



A Novel Approach to Using Seabed Geomorphology as a Predictor of Habitat Use in Highly Mobile Marine Predators: Implications for Ecology and Conservation

Hannah M. E. Wyles*, Lars Boehme, Debbie J. F. Russell and Matt I. D. Carter*

Sea Mammal Research Unit, Scottish Oceans Institute, University of St Andrews, St Andrews, United Kingdom

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*Correspondence:

Matt I. D. Carter
midc@st-andrews.ac.uk
Hannah M. E. Wyles
hw59@st-andrews.ac.uk

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Understanding how marine predators find patchily distributed prey resources in a dynamic environment is key to identifying important ecological areas for ecosystem-level conservation management. However, the mechanisms underpinning important foraging areas often result from complex interactions between static and dynamic covariates (e.g. topography and currents). Modelling habitat associations with hydrodynamic processes is rarely useful when attempting to identify and characterise foraging areas across an individual's foraging range. Investigating the influence of static habitat features on predator behaviour can provide a more tractable baseline understanding of habitat associations, upon which additional complexity can be added. Seabed gradient covariates (e.g. slope and aspect) are often used, yet such metrics are computed at singular user-defined resolutions, and provide limited ecological insight when used in isolation. Instead, categorising the seabed into geomorphological features may provide better characterisation of seabed structure. Here we explore the utility of a pattern recognition algorithm to delineate whole geomorphological features ("geomorphons") on the seabed (e.g. valleys, ridges, footslopes) from bathymetry data, and examine the influence of geomorphology on marine predator habitat use. We demonstrate the potential application of this approach in a case study, examining the influence of geomorphons on the at-sea behaviour of a highly mobile predator inhabiting shelf seas: the grey seal (*Halichoerus grypus*). We analyse GPS tracking data from three seals tagged in the southern North Sea, an area with heterogeneous geomorphology. We use hidden Markov models (HMMs) to infer foraging and travelling behaviour and model the effect of different feature types on the probability of switching between states. All three seals showed an increased probability of transitioning from travelling to foraging when encountering slopes, footslopes and hollows, and foraging activity was concentrated at slopes on the fringes of the Dogger Bank. We hypothesise that such features may host prey aggregations, and/or lead to increased prey capture success. The results suggest the importance of such areas for grey seals in the southern North Sea, a region

undergoing rapid and widespread anthropogenic habitat change. This method could be incorporated into future species distribution models to improve estimates of predator distribution, informing conservation management and marine spatial planning.

Keywords: hidden Markov models (HMMs), movement ecology, North Sea, geomorphons, grey seal (*Halichoerus grypus*), satellite telemetry and tracking

INTRODUCTION

Understanding how animals utilise their environment to optimise food intake and maximise fitness is a fundamental question for ecologists (Stephens and Krebs, 1986). Studying the intrinsic and extrinsic mechanisms which underpin the foraging behaviour of animals can provide insights into the functioning of ecosystems and ecologically important areas (Schmitz et al., 1997). It is particularly important to understand the processes which shape the foraging behaviour of high trophic level predators, as they play a vital role in the structure of marine and terrestrial communities through the top-down regulation of prey (Williams et al., 2004; Heithaus et al., 2008). Marine ecosystems are inherently dynamic and prey resources are often patchily distributed (Haury et al., 1978). Therefore, highly mobile predators (e.g. marine mammals, turtles, pelagic fish and seabirds) may adjust their foraging behaviour to maximise time in the most productive areas (Kie, 1999; Weimerskirch, 2007; Kirchner et al., 2018). Understanding how predators use environmental features to optimise foraging is necessary to allow ecologically important areas to be identified, and thus to inform marine spatial planning (Boyd and Murray, 2001; Hindell et al., 2020). Such areas are not easy to identify at sea because we cannot easily observe them, but spatial aggregations of predators can be used as indicators (Block et al., 2011; Montevecchi et al., 2012; Grecian et al., 2016; Hindell et al., 2020).

Observing the behaviour of highly mobile marine predators is challenging as they spend most or all of their time at sea, often far from land or underwater, and can cover large distances (Fedak et al., 2002; Luschi et al., 2003; Skomal et al., 2017). Animal-borne sensors allow for the collection of fine-scale data from which the movements of marine predators can be reconstructed (Wilmers et al., 2015). Such data can be analysed to infer behaviours (Patterson et al., 2008; Carter et al., 2016), to identify important foraging areas (Camphuysen et al., 2012), and to understand the environmental characteristics of these areas using ancillary oceanographic data from animal-borne tags (Lydersen et al., 2002; Boehme et al., 2008a; Boehme et al., 2008b). Locational data collected from animal-borne tags are frequently used to infer discrete behaviours, such as travelling (e.g. commuting to, from and between foraging sites) and Area-Restricted Search (ARS), which in many vagile species has been associated with foraging activity, i.e. searching for, capturing and handling prey (Kareiva and Odell, 1987; Pinaud and Weimerskirch, 2007). Identifying discrete behaviours from animal tracking data is commonly done by analysing aspects of track geometry, such as changes in step lengths (the distance

between two consecutive locations) and turning angles through time (Boyd, 1996; Fauchald and Tverra, 2003; Barraquand and Benhamou, 2008). During ARS, an animal will typically exhibit large turning angles compared to while travelling, combined with a reduction in speed, as a result of searching for, encountering and responding to a food source or in response to environmental cues, for example in areas where prey was previously encountered (Kareiva and Odell, 1987). In recent years, hidden Markov models (HMMs) have emerged as a popular and flexible analytical tool which can be used to identify discrete movement modes (from which behaviours can be inferred) from animal movement data (Patterson et al., 2008; Langrock et al., 2012). The movements of many highly mobile marine predators, including pelagic fish (e.g. Patterson et al., 2009; Towner et al., 2016), seabirds (e.g. Pirodda et al., 2018; Clay et al., 2020) and marine mammals (e.g. Isojunno et al., 2017; Carter et al., 2020) have been investigated using tracking data and HMMs. A major advantage of HMMs over other movement models is that they can be used to investigate the mechanisms that shape animal behaviour through the inclusion of covariate effects, such as environmental variables, on state transition probabilities (Morales et al., 2004; Patterson et al., 2009; Photopoulou et al., 2020). In this way, the effects of encountering a specific feature or habitat type on the probability that an animal will switch from one state to another can be quantified (Morales et al., 2004).

