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Article in *Marine Ecology Progress Series* · May 2015

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# 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 2 approaches: time-in-area and kernel density (KD) analyses, which are widely employed to detect highly-used areas and interpret foraging behaviour from positional data. For KD analyses, the smoothing parameter ( $h$ ) was calculated using the ad hoc method ( $KD_{ad\ hoc}$ ), and  $KD_{h=9.1}$ , 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  $KD_{ad\ hoc}$ ,  $KD_{h=9.1}$  and time-in-area. Our findings demonstrate that foraging activity occurs in areas where seabirds spend more time, and that both KD 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 in 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.

**KEY WORDS:** Northern gannet · Biologging · Marine Spatial Planning · Accelerometer · GPS tracking · *Morus bassanus*

## INTRODUCTION

Marine Spatial Planning (MSP) is a key tool to address trade-offs between the economic, ecological and social objectives of marine management (Ehler & Douvère 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).

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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 ideal 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 et al. 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 et al. 2000). They exhibit 2 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 et al. 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 KD 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.

## MATERIALS AND METHODS

### Data collection

Fieldwork was licensed by the States of Alderney and conducted at the breeding colony of northern

gannets on Les Etacs, Alderney, Channel Islands (49°42'N, 2°14'W) between 10 June and 1 July 2013. A total of 15 birds with chicks approx. 2–4 wk 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 15 m (IgotU GT-600, Mobile Action Technology) and a tri-axial accelerometer (X6-2, Gulf Coast Data Concepts). The GPS devices were set to record a location every 2 min and the accelerometers at 25 Hz. Acceleration was measured along 3 axes, longitudinal (*X*, surge), dorso-ventral (*Z*, heave), and lateral (*Y*, sway). The devices were wrapped in heatshrink plastic and Extra Power tape (Tesa) 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 44 g, on average <2% of the birds' body mass. The total capture and tag attachment process lasted <10 min 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 2 to 3 wk 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 approx. 1 mo. 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 3 accelerometry channels were interpolated to a regular 25 Hz 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 s). The pitch i.e. the body angle of the bird relative to

horizontal, was calculated using all 3 acceleration signals:

$$\text{Pitch} = \tan^{-1} [X/\sqrt{Y^2 + Z^2}] \times (180/\pi)$$

and smoothed using a moving average (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 2 stage process. Firstly, the *X*, *Y*, *Z* and pitch data were visualised using IGORPro (ver. 6.34, WaveMetrics), 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, 2009, Vandenabeele et al. 2014) (Fig. 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. Identifying surface foraging was more challenging since 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 4 behaviours automatically based on unsupervised analysis of the acceleration signals. This method uses spectrogram analysis by continuous wavelet transformation (1 s 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 3 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

