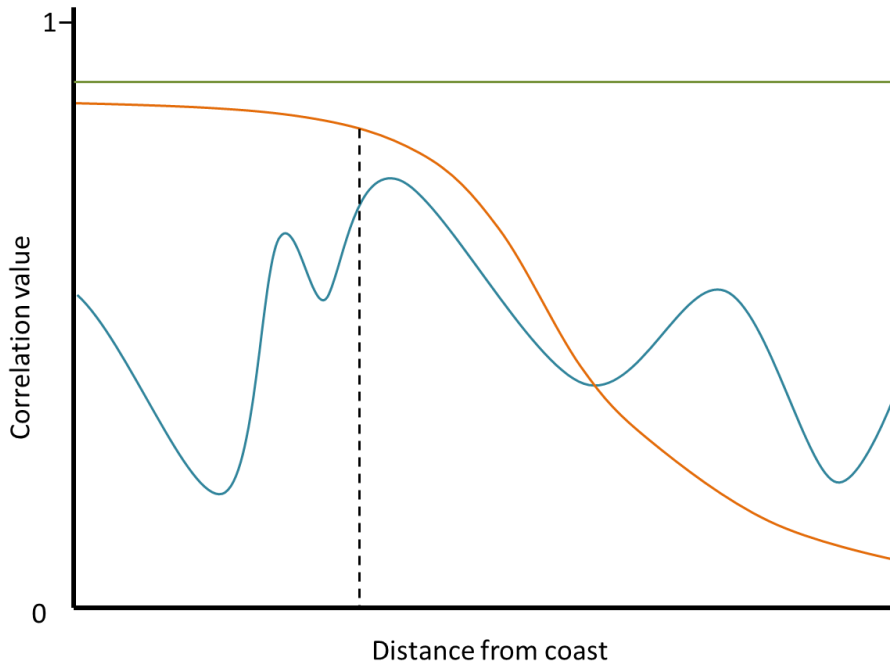


Figure 6.1 Potential relationships between correlation values for distribution comparisons (between foraging radius and empirical distributions) and distance from the coast. The green line represents a scenario where correlation values are consistent regardless of distance from the coast. The orange line illustrates what could be expected if the influence of density dependent competition drops off after a certain distance. The blue line represents a scenario where there is no clear relationship between correlation values and distance from the coast.

Another potential explanation for the lower correlations between foraging radius distributions and survey data is that both distributions are capturing different populations. Foraging radius distributions from the central breeding colony will only account for breeding birds, whereas aerial surveys do not discriminate between breeders, juveniles, immature birds and non-breeders. However, this is unlikely to contribute much to the discrepancy given that for most species only breeders will be foraging in areas surrounding the colony, with the majority of other birds moving further offshore or to completely different regions in order to avoid competition (Fayet et al., 2015; Votier et al., 2017; Furness, 2015).

The use of colony-specific foraging ranges or a different decay rate from the colony may also help to improve the accuracy of the model. Maximum foraging range is related to the size of a colony, with birds in larger colonies generally needing to travel further to avoid competition and resource depletion (Ashmole, 1963). However, whilst the relationship between colony size and foraging range has been defined mathematically for gannets (Lewis et al., 2001) it is not so clear for other species, and generalisations would need to be made, possibly based on foraging mode. Alternative colony decay rates could be established using previously collected data from either tracking or surveys (ideally from multiple colonies) but again, as this data would not be available for all species, surrogates would need to be used. Furthermore, all of these improvements would need to be implemented on a species by species basis, increasing the time and resources needed to generate distributions for an entire seabird community.

As it stands, the basic foraging radius model is a useful method for a quick assessment of community level distributions, and is beginning to be utilised more widely. A recent study applied the method to 14 breeding seabird species in Patagonia, also demonstrating how the distributions could be utilised for spatial prioritisation assessments (Afán et al., 2018). Although the method can be a surrogate for more costly tracking or survey studies, it is still only as good as the available input data, i.e. reliable colony count data and representative foraging ranges. So the usefulness of the approach may come down to a trade-off between the costs of collecting robust colony data or the costs of extensive at-sea surveys. In this instance the foraging radius method would be most appropriate for small island states with a limited coastline but large EEZ, where it would be far more cost-effective to census all of the breeding colonies rather than survey the entire territorial waters. Alternatively, if colony locations are known but there is large uncertainty in population estimates the

foraging radius method could be applied without population data and be based solely on percentage of population at-sea. This would provide a baseline distribution to which additional data, e.g. habitat features or tracking data from important colonies, could be added to.

6.2 Assessing seabird vulnerability to oil pollution and mapping risks

The review of vulnerability indices in Chapter 4 revealed the range of formulae that have been utilised for assessing seabird vulnerability to impacts from anthropogenic activities. In order to compare impacts from a variety of risks and combine vulnerability scores effectively it is essential that a universal method is used for all risks and in all regions. The OVI I have developed here, and which builds on that of Certain et al. (2015) and Wade et al. (2016) for wind farms, can be adapted and applied to any risk to seabirds.

To ensure that the Oil Vulnerability Index (OVI) developed in Chapter 4 was as accurate as possible for the region of interest - Britain and Ireland - multiple conservation factors specific to those populations were included. Whilst this might mean that the OVI scores presented in Chapter 4 are not globally applicable, the inclusion of regional level conservation factors is important, as they do have some influence over the final rankings. For example, Atlantic puffin and European storm-petrel have a higher level of vulnerability when accounting for conservation factors rather than just individual risk factors, most likely due to their status as birds of conservation concern in Ireland and the UK (Colhoun & Cummins, 2013; Eaton et al., 2015). However, it is essential that the OVI can be adapted in order to be globally applicable, and its construction in two parts allows for this. Individual risk to oiling/collision and population vulnerability to any additional mortality are calculated separately (see Appendix E.2 for Chapter 4) and then combined to generate an overall OVI score per species (Table 4.2, Chapter 4). Individual risk will remain the same for any species and only the conservation factors for population vulnerability would need to be updated to modify the OVI for a different region. Therefore, I provide a formula in Chapter 4 that can be used anywhere in the world by following a set protocol and updating factors on local conservation status and population sizes.

Mapping vulnerability in an informative way for conservation and policy decisions is challenging. The vulnerability maps produced in Chapter 4 are heavily influenced by abundance per grid square (even when it is log-transformed), resulting in some of the variation in vulnerability across areas being lost e.g. areas containing large numbers of low

risk species (e.g. terns) could show up as more important than areas containing a single high risk species such as the Atlantic puffin. A case could be made for not including abundance in vulnerability maps and instead solely plotting a measure of community vulnerability, as suggested by Certain et al. (2015). The authors propose that community vulnerability values in a grid square be calculated as the sum of species' vulnerability scores weighted by the proportional abundance of that species within a grid square. This can then be overlaid or compared side by side with maps of total abundance. However, this introduces an extra level of interpretation, which may cause confusion, particularly for policy makers or industry planners who have limited experience of working with ecological data. There is the potential that areas with high numbers of the most vulnerable species may be overlooked if they also contain multiple species of lower vulnerability. Including both vulnerability and abundance on the same map is still likely to be the most useful solution but more consideration needs to be given to how they are combined and how much weighting is given to each element in order to increase the importance of species vulnerability. Calculating OVI scores on a larger scale (e.g. from 0 to 100) to create a greater difference between low and high vulnerability scores may be one solution worth exploring.

The maps of petroleum industry risk in Chapter 4 demonstrate how accounting for both vulnerability distribution and the location of anthropogenic activities highlights areas of greatest risk, which might not always be the areas of highest vulnerability. However, it should be noted that the maps of petroleum industry risk produced here do not account for the intensity of petroleum activity occurring in the area. This could be improved by weighting oil licence blocks according to the phase of exploration or production; using historic oil spill data for the region (See Fox et al. (2016) for an example of seabird density – oil interaction maps in British Columbia); or linking risk (location of petroleum activities) with dynamic oceanographic models to reflect where oil from any spills is likely to disperse to. Maps of the density of commercial shipping in the region could be generated using automatic identification system (AIS) ship-tracking data and also be used to weight exposure risk scores, e.g. risk would be a product of abundance, vulnerability and shipping density (following methods similar to Pirotta et al., 2018).

6.3 Distribution, vulnerability and conservation of seabirds in Britain and Ireland

The combined distribution (Chapter 2), vulnerability (Chapter 4) and prioritisation (Chapter 5) maps for the entire community of breeding seabird species in Ireland clearly highlight

how the areas that are most important for seabird populations in the region, and which should be prioritised for conservation, are also the areas that are experiencing the most pressure from anthropogenic activities. This is particularly true for the Irish Sea, a region which is also important for seabird populations in Britain. Although highest combined densities of seabirds are found on the east coast of Britain (Figure 2.2, Chapter 2), the higher levels of species richness on the west coast of Scotland and in the Irish Sea appear to make them the most suitable regions for spatial prioritisation (Figure 5.3, Chapter 5). The addition of data layers on oil risks and anthropogenic activities in general for Chapters 4 and 5 revealed that these areas are also where seabird species in Ireland are experiencing the greatest risks. This result shows the importance of not just using hotspots of abundance for marine conservation planning, and recent studies have shown that seabird conservation at sea needs to go beyond protecting IBAs (Afán et al., 2018; McGowan et al., 2018).

On a species level, those that are most vulnerable in the region (according to IUCN red list) and have high OVI scores (Chapter 4) are also the species which currently have some of the lowest levels of protection, see Figure 6.2 and Table 6.1. For example, both the Atlantic puffin and Northern fulmar are listed as 'Endangered' on the IUCN European Red List (Choudhury et al., 2016) and have high scores on the OVI index (Chapter 4) but neither population in Britain and Ireland reaches the EU habitats directive target of 20% of the population being protected through designation of marine protected areas (Chapter 2). Indeed the negative relationship between OVI scores and level of MPA cover (Figure 6.2) is quite striking and clearly indicates that not enough has been done to protect the most vulnerable seabird species in Ireland.

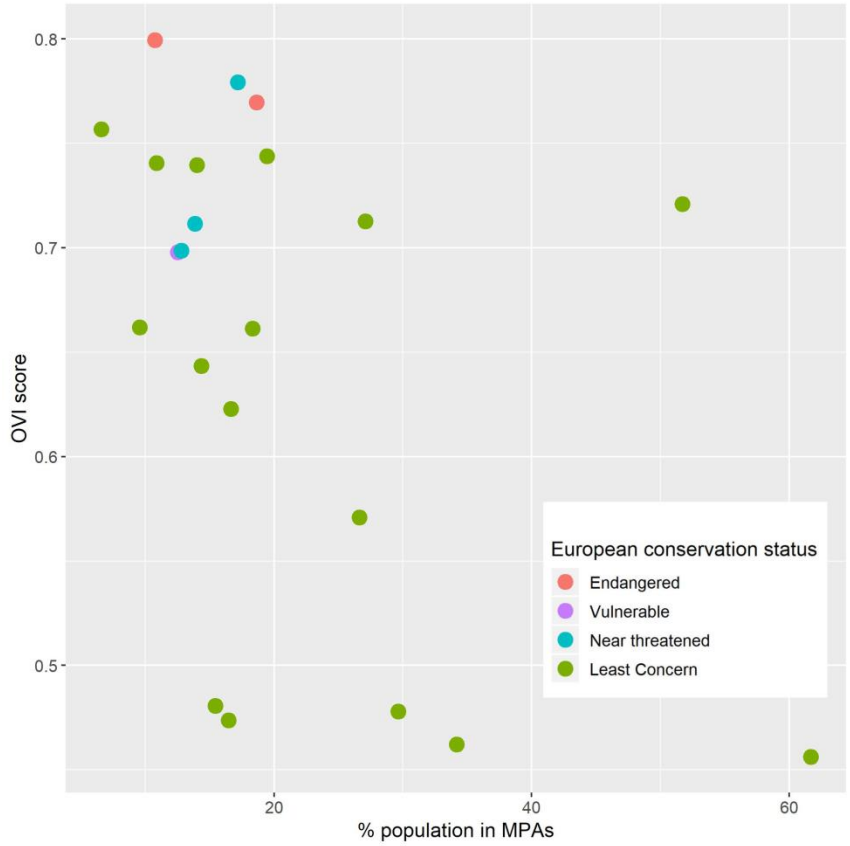


Figure 6.2 Scatterplot showing relationship between OVI score (Chapter 4) and percentage of population contained within MPAs (Chapter 2) for all species. Colour coding relates to IUCN European Conservation Status (Choudhury et al., 2016).

