Black Guillemot foraging ecology in relation to Marine Protected Area management plans for Northern Ireland

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I. Table of contents

II. List of figures

III. List of tables

IV. Executive summary

1) The Black Guillemot (*Cepphus grylle*), is the only UK seabird species included as a feature of the Marine Protected Areas (MPAs) network. The species was included as it does not qualify as a Special Protection Area (SPA) feature, being neither migratory nor listed as an Annex I species of the European Commission Birds Directive. Northern Ireland and Scotland have one Marine Conservation Zone (MCZ) and six MPAs designated respectively for Black Guillemot.
2) Northern Ireland hosts a population of ~1,600 Black Guillemots (around 4% of the UK population). Whilst the UK breeding population has been largely stable over the last 30 years, there is evidence that some Northern Irish colonies are in decline.
3) UK based research into the ecology of Black Guillemots is mostly limited to Scottish based studies, and little is known about their habitat use and movement ecology in Northern Ireland. Addressing these gaps is essential to the conservation management and protection of this species.
4) This project collected data on Black Guillemot movement and foraging ecology to inform regional MPA management plans being devised under the Marine Protected Areas Management and Monitoring (MarPAMM) project.
5) GPS tracking of breeding adult Black Guillemots was conducted to quantify distribution and habitat use at two sites in Northern Ireland during the breeding season. A total of 15 Global Positioning System (GPS) and 8 integrated GPS/ Temperature and Depth Recorder (TDR) tags were deployed across the sites of Bangor, on mainland Co. Down, and Lighthouse Island, a part of the Copeland Islands, in June 2021.
6) The movement of Black Guillemots generally remained concentrated around their breeding colonies, with birds reaching a mean-maximum distance of 1.36 ± 1.42 km (± SD) from Lighthouse Island (Copeland Island, Co. Down) and 0.94 ± 0.71 km from Bangor (Co. Down). Birds also tended to remain close inshore with birds from Lighthouse Island and Bangor reaching mean-maximum distances from the closest landmass of 0.44 ± 0.31 km and 0.34 ± 0.22 km respectively. This preference to stay close to the shore was also reflected in the maximum recorded distance of 4.90 km to the closest landmass. The furthest maximum distance recorded from the colony was 15.97 km, however this bird remained within 4 km of a landmass throughout its journey.
7) Birds deployed with TDR loggers (n = 8) exhibited mean-maximum dive depths of 13.91 m (overall max = 35.54 m). Maximum dive depths were observed to correspond with seafloor depth profiles, indicating benthic foraging behaviour.
8) Black Guillemot habitat selection for bathymetry, oceanic kinetic energy and seafloor substrate was examined using Resource Selection Functions. Environmental characteristics selected were often individual- or colony-specific. Inter-individual variation was most frequently seen in relation to kinetic energy and substrate. Overall, birds from both colonies foraged within the infralittoral (>-10 m) and shallow circalittoral (-10 to -30 m) bathymetry zones, despite greater depths despite being available at Lighthouse Island.
9) Core areas associated with behaviours of loafing or resting, commuting, and foraging were found to overlap. In addition, areas used during the day and night also overlapped. Therefore, MPAs designated to include core areas of movement may be expected to encompass multiple aspects of Black Guillemot ecology.
10) MPAs extending 5 km offshore and with bathymetry profiles reaching down to 30 m would be appropriate to encompass core areas of habitat use for Black Guillemots during the breeding season. However, the extent to which these areas would be appropriate as a

designated site during the wintering period is unknown. Given the high degree of variation in habitat use between individuals and colonies, caution is required when applying these results to other colonies.

11) Landward extensions to MPAs which encompass Black Guillemot colonies should encourage protection of nesting birds from invasive mammal predators or human disturbance and should be considered as part of the designation process.
12) We highlight the additional need for high resolution information on the benthos and tidal currents at depths less than 30 m to better understand fine scale habitat use. Further research is also required to understand the links between varying habitat characteristics, diet, and demographic trends such a breeding success and population size.

1. Introduction

Seabirds and the marine environments on which they rely are under pressure from a wide range of factors including climate change, fisheries bycatch, renewable energy developments and invasive predators (Beaugrand et al., 2002; Worm et al., 2006; Lewison et al., 2012; Dias et al., 2019). The major threats to Black Guillemots (*Cepphus grylle*) are adverse weather conditions and invasive predators affecting nest site availability (Buchadas and Hof, 2017; Johnston et al., 2019); and climate change (Smale, 2020), industrial kelp harvesting (Lorentsen et al., 2010; Christensen-Dalsgaard et al., 2020) and tidal energy development (Furness et al., 2012; Johnston et al., 2021) affecting foraging habitat.

At a UK scale the Black Guillemot breeding population has been largely stable over the last 30 years (JNCC, 2021). Northern Ireland supports around 1,600 Black Guillemots, approximately 4% of the UK's breeding population (JNCC, 2021; Booth Jones, 2022) but some of these colonies are declining, notably Rathlin Island (Booth Jones, 2021). Potential impacts of climate change may be exacerbated within Northern Ireland and the Republic of Ireland as they form the southern edge of the global range of Black Guillemots (BirdLife International, 2020) corresponding to the limit of their physiological and habitat suitability. Long-term monitoring, conducted in Northern Ireland in Bangor Marina, reported laying date to correlate with Sea Surface Temperature (SST) (Greenwood, 2007), although the potential underlying drivers behind this correlation are unknown, SST may impact prey migration or abundance (Shorty and Gannon, 2013). Within the UK and Republic of Ireland, Butterfish (*Pholis gunnellus*) has been identified as a key prey (Ewins, 1990; Leonard and Wolsey, 2015). However, butterfish remain a poorly studied species when compared to sandeels in the North Sea (Johnston et al., 2020), in terms of understanding environmental factors such as climate on their abundance and availability.

One of the key legislative tools to mitigate these impacts and alleviate anthropogenic pressure on seabird populations is through the creation of Special Protection Areas (SPAs) or Marine Protected Areas (MPAs). MPAs and Marine SPAs are designated maritime areas which provide legal protection to marine features or species of conservation priority (Lascelles et al., 2012). SPAs have been classified for all UK seabird species with the exception of Black Guillemots which fail to qualify on the grounds of not being migratory or listed under Annex 1 of the European Commission Birds Directive. Measures to support Black Guillemots are therefore provided through MPAs. The regional devolved governments of the UK and the government of the Republic of Ireland are dedicated to forming networks of MPAs to retain biodiversity and productivity within favourable condition (JNCC, 2018; DAERA, 2019; Marine Protected Area Advisory Group, 2020). Within Northern Ireland, the initiative for MPA creation is underpinned by Marine Act (2013) (DAERA, 2019). In contrast to Scotland where six Nature Conservation MPAs are designated for Black Guillemot, there is only one Marine Conservation Zone (MCZ) in Northern Ireland, and no MPAs. Therefore, Black Guillemots have been highlighted as an ecological gap (JNCC, 2018), requiring improved knowledge of core areas of habitat use and the environmental characteristics essential for foraging and survival, to better inform MPA designation and management. Furthermore, MPAs designated in the UK and the Republic of Ireland are of potentially greater importance to Black Guillemots since they are resident all year round (Johnston et al., 2018a), although it is unclear whether habitat preference and area use changes over the course of the annual cycle.

MPAs designated for Black Guillemots aim to conserve their foraging and breeding areas (Swann, 2014). Black Guillemots are relatively understudied in the UK, and new insights into their foraging ecology are continually being gained through modern Global Positioning System (GPS) tracking technology (Owen et al., 2019; Johnston et al., 2021). Recent studies have shown that Black Guillemots are likely to associate closely with attributes of inshore bathymetry and tidal currents (Johnston et al., 2021). Bathymetry is a potentially important determinant of the foraging locations of Black Guillemots as they are benthic foragers (Ostaszewska et al., 2017). Previous analysis of Black Guillemot dive depths from Lighthouse Island inferred that they likely correlate with available bathymetry (Shoji et al., 2015). Additionally, tidal currents and ocean fronts have previously been displayed to influence Black Guillemot habitat use as shown by inshore surveys (Waggitt et al., 2017). Seafloor substrate is also likely to be an important factor and previous studies explored possible links between the foraging areas of Black Guillemots and the presence of sand and gravel substrates and kelp (Sawyer, 1999; Owen, 2015; Johnston, 2019). To improve our understanding of the foraging habitat requirements of Black Guillemots further investigation combining movement data with environmental characteristics, such as depth, tides, sediment, marine flora (kelp), and diet, is required. Improved knowledge on the spatial, and diel and seasonal temporal influences on Black Guillemot movement may be used to assess the suitability of MPAs.

Improved knowledge of Black Guillemot ecology to inform MPA management is a key facet of the Marine Protected Areas Management and Monitoring (MarPAMM)[1] project. This project aims to support development of management plans for MPAs within the cross-border INTERREG VA, which comprises Northern Ireland, the Republic of Ireland (Border Counties) and Western Scotland (Figure A1). The MarPAMM project brings together statutory organisations, academic institutions, NGOs and stakeholders with the aim of developing a toolkit for monitoring and managing cross-border MPAs. Key outputs of the MarPAMM project are the delivery of six MPA management regional management plans including Co. Down – Co. Louth region (cross-border), and North Coast Ireland - North Channel region (cross-border) which are likely to be relevant to Black Guillemots.

1.1 Aims and objectives

This project used a combination of GPS and GPS/Temperature and Depth Recorder (TDR) loggers to examine Black Guillemot movements during the breeding season at two colonies in Co. Down, Northern Ireland, including: Bangor Harbour; and Lighthouse Island, in the Copeland archipelago. Using this movement data, we aim to:

1) Quantify at-sea foraging distributions.
2) Identify key foraging areas on both colony and individual levels.
3) Describe the characteristics of dive behaviour.
4) Investigate the relationships between foraging and environmental characteristics at both colony and individual levels.
5) Explore the influence of diurnal patterns on dive behaviour and space use.

2. Methods

2.1 Data collection

Fieldwork took place at Bangor (54°41'44.0"N 5°31'20.0"W) and Lighthouse Island (54°39'55.0"N 5°40'06.5"W) (Figure 1) from the 10th June to the 10th July 2021. Fieldwork was timed to coincide with the Black Guillemot incubation period, when adults are the most easily caught during nest

[1] https://www.mpa-management.eu/

attendance. Deployments included GPS-only loggers (PathTrack nanofix-geo: ~8.6 g, 50 x 15 x 10 mm; ~10.9 g, 51 x 24 x 10 mm) and GPS loggers integrated with TDR (Ecotone Uria-100: ~8.5 g, 35 x 16 x 11 mm). All loggers were encased in a dive-proof housing (tested at 50 m – 100 m) and equipped with the capacity to remotely download data to a land-based base station via ultra-high frequency (UHF) radio waves. Tags were attached to the bird's lower back feathers using three strips of Tesa© (4561) tape. Attachment methods were approved by British Trust for Ornithology (BTO) Special Methods Technical Panel. All birds were ringed, measured (wing, tarsus, bill length/depth), and weighed upon capture. Body mass was assessed to ensure tags and tape were within the acceptable limits for deployment (< 3% body mass) (Phillips and Croxall, 2003). Tags were set to record GPS fixes at five-minute intervals. This fix rate was selected as a compromise between extending battery life and recording data to an appropriate resolution for the examination of habitat use. Within the TDR integrated loggers, following a dive greater than four seconds, subsequent depths were recorded at one second intervals. A total of 23 adult birds were deployed with tags, of which 15 had PathTrack nanofix-geo tags (~8.6 g models, n=13 birds and ~10.9 g models, n = 2 birds). Of these deployments, 12 were at Bangor and the remaining three were on Lighthouse Island. All eight Ecotone Uria-100 deployments were made on Lighthouse Island due to limitations over location and the number of base stations available.

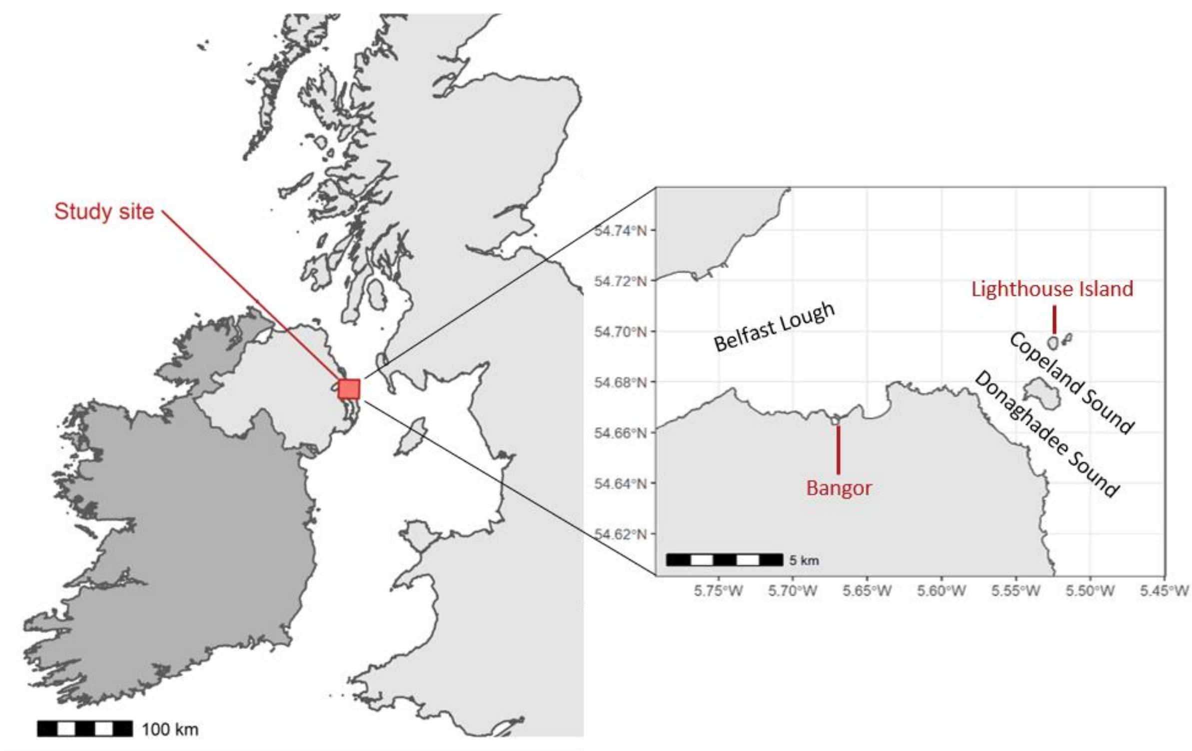

Figure 1. Study site area within the United Kingdom shown in light grey, and Republic of Ireland shown in dark grey. Expanded map of displays the study sites within Northern Ireland.

2.1.1 Nest monitoring

Where possible, nests on Lighthouse Island were visited once every five days and contents were recorded with the aim of assessing hatching success. The contents of 23 nests were monitored, of which 11 belonged to tagged birds and another 12 belonged to a control group, where no tagging had occurred. For one of the birds deployed with a PathTrack nanofix-geo tag it was not possible to ascertain a nest outcome, as hatching potentially occurred after fieldwork on the Island had concluded. Due to constraints over nest site access within Bangor Marina, hatching success could only be monitored reliably at four of the 12 nests where birds had been tagged. A comparison of hatching success between nests of tagged and untagged birds was conducted to provide an indication of the potential effects of catching, handling and tag deployment on breeding success.

2.2 Behavioural modelling

2.2.1 Data processing

The work-flow of data processing and analysis is presented below in Figure 2. Prior to analyses, all GPS data was processed to remove potentially erroneous positional coordinates. This was carried out by removing duplicate data, GPS fixes attained from three or fewer satellites, and fixes of unrealistic speeds above an average speed threshold of 20 m/s (Bradstreet, 1982).

For each individual, the distance of locational fixes from individual specific nest locations was calculated. Trips were defined by a start and end point using a 300 m perimeter from the nest. This perimeter was selected to examine genuine departures from the colony, thereby excluding nearshore loafing often exhibited by Black Guillemots adjacent the nest site (See section 3.2). GPS data overlapping with land (OSNI, 2021) and navigational buoys (British Crown and OceanWise, 2020) were also defined. Periods when birds are onshore or sitting stationary on offshore buoys were excluded in the analysis of offshore movement and marine habitat use, as patterns of movement will differ while on land or sitting on stationary objects and interfere with the classification of behavioural states (See section 2.2.3).

The maximum distances reached from the colony and from the shore, defined as distance to the nearest land mass, during each individual trip were calculated. Measurement of distance from shore was to provide an indication as to whether movement was confined to the inshore or offshore pelagic environment, regardless of the distance travelled from the colony e.g. keeping relatively close to the shore rather than heading further out to sea. Summary statistics of trip distances were calculated for each individual, presenting both the maximum and mean-maximum trip distances. This information is potentially useful when considering the suitability of MPA boundaries in relation to their distance offshore and distance from colonies of interest.

Periods of night and day were assigned to the time stamps of the GPS tracking and dive depth data using the R package ‘suncalc’ (Version 0.5.0) (Thieurmel and Elmarhraoui, 2019) within R (Version 4.0.3) (R Development Core Team 2020). Start and end times for periods of “day” and “night” were allocated using dawn (corresponding to the end of morning nautical twilight) and dusk (start of evening nautical twilight) assigned using the positional coordinates of each GPS fix.

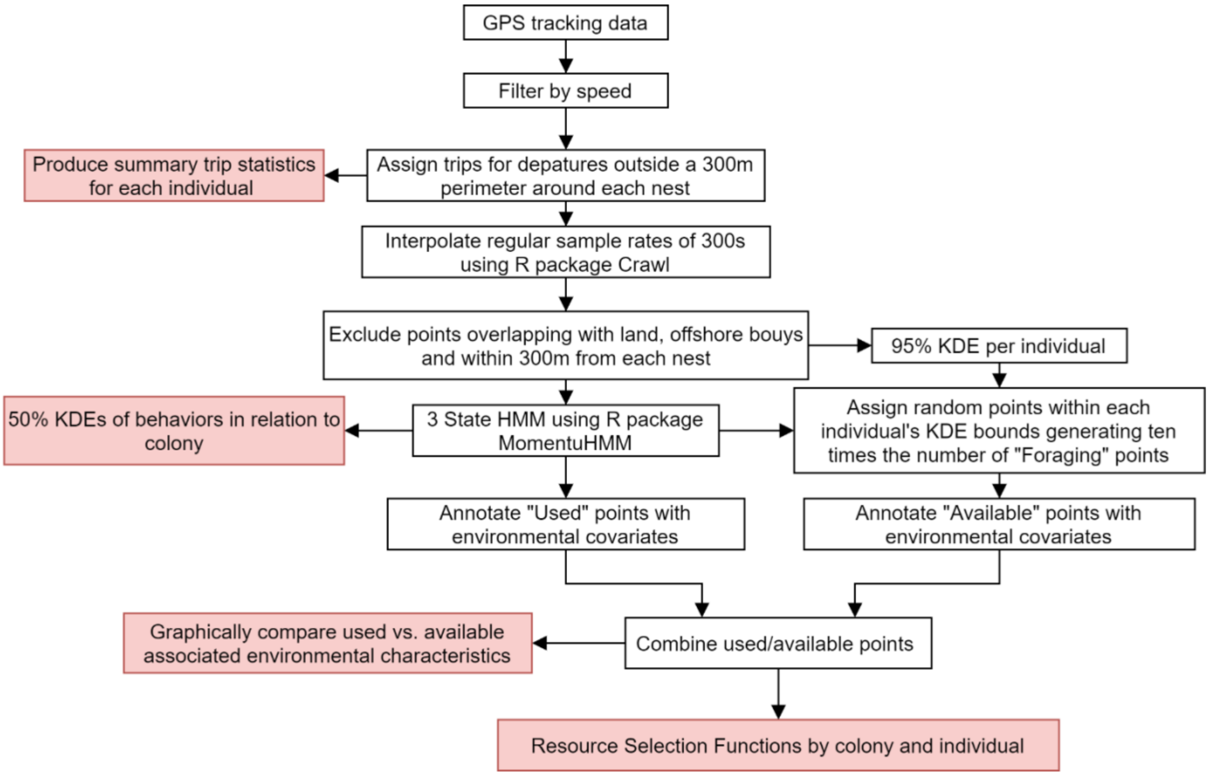

Figure 2. Analysis work-flow

2.2.2 Interpolation of GPS tracks

GPS tracking data may contain gaps between fixes potentially attributed to periods where the birds were out of satellite range, or issues arising from signal retention or time-to-fix within GPS data. Regular intervals between GPS fixes are required to remove bias in sampling rate and are a requirement for conducting behavioural analysis using attributes of step length and turning angle. Regular sampling rates of five minutes were interpolated for each individual using continuous-time correlated random walk (CTCRW) models (Johnson et al. 2008) provided by the 'Crawl' function, a part of the 'momentuHMM' package (Version 1.5.4) (McClintock & Michelot 2018).

2.2.3 Hidden Markov models

Modelling was carried out to infer behavioural states within tracking data to aid in identifying areas of ecological importance for Black Guillemots. Multivariate discrete-time Hidden Markov models (HMMs) were used to assign states of foraging, commuting and floating/resting based on movement characteristics including distance and turning angles between successive locations. This time series modelling reveals 'hidden' states through a Markov-chain modelling process; these states in turn may align with behaviours of ecological relevance for the species (McClintock and Michelot, 2018).

A three state HMM was specified to represent foraging (State 1), loafing/floating on the sea (State 2) and commuting (State 3). Parameters for each hidden state (Table 1) were applied to characterize foraging (State 1) as successive fixes exhibiting medium speed and acute turning angles; loafing/floating (State 2) slower speeds of obtuse turning angles, and commuting (State 3) as fast speeds of obtuse turning angles. We specified a gamma distribution for step length and a von Mises distribution for turning angles (McKellar et al., 2015).

Table 1. Model parameters of step length (mean and SD) and turning angle parameters (mean and concentration from Von Mises) applied to HMM. State 1, foraging; State 2, loafing/floating on sea; State 3, commuting.

