Drivers of marine top predator occurrence, movement and foraging behaviour

A thesis presented for the degree of Doctor of Philosophy in Marine Biology at the University of Aberdeen.

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Dedication

To my family, both given and chosen

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Author’s Declaration

I, hereby, declare that the work presented in this thesis is of my own composition, was undertaken by me, or principally by myself in collaboration with others as acknowledged below.

Chapter 4 was published in a peer-reviewed journal and therefore include contributions from co-authors. In particular, Geert Aarts carried out the post-hoc calibration of accelerometery data detailed in Appendix 4A. Furthermore, the data collection for Chapter 3 was done by members of the Lighthouse Field Station team and Whale and Dolphin Conservation volunteers. Oihane Fernandez has provided support with the processing of the CPOD data in Chapter 3. In addition, my supervisors, Paul Thompson and Isla Graham, provided suggestions to the core manuscript for all chapters.

No part of this work has been accepted in any previous application for a degree. All quotations have been distinguished by quotation marks and the sources of information specifically acknowledged.

Virginia Iorio

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Abstract

The study of marine megafauna movement ecology has improved our understanding of many species' distribution, habitat use and behaviour. Furthermore, this knowledge has been critical in conservation and management plans. However, uncertainties remain over how different drivers influence and shape animal movement patterns. The aim of this thesis is to test hypotheses on the role that prey distribution, animal cognitive abilities, environmental and individual characteristics have as drivers of marine top predator occurrence and movement. Using a long-term dataset on harbour seal at-sea distribution, it was found that inter-individual variability in movement patterns explained the temporal variation in population distribution. Furthermore, seal individual characteristics and dynamic environmental processes influenced individual repeatability of foraging areas. Then, passive acoustic and biologging data were used to assess the drivers of the initiation of area restricted search (ARS) behaviour for a free-ranging predator (bottlenose dolphin) and a central place forager (harbour seal), respectively. Both predators initiated ARS in response to prey encounters and proxies of previously acquired knowledge on prey distribution in the area. Prey predictability at both long and short temporal scales influenced predator foraging behaviour and occurrence. This thesis provides evidence that the distribution of resources and the mechanisms that influence its predictability are key drivers of predator movement, and it illustrates how a population distribution is a composite of its individuals' movement decisions. These results highlight the importance of accounting for predator reliance on predictable resources and inter-individual variability in movement patterns within conservation plans for marine megafauna.

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Chapter 1

General introduction

Chapter 1

General Introduction

Marine megafauna play a key role in our ecosystems (Myers & Worm 2003; Springer *et al.* 2003; Scheffer *et al.* 2005; Hammerschlag *et al.* 2019; Pimiento *et al.* 2020), from controlling top-down processes to nutrient cycling in both coastal and pelagic habitats (Myers *et al.* 2007; Estes *et al.* 2011; Doughty *et al.* 2016). Many marine predator populations remain threated by anthropogenic uses of the marine environment and environmental changes (Kovacs *et al.* 2012; Erbe *et al.* 2016; Avila *et al.* 2018; Harris *et al.* 2018; Orgeret *et al.* 2022), and they have been suggested as potential sentinels for our ocean's health (Hazen *et al.* 2019). Movement ecology of marine megafauna has been a critical field of research which has led to the understanding of species distributions and behaviour, from shelf-sea areas (Thompson *et al.* 1996; Hamer *et al.* 2001; Daunt *et al.* 2002) to highly remote parts of our oceans (Mcconnell *et al.* 1992; Davis *et al.* 2001; Pinaud & Weimerskirch 2007; Breed *et al.* 2017). This knowledge has underpinned the conservation and management of highly mobile and migratory species, which are considered endangered or threatened (Hyrenbach *et al.* 2000; Wilson *et al.* 2004b; Cañadas *et al.* 2005; Shillinger *et al.* 2008; Gallus *et al.* 2012). Although much effort has been put into studying megafauna movement and behaviour, many questions on the drivers and processes that determine movement patterns still remain unanswered (Hays *et al.* 2016).

Movement ecology in conservation and management

Understanding predator movement patterns, occurrence and behaviour is key to informing effective management plans and conservation measures (Allen & Singh 2016; Lascelles *et al.* 2016; Fraser *et al.* 2018; Hays *et al.* 2019). A review of management plans for mobile predators at risk, in North America, found that, on average, 60% of the literature available on each species' movement ecology was used for conservation planning (Fraser *et al.* 2018). In particular, telemetry studies have been instrumental in providing the first insights into predator distribution, range and at-sea behaviour (Costa *et al.* 2012; Hays *et al.* 2019). Movement data aid in the identification of critical habitats and predator hotspots, which can then be protected through the establishment of Marine Protected Areas (MPAs) (Wilson *et al.* 2009; Schofield *et al.* 2013; Trathan *et al.* 2018; Handley *et al.* 2020; Davies *et al.* 2021). Identification of hotspots used by multiple predators is particularly important, therefore multi-species biologger deployments as part of programs like Tagging of Pacific Predator (TOPP) (Block *et al.* 2011) or SEATRACK (Strøm *et al.* 2021) are particularly valuable. The TOPP program coordinated the deployment of 4,306 biologgers on 23 species of marine megafauna in the North Pacific Ocean (Block *et al.* 2011). The results of this program identified critical habitats used by multiple predators in the Pacific Ocean such as the California Current. On the other hand, the SEATRACK project aims to assess the non-breeding distribution of seabirds across the North Atlantic using data from eleven seabird species (Strøm *et al.* 2021). Results from this project have led, for example, to estimates in the abundance of seabird species across the Northeast Atlantic (Fauchald *et al.* 2021). The MegaMove project is another example of large scale data collaboration, which allowed to comparison of movement of over 2,500 individuals from 50 different species of marine vertebrate, finding that differences in movement patterns were mostly defined by the different species and by the habitat (open *vs* coastal oceans) the animals were inhabiting (Sequeira *et al.* 2018).

Movement ecology can further support conservation measures by describing species geographic ranges, their habitat association, and connectivity between subpopulations (Cooke 2008). Movement studies using telemetry devices have shown how marine megafauna movement and distribution crosses geo-political boundaries and ocean basins, a challenge for conservation measures that may require international agreements (Guilford *et al.* 2009; Block *et al.* 2011; Witt *et al.* 2011). For example, by tracking the movement of leatherback turtles (*Dermochelys coriacea*) in the South Atlantic, Witt *et al.* (2011) highlighted that 11 nations should get involved in a conservation plan for this population. Habitat association, and habitat use studies are fundamental for identifying critical areas in species distributions, such as foraging areas (Jonsen *et al.* 2007; Hindell *et al.* 2016) and migratory routes (Shaffer *et al.* 2006; Lea *et al.* 2015). Furthermore, for highly mobile species it can be challenging to differentiate subpopulations or stocks (Cooke 2008), thus studying movement of individuals can provide information on connectivity between populations and assess their resilience (Laidre *et al.* 2018; Dunn *et al.* 2019).

Movement studies have also been particularly important in assessing the impacts of anthropogenic disturbance and building the knowledge necessary to forecast the impacts of climate change (Hazen *et al.* 2013a; Rutterford *et al.* 2015; Avila *et al.* 2018). For example, research has used movement data to investigate the overlap of migration paths of large whales with ship traffic lanes (Redfern *et al.* 2013; Hazen *et al.* 2017; Pirotta *et al.* 2019), marine predator interactions with fisheries (Lewison *et al.* 2014; Queiroz *et al.* 2016; Hinke *et al.* 2017; Darby *et al.* 2021), and impacts of disturbance from renewable energy developments occurring within the species range (Cook *et al.* 2018; Whyte *et al.* 2020; Onoufriou *et al.* 2021). On the other hand, understanding the interaction between species movement and environmental processes has been the first necessary step to assess species responses to environmental changes (New *et al.* 2014; Schlaff *et al.* 2014). For example, species habitat models resulting from the TOPP program (Block *et al.* 2011) were used to assess species-specific distribution shifts under the prediction of Sea Surface Temperature (SST) rising due to climate change (Hazen *et al.* 2013a). Results showed a northward shift in distribution, with an increase in species distribution overlap. By incorporating data from 23 different species, Hazen *et al.* (2013a) were able to explore how predators with different foraging strategies would respond to environmental changes, showing that species with specialized diets might be more affected as they may have less capacity for adaptation. Furthermore, comparison of species distribution over time, as done in Hazen *et al.* (2013a), allowed for inferences on the drivers of these species occurrence.

Although it is possible to use current knowledge on species ecology to forecast future distributions, climatic anomalies already provide case studies on how individuals respond to such climatic variability and its impact on populations (Thompson & Ollason 2001; Trathan *et al.* 2007; Ropert-Coudert *et al.* 2009; Cleasby *et al.* 2017). For example, a study on the impact of El Niño Southern Oscillation (ENSO) on king penguins (*Aptenodytes patagonicus*) found that variability in SST had major effects on their foraging habitat and diving behaviour (Bost *et al.* 2015). The authors suggested that this was possibly due to a decrease in prey availability at lower trophic levels. Furthermore, they found that as anomalous SST occurred during the predator breeding period, this had particular impact on individuals breeding success and population dynamics (Bost *et al.* 2015). Changes in environmental conditions and species distribution due to climate change will impact the efficacy of MPAs (Bruno *et al.* 2018; Gilmour *et al.* 2022). Thus, conservation measures and management plans will have to move towards more dynamic approaches that allow to account for such changes (Hobday *et al.* 2010; Hobday *et al.* 2013; Maxwell *et al.* 2015; Hazen *et al.* 2017).

One of the challenges faced by movement studies using telemetry data is that the number of individuals tagged, although sometimes high (e.g. >100 individuals - Block *et al.* 2011), will always represent only a relatively small sample of the population (Lindberg & Walker 2007; Hebblewhite & Haydon 2010; Sequeira *et al.* 2019). Furthermore, growing evidence on inter-individual variability within populations poses new challenges for inferring population level demographic changes from individual behavioural data (Bolnick *et al.* 2003; Gutowsky *et al.* 2015; Merrick & Koprowski 2017; Patrick & Weimerskirch 2017). This is particularly important for conservation measures, as individuals following different movement patterns or migratory routes may be exposed to different threats (Thiers *et al.* 2014; Patrick *et al.* 2015). Individual variability has often been associated with characteristics such as age (Peron & Gremillet 2013; Riotte-Lambert & Weimerskirch 2013; Votier *et al.* 2017), sex (Lewis *et al.* 2002; Kernaleguen *et al.* 2012; Clark *et al.* 2021) or body size (Thompson *et al.* 1998; Lewis *et al.* 2005; Cronin *et al.* 2013). However, other personality traits, such as boldness or shyness, may influence an individual's movement (Patrick & Weimerskirch 2014; Allegue *et al.* 2022). Thus, understanding and describing inter-individual variability within populations is critical to contextualise population-level patterns and adapt the scale of management (Cooke 2008; Allen *et al.* 2016).

Many studies have tried to describe predator spatial patterns and movement by applying methods such as Levy flights and Brownian motion to explore how predators search for resources (Benhamou 2007; Sims *et al.* 2008; Regular *et al.* 2013). Some evidence of predators using these more probabilistic strategies has been found (Sims *et al.* 2008; Humphries *et al.* 2010; Sims *et al.* 2012). However, other studies have shown that these theoretical models cannot fully capture and describe predator searching strategies (Austin *et al.* 2004; Boyer & Walsh 2010; James *et al.* 2011; Reynolds 2012; Auger-Methe *et al.* 2016; Bennison *et al.* 2019). For example, when comparing adult basking shark (*Cetorhinus maximus*) movements with random-walk simulations, sharks consistently yielded higher prey encounter rates compared to their simulated counterpart (Sims *et al.* 2006). The authors suggested that knowledge acquired from previous encounters with prey could have successfully recreated the patterns observed in the animal tracks. Furthermore, other studies have suggested that predator cognitive abilities, such as remembering the distribution of resources, should be accounted for when investigating predator search strategies (Weimerskirch *et al.* 2007; Boyer & Walsh 2010; Auger-Methe *et al.* 2016), whereas simplified movement models have generally assumed predators to be naïve (Sims *et al.* 2008) or omniscient (Marshall *et al.* 2013).

Prey distributions

For a predator, successful foraging determines fitness, survival, and reproductive success, which is why searching for prey is considered to be the main driver of predator movements (Fauchald *et al.* 2000; Goldbogen *et al.* 2015). Thus, predator distributions are expected to match those of their prey (Hazen *et al.* 2009; Carroll *et al.* 2017) and their movements adjusted in response to prey encounters (Enstipp *et al.* 2007; Hazen *et al.* 2015). However, this has not always been found to be the case (Weimerskirch *et al.* 2007; Grémillet *et al.* 2008; Benoit-Bird *et al.* 2013; Boyd *et al.* 2015). Evidence of direct predator and prey association might have been constrained by the spatial and temporal scale in which data have been analysed (Fauchald & Tveraa 2003; Wakefield *et al.* 2009). However, knowledge of prey distributions has sometimes been critical to contextualise predator movements. For example, results obtained from Regular *et al.* (2013) on the foraging behaviour of common murres (*Uria aalge*) supported the hypotheses that murres were adopting a Brownian foraging strategy to search for uniformly distributed capelin (*Mallotus villosus*). However, previous research in the same study area revealed the spatio-temporal persistence of patchily distributed capelin shoal (Davoren *et al.*

2003). This information led to the conclusion that murres were employing a more deterministic foraging strategy than results might have indicated (Regular *et al.* 2013).

Investigating predator-prey relationships can be particularly challenging in marine environments, where most marine megafauna foraging occurs underneath the surface, and often at depth, making it difficult to directly observe foraging behaviour. Various techniques have been adopted to infer marine predators foraging behaviour, such as their large-scale movement (e.g. Pinaud & Weimerskirch 2007), body acceleration (e.g. Ydesen *et al.* 2014), and the use of vocalizations (e.g. Madsen *et al.* 2002). At large scales, detections of area restricted search (ARS) behaviour in movement data have been widely used to identify foraging areas (Pinaud & Weimerskirch 2007; Dragon *et al.* 2012). ARS is a movement strategy adopted by predators to maximize their energy gains in environments where resources are heterogeneously distributed. It predicts that predators should transit across low quality areas, with a fast directed movement, and slow down once resources are encountered by using a tortuous path to remain in the same area (Kareiva & Odell 1987; Benhamou 1992). Marine megafauna have been observed displaying ARS behaviour at different spatial scales (Weimerskirch *et al.* 2007; Bailey & Thompson 2010; Thums *et al.* 2011) and prey encounters have been shown to be one of the main drivers of ARS behaviour (Hamer *et al.* 2009; Bailey *et al.* 2019).

With technological advances, more sensors have been integrated into biologgers, allowing researchers to use other data sources to infer foraging behaviour. For example, dive characteristics have been widely used to detect foraging in marine predators, with U-shaped dives of deep diving pinnipeds interpreted as foraging dives (Hindell *et al.* 1991b; Baechler *et al.* 2002), while the inclusion of accelerometers allowed for detection of prey catch attempts (Mori *et al.* 2007; Viviant *et al.* 2010; Iwata *et al.* 2015). For example, Gallon *et al.* (2013) deployed the first accelerometer tags on southern elephant seals (*Mirouga leonina*) characterising relationships between dive metrics and foraging behaviour. Furthermore, the inclusion of other sensors has allowed the identification of prey species and successful feeding events (Watanabe & Takahashi 2013; Adachi *et al.* 2018; Goulet *et al.* 2019; Yoshino *et al.* 2020). On the other hand, specific vocalizations have been used to identify foraging behaviour for some cetacean species (Tyack & Clark 2000). For example, the foraging behaviour of bottlenose dolphins (*Tursiops truncatus*) has been studied using the detection of foraging buzzes (Nuuttila *et al.* 2013; Pirotta *et al.* 2014; Brough *et al.* 2020) and bray calls (Janik 2000a; King & Janik 2015).

