The Ornithodolite as a tool to quantify animal space use and habitat selection; a case study with birds diving in tidal waters

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Abstract

Animal-attached technologies can be powerful means to quantify space-use and behaviour, however, there are also ethical implications associated with capturing and instrumenting animals. Furthermore, tagging approaches are not necessarily well-suited for examining the movements of multiple individuals within specific, local areas of interest. Here, we assess a method of quantifying animal space use based on a modified theodolite with an inbuilt laser rangefinder. Using a database of > 4,200 tracks of migrating birds, we show that detection distance increases with bird body mass (range 5 g - >10 kg). The maximum distance recorded to a bird was 5500 m and measurement error was ≤ 5 m for targets within this distance range; a level comparable to methods such as GPS tagging. We go on to present a case study where this method was used to assess habitat selection in seabirds operating in dynamic coastal waters close to a tidal turbine. Combining positional data with outputs from a hydrographic model revealed that great cormorants (*Phalacrocorax carbo*) appeared to be highly selective of current characteristics in space and time; exploiting areas where mean current speeds were < 0.8 m s^{-1}, and diving at times when turbulent energy levels were low. These birds also orientated into tidal currents during dives. Taken together, this suggests that collision risks are low for cormorants at this site, as the two conditions avoided by cormorants (high mean current speeds and turbulence levels), are associated with operational tidal turbines. Overall, we suggest that this modified theodolite system is well-suited to the quantification of movement in small areas associated with particular development strategies, including sustainable energy devices.

Keywords: GPS, movement ecology, seabird, tidal turbine, habitat use

Competing interests: We have no competing interests.

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Introduction

Electronic tagging can now be used to provide data on the spatial movements of animals with sub-second temporal resolution (Ropert-Coudert & Wilson 2005). Nonetheless, the size of loggers providing reasonably high frequency data for significant durations (i.e. substantial battery life) means that the use of this technology is still limited to relatively large animals (Chittenden *et al.* 2009; Ropert-Coudert & Wilson 2005; Wilson *et al*. 1986). The present recommendation followed by many scientists, that the weight of the logger should not exceed 3 % of the weight of the bird, is a contentious issue. Indeed, the only way to know that there are no deleterious impacts would be to compare and evaluate the behaviour of “control” birds without any device attached (Nicolaus *et al*., 2008). There are also ethical considerations associated with the capture, handling and instrumentation of individuals (Wilson & McMahon 2006). In some cases, tags can affect the behavior of the individual and hence influence the very measurements such devices are designed to make (Elliot 2016; Saraux *et al*. 2011; Stothart *et al.* 2016).

Beyond the ethical implications of instrumenting animals, biotelemetry may not be the best approach for addressing particular study questions. For instance, questions such as how animals operate with respect to specific developments may be concerned with the movements of large numbers of individuals, or even different taxa, in a relatively small area. In these cases, tagging may not be ideal, as tagged individuals may not necessarily use the site of interest, or if they do, patterns of resource selection may be based on a low number of individuals, relative to the number using the site.

Eulerian, or static measurements, have also been important in quantifying animal locations (Turchin 1998). Like tagging, the range and resolution of resulting data varies among the different techniques. Aerial surveys can provide accurate information on the distribution of individuals over large areas (Camphuysen *et al*. 2004); however, the costs of this technique mean that few surveys tend to be run per study, limiting the ability to monitor changes in space-use through time. This method also provides point counts rather than movement trajectories. Radar can provide vast, high resolution datasets on space-use relative to a particular location, or series of connected locations (Alerstam 1990; Chapman & Graber 1997; Eastwood 1967; Gauthreaux & Belser 2003; Gürbüz *et al*., 2015) and it can also be used to derive movement trajectories. However, it is rarely possible to automate the identification of targets or even achieve identification at all (McCann & Bell 2017). The data processing requirements (e.g. to remove signal backscatter, from the movement of non-target objects) are also substantial, although international initiatives such as the European Network for the Radar surveillance of Animal Movement may lead to advances here (Alves *et al*. 2014).

Theodolites are instruments originally used for land surveying, and have also been used for animal tracking (Bailey & Thompson 2006, Piersma et al. 1990). This approach to animal tracking combines aspects of both Eulerian and Lagrangian methods, as whilst it is place-based, individuals can be identified and, in some cases, selected according to species or behavior. Individuals can also be followed, allowing users to reconstruct movement tracks (Bailey & Thompson 2006). Theodolites are relatively straightforward when it comes to the collection and processing of data (relative to radar data, for instance). They can also provide locations with high accuracy and precision when compared to land-based or seagoing surveys that use grids to allocate observations to geographic areas. Traditional theodolites measure azimuth and elevation angles and do not measure distance directly. If the height of the observer is known, relative to the target, a single theodolite can be used to derive the 2D position of an object on a flat substrate (McCormack 1991). Otherwise, a dual theodolite system is needed to derive the target's 3D position (Tucker & Schmidt-Koenig 1971). Other non-invasive static methods like 3D video tracking can yield similar precision with finer temporal resolution than theodolites (positional error of 3D video tracking can be a few centimetres at closer ranges) but these operate across ranges of up to a few hundred metres (Cavagna *et al*. 2008; De Margerie *et al*. 2015; Evangelista *et al*. 2017).

Theodolites that incorporate a distance measure can be used to estimate a target's position accurately whether the animal is on the substrate or in flight (Wilson & Wilson 1988; Hedenstrom & Alerstam 1994; Piersma *et al*. 1990). Various researchers have developed the system further in order to estimate the airspeeds of flying animals. Double theodolite systems were first used to quantify airspeeds using triangulation of horizontal and vertical angles to resolve distance and subsequently combining positional data with measurements of wind speed (Tucker & Schmidt-Koenig 1971). This superseded previous methods where birds were followed by vehicles to estimate ground speed (Michener & Walcott 1967). A further modification was proposed by Pennycuick (1982), who combined an anemometer and a coincidence rangefinder to produce a single, portable system that could track objects in flight and estimate their airspeed. This system is now based on a laser rangefinder incorporated in a pair of Vector 21 binoculars (Pennycuick *et al*. 2013), which measure distances directly and provide improved accuracy and precision. As this system was specifically developed to quantify airspeed in birds, it is only very recently that it has been used to examine animal distributions (Hedenström & Åkesson 2016; Shepard *et al*. 2016). We suggest that this technique has potentially broad ecological applications, which have yet to be fully realised. We note, however, that the incorporation of the laser range-finder means that the system cannot get a return from the water surface or the smooth, water-covered surfaces of most cetaceans.

In this study, we use the Vector Ornithodolite (hereafter, VOD) to examine the factors affecting the fine-scale space-use of seabirds operating in a highly dynamic tidal environment. Data were collected in Ramsey Sound, Pembrokeshire, UK, where a tidal turbine is currently installed but non-operational (Evans *et al*., 2015). We use hydrodynamic numerical model simulations of current flows in the Sound to investigate the conditions that birds select during foraging. The utility and limitations of the equipment for the wider community of movement ecologists are also examined, specifically through the assessment of the measurement error and whether maximal detection distances vary according to body size. The latter was investigated using a large database of 4,284 positional fixes taken from birds during migration.