State	Behaviour	Step length mean (m)	Step length SD (m)	Turning angle mean	Turning angle concentration
1	Foraging	200	100	0	1
2	Loafing/floating	100	50	0	50
3	Commuting	1000	500	0	30

2.3 Resource selection

2.3.1 Kernel density estimation

To estimate the home range area of each colony and individual 95% kernel density estimate (KDE) contours of utilisation distributions (UDs) were calculated using the 'KernelUD' function a part of the 'adehabitatHR' R package (Version 0.4.19) (Calenge, 2015). KDEs (50%) were additionally calculated for GPS data categorized by behavioural state or night and day to facilitate visual comparison of space use between categories. UD contours of varying values can be used to investigate different aspects of movement (see Fayet et al., 2017; Cleasby et al., 2020 for further details) and based on this, 95% UDs were selected to examine the outer limits of Black Guillemot area use, while 50% UDs were used to examine core area use.

2.3.2 Random point allocation

Using individual home ranges as indicated by 95% UD contours, a boundary of potentially available habitat was allocated to each individual (DeCesare et al., 2012). A set of random points was generated within this boundary using the 'spsample' function in the R package 'sp' (Version 1.4-5) (Pebesma and Bivand, 2005), to sample the surrounding available habitat. The number of random points varied by individual and was calculated as 10 times the number of foraging points (See Appendix A2), as defined by HMM.

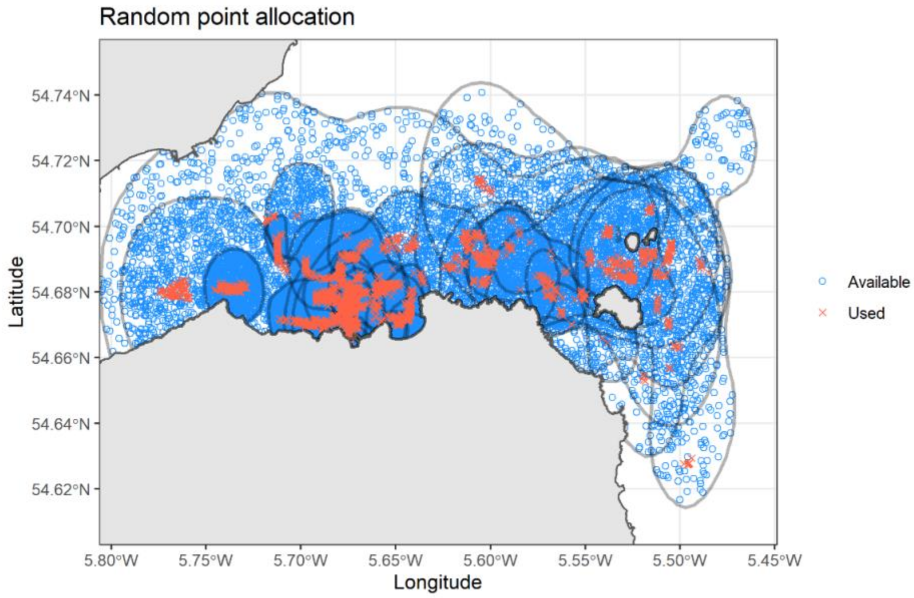

Figure 3. Random point allocation within 95% UD for each individual. Semi-transparent black lines indicate the 95% UDs produced across individuals.

2.3.3 Environmental covariates

Spatially corresponding environmental variables of bathymetry, ocean current kinetic energy, and benthic substrate were generated for all GPS and random point location data (Figure 4). All environmental variables were obtained from the open-source European Marine Observation and Data Network (EMODnet). Bathymetry was defined as water depth from Lowest Astronomical Tide (LAT) and measured in metres (EMODnet, 2016a). Oceanic current kinetic energy was selected to indicate potential areas of dynamic flowing water. This was measured in newtons per metre squared (N/m^2) and was calculated as the 90th percentile kinetic energy at the seabed due to currents within the Atlantic (Mcbreen et al., 2011; EMODnet, 2016b). Lastly, modelled categorical substrate (e.g. fine mud, rock, sand) was obtained from the EUSeaMap broad-scale predictive model (EMODnet, 2021). For definitions of the substrate categories see: https://www.emodnet-geology.eu/data-products/seabed-substrates/ .

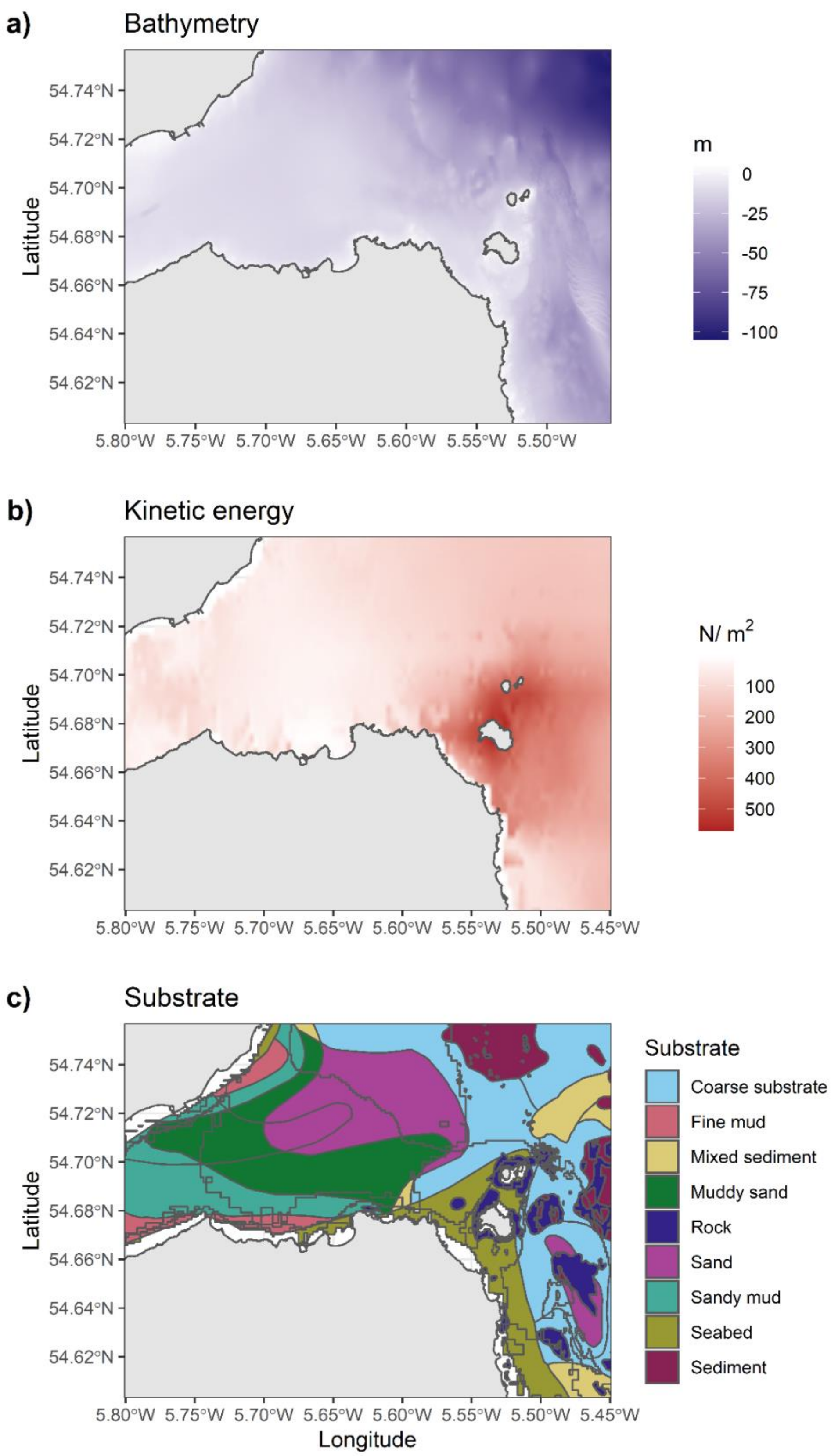

Figure 4. Map of environmental variables within the study region including a) bathymetry (m) b) kinetic energy (N/m²) at the seabed due to Atlantic oceanic currents and c) benthic substrate.

2.3.4 Tidal height and phase

Information on tidal height was attained using the British Oceanographic Data Centre (BODC) tidal gauge located at Bangor Harbour, where the tidal height is measured against Chart Datum at a temporal resolution of 15 minutes. Tidal height data was then converted to elevation in relation to Mean Sea Level (MSL) by calculating the mean tidal height from June and July 2021.

Tidal elevation data were categorized into four phases based on elevation above and below MSL and the trend over time (Table 2). For each tidal cycle above or below the MSL, the percentage of each elevation value in relation to the maximum tidal elevation (100%) and MSL (0%) was taken. Elevation values of >=80% were classified as High/Low, while values <80% were classified as flood and ebb phases based the increasing or decreasing direction of values (Embling et al., 2008; Cox et al., 2013). The association of diving behaviour with tidal phase was assessed by calculating the proportion of all available tidal phases occurring over the tracking period during hours of diving activity (14th June - 24th June, 03:00 - 21:00), and visually comparing this with the proportion of phases that occurred during recorded dives (see Section 3.4.1).

Table 2. Tidal phase description

Tidal Phase	Description
Low tide	>= 80% of negative elevations below MSL
Flood	< 80% of elevations above and below MSL of increasing value
High tide	> =80% of positive elevations above MSL
Ebb	< 80% of elevations above and below MSL of decreasing value

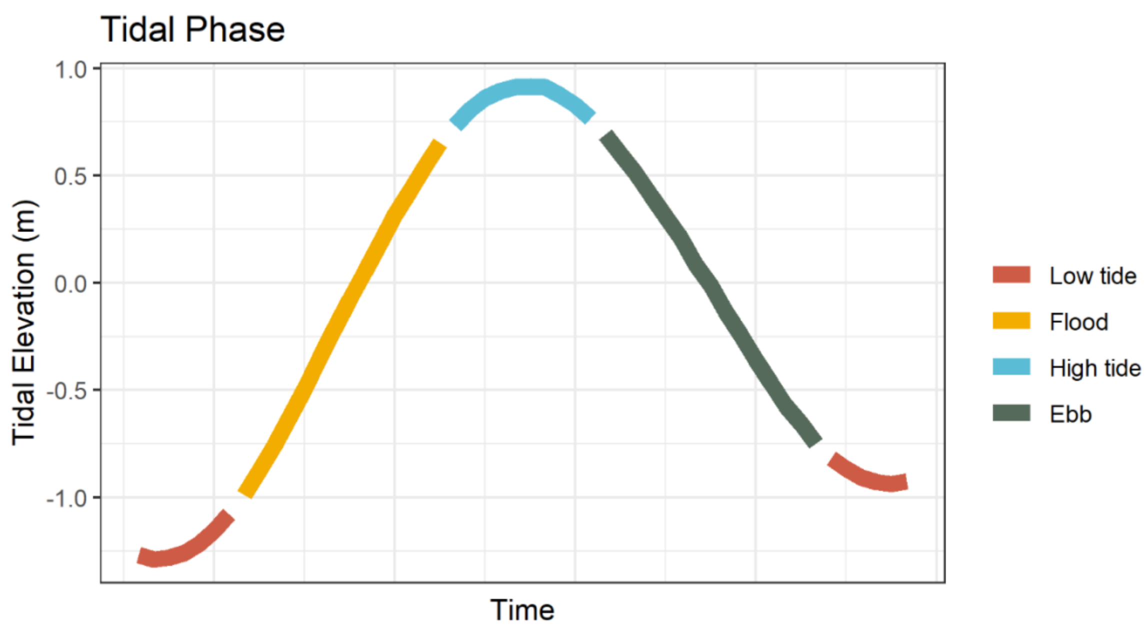

Figure 5. Tidal phase allocation

2.3.5 Resource selection functions

To assess the selection of foraging locations relative to other areas available, environmental covariates at foraging (used) locations were compared to random (available) locations (see section 2.3.2). Used versus available habitat were compared graphically, while the potential existence of preference towards particular environmental characteristics for foraging investigated using Resource Selection Functions (RSFs) constructed with binomial logistic regression models. These functions assess the relative probability of a habitat characteristic being used in relation to the availability of that habitat, providing an indication of habitat preference (Fieberg et al., 2021). Resource selection was investigated on both colony (all birds combined for Lighthouse Island or Bangor where appropriate) and individual (each bird selected in turn) levels. Colony-level models were carried out using the Generalized linear mixed effect models provided by the R package 'lme4' (Version 1.1-27.1) (Bates et al., 2015), and included individual birds as a random effect. Individual models were carried out using logistic regressions provided by GLM function in R (R Development Core Team, 2020). Within both the colony and individual logistic regressions, available data were assigned "weights" of 5000 and used data were weighted by one. This step allows for more robust interpretation of the coefficient estimates (Fithian and Hastie, 2013).

A global model consisting of used/available binomial dependent variable, and scaled independent variables of kinetic energy and bathymetry, and categorical variables of individual and substrate were used on both colony- and individual-level analysis. To identify the best fitting combination of parameters describing habitat selection, Akaike's Information Criterion (AIC) model weighting was used (Burnham et al., 2011). AIC provides a measure of a model's goodness of fit, penalised by the number of parameters to attain that fit. Lower AIC values indicate a better fitting model. A series of eight candidate models were compared for each study site and individual, and model averaging was carried out for the models within the lowest five AIC units.

2.4 TDR analysis

2.4.1 TDR processing

Dive depth data recorded by TDRs integrated within the Ecotone Uria-100 tags were used to study vertical movements within the water column. Tags were programmed to record hydrostatic pressure (mbar; 1 metres of water = 98.06 mbars) at one second intervals, sensing changes in pressure >2 mbar.

Data from the dive sensors were analysed using R version 4.0.4 (R Development Core Team, 2021) and the open-source package 'diveMove' (Luque and Fried, 2011; Luque, 2007) to determine the depth and duration of all dives deeper than 2 m. Dives shallower than two metres appeared to occur during activities other than foraging, and so were excluded from the analysis. In addition, two apparent dives were removed from the data as they were unfeasibly long. Dive data were not corrected for surface drift (zero offset correction) because logger deployments were for a restricted period of time only i.e. a few days and visual inspection of the data deemed this unnecessary, as surface values were zero, as would be expected.

2.4.2 Assigning environmental covariates

Values of dive depth did not intrinsically contain information indicating their planar location i.e. latitude or longitude. Coordinates and the corresponding environmental covariates (bathymetry, kinetic energy, and substrate) were therefore assigned from the nearest GPS fix in time. Where the time difference between the nearest GPS fix and dive value were greater than one hour, these values were excluded from examination of dive characteristics in relation to environmental covariates.

3. Results

3.1 Hatching success

Of the monitored nests on Lighthouse Island for the tagged group, a total of 9 hatched chicks hatched from 18 eggs (n = 11 nests) and for the control group, a total of 11 chicks hatched out of 22 eggs (n = 12 nests). Therefore, both groups had the same hatching successes of 0.5 hatched per egg. The hatching success for the nests (n = 2) containing a bird tagged with a PathTrack nanofix-geo was 0.33 (1 hatched, 3 eggs), whilst the nests (n = 8) containing a bird tagged with Ecotone Uria-100 loggers exhibited hatching success of 0.53 (8 hatched, 15 eggs). Sample sizes to assess the effect of tag type were too small to be able to make any meaningful comparison of hatching success however. It was apparent that there is large plasticity in laying dates, and one monitored nest may have hatched following our last visit.

3.2 GPS data

Tracking data was successfully obtained from 21 individuals (Table 3). However, data from three individuals (P10B, E1C and E7C) were insufficient to be eligible for analysis as the sample size was too small to be able to produce Utilization Distributions (UDs - see section 3.5 below). Tag deployments lasted for a mean of 1.84 ± 0.74 (± SD) days, ranging in tracking periods of 0.67-3.39 days (Table 3). Interindividual variability in deployment length was primarily related to tags being shed prematurely though preening prior to the battery being exhausted. Two birds which nested in the harbour wall at Bangor Harbour failed to transmit data from their tags, potentially due to electromagnetic shielding of radio waves attributed to the thick concrete construction.

The GPS tracking data showed that individuals from Bangor primarily travelled directly north and moved both east and westwards along the coast (Figure 6a). Collectively, individuals from Lighthouse Island moved southwest (Figure 6b), visiting the sounds connecting the Copeland Islands. Some individuals from Lighthouse Island travelled directly west into Belfast Lough, or moved nearshore, parallel the mainland coast.

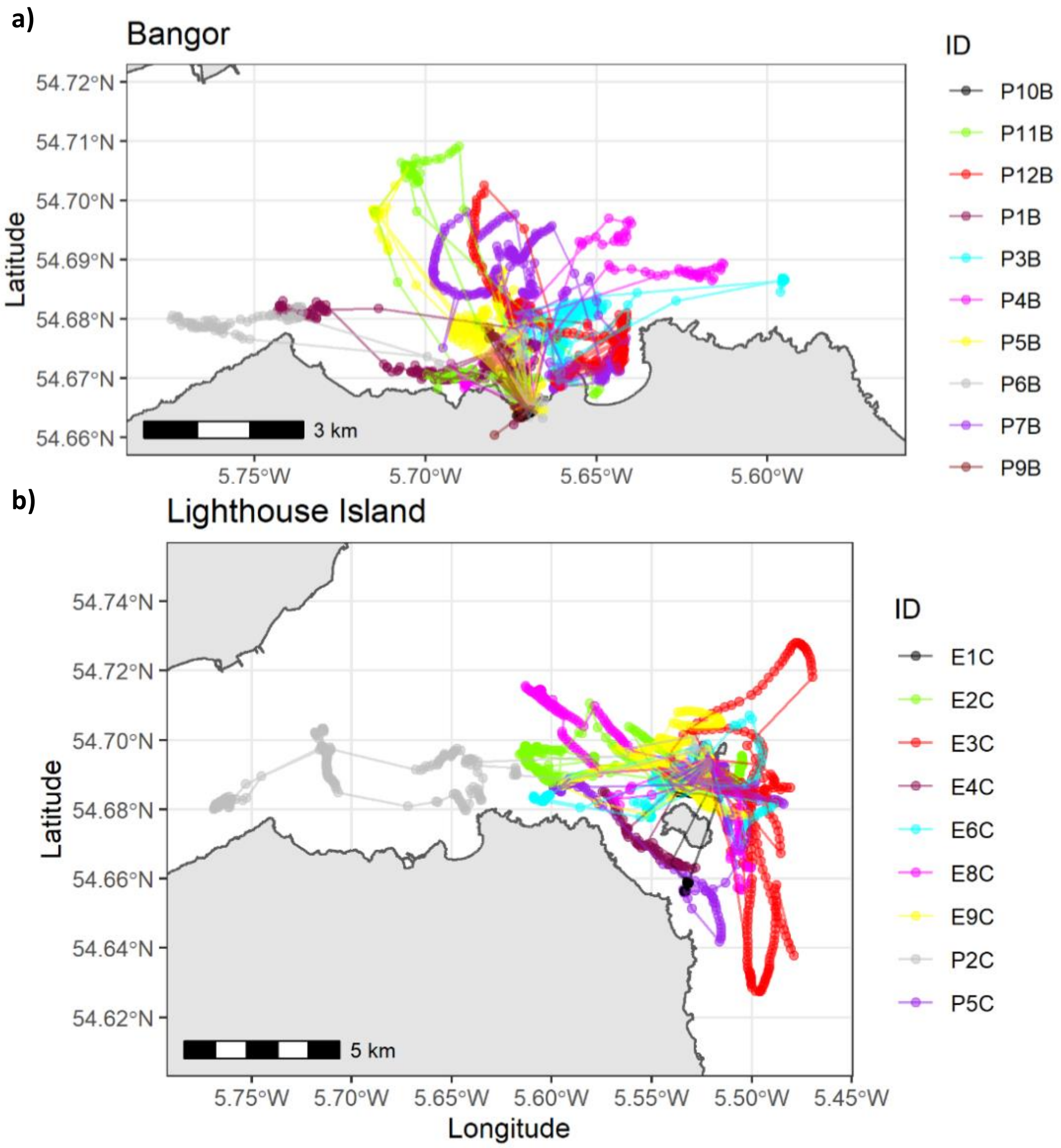

Figure 6. Individual tracking data obtained from a) Bangor and b) Lighthouse Island, with individuals uniquely coloured.

3.3 Trip statistics

A total of 179 trips away from the colonies of Bangor and Lighthouse Island were defined across 21 individuals. The mean-maximum distances from the colony location, for all the trips combined, were 1.15 km ± 1.17 km (± SD), while mean-maximum distances from the nearest landmass were of 0.37 ± 0.27 km. Mean-maximum trip distance from colony was slightly less from Bangor than Lighthouse Island, with distances of 0.94 ± 0.71 km, and 1.36 ± 1.42 km respectively. This difference was less distinct in mean-maximum distances from nearest landmass with trips reaching 0.34 ± 0.22 km from the coast when originating from Bangor, and 0.44 ± 0.31 km from Lighthouse Island. Black Guillemots travelled an absolute maximum distance of 15.97 km (mean absolute maximum= 5.29 ± 2.93 km) from the colony, and an absolute maximum of 4.90 km (2.48 ± 1.16 km) from the nearest land mass.

Table 3. Trip characteristics of the tracked birds including: duration of tracking, breeding status and foraging range.

