

Fine scale foraging habitat selection by two diving central place foragers in the Northeast Atlantic

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Abstract

1. Understanding the animal-habitat relationship at local scale is crucial in ecology, particularly to develop strategies for wildlife management and conservation. As this relationship is governed by environmental features and intra and inter-specific interactions, habitat selection of a population may vary locally between its core and edges. 2. This is particularly true for central place foragers, such as grey and harbour seals, whose trends in numbers vary among different regions in the Northeast Atlantic. Here, we aimed at studying how foraging habitat selection may vary locally with the influence of population trends and physical habitat features 3. Using GPS/GSM tags deployed in grey and harbour seal colonies of contrasting sizes, we investigate spatial patterns and foraging habitat selection by comparing trip characteristics and home range similarities, and fitting GAMM to the seal distribution and environmental data respectively. 4. We show that grey seal foraging habitat selection and spatial patterns differed markedly between regions. Grey seals may select environmental characteristics for their foraging habitat accounting for local differences in prey consumed. Spatial patterns were different might depend on local seal density and regional productivity, located from inshore to offshore areas for the limit ranges and core population respectively. Our results on foraging habitat selection reflected the coastal and sedentary behaviour of harbour seals. We found no difference in spatial patterns between colonies, except for the Inner Hebrides where seals foraged further, potentially reflecting density dependence pressure, as the number in this colony is higher. 5. These results suggest that local conditions might have a strong influence on population spatial ecology, highlighting as well the relevance of studying foraging habitat selection based on foraging behaviour at fine geographical scale, particularly if species are managed within regional units.

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ABSTRACT

1. Understanding the animal-habitat relationship at local scale is crucial in ecology, particularly to develop strategies for wildlife management and conservation. As this relationship is governed by environmental features and intra and inter-specific interactions, habitat selection of a population may vary locally between its core and edges.

2. This is particularly true for central place foragers, such as grey and harbour seals, whose trends in numbers vary among different regions in the Northeast Atlantic. Here, we aimed at studying how foraging habitat selection may vary locally with the influence of population trends and physical habitat features
3. Using GPS/GSM tags deployed in grey and harbour seal colonies of contrasting sizes, we investigate spatial patterns and foraging habitat selection by comparing trip characteristics and home range similarities, and fitting *GAMM* to the seal distribution and environmental data respectively.
4. We show that grey seal foraging habitat selection and spatial patterns differed markedly between regions. Grey seals may select environmental characteristics for their foraging habitat accounting for local differences in prey consumed. Spatial patterns were different might depend on local seal density and regional productivity, located from inshore to offshore areas for the limit ranges and core population respectively. Our results on foraging habitat selection reflected the coastal and sedentary behaviour of harbour seals. We found no difference in spatial patterns between colonies, except for the Inner Hebrides where seals foraged further, potentially reflecting density dependence pressure, as the number in this colony is higher.
5. These results suggest that local conditions might have a strong influence on population spatial ecology, highlighting as well the relevance of studying foraging habitat selection based on foraging behaviour at fine geographical scale, particularly if species are managed within regional units.

Key words : Central place foragers; diving behaviour; foraging activity; grey seal; GPS/GSM telemetry; habitat selection; harbour seal; local scale.

INTRODUCTION

Understanding species distribution and their relationship with habitat is central in ecology and to the development of strategies for wildlife management and conservation (Morris, 2003; Rhodes et al., 2005). This is particularly true in marine ecosystems, as nowadays oceans face increasing threats from overexploitation and habitat destruction (Halpern et al., 2008; Jones et al., 2018). In this ecosystem, distribution of a species is shaped by interactions between internal (*i.e.* species' physiological tolerance, dispersal and reproductive strategies) and external factors (*i.e.* environmental features, regional richness *etc.*). Intra and inter-specific interactions can also drive species distribution. For example, competition, through resource exploitation and then reduction of limited resource (*i.e.* prey depletion, Vance, 1984), leads to spatial and temporal segregation, and/or diet specialization among individuals or species (Leung et al., 2012). In a metapopulation composed of different local populations in distinct geographical areas, these interactions will vary locally due to variation in physical habitat features and community structures (Thomas et al., 1999). The local abundance of species, particularly in top-predator case, tends to be greater towards the centre of their ranges, increasing the consumption pressure on prey resources, therefore leading to a higher degree of density dependence (Oliver et al., 2009). Subsequently, individuals living in the core population use a wider range of subordinate habitats (Brown, 1988). Depending on these different pressures, individuals disproportionately use the available conditions and resources, defining habitat selection (Mayor et al., 2009). This habitat selection differs from use or association, it implies choice, and is commonly measured as use relative to availability or as use versus non-use (Mayor et al., 2009). Understanding the causes of variations in habitat selection for local populations, and determining how trends in selection can be organized in space and time represents a major challenge in ecology (Fortin et al., 2008).