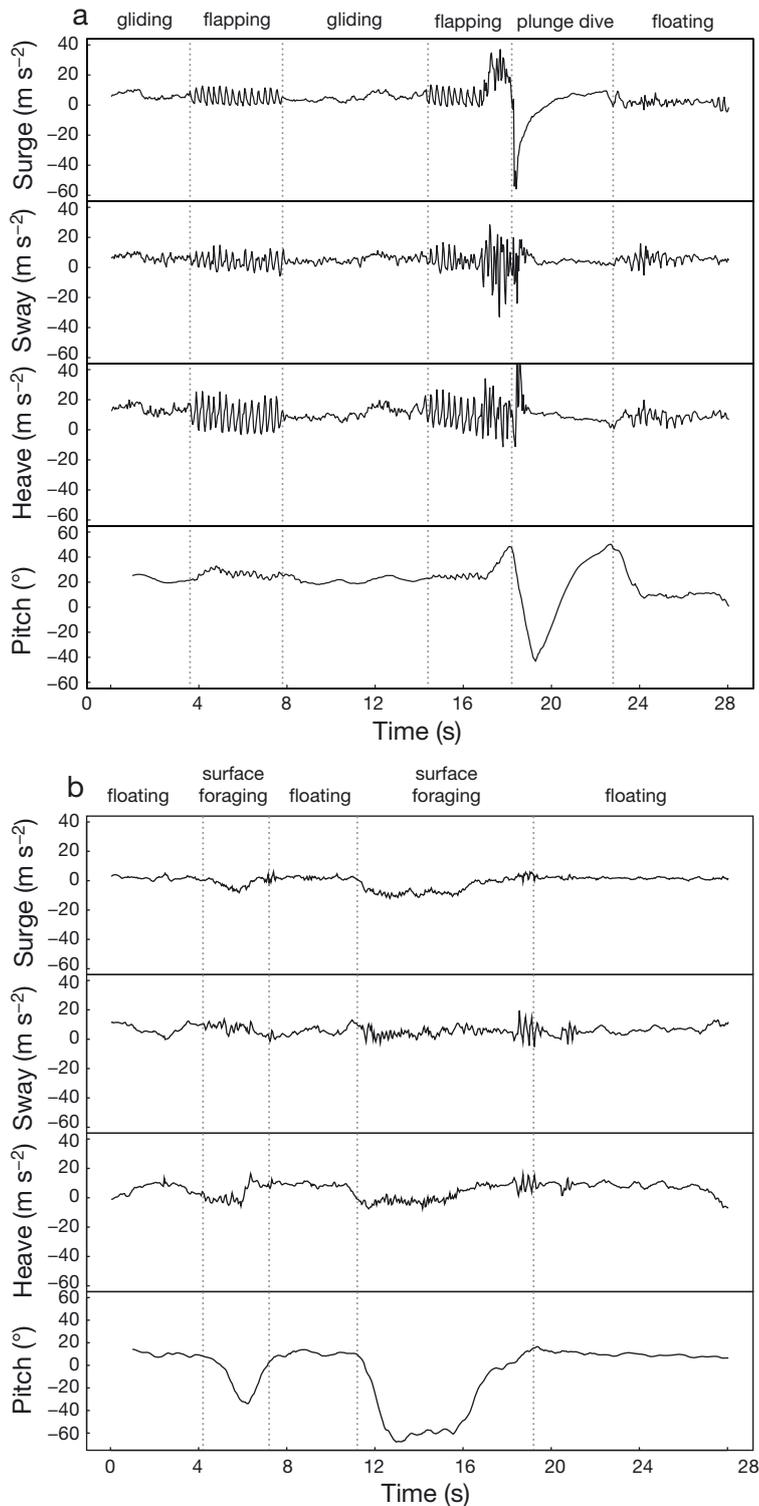


Fig. 1. Surge, sway, heave and pitch acceleration signals describing (a) flapping, gliding, plunge diving, and floating, and (b) floating and surface foraging. Flapping is classified by the oscillating patterns on the surge and heave axes. The gliding and floating behaviours are separated by pitch ( $\sim 20^\circ$  and  $0^\circ$ , 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  $-20^\circ$

the *adehabitatLT* package (Calenge 2006), in R (ver. 3.0.2, R Core Team 2013). The colony was defined as Les Etacs rocks with a 30 m surrounding buffer, based on personal observations of gannet behaviour. Trip duration (h), trip length (total distance covered, km) and range (max. 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 min in duration, whereas the second mode represented foraging trips lasting many hours. Foraging trips were therefore defined as any trip which was over 40 min 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 ver. 10).

Firstly, utilisation distributions were estimated for each trip for each bird by calculating the kernel density (KD) using a UTM zone 30 projection and a grid size of 1 km<sup>2</sup> in the *adehabitatHR* package in R (Calenge 2006). The smoothing parameter ( $h$ ) was calculated using (1) the ad hoc method ( $KD_{ad\ hoc}$ ):  $h = \sigma n^{-1/6}$ , whereby  $\sigma^2 = 0.5(\text{var } x + \text{var } y)$ , where  $x$  and  $y$  are 2-dimensional coordinates, and (2)  $KD_{h = 9.1}$ , where  $h = 9.1$  km, based on the mean scale of area restricted search (ARS) behaviour in gannets of 9.1 km (Hamer et al. 2009); 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 (s) in each 16.1 × 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 =  $\pi \times 9.1^2$ ). We also tested grid sizes of 5 × 5 km and 10 × 10 km and provide results from a comparison of grid sizes (see Table S1, Figs. S1 & S2 in Supplement 1 at [www.int-res.com/articles/suppl/m527p233\\_supp.pdf](http://www.int-res.com/articles/suppl/m527p233_supp.pdf)). 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 et al. 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 > 9 m s<sup>-1</sup>) and resting on the water (speed < 1.5 m s<sup>-1</sup>) (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 > 1 m s<sup>-1</sup> (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<sub>-480</sub> and L<sub>480</sub>, where L<sub>0</sub> is the focal location and L<sub>-480</sub> and L<sub>480</sub> are the locations 480 s before and after the focal location, i.e. over a 16 min duration (Wakefield et al. 2013).

The size of these core foraging areas (km<sup>2</sup>) were calculated for each trip for each bird using all 3 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 2 and 4 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 Boot package in R (Canty & Ripley 2014). This method involved sampling 9

birds with replacement (i.e. the same bird can 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 CI 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<sup>2</sup> (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 2 and 4 trips with a mean ( $\pm$ SD) trip duration of 26.0  $\pm$  10.0 h, mean trip length of 465  $\pm$  186 km and mean maximum distance from colony of 129  $\pm$  46 km (Table 1). Foraging activity occurred throughout the day and night, though at considerably reduced frequency between 21:00 and 02:00 h (Fig. 2). Figs. 3 & 4 show how the core foraging areas and the foraging events overlap using different filters and the KD and time-in-area approaches, respectively.

The proportion of foraging events occurring in the core foraging area was always very similar when KD<sub>ad hoc</sub> and KD<sub>h=9,1</sub> were used. Therefore, we report only results for KD<sub>h=9,1</sub>, 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 the time-in-area approach. Results for KD<sub>ad hoc</sub> are included in Table S2 in Supplement 2.