Examining animal behaviour in relation to the variety of environmental conditions that an individual encounters whilst searching for prey can help us to understand what ultimately drives foraging decisions. A wide range of environmental factors are often considered in studies of marine predator habitat associations, including static covariates such as bathymetric depth, which can influence prey accessibility for benthic foragers (e.g., Burns et al., 2004), as well as dynamic covariates that may influence prey distribution, such as sea ice presence for polar species (e.g., Pagano and Williams, 2021) and sea surface temperature in seasonal seas (e.g., Georges et al., 2000; Speakman et al., 2020). Seabed topography (i.e. spatial variation in seabed terrain) can influence predator behaviour and distribution through a variety of complex mechanisms (Cox et al., 2018). These mechanisms may be indirect, for example static features in the open ocean such as seamounts are associated with increased primary productivity (Genin and Boehlert, 1985), creating predictable foraging conditions for marine predators (Morato et al., 2010; Maxwell et al., 2012; Letessier et al., 2019). Similarly, in shelf seas tidal currents moving over offshore banks and uneven terrain can lead to subsurface aggregations of small fish, either through increased plankton concentration (Embling et al., 2012), or the mechanical influence of internal waves

(Embling et al., 2013). Such phenomena create spatially and temporally predictable foraging opportunities (Embling et al., 2012; Scott et al., 2013). Topography may have a more direct relationship to predator foraging behaviour; known foraging areas of bottlenose dolphins (*Tursiops truncatus*) in the Moray Firth (Northeast Scotland) are characterised by steep seabed gradients, which may act as a physical barrier against which to herd prey (Hastie et al., 2003; Bailey and Thompson, 2010). While the individual oceanographic components that characterise foraging sites (e.g. currents, water column stratification, tidal fronts) can be modelled at high resolution, processing and interpretation of such data can be challenging, often requiring specific expertise. Moreover, the hydrodynamic conditions that characterise foraging sites may vary spatially and temporally (e.g. across seasons). Capturing such complexities in models of predator-habitat association is challenging, particularly when studying a species across entire movement tracks rather than at isolated known foraging sites. Furthermore, although hydrodynamic covariates have been shown to be important for a range of species including some aerial and pelagic predators (Cox et al., 2018), the habitat associations of benthic predators may be better described by covariates relating to seabed characteristics. Such static metrics may prove more accessible and tractable indicators of important ecological areas, upon which dynamic covariates can later be added to investigate the specific mechanisms underpinning the importance of discrete areas. Singular metrics of topographic gradients, such as slope and aspect, are frequently used in such studies of marine predator habitat associations. An advantage of such metrics is that they can be computed across wide spatial extents, such as ocean basins. However, given the complexity of processes linking topography to prey described above, such metrics only provide limited ecological insight into predator-habitat associations, especially when used in isolation (Bouchet et al., 2015). Moreover, gradients are computed at a singular user-defined spatial scale, and do not provide insight into geological context or function. For example, it is impossible to determine the relative importance of areas near the top or bottom of a slope using gradient alone. Instead, classification of the seabed into features which have distinct geomorphological shapes provides more information about the underlying structure of the seabed (Bouchet et al., 2015).

In the terrestrial environment, geomorphology has been used to investigate the drivers of movements of wide-ranging species, such as elk (*Cervus* sp.), where the direction of movement was found to be dependent on the topography of the landscape (Kie et al., 2005). For snow leopards (*Uncia uncia*), geomorphology has also been found to influence behaviour, with features such as ridgelines and cliffs being used for both daytime resting and travelling (Jackson, 1996). In the marine environment, seabed geomorphology has been mapped for the global ocean for geological applications, categorising seabed features into a set of landforms (Harris et al., 2014), and a study has combined bathymetric data with seabed backscatter data from acoustic surveys to generate high resolution seabed classifications (“bathymorphons”) for a specific study area (Masetti et al.,

2018). However, only a handful of studies have considered such data in the context of predator-habitat associations (Torres et al., 2013; Bouchet et al., 2020; Claro et al., 2020). These studies have generally investigated the influence of broadscale features, such as canyons, seamounts and plateaus on pelagic species, and the influence of topographic features on shelf sea predators remains largely unstudied using geomorphology. Moreover, the geomorphological dataset presented in Harris et al. (2014) is not resolved to identify discrete features in shelf seas. However, the “geomorphon” pattern recognition algorithm developed by Jasiewicz and Stepinski (2013) presents an opportunity to generate new geomorphological datasets from digital elevation model (DEM) or digital terrain model (DTM) data. Importantly, the algorithm is customisable such that a range of spatial resolutions can be explored, allowing the user to generate a landform map that is relevant to their research question and study area (Jasiewicz and Stepinski, 2013). Moreover, the pattern recognition process accounts for variation in the spatial magnitude of individual features, thus allowing features to be mapped at a range of scales (e.g. capturing both narrow and wide valleys). To our knowledge this approach has not been widely used in marine ecological studies, but when applied to bathymetry data, it provides an opportunity to investigate the potential influence of seabed topographic features on the behaviour of shelf sea predators at a spatial scale which is relevant to individual animals.

This study explores the utility of seabed geomorphological features as predictors of habitat use for highly mobile predators. Here we present a case study to: (i) employ the “geomorphon” algorithm to generate a dataset of seabed geomorphological features on a spatial scale that is relevant to the study species; (ii) examine whether inclusion of geomorphology as a covariate on state transition probabilities in a HMM applied to tracking data for three grey seals (*Halichoerus grypus*) in the southern North Sea improves the model fit over a null model (i.e. with no covariate effects); and (iii) consider to what extent this approach has the potential to provide ecological insights that will contribute information towards identifying important ecological areas for conservation management.

Grey seals are an ideal study species to explore the above research questions, as they are high trophic level predators inhabiting shelf seas of the North Atlantic. They regularly undertake multi-day foraging trips at sea, travelling up to hundreds of kilometres from terrestrial haulout sites, and thus are likely to encounter a wide range of topographic conditions (McConnell et al., 1999; Breed et al., 2009; Nowak et al., 2020). Moreover, their ecology has been studied in detail for decades (Thompson et al., 1991; McConnell et al., 1992; Russell et al., 2013), but understanding of the environmental mechanisms that underpin foraging behaviour remains incomplete. Grey seals have been model species for the development of animal movement HMM techniques (Jonsen et al., 2005; McClintock et al., 2012; Carter et al., 2020), and recent studies have begun to use HMMs to investigate the influence of environmental covariates on grey seal behaviour (van Beest et al., 2019; Nowak et al., 2020). However, no studies have examined how

different static geomorphological features might influence their foraging decisions. The North Sea is particularly important habitat for this species, with the United Kingdom (UK) coast of the North Sea alone hosting ~25% of the global population (SCOS, 2020). Yet, this area is undergoing a process of intense change with the decommissioning of oil and gas infrastructure and the large-scale construction of wind farms, which overlap with seal habitat (Russell et al., 2014; Russell et al., 2016). Grey seals are protected in the UK under specific national legislation, as well as 2019 amendments to species and habitats regulations which retained the basic requirements of the European Union (EU) Habitats Directive in UK law after Brexit in 2021. As such, grey seal populations must still be maintained in “favourable conservation status”, in line with the EU Habitats Directive. Special Areas of Conservation (SACs) have been designated around the UK (Russell et al., 2019), yet these SACs are largely centred on coastal pupping and haulout sites and adjacent coastal areas. Moreover, the foraging distribution of grey seals may be hundreds of kilometres away from breeding and haulout sites (McConnell et al., 1999; Russell et al., 2013). Delineating important ecological areas offshore in the North Sea is therefore critical for effective marine spatial planning, and understanding the environmental characteristics of key foraging grounds is a research priority.