Selection of resources can be regarded as the expression of different behaviour forms (*i.e.* dispersal, migration *etc.*) of an animal in a particular environment (Schoener, 1969). It is important to consider behaviour when studying habitat selection. At local scale, foraging behaviour is perceived as the major behaviour which ultimately influences reproductive success and survival rates (Breed et al., 2009), and was already taken into account in different studies focusing on habitat selection (Donazar et al., 1993; Duchamp et al., 2004; Monsarrat et al., 2013). Recently, several studies on the ecology of marine central place foragers, such as pinnipeds and seabirds, used telemetry devices to incorporate foraging behaviour in their analyses (Guinet et al., 1997; Hamer et al., 2001; Jonsen et al., 2007; Shiel et al., 1999).

In the Northeast Atlantic, grey seals (*Halichoerus grypus*) and harbour seals (*Phoca vitulina*) are two sympatric species occurring along the European continental, Irish and British coasts, with differing population trends (SCOS, 2017). Grey seals and harbour seal's core populations are located in the UK with an estimated 141,000 and 43,500 seals respectively (SCOS, 2017). In France and Ireland, colonies of both species are located at their southern and western range limit respectively. They are located across a range of habitats, local abundances at the colonies and trends in abundance. Seals move regularly between colonies and can remain at sea for a long period. However, they display a high degree of site fidelity with foraging concentrated around their haulout sites (Cronin et al., 2013; Huon et al., 2015; McConnell et al., 1999; Sjöberg and Ball, 2000).

This context represents an excellent case for comparing intra and inter-specific of seals' foraging habitat selection and spatial usage. Many grey and harbour seals have been tracked from different colonies in the Northeast Atlantic, some of these data were already used to study habitat selection of both species, separately at the colony scale (*i.e.* local) from only one or two study sites (Aarts et al., 2008; Bailey et al., 2014; Huon et al., 2015); or at the population scale (*i.e.* global, Jones et al., 2015) pooling multiple datasets. In this study, we will combine for the first time several datasets for the assessment of foraging habitat selection at a local scale. Incorporating the results in a global context together represents a unique opportunity to bring new key elements on grey and harbour seal's ecology in the Northeast Atlantic. We aimed at 1) studying the foraging habitat selection of grey and harbour seals at a colony (*i.e.* local) scale, and 2) investigating the influence of population trends in contrasted haulout areas and physical habitat features on the seals' spatial patterns and foraging habitat selection.

MATERIALS AND METHODS

2.1 Study areas

Grey seals were tracked in 5 regions (Fig 1, Appendix 1): the Irish Continental Shelf (*ICS*), the Irish Sea, the Firth of Tay (*FoT*, representing the core population), the Eastern English Channel (*EEC*) and the Iroise Sea (, where grey seals are at their southern limit range). Local seal numbers in these studied colonies are 1,200 (Cronin et al., 2013), 800 (Cronin et al., 2016), 10,000 (SCOS, 2017), 100, and 130 (Vincent et al., 2017) seals respectively. Harbour seals were tracked in 4 regions: the Kenmare Bay, the Inner Hebrides, the Firth of Tay and the English Channel, including the haulout sites of the *Baie du Mont Saint Michel* (*BdM*), the *Baie des Veys* (*BdV*) and the *Baie de Somme* (*BdS*). Colony numbers of harbour seals in these regions are 390 (Kavanagh et al., 2010), 1,500, 280 (SCOS, 2017), 80, 200, and 600 (Vincent et al., 2017) seals respectively. Within all regions where both species are breeding (Inner Hebrides, FoT and EEC), we obtained tracking data from both species at FoT and EEC, providing the opportunity to study potential influence of interspecific interactions on foraging habitat selection and spatial usage.