Environmental variability and predictability

Static and dynamic environmental characteristics have been highlighted as another important driver of predator movement, especially as they will influence prey distributions (Hunt *et al.* 1999; Bertrand *et al.* 2014; Boyd *et al.* 2015). Static environmental variables (e.g. bathymetry, sediment type, seabed slope) can determine suitable habitats for prey and large scale predator distribution (Tollit *et al.* 1997; Bailey & Thompson 2009). Whereas dynamic oceanographic processes influence prey and predator distribution at a finer spatial and temporal scale (Hunt *et al.* 1998; Johnston *et al.* 2005; Embling *et al.* 2012).

Amongst the various oceanographic processes influencing prey distribution (Cox *et al.* 2018a), it is probably the vertical stratification of the water column through the formation of the thermocline that is most relevant to predators in coastal and mid-shelf waters (Baumgartner & Mate 2003; Pelletier *et al.* 2012; Nordstrom *et al.* 2013). Other important processes are tidal-mixing fronts (Hamer *et al.* 2009; Scott *et al.* 2010) and the interaction between hydrographic processes with land features, such as deep-water channels (Bailey & Thompson 2010; Jones *et al.* 2014) or islands and headlands (Johnston *et al.* 2005; Bailey *et al.* 2014). The association of marine predators with oceanographic and hydrographic processes is due to changes in prey availability and accessibility (Davoren *et al.* 2003; Ropert-Coudert *et al.* 2009; Bertrand *et al.* 2014; Boyd *et al.* 2015), as these can influence the abundance and density of prey aggregations, and their spatial distribution both horizontally and in the water column (Embling *et al.* 2013; Scott *et al.* 2013).

One of the key characteristics shared by these dynamic features is that they occur predictably in the marine environments, thus allowing predators to take advantage of predictable prey aggregations (Weimerskirch 2007; Scales *et al.* 2014; Afan *et al.* 2015). Environmental predictability allows predators to reduce uncertainty in the environmental conditions they will encounter and the distribution of their resources (Riotte-Lambert & Matthiopoulos 2020). Thus, marine predator distribution and occurrence has often been associated with predictable environmental features (Gende & Sigler 2006; Davoren 2013). Understanding how predators associate with specific habitats and dynamic oceanographic features has been critical to understanding how predator distribution might be influenced in the future (Hazen *et al.* 2013a; Morley *et al.* 2018). Furthermore, although MPAs might be effective at protecting species that associate with predictable resources linked with static environmental features, a more dynamic approach is required for individuals that rely on spatio-temporal varying environmental processes (Hazen *et al.* 2013a).

Memory and learning

The use of memory by marine megafauna was initially inferred by their display of site fidelity to breeding grounds (Naves *et al.* 2006; Rosenbaum *et al.* 2009; Cordes *et al.* 2011), foraging areas (Bradshaw *et al.* 2004; Arthur *et al.* 2015; Votier *et al.* 2017) and migratory routes (Broderick *et al.* 2007; Horton *et al.* 2020; Kurten *et al.* 2022). Especially given that individuals were able to return to specific areas located outside their perceptual ranges, as for example outside their olfactory or visual capabilities (Davoren *et al.* 2003; Bradshaw *et al.* 2004). In the field of movement ecology, the role of memory has received particular focus around the display of home range behaviour and how animals performed biased movement towards locations they had previously visited (Van Moorter *et al.* 2009; Nabe-Nielsen *et al.* 2013; Riotte-Lambert *et al.* 2015). Over the last decade, investigating animal cognitive abilities, such as learning information about the environment and retaining them, as drivers of movement has become a growing field of research (Merkle *et al.* 2014; Riotte-Lambert *et al.* 2015; Bracis *et al.* 2018; Abrahms *et al.* 2019a; Ranc *et al.* 2021).

In their review on the role of spatial memory in animal movement, Fagan *et al.* (2013) discussed in detail the physiological costs and benefits of memory. Here, I focus on the ecological aspects and connections with the field of movement ecology. The relevance of memory has been particularly recognised in relation to the spatio-temporal complexity and predictability of the environment (Figure 1.1) (Riotte-Lambert & Matthiopoulos 2020). Completely homogenous environments would fail to provide distinguishable features to memorise, while a highly complex environment may require too much information to be memorised (Fagan *et al.* 2013). Furthermore, the temporal or spatial scale at which resources are predictable is thought to drive different movement patterns (Riotte-Lambert & Matthiopoulos 2020). For example, species can migrate in response to large scale spatio-temporal predictability, while at smaller scales predictability can lead to movement recursions and ARS behaviour (Jessopp *et al.* 2013a; Shaw & Couzin 2013; Berger-Tal & Bar-David 2015; Riotte-Lambert & Matthiopoulos 2020).

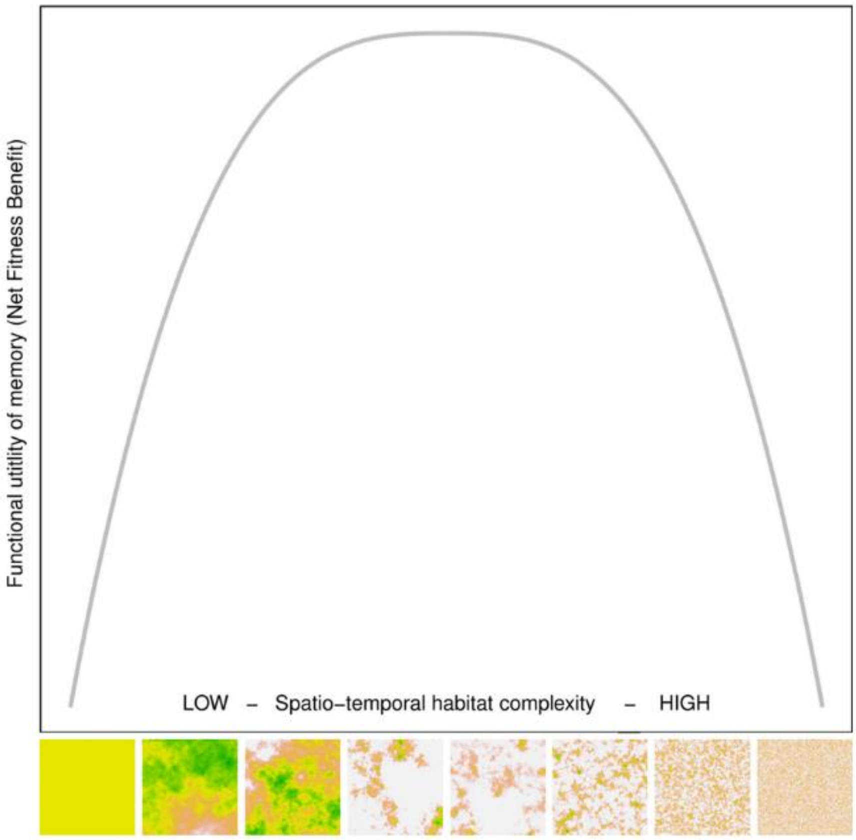

Figure 1.1. *Representation of memory functional utility in relation to spatio-temporal habitat complexity. Figure from Fagan et al. (2013).*

Support for the use of memory in animal movement has been explored using animal recursive or goal-oriented movements towards previously visited locations, and systematic searches of specific areas (Fagan *et al.* 2013). Frequent returns to previously visited sites have also been quantified to characterise individual repeatability, especially in the context of foraging behaviour. Various metrics have been used to quantify repeatability, for example the use of similar locations over time, measured as both overall area used (Arthur *et al.* 2015; Wakefield *et al.* 2015) or the distal point of a foraging trip (Votier *et al.* 2017), direction in which animals left a colony (Hamer *et al.* 2001; Davoren *et al.* 2003), foraging trip duration (Patrick *et al.* 2014; Speakman *et al.* 2021) and trajectory similarities (Cleasby *et al.* 2019). Many of these studies found inter-individual variability in repeatability suggesting that individuals might be adopting different strategies (Bolnick *et al.* 2003; Harris *et al.* 2020).

In terms of cognitive abilities, Fagan *et al.* (2013) also highlighted an important process that could be used by predators to memorise the distribution and location of resources. Cognitive mapping is a process by which spatial information is encoded with attributes in the individual memory (Burt de Perera 2004; Bingman & Cheng 2005; Normand & Boesch 2009). Whether the cognitive maps represent the spatial information from an individual perspective (i.e. egocentric) or in relation to landscape features (i.e. exocentric), or both, is still uncertain (Benhamou 1997). It has been hypothesised that individuals may initially acquire information in an egocentric way, that becomes increasingly connected and leads to a more exocentric representation (Benhamou 1997; Fagan *et al.* 2013). In this way, cognitive maps may be particularly important for predators to minimize search time and maximizing overlap with resources' distribution (Boyer & Walsh 2010; Regular *et al.* 2013).

Some limitations in the interpretation of these patterns are that not all goal-oriented movement can be considered an indication of memory, as species perceptual ranges can drastically vary (Fagan *et al.* 2017). For example, yellowfin tuna (*Thunnus albacares*) can detect cues occurring 10 km away (Girard *et al.* 2004), or animals may display innate behaviour like migrations (Åkesson & Weimerskirch 2005; Peron & Gremillet 2013). Thus, it is critical to understand a species ecology and life history when interpretating how memory may influence movement patterns. Furthermore, memory is a complex cognitive process that occurs over varying spatial and temporal scales, and interacts with an individual's environment (Fagan *et al.* 2013; Riotte-Lambert & Matthiopoulos 2020). Thus, memory needs to be simplified to be included in quantitative models.

Studying occurrence, movement and foraging in the marine environment: Biologging and Passive Acoustic Monitoring (PAM)

Marine megafauna can range over hundreds of kilometres and animals can move across ocean basins, posing challenges to the study of their movement (Block *et al.* 2005; Bonfil *et al.* 2005). Technological advances such as the development of autonomous transmitters (or "tags") that can be deployed on individual animals (Block 2005; Hussey *et al.* 2015; Wilmers *et al.* 2015) and of passive acoustic devices (Mellinger *et al.* 2007; Van Parijs *et al.* 2009) have revolutionised the field of megafauna movement ecology.

Biotelemetry and biologging

Biotelemetry and biologging studies use the deployment of tags on animals to autonomously collect data on their movement and behaviour. The main difference between biotelemetry and biologging is based on how data is recovered from the tags; biologging devices need to be recovered in order for the data to be accessed, while in biotelemetry data are relayed to logging stations (Cooke *et al.* 2004; Block 2005; Cooke *et al.* 2021). Biologgers allow for the collection of large amounts of data but need to be deployed on animals that can be reliably recaptured. On the other hand, biotelemetry tags do not need to be recovered but are more limited in the data they can relay. Furthermore, due to the challenges posed by the marine environment, biotelemetry tags can transmit data either using acoustic signals, that can be detected by fixed receivers, or for air-breathing animals, that are forced to return to the surface, data can be relayed ashore using VHF (Very High Frequency) or UHF (Ultra High Frequency) radio transmissions or satellites (Hussey *et al.* 2015).

Here, I will focus on the use of satellite telemetry tags to collect movement data and how they have been combined with biologgers to collect data using auxiliary sensors. Starting from the first deployment, in the marine environment, of an Argos (Advanced Research and Global Observation Satellite) tag on a basking shark off the West coast of Scotland (Priede 1984), satellite telemetry tags have now been deployed on a wide range of taxa (Guinet *et al.* 2001; James *et al.* 2005; Weng *et al.* 2005; Pinaud & Weimerskirch 2007). Argos uses the Doppler's shift of radio frequency to calculate animal geolocations. For more coastal species, VHF tags have been used to triangulate animal locations from vantage points and to study their activity patterns (Thompson & Miller 1990; Grémillet *et al.* 2004). However, given the uncertainty that some studies found around Argos locations and the limited spatial range of VHF, newer tags were developed using GPS systems (Weimerskirch *et al.* 2002; Weimerskirch *et al.* 2007). Although, first GPS tags were battery limited, now they can be used to track large marine animals for months with an accuracy of a few meters (Kuhn *et al.* 2009b; Costa *et al.* 2010b), although limitations still remain for smaller tags.

Early biologgers deployed on marine predators were equipped with time-depth recorders (TDRs) to collect data on individual diving behaviour (La Boeuf *et al.* 2000a; Schreer *et al.* 2001). TDRs allowed researchers to explore the third dimension of the ocean and study in more detail the underwater behaviour of megafauna. Technological advances in satellite telemetry allowed biologger data to be processed on board and relayed through the Argos system (Boehme *et al.* 2009), or for more coastal species through cell phone networks (McConnell *et al.* 2004) or UHF base stations (Onoufriou *et al.* 2016; Jones *et al.* 2017). With these new advances, more auxiliary sensors were incorporated into tags that could collect environmental data, such as conductivity-temperature-depth (CTD) sensors (Boehme *et al.* 2009), light intensity sensors to detect bioluminescence (Vacquie-Garcia *et al.* 2017) and fluorometers to collect chlorophyll *a* concentrations (Blain *et al.* 2013).

The availability of environmental data as experienced by the animal opened up avenues of research into how predators interact with their environment at a new spatial scale (Hindell *et al.* 1991a; Thums *et al.* 2013). Furthermore, environmental data collection from biologgers deployed on megafauna also found new applications in oceanographic models and databases (Weimerskirch *et al.* 1995; Boehlert *et al.* 2001; Charrassin *et al.* 2002; Costa *et al.* 2010a). With animals ranging across the most remote parts of our oceans, researchers could now collect environmental data in areas previously inaccessible due either to costs or because they were under ice for much of the year (Lydersen *et al.* 2004; Grist *et al.* 2011). In this way, transmitters deployed on seals have provided the data to understand the Circumpolar oceanographic current in the Southern Ocean (Boehme *et al.* 2008; Roquet *et al.* 2013).

Biologgers have also been equipped with sensors that collect data on animal behaviour, such as accelerometers to measure underwater movement (Nowacek *et al.* 2001; Viviant *et al.* 2010; Gallon *et al.* 2013). These have been followed by the inclusion of cameras (Hooker *et al.* 2002; Watanabe & Takahashi 2013; Yoshino *et al.* 2020), echosounders (Goulet *et al.* 2019) and acoustic sensors (Matthews *et al.* 2001; Nowacek *et al.* 2001). Collecting concurrent data on all these aspects of animal behaviour has led to new insights into their at-sea behaviour (Mikkelsen *et al.* 2019; Oestreich *et al.* 2020). For example, the combination of movement, accelerometer and acoustic data led to new insights into the migratory behaviour of blue whales (*Balaenoptera musculus*) showing distinct diel patterns in acoustic and foraging behaviour, and changes in their overall behaviour in response to the onset of migration (Oestreich *et al.* 2020).

However, the use of tags to study marine animals comes with limitations and challenges. Most importantly there are ethical issues associated with the deployment of tags on animals to answer research questions that need to be addressed (Cooke 2008). Where required, procedures have to be developed that minimize the stress related to the capture and handling of animals, as well as minimising the potential impact of devices on animal behaviour (Bodey *et al.* 2018b; Williams *et al.* 2020). Furthermore, both the devices themselves and the process of deploying them are frequently expensive, often constraining the number of devices that can be deployed (Hebblewhite & Haydon 2010). In turn, where the number of individuals used in a study is limited, the population-level inferences that can be drawn from the dataset will be constrained (Hebblewhite & Haydon 2010; Hays *et al.* 2016). Thus, where research questions can be answered using alternative, non-invasive methods, such as passive acoustic monitoring, these should be considered.

Passive acoustic monitoring

Passive acoustic monitoring (PAM) involves the deployment of hydrophones or acoustic detectors to record the presence and the behaviour of marine animals (Zimmer 2011). They have been successfully used to study marine mammals (Mellinger *et al.* 2007; Risch *et al.* 2007), soniferous fish species (Wilson *et al.* 2004a; Caiger *et al.* 2020) and more recently to characterise ecosystems through their soundscapes (Weiss *et al.* 2021). PAM has also played a key role in assessing the impacts of underwater noise on marine megafauna (Merchant *et al.* 2014; Nabe-Nielsen *et al.* 2018; Graham *et al.* 2019), and supporting conservation and management plans (Van Parijs *et al.* 2009; Van Parijs *et al.* 2015; Todd *et al.* 2020). PAM devices are particularly suited to highly vocal species such as marine mammals, as in addition to recording presence, different vocalizations can be used to infer behaviour (Van Parijs & Clark 2006; Garland *et al.* 2011), in particular foraging activities (Pirotta *et al.* 2014; King & Janik 2015).