METHODS

Tag Deployment and Study Area

The data used in this case study were from three adult grey seals tagged with Fastloc[®] GPS/GSM (Global System for Mobile Communications) devices (SMRU Instrumentation, UK) as part of a larger deployment in May 2015 ($n = 20$) at two haulout sites in Southeast England (Blakeney Point and Donna Nook) (see Russell, 2016). Seals were captured using hand nets, and anaesthetised with intravenous Zoletil100[®] (Virbac, France). The tagging procedure followed that of Sharples et al. (2012). Tags were glued to the fur on the back of the neck at the base of the skull using Loctite[®] 422TM cyanoacrylate instant adhesive (Henkel, UK); the tags then fall off by or during the annual moult. The tags collect positional information using Fastloc[®] GPS when the seal is at the surface or on land, as well as haul-out status using a wet/dry sensor. Data are stored in the buffer memory to be transmitted when the seal enters GSM range (McConnell et al., 2004). **Table 1** outlines the tag deployment information for each seal.

The three individuals used in this case study were chosen as they had the widest ranging movements of the 20 tagged seals and thus were most likely to encounter a variety of different

geomorphological features. The spatial extent of seal tracking data is shown in **Figure 1**. All three seals were either tagged in, or visited, haulout sites within the Humber Estuary SAC (Donna Nook) for which grey seals are a qualifying feature. The habitat covered by seal tracks encompasses much of the southwestern quadrant of the North Sea; an area of shallow but variable water depth (on average ~30 m deep; bathymetry shown in **Figure 1**). This area is predominantly sandy, featuring a large sandbank (Dogger Bank), rising to ~15 m below the surface, which separates seasonally stratified deeper waters of the northern North Sea from the shallower, mixed waters of the southern North Sea (Hill et al., 1993). This division of water bodies is punctuated by the Flamborough tidal mixing front, extending eastwards from the English coast around the fringes of the Dogger Bank (Hill et al., 1993). Dominant prey species for seals in this region include sandeels (*Ammodytes* spp.), flatfish, gadids and other benthic species associated with sandy substrates [e.g. dragonet (*Callionymus lyra*) and goby] (Wilson and Hammond, 2019).

Processing of Movement Data

Location data for the three seals were cleaned to remove erroneous estimates following the protocol from Russell et al. (2015) using residual error threshold and number of satellites. Trips with < 10 observations were removed as they were unlikely to consist of foraging behaviour at sea and were more likely to be near-shore behaviour related to waiting for tidal haulout sites to become available (Thompson, 1989) (See **Supplementary Material**). Location data were regularised to a consistent time step of 1 hour using linear interpolation between pre- and post-location estimates, then any location that fell during a haul-out event was excluded, leaving only at-sea locations. For detail on the selection of a regularisation interval, see **Supplementary Material**. Any time interval for which there was a gap of > 2 hours between observed locations surrounding the interpolated point was flagged as ‘unreliable’ (Russell et al., 2015). These unreliable data points were included in the model, but the associated step lengths and turn angles were omitted. A state was assigned to these intervals by the HMM based on the Markov property, not on the state-dependent parameters, thus they did not influence the state distributions (Carter et al., 2020). See “Statistical Analysis” section below for HMM formulation. The location at the midpoint of the regularised time intervals was used for matching with environmental data (geomorphons; see below). The data were separated into trips, with the start of a trip identified by the end of a haul-out event, and the end of a trip when another haul-out event was initiated. Data within 10 km of the coast at mean high water were excluded using QGIS (QGIS Development Team, 2019) as it is impossible to distinguish

TABLE 1 | Tag deployment information.

Seal reference	Tag start date	Tag end date	Deployment Location	Mass (kg)	Sex
Seal 1	05/05/2015	27/08/2015	Blakeney	157.2	Male
Seal 2	05/05/2015	24/11/2015	Blakeney	174.6	Male
Seal 3	02/05/2015	26/12/2015	Donna Nook	150.4	Female

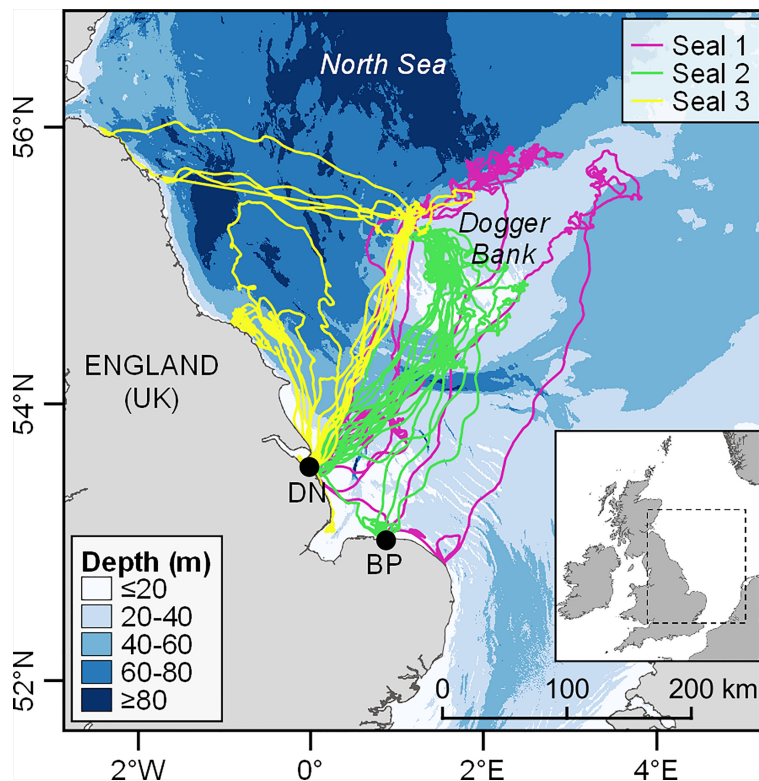


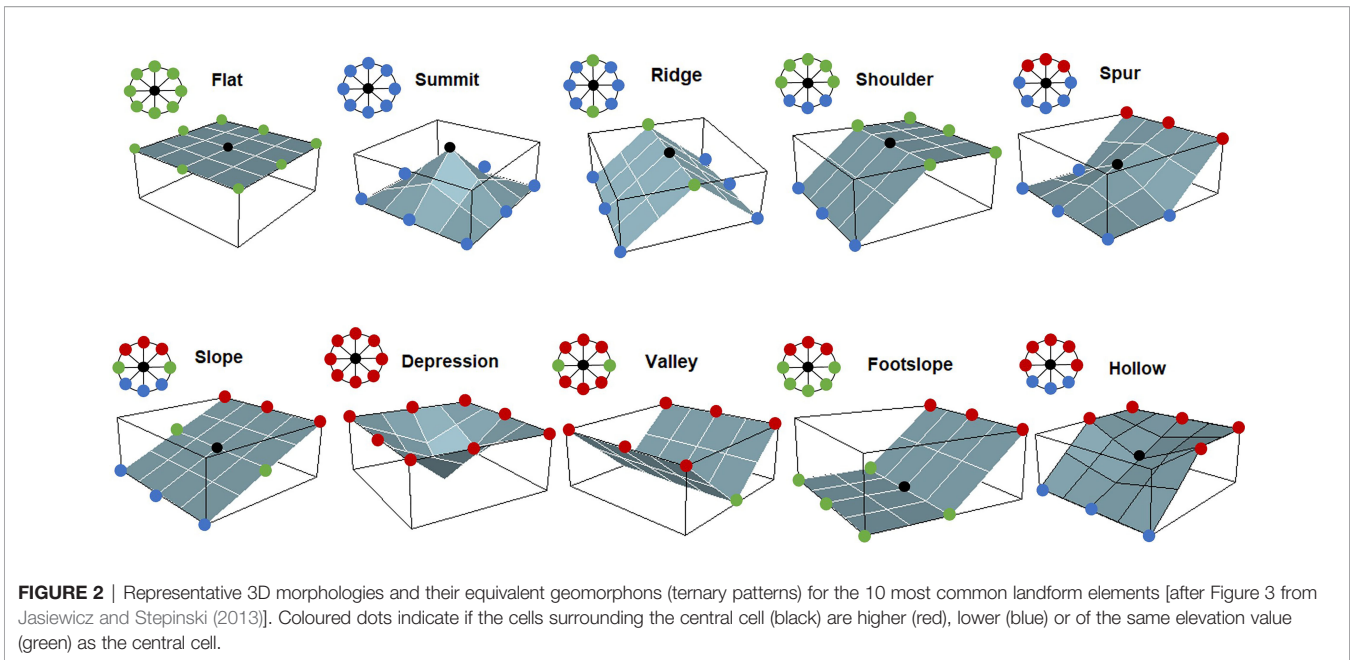
FIGURE 1 | At-sea movements of the three tagged grey seals. Black dots indicate the tagging sites (DN = Donna Nook, BP = Blakeney Point). Bathymetry data: EMODnet Digital Bathymetry (DTM) (2016).