2.2 Data description

Seal handling and tagging - One hundred and two seals were caught and tagged in total (all tagging sites combined) between 2008 and 2014 by the University of La Rochelle (France), the Sea Mammal Research Unit (St Andrews University, UK) and University College Cork (Ireland), representing 46 grey seals and 56 harbour seals (Table 1). Seals were caught around and/or on their haulout sites and fitted with Fastloc GPS/GSM tags developed by the Sea Mammal Research Unit. These tags collect data and information on animal diving, haulout activities and location, and relayed through onboard mobile phone with GSM modem (Sea Mammal Research Unit, St Andrews University, full specifications available at http://www.smru.st-and.ac.uk/Instrumentation/downloads/GPS_Phone_Tag22.pdf).

Breeding and moulting period - During the breeding and moulting periods, seals tend to strongly reduce their foraging activities, increasing the amount of time spent hauled out, or staying close to their haulout sites (Boness, 1984; Caudron et al., 2009; Lidgard et al., 2003). As we aimed to focus on their foraging activities to model habitat selection, data obtained during the breeding (September to December for grey seals) and early moulting (January to February for grey seals) periods were excluded from the analyses. All harbour seal data were obtained outside the species' breeding and moulting seasons. Changes in the diving and haulout

behaviour were tracked during the reproductive and moulting periods with the *MamVisAd* software (Sea Mammal Research Unit, Saint Andrews University). When a strong reduction in proportion of time in diving was observed during these two periods and the seal hauled out for prolonged periods in a known breeding or moulting area, the data were excluded.

Return-trip selection – In the Northeast Atlantic, harbour seals are relatively sedentary, showing short movements from their haulout sites (10-20 Km) and long-term fidelity (Ries et al., 1997; Tollit et al., 1998; Vincent et al., 2010). In contrast, telemetry on grey seals showed frequent movements between colonies (McConnell et al., 1999). They can alternate return trips to their haulout site in specific areas (within areas where most of their foraging activities occur) but they also frequently travel over hundreds of kilometres to distinct haulout site (SCOS, 2017). To study habitat selection and spatial usage of grey seals, we chose to focus on foraging trips and therefore only selected return trips to the same haulout areas (McConnell et al., 1999).

Explanatory variables - We used three environmental variables to identify the foraging habitat selection of grey and harbour seals (Appendix 2). These variables were chosen due to their expected role in the seals' foraging ecology (Aarts et al., 2008; Bailey et al., 2014; Huon et al., 2015). Bathymetry was obtained from the European Marine Observation and Data Network (*EMODnet*), with a grid size resolution of 0.125*0.125 minutes (<http://www.emodnet.eu/bathymetry>). Sediment data were obtained from the *MESH-EUNIS* model (Mapping European Seabed Habitat project), which predicts habitat types with a spatial resolution of 300 meters. Sediment types were based on a simplified FOLK classification system (Folk, 1954) and limited to the most dominant types: rock, mud, sand, gravel, coarse, and mixed sediments. We used different tidal current datasets for Irish, Scottish and French areas, scaled to similar resolutions for inter-site comparisons. Datasets for the French study areas were obtained from *Previmer* (Lecornu and De Roeck, 2009) for the tracking period. These were created from the MARS 2D model with a resolution of 250m and were available at an hourly scale. The Irish Marine Institute provided tidal current data for the Irish Continental Shelf and the Irish Sea (<https://www.marine.ie/Home/home>). Data was obtained from a numerical model with a spatial resolution varying between 1.2 Km and 1.5 Km and corresponded to surface tidal current at 3 hours interval. This dataset did not cover the Kenmare bay (for which no tidal current data was available). We averaged model datasets for the French and Irish areas respectively, in order to represent the tidal strength in space irrespective of instant tidal phases (ebb, slack or rising tide). Tidal current data for Scottish sites was obtained from the Web vision renewable website and was calculated from the ABP mer model (*Atlas of UK marine Renewable Energy Resources 2008. ABP mer*, <http://renewables-atlas.info/>). This data corresponded to the peak current speed of a mean spring tide (m.s^{-1}), with a spatial resolution decreasing from 200m to 5 Km from inshore to offshore areas.

