Quantifying pursuit-diving seabirds' associations with fine-scale physical features in tidal stream environments

James J. Waggitt[1,2,3]*, Pierre W. Cazenave[4], Ricardo Torres[4], Benjamin J. Williamson[2] and Beth E. Scott[2]*

[1]*School of Ocean Sciences, Bangor University, Menai Bridge LL59 5AB, UK;* [2]*Institute of Biological and Environmental Sciences, University of Aberdeen, Aberdeen AB24 2TZ, UK;* [3]*Marine Scotland Science, Aberdeen AB11 9DB, UK;* and [4]*Plymouth Marine Laboratory, Plymouth PL1 3DH, UK*

Summary

1. The rapid increase in the number of tidal stream turbine arrays will create novel and unprecedented levels of anthropogenic activity within habitats characterized by horizontal current speeds exceeding 2 ms^{-1}. However, the potential impacts on pursuit-diving seabirds exploiting these tidal stream environments remain largely unknown. Identifying similarities between the fine-scale physical features (100s of metres) suitable for array installations, and those associated with foraging pursuit-diving seabirds, could identify which species are most vulnerable to either collisions with moving components, or displacement from these installations.

2. A combination of vessel-based observational surveys, Finite Volume Community Ocean Model outputs and hydroacoustic seabed surveys provided concurrent measures of foraging distributions and physical characteristics at a fine temporal (15 min) and spatial (500 m) resolution across a tidal stream environment suitable for array installations, during both breeding and non-breeding seasons. These data sets were then used to test for associations between foraging pursuit-diving seabirds (Atlantic puffins *Fratercula arctica*, black guillemots *Cepphus grylle*, common guillemots *Uria aalge*, European shags *Phalacrocorax aristotelis*) and physical features.

3. These species were associated with areas of fast horizontal currents, slow horizontal currents, high turbulence, downward vertical currents and also hard–rough seabeds. The identity and strength of associations differed among species, and also within species between seasons, indicative of interspecific and intraspecific variations in habitat use. However, Atlantic puffins were associated particularly strongly with areas of fast horizontal currents during breeding seasons, and European shags with areas of rough–hard seabeds and downward vertical currents during non-breeding seasons.

4. *Synthesis and applications.* Atlantic puffins' strong association with fast horizontal current speeds indicates that they are particularly likely to interact with installations during breeding seasons. Any post-installation monitoring and mitigation measures should therefore focus on this species and season. The multi-species associations with high turbulence and downward vertical currents, which often coincide with fast horizontal current speeds, also highlight useful pre-installation mitigation measures via the omission of devices from these areas, reducing the overall likelihood of interactions. Environmental impact assessments (EIA) generally involve once-a-month surveys across 2-year periods. However, the approaches used in this study show that more focussed surveys can greatly benefit management strategies aiming to reduce the likelihood of negative impacts by facilitating the development of targeted mitigation measures. It is therefore recommended that these approaches contribute towards EIA within development sites.

*Correspondence author. E-mail: j.waggitt@bangor.ac.uk; b.e.scott@abdn.ac.uk

Introduction

The rapid increase in the number of tidal stream turbine arrays will create novel and unprecedented levels of anthropogenic activity within habitats characterized by horizontal current speeds exceeding 2 ms^{-1} (Pelc & Fujita 2002). However, the environmental impacts of array installations remain largely unknown (Inger *et al.* 2009). It is known that these tidal stream environments are exploited by a range of seabird species (Hunt *et al.* 1999; Benjamins *et al.* 2015), and identifying potential impacts of array installations on these species remains a research priority (Furness *et al.* 2012; Scott *et al.* 2014). Two major concerns are the possibility of collisions between pursuit-diving seabirds (*Alcidae* and *Phalacrocoracidae*) and the moving components of devices during foraging activities (Wilson *et al.* 2007), and also the possibility of displacing such species during device installation, operation and maintenance (Langton, Davies & Scott 2011). A key component of determining whether collisions and displacement could impact pursuit-diving seabirds is estimating the extent of spatial overlap between their foraging distributions and the preferred locations of array installations in development sites (Waggitt & Scott 2014).

Whilst generally covering small areas (<10 km^2), tidal stream environments can usually be further divided into several fine-scale and ephemeral physical features (100s of metres) identified by different physical characteristics. Substrates can include rocky reefs, exposed bedrock and sedimentary substrates, whilst a broad range of different seabed depths usually exist (Moore 2010). Areas of fast horizontal currents are found within and around areas of constricted coastlines, and these are usually bounded by areas of considerably slower horizontal currents. Intense turbulence typically forms between these water bodies, whereas areas of high vertical speeds (upward or downward) are found when fast horizontal currents are intercepted by bathymetric features (Benjamins *et al.* 2015). The location and extent of these hydrodynamic features varies across ebb–flood and spring–neap tides due to variations in horizontal current speeds and directions, which culminate in the creation of spatiotemporally dynamic and physically complex habitats.

The range of physical features characterizing tidal stream environments can influence the spatiotemporal foraging distributions of pursuit-diving seabirds by affecting prey availability. Fast horizontal currents and high turbulence could disorientate and disintegrate shoals of fish (Liao 2007) whereas upward vertical currents can force these fish towards the water surface (Hunt *et al.* 1998; Zamon 2003), increasing their catchability (Enstipp, Grémillet & Jones 2007; Crook & Davoren 2014). Certain substrates could

promote benthic and epi-benthic prey abundances. For example, rocky reefs may support diverse fish and invertebrate assemblages whereas sedimentary substrates may be occupied by dense shoals of burrowing sandeels (Watanuki *et al.* 2008). Moreover, as the energetic cost of diving to the seabed is known to increase with depth (Butler & Jones 1997) and horizontal current speeds (Heath & Gilchrist 2010), the accessibility of these benthic and epi-benthic resources could increase in areas of shallower depth and/or slower horizontal currents (Ronconi & Clair 2002; Drew, Piatt & Hill 2013). In addition to influencing the foraging distributions of pursuit-diving seabirds, hydrodynamic and bathymetric features also influence the location of array installations by affecting energy returns, ease of attachment to the seabed, operation and maintenance. Areas containing fast horizontal currents, depths >30 m and relatively hard–smooth seabeds are typically considered suitable for array installations (Fraenkel 2006). Identifying similarities between the physical features suitable for array installations, and those associated with foraging pursuit-diving seabirds, could identify which species are relatively likely to forage near such installations within development sites (Waggitt & Scott 2014).

Associations between foraging pursuit-diving seabirds and physical features have been noted previously in tidal stream environments (reviewed by Benjamins *et al.* 2015). However, these previous studies have lacked concurrent and quantitative measurements of multiple physical characteristics in continuous time and space. This absence limits the number of physical features that can be identified and also prevents species' use of different physical features being quantified and compared. Moreover, previous studies have been performed in either breeding or non-breeding seasons, and exclusively in North America. It is therefore unknown whether species have similar associations across seasons, or whether ecologically similar species share associations across regions. The expected increase in array installations world-wide creates the need for a more detailed exploration of associations within tidal stream environments suitable for array installations across breeding and non-breeding seasons, particularly outside North America (Waggitt & Scott 2014).