between foraging and other near-shore behaviour (such as waiting for tidal haulout sites to become available) using location data.

Environmental Data

The “geomorphon” pattern recognition algorithm generates a raster layer of discrete landforms from DTM input data (Jasiewicz and Stepinski, 2013). A DTM for the North Sea was obtained from the European Marine Observation and Data Network (EMODnet Bathymetry Consortium, 2016) with a grid resolution of 250 m. The Geographic Resources Analysis Support System (GRASS GIS) (Neteler and Mitasova, 2007) extension *r.geomorphon* (Jasiewicz and Stepinski, 2013) was used to calculate the geomorphons in R (R Core Team, 2021). A raster was produced with grid cell values corresponding to one of the 10 landform elements which are most commonly recognisable in a typical terrestrial landscape (Figure 2). The algorithm requires three parameters to be set by the user, which can influence the geomorphology classification: (i) the maximum extent of a landform, known as the maximum lookup distance (this value needs to be relatively large for the landform elements across a range of sizes to be classified), (ii) the flatness threshold (degrees), below this value any terrain is classified as flat, and (iii) the spatial resolution of the DTM data (Stepinski and Jasiewicz, 2011). This

method uses a line-of-sight principle (Yokoyama et al., 2002) for identifying the relationship of a central cell in the DTM raster with its neighbouring cells. This line-of-sight principle allows an incremental increase in lookup distance (up to the predefined maximum value) until minimum zenith and nadir angles along the eight compass directions are obtained between the central cell and the neighbouring cells (Stepinski and Jasiewicz, 2011). These minimum zenith and nadir angles are compared by the algorithm to identify if the central cell is higher, lower or the same elevation as its neighbours and this is converted into a ternary pattern which represents the geomorphon (Stepinski and Jasiewicz, 2011). There are, theoretically, 6561 possible topographic patterns, and in order to reduce this for mapping, the patterns are grouped into the ten most common landforms: flat, summit, ridge, shoulder, spur, slope, hollow, depression, valley and footslope (Jasiewicz and Stepinski, 2013) (Figure 2). The output of this algorithm is a raster with values for each grid cell corresponding to one of the ten common landform elements mentioned above. Importantly, the algorithm allows the final lookup distance for each cell to be determined automatically, and to be self-adaptive. This means that the geomorphons are mapped at a range of spatial extents, thus allowing for the recognition of landforms of a variety of sizes (e.g., identifying both narrow and broad valleys) (Stepinski and Jasiewicz, 2011). Moreover, the option to customise algorithm parameters allows the user to produce a landform map that is



relevant to their research question, depending on the spatial extent and resolution of interest.

In order to find the most suitable terrain classification for investigating how geomorphological features influence grey seal movements, a range of values for the three parameters (lookup distance, flatness threshold and spatial resolution of the DTM) were trialled. A stepwise procedure was applied by creating a matrix encapsulating all possible combinations of four distinct values for each parameter, giving a total of 64 combinations. The values in the matrix were chosen as they provided a large range in the possible geomorphology rasters; it was unknown which geomorphological scale would be most biologically relevant. Four different bathymetry resolutions were trialled (250 m, 500 m, 1000 m and 2000 m), with four different lookup distances (5 cells, 15 cells, 40 cells and 60 cells) and four different flatness thresholds (0.1, 0.25, 0.5 and 0.7 degrees). Relatively large values of lookup distance and flatness threshold would result in a terrain classification from a higher and broader viewpoint than from smaller values; smaller values would give a classification of the terrain from a finer spatial resolution and thus finer detailed features (Stepinski and Jasiewicz, 2011). Because the final lookup distance is determined automatically, and is self-adaptive, larger values of lookup distance would allow the identification of landforms of a variety of sizes (Stepinski and Jasiewicz, 2011). Higher flatness thresholds produce maps that are flatter, and the influence of this threshold increases disproportionately with coarseness of the resolution of the terrain data. Thus, values of < 1 degree were used to avoid over-classification of flat areas (Stepinski and Jasiewicz, 2011). For each combination of parameter values, a geomorphology raster was created, resulting in 64 candidate rasters. For each candidate raster, geomorphons were extracted for each seal location, and included in a HMM as a covariate effect on state transition probabilities (see “Statistical Analysis” section below). The R package *momentuHMM* (McClintock and Michelot, 2018) was

used to formulate the HMM. The best configuration of parameters for the pattern recognition algorithm was determined using model selection by Akaike Information Criterion (AIC) (Burnham and Anderson, 2002).

To allow comparison among individuals in the effect of geomorphology on behaviour, one individual (Seal 1) was used for defining the best parameters for the pattern recognition algorithm, as this seal covered the widest area and the largest variety of geomorphons (**Figure 1**). Thus, it was assumed that the scale of the geomorphology perceived by each seal would be similar. The values for the different parameters that produced the geomorphology raster with the lowest AIC score when used in the covariate HMM for Seal 1 were: a bathymetry resolution of 2000 m; a lookup distance of 15 cells and a flatness threshold of 0.1 degrees. This configuration produced the model with lowest AIC score compared to other parameter configurations (4.67 points lower than the next best model; see **Supplementary Material Table S1**). The resulting geomorphology raster is shown in **Figure 3**. This geomorphology raster was used for extracting the geomorphons for each location for each seal using the “raster” package (Hijmans and van Etten, 2021) in R.