The distance between each GPS location and the last haulout and the distance to the shore were also included as explanatory variables to describe accessibility to the environment (Aarts et al., 2008). The geodesic distance to the last haulout visited was calculated using the *LC.dist* function from the *Marmap* package (Pante and Simon-Bouhet, 2013) in R *v 3.3.3* (R core Team 2017). Distance from shore was calculated as the straight-line distance to the closest point along the coast using ArcGIS *v 10.5* (Environmental Systems Research Institute, Inc., Redlands, CA, 2017) "*Nearest*" function.

2.3 Foraging habitat selection

Assessment of the seals' foraging locations - We analysed the seals' dives to identify their foraging behaviour following (Planque et al., 2020). Dives with a maximum depth < 3 meters and a dive duration < 30 seconds were removed, considering that very shallow and short dives are unlikely representing foraging behaviour. We applied two diving criteria related to the seals' benthic foraging behaviour: the dive shape and vertical descent speed (Vincent et al., 2016). These criteria were determined for each individual because of possible inter-individual variability in diving strategies linked with physiological or behavioural characteristics (Austin et al., 2006; Beck et al., 2003). Dive-shape was assessed through the *Time Allocation at Depth* index (TAD, Fedak et al., 2001), usually varying from 0 and 1, where 0 correspond to dives close to the surface and 1 to "U-shape" dives. These square dives are assumed to represent foraging (Bjørge et al., 1995; Hindell et al.,

1991; LeBoeuf et al., 1988; Thompson et al., 1991). We set a minimum TAD threshold to the 3rd quartile (*i.e.* 75% of dives) of each individual dive distribution according to their shape in order to select 25% most U-shaped individual dives (Planque et al., 2020). Long duration dives with a very low vertical descent speed (assumed to be sleeping dives) were excluded from the analysis for each individual: we excluded 10% of the most U-shaped dives characterized by the lowest vertical descent speeds.

Use-availability design – Following the use-availability design (Keating and Cherry, 2004), we assessed the foraging habitat selection by comparing the environmental characteristics of points (*i.e.* foraging dive locations) to those of randomly generated points, representing the habitat availability (Aarts et al., 2008; Johnson et al., 2006; Keating and Cherry, 2004; Lele and Keim, 2006). Two random points per foraging dive point were created locally within the different study areas using the *sp* R package. These random points were created in each study area within buffers three times the size of the Minimum Convex Polygon (*MCP*, Burgman and Fox, 2003) of the seals’ dive locations in each study area, limited by the continental shelf (seals do not travel further). For the *EEC* and the *FoT*, where both species were present, one buffer was created for each species.

Modelling analyses – We fitted *Generalized Additive Mixed Models* (GAMM) to the data, with the *gam* function *mcmc* R package. We used a binomial family argument with a *logit-link* function to estimate the parameters of an *inverse-logit* selection model based on seal foraging dives and random points (Johnson et al., 2006). Foraging dives and random points were the response variable, taking the value 1 and 0 respectively. To consider the intra-individual autocorrelation, we treated the individual as a random effect. Environmental variables were treated as fixed effects. The bathymetry, tidal current, distance from shore, and distance from the last haulout were included as discrete variables; sediments were treated as categorical variable. When one sediment type was over-represented, the model was forced to consider this sediment type as reference level (otherwise reference sediment type was included alphabetically). The multi-collinearity between covariates was assessed using the VIF value (*Variance Inflation Factor*, Kutner et al., 2004). The best model was selected using the AIC criteria (*Akaike’s Information Criteria*, Akaike, 1973). Furthermore, we calculated the importance of each covariate with the prediction function of the GAMM, providing an index of the relative importance of each covariate in the chosen model. The maps of habitat selection predicted by the model were created with ArcGIS for all sites.