Methods

System performance

The workings of the VOD have been described in detail elsewhere in terms of the use of this equipment for the measurement of animal location and airspeed (Pennycuick *et al*. 2013), hence only a summary will be given here. The Vectronix USMC Vector 21 is a pair of binoculars with an inbuilt laser rangefinder, digital compass (giving azimuth angle), and inclinometer, providing both inclination and azimuth angles (Vectronix™ 2004). The user obtains co-ordinates of a target by pressing and releasing two buttons when the target is between the cross-hairs in the view finder and positions are sent to a laptop via a cable. In this study, a simple programme was written in Visual Basic (Microsoft) to enable users to append information including species and behavior to each set of co-ordinates.

The Vector measures distances from 5 m to over 10 km (Vectronix™ 2004). The error associated with distance measurement must be ascertained by the user. We therefore used the following protocol to quantify this: Locations were taken to a fixed target, in this instance an area next to a prominent ledge, approximately 1 m^2 situated on

Mumbles boat house (51°34'12.0"N 3°58'32.4"W) in Swansea Bay. Fixes were taken at increasing distances from 50 m to 5 km, with 10 fixes being taken at each of 12 distance intervals. Intervals were selected based on the ability to have a clear view of the target.

The ability to get returns from the laser (and hence record the target's co-ordinates) in some cases, may be related to the target characteristics (i.e. size, color etc.) and the experience of the observer. In order to examine how maximum distance varied in relation to body size, multiple, sequential, locations of birds migrating past Ottenby observatory, southern Sweden, were collected from 2012 to 2017. The methods are detailed in full by Hedenström and Åkesson (2016). Each series of locations from an individual bird is hereafter referred to as a 'run'. The furthest distance measurement per run was selected for further analysis. We note that observers were not aiming to get returns from the furthest targets they could observe and the resulting distances are therefore only an indication of those that could be attained. Data were collected by experienced ornithologists, with one observer operating the VOD and the other identifying birds using a telescope, although it is possible for a single person to operate the system using a telescope to identify distant targets where necessary. This approach thus provides an insight into the distances that can be obtained where experience in bird identification is not a limiting factor.

Data analysis

Generalised Linear Models were used to assess whether the maximum distances were affected by the mass, wingspan and flock size of the target, with the global model including these terms and an interaction between body mass and flock size. As mass and wingspan are related, the residual variation from the allometric prediction of wingspan was used in the model, with the predicted wingspan being taken as mass$^{0.39}$ for each of the 151 study species (Pennycuick 2008). Distance and body mass were log10 transformed and regressions were run in base R (R core group 2017). Models were compared using their AIC scores.

Space use within Ramsey Sound

Data collection took place in Ramsey Sound, Pembrokeshire, from a vantage point based near St Justinian 51°52'42.4"N 5°18'38.4"W, which provided views of the entire Sound. Data collection began on the 24th April 2017 and included a total of 35 visits. Surveys were conducted in periods of calm and dry weather with good visibility (i.e. where the horizon remained visible), and for sea states of ≤ 2 on the Beaufort scale (corresponding to wind speeds of <= 3 m s^{-1}). The locations of seabirds within the Sound were recorded across the entire tidal cycle using the VOD. A full scan of the area was completed every 15 minutes for a minimum session length of 4 hours and the tidal state was noted (flood, ebb or slack water which occurred 2.5 hours after high and low water respectively). Locations were recorded for all birds observed within a scan, with birds being identified to species level (distance permitting). Group size and behavior were also recorded. If foraging behavior was observed, individuals were followed after the main scan in order to take positional fixes at the start and end points of individual dives. Care was taken to ensure the entire Sound was searched systematically during each 15-minute scan to reduce any spatial bias in sightings.

Azimuth, elevation angle and distance data for bird observations were subsequently converted to latitude and longitude, using the observer's known GPS position. These polar coordinates were then used to identify areas of high general use within the Sound and areas specifically associated with foraging. Distributions were plotted using fixed kernel density estimation (KDE) in the statistical analysis software R using the packages 'ggmap' (Khale and Wickham 2016) and 'MASS' (Ripley *et al.* 2017). An estimate of all-encompassing foraging range of great cormorants (*Phalacrocorax carbo*), was provided by the 90% KDE contour (as the most frequent diving species).

To investigate how cormorants dived in relation to current vectors, the horizontal distance covered between the start and end points of a dive was calculated using the Haversine formula (Jenness 2011). The dive bearing was also calculated, assuming the bird followed a straight line from its start to end position (Wilson & Wilson 1988). The convention with axial data, such as those collected here, is to transform the bearings so they lie between 0 and 180°, calculate the mean, and finally back-transform to plot the data as a circle diagram (Cox 2001). These data were visualised using Oriana, which was also used to perform a Rayleigh's Z test to assess whether bearings conformed to a uniform distribution (Kovach 2011).

The Telemac-2D (v7r2) open-source hydrodynamic ocean modelling software suite was used to quantify spatial and temporal variation in current speed (m s^{-1}), turbulent energy (J kg^{-1}) and water depth (m) within Ramsay Sound for the entire study period. This model solves the depth integrated Saint-Venant free surface flow equations, derived from the full Reynolds Averaged Navier Stokes (RANS) equations for momentum and continuity (Hervouet 2007). The finite element unstructured mesh varies from coarse (approximately 10 km at model boundaries) to fine (approximately 50 m around the North Wales coast) for a domain encompassing the Irish Sea (50^{o}N to 56^{o}N, 8^{o}W to 3^{o}W). Values of hydrodynamic conditions were provided at approximately 300 m and 10-minute resolution in Ramsay Sound. Model simulations are forced at domain boundaries with tidal harmonic constituents only and no other influences to dynamics are considered. However, in shallow coastal regions were the water column remains well mixed, vertically homogenous velocities can be expected above the bottom boundary layer. Therefore depth-averaged approximations provide good estimation of flow characteristics. Full details of numerical model set up, calibration and validation are detailed elsewhere (Piano *et al.* 2017; Piano *et al.* 2015).

To facilitate comparisons with the spatial and temporal distributions of dives, values of hydrodynamic conditions were transposed onto an orthogonal grid of 100 m resolution using kriging interpolation. Kriging was performed using the 'automap' package in R

(Hiemstra *et al.* 2009). The spatial distribution of dives was compared to that of mean current speeds in Ramsay Sound. As tidal environments are broadly divisible into areas of comparatively fast and slow mean current speeds (Benjamins *et al*. 2015, Waggitt *et al*. 2017), such comparisons provide useful insights into general habitat-use. Furthermore, as tidal stream turbines generally occupy areas of faster mean current speeds (Fraenkel 2006), these comparisons would also identify the likelihood of interactions between diving birds and installations (Waggitt & Scott 2014). The temporal distribution of dives across tidal states (ebb-flood) within persistently used areas was also examined in relation to current speed, turbulent energy and depth. These comparisons would identify the hydrodynamic conditions experienced by individuals during dives. Estimates of hydrodynamic conditions were extracted using the mean coordinates of dives, which were highly aggregated.

Results

System performance

Variance in distance measurements increased with distance (Figure 1). The standard deviation was around 1-2 m for distances < 2 km and was close to 0.1% of distance measurements overall. Note that the error measured here reflects random deviation only. The overall accuracy given in the user manual is ± 1 m (Vectronix™ 2004).