Bird ID	Site	Tag Type	Tag Weight (g)	Deployment Date	Body Weight (g)	Nest Contents	Deployment Duration (days)	Maximum Distance from Nearest Landmass (km)	Mean Maximum Distance from Nearest Landmass (km)	Maximum Distance from Colony (km)	Mean Maximum Distance from Colony (km)	Trips (n)	Fixes (n)
E1C	L. Isl.	Ecotone	8.47	17/06/2021	425	2E	1.02	1.06	0.53	4.36	2.18	2	192
E2C	L. Isl.	Ecotone	8.47	19/06/2021	390	2E	2.62	3.29	0.41	6.03	0.86	8	445
E3C	L. Isl.	Ecotone	8.47	19/06/2021	388	1E, 1C	3.39	4.90	0.24	7.68	0.38	20	756
E4C	L. Isl.	Ecotone	8.47	16/06/2021	367	2E	0.67	1.17	0.39	3.69	1.23	3	139
E6C	L. Isl.	Ecotone	8.47	16/06/2021	382	1E	1.99	2.87	0.26	5.74	0.48	11	427
E7C	L. Isl.	Ecotone	8.47	20/06/2021	440	2E	1.23	1.07	0.13	1.31	0.19	8	294
E8C	L. Isl.	Ecotone	8.47	20/06/2021	375	2E	2.06	3.67	0.91	6.28	2.09	4	464
E9C	L. Isl.	Ecotone	8.47	17/06/2021	372	2E	2.98	2.47	0.15	4.71	0.36	16	622
P2C	L. Isl.	PathTrack	10.9	26/06/2021	405	1E	1.36	3.47	1.15	15.98	5.33	3	360
P5C	L. Isl.	PathTrack	8.64	26/06/2021	407	2E	1.92	3.75	0.25	5.91	0.49	15	349
P13C	L. Isl.	PathTrack	8.70	27/06/2021	377	2E	1.89	2.51	0.42	5.47	0.91	6	266
P1B	Bangor	PathTrack	10.9	29/06/2021	420	NA	3.26	1.37	0.077	5.10	0.39	18	504
P3B	Bangor	PathTrack	8.64	12/06/2021	382	2E	1.95	1.41	0.23	4.68	0.69	6	311
P4B	Bangor	PathTrack	10.9	27/06/2021	390	NA	0.74	2.20	0.73	4.45	1.48	3	134
P5B	Bangor	PathTrack	8.69	14/06/2021	397	NA	2.8	3.29	0.33	5.02	0.34	10	632
P6B	Bangor	PathTrack	8.63	10/06/2021	385	NA	1.41	1.29	0.43	6.95	2.31	3	363
P7B	Bangor	PathTrack	8.61	14/06/2021	395	2E	2.05	2.98	0.17	3.70	0.33	18	388
P9B	Bangor	PathTrack	8.6	12/06/2021	380	NA	0.8	0.98	0.33	1.73	1.73	3	174
P10B	Bangor	PathTrack	8.64	11/06/2021	425	NA	1.14	NA	NA	NA	NA	0	25
P11B	Bangor	PathTrack	8.69	14/06/2021	370	NA	1.79	4.11	0.69	5.25	1.06	6	300
P12B	Bangor	PathTrack	8.70	10/06/2021	375	2E	1.76	1.55	0.10	1.85	0.18	16	282
NA	Bangor	PathTrack	8.62	10/06/2021	415	2E	0	NA	NA	NA	NA	0	0
NA	Bangor	PathTrack	8.61	11/06/2021	399	NA	0	NA	NA	NA	NA	0	0

3.4 Dive characteristics

3.4.1 Dive statistics

The total number of dives recorded that exceeded two metres was 1,622, however the number of dives varied by individual (Table 4). The mean-maximum dive depth for all data combined was -13.91 m, with a mean dive duration of 62.45 seconds. The absolute maximum depth reached was -35.54 m and the maximum dive duration was 173 seconds.

Table 4. Summary table of dive statistics for data from eight Ecotone loggers and combined results for all dive data.

		Max dive depth (m)		Dive duration (s)	
Logger ID	Number of dives	Mean	Range	Mean	Range
FOL01- E1C	127	-11.22	-2.07 – -19.50	55.47	1.00 – 100.00
FOL02- E2C	214	-18.45	-2.12 – -25.87	75.39	1.00 – 110.00
FOL03- E3C	352	-14.01	-2.07 – -35.54	59.28	1.00 – 118.00
FOL04- E4C	174	-10.43	-2.01 – -18.28	51.36	1.00 – 173.00
FOL05- E6C	217	-12.80	-2.51 – -19.44	65.59	2.00 – 112.00
FOL06- E7C	63	-14.17	-2.63 – -19.36	69.32	6.00 – 96.00
FOL07- E8C	188	-18.58	-2.56 – -30.60	73.96	2.00 –120.00
FOL08- E9C	287	-11.43	-2.04 – -17.82	54.97	1.00 – 93.00
Combined	1622	-13.91	-2.01 – -35.54	62.45	1.00 – 173.00

3.4.2 Dive characteristics in relation to environmental covariates

Dive duration (Figure 7a) and maximum dive depth (Figure 7b) did not appear to vary greatly by hour of day. However, the number of dives (Figure 7c) appeared to be slightly bimodal, with more dives in the morning and the evening than in the middle of the day. In contrast to hour of day, the number of dives was not observed to vary in relation to tidal phase (Figure 8). The number of dives seemed to vary according to substrate classification (Figure 9c), with more dives occurring over muddy sand and seabed classifications. When considering maximum dive depth over different substrates (Figure 9b), dives were deeper over sediment, muddy sand and course substrate, than over seabed, rock or mixed sediment. However, dive duration did not vary according to substrate (Figure 9a). Increasing maximum dive depths maintain some correlation with deeper bathymetries (Figure 10a). Dive duration shows a similar correlation between increasing dive periods and bathymetries (Figure 10b). No correlation between kinetic energy and dive depth (Figure 11a) or duration (Figure 11b) was apparent. Time series of dive depths in relation to bathymetry, kinetic energy, and substrate are explored in Figure 12, which presents two example individuals. Maximum dive depths often converged with bathymetry, indicating that birds were diving to the seafloor (Figure 12).

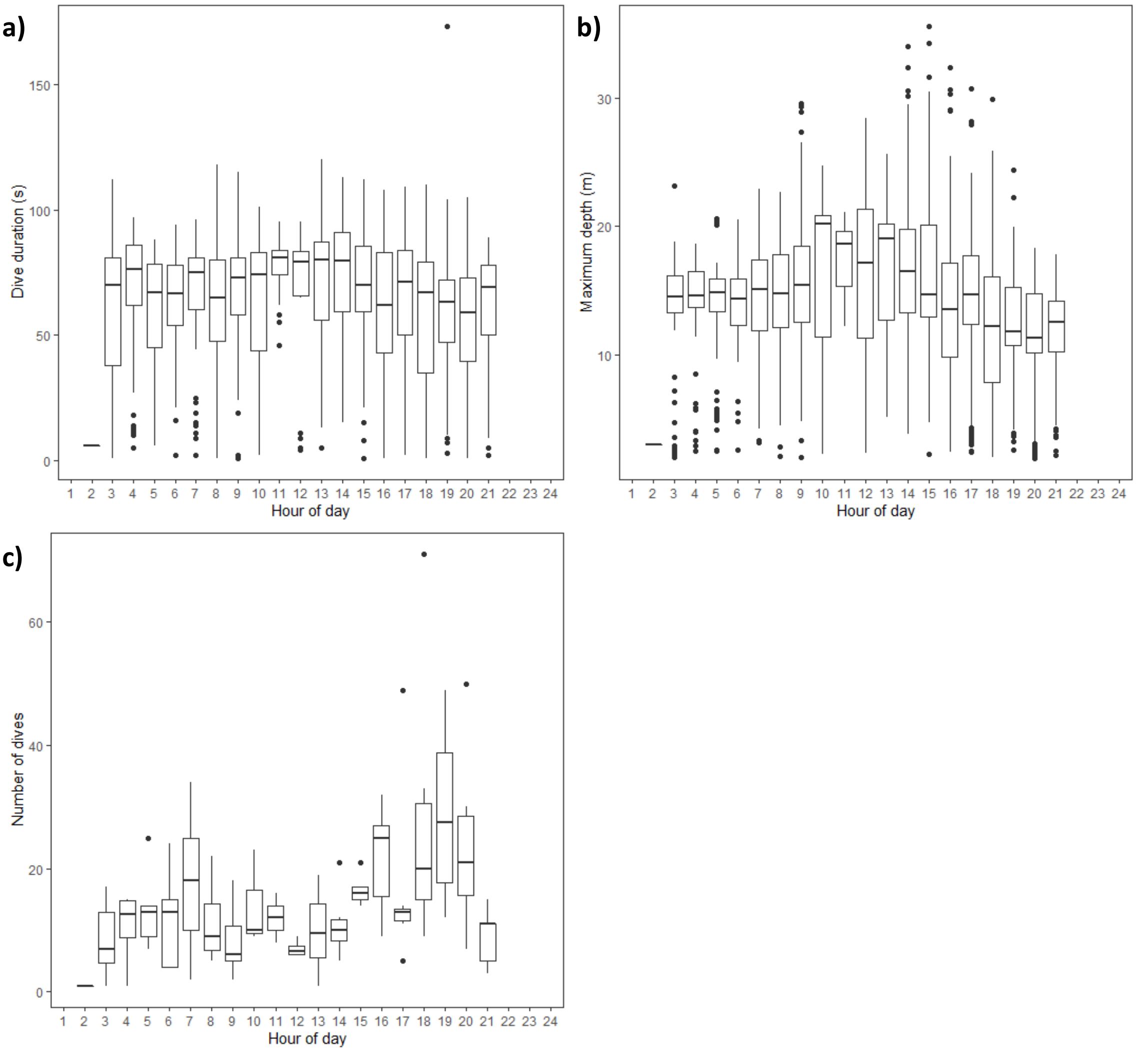

Figure 7. Boxplot of a) dive duration in seconds b) maximum dive depth in metres c) number of dives according to hour of the day. Black dots represent outliers.

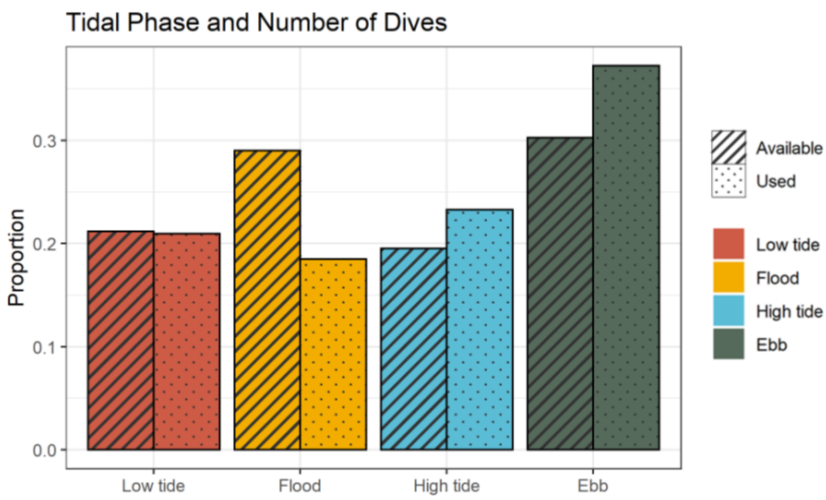

Figure 8. Proportion of dives in relation tidal phase, compared to concurrent available tidal phases.

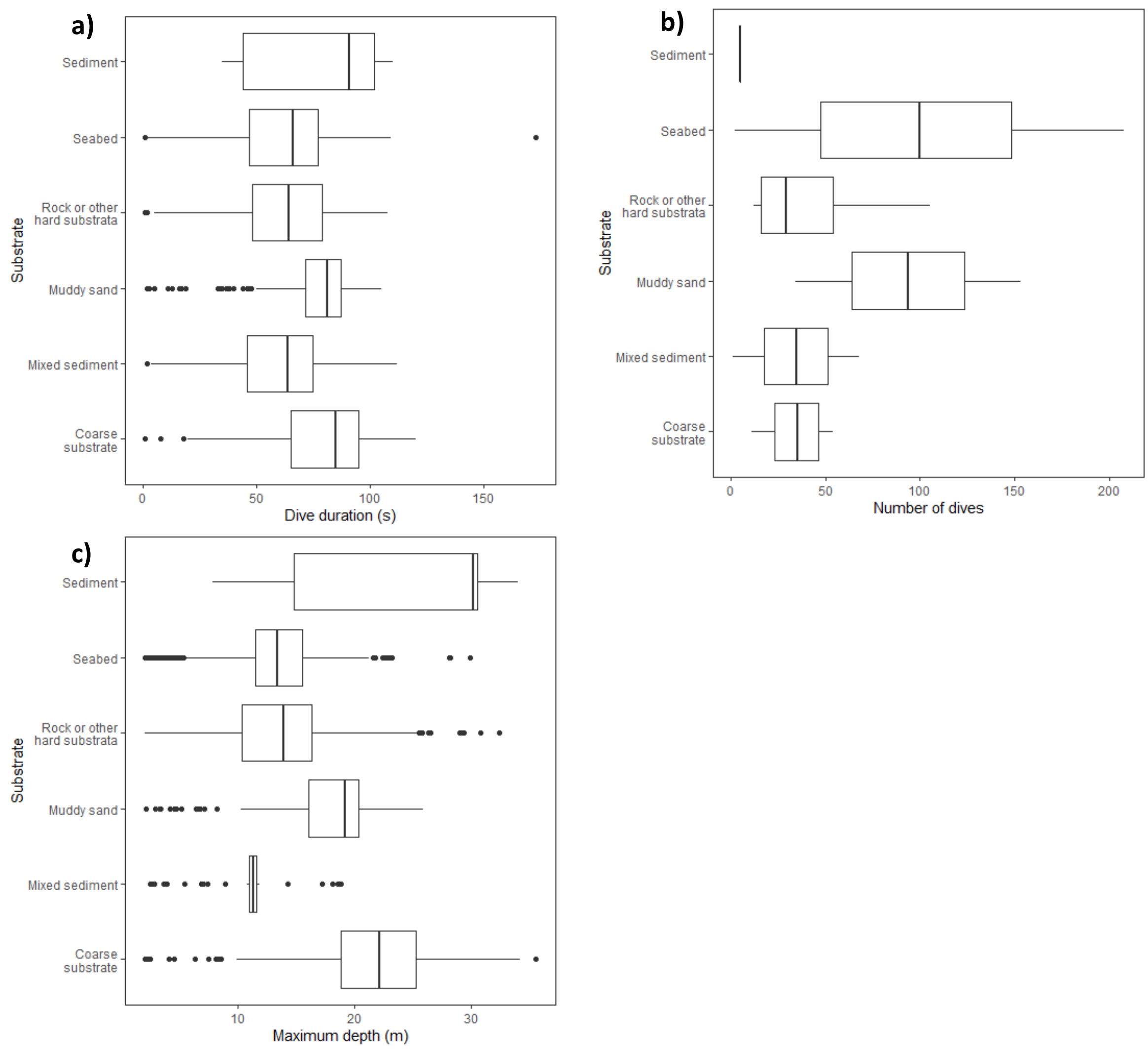

Figure 9. Boxplot of a) dive duration in seconds, b) maximum dive depth in metres and c) number of dives according to substrate classification. Black dots represent outliers.

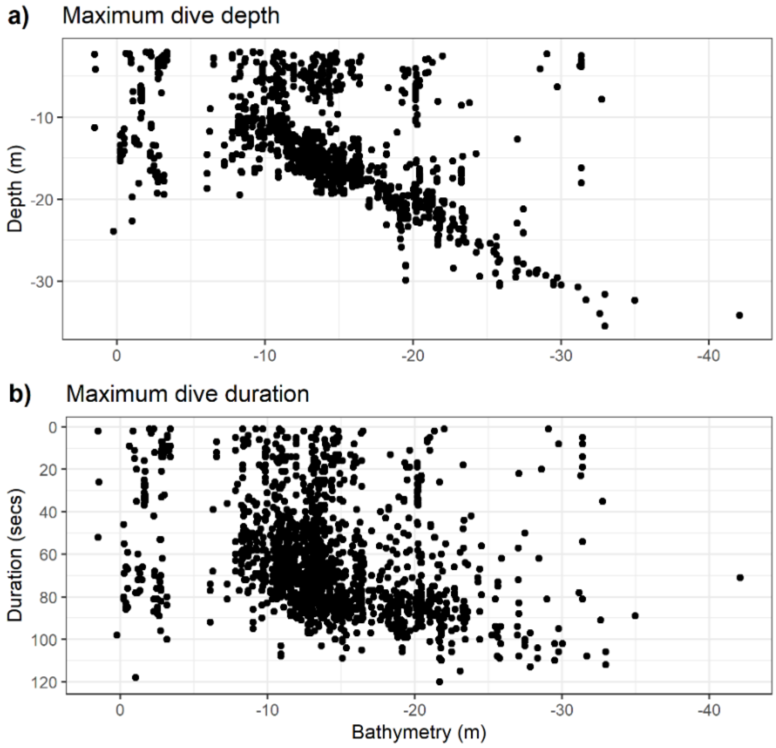

Figure 10. Scatterplot of a) maximum dive depth (m) and b) duration (seconds) in relation to bathymetry (m).

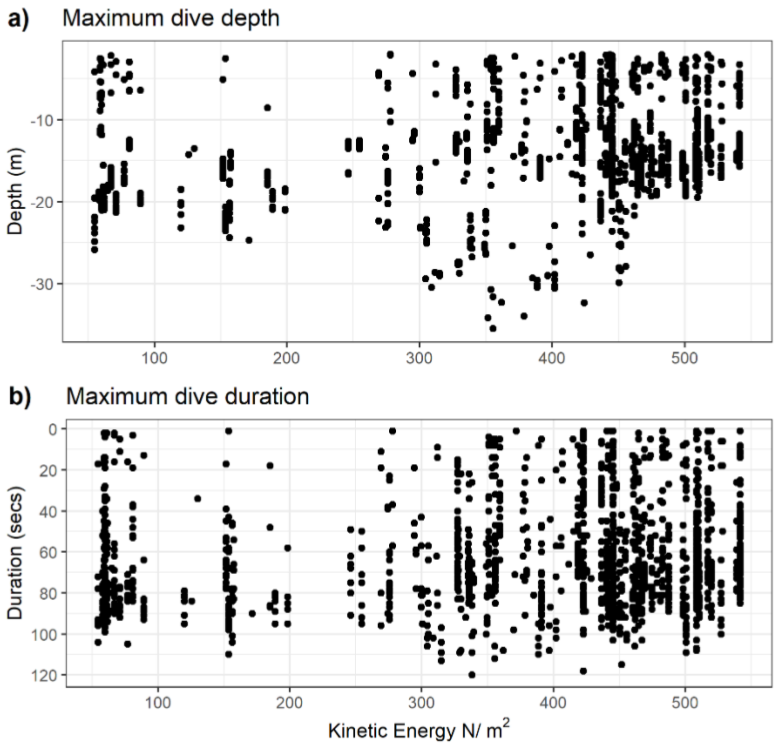

Figure 11. Scatterplot of a) maximum dive depth (m) and b) duration (seconds) in relation to kinetic energy (N/m²).

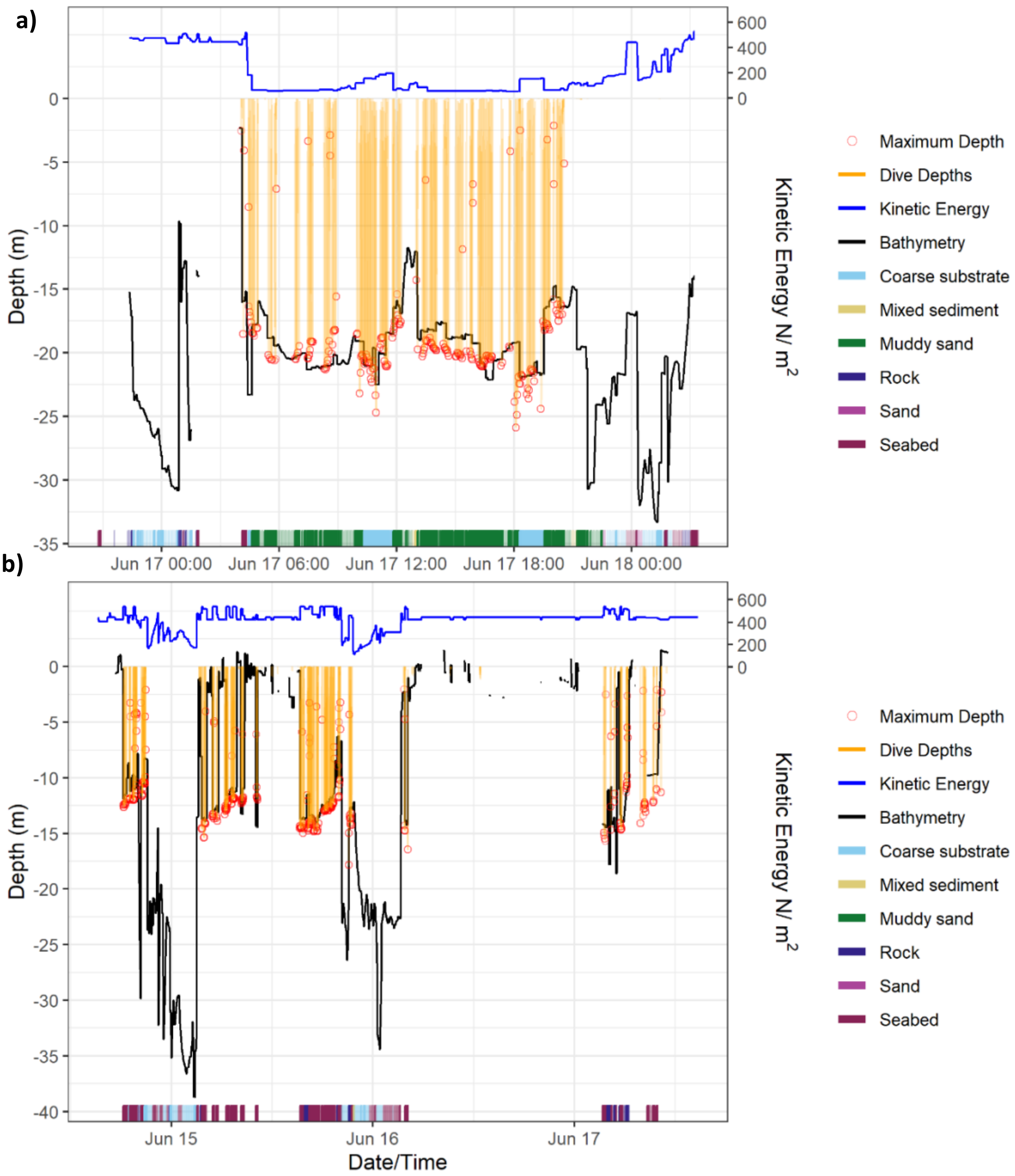

Figure 12. Time series dive depths in relation to maximum bathymetry (m) and kinetic energy (N/m²) for individuals a) E2C, and b) E9C. Further individuals can be found in Appendix A8.

3.5 Utilisation distributions

3.5.1 95% UDs by colony

Overlap between colony-level 95% UD's occurred only at the eastern and western most reaches of movement from Bangor and Lighthouse Island respectively, but otherwise there was very little overlap (Figure 13). Black Guillemots from Bangor tended to head directly to the north, spreading laterally east and west relatively close to the shore, whereas birds from Lighthouse Island used areas directly around the Copeland Islands, reaching furthest directly west and south from the colony. There is relatively little movement offshore and to the north of Lighthouse Island compared to movement seen west and south along the coastal mainland.