Table 1. Details of foraging trips (mean  $\pm$  SD) undertaken by 9 northern gannets from the Les Etacs colony, Alderney

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

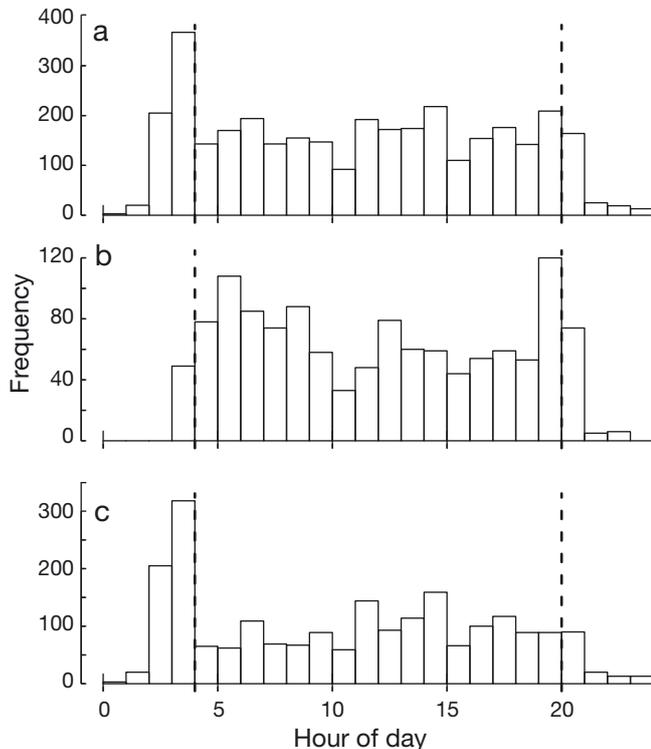


Fig. 2. Diurnal variation in foraging events from 26 foraging trips from 9 northern gannets from Les Etacs colony, Alderney. (a) All foraging events, (b) plunge dives and (c) surface foraging events. (Dashed lines) = sunrise and sunset. Time of day given in GMT

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). 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 (Fig. 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). 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 3). In contrast, when considering solely surface foraging, the results indicated a lower propor-

tion of foraging events occurred in the core foraging area when night-time data were removed (Table 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  $<1.5 \text{ m s}^{-1}$  and  $>9 \text{ m s}^{-1}$ , results in a lower proportion of all foraging events occurring in the core foraging areas designated using either of the methods (Table 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 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 3). Filtering the data for both speed and day results in very similar conclusions to data filtered for speed alone (Tables 2–4, Fig. 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  $>1 \text{ m s}^{-1}$ ) 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 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 3), however it did result in a more efficient designation of core foraging areas (Fig. 5). Filtering the data for both tortuosity and day results in very similar conclusions to data filtered for tortuosity alone (Tables 2–4, Fig. 5).