Over 4,200 runs were recorded for migrant birds in Sweden. These were filtered to obtain a “maximum distance” for each of the 151 species in the dataset. The smallest species recorded was a goldcrest (*Regulus regulus*) weighing ~ 6 g, and the maximum distance achieved for this species was 913 m. A whooper swan (*Cygnus cygnus*) with a weight of ~ 9 kg, was recorded 2,742 m from the observer, and the largest overall distance, obtained from a migrating flock of barnacle geese (*Branta leucopsis*), was 5,498 m. The majority of observations were from single birds, with 56 observations being from flocks of between 2 and an estimated 450 individuals.

Maximum distance was best explained by a model with bird body mass as the sole explanatory variable (beta = 0.12, F=120.9, df=149, p<0.001, adj R^2 = 0.44) (Figure 2). A model including both mass and the residual wingspan received equivalent support (ΔAIC < 2), although wingspan had a low effect size and was non-significant (beta < 0.001, p = 0.4). The global model that also included flock size and the interaction between flock size and body mass, showed that this interaction did not significantly influence maximum distance (z =1.178, df =150, p>0.1) and neither did flock size in isolation (z =1.531, df=150, p>0.1).

Current selection within Ramsey Sound

Seven seabird species were recorded in 140 hours of survey effort: common guillemot (*Uria aalge*), razorbill (*Alca torda*), European shag (*Phalacrocorax aristotelis*), Northern gannet (*Morus bassanus*), great black-backed gull (*Larus marinus*), lesser black-backed gull (*Larus argentatus*) and the great cormorant (Table 1). The majority of all bird locations were of individuals rafting or flying, these were not included in the analysis (see supplementary information, S1). The cormorant was the only species with > 10 dives recorded across all surveys (n = 56). Birds avoided the main channel where mean current speeds were > 1.5 m s^{-1}, preferring to both loaf and forage in relatively slack waters, where mean current speeds were < 0.8 m s^{-1} (Figure 3). Cormorants foraged close to the mainland (0.1 - 0.7 km from the vantage point) in a highly restricted area which is characterised by low current speeds (min = 0.29 m s^{-1}, max = 0.81 ms^{-1}, mean = 0.48 ms^{-1}) and water depths of 24.5 - 26 m.

When it comes to the particular times that cormorants dived, over 80% of cormorant dives occurred 4 hours after high water or later, when tidal height was rising (Figure 4). There was no clear pattern when it came to the selection of current speeds, which varied from ~ 0.2 - 1.0 m s^{-1} in this area across the tidal cycle (Figure 4). However, dive times did coincide with periods of falling turbulence, with over 80 % of dives occurring when the turbulence was < 0.02 J kg^{-1} (with turbulence increasing up to a mean of 0.04 J kg^{-1}).

Dive bearings were not uniformly distributed (n= 40, Rayleigh's $Z_{5.503}$, p< 0.005) and the mean orientation (mean=168.8 ± 8.3°) was into the current (Figure 5). Birds also covered short distances during dives (mean = 44.5 m, median = 17.8 m, max = 261 m, min = 0.6 m) supporting the notion that birds are orientating into the flow. However, birds can be drifted backwards where swim speed is less than the current strength, effectively producing a bearing that is coincident with the current vector.

Discussion

System performance

Our results show that the standard deviation of distance measurements is 1- 2 m within a 2 km range. The real 3D positional error for moving birds may be increased by (i) systematic error of the laser distance measurement, and (ii) possible influences of target size and color (the latter would be difficult to test as this may vary depending on whether the upper or lower surface of the wing is visible, which varies within the wingbeat cycle). Errors are also likely in (iii) azimuth and inclination angles, in fact, azimuth error is probably the main source of positioning error within the VOD. Measuring these effects is beyond the scope of the present study, but we assume that these additional sources of position error are of the same order of magnitude as the random error we measured for distance. Therefore, VOD positioning error is probably comparable to what is generally accepted for GPS data, which is estimated to be in the range of 3-28 m (Frair et al. 2010). However, while spatial error in tagging technology can lead to the misrepresentation of behaviors in a scale-dependent manner (Browning *et al*. 2017; Costa *et al*. 2010), animal locations can be coded according to behavior (as well as species, age, and other factors that may be of interest) with the VOD. The downside of the VOD is that it has relatively intensive requirements when it comes to survey effort.

The “maximum” distance recorded to birds migrating past the Swedish coast increased with bird body mass. This suggests that larger birds are detected more readily at greater distances (the same may be true of larger flocks), which could lead to some sampling bias in studies recording locations of smaller species. Although large flocks of birds may be detected by an observer earlier than individuals, this did not influence the ability to obtain a fix using the VOD in our study. However, flocking may have more complex effects on the ability to detect targets, for instance the type of flock formation may influence detection ability: echelon formations may be easier for observers to spot at distance as opposed to clustered flocks, and these flocking principles could also be affected by body mass. Larger species, such as geese and swans (*Anatidae & Cygnus sp.*) tend to form echelon formations whilst smaller birds, like doves (*Columbidae*), form clusters. Our experiences during data collection also suggest that it can be difficult to obtain a fix from species at the smaller end of the size spectrum, even when they have been detected with optics and are within range. Nonetheless, a location was obtained from the smallest species (5.5 g) when it was ~ 1 km from the observer and there were several instances where birds weighing 50 - 100 g were recorded ~ 2 km away, demonstrating that small birds (including those too small to be tagged) can be detected and recorded at substantial distances. When it comes to the model predictions of how the VOD generally performed, birds of 10, 100 and 1,000 g were readily recorded at distances of 500, 1,000 and 2,000 m, respectively.

Spatial bias is well documented for land-based surveys, which use distance bands or grid systems for assessing the locations of birds foraging in near-shore tidal habitats (Waggitt *et al*. 2014; Waggitt *et al*. 2016a). Here, birds are less likely to be detected if they forage further from the shore. It seems unlikely that this affected the results in the present study, given that the full length of Ramsey Sound (1.9 km) is less than the distance over which large birds such as seabirds can be detected and recorded (see S1 for a map of the raw data), and that surveys were conducted in periods of low swell height. Therefore, while some of the limitations of shore-based surveys still apply to the use of the VOD in a general sense, with both being based on the use of a telescope and binoculars to scan for birds, we consider it unlikely that we have underestimated the usage of fast flowing currents that lie further from the coastline.

Like GPS tagging and land-based surveys, the VOD can be affected by environmental conditions. The probability of detecting a target or getting a return with the VOD may be influenced by sea state and surface conditions (although these factors were not investigated directly here), and false returns can be given from fog or cloud, although spurious returns are easy to identify and remove. The system can also be affected by high winds that make the equipment unsteady to hold and difficult to obtain a fix on the target bird.

Many studies have discussed the potential impacts of bird capture and recapture and the deleterious effects of tags (Bennisson *et al*. 2017; Calvo & Furness 1992; Götmark 1992; Phillips *et al*. 2003; Vandenabeele *et al*. 2011; Wilson & Vandenabeele 2012). The VOD has advantages here, as it does not involve marking animals and in fact observers can be placed at a vantage point away from breeding colonies, thereby reducing disturbance. The operational range of the system also far exceeds predicted flushing distances, which can be a factor in other surveys, including boat-based work (Schwemmer *et al*. 2011). Finally, the VOD uses a laser tachometer to measure distance. It seems unlikely that this could have adverse effects on target animals, as medical literature citing retinal injuries from handheld laser devices indicates that risk of injury is high if the primary light source is in the 'green' end of the light spectrum and if pointed directly at the eye from less than one metre away (Luttrull & Hallisey 1999; Mainster *et al*. 2004; Wyrsch & Baenninger 2010).