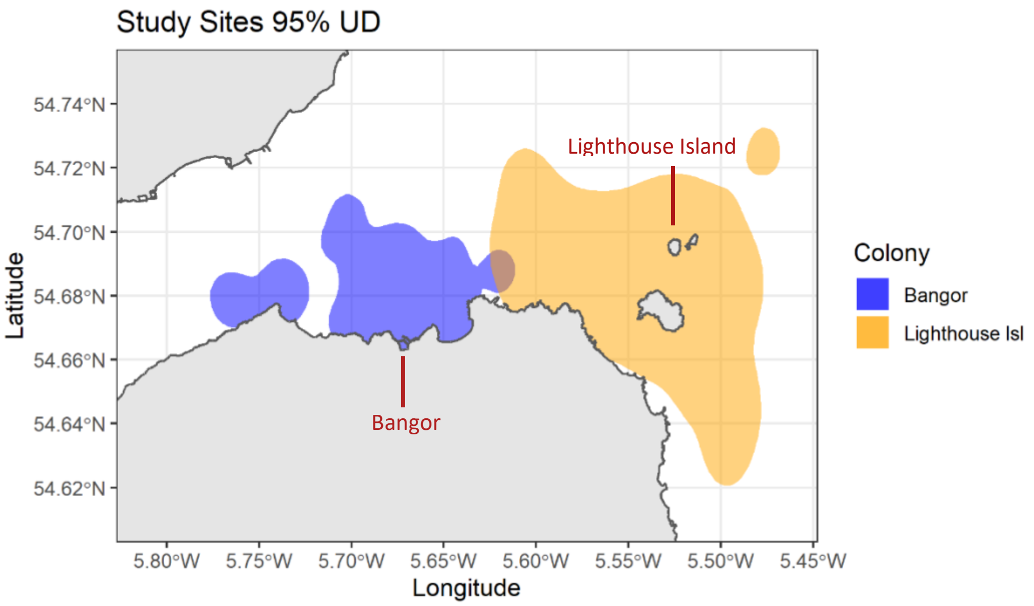

Figure 13. 95% Utilisation Distribution contours produced from tracking data from Bangor and Lighthouse Island.

3.5.2 95% UDs by individual

Individual 95% UD contours of birds tracked from Bangor (Figure 14a) and Lighthouse Island (Figure 14b) indicate that individuals from the same colony generally overlapped strongly in area use. Although there was an apparent preference of birds from Bangor to head directly north (see section 3.5.1), a few individuals diverged from this pattern with bird's P3B and P4B travelling northeast, whilst bird P6B used areas westwards along the coast (Figure 6a, Figure 14a). From Lighthouse Island, bird P2C produced a 95% UD which encompassed a large area of Belfast Lough, this was quite distinct compared to areas used by other birds, and was linked to an single trip from the colony (Figure 6b, Figure 14b).

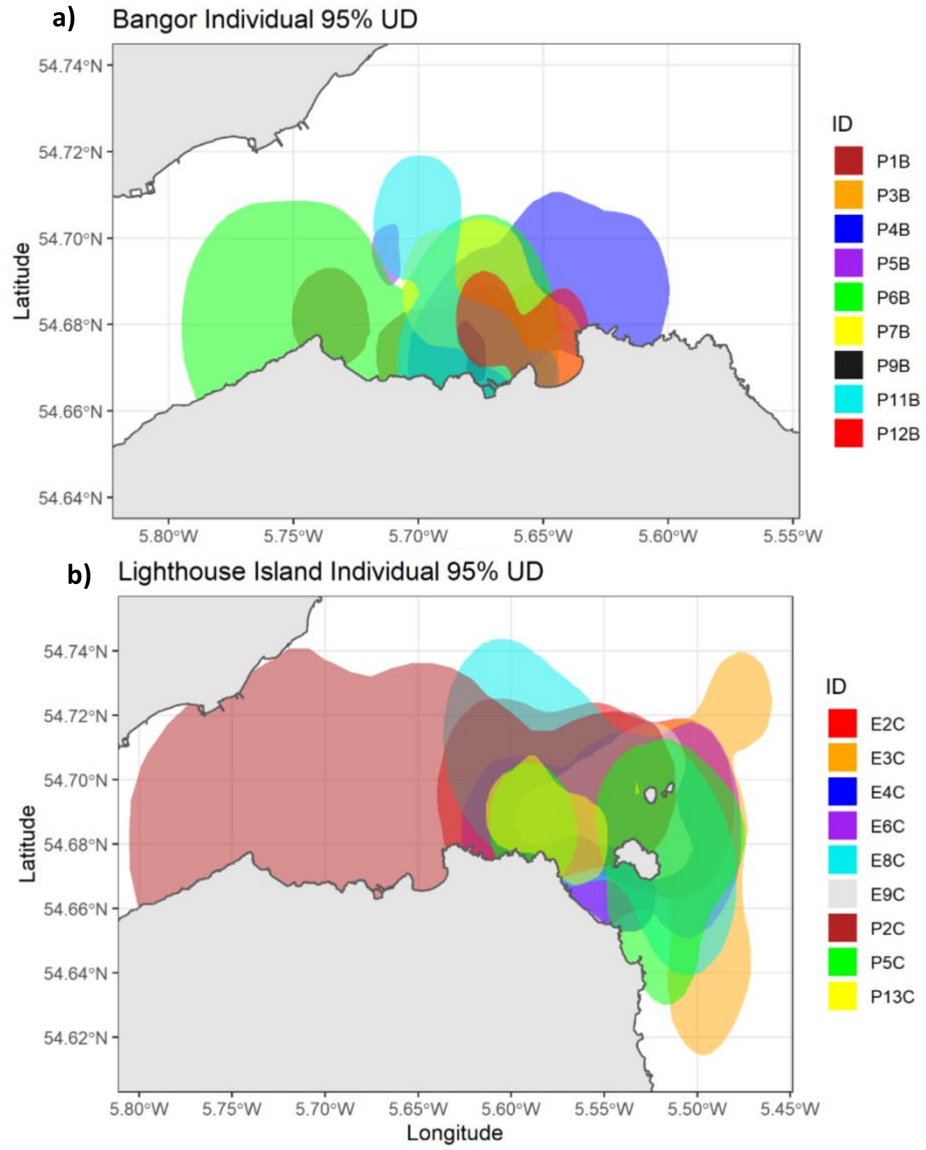

Figure 14. 95% Utilisation Distribution contours produced from individual tracking data from a) Bangor and b) Lighthouse Island.

3.6 50% UDs of behavioural states

Area use for the three different behavioural states of Black Guillemots originating from Bangor overlapped to a large extent (Figure 15a) although foraging and commuting were both encompassed within the area covered by loafing behaviour. The behavioural states of individuals from Lighthouse Island overlapped within a core area surrounding the island (Figure 15b). However, foraging behaviour from this colony extended westwards along the mainland coast, beyond the areas used for loafing and commuting.

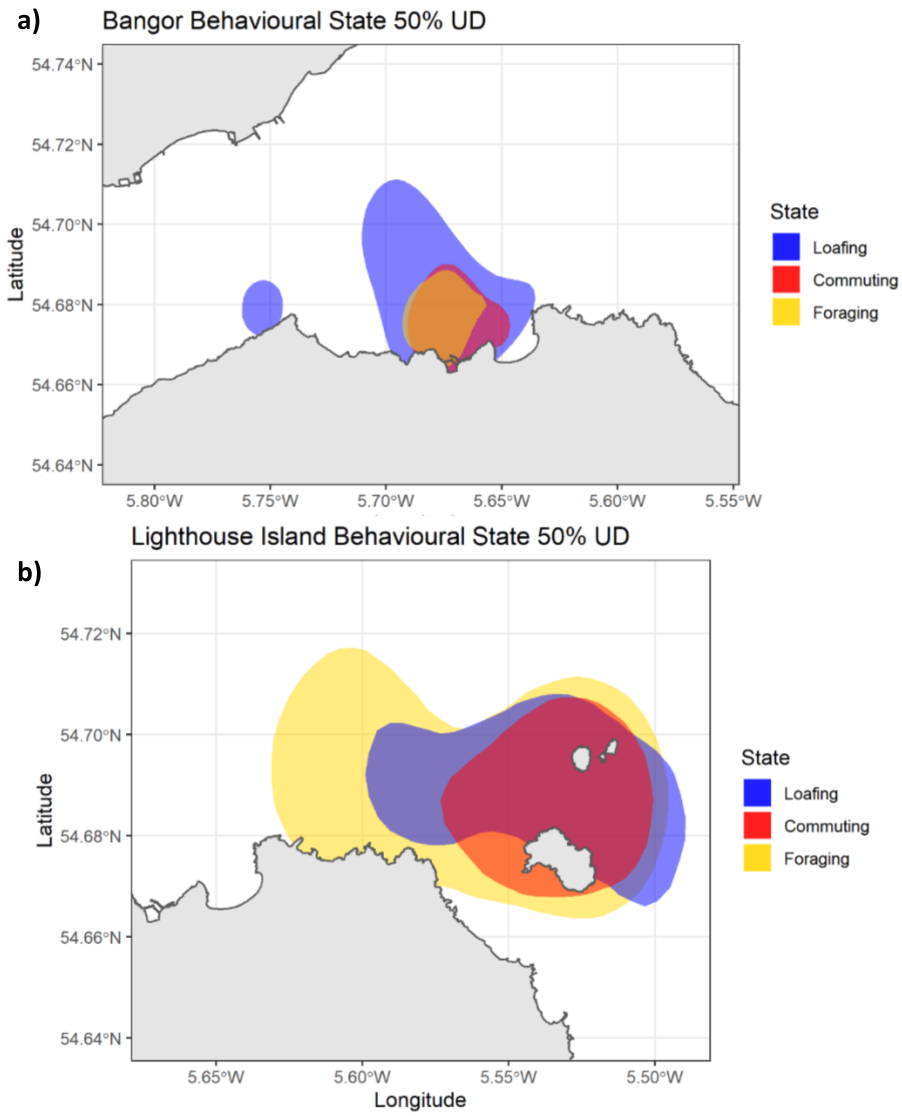

Figure 15. 95% Utilisation Distribution contours produced for behavioural states from a) Bangor and b) Lighthouse Island.

3.7 Foraging habitat characteristics

Model selection of RSFs, using AIC values weighted by 5 units, indicated the global model—containing all the covariates of bathymetry, kinetic energy, and substrate—to be the best fitting model for each study site and separate individual (See Appendix A6). However, each model must be examined individually as covariates varied in influence (See Appendix A7).

Bathymetry associated with the foraging locations of birds originating from Bangor were generally similar across all individuals (mean range = -8.06 to -11.82 m) (Table 5). All individuals were restricted to a maximum depth of -12.75 m indicative of the local depth characteristics within the distances travelled from the shore (max = 4.1 km). Birds from Lighthouse Island displayed a wider range of foraging depths (mean range= -9.82 to -18.95 m) (Table 5). The dive depths were likely reflective of bathymetry (Figure 12) which tended to be fairly homogeneous surrounding Bangor compared to the depths surrounding Lighthouse Island, which were more variable (Figure 16, Figure 17). The lack of variation in surrounding bathymetry may have been the reason that this was found to be a non-significant descriptor habitat selection ($p > 0.05$) in birds from Bangor (Table A4). RSFs for Lighthouse Island show a large difference in the AIC values between models which contained or excluded bathymetry, this indicated that bathymetry is an important habitat determinant for this colony (Table A1). Birds from Lighthouse Island significantly selected for shallower bathymetries than were generally available in their home range (Table A4, Figure 16d). Non-normal distributions were seen to exist in the selected bathymetries from Bangor and Lighthouse Island (Figure 17c,d). Peaks in used bathymetries by individuals from Bangor were present at depths of -7.5 m and -12.5 m (Figure 17c). The distribution of selected bathymetries by individuals from Lighthouse Island concentrated around a single peak at -15 m (Figure 17c), however inidividuals were also seen to use bathymetries as deep as – 33 m (Table 5, Figure 10).

Dynamic tidal currents were not as strong within the area of Belfast Lough which surrounded Bangor (Figure 4b) in comparison to Lighthouse Island, which is surrounded by the Donaghadee and Copeland Sounds (Figure 1, Figure 6b). Therefore, available kinetic energy varied significantly between Bangor (mean=34.22 ± 26.73 N/m^2) (Figure 16a, Table 5) and Lighthouse Island (mean=216.51 ± 140.69 N/m^2) (Figure 16b, Table 5). While kinetic energy was a significant descriptor of habitat selection for both Bangor and Lighthouse Island, coefficients indicated that individuals from Bangor selected lower kinetic energy than the available habitat, while Lighthouse Island birds selected higher kinetic energy (Table A4). However, a notable non-normal distribution was apparent in the associated kinetic energies from Lighthouse Island (Figure 17b), where there was a bimodal distribution at low (<200 N/m^2) and high (>400 N/m^2) values of used kinetic energy (Figure 17b, Figure 20a).

Large differences in AIC values between RSFs with and without substrate indicated substrate was likely to be an important habitat determinant for Bangor (Table A1). Between the two study sites, differing substrates dominated the available habitat, with sandy mud being the most prominent surrounding Bangor (Figure 18a), while only making up a small proportion of available habitat corresponding to Lighthouse Island (Figure 18b). Coarse substrate constituted the greatest proportion of available substrate associated with Lighthouse Island; however, this was not present in the available habitat of Bangor. Birds from Bangor preferentially selected fine mud and undefined seabed, and avoided muddy sand (Table A4). From Lighthouse Island the number of substrate types both available and selected were more varied by comparison (Figure 18). Of the seven substrate types used, muddy sand, sandy mud, and mixed sediment were significantly selected, while course substrate and rock were significantly avoided (Table A4). These results demonstrate that no single sediment type, based on the classification used, was of great importance across the colonies.

The distribution of used and available bathymetry and kinetic energy in relation to substrate surrounding Bangor and Lighthouse Island are visually explored in Figure 19 and Figure 20. From Bangor, used locations clustered around depths of -12 m, coinciding with lower kinetic energies of <50 N/m^2, and aligning with sandy mud (Figure 19). Used locations from Lighthouse Island appeared to reside around depths >-25 m with two groupings around kinetic energies < 200 and > 300 N/m^2, associated substrates are varied (Figure 20).

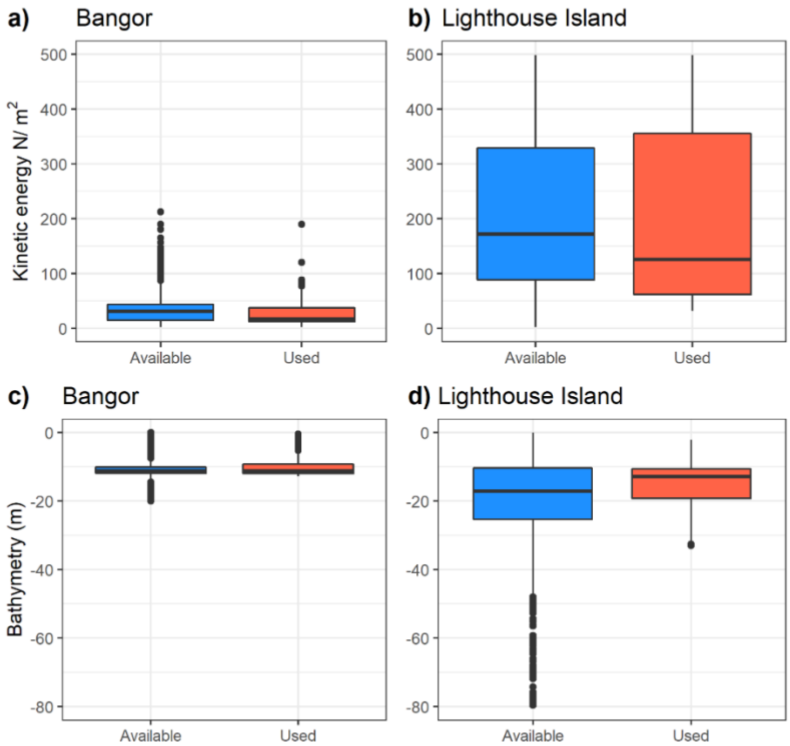

Figure 16. Distribution of kinetic energy (a, b) and bathymetry (c, d) at used and available locations in relation to Bangor (a, c), and Lighthouse Island (b, d).

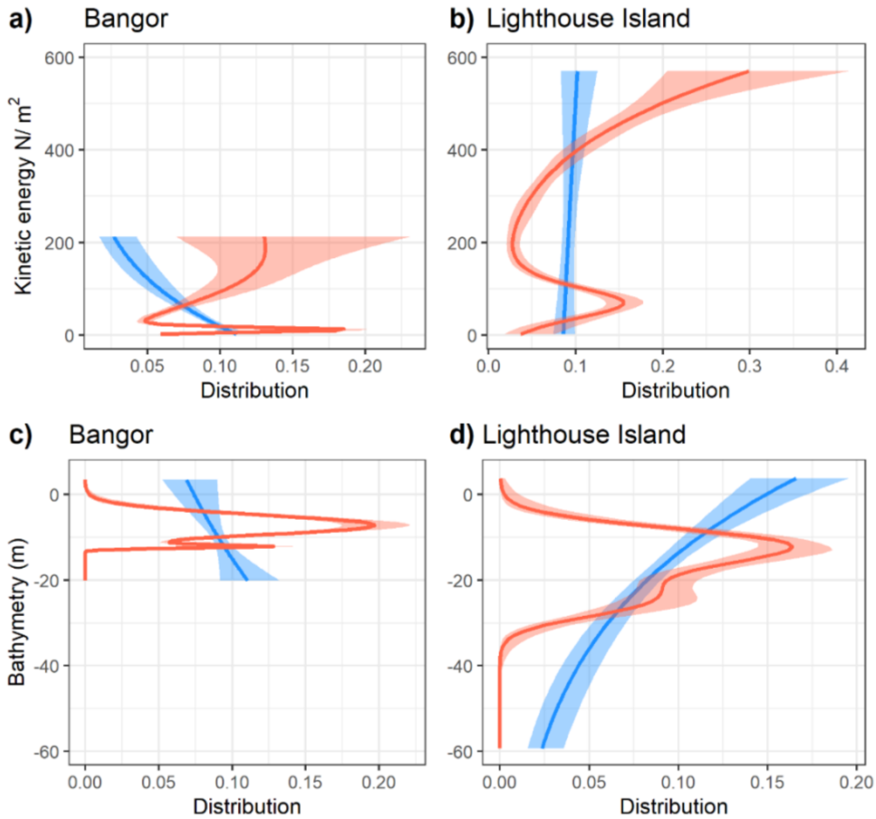

Figure 17. Smoothed conditional means displaying the distribution of kinetic energy (a, b) and bathymetry (c, d) at used (red) and available (blue) locations relating to Bangor (a, c), and Lighthouse Island (c, d). Conditional means are produced through binominal logistic regression.

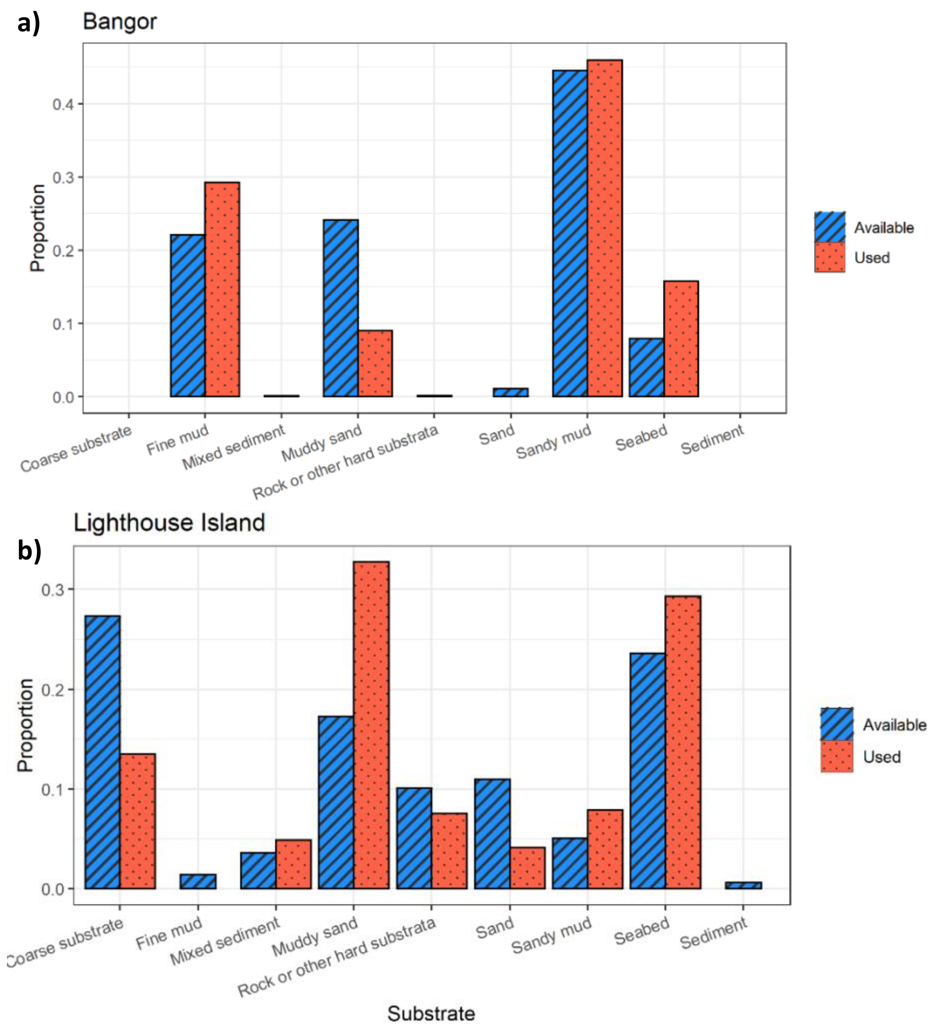

Figure 18. Proportion of used and available locations distributed among benthic substrate categories in relation to a) Bangor and b) Lighthouse Island.