PAM devices can also be used to collect data on animal movement, using triangulation to detect an individual location from recordings on multiple devices (Stanistreet *et al.* 2013; Macaulay *et al.* 2017). Thus, one advantage of PAM compared to biologging, is that multiple animals in the population can be detected and tracked using the same hydrophones, permitting population level inference using a less invasive technique (Hebblewhite & Haydon 2010; Marques *et al.* 2013; Nowacek *et al.* 2016)**.** Arrays of PAM devices are particularly useful for long-term data collection (Davis *et al.* 2017; Fernandez-Betelu *et al.* 2021), and to study both fine and large scale movements (Risch *et al.* 2014; Gillespie *et al.* 2020).

Study system

In this thesis, I used these techniques to investigate the drivers of movement patterns of two species of coastal marine mammal, the harbour seal (*Phoca vitulina*) and the bottlenose dolphin. These marine predators display two contrasting movement patterns, as seals are central place foragers (Orians & Pearson 1979), while dolphins are free ranging predators. The study was conducted in the Moray Firth, NE Scotland, where resident populations of these two species occur (Cordes *et al.* 2011; Cheney *et al.* 2014). The Moray Firth is a large coastal embayment dominated by shallow (<100m) waters (Figure 1.2) (Eleftheriou *et al.* 2004). Seabed sediments in the area largely consist of sand, gravelly sand and muddy sand (Holmes *et al.* 2004), and as a shelf-sea, it becomes seasonally thermally stratified (Simpson & Sharples 2012). The south-western part of the embayment is known as the Inner Moray Firth (Wilson *et al.* 1997), where the complex coastline and topography create a series of localised hydrographic processes, such as tidal fronts (Hastie *et al.* 2004; Bailey & Thompson 2010).

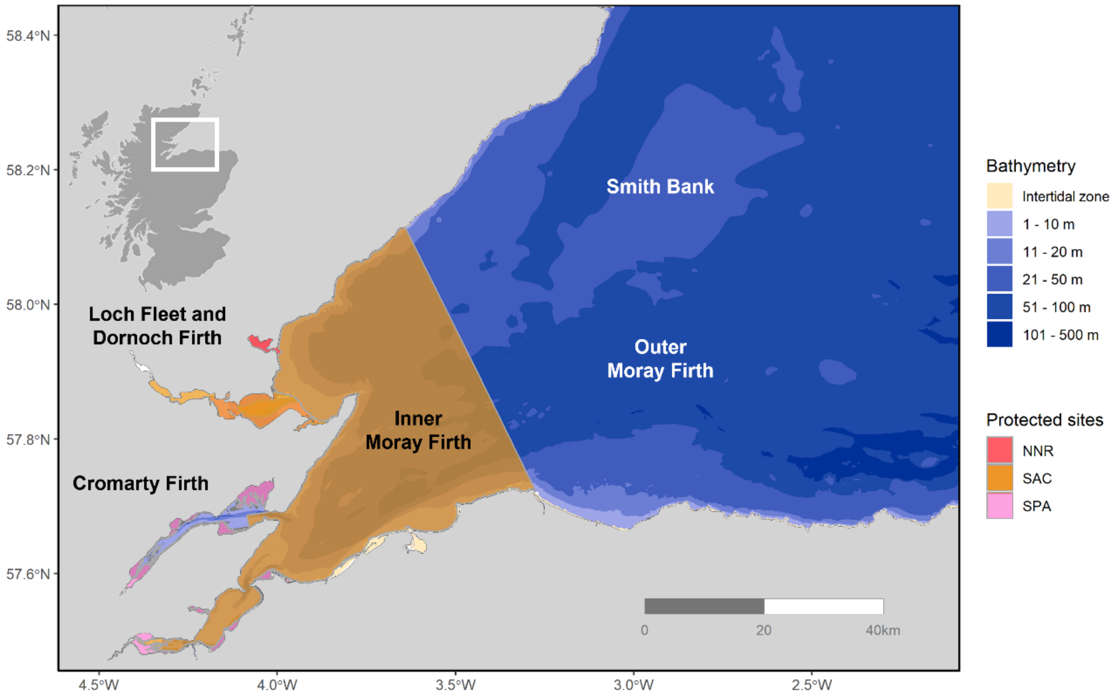

Figure 1.2. *Map of the Moray Firth (NE Scotland, UK). Highlighted on the map the Special Areas of Conservation (SACs), Special Protection Areas (SPAs) and National Nature Reserve (NNR).*

The Moray Firth is a recognised hotspot for marine megafauna, which has driven research on their occurrence and behaviour. Studies on marine predator foraging behaviour and diet have revealed that sandeels (*Ammodyte spp.*) are a critical resource for seabirds and pinnipeds (Furness & Tasker 2000; Wilson & Hammond 2019). However, other studies have highlighted seasonal variation in the relative importance of sandeels in Moray Firth predators' diet with other species such as gadoids (cod - *Gadus morhua*, haddock - *Melanogrammus aeglefinus*, and whiting - *Merlangus merlangius*) and clupeids (herring - *Clupea harengus*, and sprat - *Sprattus sprattus*) as more common prey species in autumn and winter (Pierce *et al.* 1991; Greenstreet *et al.* 1998). In addition, during the summer months, Atlantic salmon are another key prey species for many predators (Hastie *et al.* 2004; Butler *et al.* 2008). With eighteen major rivers flowing into the Moray Firth, this area was historically important for salmon (Williamson 1988), but populations have been declining in recent decades. Furthermore, interactions amongst marine top predators have been studied to elucidate competition for resources among the species (e.g. harbour and grey seals - Thompson *et al.* 1996; harbour porpoise and bottlenose dolphin - Williamson *et al.* 2022), or occasionally violent interactions (e.g. between bottlenose dolphins and harbour porpoises Ross & Wilson 1996).

Research has characterised the occurrence and distribution of marine mammals in the Moray Firth, such as for the bottlenose dolphin (Cheney *et al.* 2013), harbour porpoise (*Phocoena phocoena*) (Williamson *et al.* 2017), minke whale (*Balaenoptera acutorostrata*) (Robinson *et al.* 2009), harbour seal (Sharples *et al.* 2012; Thompson *et al.* 2019) and grey seal (*Halichoerus grypus*) (Matthiopoulos *et al.* 2004). This research has underpinned conservation and management of these populations. Under the European Union (EU) Habitats Directive (92/43/EEC), the Inner Moray Firth was established as a Special Area of Conservation (SAC) in 2005 to protect the core distribution area of the resident population of bottlenose dolphins (Figure 1.2) (Wilson *et al.* 1997; Cheney *et al.* 2013). Under the same directive, the Dornoch Firth and Morrich More SAC was established to protect important breeding sites of harbour seals (Figure 1.2) (Butler *et al.* 2008). More recently Loch Fleet has been recognised as another important haul-out site for harbour seals (Figure 1.2) (Cordes *et al.* 2011), this site has been further classified as a National Nature Reserve (NNR) by NatureScot. Occasionally other megafauna species have been sighted in the Moray Firth, as for example sightings of killer whales (*Orcinus orca*) (Robinson *et al.* 2017) and other delphinid species (Thompson *et al.* 2015).

The Moray Firth has also been an area important to the commercial and industrial sector. Historically, the Moray Firth was an important fishing area, while in the last decades, it became more relevant to the energy sector, initially with oil and gas exploration (Peters *et al.* 1989) and more recently to the marine renewable sector (Bailey *et al.* 2010; Graham *et al.* 2019). This area is also impacted by a high level of commercial and recreational shipping traffic (Merchant *et al.* 2014; Pirotta *et al.* 2015a). Given the increase in commercial use and high number of protected sites in the Moray Firth, it is important to keep monitoring marine predator populations and how they use these areas to support their management and conservation.

Thesis aims and objectives

To improve our understanding of the movement ecology of marine megafauna, this thesis aims to test hypotheses about the drivers of marine top predator occurrence and movement, in relation to prey distribution and environmental characteristics within this study system.

Assessing population distribution over time can elucidate drivers on the occurrence of species. However, this should be done while accounting for possible differences between individuals in the population. In Chapter 2, I used a long-term dataset on the movement of harbour seals in the Moray Firth, to assess the temporal variation of this populations distribution and to investigate if it was explained by the inter-individual variability in movement patterns occurring within the population. Then, to better understand the variability observed, I explored the repeatability of individual foraging behaviour and tested the hypothesis that this could, in turn, be influenced by individual life histories and responses to dynamic environmental changes. Data from three different biologger types (VHF, Argos and GPS), spanning over 30 years, were combined to investigate long-term and seasonal changes in the population distribution of harbour seals and to describe the inter-individual variability in their distribution. Finer-scale GPS data from the more recent deployment were then used to assess individual repeatability of foraging behaviour at different temporal scales and factors that might be influencing it.

Many studies, which have focussed on assessing the drivers of predators searching behaviour (e.g. ARS), used central-place foragers as case studies. In Chapter 3, I investigated the drivers of ARS behaviour in a free-ranging predator: the bottlenose dolphin. Specifically, I first tested the hypothesis that predators use both long-term memory and prey encounters to adjust their fine-scale movement. Second, I tested the hypothesis that recent foraging success would influence a predator's occurrence in a foraging hotspot. I used passive acoustic methods to collect information on dolphin occurrence, movement and foraging behaviour within the study area. I then used the variation in the directionality of clicks detected on an array of PAM recorders to infer dolphin movements and assess whether predator behaviour changed in response to their presence in a historically favoured foraging area and in relation to more recent proxies of prey availability. Finally, I assessed if recent prey encounters increased the probability of dolphin occurrence at foraging hotspots.

Following on from the results of Chapter 3, I aimed to investigate the role of spatial memory in the fine-scale movement of harbour seals. Mixed evidence has been found on the role that prey encounters play in the transition to ARS behaviour of central place foragers, and spatial memory has been hypothesised as a possible additional driver (Weimerskirch *et al.* 2007). In Chapter 4, I tested the hypothesis that both spatial memory and prey encounters would increase the probability of an individual to initiate ARS behaviour. I used biologgers with a GPS sensor, to collect data on the seals at-sea movement, and accelerometers to detect seal prey capture attempts. Hidden Markov Models were then used to classify the seal at-sea movement into behavioural states, in particular to identify times when seals where displaying ARS behaviour, and to identify which drivers influence seals changing behavioural state. To test whether these predators were using spatial memory, I first assessed the repeatability of foraging areas used over consecutive months. Then, I investigated how spatial memory (represented by the areas used during the previous month), and prey encounters influenced the probabilities of seals to initiate ARS behaviour.

Finally, the general discussion summarises the main findings of the thesis (Chapter 2 to 4), discusses some of the wider implications of the results and suggests directions for future studies.

Chapter 2

Individual variability and repeatability as drivers of temporal variation in population distributions

Chapter 2

Individual variability and repeatability as drivers of temporal variation in population distributions

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Abstract

Understanding temporal variation in population distribution is a critical component of any assessment of disturbance impacts or climate change. However, the overall distribution of a population results from the combination of individual movements and home ranges. These, in turn, may be influenced by the life histories and individual responses to the environment. In this study, I used data spanning over 30 years on the at-sea distribution of harbour seals (*Phoca vitulina*) in NE Scotland to assess temporal variation in overall population distribution in relation to observed inter-individual variability. Then I used a Hidden Markov Model to classify movements and identify areas where seals displayed searching behaviour to investigate individual's repeatability of foraging areas and how sexual, seasonal and environmental factors might be influencing it. I found that this population of seals used consistently similar core areas over time, with slight differences in their overall long-term and seasonal distribution, which could be explained by inter-individual variation. I demonstrate that individuals were highly repeatable in their foraging areas over time. There were sexual and seasonal differences in repeatability and the size of foraging areas, with pre-breeding females being more repeatable and using a smaller area than males in the same season. Finally, I found that the stratification of the water column, in particular the depth of the thermocline, influenced the distance between foraging areas visited over two consecutive trips. In conclusion, predator foraging behaviour and distribution was influenced by a variety of factors at different spatial and temporal scales. Quantifying the inter-individual variability in movement and foraging patterns contextualised the variability in population distribution, supporting the importance of accounting for individual preferences and characteristics in conservation and management plans.

Introduction

Describing population distributions is a fundamental starting point for understanding a species' ecology. Typically, this includes identifying critical habitats (Reisinger *et al.* 2018; Hays *et al.* 2019; Lennox *et al.* 2019), describing habitat preferences (Block *et al.* 2011; Pirotta *et al.* 2011; Wilmers *et al.* 2013; Thiers *et al.* 2017) and exploring community interactions (Hebblewhite & Merrill 2007; Matich *et al.* 2011; Roman *et al.* 2014; Breed *et al.* 2017). This information is also required within forecasting tools to assess the impacts of climate change (Hazen *et al.* 2013a; Rutterford *et al.* 2015; Synes *et al.* 2015; Chmura *et al.* 2018; Berteaux & Lai 2021). In particular, the assessment of population distributions over time has been fundamental to detect shifts in distributions (Peschko *et al.* 2016) and to support the efficacy of conservation measures (Arso Civil *et al.* 2019). However, the observed home range of a population and its habitat use are the result of the combination of the movement and preferences of its individuals (Leclerc *et al.* 2016; Van Moorter *et al.* 2016). Across both terrestrial and marine species, more focus has been put into studying individual movement, behaviour and personality (Biro & Stamps 2008; Araujo *et al.* 2011; Patrick & Weimerskirch 2014; Harrison *et al.* 2015; Spiegel *et al.* 2017; Webber *et al.* 2020).

For central place foragers, individuals are often constrained to foraging areas close to their central place (e.g. land haul-out sites for pinnipeds or nests sites for birds), and inter-individual competition for resources can be high (Lewis *et al.* 2001; Wakefield *et al.* 2013; Jessopp *et al.* 2020). To combat negative effects of competition, individuals may specialise in their foraging tactics (Navarro *et al.* 2013; Boyd *et al.* 2014), habitat preferences (Pinaud & Weimerskirch 2007; Kernaleguen *et al.* 2012; Photopoulou *et al.* 2020) and diet (Saulitis *et al.* 2000; Cherel *et al.* 2009; Bodey *et al.* 2018a). Like other personality traits, foraging preferences may change or remain stable over time, resulting in individual behaviour plasticity or repeatability (Patrick & Weimerskirch 2014; Harris *et al.* 2020). Behavioural repeatability has been studied across many species (Bell *et al.* 2009; Patrick *et al.* 2013; Jacoby *et al.* 2014; McHuron *et al.* 2018), in particular in relation to the spatio-temporal complexity and predictability in the distribution of resources, with repeatable movement patterns developing in response to predictable resources (Abrahms *et al.* 2018; Riotte-Lambert & Matthiopoulos 2020). For example, it was found that more heterogeneous and/or predictable habitats should favour a higher level of repeatability (Switzer 1993; Trevail *et al.* 2021).

Predator foraging and movement decisions are shaped by a variety of factors, most of which stem from ecological needs and the characteristics of the surrounding environment (Getz & Saltz 2008; Goossens *et al.* 2020; Williamson *et al.* 2022). The life history and reproductive status of many species will impose different needs and constraints on individuals. For example, lactating fur seals (*Arctocephalus forsteri*) or chick rearing wandering albatrosses (*Diomedea exulans*) must return to their colonies to feed offspring more regularly during the breeding period, which constrain the adults' movement at-sea (Shaffer *et al.* 2003; Page *et al.* 2005). Furthermore, some species display high sexual differences in foraging strategies, such as in their foraging areas (La Boeuf *et al.* 2000b; Phillips *et al.* 2004; Kienle *et al.* 2022), duration and distance travelled during a foraging trip (Thompson *et al.* 1998; Weimerskirch *et al.* 2009; Cleasby *et al.* 2015) and diving depth (Lewis *et al.* 2002; Beck *et al.* 2003). All these factors can influence, and sometimes limit, the habitats available to an individual and therefore affect its decisions. Moreover, the environment can influence predator foraging behaviour directly or indirectly (Nowak *et al.* 2020). For example, predators can be directly influenced by dynamic environmental conditions, such as winds or ocean currents, which can increase or decrease the cost of movement (Lambardi *et al.* 2008; Amelineau *et al.* 2014). More indirectly, environmental conditions also shape the distribution of prey and resources, and thus influence predator's foraging areas (Dragon *et al.* 2010; Cox *et al.* 2018a).

