Assessing the potential impacts of anthropogenic disturbance on seabirds: A case study from Alderney

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Abstract

Seabirds are threatened by multiple anthropogenic pressures in the marine environment. These pressures may be short- or long- term and impacts may be either direct or indirect and affect reproduction or survival. Marine Renewable Energy Installations (MREIs) provide a relevant, and spatially explicit, example of such pressures. However, there is currently very little empirical evidence as to how MREIs will impact seabirds. Studies have shown that potential impacts are likely to be species and device specific, temporary or long term, and both positive and negative. Current approaches to predict and assess these impacts from MREIs rely on understanding the species- specific risk of devices (e.g. by making predictions based on the ecology of the seabird), the occurrence of individual species at-sea (e.g. from boat-based surveys), and demographic studies of breeding populations (e.g. through long-term ringing studies). However, these approaches are limited in their ability to detect changes in the distribution of seabirds at-sea and at breeding colonies. They may omit the impacts on non-breeding birds, and overlook the cumulative impacts of multiple pressures on specific populations when predicting potential impacts.

Alderney in the English Channel hosts internationally and nationally important seabird colonies, in addition to providing a suitable environment for the installation of tidal turbines. Additionally, the home range area of the colony of Northern gannets *Morus bassanus* breeding just offshore of Alderney overlaps with nine sites proposed for the development of MREIs, thus Alderney provides an ideal site for this type of study. This thesis explores simple approaches to predict and assess the impacts of proposed MREIs on seabirds, and demonstrates how the large amount of existing seabird tracking data can be used to predict the colony specific impacts of spatial change on seabirds. These approaches are developed at our Alderney study site but are broadly applicable elsewhere.

Overall our results suggest that the MREIs proposed for development around Alderney and the English Channel are unlikely to cause population level impacts to the seabirds breeding on, and around, Alderney. With ever increasing human pressures on the marine environment it is vital that we identify robust approaches with which to predict and monitor the impacts of these pressures. This thesis provides simple, robust and cost-effective approaches to predict and assess the potential impacts of spatial change on seabirds, and could be easily adapted for other sites, and for alternative types of spatial change.

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Chapter 1

General Introduction

Seabirds and anthropogenic pressures in the marine environment

It has become widely accepted that seabirds are threatened by anthropogenic changes in the marine environment. Pressures on seabirds in marine systems may be long-term and occur as a result of activities such as; overfishing, pollution and offshore developments (Croxall *et al.* 2012), or they may be the result of one off events such as oil spills (Votier *et al.* 2005). Thus, resulting impacts may be direct or indirect (Lorance *et al.* 2009), chronic or acute (Breen *et al.* 2012) and affect productivity and/or survival (Lewison *et al.* 2012). Seabirds are long lived animals with high adult survival rates combined with low reproductive rates. Thus, they are especially impacted by increased adult mortality (Sæther & Bakke 2000), and minor declines in survival can result in major changes to the population growth rate (Wanless *et al.* 2006).

The impacts of spatial change in marine systems are likely to be both species- and population- specific, and it is vital that we identify robust approaches with which to predict and monitor their impacts. The increasing proposals for the development of Marine Renewable Energy Installations (MREIs) in the UK and European waters provides a relevant example of spatial change in the marine environment, and forms the basis of this thesis.

Marine Renewable Energy Installations (MREIs)

Potential impacts from MREIs

There is currently very little empirical evidence as to the effect that MREIs will have on seabirds (Grecian *et al.* 2010; Masden *et al.* 2010). While various studies have attempted to establish the potential impacts of these devices on seabirds (e.g Gill 2005; Wilson *et al.* 2010; Furness *et al.* 2012), very few are based on empirical evidence from existing development sites (e.g Lindeboom *et al.* 2011; Petersen *et al.* 2011). This is likely to be because there have not yet been enough deployments of tidal and wave power devices to study (Witt *et al.* 2012), and monitoring at offshore windfarm sites can be difficult and expensive (Fox *et al.* 2006). However, studies have shown that potential impacts are likely to be species and device specific (Furness *et al.* 2012), temporary or long term (McCluskie, Langston & Wilkinson 2012), and both positive and negative (Inger *et al.* 2009).

Positive impacts through habitat enhancement may occur if development sites act as artificial reefs, fish aggregation devices and de-facto Marine Protected Areas (MPAs) (Inger *et al.* 2009). Negative impacts may occur as a result of direct collisions with devices, or by altering the energy budgets of the birds (Garthe & Hupop 2004). This may occur if the development site is situated between important foraging and breeding grounds, creating a barrier to movement, or if devices are placed within important foraging areas, forcing birds to be displaced from these locations (Langston, Allen & Crutchfield 2010). For windfarms, we currently know very little about these behavioural responses of seabirds (Fox *et al.* 2006), though it has been shown that some birds show avoidance behaviour and others are attracted to these areas (Lindeboom *et al.* 2011; Poot *et al.* 2012). The threat from direct mortality as a result of collision with MREIs is particularly important in seabirds because, as mentioned previously, their demographic rates mean that minor declines in adult survival can have major implications at a population- level (Wanless *et al.* 2006).

Current approaches to predict (pre-construction) and assess (post-construction) the impacts of MREIs on seabirds

In order to predict the potential impacts from proposed MREIs we need to know two things; the species- specific risk imposed by the device, and the occurrence of seabirds within the development area (Langton, Davies & Scott 2011).

Firstly, the species-specific risks imposed by the device can be estimated using knowledge of the behaviour and ecology of the species (Furness *et al.* 2012). For example auks *Alcida sp*, cormorants *Phalacrocorax sp* and divers *Gavia sp* are likely to be most at risk when considering tidal turbines because not only do they dive to the depths where they risk colliding with moving components, they also exploit habitats suitable for the installation of tidal turbines (Furness *et al.* 2012). Correspondingly, Northern gannets *Morus bassanus* and Skuas *Stercorarius sp* are amongst the groups most at risk of collision with offshore wind turbines because they fly at the same altitudes as the turbine blades, and spend a high proportion of time at sea flying (Furness, Wade & Masden 2013).

Secondly, the current approaches to estimate the occurrence of seabirds within proposed development areas primarily depend on estimates of the distribution of seabirds-at-sea gained from ship-based, aircraft or vantage point observations (Camphuysen *et al.* 2004; Waggitt, Bell & Scott 2014). Records of the distribution of seabirds-at-sea acquired from these surveys using standardised methodologies have resulted in a substantial long-term database of all European-Seabirds-At-Sea surveys conducted in European waters (Reid & Camphuysen 1998). We can use this baseline information to make predictions about the potential impacts proposed MREIs may have, or to observe changes after the installation of these devices. However, these surveys are based mainly offshore and at the scale of tens to hundreds of kilometres (Louzao *et al.* 2009), and currently very little data exists about the near-shore fine-scale distribution of seabirds.

Although vantage point observations have been used in order to understand the distribution of seabirds within proposed development sites (Waggitt & Scott 2014), these observations are very location specific and only occur at the timescale required for Environmental Impact Assessments. Tidal turbines are likely to be located in these near-shore waters, and during the breeding season seabirds are constrained to coastal areas, often rafting and foraging in the waters adjacent to breeding sites (Wilson *et al.* 2009). Additionally, certain species such as shags and divers forage in the fast flowing habitats suitable for the placement of tidal turbines (Furness *et al.* 2012). Furthermore, other types of spatial change could be impacting these near-shore fine-scale seabird distributions, since human activities are concentrated in near-shore locations (Halpern *et al.* 2008). Therefore the potential for negative interactions with humans is high in these near-shore waters, and these may remain undetected due to the deficiency of monitoring the distribution and abundance of seabirds in these locations.

The approaches currently applied to assess and quantify the post-construction impacts from the installation of offshore developments involve monitoring at the colony, and monitoring seabirds-at-sea (Drewitt & Langston 2006). Population counts at seabird breeding colonies are the best method to monitor long-term population trends of breeding birds (Maclean *et al.* 2013), and increased adult mortality from collisions with offshore developments may manifest in observable declines in seabird numbers at nearby breeding colonies (Furness & Wanless 2014). However, a high proportion of individuals at breeding colonies are non-breeders (Aebischer & Wanless 1992) thus disproportionate effects on juveniles would not be detected, and the UK hosts internationally important numbers of certain species during the non-breeding season (Stroud *et al.* 2001), thus declines in the abundance of seabirds-at-sea may not be observable through population monitoring at breeding colonies (Harris & Wanless 1995).

Alternatively, the distribution and abundance of seabirds-at-sea can be monitored using ship-based, aircraft and vantage point observations, and novel tracking studies, and these methods may be used to detect any changes in the abundance of seabirds within the development zone as a result of the installation of devices (Lindeboom *et al.* 2011). However, the distribution of seabirds-at-sea is subject to large temporal variation and thus in order to detect consistent directional changes in the abundance of seabirds within development zones these changes would need to be extreme (Maclean *et al.* 2013). Furthermore, information about the distribution and abundance of seabirds-at-sea collected through ship-based and vantage point surveys cannot establish a colony of origin of the individuals observed (Camphuysen *et al.* 2004). However, legislation provides a legal framework to manage populations of seabirds at the level of the colony through the designation of SPAs (Wilson *et al.* 2009), and this creates a mismatch between what is occurring at-sea and impacts observed at the colony (Grecian *et al.* 2012) due to the inability to apportion birds observed at-sea to their colony of origin. Additionally, this means that any cumulative impacts of multiple pressures on specific populations will not be accounted for. The MREI industry is continuing to expand, thus there will be sustained pressure to predict and assess the impacts from these devices on seabirds.

Alternative approaches to predict and assess the impacts of MREIs on seabirds

Against this backdrop, scientists (ornithologists), have a key role to play in bringing the latest approaches to this challenge, and provide robust, cost-effective, methods with which to address these limitations. In the current economic climate research funding is limited and therefore there is increased value in establishing robust methods which allow us to make the most of data that is collected regularly and on a large scale. For example, there has been a rapid increase in the number of tracking studies from multiple species of seabirds, at a number of populations worldwide, as tracking devices have become smaller and more affordable (Block *et al.* 2011). In most cases tracking data are used to identify the at-sea areas where seabirds spend most time, and thus location data is often used as a proxy for important foraging areas (Le Corre *et al.* 2012). However, until now there has been little evidence to support this assumption, and thus inferences from this must be taken with a precautionary approach. Additionally, it is important to know which behaviours birds are exhibiting in these areas where they have the potential to interact with MREIs, as specific behaviours may influence the risk of these devices to seabirds (Furness *et al.* 2012).

The application of many tracking studies is to identify important at-sea areas for the purposes of conservation or marine spatial planning (Louzao *et al.* 2009; Harris *et al.* 2012). Therefore it is essential to consider the long-term variation in the distribution of these important at-sea areas, in order to understand the long-term impacts of marine spatial change (Robertson *et al.* 2014). It has previously been demonstrated that inter-annual variation in the location of foraging areas occurs as a result of variation in oceanographic conditions (Garthe, Montevecchi & Davoren 2011). Additionally inter-individual variation in foraging behaviour has been widely reported for seabirds (Kato *et al.* 2000; Bearhop *et al.* 2006). However, few studies have looked at how inter-individual variation differs between years, and what the consequences of this may be at a population level. If all individuals in the population visit larger areas, then all individuals are likely to have an increased risk of interacting with spatially explicit environmental pressures. Conversely, if inter-annual variation is driven by individual birds visiting more, different areas between trips, then spatial pressures may affect individuals in the population differently. Thus, it is important to understand the drivers behind inter-annual variation in the location of important at-sea areas at an individual level in order to understand the population level impacts from the development of MREIs.

In addition to solely identifying important at-sea areas from detailed, large scale tracking studies, this information can be used to parameterise spatially explicit models in order to predict the impacts that MREIs, or other types of spatial change, may have on seabirds (Patterson *et al.* 2008). This provides a colony-specific approach, thus can take into account the cumulative impact of multiple disturbances within the home range area of a defined population, which has not been possible to do using existing methods. By combining physiological and ecological traits of the birds with knowledge of their at-sea behaviour and the spatial variation of potential pressures, then predictions can be made about the impacts these pressures may have on the physiological state and demographic rates of seabirds. Subsequently, the predicted changes in demographic rates of individuals such as survival and productivity can be used to predict the long term impacts of spatial change at the population level.

Indeed, demographic rates may also be estimated empirically through long-term ringing projects at breeding colonies (Baillie 1995), and thus used to monitor the impacts of spatial change in the long term. For example, it has been proposed that monitoring adult survival rates through ringing projects at breeding colonies near to MREIs and control colonies further away could provide clear evidence as to whether collision mortality has a significant effect on survival rates in seabirds (Furness & Wanless 2014). However, demographic analysis of ringing data may not necessarily reflect current conditions. This is because the time lag between real-time changes in demographic rates and conclusions from population modelling may result in the detection of changes years after they occur in the population (Beissinger & Westphal 1998), and thus these conclusions should be interpreted with caution.

This thesis attempts to identify critical gaps in the approaches currently used to predict and assess the impacts of MREIs and other types of spatial change on seabirds and to identify alternative approaches. Current approaches are limited in their ability to detect changes in the distribution of seabirds at-sea and at breeding colonies, potentially overlooking impacts on non-breeding birds, and cumulative impacts of multiple pressures on specific populations. Additionally, very little is known about what drives the near-shore distribution of seabirds, or how inter-individual variation affects inter-annual variation in foraging behaviour.

Study site

Alderney and its surrounding islands in the English Channel (49 42' 50" N, 2 12' 18" E) are important breeding grounds for many species of seabird. The island of Burhou*,* approximately 2 km offshore is host to a nationally important colony of lesser black-backed gulls *Larus fuscus* and European shags *Phalacrocorax aristotelis,* a regionally important colony of storm petrel *Hydrobates pelagicus* and the largest puffin *Fratercula arctica* colony in the English Channel (Morley & Broadhurst 2014). Additionally, Les Etacs, a stack a few hundred metres offshore of Alderney, is host to an internationally important colony of Northern gannets *Morus bassanus*. However, Alderney is also one of the best locations world-wide in its potential for harvesting tidal stream energy on a large-scale (Neill, Jordan & Couch 2012). Yet, the high current speeds, and appropriate depths appropriate for the operation of tidal turbines (Myers & Bahaj 2005) also provide important foraging habitat for some of the local seabirds (Furness *et al.* 2012). Furthermore, the foraging range of Alderney's gannet population overlaps with nine sites proposed for the development of MREIs (Soanes *et al.* 2013). Consequently, the Alderney Wildlife Trust who are responsible for species and habitat conservation on Alderney, are concerned about the implications that these developments may have on the valued populations of breeding seabirds. Thus, Alderney has specific issues but also represents a model system which reflects the broader concerns about how MREIs may impact the marine environment at a larger scale.

Thesis aims and structure

This thesis aims to address some of the limitations in the current approaches to predicting and assessing the impacts of spatial change in the marine environment on seabirds, specifically regarding the development of MREIs. It considers the most efficient way to apply novel, yet simple and easily adaptable approaches to the analyses of widely collected data, in order to achieve these aims. The chapters have been written to be stand alone, linked by the common theme of predicting and assessing impacts of spatial change on seabirds, thus some information may be repeated between chapters, and formatting may differ according to journal requirements. These are the main questions that the thesis aims to address:

Chapter 2 aims to provide evidence to support the assumption that core foraging areas can be identified simply by locating areas where seabirds spend more time. The purpose of this is to justify the application of the time-in-area approach to identify core foraging areas in seabirds for the remainder of the thesis. This chapter has been published in Marine Ecology Progress Series.

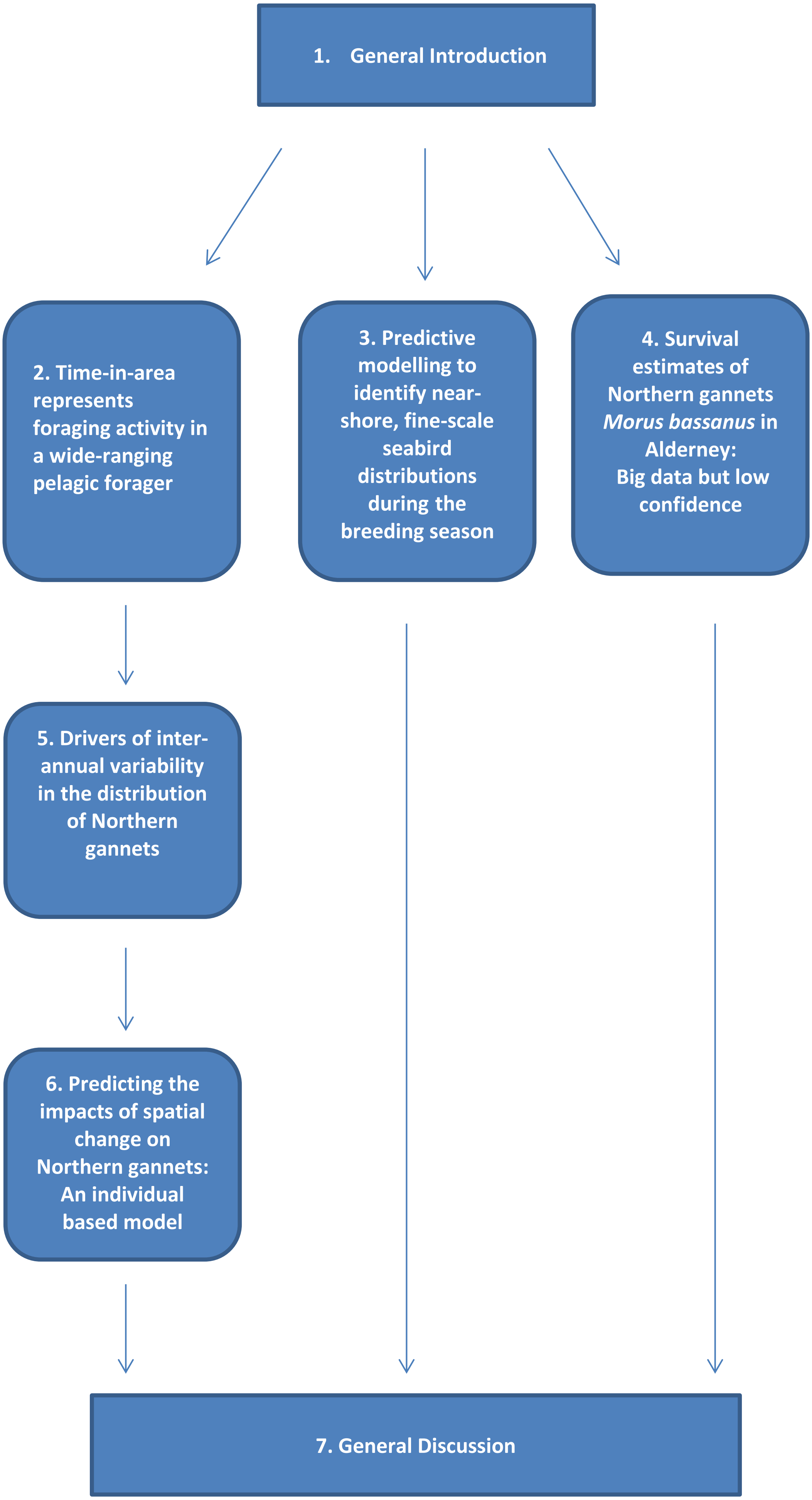
Chapter 3 aims to address the gap in the literature concerning the environmental drivers behind the near-shore fine-scale distribution of seabirds during the breeding season. This information can be used in order to assess the potential impacts of anthropogenic disturbance on seabirds during the breeding season. This chapter has been published in PlosOne.

Chapter 4 aims to apply age-specific survival analysis to long-term ringing records collected from the population of Northern gannets breeding on Les Etacs. This can be used as a baseline from which we can monitor changes in survival as a result of the installation of MREIs. This chapter is in press in Bird Study.

Chapter 5 aims to identify the inter-individual variation underpinning the inter-annual variation in the location of core foraging areas and home range areas of Alderney's population of Northern gannets. The purpose of this is to understand how potential interactions between seabirds and MREIs may vary between years. This chapter is in press in Marine Biology.

Chapter 6 aims to develop a flexible Individual Based Model in order to quantify the potential impacts of spatial change in the marine environment on seabirds. Specifically this model quantifies the impacts from proposed windfarms in the English Channel and North Sea on the survival, productivity and physiological state of Alderney's population of Northern gannets. However, this IBM is easily adaptable for other species of seabird and provides a robust approach to predict the impacts of various types of spatial change on seabirds. This chapter is under review in the Journal of Applied Ecology.

Chapter 7 aims to summarise the key approaches and lessons learned. The interrelations between the individual chapters and Chapter 7 are shown in the following schematic.


1. General Introduction
2. Time-in-area represents foraging activity in a wide-ranging pelagic forager
3. Predictive modelling to identify near-shore, fine-scale seabird distributions during the breeding season
4. Survival estimates of Northern gannets *Morus bassanus* in Alderney: Big data but low confidence
5. Drivers of inter-annual variability in the distribution of Northern gannets
6. Predicting the impacts of spatial change on Northern gannets: An individual based model
7. General Discussion

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Chapter 2

Time-in-area represents foraging activity in a wide-ranging pelagic forager

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Abstract

Successful Marine Spatial Planning depends upon the identification of areas with high importance for particular species, ecosystems or processes. For seabirds, advancements in biologging devices have enabled us to identify these areas through the detailed study of at-sea behaviour. However, in many cases, only positional data are available and the presence of local biological productivity and hence seabird foraging behaviour is inferred from these data alone, under the untested assumption that foraging activity is more likely to occur in areas where seabirds spend more time.

We fitted GPS devices and accelerometers to Northern gannets *Morus bassanus* and categorised the behaviour of individuals outside the breeding colony as plunge diving, surface foraging, floating and flying. We then used the locations of foraging events to test the efficiency of time-in-area and Kernel Density (KD) analyses, defining the smoothing parameter (h) using the *ad-hoc* method, and where h=9.1 km, to designate core foraging areas from location data. A high proportion of foraging events occurred in core foraging areas designated using $KD_{ad\text{-}hoc}$, $KD_{h=9.1}$, and time-in-area. Our findings demonstrate that foraging activity occurs in areas where seabirds spend more time, and that both Kernel Density analysis and the time-in-area approach are equally efficient methods for this type of analysis. However, the time-in-area approach is advantageous in its simplicity, and its ability to provide the shapes commonly used in planning. Therefore, the time-in-area approach can be used as a simple way of using seabirds to identify ecologically important locations from both tracking and survey data.

Introduction

Marine Spatial Planning (MSP) is a key tool to address trade-offs between the economic, ecological and social objectives of marine management (Ehler & Douvere 2009). It is largely accepted that an ecosystem-based approach to management such as MSP is required to deal with the increasing human use of the marine environment (Crain *et al.* 2009; Tallis *et al.* 2010; Halpern *et al.* 2012). Among other factors, MSP relies upon the identification of those areas which are most important to conserve for biological and/or ecological functions (Crowder & Norse 2008). One approach is to identify the core foraging areas of pelagic species, specifically marine top predators (Le Corre *et al.* 2012), because they tend to aggregate in specific areas influenced by increased local productivity and dense prey patches (Louzao *et al.* 2009). Seabirds are a convenient group to study in this context as they are relatively easy to monitor because they nest on land, often in large aggregations, and are visible when foraging. Furthermore they are a good indicator of environmental conditions over broad spatio-temporal scales (Piatt *et al.* 2007).

Our understanding of seabird behaviour and spatial ecology has improved recently, due to the advancement of biologging technologies, which has resulted in loggers becoming smaller and more affordable (Burger & Shaffer 2008). Devices such as time depth recorders (Tremblay *et al.* 2003) and accelerometers (Ropert-Coudert *et al.* 2003) can be used to measure the behaviour of seabirds. Combining these tools with tracking devices, such as GPS loggers, would be the most suitable method to identify foraging areas (Burger & Shaffer 2008). However, this is often not possible as recommended guidelines on the load of biologging devices (Hawkins 2004) preclude small birds from carrying multiple devices and these devices can be costly. As a result of these limitations, only location data are collected in many biologging studies. However, without behavioural information, the precise ecological significance of highly used areas is unknown (Camphuysen *et al.* 2012). The usual assumption is that highly-used areas reflect regions of important ecological processes, where individuals congregate to forage (Le Corre *et al.* 2012), though it should be noted that seabirds also flock together for other reasons such as information exchange (Burger 1997).

Two widely used methods to detect highly-used areas and interpret foraging behaviour from positional data are Kernel Density (KD) analysis and time-in-area analysis. Other methods exist for this type of analysis, such as state-space modelling (Patterson *et al.* 2008), area restricted search analysis (Fauchald & Tveraa 2003) and track segmentation (Thiebault & Tremblay 2013), however, these methods are often computationally challenging. KD analysis uses location densities to calculate probability density estimates which are often used as a proxy for foraging areas (Wood *et al.* 2000) although they may also represent resting and moulting areas. Disadvantages of KD analysis are its dependence on a user-defined smoothing parameter which can lead to considerable over- or under- estimation of the extent of seabird habitat use (Soanes *et al.* 2014). Various methods exist to calculate the smoothing parameter including the *ad-hoc* method, Least Squared Cross Validation (LSCV, Worton 1995), and using Area Restricted Search behaviour to measure the scale of interaction between the animal and the environment (Pinaud 2008). Clustered locations, which are prevalent in seabird tracking data, cause complications with both the *ad-hoc* method, due to over-smoothing, and with the LSCV method as it causes errors due to the algorithms not converging (Hemson *et al.* 2005). In addition, analysing each bird or trip individually will result in a different smoothing parameter than if the population is analysed together.

Alternatively, the time-in-area approach is a simple yet efficient method frequently used to identify areas of high bird density and/or usage (Le Corre *et al.* 2012; Soanes *et al.* 2013). It merely sums the amount of time spent in each cell of a pre-defined grid, though the size of the grid cell will affect the outcome (Soanes *et al.* 2014). In addition grid cells are commonly used units in Marine Spatial Planning (e.g Gilliland & Laffoley 2008; White, Halpern & Kappel 2012) and compatible with decision making tools such as C-Plan and MARXAN (Lombard *et al.* 2007). With all of these approaches, bird density is often used as a proxy for foraging activity, under the assumption that an animal will spend more time in an area when foraging than when transiting (Gremillet *et al.* 2004). However, evidence in support of this assumption is limited.

We set out to evaluate the efficiency of kernel density analysis and time-in-area analysis to define core foraging areas, using Northern gannets *Morus bassanus* as a model species. Northern gannets are generalist predators, feeding on a variety of pelagic fish and fisheries discards (Garthe, Benvenuti & Montevecchi 2000). They exhibit two feeding modes, plunge diving and foraging/diving from the surface (Ropert-Coudert *et al.* 2004), and have a large foraging range (up to 640 km) during the breeding season (Langston, Allen & Crutchfield 2010). Here, we combine positional data from GPS loggers and behavioural data from accelerometers to calculate the proportion of dives occurring in the core foraging areas defined using KD analysis and the time-in-area approach. We also examine the effect of applying commonly used filters that attempt to proxy foraging behaviours, such as speed, time of day, and tortuosity. We demonstrate that for Northern gannets both Kernel Density and the time-in-area approach are effective methods to identify core foraging areas when more detailed behavioural data are not available, giving confidence to the use of seabirds to indicate areas of high biological productivity for use in MSP.

Methods

Data collection

Fieldwork was licensed by The States of Alderney and conducted at the breeding colony of Northern gannets on Les Etacs, Alderney (49°42’N, 2°14’W) between 10th June and 1st July 2013. A total of 15 birds with chicks approximately 2-4 weeks old were caught at their nest using a noose pole, as they were encountered throughout the colony. All birds were fitted with a GPS data recorder accurate to 15m (IgotU GT-600, Mobile Action Technology, Taiwan) and a tri-axial accelerometer (X6-2, Gulf Coast Data Concepts, Waveland, USA). The GPS devices were set to record a location every two minutes and the accelerometers at 25 Hz. Acceleration was measured along three axes, longitudinal (X, surge), dorso-ventral (Z, heave), and lateral (Y, sway). The devices were wrapped in heatshrink plastic and Tesa ® Extra Power tape was used to attach them at the base of the tail between the central tail feathers in order to reduce any aerodynamic or hydrodynamic impacts (Ropert-Coudert *et al.* 2009). The GPS and accelerometer package weighed 44g, on average

< 2% of the birds' body mass. The total capture and tag attachment process lasted < 10 minutes in each case, and the birds appeared to behave normally when released. Previous studies show that this type of device (and larger devices) have no impact on the foraging duration, breeding success or body condition of Northern gannets (Hamer *et al.* 2000; Lewis *et al.* 2002; Gremillet *et al.* 2004), however due to the inaccessibility of this site we were unable to test for these impacts in this study. Nine birds were recaptured two to three weeks later and the loggers detached and downloaded. The remaining 6 birds could not be recaptured during the limited time available and devices would have been lost at sea within approximately one month. This is unlikely to have had any impact on breeding success.

Data processing and analysis

Behaviour analysis

Information on foraging trips from the GPS data (as described below) were combined with acceleration signals. Time spent in the colony (as defined below) was excluded from the analysis of all data. The accelerometer stored a time-stamp for each data recording. To account for clock drift and occasional missing data points (<0.01%), all three accelerometry channels were interpolated to a regular 25Hz data frame. Synchronisation of devices were checked by simultaneously visualising GPS data and acceleration signals each time each gannet departed from and arrived at the colony (4 - 8 times per bird), which confirmed that device drift was negligible (<30 seconds). The pitch i.e. the body angle of the bird relative to horizontal, was calculated using all three acceleration signals

$$Pitch = atan ((X / (sqrt ((Y^2) + (Z^2))))) * (180/pi)$$

and smoothed using a box window (window size = 25 points). To account for variation in logger attachment position on each bird, the pitch data were corrected on the assumption that a period where the bird was resting on the water would have a pitch of zero (Watanuki *et al.* 2003). Acceleration data were then analysed using a two stage process. Firstly, the X, Y, Z and pitch data were visualised using IGORPro (Version 6.34, WaveMetrics, USA), and behavioural activities were assigned by visual inspection of acceleration and pitch, based on published examples from closely related species (Ropert-Coudert *et al.* 2004; Ropert-Coudert *et al.* 2009; Vandenabeele *et al.* 2014) (Figure 2.1).

Four key behaviours (flying, floating, plunge diving and surface foraging) could be identified. Flying consisted of both flapping and gliding behaviours, which in addition to plunge diving and floating were clearly identified from the acceleration signals. It was more challenging to identify surface foraging, as acceleration signals from this behaviour may have incorporated a number of behaviours including; scooping from the surface, feeding on fisheries discards, preening and diving from the surface. Secondly, the package *Ethographer* for IGOR Pro (Sakamoto *et al.* 2009) was used to extract these four behaviours automatically based on unsupervised analysis of the acceleration signals. This method uses spectrogram analysis by continuous wavelet transformation (1 second window), followed by unsupervised cluster analysis, using the *k*-means clustering algorithm (Sakamoto *et al.* 2009) to identify repetitive cycles in acceleration signals, assigning a cluster every second on each of the three axes. To distinguish between behaviours with apparently similar acceleration signals, for example floating and periods of flight when birds were gliding, further logical arguments predominantly based on the pitch of the bird were used and behaviour was classified as flying, floating, plunge diving or surface foraging for every second. Together, we refer to plunge dives and surface foraging events as foraging events, and it is the time of initiation of these events that were used in all subsequent analysis.

Spatial analysis

GPS positions were interpolated to every second, to allow integration with behavioural data and to assign exact GPS locations to foraging events, using the *adehabitatLT* package (Calenge 2006), in R (version 3.0.2, R Development Core Team 2013). Additionally, this interpolation accounted for missing data points when the bird was diving, or through missed GPS locations. These missing points would result in a value of zero when calculating time-an-area, and thus exclude cells which the bird must have passed through, and yet where no data was recorded. The

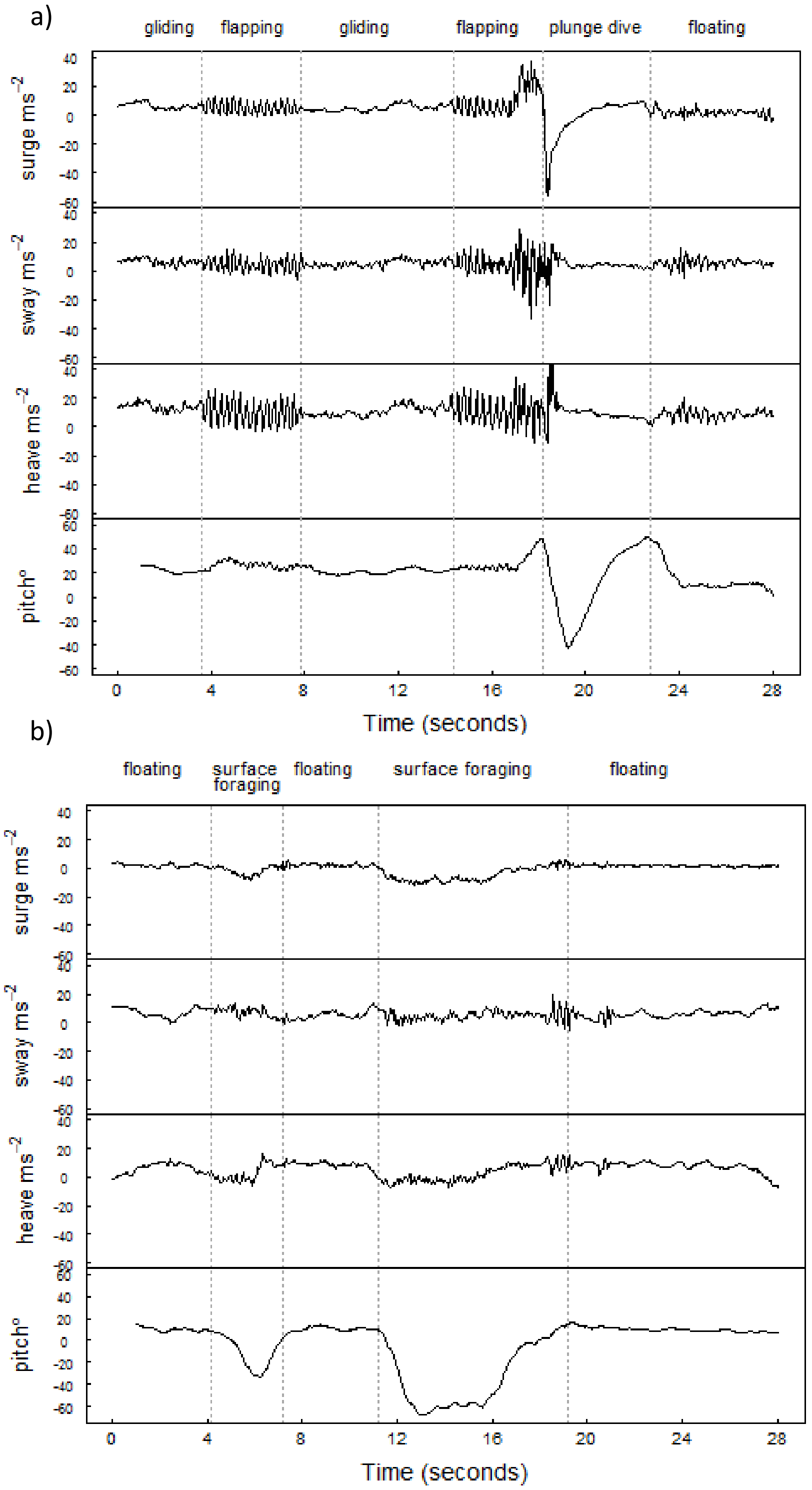


Figure 2.1. Acceleration signals describing a) flapping, gliding and plunge diving and b) floating and surface foraging behaviour of Northern gannets. Flapping is classified by the oscillating patterns on the surge and heave axes. Gliding and floating are separated by pitch (≈ 20^{0} and 0^{0} respectively). Plunge dives are characterised by a sudden deceleration in surge combined with a negative pitch and surface foraging by a slight deceleration combined with a negative pitch of more than -20^{0}.

colony was defined as Les Etacs rocks with a 30 m surrounding buffer, based on personal observations of gannet behaviour. Trip duration (hours), trip length (total distance covered, km) and range (maximum distance from the colony, km) were calculated. A frequency histogram of trip duration showed a clear bimodal distribution. One mode represented short trips, up to 40 minutes in duration, whereas the second mode represented foraging trips lasting many hours. Foraging trips were therefore defined as any trip which was over 40 minutes in duration. Foraging events were observed on every trip defined in this way. Each interpolated GPS location was assigned a behaviour and plotted in Arcmap (ArcGIS Desktop: Release 10. Redlands, CA: Environmental Systems Research Institute).