Finally, the research in this thesis relates only to distribution of seabirds in the breeding season, due to the foraging radius model only being suitable for central place foragers. This in particular has significant implications for assessing vulnerability to oil outside the breeding season, and species compositions at offshore oil platforms have been observed to change considerably throughout the year (Tasker et al., 1986). For example, regular oil spills are known to occur in the English Channel and Bay of Biscay which are important over-wintering areas for auks, including the Erika spill in 1999 which killed up to 130,000 auks (Le Rest et al., 2016). The mid-Atlantic Ridge is also an important over-wintering area and migration route for multiple species (Bennison & Jessopp, 2015; Montevecchi et al., 2012; Frederiksen et al., 2012). Whilst areas such as the Irish Sea and Celtic Sea retain high densities of seabirds throughout the year, the species composition will change seasonally. Future work on the vulnerability and conservation of seabirds in Ireland should also utilise data on distributions during the winter season, such as from the recently published ObSERVE aerial survey reports (Jessopp et al., 2018; Rogan et al., 2018).

Table 6.1 Summary of results from Chapter 2 and Chapter 4

Species	Population size (individuals)	European conservation status	Proportion of European population	% Population in MPAs	OVI score
Arctic skua *Stercorarius parasiticus*	4740	Least concern	4.23	15.46	0.48
Arctic tern *Sterna paradisaea*	116472	Least concern	6.43	16.48	0.47
Atlantic puffin *Fratercula arctica*	869690	Endangered	7.5	18.64	0.77
Black guillemot *Cepphus grylle*	38529	Least concern	5.19	18.36	0.66
Black-headed gull *Larus ridibundus*	184240	Least concern	7.44	51.74	0.72
Black-legged kittiwake *Rissa tridactyla*	704028	Vulnerable	15.96	12.51	0.7
Common guillemot *Uria aalge*	1271624	Near threatened	41.56	13.83	0.71
Common gull *Larus canus*	48110	Least concern	4.76	16.64	0.62
Common tern *Sterna hirundo*	35468	Least concern	3.11	34.21	0.46
European shag *Phalacrocorax aristotelis*	61798	Least concern	39.36	27.11	0.71
European storm-petrel *Hydrobates pelagicus*	178138	Least concern	17.29	6.6	0.76
Great black-backed gull *Larus marinus*	36528	Least concern	13.73	14	0.74
Great cormorant *Phalacrocorax carbo*	27084	Least concern	3	26.65	0.57
Great skua *Stercorarius skua*	16016	Least concern	46.42	14.35	0.64
Herring gull *Larus argentatus*	278340	Near threatened	17.82	17.2	0.78
Leach's storm-petrel *Oceanodroma leucorhoa*	96714	Least concern	17.68	9.7	N/A
Lesser black-backed gull *Larus fuscus*	180790	Least concern	26.79	19.43	0.74
Little tern ***Sterna albifrons***	3424	Least concern	3.23	61.65	0.46
Manx shearwater *Puffinus puffinus*	658798	Least concern	83.92	10.85	0.74
Mediterranean gull *Larus melanocephalus*	1026	Least concern	0.16	71.37	N/A
Northern fulmar *Fulmarus glacialis*	1075514	Endangered	15.36	10.76	0.8
Northern gannet *Morus bassanus*	576088	Least concern	42.05	9.56	0.66
Razorbill *Alca torda*	178773	Near threatened	17.53	12.8	0.7
Roseate tern *Sterna dougallii*	3060	Least concern	52.76	21.98	N/A
Sandwich tern *Sterna sandvicensis*	34166	Least concern	11.58	29.66	0.48

6.4 Conclusions and future directions

In this thesis I have demonstrated how the collation of large amounts of existing colony-based data can be utilised for the spatial assessment of a seabird community without the need to collect additional empirical data at sea. In some cases, the foraging radius method can be just as good at assessing species' distributions as more complicated models, and provides a very useful tool for rapidly mapping distributions in order to inform marine spatial planning and predict spatial vulnerability to risks. Furthermore, my thesis highlights the species for which the basic foraging radius method is less suitable and for which additional factors that drive their distributions need to be considered. Further work is needed to identify ways to incorporate colony-specific foraging ranges, species-specific colony decay rates, and general rules for spatial segregation into the universal model. This requires the collection and collation of data from multiple colonies of varying sizes to identify these species' specific parameters, as has previously been done for gannets. The baseline foraging radius distributions can be further enhanced by the addition of empirical distribution data (e.g. from surveys or GPS tracking), which would provide greater confidence in their utility for offshore regions.

When assessing species vulnerability to any anthropogenic risk, it is vital that the methods used are transparent, replicable, and easily communicated for conservation and policy purposes. The OVI that I have developed and presented in this thesis meets these requirements, and can be easily adapted for use across different regions of the world, or for other anthropogenic risks. While the best way to map these results for rapid risk assessments remains unclear, further work should assess the importance of weighting the different elements in a vulnerability or risk exposure map.

Finally, combining the results on species' distributions, vulnerability to oil pollution, and overlap with both existing MPAs and anthropogenic activities has allowed me to provide a community scale assessment of breeding seabird species in Irish waters. It is clear that Ireland is still failing to meet national, EU, and international targets for protecting its seabird community. However, it is promising that there is now a significant amount of data and readily applicable methods available to better inform seabird conservation planning in the region.

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Appendices

Appendix A – Supplementary figures for Chapter 2

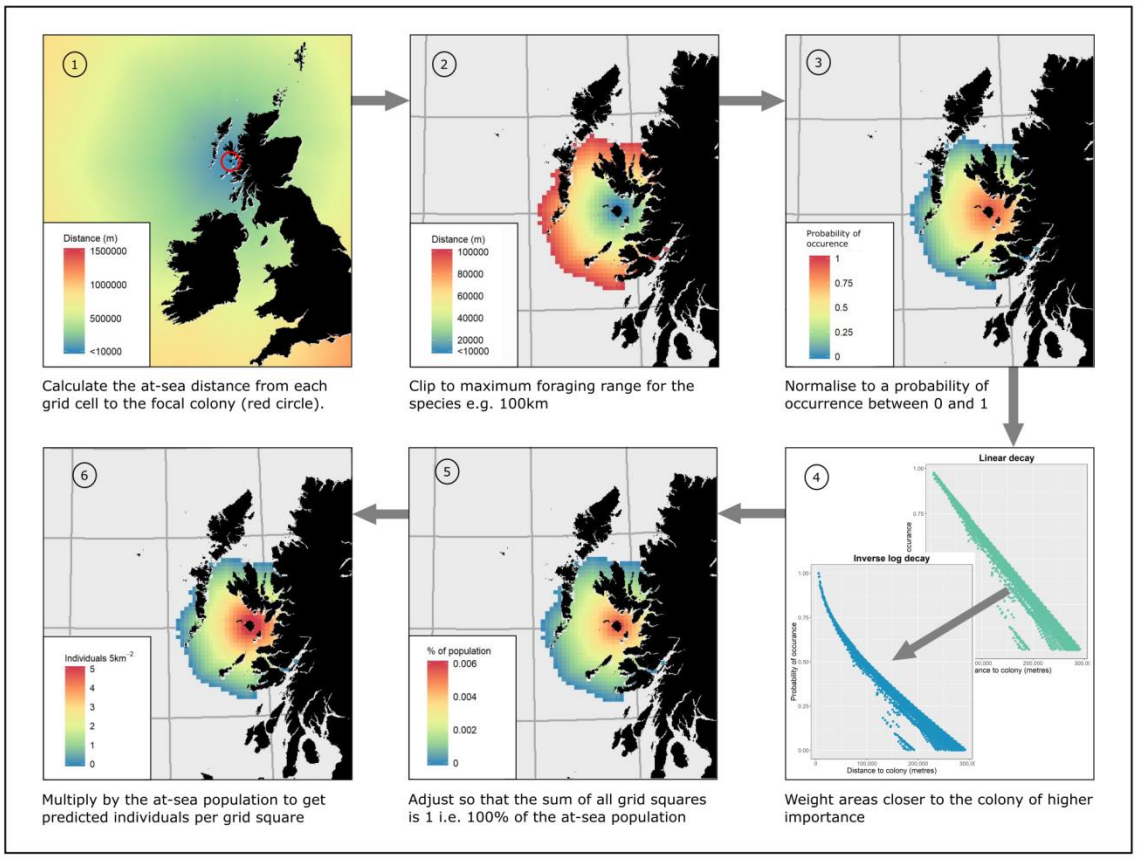
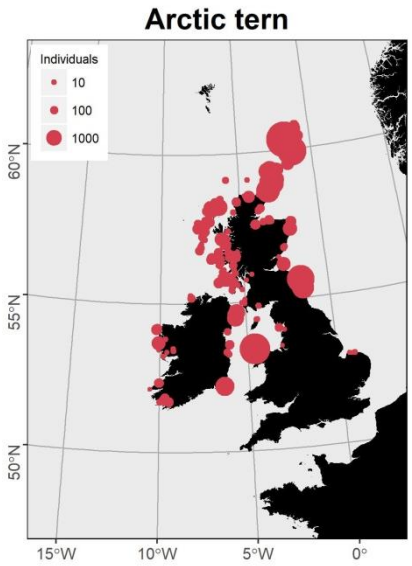
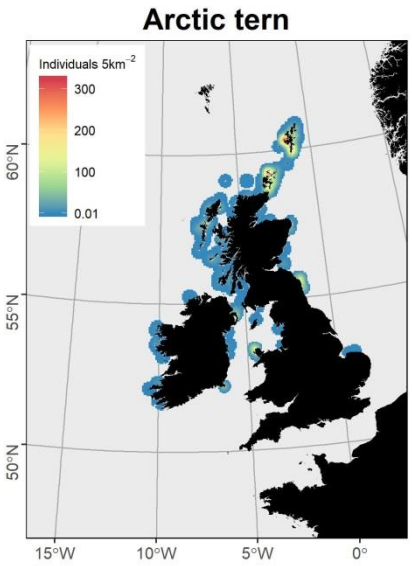
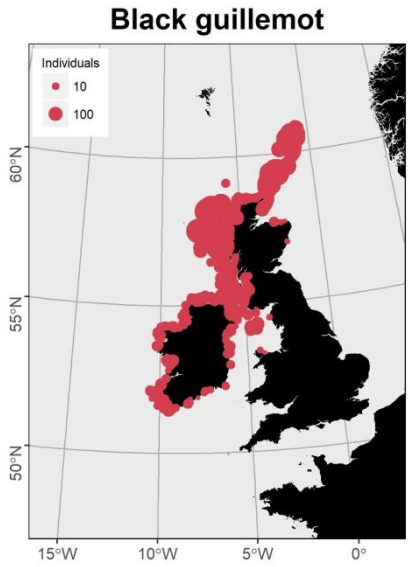
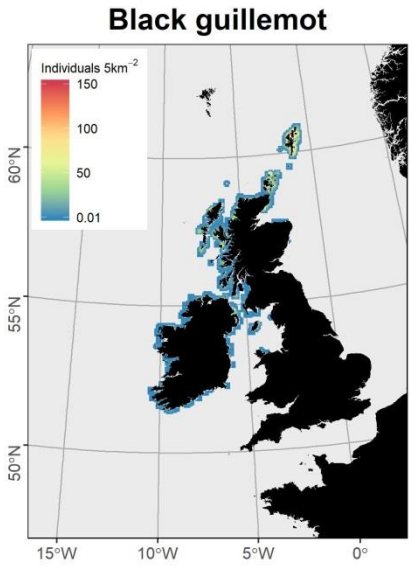


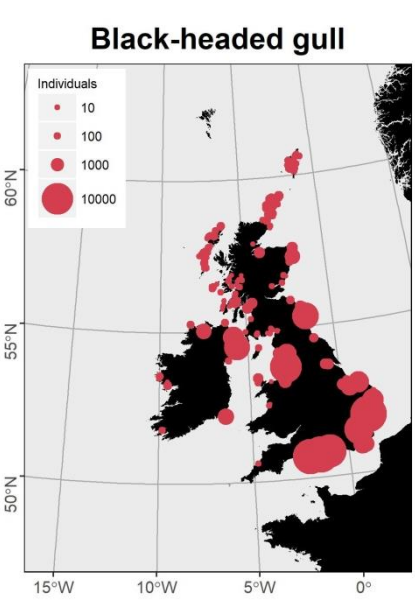
Figure A.1 Schematic of steps followed to produce a foraging radius distribution for a single colony. Example shown is for a hypothetical colony of 1,000 individuals with a maximum foraging range of 100 km. All colony distributions are then combined to generate the complete regional distribution. See methods (Chapter 2) for further details.