Statistical Analysis

To test the hypothesis that there is a relationship between seabed topography and seal behaviour, a two state HMM was fitted for each seal independently with a covariate effect of geomorphology (10 level factor) acting on state transition probabilities (covariate model). This covariate model was then compared to a two state HMM for each seal with no covariate effects (null model). The covariate model was deemed superior to the null model (no covariate effects) if it resulted in a reduction in AIC score of 2 points or more (Burnham and Anderson, 2002). The package *momentuHMM* (McClintock and Michelot, 2018) was used to formulate the models in R. HMMs were fitted with step lengths

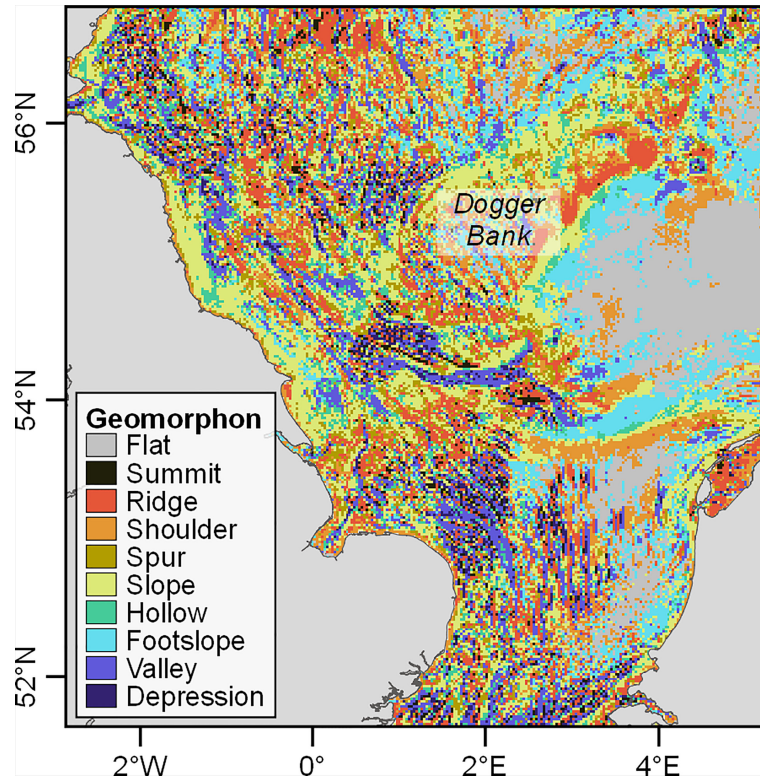


FIGURE 3 | The geomorphology raster of the southern North Sea showing the distribution of the different geomorphons.

and change in bearing (turn angle) as the state-dependent data streams, in line with other studies of grey seal behaviour (Jonsen et al., 2005; Breed et al., 2009; Russell et al., 2015; Nowak et al., 2020). Models were fitted with two discrete movement states for each individual to provide a simple framework for testing the effect of geomorphology on behavioural state. The Viterbi algorithm was used to calculate the most probable state at each time step (Zucchini et al., 2016), and states were inferred as foraging or travelling based on prior knowledge of seal behaviour, and published examples of similar models (i.e. short step lengths and high turn angles = ARS (foraging), long step lengths and low turn angles = travelling) (Carter et al., 2020; Nowak et al., 2020). A Gamma distribution was assumed for the step lengths and a wrapped Cauchy distribution was assumed for the turn angles (see Carter et al., 2020 for mathematical notation). Starting values for the state-dependent parameters (mean and standard deviation for step lengths and the wrapped Cauchy concentration parameter for turn angles) must be

specified for each state. A range of starting values for each state-dependent parameter were trialled until arriving at the global optimum for the negative log-likelihood (Michelot et al., 2016). Model validation checks were carried out by graphical checking of the pseudo-residuals (Zucchini et al., 2016), and no indication of issues relating to poor model fit were found. To facilitate a qualitative comparison of habitat use among individuals, the overall activity budgets (percentage of time spent foraging versus travelling) were estimated for each seal, alongside the percentage of total time spent per state at each geomorphon type.

RESULTS

HMMs successfully identified two discrete movement states for each seal, inferred here as foraging and travelling

TABLE 2 | AIC values for the null model and covariate model for each seal.

Seal	Null model	Covariate model	Δ AIC
1	7483.1	7465.8	-17.3
2	13405.6	13391.4	-14.2
3	8829.8	8820.2	-9.6

Δ AIC indicates the difference in Akaike Information Criterion score between the null and covariate model. Where Δ AIC < -2, the covariate model is deemed superior.

(**Supplementary Material Figure S5**). Model selection by AIC score showed clear support for the covariate model (effect of geomorphons on state transition probabilities) over the null model (no covariate effects) for all three seals (**Table 2**). The AIC score of the covariate model was substantially lower than that of the null model for all three seals ($\Delta\text{AIC} = -17.3, -14.2$ and -9.6 for Seals 1, 2 and 3 respectively; **Table 2**). **Figure 4** shows the distribution of foraging locations for each seal, as inferred from the covariate model, colour-coded by the underlying geomorphology. Foraging sites for all seals occurred either within 50–70 km of the coast, or at sites approximately 200 km away from the haulout, overlapping with a variety of geomorphons (**Figure 4**). Foraging appeared to occur mostly on the fringes of the Dogger Bank for Seals 1 and 3, and on the bank itself for Seal 2. The foraging areas of Seal 3 appeared to overlap slightly with those of Seal 1, near the northern edge of the Dogger Bank (**Figure 4**). Foraging also occurred within 20 km of the coast for Seals 2 and 3 (**Figure 4**). The number and distribution of locations inferred as foraging was similar between the covariate model and the null model for all three seals. The total percentage of state assignments which agreed between the two models was 97.8% for Seal 1, 98.1% for Seal 2 and 91.3% for Seal 3.

According to the covariate model, the activity budgets were qualitatively similar among all three seals; Seal 1 was in the putative foraging state 63% of the time, versus 61% for Seal 2 and 59% for Seal 3. **Figure 5A** and **Table 3** show the mean effect of different geomorphons on the probability of switching from travelling to foraging states with associated 95% confidence intervals (CIs). **Figure 5B** shows the percentage of time spent in each state at each of the geomorphons across the whole track for each seal, alongside the relative mean percentage of time seals are expected to be in the foraging state based on activity budgets. There was a positive effect of footslope, slope and hollow on the probability of transitioning from travelling to foraging for all three seals, but the respective effect sizes varied among individuals. While the largest effect size for Seal 1 was recorded for footslope (0.3, 0.16–0.51 95% CIs) (**Table 3**, **Figure 5A**), the seal only encountered this feature on 4.9% (83) of locations (**Table 3**), and the ratio of foraging to travelling states at this feature appeared to be proportional to the overall activity budget (**Figure 5B**). Slope was the most frequently encountered feature for all three seals, and Seal 1 appeared to show a disproportionately high amount of foraging at this feature type (**Figure 5B**). The largest effect sizes for Seal 2 were recorded for footslope (0.21, 0.1–0.38) and shoulder (0.3, 0.19–0.43) and the seal appeared to show a disproportionately high amount of foraging at these feature types. Seal 2 also encountered these two feature types more frequently than the other two seals. The largest effect sizes for Seal 3 were recorded for footslope (0.1, 0.03–0.29) and slope (0.09, 0.06–0.13). Seal 3 appeared to show a disproportionately high amount of foraging at ridges and shoulders, despite these features not having a large influence on the transition probability from travelling to foraging. There was no effect of flat on state transition probability for any of the seals, but the number of locations that overlapped with this feature type was low (**Table 3**).