Firstly Utilisation Distributions were estimated for each trip for each bird by calculating the Kernel Density (KD) using a UTM 30 projection and a grid size of 1 km^2 in R package *adehabitatHR* (Calenge 2006). The smoothing parameter (h) was calculated using both the *ad-hoc* method ($KD_{ad\text{-}hoc} = h = \sigma n^{-1/6}$ where $\sigma^2=0.5(var(x)+var(y))$) and h=9.1 km ($KD_{h=9.1}$), based on the mean scale of Area Restricted Search (ARS) behaviour in gannets of 9.1 km (Hamer *et al.* 2009), and a similar value to that used in previous studies where h=10, also based on the mean scale of ARS behaviour identified by Hamer *et al.* 2009 (Stauss *et al.* 2012). The Least Squared Cross Validation (LSCV) method was tested, but deemed inappropriate for this data as the algorithms failed to converge and thus failed to identify the optimal smoothing parameter. Secondly, the R package *Trip* (Sumner 2011) was used to calculate the time spent (seconds) in each 16.1 x 16.1 km cell of a pre-defined grid around the colony. Grid size was calculated in order to result in an area consistent with that used in KD analysis with a smoothing parameter of 9.1 km (i.e. area= $\pi*9.1^2$). We also tested grid sizes of 5 x 5 km and 10 x 10 km and provide results from a comparison of grid sizes in table S2.2 and figures S2.1 & S2.2. Utilisation Distributions of 25%, 50% and 75% probability of use were calculated for each method.

It has been suggested that removing night time positions before defining core foraging areas may increase the level of association between foraging events and time spent in a given area for gannets as they are assumed not to feed at night (Hamer *et al.* 2000; Garthe, Montevecchi & Davoren 2007). Preliminary analysis identified there was no effect on the conclusions when different definitions of night-time (sunrise and sunset, and civil, nautical and astronomical dawn and dusk) were investigated, so cut-offs at sunrise and sunset were used in the analysis. Filtering the data by speed is another method to improve the accuracy of identification of foraging areas, so the effect of removing periods assumed to represent transiting (speed >9m/s) and resting on the water (speed <1.5m/s) (Wakefield *et al.* 2013) were also considered in this analysis. Another common method is to filter the data by a tortuosity index with a speed threshold, on the basis that tortuosity of the track most likely represents the intensity of search behaviour, and thus foraging (Fauchald & Tveraa 2003), which would occur whilst the bird is in flight. Therefore the effect of filtering the data to include points with a tortuosity index of <0.9 combined with a speed >1m/s (Wakefield *et al.* 2013) was also tested in the analysis. The tortuosity index was calculated as a ratio of the straight line distance to the total distance travelled between L_{-480} and L_{480} when L_0 is the focal location, and L_{-480} and L_{480} are the locations 480 seconds before and after the focal location i.e. over a 16 minute duration as per Wakefield *et al.* (2013).

The size of these core foraging areas (km^2) were calculated for each trip for each bird using all three methods and contours outlined above (9 areas). Furthermore the time of day, speed and tortuosity filters, were also considered separately and in combination to generate a total of 54 definitions of core foraging area. The proportions of different foraging events falling within each area was calculated for each trip for each bird. Each bird made between two and four trips. To account for this uneven sample size, whilst still using the entire data set, the areas and proportions for each trip for each bird were bootstrapped with replacement 10,000 times, using the package *Boot* (Canty & Ripley 2014). This method involved sampling 9 birds with replacement (i.e. the same bird could be sampled twice), and for each bird sampling 2, 3, or 4 trips with replacement. The bootstrap was weighted to take into account the probability of recording 2, 3, or 4 trips. This was carried out 10,000 times in order to calculate a mean and confidence intervals for the proportion of dives occurring in core foraging areas, and the size of these areas. Consideration of these ranges allows us to consider the effects of methods and filtering approaches. Efficiency was calculated as the proportion of total dives per km^2 (i.e. by dividing the proportion of dives occurring in the core foraging area, by the size of the core foraging area).

Results

Proportion of foraging events in core foraging area

The gannets each made between two and four trips with a mean (± SD) trip duration of 26.0 ± 10.0 h, mean trip length of 465 ± 186 km and mean maximum distance from colony of 129 ± 46 km (Table 2.1). Foraging activity occurred throughout the day and night, though at considerably reduced frequency between 21:00 and 02:00 (Figure 2.2). Figures 2.3 and 2.4 show how the core foraging areas and the foraging events overlap using the different approaches and filters.

Table 2.1. Details of foraging trips (mean ± SD) undertaken by nine Northern gannets from the Les Etacs colony, Alderney, Channel Islands

Gannet ID code	No. of trips	Trip duration (hrs)	Trip length (kms)	Max distance from colony (kms)	No. plunge dives	No. surface foraging events
1	3	23.4 ± 2.9	393 ± 86	95 ± 11	61 ± 22	78 ± 31
5	3	17.3 ± 3.4	262 ± 84	74 ± 10	25 ± 7	47 ± 19
7	3	40.4 ± 16	658 ± 130	152 ± 37	96 ± 39	154 ± 54
9	2	24.6 ± 4	454 ± 75	116 ± 5	37 ± 5	53 ± 15
13	2	42.4 ± 6	726 ± 29	186 ± 15	76 ± 28	143 ± 34
15	3	20.3 ± 0.9	342 ± 55	130 ± 21	18 ± 1	87 ± 5
19	4	25.5 ± 4.2	612 ± 193	147 ± 56	42 ± 12	41 ± 19
22	4	21.6 ± 3.5	353 ± 127	119 ± 54	35 ± 6	89 ± 13
23	2	25.7 ± 2.3	458 ± 65	164 ± 12	51 ± 6	84 ± 6

The proportion of foraging events occurring in the core foraging area was always very similar when $KD_{ad\text{-}hoc}$ and $KD_{h=9.1}$ were used. Therefore, we report only results for $KD_{h=9.1}$, as this is similar to values commonly used in the analysis of gannet spatial data (Stauss *et al.* 2012; Waggitt *et al.* 2014) and directly comparable with

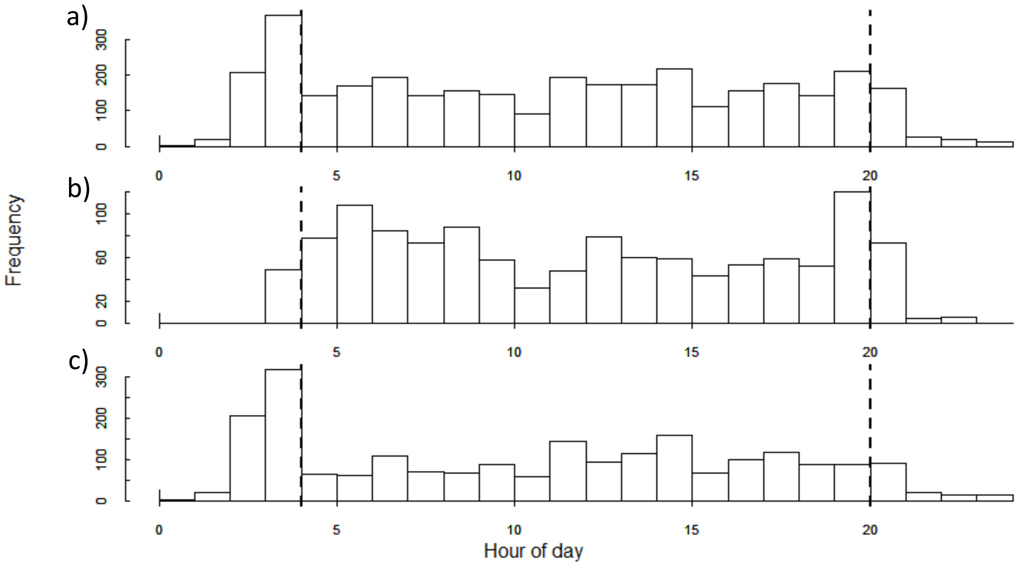


Figure 2.2. Diurnal variation in foraging events from 26 foraging trips from nine Northern gannets from Les Etacs colony, Alderney. a) all foraging events, b) plunge dives, c) surface foraging events. Dotted lines represent sunrise and sunset. Times are in GMT.

the time-in-area approach. Results for $KD_{ad\text{-}hoc}$ are included in Table S2.1. The mean bootstrapped proportion of all foraging events occurring in the core foraging area at 25%, 50% and 75% probability of use was larger when designated using KD analysis than with the time-in-area approach (Table 2.2). However, these contours are not directly comparable and the values do not take into account the size of the designated core foraging area. When standardised by the size of the core foraging area defined both approaches were equally efficient (Figure 2.5).

Effect of night time cut-off, and foraging type

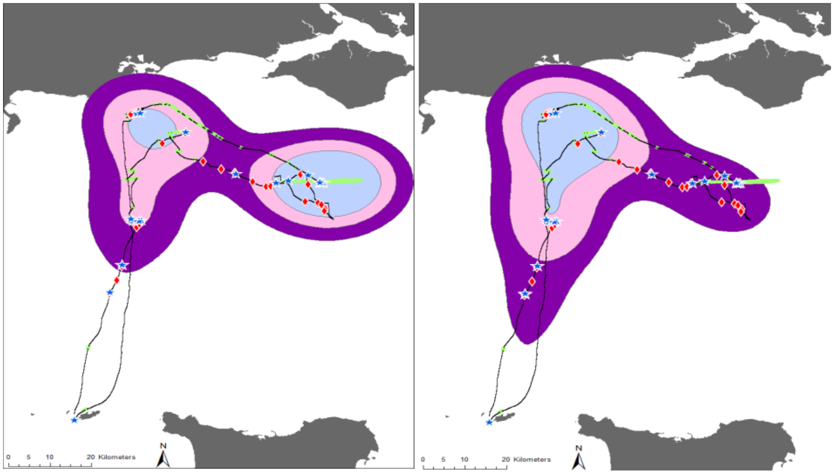
We found little evidence to suggest that the removal of night-time data results in a higher proportion of all foraging events occurring in the core foraging areas designated using either of the methods (Table 2.2). However, there is evidence to suggest that the proportion of plunge dives occurring in the core foraging area, using either method of designation, was higher when night-time data were removed (Table 2.3). In contrast, when considering solely surface foraging, the results indicated a lower proportion of foraging events occurred in the core foraging area when night-time data were removed (Table 2.4). These divergent results suggest the gannets exhibited different foraging behaviours in different places and at different times.

Effect of speed

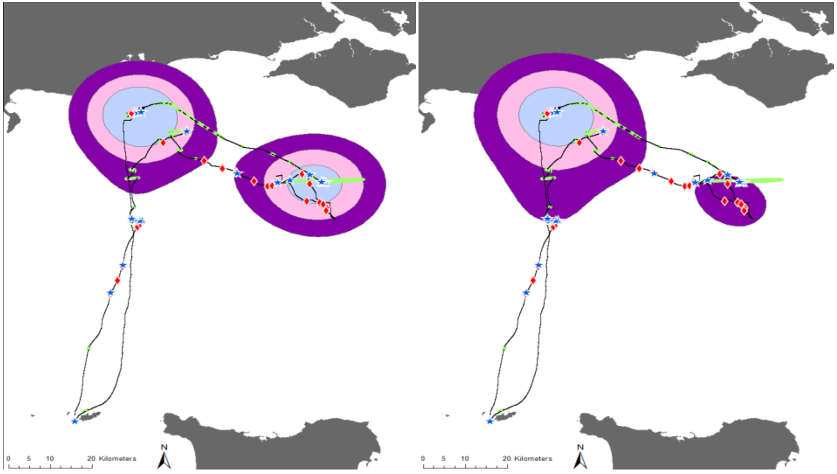
There is some evidence to suggest that filtering the data to remove speeds of <1.5m/s and >9m/s, results in a lower proportion of all foraging events occurring in the core foraging areas designated using either of the methods (Table 2.2). There is strong evidence suggesting that when surface foraging alone is considered, filtering for speed considerably reduces the proportion of foraging events which occur in the core foraging areas designated using any of the methods (Table 2.4). When considering only plunge dives, filtering the data for speed did not change the probability of dives occurring in the core foraging area (Table 2.3). Filtering the data for both speed and day results in very similar conclusions to data filtered for speed alone (Tables 2.2 – 2.4, Figure 2.5).

Effect of tortuosity

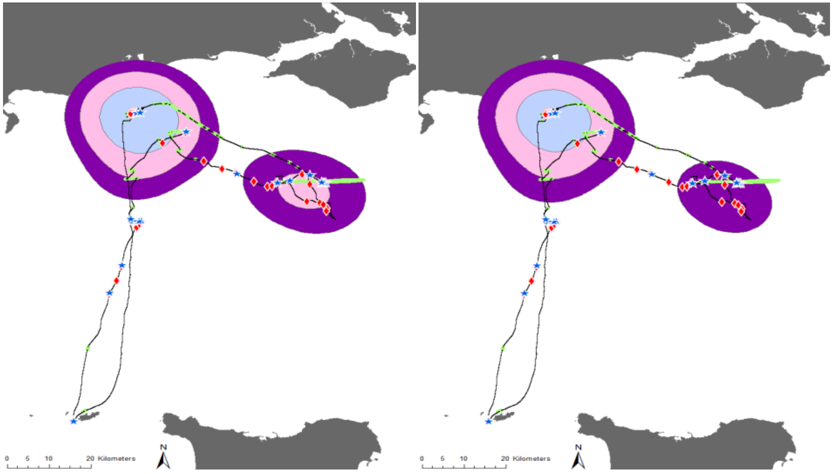
There is some evidence to suggest that filtering the data to include areas with a more tortuous track (<0.9 combined with a speed of >1m/s) results in a lower proportion of all foraging events occurring in the core foraging areas designated using either method. There is strong evidence suggesting that when surface foraging alone is considered, filtering for tortuosity considerably reduces the proportion of foraging events which occur in the core foraging areas designated using any of the methods (Table 2.4). When considering only plunge dives, filtering the data for tortuosity did not change the probability of dives occurring in the core foraging area (Table 2.3), however it did result in a more efficient designation of core foraging areas (Figure 2.5). Filtering the data for both tortuosity and day results in very similar conclusions to data filtered for tortuosity alone (Tables 2.2 – 2.4, Figure 2.5).



a) None b) Day

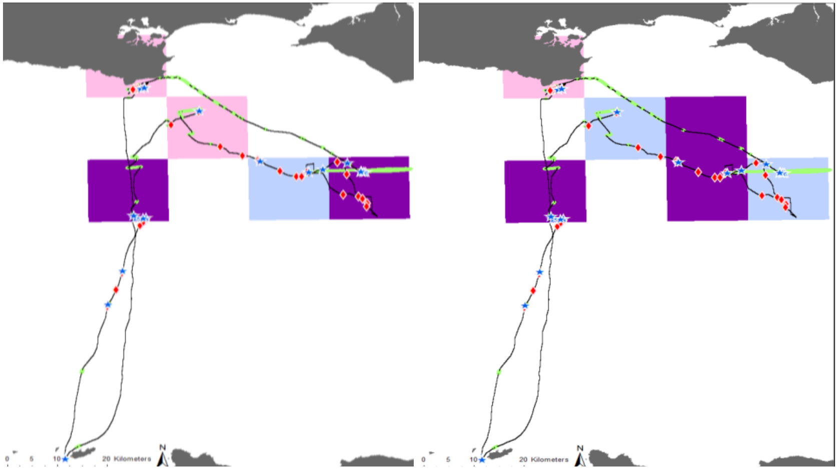


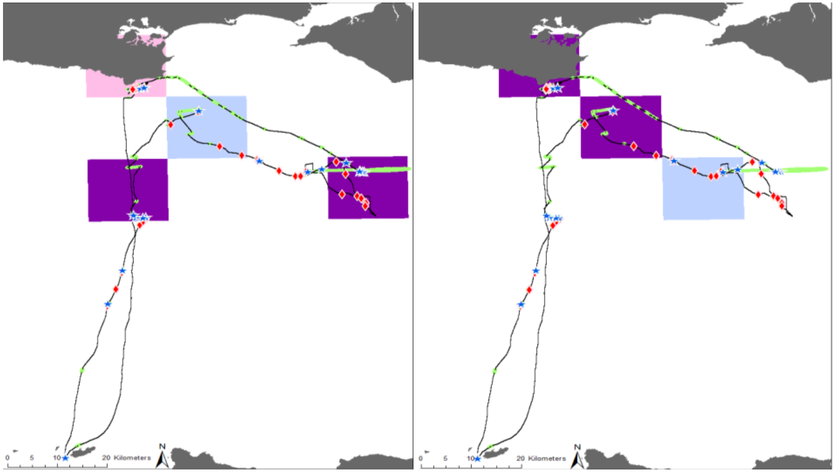
c) Speed d) Speed and day



e) Tortuosity f) Tortuosity and day

Figure 2.3. Example of foraging events occurring in core foraging areas defined by KDh=9.1 and filtered for a) nothing, b) day, c) speed, d) speed and day e) tortuosity and f) tortuosity and day for one trip from a Northern gannet. Colours and shapes indicate behaviours – flying (black line), floating (green circle), plunge diving (red diamond), surface foraging (blue star). Core foraging areas are 25% (pale blue), 50% (pink), 75% (purple).


a) None
b) Day


c) Speed
d) Speed and day

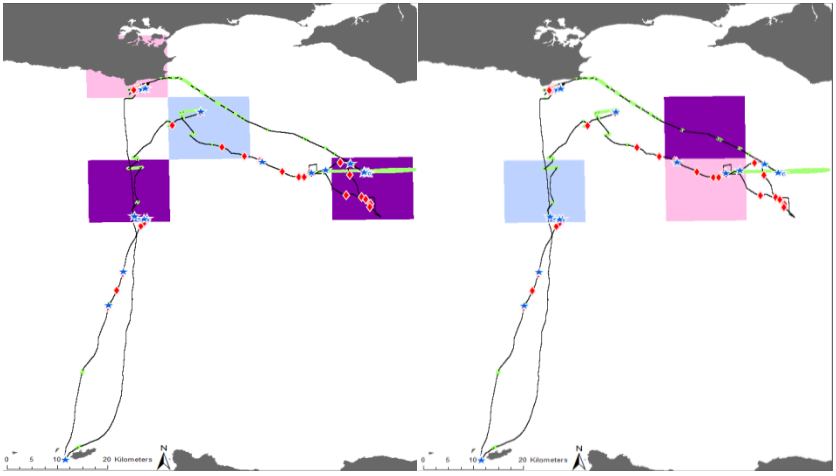

e) Tortuosity
f) Tortuosity and day

Figure 2.4. Example of foraging events occurring in core foraging areas defined by the time-in-area approach and filtered for a) nothing, b) day, c) speed, d) speed and day e) tortuosity and f) tortuosity and day for one trip from a Northern gannet. Colours and shapes indicate behaviours – flying (black line), floating (green circle), plunge diving (red diamond), surface foraging (blue star). Core foraging areas are 25% (pale blue), 50% (pink), 75% (purple).

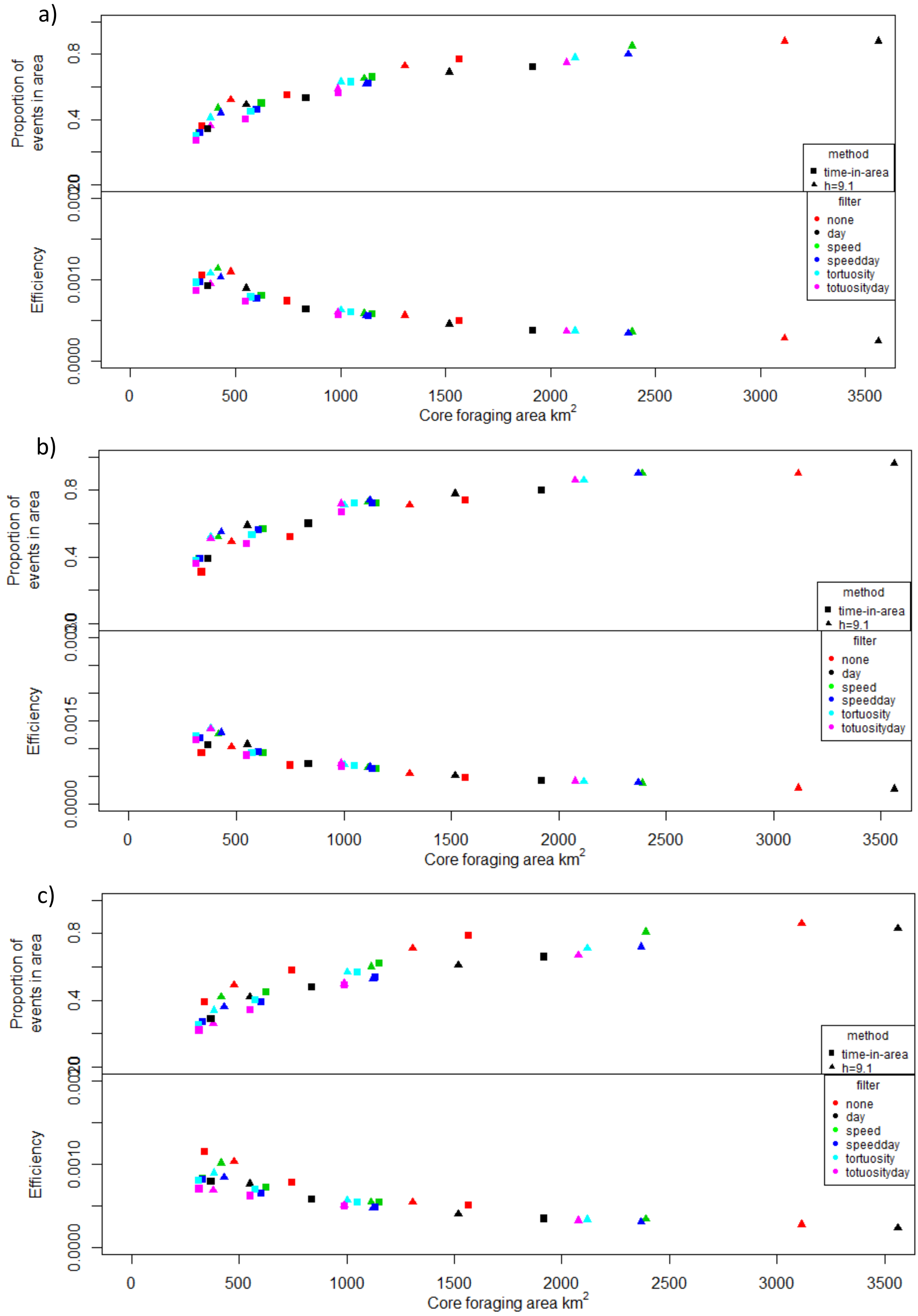


Figure 2.5. The proportion and efficiency (proportion/km2) of a) all foraging events, b) plunge dives, c) surface dives occurring in the core foraging areas defined using KDh=9.1 and the time-in-area approach. Points represent the 25%, 50% and 75% probability of use for unfiltered data and data filtered for day, speed, tortuosity, speed and day and tortuosity and day (see Tables 2.2 - 2.4).

Table 2.2. Bootstrapped proportion with 95% confidence intervals (CI) of all foraging events occurring in the core foraging areas defined by the 25%, 50% and 75% Utilisation Density contours and various filters, using the Kernel Density and time-in-area approaches for 26 trips from nine Northern gannets from the Les Etacs colony, Alderney, Channel Islands

Filter	Contour (%)	Proportion of dives occurring in core foraging area	
		$KD_{h=9.1}$ (CI)	Time-in-area (CI)
None	25	0.52 (0.44-0.59)	0.36 (0.28-0.45)
	50	0.73 (0.67-0.79)	0.55 (0.48-0.63)
	75	0.88 (0.83-0.92)	0.77 (0.71-0.83)
Day	25	0.49 (0.41-0.58)	0.34 (0.26-0.42)
	50	0.69 (0.61-0.77)	0.53 (0.43-0.63)
	75	0.88 (0.83-0.93)	0.72 (0.62-0.80)
Speed	25	0.47 (0.39-0.55)	0.32 (0.26-0.41)
	50	0.65 (0.58-0.72)	0.50 (0.42-0.58)
	75	0.85 (0.80-0.90)	0.66 (0.58-0.74)
Speed and day	25	0.44 (0.37-0.51)	0.32 (0.24-0.41)
	50	0.62 (0.54-0.71)	0.46 (0.34-0.56)
	75	0.80 (0.73-0.87)	0.62 (0.53-0.71)
Tortuosity	25	0.41 (0.33-0.50)	0.30 (0.22-0.38)
	50	0.63 (0.57-0.70)	0.45 (0.37-0.54)
	75	0.78 (0.72-0.83)	0.63 (0.55-0.70)
Tortuosity and day	25	0.36 (0.30-0.43)	0.27 (0.21-0.35)
	50	0.59 (0.52-0.67)	0.40 (0.31-0.50)
	75	0.75 (0.69-0.82)	0.56 (0.47-0.66)

Table 2.3. Bootstrapped proportion with 95% confidence intervals (CI) of all plunge dives occurring in the core foraging areas defined by the 25%, 50% and 75% Utilisation Density contours and various filters, using the Kernel Density and time-in-area approaches for 26 trips from nine Northern gannets from the Les Etacs colony, Alderney, Channel Islands

Filter	Contour (%)	Proportion of dives occurring in core foraging area	
		$KD_{h=9.1}$ (CI)	Time-in-area (CI)
None	25	0.49 (0.39-0.58)	0.31 (0.20-0.43)
	50	0.71 (0.62-0.79)	0.52 (0.44-0.60)
	75	0.90 (0.86-0.94)	0.74 (0.65-0.82)
Day	25	0.59 (0.48-0.68)	0.39 (0.30-0.49)
	50	0.78 (0.70-0.84)	0.60 (0.49-0.70)
	75	0.96 (0.93-0.98)	0.80 (0.70-0.86)
Speed	25	0.52 (0.40-0.63)	0.39 (0.31-0.49)
	50	0.73 (0.65-0.81)	0.57 (0.46-0.66)
	75	0.90 (0.86-0.93)	0.72 (0.65-0.79)
Speed and day	25	0.55 (0.46-0.63)	0.39 (0.31-0.49)
	50	0.74 (0.66-0.81)	0.56 (0.48-0.64)
	75	0.90 (0.85-0.93)	0.72 (0.65-0.78)
Tortuosity	25	0.52 (0.43-0.62)	0.38 (0.30-0.47)
	50	0.71 (0.64-0.79)	0.53 (0.44-0.61)
	75	0.86 (0.82-0.90)	0.72 (0.64-0.79)
Tortuosity and day	25	0.51 (0.42-0.61)	0.36 (0.28-0.45)
	50	0.72 (0.64-0.78)	0.48 (0.39-0.58)
	75	0.86 (0.82-0.90)	0.67 (0.59-0.75)

Table 2.4. Bootstrapped proportion with 95% confidence intervals (CI) of all surface foraging events occurring in the core foraging areas defined by the 25%, 50% and 75% Utilisation Density contours and various filters, using the Kernel Density and time-in-area approaches for 26 trips from nine Northern gannets from the Les Etacs colony, Alderney, Channel Islands.

Filter	Contour (%)	Proportion of dives occurring in core foraging area	
		$KD_{h=9.1}$ (CI)	Time-in-area (CI)
None	25	0.49 (0.39-0.58)	0.39 (0.30-0.48)
	50	0.71 (0.62-0.79)	0.58 (0.48-0.67)
	75	0.86 (0.79-0.92)	0.79 (0.72-0.85)
Day	25	0.42 (0.30-0.54)	0.29 (0.21-0.38)
	50	0.61 (0.49-0.73)	0.48 (0.36-0.61)
	75	0.83 (0.74-0.91)	0.66 (0.53-0.78)
Speed	25	0.42 (0.32-0.53)	0.27 (0.19-0.37)
	50	0.60 (0.50-0.69)	0.45 (0.35-0.55)
	75	0.81 (0.71-0.88)	0.62 (0.50-0.73)
Speed and day	25	0.36 (0.26-0.46)	0.27 (0.18-0.38)
	50	0.53 (0.40-0.67)	0.39 (0.27-0.53)
	75	0.72 (0.61-0.83)	0.54 (0.41-0.67)
Tortuosity	25	0.34 (0.23-0.45)	0.25 (0.15-0.35)
	50	0.57 (0.48-0.66)	0.40 (0.30-0.51)
	75	0.71 (0.61-0.80)	0.57 (0.46-0.68)
Tortuosity and day	25	0.26 (0.18-0.35)	0.22 (0.15-0.30)
	50	0.50 (0.38-0.62)	0.34 (0.24-0.47)
	75	0.67 (0.55-0.78)	0.49 (0.37-0.62)

Discussion

The ability to determine where and how pelagic species use the marine environment can greatly add to the information used in Marine Spatial Planning (Le Corre *et al.* 2012). This study demonstrates that for Northern gannets at least, spatial data alone can indeed be used to identify core foraging areas. Devices such as accelerometers are a valuable mechanism from which to identify foraging behaviour, however the interpretation of behaviours derived from these devices are also subjective, and often not validated due to the nature of seabird foraging occurring far from land. Filtering the data for day-time, speed and tortuosity had little impact on the usefulness of this approach when all foraging events were considered. When considering only plunge dives, any of the filters resulted in a more efficient designation of core foraging area than using unfiltered data. In contrast, when considering only surface foraging events the use of any filter resulted in a less efficient designation of core foraging area. However different modes of foraging may be more likely at different times of day and thus the decision on which foraging modes to include for species which have more than one should depend on the purpose of the analysis and ecological context.

Comparison of kernel density and time-in-area analyses

Kernel density analysis (Stauss *et al.* 2012) and the time-in-area approach (Soanes *et al.* 2013) are commonly used techniques to define core foraging areas for marine predators such as seabirds. Our analysis suggests that both of these approaches have varying degrees of accuracy dependent upon the methods used to identify the smoothing parameter and the filters applied to the data. However, while accurately encompassing a high proportion of dives, both methods had a tendency to overestimate the size of the area where these dives occurred (Figures 2.3 and 2.4). It is widely recognised that the Least Squared Cross Validation method reduces this tendency in KD analysis (Worton 1995), but this type of analysis is frequently inappropriate for seabird tracking data as the clustered data points cause the algorithms to fail (Hemson *et al.* 2005). The size of the grid cell used in the time-in-area approach affects the efficiency of designation (Soanes *et al.* 2014), and we establish that in this instance a 5 x 5 km grid cell is more efficient in its ability to identify core foraging areas than larger grid cells (Table S2.2, Figures S2.1 & S2.2). This does, however, result in a more fragmented designation of core foraging area, which can have its own implications (Hughes *et al.* 2005). However for highly mobile species with discrete foraging areas such as seabirds it may be advantageous to identify multiple important areas, rather than focussing on one or two key areas which KD analysis has a tendency to do.

Previous applications of KD analysis have defined core foraging area as the 25% (Stauss *et al.* 2012) or 50% (Worton 1995) probability of use. For gannets, areas of 50% and 75% probability of use identified a substantially greater proportion of all types of foraging event, however when standardised for the size of these areas they were less efficient (Figure 2.5). It is clear that for the time-in-area approach, an area of 25% probability of use will not incorporate a high proportion of foraging events and the 50% and 75% areas of use are analogous to the 25% and 50% KD usage respectively. Therefore, it is recommended that a 50% or 75% probability of use should be used with this approach depending on the purpose of the analysis. It is also important to consider the size of the grid cell, as a larger cell would undoubtedly include a higher proportion of foraging events but may result in an overestimation of core foraging area (Soanes *et al.* 2014). In this instance the use of 5 x 5 km grid cells was more efficient than larger cells in terms of maximising the proportion of foraging events incorporated whilst minimising the size of the core foraging area (Figure S2.2).

Foraging events and core foraging areas

A high proportion of foraging events were recorded in the core foraging areas designated by both methods, which supports the assumption that spatial movement analyses can be used to identify high-use areas associated with foraging activity. Gannets exhibit site fidelity and frequently commute to previously used foraging areas, transiting relatively rapidly to them (Gremillet *et al.* 2004; Patrick *et al.* 2014). More time is spent in these areas due to the higher dive frequency at foraging sites (Hamer *et al.* 2000) interspersed with periods resting on the water (Ropert-Coudert *et al.* 2004). Gannets frequently perform opportunistic plunge dives when in transit (Lewis *et al.* 2004; Garthe, Montevecchi & Davoren 2007), however given these have short durations (Green *et al.* 2010), isolated dives would only marginally increase the time spent in those areas. When combined with overnight periods resting on the water with reduced foraging activity, these behaviours may explain the remainder of the variability in the proportion of dives occurring in the designated core foraging areas.

An assumption of this study is that increased foraging events signify an area with a higher encounter rate of prey, rather than an area where more foraging events are required in order to catch the same number of prey items. We suggest this can be supported by the fact that seabirds are predominantly visual predators, diving after detecting prey (Garthe, Benvenuti & Montevecchi 2000), and that ingestion in Cape gannets *Morus capensis* and Australasian gannet *Morus serrator* occurred in over 75% and 91% of plunge dives, respectively (Ropert-Coudert *et al.* 2004; Machovsky-Capuska *et al.* 2012). This not only supports our assumption but also suggests that this approach may be equally effective for other visual-foraging pelagic seabirds. However to be certain of the applicability to other groups this study would need to be expanded to other species.