## 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

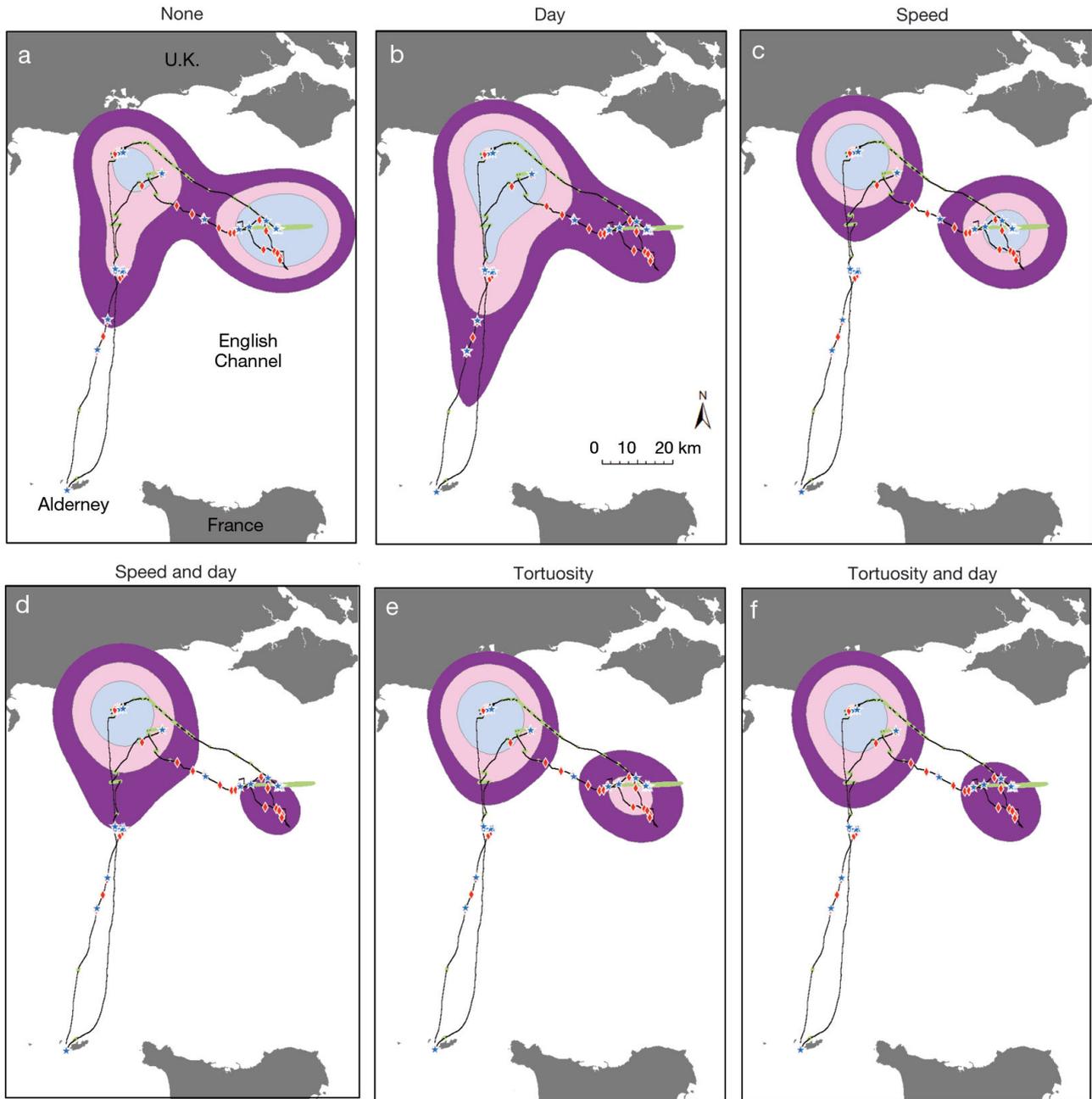


Fig. 3. Example of foraging events occurring in core foraging areas defined by  $KD_{h=9.1}$  and filtered for (a) no filter, (b) day, (c) speed, (d) speed and day, (e) tortuosity, and (f) tortuosity and day for one trip of a northern gannet. Colours and shapes indicate behaviours: flying (black line), floating (●), plunge diving (◆), surface foraging (★). Core foraging areas are 25% (pale blue), 50% (pink), 75% (purple)

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 is also subjective, and often not validated due to the nature of seabird foraging occur-