2.4 Influence of intra and interspecific interactions on spatial patterns and home range segregation

Trip characteristics and measure of similarity between home ranges were used to evaluate the influence of intra and inter-specific interactions on spatial patterns, to get complementary information to foraging habitat selection. For each species, trips with duration lower than 3h were removed as they were considered to be in the vicinity of haulout sites (Cronin et al., 2013). We used trip duration and maximum extent from the haulout sites (values were log transformed to correct for non-normal distribution). Interpolated tracks were used for these trip characteristics. To reduce sampling bias (between areas where seals spend more time diving or out of the water), we interpolated all GPS locations every 20 minutes using straight-line interpolation. We assumed that each trip made by an individual seal was independent from the others. Shapiro and Bartlett tests were firstly used to test the normality and homoscedasticity of the data by using the functions *shapiro.test* and *bartlett.test* from the *Stat* R package. If the normality and homoscedasticity were validated, ANOVA was used for inter-specific site comparison; if not, we used a Kruskal Wallis test (respectively *aov* and *kruskal.test* function). When the inter-variability was validated, a post-hoc test was used for pairwise comparison. We used a Tukey HSD test (*tukey HSD* function) in the case of ANOVA; and the dunn test (*dunn.test* function in the *dunn.test* R package) in the case of Kruskal Wallis. We used the *Bhattacharyya’s affinity* index (BA, (Bhattacharyya, 1943) to quantify home range spatial overlap. This method quantifies the spatial overlap between two population spatial distribution (Fieberg et al., 2005) and provides a value ranging from 0 (*i.e.* no overlap or complete segregation) to 1 (*i.e.* complete overlap). We applied the BA on the 95% Kernel density of foraging dive locations between individuals of the same colony to study the influence of colony size (*i.e.* indirectly the density dependence), and between species when both species were tracked around the same colony (*i.e.* FoT and EEC) to study the influence of inter-specific

interactions. We used the *Kerneloverlap* function of the *adehabitatHR* R package (Calenge, 2006).

RESULTS

3.1 Foraging habitat selection

Grey seal foraging habitat selection – 438,314 dive points were identified as foraging dive locations for all study areas (Table 1, Appendix 3). The details of the model selected for each site are presented (Table 2). The explained deviances for all sites were relatively high (Table 2), varying between 31% (for the EEC) and 78% (for the Iroise Sea). For most sites, the distance from the last haulout accounted for most of the explained variance, varying from 45% (FoT) to 76% (Iroise Sea). The second variable having a strong influence on the habitat selection was the bathymetry, varying from 15% (Iroise Sea) to 40% (FoT) of the explained deviance. These two parameters had a negative influence on foraging habitat selection, grey seals tended to select foraging habitat close to their haulout sites and in shallower waters. Distance from shore, tidal current and sediments combined accounted for less than 10% of the explained deviance, but the influence of these variables differed among sites. In the EEC and ICS, grey seals selected habitat further than 20Km and 150Km from shore respectively. Conversely, grey seals selected their foraging habitat less than 50Km from shore in the Irish Sea. Tidal current speed had a positive influence on grey seals' foraging habitat selection in the Irish Sea. In the ICS, they selected an optimum tidal current of 0.15 m/s. For the other sites, seals selected a minimum value of tidal current speed (0.4 m/s for the Iroise Sea and the FoT, and 0.6m/s for the EEC). Grey seals selected different types of sediments in the different study areas. Habitat close to the colonies was highly selected in all study areas (Fig 3). This was particularly true for the Iroise Sea and the Irish Sea, where grey seals mainly selected their foraging habitat in shallow waters around tidal areas, where they haul out.

Harbour seal foraging habitat selection – 359,001 dives points were identified as foraging dive locations for all study area (Table 1, Appendix 3). Details of the models selected for each site are presented in Table 3. The overall explained deviance (ED) was relatively high (Table 3) varying from 30.9% (BdV) to 78.3% (BdM). Distance from the last haulout (91% of ED for the Inner Hebrides), the distance from shore (92% of ED for the BdS), and the bathymetry (62% of ED for the BdV) predominantly explained the deviances. The distance from the last haulout had a negative influence for all sites, *i.e.* harbour seals selected their foraging habitat close to their haulout sites. The influence of distance from shore and bathymetry were more contrasted. For BdS and Kenmare bay, harbour seals selected short distances from shore. Nevertheless, in the Inner Hebrides and FoT, harbour seals selected their foraging habitat at 40 Km from the coast. Harbour seals selected habitat in shallow waters in the BdM and the BdV. In the Inner Hebrides and the FoT, they selected depths at 20 and 25m respectively. Tidal current and sediment together only explained less than 10% of the deviance, except for the Firth of Tay where tidal current explained 55% of the deviance. Habitat selection was highest along the coastline for the BdS, and within the bays for the BdM, the BdV and Kenmare bay (Fig 3). In the Inner Hebrides and the FoT, harbour seals selected their foraging habitat in inshore and in distance to the shore.