Nocturnal foraging

Previous studies have suggested that gannets do not forage at night (Hamer *et al.* 2000; Garthe, Montevecchi & Davoren 2007). However, these studies refer only to plunge diving. In line with these previous studies, we found strong evidence to suggest that the proportion of plunge dives occurring in core foraging areas is higher when night-time location data are removed. Gannets are visual predators when plunge diving (Machovsky-Capuska *et al.* 2012) and, therefore, unlikely to actively forage in hours of darkness when visibility is reduced. Our results indicate that plunge diving did not occur throughout the night but that this behaviour re-commenced as early as 3 am. This suggests that if interested solely in plunge diving behaviour, the removal of night-time data would result in a higher proportion of dives occurring in core foraging areas.

However, in addition to plunge diving, gannets forage from the water surface (Garthe, Benvenuti & Montevecchi 2000). Our study suggests that this is an important behaviour in Northern gannets with 64% of all foraging events being surface foraging events, with 31% of these occurring during darkness. While our approach is likely to overestimate the amount of surface foraging (see below), this is an interesting finding as surface foraging is rarely studied, highlighting the need for further investigation. Northern gannets have been observed swimming from the surface to forage (Garthe, Benvenuti & Montevecchi 2000), however this behaviour is not identifiable from time-depth recorders, and previous studies using accelerometers do not attempt to classify it. In addition most studies analysing gannet spatial data remove night time fixes, which is when a high proportion of surface foraging events occurred. Gannets display opportunistic foraging behaviour (Montevecchi *et al.* 2009) and a gannet resting on the sea surface may detect a fish reflecting moonlight resulting in nocturnal surface foraging. Alternatively, scavenging for fisheries discards could explain these nocturnal foraging events, as this practice occurs during both day and night (Enever, Revill & Grant 2007).

Votier *et al.* (2010) excluded night-time data when investigating utilisation of fisheries discards by gannets, as it is frequently assumed that this period is spent solely resting on the water. However, we found evidence to suggest that removing night-time data would result in a lower proportion of surface foraging events occurring in designated core foraging areas. Overall, we found little evidence to suggest that the removal of night-time data results in a higher proportion of all foraging events occurring in the core foraging areas. As a result, we recommend that for gannets at least, all data, from both day and night periods should be incorporated in analyses.

Effects of filtering for speed and foraging mode

The proportion of all foraging events and surface foraging events occurring in core foraging area*s* was reduced when the data was filtered for speeds <1.5m/s and >9m/s, and for the combination of speed and day. This is logical given that surface foraging accounted for a large proportion of all foraging events and occurred when the bird was resting on the water and, therefore, likely to be travelling at low speeds, and frequently at night. When considering only plunge dives the efficiency of designating core foraging areas was higher when the speed filter was applied. This is also logical given that periods of transiting and resting on the water were excluded (Wakefield *et al.* 2013), leading to the analysis of data where only speeds where it is rational for a bird to be plunge diving were included. There is evidence to suggest that when analysed separately, the proportion of plunge dives and surface foraging events occurring in designated core foraging areas differ. This strongly suggests birds are exhibiting different behaviours in different locations and/or at different times. For example, gannets are known to have different foraging strategies when actively searching for different prey types (Garthe, Benvenuti & Montevecchi 2000) and when feeding on discards from fishing vessels (Bartumeus *et al.* 2010; Votier *et al.* 2010). This suggests there is an additive effect of foraging behaviours and that all behaviours should be incorporated when identifying areas of high foraging activity.

Effect of filtering for tortuosity

Tortuosity is an indicator of ARS behaviour under the assumption that a more tortuous track represents a bird circling an area looking for prey (Bovet & Benhamou 1991). This is clearly only relevant to aerial search behaviour associated with plunge diving. Given that surface foraging accounted for a large proportion of all foraging events it is logical that the filter for tortuosity resulted in a lower proportion of all foraging events occurring in the core foraging areas. Filtering for more tortuous tracks excludes areas where the bird is transiting or resting. In addition it excludes opportunistic plunge dives in transit and tracks heading directly towards fishing vessels, which can impact foraging tortuosity from a distance of 11km (Bodey *et al.* 2014). Only data points where the bird appears to be actively searching are maintained, explaining why designating core foraging events is more efficient using this filter when considering only plunge dives.

The use of accelerometers to measure behaviour

The continuing improvement of biologging devices enables us to develop an increasingly detailed understanding of at-sea behaviours of seabirds. Efficient methods to extract behaviours from large files of acceleration data are still in development (Bidder *et al.* 2014). The unsupervised method for behaviour classification used in this study will undoubtedly have introduced some error due to variability in behaviours within and between individuals. However, visual comparisons between raw acceleration data and behaviour classifications suggest this error is very small and unlikely to be greater than in other similar studies. Behaviours were classified based on the logical interpretation of acceleration signals. However, due to the fact that these behaviours are occurring while birds are away from land and unable to be monitored, they have not been validated. In the case of surface foraging, events include both pecking, scooping and diving from the surface. Washing or preening may have been classified as surface foraging if the pitch of the bird exceeded -20^{0}. This threshold was identified by visual inspection of the acceleration signals, and seemed to reflect more extreme movements including those of longer duration which appeared to represent surface foraging events. Ideally, these behaviours should be classified separately, however this is highly challenging with an unsupervised classification method and therefore surface foraging events are likely to have been overestimated. Despite this, we show that surface foraging is an important foraging mode for Northern gannets and worthy of consideration and validation.

Conclusion

The time-in-area approach and Kernel Density analysis were equally efficient methods to designate core foraging areas using location-only data for Northern gannets. Both methods support the hypothesis that foraging activity is more likely to occur in areas where seabirds spend more time. However the time-in-area approach is advantageous in its simplicity. In addition, grid cells are commonly used units in Marine Spatial Planning (Gilliland & Laffoley 2008; White, Halpern & Kappel 2012) and compatible with decision making tools such as C-Plan and MARXAN (Lombard *et al.* 2007). We recommend the time-in-area approach is used in the analysis of tracking and survey data when behavioural data are unavailable, in order to identify core foraging areas to be used in Marine Spatial Planning.

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Supporting Information

Utilisation distributions were estimated for 26 foraging trips from nine Northern gannets from Les Etacs colony, Alderney, by calculating the Kernel Density (KD) using a UTM 30 projection and a grid size of 1 km^2 in R package *adehabitatHR* (Calenge 2006). The smoothing parameter (h) was calculated using both the *ad-hoc* method ($KD_{ad\text{-}hoc} = h = \sigma n^{-1/6}$ where $\sigma^2=0.5(var(x)+var(y))$) and h=9.1 km ($KD_{h=9.1}$). The proportion of foraging events occurring within the core foraging area designated using each method was calculated. Results from $KD_{h=9.1}$ are discussed in the main text.

The R package *Trip* (Sumner 2011) was used to calculate the time spent (seconds) in each cell of a pre-defined grid, for 26 foraging trips from nine Northern gannets from the Les Etacs colony, Alderney. Cell size of 5 x 5 km and 10 x 10 km were tested. The proportion of dives occurring in the core foraging area was similar using the either grid size (Table S2.1), however the designation was much more efficient when the 5 x 5 km grid cells were used (Figure S2.1), demonstrated in figure 2.

Table S2.1. Bootstrapped proportion with 95% confidence intervals (CI) of all foraging events occurring in the core foraging areas defined by the 25% and 50% Utilisation Density Contours and various filters, defined using $KD_{ad\text{-}hoc}$ for 26 trips from nine Northern gannets from the Les Etacs colony, Alderney, Channel Islands

Filter	Contour (%)	Proportion of dives occurring in core foraging area		
		All foraging events	Plunge dives	Surface foraging
None	25	0.49 (0.4-0.57)	0.46 (0.35-0.56)	0.51 (0.41-0.61)
	50	0.71 (0.65-0.76)	0.68 (0.57-0.77)	0.72 (0.66-0.78)
Day	25	0.47 (0.39-0.56)	0.56 (0.44-0.66)	0.40 (0.28-0.52)
	50	0.70 (0.62-0.77)	0.78 (0.70-0.85)	0.63 (0.53-0.73)
Speed	25	0.42 (0.33-0.50)	0.46 (0.34-0.56)	0.38 (0.27-0.49)
	50	0.63 (0.54-0.70)	0.70 (0.58-0.80)	0.57 (0.46-0.66)
Speed and day	25	0.42 (0.34-0.51)	0.51 (0.40-0.62)	0.36 (0.25-0.46)
	50	0.62 (0.52-0.72)	0.72 (0.63-0.80)	0.54 (0.42-0.66)
Tortuosity	25	0.28 (0.23-0.34)	0.41 (0.34-0.39)	0.20 (0.12-0.28)
	50	0.48 (0.41-0.54)	0.61 (0.51-0.7)	0.38 (0.29-0.47)
Tortuosity and day	25	0.24 (0.19-0.29)	0.38 (0.28-0.47)	0.16 (0.09-0.21)
	50	0.43 (0.36-0.50)	0.56 (0.46-0.67)	0.32 (0.23-0.42)

Table S2.2. Bootstrapped proportion with 95% confidence intervals (CI) of all foraging events occurring in the core foraging areas defined by the 25%, 50% and 75% Utilisation Density Contours and various filters, defined using the time-in-area approach with 5 x 5 km and 10 x 10 km grid cells for 26 trips from nine Northern gannets from the Les Etacs colony, Alderney, Channel Islands

Filter	Contour (%)	Proportion of dives occurring in core foraging area	
		5 km grid cell (CI)	10 km grid cell (CI)
None	25	0.28 (0.23-0.32)	0.28 (0.23-0.34)
	50	0.50 (0.43-0.57)	0.51 (0.52-0.59)
	75	0.82 (0.75-0.88)	0.78 (0.71-0.82)
Day	25	0.27 (0.20-0.35)	0.32 (0.23-0.40)
	50	0.49 (0.39-0.57)	0.48 (0.38-0.58)
	75	0.75 (0.66-0.81)	0.72 (0.62-0.80)
Speed	25	0.19 (0.15-0.23)	0.22 (0.16-0.28)
	50	0.38 (0.29-0.47)	0.43 (0.34-0.51)
	75	0.59 (0.50-0.67)	0.59 (0.51-0.68)
Speed and day	25	0.16 (0.12-0.21)	0.21 (0.15-0.28)
	50	0.30 (0.25-0.36)	0.35 (0.29-0.42)
	75	0.57 (0.48-0.66)	0.49 (0.42-0.56)

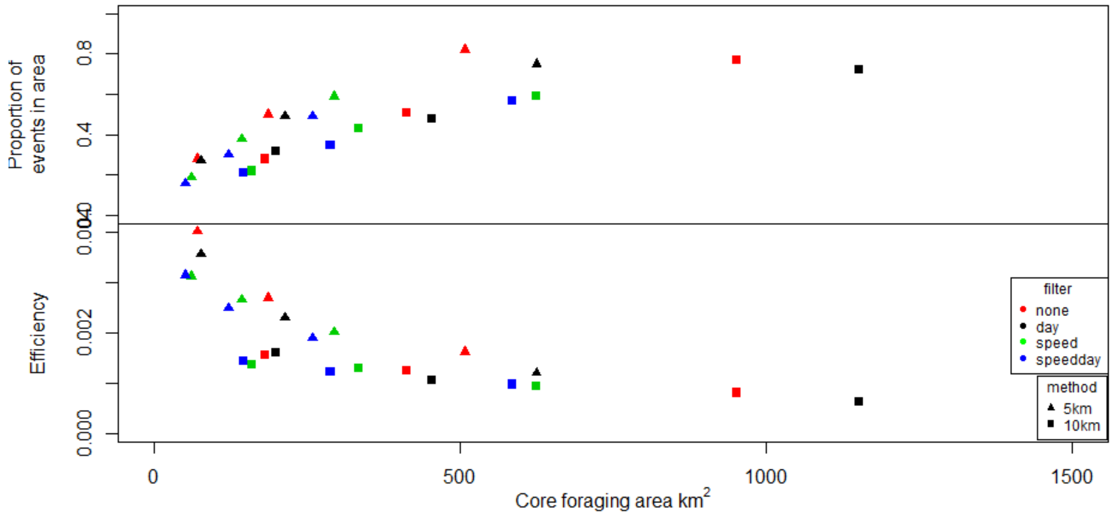

Figure S2.1. The proportion of all foraging events occuring in the core foraging areas defined using 5 x 5 km and 10 x 10 km grid cells using the time-in-area approach. Points represent the 25%, 50% and 75% probability of use for unfiltered data and data filtered for day, speed, speed and day.

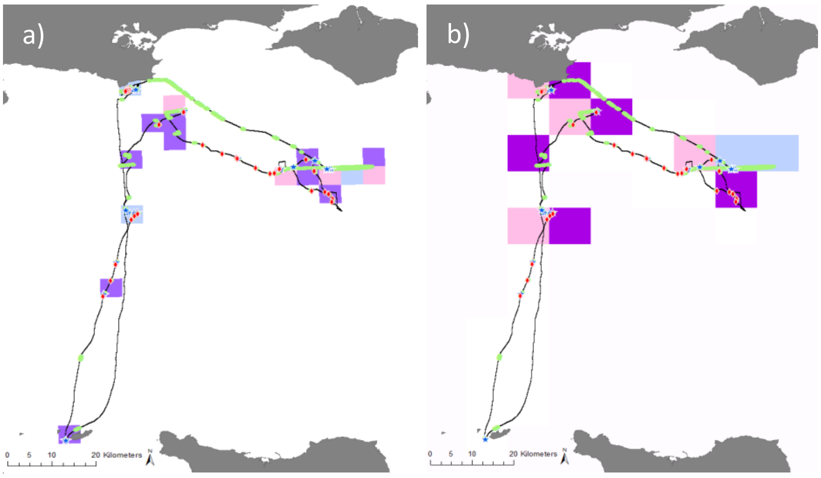

Figure S2.2. Example of foraging events occuring in core foraging areas defined by the time-in-area approach using a) 5 x 5 km and b) 10 x 10 km grid cells for one trip from a Northern gannet. Colours and shapes indicate behaviours – flying (black line), floating (green circle), plunge diving (red diamond), surface foraging (blue star). Core foraging areas are 25% (pale blue), 50% (pink), 75% (purple).

Chapter 3

Predictive modelling to identify near-shore, fine-scale seabird distributions during the breeding season

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Abstract

During the breeding season many seabirds are constrained to coastal areas and are restricted in their movements, spending much of their time in near-shore waters either loafing or foraging. However, in using these areas they may be threatened by anthropogenic activities such as fishing, watersports and coastal developments including Marine Renewable Energy Installations (MREIs). Although many studies describe large scale interactions between seabirds and the environment, the drivers behind near-shore, fine-scale distributions are not well understood. For example, Alderney is an important breeding ground for many species of seabird and has a diversity of human uses of the marine environment, thus providing a suitable location to investigate the near-shore fine-scale interactions between seabirds and the environment. We used vantage point observations of seabird distributions, collected during the 2013 breeding season in order to identify and quantify some of the environmental variables affecting the near-shore, fine-scale distribution of seabirds in Alderney's coastal waters. We validate the models with observation data collected in 2014 and show that water depth, distance to the intertidal zone, and distance to the nearest seabird nest are key predictors in the distribution of Alderney's seabirds. AUC values for each species suggest that these models perform well, although the model for shags performed better than those for auks and gulls. While further unexplained underlying localised variation in the environmental conditions will undoubtedly effect the fine-scale distribution of seabirds in near-shore waters, we demonstrate the potential of this approach in marine planning and decision making.

Introduction

Seabirds are primarily suited to life at sea, however during the breeding season many species are constrained to coastal areas, often breeding in large colonies, and rafting and foraging in the coastal waters adjacent to breeding sites (Wilson *et al.* 2009). At the same time, the potential for negative interactions between humans and seabirds is particularly acute in coastal areas, since seabirds have to use these areas and many human activities are concentrated in near-shore locations (Halpern *et al.* 2008). Understanding how the vulnerability of seabirds varies for different types of anthropogenic disturbance, requires information on how likely they are to interact with an activity (exposure) and the severity of effects where interaction occurs (sensitivity) (Hope 2006; Knights *et al.* 2014). Severity of effects is well documented for some interactions (e.g. Carney & Sydeman 1999; Favero & Seco Pon 2014) and less well understood for others (e.g. Furness *et al.* 2012; Witt *et al.* 2012). Likely exposure to activities requires an understanding of the factors driving distributions of seabirds in space and time.

The factors associated with seabird distributions include, but are not limited to, environmental factors such as bathymetry (Wanless *et al.* 1993; Amorim *et al.* 2009), distance to land and nest site (Davoren, Montevecchi & Anderson 2003; Amorim *et al.* 2009), substrate type (Watanuki *et al.* 2008), chlorophyll levels (Suryan, Santora & Sydeman 2012), sea surface temperature (Guinet *et al.* 1998) and oceanographic processes (Hunt *et al.* 1999; Scales *et al.* 2014). Many of these and their interactions may be proxies for the underlying factors influencing seabird distribution which are primarily prey availability and energetic constraints. In addition, ecological interactions, such as local enhancement (Buckley 1997) or competition (Fauchald 2009) may be important. Furthermore, prey availability and important at-sea areas, may vary temporally (Hunt Jr & Schneider 1987; Amorim *et al.* 2009; Cox, Scott & Camphuysen 2013), or be dependent on weather conditions (Daunt *et al.* 2006; Amorim *et al.* 2009). Although widely studied, most research into the factors driving seabird distribution is conducted at moderate to large spatial scales, and very fine-scale distributions are rarely considered. Yet it is the factors affecting near-shore, fine scale distribution that are most pertinent when considering marine spatial planning issues, such as the licensing of new human activities in coastal areas.

Methods for studying seabird distributions include: large-scale ship-based or aircraft surveys of all species in a pre-defined area (Camphuysen *et al.* 2004); and novel tracking technologies which provide very fine-scale location and behavioural information for a sample of individuals from a known colony (e.g. Soanes *et al.* 2013b). These methods have improved our understanding of seabird habitat use and at-sea distributions, as the interactions between the physical and biological environments and how they influence seabird distributions are explored. However, while seabird tracking studies, in particular, have improved our understanding of seabird ecology, they are not always feasible, as recommended guidelines on the load of biologging devices (Hawkins 2004) preclude small birds from carrying some devices, and some species and populations are not amenable to tracking (Harris *et al.* 2012). Additionally, often only subsets of the population are tracked which could induce bias (Soanes *et al.* 2013a), and tracking data is colony specific rather than site specific i.e. birds from that colony may not enter the area of interest. Additionally, large scale aircraft or ship-based surveys are expensive, and can be problematic in shallow and topographically complex habitats.

Shore-based surveys overcome these aforementioned issues, and for near-shore fine-scale studies, it should be possible to use vantage point observations. Vantage point observations have been used to gain presence-absence data of seabirds in areas proposed for the development of offshore renewable energy devices, however these distributions have not been related to the underlying environmental variables, presumably because most surveys in coastal environments are driven by Environmental Impact Assessments which only focus on quantifying numbers of birds in the site, rather than their habitat use (Camphuysen *et al.* 2004). This approach has been used successfully to investigate distributions of marine mammals in this context (e.g. Jones *et al.* 2014). Furthermore these observations could allow behaviours such as flocking, foraging and fine-scale interactions between seabirds and the environment to be monitored.

For example, Alderney and its surrounding islands in the English Channel are important breeding grounds for many species of seabird (Table 3.1), and also one of the best locations world-wide in its potential for harvesting tidal stream energy on a large-scale (Neill, Jordan & Couch 2012). With consistently high current speeds coupled with depths of 25 m - 45 m it is a suitable environment for the operation of tidal turbines (Myers & Bahaj 2005), and Alderney Renewable Energy (ARE) has been granted the licence to install a tidal stream array to exploit this resource. In addition Alderney is a popular destination for recreational boating, and proposals for a marina are being discussed, thus there is the potential for high levels of exposure to anthropogenic disturbance. In order to understand how developments such as these are likely to affect seabird populations, such as those in Alderney, it is necessary to understand the drivers behind their fine-scale distribution in near-shore waters (Waggitt & Scott 2014). We use vantage point observations of the distributions of seabirds around Alderney, collected during the 2013 breeding season, to identify and quantify some of the environmental variables affecting their fine-scale distributions. We validate the model using observation data collected in 2014. In doing so we have developed a simple, yet powerful, observation and modelling approach that could be used in other locations in order to examine potential impacts of anthropogenic disturbance operating in the near-shore environment.

Table 3.1. Seabirds breeding on Alderney and its surrounding islands

Species	Number of breeding pairs	Importance
Atlantic puffin *Fratercula arctica*	143	Largest in English Channel
Storm petrel *Hydrobates pelagicus*	2800[a]	Regionally important
Lesser black-backed gulls *Larus fuscus*	1392	Nationally important
European shag *Phalacrocorax aristotelis*	167	Nationally important
Common guillemot *Uria aalge*	120[b]	
Razorbill *Alca torda*	90[b]	
Northern gannet *Morus bassanus*	7885	Internationally important

a.Number of individuals (2008)

b. Approximation (Pers Comms, Alderney Wildlife Trust)

Data extracted from (Morley & Broadhurst 2014)

Methods

Study site

Alderney, Channel Islands (49 42' 50" N, 2 12' 18" E), is renowned for its fast flowing tidal stream which divides around the island creating The Race to the south and The Swinge to the north (Figure 3.1). Currents in these waters can exceed speeds of 2.5 ms^{-1} (Neill, Jordan & Couch 2012). In addition the tidal range is large, so there are large intertidal zones and many of the rocks and islets which are prevalent in Alderney's near-shore waters only protrude from the water at low tide.

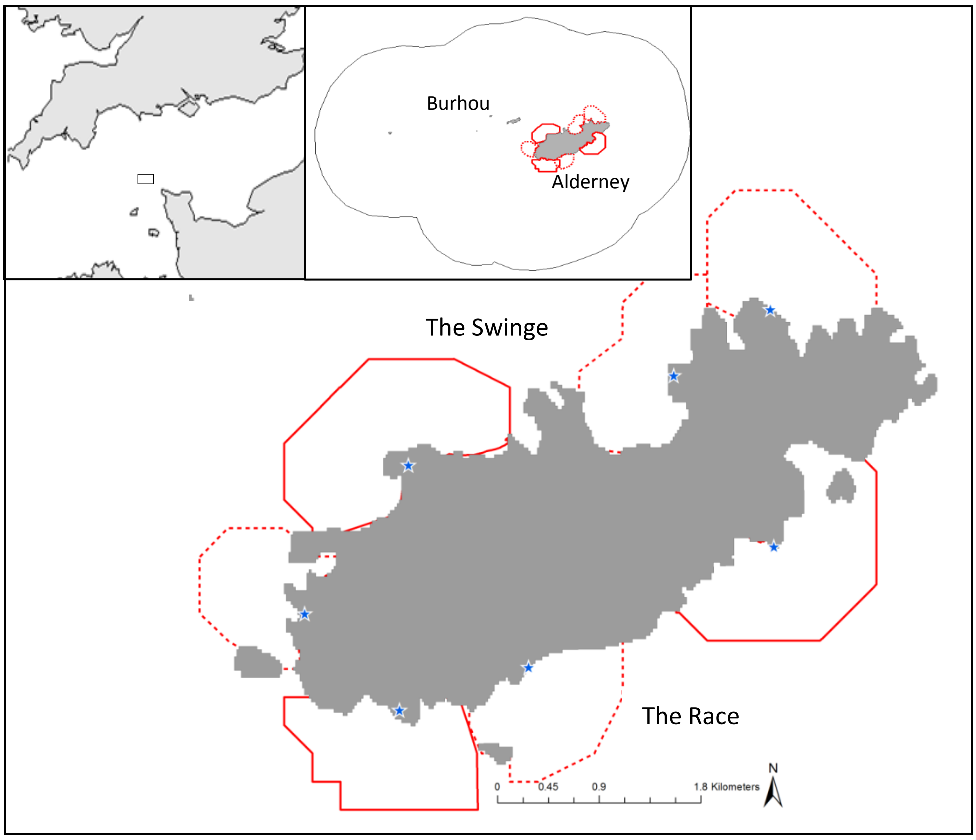

Figure 3.1. Alderney and the island of Burhou (inset). The locations of vantage point observations conducted in 2013 (solid red lines) and 2014 (dotted and solid red lines) are marked on the map

We attempted to quantify this spatial variability in the near-shore environment by defining a number of environmental variables on a 250 m x 250 m grid which included all areas up to 1 km from the coast of Alderney using ArcGIS 10.2 (ArcGIS Desktop: Release 10. Redlands, CA: Environmental Systems Research Institute,

Figure S3.1). These variables were: euclidean distances to intertidal areas (low water mark, including offshore intertidal rocks), to land (high water mark), to nearest nest and to groups of 5, 10 and 20+ nests, mean depth (extracted from an admiralty chart, range from 0 (in the intertidal zone) to 30 m), and the substrate type (coarse sediment or circalitoral rock (Martin, Brown & Hull 2014)). Unfortunately, no data was available on the fine-scale tidal flow speeds in Alderneys near- shore waters, and therefore we were unable to include this in the model. All maps were downloaded from the GADM database of global administrative areas (2016).

Data collection

The number of nests and their locations on Alderney and Burhou was mapped for shags, auks and gulls from boat and foot-based surveys. The number and location of nests of the remaining species were gained from Morely and Broadhurst (2014) and from Alderney Wildlife Trust (pers comms). Shags, gulls, large auks and gannets nest on the south cliffs of Alderney and the islets to the south and west while the island of Burhou, approximately 2.5 km to the north west, hosts more shags, gulls, puffins and storm petrels (Figure 3.2). Land based vantage point observations of birds at sea were carried out on Alderney, during the seabird breeding season (April - July) in 2013 and 2014. Fieldwork on Burhou (i.e nest counts) was carried out as part of the RAMSAR management plan which is authorised by the states of Alderney and maintained by the Alderney Wildlife Trust. No permission was necessary for fieldwork on Alderney as this was all carried out on public land, and nests were not approached. The fieldwork did not require handling any animals therefore no permissions from animal ethics committees were required.

In 2013 three vantage points were selected, one site overlooking The Swinge, and two overlooking The Race (Figure 3.1). In 2014 a further four sites were added. Each vantage point was over 30 m above sea level in order to obtain a good view over the observation area, which extended up to 1 km from the vantage point in all seaward directions. On each visit 4 seabird distribution scans were conducted in order to maximise the likelihood of detecting diving birds, each taking approximately 15 minutes. For each scan, binoculars (7x50) were used to scan the observation area and birds on the water were identified, a bearing was taken, and a rangefinder was used to estimate the distance to the bird at the location the bird was first sighted. Identification of the birds to species level was not consistently possible, therefore birds were classified into broader groups of large gulls (comprising great black-backed *Larus marinus,* lesser black-backed and herring gulls *Larus argentatus*), large auks (comprising common guillemots and razorbills), and European shags. The occasional Atlantic puffin was also observed, but the sample size (4 observations) was insufficient for these to be included in the analysis. Northern gannets were also excluded from the analysis as there were very few sightings of foraging birds (on only one occasion there were plunge diving gannets in the observation area), and many loafing adjacent to the large colony at Les Etacs, with few sightings elsewhere around the island. No other species of seabird were observed in the observation areas.

Although behaviour was not recorded, all species were observed loafing on the water and foraging, either by diving (large auks and shags), or dipping from the surface (large gulls), in all locations where they were observed. In 2013, observations were carried out at all sites up to 6 days a week for 4 months (April – July) resulting in a total of 65 days of data for each site. In 2014, each of the seven vantage points was visited weekly, resulting in a total of 16 days of observation data for each observation area (Table S3.1). Observations were not carried out in bad visibility (< 2000 m) or in sea state greater than 4 (~ 95% were in sea state 1-3), and this, combined with the height of the vantage points and the relatively close distance to the edge of each site, means we were confident that all birds in the observation area were seen. There was not sufficient time to incorporate the potential effects of the state of tide with either time of day or day of year with a suitable number of repeats. Thus, the vantage points were visited at the same time every morning (08:00 - 12:00), to ensure that the time of day was consistent, but all states of tide were incorporated in the observations. The state of tide (ebb, flood or slack) and the time since high tide (expressed as both a continuous variable, and categorically grouped into two hour blocks) at each site was calculated for every visit.

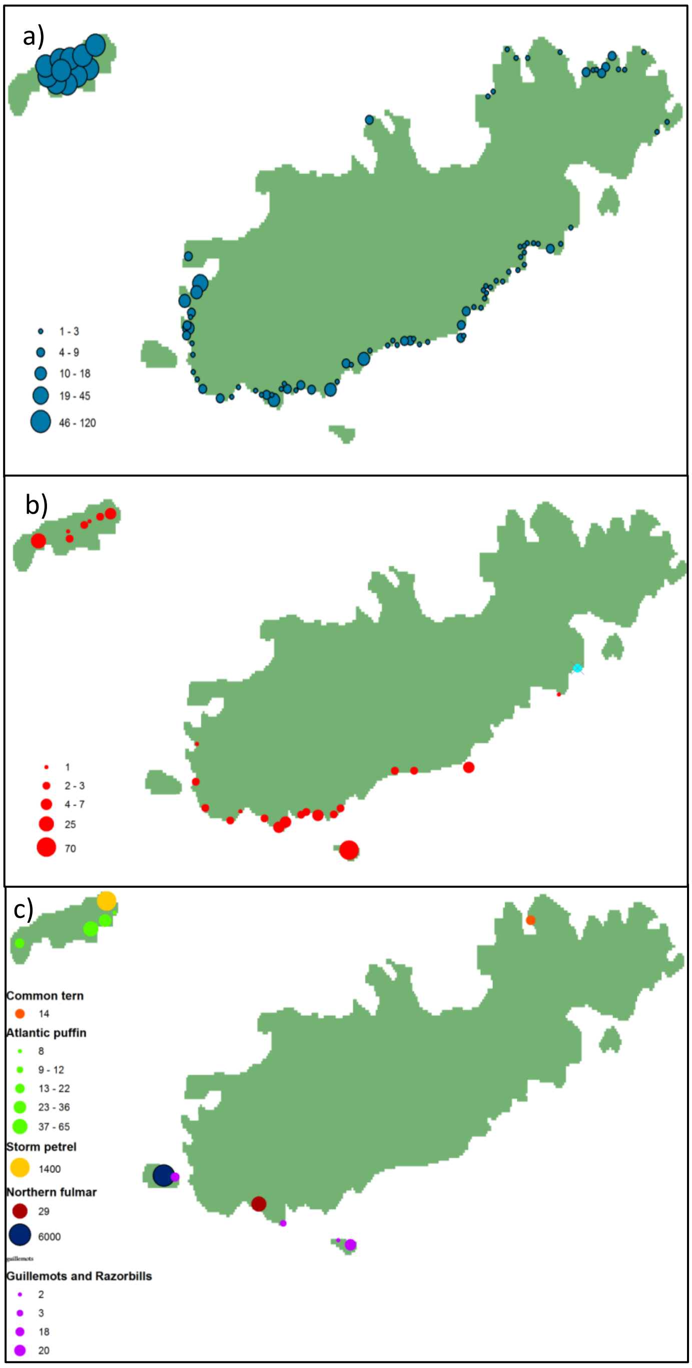

Figure 3.2. Distribution of seabird breeding sites on Alderney (a) large gulls, (b) shags, (c) other seabirds nesting on Alderney in 2013.

Data processing and analysis

Each group (shags, large gulls and large auks) was analysed separately owing to differences in the ecology and foraging behaviour between the three groups. The latitude and longitude for each bird sighting was calculated from the distance and bearing from the vantage point using the geosphere package in R (Hijmans, Williams

& Vennes 2014). For each visit, a single scan containing the maximum number of sightings was selected, with the aim of including all birds that were in the observation area, including those that were diving during some scans, whilst avoiding double counting. The bird locations were added to the grid of environmental data and mean values of all explanatory variables were calculated for each grid cell. These values, as well as the presence or absence of seabirds in each grid cell on each visit, were exported from GIS and analysed using R (version 3.0.2, R Development Core Team 2013).

For each group a generalised linear mixed model with a binomial error structure was created using the *glmer* function in package *lme4* (Bates *et al.* 2013). Presence - Absence models were used due to their robustness in situations such as ours with zero-inflated datasets, additionally our aim was to keep the analysis simple, thus more complex methods to calculate spatial distributions were not used in this instance. Models were constructed to calculate which of the environmental variables affected the probability of finding at least one bird of that group in a given grid cell using data collected in 2013. In each case, the explanatory variables in the starting model were distance to land, distance to the intertidal zone, distance to the nearest conspecific nest, distances to nearest groups of conspecific nests (5-9, 10-19, 20+), depth, substrate type, and all measures of tidal state for each observation. We did not have sufficient data to include either time of day or day of year as a variable, thus the whole breeding season was treated as a single time period. Each grid cell was included as a random effect in order to take account of the repeated observations in each cell. Variables were scaled and centred in order to improve interpretation (Schielzeth 2010).

The model with the lowest Akaike Information Criterion (AIC) score of all of the possible combinations of explanatory variables was determined using the *dredge* function in the *MuMIn* package (Barton 2014). Likelihood ratio tests were used to obtain the significance for each explanatory variable in the final model. The model was then used to predict the probabilities of observing a bird of that group in each cell within the seven observation sites surveyed in 2014. There was some nonindependence between the covariates, however a correlation coefficient of 0.65 between our most correlated variables; depth and distance to the intertidal zone, is below the accepted threshold of 0.7 for regression models (Dormann *et al.* 2013). Plots of the shape of these correlations were curved, suggesting that the variables were not simply covarying, thus justifying their retention (Dormann *et al.* 2013). The model was validated against the proportion of times a bird of that group was observed in each grid cell over 16 visits in 2014. The difference in area between grid cells which consisted entirely of sea, and those which intersected the coast were ignored.

A Receiver Operating Characteristic (ROC) curve was created in R package pROC (Robin *et al.* 2014) in order to test the model for errors of omission (falsely predicted negative values) and commission (falsely predicted positive values) (Fielding & Bell 1997). The ROC curve is a plot of true positive values (sensitivity) against 1- the false positive values (specificity), for all available thresholds of movement between classes (i.e the point at which absent becomes present). The "best" threshold is considered to be that where the difference between sensitivity and specificity is least (Fielding & Bell 1997). The Area Under the Curve (AUC) was calculated to test the overall performance of the model (Hernandez *et al.* 2006). AUC may range from 0.5 to 1, where a value of 0.5 is no better than random, and a value of 1 would be a perfect model (Fielding & Bell 1997). Accepted thresholds for model performance are; low accuracy (0.5 - 0.7), useful applications (0.7 - 0.9) and high accuracy >0.9 (Manel, Williams & Ormerod 2001). In addition, the positive predictive power (ppp), negative predictive power (npp), sensitivity and specificity were calculated (Figure 3.3).