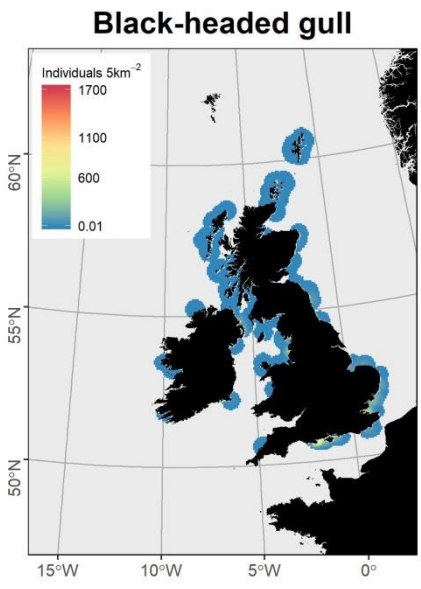

Arctic tern
Individuals
10
100
1000
60°N
55°N
50°N
15°W
10°W
5°W
0°


Arctic tern
Individuals 5km^{-2}
300
200
100
0.01
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15°W
10°W
5°W
0°

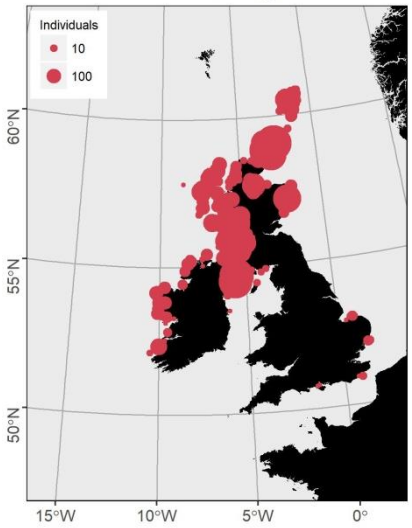

Black guillemot
Individuals
10
100
60°N
55°N
50°N
15°W
10°W
5°W
0°


Black guillemot
Individuals 5km^{-2}
150
100
50
0.01
60°N
55°N
50°N
15°W
10°W
5°W
0°

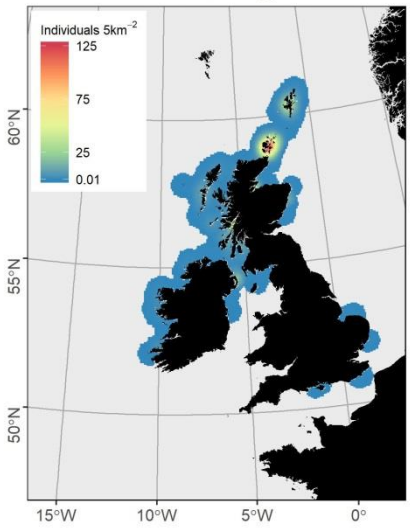

Black-headed gull
Individuals
10
100
1000
10000
60°N
55°N
50°N
15°W
10°W
5°W
0°


Black-headed gull
Individuals 5km^{-2}
1700
1100
600
0.01
60°N
55°N
50°N
15°W
10°W
5°W
0°