3.2 Influence of intra and inter-specific interaction on spatial usage and home range segregation

For each site and species, the hypotheses of normality and homoscedasticity of trip duration and maximum extent were rejected ($p < .05$); leading to the use of the non-parametric Kruskal Wallis test, and Dunn-test as a post-hoc test.

Grey seals' trip characteristics – Medians of trip durations were significantly different between sites ($p < 0.05$, Table 1, Fig 3, Appendix 4). Most of the pairwise-site comparisons were significantly different (8/10, $p < 0.05$). Trip durations were higher for the Irish Sea (median=3.17 hours; IQR=1.98 hours) and shorter in the EEC (median=1.92 hours; IQR= 1.17 hours). Medians of maximum extent differed among areas ($p < 0.001$, Table 4). All pairwise comparisons were significantly different ($p < 0.05$) except for the EEC vs FoT ($p = 0.09$). Maximum extents were longer for the FoT (median=2.70 Km; IQR=2.63 Km) and lower for the ICS (median=0.626 Km; IQR=4.30 Km).

Harbour seals' trip characteristics – Medians of trip duration were significantly different between study areas ($p < 0.001$, Table 2, Fig 3, Appendix 5). Most of the pairwise-site comparisons were significant. Trip durations were higher for the Inner Hebrides (median=2.90 hours; IQR=1.29 hours), where the individual range was also high) and lower for the FoT (median=2.26 hours; IQR=1.19). Median maximum extents differed among sites ($p < 0.05$). Ten pair-sites over were significantly different (Table 5, Fig 4). The trip maximum extents were higher for the Inner Hebrides (median=1.94 Km; IQR=1.94 Km) and lower in the Firth of Tay (median=1.53 Km; IQR=1.37 Km).

Measure of similarity in home ranges – Within each site, grey seals individually segregated their spatial usage, indicated by a relative low BA values varying from 0.02 ± 0.12 (Irish Sea) to 0.18 ± 0.18 (ICS), (Fig 4). Overlaps of individual spatial usage were highlighted for harbour seals in the BdM (0.87 ± 0.12), BdV (0.75 ± 0.19), BdS (0.73 ± 0.15) and the Kenmare Bay (0.65 ± 0.19). Conversely, a low BA value was observed for the Inner Hebrides (0.04 ± 0.22). The interspecific comparison between grey seals and harbour seals showed low median value for the FoT (0.01 ± 0.05) and the EEC (0.09 ± 0.17), indicating spatial segregation.

DISCUSSION

This study highlighted the importance of considering the local scale in the understanding of the relationship between animal and its environment; particularly in the case of meta-populations where local population trends and physical habitat features vary regionally. By incorporating tracking data from contrasted colonies in the Northeast Atlantic (*i.e.* core population versus limit range), our study provides new knowledge on local foraging habitat selection of grey and harbour seals. To avoid the problem of homogenization (Matthiopoulos, 2017), we chose to create a model for each haulout group in order to consider local habitat availability and difference of intraspecific interactions. Furthermore, we chose to focus on foraging activities by using dive characteristics as seals are predominantly considered as benthic divers (Gosch et al., 2019). This is the first time that habitat modelling on harbour and grey seals was performed by considering likely foraging behaviour while diving.

Grey seal foraging habitat selection and spatial patterns

The distance from the last haulout was the most important factor influencing the foraging habitat selection of grey seals in all study areas (from 45% to 76% of the explained deviance in the model respectively for the FoT and the Iroise Sea). Our data shows that when performing return trips, they spend the majority of their time close to the haulout sites. These results are consistent with previous studies throughout the range of grey seals in the Northeast Atlantic. Grey seals in the North Sea spent 43% of their time within 10Km of the haulout sites (McConnell et al., 1999) and preferentially selected habitat closer to haulout-sites with a gradual decrease of habitat selection beyond tens of kilometres (Aarts et al., 2008). In the Baltic Sea, Sjöberg and Ball, (2000) noted short distance trips (from 10 to 15 Km), grey seals spending 75% of their time within a radius smaller than 50Km around their haulout sites. In the Iroise Sea, grey seals mostly undertook trips within 40Km of haulout sites (Huon et al., 2015). Foraging habitat selection by grey seals was negatively influenced by bathymetry, but to a lesser extent than distance from haulout sites (varying from 10 to 40% in the explained deviance). Depending on study sites, the depth selection decreased until a depth of 50m (Irish and Iroise Sea) and 100m (FoT). These results are consistent with previous studies on grey seals habitat selection, with usual dive depth between 10 to 80 m (Aarts et al., 2008; Tollit et al., 1998). Grey seals are generally considered as benthic feeders (Beck et al., 2003; Lydersen et al., 1994) and the influence of bathymetry on foraging habitat selection will presumably vary locally depending on the seabed topography and sediment type. Furthermore, distance from the shore and tidal current must also influence the behaviour of seals, as they use them to orientate, to move, and to forage (Zamon, 2003, 2001). These three variables did not contribute much to the explained deviance of the models, and their influence varied among sites. Distribution of seals' prey resources was not included in the model, as the data were not available for some of the study areas.