This study aimed to provide a detailed exploration into associations between foraging pursuit-diving seabirds and physical features within a tidal stream environment (3 × 3 km) suitable for array installations, across breeding and non-breeding seasons and in north-west Europe. Several approaches were used to provide the novel combination of data sets needed for this exploration. First, multi-beam sonar and echosounder surveys provided measurements of depth (Courtney & Shaw 2000) and

substrate characteristics (Chivers, Emerson & Burns 1990) in continuous space, respectively. This fine-resolution data were then coupled with a Finite Volume Community Ocean Model (FVCOM) (Chen, Liu & Beardsley 2003) to quantify multiple hydrodynamic characteristics continuously in time and space at a similar resolution, something which *in situ* oceanographic instruments cannot achieve (Tremblay *et al.* 2009). Secondly, vessel-based transects (Camphuysen *et al.* 2004), rather than more commonly used shore-based scans, were used to record the foraging distribution of seabirds at a fine resolution within the study area across multiple tidal states. The use of vessel-based transects overcame issues of spatially biased recordings of foraging distributions, encountered when using shore-based scans over areas spanning several square kilometres (Waggitt, Bell & Scott 2014).This data set was then used to test whether (i) the probability of encountering foraging seabirds varied as a function of physical characteristics (horizontal current speed, vertical current speed, horizontal eddy viscosity, water elevation, seabed roughness, seabed hardness), indicative of associations with physical features; (ii) these associations with physical features differed among species within seasons, or within species between seasons, indicative of interspecific and intraspecific variations in habitat use. Results were then used to identify which species were most likely to forage in areas suitable for array installations.

Materials and methods

STUDY SITE

The study was performed at the Fall of Warness (FOW), Orkney, UK (Fig. 1), across a total of 6 and 8 days in May and October, respectively, during both 2012 and 2013. May represented breeding seasons and October represented non-breeding seasons. Information on study dates is shown in the Appendix S1 in Supporting Information. The FOW is a tidal stream environment

(3 × 3 km) situated between the island of Eday to the east, and the much smaller islands of Muckle Greenholm and Little Greenholm to the south-west (Fig. 1). The FOW is also a tidal stream turbine test site which is managed by the European Marine Energy Centre (EMEC) and currently contains eight device berths (Fig. 1). Information on which devices were operational during study periods was not available due to confidentiality agreements with companies. However, it was known that device operations were relatively minimal across study periods; two devices were operational on 1 day, one device was operational on 9 days, and no devices were operational on 4 days.

PHYSICAL CHARACTERISTICS

Hydrodynamics

Finite Volume Community Ocean Model (Chen, Liu & Beardsley 2003) (Appendix S1) was used to quantify spatiotemporal variances in horizontal current speeds (ms^{-1}: *HSpd*), turbulence (horizontal eddy viscosity in m^2 s^{-1}: *Visc*), vertical current speeds (cms^{-1}: *VSpd*) and water elevation (m: *Elev*). *HSpd, Visc* and *VSpd* identified when and where prominent hydrodynamic features were found (Fig. 2), whereas *Elev* quantified spatial and temporal variations in depth linked to bathymetry (Fig. 3) and tidal cycles, respectively.

Substrate properties

A vessel mounted Simrad EK60 multi-frequency echosounder (38, 120, 200 kHz) was used in conjunction with the RoxANN software package (Sonavision Ltd., Aberdeen, UK) to record an arbitrary measure of seabed roughness (*SRH*) and hardness (*SHD*) between 0 and 10 (Chivers, Emerson & Burns 1990) (Appendix S1). Higher values of *SRH* and *SHD* are indicative of rougher and harder substrates, respectively. A combination of *SRH* and *SHD* provided information on seabed characteristics (Fig. 4), information which would not be provided from multibeam sonar-derived bathymetry. Seabed surveys in the FOW suggest that a combination of high *SRH*–high *SHD* likely represents rocky reefs, low *SRH*–high *SHD* represent exposed bedrock, and
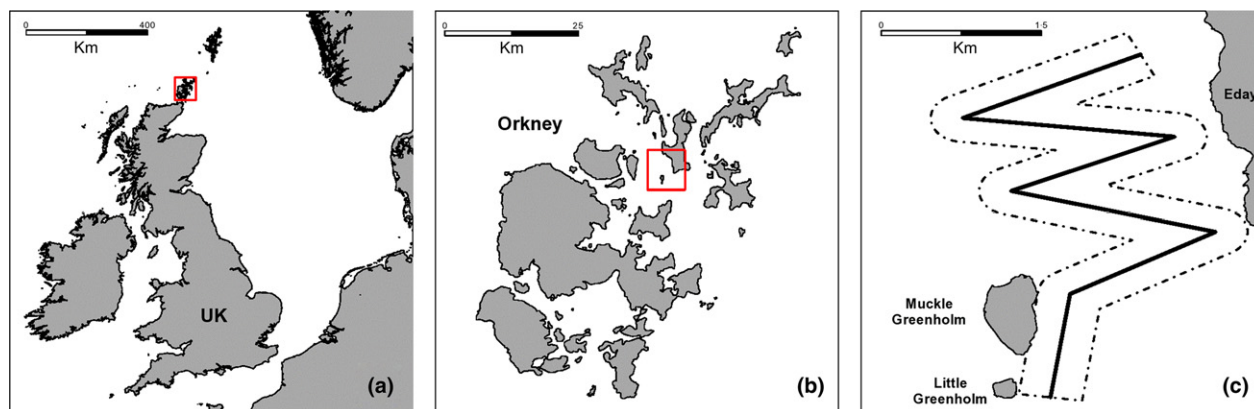

Fig. 1. The Fall of Warness is a high-tidal energy environment in Orkney, UK, situated between the island of Eday to the east and the islands of Muckle Greenholm and Little Greenholm to the south-west. Vessel-based transects recorded the distribution of foraging seabirds within the Fall of Warness, with the survey area spanning 300 m either side of the transect route. The Fall of Warness is a tidal stream turbine test site, with the capacity to deploy up to eight devices.
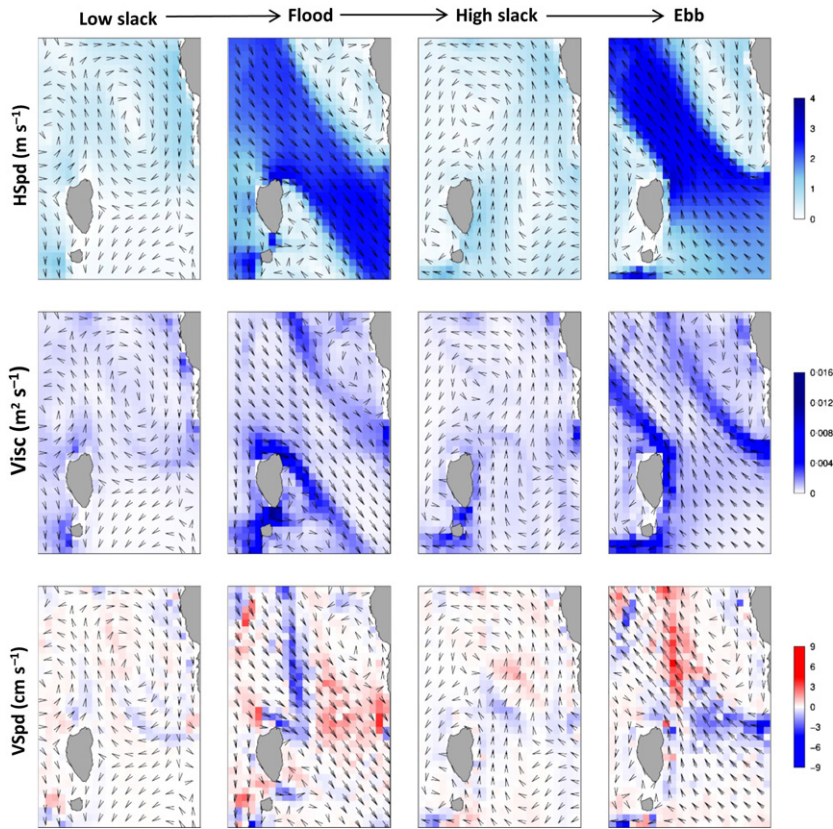
Fig. 2. FVCOM outputs showing spatiotemporal variances in *HSpd*, VSpd and *Visc* at 100-m resolution across a typical ebb–flood cycle (20 May 2012) in the Fall of Warness, Orkney, UK. *HSpd*, *Visc* and *VSpd* quantify horizontal current speeds, eddy viscosity (indicative of turbulence) and vertical current speeds, respectively.
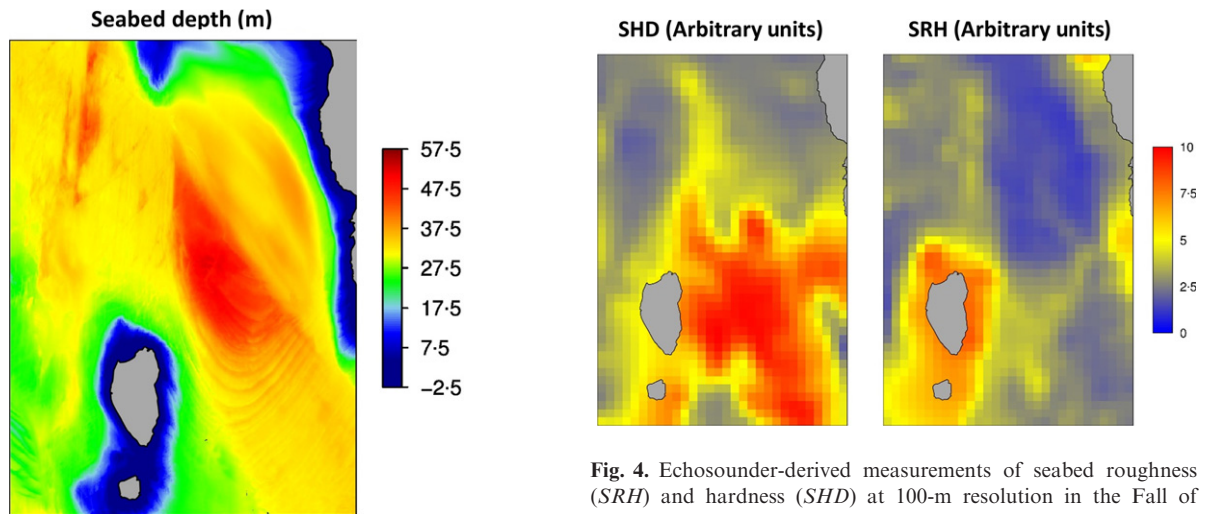