Habitat Selection

Relatively few studies have quantified habitat use at very fine scales in seabirds (Holm & Burger 2002; Waggitt *et al*.. 2016a; Waggitt *et al.*. 2016b; Zamon 2003). Here we show that cormorants were highly selective in terms of both the area and the time of the tidal cycle they chose to dive. Ramsey Sound experiences extreme tidal variation with current speeds > 3.5 m s^{-1} and strong eddy formation over the rocky reefs. Cormorants dived in a highly localised area of the Sound, showing a general avoidance of high current speeds in the main channel and areas of high turbulence caused by rocky reefs at 'the Bitches' and 'Bishop's and Clerks'. While we did not test whether current speed was the ultimate driver of space-use, it seems likely that birds were responding to low current speed, prey availability, or a combination of both these factors. This follows from the observation that birds were orientating into the current during their dives, as has been hypothesised by previous studies (Gremillet et al., 1998;

Wilson & Wilson 1988), and travelling short distances. This pattern of diving repeatedly in the same place, suggests that cormorants are more likely to be foraging mid-water, as the rate at which benthic prey would be replenished by the changing tide would be negligible (Rahel 1988; Schneider & Piatt 1986). Furthermore, the sea bed in Ramsey Sound consists of gravel and hard rock which is less suitable for benthic fish species (Fischer 2000). It therefore seems likely that cormorants were targeting shoaling fish in highly specific areas of the Sound.

Pelagic fish tend to shoal in areas of minimal water turbulence where current speeds are relatively low (Cury & Roy, 1989; Fréon & Misund 1999), which generally accords with the conditions that cormorants selected. As stated above, the area where birds were diving was characterised by a relatively low current speed compared to the main channel. Within this, and over the changing conditions of the tidal cycle, birds showed less selectivity of current speed, diving over a reasonably wide range of available speeds, up to ~ 0.75 m s^{-1}, and only appearing to avoid the strongest currents of ~ 1 m s^{-1}. What was striking, however, was the tendency to dive on the flood tide, which appeared to be strongly related to turbulence levels, with birds selecting times of low turbulence.

Overall therefore, when and where cormorants dive appears to be influenced by a hierarchy of factors operating in space and time. In contrast to these findings, Holm and Burger (2002) showed that pelagic cormorants (*Phalacrocorax pelagicus*) showed no significant response to tidal height or current strength. In fact, individuals were more likely to dive in areas of high turbulence within eddies (although values of current speed and turbulence coefficients are not known) (Sealy 1975). Whilst Waggitt *et al.* (2017) found that European shags *Phalacrocorax aristotellis* were generally associated with areas of low mean current strengths among five locations in Scotland, there were exceptions to this rule. These differences may well be driven by patterns of prey availability, which can vary between sites and predator species. Nevertheless, this study agrees with a growing consensus that associations with areas of fast mean currents are comparatively rare among UK cormorant species (Waggitt *et al*. 2017).

The need for detailed information on foraging patterns, including how tidal stream features contribute to foraging success and the direction of travel in relation to currents, has been highlighted in a recent review by Benjamins *et al*. (2015), as these factors will ultimately influence the likelihood of animals exploiting hydrodynamic features. Such associations are important in advancing our understanding of the species and sites where collisions between seabirds and tidal turbines are most likely. The risk of diving seabirds being pulled into the path of moving components of tidal stream devices persists through either being i) passively dragged by strong currents or by ii) birds actively foraging *with* the direction of the coincident current vector (Benjamins *et al*.. 2015; Waggitt & Scott 2014). However, there are several indicators that the tidal turbine may represent a relatively low risk to seabirds in Ramsey Sound. The Sound appears to be used by relatively few seabirds, at least in the conditions sampled during this study, despite the fact that around 2,000 pairs of auks breed on Ramsey Island (Mitchell *et al.* 2004). Furthermore, seabirds tended not to use the main channel, which has the greatest current speeds, making it most suitable for marine energy (ME) installations (Mueller & Wallace 2008; Pelc & Fujita 2002; Piano *et al*. 2017).

Cormorants have previously been identified as one of the species most at risk from tidal turbine developments (Furness *et al*. 2012; Langton *et al*. 2011) due to their high usage of tidal races for foraging and their propensity to forage on benthic prey (Furness *et al*. 2012; Garthe & Hüppop 2004). Cormorants were the birds most commonly diving in Ramsey Sound, even though no cormorants are recorded as breeding on Ramsey and the nearest sizeable colony (Thorn Island, 32 pairs) is located 25 km away (Mitchell *et al*. 2004). Therefore, the cormorants observed in our study were likely to be non-breeding individuals or those choosing to forage some distance from the main colony. These individuals may be exposed to lower risk of collision with tidal turbines than would have been predicted based on previous studies, due to their tendency not only to forage in areas of low current strength, but also to cover far less distance than is typical of cormorants diving in other areas (Holm & Burger, 2002; Schneider & Piatt 1986). If these birds are avoiding areas of high turbulence, then this would also tend to keep them away from the downstream end of operational turbines, due to turbulence in the wake (Chen *et al*. 2015). However, further research is required to ascertain whether cormorants show a general avoidance of turbulence, or whether this represents a site, or individual-specific phenomenon.

In conclusion, we suggest that the VOD is a potentially valuable addition to the armoury of tools being used to quantify animal responses to specific, small-scale anthropogenic impacts, such as renewable energy devices. The system provides 3-d coordinates within a radius of several kilometres with a measurement error that is commensurate with GPS tags. Though the initial start-up costs for the VOD are relatively high ($18,900 at the time of this study), there is no requirement to pay data subscriptions over the lifetime of the product or recover any technology from animals to access data. The variety and quantity of data that can be collected mean that it is likely to prove cost effective in the longer term, particularly when compared to anima-borne tags, with each GPS tag costing $70 - $800 depending on the method of data transmission and the hardware itself (Hebblewhite *et al*. 2007). The VOD system has relatively low training requirements and simple post-processing of the resulting data, but above all, it represents a method of tracking animals that has little to no ethical implications for the target animals. Finally, the ability to track even the smallest passerines means that opportunities arise to assess how a wide range of animals may respond to developments on land, as well as at sea, from patterns of land use to the installation of wind farms (Hedenström & Alerstam 1994; Piersma *et al*. 1990).

References

Alerstam T, Lindström Å (1990). *Optimal bird migration: the relative importance of time, energy, and safety. Bird migration: physiology and ecophysiology,* 1st edn. Springer, Berlin, Heidelberg.

Alves JA, Shamoun-Baranes J, Desmet P, Doktar A, Bauer S, Hüppop O, Koistinen J, Leijnse H, Liechti F (2014). Monitoring continent-wide aerial patterns of bird movements using weather radars. *Movement Ecology* **2**(9).

Bailey H, Thompson P (2006). Quantitative analysis of bottlenose dolphin movement patterns and their relationship with foraging. *Journal of Animal Ecology* **75**, 456-465.

Benjamins S, Dale AC, Hastie G, Waggitt JJ, Lea MA, Scott B, Wilson B (2015). Confusion reigns? A review of marine megafauna interactions with tidal-stream environments. *Oceanography and Marine Biology: An Annual Review* **53**, 1-54.