Biologgers are often used to study individuals' movement (Cecere *et al.* 2020), their repeatability (Arthur *et al.* 2015) and factors that influence movement decisions (Iorio-Merlo *et al.* 2022). These have been deployed on many species in both terrestrial and marine environments, underpinning a wealth of studies on many aspects of animal behaviour (Merkle *et al.* 2014; Auger-Methe *et al.* 2016; Carter *et al.* 2016; Cox *et al.* 2016). In addition to providing information on animal locations, biologgers can now also provide greater insights into one of the main drivers of a predator movement: the searching and foraging on prey (Benoit-Bird *et al.* 2013). In particular, area-restricted-search (ARS) behaviour has been used as a common method to characterise foraging behaviour from movement data (Dragon *et al.* 2012). ARS is a movement strategy adopted by predators to maximize their energy intake. In environments where resources are heterogeneously distributed, predators should transit through low quality areas, with highly directed movement, and remain in highly quality areas using a tortuous path (Kareiva & Odell 1987; Benhamou 1992). Studies have used ARS to quantify the repeatability of foraging behaviour, for example by calculating the overlap of foraging patches visited over time (Arthur *et al.* 2015). Furthermore, advances in biologgers now permit the concurrent collection of environmental and movement data (Boehme *et al.* 2009), enabling researchers to investigate the influence of dynamic environmental variable on animal’s movement (Biuw *et al.* 2007; Nowak *et al.* 2020).

The harbour seal (*Phoca vitulina*) is a central place forager inhabiting coastal temperate and arctic waters, and also found along the coasts of the UK (Sharples *et al.* 2012; Thompson *et al.* 2019). Aerial counts and large-scale biologger deployments have been used to monitor populations and describe their at-sea distribution (Thompson *et al.* 2019; Carter *et al.* 2022). Harbour seals in the UK are listed in the Annex II of the EU Habitat Directive (Council of the European Communities 1992) and they are protected under more local legislations such as the Marine Act 2010 in Scotland (Thompson *et al.* 2019). For their conservation and management in the UK, the harbour seal population has been divided into seal management units (SMUs) (Thompson *et al.* 2019; Carroll *et al.* 2020). The population in the Moray Firth, in the North East of Scotland, has been extensively studied since the early 90’s with research focussing on their movement (Thompson 1993; Thompson *et al.* 1994), habitat use (Cordes *et al.* 2011; Bailey *et al.* 2014), foraging behaviour (Thompson & Miller 1990; Tollit *et al.* 1998), diet (Tollit & Thompson 1996; Tollit *et al.* 1997) and more recently on their life histories through a long-term individual based study (Cordes & Thompson 2013, 2014). Although the population of the Moray Firth was not particularly impacted by the Phocine Distemper Virus outbreak in 1988 (Thompson & Miller 1992), the number of individuals remained constrained by active shooting of seals particularly close to protected areas (Thompson *et al.* 2007). Following implementations on shooting regulations, the population has slowly recovered (Matthiopoulos *et al.* 2014).

Recent studies on harbour seal habitat association around the UK found inter-regional differences in the environmental covariates driving populations at-sea distribution (Carter *et al.* 2022). These results highlighted that harbour seal habitat association may vary at smaller spatial scales than their species range, and thus the importance of obtaining data from throughout the population. However, small scale variation in habitat preferences could also arise from inter-individual variability in habitat association (Baylis *et al.* 2012). Furthermore, Carter *et al.* (2022)'s results built on previous studies on habitat association in the Moray Firth (Bailey *et al.* 2014) suggesting that seasonally dynamic environmental features, such as frontal intensity, may also be important drivers of harbour seal distribution in this region. However, as out of the scope of their study, Carter *et al.* (2022) did not explore seasonal changes in harbour seal distribution, and dynamic variables were averaged across the year. The extensive knowledge acquired on the Moray Firth population makes them a good study system to investigate temporal variations in population and individual spatial variability and repeatability.

In this study, I integrated movement data derived from biologgers deployed on individuals from this study population during the last three decades (Thompson *et al.* 1998; Cordes *et al.* 2011; Sharples *et al.* 2012), and aim to: (i) investigate temporal variation in harbour seal distribution, (ii) quantify variability in individual distribution and (iii) repeatability of foraging behaviour, and (iv) assess factors influencing individual repeatability. First, building on previous studies (Bailey *et al.* 2014),I used habitat models to predict seals at-sea distribution over a 4 x 4 km grid and used the Structural Similarity Index to compare model predictions (Jones *et al.* 2016). I used this analysis to assess both long-term (between decades) and seasonal (pre- vs. post-breeding) changes in distribution. Second, I quantified individual variability in at-sea distribution by investigating the number of individuals using each grid cell and assessed temporal changes of core areas distribution. To quantify individual repeatability, I focussed on seal's foraging areas and the spatial overlap of foraging areas in consecutive time periods. Finally, I assessed if seasonal or sexual factors influenced seals foraging site repeatability and foraging area size. While at a finer temporal scale, I investigated how dynamic environmental variables, measured from biologgers, and in particular water column stratification (Carter *et al.* 2022), influenced the distance between foraging patches visited over consecutive trips (Carroll *et al.* 2018).

Methods

Case study species and study area

Between 1988 and 2017, 94 individual seals (42 males and 52 females) were captured at sites within the northern region of the Moray Firth (Loch Fleet or the Dornoch Firth) and tagged with various biologger devices (Table 2.1). Individuals were captured onshore either in September, post moult, or in the late winter (February - March) during the pre-breeding season (Table 2.1). Biologgers were placed on top of their head or at the back of the neck of the animals by attaching them to the animal's hair. For details on the capture and handling methods see Thompson *et al.* (1992) and Russell *et al.* (2016). The capture and handling of animals were carried out under Home Office Licences issued to the University of Aberdeen (Licence No. PPL 60/0126, PPL 60/01351, PPL 60/191) and the Sea Mammal Research Unit (Licence No. 30/2589, 60/3303, 60/4009, 70/7806) with approvals from the respective University Animal Welfare and Ethics Committees. Following technological advancements, tags deployed on seals varied during the study period. Initially, with Very High Frequency (VHF) tags that required manual triangulation of the seal location (Thompson & Miller 1990), followed by ARGOS (Advanced Research and Global Observation Satellite) telemetry tags, which relayed data ashore using satellites (Costa *et al.* 2010b), and more recently with GPS (Global Positioning System) tags that relayed the data using the GSM (Global System) network (McConnell *et al.* 2004) (Table 2.1).

VHF telemetry

To study harbour seal behaviour and foraging ecology, VHF tags were attached to harbour seals between 1989 and 1991 (Thompson *et al.* 1998). VHF tags were used to track individuals' movement at-sea, collecting one position per day, for 6 days per week (Bailey *et al.* 2014). For details on obtaining radio-fixes and uncertainty around the bearings see Springer (1979) and Thompson and Miller (1990).

Table 2.1. *Summary of data available from biologgers deployed on harbour seals in the Moray Firth. Over the last 30 years, seals have been tagged using Very High Frequency (VHF) radio tracking devices, Argos satellite and Global Positioning System (GPS) sensors combined with the mobile phone Global System (GSM) network to relay data ashore.*

Tag type	**Deployment years**	**Number of tags**	**Mean duration (days)**	**Tracked months**	**Sex ratio (Male:Female)**
VHF	1989-1991	21	58	May-Jul, Oct-Feb	12:9
Argos satellite	2004-2007	11	109	Mar-Jul, Sept-Apr	6:5
GPS-GSM	2009, 2014-2017	61	110	Feb-Aug, Sept-March	23:38
Total		93			41:52

Satellite telemetry

As part of a larger study on seal foraging distribution around the UK, eleven satellite relay data loggers (SRDLs) were deployed between 2004 and 2007 (Sharples *et al.* 2012). These biologging devices transmit animal locations using the Argos system. Argos locations are assigned to classes depending on their quality. Low quality locations may have low accuracy and locations errors up to several kilometres (Costa *et al.* 2010b).

GPS-GSM telemetry

Between 2009 and 2017, sixty-one GPS-GSM tags were attached to animals captured at Loch Fleet Nature Reserve to investigate harbour seal foraging areas (Cordes *et al.* 2011) and characterise at sea distribution in relation to offshore windfarm developments (Graham *et al.* 2017). These tags are equipped with a GPS sensor which aims to record a location every time a seal reaches the surface, and then uses the GSM network to relay the data ashore (McConnell *et al.* 2004). On average, locations were recorded every 18 (± 54) minutes which resulted in on average 78 (± 41) locations per day. GPS positions are more accurate than previously deployed sensors, with a measurement error estimated to be within 40 m (Hazel 2009).

GPS-GSM tags were also equipped with a temperature sensor to collect measurements associated with the seal's dive data (Table 2.2). A wet-dry sensor was used to determine when the seals were hauled-out or when they were at-sea. While in the water, temperature was measured every four seconds and data were stored and processed onboard the tag. For the two deepest dives in each hour, twelve temperature readings collected during the ascent phase of the dive were relayed through the GSM network. The relayed temperature readings were those taken at the maximum and minimum depth of the dive, and at 10 broken-stick-points along the ascent phase of the dive (Fedak *et al.* 2001). Given that these where not equally spread through the water column, I first used an interpolation method from the R package *RchivalTag* (Bauer 2017) to obtain a temperature value every 0.5 meters. From the interpolated values I was then able to obtain four metrics. Sea surface and bottom temperature calculated as the mean water temperature between the first two and last two meters of the water column. A stratification index calculated using the standard deviation of the whole water column and, finally, the thermocline depth determined using the 3 m window with the highest temperature gradient through the water column (Bauer 2017).

Table 2.2. *Summary of the number of temperature profiles collected in each year.*

Year	Deployment start	# of animals tagged	Total # temperature profile	Average # of temperature profile per seal
2014	October	12	40,008	3,334
2015	March	12	30,334	2,528
2017	Feb	30	68,574	2,286

State-space modelling to integrate data from different biologgers

I used a state-space model (SSM) to predict seal daily locations while accounting for difference in the error structure between the different biologgers (Bailey *et al.* 2014). The approach was based on models developed by Jonsen *et al.* (2005); (2007), which were originally developed for Argos satellite telemetry data. For the processing of the data collected by VHF and Argos biologgers see Bailey et al. (2014). Here, I combined outputs of this previous study with more recent GPS-GSM data using a similar processing approach within the *bsam* package in R (Jonsen *et al.* 2016), providing estimated GPS locations at daily intervals (Pistorius *et al.* 2017). This state-space model combines a hypothetical movement model with an observation model to provide a probability of obtaining a particular observation given the animal's true locations (Patterson *et al.* 2008; Reid *et al.* 2014). The output of the SSM, or the probability of the states, represents the daily animal spatial locations (Patterson *et al.* 2008). The *bsam* package uses a Bayesian approach with a Markov chain Monte Carlo to estimate daily locations (Jonsen *et al.* 2016). Here, I used 20,000 iterations after a burn-in of 10,000 iterations to remove the effect of initial values. The chain was thinned by keeping every 30th location, to remove the majority of the autocorrelation (Reid *et al.* 2014). Although the *bsam* package (Jonsen *et al.* 2016) was built to be used on Argos satellite telemetry data, it is possible to specify that the locations are to be considered "fixed" (i.e. with very little spatial error - Jonsen *et al.* 2016). Thus, when modelling GPS data, the model assumes the location error to be normally distributed (Jonsen *et al.* 2005).

Habitat modelling

To predict harbour seals at-sea distribution I took a habitat modelling approach using a generalised additive model (GAM) to predict seal occurrence over a 4x4 km grid based on static environmental covariates (Bailey *et al.* 2014). As one of the aims of this study was to assess temporal variation in at-sea distribution of harbour seals over time, the data were split: 1) between 1989-2009 (see Bailey *et al.* 2014) and 2014-2017 for a long-term comparison; and 2) between the pre- (March - July) and post- (September - February) breeding period for a seasonal comparison. Seals were assigned to either season based on the date they were captured (Table S2.1), and data were truncated according to the above defined time periods. The output of the SSM was summarised over a 4 x 4 km grid over the study area, allocating a binary value to each cell representing the presence or absence of any seal daily locations (i.e. 0-1). The entire Moray Firth was considered to be available habitat, but grid cells within 2km of haul-out sites were removed to reduce the bias towards these areas (Bailey *et al.* 2014).

As the main goal of the models was to compare harbour seal distribution between selected time periods, I selected environmental covariates that have been used in previous studies using data from this population (Bailey *et al.* 2014; Carter *et al.* 2022). I used water depth, seabed slope, distance to the nearest haul out site, seabed sediment type and the probability of lesser sandeel (*Ammodytes marinus*) occurrence as environmental covariates in the model (Figure 2.1). Water depth data were derived from SeaZone Hydrospatial Bathymetry (grid tiles: NW25600020, NW25600040, NW25600060 and NW25800040) at a resolution of 6 arcsecond grid. As the resolution of the data was at a finer scale than the 4 x 4 km grid, the mean depth for each cell was calculated (Figure 2.1A). The seabed slope was obtained from the bathymetry data using the terrain function of the *raster* package in R (Figure 2.1B) (Hijmans & van Etten 2012). The seabed sediment type data were also obtained from SeaZone Seabed Sediment (1:250,000 scale, SeaZone Solutions Ltd., UK), and 4 x 4 km grid cells were assigned with the predominant sediment type. Sediment classification was based on Folk (1954) but, following Bailey *et al.* (2014), I initially simplified the classification into sandy mud, muddy sand, gravelly sand, sandy gravel and gravel (Figure 2.1C). However, some sediments were dominant in only a small number of cells (Table S2.2) so, for this analysis, they were further grouped with the most similar sediment type. Distance to the nearest haul out was calculated using the locations of known harbour seal haul-out locations (Bailey *et al.* 2014; SCOS 2020), as well as some additional haul-out sites identified by the GPS data used in this study (Figure 2.2). The probability of lesser sandeel occurrence were obtained at a 200 meters resolution from Marine Scotland (Langton *et al.* 2021), and a mean value taken for each 4 x 4 km grid cell (Figure 2.1D).