Fig. 3. Multi-beam sonar-derived measurements of seabed depth (difference from mean water elevation) at 5-m resolution in the Fall of Warness, Orkney, UK.

Fig. 4. Echosounder-derived measurements of seabed roughness (*SRH*) and hardness (*SHD*) at 100-m resolution in the Fall of Warness, Orkney, UK.

low *SRH*–low *SHD* represent sedimentary substrates (Aurora 2005).

SEABIRD DISTRIBUTIONS

Design

A total of 101 zig-zag and vessel-based transects were performed using the Marine Scotland Science research vessel FRV *Alba-na-Mara* (Fig. 1). During transects, the vessel moved against the prevailing horizontal currents. This unconventional design allowed the vessel to maintain a reasonably consistent trajectory despite the fast horizontal currents, and also sustain speeds suitable for recording foraging seabirds (5–15 km) (Camphuysen *et al.* 2004) (Appendix S1). Transects were spread across different tidal states to capture variance in the location and extent of hydrodynamic features (Appendix S1). Whilst transects were biased towards either ebb or flood tides within each season, there should have been enough transects across ebb and flood tides to provide representative recordings of foraging distributions per tidal state and season. Transects were only performed when the sea state was less than 3 (Beaufort scale) and visibility was at least 300 m.

Performance

During transects, two observers sat 5·6 m above sea level at the bow of the vessel and only recorded seabirds seen on the water surface. Flying seabirds were not recorded as they would not be actively foraging. Survey methods were based upon those outlined within the European Seabird at Sea (ESAS) methodology (Camphuysen *et al.* 2004). To provide accurate positions, observers recorded seabirds seen on the sea surface into 1-min intervals, and only when they were perpendicular to the bow. Whenever seabirds on the sea surface were seen flushing before they were perpendicular to the bow, observers noted their approximate distance ahead of the vessel. Each observer covered one side of the vessel, and it was noted on which side seabirds on the sea surface were observed. These approaches enabled the position of any seabirds seen on the sea surface to be quantified with an estimated accuracy of approximately 300 m in most cases. Observers also recorded the behaviour of seabirds seen on the sea surface to discriminate between those which were actively foraging (diving or searching) and those which were resting.

Processing

Data sets collected during vessel-based transects were subjected to several stages of processing before analyses. First, to provide a sufficient number of sightings for statistical analysis, only the most prevalent and abundant species were considered for analysis (Table S1–2). In breeding seasons, these species were deemed to be Atlantic puffins *Fratercula arctica,* black guillemots *Cepphus grylle*, common guillemots *Uria aalge* and European shags *Phalacrocorax*

aristotelis. In non-breeding seasons, these were deemed to be black guillemots and European shags. Secondly, any seabird that was seen < 100 m from coastlines was omitted from analysis during breeding seasons to remove those likely to be engaged in maintenance/resting activities immediately alongside their nest site (McSorley *et al.* 2003). The distance of 100 m was based upon observations of seabirds performing maintenance/resting activities particularly sheltered and shallow areas alongside coastlines. Thirdly, any seabird that was seen flushing >100 m ahead of the vessel was also omitted from analysis to ensure that the positions of sightings were as accurate as possible, although only 4% of seabirds seen on the sea surface were recorded doing this. Finally, observer effort per minute (*EF*) for each side of the vessel was determined by quantifying the total sea surface area (km^2) that they covered (Appendix S1).

ANALYSIS

The presence/absence of foraging seabirds, total *EF* and mean values of physical characteristics were calculated within 500 × 500 m cells for every 15-min time period (Fig. 5). In all cases, mean values of physical characteristics retained prominent physical features of interest across the study area. The choice of cell resolution was determined by the estimated accuracy of seabird sightings (approximately 300 m) rather than the resolution of physical characteristics (100 m). The use of a cell resolution which was slightly larger than the estimated accuracy of seabird sightings accounted for discrepancies when assigning point data (the location of sightings) to particular cells, that is point data
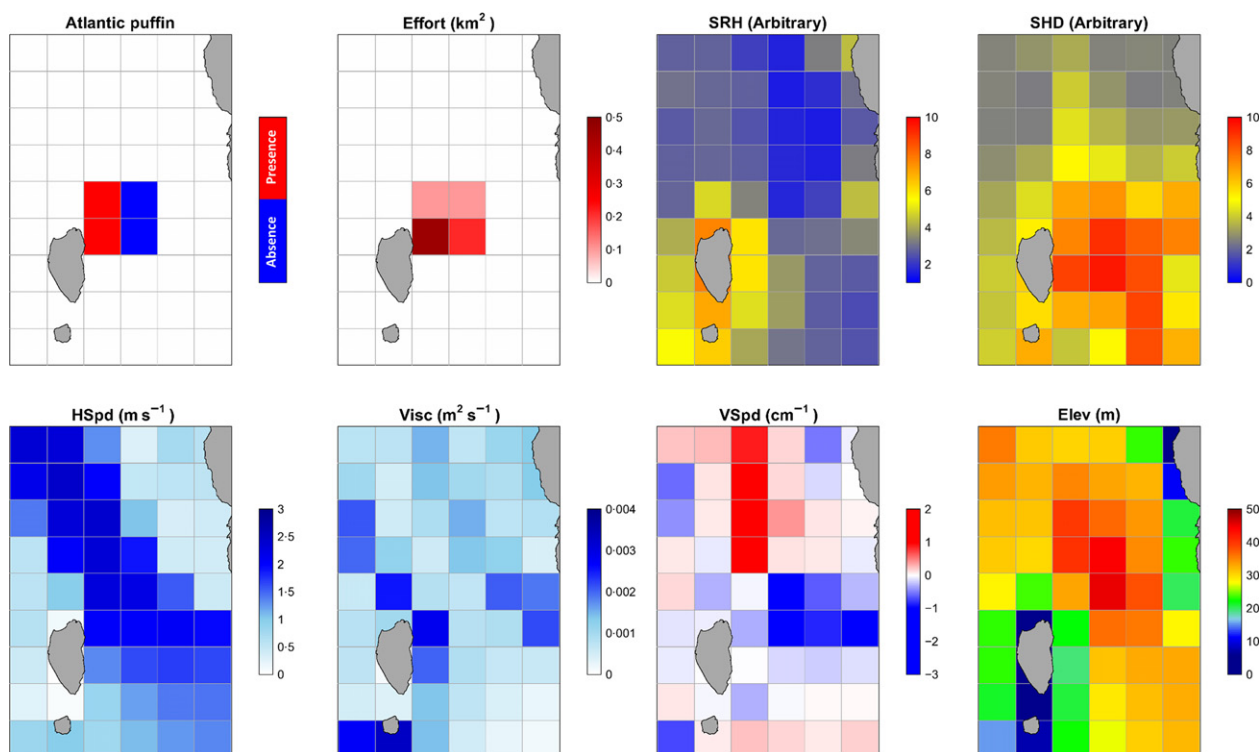