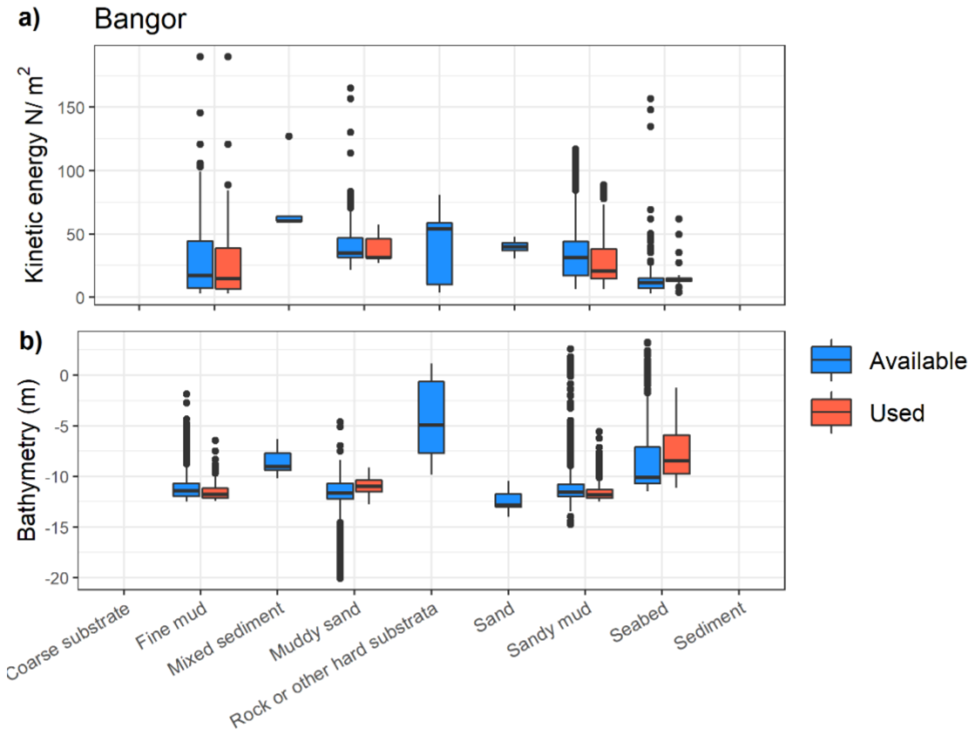

Figure 19. Distribution of substrate classes at used and available locations corresponding to Bangor in relation to a) kinetic energy and b) bathymetry.

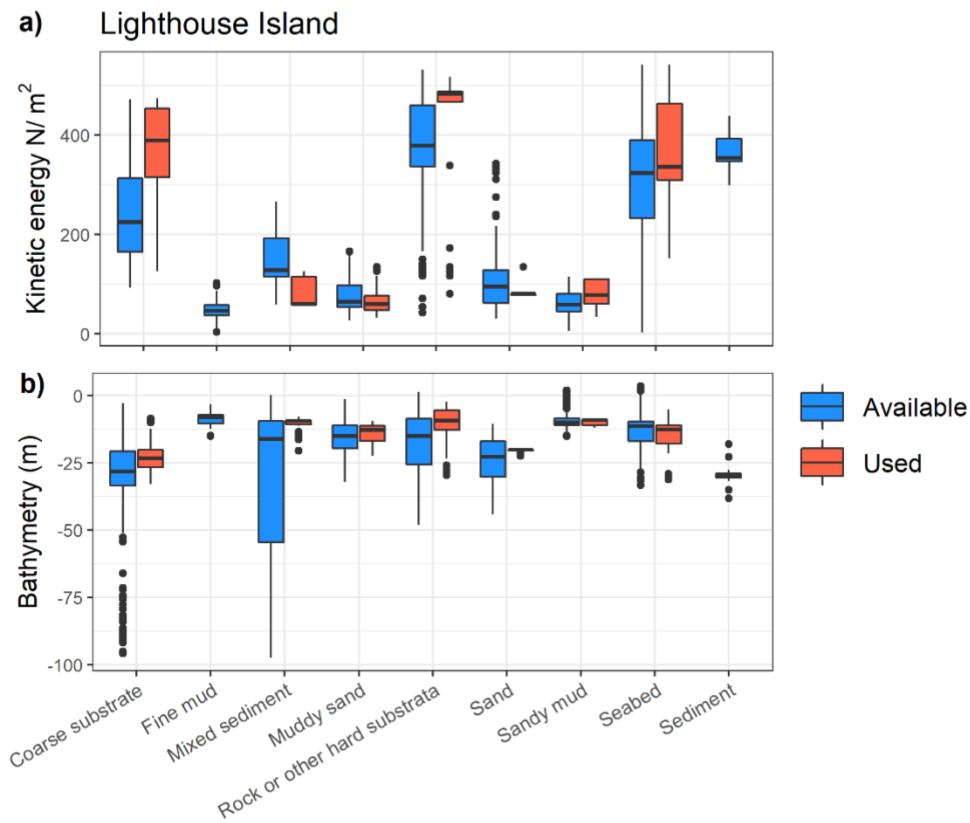

Figure 20. Distribution of substrate classes at used and available locations corresponding to Lighthouse Island in relation to a) kinetic energy and b) bathymetry

Table 5. Used environmental covariates at foraging locations for all birds (Individuals combined) and individuals originating from Bangor and Lighthouse Island, and the characteristics of the surrounding available habitat (Available).

Colony	ID	Bathymetry (m)			Kinetic Energy (N/m^2)			Substrate (n)							
		Mean	Max	Min	Mean	Max	Min	Coarse substrate	Fine mud	Mixed Sediment	Muddy sand	Rock	Sand	Sandy mud	Seabed
Bangor	Available habitat	-10.18	-20.07	3.44	34.22	212.74	2.82	0	2404	13	2617	17	118	4843	863
Lighthouse Island		-18.7	-97.3	3.84	216.52	570.17	2.86	1435	74	189	908	531	576	266	1240
Bangor	Individuals combined	-10.38	-12.75	-0.56	29.79	190.14	2.82	0	322	0	99	0	0	506	173
Lighthouse Island		-14.79	-33.02	-2.21	223.45	541.5	32.63	75	0	27	182	42	23	44	163
Bangor	P1B	-9.68	-12.4	-5.72	40.04	190.14	2.82	0	69	0	0	0	0	40	88
	P3B	-11.82	-12.42	-5.57	15.85	43.91	4.19	0	19	0	0	0	0	167	3
	P4B	-10.75	-12.44	-3.8	27.80	57.37	4.42	0	35	0	31	0	0	15	0
	P5B	-11.72	-12.49	-0.56	30.20	88.53	3.84	0	82	0	5	0	0	103	0
	P6B	-10.47	-12.41	-7.64	38.60	86.56	3.25	0	55	0	0	0	0	57	0
	P7B	-9.81	-12.34	-1.24	24.44	46.61	3.61	0	0	0	60	0	0	71	14
	P9B	-11.07	-12.14	-6.13	11.68	18.58	4.42	0	29	0	0	0	0	0	3
	P11B	-8.06	-12.75	-1.6	49.39	120.66	11.41	0	32	0	3	0	0	0	18
	P12B	-8.95	-12.28	-4.44	22.67	61.84	4.60	0	1	0	0	0	0	53	47
Lighthouse Island	E2C	-18.95	-28.16	-9.98	183.02	474.38	54.81	30	0	2	61	0	0	0	0
	E3C	-16.06	-31.75	-2.32	413.29	500.84	116.50	7	0	0	0	18	0	0	16
	E4C	-9.82	-11.48	-6.66	345.27	414.92	327.30	0	0	0	0	0	0	0	11
	E6C	-13.55	-23.46	-6.15	279.41	509.71	59.18	5	0	19	5	8	0	0	31
	E8C	-19.14	-26.41	-5.12	182.51	510.87	78.33	7	0	0	1	3	22	0	6
	E9C	-17.2	-33.02	-8.91	400.14	541.50	267.39	5	0	0	0	1	0	0	50
	P2C	-10.77	-17.36	-8.73	58.13	111.49	32.64	0	0	0	73	1	0	44	0
	P5C	-12.21	-24.77	-2.22	435.03	498.34	287.49	16	0	0	0	11	0	0	11
	P13C	-14.5	-21.67	-9.41	158.26	378.09	58.14	5	0	6	42	0	1	0	38

3.8. Near-shore area use

Birds were often concentrated in nearshore areas close to nest sites. This aspect of movement was excluded from the analysis of foraging habitat as it occurred within 300 m of nest sites and was regarded as being distinct to foraging trips. Use of the nearshore adjacent to the colony is potentially an important area for the exhibition of other behaviours such as loafing and resting. This was confirmed by visual observations in the field.

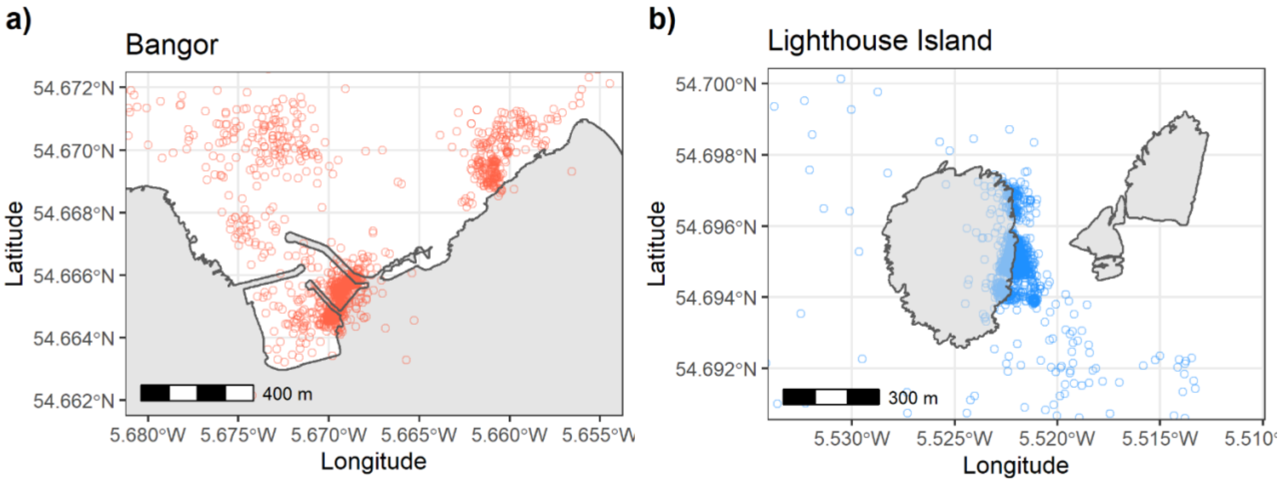

Figure 21. Nearshore GPS locations of Black Guillemots adjacent to nesting sites for a) Bangor and b) Lighthouse Island.

3.9. Night vs. day area use

Night and day space use appeared to overlap in core areas surrounding each colony (Figure 22). Some divergences from the main areas of overlap can be seen during the day, with birds originating from Bangor using a bay east of the colony (Figure 30a). From Lighthouse Island (Figure 30b), area use specifically associated with day-time can be seen to the west of the colony in nearshore areas of the mainland. Use of an area north west of Bangor at night was likely related to the location of a navigational buoy providing a roosting platform.

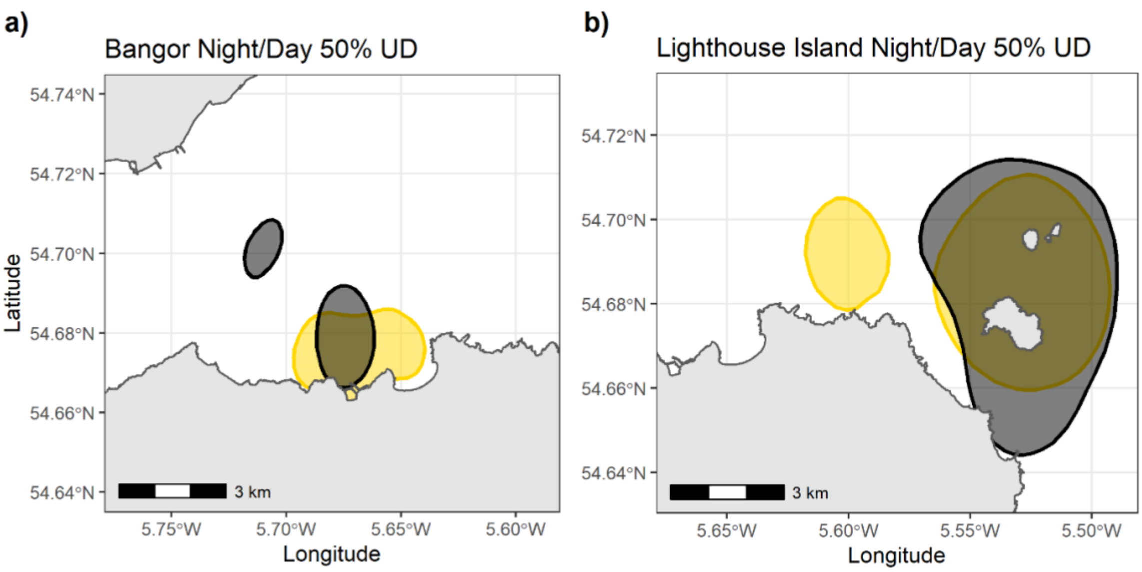

Figure 22. 50% Utilisation Distribution contours of Black Guillemot space use categorised by night (black) and day (yellow) for a) Bangor and b) Lighthouse Island.

4. Discussion

Improved protection of Black Guillemot populations through MPA designation aims to mitigate the negative impacts potentially arising from degradation of foraging or breeding habitat. Foraging habitat may be impacted by fisheries practices (Žydelis et al., 2009; Barrett et al., 2016), marine renewable energy devices (Furness et al., 2012; Masden et al., 2013), or climate change (Smale, 2020), amongst other factors. Breeding habitat may be vulnerable to human disturbance (Cairns, 1980), or native (Ewins, 1985; Johnston et al., 2019) and invasive predators (Craik, 1997). The impacts of these stressors may be compounded by the non-migratory behaviour of Black Guillemots, potentially exposing the species to negative impacts year-round (Ewins and Kirk, 1988). More broadly within the UK, Black Guillemots have been found to be increasing (JNCC, 2021), while in Northern Ireland some colonies are in decline and the overall population appears to have increased only slightly since the last census (Booth Jones, 2022). Maintaining foraging habitat to a 'favourable condition' within MPAs (The Scottish Government, 2010), may provide a buffer against potential environmental impacts of climate change on benthic habitat and prey species. Additionally, landward boundaries attributed to MPAs encompassing colony areas may encourage the maintenance of nest sites from degradation by invasive predators or human disturbance.

4.1 Habitat characteristics relevant to MPA management

4.1.1 Bathymetry

Black Guillemots from Bangor and Lighthouse Island primarily foraged within 5 km of their nest sites, selecting environmental characteristics site specific to that area. Data from TDR loggers indicated that birds were frequently diving to the benthos, therefore seafloor characteristics potentially had the greatest influence on foraging locations. One aspect of the seafloor that was found to influence foraging across colonies was a preference towards shallower bathymetries (>-20 m). Overall, birds from both colonies largely remained within the infralittoral (>-10 m) and shallow circalittoral (-10 to -30 m) bathymetry zones (EMODnet, 2021). Between the two colonies, selection of specific depths was more apparent in relation to Lighthouse Island with preference shown towards shallower locations. This was likely attributed to a greater range in bathymetry surrounding Lighthouse Island, while from Bangor the available habitat was limited to a maximum depth of 12 m, well within the dive range of Black Guillemots (Masden et al., 2013; Shoji et al., 2015).

4.1.2 Substrate

While bathymetry was not a confining factor in relation to Bangor, substrate was found to be the most important habitat determinant for this site. The active selection of specific substrate type and benthic biotopes has previously been identified in Black Guillemots, including sand, gravel, and kelp (Sawyer, 1999; Owen, 2015; Johnston, 2019). Dive behaviour examined here found a potential link between mid-water (approx. -15 m) muddy sand and more frequent dives, while coarse substrate was attributed to deeper (approx. -25 m) but less frequent dives. More research is required to identify the prey communities held within coarse substrate and muddy sand, to examine the benefits of these differing habitats. No substrate types were found to be commonly selected by individuals. This may be due to the foraging habitat of Black Guillemots being more influenced by benthic biotope, which may have a complex relationship with depth, kinetic energy, and substrate type. One indicator of this is the narrow band of relatively shallow depths selected. Increased light penetration at shallower depths of > -20 m allows the growth of kelp species *Laminaria saccharina* in sheltered areas of mixed sediment, and *Laminaria hyperborean* in areas moderately exposed to wave action and tidal currents (Foster-Smith, 2010). Kelp habitats are highly biodiverse (Smale et al., 2013; Burrows et al., 2014) and include Black Guillemot prey species such as Butterfish, Gadoid spp.

and Cottidae spp. (Sawyer, 1999). Data on biotope distribution for this area was not available for this analysis; therefore, to more accurately assess habitat selection of substrate, higher resolution data on seafloor habitats are required.

4.1.3 Kinetic energy

Another consideration of proposed MPAs are the potential foraging opportunities provided by fast flowing currents. Strong oceanic currents present potential foraging opportunities for seabirds through the formation of fronts and upwellings which aggregate prey (Benjamins et al., 2015). We found the selection of kinetic energies to differ between birds from Bangor and Lighthouse Island. This was attributed to the presence of tidally active sounds between the three constituent islands of the Copelands, causing a large variation in available kinetic energy between the two study sites. Variation in preferred kinetic energies was apparent between individuals from Lighthouse Island, which selected for properties of either high (> 400 N/m^2) or low kinetic energy (< 200 N/m^2). This broadly reflects other studies examining Black Guillemot association with fast tidal currents, where some individuals associated strongly with tidal streams, while others foraged in more sheltered low energy habitats (Johnston et al., 2021). While Black Guillemots are often identified as associating with fast flowing currents, this varies between sites (Waggitt et al., 2017), however the underlying cause of this variation is unknown. Although the fast flowing currents may form an important foraging habitat of potentially high protection value, it is important to consider that Black Guillemots may only use spatially or temporally restricted attributes of available currents linked with tidal eddies and upwellings of prey (Benjamins et al., 2015; Johnston et al., 2021).

4.1.4 Behaviours

Nearshore areas adjacent to the nests of Black Guillemots are important for courtship and social display, and have been suggested to influence breeding synchrony, regulate colony size, and provide areas for copulation and predator alarm (Hilden, 1994). We observed nearshore areas adjacent to the nest sites off Lighthouse Island and Bangor Harbour to be frequently used by multiple individuals during the morning for social display. These behaviours, and the nearshore areas in which they occur, are a potentially important consideration for both the continuation of Black Guillemot nest establishment and ongoing recruitment of individuals to a colony. Black Guillemots have acclimatised to human activity within Bangor Harbour enabling them to nest within a busy urban centre. However, the consequences of this disturbance on breeding success, nest site preference, and colony population are unknown. At colonies less exposed to human activity, such as Lighthouse Island, disturbance to nearshore and onshore breeding areas may have a detrimental effect on colony attendance or breeding success. Therefore, both onshore and nearshore areas adjacent to colonies are important to consider for protecting spaces used by Black Guillemots to exhibit a complex range of behaviours.

We found that the areas used by Black Guillemots when loafing, commuting and foraging overlapped to a large extent. Fine scale variation in areas selected for specific behaviours are likely to exist within an individual Black Guillemot's home-range, however this was not able to be investigated here. Temporal variation in behaviour was exhibited between day and night, with diving ceasing at night, potentially related to an extended period of birds loafing or roosting. This change in behaviour may be related to light level, the reduction of which may impede the ability to forage visually. During the day, the number of dives was observed to be distributed bimodally with more activity in the morning and evening, and less in the middle of the day, as has also been observed by others (Ewins, 1986). Despite this temporal variation, the location of areas associated with nocturnal and diurnal activity broadly overlapped. Further investigation is required into temporal and behavioural variation in Black Guillemot space use; however, these initial results indicate that appropriately placed MPAs may encompass multiple aspects of Black Guillemot movement and behaviour.

4.2 Recommendations for future work

This work was carried out within a restricted time period during the breeding season, a period in which seabirds exhibit distinct foraging and nest attendance behaviours. This was due to technological restrictions of tag battery life and data retrieval, and methodological restrictions in catching techniques. Advances in tracking technology, for example the use of Global Location Sensors (GLS) coupled with stable isotope analysis (Baak et al., 2021), allowing for the study of movement over longer periods and across seasons would greatly improve our knowledge of Black Guillemot habitat use throughout the year.

Analyses carried out within this report focussed on three core environmental variables using open-access data (EMODnet, 2021). This analysis could have been improved upon through the use of supplementary environmental covariates such as tidal velocity, and benthic biotope. These data were unfortunately not openly available. The analysis could also have been improved by using environmental data of higher spatial resolution, potentially acquired through bespoke habitat surveys, allowing the identification of specific benthic biotopes associated with foraging. Additionally, higher resolution tracking data (<5 mins) would be beneficial; however, with the current available technology this would drastically curtail a tag's battery life. This would be of greatest benefit within the dive depth analysis where some dives were found to exceed bathymetry. This was likely due to the resolution of the bathymetry data, or spatial error linked to assigning environmental characteristics from the nearest GPS point in time. This could be improved upon through higher resolution of GPS fix rates and higher resolution of habitat data.

We have shown that Black Guillemots foraged within the immediate 5 km area surrounding the breeding colony, but inter-colony and inter-individual variation in habitat selection was high. Therefore, the importance of habitat selected for foraging identified in our study may not be transferrable to other colonies in Northern Ireland or elsewhere in the INTERREG VA region, which are potentially surrounded by different environmental characteristics of bathymetry, substrate, and tidal currents. However, protection of a diverse suite of habitats within MPAs may ensure resilience in Black Guillemot populations to environmental change and anthropogenic pressures. Further study of other Black Guillemot colonies would be beneficial, identifying the potential influence of site-specific foraging habitat attributes on colony size, breeding success, and adult condition and survival. Additional study of the foraging habitat between seasons and years may identify temporally important aspects of Black Guillemot foraging ecology with implications for the suitability of MPA coverage (Baak et al., 2021).

This report addresses the foraging habitat requirements of Black Guillemots during the breeding season. However, little is known about the potential drivers of population change in Northern Ireland and therefore the relative benefit of at-sea MPA protection to Black Guillemots is not well understood. For example, Rathlin Island is the only colony in Northern Ireland for which Black Guillemot foraging habitat protection exists, and this colony has declined since by ~62% from the last census (Booth Jones et al., 2022), while monitoring of the Lighthouse Island population suggests that this population has increased by ~42% since the last census (Booth Jones, 2022). In contrast to Rathlin Island, the Lighthouse Island colony appears to have benefitted from the installation of artificial nest boxes (Leonard and Wolsey, 2015) and remains free of introduced mammalian predators. Therefore, while at-sea MPA protection is vital to support Black Guillemot populations in the face of increasing environmental change and human activities, conservation management for Black Guillemots should also consider information gaps around the impacts of predation on breeding success and availability of nesting habitat.