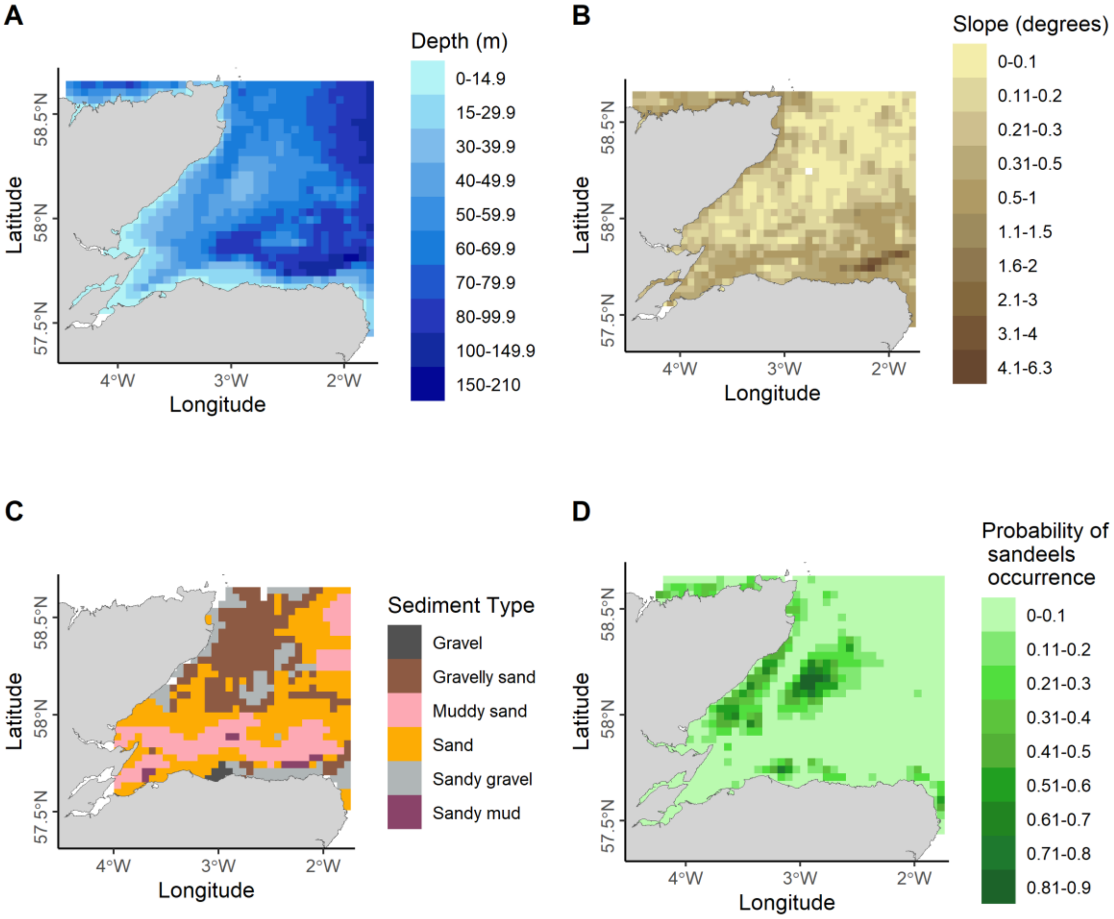

Figure 2.1. *Environmental covariates included in the GAM summarised over the 4 x 4 km grid. A) water depth, B) seabed slope, C) seabed sediment type and D) probability of sandeels occurrence.*

Seal occurrence across the study area was modelled using a GAM with a binomial error distribution and logit link function. The models were fitted using the R package *mgcv* (Wood 2017). The smoother terms for water depth, seabed slope, distance to the nearest haul-out and sandeel probability were derived using penalized regression splines with a shrinkage term (Wood 2017). Validation of the model was carried out using the *DHARMa* R package (Hartig 2021). Spatial correlation between the data was checked using the spline correlogram (Zuur *et al.* 2009). Model selection was performed using a multi-model inference approach, following the one described by Grueber *et al.* (2011). Starting from a model with all the available covariates, Akaike's Information Criterion (AIC) was used for model selection using the *dredge* function in the *MuMIn* package (Burnham & Anderson 2002). A cut off of 2 ΔAIC was used to select candidate models for each time period and season (Burnham & Anderson 2002). Candidate models were then averaged using the function *model.avg* in the *MuMIn* package. The average model was used to predict seal at-sea distribution.

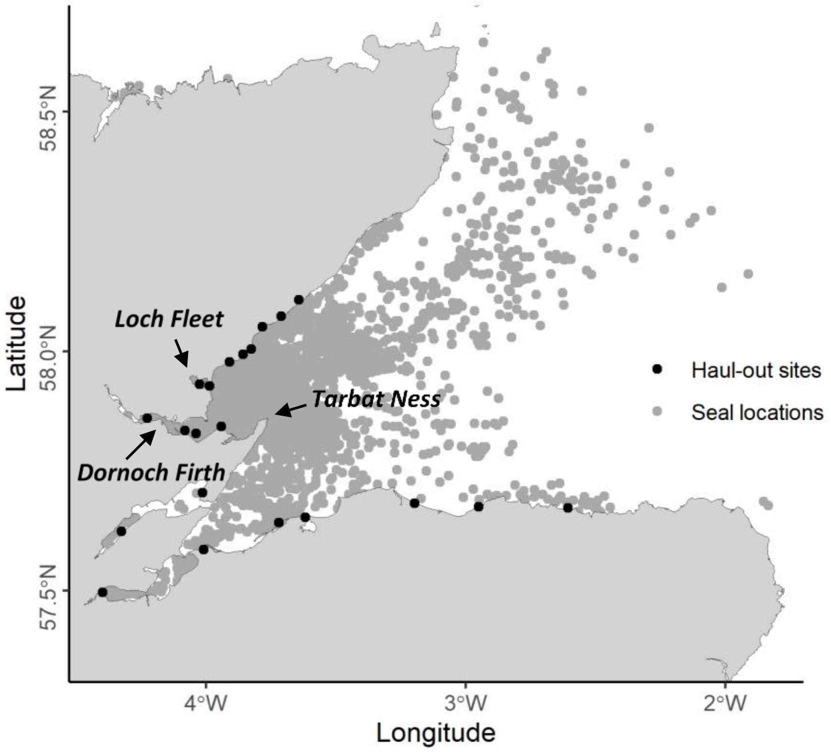

Figure 2.2. *Map showing harbour seal daily locations estimated by the state-space model from all tagging deployments, and the locations of the haul-out sites used to calculate the distance to the nearest haul-out.*

Comparing seal distributions

To investigate variation in distribution between the two time periods (1989-2009 and 2014-2017) and between seasons, I used the method described by Jones *et al.* (2016) to calculate the Structural Similarity Index (SSIM). The index is used to compare ecological maps accounting for prediction uncertainty, and estimates local similarities in the mean, variance and spatial correlation between maps. I compared the GAM models predictions by visualising differences using the similarity in means (SIM), similarity in variance (SIV), similarity in patterns (SIP) and SSIM. These metrics take a value either between 0 and 1, or -1 to 1, representing differences and similarities between the maps, respectively.

Variability in individual distributions

I explored variability in individual seal distributions by calculating the proportion of individuals tagged in each time period, or season, that used each grid cell. In this instance to compare the two maps, I calculated the absolute difference between corresponding cells in each map. The difference took a value between 0 and 1. Values closer to 1 highlighted cells that were disproportionally used by individuals in either time periods.

Identification of ARS behaviour

In addition to assessing temporal variation in overall patterns of at-sea distribution and habitat use, I also used finer-scale GPS data to identify areas in which harbour seals were more likely to forage. To characterise foraging distribution, I analysed harbour seal movement data from 2014-2017 with a Hidden Markov Model (HMM) to identify locations where seals displayed ARS behaviour. Furthermore, I focussed this analysis on foraging trips that were longer than twelve hours and which were return central place trips that started and ended in the same haul-out location (Thompson *et al.* 1998). To avoid misclassification of movement near the haul-out site, I further removed all the locations that occurred within 2km of the haul-out site (Cordes & Thompson 2013).

The HHM used step length and turning angle distributions to classify seals movement into two behavioural states; “Transit”, long directional displacement, and “ARS”, short tortuous path (McClintock *et al.* 2017). I fitted the model using the R package *momentuHMM* (McClintock & Michelot 2018). As HHMs require data to be at fixed time intervals I used a dive batch approach and grouped data into batches of five dives (Iorio-Merlo *et al.* 2022). Dive locations were linearly interpolated from raw GPS locations using the manufacturer software. I used the location of the first dive of each batch to calculate the step length and turning angle between consecutive dive batches.

I assumed these observations followed a state-dependent gamma and wrapped Cauchy distribution respectively (Langrock *et al.* 2012). Large gaps can occur in the GPS data, thus if dive batches were not associated with a raw GPS location, the step length and turning angle were set to “NA” and the state was assigned based solely on the Markov property (for details see Russell *et al.* 2015; Carter *et al.* 2020; Iorio-Merlo *et al.* 2022 and Appendix 4B). Initial values for parameters were selected by using the lowest AIC scoring model out of 50 iterations with randomly selected initial values. Finally, the most likely state sequence was decoded using the Viterbi algorithm (Zucchini & MacDonald 2009).

Individual repeatability of foraging areas

Repeatability of individual foraging areas was assessed by comparing Kernel utilization distributions (UD). Kernel UD were defined using the *adehabitatHR* R package (Calenge 2006), using only those locations classified by the HMM as ARS. This analysis aimed at quantifying individual spatial and temporal repeatability of foraging behaviour. First, I compared the size of the core foraging areas and number of distinct foraging patches used by each individual during the period in which they were tagged. Second, I assessed individual repeatability in foraging patches visited over time by calculating the overlap of utilization distribution of foraging patches between consecutive time periods.

To quantify the size of foraging areas and number of foraging patches used, I calculated the 50% UD of all the ARS classified locations for each individual. A 50% UD was selected to represent the core foraging area used by an individual over time and excludes the occasional foraging site that would be included with a higher percentage (Figure S2.1). Foraging area size was defined as the size in km square of the 50% utilization distribution. As I observed a variability in the number of distinct polygons that represented the 50% UD, I considered the distinct polygons to represent different foraging patches used by an individual. Thus, I used the number of different polygons identified to calculate the number of foraging patches used. If more than one polygon was identified, I summed the size of each polygon to calculate the total foraging area. For the individuals that used more than one patch, I also calculated a median foraging patch size where the median value across polygons was taken.

Furthermore, I assessed an individual's repeatability of foraging behaviour over time at three temporal scales between: consecutive months, consecutive two-weeks periods and consecutive trips. I calculated the 95% UD distribution of ARS locations at the three temporal scales. For this analysis I chose a higher threshold as I wanted to assess the overlap in distribution between two consecutive time periods, considering all the area visited by an individual. To estimate repeatability, I calculated the overlap between kernel distributions using the Bhattacharyya's affinity (BA) index (Bhattacharyya 1943). The BA index takes a value between 0 and 1, indicating no overlap or identical distribution respectively. I calculated UD overlap at all three temporal scales in pair-wise comparison and took a mean value for each individual for each time period (Figure 2.3). At the monthly scale, I split the data into calendar months and calculated the overlap between each pair of consecutive months. While for the two-week period, I split the data into two-weeks blocks starting from the first day of data available. For each individual the observed repeatability was then compared with a null distribution calculated comparing the second month, two-week period or trip, with the first period of another randomly selected individual of the population that was tagged at the same time as described in Figure 2.3.

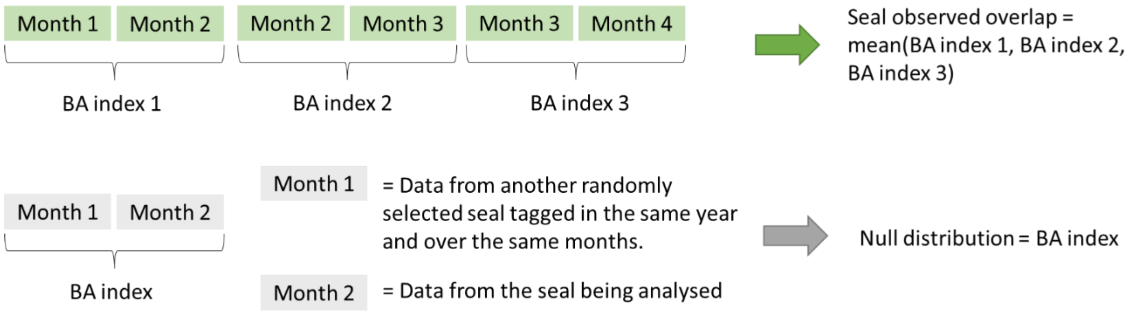

Figure 2.3. *Diagram showing how seals repeatability was assessed at the monthly scale, as an example. The observed seal overlap was calculated using the mean value of BA indices over consecutive months. The null distribution was obtained by calculating the BA index between a seal month 2 data and another randomly selected individual month 1.*

Factors influencing individual's repeatability

Given previous observation of sexual and seasonal differences in harbour seal foraging behaviour (Thompson *et al.* 1998; Sharples *et al.* 2012), I investigated whether these factors also influenced individual repeatability of foraging area. Furthermore, as water column stratification was recognised as an important factor shaping the overall distribution of this seal population (Carter *et al.* 2022), I assessed, at a finer temporal scale, whether the water column stratification encountered by a seal during a foraging trip would influence proximity to the foraging area visited in the following trip.

First, I used Kruskal-Wallis tests to assess if there were differences between males and females and/or between the pre- and post-breeding season in individual's repeatability and the total size of the foraging area used. Where multiple Kruskal-Wallis test were performed, multiple testing was corrected using a pairwise Wilcoxon rank sum test using a Bonferroni correction. Second, I followed the methods by Carroll *et al.* (2018) to assess the influence of water column stratification on the distance between consecutive foraging patches. To determine the distance between foraging areas visited over consecutive trips, I extracted, for each foraging trip, the centroid location of the 95% UD of ARS locations and calculated the distance between the centroids of consecutive trips to obtain a measure of spatial repeatability. I used the temperature data collected by the tags to obtain in situ measurements of the environmental conditions encountered. To increase the sample size of temperature data available for each individual, I extracted all data available from other seals that were within a 5 km buffer of the centroid location during that individual foraging trip. I then took an average value of all four metrics (i.e. sea surface and bottom temperature, stratification index and thermocline depth) from the available dataset. I used a linear mixed effect model with distance between centroids as a response, and the temperature metrics recorded during the first trip, of each pair, as predictors. Bottom and surface temperature were modelled separately due to high collinearity. I also included sex as an additive factor in the model and seal ID as a random effect. To improve model fit I log transformed the distance between centroids. I fitted the model using the functions available in the *lme4* R package (Bates *et al.* 2015). Validation of the model was done using the *DHARMa* R package (Hartig 2021). Temporall correlation was assessed using autocorrelation plots. All analyses were carried out in R (*version 4.1.1*) (R Core Team 2021).

Results

A total of 94 tags were deployed between 1989 and 2017 (Table 2.1). Argos and GPS tags lasted a similar duration, while VHF tags collected data over a shorter time period (Table 2.1). The locations derived from the SSM showed a high degree of overlap between the three tag types within the Inner Moray Firth, with the majority of locations occurring near Loch Fleet, the Dornoch Firth and the nearby headland (Figure 2.4). The Argos locations had the greatest dispersal in particular in the northeast part of the Moray Firth (Figure 2.4A). While the GPS tags deployed between 2014 and 2017 highlighted a higher usage of the coastal areas around the northern coast of the Moray Firth, which was not observed in the earlier dataset (Figure 2.4B). SSM daily summary locations well represented the variability observed in the raw GPS locations collected by the GPS-GSM tags deployed between 2014 and 2017 (Figure S2.2).

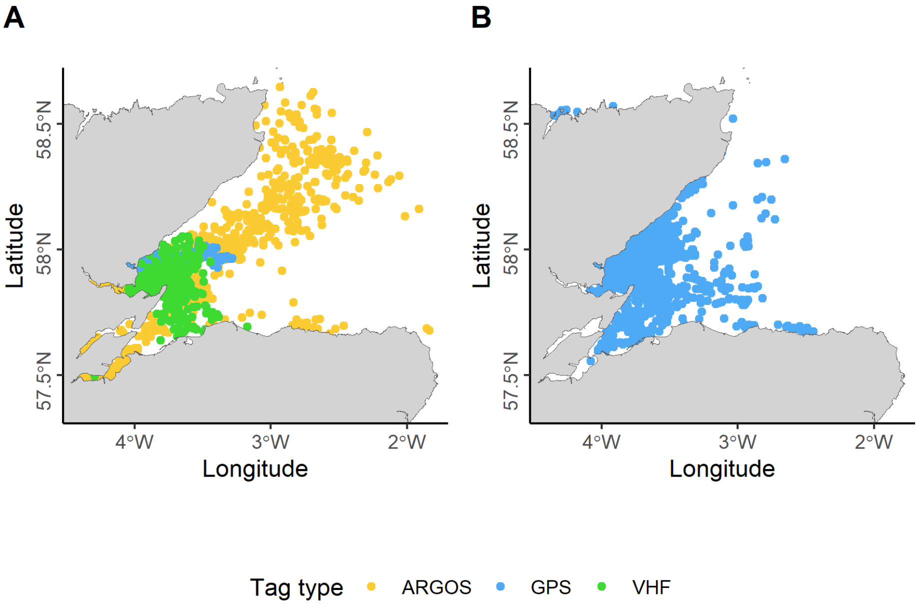

Figure 2.4. *Daily harbour seal locations estimated by the state-space model (SSM) from for the three biologgers types: VHF (green), Argos (yellow), GPS (blue). A) Tags deployed between 1989 and 2009 (VHF = 21, Argos = 11, GPS = 5). B) Tags deployed between 2014 and 2017 (GPS = 56).*

Temporal patterns in seal distributions

The GAM models confirmed that similar factors influenced harbour seal distribution in the two time periods (Table S2.3), all covariates being retained in the candidate models (Table S2.4 and Table S2.5). Bathymetry, distance to the nearest haul-out site and seabed slope all had an overall negative relationship with higher seal probability of occurrence in shallower flat coastal areas (Figure S2.3 and Figure S2.4). In both time periods seals were negatively associated with sandy gravel sediment (Figure S2.3 and Figure S2.4), while in the most recent dataset, seals were positively associated with muddy sand sediment (Figure S2.4). Although sandeel probability was retained in the candidate models for both time periods, it had no influence on seal occurrence with the oldest dataset (Figure S2.3), and bell-shaped relationship with the most recent data, with the highest probability of seal occurrence at intermediate sandeel probability (Figure S2.4). Both models predicted a high probability of seal occurrence in the inner part of the Moray Firth, with some variability between models in the predictions in the offshore areas (Figure 2.5).