Fig. 5. An example of concurrent, quantitative and continuous data sets on the foraging distributions of seabirds (Atlantic puffins *Fratercula arctica*) and physical characteristics at fine spatial (500 m) and temporal (15 min) resolution on 20 May 2012 at 12 : 45 GMT. *Elev*, *HSpd*, *Visc*, *VSpd*, *SRH* and *SHD* quantify water depth, horizontal current speeds, eddy viscosity (indicative of turbulence), vertical current speeds, seabed roughness and seabed hardness, respectively.

rarely occurred in the centre of a cell. Presence/absence data were used because of heavily zero-inflated (zero counts from 67% to 89%) and overdispersed (variance to mean ratios from 2·48 to 43·60) abundance data, which hindered the performance of robust statistical analysis. All seabirds seen on the sea surface were deemed to be foraging because relatively few were recorded as diving or searching (4–26% of sightings, depending upon the species and season), which provided insufficient sample sizes for robust statistical analysis. Whilst this approach inevitably classed some resting seabirds as foraging seabirds, temperate *Alcidae* and *Phalacrocoracidae* spend most of their time on the sea surface actively foraging during both breeding (Wanless *et al.* 1997; Evans *et al.* 2013) and non-breeding seasons (Daunt *et al.* 2006; Fort *et al.* 2013), and most were probably detected during diving bouts. Although seabirds could have drifted away from the precise location of dives, time intervals between successive dives rarely exceed 1–2 min (Wanless *et al.* 1997; Falk *et al.* 2000), meaning that most would probably have been assigned to a cell where they performed diving bouts. Data processing was performed using the 'maptools' (Bivand & Lewin-Koh 2015) and 'raster' packages (Hijmans 2013) in 'ʀ' (version 3.0.2, R Development Core Team 2013).

Generalized linear mixed effect models (GLMM) with binomial distributions were used to test for relationships between seabird presence/absence and the six different physical characteristics. Models were performed for each species in each season, using a combination of data from 2012 and 2013. Foraging seabird presence/absence was a response variable, with physical characteristics as continuous explanatory variables. The substrates likely encountered within the FOW would be characterized by different combinations of SRH and SHD values (see 'Substrate Properties' above). Therefore, SRH and SHD were modelled together as a two-dimensional explanatory variable. A time variable was used as a random factor to account for any temporal variation in foraging seabird presence that was not explained by physical characteristics, such as weather conditions influencing the detectability of foraging seabirds, as well as any spatial or temporal autocorrelation in the residuals. This time variable represented each 15-min period during vessel surveys. EF was included as a statistical offset to account for unequal coverage of sea surface areas.

Model selection was performed using a multi-model inference approach, based upon Akaike's Information Criterion (AIC) values (Burnham & Anderson 2002). All combinations of explanatory variables were tested in a series of 32 candidate models, and AIC values were calculated for each candidate model. AIC weights were then used to calculate model-averaged parameter estimates, which were subsequently assessed for statistical significance ($P < 0.05$). All 32 candidate models were used in the calculation of model-averaged parameter estimates (Appendix S2). Plots of residuals associated with fixed effects showed no evidence of spatial or temporal autocorrelation (Figs S1 and S2), and plots of residuals associated with random effects resembled normal distributions (Fig. S3). Values of variance inflation factors (VIF) were <3·41, indicating that collinearity among explanatory variables was not an issue. Fitted lines with standard errors were calculated for each statistically significant relationship, using model-averaged parameter estimates. In these calculations, the physical characteristic of interest was varied between its minimum and maximum values (excluding extreme outliers, encountered on deviations from the usual transect route), whilst other physical characteristics and EF were held at their median and mean values, respectively. Statistical analysis was performed using the 'lme4' (Bates *et al.* 2013), 'car' (Fox & Weisberg 2011) and 'MuMln' (Barton 2014) packages in 'ʀ' (version 3.0.2, R Development Core Team 2013).

Results

BREEDING SEASONS

Atlantic puffins

The most frequent sightings of Atlantic puffins occurred within the central channel (Fig. 6) across ebb and flood tides, coinciding with higher $HSpd$ values (Fig. 2). The distribution of the most frequent sightings closely resembled the distribution of maximum $HSpd$ values, with frequent sightings occurring throughout the central channel during ebb tides but constrained to southern areas of the central channel during the flood tides. This relationship with $HSpd$ was significant (Table 1) and particularly strong; probabilities were 8·48 times larger for the highest than for the lowest $HSpd$ values (Fig. 7). Relatively frequent sightings also occurred on the north-east corner of Muckle Greenholm (Fig. 6) coinciding with high $HSpd$ and elevated $Visc$ values (Fig. 2). This relationship with $Visc$ was significant (Table 1) but relatively weak; probabilities were only 3·21 times larger for the highest than for the lowest $Visc$ values (Fig. 7). This relatively weak effect may reflect low sightings in areas of slower $HSpd$ and elevated $Visc$ values (Figs 2 and 6), highlighting the strong effect of $HSpd$.

Common guillemots

The most frequent sightings of common guillemots generally occurred within the central channel across ebb and flood tides (Fig. 6), coinciding with higher $HSpd$ values (Fig. 2). The frequency of sightings within this central channel peaked during ebb tides when the extent of maximum $HSpd$ values along the transect line increased (Fig. 2). This relationship with $HSpd$ was significant (Table 1) and moderately strong; probabilities were 3·27 times larger for the highest than for the lowest $HSpd$ values (Fig. 7). The absence of a particularly strong effect may reflect frequent sightings in a few areas with considerably lower $HSpd$ values (Figs 2 and 6) and/or because the distribution of the most frequent sightings did not closely resemble the distribution of maximum $HSpd$ values within this central channel (Figs 2 and 6).