ring 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

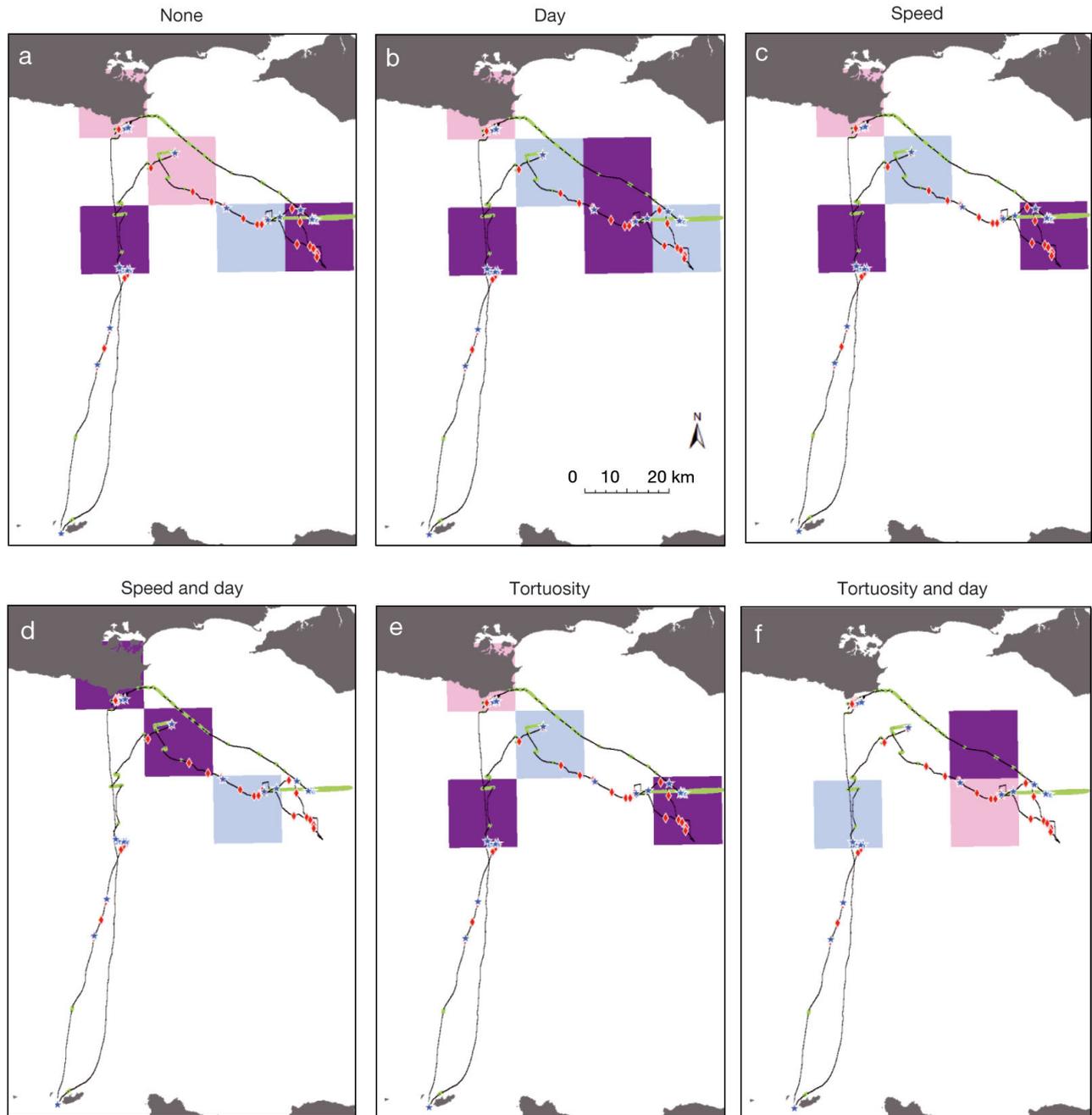


Fig. 4. Example of foraging events occurring in core foraging areas defined by time-in-area and filtered for (a) no filter, (b) day, (c) speed, (d) speed and day, (e) tortuosity, and (f) tortuosity and day for one trip of a northern gannet. Colours and shapes indicate behaviours: flying (black line), floating (●), plunge diving (◆), surface foraging (★). Core foraging areas are 25% (pale blue), 50% (pink), 75% (purple)

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

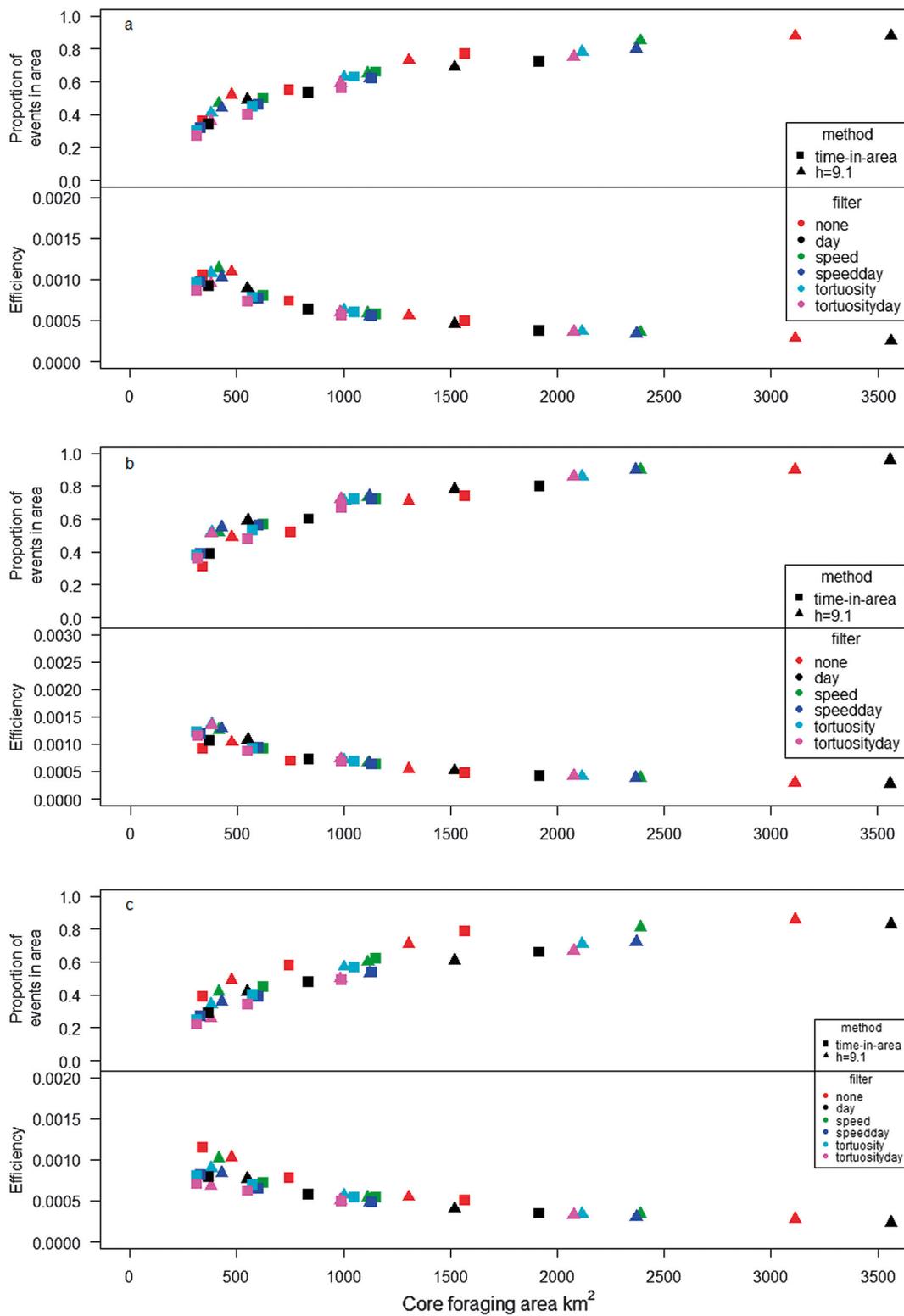


Fig. 5. Proportion and efficiency (proportion per km<sup>2</sup>) of (a) all foraging events, (b) plunge dives, and (c) surface dives occurring in the core foraging areas defined using  $KD_{h=9.1}$  and the time-in-area approaches. Points represent the 25, 50 and 75% probability of use for unfiltered data and data filtered for day, speed, tortuosity, speed and day and tortuosity and day (see Tables 2–4). Data presented are bootstrapped mean values for 26 foraging trips from 9 northern gannets from the Les Etacs colony, Alderney