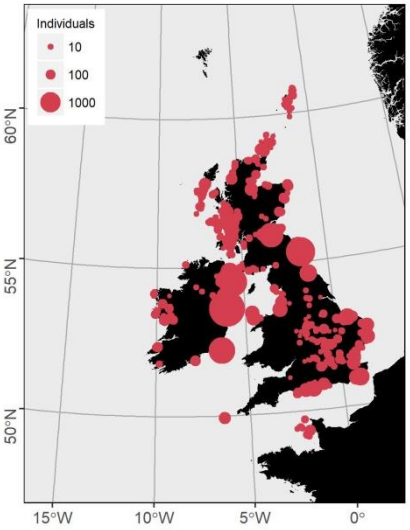
Common gull



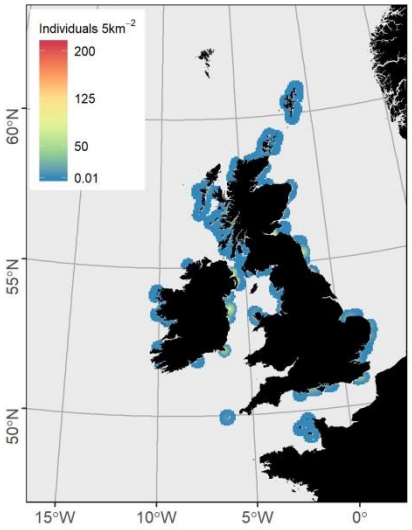
Common gull



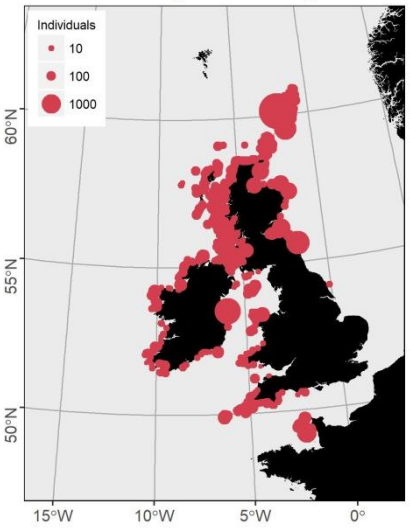
Common tern



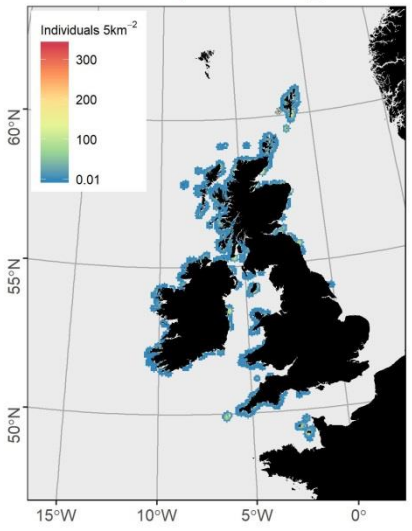
Common tern



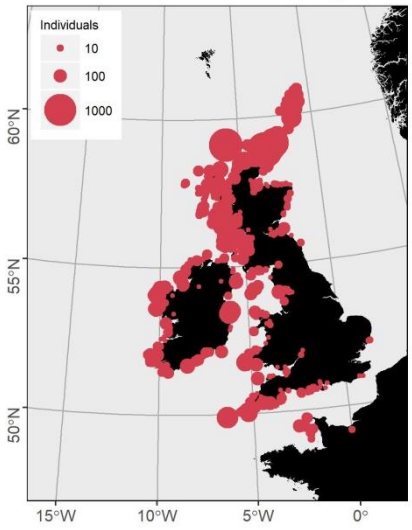
European shag



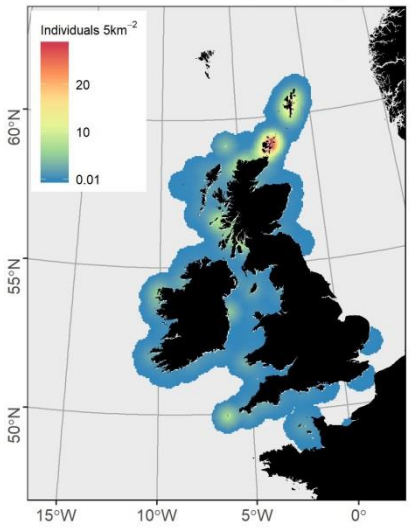
European shag



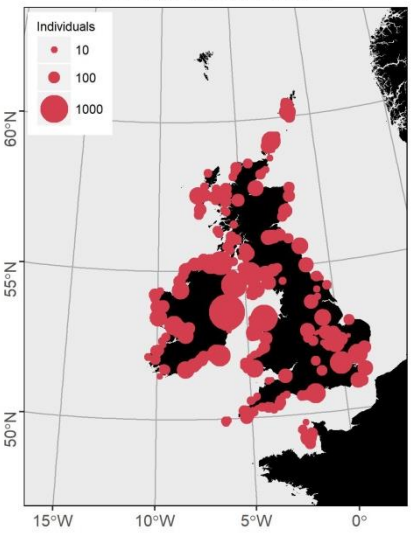
Great black-backed gull



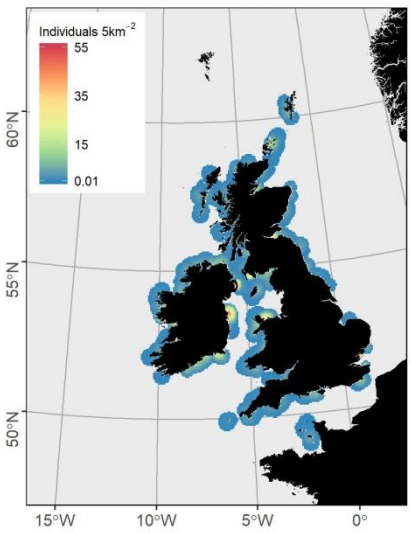
Great black-backed gull



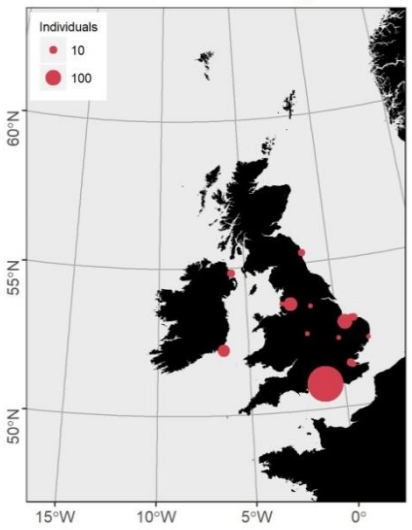
Great cormorant



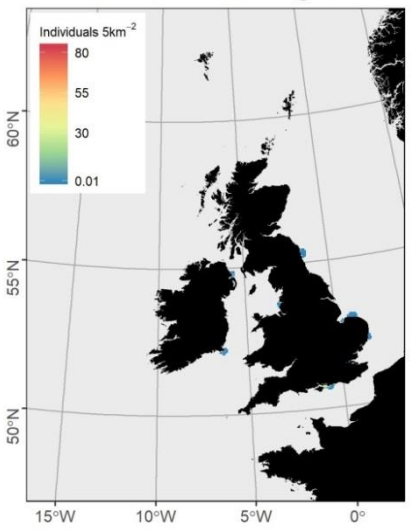
Great cormorant



Mediterranean gull



Mediterranean gull



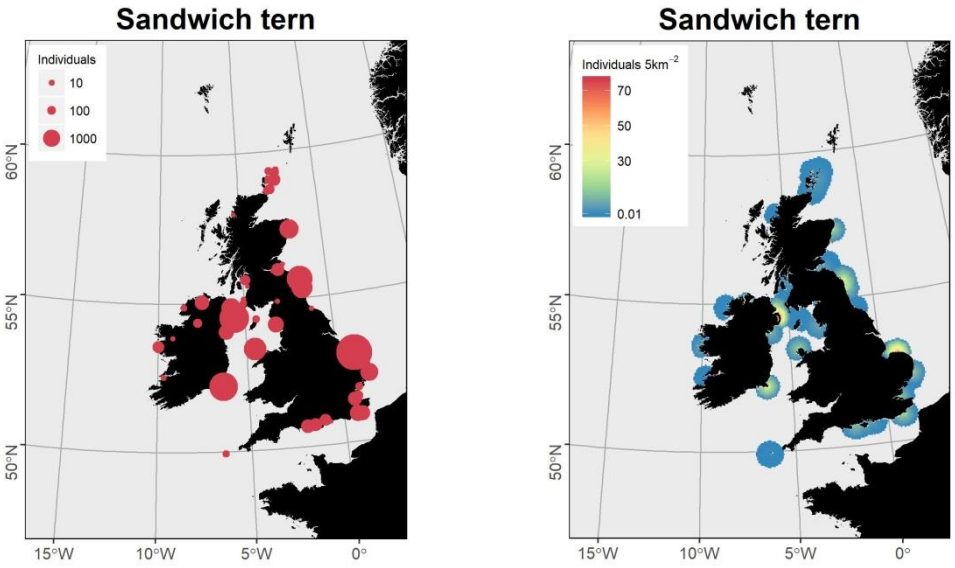
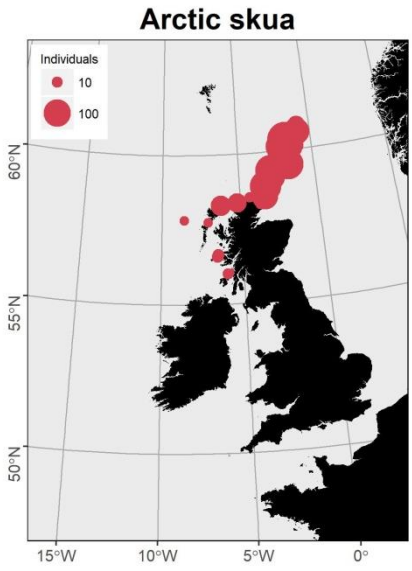
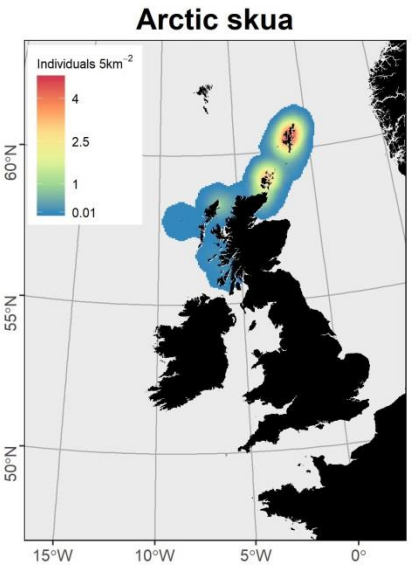
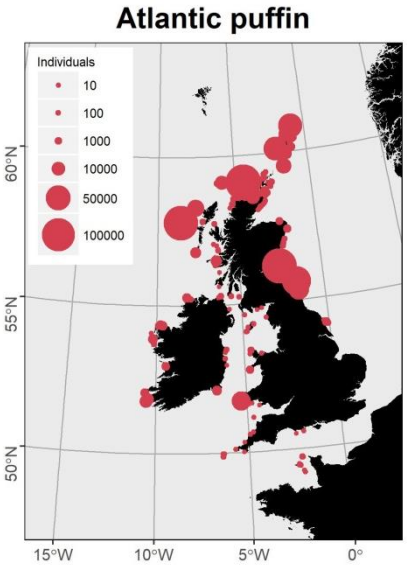
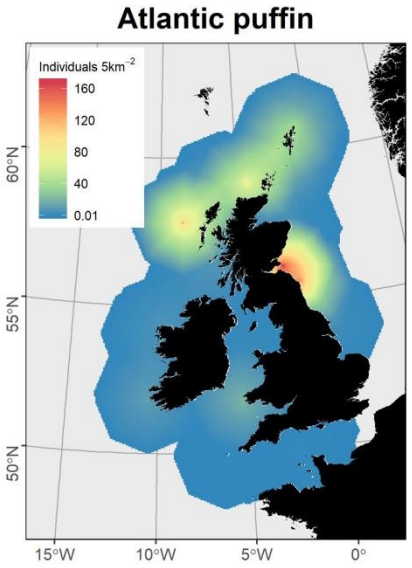


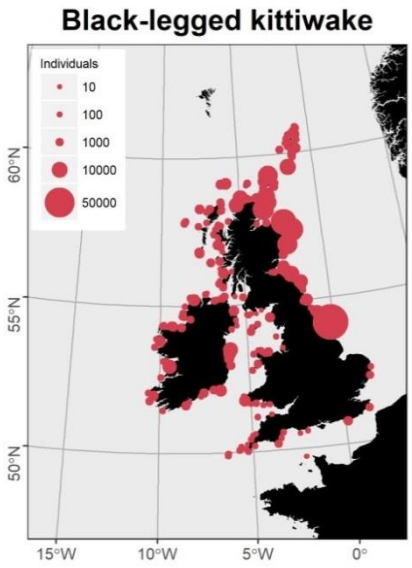
Figure A.2 Maps for each coastal seabird species occurring in Britain and Ireland (apart from sensitive species) showing a) colony location and population size and b) foraging radius distributions

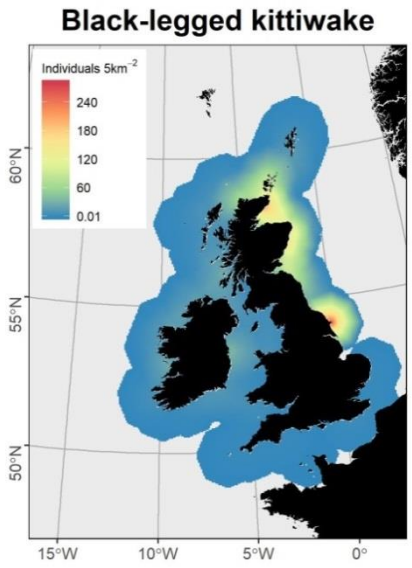

Arctic skua
Individuals
10
100
60°N
55°N
50°N
15°W
10°W
5°W
0°


Arctic skua
Individuals 5km^{-2}
4
2.5
1
0.01
60°N
55°N
50°N
15°W
10°W
5°W
0°

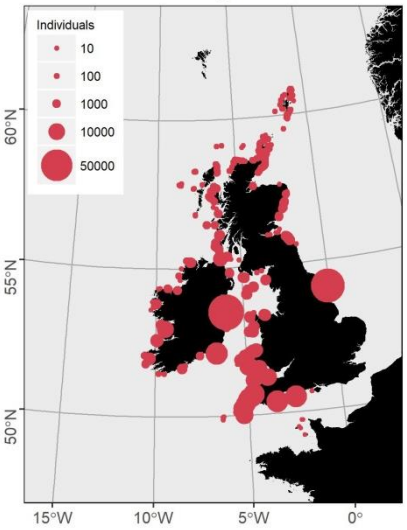

Atlantic puffin
Individuals
10
100
1000
10000
50000
100000
60°N
55°N
50°N
15°W
10°W
5°W
0°


Atlantic puffin
Individuals 5km^{-2}
160
120
80
40
0.01
60°N
55°N
50°N
15°W
10°W
5°W
0°

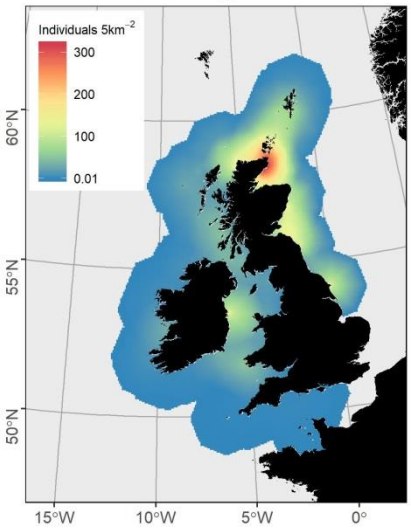

Black-legged kittiwake
Individuals
10
100
1000
10000
50000
60°N
55°N
50°N
15°W
10°W
5°W
0°


Black-legged kittiwake
Individuals 5km^{-2}
240
180
120
60
0.01
60°N
55°N
50°N
15°W
10°W
5°W
0°