Bennison A, Bearhop S, Bodey TW, Votier SC, Grecian WJ, Wakefield ED, Hamer KC, Jessopp M (In Press). Search and foraging behaviors from movement data: A comparison of methods. *Ecology and Evolution*

Browning E, Bolton M, Owen E, Shoji A, Guilford T, Freeman R (In Press). Predicting animal behavior using deep learning: GPS data alone accurately predict diving in seabirds. *Methods in Ecology and Evolution*

Calvo B, Furness RW (1992). A review of the use and the effects of marks and devices on birds. *Ringing & Migration* **13**, 129-151.

Camphuysen CJ, Fox AD, Leopold MF, Petersen IK (2004). Towards Standardised

Seabirds at Sea Census Techniques in Connection with Environmental Impact Assessments for Offshore Wind Farms in the UK: a comparison of ship and aerial sampling methods for marine birds and their applicability to offshore wind farm assessments. Royal Netherlands Institute for Sea Research, Netherlands, Texel.

Cavagna A, Cimarelli A, Giardina I, Orlandi A, Parisi G, Procaccini A, Santagati R, Stefanini F (2008). New statistical tools for analyzing the structure of animal groups. *Mathematical Biosciences* **214**, 32-37.

Chapman RD, Graber HC (1997). Validation of HF radar measurements. *Oceanography* **10**, 76-79.

Chen Y, Lin B, Lin J, Wang S (2015). Effects of stream turbine array configuration on tidal current energy extraction near an island. Computers and *Geosciences* **77**, 20–28

Chittenden CM, Butterworth KG, Cubitt KF, Jacobs MC, Ladouceur A, Welch DW, McKinley RS (2009). Maximum tag to body size ratios for an endangered coho salmon (*O. kisutch*) stock based on physiology and performance. *Environmental Biology of Fishes* **84**, 129-140.

Costa DP, Robinson PW, Arnould JP, Harrison AL, Simmons SE, Hassrick JL, Hoskins AJ, Kirkman SP, Oosthuizen H, Villegas-Amtmann S, Crocker DE (2010). Accuracy of ARGOS locations of pinnipeds at-sea estimated using Fastloc GPS. *PloS one* **5**, 8677.

Cox N (2001). Analysing circular data in Stata. *NASUG, Boston, MA*.

Cury P, Roy C (1989). Optimal environmental window and pelagic fish recruitment success in upwelling areas. *Canadian Journal of Fisheries and Aquatic Sciences* **46**, 670-680.

De Margerie E, Simonneau M, Caudal JP, Houdelier C, Lumineau S (2015). 3D tracking of animals in the field using rotational stereo videography. *Journal of Experimental Biology* **218**, 2496-2504.

Eastwood E (1967). *Radar ornithology*, 1st edn. Methuen & co, London.

Elliott KH (2016). Measurement of flying and diving metabolic rate in wild animals: review and recommendations. *Comparative Biochemistry and Physiology Part A: Molecular & Integrative Physiology* **202**, 63-77.

Evangelista DJ, Ray DD, Raja SK, Hedrick TL (2017). Three-dimensional trajectories and network analyses of group behavior within chimney swift flocks during approaches to the roost. *Proceedings of the Royal Society B: Biological Sciences* **284**, 2016-2602).

Evans P, Mason-Jones A, Wilson CAME, Wooldridge C, O'Doherty T, O'Doherty D (2015). Constraints on extractable power from energetic tidal straits. *Renewable Energy* **81**, 707-722.

Fischer P (2000). Test of competitive interactions for space between two benthic fish species, burbot *Lota lota*, and stone loach *Barbatula barbatula*. *Environmental Biology of Fishes* **58**, 439-446.

Fraenkel PL (2006) Tidal current energy technologies. *Ibis* **148**, 145–151.

Frair JL, Fieberg J, Hebblewhite M, Cagnacci F, DeCesare NJ, Pedrotti L (2010).

Resolving issues of imprecise and habitat-biased locations in ecological analyses using GPS telemetry data. *Philosophical Transactions of the Royal Society of London B: Biological Sciences* **365**, 2187-2200.

Fréon P, Misund OA (1999). *Dynamics of pelagic fish distribution and behaviour,* 1st edn. Fishing News Books, Oxford.

Furness RW, Wade HM, Robbins AM, Masden EA (2012). Assessing the sensitivity of seabird populations to adverse effects from tidal stream turbines and wave energy devices. *ICES Journal of Marine Science* **69**, 1466-1479.

Garthe S, Hüppop O (2004). Scaling possible adverse effects of marine wind farms on seabirds: developing and applying a vulnerability index. *Journal of Applied Ecology* **41**, 724-734.

Gauthreaux Jr SA, Belser CG (2003). Radar ornithology and biological conservation. *The Auk*, **120**(2), 266-277.

Götmark F (1992). The effects of investigator disturbance on nesting birds. In *Current ornithology*. Springer US, New York, 63-104.

Gürbüz SZ, Reynolds DR, Koistinen J, Liechti F, Leijnse H, Shamoun-Baranes J, Dokter AM, Kelly J, Chapman JW (2015). Exploring the skies: Technological challenges in radar aeroecology. In *Radar Conference (RadarCon), 2015 IEEE*, 0817-0822

Hebblewhite M, Percy M, Merrill EH (2007). Are all global positioning system collars created equal? Correcting habitat-induced bias using three brands in the Central Canadian Rockies. *Journal of Wildlife Management* **71**, 2026-2033.

Hedenström A, Alerstam T (1994). Optimal climbing flight in migrating birds:

predictions and observations of knots and turnstones. *Animal Behaviour* **48**, 47-54.

Hedenström A, Åkesson S (2016). Ecology of tern flight in relation to wind, topography and aerodynamic theory. *Philosophical Transactions of the Royal Society of London B: Biological Sciences* **371**.

Heath JP, Gilchrist HG (2010). When foraging becomes unprofitable: energetics of diving in tidal currents by common eiders wintering in the Arctic. *Marine Ecology Progress Series* **403**, 279-290.

Hiemstra PH, Pebesma EJ, Twenhofel CJW, Heuvelink GBM (2009). Real-time automatic interpolation of ambient gamma dose rates from the Dutch radioactivity monitoring network. *Computers & Geosciences* **35**, 1711–1721.

Hervouet JM (2007). *Hydrodynamics of free surface flows*, 1st edn. John Wiley and Sons, London.

Holm KJ, Burger AE (2002). Foraging behavior and resource partitioning by diving birds during winter in areas of strong tidal currents. *Waterbirds* **25**, 312-325.

Hoover AL, Shillinger GL, Swiggs J, Bailey H (2017). Comparing Acoustic Tag Attachments Designed for Mobile Tracking of Hatchling Sea Turtles. *Frontiers in Marine Science* **4**, 225.

Jenness J (2011). *Tools for Graphics and Shapes*. Jenness Enterprises, USA.

Kahle D, Wickham H (2013). ggmap: Spatial Visualization with ggplot2. *R Journal*, ***5***.

Kovach WL (2011). *Oriana–circular statistics for windows, ver. 4.* Kovach Computing Services, Pentraeth, Wales, UK.

Langton R, Davies IM, Scott BE (2011). Seabird conservation and tidal stream and wave power generation: Information needs for predicting and managing potential impacts. *Marine Policy* **35**, 623-630.