Table 2. Bootstrapped proportion of foraging events (95% CI) occurring in the core foraging areas defined by utilisation density contours (25, 50 and 75%), filters, and using the kernel density and time-in-area approaches for 26 trips from 9 northern gannets from the Les Etacs colony, Alderney

Filter	Contour (%)	Proportion of forage events occurring in core foraging area	
		KD <sub>h=9.1</sub> (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 3. Bootstrapped proportion of all plunge dives (95% CI) occurring in the core foraging areas defined by utilisation density contours (25, 50 and 75%), filters, and using the kernel density and time-in-area approaches for 26 trips from 9 northern gannets from the Les Etacs colony, Alderney

Filter	Contour (%)	Proportion of foraging events occurring in core foraging area	
		KD <sub>h=9.1</sub> (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 4. Bootstrapped proportion of all surface foraging events (95% CI) occurring in the core foraging areas defined by the utilisation density contours (25, 50 and 75%), filters, and using the kernel density and time-in-area approaches for 26 trips from 9 northern gannets from the Les Etacs colony, Alderney

Filter	Contour (%)	Proportion of foraging events occurring in core foraging area	
		KD <sub>h=9.1</sub> (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)

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 (Figs. 3 & 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 established that in this instance a 5 × 5 km grid cell is more efficient in its ability to identify core foraging areas than larger grid cells (Table S1, Figs. S1 & S2 in the Supplement). 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 focusing on 1 or 2 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 (Fig. 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  $5 \times 5$  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 (Table S1, Figs. S1 & S2 in the Supplement).

### 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 et al. 2007), however given that these have short durations (Green et al. 2009), 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 num-

ber of prey items. We suggest this can be supported by the fact that seabirds are predominantly visual predators, diving after detecting prey (Garthe et al. 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 et al. 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 03:00 h. 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 et al. 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 et al. 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 et al. 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 areas was reduced when the data was filtered for speeds  $<1.5 \text{ m s}^{-1}$  and  $>9 \text{ m s}^{-1}$ , 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 that include only speeds where it is rational to assume that a bird is plunge diving. 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 et al. 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 area restricted search (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 11 km (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.

#### **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  $-20^\circ$ . 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.

### Conclusions

The time-in-area approach and KD 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 et al. 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.

*Acknowledgements.* The project was funded by a CASE PhD studentship from NERC and the Alderney Commission for Renewable Energy. Permission to carry out field work was granted by The States of Alderney. The Channel Island Bird Ringing Scheme gave permission to ring the gannets. We thank Tim Morley for help in the field, boat skipper Dave McAllister, Matt Spencer who assisted in the bootstrapping and James Grecian for assisting with the kernel density analysis. Three anonymous referees provided valuable comments on the manuscript.