DISCUSSION

This study aimed to explore the utility of a pattern recognition algorithm for classifying seabed geomorphological features (see Jasiewicz and Stepinski, 2013) to better understand the habitat use of mobile marine predators, using grey seals tagged in the southern North Sea as a case study. By modelling the seal movement data in a HMM framework with geomorphological features as a covariate acting on state transition probabilities, we found that geomorphological data improved the identification of behavioural states for the three seals studied, and offered new insights into foraging ecology which will aid the identification of important habitat.

Geomorphons impacted the state transitions for all three seals, providing evidence that seabed geomorphology does influence seal foraging behaviour. There were commonalities among the three individuals in the types of seabed geomorphology that had a positive influence on switching from travelling to foraging; slopes, footslopes and hollows were all associated with an increase in the probability of seals switching to foraging upon encountering them (**Figure 5A**). However, there was a mismatch between the feature types that were likely to increase the probability of switching from travelling to foraging, and feature types where the majority of foraging activity was concentrated. For example, Seal 3 was most likely to transition into ARS upon encountering footslopes and slopes compared to other feature types, but appeared to spend a disproportionately large amount of time foraging at ridges and shoulders (**Figure 5**). A seal travelling through the landscape towards an area of raised seabed, such as the Dogger Bank, is likely to encounter footslopes and slopes before arriving at shoulders or ridges (**Figure 3**). The mechanism underlying the influence of slopes and footslopes on the decision to switch to foraging may therefore be related to overspill of prey patches from good foraging habitat (i.e. ridges and shoulders) into surrounding areas. Similarly, the geomorphon with the largest influence on behaviour switching for Seal 1 was footslope, but the seal did not encounter this feature type frequently (only 4.9% of locations). HMMs are commonly used to understand the environmental drivers of foraging behaviour by examining covariate effects on state transition probabilities (Morales et al., 2004; Patterson et al., 2009; van Beest et al., 2019). However, our results highlight that the mechanisms that influence switching into foraging behaviour may be associated with different habitat characteristics to areas where foraging activity is concentrated. This is a key consideration when identifying important ecological areas for conservation management based on inference from covariate effects on state transitions in HMMs, particularly if the covariate is a categorical representation of habitat. We therefore recommend that habitat characteristics associated with state-switching behaviour should be considered in conjunction with the characteristics of areas where foraging activity is concentrated for a more complete understanding of the relationship between habitat and predator behaviour.

Slopes were the most frequently encountered feature type, associated with the greatest proportion of foraging activity, and had a positive effect on state transitions for all three seals

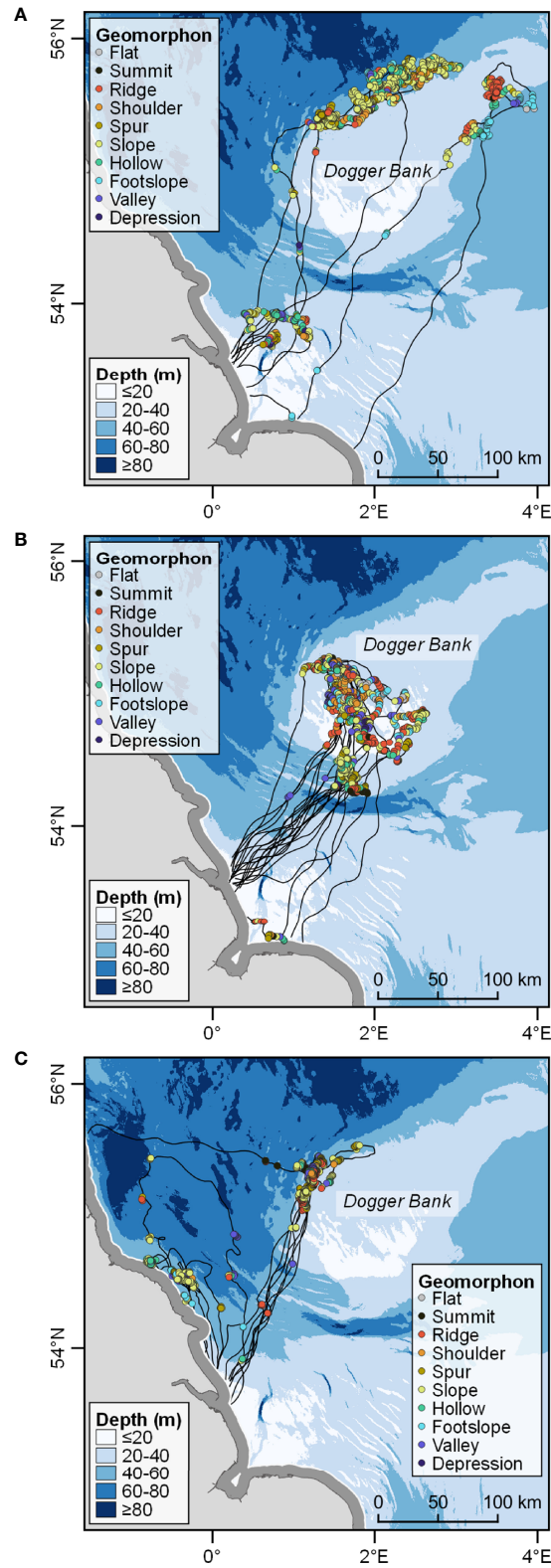


FIGURE 4 | Movement of (A) Seal 1, (B) Seal 2 and (C) Seal 3 with foraging locations classified according to the geomorphology for each location and travelling indicated by black lines. The 10 km coastal buffer within which locations were excluded is shown in dark grey. All three seals foraged in the vicinity of the Dogger Bank.