Black guillemots

The most frequent sightings of black guillemots occurred alongside Muckle Greenholm across ebb and flood tides (Fig. 6), downstream of the south-western Eday headland during ebb tides and in the northern main channel during flood tides; these areas all coincided with elevated $Visc$ values (Fig. 2). This relationship with $Visc$ was significant

(Table 1) and moderately strong; probabilities were 3·07 times larger for the highest than for the lowest *Visc* values (Fig. 7). Sightings generally increased outside the central channel (Fig. 6) coinciding with lower *HSpd* values (Fig. 2). This relationship with *HSpd* was significant (Table 1) but relatively weak; probabilities were 2·02
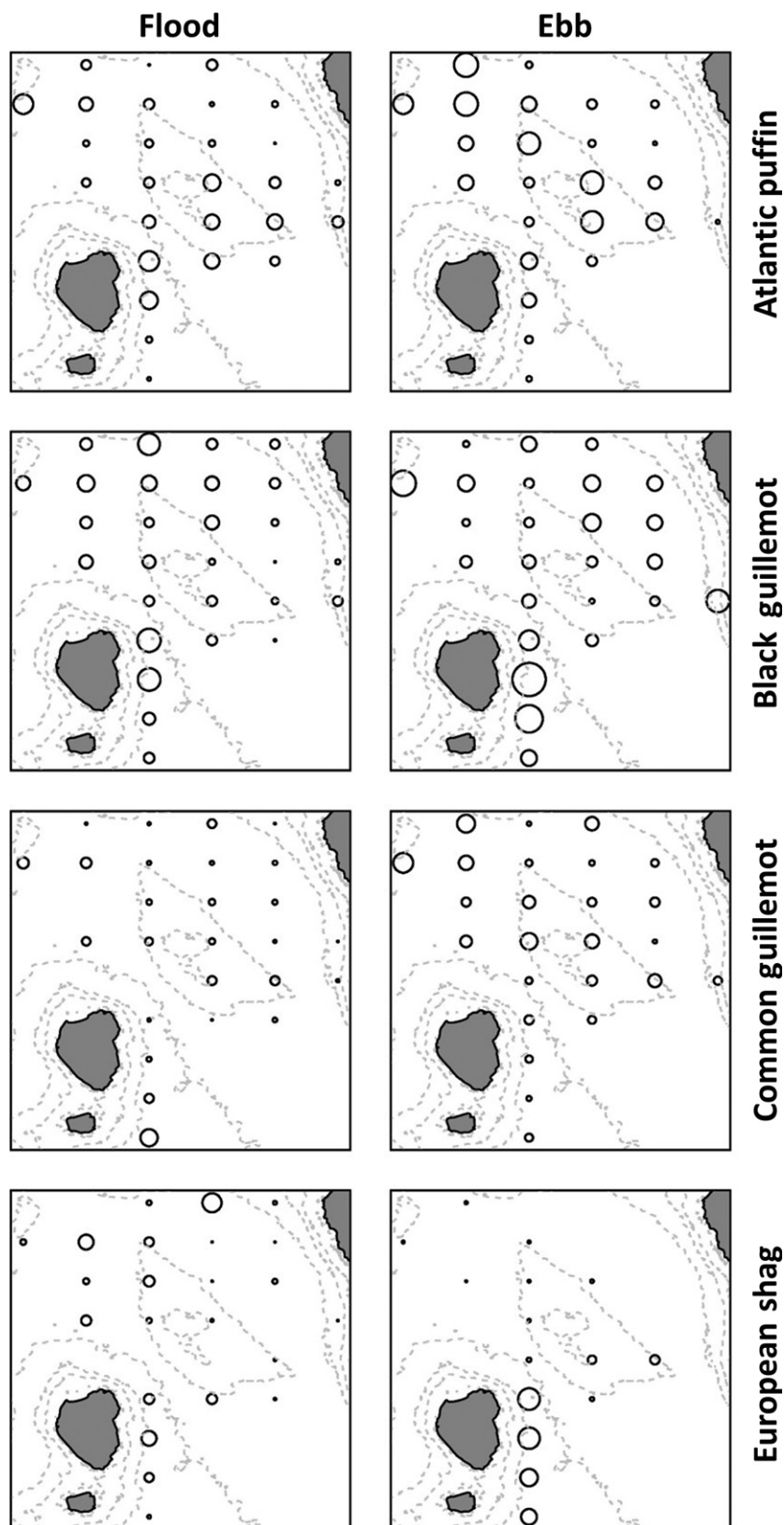

Fig. 6. The frequency of sightings per 500-m resolution cell as a function of species and tide in breeding seasons. The size of the circle represents the proportion of vessel visits where a foraging seabird was encountered. Dashed lines represent 10-m bathymetry contours. Cells that were visited less than ten times were omitted.

Table 1. Model-averaged model parameters (±SE) showing relationships between the probability of encountering foraging seabirds and physical characteristics. Standardized coefficients are shown to enable direct comparisons among physical characteristics. *Elev, HSpd, Visc, VSpd, SRH* and *SHD* quantify water depth, horizontal current speeds, eddy viscosity (indicative of turbulence), vertical current speeds, seabed roughness and seabed hardness, respectively. Relationships were modelled using generalized linear mixed effect models (GLMM). Statistically significant relationships ($P < 0.05$) are shown in bold. Breeding seasons $n = 1420$; non-breeding seasons $n = 1727$

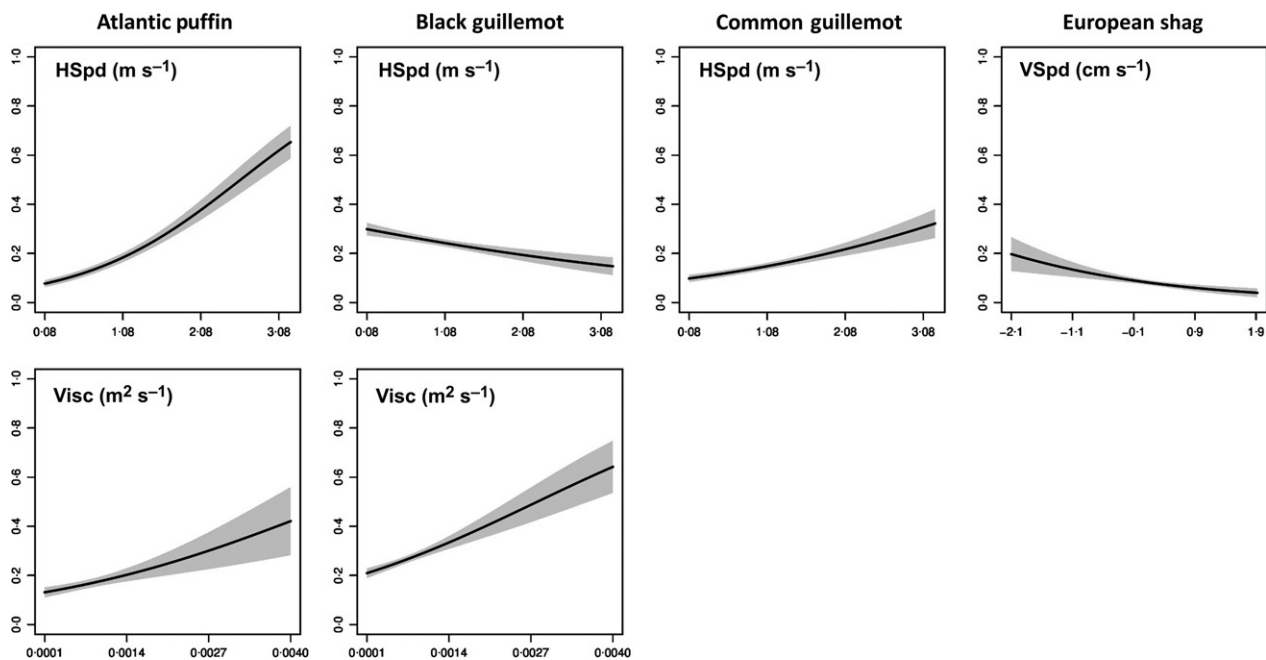| Season	Species	Intercept	Elev (m)	HSpd (ms^{-1})	Visc (m^2 s^{-1})	VSpd (cm s^{-1})	SRH (Arbitrary)	SHD (Arbitrary)
Breeding	Atlantic Puffin	-1.86 ± 0.12	0.17 ± 0.10	**0.69 ± 0.09**	**0.23 ± 0.08**	0.02 ± 0.06	0.03 ± 0.15	0.01 ± 0.10
Breeding	Black Guillemot	-1.34 ± 0.07	-0.05 ± 0.10	**-0.21 ± 0.07**	**0.27 ± 0.07**	-0.07 ± 0.06	0.15 ± 0.09	-0.07 ± 0.08
Breeding	Common Guillemot	-2.16 ± 0.10	0.12 ± 0.12	**0.33 ± 0.08**	-0.09 ± 0.09	0.04 ± 0.07	-0.04 ± 0.13	-0.14 ± 0.10
Breeding	European Shag	-2.57 ± 0.11	-0.24 ± 0.13	0.05 ± 0.10	0.04 ± 0.10	**-0.23 ± 0.08**	0.18 ± 0.15	0.14 ± 0.11
Non-Breeding	Black Guillemot	-1.12 ± 0.08	0.04 ± 0.11	**0.20 ± 0.07**	**0.18 ± 0.07**	**-0.18 ± 0.06**	0.11 ± 0.09	-0.14 ± 0.08
Non-Breeding	European Shag	-2.27 ± 0.10	-0.22 ± 0.12	-0.20 ± 0.10	0.13 ± 0.08	**-0.30 ± 0.08**	**0.34 ± 0.13**	**0.30 ± 0.09**