### LITERATURE CITED

- Bartumeus F, Giuggioli L, Louzao M, Bretagnolle V, Oro D, Levin SA (2010) Fishery discards impact on seabird movement patterns at regional scales. *Curr Biol* 20: 215–222
- Bidder OR, Campbell HA, Gómez-Laich A, Urgé P and others (2014) Love thy neighbour: automatic animal behavioural classification of acceleration data using the k-nearest neighbour algorithm. *PLoS ONE* 9:e88609
- Bodey TW, Jessopp MJ, Votier SC, Gerritsen HD and others (2014) Seabird movement reveals the ecological footprint of fishing vessels. *Curr Biol* 24:R514–R515
- Bovet P, Benhamou S (1991) Optimal sinuosity in central place foraging movements. *Anim Behav* 42:57–62
- Burger AE (1997) Arrival and departure behavior of common murres at colonies: evidence for an information halo? *Colon Waterbirds* 20:55–65
- Burger AE, Shaffer SA (2008) Perspectives in ornithology application of tracking and data-logging technology in research and conservation of seabirds. *Auk* 125:253–264
- Calenge C (2006) The package ‘adehabitat’ for the R software: A tool for the analysis of space and habitat use by animals. *Ecol Modell* 197:516–519
- Camphuysen KCJ, Shamoun-Baranes J, Bouten W, Garthe S (2012) Identifying ecologically important marine areas for seabirds using behavioural information in combination with distribution patterns. *Biol Conserv* 156:22–29
- Canty A, Ripley B (2014) boot: Bootstrap R (S-Plus) functions. R Package version 1.3–15.
- Crain CM, Halpern BS, Beck MW, Kappel CV (2009) Understanding and managing human threats to the coastal marine environment. *Ann NY Acad Sci* 1162:39–62
- Crowder L, Norse E (2008) Essential ecological insights for marine ecosystem-based management and marine spatial planning. *Mar Policy* 32:772–778
- Ehler C, Douvère F (2009) Marine Spatial Planning: a step-by-step approach towards ecosystem-based management. Intergovernmental Oceanographic Commission and Man and the Biosphere Programme. IOC Manual and Guides No. 53, ICAM Dossier No. 6, UNESCO, Paris
- Enever R, Revill A, Grant A (2007) Discarding in the English Channel, Western approaches, Celtic and Irish seas (ICES subarea VII). *Fish Res* 86:143–152
- Fauchald P, Tveraa T (2003) Using first-passage time in the analysis of area-restricted search and habitat selection. *Ecology* 84:282–288
- Garthe S, Benvenuti S, Montevecchi WA (2000) Pursuit plunging by northern gannets (*Sula bassana*) feeding on capelin (*Mallotus villosus*). *Proc R Soc B* 267:1717–1722
- Garthe S, Montevecchi WA, Davoren GK (2007) Flight destinations and foraging behaviour of northern gannets (*Sula bassana*) preying on a small forage fish in a low-Arctic ecosystem. *Deep-Sea Res II* 54:311–320
- Gilliland PM, Laffoley D (2008) Key elements and steps in the process of developing ecosystem-based marine spatial planning. *Mar Policy* 32:787–796
- Green JA, White CR, Bunce A, Frappell PB, Butler PJ (2009) Energetic consequences of plunge diving in gannets. *Endang Species Res* 10:269–279
- Gremillet D, Dell’Omo G, Ryan PG, Peters G, Ropert-Coudert Y, Weeks SJ (2004) Offshore diplomacy, or how seabirds mitigate intra-specific competition: a case study based on GPS tracking of Cape gannets from neighbouring colonies. *Mar Ecol Prog Ser* 268:265–279
- Halpern BS, Longo C, Hardy D, McLeod KL and others (2012) An index to assess the health and benefits of the global ocean. *Nature* 488:615–620
- Hamer KC, Phillips RA, Wanless S, Harris MP, Wood AG (2000) Foraging ranges, diets and feeding locations of gannets *Morus bassanus* in the North Sea: evidence from satellite telemetry. *Mar Ecol Prog Ser* 200:257–264
- Hamer KC, Humphreys EM, Magalhães MC, Garthe S and others (2009) Fine-scale foraging behaviour of a medium-ranging marine predator. *J Anim Ecol* 78: 880–889
- Hawkins P (2004) Bio-logging and animal welfare: practical refinements. *Mem Nat Inst Polar Res, Spec Issue* 58: 58–68
- Hemson G, Johnson P, South A, Kenward R, Ripley R, Macdonald D (2005) Are kernels the mustard? Data from global positioning system (GPS) collars suggests problems for kernel home-range analyses with least-squares cross-validation. *J Anim Ecol* 74:455–463
- Hughes TP, Bellwood DR, Folke C, Steneck RS, Wilson J (2005) New paradigms for supporting the resilience of marine ecosystems. *Trends Ecol Evol* 20:380–386
- Langston R, Allen S, Crutchfield Z (2010) Birds. In: Huddle-