The validated model was then used to predict the distribution of seabirds in the coastal waters surrounding Alderney. Predictions of the probability of finding a bird in a given cell were made up to 1 km from the coast of these islands. The environmental conditions of these waters were all within the same ranges as those in the original observation areas.

		Observed			
		Present	Absent		
Predicted	Present	a	b	Positive predictive power	a/(a+b)
	Absent	c	d	Negative predictive power	d/(c+d)
		Sensitivity	Specificity	Accuracy = (a+d)/(a+b+c+d)	
		a/(a+c)	d/(b+d)		

Figure 3.3. A confusion matrix. This describes how accuracy, sensitivity, specificity, negative predictive power and positive predictive power are calculated.

Results

Of the 117 grid cells surveyed in 2013 there were 83, 49 and 65 cells with at least one observation of a shag, auk and gull respectively. Of the 217 grid cells surveyed in 2014 there were 78, 48 and 78 cells with at least one observation of a shag, auk and gull respectively. This difference in the number of grid cells used was due to the birds tending to use the same grid cells in both years. Few seabirds were found in the new observation areas.

The near-shore, fine-scale distribution of all three groups of seabirds which make up the majority of the birds observed around Alderney can be partially explained by distance to the nearest seabird nest, distance to the intertidal zone and depth (Table 3.2). Substrate type was also important for shags. The probability of observing a shag (Figure 3.4), auk (Figure 3.5) or gull (Figure 3.6) was higher in areas closer to the nest and the intertidal zone, and in deeper water (Table 3.2). The probability of observing a shag was higher over coarse sediment substrates (Figure 3.4).

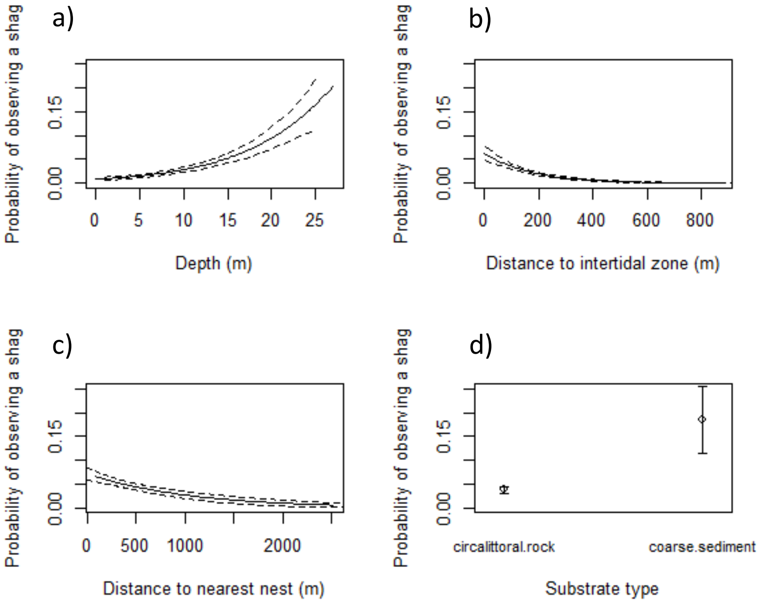

Figure 3.4. Explanatory variables to describe the near-shore distribution of European shags. The probability (and standard error) of observing a European shag as a function of a) depth, b) distance to intertidal zone, c) distance to nearest nest and d) substrate type considered independently, and not accounting for the combined effects of these environmental variables, and are adjusted for the median value for the other numerical predictors in the model, and for the reference level for factors. Based on vantage point observations of the distribution of auks in Alderneys coastal waters over 65 days during the 2013 breeding season.

AUC values of 0.66 - 0.78, calculated from the ROC curve suggest that overall the performance of all the models was fairly good. However, correct classifications of 57 - 77% suggest that the model for shags was good and superior to that for auks and for gulls (Table 3.3). Sensitivity (the correctly predicted presence observations) and specificity (the correctly predicted absence observations) of the models were also good (0.63 - 0.82 and 0.56 - 0.78 respectively, Table 3.2). In addition, the negative predictive power (i.e. the proportion of predicted absences which are also observed absences) was extremely high (97 – 99%). However the positive predictive power (i.e. the proportion of predicted presences which were observed presences) was low (6 - 13%, Table 3.3).

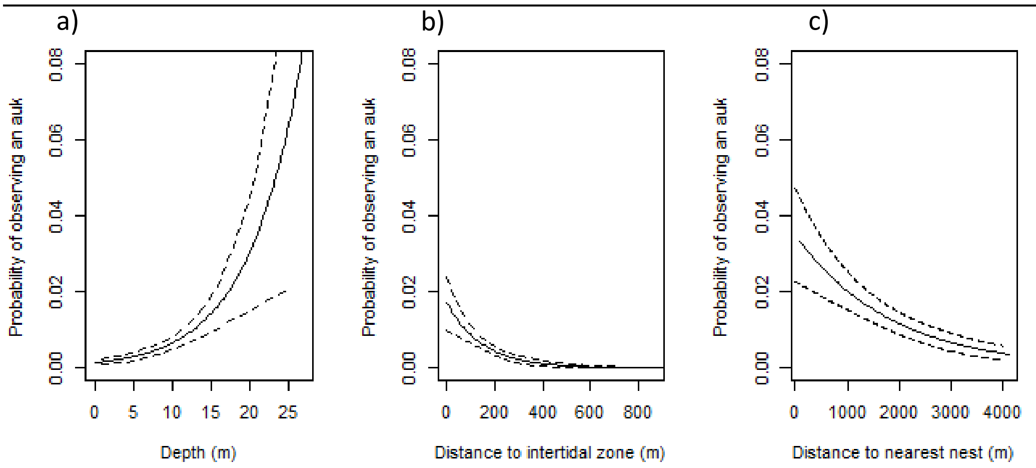

Figure 3.5. Explanatory variables to describe the near-shore distribution of large auks. The probability (and standard error) of observing an auk as a function of a) depth, b) distance to intertidal, c) distance to nest considered independently, and not accounting for the combined effects of these environmental variables, and are adjusted for the median value for the other numerical predictors in the model. Based on vantage point observations of the distribution of shags in Alderneys coastal waters over 65 days during the 2013 breeding season.

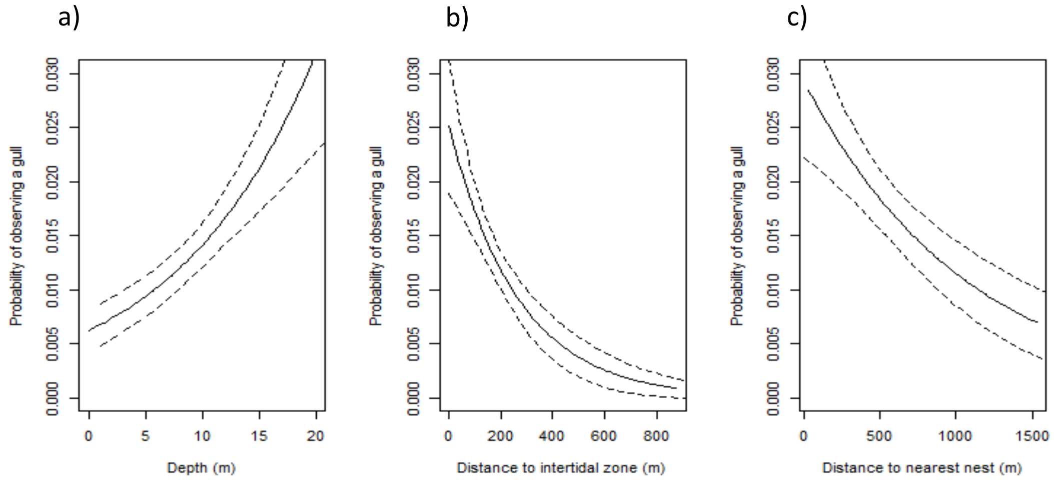

Figure 3.6. Explanatory variables to describe the near-shore distribution of large gulls. The probability (and standard error) of observing a large gull as a function of a) depth, b) distance to intertidal, c) distance to nest considered independently, and not accounting for the combined effects of these environmental variables, and are adjusted for the median value for the other numerical predictors in the model. Based on vantage point observations of the distribution of gulls in Alderneys coastal waters over 65 days during the 2013 breeding season.

Table 3.2. Environmental variables to describe the distribution of Alderney's seabirds. Significant environmental variables scaled and centred (likelihood ratio p-values) in the models to predict the distribution of seabirds in Alderney's coastal waters.

Group	Variable	Estimate	Std Error	p-value
European shags	Distance to the intertidal zone	-1.2	0.23	<0.001
	Depth	1.11	0.21	<0.001
	Distance to nearest nest	-0.72	0.27	0.007
	Substrate (coarse sediment)	0.83	0.27	0.003
Large auks	Distance to the intertidal zone	-1.29	0.45	0.002
	Depth	1.35	0.39	<0.001
	Distance to nearest nest	-0.67	0.21	0.001
Large gulls	Distance to the intertidal zone	-0.71	0.26	<0.001
	Depth	0.63	0.20	0.001
	Distance to nearest nest	-0.33	0.14	0.02

Table 3.3. Model scores from a ROC curve. Based on a presence-absence model using environmental variables to predict the fine-scale distribution of seabirds in Alderney's coastal waters

Group	Threshold	Correct classification (%)	Positive Predictive Power (%)	Negative Predictive Power (%)	Sensitivity	Specificity	Area under curve
European shags	0.09	77	13	98	0.63	0.78	0.73
Large auks	0.006	61	6	99	0.82	0.61	0.78
Large gulls	0.014	57	7	97	0.68	0.56	0.66

In 2014 birds from all three groups were observed most often in waters off the south west coast of Alderney, nearest the majority of nest sites and in line with predictions of suitable habitats by the models. Shags and gulls (Figures 3.7a and 3.7b) were observed along the south coast and tended to remain within 500 m from the coast. Auks were rarely observed off the south-east coast and tended to remain towards the west of the island (Figure 3.7c).

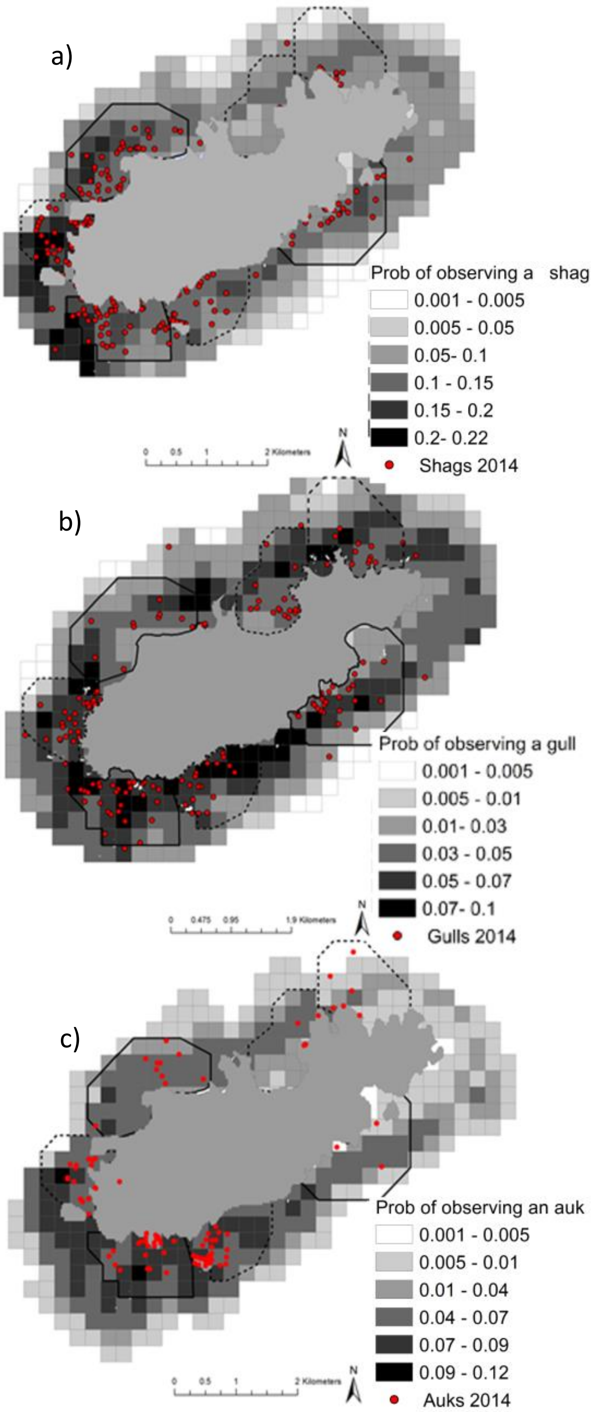

Figure 3.7. Predicted and observed distributions of Alderney's seabirds. The probability of observing a) a shag, b) a gull, c) an auk within 1 km from the coastline of Alderney. Sites surveyed for birds in 2013 (continuous black line) and 2014 (dotted and continuous black line) are marked. Predictions were made based on a presence-absence model using observations made in 2013 and verified with observations made in 2014.

Discussion

In order to understand the potential for any negative impacts from human activities a comprehensive knowledge of the distribution of seabirds with the potential to be affected, at a relevant spatial scale, is vital. Presence-absence models show that the near-shore, fine-scale distribution of seabirds in Alderney's coastal waters can partially be explained by distance to the intertidal zone, distance to the nearest seabird nest, depth and substrate type. Overall classification rates and AUC values indicate that the binomial models perform reasonably well for shags and auks, and less well for gulls. In particular, the models were highly accurate at predicting where the birds were unlikely to be found, but tended to over-estimate the presence of birds, suggesting that factors other than those considered in our study are important in determining habitat use and at-sea distribution.

Studies of seabird biology tend to focus on foraging trips, and the literature on seabird habitat use is dominated by telemetry studies of presumed foraging birds at sea. However, a bird observed at sea is not necessarily foraging; seabirds also rest and raft at sea (Burger 1997; Wilson *et al.* 2009), and this aspect of their behaviour is understudied. Some of our birds were observed foraging, but our study shows that whether foraging or not, at a fine-scale, birds do not use the near-shore environment randomly and have clear preferences for some areas. Thus, the factors underlying their distribution should be considered with respect to decision making for coastal developments. The following discussion will focus on the important variables driving the near-shore fine-scale distribution of seabirds as identified in the model.

Environmental variables

At-sea distributions of foraging seabirds are considered to be driven primarily by prey distribution, but restricted by behavioural, morphological and energetic constraints of the bird (Hunt Jr & Schneider 1987). Many previous studies describe the influence of various environmental and oceanographic variables on the at-sea distribution of seabirds (e.g Amorim *et al.* 2009; Scales *et al.* 2014), however most studies are conducted at a relatively large spatial scale in comparison to this one.

Seabirds appear to make hierarchical decisions, firstly to identify large-scale suitable foraging areas, and then, nested within these areas, to utilise fine-scale habitat features which aggregate prey (Becker & Beissinger 2003). Therefore, environmental and oceanographic variables may have different relative importance at different spatial scales (Hunt Jr & Schneider 1987). In addition seabirds display temporal variation in their distributions, most prominently between the breeding and non-breeding seasons, and it is important to understand their distributions during both of these periods. Tidal state, which can be linked to current speed (Benjamins *et al.* 2015) was found not to be important in our model. This contrasts with other studies of seabirds in areas of high tidal flow. Since most of our birds were close to the intertidal zone they may have been isolated from these current effects found in the water further offshore. As noted earlier, unfortunately we were unable to obtain fine-scale current data for this area. We establish that depth, distance to the nearest seabird nest, distance to the intertidal zone and substrate type are important factors influencing the distribution of Alderney's seabirds.

Distance to the intertidal zone

A higher probability of observing all three bird groups closer to the intertidal zone may be explained by an increase in prey availability in these locations. Many intertidal and sub-tidal rock formations surround Alderney's coastline, and birds were frequently observed in these areas. This type of feature is likely to enhance the occurrence of small scale eddies and shear lines which can aggregate prey in predictable locations (Stevick *et al.* 2008). These oceanographic processes are important for foraging seabirds, at both large (Cox, Scott & Camphuysen 2013; Scales *et al.* 2014) and small (Becker & Beissinger 2003; Scott *et al.* 2010) spatial scales. Sandeels are the primary prey type for auks and shags during the breeding season and are likely to aggregate in these areas. Furthermore, previous studies have revealed that they are able to supplement their diet with crustaceans (Barrett & Furness 1990; Thompson *et al.* 1999; Mehlum 2001), which are common in this habitat type. In addition, gulls frequently forage in the low intertidal and shallow sub-tidal zones (Rome & Ellis 2004) on benthic crustacean and small fish (Kubetzki & Garthe 2003).

Distance to nest

The energetic cost of foraging increases with the distance travelled to foraging locations, unless there is variability in the cost of foraging, or the energy gained from prey. Thus, it is logical for birds to exploit available prey patches in close proximity to the nest. Previous studies demonstrate how distance from the colony is an important factor in the at-sea distributions of guillemots (Oedekoven, Ainley & Spear 2001) and shags (Wanless, Harris & Morris 1991). In addition, although we know that time spent in an area can be used as a proxy for foraging behaviour (Warwick-Evans *et al.* 2015), seabirds also spend time rafting near to their colonies for purposes such as information exchange (Burger 1997). Although foraging behaviour was observed in all groups, the frequency of this behaviour was not recorded, and these areas may be used primarily for loafing rather than foraging. However, as the focus of the study is to understand seabird distribution and not specifically active foraging sites, all locations are relevant.

Depth

Many species of seabird forage in water of a preferred depth (Wanless, Harris & Morris 1991; Stone, Webb & Tasker 1995), presumably due to increased prey availability in these locations. It has been suggested that when considering the fine-scale distribution of top-predators, processes which increase prey aggregation are more important than the oceanographic processes driving primary production (Becker & Beissinger 2003). In the absence of detailed data on preferential prey and the distribution of prey, we can only assume that birds select these greater depths based on increased prey availability. In addition, this deeper water may contain topographical features such as sea banks, and tidal forcing associated with these features may cause the aggregation of zooplankton (Embling *et al.* 2013), leading to fish aggregation and therefore superior foraging locations.

Substrate type

Shags were encountered more often over areas of coarse sediment than over rocky substrates. Although shags are able to forage for sandeels in both the pelagic and benthic zones (Gremillet *et al.* 1998), their diving strategy is considered to be primarily benthic (Watanuki *et al.* 2008), consuming bottom living fish and probing the sand for buried sandeels (Watanuki *et al.* 2008). Consequently, this explains the increased probability of observing a shag in areas of coarse sediment. Although guillemots and razorbills also primarily forage for sandeels during the breeding season (Wanless, Harris & Greenstreet 1998), they are pelagic feeders, and do not exploit sand dwelling fish, hence substrate type is likely to be less important in the distribution of auks. Gulls do not dive at all, and forage by scooping fish from surface waters. Thus, substrate type is not an important variable driving their at-sea distribution.

Model performance

The models predicting the distribution of shags and auks perform reasonably accurately when evaluated using the AUC values and the percentage of correct classifications. AUC values are frequently used to assess the performance of presence-absence models (Austin 2007; Marmion *et al.* 2009). However these may not accurately represent key aspects of model performance (Manel *et al.* 1999; Lobo, Jiménez-Valverde & Real 2008) such as errors of commission and omission. Deconstructing models to evaluate separate measures of prediction success, based on errors of commission or omission may be more suitable (Fielding & Bell 1997; Manel *et al.* 1999). Sensitivity and specificity measure the proportion of observed presences and absences which are correctly predicted, respectively. Positive predictive power (ppp) and negative predictive power (npp) measure the proportion of predicted presences and absences which were also observed i.e the proportion of true presences out of all predicted presences, and similarly for absences. Whilst the values of sensitivity and specificity were reasonable and values of negative predictive power were high in all models, the values of positive predictive power were low, i.e. the models over-predicted presences.

Environmental conditions, in terms of the variables we measured, may be suitable in these areas where the predicted probability of occurrence is high yet birds are not observed. It is likely that populations of birds present on Alderney are relatively small in comparison to the potential area of suitable habitat available, with limitations on suitable nesting sites or other factors on shore being more limiting than habitat at sea. Baldessarini *et al.* (1983) illustrate how positive predictive power significantly decreases, and negative predictive power significantly increases, as prevalence of occurrence decreases. Therefore a low positive predictive power may not necessarily signify a bad model. Additionally, birds in areas which are rarely used may not have been observed during the 16 surveys conducted in 2014. Furthermore, within the areas identified by the model as having a higher probability of occurrence, other factors such as competition (Fauchald 2009), or local enhancement (Buckley 1997), may determine which of these areas are actually used. Habitual behaviour may also be an important factor, but not much is yet known about this.

The relative importance of false positives and false negatives is highly dependent on the application of the predictions (Fielding & Bell 1997). In the context of this study it is arguably less serious to over-predict presences than absences, as this would provide a precautionary approach to guide offshore developments. Our findings support previous suggestions that equal weightings of errors of omission (falsely predicted negative values) and commission (falsely predicted positive values) may not be a representative way to assess model accuracy (Lobo, Jiménez-Valverde & Real 2008). Methods exist to define costs to false positives and false negatives, and weight these accordingly, but these can be subjective and vary depending on the application (Fielding & Bell 1997).

Extending predictions into unobserved areas

Predictions in those sites in close proximity to the initial observation sites, where environmental conditions were similar, appeared to be superior to those further away, and certainty of predictions will decrease significantly in areas which were not previously surveyed. Ecological and oceanographic features can change at scales of only a few metres (Hunt Jr & Schneider 1987), and new areas may be subject to untested environmental or anthropogenic pressures. As models will never take into account all of the underlying variables explaining the distribution of seabirds, any predictions made outside of the study area should be interpreted cautiously.

Recommendations

The near-shore, fine-scale distribution of seabirds in Alderney's coastal waters is related to depth, distance to the nearest seabird nest, distance to the intertidal zone and substrate type. Overall, the models performed reasonably well at identifying areas with suitable habitat types for all three groups, although other factors are undoubtedly involved in determining the near-shore fine-scale distributions of Alderney's seabirds. In the absence of observation data, and as a precautionary approach, these models of habitat use could therefore be applied when recommending areas in which to limit human disturbance, for example in this instance boating and fisheries disturbance around Alderney could be directed away from rocky deep water areas near nests and intertidal zones.

In this instance we could not view the site currently proposed for development of tidal turbines in Alderney (2km offshore) though this would not necessarily always be the case. Furthermore, installations may affect birds in close proximity to the site during construction and decommissioning and due to changes in energy and prey distribution as a result of mixing and sediment transport. Furthermore these changes in sedimentation processes which may occur through altered current regimes, and changes in tidal ranges due to the removal of energy around installations may effect near-shore seabird distributions. European shags may be particularly vulnerable in this respect due to their association with both the substrate type and proximity to intertidal zones (Shields *et al.* 2011).

Our example from Alderney shows that vantage point analyses are complementary to GPS tracking and ship-based and aircraft surveys in their ability to collect large quantities of highly accurate near-shore data at minimal expense. Additionally this method is site specific, rather than colony specific, allowing all birds in the area of interest to be monitored. However, the observable distance from the shore is limited and detection rates become a problem at distances greater than approximately 1km. Additionally, observations cannot be conducted in poor weather conditions. Thus we suggest vantage-point observations are an appropriate method in which to monitor bird distributions in near-shore coastal waters under the right conditions (Waggitt, Bell & Scott 2014). Therefore, we suggest that when assessing potential impacts of marine disturbance on seabirds, observations and subsequent modelling to evaluate the active use of a site by seabirds can make a valuable contribution to the decision making process.

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Supporting Information

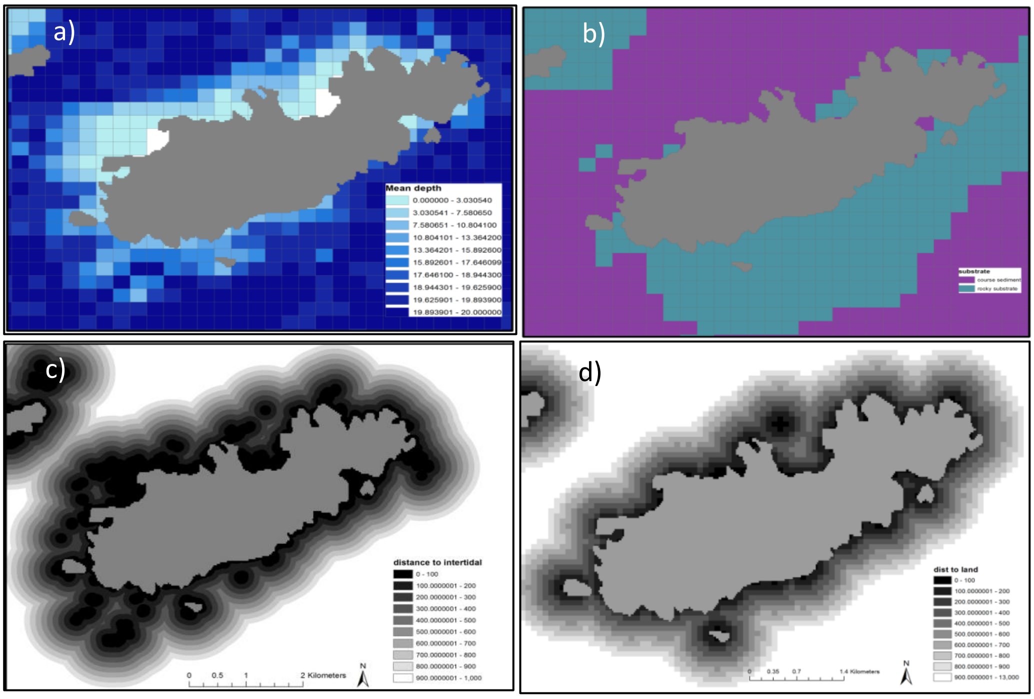

Figure S3.1 The environmental variables describing the near-shore fine-scale distribution of Alderneys seabirds a) depth, b) substrate type, c) distance to the intertidal zone, d) distance to land.

Table S3.1 The number of scans conducted at each vantage point over the different states of tide and months of the year. The state of tide was not calculated for 2014 because it was not significant in the model based on 2013 data.

Year	Month	Tide	Number of Scans
2013	April	Ebb	4
		Flood	9
		Slack	3
	May	Ebb	6
		Flood	11
		Slack	4
	June	Ebb	4
		Flood	8
		Slack	0
	July	Ebb	1
		Flood	10
		Slack	6
2014	April		3
	May		4
	June		4
	July		5

Chapter 4

Survival estimates of Northern gannets *Morus bassanus* in Alderney: Big data but low confidence

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Author contributions: VWE, PWA & JAG designed the study, VWE analysed and wrote this manuscript with support from JAG & PWA.

Summary

Capsule: There has been a linear increase in the survival rates for both adult and juvenile Northern gannets breeding on Alderney in the English Channel. However, large confidence intervals surrounding these estimates highlight the need for improved monitoring.

Aims: To estimate the age specific survival and reporting rate from an internationally important population of Northern gannets breeding at one of the southern-most colonies for this species.

Methods: We use 28 years of ringing and recovery data from birds ringed in Alderney in order to estimate age specific survival and reporting rates for this population of Northern gannets.

Results: We find that adult and juvenile survival rates differ, and that both survival and reporting rates are considerably lower in first year birds than older birds. Additionally, there is an increasing linear trend in survival rates over time, and a decreasing trend in reporting rates.

Conclusion: While these parameters point towards continued growth of this population, the confidence intervals around our estimates are large, highlighting the need for improved re-sighting efforts in long-term studies of this nature.

Introduction

Seabirds are threatened by anthropogenic changes to the marine environment (Croxall *et al.* 2012). To assess the past, current and future impacts of these threats it is essential to understand the age-specific demographic rates of seabirds, and the temporal trends associated with them. Furthermore, since different populations of the same species face different threats and demographic rates can show divergent trends (Crawford *et al.* 2008), it is important to study multiple populations from across each species range. However, demographic studies of long-lived birds such as seabirds require long-term data sets, which, by their nature, are challenging and resource intensive to accumulate. As a result, there are very few ongoing studies which consistently gather sufficient data (usually through ringing and re-sighting birds) to allow for meaningful analysis. Therefore all studies which do generate sufficient data are valuable, even if they focus on the ringing of pulli, which can limit analysis and interpretation (Francis 1995).

Northern gannets *Morus bassanus* breed in large colonies in the North Atlantic, with 75% of the worldwide population breeding in Europe (Gremillet *et al.* 2006). The population of Northern gannets breeding on Alderney in the English Channel inhabits the offshore stacks of Ortac and Les Etacs (Figure 4.1). Although relatively small in comparison to some nearby UK populations, the size of the colony has increased rapidly since the first recorded nest on Ortac in 1940 (Nelson 1978). In 1967, Alderney supported 3,000 breeding pairs and by 2011 the population had reached 7,885 breeding pairs (Bohan 2012), having increased at an average of 3.6% per year since 1967. However, increasing colony size does not necessarily signify a population with highly profitable foraging conditions, and may be a result of birds working hard to forage during the breeding season (Gremillet *et al.* 2006) and/or the immigration of new breeders from other colonies (Siorat & Rocamora 1995).

Despite the healthy rate of population growth throughout the European colonies, gannets may be threatened by anthropogenic impacts, such as the installation of offshore windfarms, over-fishing, fishing gear induced mortality, decreases in fisheries discards and climate change (Grecian *et al.* 2012). As with gannets breeding at Rouzic (Figure 4.1) which are thought to be operating at their energetic limits (Gremillet *et al.* 2006), Alderney's population may be particularly vulnerable due to its position near the southern limit of the species range (Brown, Stevens & Kaufman 1996). Furthermore this population's foraging areas overlap with 9 sites proposed for the development of marine renewable energy installations (Soanes *et al.* 2013). Variation in the behaviour of gannets throughout their life cycle will result in different threats between the age classes. For example, many of Alderney's gannets migrate to West Africa soon after fledging where they remain for the first year or two of life (Veron & Lawlor 2009), thus first year survival is most likely to be impacted by the industrial fishing practices occurring off West Africa. Conversely, Alderney's adult gannets overwinter from the North Sea, to the Bay of Biscay and North Africa (Veron & Lawlor 2009), returning to the English Channel during the breeding season, hence adult survival will be impacted by environmental conditions and fishing practices in these areas (Gremillet *et al.* 2015).

Given the different threats to gannets in different locations and that these threats will change throughout their life cycle, a robust approach to monitor colony specific survival rates must be developed in order to determine which stages of each population are likely to be impacted by changes in local conditions and to what extent (Furness & Wanless 2014). We use 28 years of ringing data to calculate the age-specific survival rates for the Alderney population of Northern gannets.

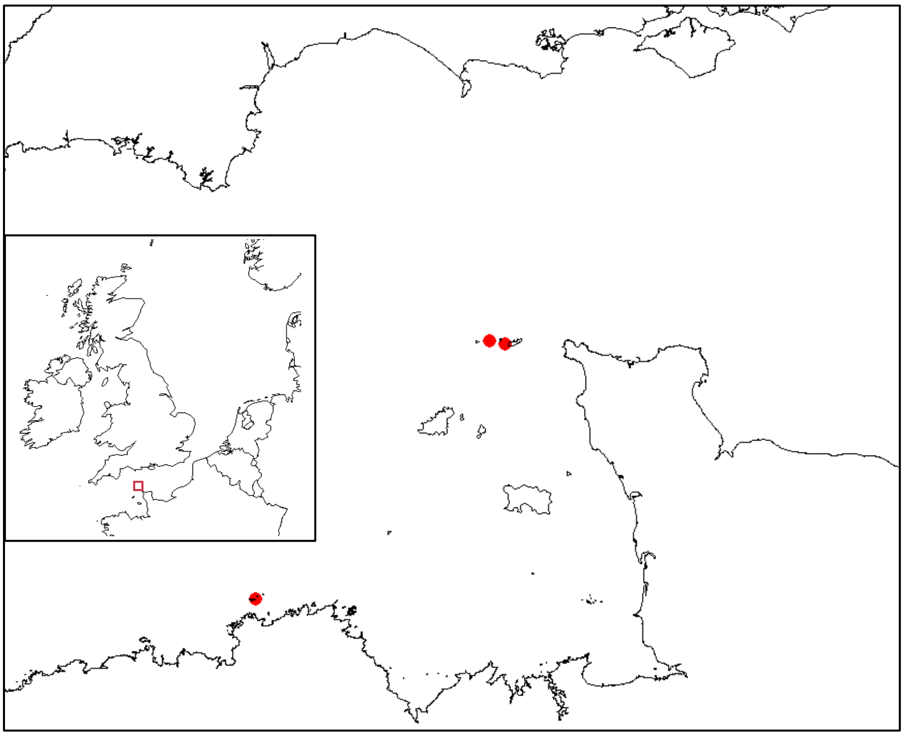

Figure 4.1. The Alderney population of Northern gannets on Ortac and Les Etacs. Rouzic is the southern boundary for European Northern gannets.

Methods

Ringing of Northern gannets in Alderney, Channel Islands, (49 42' 50" N, 2 12' 18" E) by ringers operating under the Channel Island Bird Ringing Scheme began in 1947. However, there were many years where birds were not ringed and regular annual ringing began in 1983, with only one year missing between 1983 and 2010. For this reason, the analysis was conducted using the 19,732 individual birds ringed as chicks in Alderney during this period. Recoveries of birds found dead were used in order to calculate age specific survival and reporting estimates. All birds recovered dead in the colony were removed from the analysis to avoid bias in the estimation of reporting rate, as the prospects of such birds being reported are likely to be atypical (Wanless *et al* 2006), resulting in a total of 530 recoveries of birds ringed in Alderney and recovered dead outside the colony.

Most of the birds ringed in Alderney were ringed as pulli (>99%), which creates a problem when calculating the independent estimate of reporting rates in adult birds, necessary for dead recovery analysis (Francis 1995). Indeed, Furness and Wanless (2014) highlight the shortcomings in current demographic analysis of gannets whereby a high proportion of birds ringed are pullus, and very few adult birds are ringed. Therefore, to enable the calculation of survival rates for Alderney's gannets, we adopted a method previously used by Wanless *et al.* (2006), whereby the birds ringed as pullus in Alderney were combined with data from birds ringed as adults in the UK in the same time period (a total of 1,731 ringed of which 94 were recovered), allowing the calculation of age specific survival estimates for juvenile birds specific to Alderney, and adult survival rates as a combination of Alderney and UK birds. This assumes that Northern gannets from Alderney have similar survival and reporting rates to those ringed in the UK. Kubetzki *et al.* (2009) show that Northern gannets from the Bass Rock colony overwinter in areas ranging from the North Sea down to West Africa. Rings recovered from Alderney's population show a similar overwintering distribution (Veron & Lawlor 2009). This suggests that reporting rates would be similar for UK and Alderney adult gannets, thus supporting this approach. Additionally, the number of pullus ringed in Alderney (19,732), which will, after 5 years, contribute to the adult survival estimates is substantially larger than those ringed in the UK (1,731), thus the estimates of adult survival will be based largely on gannets breeding on Alderney.