I used the Similarity in Means (SIM), Similarity in Variance (SIV), Similarity in Patterns (SIP) and the overall Structural Similarity Index (SSIM) to investigate differences in the predicted probability of seal occurrence in the two time periods (Figure 2.6). Figure 2.6A shows the Similarity in Means. Areas where the SIM value was close to 1 (yellow) were those where predictions were high or low in both time periods. For example, both maps predicted a high probability of occurrence in the inner part of the Moray Firth and in most coastal areas (Figure 2.5B). On the other hand, values of SIM close to 0 (red) were areas with contrasting probabilities of occurrence. Offshore areas that were used between 1989 and 2009, particularly by Argos tagged seals (Figure 2.4), were not equally used in the more recent years. In contrast, I observed a higher probability of seal occurrence associated with the two deep water pockets along the southern coast (Figure 2.5B) in recent years. Figure 2.6B shows the Similarity in Variance, with areas where the two maps were similar (yellow) or differed (red) in variance. This metric accounts for the variability associated with the predictions. For example, the areas around the South coast were less marked compared to the SIM (Figure 2.6A) indicating that, although these were used in the more recent years, their use was more sporadic and associated with specific areas (Figure 2.5B).

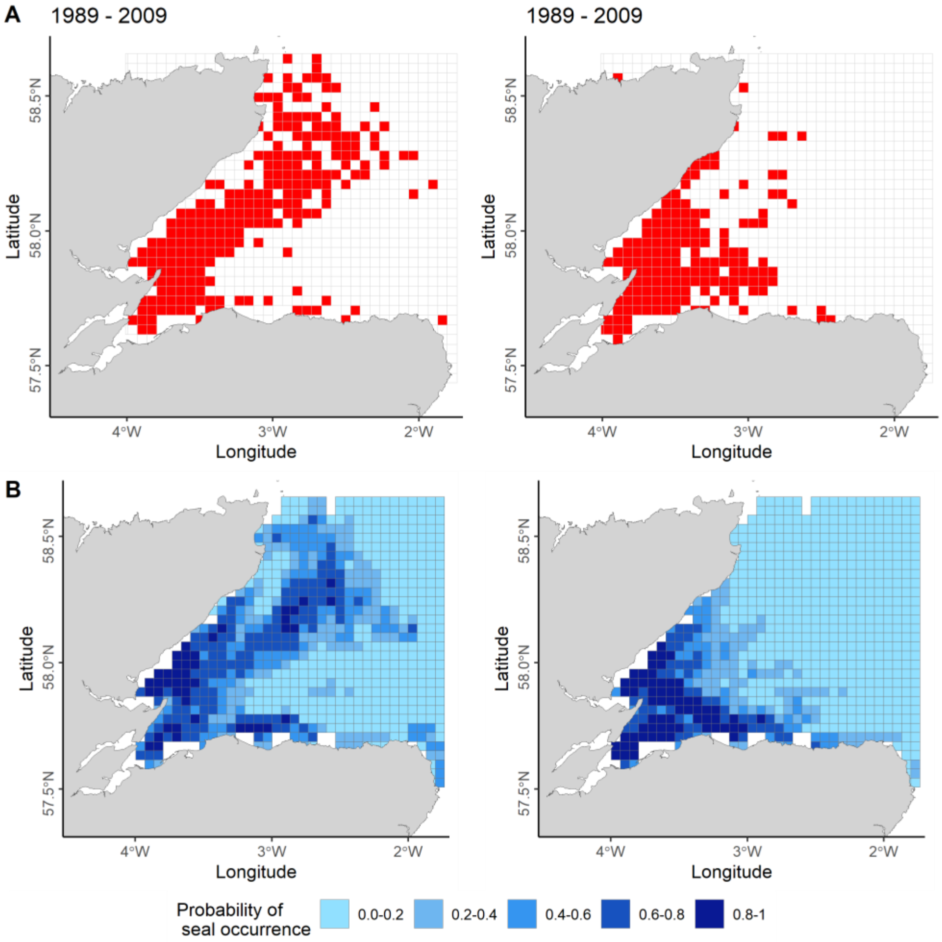

Figure 2.5. *A) Presence (red) and absence (white) of harbour seal daily locations in each 4 x 4 km cell grid. B) GAM predicted probabilities of harbour seal occurrence in each cell grid.*

The SIP showed the spatial covariance between the two maps accounting for the spatial structure of low and high predictions. In areas where the SIP values were close to 1 (yellow), the spatial structure between the probabilities was similar, meaning areas with high and/or low variance overlapped between the two maps (Figure 2.6C). This highlighted areas where the population was either using or not using the same areas in the two time periods. For example, offshore areas had a widespread high probability in the first time period but a low probability across the area in the more recent ones (Figure 2.5B). Thus, the spatial structure was similar between the two maps. Where SIP values were close to 0 (orange) the two maps were independent of each other. While areas where the SIP was close to -1 (red) highlighted areas where seal use differed between the two maps. For example, the coastal areas along the north coast of the Moray Firth were highly variable in probability in both maps, and there was little correspondence between high and low probabilities (Figure 2.5B). Finally, the SSIM is a product of the three values (Figure 2.6D). The mean value of the SSIM (SSIM = 0.36) showed a positive spatial structure between the underlying maps.

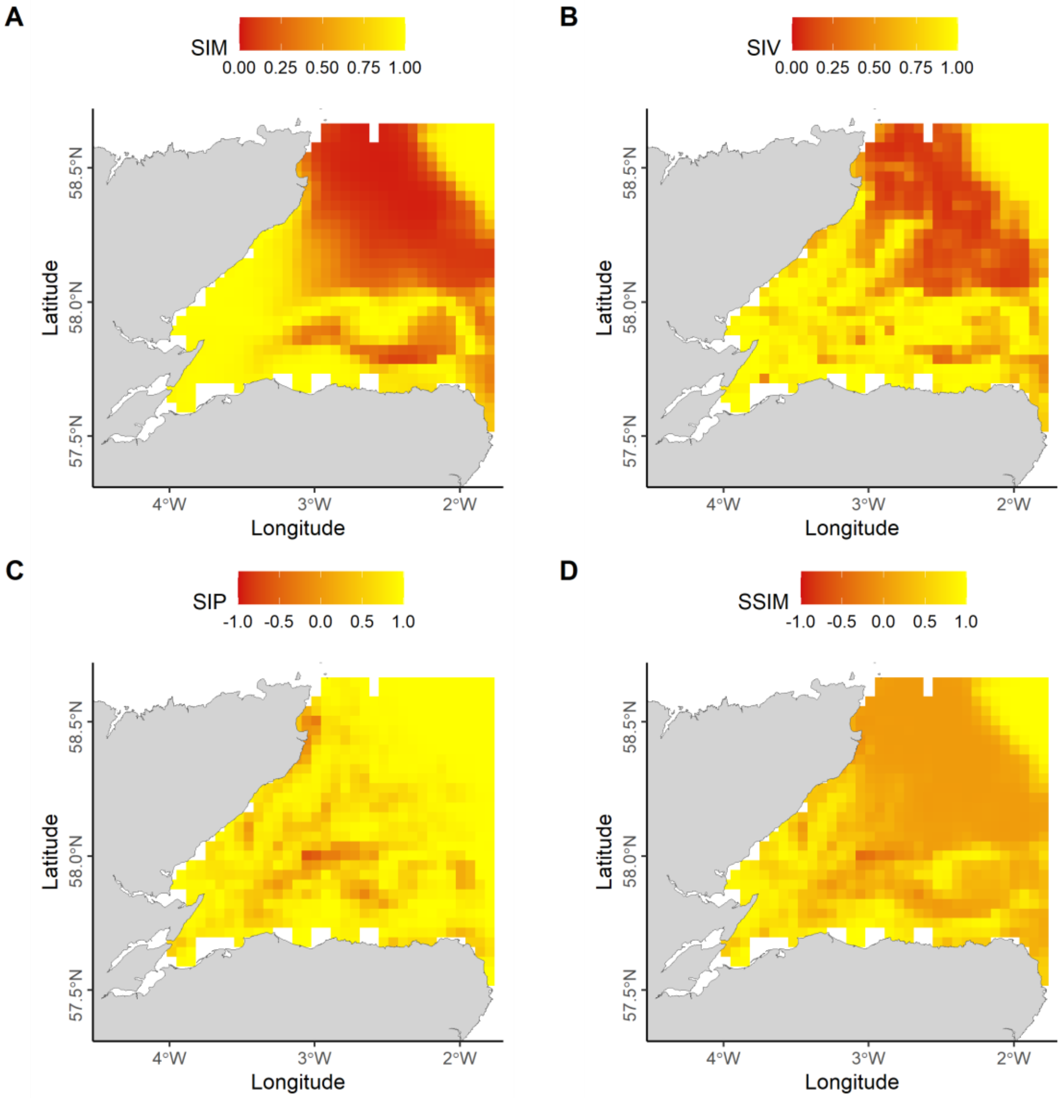

Figure 2.6. *Map comparison of the predicted probability of harbour seal occurrence between 1989-2009 and 2014-2017. The methods by Jones et al. (2016) were used to calculate: A) Similarity in Mean, B) Similarity in Variance, C) Similarity in Pattern and D) Structural Similarity Index.*

Harbour seal seasonal distribution

The GAMs results showed that all covariates were retained in the final models fort both the pre- and post-breeding season (Table S2.6, Table S2.7 and Table S2.8). I found that both models predicted harbour seal distribution to respond similarly to the covariates (Figure S2.5 and Figure S2.6). Seal probability of occurrence was highest in the Inner Moray Firth in both periods (Figure 2.7A) but, during the post-breeding season, the model predicted a higher probability of occurrence in the offshore areas (Figure 2.7A). Overall, all SSIM indices highlighted an agreement between the predictions of the two maps (Figure 2.7B).

Variability in individual's distribution

To investigate the extent to which individual distributions reflected the wider population distribution (Figure 2.5 and Figure 2.7A), I compared the spatial variation in the proportion of individuals using each grid cell during the two time periods (Figure 2.8). The majority of the cells in the grid were used by less than 10% of the seals tagged (Figure 2.8A). However, cells in areas close to the haul-out sites, Loch Fleet, the Dornoch Firth and the water surrounding Tarbat Ness, were used by a high proportion of seals. This pattern was similar between the two time periods, although more recent data showed a greater use in the cells closest to Loch Fleet (Figure 2.8B).

Similar patterns were observed comparing the individual distributions in the pre- and post-breeding season (Figure 2.9). Heavily used areas were those close to haul-out sites, with the rest of the cells being used by just a few individuals. There was a higher proportion of individuals using the foraging areas eastward from Tarbat Ness in the postbreeding season (Figure 2.9A), which was highlighted as one of the areas used differently in the two seasons (Figure 2.9B).

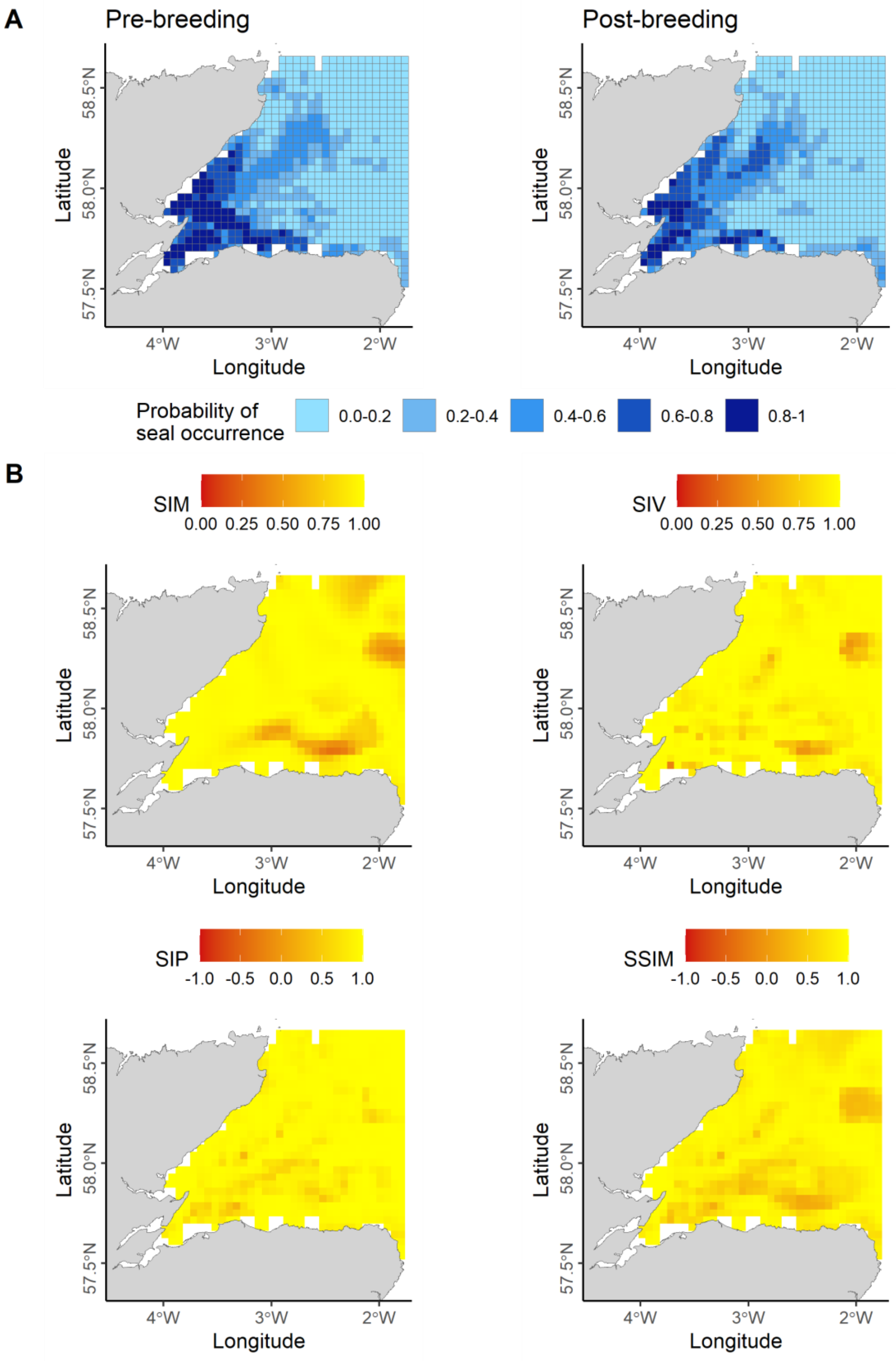

Figure 2.7. *A) GAM predicted probabilities of harbour seal occurrence during the pre- and post-breeding season. B) Map comparison of predicted seal probability occurrence during the pre- and post-breeding season using Jones et al. (2016) methods. In order left to right, top to bottom, the Similarity in Means, the Similarity in Variance, the Similarity in Patterns and the Structural Similiarity Index.*