- ston J (ed) Understanding the environmental impacts of offshore windfarms. Information Press, Oxford
- Le Corre M, Jaeger A, Pinet P, Kappes MA and others (2012) Tracking seabirds to identify potential Marine Protected Areas in the tropical western Indian Ocean. *Biol Conserv* 156:83–93
- Lewis S, Benvenuti S, Dall–Antonia L, Griffiths R and others (2002) Sex-specific foraging behaviour in a monomorphic seabird. *Proc R Soc B* 269:1687–1693
- Lewis S, Benvenuti S, Daunt F, Wanless S and others (2004) Partitioning of diving effort in foraging trips of northern gannets. *Can J Zool* 82:1910–1916
- Lombard A, Reyers B, Schonegevel L, Cooper J and others (2007) Conserving pattern and process in the Southern Ocean: designing a marine protected area for the Prince Edward Islands. *Antarct Sci* 19:39–54
- Louzao M, Bécarea J, Rodriguez B, Hyrenbach KD, Ruiz A, Arcos JM (2009) Combining vessel-based surveys and tracking data to identify key marine areas for seabirds. *Mar Ecol Prog Ser* 391:183–197
- Machovsky-Capuska GE, Howland HC, Raubenheimer D, Vaughn-Hirshorn R, Würsig B, Hauber ME, Katzir G (2012) Visual accommodation and active pursuit of prey underwater in a plunge-diving bird: the Australasian gannet. *Proc R Soc B* 279:4118–4125
- Montevicchi W, Benvenuti S, Garthe S, Davoren G, Fifield D (2009) Flexible foraging tactics by a large opportunistic seabird preying on forage- and large pelagic fishes. *Mar Ecol Prog Ser* 385:295–306
- Patrick SC, Bearhop S, Grémillet D, Lescroël A and others (2014) Individual differences in searching behaviour and spatial foraging consistency in a central place marine predator. *Oikos* 123:33–40
- Patterson TA, Thomas L, Wilcox C, Ovaskainen O, Matthiopoulos J (2008) State–space models of individual animal movement. *Trends Ecol Evol* 23:87–94
- Piatt J, Sydeman W, Sydeman W, Piatt J, Browman H (2007) Seabirds as indicators of marine ecosystems. *Mar Ecol Prog Ser* 352:199–204
- Pinaud D (2008) Quantifying search effort of moving animals at several spatial scales using first-passage time analysis: effect of the structure of environment and tracking systems. *J Appl Ecol* 45:91–99
- R Core Team (2012) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. Available at: [www.r-project.org](http://www.r-project.org)
- Ropert-Coudert Y, Grémillet D, Ryan P, Kato A, Naito Y, Le Maho Y (2003) Between air and water: the plunge dive of the Cape Gannet *Morus capensis*. *Ibis* 146:281–290
- Ropert-Coudert Y, Grémillet D, Kato A, Ryan PG, Naito Y, Le Maho Y (2004) A fine-scale time budget of Cape gannets provides insights into the foraging strategies of coastal seabirds. *Anim Behav* 67:985–992
- Ropert-Coudert Y, Daunt F, Kato A, Ryan PG and others (2009) Underwater wingbeats extend depth and duration of plunge dives in northern gannets *Morus bassanus*. *J Avian Biol* 40:380–387
- Sakamoto KQ, Sato K, Ishizuka M, Watanuki Y, Takahashi A, Daunt F, Wanless S (2009) Can ethograms be automatically generated using body acceleration data from free-ranging birds? *PLoS ONE* 4:e5379
- Soanes LM, Arnould JP, Dodd SG, Sumner MD, Green JA (2013) How many seabirds do we need to track to define home-range area? *J Appl Ecol* 50:671–679
- Soanes LM, Bright JA, Bolton M, Millett J, Mukhida F, Green JA (2014) Foraging behaviour of Brown Boobies *Sula Leucogaster* in Anguilla, Lesser Antilles: Preliminary identification of at-sea distribution using a time-in-area approach. *Bird Conserv Int* 25: 87–96
- Stauss C, Bearhop S, Bodey T, Garthe S and others (2012) Sex-specific foraging behaviour in northern gannets *Morus bassanus*: incidence and implications. *Mar Ecol Prog Ser* 457:151–162
- Sumner MD (2011) trip: Spatial analysis of animal track data. R package version 1.1–10.
- Tallis H, Levin PS, Ruckelshaus M, Lester SE, McLeod KL, Fluharty DL, Halpern BS (2010) The many faces of ecosystem-based management: making the process work today in real places. *Mar Policy* 34:340–348
- Thiebault A, Tremblay Y (2013) Splitting animal trajectories into fine-scale behaviorally consistent movement units: breaking points relate to external stimuli in a foraging seabird. *Behav Ecol Sociobiol* 67:1013–1026
- Tremblay Y, Cherel Y, Oremus M, Tveraa T, Chastel O (2003) Unconventional ventral attachment of time–depth recorders as a new method for investigating time budget and diving behaviour of seabirds. *J Exp Biol* 206: 1929–1940
- Vandenabeele SP, Grundy E, Friswell MI, Grogan A, Votier SC, Wilson RP (2014) Excess baggage for birds: Inappropriate placement of tags on gannets changes flight patterns. *PLoS ONE* 9:e92657
- Votier SC, Bearhop S, Witt MJ, Inger R, Thompson D, Newton J (2010) Individual responses of seabirds to commercial fisheries revealed using GPS tracking, stable isotopes and vessel monitoring systems. *J Appl Ecol* 47: 487–497
- Waggitt J, Briffa M, Grecian W, Newton J, Patrick S, Stauss C, Votier S (2014) Testing for sub-colony variation in seabird foraging behaviour: ecological and methodological consequences for understanding colonial living. *Mar Ecol Prog Ser* 498:275–285
- Wakefield ED, Bodey TW, Bearhop S, Blackburn J and others (2013) Space partitioning without territoriality in gannets. Science, New York, NY
- Watanuki Y, Niizuma Y, Geir WG, Sato K, Naito Y (2003) Stroke and glide of wing-propelled divers: deep diving seabirds adjust surge frequency to buoyancy change with depth. *Proc R Soc B* 270:483–488
- White C, Halpern BS, Kappel CV (2012) Ecosystem service tradeoff analysis reveals the value of marine spatial planning for multiple ocean uses. *Proc Nat Acad Sci USA* 109: 4696–4701
- Wood A, Naef Daenzer B, Prince P, Croxall J (2000) Quantifying habitat use in satellite tracked pelagic seabirds: application of kernel estimation to albatross locations. *J Avian Biol* 31:278–286
- Worton BJ (1995) Using Monte Carlo simulation to evaluate kernel-based home range estimators. *J Wildl Manag* 59: 794–800