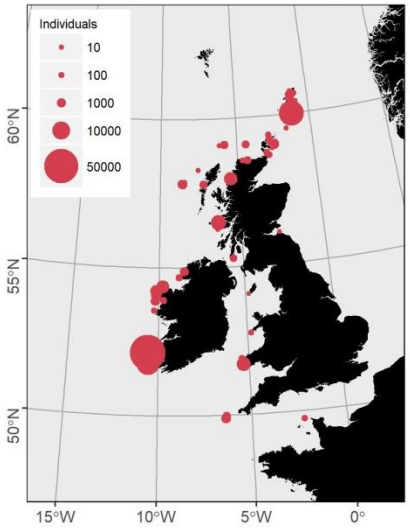
Common guillemot



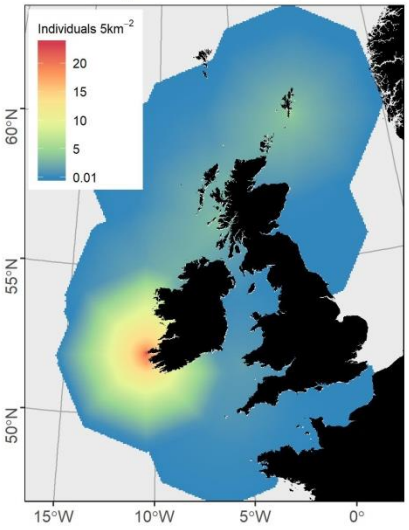
Common guillemot



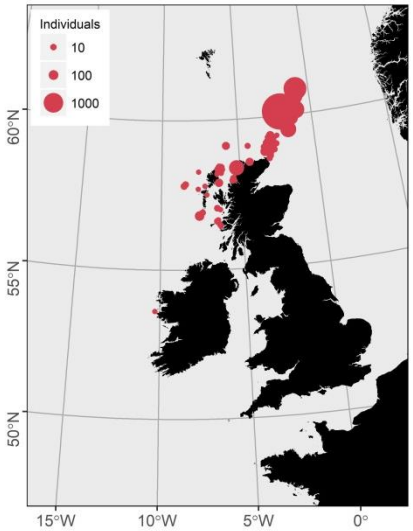
European storm-petrel



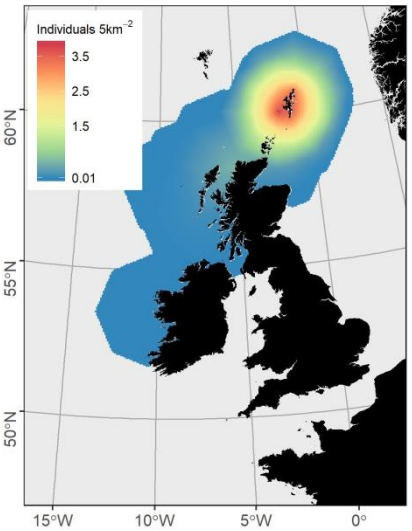
European storm-petrel



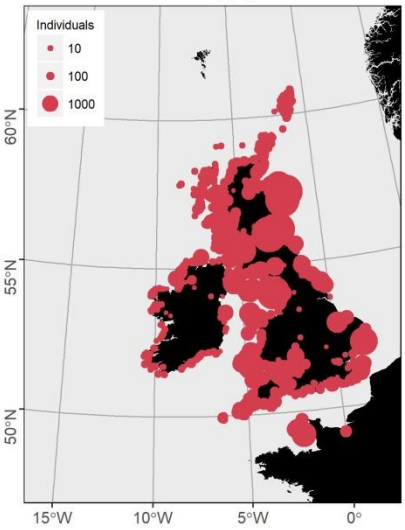
Great skua



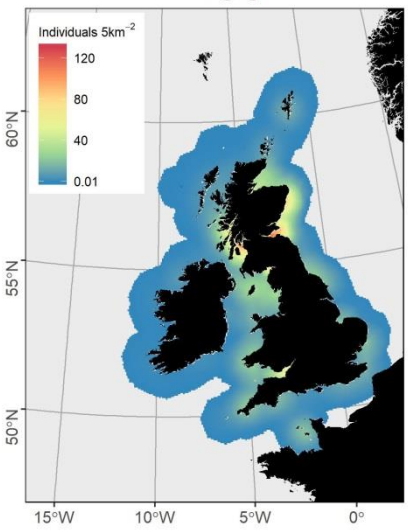
Great skua



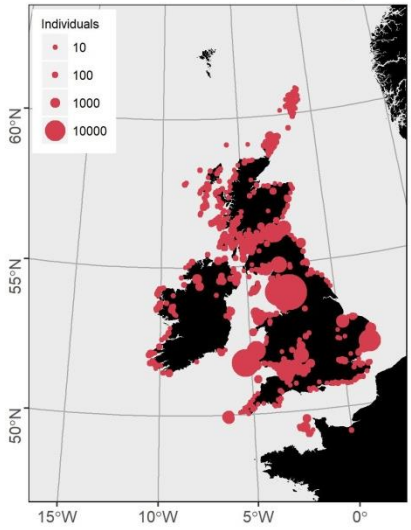
Herring gull



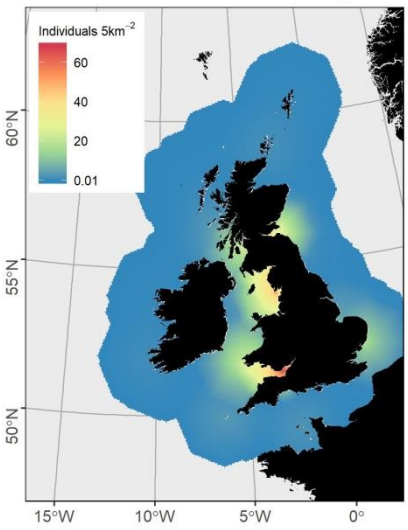
Herring gull



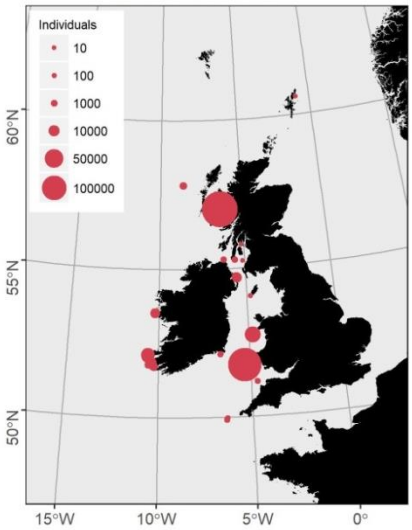
Lesser black-backed gull



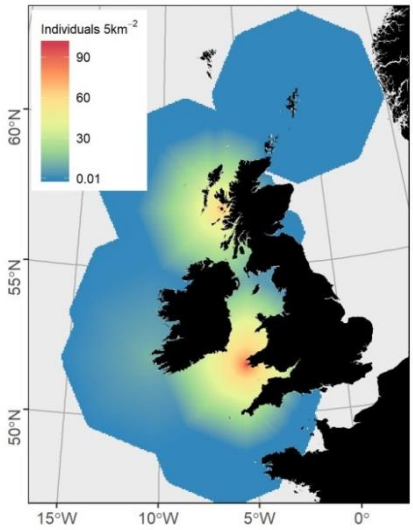
Lesser black-backed gull



Manx shearwater



Manx shearwater



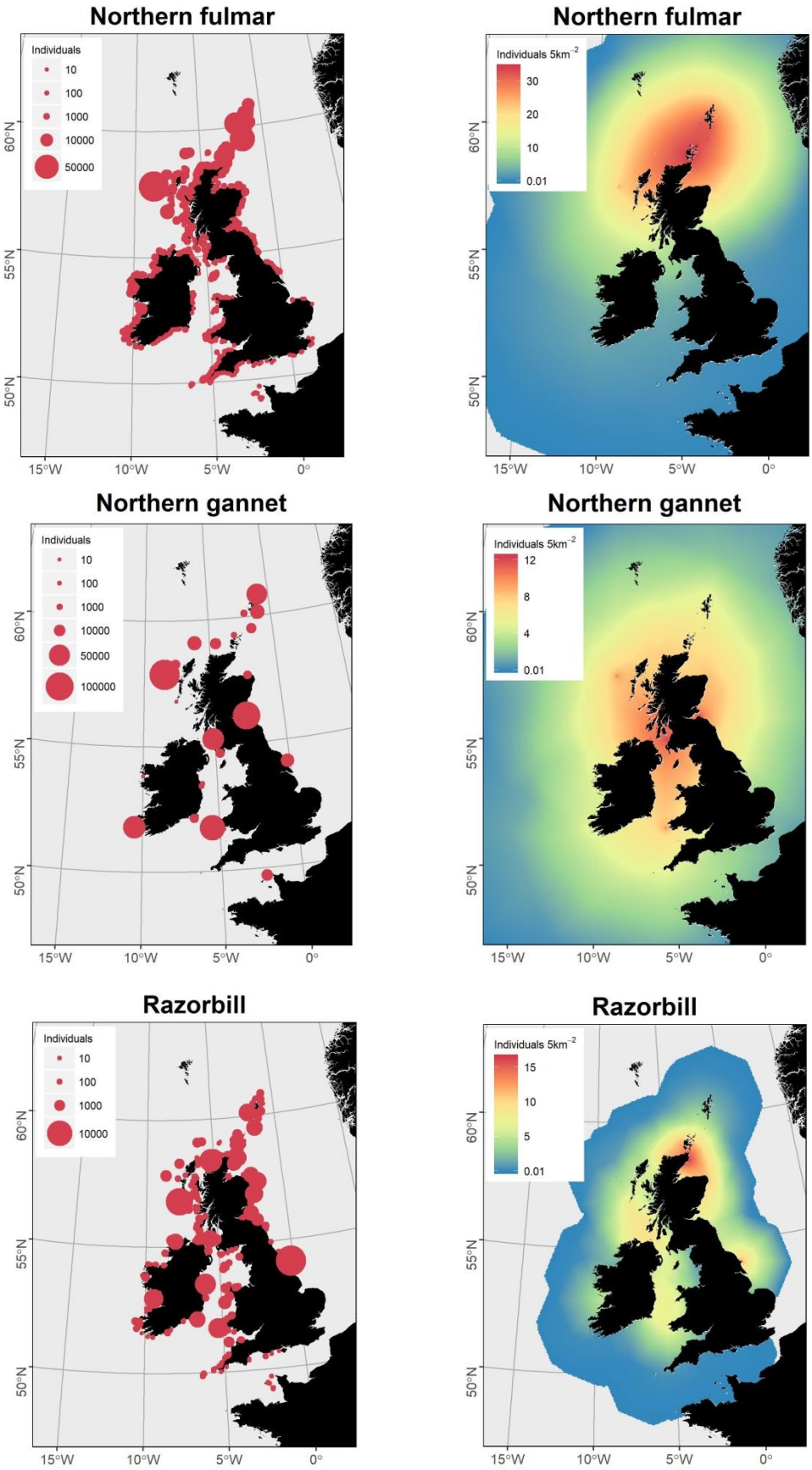
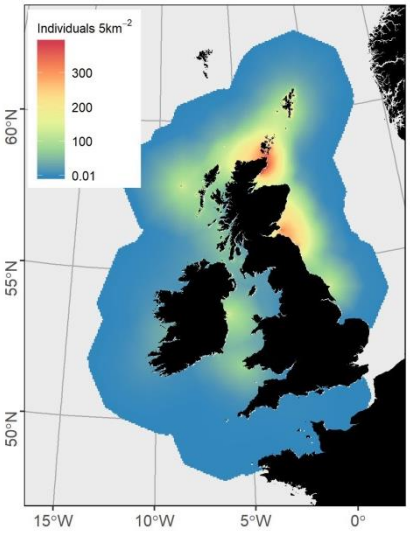
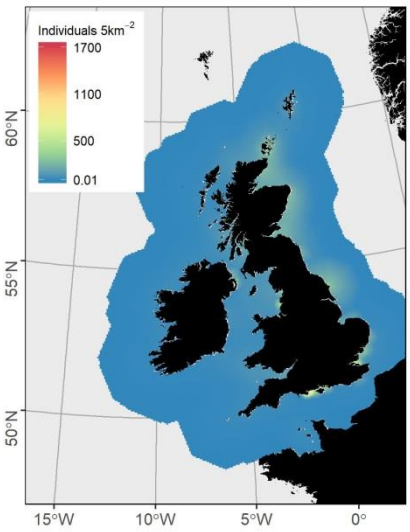


Figure A.3 Maps for each pelagic seabird species occurring in Britain and Ireland showing a) colony location and population size and b) foraging radius distributions

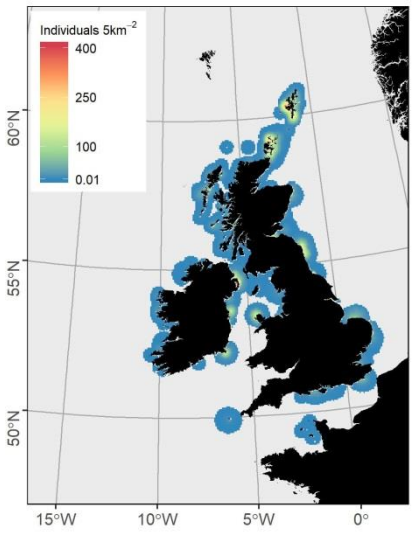
Alcidae



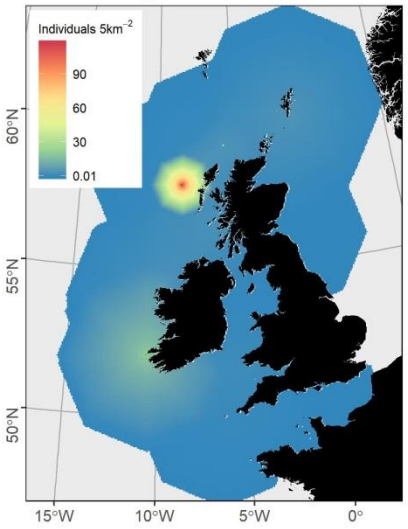
Laridae - Gulls



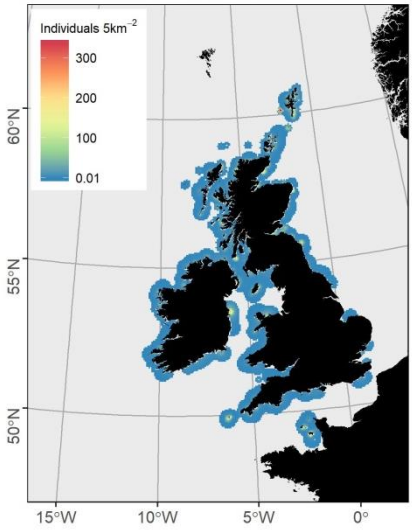
Laridae - Terns



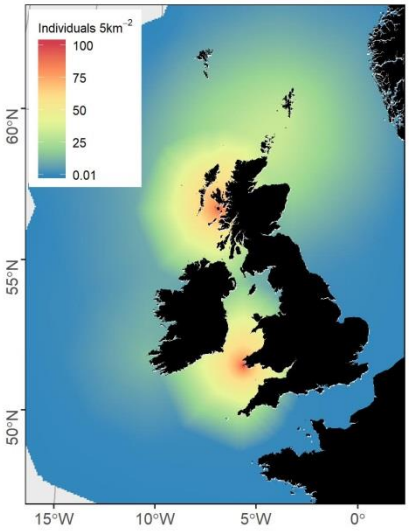
Hydrobatidae



Phalacrocoracidae



Procellariidae



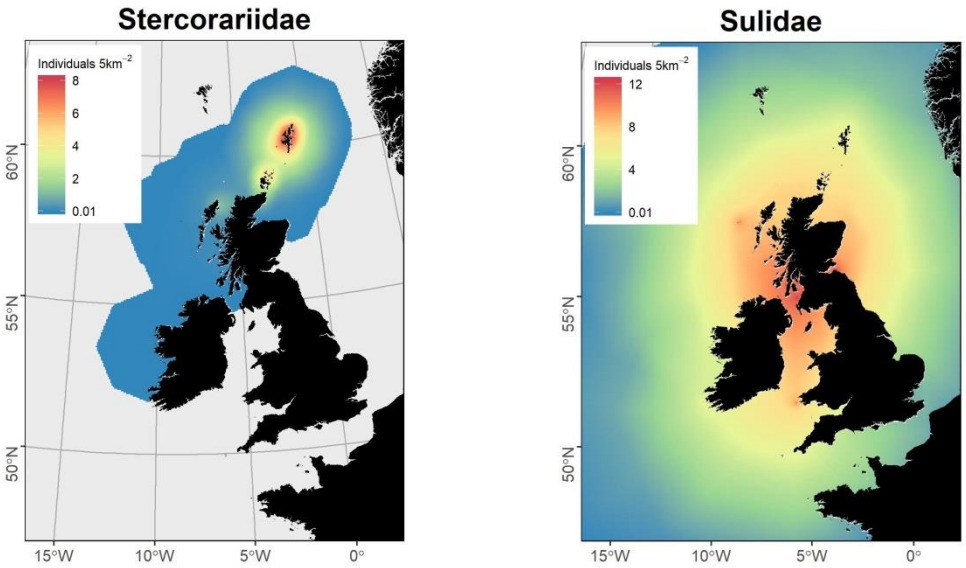


Figure A.4 Maps for each seabird family group occurring in Britain and Ireland showing foraging radius distributions