Grey seals in the Firth of Tay and in the Eastern English Channel made longer trips but of shorter duration compared to grey seals in the other sites. In the Northeast Atlantic, the core population is in the North Sea

with 141,000 individuals (SCOS, 2017). In this area, due to the important pressure on prey resources located in inshore areas, grey seals tend to travel long distances directly to offshore areas on specific sandbanks where sandeel availability is high (Hammond et al., 1994; McConnell et al., 1999; Wilson and Hammond, 2019). It may be a process to reduce the effect of density dependence and to avoid the indirect competition for resources with fisheries. This offshore behaviour is in accordance with our results for the FoT. Grey seals in the EEC performed their trips mostly in specific areas along the coast, as the EEC is known to be a major ground for flatfish (Carpentier et al., 2009; Riou et al., 2001; Selleslagh et al., 2009), which are observed in grey seal diet (Planque *pers. com*). In the ICS and Iroise Sea, grey seals made shorter trips. These two sites are known as highly biologically productive regions in the Eastern North Atlantic (upwelling and area enclosed by specific currents, respectively for the ICS and the Iroise Sea (Hily and Glémarec, 1999; Raine and McMahon, 1998). Furthermore, grey seals in these areas mainly feed on fish species not targeted by commercial fisheries (Ridoux et al., 2007; Vincent et al., 2016), and as a result, a low spatial overlap and low resource competition were found between seals and fisheries (Cronin et al., 2012). This low degree of competition with fisheries and high prey availability could explain the shorter trips performed by these grey seals, as they can find sufficient resource close to their haulout sites. Furthermore, in the Iroise Sea, this was also supported by the size of the colony (*i.e.* small local abundance at the southern limit range), indicating a low effect of density dependence. Grey seals in the Irish Sea adopted a different spatial usage compared to the four other sites, with the highest trip duration. The numbers of seals between the East and West parts of Ireland are of the same order of magnitude (800 *versus* 1200 respectively), so colony size may not explain the difference in spatial usage. However, a high degree of interactions (*i.e.* spatial overlaps) between fisheries and grey seals in the Irish Sea was recently highlighted (Cronin et al., 2016; Gosch et al., 2019). These interactions with anthropic activities could explain why grey seals made longer trips with an intermediate maximum extent in this area compared to the other sites. But most of all, grey seal selected foraging habitat matching those of their prey (Alheit and Hagen, 1997; Gosch et al., 2014; Hammond et al., 1994; Ridoux et al., 2007).

Harbour seal foraging habitat selection and spatial patterns

Distance from the last haulout, distance from shore and/or bathymetry explained an important part of the deviance (>90%) in harbour seal foraging habitat selection. These three variables had a negative influence, but at different degrees depending on the site configuration. Harbour seals were very coastal and sedentary in the six study areas, which is consistent with previous findings on the species: in the Moray Firth (East of Scotland) for instance, seals forage within 30 Km of their haulout sites and dive at a maximum depth of 50m (Bailey et al., 2014; Tollit et al., 1998). This was also highlighted on the other side of the Atlantic, in the Saint Laurent estuary (Lesage et al., 2004), seals were coastal (with distances shorter than 11 Km from the shore) and in shallow waters (<50m deep). Tidal current and sediment types accounted less in the explained deviance than the other variables. Their influence was generally very low, with the exception of the tidal current for the FoT. Harbour seals feed on diverse fish species and their diet vary locally (Hall et al., 1998). At their southern limit range, in the English Channel, harbour seals mainly selected foraging habitat over mixed sediments in front of estuaries, corresponding to the habitat of juvenile of flatfish that constituted most of harbour seal diet in BdS (Spitz et al., 2015). Seal diet in BdM was not available, we could not compare seals' foraging habitat selection and their main prey's habitat there. On the East coast of Scotland, harbour seals selected habitat over sandy areas in front of the Tay river mouth, corresponding to the habitat of sandeel - the main harbour seal prey in the area (Wilson and Hammond, 2019). Harbour seals were more pelagic in the Inner Hebrides, selecting habitat along the sounds of the fjords, corresponding to the habitat of pelagic species such as whiting, scads and herring (Wilson and Hammond, 2019). Sediment and current features selected by harbour seals might correspond to the habitat features of their prey.