Luttrull JK, Hallisey J (1999). Laser pointer–induced macular injury. *American journal of ophthalmology* **127**, 95-96.

Mainster MA, Stuck BE, Brown J (2004). Assessment of alleged retinal laser injuries. *Archives of ophthalmology* **122**, 1210-1217.

McCann DL, Bell PS (2017). Visualising the aspect-dependent radar cross section of seabirds over a tidal energy test site using a commercial marine radar system. *International Journal of Marine Energy* **17**, 56-63.

McCormac JC (1991). Surveying fundamentals. *Prentice Hall*.

Michener MC, Walcott C (1967). Homing of single pigeons--analysis of tracks. *Journal of Experimental Biology* **47**, 99-131.

Mitchell P, Newton S, Ratcliffe N, Dunn TE (2004). *Seabird populations of Britain and Ireland*, 1st edn. T &AD Poyser, London, UK.

Mueller M, Wallace R (2008). Enabling science and technology for marine renewable energy. *Energy Policy* **36**, 4376-4382.

Nicolaus M, Bouwman KM & Dingemanse NJ (2008). Effect of PIT tags on the survival and recruitment of great tits Parus major. *Ardea*, **96**(2), 286-292.

Patrick SC, Bearhop S, Grémillet D, Lescroël A, Grecian WJ, Bodey TW, Hamer KC, Wakefield E, Le Nuz M, Votier SC (2014). Individual differences in searching behaviour and spatial foraging consistency in a central place marine predator. *Oikos* **123**, 33-40.

Pelc R, Fujita RM (2002). Renewable energy from the ocean. *Marine Policy* **26**, 471-479.

Pennycuick CJ (1982). The VOD: an instrument for collecting large samples of bird speed measurements. *Philosophical Transactions of the Royal Society of London B: Biological Sciences* **300**, 61-73.

Pennycuick CJ, Åkesson S, Hedenström A (2013). Air speeds of migrating birds observed by VOD and compared with predictions from flight theory. *Journal of the Royal Society Interface* **10**.

Piano M, Neill SP, Lewis MJ, Robins PE, Hashemi MR, Davies AG, Ward SL, Roberts MJ (2017). Tidal stream resource assessment uncertainty due to flow asymmetry and turbine yaw misalignment. *Renewable Energy* **114***,* 1363-1375.

Piano M, Ward S, Robins P, Neill S, Lewis M, Davies AG, Powell B, Wyn-Owen A, Hashemi MR (2015). Characterizing the tidal energy resource of the West Anglesey Demonstration Zone (UK), using Telemac-2D and field observations. In *XXII Telemac and Mascaret User Club Conference*. Daresbury, UK.

Piersma T, Zwarts L, Bruggemann JH (1990). Behavioural aspects of the departure of waders before long-distance flights: flocking, vocalizations, flight paths and diurnal timing. *Ardea* **78**, 157-184.

Phillips RA, Xavier JC, Croxall JP (2003). Effects of satellite transmitters on albatrosses and petrels. *The Auk* **120**, 1082-1090.

R Core Team (2016). R: A language and environment for statistical computing. *R Foundation for Statistical Computing*, Vienna, Austria. URL https://www.Rproject.org/.

Rahel FJ, Stein RA (1988). Complex predator-prey interactions and predator intimidation among crayfish, piscivorous fish, and small benthic fish. *Oecologia* **75**, 94-98.

Ripley B (2015). MASS: Support functions and datasets for Venables and Ripley's MASS. *R package version* 7.3-40.

Ropert-Coudert Y, Wilson RP (2005). Trends and perspectives in animal-attached remote sensing. *Frontiers in Ecology and the Environment* **3**, 437-444.

Saraux C, Le Bohec C, Durant JM, Viblanc VA, Gauthier-Clerc M, Beaune D, Le Maho Y (2011). Reliability of flipper-banded penguins as indicators of climate change. *Nature*, **469**(7329), 203.

Schneider DC, Piatt JF (1986). Scale-dependent correlation of seabirds with schooling fish in a coastal ecosystem. *Marine Ecology Progress Series*, 237-246.

Schwemmer P, Mendel B, Sonntag N, Dierschke V, Garthe S (2011). Effects of ship traffic on seabirds in offshore waters: implications for marine conservation and spatial planning. *Ecological Applications* **21**, 1851-1860.

Sealy SG (1975). Feeding ecology of the ancient and marbled murrelets near Langara Island, British Columbia. *Canadian Journal of Zoology* **53**, 418-433.

Shepard EL, Williamson C, Windsor SP (2016). Fine-scale flight strategies of gulls in urban airflows indicate risk and reward in city living. *Philosophical Transactions of the Royal Society of London B: Biological Sciences*, **371**.

Stein JE, Collier TK, Reichert WL, Casillas E, Hom T, Varanasi U (1992). Bioindicators of contaminant exposure and sub-lethal effects: studies with benthic fish in Puget Sound, Washington. *Environmental Toxicology and Chemistry* **11**, 701-714.

Stothart MR, Elliott KH, Wood T, Hatch SA, Speakman JR (2016). Counting calories in cormorants: dynamic body acceleration predicts daily energy expenditure measured in pelagic cormorants. *Journal of Experimental Biology* **219**, 21922200.

Tucker VA, Schmidt-Koenig K (1971). Flight speeds of birds in relation to energetics and wind directions. *The Auk* **88**, 97-107.

Turchin P (1998). *Quantitative analysis of movement*. Sinauer assoc., Sunderland, UK.

Vandenabeele SP, Wilson RP, Grogan A (2011). Tags on seabirds: how seriously are instrument-induced behaviours considered? *Animal Welfare-The UFAW Journal* **20**, 559.

Vectronix (2004). *Vector operating and operator maintenance instructions*, version 0.3. Heerbrugg, Switzerland.

Waggitt JJ, Scott BE (2014). Using a spatial overlap approach to estimate the risk of collisions between deep diving seabirds and tidal stream turbines: A review of potential methods and approaches. *Marine Policy* **44**, 90-97.

Waggitt JJ, Bell PS, Scott BE (2014). An evaluation of the use of shore-based surveys for estimating spatial overlap between deep-diving seabirds and tidal stream turbines. International Journal of Marine Energy **8**, 36–49.

Waggitt JJ, Cazenave PW, Torres R, Williamson BJ, Scott BE (2016a). Quantifying pursuit-diving seabirds' associations with fine-scale physical features in tidal stream environments. *Journal of Applied Ecology* **53**, 1653-1666.

Waggitt JJ, Cazenave P, Torres R, Williamson BJ, Scott BE (2016b). Predictable hydrodynamic conditions explain temporal variations in the density of benthic foraging seabirds in a tidal stream environment. *ICES Journal of Marine Science* **73**, 2677–2686.

Wickham H (2011). ggplot2. *Wiley Interdisciplinary Reviews: Computational Statistics* **3**, 180-185.

Wilson RP, Grant WS, Duffy DC (1986). Recording devices on free-ranging marine animals: does measurement affect foraging performance? *Ecology* **67**, 10911093.

Wilson RP, Wilson MPT (1988). Foraging behaviour in four sympatric cormorants. *The Journal of Animal Ecology* **57**, 943-955.

Wilson RP, Vandenabeele SP (2012). Technological innovation in archival tags used in seabird research. *Marine Ecology Progress Series* **451**, 245-262.