Data processing and analysis

Dead recovery analysis was carried out using Seber models (Seber 1970) in order to estimate survival rate (S) and reporting probability (r) using Program MARK software (White & Burnham 1999), combined with the RMark package (Laake 2013), in statistical software R (R Core team 2013).

Initially we fitted a range of age-dependent models, ranging from 0 - 5+ years for both the survival and reporting parameters before considering time-dependent factors (Table S4.1). These preliminary models suggested that it was necessary to cap the number of age classes for the reporting rate to 2 in order for the algorithms to converge, and the models to run. The model which best fitted the data, and thus was used in all further models, was that with 4 age classes in the survival parameter (i.e variation between each of the first three years preceding adulthood), and 2 age classes for the reporting rate, although the improvement over a two age class model was small. A median c-hat goodness of fit test was carried out on the full *age* and *time* dependent model ($S_{age4*time}$, $r_{age2*time}$) in MARK and the variance inflation factor was calculated (c-hat = 2.66). All subsequent models were adjusted to account for this and the best model was identified using $QAIC_C$. Models with all combinations of *age (*as an additive effect*), time* (where all years have an individual parameter estimate) and *Time* (a linear trend in change over time) and with both an additive effect of time and a multiplicative effect of time for both survival and reporting rate were run and ranked by QAICc (Table S4.2). This resulted in a total of 25 models. Weighted mean estimates and 95% confidence intervals of annual survival were calculated for each age class using the *weighted.mean* function in R.

Results

The model with the lowest QAICc value was the one in which survival rates were dependent on *age* and *Time* (as a linear trend), where *Time* had an additive effect on *age* i.e the trend ran parallel between the age classes ($S_{age+Time}$ r_{age}). Reporting rate was dependent on *age*. There was not a large difference in QAICc values for the top models (Table 4.1), therefore model averaging was used to obtain final parameter estimates. Overall there was a gradual increasing linear trend in estimated survival from 1983 – 2010 (Figure 4.2). This trend was more pronounced in first-year birds (from 0.43 - 0.69) than in older age classes (Figure 4.2). Gannets in their second year or older all had high estimates of survival rates ranging from 0.91 – 0.98 (Figure 4.2). Mean estimates of annual survival were considerably lower for first year birds than those in older age classes (Table 4.2). Given that some of the adults were ringed in the UK there is a chance that the difference in survival estimates between adult and juvenile birds may be down to location rather than age. However the 2nd and 3rd year birds would be those ringed as pullus in Alderney and thus it is unlikely that these would also have a higher survival rate if location rather than age were the cause. Overall there was a decreasing trend in reporting rate during the study period, with reporting rate for first year birds considerably lower than for older birds (Figure 4.3).

Table 4.1. The top 6 models comprising 99% of the weighting of all models averaged in order to calculate survival rates between 1983 and 2010 for the Alderney population of Northern gannets.

Model	DeltaQAICc	No. parameters	weight
$S_{age+Time}$, r_{age}	0	7	0.50
S_{age}, $r_{age+Time}$	1.44	7	0.24
$S_{age+Time}$, $r_{age*Time}$	3.24	9	0.1
$S_{age*Time}$, r_{age}	3.84	10	0.07
$S_{age*Time}$ $r_{age*Time}$	4.24	12	0.06
$S_{age*Time}$, $r_{age+Time}$	5.82	11	0.03

Table 4.2. Mean estimates (and 95% confidence intervals) of survival rates for Alderneys Northern gannet population from 1983 – 2010.

Age class	Survival Rate
1st year	0.57 (0.29 – 0.79)
2nd year	0.95 (0.86 – 0.98)
3rd year	0.97 (0.91 – 0.99)
4+ year	0.95 (0.87 – 0.98)

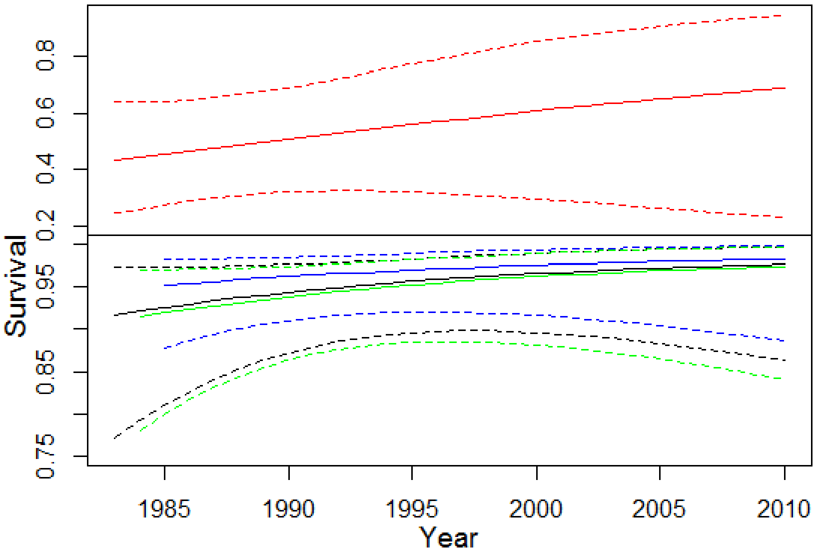

Figure 4.2. Estimates of survival rates (with 95% confidence intervals) for the Alderney gannet population, combined with adults ringed in the UK, with age classes a) pullus, b) 2nd year (green), 3rd year (blue) 4+years (black). Estimates are based on weighted averages from all models.

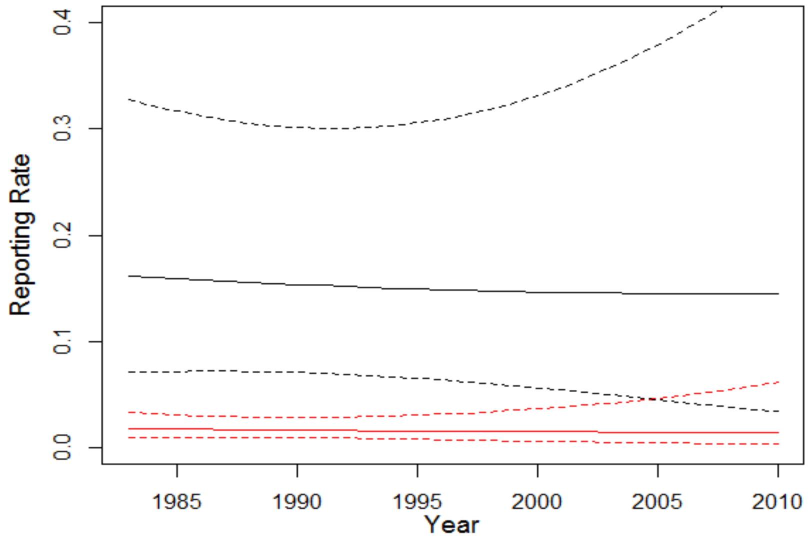

Figure 4.3. Estimates of reporting rates (with 95% confidence intervals) for the Alderney gannet population with age classes: first year (red), 2+yr (black). Estimates are based on weighted averages from all models.

Discussion

The high mean adult survival rate for Alderney's gannet population (combined with gannets ringed in the UK, 0.95) is consistent with high survival rates estimated for the UK and Ireland populations (0.92, Wanless *et al.* 2006). High adult survival rates are expected in seabirds, as they are long lived and slow to reach maturity (Bell 1980), traits which result in prioritising survival over reproduction in years when environmental conditions are poor (Pichegru *et al.* 2010). Although the model which most parsimoniously fitted the data was structured with 4 age classes for survival, survival rates for 2nd and 3rd year birds were very close to those of adult birds (Figure 4.3), and only first year birds showed a considerably lower rate of survival. This is consistent with previous studies of Northern gannets (Nelson 2002; Wanless *et al.* 2006) and possibly due to problems when learning how to feed themselves (Hamer 2002).

A linear increase in survival rate over time was found for all age groups. This is the most parsimonious explanation of the data and is consistent with recent increases (up to 2011 at least) in Alderney's gannet population (Bohan 2012), although increasing productivity could also play a role. Thus, despite being near the southern limit for the range of the Northern gannet, the population is continuing to grow, consistent with the global increase in populations of this species (BirdLife-International 2015). This reflects improving conditions for Northern gannets, most likely due to their propensity to feed on fisheries discards (Votier *et al.* 2013). However, seabirds are threatened by many anthropogenic activities (Croxall *et al.* 2012), such as fishing, climate change and offshore development, and threats will change throughout the life cycle of the bird. For example juveniles migrating to West Africa are likely to be impacted by industrial fisheries in this region (Gremillet *et al.* 2015), whereas adult birds are likely to be disproportionately affected by conditions further north and in the English Channel, where they return annually to breed.

Alderney's gannets forage in areas which overlap with 9 sites proposed for the development of marine renewable energy installations (Soanes *et al.* 2013), which may result in increased mortality for adult birds (Furness & Wanless 2014). Populations of long lived seabirds with high survival rates are especially impacted by increased adult mortality (Sæther & Bakke 2000), and minor declines in survival can result in major changes to population growth rate (Wanless *et al.* 2006). Alderney's population of Northern gannets may be particularly vulnerable to climate change due to their location towards the southern tip of the range for this species. It is predicted that northern hemisphere populations of any species which reside near their southern boundaries will be more strongly effected by climate change (Brown, Stevens & Kaufman 1996), as the environmental conditions for themselves and their prey become unsuitable. Nelson (1978) suggests that the southern limits of the breeding range for Northern gannets may be fixed by the abundance of principal prey items, although Hamer *et al.* (2007) suggest that the ability of gannets to consume a wide variety of prey may overcome this potential impact. Montevecchi (2012) observed starving gannet chicks in Newfoundland after sea temperatures were 4^{o}C higher than average and suggested the fish were distributed in deeper waters than usual and at depths which were unavailable to diving gannets. These previous studies identify the multiple threats to seabirds, which can operate across all life-history stages. Furthermore, the balance of these threats may vary between locations, which again highlights the need to estimate age-specific demographic rates for as many populations as possible.

Dead recovery analysis of seabirds can be problematic if the majority of birds are ringed as pullus, because this may create problems when estimating the reporting rate for adult birds (Francis 1995). In this instance we were able to partially overcome this by combining birds ringed in the UK as adults with pullus ringed on Alderney, although by using this method we do not know Alderney specific reporting rates for adult birds, which could introduce a source of error. Reporting rates were lower for first year birds than older birds. Northern gannets do not reach maturity until their 5th year, and until this time spend long periods at sea (Nelson 1978). First year birds from Alderney migrate south towards the Mediterranean and Africa (Veron 1988) often remaining in these areas into their second year in order to take advantage of the calmer waters and more easily handled prey (Nelson 2002). Fewer recoveries are expected from these areas with low human population density (Veron & Lawlor 2009), and the combination of this, and longer periods at sea are likely to explain the lower reporting rate for first year birds which is supported by previous findings for UK and Irish gannets (Wanless *et al.* 2006).

On top of this limitation, reporting rates for Alderney's gannets have declined in recent years which is also consistent with findings from the UK and Ireland (Wanless *et al.* 2006). The declining trend in reporting rates for both juvenile and adult birds results in challenges when estimating the impacts of anthropogenically-induced changes in the marine environment. Therefore it is imperative that a robust system is developed in order to obtain precise colony specific estimates of demographic rates for Northern gannets, particularly for adults. Currently the high levels of uncertainty surrounding the survival estimates for recent years, due to lower rates of recovery (Wanless *et al.* 2006), results in demographic analysis of ringing data that may not necessarily reflect current conditions in their environment. This is because the time lag between real-time changes in demographic rates and results from population modelling may result in the detection of changes years after they occur in the population (Beissinger & Westphal 1998). Wanless *et al.* (2006)

conclude that it is necessary to ring more adult gannets in order to gain more accurate, colony specific survival estimates, and Furness & Wanless (2014) recommend a large-scale colour-ringing programme be initiated immediately in order to thoroughly assess the impacts to gannet populations from offshore windfarms. The lack of adult data from our study supports this move. Not only will this overcome the problem when calculating reporting rates for adult birds, but colour ringing adults will increase the precision of estimates for more recent years, reducing the lag phase, and enable combined live-dead survival analysis.

Our study is the first to provide any demographic parameters for Alderney's population of Northern gannets. If survival of both juveniles and adults is maintained, then the population is likely to continue to grow. However despite the considerable efforts in both ringing and recovery, estimates of survival have large confidence intervals and there are limitations surrounding our understanding of adult survival. Further data are still required in order to investigate threats to gannets throughout their life cycle, predict population trajectories in the presence of windfarms, or under different environmental conditions, and implement successful management strategies. Our study demonstrates that even substantial datasets, such as this one, require re-sightings, particularly of birds ringed or re-sighted as adults. This can be achieved relatively easily by the instigation of large-scale colour-ringing schemes of adult birds.

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Supporting Information

Table S4.1. Comparison of model performance in relation to the number of age classes in models to calculate the survival rate of Alderney's population of Northern gannets.

Number of age classes	AICc
1	8659.9
2	8630.9
3	8632.1
4	8628.9
5	8630.5
6+	8631.2

Table S4.2. All models that were averaged in order to calculate survival rates between 1983 and 2010 for Alderney's population of Northern gannets.

Model	QAICc	No. parameters	weight
$S_{age+Time}$, r_{age}	0	7	0.50
S_{age}, $r_{age+Time}$	1.44	7	0.24
$S_{age+Time}$, $r_{age*Time}$	3.24	9	0.1
$S_{age*Time}$, r_{age}	3.84	10	0.07
$S_{age*Time}$ $r_{age*Time}$	4.24	12	0.06
$S_{age*Time}$, $r_{age+Time}$	5.82	11	0.03
$S_{age+Time}$, $r_{age+Time}$	13.51	8	<0.01
S_{age}, $r_{age*Time}$	13.89	8	<0.01
S_{age}, r_{age}	15.40	6	<0.01
$S_{age+time}$, r_{age}	31.32	33	<0.01
$S_{age+time}$ $r_{age*Time}$	35.08	35	<0.01
$S_{age+Time}$, $r_{age+time}$	45.75	34	<0.01
S_{age}, $r_{age+time}$	46.77	33	<0.01
$S_{age*Time}$, $r_{age+time}$	49.10	37	<0.01
$S_{age+time}$, $r_{age+Time}$	49.51	34	<0.01
$S_{age+time}$, $r_{age+time}$	76.21	60	<0.01
$S_{age+Time}$ $r_{age*time}$	79.89	61	<0.01
$S_{age*Time}$, $r_{age*time}$	86.07	64	<0.01
S_{age}, $r_{age*time}$	94.53	60	<0.01
$S_{age+time}$, $r_{age*time}$	128.74	87	<0.01
$S_{age*time}$, $r_{age*Time}$	149.94	115	<0.01
$S_{age*time}$, r_{age}	150.98	113	<0.01
$S_{age*time}$ $r_{age+Time}$	155.60	114	<0.01
$S_{age*time}$, $r_{age+time}$	207.47	140	<0.01
$S_{age*time}$, $r_{age*time}$	247.35	167	<0.01

Chapter 5

Changes in behaviour drive inter-annual variability in the at-sea distribution of Northern gannets

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Abstract

The at-sea distribution of seabirds primarily depends on distance from their breeding colony, and the abundance, distribution and predictability of their prey, which are subject to strong spatial and temporal variation. Many seabirds have developed flexible foraging strategies to deal with this variation, such as increasing their foraging effort or switching to more predictable, less energy-dense, prey, in poor conditions. These responses may vary both within and between individuals, and understanding this variability is vital to predict the population-level impacts of spatially explicit environmental disturbances, such as offshore windfarms. We conducted a multi-year tracking study in order to investigate the inter-annual variation in the foraging behaviour and location of a population of Northern gannets breeding on Alderney in the English Channel. To do so, we investigated the link between individual-level behaviour and population-level behaviour. We found that a sample of gannets tracked in 2015 had longer trip durations, travelled further from the colony and had larger core foraging areas and home range areas than gannets tracked in previous years. This inter-annual variation may be associated with oceanographic conditions indexed by the North Atlantic Oscillation (NAO). Our findings suggest that this inter-annual variation was driven by individuals visiting larger areas in all of their trips rather than individuals diversifying to visit more, distinct areas. These findings suggest that, for gannets at least, if prey becomes less abundant or more widely distributed, more individuals may be required to forage further from the colony, thus increasing their likelihood of encountering pressures from spatially explicit anthropogenic disturbances.

Introduction

The distribution of seabirds in the marine environment is driven primarily by the abundance, distribution and predictability of their prey items (Hunt *et al.* 1999). Seabirds forage near predictable features with increased productivity, such as fronts and shelf edges (Hunt *et al.* 1999) and where prey is aggregated by bathymetric features (Yen, Sydeman & Hyrenbach 2004). Within these large-scale features, the distribution of prey items can be patchy (Fauchald, Erikstad & Skarsfjord 2000) and subject to strong spatial and temporal variation (Shealer, Schreiber & Burger 2002; Fauchald & Tveraa 2006), primarily as a result of fluctuations in oceanographic conditions (Hunt Jr & Schneider 1987; Chavez *et al.* 2003; Burke & Montevecchi 2009).

It is widely accepted that seabirds have developed flexible foraging strategies as a mechanism with which to respond to seasonal and/or annual variation in the abundance and distribution of prey (Weimerskirch *et al.* 2005). For example, in response to poor prey availability, seabirds may exploit more predictable prey types, lower in energetic-value (Wanless *et al.* 2005), or they may increase foraging effort (Monaghan *et al.* 1994). This may vary through alterations to the time budget of the birds while at-sea (Ronconi & Burger 2008), or to the duration or range of foraging trips (Monaghan *et al.* 1994; Uttley *et al.* 1994; Garthe, Montevecchi & Davoren 2011). However, this variability in foraging behaviour can have consequences for reproductive success and, thus, variation in productivity is linked to oceanographic variability (Becker, Peery & Beissinger 2007). This is because seabirds are central place foragers during the breeding season, constrained to return to the colony regularly throughout incubation and chick-rearing to incubate the egg and provision offspring. Thus, increased foraging trip duration may result in both parents undertaking simultaneous foraging trips, leaving eggs or chicks unattended at the nest and subject to attacks by predators or conspecifics (Lewis *et al.* 2004). Therefore, both energy limitation and predation or competition can have implications on reproductive success. Ultimately, as long-lived animals, seabirds will prioritise their own survival over that of their offspring, and abandon breeding attempts when prey availability is very low (Ponchon *et al.* 2014).

While research efforts have focussed on linking variation in oceanographic conditions to productivity at the population level, the role of intra- and inter-individual variation in behaviour has received little attention (Wakefield *et al.* 2015). Indeed, in most cases variation amongst individuals in the population has been overlooked, under the classical assumption that individuals in a population behave in similar ways. Yet variation in foraging behaviour can occur both within and between individuals (e.g. Kato *et al.* 2000; Barlow & Croxall 2002; Woo *et al.* 2008). However, few studies have looked at how intra- and inter-individual variation differs between years, and what the consequences of this may be at a population level.

Low inter-individual variation in trip duration or foraging area may occur because prey are concentrated in particular areas, attracting all individuals in a population, or may be because prey are sparsely distributed, and all individuals in the population have large searching areas i.e. all individuals are going everywhere. Alternatively, high inter-individual variation suggests that prey are abundant and patchy in their distribution and individuals can target different patches. Thus, inter-annual variation in both the abundance and distribution of prey, might lead to variation in inter-individual variability in foraging location. Additionally, intra-individual consistency in foraging locations of seabirds has been observed at various temporal scales across months and years in some individuals, yet others show high intra-individual variability (Ceia & Ramos 2015; Wakefield *et al.* 2015). These diverging strategies suggest that some individuals in a population may have greater specialisation with regards to diet and habitat use than others (Bearhop *et al.* 2006). This inter-individual variation is essential to consider when tracking studies are used to identify important areas for conservation, because often only a small proportion of the population is tracked, and few studies take into account how well the sampled individuals represent the foraging locations of the entire population (Soanes *et al.* 2013a). However, by using what we know about the size and location of the foraging areas of tracked birds, it is possible to incorporate this limitation, and predict the size of foraging areas used by the entire population (Soanes *et al.* 2013a).

Consistency in foraging locations as a result of individual dietary and habitat specialisation has been observed in Northern gannets *Morus bassanus* (Patrick *et al.* 2014; Wakefield *et al.* 2015). This challenges their traditional classification as generalist predators that feed on a variety of pelagic fish and fisheries discards (Nelson 1978; Votier *et al.* 2010). Additionally, Northern gannets, and congeneric populations, show inter-annual variation in foraging behaviour and reproductive success as a result of sea temperature, primary productivity and the type and abundance of prey (Montevecchi 2007; Garthe, Montevecchi & Davoren 2011; Angel *et al.* 2015). However, most studies overlook the link between this individual consistency and inter-annual variation. This is important because while Northern gannet populations are increasing at an average of 3% per year across the UK and Ireland (Wanless *et al.* 2006), they have high conservation importance due to their restricted ranges, with 75% of the world's population breeding in Europe (Gremillet *et al.* 2006). Consequently, there is concern that populations may be impacted by anthropogenic pressures such as prey exploitation by fisheries (Gremillet *et al.* 2015), changes in the bycatch policy (Votier *et al.* 2013) or the installation of windfarms (Furness, Wade & Masden 2013). To understand how gannets are going to be affected by these pressures a better understanding of inter-annual variation in foraging behaviour at both the individual and the population level is required. Many of these pressures are spatially explicit, and thus if in years of low prey availability, all individuals in the population visit larger areas, then all individuals are likely to have an increased risk of interacting with these pressures. Conversely, if inter-annual variation in foraging behaviour is driven by individual birds visiting different areas, then spatial pressures may have differential effects on individuals in the population.

Here we use four years of tracking data to investigate the inter-annual variation in the foraging behaviour and space-use by a population of Northern gannets breeding on Alderney, Channel Islands. Alderney's population may be particularly vulnerable due to its position near the southern limit of the species range (Brown, Stevens & Kaufman 1996), the overlap in home range with offshore developments (Soanes *et al.* 2013b), and the limitation in extending its range due to competition from conspecifics in nearby colonies (Wakefield *et al.* 2013). We investigate the link between individual-level and population level behaviour. Specifically, we determined whether in years when the population has a larger foraging area, if this is driven by individual birds diversifying to visit more distinct areas (e.g. Figure 5.1d), or by each bird increasing its own foraging area (e.g. Figure 5.1b).

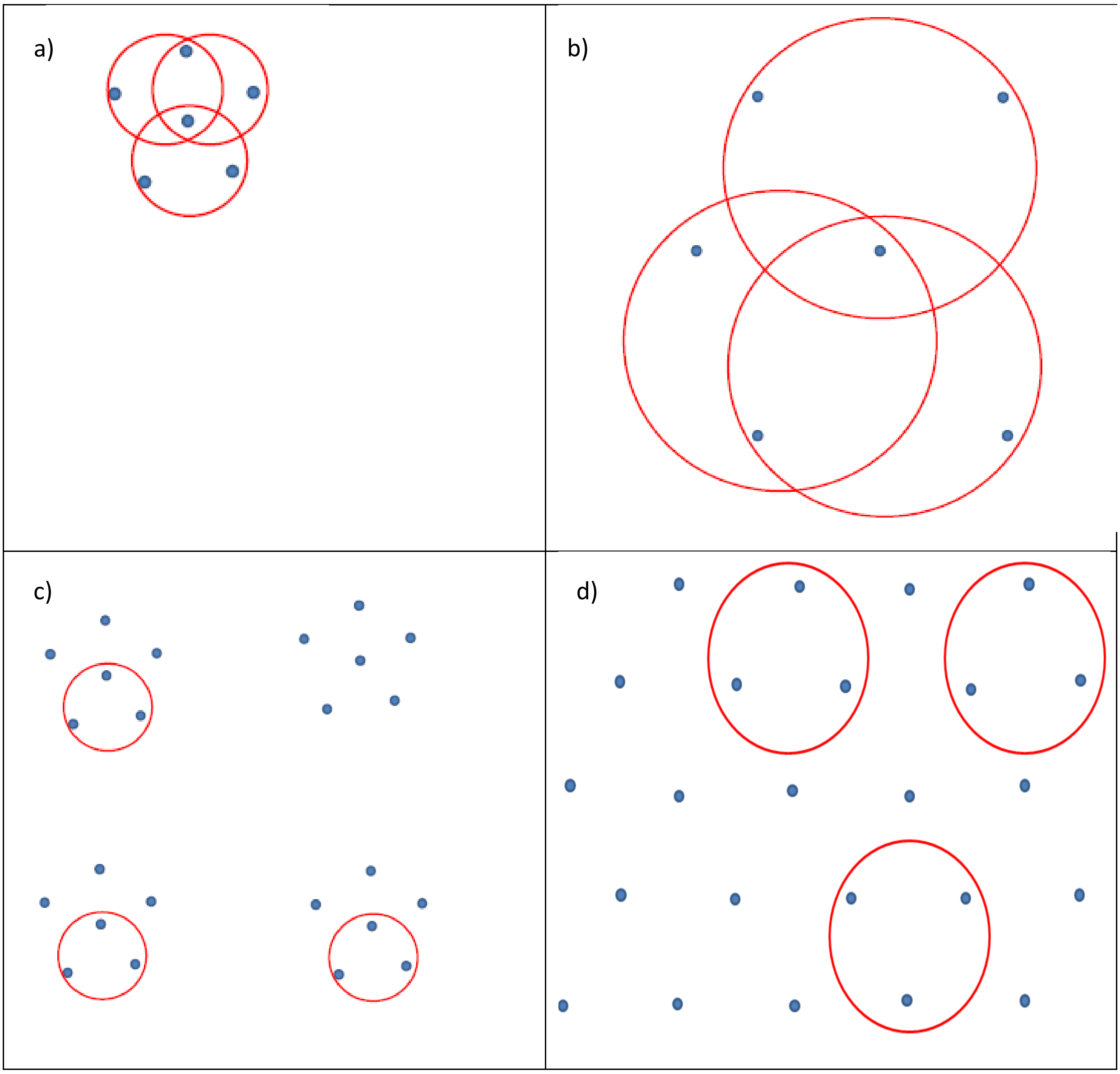

Figure 5.1. Four hypothetical scenarios to describe the distribution of prey (blue dots), and the foraging location of seabirds (red circles); a) Low resource + high patchiness = small foraging area and high inter-individual overlap, b) low resource + low patchiness = large foraging area and high inter-individual overlap, c) high resource + high patchiness = small foraging area and small inter-individual overlap, d) high resource and low patchiness = large foraging area and small inter-individual overlap.

Methods

Data collection

Fieldwork was conducted at the breeding colony of Northern gannets on Les Etacs, Alderney (49^{o}42'N, 2^{o}14'W) during the early chick rearing period in early June of 2011 and 2013 – 2015. All procedures were licensed by the States of Alderney. Birds with chicks approximately 2–4 weeks old were captured at their nest using a noose pole. GPS data recorders, logging positions every 2 minutes (IgotU GT-120 (2011), IgotU GT-600 (2013-2015), Mobile Action Technology), packaged in plastic heatshrink, were attached to the base of the tail using Tesa Extra Power tape. The devices weighed ~ 1% of the birds' body mass (22 g or 33 g). Loggers were removed 2 to 3 weeks later and birds not recaptured would have lost their devices within approximately one month (pers obs). Devices of 1 % body mass have previously been shown to have no effect on foraging duration, breeding success or body condition in Northern gannets (Hamer *et al.* 2000).

Breeding success was monitored at the colony in 2013-15. At the start of the chick-hatching period five plots were designated, each containing 50 Apparently Occupied Sites (AOSs), and the number and age of the chicks were recorded every 7-10 days throughout the breeding season. The number of chicks which fledged in each plot were divided by 50 and averaged across the five plots in order to obtain a value of chicks fledged per pair for the colony. Due to the inaccessibility of the colony these productivity counts were conducted via a telescope from the main island of Alderney, thus only nests on the edge of the colony could be observed, probably resulting in a biased sample of newer, less successful breeders (Nelson 2002). Consequently, estimates of fledging success obtained in the present study may not be comparable to those obtained elsewhere. However, this potential bias should remain consistent between years, allowing for inter-annual comparisons.

Data processing and analysis

GPS positions were interpolated to every 10 s using the *adehabitatLT* package (Calenge 2006) in R (R Core team 2013) to account for occasional missing data associated with diving behaviour or missed GPS locations, which would result in a value of zero when calculating time-in-area, and thus exclude cells which the bird must have passed through, yet which no data was recorded. The colony was defined as Les Etacs rocks with a 30 m surrounding buffer, based on personal observations of gannet behaviour, and for each bird, each trip was defined as all points between leaving and returning to this area. Trip characteristics including: duration (hours); trip length (total distance, km); maximum distance from the colony (km); and directness (trip length/maximum distance from the colony) were calculated for all trips, independent of the gannet ID. Directness is a measure of deviation from a straight line, with a value of 2 representing direct movement between the colony and furthest point, and anything above this representing a less direct track. A frequency histogram of trip duration showed a clear bimodal distribution. One mode represented trips up to 40 minutes in duration, whereas the second mode represented trips lasting many hours. Foraging trips were, therefore, defined as any trip over 40 minutes in duration to discount birds loafing adjacent to the colony, or short periods of flight following disturbance at the colony.

General linear mixed effects models were used in package *nlme* (Pinheiro *et al.* 2016) to identify inter-annual variation in trip characteristics. Year was the fixed effect and individuals were included as random effects to account for pseudo-replication. Diagnostic plots were carried out and all model assumptions were met. *Post hoc* Tukey tests were conducted in package *multcomp* (Hothorn, Bretz & Westfall 2008) to identify between which years differences lay, and least squared means were calculated using package *lsmeans* (Lenth 2016) to calculate annual mean values of all trip characteristics. The R package *Trip* (Sumner 2011) was used to calculate the proportion of time spent (s) in each 5 × 5 km cell of a pre-defined grid around the colony for each bird for each year, and averaged across the birds. Warwick-Evans *et al.* (2015) demonstrate that this was the most efficient scale to capture the search behaviour of this population of northern gannets. The cells used were ranked in order of time spent and the top 95% were defined as the Home Range Area (HRA) and the top 50% the Core Foraging Area (CFA). Subsequently, time spent in each 5 × 5 km grid cell was calculated each year for all of the tracked birds combined (i.e. not calculated independently for each bird) and the CFA and

HRA were plotted in ArcGIS (ArcGIS ver.10.2). Time spent in each grid cell can be used as a proxy for foraging behaviour, because individuals of this species spend more time in areas with increased foraging activity (Warwick-Evans *et al.* 2015).

In order to calculate how well the individuals that we tracked represented the HRA and CFA of the entire population in a specific year, we followed the methodology devised by Soanes *et al.* (2013a). For each year independently, the HRA and CFA were calculated initially for one individual and subsequently for an increasing number of individuals. The individuals included in each calculation were sampled at random from all of the tracked birds, until the total number of gannets tracked that year had been sampled. This data was then bootstrapped 10,000 times using R package *boot* (Canty & Ripley 2014) to determine the mean values of CFA and HRA. These data were then fitted to the Michaelis-Menten model as per Soanes *et al.* (2013a). This allowed us to extract the asymptotic value of the y axis (a) i.e. the size of the CFA/HRA predicted for the entire population, and the value at which half of the maximum response is attained (b) i.e. the number of individuals necessary to sample in order to reach half of the CFA/HRA for the entire population (Figure 5.2).

Michaelis –Menten: $y = a*x / (b + x)$

These values were then used to extrapolate the CFA and HRA for the entire population of approximately 10,000 birds breeding on Alderney, for that specific year. We then calculated the proportion of the population level CFA and HRA that was represented by our sample of gannets for each year independently. Subsequently, this approach was modified in order to determine how well the trips we sampled from each individual represented the entire foraging area for that individual, and thus how consistent each individual was between trips. This was done by calculating the HRA and CFA for one trip, and subsequently for an increasing number of trips, and following the bootstrapping and model fitting approach described above. In 2011 only four individuals recorded three or more trips, thus the Michaelis-Menten equation could only be fitted for these four

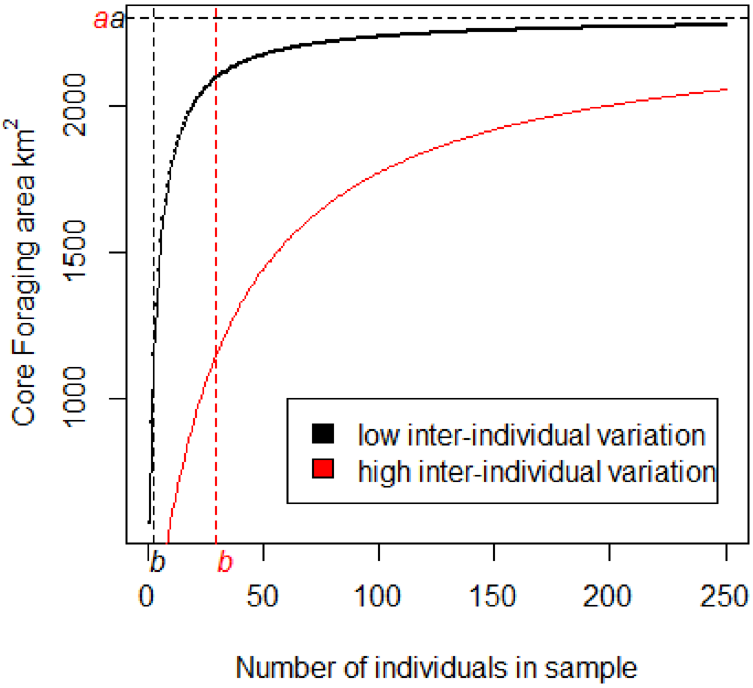

Figure 5.2. A hypothetical relationship between the number of individuals sampled and the size of the core foraging area for seabirds showing high and low inter-individual variation in core foraging area locations.

individuals, and conclusions about consistency within individuals in 2011 should be interpreted cautiously. In order to measure the overlap in space-use between individuals, the number of birds that used each 5 × 5 km grid cell within a single year was calculated. Subsequently, in order to measure overlap in space-use between years, the number of years that each 5 × 5 km grid cell was used was calculated. Additionally for each pairwise combination of two years, and in both directions, the proportion of cells that were used in the mean HRA and CFA in year X that were also used in year Y was calculated in order to investigate the sample overlap in foraging locations between specific years. Given that the sample of the population we tracked did not represent the entire population, we calculated the population overlap using the equation

Population overlap = $O * 100 / S_{Y2}$

Where O is the sample overlap (%) and S_{Y2} is the percentage of the total predicted HRA or CFA in our second year sample (See Supporting Information). This calculation assumes that for both CFA and HRA areas which are visited but not observed are as likely to have been visited as those which have been visited and observed, i.e. detection rate is equal in overlapping, and non-overlapping cells.