Fig. 7. Fitted lines ± standard error from generalized linear mixed effect model (GLMM) outputs in breeding seasons showing statistically significant ($P \leq 0.05$) relationships between the probabilities of encountering foraging seabirds and physical characteristics. *HSpd, Visc* and *VSpd* quantify horizontal current speeds, eddy viscosity (indicative of turbulence) and vertical current speeds, respectively.

times larger for the lowest than for the highest *HSpd* values (Fig. 7). This relatively weak effect may reflect frequent sightings in areas of elevated *Visc* and high *HSpd* values alongside Muckle Greenholm.

European shags

The most frequent sightings of European shags occurred alongside Muckle Greenholm across ebb and flood tides and in the northern main channel during flood tides (Fig. 6), areas coinciding with generally negative *VSpd*

values (Fig. 2). This relationship with *VSpd* was significant (Table 1) and moderately strong; probabilities were 4·94 times larger for the lowest than for the highest *VSpd* values.

NON-BREEDING SEASONS

Black guillemots

The most frequent sightings of black guillemots occurred downstream of Muckle Greenholm and the south-western

Eday headland during ebb tides, and in the northern central channel during flood tides (Fig. 8); these areas all coincided with elevated *Visc* and/or negative *VSpd* values (Fig. 2). These relationships with *Visc* and *VSpd* were significant (Table 1) and moderately strong; probabilities were 2·43 times larger for the highest than for the lowest *Visc* values, and 3·12 times larger for the lowest than for the highest *VSpd* values (Fig. 9). Sightings generally increased away from the Eday coastline and its minimal *HSpd* values (Figs 2 and 8). This relationship with *HSpd* was significant (Table 1) but relatively weak; probabilities were only 2·00 times larger for the highest than for the smallest *HSpd* values (Fig. 9). This relatively weak effect may reflect frequent sightings across the broad range of *HSpd* values found away from the Eday coastline (Figs 2 and 6).

European shags

The most frequent sightings of European shags were concentrated alongside Muckle Greenholm across ebb and flood tides (Fig. 8), coinciding with rough–hard seabeds (Fig. 4) and generally negative *VSpd* values (Fig. 2). These relationships with *VSpd* and rough–hard seabeds were significant (Table 1) and particularly strong; probabilities were 10·56 times larger for the lowest than for the highest *VSpd* values, and 6·35 times larger for the roughest–hardest than for the smoothest–softest seabeds (Fig. 9). The higher effect of the former could reflect frequent sightings in areas of negative

VSpd within the southern main channel during flood tides (Figs 2 and 8).

Discussion

This study aimed to identify associations between foraging pursuit-diving seabirds and fine-scale (100 s of metres) physical features within a tidal stream environment. This is the first study to provide concurrent and quantitative measures of foraging distributions and multiple physical characteristics in continuous time and space across a tidal stream environment (3 × 3 km) suitable for array installations of tidal stream turbines, during both non-breeding and breeding seasons. This study therefore provides the most comprehensive exploration of pursuit-diving seabirds' use of tidal stream environments to date. There were two main findings from this study. First, significant relationships were seen between the probability of encountering foraging seabirds and certain physical characteristics in both breeding and non-breeding seasons, indicative of associations with physical features. Secondly, the identity and strength of associations with physical features differed between species in non-breeding and breeding seasons, and also within species between these two seasons, indicative of interspecific and intraspecific variations in habitat use. These two main findings are first discussed with regard to biophysical mechanisms and habitat use, and then with regard to their application in the environmentally sustainable management of sites earmarked for array installations.
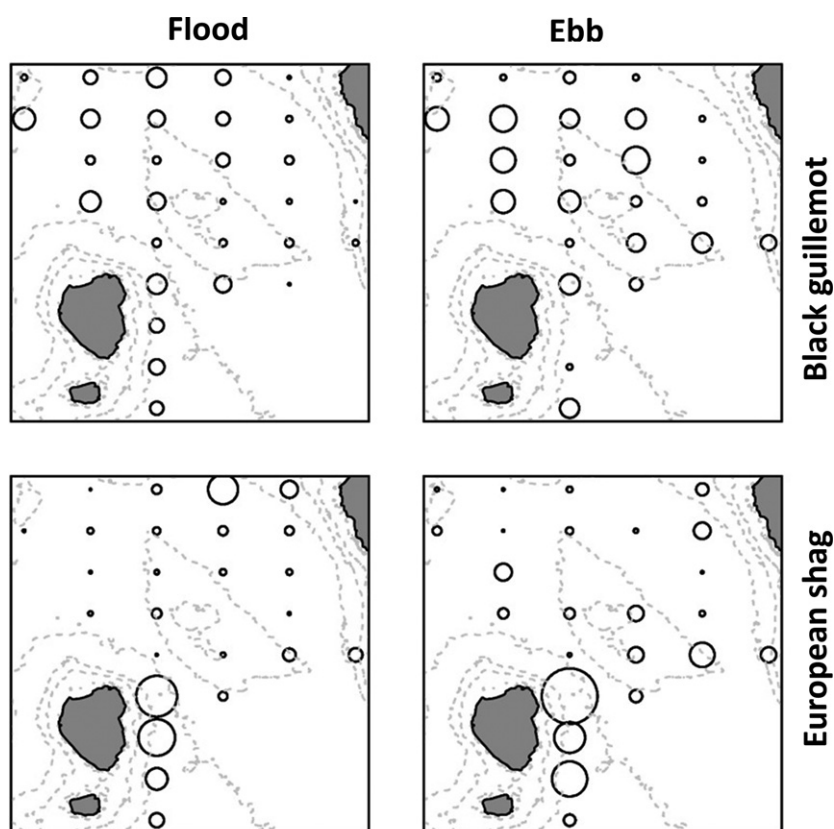