Wilson RP, McMahon CR (2006). Measuring devices on wild animals: what constitutes acceptable practice? *Frontiers in Ecology and the Environment* **4**, 147-154.

Wyrsch S, Baenninger PB, Schmid MK (2010). Retinal injuries from a handheld laser pointer. *New England journal of medicine* **363**, 1089-1091.

Zamon JE (2003). Mixed species aggregations feeding upon herring and sandlance schools in a nearshore archipelago depend on flooding tidal currents. *Marine Ecology Progress Series* **261**, 243-255.

Table 1. The number of individual locations recorded with the VOD in Ramsey Sound for animals that were performing behaviour on the water surface (n=301 positional fixes).

Species	Rafting	Diving	Flying
Guillemot	48	6	9
Shag	2	1	0
Gannet	1	7	38
Great black-backed gull	2	0	0
Lesser black-backed gull	66	0	0
Cormorant	43	56	19
Razorbill	4	0	2

Figures

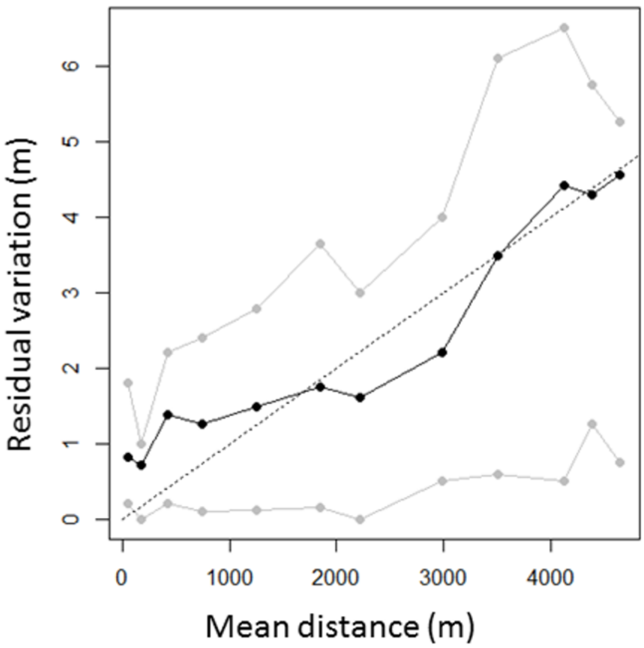

Figure 1. The residual variation of range measurements as a function of distance to a fixed, 1 m^2 target, as measured by the VOD (n = 120 fixes, 10 fixes per distance interval). The standard deviations are given in black, while the minimum and maximum deviations are given in grey for each distance. The dashed line indicates the variance that would be equivalent to 0.1% of the distance value.

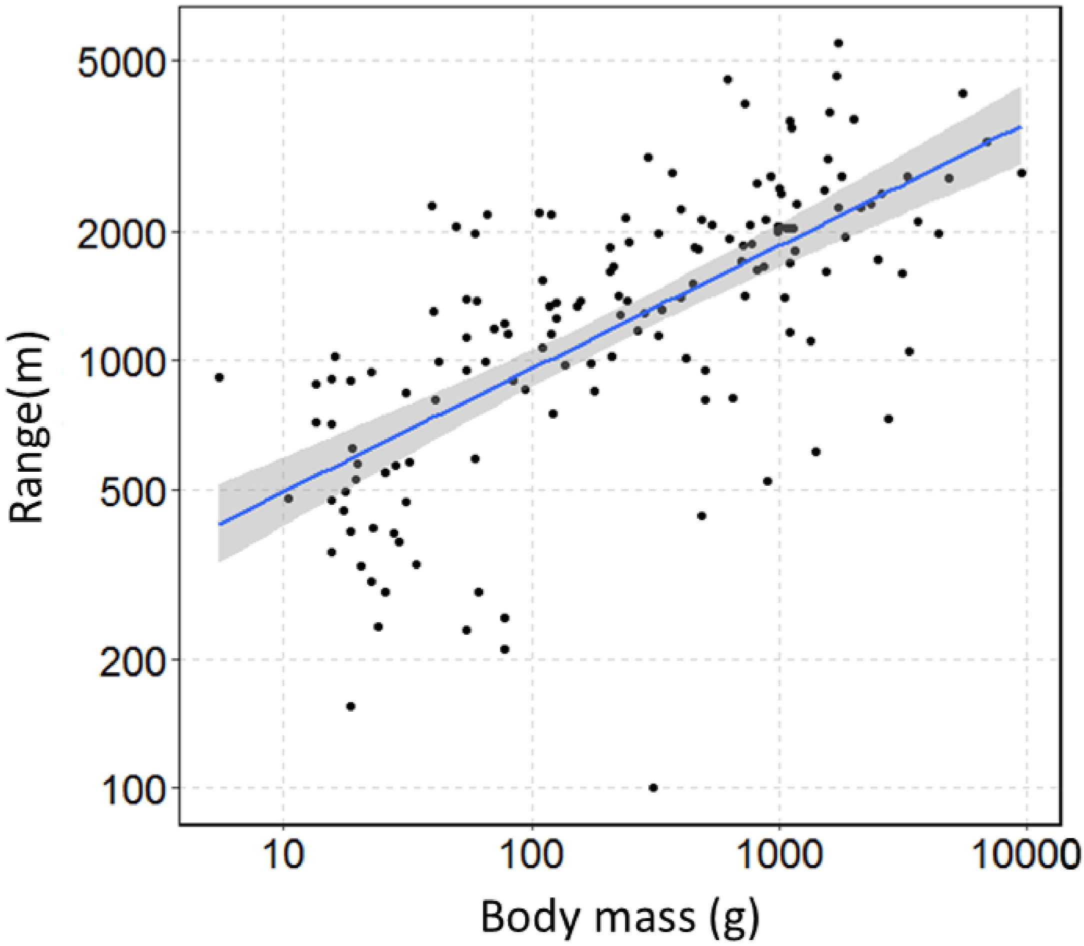

Figure 2. The maximum range of avian targets from the VOD, in relation to body mass. The blue line equates to the model prediction.