Foraging habitats of Northern gannets have previously been linked to chlorophyll a, sea-surface temperature, bathymetry and copepod abundance (Hamer *et al.* 2000; Votier *et al.* 2010; Scott *et al.* 2013). Thus, further evidence to support these links are not addressed in this study. Additionally, this study deals with predicted population metrics, and thus an index of oceanographic conditions at a larger scale is more relevant. Thus, the association between inter-annual variation in foraging effort, and oceanographic conditions can be investigated using the North Atlantic Oscillation (NAO, downloaded from www.cgd.ucar.edu/cas) as an index of annual oceanographic conditions. The NAO is a climatic event where fluctuations in atmospheric pressure at sea level result in warmer, wetter and windier climates (Hurrell 1995), with warmer sea temperatures (Sims *et al.* 2001) in years with a high NAO index. Warmer sea temperatures influence the type and abundance of fish communities (Planque & Taylor 1998; O'Brien *et al.* 2000), which in turn influence the foraging behaviour of seabirds (Garthe, Montevecchi & Davoren 2011). Additionally, years of high NAO have been associated with lower overwintering survival (Votier *et al.* 2005) and breeding performance of seabirds (Thompson & Ollason 2001).

Results

Northern gannets tracked on Alderney between 2011 and 2015 consistently foraged within the English Channel, though were also recorded, on occasion, in the North Sea (Figure 5.3). Mean trip duration ranged from 17 hrs in 2011 to 27 hrs in 2015, corresponding with mean length of 330 km and 470 km, and mean maximum distance from the colony of 105 km to 135 km, respectively.

Inter-annual variation in foraging areas

Both the Core Foraging Areas (CFA) and the Home Range Areas (HRA) of tracked gannets varied between years (Figure 5.3). While commonly used areas around the North coast of France in the CFA and around Alderney in the HRA were observed in multiple years, sampled birds used relatively few areas consistently in all four years of study, especially in terms of CFA (Figure 5.4). Scaling these samples up to population level predictions also revealed differences between years in the extent of predicted CFA and HRA (Table 5.1). Predicted CFA was greater in 2015 than 2011, 2013, and 2014, respectively, with an increase in size of 30% from smallest to largest. Similarly the predicted HRA was greater in 2015 than 2013, 2014 and 2011, respectively, with an increase in size of 60% from smallest to largest (Table 5.1).

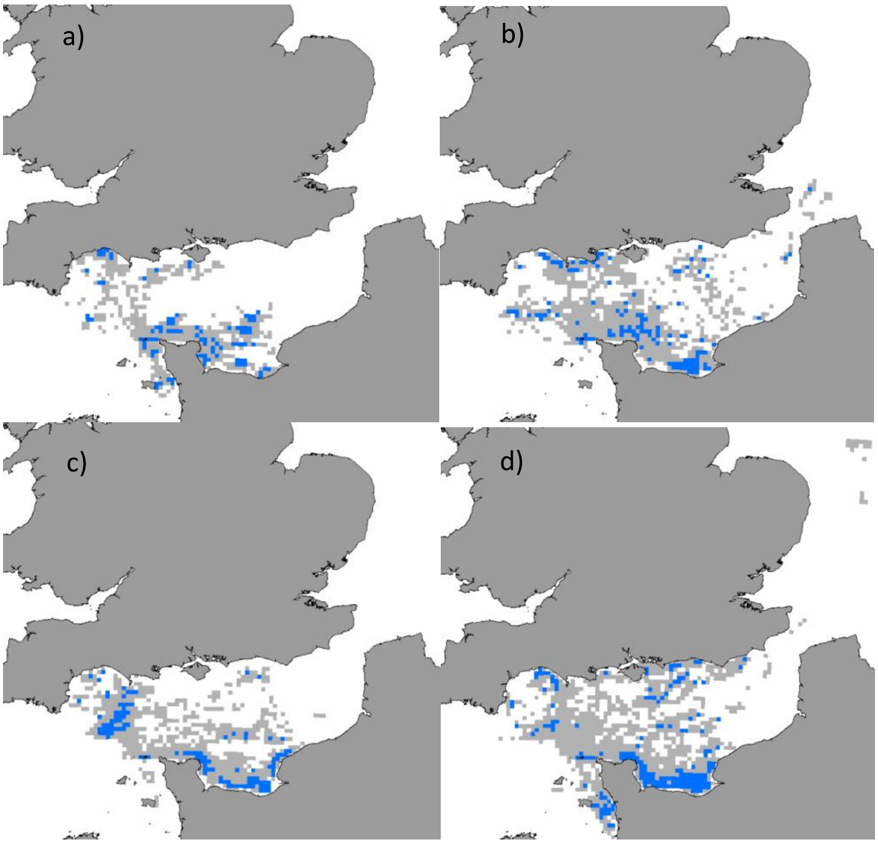

Figure 5.3. The proportion of time spent in the CFA (blue cells) and HRA (grey cells) of a sample of Northern gannets breeding on Alderney, Channel Islands in a) 2011, b) 2013, c) 2014, d) 2015. This approach combines the data from all birds in order to calculate the time-in area for each year.

A similar pattern was seen in terms of population and sample overlap in the number of grid cells used in different years. For CFA, 2015 encompassed a greater proportion of cells than the other three years (Table 5.2). More dramatically, HRA in 2015 was predicted to encompass all of the cells also predicted to be used by the birds in 2014 and 2011, and nearly all of those used in 2013 (Table 5.3). A value of > 100% was calculated for the population overlap as a result of the slight discrepancies when extrapolating up from the sample overlap. The value of *b* from the Michaelis-Menten equation, which indicates how similar birds are to each other in their foraging areas, also varied between years (Table 5.1). Birds from 2015 were the most similar to each other (lowest value of *b*) for both CFA and HRA and in 2011 were the most different.

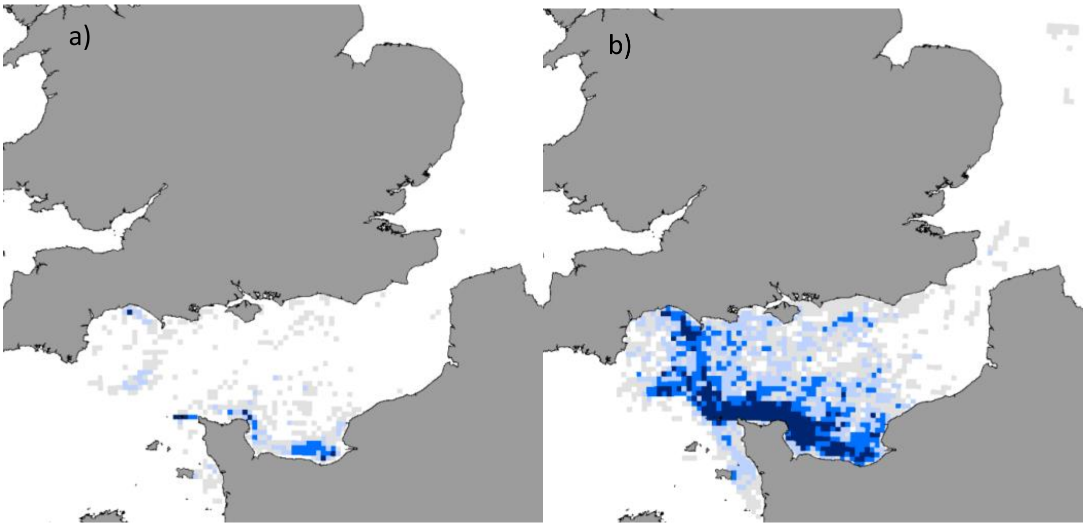

Figure 5.4. Overlap of a) CFA and b) HRA cells used by the tracked sample of Northern gannets breeding on Alderney in 1 (grey), 2 (pale blue), 3 (mid blue) or all 4 (dark blue) years.

Table 5.1. A tracked sample of Northern gannets and indices to measure how well the sample each year represents the HRA and the CFA of the entire population (~10,000 birds). *a* is the asymptote value (i.e. the predicted size of the CFA/HRA for the entire population), *b* is the value of *x* (i.e. the number of individuals) at which half of the maximum response is attained and both are derived from the Michaelis-Menten equation. P is productivity, and the NAO index for June each year is also shown

Year	Sample size	Number of trips recorded per bird	CFA *a*	HRA *a*	CFA *b*	HRA *b*	CFA Km^2	HRA Km^2	Prop. of total CFA sampled	Prop. of total HRA sampled	No. of individuals needed to represent 95% of CFA	No. of individuals needed to represent 95% of HRA	P	NAO June
2011	17	2.2	6987	21871	35.7	14.4	2254	11823	0.32	0.54	633	267	na	-1.15
	10000						6962	21840						
2013	15	4.8	6175	30010	14.8	8.5	3103	19126	0.50	0.63	274	160	0.51	0.59
	10000						6166	29989						
2014	13	6.4	5455	25647	11.7	8.2	2874	15683	0.53	0.61	217	155	0.61	-0.58
	10000						5449	25627						
2015	15	6.4	7026	34830	10.2	6.9	4287	24296	0.61	0.70	191	130	0.48	0.17
	10000						7019	34803						

Table 5.2. Inter- annual population (and sample) overlap (%) in the 5 km by 5 km grid cells used in the Core Foraging Area of a population of Northern gannets breeding on Alderney, Channel Islands

	2011	2013	2014	2015
2011	X	37 (18)	28 (15)	49 (30)
2013	42 (13)	X	46 (24)	54 (33)
2014	39 (12)	55 (28)	X	72 (44)
2015	49 (16)	47 (24)	52 (28)	X

Table 5.3. Inter-annual population (and sample) overlap (%) in the 5 km by 5 km grid cells used in the Home Range Area of a population of Northern gannets breeding on Alderney, Channel Islands

	2011	2013	2014	2015
2011	X	96 (60)	90(55)	102(71)
2013	70 (38)	X	80(49)	92(64)
2014	78 (42)	95 (60)	X	106(74)
2015	64 (35)	80(51)	77(47)	X

Inter-annual variation in foraging trip characteristics

We found strong evidence of inter-annual variation in trip duration, trip length, maximum distance from the colony, core foraging area, and home range area from the tracked gannets (Figure 5.5). In addition there was weak evidence of inter-annual variation in the directness of foraging trips (Figure 5.5). Broadly speaking, trips in 2015 were longer in duration, distance travelled, maximum distance from the colony, directness, and birds had larger CFA and HRA than 2013, 2014 and 2011 respectively. Correspondingly, the June NAO index was negative in 2011 and 2014, and positive in 2013 and 2015, also coinciding with lower reproductive success in 2013 and 2015 (Table 5.1).

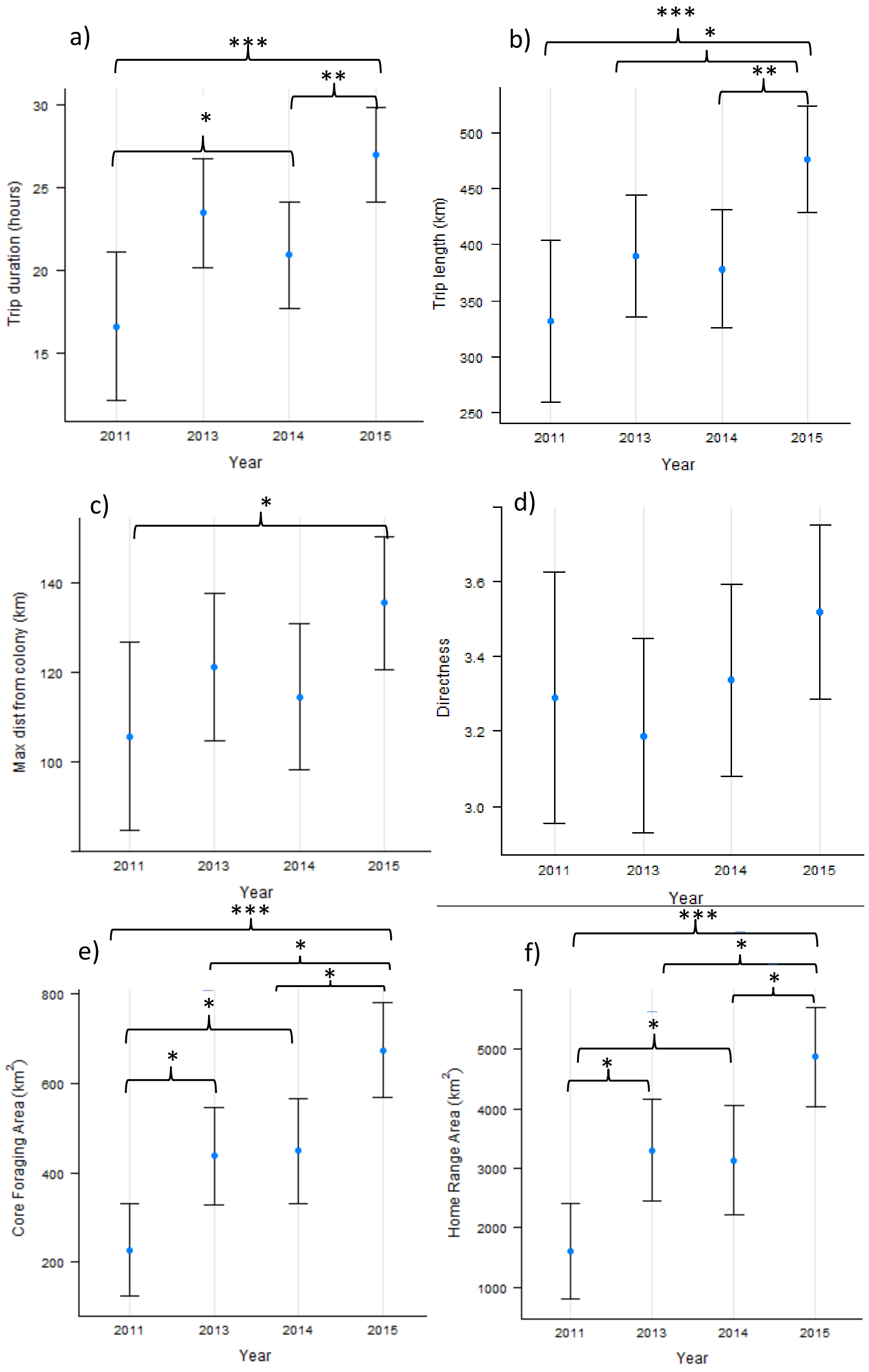

Figure 5.5. Inter-annual variation in the least squares mean (± standard errors) values for a) trip duration (T_{283} = 3.85 p < 0.001), b) trip length (T_{283} = 3.83 p < 0.001), c) maximum distance from the colony (T_{283} = 2.71 p < 0.01), d) directness (T_{283} = 1.86 p = 0.06) e) Core Foraging Area (T_{60}=5.7 p<0.001) f) Home Range Area (T_{60}=5.2 p<0.001) from a sample of Northern gannets breeding on Alderney, Channel Islands. Brackets indicate significant differences between the end points of each bracket. Asterisks indicate significance level: * 0.05, ** 0.01, *** 0.001.

The sample CFAs and HRAs of individual tracked birds overlapped with each other more often in 2015 than in 2011, with 2013 and 2014 having intermediate amounts of inter-individual overlap (Tables 5.4 and 5.5). The greater sample size in 2015 may have resulted in a higher overlap than in 2011, when fewer trips were sampled. However, similar numbers of trips were sampled in 2014 and 2015, and a different degree of overlap was observed which suggests that these differences are not entirely down to the number of trips sampled. Additionally, there was inter-annual variation in the size of the predicted CFA for individual birds (Figure 5.6a), and the higher mean and larger error bars in 2015, suggest that the CFA for individual birds was larger with higher inter-individual variation in size than in previous years. The predicted HRA for individual birds was not significantly different between the years, however the large variation within years in these values suggests that the inter-individual variation in the size of HRA was also considerably higher in 2013 and 2015 (Figure 5.6b).

The number of trips necessary for a sample to represent half of both CFA and HRA for individual birds (*b*) predicted using the Michaelis-Menten equation did not vary significantly between the years, suggesting that between trips, individual birds were similarly consistent in their habitat use between years. However, the within year variation surrounding these values represents the inter-individual variation in consistency i.e. some birds were very consistent in their foraging locations, whereas others were more variable. This variation was also lowest in 2011 and 2014 which suggests there was smaller inter-individual variation in the consistency of the location of HRA of individuals in those years (Figure 5.6d).

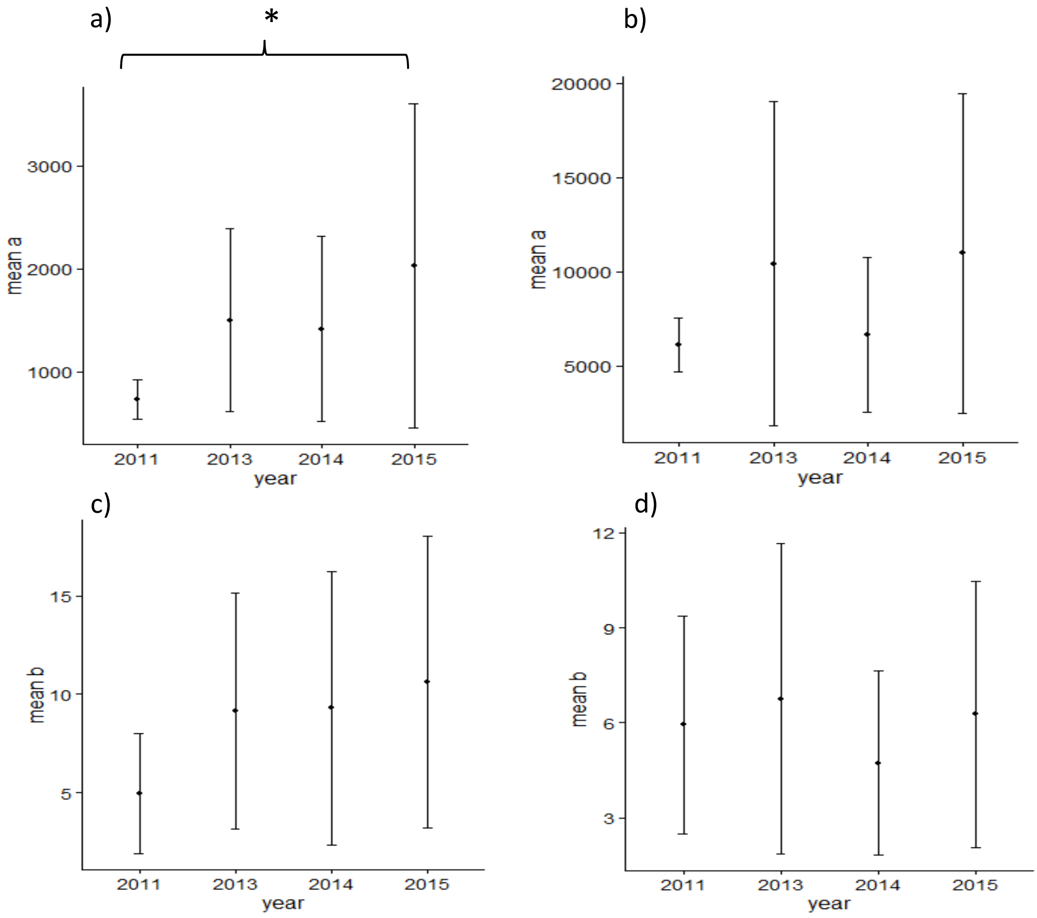

Figure 5.6. Mean size (value *a* from the Michaelis-Menten equation) of the a) Core Foraging Area (T_{42}=2.17 p=0.036) and b) Home Range Area (T_{42}=1.63 p=0.11) and the mean number of trips per individual (value *b* from the Michaelis-Menten equation) necessary in order to reach half of the c) Core Foraging Area (T_{42}=0.92 p=0.37), d) Home Range Area (T_{42}=0.12 p=0.90) for an individual bird, predicted using the Michaelis-Menten equation from a sample of tracked Northern gannets from Alderney, Channel islands. The brackets indicate significant differences between the two end points of each bracket. The Asterisks indicate levels of significance: * 0.05, ** 0.01, *** 0.001.

Table 5.4. The overlap between individuals in the number of 5 km by 5 km grid cells used in the Core Foraging Area for Northern gannets tracked from Alderney, Channel Islands in a single year

	Number of cells used by n birds					
Year	1	2	3	4	5	6
2011	124	14	1	0	0	0
2013	195	25	4	0	0	1
2014	175	18	5	2	0	0
2015	273	45	16	4	1	0

Table 5.5. The overlap between individuals in the number of 5 km by 5 km grid cells used in Home Range Area for Northern gannets tracked from Alderney, Channel Islands in a single year

	Number of cells used by n birds															
Year	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16
2011	391	134	52	23	7	10	5	4	0	1	0	0	0	0	0	1
2013	575	293	89	60	24	11	6	2	2	0	2	1	0	1	0	0
2014	490	193	81	43	26	11	7	3	5	1	0	0	1	0	0	0
2015	694	358	185	83	30	27	21	11	13	8	4	0	0	0	1	1

Discussion

Seabirds are known to exhibit inter-annual variation in foraging behaviour at the population level, and intra- and inter- individual flexibility, however, few studies link the two. We show strong evidence of inter-annual variation in the size and location of Core Foraging Areas and in foraging trip characteristics recorded from a sample of Northern gannets breeding on Alderney, Channel Islands. Gannets tracked in 2015 undertook trips with a longer duration, length and maximum distance from the colony as well as larger CFA and HRA than those recorded in other years. This corresponded with a lower breeding success than previously recorded. This large foraging range in 2015 combined with the largest overlap of HRA and CFA between individuals suggests that all individuals travelled extensively in search of prey. Thus inter-annual variation in the size of the foraging area for the entire population is driven by individual birds visiting larger areas in all of their trips, not by individual birds diversifying to visit more, different areas.

Inter-annual variation in foraging areas and trip characteristics

Variation in physical oceanographic processes can alter the distributions of plankton and fish and, thus, prey availability to seabirds (Shealer, Schreiber & Burger 2002) resulting in inter-annual variation in foraging locations for many species (Burke & Montevecchi 2009). Seabirds have developed a flexible foraging strategy as a mechanism with which to deal with this spatial and temporal variation in prey distribution (Weimerskirch *et al.* 2005; Montevecchi *et al.* 2009) and the inter-annual variation in foraging areas and trip characteristics of Alderney's Northern gannets may be explained by this.

Reduced prey availability can result in longer foraging trip duration, range and core foraging area in seabirds (Monaghan *et al.* 1994; Suryan, Irons & Benson 2000). Thus, the longer foraging trips and larger CFAs from gannets tracked in 2015 than those tracked in 2011 and 2014, may be due to lower prey availability as a result of oceanographic conditions (Burke & Montevecchi 2009). The June NAO index in 2013 and 2015 was higher than in 2011 and 2014 (Table 5.1), which is consistent with years of increased trip duration and range. This suggests that the NAO might be influencing the type and abundance of prey and, thus, seabird foraging behaviour in the English Channel. Northern gannets have been observed to travel further with a larger home range in years where larger pelagic fish were more abundant than small fish (Garthe, Montevecchi & Davoren 2011), potentially explaining the larger CFA and HRA in 2015 when the NAO index was high. However, the NAO index was even higher in 2013, and although trip duration was longer and CFA and HRA were larger than in 2011 and 2014 when the NAO indexes were negative, they were not as extreme as in 2015; this suggests other factors were also involved, which we could not evaluate within the scope of our study.

The combination of the increased foraging range and large overlap of HRA and CFA between individuals in 2015 implies that all individuals had large searching areas i.e. all birds were going everywhere in search of prey, rather than to consistent individual-specific foraging areas. This suggests that prey was widespread and thinly dispersed, which is consistent with the less direct path between the colony and foraging areas observed in that year. Gannets showed the most direct path between the colony and the foraging areas in 2013, suggesting that prey may have been in more predictable locations in that year (Pettex *et al.* 2010). Trip duration was higher and CFA and HRA smaller in 2013, than in 2011 and 2014 and this, combined with a more direct commuting path, suggests that gannets were foraging in more predictable locations, further from the colony in 2013. However, the directness of foraging trips may also be related to other behaviours, such as wind direction (Gremillet *et al.* 2004), or following fishing vessels (Votier *et al.* 2010), or conspecifics (Buckley 1997). The lower HRA combined with fairly direct trips and shorter trip durations in 2011 and 2014 suggest that birds were foraging at predictable locations closer to the colony in these years.

Breeding success was also lower in 2013 and 2015 than in 2014, and may be a result of the increased foraging trip duration in those years. If adults have had to travel further from the colony in order to forage, they may have failed to return with sufficient food for chick provisioning (Baird 1990), or at a sufficient rate in order to maximise reproductive success (Suryan *et al.* 2002). Additionally, chicks left unattended at the colony are open to attacks by predators or conspecifics (Lewis *et al.* 2004). Trip duration is directly related to foraging range in seabirds (Weimerskirch 2007), thus explaining the increased trip length, and maximum distance from the colony in years with a longer trip duration.

In general, there was little overlap in the locations of sampled CFA between years, with only 8 of the 5 km by 5 km cells being used in all four years. This suggests that the distribution of prey varied between the years. However, the 5 km x 5 km cells used for these analyses are small in comparison with the scale of some Area Restricted Search (ARS) behaviour observed in gannets (Hamer *et al.* 2009), thus overlap in foraging location at these larger scales is omitted. However, a previous study of the foraging behaviour of Alderney's gannets found that this was the most efficient scale to capture their search behaviour (Warwick-Evans *et al.* 2015). Furthermore we know that our sample under-represents the population CFA and HRA, and that sample overlap is thus lower than population overlap (Tables 5.2 & 5.3). Thus, we can assume that more cells are actually visited in multiple years.

Overlap in HRA between the years was much larger, as birds tended to commute along similar paths to reach foraging areas, particularly towards Northern France, and South West UK where foraging occurred in all 4 years. In fact, sampled birds in 2015 used all of the HRA cells used in 2011 and 2014, and most of those used in 2013. This is further evidence that it was necessary for these gannets to travel further in order to forage in 2015, and thus prey items were more widely dispersed.

Intra- and inter-individual variation

The value of *b* from the Michaelis-Menten equation can inform us of the number of trips necessary to sample from an individual in order to represent half of its entire CFA or HRA (Soanes *et al.* 2013a). Thus, it can be used to describe intra-individual variation, or consistency, in the location of CFA and HRA. For example, if the entire CFA or HRA of an individual could be determined from just one trip then the value of *b* would be low, and intra-individual variation, in terms of the location of CFA or HRA, would be low, thus consistency would be high. Gannets tracked on Alderney in 2011 required fewer trips to be tracked in order to represent half of the CFA of individual birds than in subsequent years i.e. these birds displayed lower intra-individual variation (higher consistency) in the location of the CFA of individual trips than those tracked in later years (Figure 5.6c). However, these results were not significant, probably due to the low sample size of individuals with multiple trips recorded in this year. The values of *b*, in terms of CFA, were similar amongst the subsequent three years, and thus inter-annual variation in this intra-individual variation cannot be confirmed. The low inter-annual variation in *b* in terms of HRA illustrates that intra-individual variation in the location of the HRA was similar between years. However, the variability in this value, described by the error-bars, was considerably larger in 2013 and 2015, than 2011 and 2014, demonstrating higher inter-individual variation in their intra-individual variation in 2013 and 2015.

The value of *b* from the Michaelis-Menten equation can also inform us of the number of individuals necessary to sample from a population in order to represent half of the entire CFA or HRA for a population (Soanes *et al.* 2013a). Thus, it can be used to describe inter-individual variation in the location of CFAs and HRAs. Gannets tracked on Alderney in 2015 displayed lower inter-individual variation in the locations of CFAs and HRAs than in previous years, as described by the low b value (Table 5.1). Low levels of inter-individual variation in the location of CFAs suggest that either prey is concentrated in small areas, attracting all individuals (e.g. Figure 5.1a), or that prey is sparsely distributed and all individuals in the population have large searching areas. The low inter-individual variation observed in 2015, combined with the larger CFA strongly suggests that, of these two alternatives, this inter-individual variation was driven by individual birds visiting larger areas (Figure 5.1b). Combining this low inter-individual variation with the large overlap in CFA between sampled individuals in that year, we can suggest that the inter-annual variation in the size of the CFA for the entire population is also driven by individual birds visiting larger areas, and not by individual birds visiting more, different areas (Figure 5.1d).

Consistency in foraging locations within and between individuals has been shown in Northern gannets (Patrick *et al.* 2014; Wakefield *et al.* 2015) and other seabirds (Irons 1998; Weimerskirch 2007) and may be due to individual specialisation in diet (Bearhop *et al.* 2006; Woo *et al.* 2008; Patrick *et al.* 2014) or predictability of prey patches (Hamer *et al.* 2001; Weimerskirch 2007). However, this consistency is rarely considered at an inter-annual level, although Wakefield *et al.* (2015) demonstrated that gannets show intra-individual consistency in foraging areas across years, due to long term dietary specialisation, and site familiarity gained in early life. Our data suggest that in the more challenging foraging conditions of 2013 and 2015, more individuals in the population were generalist in terms of foraging locations, however this may be due to selecting different proportions of individuals with different foraging strategies, in terms of generalist or specialist, in different years.

Limitations and implications

Predictions from the Michaelis-Menten equation indicate that in no year did our sample of gannets fully represent either the HRA or CFA predicted for the entire population breeding on Alderney. This is likely to be the case in the majority of seabird tracking studies as devices can be costly, and logistics of getting to colonies may limit the frequency of fieldwork, which can result in only sampling a small proportion of the population. The relative importance of this limitation depends on the question being asked. If differences in the trip characteristics between groups, for example males and females (e.g. Cleasby *et al.* 2015), are being investigated then it could be assumed that under-representation of the entire population in terms of trip characteristics would not be biased in either direction, thus would not influence the conclusions. However, if the location of CFAs or HRAs is being explored then this can have important consequences, particularly if tracking studies are being used to identify important areas for conservation or marine spatial planning.

In this study, the number of birds necessary to track in order to represent the CFA for the entire population varied annually, as a result of differences, between years, in the inter- individual variation in the location of CFA. It would have been necessary to track many more birds in 2011 than in the subsequent years. However, only 2.4 trips per individual were recorded in 2011, considerably fewer than in subsequent years, and this supports the idea that gannets display intra-individual variation in foraging locations and highlights the importance of sampling multiple trips per individual (Soanes *et al.* 2013a). This inter-annual variation in the number of birds necessary to track to represent the CFA of the whole population was also observed in years where similar numbers of trips per individual were recorded (2013 - 2015). This indicates that inter-individual variation in the location of CFA differs between years, and should be an important consideration in tracking studies.

Gannets tracked in 2015 undertook foraging trips with a longer duration and length and a larger CFA and HRA than gannets tracked in previous years. These inter-annual differences in foraging behaviour are driven by differences in the intra- and inter- individual variation in foraging behaviour and location between the years, and may be associated with variation in oceanographic conditions, and a lower breeding success. Years with sparsely distributed or low abundance of prey, may become more frequent as a result of exploitation by commercial fisheries or climate change (Perry *et al*. 2005). This may result in increased trip duration, potentially leading to lower reproductive success through both energy limitation and predation or competition. Additionally, if core foraging areas and home range areas of individual birds increase, then more individuals are likely to encounter pressures from spatially variable anthropogenic disturbances, such as the development of windfarms. Indeed, gannets tracked in this study overlapped with windfarm sites less often in 2011 and 2014, than in 2013 and 2015 with 3, 15, 22 and 33 trips entering proposed development areas each year respectively (Warwick-Evans *et al*. unpublished data).

Furthermore, intra-specific competition from the large North Sea gannetries may limit the foraging range of Alderney's gannets (Wakefield *et al.* 2013). Interestingly, Alderneys gannets show consistency in their westward boundaries, most likely because the gannets from Les Sept Iles forage in the western English Channel (Gremillet *et al.* 2006), thus limiting the potential range of Alderney's gannets. If North Sea gannets limit the northern boundaries then Alderney's gannets may be forced to alter their time budgets or prey type in years of poor food availability. This may have negative impacts on reproductive success, as alternative prey items may have a lower energetic value, or altered time budgets may be more energetically costly.

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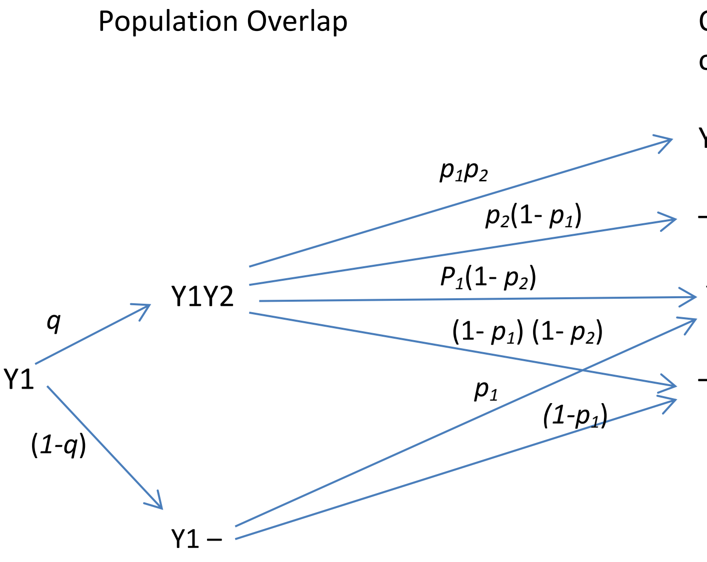
Supporting Information

The equation to calculate the overlap in cells used for the CFA/HRA between years, for the entire population is: Population overlap = O *100 / S_{Y2}, where O is the observed overlap (i.e. the % overlap in cells used for the CFA/HRA between years in our tracked birds) and S_{Y2} is the percentage of the total predicted CFA/HRA sampled in year 2. Y1 and Y2 represent year 1 and year 2 respectively. This equation was derived from a series of possible overlap scenarios: 1: If a cell was used in the CFA/HRA in year 1 and year 2 (Population overlap = Y1Y2) then the cell could be observed in year 1 and year 2 (Y1Y2), observed only in year 2 (– Y2), observed only in year 1 (Y1 –), or not observed at all (– –). Alternatively, if a cell was used in the CFA/HRA in year 1 but not in year 2 (population overlap = Y1 –) then the cell could be observed only in year 1 (Y1 –), or not observed at all (– –).