Networks of MPAs, rather than individual sites, have been suggested to be of greater conservation benefit to seabirds (JNCC, 2018). Should individual colonies experience years of catastrophic nest failure, driven either by predation or adverse weather conditions, networks of MPAs may provide source populations to drive colony re-establishment (JNCC, 2018). However the appropriate distance between Black Guillemot colonies at which a MPA network may influence metapopulation dynamics is currently unknown (Johnston et al., 2018a, 2018b). To better understand whether MPAs provide effective protection to Black Guillemots, long-term monitoring of breeding success, adult survival, dispersal, and diet will be important to identify potential demographic or ecological trends. Long-term demographic monitoring and a greater understanding of threats - posed by predation, disturbance, and climate change - is essential to identifying drivers of population change.

4.3 Conclusions

Tracking data gathered from Bangor and Lighthouse Island during the breeding season of 2021 contributes to a growing knowledge base of Black Guillemot foraging ecology. Findings of space use, diving behaviour and foraging habitat can be directly applied as guidance for MPA management undertaken within the MarPAMM project. Our results indicate that proposed MPAs for Black Guillemots would be of greatest benefit within 5 km of colonies and with bathymetry profiles shallower than 30 m. However, the extent to which these areas would be appropriate as a designated site during the wintering period is unknown. Also, given the high degree of variation in habitat use between individuals and colonies, the results may not necessarily be applicable to other colonies. Landward extensions to MPAs, which encompass Black Guillemot colonies, should encourage protection of nesting birds from invasive mammal predators or human disturbance and should be considered as part of the designation process. A primary recommendation from our findings is the additional need for high resolution information on the benthos and tidal currents at depths shallower than 30 m to inform of fine scale habitat selection. Further research is required to understand the links between varying habitat characteristics and diet on demographic trends, such as breeding success and population size. Addressing these knowledge gaps will bring to light the mechanisms influencing Black Guillemot foraging ecology, which may provide the focus of future MPA management effort.

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The raw data presented here is archived on Movebank (https://www.movebank.org/). Further details on accessing the data are outlined within Appendix A10. The copyright for the data belongs to AFBI, with data collected as a partnership between BTO and AFBI.

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Appendix

Ai. Appendix list of figures

Aii. Appendix list of tables

A1. INTERREG VA region

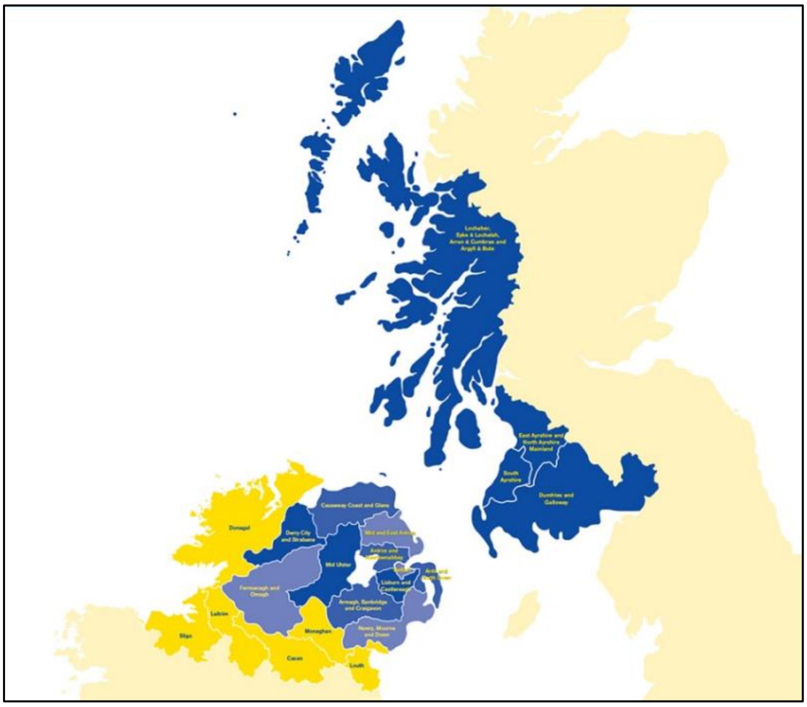

Figure A1. Map of the INTERREG VA region (as shown by the labelled areas). Image taken from: The EU Special Programmes Body https://www.seupb.eu/iva-overview

A2. Random point ratio selection

Selection of the number of appropriate random points was carried out by generating 30 combinations of increasing numbers of random points per the number of foraging points (1:1, 5:1, 10:1, 15:1, and 20:1). Binomial logistic regression models (see section 2.3.5) were run comparing “used” points to each combination of “available” random points (Fieberg et al., 2021). Parameter estimates from the 30 models run for each group of random points were compared graphically (Figure A2), indicating that estimates of each parameter stabilised in models produced using random points ≥10 times the number of used points. The selection of 10:1 random to used points was therefore deemed to be unlikely to influence intepretation of the final model compared to smaller ratios.

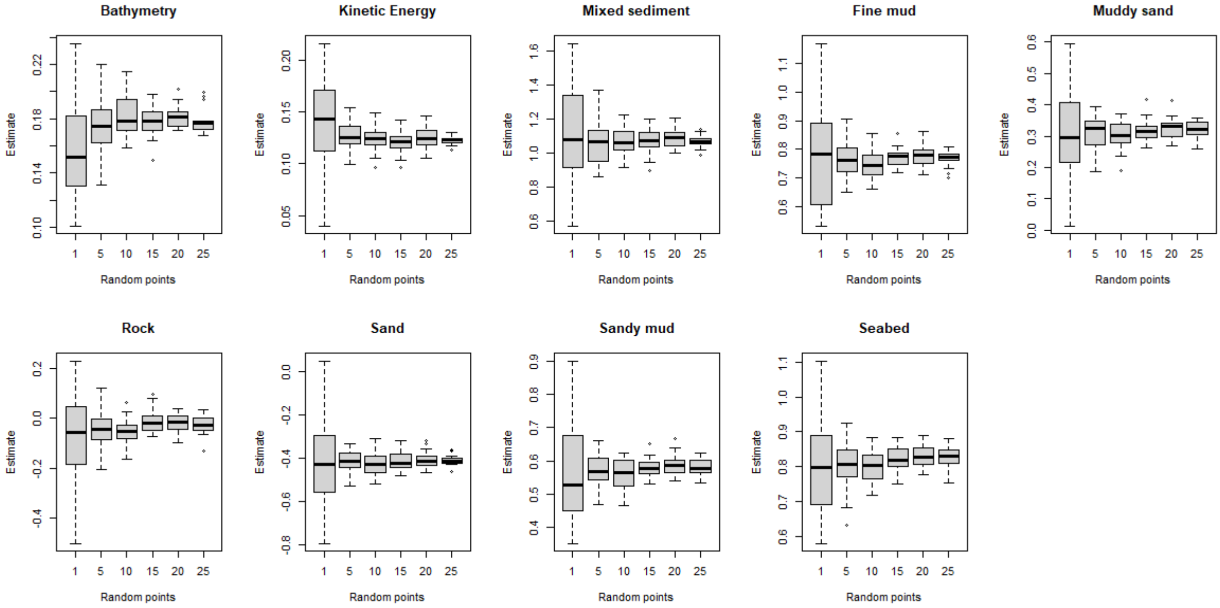

Figure A2. Parameter estimates of Resource Selection Functions in relation to increasing numbers of randomly generated available points.

A3. Individual selection of bathymetry

Inter-individual variation in selection of bathymetry was seen between individual RSFs. For four individuals originating from Bangor, bathymetry was found to play no role in habitat selection. Two individuals selected shallower habitats (P7B and P11B), while three individuals selected deeper habitats (P1B, P5B, and P6B) (Figure A3). However, the contrast between the mean depths selected by these individuals was slight (±2 m) (Table 5), therefore individuals selected similar depths around -10 m. The selection of distinct bathymetries in individuals from Lighthouse Island was more apparent. From this colony bathymetry did not describe selection for three individuals. However, five individuals (P2C, P5C, E2C, E6C, and E8C) preferred bathymetry significantly shallower than the available depths. While mean and maximum bathymetry associated to foraging varied to a greater extent at Lighthouse Island in comparison to Bangor, depths selected were consistently shallower than the available bathymetry (Figure A4).

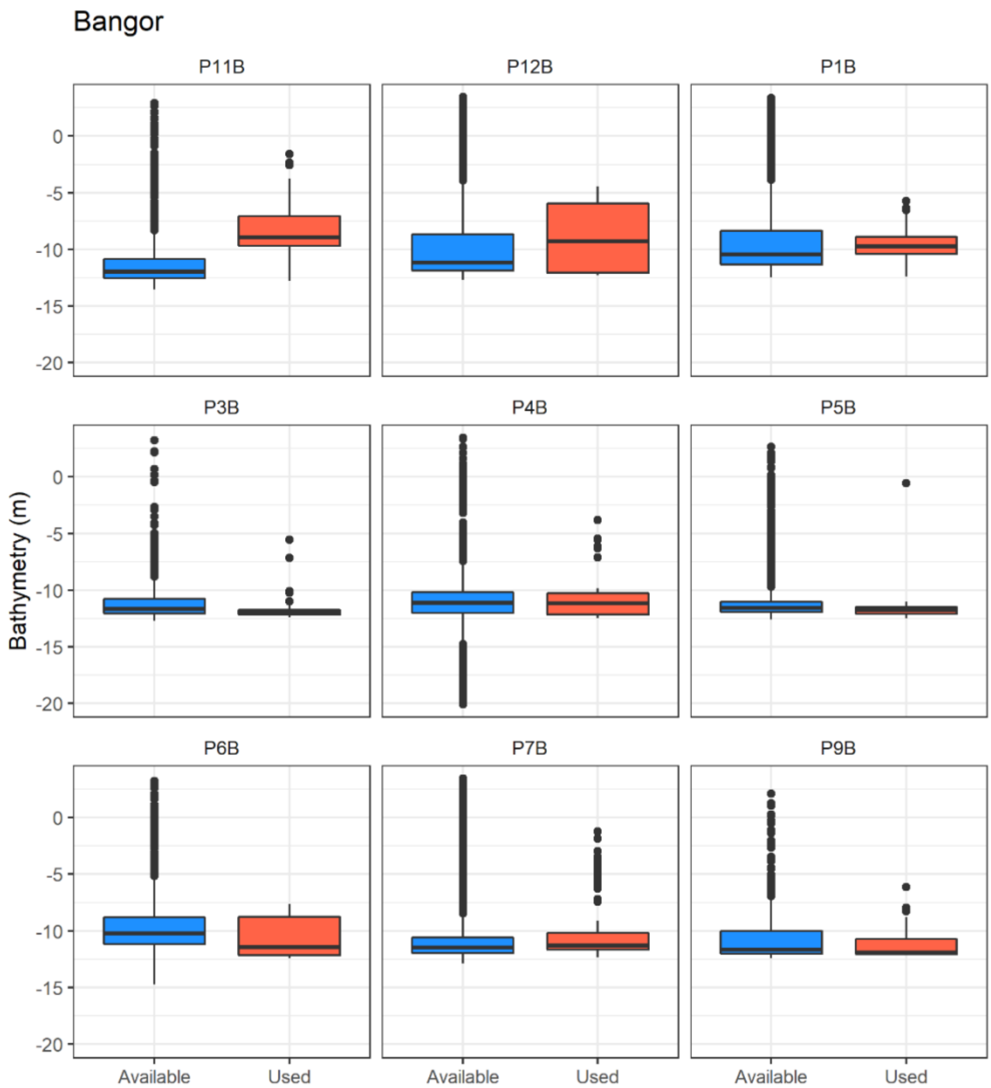

Figure A3. Distribution of bathymetry at used and available locations corresponding to individuals originating from Bangor.

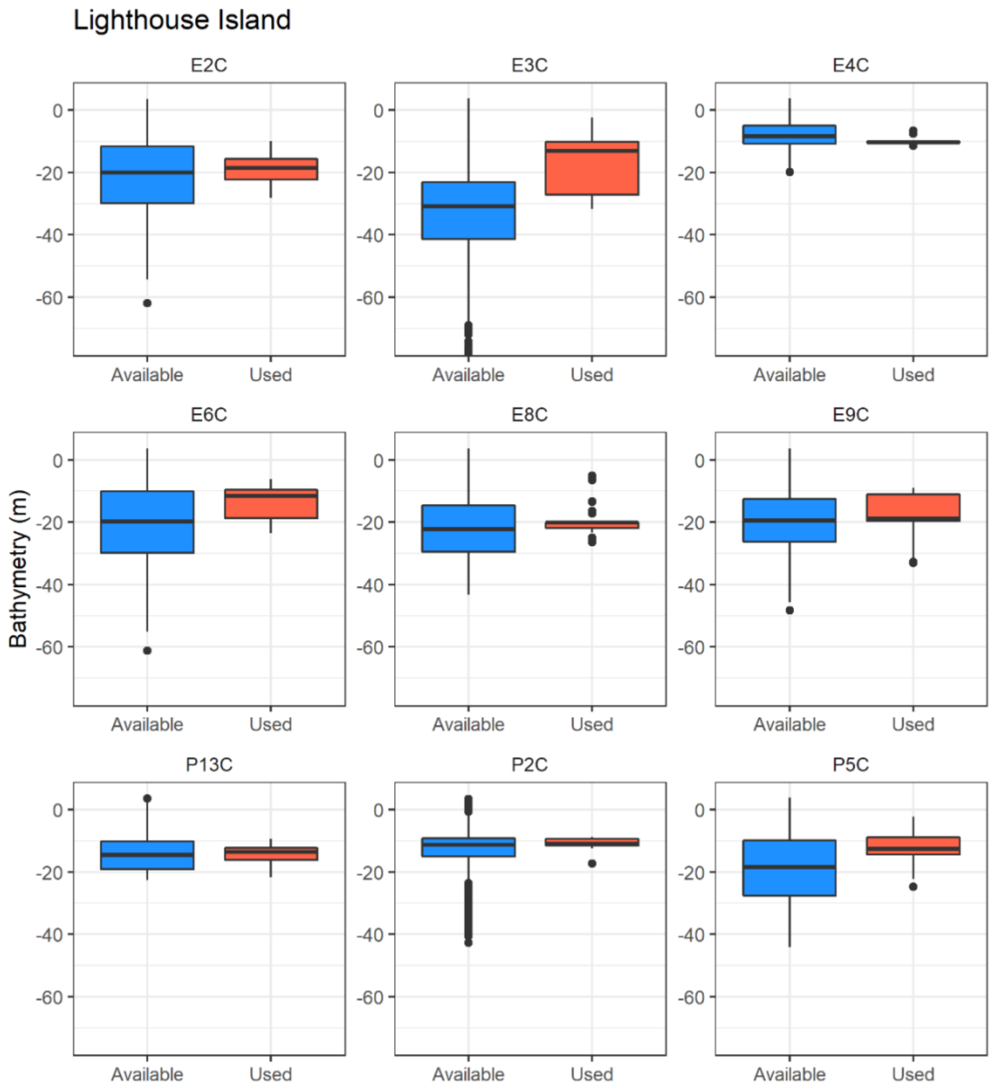

Figure A4. Distribution of bathymetry at used and available locations corresponding to individuals originating from Lighthouse Island.

A4. Individual selection of kinetic energy

Selected ocean current conditions were similar between individuals Bangor, likely related to kinetic energy being homogenous around this colony (Table 5, Figure A5). This narrow range of kinetic energies associated with Bangor may have in turn influenced the lack of consistent preference towards higher or lower energy values as identified by RSFs. The influence of kinetic energy on selection was found to be significant in seven of nine Bangor individuals, three individuals (P1B, P5B, and P11B) preferred higher kinetic energy compared to the available habitat, and four individuals (P3B, P4B, P6B, and P11B) selected lower values, indicating a lack of consistent response (Table A4). Alternatively, five individuals from Lighthouse Island selected higher kinetic energies (P5C, E2C, E3C, E6C and E9C), while the remaining four showed no preference (P2C, E4C, E8C, P13C) (Table A5). Suggesting bimodal selection of either low (<200 N/m2) or high (>400 N/m2) kinetic energies (Table A5, Figure A6).

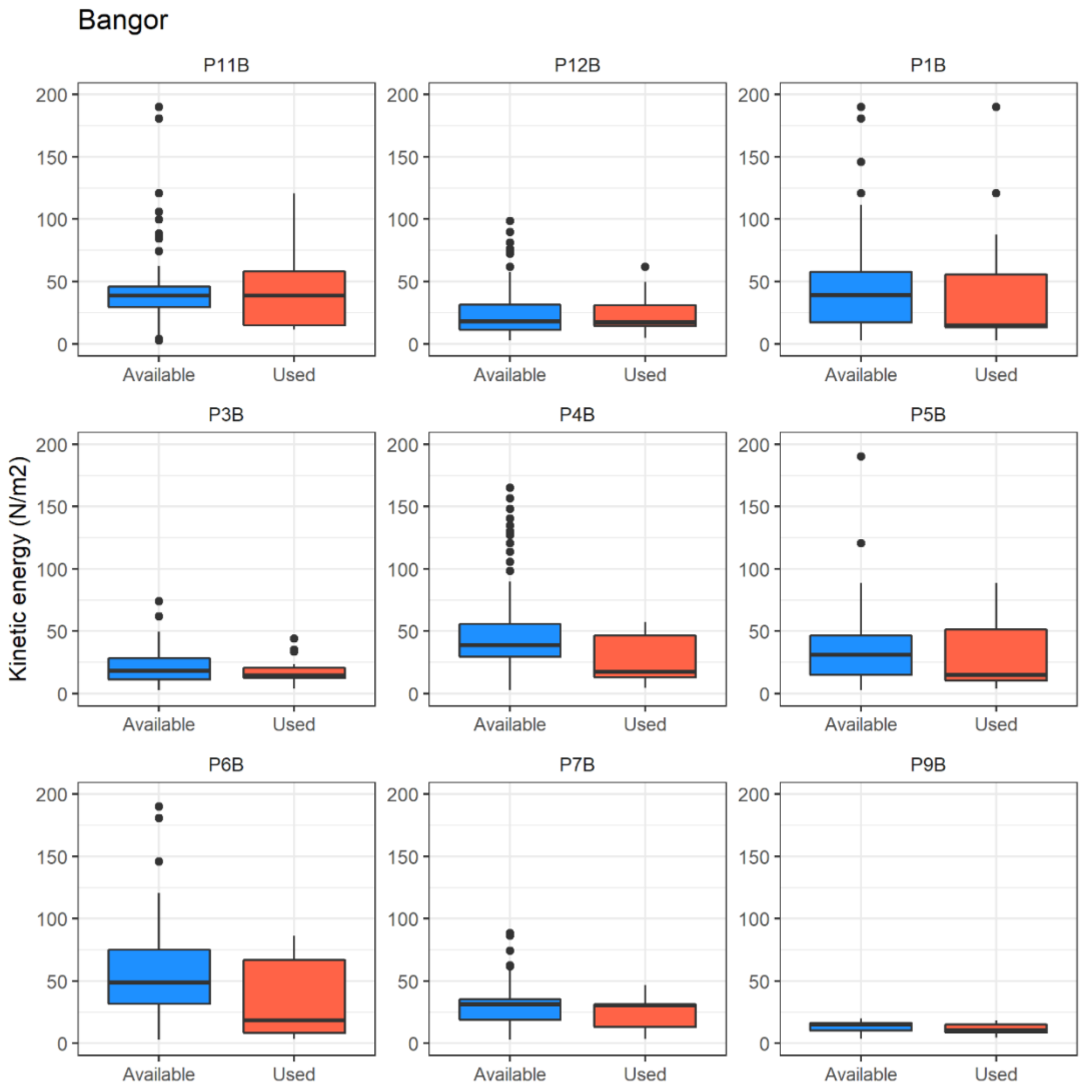

Figure A5. Distribution of kinetic energy at used and available locations corresponding to individuals originating from Bangor.

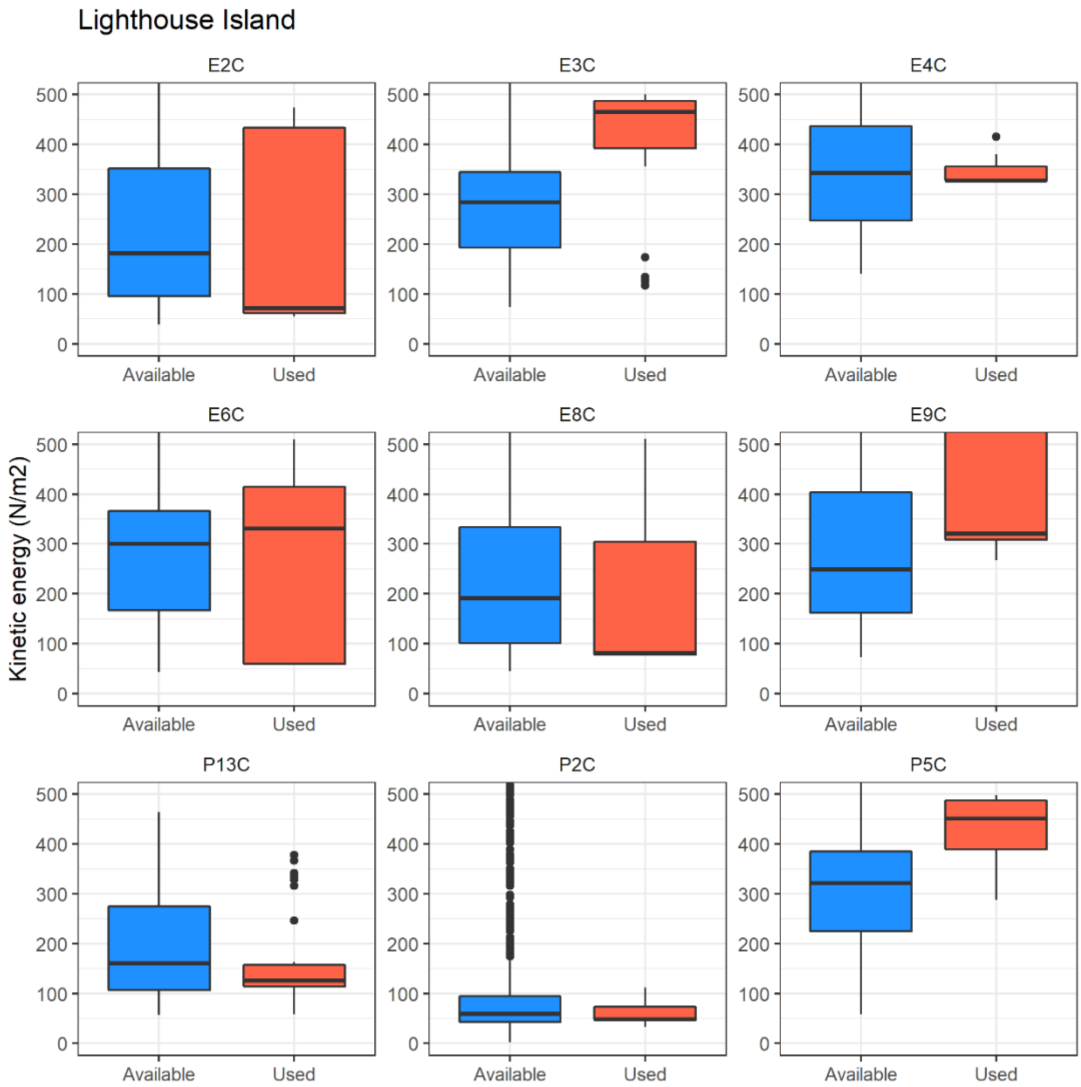

Figure A6. Distribution of kinetic energy at used and available locations corresponding to individuals originating from Lighthouse Island.