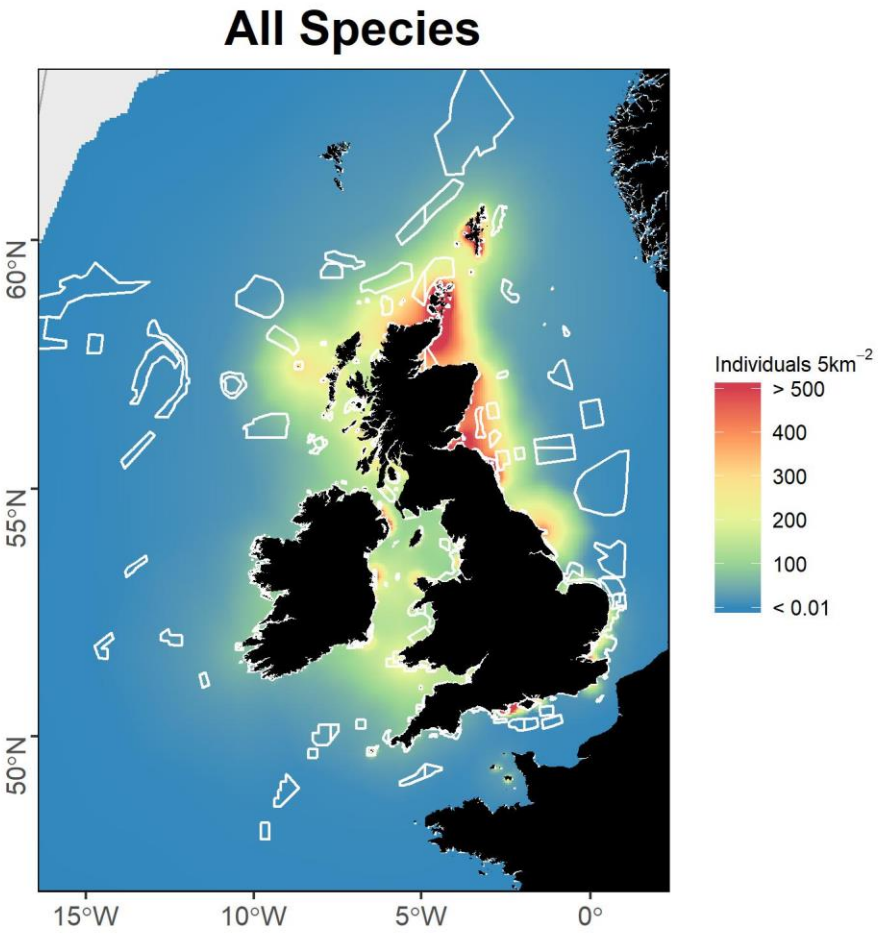


Figure A.5 Map showing the foraging radius distribution for all species with protected areas overlaid (white polygons). Grid squares with over 500 individuals are red and grid squares containing less than 0.01 are blue.

Appendix B – Supplementary tables for Chapter 2

Table B.1 Percentage of predicted at-sea population contained within a currently designated protected area. Percentage values are not additive as there is spatial overlap between the different protected area types.

Species	Percentage of population contained in:		
	SPAs	OSPAR MPAs	All PAs
Coastal species			
Arctic tern	5.43	13.66	16.48
Black guillemot	8.66	17.45	18.36
Black-headed gull	36.22	47.99	51.74
Common gull	5.06	15.95	16.64
Common tern	16.44	25.94	34.21
European shag	9.37	22.59	27.11
Great black-backed gull	3.29	12.57	14.00
Great cormorant	10.74	20.45	26.65
Little tern	40.71	48.18	61.65
Mediterranean gull	64.38	57.82	71.37
Roseate tern	7.53	2.00	21.98
Sandwich tern	9.70	20.78	29.66
Pelagic species			
Arctic skua	3.47	15.46	15.46
Atlantic puffin	1.30	13.77	18.64
Black-legged kittiwake	1.86	10.77	12.51
Common guillemot	2.04	12.46	13.83
European storm-petrel	0.70	5.21	6.60
Great skua	0.92	14.35	14.35
Herring gull	5.21	15.91	17.20
Leach's storm-petrel	3.40	9.67	9.70
Lesser black-backed gull	7.59	17.23	19.43
Manx shearwater	1.91	9.27	10.85
Northern fulmar	0.59	10.36	10.76
Northern gannet	0.95	8.52	9.56
Razorbill	1.66	11.61	12.80
Family group			
Alcidae	1.85	12.96	14.29
Laridae – gulls	7.83	17.62	19.55
Laridae – terns	8.87	17.60	22.96
Hydrobatidae	1.65	6.78	7.69
Phalacrocoracidae	9.79	21.94	26.97
Procellariidae	1.09	9.94	10.79
Stercorariidae	1.50	14.60	14.61
Sulidae	0.95	8.52	9.56

B.2 List of species contained within each family group

Alcidae: Atlantic puffin, black guillemot, common guillemot, and razorbill.

Laridae – gulls: Black-headed gull, black-legged kittiwake, common gull, great black-backed gull, herring gull, lesser black-backed gull, and Mediterranean gull.

Laridae – terns: Arctic tern, common tern, little tern, roseate tern, and sandwich tern.

Hydrobatidae: European storm-petrel and Leach's storm-petrel.

Phalacrocoracidae: European shag and great cormorant.

Procellariidae: Manx shearwater and northern fulmar.

Stercorariidae: Arctic skua and great skua.

Sulidae: Northern gannet.

Appendix C – R code for foraging radius model

```
## Marine Protected Areas show low overlap with projected distributions of seabird
populations in Britain and Ireland
## Critchley et al. 2018
## Appendix C
## Example of a complete script for creating projected distributions, with all the steps
included

#Require dependencies
library(raster)
library(gdistance)
library(maptools)
library(rgdal)
library(rgeos)
library(colorRamps)

rm(list=ls())

setwd("C:/") #set the working directory

# ------------------------------------------------------------------------------
# Create base map in UTM

# Define projection
UTMCRS <- CRS("+proj=utm +zone=29 +ellps=WGS84 +datum=WGS84 +units=m
+no_defs") # UTM 29 is used for Ireland
# Load in high resolution shapefile to generate distribution model from
map_shp <- readOGR(dsn = "path", layer = "file") # Replace with path to file and file name
# Clip and project to UTM
CP <- as(extent(-15, 15, 45, 75), "SpatialPolygons") # set to extent of region
proj4string(CP) <- CRS(proj4string(map_shp)) # Match projections
# Clip the map and overwrite
map_shp <- gIntersection(map_shp, CP, byid = T, drop_lower_td = T)
# Transform to UTM
map_utm <- spTransform(map_shp, UTMCRS)
plot(map_utm)
# Remove large file that isn't needed
rm(map_shp)
```

```
# ------------------------------------------------------------------------
# Transform and plot colonies

# Load colonies
Colonies <- read.csv("colony_table.csv") # replace with file containing colony locations and
population sizes
# Convert to SpatialPointsDataFrame
Colonies <- SpatialPointsDataFrame(coords = cbind(Colonies$Lon, Colonies$Lat),
                          data = Colonies, proj4string = CRS("+proj=longlat +datum=WGS84"))
# Transform from Lon Lat to UTM
Colonies <- spTransform(Colonies, UTMCRS)
# Check colonies are in the right place
plot(Colonies, pch = 19, add = T)

# Create list of population counts for each colony
Populations <- data.frame(Colonies@data$Count)

#set foraging radius distance (in metres) to be used in model
MaxDist <- 100000

# ------------------------------------------------------------------------
# Generate raster from map for distance calculations

# Create blank raster of 5km resolution that covers full extent of region
ras <- raster(xmn = -600000, xmx = 1400000, ymn = 4900000, ymx = 7500000, resolution =
5000)

crs(ras) <- crs(map_utm) # match projection of raster to map
# rasterize will set ocean to NA so inverse it and set water to "1"
# land is equal to zero because it is "NOT" NA
mask <- rasterize(map_utm, ras)
ras <- is.na(mask)

# Set land to 2 to make it more expensive to cross
ras[ras==0] <- 2
# Each cell now has value of 1 or 2, nothing else

# Create a Transition object from the raster
# this calculation will take time when resolution is small
tr <- transition(ras, function(x) 1/mean(x), 8)
```

```
tr <- geoCorrection(tr, scl = FALSE) # correct for diagonal distances

# ------------------------------------------------------------------------
# Set up loop & progress bar

# Set up loop through colonies
Colonies <- data.frame(coordinates(Colonies))

# Create a stack to store each raster in the loop,
# these will then be summed at the end
ColonyStack <- stack()

# Create progress bar to track percentage of loops completed
# This is useful when there are a large number of colonies
# but it does slow down the loop slightly
pb <- winProgressBar(title="Raster loop progress bar", label="0% done",
                     min=0, max=100, initial=0)

# ------------------------------------------------------------------------
# Generate distribution for each colony and sum

for (i in 1:length(Colonies[,1])){
  R <- accCost(tr, SpatialPoints(Colonies[i,]))

  # now raster still shows the expensive travel over land
  # so we mask it out for sea travel only
  R <- mask(R, mask, inverse = TRUE)

  R[R > MaxDist] = NA

  R <- -1*(R/MaxDist)+1  # normalise to 0 and 1 probability of occurance

  # Calculate ditance from each cell to the colony
  dist.R <- distanceFromPoints(R, (Colonies[i,]))
  R<- R*(1/log(dist.R)) # weight areas closer to the colony of higher importance

  # normalise to 0 and 1 probability of occurance
  R <- ((R-cellStats(R,"min"))/(cellStats(R,"max")-cellStats(R,"min")))

  # whole area sums to one
```

```
  R <- R/sum(getValues(R), na.rm = T)

  # multiply by the number of pairs at each colony
  R <- R*(Populations[i,1])

  # Plot raster to check it worked
  # This will slow down the loop so this step can be removed to speed things up
  par(ask = F)
  plot(R)

  # Save raster for each colony into stack
  ColonyStack <- stack(ColonyStack, R)

  rm(R) # Remove large file that is no longer needed

  # run progress bar - can be removed to speed up loop
  Sys.sleep(0.1)  # slow down the code for illustration purposes
  info <- sprintf("%d%% done", round((i/length(Colonies[,1]))*100))
  setWinProgressBar(pb, i/(length(Colonies[,1]))*100, label=info)

}

output <- sum(ColonyStack, na.rm = T) # sum cell values across colonies

writeRaster(output, filename = "Raster_name", format = "GTiff", overwrite = TRUE) # Write
to raster file

# ------------------------------------------------------------------------------
# Plot distribution map

par(ask = F)
plot(output)
lines(map_utm, lwd = 0.25)
points(Colonies, pch = 19, cex = 0.75, col = 2)
```

Appendix D – Supplementary material for Chapter 3

Table D.1 Details of foraging range values (mean and mean maximum), and sources, used in foraging radius distributions. See D.2 for a full reference list of sources.