Coastal behaviour of harbour seals in the Northeast Atlantic was also identified in their spatial usage for each study area. The median distance from the last haulout was highest for the BdM with 6 Km. However, two patterns were highlighted when performing intraspecific comparisons of spatial distribution of foraging areas for each study sites (BA index). The FoT, Kenmare bay and the study areas in the English Channel showed a high degree of intraspecific spatial overlap (high BA values; [?]0.65). Prey resources might be

sufficient to sustain all individuals around these colonies, suggesting a low influence of density dependence. Even though the species is capable of long trips at sea (Lesage et al., 2004), harbour seals in the FoT and Kenmare bay may not need to perform such long trips to find their prey. Conversely, we highlighted a lower degree of intraspecific spatial overlap in the Inner Hebrides (BA value=0.04+-0.22). The individual range of trip duration and maximum extent were higher. These results may be explained by the influence of intraspecific interactions, as the colony number in this area is more important than the others (15,200 *versus* few hundreds, SCOS, 2017). Inter-specific interactions may also have an impact on harbour seals' spatial usage, as grey seals also breed in the Inner Hebrides ((i.e. 8,700 individuals, Duck et al., 2013; SCOS, 2017; Wilson and Hammond, 2019). This suggests that harbour seals in this area may use a larger area in order to reduce intra- and interspecific indirect competition for resources.

The number of harbour seals at some colonies in the North Sea declined during the last decade (Thompson et al., 2019). The decline of sandeel numbers (main prey of harbour seals around these colonies) and the interspecific competition with grey seals were suggested as potential causes in local harbour seal declines (Wilson and Hammond, 2019). In our study, grey seals and harbour seals were tracked in two areas, where both species haul-out. In this context, it was interesting to compare the two species' foraging habitat selection and spatial usage. Spatial partitioning between seal species was highlighted in habitat selection and spatial patterns in the FoT and EEC, where both species coexist and were tracked. Grey seals made longer trips than harbour seals (15 Km for median maximum extents in grey seals in both areas, versus 5Km and 4 Km respectively for harbour seals in the EEC and FoT). In both cases, harbour seals tended to forage in inshore areas, while grey seals went further offshore. The two species also selected distinct sediment types. In the EEC, grey seals selected muddy seabed and harbour seals sand, rock and mixed sediments. These findings are in accordance with previous studies, that also found differences in the use of marine environment between these two species (Jones et al., 2015; Sharples et al., 2012).

In the North Atlantic, grey seals and harbours seals are managed at local scales, and in the absence of genetic information on population structuring, haulout groups are often considered as "Seal Management Units" (Russell et al., 2013). Both species are considered as generalist, using a variety of habitat and prey. This study highlights the importance of studying foraging habitat selection at local scale, and considering the variability between colonies, as physical habitat features and seals' prey resources vary between regions. As marine top predators, both seal species are listed in the Annex II of the European habitat directive requiring establishment of protected areas to maintain favourable conservation status. At a local scale, our predictive maps of foraging habitat selection could be used by managers to implement specific areas of conservation to maintain a good ecological state of their habitat and prey resources potentially at risk due to anthropic activities. Such a foraging habitat selection analysis could be applied and/or adapted for other central place foraging species, in both the marine and terrestrial ecosystems.

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AUTHORS' CONTRIBUTION

MH and CV conceived the ideas and developed the methodology with the help of YP. CV, MC and MJ collected the data. MH analysed the data and led the writing of the manuscript. All authors contributed critically to the drafts and have final approval for publication.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study will be available on GitHub as manuscript will be accepted.

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