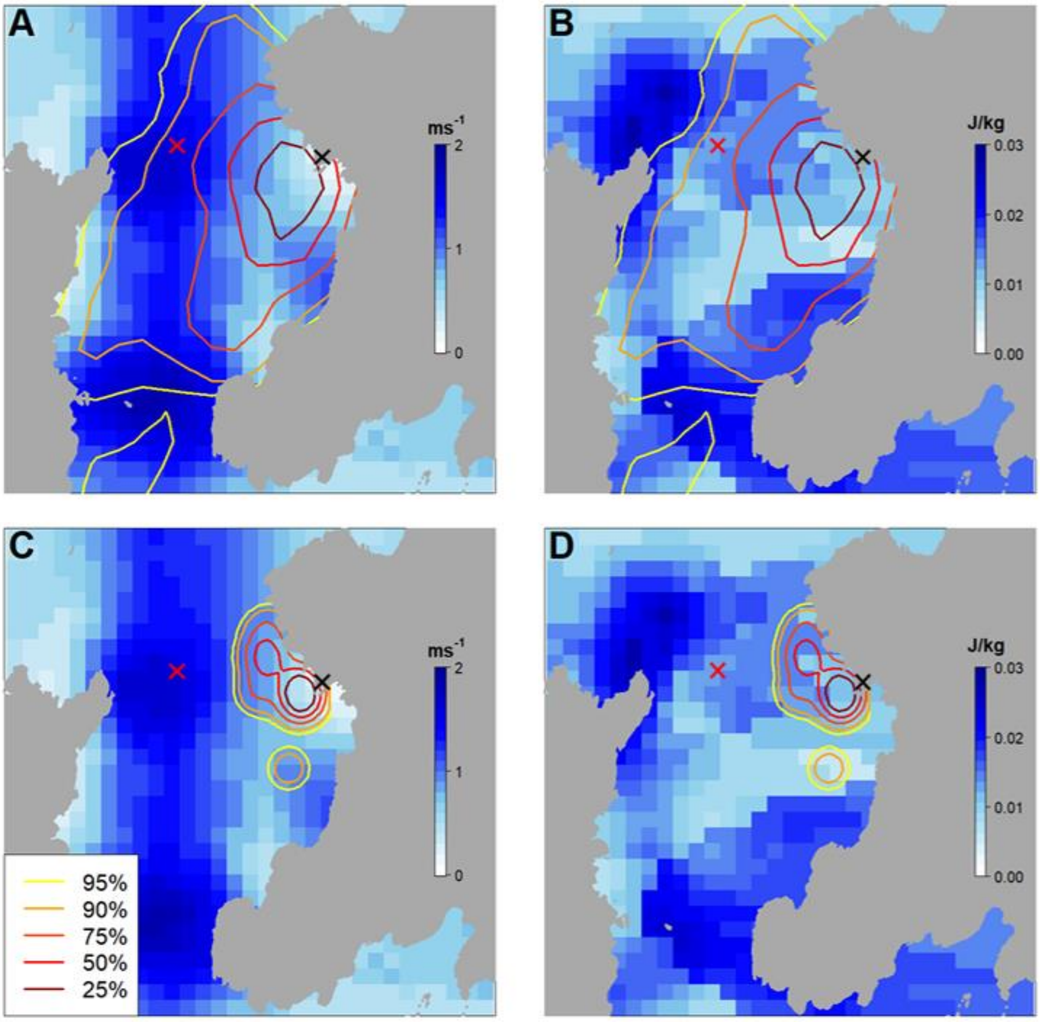

Figure 3. Kernel density contours showing distributions of A) all seabirds and all behaviours plotted in relation to mean current speed, B) all species and behaviours over mean turbulence, C) all cormorant dives plotted against mean horizontal current speed and D) all cormorant dives plotted against mean turbulence in Ramsey Sound. The black cross represents the vantage point at St Justinian’s (51°52'42.4"N 5°18'38.4"W) whilst the red cross marks the location of the DeltaStream tidal turbine device.

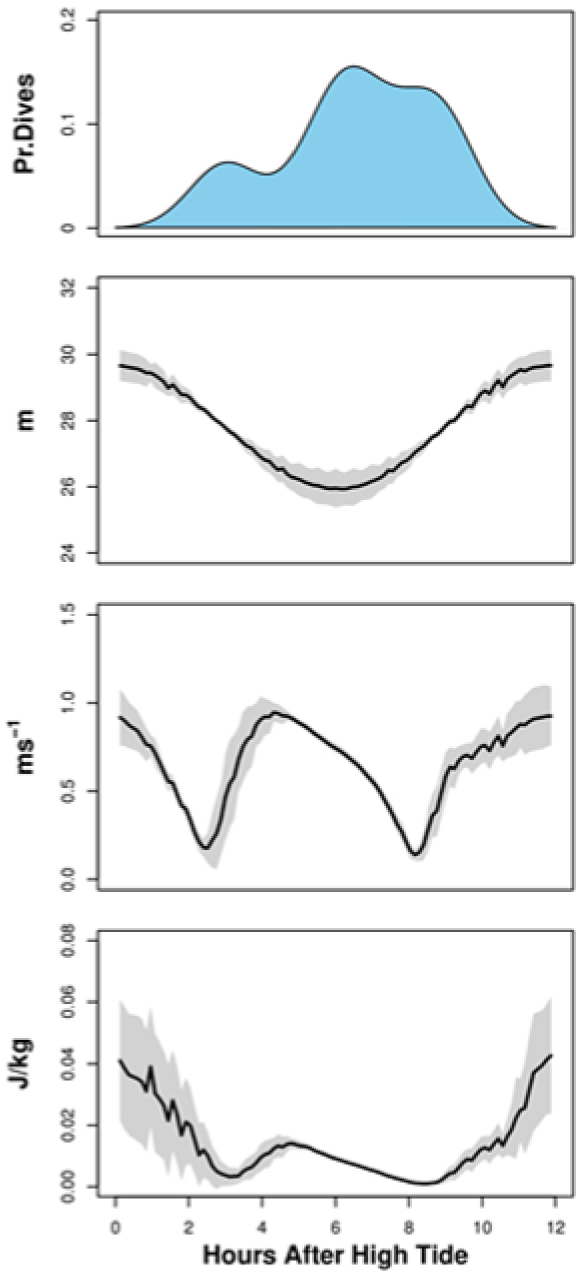

Figure 4. The times when cormorants were diving are given in relation to i) tidal height, ii) current strength and iii) turbulence, as modelled using the hydrodynamic model. A density plot is used to show the proportion of dives in relation to time.

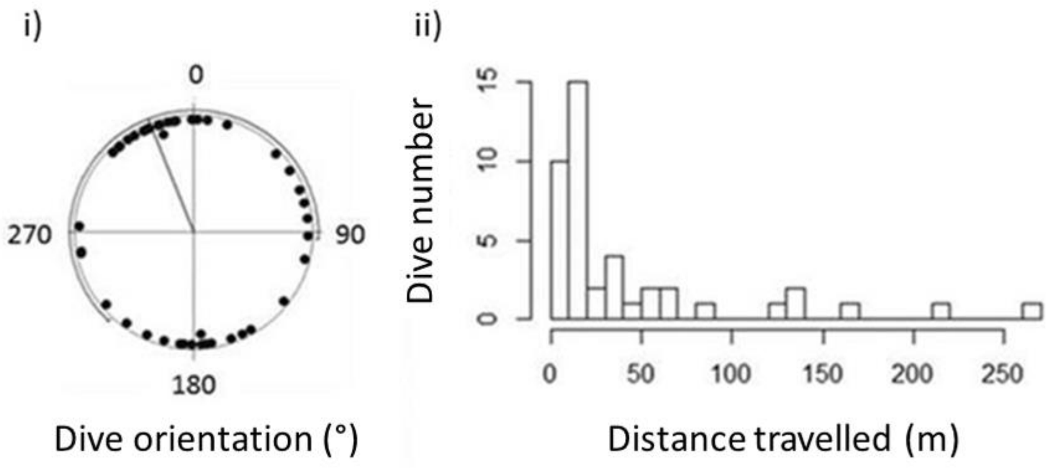

Figure 5. (i) The dive bearings for cormorants foraging in Ramsey Sound illustrate that birds forage into the current (mean bearing is given by the line from the centre of the circle and the line around the outside indicate the inter-quartile range), which was flowing in a Southerly direction from 0 to 180 degrees. The strategy of orientating into the flow resulted in birds travelling relatively low horizontal distances during dives, as displayed in (ii).