Fig. 8. The frequency of sightings per 500-m resolution cell as a function of species and tide in non-breeding seasons. The size of the circle represents the proportion of vessel visits where a foraging seabird was encountered. Dashed lines represent 10-m bathymetry contours. Cells that were visited less than ten times were omitted.
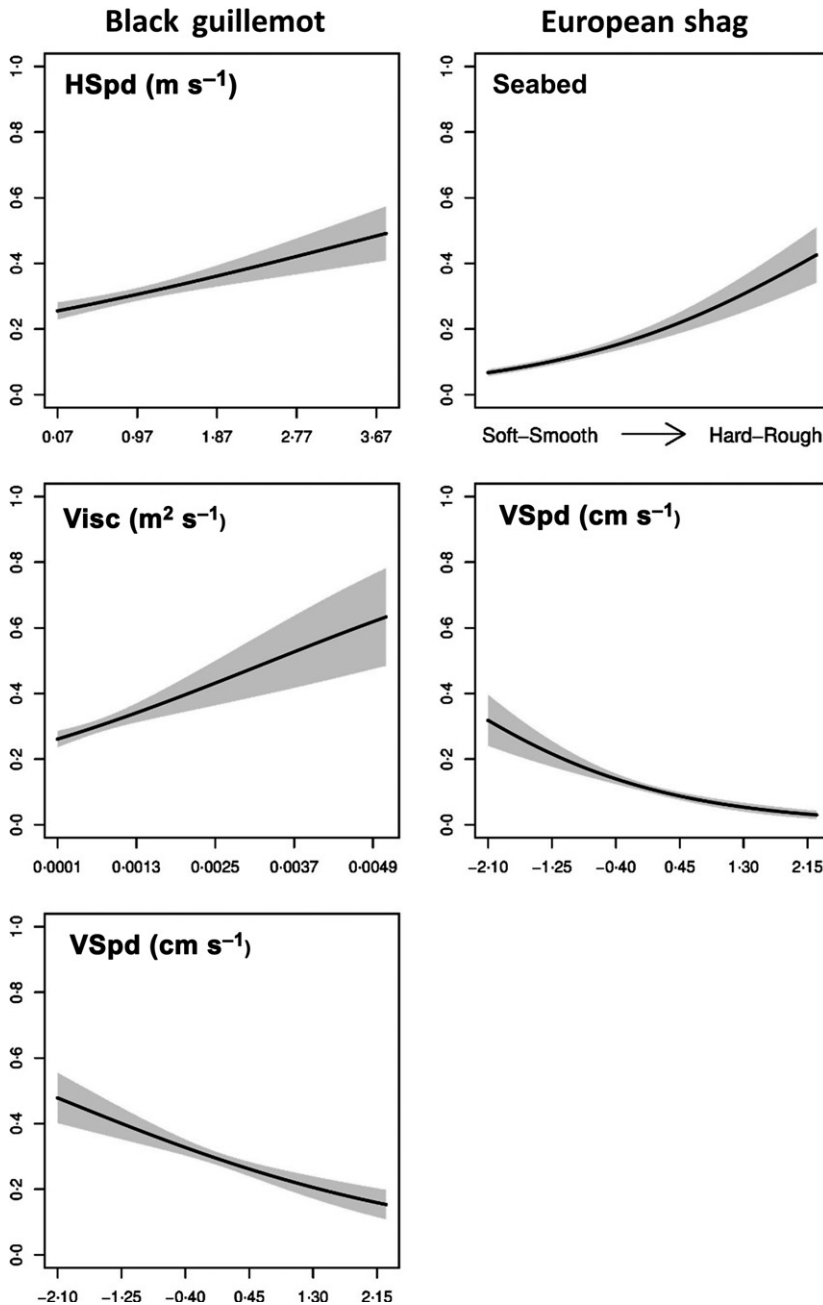
Black guillemot

HSpd (m s⁻¹)

Visc (m² s⁻¹)

VSpd (cm s⁻¹)

European shag

Seabed

Soft–Smooth ⟶ Hard–Rough

VSpd (cm s⁻¹)

Fig. 9. Fitted lines ± standard errors from generalized linear mixed effect model (GLMM) outputs in non-breeding seasons showing statistically significant ($P \leq 0.05$) relationships between the probabilities of encountering foraging seabirds and physical characteristics. *HSpd, Visc* and *VSpd* quantify horizontal current speeds, eddy viscosity (indicative of turbulence) and vertical current speeds, respectively.

FINE-SCALE PHYSICAL FEATURES

Within tidal stream environments, a small number of studies have found associations between foraging seabirds and areas of fast horizontal currents, slow horizontal currents, high turbulence and strong vertical currents (Hunt *et al.* 1999; Benjamins *et al.* 2015). However, this is the first study to identify relationships between foraging seabirds and physical features within these habitats outside North America. Despite the scarcity of comparable studies, results from this study indicate some generalities among pelagic foraging *Alcidae* (Atlantic puffins, common guillemots); the moderate and strong associations with fast horizontal currents match those from similar species

in North America (Hunt *et al.* 1998; Holm & Burger 2002; Ladd *et al.* 2005; Drew, Piatt & Hill 2013). By contrast, these results highlight some discrepancies among benthic foraging *Alcidae* (black guillemots) and *Phalacrocoracidae* (European shags); the moderate and strong associations with hydrodynamic and seabed features both match and contrast those from similar species in North America (Holm & Burger 2002; Zamon 2003; Drew, Piatt & Hill 2013). Evidence therefore suggests that benthic foraging species exploit different physical features in different sites, indicative of site-specific habitat use. However, benthic foraging *Alcidae* and *Phalacrocoracidae* are known to exploit a broad range of fish and invertebrate prey (Bradstreet 1980; Ewins 1990; Wanless & Harris 2004). As

habitat use within tidal stream environments could depend upon prey resources (Elliott *et al.* 2008), regardless of physical similarities, identifying links between prey selection and associations could explain these discrepancies among benthic foraging *Alcidae* and *Phalacrocoracidae*.

BIOPHYSICAL MECHANISMS

An increasing number of studies within shallow water habitats (<500 m) highlight the importance of hydrodynamic features originating from interactions between tidal currents and bathymetry for foraging seabirds including internal waves (Stevick *et al.* 2008; Embling *et al.* 2012; Scott *et al.* 2013), eddies (Allen *et al.* 2001) and physical forcing (Lavoie, Simard & Saucier 2000; Cotte & Simard 2005). All species studied here showed associations with hydrodynamic features originating from these interactions, features which emerge and intensify during maximum tidal currents. This study provides further evidence of the influence of these interactions, and also of foraging opportunities generally increasing during maximum tidal currents (Hunt *et al.* 1998; Zamon 2003; Embling *et al.* 2012; Jones *et al.* 2014), within shallow water habitats. As numerous species known to exploit both pelagic and benthic prey items were associated with hydrodynamic features, these features seem to enhance the availability of several prey species through different mechanisms. The underlying mechanism, however, could be the disorientation of mobile fish in strong and three-dimensionally dynamic flows (Liao 2007) which may provide seabirds with isolated, less responsive and more exploitable prey items (Enstipp, Grémillet & Jones 2007; Crook & Davoren 2014).