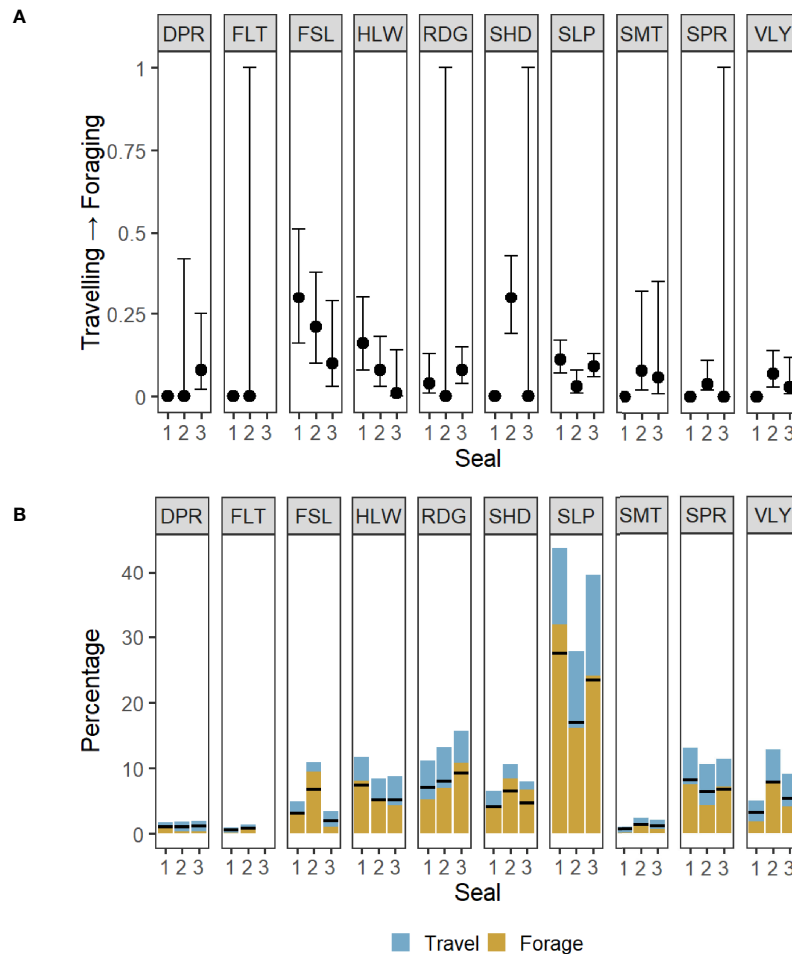


FIGURE 5 | (A) Mean transition probabilities between behavioural states inferred from the states assigned by the covariate HMM with 95% confidence intervals. There was an increased likelihood of switching from travelling to foraging for all three seals in association with the following geomorphons: footslope (FSL), slope (SLP) and hollow (HLW). Where the confidence intervals are 0, seals never transitioned out of the state they were in upon encountering that feature. But where CIs are wide (0-1), although there may have been an influence of that feature on transitioning from foraging to travel, there was no instance of the seal transitioning out of travelling upon encountering that feature. **(B)** Percentage of total time (per seal) spent in foraging or travelling state at each feature type. Horizontal black bars show the relative mean percentage of time seals are expected to be in the foraging state based on activity budgets: Seal 1 = 63%, Seal 2 = 61%, Seal 3 = 59%. A disproportionately large amount of time was spent foraging over slope features for Seal 1, footslopes (FSL) and shoulders (SHD) for Seal 2, and ridges (RDG) and shoulders for Seal 3. For all feature type abbreviations see **Table 3**.

(**Figure 5**). Slopes exposed to currents (e.g. on the fringes of the Dogger Bank where Seals 1 and 3 foraged) are known to produce tidal fronts and upwellings, leading to increased productivity and accumulation of plankton, and in turn, increased numbers of prey species (Ingram et al., 2007; Morato et al., 2010; Reisinger et al., 2018; Bouchet et al., 2020). Beyond the importance of slopes, there were differences among individuals in the variety of geomorphons that influenced the transition from travelling to foraging behaviour, and where foraging was concentrated (**Figure 5**). These differences between the seals could be caused by various factors. Firstly, individual preference has been shown to be an important factor in foraging behaviour of seals and other marine predators (Ostfeld, 1982; Tollit et al., 1998; Sargeant et al., 2005). Some individuals might have prior spatial memory of where

certain geomorphological features exist, but different individuals might also have varying prey preferences and distinct prey capture strategies. Indeed, Carter et al. (2020) found that, for grey seal pups, foraging patches encountered on initial exploration after first leaving the natal colony are re-visited in subsequent directed foraging trips throughout early life, suggesting that spatial memory plays a key role in the development of foraging habitat preferences. Maxwell et al. (2012) also found that some individual northern elephant seals (*Mirounga angustirostris*) returned to the same seamount chain in the North Pacific Ocean on discrete trips, suggesting a maintained knowledge of profitable foraging areas. As well as differences in previous experience, sex differences in diet composition have been reported for grey seals in the Northwest Atlantic, which may relate to sex differences in body size and

TABLE 3 | Effect sizes with 95% confidence intervals (CIs) for the probabilities of transitioning between travelling and foraging for each seal for each geomorphon.

Geomorphon	Seal reference					
	1		2		3	
	Effect size (CIs)	No. of locations (Forage: Travel)	Effect size (CIs)	No. of locations (Forage: Travel)	Effect size (CIs)	No. of locations (Forage: Travel)
Depression (DPR)	0 (0, 0)	30 (16:14)	0 (0, 0.42)	54 (10:44)	0.08 (0.02, 0.25)	42 (8:34)
Flat (FLT)	0 (0, 0)	17 (2:15)	0 (0, 1)	42 (30:12)	NA	0 (0:0)
Footslope (FSL)	0.30 (0.16, 0.51)	83 (55:28)	0.21 (0.10, 0.38)	328 (284:44)	0.10 (0.03, 0.29)	74 (22:52)
Hollow (HLW)	0.16 (0.08, 0.3)	199 (138:61)	0.08 (0.03, 0.18)	253 (148:105)	0.01 (0, 0.14)	191 (95:96)
Ridge (RDG)	0.04 (0.01, 0.13)	190 (90:100)	0 (0, 1)	394 (209:185)	0.08 (0.04, 0.15)	341 (235:106)
Shoulder (SHD)	0 (0, 0)	110 (73:37)	0.30 (0.19, 0.43)	317 (254:63)	0 (0, 1)	175 (146:29)
Slope (SLP)	0.11 (0.07, 0.17)	743 (543:200)	0.03 (0.01, 0.08)	834 (485:349)	0.09 (0.06, 0.13)	864 (525:339)
Summit (SMT)	0 (0, 0)	19 (2:17)	0.08 (0.02, 0.32)	71 (38:33)	0.06 (0.01, 0.35)	45 (15:30)
Spur (SPR)	0 (0, 0)	222 (127:95)	0.04 (0.02, 0.11)	316 (132:184)	0 (0, 1)	247 (156:91)
Valley (VLY)	0 (0, 0)	86 (32:54)	0.07 (0.03, 0.14)	385 (234:151)	0.03 (0.01, 0.12)	199 (91:108)

Where the confidence intervals are 0, seals never transitioned out of the state they were in upon encountering that feature. But where CIs are wide (0-1), although there may have been an influence of that feature on transitioning from foraging to travelling, there was no instance of the seal transitioning out of travelling upon encountering that feature.

metabolic strategies (Beck et al., 2007). Sex-specific diet may translate to sex-specific associations with habitat. Given that we selected three seals which show reasonably discrete foraging areas for this case study, a further study on a larger dataset is required to examine possible sex differences in habitat associations, and if features used by all three seals studied here remain important at the population level.