Let q be the probability that a cell that was visited in Y1 was also visited in Y2 (i.e. the population overlap), let p_1 be the probability of observing a cell that was visited in year 1, and p_2 be the probability of observing a cell that was visited in year 2 (i.e. the proportion of the total predicted HRA or CFA that was sampled). Then the probability of each outcome can be calculated as follows:



Observed overlap	Probability	Count
Y1 Y2	qp_1p_2	n_1
– Y2	$qp_2(1- p_1)$	n_2
Y1 –	$qP_1(1- p_2) + (1-q)\ p_1$	n_3
– –	$q(1- p_1)\ (1- p_2) + (1-q)\ (1- p_1)$	n_4

Thus, the proportion of cells observed in year 2 which overlap with cells observed in year 1

$= n_1/(n_1 + n_3)$ (i.e. the number of cells visited and observed divided by the total number of cells visited, whether or not they were observed), thus the percentage overlap (O) = $100*n_1/(n_1 + n_3)$. We know that $n_1 = nqp_1p_2$, where n is the total number of cells and that

$n_3 = n(qp_1(1- p_2) + (1-q)\, p_1)$

$= n(qp_1 - qp_1p_2 + P_1 - qp_1)$

$= n(p_1 - qp_1p_2)$

$= np_1(1-qp_2)$

Thus O = $100*nqp_1p_2 / (n(qp_1p_2 + p_1(1-qp_2)))$

$= 100*nqp_1p_2 / (np_1)$

$= 100*qp_2$,

so q = O/ $(100*p_2)$.

We know that $S_{Y2} = p_2* 100$

Thus population overlap (%) = O *100 / S_{Y2}.

Chapter 6

Predicting the impacts of marine spatial change on Northern gannets: An individual based model

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Summary

1. Individual Based Models (IBMs) are a powerful tool to predict the consequences of environmental change on animal populations and support evidence-based decision making for conservation planning.
2. In the UK marine environment there are increasing proposals for windfarm developments, and seabirds are a vulnerable group which may be at risk from these developments.
3. We developed a spatially-explicit IBM to investigate the potential impacts of the installation of windfarms in the English Channel and North Sea on body mass, productivity and mortality of a breeding population of Northern gannets for which we have tracking data.
4. A baseline model with no windfarms accurately represented the status of a sample of tracked gannets at the end of the 90 day chick-rearing period, and the behaviour-time budget was similar to that of tracked gannets.
5. Model simulations in the presence of windfarms indicated that installations should have little impact on the gannet population, when either avoidance behaviour or collision risk scenarios were simulated.
6. *Synthesis and applications. IBMs provide a robust approach to predict the impact of spatial change on seabirds. They are location-specific, thus can specifically take into account the cumulative impact of multiple disturbances within the home range area of a defined breeding population which has not been possible to do using existing methods. Our model can be adapted for other seabird populations or to predict the impacts from other types of spatial change in the marine environment.*

Introduction

The marine environment is under increasing pressure from anthropogenic activities such as overfishing, climate change and offshore developments (Halpern *et al.* 2012). Evidence-based decision making is the preferred approach when responding to such pressures (Solesbury 2001), but this may be challenging when there is little empirical evidence as to how the system will respond to environmental change (Botsford, Micheli & Hastings 2003). Predictive modelling can fill this gap and Individual Based Models (IBMs, Sutherland 1996; Grimm & Railsback 2013) are widely used in many disciplines to model complex systems, for example to predict the impacts of environmental change on shorebirds and seabirds (Stillman *et al.* 2003; West & Caldow 2006; Langton, Davies & Scott 2014). They differ from conventional models by modelling autonomous entities, and each individual’s behavioural and physiological traits determine the properties of the system, e.g. taking into account individual variation and an individual’s interaction with the environment (Grimm *et al.* 2006). For example, the functional response (relationship between intake rate and prey density) is often a key relationship underpinning IBMs, thus the individual’s behaviour is a result of its own decision-making which, in turn, is a result of its physiological state (Stillman 2008). IBMs provide a powerful approach to predict the consequences of environmental change in a variety of systems as the modelled individuals reflect real animal behaviour (Stillman 2008).

As anthropogenic pressures are largely spatially explicit, IBMs are appropriate to predict the impacts of environmental change in the marine environment, e.g. the development of windfarms. These installations may enhance the environment by creating *de facto* no fishing zones (Inger *et al.* 2009) but there is concern about the negative impacts they may have on Europe’s breeding seabirds (Garthe & Hupop 2004). These include indirect effects (exclusion from windfarm sites, barriers to movements), as well as direct mortality from collisions (Drewitt & Langston 2006). While studies have looked at the potential impacts of windfarms (Gill 2005; Fox *et al.* 2006), very few are based on empirical evidence from existing windfarms (e.g Krijgsveld *et al.* 2011; Lindeboom *et al.* 2011), due to the relatively small number currently operating and the difficulty and high cost of monitoring them (Fox *et al.* 2006).

Indirect effects have the potential to alter energy budgets by forcing birds to travel further to forage (Masden *et al.* 2010), or increasing competition in alternative foraging areas. Knowledge regarding seabird behavioural responses to windfarms is sparse (Fox *et al.* 2006); some birds show avoidance behaviour whereas others are attracted to these sites (Lindeboom *et al.* 2011; Poot *et al.* 2012). As an example of this uncertainty, Northern gannets *Morus bassanus* displayed the strongest avoidance behaviour at existing windfarm sites (Petersen, Clausager & Christensen 2004; Krijgsveld *et al.* 2011), additionally, Furness, Wade and Masden (2013) assessed that they are one of the most vulnerable species to collision mortality from windfarms. This demonstrates a demand to establish a robust methodology to predict the impacts from these devices on seabirds, and we propose that IBMs are suitable as they integrate both direct and indirect effects. Additionally, being colony specific, IBMs take into account the cumulative impact of disturbances within the foraging area of a specific colony, thus are superior to methods currently used to predict the impact from these devices which focus solely on development sites (Drewitt & Langston 2006).

We have developed a spatially-explicit IBM in order to predict how the construction of proposed windfarms in the English Channel and North Sea may impact the mortality and breeding success of a population of Northern gannets breeding in the English Channel. We then introduce the proposed windfarms and simulate the population both with and without windfarms, allowing a) the gannets to perform complete avoidance behaviour and b) allowing them to enter the windfarm areas with a risk of collision when doing so. The framework that we outline could be modified both for other species of mobile marine organism and other environmental pressures.

Methods

Data collection

Fieldwork, licensed by the States of Alderney, to determine the behaviour and habitat use of Northern gannets took place at the breeding colony (~5,000 pairs), on Les Etacs, Alderney, Channel Islands (49°42’N, 2°14’W) during the early chick-rearing period in June of 2011 and 2013–2015. Adults with chicks approximately 2–4 weeks old were caught at their nest using a noose pole, as they were encountered throughout the colony. GPS data recorders, logging positions every 2 minutes (IgotU GT 120 or IgotU GT-600, Mobile Action Technology), were attached to the base of the tail using heatshrink plastic and Tesa Extra Power tape. In 2013, nine birds were also fitted with a tri-axial accelerometer (X6-2, Gulf Coast Data Concepts), set to record at 25hz. The weight of the devices was < 2% of the birds’ body mass (GPS 33 g; GPS + accelerometer 44 g). The loggers were removed 2 to 3 weeks later.

Data processing and analysis

GPS positions were interpolated to every 10 seconds using the *adehabitatLT* package (Calenge 2006) in R (ver. 3.0.2, R Core Team 2013). The R package *Trip* (Sumner 2011) was used to calculate the time spent (s) in each 5 × 5 km cell of a pre-defined grid around the colony for each bird for each year (Time-in-area or TIA grid). In order to identify important foraging areas a second grid was created (foraging grid) by filtering the data for track tortuosity, which represents searching behaviour (Wakefield *et al.* 2013). The tortuosity index was calculated as a ratio of the straight line distance to the total distance travelled between L_{-48} and L_{48}, where L_0 is the focal location, i.e. over a 16 min duration (Wakefield *et al.* 2013). Individuals were defined as searching where GPS points had a tortuosity index of < 0.9 and a speed >1 m s^{-1}. The cells in this grid comprising the top 25% of time spent undertaking searching behaviour were identified as key foraging areas. A third grid (behaviour grid) was generated from the other two grids by expressing a value for each cell as the proportion of points classified as searching behaviour from the total number of points in the cell. This was used to determine the probability of foraging in each cell, rather than flying straight through it.

Ethographer for IGOR Pro (Sakamoto *et al.* 2009) was used to extract behaviours from the acceleration data automatically, based on unsupervised cluster analysis of the acceleration signals as described in full in Warwick-Evans *et al.* (2015). We were able to classify all periods within the first 5 days of data per bird as foraging, flying, resting on the water and diving behaviours from the accelerometer data. These were used to understand the time budgets of the gannets, in order to create the behaviour decision trees, and to assist in model validation.

Model

Model description

The four years of tracking data were combined with key parameters from peer-reviewed literature (Table 6.1) to design a spatially explicit model using NetLogo (Wilensky 1999). We describe the model using the ODD protocol (Grimm *et al.* 2010). Our model builds on the IBM for guillemots devised by Langton, Davies and Scott (2014) and incorporates characteristics of the surrounding environment.

Purpose

The purpose of the model is to predict how the construction of proposed windfarms in the English Channel and North Sea (Figure S6.1) may impact the body mass, mortality rate and breeding success of Northern gannets.

State Variables and scales

The model is composed of 5,000 family groups, each comprising an adult male, an adult female and a chick. The landscape is a grid of 5 km by 5 km patches, each with attributes such as number of fish and probability of foraging. The key state variables are described in Table 6.2 (see Table S6.1 for all state variables). The model runs in 6 minute timesteps, with 240 timesteps per day. The first 200 timesteps in a day are

Table 6.1. The parameter estimates used in the IBM. Please see Table S6.3 for further justification.

Parameter	Value	Explanation and Source
Initial mass of adults (g)	3286 ± 226	(Wanless & Okill 1994)
Initial mass of chicks (g)	79.3 ± 11.2	(Montevecchi *et al.* 1984)
Full (g)	745	(Garthe, Grémillet & Furness 1999)
Flyfull (g)	550	Derived through iteration
Fish size (g)	100 ± 10	(Garthe, Grémillet & Furness 1999)
Chick-Food-Max (g)	Calculated daily	(Montevecchi *et al.* 1984)
Assimilation Efficiency	0.76	(Cooper 1978)
Energy density of adult gannet tissue (kJ/g)	13	(Montevecchi *et al.* 1984)
Energy density of gannet chick tissue (kJ/g)	Calculated daily	Derived from (Montevecchi *et al.* 1984)
Energy density of prey (kJ/g)	7	(Lewis *et al.* 2003)
Metabolic rate at nest (kJ/g/min)	0.0007	(Birt-Friesen *et al.* 1989)
Metabolic rate at rest (kJ/g/min)	0.0007	(Birt-Friesen *et al.* 1989)
Metabolic rate at flight (kJ/g/min)	2.36	(Pennycuick 1998)
Metabolic rate at forage (kJ/g/min)	2.36	(Pennycuick 1998)
Flight speed (m/s)	15.3	(Hamer *et al.* 2000)
Foraging efficiency	0.75	Hennicke *et al*. in (Ropert-Coudert *et al.* 2004)
Mass below which adult is dead (g)	1800	(Garthe *et al.* 2012)
Mass below which chick is dead (g)	1800	(Garthe *et al.* 2012)

day-time, the remainder are night-time, corresponding with early June at the study location. The model runs for the 90 day chick-rearing period.

Process overview and scheduling

The main processes in the model are decision making, performing behaviours and updating mass. Behavioural processes are undertaken by adults each timestep at which point behaviour counters are updated. Adult and chick mass are updated during the last minute of each day. Adult mortality occurs if body mass drops below a specific threshold. Mortality in chicks occurs if on day 90 body mass has not attained a specific threshold.

Design concepts

Basic principles

The state and mortality rate of adults and chicks throughout the chick rearing period are impacted by the energy and time budgets of the adults which, in turn, are affected by the amount and distribution of prey. Energy is gained through food intake and lost through maintenance and activity. Northern gannets, like most seabirds, are long-lived and will prioritise their own survival above that of the chick.

Adaptation

Behavioural decisions are based on the physical state of the adult and the attributes of the surrounding environment and are made using decision trees (Figures S6.2 & S6.3).

Objectives

The adults aim to brood a chick to fledging whilst maintaining their own state at a healthy level.

Sensing

Adults have a memory of their behaviour during the previous timestep. They are aware of their own stomach content, whether they have previously been full during the current trip, if their chick has been fed and if it has been given the maximum food intake for the day. If an adult is on the nest they are aware of whether their partner is on the nest and who has been there longer. Adults are aware of how much food is in the patch they are on, the probability that they should forage there and if it is day or night time.

Interaction

The adults interact directly with the chick during feeding events and indirectly with one another via competition for food.

Table 6.2. Key state variables for the model entities**.**

globals	
day-night	Day-time or night-time
minute	Minute of the day
day	Day of the simulation
chick-food-max	Maximum mass of food the chick can consume this day
adults	
pair	Identifies the partnership of the individual
chicknum	Identifies the chick belonging to each pair
gender	Sex of the individual
mass	Body mass on the current day
stomach-content	Mass of food in the stomach
behav	Behaviour the bird is performing this timestep
duration-nest	Time the adult has been on the nest (without leaving)
flight	Minutes flying on this trip
rest	Minutes resting on this trip
forage	Minutes foraging on this trip
forage-type	Whether the adult is foraging for itself or the chick
catch	Mass of the fish caught
fish-counter	Total number of fish caught this trip
food-given-to-chick	Total amount of food given to chick that day
energy-gain	Amount of energy the adult has gained that day
tot-energy-expend	Total energy expended that day
chicks	
pair	Pair number of the chicks parents
chick-mass	Mass of the chick
energy-tissue-chick	Energy density of chick tissue that day
egain	Energy gained by the chick that day
eexpend	Energy expended by the chick that day
patches	
use	Use of the patch (i.e. home, windfarm)
fish-number	Number of fish currently in each patch
start-fish	Number of fish each patch started with
tortuosity	Tortuosity (proportion of time searching behaviour was observed in the patch)
probnorth	Probability of heading north when leaving each patch
probeast	Probability of heading east when leaving each patch
probsouth	Probability of heading south when leaving each patch
probwest	Probability of heading west when leaving each patch

Stochasticity

Initial masses of adults and chicks are drawn randomly from normal distributions based on the literature. The success or failure of catching a fish is stochastic, based on foraging efficiency from the literature. The destination an adult is given when leaving the nest to forage is randomly selected from the foraging grid. It is clear from the tracking data and other studies (Pettex *et al.* 2010) that gannets fly straight through some patches (commuting behaviour), whereas searching behaviour is observed in others. The behaviour grid gives the probability of a gannet foraging there, with higher probability of foraging in patches where increased searching behaviour was observed. After a gannet has reached its foraging destination the probability of moving in a given direction is determined by the amount of time tracked birds spent in the surrounding patches from the TIA grid.

Observation

Adult and chick mortality rate and mass are the main outputs. Mean trip length and behaviour budgets of adults are used for model validation.

Initialisation

The first minute of the model is the first minute of daylight on the day the chicks hatch (the model assumes all chicks hatch on the same day). Individuals start on the nest and all behaviour counters and stomach contents initialise at zero except for the duration at the nest for males. This initialises at 1 minute in order to be higher than that of the female, instigating the departure on a foraging trip.

Input Data

The attributes of patches, such as the probability of movement between patches (from the TIA grid), the probability of heading to a particular patch (from the foraging grid) and the probability of foraging (from the behaviour grid) were input into the model. Areas where gannets spend more time represent areas of increased foraging, and hence areas of higher fish availability (Warwick-Evans *et al.* 2015). The distribution of fish amongst the patches was therefore assigned by multiplying the proportion of time the tracked birds spent in each 5 km by 5 km patch by a numerical constant (Table S6.2). This value was assigned iteratively in the baseline models until the physiological state of both adults and chicks at the end of the breeding season represented values observed in natural populations.

Sub-models

Sub-models were created to decide and perform behaviours of adults, and to calculate the maximum quantity of food a chick can consume each day, the amount of energy expended by the adults and the amount of food in the stomach each timestep, and the mass of the adult and chick at the end of each day (see Supporting information).

Model validation

To test the performance of the model we compared the body mass of adults and chicks with values from the literature, and the trip length of adults with those from our tracked birds. Additionally, the proportion of the simulated birds performing each of the behaviours (on the nest, flying and foraging combined, and resting on the water) was plotted against time of day, and compared to the time budgets of the birds fitted with accelerometers.

*Simulation*s

Initially baseline models were simulated using the tracking data from all four years combined, which represents the mean state of the population over the four years without windfarms. Subsequently model simulations were carried out independently for each year, parameterised using year-specific tracking data. Both the baseline and the year-specific models were run in the presence and absence of windfarms. For the simulations in which the windfarms exist, the birds either show complete avoidance behaviour or are able to enter this area but risk mortality due to direct collision with a turbine as described below.

Avoidance

When the birds show avoidance behaviour they are unable to enter patches with windfarms. Instead, birds must move to nearby patches, increasing the competition in these patches. As a result they may have to travel further in order to gain enough food, with energetic consequences for themselves and their offspring.

Collision risk

If birds enter the windfarm area, there is a chance there will be direct mortality as a result of hitting a turbine. The risk was calculated individually for each windfarm site using the extended Band model (Band & Band 2012, see Supporting information). It was not possible to calculate exact values for each site, as some information (e.g. the amount of time the turbines would be operational) was unavailable. Furthermore the micro-avoidance rates (avoidance of individual turbines when in the windfarm area) of gannets are unknown and industry standard values are used (Cook *et al.* 2014) using a best and worst case scenario for each windfarm site. The best case is with the lowest operational rate (64%) and the highest avoidance rate (99.5%), and the worst case is the highest operational rate (90%) and the lowest avoidance rate (98.9%).

Sensitivity analysis

To determine the robustness of the model and the parameters that impacted most on the mortality rate and body mass of the adults and chicks, an individual parameter perturbation sensitivity analysis was carried out. Multiple simulations were carried out on the baseline model, where each of a key subset of the model parameters were varied singly and sequentially by a standard variability of ± 10 %, whilst maintaining the initial values for all other variables. To account for stochasticity in the outputs, simulations were repeated three times, and the mean and standard deviation of mortality rate and body mass for both adults and chicks was calculated and expressed as the percentage difference from the baseline model. Subsequently, a best-case and a worst–case scenario were simulated, where all values of model parameters which resulted in an increase/decrease in mortality or body mass were adjusted by ± 10 %, respectively.

Results

The baseline model accurately represented the mortality rate and physiological state of the tracked gannets at the end of the 90 day chick-rearing period (Table 6.3). The model predicts increased mortality only as a result of direct collision with turbines, or due to starvation as a consequence of the addition of windfarms, through alteration to the energy budget or increased competition. Gannets are undoubtedly subject to mortality from other causes, and we know that neither adult nor chick survival are 100%. However for the purposes of this model, we use zero mortality for both adults and chicks as a baseline from which to quantify the increased mortality from the installation of windfarms, although we know that in reality mortality rates will be higher than this. Both simulated and tracked birds spent similar amounts of time per day engaged in the key behaviours of being on the nest, in flight and resting on the water (Figure 6.1). The diel pattern was also similar suggesting that the behaviour of the modelled birds was comparable to that of the natural population. Windfarms occupied 4% of the patches which the tracked gannets visited (Figure 6.2) and there was little evidence to suggest that the installation of the proposed windfarms would impact Alderney's population of Northern gannets. No differences were observed in the physiological state or mortality rate of the gannets between the baseline model and models where gannets showed avoidance behaviour either for all years combined (Table 6.4) or for individual years (Table 6.5). Simulations where the gannets entered the windfarm area and were exposed to collision risk showed minimal adult and chick mortality and no change in physiological state (Tables 6.4 & 6.5). There was some evidence of inter-annual variation in the baseline models, with a lower than normal fledging mass of chicks in 2015, yet no evidence of inter-annual variation in the impacts from windfarms (Table 6.5).

Table 6.3. Mortality rate and physiological state of natural and simulated gannets. Mortality rate is a measure of increased mortality from collision or starvation as a result of the addition of the proposed windfarms, thus for the baseline model simulation, and empirical data this value is zero.

Parameter	Empirical data	Baseline model output
Adult mortality (%)	0	0
Adult mass (kg)	3.3	3.3
Chick mortality (%)	0	0
Chick mass (kg)	3.7	3.7
Trip duration (h)	24	24

Table 6.4. The state and mortality rates of birds under different model simulations: parameterised with data from all years combined.

Parameter	Baseline	Avoidance	Collision	
			Best case	Worst case
Adult mortality	0	0	0	0.02
Adult mass	3.3	3.3	3.3	3.3
Chick mortality	0	0	0	0.04
Chick mass	3.3	3.3	3.3	3.3

Table 6.5. State and mortality rates from model simulations parameterised individually for each year

Year	Parameter	Baseline	Avoidance	Collision	
				Best case	Worst case
2013	Adult mortality (%)	0	0	0.02	0.04
	Adult mass (kg)	3.3	3.3	3.3	3.3
	Chick mortality (%)	0	0	0.02	0.06
	Chick mass (kg)	3.7	3.9	3.8	3.8
2014	Adult mortality (%)	0	0	0.01	0.08
	Adult mass (kg)	3.3	3.3	3.3	3.3
	Chick mortality (%)	0	0	0.02	0.08
	Chick mass (kg)	3.7	3.7	3.7	3.7
2015	Adult mortality (%)	0	0	0.02	0.03
	Adult mass (kg)	3.3	3.3	3.3	3.3
	Chick mortality (%)	0	0	0.04	0.08
	Chick mass (kg)	3.1	3.1	3.1	3.1

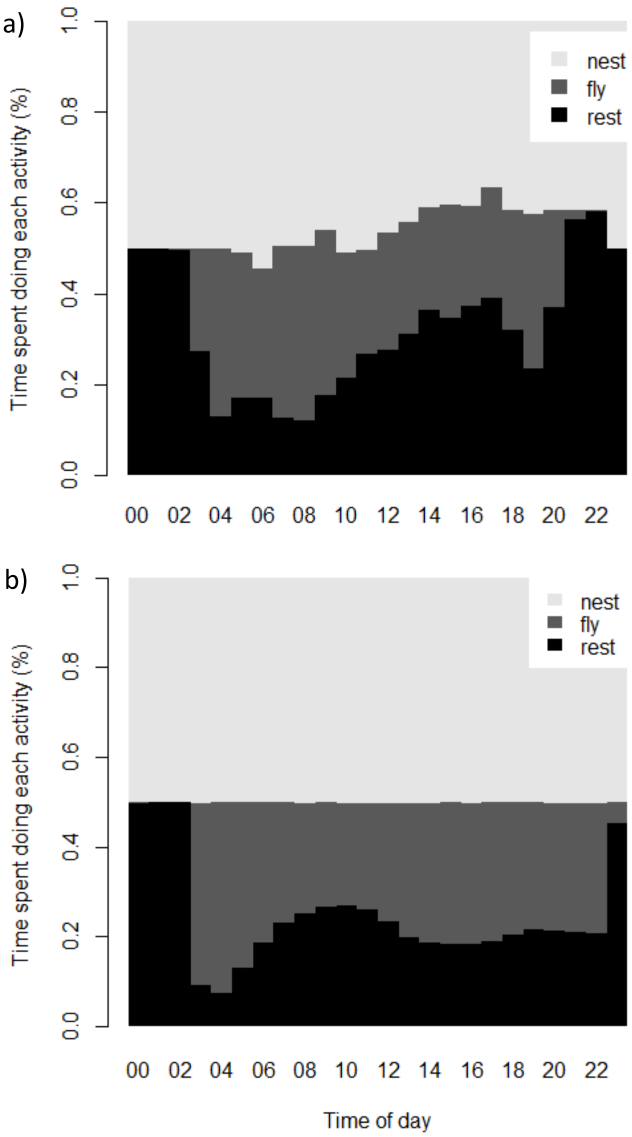

Figure 6.1. Behaviour budgets for a) GPS tracked and accelerometer equipped Northern gannets, and b) outputs from a baseline IBM simulation for all years of data combined. Only the first second of diving behaviour was extracted from the accelerometer data, therefore there is no time budget for diving behaviour in the tracked gannets, thus flight and foraging behaviour are combined for both datasets.

Sensitivity analysis

The model was fairly robust to changes in the parameter values, with changes of <10% being recorded as a result of a 10% change in the parameter value in almost all cases (Table 6.6). Both the adults and chicks in the model were most sensitive to changes in the energy density of fish. This effect was much larger on the chicks, because the adults were able to compensate by catching more fish, whereas the chicks were limited by the quality and quantity of food the adult could carry. Furthermore, chicks were more sensitive in general to perturbations in model parameters than adults, as they had less ability to compensate for smaller, less energy dense fish, or for higher energetic costs, as their food intake was constrained by the behaviour of adults. This reflects the principle that adults prioritise themselves over their chicks in times of lower food availability, or higher costs of foraging. Even in the unlikely worst-case scenario that all model parameters were inaccurate, a change in approximately 30% of the adult body mass is driven mostly by the energy density and size of fish, which can be justified biologically, and could easily be adjusted in the model based on more accurate data from a given study site.

Table 6.6 Sensitivity analysis of adult and chick mortality and body mass. Each of the model parameters were varied singly and sequentially by a standard variability of ± 10 %.

Parameter	Value	Chick mortality (%)	Adult mortality (%)	Difference in chick mass (%)	Difference in adult mass (%)
Foraging efficiency	0.675	0	0	-4.1 ± 2.3	-3.3 ± 0.2
Foraging efficiency	0.825	0	0	-0.1 ± 0.4	1.9 ± 0.1
Full (g)	670.5	0	0	0.4 ± 1.5	-2.6 ± 0.3
Full (g)	819.5	0	0	-3.7 ± 1.6	0.9 ± 0.3
Flyfull (g)	495	0	0	-8.8 ± 0.3	-2.2 ± 0.1
Flyfull (g)	605	0	0	4.0 ± 2.2	0.6 ± 0.7
Fish size (g)	90	0	0	-2.3 ± 3.8	-6.2 ± 0.8
Fish size (g)	110	0	0	-0.2 ± 2.7	3.7 ± 0.3
Metabolic rate at nest (kJ/g/min)	0.00057	0	0	-1.0 ± 3.0	4.0 ± 0.3
Metabolic rate at nest (kJ/g/min)	0.00083	0	0	-0.8 ± 2.4	-4.9 ± 0.1

Metabolic rate at rest (kJ/g/min)	0.00057	0	0	1.0 ± 1.9	1.6 ± 0.1
Metabolic rate at rest (kJ/g/min)	0.00083	0	0	-1.5 ± 1.6	-3.1 ± 0.1
Number of fish	63000	0	0	-6.5 ± 5.3	-3.9 ± 0.4
Number of fish	77000	0	0	1.1 ± 1.2	1.6 ± 0.0
Energy density of fish (kJ/g)	6.3	0	0	-23.0 ± 0.2	-8.7 ± 0.1
Energy density of fish (kJ/g)	7.7	0	0	20.1 ± 0.5	7.2 ± 0.2
Assimilation Efficiency	0.684	0	0	-2.5 ± 0.9	-8.6 ± 0.0
Assimilation Efficiency	0.836	0	0	-1.3 ± 0.7	7.1 ± 0.1
Energy density of chick tissue (kJ/g)	0.9*	0	0	10.8 ± 1.6	-1.3 ± 1.2
Energy density of chick tissue (kJ/g)	1.1*	0	0	-10.6 ± 0.6	-0.7 ± 0.2
Maximum chick food	0.9*	0	0	-16.0 ± 3.6	-0.0 ± 0.7
Maximum chick food	1.1*	0	0	11.4 ± 0.9	-1.7 ± 0.2
Best-case	na	0	0	36.2 ± 1.4	38.3 ± 0.4
Worst-case	na	18 ± 0.8	82 ± 1.6	-33.5 ± 1.3	-29.3 ± 0.4

* The value for this parameter was calculated daily then multiplied by 0.9 or 1.1 for the perturbation

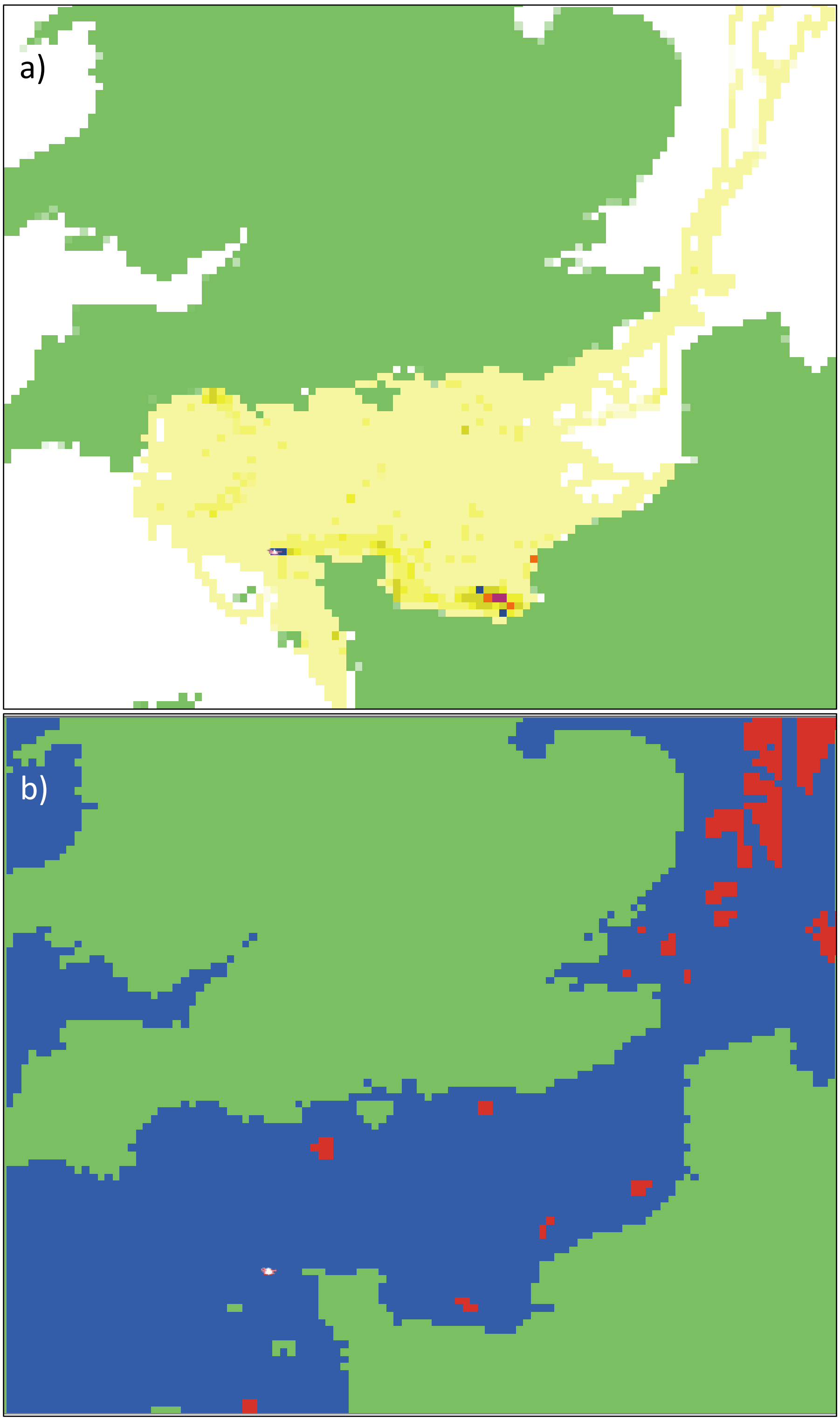

Figure 6.2 a) Time-in-area plot for Alderney's population of Northern gannets tracked in 2011 - 2015, b) windfarms proposed for development in the English Channel and North Sea.

Discussion

The use of individual based models to predict the effects of environmental change is a powerful tool that is widely used in many disciplines (Grimm 1999). We have developed the most complex and comprehensive model yet for seabirds where baseline models accurately represented the behaviour and physiological state of the Les Etacs gannets, and model simulations successfully explored the potential impacts from environmental change. We found no impact of existing or proposed windfarms on the mortality rate, productivity or physiological state of Alderney's Northern gannets. Our model indicated that there were no changes to mortality rate, productivity or physiological state if Northern gannets avoided the site and negligible mortality and no change in physiological state if the birds entered the windfarm areas (and hence risked colliding with the turbines). Concerns that in poor years windfarms would have increased impact on gannets were not supported by the model outcomes.

The home range of the gannets was large in comparison to the area occupied or proposed for windfarms (Figure 6.2) which represented only 4% of the 5 x 5 km cells which the gannets visited. Consequently, the proportion of foraging behaviour in these areas was low and, as the areas were relatively small, the displacement distances were small, resulting in negligible effects on the energy budget of the birds. Other windfarm developments may pose greater threats to different colonies. For example, the area of proposed windfarms in the North Sea is much larger (4cOffshore 2015), and may be harder to avoid, thus posing a higher risk to gannet colonies nearby. Northern gannets avoidance rates to entire windfarm sites (macro-avoidance) is estimated to be 64% and the rate at which birds avoid individual turbines whilst inside the windfarm area (micro-avoidance) is 98.9% - 99.5% (Cook *et al.* 2014). Industry standard data on the flight height of gannets indicates that only 11.3% of Northern gannets fly at a height with a risk of collision with a rotor (Cook *et al.* 2012) and when these data are combined in the extended Band model, used to calculate collision risk in this model, the probability of a gannet entering the windfarm and colliding with a rotating turbine is small. There is some debate surrounding the visual observation method to determine flight heights, and Cleasby *et al.* (2015) proposed that it may underestimate collision risk, and therefore the risk of mortality may be underestimated using current methods. Should gannet collision risk be re-evaluated and confirmed, our modelling approach allows the population-level impacts to rapidly be reassessed.

Current approaches to assess the potential impacts on seabirds from proposed windfarms are based on observation data collected within windfarm sites, making assumptions about the origins of these birds. However, legislation manages seabirds at the level of the colony through the designation of SPAs (Wilson *et al.* 2009). Detecting change (impact) in the numbers of birds offshore is hard using this approach, as there is large spatial and temporal variation in seabird numbers at any given offshore location (Maclean *et al.* 2013). Individual based models are colony specific, thus, we propose that predictions from IBMs are superior to predictions based on observation data only, as they take into account the cumulative impact of disturbances within the foraging area of a colony, which current approaches cannot do. Although, the model was parameterised for breeding adults, with hatched chicks, it can be easily adapted for other individuals in the colony (e.g. non-breeders, incubating birds) and for other gannetries (in some cases using existing data, Wakefield et al. 2013) by maintaining the model structure and input parameters and simply changing the spatial environment.

With knowledge of environmental parameters, this IBM could be modified to predict the impacts from other examples of spatial change, such as oil spills (Montevecchi *et al.* 2012), fisheries depletion (Gremillet *et al.* 2015), changes to fisheries bycatch policies (Votier *et al.* 2010) or comparing the likely success of proposed MPAs. Furthermore, in the way that this model was based on a model of foraging behaviour by guillemots (Langton, Davies & Scott 2014), this IBM could be modified for other seabird species for which tracking data is available if the behaviour and physiology of the species is reasonably well understood.