Species	Maximum foraging range (km)	Source	Mean maximum foraging range (km)	Sources
Arctic skua	75	Thaxter et al. 2012	62.5	Thaxter et al. 2012
Arctic tern	30	Thaxter et al. 2012	24.2	Thaxter et al. 2012
Atlantic puffin	66	Harris et al. 2012	53	Harris et al. 2012 & Bennison (unpublished data)
Black guillemot	15	Thaxter et al. 2012	7.35	Jovani et al. 2015
Black-headed gull	40	Thaxter et al. 2012	25.5	Thaxter et al. 2012
Black-legged kittiwake	304	Christensen-Dalsgaard et al. 2018	162.4	Christensen-Dalsgaard et al. 2018 & Thaxter et al. 2012
Common guillemot	135	Thaxter et al. 2012	84.2	Thaxter et al. 2012
Common gull	50	Thaxter et al. 2012	50	Thaxter et al. 2012
Common tern	30	Thaxter et al. 2012	15.2	Thaxter et al. 2012
European shag	23	Soanes et al. 2014	17.3	Soanes et al. 2014 & Thaxter et al. 2012
European storm-petrel	398	Bolton & Kane (unpublished data)	266.3	Bolton & Kane (unpublished data) & Thaxter et al. 2012
Great Black-backed gull	60	Jovani et al. 2015	35	Jovani et al. 2015
Great cormorant	70	Potier et al. 2015	36.25	Potier et al. 2015 & Thaxter et al. 2012
Great skua	219	Thaxter et al. 2012	86.4	Thaxter et al. 2012
Herring gull	92	Jovani et al. 2015	61.1	Thaxter et al. 2012
Leach's storm-petrel	700	Pollet et al. 2014	245	Pollet et al. 2014 & Thaxter et al. 2012
Lesser Black-backed gull	181	Thaxter et al. 2012	130.5	Juvaste et al. 2017, Thaxter et al. 2015 & Thaxter et al. 2012
Little tern	11	Thaxter et al. 2012	6.3	Thaxter et al. 2012
Manx shearwater	1456	Wischnewski (unpublished data)	927.5	Thaxter et al. 2012 & Wischnewski

				(unpublished data)
Mediterranean gull	20	Thaxter et al. 2012	20	Thaxter et al. 2012
Northern fulmar	580	Thaxter et al. 2012	400	Thaxter et al. 2012
Northern gannet	709	Wakefield et al. 2013	289.4	Thaxter et al. 2012 & Wakefield et al. 2013
Razorbill	95	Thaxter et al. 2012	47	Thaxter et al. 2012 & Wischnewski (unpublished data)
Roseate tern	30	Thaxter et al. 2012	16.6	Thaxter et al. 2012
Sandwich tern	54	Thaxter et al. 2012	49	Thaxter et al. 2012

D.2 Reference list for foraging range sources

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D.3 Details of methods to create Generalised Additive Models of seabird distribution from the broad-scale offshore aerial survey data.

In the broad scale surveys, summer seabird abundance and distribution was modelled using Generalized Additive Models (GAM) with a logarithmic link function, and a Tweedie error distribution following Cañadas and Hammond (2008). A spatial grid of resolution 0.10 x 0.06 degrees (latitude x longitude) was created covering the survey areas. This resolution was chosen as it was the finest consistent resolution that captured all available environmental covariates. This approach yielded a total of 4,129 grid cells within the study area. The empirical data from the surveys used for distribution comparisons consisted of total density recorded along track segments. Segment length was determined by transect length travelled within each grid square. Environmental variables were derived from a large number of data sources summarised in D.4. Water depth (m), distance to the 0 m, 200 m and 2000 m contours (as proxies for coastal, continental shelf and oceanic habitats, respectively), slope and contour index, sea surface temperature (C°), sea bottom temperature (C°), mixed layer depth (m) and chlorophyll-a concentration (mgC/l) were assigned to the centre of each grid cell and used to provide values of environmental covariates for the effort segments and to predict abundance spatially. As group sizes had a very wide range and varied spatially, group size was modelled and overall seabird density per grid cell obtained by multiplying the abundance of groups per grid cell (using the best fitting model), by the predicted group size, and dividing by the area of the grid cell. To obtain the coefficient of variation and percentile-based 95% Confidence Intervals, using transect-day as the resampling unit, 400 non-parametric bootstrap re-samples were applied to the whole modelling process. In each bootstrap replicate, the degree of smoothing of each model term was selected by the statistical package, thus incorporating some model selection uncertainty in the variance (Cañadas and Hammond, 2008).

The best fitting model was determined by stepwise selection in the model settings, and then based on the comparison of AIC values, significance of terms and the deviance explained. All modelling was carried out using the statistical software R (R Core Team, 2017) using the *mgcv* package (Wood, 2006).

Table D.4 Details of Environmental covariates used in Generalised Additive Models of seabird distribution from the broad-scale offshore aerial survey data.

Name	Description	Source
depth	Average depth in the grid cell	2-Minute Gridded Global Relief Data (ETOPO2v2). National Geophysical Data Center (NGDC). NOAA Satellite and Information Service.
depthsd	Standard deviation of the depth data points within the grid cell	Derived from ETOPO2 bathymetric data
dist0	Distance to the 0 m depth contour (coast), in decimal degrees	Calculated with the Spatial Analyst extension of ArcGis 9.2, using GEBCO bathymetric data.
dist200	Distance to the 200 m depth contour, in decimal degrees	Calculated with the Spatial Analyst extension of ArcGis 9.2, using GEBCO bathymetric data.
dist2000	Distance to the 2000 m depth contour, in decimal degrees	Calculated with the Spatial Analyst extension of ArcGis 9.2, using GEBCO bathymetric data.
slope	Slope of the sea floor in m per km, calculated as follows: $\frac{\left(\frac{depth_{max} - depth_{min}}{distance\ in\ km_{(depth_{max} - depth_{min})}}\right)}{10}$	Derived from ETOPO2 bathymetric data
ci	Contour index of the sea floor, calculated as follows: $\frac{(depth_{max} - depth_{min})}{depth_{max}} * 100$	Derived from ETOPO2 bathymetric data
ssh	Average Sea Surface Height Anomaly for the months of June to August 2005 and 2007, calculated as the difference between measured SSH and the expected mean SSH.	Altimetry Sensors on multiple spacecrafts (JASON-1, TOPEX/POSEIDON, ENVISAT, GFO, ERS 1/2, GEOSAT). Resolution: 0.25 degrees. NOAA CoastWatch Program
sst	Average Sea Surface Temperature for the months of June to August 2005 and 2007.	Sensor: Moderate Resolution Imaging Spectroradiometer (MODIS) on Aqua, Advanced Very High Resolution Radiometer (AVHRR) on POES, Imager on GOES, Advanced Microwave Scanning Radiometer (AMSR-E) on Aqua. Resolution: 0.1 degrees. NOAA CoastWatch Program
sst_sd	Standard deviation of Sea Surface Temperature for the months of June to August 2005 and 2007.	Derived from NOAA CoastWatch Program sea surface temperature data.

Table D.5 Details of environmental covariates retained in GAM models of sightings (groups) and group size used for seabird distribution from broad-scale aerial surveys, and deviance explained.

		Groups				Group size			
Species	**Season**	**Covariates**	**edf**	**p**	**Deviance explained (%)**	**Covariates**	**edf**	**p**	**Deviance explained (%)**
Fulmar	Summer	Lon*Lat	25.7	<<0.001	13.3	Lon*Lat	27.8	<<0.001	46.0
		Depth	4.8	<<0.001					
Auks	Summer	Lon*Lat	13.9	<<0.001	81.5	Lon*Lat	15.5	<<0.001	8.3
Gannet	Summer	Lon*Lat	18.6	<<0.001	25.6	Lon*Lat	26.7	<<0.001	26.5
Manx	Summer	Lon*Lat	17.8	<<0.001	36.9	Lon*Lat	24.2	<<0.001	35.7
		chl_sum	4.5	0.0017					
Petrels	Summer	Lon*Lat	28.0	<<0.001	27.4	Mean group size			
		sst_sum	8.3	0.0022					
Black-backed gull	All	Lon*Lat	18.8	<<0.001	34.5	Lon*Lat	17.8	<<0.001	83.9
common/ herring gull	All	Lon	6.9	<<0.001	54.8	Dist_0	7.3	0.068	35.5

Table D.6 Pearson correlation coefficients between individual colony kernel densities (from GPS tracking data) and foraging radius distributions for that colony. *p* values were calculated after accounting for spatial autocorrelation using Dutilleul's (1993) method. Significant correlations ($p < 0.05$) are marked in bold. Values for mean max and max foraging ranges can be found in Table D.1.

Species	Region	Resolution	Year	Foraging range	Correlation value	p-value
Atlantic puffin	Little Saltee, Wexford	2km	2017	Max	0.5	**< 0.001**
Atlantic puffin	Little Saltee, Wexford	2km	2017	Mean max	0.557	**< 0.001**
European storm-petrel	High Island, Galway	2km	2016	Max	0.532	**0.01**
European storm-petrel	High Island, Galway	2km	2016	Mean max	0.574	**0.003**
Manx shearwater	High Island, Galway	5km	2014-16	Max	0.211	**0.002**
Manx shearwater	High Island, Galway	5km	2014-16	Mean max	0.344	**< 0.001**
Manx shearwater	Great Blasket, Kerry	5km	2014-15	Max	0.2	**0.01**
Manx shearwater	Great Blasket, Kerry	5km	2014-15	Mean max	0.282	**0.001**
Razorbill	Great Saltee, Wexford	2km	2014	Max	0.473	**< 0.001**
Razorbill	Great Saltee, Wexford	2km	2014	Mean max	0.645	**< 0.001**

Table D.7 Pearson correlation coefficients between distributions from aerial fine-scale surveys and foraging radius distributions in the Irish Sea. *p* values were calculated after accounting for spatial autocorrelation using Dutilleul's (1993) method. Significant correlations ($p < 0.05$) are marked in bold. Values for mean max and max foraging ranges (FR) can be found in Table D.1

Species	Predictive model	Correlation with empirical data	p-value
All species	Max FR	0.315	0.083
All species	Mean max FR	0.369	0.078
Arctic & Common tern	Max FR	**0.339**	**0.003**
Arctic & Common tern	Mean max FR	**0.166**	**0.014**
Atlantic puffin	Max FR	0.038	0.683
Atlantic puffin	Mean Max FR	0.045	0.604
Auks	Max FR	0.49	0.063
Auks	Mean max FR	0.527	0.062
Black guillemot	Max FR	0.066	0.146
Black guillemot	Mean max FR	0.048	0.272
Black-headed gull	Max FR	-0.003	0.94
Black-headed gull	Mean max FR	-0.003	0.942
Black-legged kittiwake	Max FR	0.065	0.461
Black-legged kittiwake	Mean max FR	0.15	0.152
Cormorant & Shag	Max FR	-0.001	0.985
Cormorant & Shag	Mean max FR	0.009	0.86
Gulls	Max FR	0.023	0.749
Gulls	Mean max FR	0.01	0.853
Herring and Common gull	Max FR	-0.006	0.936
Herring and Common gull	Mean max FR	0.053	0.548
LBB & GBB gull	Max FR	-0.1	0.314
LBB & GBB gull	Mean max FR	-0.031	0.672
Little tern	Max FR	-0.013	0.762
Little tern	Mean max FR	-0.007	0.87
Manx shearwater	Max FR	**0.112**	**0.035**
Manx shearwater	Mean max FR	**0.112**	**0.039**
Northern fulmar	Max FR	0.082	0.086
Northern fulmar	Mean max FR	0.082	0.079
Northern gannet	Max FR	0.057	0.256
Northern gannet	Mean max FR	-0.097	0.33
Petrels	Max FR	0.038	0.355
Petrels	Mean max FR	0.051	0.285

Razorbill & Common guillemot	Max FR	0.487	0.064
Razorbill & Common guillemot	Mean max FR	0.508	0.101
Roseate tern	Max FR	**0.313**	**< 0.001**
Roseate tern	Mean max FR	**0.391**	**< 0.001**
Sandwich tern	Max FR	**0.194**	**0.015**
Sandwich tern	Mean max FR	**0.209**	**0.009**
Terns	Max FR	**0.335**	**0.001**
Terns	Mean max FR	**0.392**	**< 0.001**

Table D.8 Correlations between combined data from two summers of aerial broad-scale surveys and both foraging radius distributions and GAM distributions. Values for correlations between foraging radius distributions and GAM distributions are also shown. *p* values were calculated after accounting for spatial autocorrelation using Dutilleul's (1993) method. Significant correlations ($p < 0.05$) are marked in bold. Values for mean max and max foraging ranges (FR) can be found in Table D.1.