A5. Individual selection of substrate

Individuals that from Bangor were found to select fine mud in six instances, and sandy mud in four instances (Figure A7,Table A4). Selection of substrate by Individuals from Lighthouse Island reflected the varied substrate composition of the surrounding area with five different substrate types preferred across nine individuals. Muddy sand was the most commonly preferred substrate type, being selected by three individuals (Figure A8, Table A5). A range of other substrate types were selected including coarse sediment/rock (two individuals), seabed (two individuals), mixed sediment (one individual), and sand (one individual). This indicated that individual specific substrate preferences may be present.

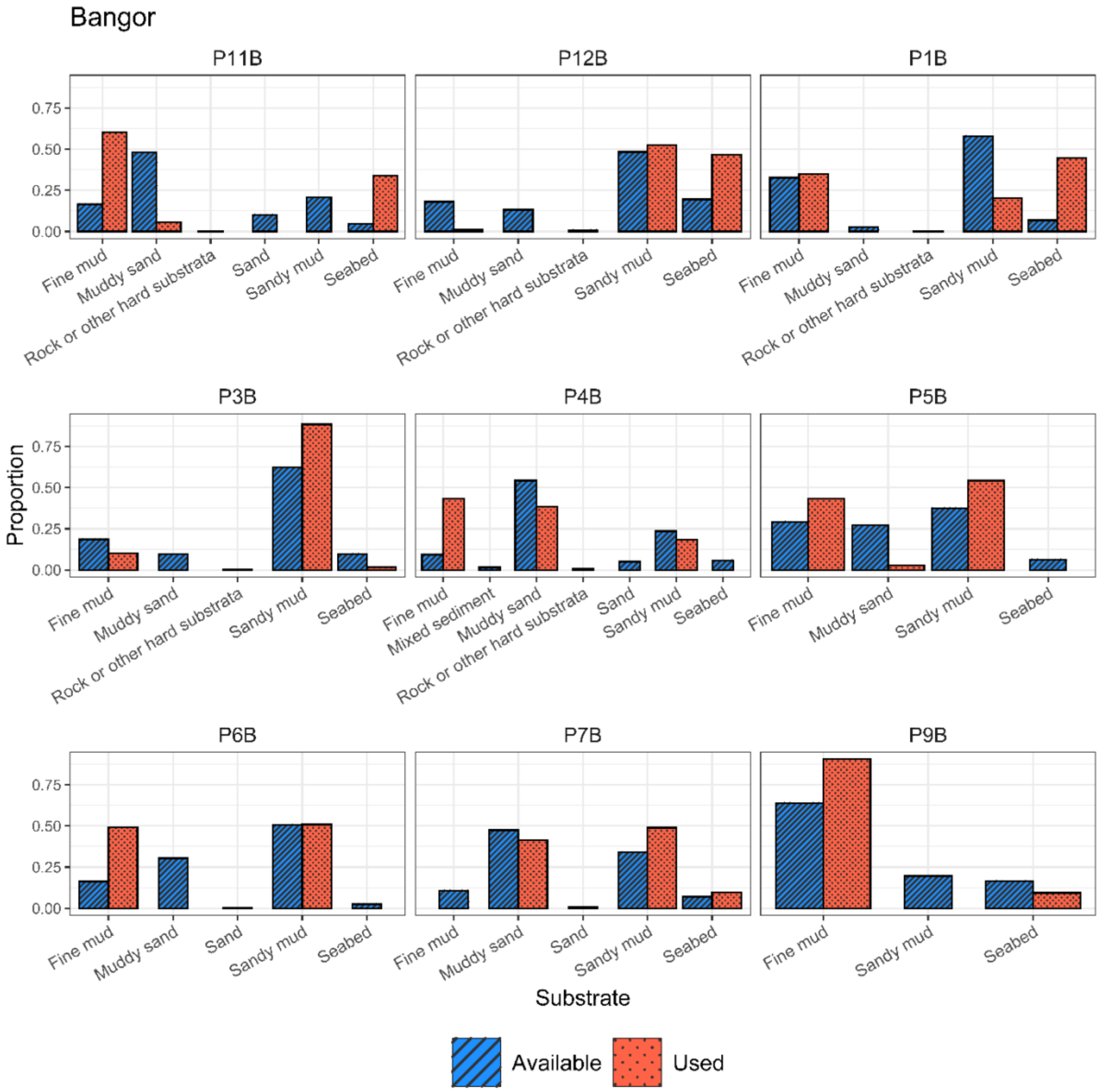

Figure A7. Proportion of used and available locations distributed among benthic substrate categories corresponding to individuals originating from Bangor.

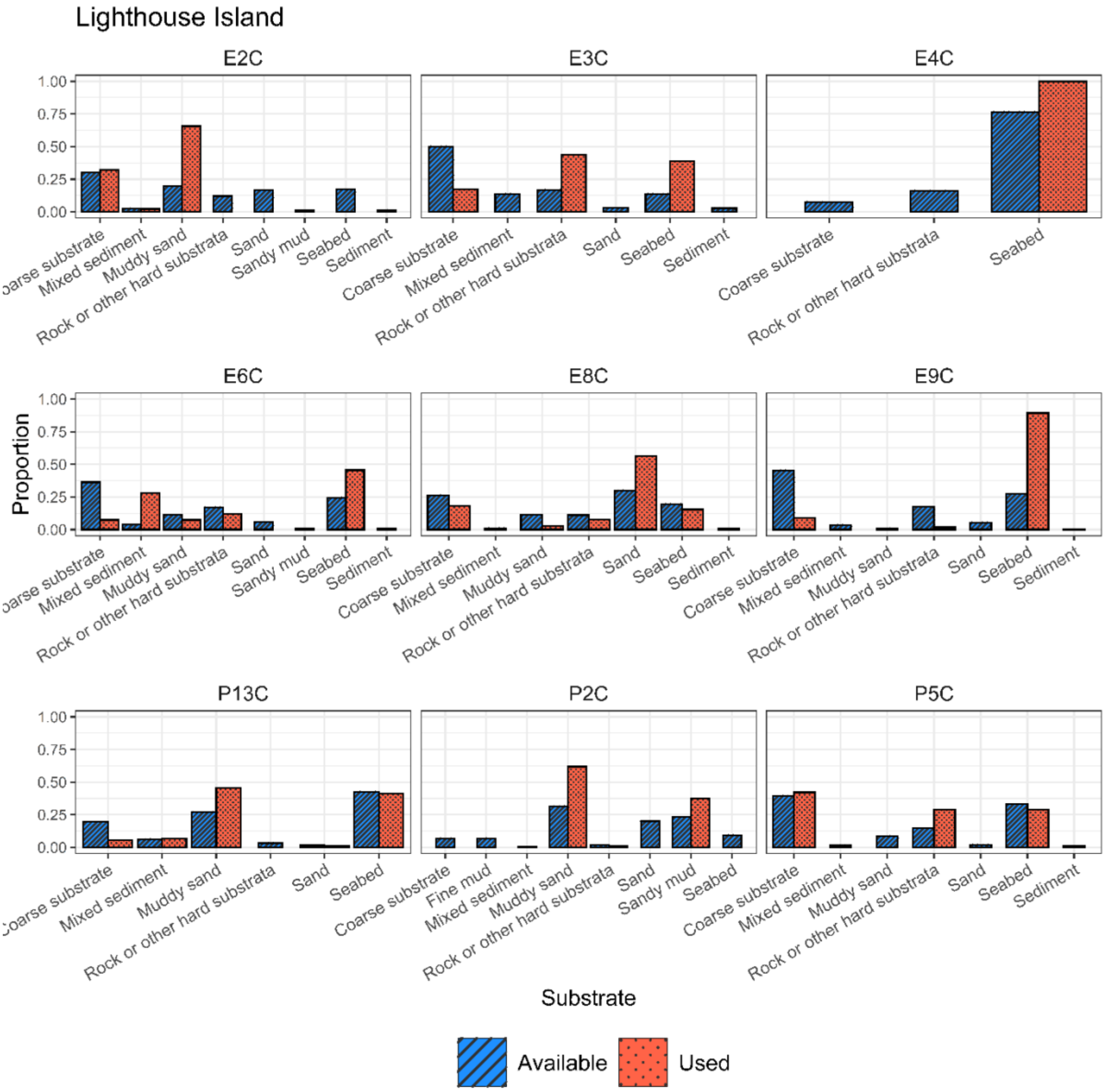

Figure A8. Proportion of used and available locations distributed among benthic substrate categories corresponding to individuals originating from Lighthouse Island.

A6. AIC model selection

Table A1. AIC ranking of Resource Selection Function (RSF) produced for each colony of Bangor and Lighthouse Island. Df= Degrees of Freedom, AICc= conditional AIC Value, Delta= difference in AIC from the model with the lowest AIC value.

	Bangor						
	ID	Bathymetry	Kinetic Energy	Substrate	df	AICc	delta AICc
1	+	NA	-0.14	+	17	25701.95	0.00
2	+	0.03	-0.15	+	18	25703.06	1.11
3	NA	NA	-0.13	+	9	25711.31	9.35
4	NA	0.03	-0.14	+	10	25712.23	10.27
5	+	NA	NA	+	16	25715.24	13.28
6	+	-0.01	NA	+	17	25717.18	15.23
7	NA	NA	NA	+	8	25722.18	20.23
8	NA	0.00	NA	+	9	25724.18	22.22
9	+	0.15	-0.33	NA	12	25896.19	194.24
10	NA	0.15	-0.30	NA	4	25896.58	194.63
11	+	NA	-0.31	NA	11	25926.03	224.07
12	NA	NA	-0.28	NA	3	25927.80	225.84
13	NA	0.13	NA	NA	3	25960.70	258.75
14	+	0.13	NA	NA	11	25967.07	265.12
15	NA	NA	NA	NA	2	25981.88	279.93
16	+	NA	NA	NA	10	25987.64	285.69
	Lighthouse Island						
1	+	0.57	0.67	+	20	12764.24	0.00
2	NA	0.53	0.71	+	12	12769.65	5.41
3	NA	NA	0.74	+	11	12826.87	62.62
4	+	NA	0.69	+	19	12834.90	70.66
5	+	0.56	NA	+	19	12837.71	73.46
6	NA	0.53	NA	+	11	12848.90	84.66
7	+	NA	NA	+	18	12907.31	143.07
8	NA	NA	NA	+	10	12909.07	144.83
9	+	0.65	NA	NA	11	12965.71	201.47
10	NA	0.61	NA	NA	3	12967.46	203.22
11	+	0.65	0.01	NA	12	12967.71	203.47
12	NA	0.59	0.05	NA	4	12968.45	204.21
13	NA	NA	0.08	NA	3	13081.28	317.04
14	NA	NA	NA	NA	2	13082.75	318.51
15	+	NA	0.11	NA	11	13094.92	330.67
16	+	NA	NA	NA	10	13097.87	333.63

Table A2. AIC ranking of Resource Selection Function (RSF) produced for each colony of Bangor. Df= Degrees of Freedom, AICc= conditional AIC Value, Delta= difference in AIC from the model with the lowest AIC value.

	Bathymetry	Kinetic Energy	Substrate	df	AICc	delta AICc
P1B						
1	-0.23	0.31	+	7.00	4421.45	0.00
2	NA	0.22	+	6.00	4433.24	11.79
3	-0.15	NA	+	6.00	4433.99	12.54
4	NA	NA	+	5.00	4438.75	17.30
5	0.23	-0.37	NA	3.00	4660.00	238.55
6	NA	-0.29	NA	2.00	4675.84	254.40
7	0.20	NA	NA	2.00	4677.17	255.72
8	NA	NA	NA	1.00	4686.05	264.60
P3B						
1	-0.27	-0.60	+	7.00	4334.42	0.00
2	NA	-0.68	+	6.00	4335.06	0.64
3	-0.63	NA	+	6.00	4364.85	30.43
4	NA	NA	+	5.00	4379.92	45.50
5	-0.86	-0.18	NA	3.00	4396.06	61.64
6	-0.93	NA	NA	2.00	4398.83	64.41
7	NA	-0.30	NA	2.00	4440.74	106.32
8	NA	NA	NA	1.00	4455.20	120.78
P4B						
1	NA	-0.99	+	8.00	1825.15	0.00
2	0.25	-1.00	+	9.00	1825.69	0.55
3	NA	NA	+	7.00	1855.81	30.67
4	0.10	NA	+	8.00	1857.43	32.28
5	NA	-1.05	NA	2.00	1876.03	50.89
6	-0.17	-1.09	NA	3.00	1876.83	51.68
7	NA	NA	NA	1.00	1922.32	97.17
8	0.00	NA	NA	2.00	1924.32	99.18
P5B						
1	-1.20	0.29	+	6.00	4300.98	0.00
2	-0.81	NA	+	5.00	4310.02	9.03
3	NA	NA	+	4.00	4343.93	42.95
4	NA	-0.09	+	5.00	4344.29	43.31
5	-0.66	NA	NA	2.00	4423.79	122.81
6	-0.63	-0.07	NA	3.00	4425.21	124.23
7	NA	-0.17	NA	2.00	4451.84	150.86
8	NA	NA	NA	1.00	4454.15	153.17

Table A2. continued

	Bathymetry	Kinetic Energy	Substrate	df	AICc	delta AICc
P6B						
1	-0.20	-0.53	+	7.00	2465.86	0.00
2	NA	-0.65	+	6.00	2467.45	1.59
3	-0.43	NA	+	6.00	2486.23	20.37
4	NA	NA	+	5.00	2506.25	40.38
5	NA	-0.67	NA	2.00	2584.40	118.54
6	0.05	-0.69	NA	3.00	2586.15	120.29
7	-0.15	NA	NA	2.00	2619.76	153.89
8	NA	NA	NA	1.00	2619.95	154.09
P7B						
1	-0.20	-0.53	+	7.00	2465.86	0.00
2	NA	-0.65	+	6.00	2467.45	1.59
3	-0.43	NA	+	6.00	2486.23	20.37
4	NA	NA	+	5.00	2506.25	40.38
5	NA	-0.67	NA	2.00	2584.40	118.54
6	0.05	-0.69	NA	3.00	2586.15	120.29
7	-0.15	NA	NA	2.00	2619.76	153.89
8	NA	NA	NA	1.00	2619.95	154.09
P9B						
1	-0.78	NA	+	4.00	744.48	0.00
2	NA	NA	+	3.00	745.83	1.35
3	-0.82	-0.12	+	5.00	746.08	1.60
4	NA	-0.10	+	4.00	747.54	3.06
5	-0.37	-0.34	NA	3.00	756.63	12.15
6	NA	-0.35	NA	2.00	756.65	12.17
7	-0.35	NA	NA	2.00	758.55	14.07
8	NA	NA	NA	1.00	758.68	14.20
P11B						
1	0.57	0.23	+	8.00	1105.25	0.00
2	0.62	NA	+	7.00	1112.19	6.94
3	NA	0.28	+	7.00	1129.59	24.33
4	NA	NA	+	6.00	1142.54	37.29
5	0.72	0.41	NA	3.00	1166.06	60.80
6	0.62	NA	NA	2.00	1188.12	82.87
7	NA	0.35	NA	2.00	1266.19	160.94
8	NA	NA	NA	1.00	1274.89	169.64
P12B						
1	0.16	NA	+	6.00	2281.27	0.00
2	0.14	0.08	+	7.00	2282.68	1.41
3	NA	NA	+	5.00	2282.92	1.65
4	NA	0.13	+	6.00	2283.18	1.91
5	0.35	NA	NA	2.00	2340.09	58.81
6	0.35	-0.06	NA	3.00	2341.75	60.47
7	NA	NA	NA	1.00	2359.23	77.96
8	NA	0.03	NA	2.00	2361.13	79.86

Table A3. AIC ranking of Resource Selection Function (RSF) produced for each colony of Lighthouse Island. Df= Degrees of Freedom, AICc= conditional AIC Value, Delta= difference in AIC from the model with the lowest AIC value.

	Bathymetry	Kinetic Energy	Substrate	df	AICc	delta AICc
			E2C			
1	0.40	2.16	+	10.00	1988.59	0.00
2	NA	2.13	+	9.00	1993.66	5.07
3	0.35	NA	+	9.00	2054.65	66.05
4	NA	NA	+	8.00	2057.96	69.37
5	0.27	-0.28	NA	3.00	2185.64	197.05
6	NA	-0.29	NA	2.00	2190.12	201.53
7	0.26	NA	NA	2.00	2190.39	201.80
8	NA	NA	NA	1.00	2194.80	206.21
			E3C			
1	1.39	0.82	NA	3.00	887.87	0.00
2	0.83	0.79	+	8.00	890.52	2.65
3	NA	1.09	+	7.00	891.28	3.41
4	NA	1.55	NA	2.00	895.99	8.12
5	2.44	NA	NA	2.00	896.74	8.87
6	1.93	NA	+	7.00	899.93	12.06
7	NA	NA	+	6.00	926.37	38.50
8	NA	NA	NA	1.00	969.21	81.34
			E4C			
1	NA	NA	+	3.00	253.69	0.00
2	NA	NA	NA	1.00	255.35	1.65
3	-0.11	NA	+	4.00	255.80	2.11
4	NA	0.09	+	4.00	255.80	2.11
5	NA	0.06	NA	2.00	257.39	3.70
6	0.04	NA	NA	2.00	257.42	3.72
7	-0.25	0.20	+	5.00	257.76	4.07
8	0.00	0.06	NA	3.00	259.53	5.83
			E6C			
1	0.66	0.39	+	10.00	1499.84	0.00
2	0.57	NA	+	9.00	1502.26	2.42
3	NA	NA	+	8.00	1525.65	25.81
4	NA	0.03	+	9.00	1527.67	27.83
5	0.82	NA	NA	2.00	1566.92	67.08
6	0.83	-0.04	NA	3.00	1568.78	68.95
7	NA	NA	NA	1.00	1600.40	100.56
8	NA	0.00	NA	2.00	1602.41	102.58

Table A3. continued

	Bathymetry	Kinetic Energy	Substrate	df	AICc	delta AICc
E8C						
1	1.00	NA	+	8.00	898.98	0.00
2	0.99	-0.17	+	9.00	900.71	1.73
3	0.44	-0.41	NA	3.00	914.36	15.38
4	0.34	NA	NA	2.00	918.71	19.74
5	NA	NA	+	7.00	919.21	20.23
6	NA	-0.33	NA	2.00	919.77	20.80
7	NA	-0.29	+	8.00	920.48	21.50
8	NA	NA	NA	1.00	921.52	22.54
E9C						
1	-0.96	1.20	+	9.00	1204.56	0.00
2	NA	0.79	+	8.00	1216.75	12.19
3	-0.45	NA	+	8.00	1233.45	28.88
4	NA	NA	+	7.00	1235.18	30.62
5	-0.56	1.50	NA	3.00	1262.55	57.99
6	NA	1.04	NA	2.00	1268.46	63.90
7	0.38	NA	NA	2.00	1315.47	110.91
8	NA	NA	NA	1.00	1320.92	116.35
P2C						
1	0.36	-0.60	+	10.00	2643.04	0.00
2	0.40	NA	+	9.00	2643.72	0.68
3	NA	-0.72	+	9.00	2644.85	1.81
4	NA	NA	+	8.00	2647.02	3.98
5	0.50	-0.60	NA	3.00	2733.96	90.92
6	NA	-0.88	NA	2.00	2745.29	102.25
7	0.58	NA	NA	2.00	2746.90	103.85
8	NA	NA	NA	1.00	2771.01	127.97
P5C						
1	1.30	2.13	+	9.00	810.59	0.00
2	NA	2.35	+	8.00	833.64	23.05
3	0.34	1.36	NA	3.00	834.84	24.25
4	NA	1.63	NA	2.00	835.53	24.95
5	1.38	NA	+	8.00	857.26	46.68
6	0.87	NA	NA	2.00	871.95	61.37
7	NA	NA	+	7.00	892.12	81.54
8	NA	NA	NA	1.00	894.06	83.48
P13C						
1	NA	-0.26	+	7.00	2149.35	0.00
2	NA	NA	+	6.00	2149.99	0.64
3	-0.05	-0.28	+	8.00	2151.22	1.86
4	0.02	NA	+	7.00	2152.00	2.65
5	NA	-0.33	NA	2.00	2162.35	13.00
6	0.03	-0.33	NA	3.00	2164.29	14.94
7	NA	NA	NA	1.00	2168.67	19.31
8	0.00	NA	NA	2.00	2170.67	21.32

A7. Resource selection function results

Table A4. GLM results for colonies of Bangor and Lighthouse Island with Individual random effect. Significant p-values (<0.05) indicated in bold and with asterisk (*). Where non-significant p-values are shown this indicates that the independent variable is not influential in classifying a sample as used or available.