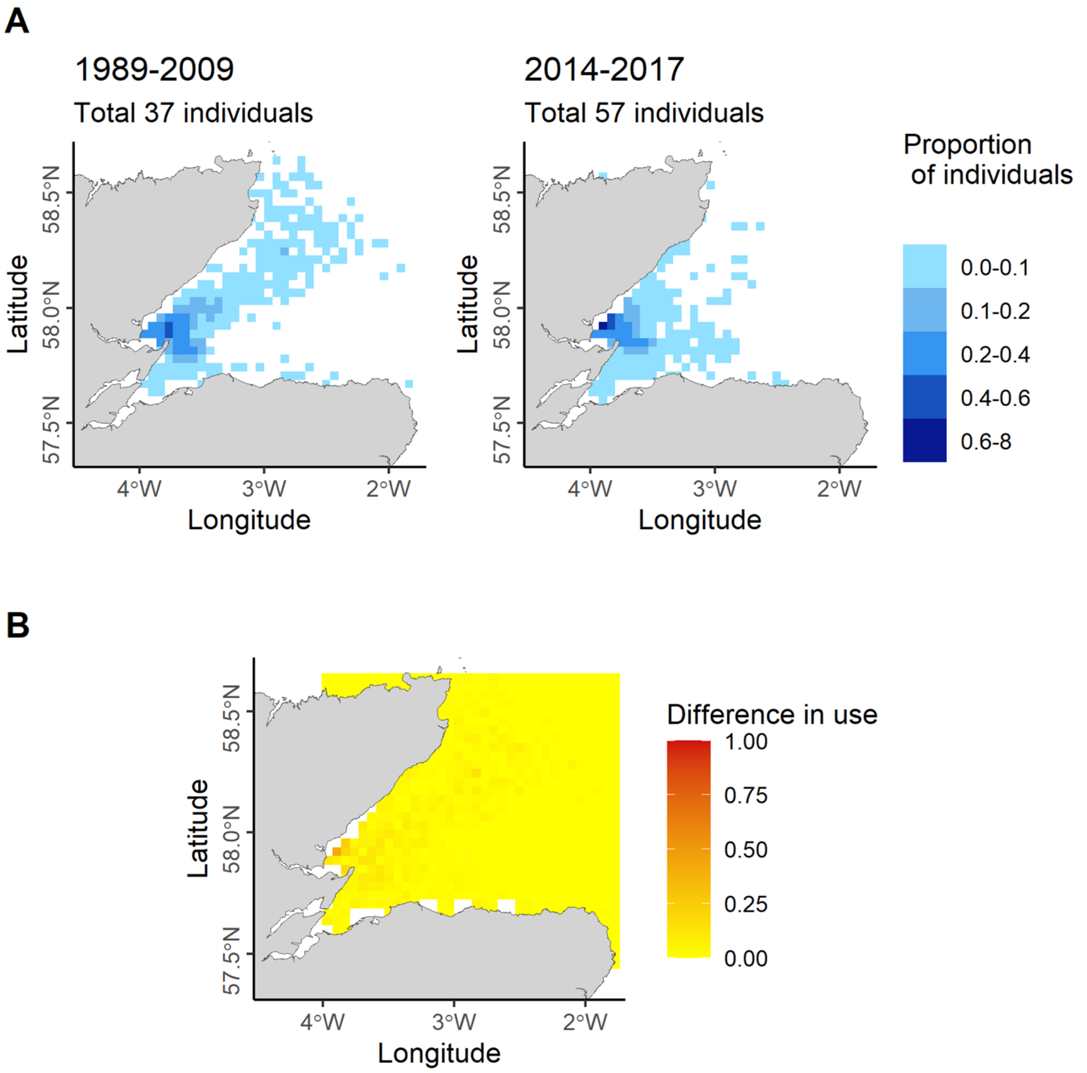

Figure 2.8. *A) Maps showing the proportion of individuals tagged in each time period for which a daily location was found in each cell. B) Absolute difference between the proportion of individuals using each cell in the two time periods.*

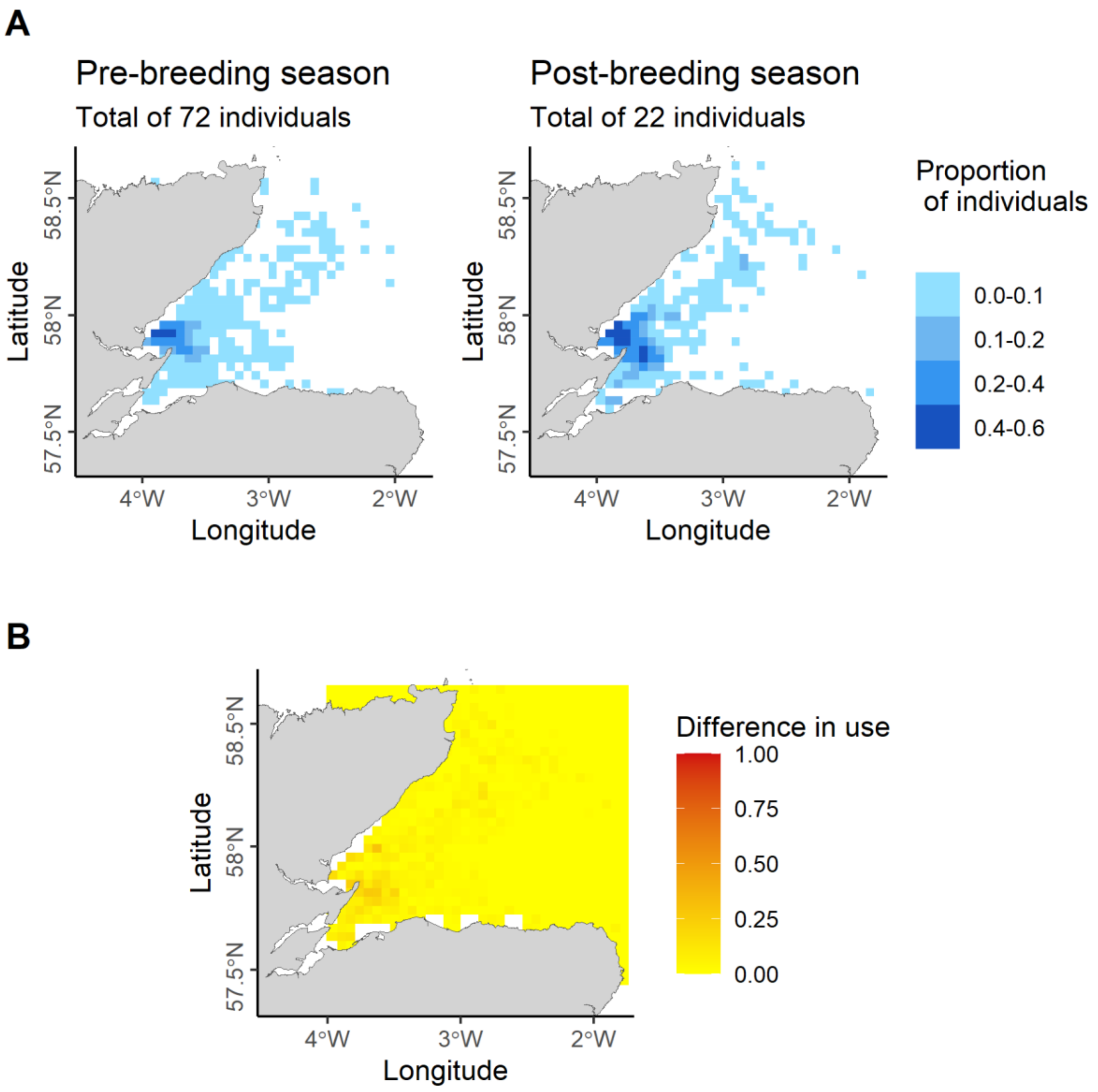

Figure 2.9. *A) Maps showing the proportion of individuals tagged in the pre-breeding and post-breeding for which a daily location was found in each cell. B) Absolute difference between the proportion of individuals using each cell in the two seasons.*

Size and repeatability of an individual's foraging area

I used an HMM to classify seal dive batches during foraging trips into two states: ARS and Transit (Figure S2.7). I assumed the state with the shortest step length (state 1: 199.67 m ± 177.10, state 2: 986.31 m ± 558.28) and highest turning angle (state 1: $\mu = 0$, $\gamma = 0.83$, state 2: $\mu = 0$, $\gamma = 0.38$) to represent the ARS state.

I was able to use the number of distinct polygons identified by the 50% UD to calculate the number of core foraging patches used by each individual (Figure 2.10). Half of the seals tagged between 2014 and 2017 concentrated their foraging effort in one foraging patch, while the other half used two or more (Table 2.3).

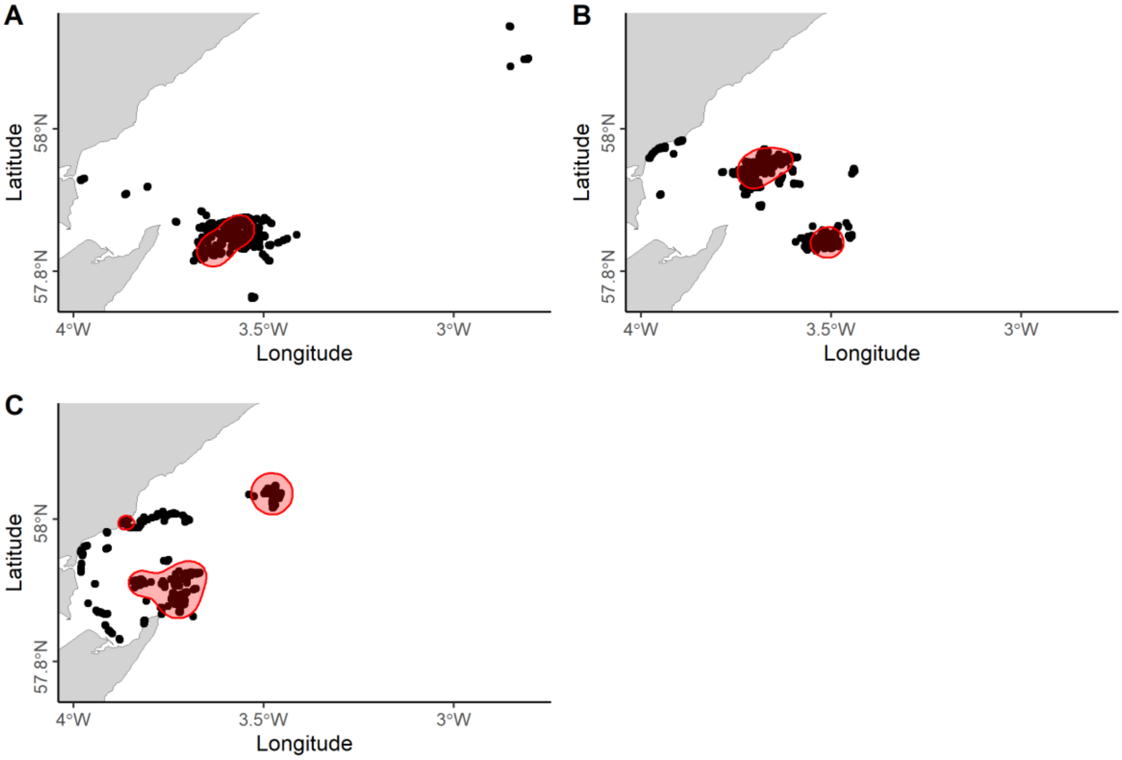

Figure 2.10. *50% kernel density utilization distribution (red) of all the locations classified as ARS (black) during the tag deployment period for three individuals for which A) one, B) two and C) three distinct foraging patches were identified. The maps represent the foraging areas used by seal ID 90 between October 2014 and February 2015, seal ID 53 between March and June 2017 and seal ID 264 between March and June 2015, respectively.*

Table 2.3. *Number of individual harbour seals by sex, and total, using one or more foraging patches during the tagging period, identified by the distinct number of polygons in the 50% kernel UD distribution of ARS locations.*

Number of foraging patches used	**Number of Females**	**Number of males**	**Total**
Highly repeatable (1 patch)	23	8	31
Switching between 2 patches	10	7	17
Highly variable (>2 patches)	0	7	7

The size of the total foraging area used by each individual significantly increased (*Kruskal-Wallis: H = 33.81, p < 0.001*) with the number of foraging patches used (Figure 2.11A). However, the size of the distinct foraging patches was not affected (*Kruskal-Wallis: H = 4.05, p = 0.132*) by the number of patches used by the individuals (Figure 2.11B). Furthermore, individual monthly repeatability of foraging areas decreased (*Kruskal-Wallis: H = 27.62, p < 0.001*) with the number of foraging patches used (Figure 2.11C).

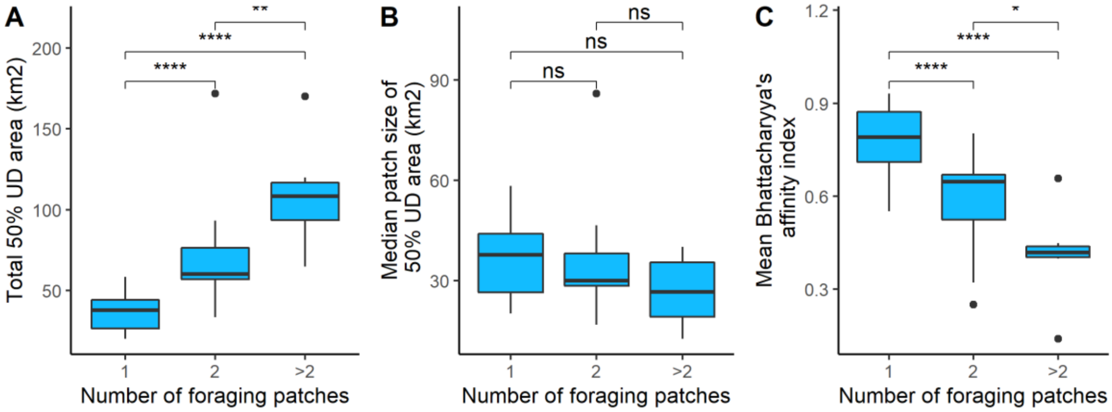

Figure 2.11. *Comparison between individuals using one or more foraging patches of A) total foraging area (50% UD) size in kilometer-squares, B) median size of the foraging patches and C) mean Bhattacharyya's affinity index (i.e. overlap) between 95% UD distribution of ARS location used by individual seals over consecutive months. Foraging patches are defined as 50% UD polygons. If more than one polygon was identified, the area of the polygons was summed. Significance of pairwise wilcox test corrected for multiple testing.*

Furthermore, I found that the individuals were highly repeatable in the foraging patches visited repeatedly over consecutive months, and this remained high at both longer and shorter temporal scales (Figure 2.12). At a longer time-scale, I was able to compare the 95% utilization distribution of foraging areas for five individuals that were tagged twice, two in different breeding seasons and three in the same season (Figure S2.8).