Species	Predictive model	Correlation with empirical data	p-value
All species	Max FR	**0.151**	**0.013**
All species	Mean max FR	**0.167**	**0.002**
All species	GAM	**0.286**	**< 0.001**
Auks	Max FR	**0.426**	**< 0.001**
Auks	Mean max FR	**0.389**	**< 0.001**
Auks	GAM	**0.57**	**< 0.001**
Gulls	Max FR	**0.141**	**0.002**
Gulls	Mean max FR	**0.161**	**0.003**
Petrels	Max FR	0.082	0.1
Petrels	Mean max FR	0.084	0.08
Petrels	GAM	**0.222**	**< 0.001**
Terns	Max FR	**0.409**	**< 0.001**
Terns	Mean max FR	**0.421**	**< 0.001**
Black-legged kittiwake	Max FR	**0.129**	**0.005**
Black-legged kittiwake	Mean max FR	**0.155**	**< 0.001**
Black-legged kittiwake	GAM	**0.274**	**< 0.001**
Manx shearwater	Max FR	0.056	0.059
Manx shearwater	Mean max FR	0.062	0.057
Manx shearwater	GAM	**0.222**	**< 0.001**
Northern fulmar	Max FR	0.007	0.82
Northern fulmar	Mean max FR	0.0173	0.559
Northern fulmar	GAM	**0.213**	**< 0.001**
Northern gannet	Max FR	0.116	0.066
Northern gannet	Mean max FR	0.052	0.338
Northern gannet	GAM	**0.258**	**< 0.001**

Appendix E – Supplementary material for Chapter 4

Table E.1 Factors used for calculating vulnerability to oil pollution and displacement. See Table 4.1 in Chapter 4 for definition of factors.

Species	A1	A2	A3	A4	A5	A6	B1	C1	C2	C3	C4	C5	C6
Arctic skua	1	1	5	2	5	5	1	3	5	4	1	2	4
Arctic tern	2	2	5	3	4	4	1	5	4	4	1	3	4
Atlantic puffin	3	3	5	3	3	3	5	3	5	4	4	3	5
Black guillemot	3	3	5	4	3	3	5	1	4	4	1	3	4
Black-headed gull	2	2	2	2	4	4	5	3	4	5	1	3	3
Black-legged kittiwake	2	2	5	2	4	4	3	3	5	4	3	4	4
Black-throated diver	5	5	5	4	1	1	3	5	4	4	1	1	4
Common eider	3	3	5	4	3	3	4	3	4	4	2	2	1
Common goldeneye	4	4	3	4	2	2	4	3	4	5	1	1	1
Common guillemot	4	3	5	3	2	3	5	3	4	4	2	5	5
Common gull	2	2	2	2	4	4	4	3	4	4	1	3	3
Common scoter	5	5	5	4	1	1	4	3	5	5	1	1	1
Common tern	2	2	5	3	4	4	1	5	4	4	1	2	4
European shag	1	4	5	3	5	2	4	3	5	4	1	5	3
European storm-petrel	1	1	5	1	5	5	3	5	4	4	1	4	5
Great black-backed gull	2	1	4	2	4	5	4	3	4	4	1	4	4
Great cormorant	1	4	4	3	5	2	4	3	2	4	1	2	3
Great northern-diver	5	4	5	3	1	2	4	5	4	4	1	1	4
Great skua	1	1	5	2	5	5	2	3	4	4	1	5	4
Great-crested grebe	3	3	3	4	3	3	3	3	1	4	1	1	2
Greater scaup	4	4	5	4	2	2	4	3	5	4	1	1	1
Herring gull	2	1	3	1	4	5	4	3	5	5	2	4	4
Lesser black-backed gull	2	1	3	1	4	5	4	3	4	4	1	5	4
Little auk	3	3	5	2	3	3	5	3	1	1	1	1	5
Little tern	2	2	5	4	4	4	1	5	4	4	1	2	4
Long-tailed duck	4	3	5	4	2	3	4	3	5	5	3	1	1
Manx shearwater	1	1	5	1	5	5	3	3	4	4	1	5	5
Northern fulmar	1	1	5	1	5	5	4	3	4	1	4	4	5
Northern gannet	4	1	5	1	2	5	3	3	4	4	1	5	5
Razorbill	4	3	5	3	2	3	5	3	4	4	2	4	5
Red-throated diver	5	5	5	4	1	1	4	5	2	4	1	1	4
Sandwich tern	2	2	5	3	4	4	1	5	4	4	1	4	4
Sooty shearwater	1	1	5	1	5	5	3	3	3	5	2	1	5
Velvet scoter	5	4	5	3	1	2	4	3	5	5	3	1	1

Table E.2 Scores and ranks for oiling risk, displacement risk, and population sensitivity. OVI 9 = Oiling risk * Population sensitivity; DVI = Displacement risk * Population sensitivity. See Table 4.2 in Chapter 4 for OVI 9 and DVI scores.

	Oiling risk		Displacement risk		Population sensitivity	
Species	**Score**	**Rank**	**Score**	**Rank**	**Score**	**Rank**
Arctic skua *Stercorarius parasiticus*	0.58	27	0.41	29	0.82	19
Arctic tern *Sterna paradisaea*	0.54	28	0.66	19	0.86	10
Atlantic puffin *Fratercula arctica*	0.84	6	0.79	14	0.91	1
Black guillemot *Cepphus grylle*	0.84	7	0.82	11	0.78	24
Black-headed gull *Larus ridibundus*	0.88	2	0.60	23	0.82	22
Black-legged kittiwake *Rissa tridactyla*	0.78	16	0.60	24	0.90	2
Black-throated diver *Gavia arctica*	0.49	34	1.00	1	0.82	20
Common eider *Somateria mollissima*	0.78	17	0.82	12	0.69	29
Common goldeneye *Bucephala clangula*	0.60	26	0.92	6	0.66	31
Common guillemot *Uria aalge*	0.79	14	0.85	9	0.90	4
Common gull *Larus canus*	0.78	18	0.60	25	0.79	23
Common scoter *Melanitta nigra*	0.54	29	1.00	2	0.69	30
Common tern *Sterna hirundo*	0.54	30	0.66	20	0.84	15
European shag *Phalacrocorax aristotelis*	0.82	12	0.73	16	0.86	14
European storm-petrel *Hydrobates pelagicus*	0.84	8	0.32	31	0.90	5
Great black-backed gull *Larus marinus*	0.88	3	0.51	26	0.84	16
Great cormorant *Phalacrocorax carbo*	0.80	13	0.73	17	0.72	28
Great northern diver *Gavia immer*	0.62	24	0.95	4	0.82	21

Great skua *Stercorarius skua*	0.74	20	0.41	30	0.86	11
Great-crested grebe *Podiceps cristatus*	0.63	23	0.82	13	0.60	34
Greater scaup *Aythya marila*	0.68	22	0.92	7	0.66	32
Herring gull *Larus argentatus*	0.86	4	0.42	27	0.90	3
Lesser black-backed gull *Larus fuscus*	0.86	5	0.42	28	0.86	12
Little auk *Alle alle*	0.84	9	0.75	15	0.65	33
Little tern *Sterna albifrons*	0.54	31	0.70	18	0.84	17
Long-tailed duck *Clangula hyemalis*	0.74	21	0.87	8	0.76	26
Manx shearwater *Puffinus puffinus*	0.84	10	0.32	32	0.88	7
Northern fulmar *Fulmarus glacialis*	0.93	1	0.32	33	0.86	13
Northern gannet *Morus bassanus*	0.75	19	0.61	22	0.88	8
Razorbill *Alca torda*	0.79	15	0.85	10	0.88	9
Red-throated diver *Gavia stellata*	0.54	32	1.00	3	0.78	25
Sandwich tern *Sterna sandvicensis*	0.54	33	0.66	21	0.88	6
Sooty shearwater *Ardenna grisea*	0.84	11	0.32	34	0.82	18
Velvet scoter *Melanitta fusca*	0.62	25	0.95	5	0.76	27

Appendix F – Supplementary material for Chapter 5

Table F.1 Spatial prioritisation results for scenarios 1, 2, 3 and 4

Feature	Scenario 1		Scenario 2 + MPAs		Scenario 3 + costs		Scenario 4 + MPAs and costs	
	Amount of individuals	Percentage of population	Amount of individuals	Percentage of population	Amount of individuals	Percentage of population	Amount of individuals	Percentage of population
Atlantic puffin	24929	61.57	23324	57.61	8195	20.24	9865	24.37
Arctic tern	2499	56.08	3217	72.19	2010	45.12	2902	65.13
Black guillemot	686	38.06	751	41.69	701	38.93	1030	57.20
Black-headed gull	2173	51.32	3666	86.57	2408	56.88	2961	69.94
Black-legged kittiwake	28251	42.77	26171	39.62	21172	32.05	22538	34.12
Common guillemot	96134	74.13	94858	73.14	31292	24.13	37570	28.97
Common gull	158	20.19	191	24.42	439	56.08	480	61.40
Common tern	99	31.78	206	65.95	189	60.59	240	77.08
European shag	4243	54.18	4601	58.75	3139	40.09	4816	61.50
European storm-petrel	25060	20.00	25106	20.04	29322	23.40	30294	24.18
Great cormorant	6456	70.87	6381	70.03	2956	32.44	3822	41.95
Great skua	1	20.17	1	21.15	2	59.45	2	62.72
Great black-backed gull	1984	41.22	2368	49.19	1735	36.04	2179	45.28
Herring gull	5146	50.19	4707	45.90	3594	35.05	4092	39.91

Little tern	50	27.78	180	100.00	180	99.98	180	99.98
Lesser black-backed gull	9259	77.16	8960	74.67	3061	25.51	3129	26.07
Manx shearwater	42951	20.01	42938	20.00	42934	20.00	42937	20.00
Northern fulmar	11626	20.04	11603	20.00	20130	34.70	19836	34.19
Northern gannet	24419	45.23	23225	43.01	11506	21.31	12149	22.50
Razorbill	18653	66.13	14776	52.39	7876	27.92	10052	35.64
Sandwich tern	4104	78.52	4572	87.48	1696	32.46	2184	41.79
Leach's storm-petrel	1187	20.27	2198	37.53	3439	58.73	3636	62.10
Roseate tern	2836	100.00	2836	100.00	588	20.75	1032	36.38
Auks - offshore	2814	94.55	2804	94.23	627	21.07	664	22.31
Northern fulmar - offshore	658	20.01	658	20.02	658	20.00	658	20.00
Northern gannet - offshore	1058	27.41	946	24.51	1076	27.88	1102	28.56
Black-legged kittiwake - offshore	407	57.44	414	58.43	150	21.20	167	23.62
Manx shearwater - offshore	4010	49.72	3984	49.40	1615	20.03	1619	20.08
Petrels - offshore	410	20.02	409	20.00	439	21.43	452	22.09
Terns - offshore	106	66.79	107	67.34	32	20.23	39	24.65