	Bangor				
	term	estimate	std.error	z-statistic	p.value
1.00	(Intercept)	-10.50	0.09	-115.28	**0.00***
2.00	Bathymetry	0.06	0.06	1.05	0.29
3.00	Kinetic Energy	-0.15	0.04	-3.62	**0.00***
4.00	Mixed sediment	-14.14	845.80	-0.02	0.99
5.00	Muddy sand	-1.34	0.12	-11.02	**0.00***
6.00	Rock	-12.54	324.19	-0.04	0.97
7.00	Sand	-15.04	436.88	-0.03	0.97
8.00	Sandy mud	-0.23	0.07	-3.06	**0.00***
9.00	Seabed	0.28	0.11	2.52	**0.01***
	Lighthouse Island				
1.00	(Intercept)	-11.40	0.15	-77.62	**0.00***
2.00	Bathymetry	0.54	0.07	7.45	**0.00***
3.00	Kinetic Energy	0.73	0.08	8.82	**0.00***
4.00	Fine mud	-22.35	48425.30	0.00	1.00
5.00	Mixed sediment	1.63	0.25	6.60	**0.00***
6.00	Muddy sand	1.99	0.19	10.49	**0.00***
7.00	Rock	-0.90	0.23	-4.01	**0.00***
8.00	Sand	0.45	0.26	1.74	0.08
9.00	Sandy mud	1.68	0.25	6.59	**0.00***
10.00	Seabed	-0.01	0.17	-0.07	0.94
11.00	Sediment	-14.80	974.24	-0.02	0.99

Table A5. GLM results of individuals from Bangor. Significant p-values (<0.05) indicated in bold and with asterisk (*). Where non-significant p-values are shown this indicates that the independent variable is not influential in classifying a sample as used or available.

term	estimate	se	z-statistic	p-value
P1B				
Bathymetry	-0.47	0.14	-3.40	**0.00***
Kinetic energy	0.35	0.08	4.14	**0.00***
Fine mud	-11.00	0.14	-81.35	**0.00***
Muddy sand	-24.33	210.90	-0.12	0.91
Rock	-23.11	1551.07	-0.01	0.99
Sandy mud	-12.21	0.17	-70.14	**0.00***
Seabed	-8.70	0.13	-68.41	**0.00***
P3B				
Bathymetry	-0.37	0.24	-1.55	0.12
Kinetic energy	-0.65	0.13	-5.14	**0.00***
Fine mud	-12.19	0.27	-45.78	**0.00***
Muddy sand	-24.31	193.06	-0.13	0.90
Rock	-23.80	1778.20	-0.01	0.99
Sandy mud	-10.56	0.12	-88.60	**0.00***
Seabed	-12.97	0.61	-21.15	**0.00***
P4B				
Bathymetry	0.31	0.24	1.25	0.21
Kinetic energy	-1.04	0.22	-4.79	**0.00***
Fine mud	-10.03	0.27	-36.82	**0.00***
Mixed sediment	-25.29	1129.62	-0.02	0.98
Muddy sand	-11.02	0.18	-60.19	**0.00***
Rock	-26.33	1714.82	-0.02	0.99
Sand	-26.24	648.06	-0.04	0.97
Sandy mud	-11.70	0.30	-38.95	**0.00***
Seabed	-27.51	586.36	-0.05	0.96
P5B				
Bathymetry	-2.95	0.46	-6.35	**0.00***
Kinetic energy	0.35	0.10	3.66	**0.00***
Fine mud	-11.06	0.18	-60.24	**0.00***
Muddy sand	-14.43	0.51	-28.23	**0.00***
Sandy mud	-11.40	0.20	-57.11	**0.00***
Seabed	-24.02	219.28	-0.11	0.91

Table A5. Continued.

term	estimate	std.error	statistic	p.value
P6B				
Bathymetry	-0.38	0.21	-1.86	0.06
Kinetic energy	-0.54	0.12	-4.31	**0.00***
Fine mud	-9.93	0.16	-61.48	**0.00***
Muddy sand	-26.61	242.18	-0.11	0.91
Sand	-26.86	4216.26	-0.01	0.99
Sandy mud	-10.68	0.15	-70.41	**0.00***
Seabed	-26.99	837.31	-0.03	0.97
P7B				
Bathymetry	0.34	0.15	2.27	**0.02***
Kinetic energy	-0.30	0.12	-2.51	**0.01***
Fine mud	-26.32	319.04	-0.08	0.93
Muddy sand	-10.82	0.15	-73.97	**0.00***
Sand	-25.94	1333.11	-0.02	0.98
Sandy mud	-10.47	0.13	-82.29	**0.00***
Seabed	-11.30	0.38	-30.05	**0.00***
P9B				
Bathymetry	-1.65	1.04	-1.58	0.11
Kinetic energy	-0.11	0.17	-0.67	0.50
Fine mud	-11.33	0.57	-19.78	**0.00***
Sandy mud	-27.19	530.96	-0.05	0.96
Seabed	-11.00	0.58	-18.97	**0.00***
P11B				
Bathymetry	1.05	0.19	5.46	**0.00***
Kinetic energy	0.28	0.08	3.26	**0.00***
Fine mud	-9.75	0.20	-48.11	**0.00***
Muddy sand	-12.60	0.59	-21.46	**0.00***
Rock	-30.53	6951.43	0.00	1.00
Sand	-26.44	859.24	-0.03	0.98
Sandy mud	-26.70	575.21	-0.05	0.96
Seabed	-10.11	0.47	-21.58	**0.00***
P12B				
Bathymetry	0.21	0.13	1.65	0.10
Kinetic energy	0.08	0.10	0.81	0.42
Fine mud	-13.39	1.00	-13.35	**0.00***
Muddy sand	-26.19	393.00	-0.07	0.95
Rock	-26.53	1585.56	-0.02	0.99
Sandy mud	-10.52	0.15	-68.48	**0.00***
Seabed	-9.85	0.16	-59.79	**0.00***

Table A6. GLM results of individuals Lighthouse Island. Significant p-values (<0.05) indicated in bold and with asterisk (*). Where non-significant p-values are shown this indicates that the independent variable is not influential in classifying a sample as used or available.

	Estimate	se	z-statistic	p-value
	P2C			
Bathymetry	0.38	0.20	1.94	0.05
Kinetic energy	-0.65	0.40	-1.62	0.10
Coarse substrate	-25.84	798.73	-0.03	0.97
Fine mud	-27.71	806.53	-0.03	0.97
Mixed sediment	-27.35	3096.71	-0.01	0.99
Muddy sand	-10.33	0.20	-52.04	**0.00***
Rock	-9.17	1.71	-5.38	**0.00***
Sand	-27.20	466.17	-0.06	0.95
Sandy mud	-10.63	0.21	-49.66	**0.00***
Seabed	-26.79	648.26	-0.04	0.97
	P5C			
Bathymetry	1.39	0.28	4.95	**0.00***
Kinetic energy	2.17	0.40	5.47	**0.00***
Coarse substrate	-10.12	0.30	-33.60	**0.00***
Mixed sediment	-23.55	1834.03	-0.01	0.99
Muddy sand	-22.69	732.98	-0.03	0.98
Rock	-13.93	0.72	-19.34	**0.00***
Sand	-23.96	1486.51	-0.02	0.99
Seabed	-13.54	0.62	-21.78	**0.00***
Sediment	-26.18	2335.45	-0.01	0.99
	P13C			
Bathymetry	-0.06	0.14	-0.41	0.68
Kinetic energy	-0.28	0.17	-1.66	0.10
Coarse substrate	-12.16	0.46	-26.26	**0.00***
Mixed sediment	-10.94	0.44	-25.10	**0.00***
Muddy sand	-10.55	0.26	-41.25	**0.00***
Rock	-23.87	292.77	-0.08	0.94
Sand	-11.29	1.03	-11.00	**0.00***
Seabed	-10.59	0.21	-50.30	**0.00***
	E2C			
Bathymetry	0.42	0.16	2.68	**0.01***
Kinetic energy	2.22	0.31	7.21	**0.00***
Coarse substrate	-12.06	0.39	-31.26	**0.00***
Mixed sediment	-9.97	0.73	-13.63	**0.00***
Muddy sand	-7.59	0.32	-23.88	**0.00***
Rock	-30.65	615.03	-0.05	0.96
Sand	-25.31	554.69	-0.05	0.96
Sandy mud	-25.35	2446.01	-0.01	0.99
Seabed	-30.02	501.01	-0.06	0.95
Sediment	-29.45	2057.58	-0.01	0.99

Table A6. Continued.

	estimate	se	z-statistic	p-value
	E3C			
Bathymetry	0.85	0.51	1.66	0.10
Kinetic energy	0.81	0.27	3.03	**0.00***
Coarse substrate	-12.03	0.40	-30.36	**0.00***
Mixed sediment	-24.30	547.97	-0.04	0.96
Rock	-11.18	0.45	-25.11	**0.00***
Sand	-26.34	1193.66	-0.02	0.98
Seabed	-10.97	0.46	-23.99	**0.00***
Sediment	-26.74	1257.69	-0.02	0.98
	E4C			
Bathymetry	-0.31	0.60	-0.52	0.60
Kinetic energy	0.23	0.44	0.52	0.60
Coarse substrate	-26.57	1721.08	-0.02	0.99
Rock	-26.36	1164.74	-0.02	0.98
Seabed	-10.34	0.36	-28.68	**0.00***
	E6C			
Bathymetry	0.68	0.14	5.03	**0.00***
Kinetic energy	0.40	0.19	2.04	**0.04***
Coarse substrate	-12.01	0.45	-26.73	**0.00***
Mixed sediment	-7.99	0.33	-24.56	**0.00***
Muddy sand	-10.84	0.53	-20.64	**0.00***
Rock	-11.83	0.44	-26.95	**0.00***
Sand	-24.67	423.71	-0.06	0.95
Sandy mud	-25.49	1271.40	-0.02	0.98
Seabed	-10.81	0.26	-41.66	**0.00***
Sediment	-24.96	1142.55	-0.02	0.98
	E8C			
Bathymetry	1.05	0.23	4.57	**0.00***
Kinetic energy	-0.18	0.30	-0.59	0.55
Coarse substrate	-10.91	0.38	-28.37	**0.00***
Mixed sediment	-26.23	763.06	-0.03	0.97
Muddy sand	-12.99	1.06	-12.30	**0.00***
Rock	-11.65	0.81	-14.42	**0.00***
Sand	-9.91	0.37	-27.09	**0.00***
Seabed	-12.01	0.56	-21.36	**0.00***
Sediment	-22.99	891.49	-0.03	0.98
	E9C			
Bathymetry	-1.01	0.27	-3.70	**0.00***
Kinetic energy	1.23	0.26	4.80	**0.00***
Coarse substrate	-12.89	0.57	-22.53	**0.00**
Mixed sediment	-23.12	580.02	-0.04	0.97
Muddy sand	-23.76	1142.66	-0.02	0.98
Rock	-13.69	1.02	-13.37	**0.00***
Sand	-24.36	471.13	-0.05	0.96
Seabed	-10.02	0.25	-40.63	**0.00***
Sediment	-25.58	2557.29	-0.01	0.99

A8. Individual dive depth time series

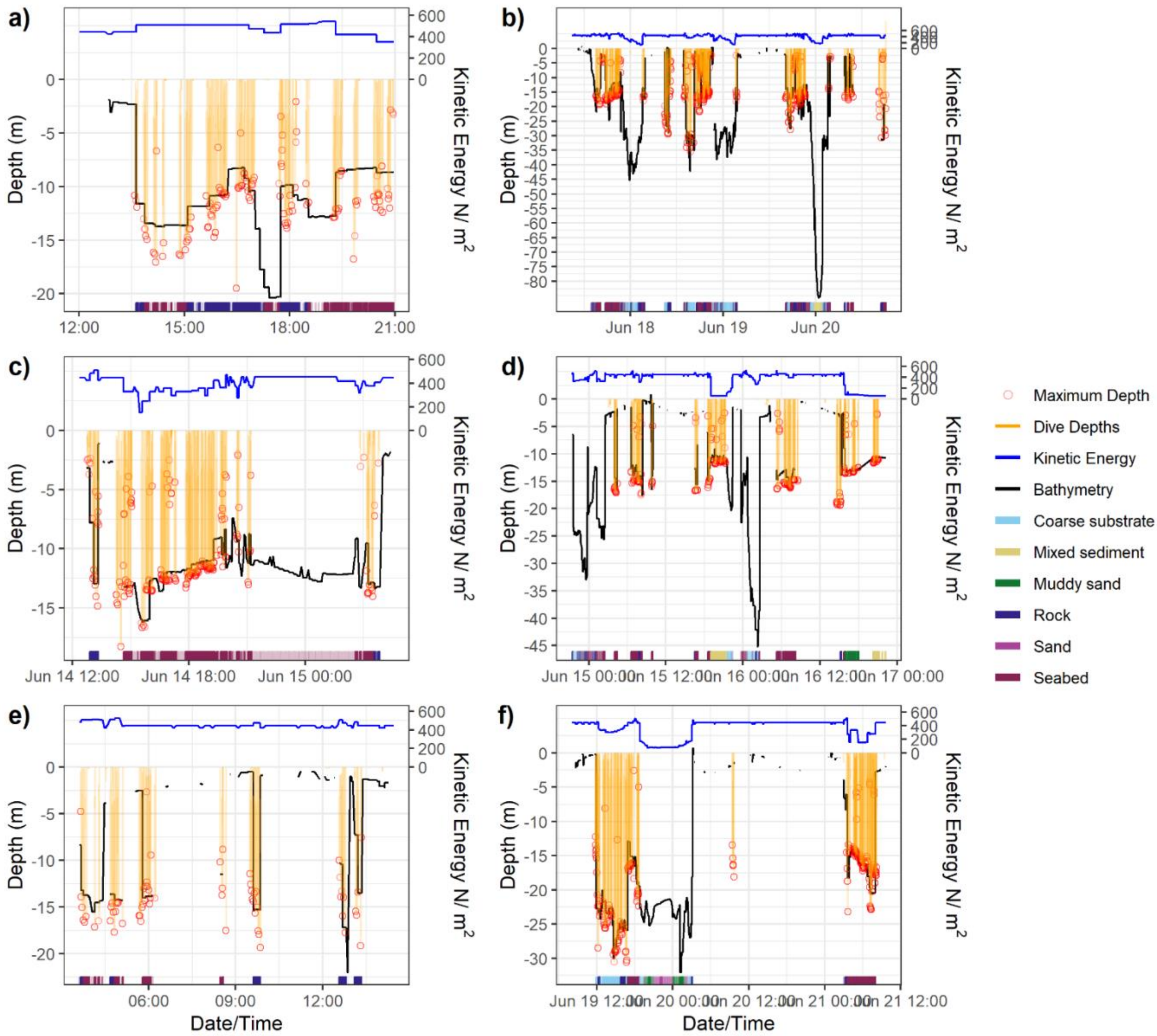

Figure A9. Time series dive depths in relation to maximum bathymetry (m) and kinetic energy (N/m²) for individuals a) E1C, b) E3C, c) E4C, d) E6C e) E7C and f) E8C.

A9. Location of dives

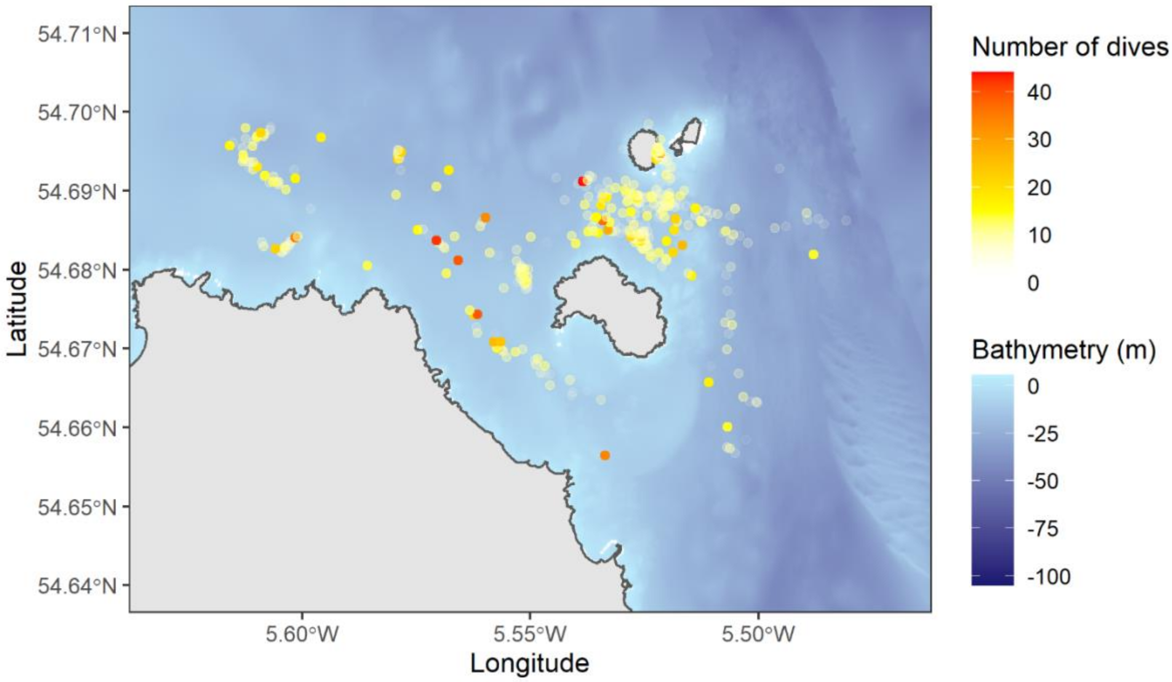

Figure A10. Number dives in relation to maximum bathymetry (m) for all individuals combined.

A10. Data archiving and access

All tracking data presented here will be stored on the Movebank online tracking data repository (Movebank.org), with full unrestricted access rights provided.

All tracking data from 21 individual birds (Table A7) will be stored within two "Studies" within Movebank, each specified by tagging colony, these are named as "BTO - Copeland 2021 – Black Guillemot" (Table A8) and "BTO - Bangor 2021 – Black Guillemot" (Table A9). Data fields contained within each tag type may differ between Pathtrack (Table A10) and Ecotone (Table A11) due to differences in hardware used by the manufacturers. Data stored within Movebank will have undergone an initial filtering step to exclude successive datapoints of unfeasibly fast speeds (>50 m/s).

Table A7. Composition of tag data

Tag type	Model type	Data type	Tags (n)	Deployed from Bangor (n)	Deployed on Lighthouse Island (n)
Ecotone	Uria-100	GPS/TDR	8	0	8
Pathtrack	nanofix-geo	GPS	13	10	3

Table A8. Summary of GPS data for Study: *BTO - Copeland 2021 – Black Guillemot*

Study Statistics	**Results**
Number of tags (n)	11
Time of First Deployed Location (Date, Time)	2021-06-14 12:26:55
Time of Last Deployed Location (Date, Time)	2021-06-22 09:28:13
Number of Deployed Locations (n)	4308

Table A9. Summary of GPS data for Study: *BTO - Bangor 2021 – Black Guillemot*

Study Statistic	**Results**
Number of tags (n)	10
Time of First Deployed Location (Date, Time)	2021-06-09 19:42:00
Time of Last Deployed Location (Date, Time)	2021-06-29 14:14:48
Number of Deployed Locations (n)	3109

Table A10. Pathtrack data fields. Replicated from the Movebank Attribute Dictionary https://www.movebank.org/cms/movebank-content/movebank-attribute-dictionary

Field	**Description**
Event Id	An identifier for the set of values associated with each event, i.e. sensor measurement. A unique event ID is assigned to every time-location or other time-measurement record in Movebank.
Visible	Determines whether an event is visible on the Movebank map.
Timestamp	The date and time corresponding to a sensor measurement or an estimate derived from sensor measurements
Location long	Longitude- WGS84
Location lat	Latitude-WGS84
Battery charging current	The battery charging current reported by the tag.
GPS: horizontal accuracy estimate	A horizontal (in)accuracy estimate, calculated by the GPS module.
GPS: satellite count	The number of GPS satellites used to estimate the location.
Height above ellipsoid	The estimated height above the ellipsoid, typically estimated by the tag.
Height raw	Raw values for the height of the tag above ellipsoid or mean sea level, typically estimated by the tag.
Sensor type	The type of sensor with which data were collected.
Individual taxon canonical name	The scientific name of the species on which the tag was deployed, as defined by the Integrated Taxonomic Information System (ITIS, www.itis.gov).
Tag local identifier	A unique identifier for the tag, provided by the data owner.
Individual local identifier	An individual identifier for the animal, provided by the data owner.
Study name	The name of the study in Movebank.

Table A11. Ecotone data fields. Replicated from the Movebank Attribute Dictionary https://www.movebank.org/cms/movebank-content/movebank-attribute-dictionary

Field	Description
Event id	An identifier for the set of values associated with each event, i.e. sensor measurement. A unique event ID is assigned to every time-location or other time-measurement record in Movebank.
Visible	Determines whether an event is visible on the Movebank map.
Timestamp	The date and time corresponding to a sensor measurement or an estimate derived from sensor measurements
Location long	Longitude- WGS84
Location lat	Latitude-WGS84
Bar:barometric depth	The barometric water pressure depth.
Bar:barometric pressure	The barometric air or water pressure.
Battery charging current	The battery charging current reported by the tag.
External temperature	The temperature measured by the tag (Celcius).
GPS:dop	Dilution of precision provided by the GPS.
GPS:hdop	Horizontal dilution of precision provided by the GPS.
GPS:horizontal-accuracy-estimate	A horizontal (in)accuracy estimate, calculated by the GPS module.
GPS:satellite-count	The number of GPS satellites used to estimate the location.
GPS:vdop	Vertical dilution of precision provided by the GPS.
Ground speed	The estimated ground speed provided by the sensor or calculated between consecutive locations.
Heading	The direction in which the tag is moving, in decimal degrees clockwise from north, as provided by the sensor or calculated between consecutive locations.
Height above ellipsoid	The estimated height above the ellipsoid, typically estimated by the tag. If altitudes are calculated as height above mean sea level, use 'height above mean sea level'.
Height raw	Raw values for the height of the tag above ellipsoid or mean sea level, typically estimated by the tag. Values are stored as raw text values because non-numeric characters are used or processing is required to derive the correct height estimate. Best practice is to define values in the reference data.
Underwater time	The amount of time the tag was underwater during the measurement period.
Vertical error numerical	An estimate of the vertical error of the location.
Sensor type	The type of sensor with which data were collected.
Individual taxon canonical name	The scientific name of the species on which the tag was deployed, as defined by the Integrated Taxonomic Information System (ITIS, www.itis.gov).
Tag local identifier	A unique identifier for the tag, provided by the data owner.
Individual local identifier	An individual identifier for the animal, provided by the data owner.
Study name	The name of the study in Movebank.
Underwater time	Dive duration

Project partners

Citation

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www.mpa-management.eu