In addition to a management tool, IBMs increase our understanding about the species' breeding ecology by mechanistically linking foraging behaviour to physiological state and breeding success. The modelled inter-annual variation in breeding performance suggests that either the amount of prey or its distribution varied across the years. Modelled breeding performance was lowest in 2015, with a 16 % reduction in mean fledging mass, coinciding with lower reproductive success in the gannets breeding on Alderney in 2015 (Chapter 5). The number of fish in the 2015 model was similar to that in 2014 (Table S6.3) when the chicks reached full fledging mass. Thus, it is likely that the distribution or quality of prey in 2015 resulted in altered energy budgets, with increased foraging costs for the gannets. This is reflected in the tracking data as longer trips into the North Sea were recorded in 2015 (Chapter 5).

As with all modelling approaches, assumptions and simplifications to the behaviour and life history of modelled species are made, e.g. the prey type and size and the foraging efficiency of gannets breeding on Les Etacs was similar to that from the literature. Additionally, some behavioural characteristics were simplified, e.g. modelled adult birds do not interact when on foraging trips, no foraging occurs at night and adults are never at the nest together for more than one timestep. Additionally, the model uses tracking data to determine the probability of a bird moving from one of the cells to any of the adjacent cells, thus cells which were not visited by our sampled birds have a probability of zero for a modelled bird to enter. We know that our sample of tracked gannets did not represent the entire home range area for the entire population, thus some cells may be under-represented in the model. However, this is unlikely to have severe implications on the model outputs, as these cells were likely to have very low usage, and thus even if they were available in the model, few birds would use them. Despite these limitations we believe that this model is a substantial improvement compared to previous models predicting the effects of environmental change on seabirds. This model could easily be adapted to predict the impacts of spatial change on other seabird colonies. We demonstrate that this is a strong approach and should be implemented widely to predict the potential impacts from environmental change and assist policy makers when establishing management plans.

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Supporting Information

Figure S6.1 Map of windfarms which overlap with the home range of Alderney's population of Northern gannets

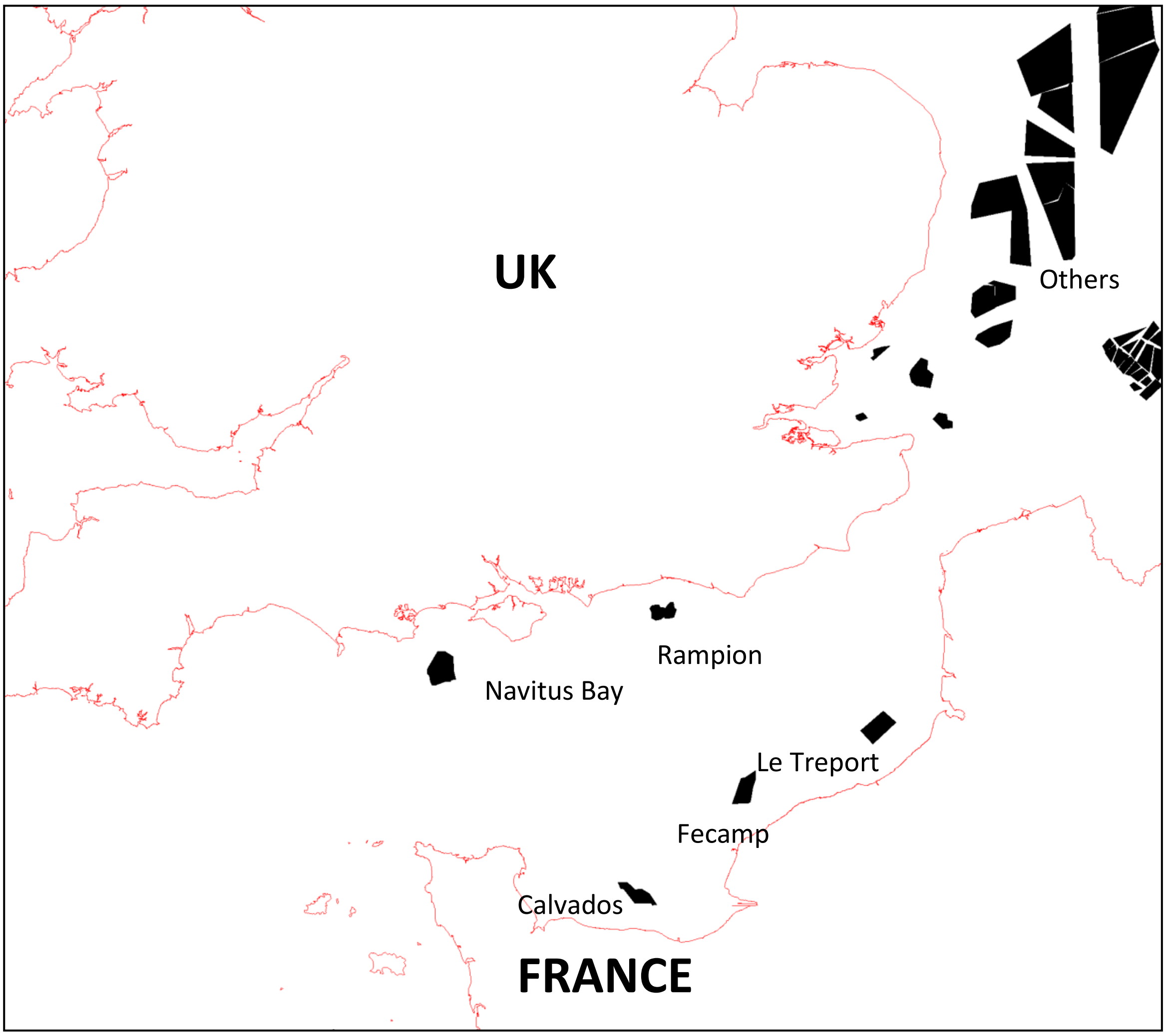

Table S6.1. All state variables in the model including parameters for coding purposes only

globals	
day-night	If it is daytime or night time
minute	The minute of the day
tot-minute	The number of minutes since the start of the simulation
day	The day of the simulation
chick-food-max	The maximum mass of food the chick can consume this day
chick-food	Food available to feed to the chick
energy-density	The energy density of prey
assim	Assimilation efficiency
energy-tissue	Energy density of adult tissue
energy-nest	The energy cost to staying at the nest (kj/g/min)
energy-rest	The energy cost to resting on the water (kj/g/min)
wing-span	The wing span of an adult gannet
air-dens	Air density at 17 m
aspect-ratio	Ratio of wing span to frontal area
bmr	Basal metabolic rate of a gannet
v	Flight speed (m/sec)
list1	List of the proportion of time a gannet spends foraging in a particular cell
list2	List of the cell ID that correspond to the proportions in list 1
f-efficiency	Foraging efficiency
full	The maximum amount of food a gannet can ingest
flyfull	The maximum stomach-content for a commuting trip
open	A list of potential patches in the find-a-path procedure
closed	A list of potential patches in the find-a-path procedure
optimal-path	A list of the best path in the find-a-path procedure
listtort	List of tortuosity index for each patch
listpnorth, listpsouth, listpeast, listpwest	List of probability of moving north etc for each patch
listtia	List of time spent in each patch
riskc	Risk of colliding with a turbine in the Calvados windfarm
riskf	Risk of colliding with a turbine in the Fecamp windfarm
riskn	Risk of colliding with a turbine in the Navitus Bay windfarm
riskr	Risk of colliding with a turbine in the Rampion windfarm
riskt	Risk of colliding with a turbine in the Treport windfarm
risko	Risk of colliding with a turbine in other windfarms (North Sea)
adults-own	
pair	Identifies which partnership the individual is in
gender	Identifies the sex of the individual
fish-counter	How many fish they have caught this trip
chicknum	Identifies the chick belonging to each pair
catch	The mass of the fish caught
cost-min	Cost of flight per minute at current mass including stomach content
stomach-content	Mass of food currently in the stomach
mass	Body mass on the current day
behav	The behaviour the bird is performing this timestep
direction	If the bird is on the way home
rest-length	Whether the bird is going to have a long or short rest

total-catch	Total mass of fish caught this day
duration-nest	How long the adult has been on the nest (without leaving)
forage-type	Whether the adult is foraging for itself or the chick
flight	How many minutes the adult has flown on this trip
rest	How many minutes the adult has rested on this trip
forage	How many minutes the adult has foraged on this trip
fish-this-trip	Total number of fish caught this trip (calculated when return to nest)
head	ID number of the patch to head to
reached-target	If the adult has reached its target (either foraging patch or home)
path	The path it should take to the foraging patch / home
current-path	The current path its taking
flight-home	How many minutes it has been flying towards home
all	The sum of the probability of movement in each direction in the fly model
trip-length	Total length of trip (calculated on return to the nest)
trip-length-list	List of the lengths of each trip
chick-forage	If the adult has foraged for the chick
feeding-time	If the adult returns to the nest and needs to feed the chick
food-given-to-chick	Total amount of food given to the chick that day
energy-gain	The amount of energy the adults have gained that day
tot-energy-expend	The total amount of energy expended that day
alive-dead	Are the adults alive or dead
last-x	X coordinate of the last patch the adult visited
last-y	Y coordinate of the last patch the adult visited
visited-patches	A list of the coordinates of the patches the adult has visited
last-five	The last 5 patches the adult visited
target-patches	The four surrounding patches
target-patches1	The four surrounding patches minus any patches in the last 5 list
dir	Choice of directions in the fly submodel
dir1	Choice of directions in the fly submodel
dir2	Choice of directions in the fly submodel
time	The time each fish was caught
time1, time2 etc	The time the first, second etc fish was caught
digesting1 , digesting2 etc	The mass of each caught fish being digested per timestep
chicks-own	
pair	Which pair number are the chicks parents
chick-mass	The mass of the chick
energy-tissue-chick	The energy density of the chick tissue during that day
egain	The energy gained by the chick that day
eexpend	The energy expended by the chick that day
my-chick-food	The amount of food the chick has consumed that day
chick-alive-dead	If the chick is alive or dead
chick-fed-list	A list of days the chick was fed
dayfed	The last day the chick was fed
patches-own	
use	The use of the patch (i.e. home, windfarm)
name	The name of the windfarm in order to specify site specific collision risk

tia	Time spent by tracked birds in each patch
tort	Tortuosity (the proportion of time searching behaviour was observed in the patch)
probnorth probeast probsouth probwest	Probability of heading north etc when leaving each patch
fish-number	The number of fish currently in each patch
start-fish	The number of fish each patch started with
aversion	If the bird is not allowed in that patch the aversion = 1
ID	The ID number of the patch
f g and h	Parameters in the find-a-path procedure
parent-patch	Next potential patch in the find-a-path procedure

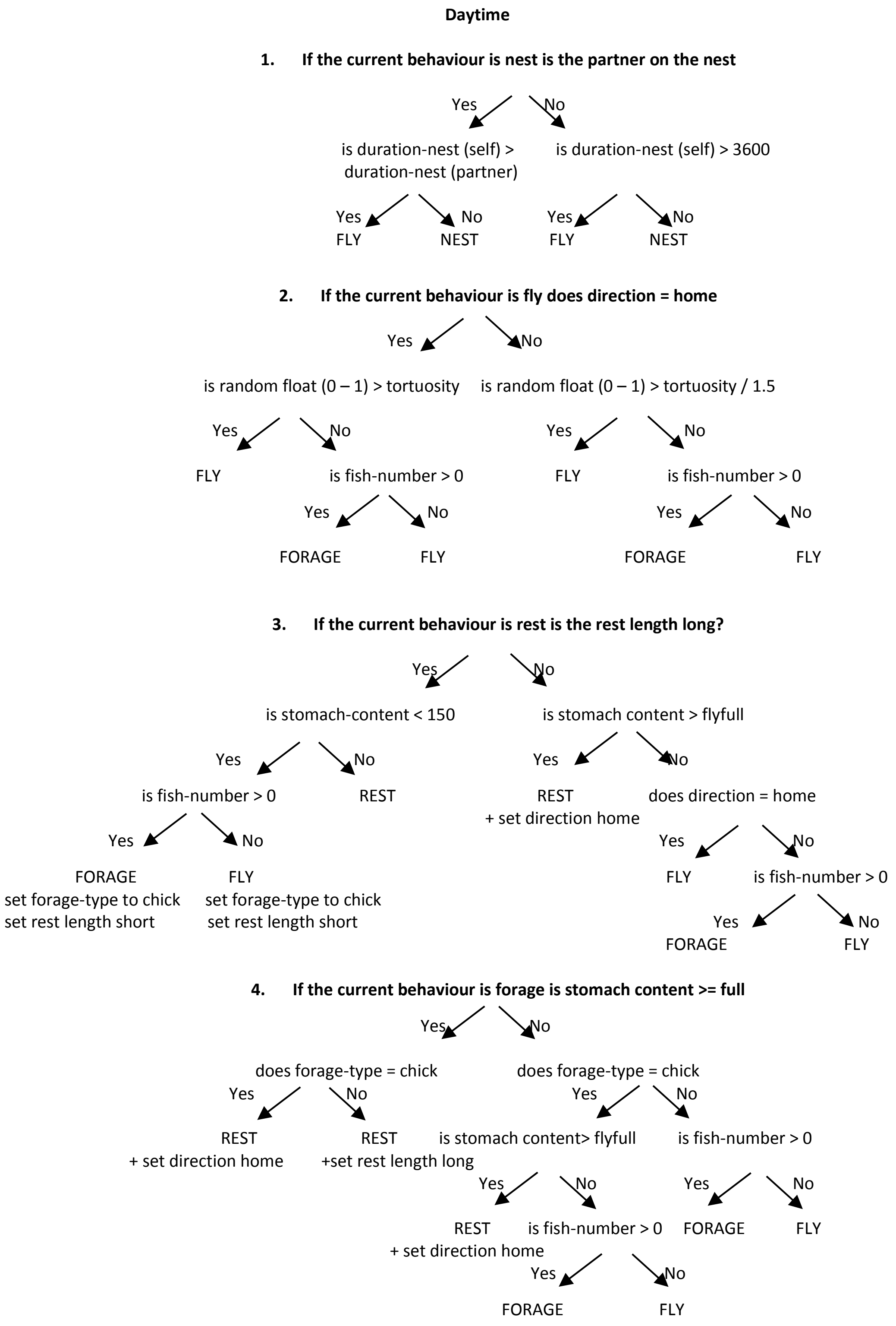

Figure S6.2. A series of decision trees followed each day-time timestep in order to decide the behaviour in the current timestep based on previous behaviours and physiological state.

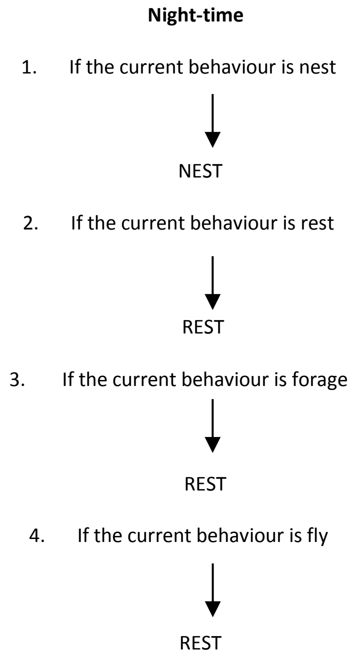

Figure S6.3. A series of decision trees followed each night-time timestep in order to decide the behaviour in the current timestep based on previous behaviours and physiological state.

Table S6.2. The constant is the number by which the time spent in each cell was multiplied in order to calculate the total number of fish in the model for the adults in to finish the breeding season at a mass of approximately 3.29kg. The number of cells which these fish were spread across is also given.

Year	Constant	Number of fish	Number of cells
2013	750,000	367,546	1,372
2014	500,000	266,494	1,126
2015	550,000	269,500	1,801
Combined	350,000	172,051	2,035

Table S6.3. Further justification of parameter estimates

Parameter	Value	Explanation and Source
Full (g)	745	The only data available on max stomach content was the maximum size of food items ingested in observations by (Garthe et al. 1999) therefore this value was used in the model.
Flyfull (g)	550	Derived through iteration. Gannets do not commute when full (Ropert-Coudert et al. 2004) but need to retain enough food in the stomach to provision the chick (~450g max) so values from 450 – 650 were tested, and the simulation which returned the most accurate physiological state of the adult and chick was used.
Fish size (g)	100 ± 10	The median mass of fish ingested by Northern gannets found by Garthe et al. (1999) was used. As no standard deviation was given in the paper a value of 10% was used.
Assimilation Efficiency	0.76	Cooper (1978). This value is for the cape gannet, however the diet and physiology of these species is very similar, and there is a narrow range of assimilation efficiencies of fish-eating seabirds in general (Dunn 1980).
Energy density of gannet chick tissue (kJ/g)	Calculated daily	The equation was derived from calculations using values based on table 2 in Montevecchi et al. (1984)
Metabolic rate at flight (kJ/g/min)	mass specific	The Pennycuick flight model (Pennycuick 1998) was used to calculate the flight cost in each timestep where the bird is foraging in order to account for the combination of the mass of the bird and the stomach content.
Metabolic rate at forage (kJ/g/min)	mass specific	The Pennycuick flight model (Pennycuick 1998), was also used to calculate the cost of foraging as this can be assumed to be similar to the cost of flight (Amélineau et al. 2014).
Mass below which adult is dead (g)	1800	Garthe et al. (2012) found two emaciated gannets with mass < 1800 g in otherwise perfect condition.
Mass below which chick is dead (g)	1800	The same value from Garthe et al. (2012) was used for chicks, as in the model they only die at the end of the breeding season, and no other data is available on the mass at which a gannet chick may die

Submodels

Behaviour decisions

A series of decision trees is used to decide which behaviour to perform each timestep (Figures S6.2 & S6.3). These decisions are based on the behaviour in previous timesteps, the behaviour of the partner, the attributes of the patch they are in and the physiological state of the adult. The behaviours which a gannet may exhibit are; at the nest (*nest*), resting on the water (*rest*), foraging (*forage*) and flying (*fly*). In natural populations male and female Northern gannets alternate chick brooding whilst the partner undertakes foraging trips (Nelson 1978). There are short periods where both the male and female are at the nest but predominantly just one adult remains (Nelson 1978). In the model only one adult is ever at the nest, except for during the changeover period. If the previous behaviour of a bird is at the nest the decision to leave is based on if the partner is also there and if so who has been there longer. An adult alone at the nest will leave the chick unattended to go foraging if they have been on the nest for more than 2.5 days. This value was decided based on the maximum trip duration observed in the tracked gannets and allows a gannet whose partner may have died (for example in a collision with a wind turbine) to leave the nest. The only behaviour which may follow being at the nest is to remain at the nest or to fly.

If a bird in the model has been flying, the probability of it foraging in a patch is decided by the proportion of time tracked gannets were observed foraging in the patch (behaviour grid), how many fish are there (TIA grid) and if it is on the way home or not. Gannets are visual pursuit predators that only dive after observing prey (Machovsky-Capuska *et al.* 2012) therefore will only forage in patches with prey available. During daylight hours the bird only stops flying if it starts foraging or if it returns to the nest.

There is good evidence to suggest that when on foraging trips gannets initially forage for themselves and this is followed by a long period of rest during which they digest (Ropert-Coudert *et al.* 2004). They subsequently forage for the chick on the way home, thus the birds in the model forage until they are completely full and subsequently rest until they are nearly empty. After this the birds in the model fly towards home, foraging for the chick *en route*. During these subsequent foraging periods birds do not get completely full, and may only forage until they are *flyfull* – too full to commute, followed by short periods resting on the water allowing them to digest enough to reduce their mass enough to fly. If there are no fish left in the patch the birds will fly. This allows birds to move whilst foraging and return to the nest with enough undigested food to provision the chick. Gannets are visual pursuit predators and primarily forage by plunge diving during daylight hours (Hamer *et al.* 2000), although there is some evidence that birds forage from the surface at night (Warwick-Evans *et al.* 2015). Thus, for simplicity, the birds in the model which are foraging or in flight when it becomes night time rest on the water, and those that are at the nest or resting on the water remain in this behavioural state until daylight.

Perform behaviours

After making a decision on which behaviour to perform, the next step in the model is to perform this behaviour.

Fly

Before leaving the nest the birds are given a heading based on relative intensity of searching behaviour in areas observed in the tracking data (foraging grid). They calculate a direct path to this destination, avoiding land, and are able to stop and forage *en route*. If the gannet has reached its destination but has not yet met the criteria to return home the gannet will fly stochastically from patch to patch depending on the time the tracked birds spent in each patch (TIA grid), and will forage in patches where fish are available, depending on the probability of foraging there (behaviour grid). Birds cannot visit the same patch within a specified number of timesteps in order to avoid becoming stuck in highly used areas. This threshold was determined iteratively to be five. When the criteria to return home has been met the bird will calculate a path directly home, also avoiding land and allowing the bird to forage and rest *en route* (Pettex *et al.* 2010).

Forage

If a random number between 0 - 1 is lower than the foraging efficiency from the literature then the bird will catch a fish. The mass of the fish (g) is drawn from a random distribution (mean 100, sd 10, Garthe, Grémillet & Furness 1999), the stomach content and fish-counter are updated, and the number of fish in the patch is reduced by one. During the first three hours birds can only catch one fish in a patch and move on, to reflect the opportunistic dives observed *en route* to the foraging patch (Ropert-Coudert *et al.* 2004). After this time the birds remain in a patch until either the fish are depleted, or the bird is unsuccessful at catching a fish at which point it will move on. The number of fish in each patch reverts to the initial value in the last minute of the day.

Rest

If the behaviour is rest the birds perform no activity.

Nest

If the birds were on the nest the previous timestep no activity is performed. If the birds are returning to the nest and if they have anything in the stomach they will transfer all the food to the chick. Chicks are able to consume a maximum volume of food each day (*chick-food-max see below for calculations*) all remaining food is retained by the adult.

Calculate stomach content

After a successful foraging event the stomach content of adults increases by the mass of the fish caught. Jackson (1992) showed that cape gannets take 10 hrs to completely digest a “normal sized meal”. Therefore the rate that food is removed from the stomach in the model is 0.01 * mass of fish per timestep for the 100 timesteps following a successful foraging event.

Calculate energy

Energy expended by adults is calculated every timestep based on the current mass of the individual and which behaviour has been performed.

$$E_{expend} = E_{activity} * \text{mass}$$

Metabolic rates are considered to be similar whilst birds are at the nest and resting on the water (Birt-Friesen *et al.* 1989) and whilst foraging and flying (Amélineau *et al.* 2014). These rates are reflected in the model. The cost of flight and foraging are calculated using the Pennycuick flight model (Pennycuick 1998) for each 6 minute timestep that the bird is flying using the mass including stomach content at that timestep.

Calculate chick food

The amount of food a chick required in order to maintain its current tissue and to grow at a normal rate (*Chick-food-max*) is calculated in the first timestep of each day using data from Montevecchi *et al.* (1984). Chicks are able to consume this amount + 10% to account for days when they are underfed. Furthermore, if a chick is not fed on a given day, the value for that day is added to the maximum amount it can be fed the following day.

Update chicks

Chicks update their mass (g) during the final timestep of every day using the equation.

$$\text{mass}_{t+1} = \text{mass}_{t} + \text{E}_{growth}$$

Chicks expend energy for growth and maintenance and receive energy from food. The energy available for growth is

$$\text{E}_{growth} = (\text{E}_{gain} - \text{E}_{expend}) * p / \text{E}_{tissue}$$

Where energy gained ($\text{E}_{gain,}$ kj/bird) is calculated using the equation

$$\text{E}_{gain} = \textit{chick-food} * a * \text{E}_{prey}$$

Where chick-food is the mass of food the chick has received that day (g), assimilation efficiency (*a*) is the efficiency at which the chick is able to absorb nutrients from prey, and E_{prey} is the energy density of the prey (kj/g).

Energy expended for maintenance ($\text{E}_{expend,}$ kj/bird) is the amount of energy the chick has expended that day in order to maintain current cell tissue and was calculated using the growth model in Montevecchi et al 1984. Productivity efficiency (*p)* is the efficiency by which the chick is able to turn energy into new cells. Energy density of the chicks tissue ($\text{E}_{tissue,}$ kj) can be calculated using the equation

$$E_{tissue} = 2.5178 + (0.2806 * day)$$

until day 56 at which point it becomes equal to that of an adult (Montevecchi *et al.* 1984).

Update adults

During the final timestep of every day adults in the model update their mass using the equation.

$$mass_{t+1} = mass_t + (E_{gain} - E_{expend}) \ / \ E_{tissue}$$

Where energy gained ($E_{gain,}$ kj/bird) is calculated using the equation

$$E_{gain} = self\text{-}food * a * E_{prey}$$

and energy expended ($E_{expend,}$ kj/bird) is the total activity specific energy used, calculated in the *calculate-energy* procedure described above. The equation used to calculate the mass gain for the adult was different to that for chicks as mass gain in adults is purely stored energy in the form of fat, rather than for somatic growth of the bird which is the case for chicks.

Collision risk model for Northern gannets encountering windfarms

The extended Band model was used in order to calculate the risk of collision for one bird for each timestep if the individual was already in the windfarm area. The model works by combining information about the density of birds in windfarm sites, and the height and speed at which they move through turbine sites with information about the number of turbines, and the area of the site in order to calculate the risk of a flying gannet striking a rotor blade in a specified time period. The parameters in the model were input into the collision modelling tool on the BTO website (http://www.bto.org/science/wetland-and-marine/soss/projects) to reflect the way model gannets interact with windfarm patches in the model (Table S6.4). The input of bird density was 0.04 (i.e. 1 individual per 25 km^2 which is the size of 1 patch in the model) and the total number of daylight hours was 0.1 (i.e. one 6 minute timestep). The flight speed was changed to 13.9 m/s as this is the speed the gannets in the model move. The generic data on the flight height of gannets (Cook *et al.* 2012) was used in order to calculate the proportion of birds flying at the height of the turbines.

Table S6.4. Parameters input into the BTOs collision risk modelling tool. Where no specific parameters were necessary for the IBM the default value for gannets was used

Parameter	Source	Value
Bird data		
Bird length (m)	Default	0.94
Wingspan (m)	Default	1.72
Flight speed (m/sec)	Speed gannets in the model move	13.9
Nocturnal activity factor (1-5)	Default	2
Flight type, flapping or gliding	Default	Gliding
Bird survey data		
Daytime bird density (birds/sqkm)	Explained in text	0.04
Proportion at rotor height (%)	Industry standard data extracted from Cook et al 2014	
Proportion of flights upwind (%)	Default	50%
Birds on migration data	The model runs throughout the breeding season, and does not include migrating birds	
Windfarm data	Site specific	
Turbine data	Site specific	

Specifications for the proposed windfarms were extracted from the website 4coffshore (4coffshore 2015) and further turbine specific specifications from the suppliers website were used. The mean rotation speed of the turbines can be calculated using wind speed frequency data, however we were unable to gain this information, therefore the maximum rotation speed was used in the model, which will give us a precautionary value. Site specific collision risk values were calculated for the 5 sites proposed for development in the English Channel. Some of the proposals for the North Sea section are still in very early phases of development, and there is no data available on the size and model of turbines proposed. Consequently, the collision risk values for the five known sites in the English

Channel were averaged in order to calculate the collision risk for the North Sea sites. The proportion of time that the wind turbines will be operational was unavailable, therefore we used parameters from the worked example on the BTO website (Band 2012). The lowest proportion of time the turbines were operational was (0.64) and the highest proportion of time was (0.90). Additionally, the total avoidance rates of gannets to rotors was also unavailable and this is believed to be between 98.9% and 99.5% (Cook et al. 2014). Consequently we simulated a best case scenario with low operational time and high avoidance rate, and a worst case scenario with high operational time and low avoidance rate.

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Chapter 7

General Discussion

General Discussion

It has become widely accepted that seabirds are threatened by anthropogenic changes in the marine environment (Croxall *et al.* 2012), and the development of Marine Renewable Energy Installations (MREIs) provides a relevant example of such pressures. However, the potential impacts of these devices on seabirds are still uncertain and studies to predict and assess these are seldom based on empirical evidence at existing sites. In the few cases where post-construction changes in the abundance of seabirds in the development zone has been quantified, species-specific behaviours have been observed, including evidence of both attraction and avoidance behaviour (Krijgsveld *et al.* 2007; Lindeboom *et al.* 2011). Thus, the continued assessment of the species-specific impacts of these devices is vital.

Current approaches to predict (pre-construction) and assess (post-construction) the impacts of MREIs on seabirds rely on understanding the species-specific risk of devices, the species-specific occurrence at-sea, (Langton, Davies & Scott 2011), and demographics of breeding populations. Although species-specific risks from both windfarms and tidal turbines have been evaluated (Furness *et al.* 2012; Furness, Wade & Masden 2013), knowledge of the distribution of seabirds at sea is limited in near-shore areas, and consistent directional changes in the abundance of seabirds within development zones would need to be extreme to be detected (Maclean *et al.* 2013). Additionally, this approach does not consider the cumulative impacts of spatial change on a specific population. Demographic studies at breeding colonies address this limitation, and provide population specific estimates of survival and reproductive rates. However, these estimates are likely to be inappropriate, due to the high numbers of non-breeding birds which may be affected, (Furness & Wanless 2014) and the time lag between real-time changes in demographic rates and results from population modelling (Beissinger & Westphal 1998).

This thesis has explored alternative approaches to predict and assess the impacts of MREIs and other types of spatial change on seabirds, and addresses some of the gaps in the literature regarding the limitations of current approaches.

Key findings

The overall aim of the study was to identify alternative approaches to predict and monitor potential impacts from environmental change in marine systems on seabirds. Firstly, it was necessary to establish a simple approach to identify important areas at-sea for seabirds, and thus **Chapter 2** demonstrates that, for Northern gannets at least, the time spent in a particular area can be used to determine the behaviour occurring there, specifically, that areas where birds spend more time correspond with important foraging areas (Warwick-Evans *et al.* 2015). This concept is applied throughout the thesis and the time-in-area approach is used in order to establish core foraging areas and home range areas in subsequent chapters.

Chapter 3 establishes that predictive models can be used to associate the near-shore fine-scale distribution of seabirds during the breeding season with environmental variables. In this case water depth, distance to the intertidal zone and distance to the nearest nest were important predictors in the near-shore fine-scale distribution of seabirds around Alderney. Such models can aid marine spatial planning in determining the potential impacts of coastal disturbances, such as tidal turbines, on seabirds. However, other, un-measurable variables must also be important to the near-shore fine-scale distribution of these seabirds. Thus, direct observations to identify the occurrence of seabirds in proposed development sites should continue to be implemented to thoroughly identify the potential for interactions with these devices.

Age-specific survival rates for Northern gannets breeding on Alderney were calculated in **Chapter 4** and underpin the continued growth of this population. However, low recovery rates of adult birds in recent years, has resulted in high levels of uncertainty surrounding these estimates. Thus, changes in demographic rates and population trends at the breeding colony, as a result of the installation of MREIs, may not be observed in the colony for many years (Beissinger & Westphal 1998). These findings support the implementation of a large scale colour ringing project, as recommended by Furness and Wanless (2014), which will enable increased precision in the estimation of age-specific survival rates, and from which we can quantify any post-construction impacts from the installation of MREIs.

Chapter 5 examines the inter-annual variation in the location and characteristics of foraging trips from Northern gannets breeding on Alderney and tracked over four breeding seasons with GPS devices. In 2015 birds went on longer foraging trips, using larger areas than in previous years. Additionally, differences in intra- and inter- individual variation in foraging locations between the years were observed. In this instance the inter-annual variation in foraging locations was driven by individuals visiting larger areas in all of their trips rather than individuals diversifying to visit more, distinct areas. Thus, if prey items become less abundant, or more widely distributed, increased numbers of gannets breeding on Alderney may encounter pressures from spatially explicit anthropogenic disturbances.

Additionally, this tracking data was used in the parameterisation of an Individual Based Model (IBM) described in **Chapter 6.** This spatially explicit model quantifies the impacts from windfarms proposed for development in the English Channel and North Sea on the survival, productivity and physiological state of Alderney's population of Northern gannets. Model outputs predict that the installation of these devices will have no effect on Alderney's gannets if avoidance behaviour is shown and a negligible effect if birds enter windfarm areas and risk mortality as a result of colliding with the turbines. Additionally, if rates of avoidance behaviour or collision risk models are re-evaluated, then these alterations may be easily incorporated into the existing model. Furthermore, this IBM is easily adaptable for other species of seabird and provides a robust approach to predict the impacts of various types of spatial change on seabirds.

Implications and future directions

This thesis provides simple, easily adaptable and cost-effective approaches to predict and assess the impacts of MREIs on seabirds. It demonstrates how the extensive datasets of seabird tracking data, from worldwide populations, can be used efficiently and cost-effectively, to predict colony specific impacts of spatial change on seabirds. However, some species of seabird are not amenable to tracking. For example, small birds cannot carry some devices and lower reproductive success has been observed in some tagged individuals (Hawkins 2004; Whidden *et al.* 2007). Thus, demographic studies are vital for long-term monitoring of breeding populations, and the implementation of long-term colour ringing studies will provide precise information about the effects of MREIs on breeding populations. Additionally, observations from land-based vantage points may provide a robust, yet inexpensive approach to monitor the near-shore, fine-scale distribution of seabirds.

In addition to the implementation of colour ringing projects, further development of these approaches could include modifications to the IBM developed in this thesis. Although this IBM provides the most comprehensive model to date with which to predict colony specific impacts of multiple sources of spatial change on seabirds, it was necessary to simplify some aspects of seabird behaviour. For example, the model overlooks some of the natural behaviour of seabirds, such as conspecific interactions on foraging trips, and time spent together on the nest (Nelson 2002), which could be addressed in future iterations of the model.

A further development in this field could build on the approach established by Soanes *et al.* (2013), and developed here for individuals, which predicts the size of the foraging area for the entire population based on the location of foraging areas for a tracked sample of the population. This provides a robust approach with which to predict the size of these areas, however, it is also important to know the location of these areas. Thus, the development of a universal model which can predict the locations of these missing areas, or the locations of foraging areas for seabirds where no tracking data exists, would enhance our ability to predict the impacts of spatial change on these populations. A combination of species-specific physiological traits, environmental features, such as bathymetry and primary productivity and knowledge of the size of the population could provide the basis for this modelling approach.

Conclusions

Overall our results suggest that MREIs proposed for development around Alderney and the English Channel are unlikely to cause population level impacts to the seabirds breeding on, and around, Alderney. Vantage point observations and predictive models suggest that the proposed tidal turbines are likely to be in deeper waters, further from nest sites and intertidal zones than locations commonly used by the seabirds during the breeding season. Additionally, a spatially explicit IBM, parameterised directly using tracking data from Alderney's population of Northern gannets, suggests that the windfarms proposed for development throughout the English Channel and North Sea will have little effect on these gannets at a population level.

With ever increasing human pressures on the marine environment it is vital that we identify robust approaches with which to predict and monitor the impacts from these disturbances. Although current approaches begin to address these, there is the need for more simple, widely applicable, and cost effective methods. The alternative approaches, described in this thesis provide simple, adaptable, and robust methodologies which could be applied when predicting and assessing the potential impacts on seabirds of proposed spatial change in the marine environment.

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