Our results show that categorising seabed topography using geomorphological shapes can provide a tractable static covariate to investigate marine predator habitat use across the foraging range of an individual. This covariate may also provide further insight into predator-habitat associations when considered in studies focussed on discrete known foraging areas, such as the fringes of the Dogger Bank identified here for grey seals. Given the complexity of interactions between topography and tidal currents that underpin a wide variety of mechanisms affecting prey behaviour and distribution (Cox et al., 2018), geomorphons could be combined with hydrographic data, such as tidal currents and frontal intensity, to elucidate patterns of predator behaviour and space use at fine spatial and temporal scales. Hydrodynamic features resulting from an interplay between topography and currents can be modelled at increasingly fine resolution and included in models of predator habitat associations (Embling et al., 2012; Scott et al., 2013). However, such spatially and temporally discrete features applied to movement data across the individual's foraging range are not likely to prove insightful. Moreover, although hydrodynamic features may provide important foraging habitat for aerial predators such as seabirds [as demonstrated by Scott et al. (2013)] and seals in tidally

energetic coastal channels (Hastie et al., 2016), the role of tides may be less important for benthic foragers in the southern North Sea; our results show that individual grey seals remain in certain foraging patches across multiple tidal cycles during multi-day foraging trips (**Figure 4**). This suggests that other static components of habitat (such as the potential for certain topographic features to aggregate benthic prey) may be more influential drivers of behaviour than hydrodynamic processes for grey seals. However, an assumption about the movement data in this analysis was that the seals exhibited two behavioural states at sea. Seals routinely spend prolonged periods at the surface, which may be conflated with ARS when using location data in movement models (McClintock et al., 2013; Russell et al., 2015). This surface behaviour is likely related to digestion (Sparling et al., 2007), and thus probably occurs in foraging areas. While not accounting for resting therefore likely does not impact our findings, future studies of switching from foraging to resting in relation to tidal state may provide further insight into the temporal dynamics of habitat use. Exploring the influence of geomorphons on behaviour in conjunction with other static covariates is also an important avenue for future research. For example, although we have shown that encountering a certain feature type can influence the decision for seals to switch from foraging to travelling, the role of the environment in shaping how seals navigate to these features remains unclear. It is possible that other metrics such as depth gradients or changes in substrate type may be useful in elucidating how individuals navigate to fine-scale features. Moreover, combining geomorphons with information from other static covariates such as aspect in

holistic habitat models may lead to better understanding of the functional significance of individual features.

The effect size of some of the geomorphons was small (< 0.1) and this could be related to the probability that a seal will encounter this feature type. For example, flat areas were not frequently encountered by any of the seals, and thus had no effect on foraging behaviour (Figure 5). However, large flat areas are present within the foraging range of the seals (Figure 3). To determine if certain features are preferentially selected or avoided, use of geomorphons could be modelled in a use-availability habitat preference framework (Aarts et al., 2008). Such models allow us to quantify if the use of a habitat type is proportionate to its availability within the environment accessible to the study animal (Aarts et al., 2008). However, a caveat of this approach is that it assumes that the individual has complete knowledge of their accessible environment, and thus chooses to go to certain areas despite the known existence of alternative habitat elsewhere. In reality this may not be the case. Nevertheless, combining insights from individual-focussed mechanistic studies such as ours with population level habitat preference models would be a valuable line of future investigation to understand the wider importance of different feature types and predict the location of important foraging areas.

Our case study has demonstrated the potential for this approach to provide useful information for conservation management. For example, the importance of the Dogger Bank is widely acknowledged for both commercial fisheries (Sell and Kröncke, 2013) and a range of predator species (Hamer et al., 2000; De Boer, 2010; Hammond et al., 2013; Gilles et al., 2016), yet the mechanisms influencing predator behaviour and distribution are less well understood. Our results suggest that slopes and slope-like features on and around the bank may be especially important for seals. The southern North Sea (and Dogger Bank in particular) is an area of rapid offshore wind development, with numerous large turbine arrays currently at various stages of planning, consenting, construction and operation. The impact of such developments on important prey species, and the implications for grey seal foraging habitat remain unknown. Russell et al. (2014) found that some individual harbour (*Phoca vitulina*) and grey seals repeatedly forage at established wind turbines and other anthropogenic structures, suggesting that novel foraging habitat is created due to artificial reef effects that arise from placing a solid structure in an otherwise sandy or soft sediment environment (Wright et al., 2020). However, artificial reefs may concentrate prey that would otherwise be distributed elsewhere, leading to increased competition and vulnerability to over-exploitation (Pickering and Whitmarsh, 1997). Moreover, seals are known to exhibit short-term avoidance of areas during pile driving for wind turbine installation (Russell et al., 2016), but it is unclear what the fitness consequences of such disturbance might be. The continued expansion of offshore anthropogenic structures in the North Sea may therefore have complex implications for marine predator foraging behaviour, as well as trophic dynamics and species interactions in the wider ecosystem. Further research is needed to understand the environmental

characteristics of important foraging habitat, and the possible long-term consequences for predator populations of modifying such habitat.

CONCLUSION

This study found that incorporating seabed geomorphology into behavioural models improved predictions of habitat use by a marine predator in the southern North Sea and provided new insights into foraging behaviour. Although originally developed for terrestrial applications, we demonstrate how the geomorphon algorithm can be used to provide geomorphology datasets for shelf seas using bathymetry data, where other datasets (e.g. Harris et al., 2014) are not resolved to detect discrete seabed features. Metrics such as slope and aspect have been used to explore the environmental drivers of foraging in cetaceans (e.g. Hastie et al., 2003), seals (e.g. Maxwell et al., 2012) and seabirds (e.g. Suryan et al., 2006; Carpenter-Kling et al., 2020), and although these studies have provided some key insights into how predators exploit seabed terrain, habitat selection may be influenced by specific patterns beyond the presence and gradient of slope. Moreover, in highly heterogeneous environments such as shelf seas, a more complex representation of the seabed topography than simple gradient metrics may be necessary to understand its relationship to predator activity (Bouchet et al., 2020). Furthermore, where gradient computation requires a single user-defined scale to be set, the geomorphon algorithm allows flexibility in the size of mapped landforms, identifying landforms at the most appropriate scale for the habitat and study species (Stepinski and Jasiewicz, 2011). This provides a more tractable representation of the habitat, allowing better visualisation of the seabed terrain that individual animals encounter, and facilitating biological interpretation of movement models. When used in conjunction with other metrics, this approach may reveal key insights about scale-dependence of habitat associations and further our understanding of how predators interact with, and respond to, their environment. Our study highlights an avenue for future research to gain more ecological understanding of the mechanistic influence of seabed terrain on marine predator behaviour and distribution, and aid the identification and delineation of important habitats. Improving our understanding of what features characterise important predator foraging habitat is essential in assessing how marine ecosystems will be affected by changes caused by anthropogenic habitat modification, overfishing and climate change (McCauley et al., 2015). Moreover, better identification of important foraging areas for marine predators will lead to more effective marine spatial planning and conservation management for the wider ecosystem.

DATA AVAILABILITY STATEMENT

Sources of environmental data are outlined in the methods section. Other data are available upon request from the authors. Requests to access these datasets should be directed to Dr Debbie Russell (dr60@st-andrews.ac.uk).

ETHICS STATEMENT

The animal study was reviewed and approved by the University of St Andrews Ethics Committee. Capture, handling and tagging of seals was carried out under UK Home Office project licence 60/4009 under the Animals (Scientific Procedures) Act 1986. The capture of seals was conducted under licence from the Marine Management Organisation (England) with necessary approvals from Natural England for work on designated sites.

AUTHOR CONTRIBUTIONS

Designed the experiment: LB, DJFR, MIDC, HMEW. Collected the data: DJFR. Processed the data: HMEW, MIDC. Analysed the data: HMEW. Wrote the manuscript: HMEW and MIDC. Edited the manuscript: DJFR and LB. All authors reviewed the final version of the manuscript and gave consent for submission.

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SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: <https://www.frontiersin.org/articles/10.3389/fmars.2022.818635/full#supplementary-material>

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