Presumably because hydrodynamic features dominate these habitats, seabed features have rarely been considered in studies investigating associations in tidal stream environments (Hunt *et al.* 1999; Benjamins *et al.* 2015). European shags were strongly associated with rough hard seabeds in non-breeding seasons, and were the only species to associate with seabed features. Previous studies found European shags concentrate their foraging efforts in areas of rough–hard seabed whilst exploiting sedentary benthic invertebrates and fish (Watanuki *et al.* 2008). Unlike *Alcidae*, *Phalacrocoracidae* could often detect and ambush prey items at close distance using tactile cues (White *et al.* 2007). These unique ambush strategies appear well suited for searching through complex habitats for the aforementioned prey items (Lovvorn & Liggins 2002), and this could explain European shags' association with rough–hard seabeds. The combination of associations with seabed features likely to enhance the availability of sedentary prey species, and with hydrodynamic features likely to concern more mobile prey species, complements previous evidence of flexible foraging strategies among *Phalacrocoracidae* (Gremillet *et al.* 1998; Velando & Freire 1999). Somewhat surprisingly, neither black guillemots nor European shags showed associations with water elevation, despite previous studies showing benthic foragers associating with times and areas of shallower depths (Ronconi & Clair 2002; Drew, Piatt & Hill 2013). However, previous studies focussed upon study sites with large depth (100 m) and/or tidal ranges (8 m), suggesting that the influence of water elevation could be restricted to these extreme scenarios.

Whilst associations have been linked to foraging opportunities, other mechanisms also merit consideration, particularly among species breeding and roosting within the FOW. For instance, Muckle Greenholm provides black guillemots and European shags with nesting opportunities in breeding seasons, and the latter with roosting opportunities across both seasons; opportunities which could explain why encounters here were particularly frequent (McSorley *et al.* 2003). However, it was noted that the Eday coastline also provides these species with nesting/roosting opportunities (J.J. Waggitt, *personal observation*), and encounters along this coastline were relatively infrequent. It is nevertheless likely that the combination of suitable roosting/nesting opportunities and foraging opportunities could encourage an accumulation of individuals alongside Muckle Greenholm.

HABITAT USE

By performing novel and comparable studies across breeding and non-breeding seasons, this study shows unique evidence of intraspecific differences in habitat use between seasons. Both black guillemots and European shags associated with a broader range of physical features in non-breeding than in breeding seasons. These seasonal differences in habitat use could result from declines in prey resources during non-breeding seasons. For instance, the migration of benthic fish into offshore habitats (Gibson 1969) and the hibernation of sandeels within substrates (Winslade 1974) could reduce resource availability, encouraging niche expansion (Chase 2011). Black guillemots also showed contrasting relationships between seasons, associating with fast horizontal currents in non-breeding seasons, but slower horizontal currents in breeding seasons. The switch from slower to faster horizontal currents coincided with the dispersal of common guillemots into offshore habitats (Kober *et al.* 2010). Whilst classed as benthic and pelagic foragers, respectively, black guillemots and common guillemots generally perform similar U-shaped dives whilst exploiting prey in the lower water column (Thaxter *et al.* 2010; Masden, Foster & Jackson 2013). Therefore, these species may share similar vertical space within the study site. It is speculated that a decline of benthic resources in combination with reduced levels of interspecific competition initiates this seasonal change in habitat use, with black guillemots in non-breeding seasons potentially exploiting similar resources to common guillemots in breeding seasons.

As noted previously, in tidal stream environments, species showed differences in their associations, indicative of

interspecific variations in habitat use (Hunt *et al.* 1998; Holm & Burger 2002; Ladd *et al.* 2005; Drew, Piatt & Hill 2013). However, the combination of more detailed physical characteristics and multi-seasonal studies showed that the extent and magnitude of these differences varied as a function of season and species families. For example, in breeding seasons, the *Alcidae* species often shared associations, whereas *Alcidae* and *Phalacrocoracidae* species never shared associations. By contrast, in non-breeding seasons, the remaining *Alcidae* (black guillemots) and *Phalacrocoracidae* species did share some associations. It is suggested that differences in fundamental foraging behaviours, in combination with the aforementioned seasonal variations in resource availability and levels of competition, could collectively determine the extent and magnitude of differences in associations among species.

CONSISTENCY

The presence of significant and strong relationships indicates that species' associations were consistent within seasons across the study period. However, changes in prey characteristics could influence a species' habitat use, particularly shifts between predominantly benthic and pelagic diets (Watanuki *et al.* 2004; Elliott *et al.* 2008). Nevertheless, regional dietary studies indicate general consistencies in species dependency on either benthic or pelagic prey items (Furness *et al.* 2012), suggesting that the aforementioned scenarios are unlikely. It is therefore argued that the associations shown in these studies are representative of typical scenarios.

VULNERABLE SPECIES

Array installations will mainly occur within areas of fast horizontal currents, depths > 30 m and relatively hard–smooth seabeds (Fraenkel 2006); most of the eight installations within the FOW occupied areas containing these four physical characteristics. Atlantic puffins showed strong associations with fast horizontal currents during breeding seasons, indicating a particularly high likelihood of interactions with any array installation. Any post-installation monitoring or mitigation measures, which could include the moderation of device operation and maintenance, should therefore focus on Atlantic puffins during breeding seasons. It was also found that multiple species were associated with areas of high turbulence and downward vertical currents, which often coincided with fast horizontal currents, across breeding and non-breeding seasons. Therefore, a potential pre-installation mitigation strategy would be the omission of array installations from these physical features, reducing the overall likelihood of interactions across species.

On a broader perspective, it was found that three out of four species showed moderate or strong associations with areas of fast horizontal current speeds within at least one season, despite their fundamental differences in foraging

behaviour. Therefore, numerous species exploiting a development site could have a relatively high likelihood of interactions with array installations, with higher levels of vulnerability not constrained to certain groups. Seasonal differences in the relative levels of vulnerability, linked to either dispersal among migratory species (Atlantic puffins, common guillemots) or changes in habitat use among resident species (black guillemots), were also found. This finding emphasizes the need to understand habitat use across the annual cycle, or at least within discrete periods of the annual cycle (e.g. breeding and non-breeding seasons), when estimating levels of vulnerability for species exploiting a development site.

MANAGEMENT ISSUES

There is a legal responsibility to consider impacts from tidal stream turbine installations on the environment (European Directive: 85/337/EEC), and environmental impact assessments (EIA) documenting biological and physical characteristics of development sites form a major component of this process (Wood 2003). With many governments adopting a 'deploy and monitor' approach with regard to marine renewable energy devices (Wright 2015), robust and informative approaches are needed to first identify potential impacts from installations and then to initiate appropriate mitigation measures to safeguard vulnerable species. Current EIA approaches typically involve performing a single transect once per month across 2 years, to quantify general abundances of different seabird species over the annual cycle (Jackson & Whitfield 2014). This study shows that management strategies aiming to reduce the likelihood of negative impacts would benefit greatly from more focussed approaches within development sites, and that identifying associations between foraging seabirds and physical features can facilitate effective risk assessment and mitigation. For instance, the identification of which and when species are strongly associated with fast horizontal currents provides clear instruction to those tasked with implementing post-installation monitoring and mitigation measures, allowing effort and resources to be focused on appropriate species and seasons. The identification of any associations between foraging seabirds and physical features which generally coincide with fast horizontal current speeds (turbulence and upward/downward vertical currents) would also allow installations to be situated in areas where the potential for negative impacts are lowest, providing compromises between energy returns and conservation. As they can facilitate the development of targeted mitigation measures, it is recommended that the approaches used in this study should contribute towards EIA within development sites.

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Data accessibility

The data sets used in this manuscript are available from Dryad Digital Repository doi: 10.5061/dryad.9r76h (Waggitt *et al.* 2016).

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Supporting Information

Additional Supporting Information may be found in the online version of this article.

Appendix S1. Additional details of methodologies for hydrodynamic models, substrate characteristics, vessel-based surveys and data processing.

Appendix S2. Details of all candidate models per species and season.

Table S1. Counts and number of sightings per species in breeding seasons.

Table S2. Counts and number of sightings per species in non-breeding seasons.

Figure S1. Diagnostic plots testing for spatial autocorrelation.

Figure S2. Diagnostic plots testing for temporal autocorrelation.

Figure S3. Diagnostic plots showing the distribution of intercepts associated with the random effect.