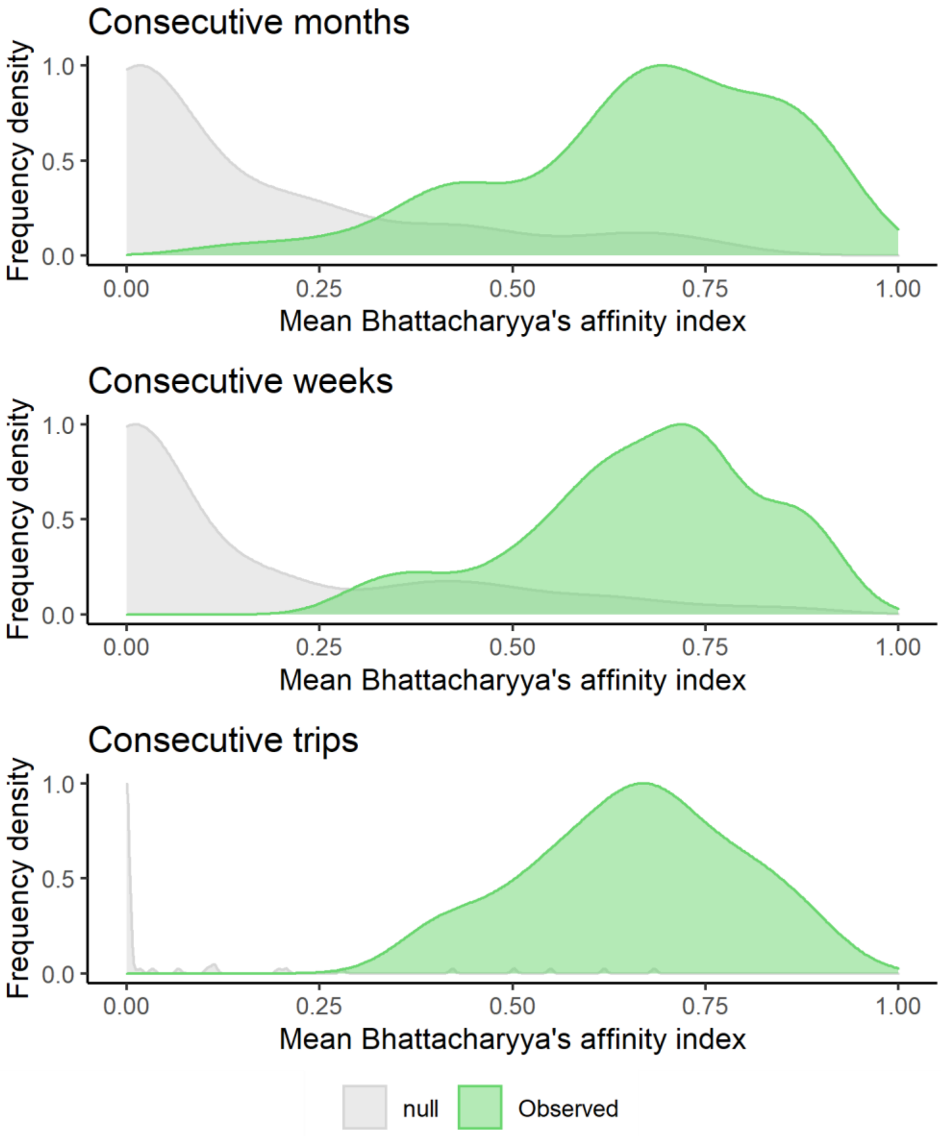

Figure 2.12. *Frequency distribution of the observed overlap (green) of an individual 95% UD of ARS locations calculated using the Bhattacharyya's affinity index at three temporal scales (consecutive months, two-weeks periods and trips), and the null distribution (grey) of Bhattacharyya's affinity index values from the overlap with the 95% UD distribution of ARS locations with another randomly selected individual.*

Sexual and seasonal differences in individual repeatability and foraging area size

Out of the fifty-seven seals tagged between 2014 and 2017, fourteen were tagged in September of 2014 providing data throughout the post-breeding season, while the other forty-three were tagged in February 2015 and 2017, providing data during the pre-breeding season (Table S2.1). I found that there was a significant difference in repeatability between the sexes and between the pre and post breeding season (*Kruskal-Wallis: H = 13.647, p = 0.003*). Specifically, there was a significant difference between male and females during the pre-breeding season (Figure 2.13A).

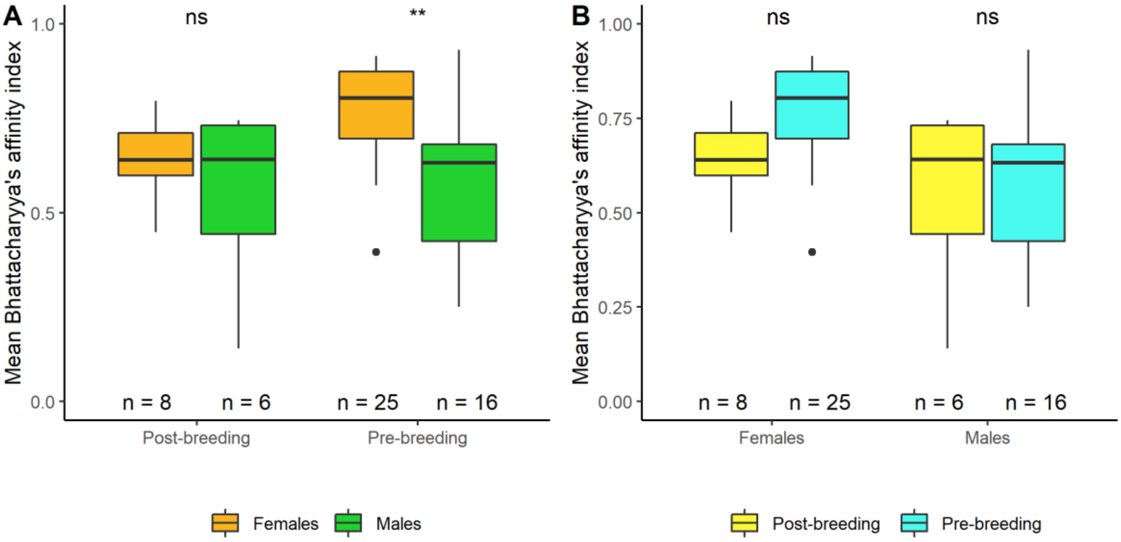

Figure 2.13. *Mean Bhattacharyya's affinity index (i.e. overlap) between 95% UD distribution of ARS locations used by individual harbour seals over consecutive months. A) Compares overlap between the sexes during the pre- and post-breeding period. B) Compares overlap between the pre- and post-breeding period within the two sexes. Significance of the Kruskal-wallis test corrected for multiple testing is reported at the top.*

Similar patterns were seen in the size of the total foraging area used by individuals (*Kruskal-Wallis: H = 12.45, p = 0.006*), with males using a significantly larger area than females during the pre-breeding season (Figure 2.14A).

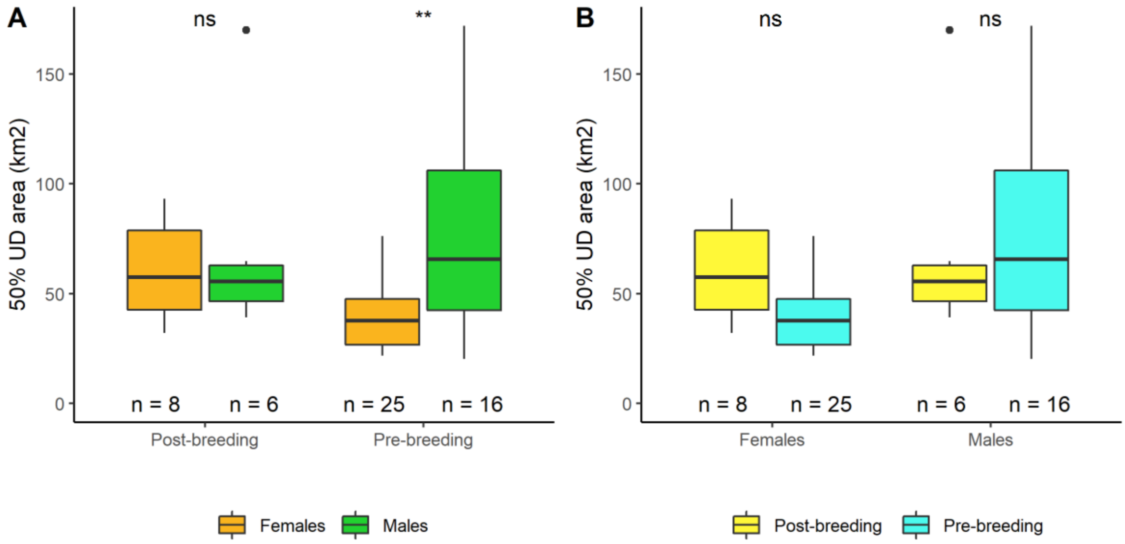

Figure 2.14. *Total area size in kilometer-squares of the 50% UD distribution of the ARS locations used by harbour seals during the tag deployment. A) Compares size between the sexes during the pre- and post-breeding period. B) Compares size between the pre- and post-breeding period within the two sexes. Significance of the Kruskal-wallis test corrected for multiple testing is reported at the top.*

Influence of water column stratification on individual’s repeatability

Pooled temperature data from all seals showed an increase in temperature during the summer months and the formation of the thermocline during spring (Figure 2.15). Although, there was some spatial variability in water column stratification in the study area (Figure 2.16).

The results of the linear mixed effect model showed that the depth of the thermocline encountered during a foraging trip and the sex of the individual significantly influenced the distance between foraging patches used by seals in consecutive foraging trips (Table 2.4). In particular, seals were more likely to return to feed near patches where the water column was more stratified (characterised by a shallower thermocline - Figure 2.17A). Furthermore, in agreement with previous results on repeatability found in this study (Figure 2.13), there was a significant difference in the distance between consecutive foraging patches between males and females, with males travelling greater distances between consecutive foraging patches (Figure 2.17B). The stratification index calculated as the standard deviation of the water column and the surface temperature, although not significant were retained during model selection as improved model fit. The marginal R^2 for this model was 0.07 and the conditional R^2 was 0.16.

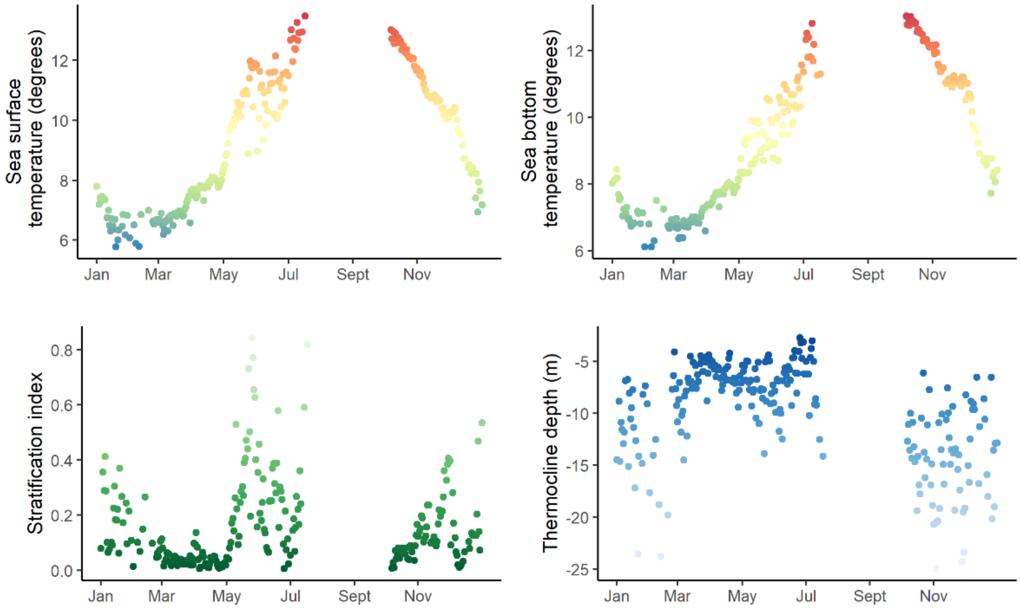

Figure 2.15. *From top to bottom, left to right: Daily median surface and bottom water temperature in degrees celsius, stratification index calculated as the standard deviation of the water column and the estimated depth of the thermocline. The plots combine data collected in 2014, 2015 and 2017.*

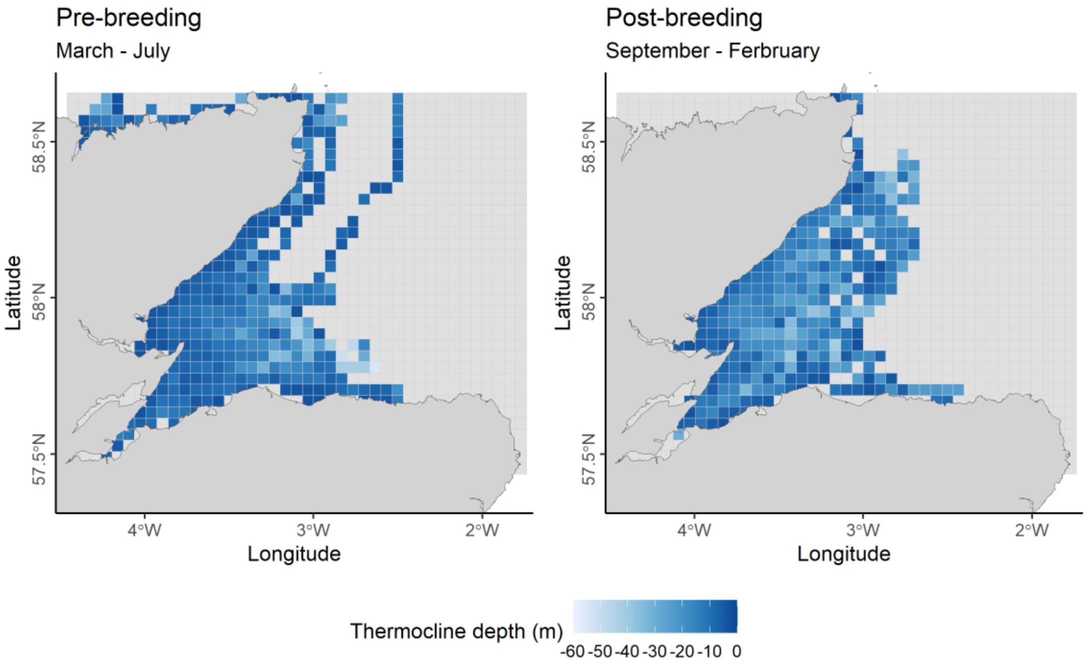

Figure 2.16. *Spatial variation of the stratification of the water column as defined by the thermocline depth. Median thermocline depth was taken for each 4 x 4 km grid cell for the two seasons.*

Table 2.4. *Linear mixed effect model results showing the significance influence of the covariates on the distance between foraging patches centroid of consecutive trips.*

	Chi-square	**DF**	**P-value**
Thermocline Depth	50.76	1	<0.001***
Surface Temperature	0.09	1	0.757
Stratification index	2.61	1	0.106
Sex	6.13	1	0.013*

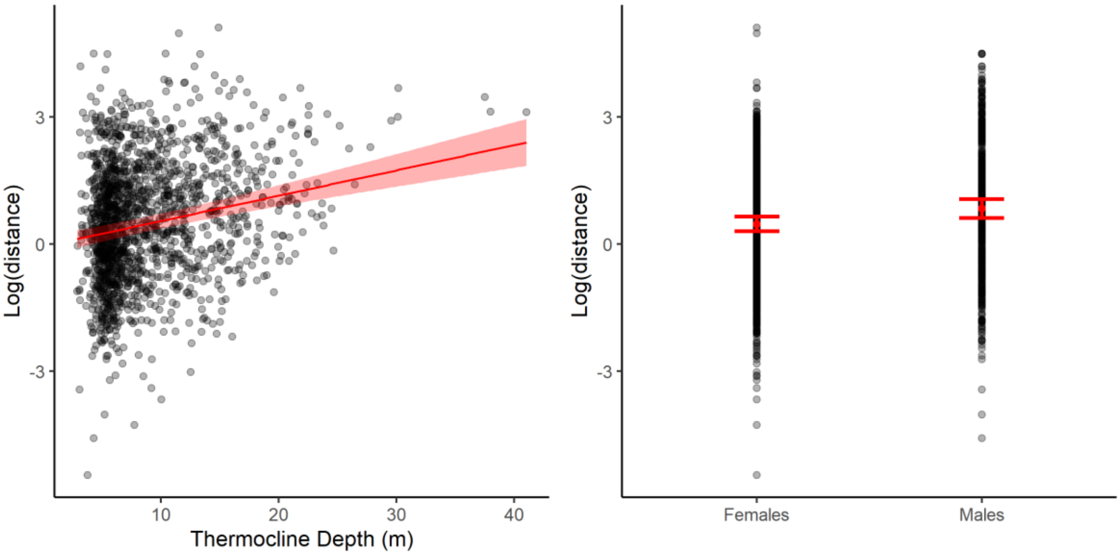

Figure 2.17. *Results of the linear mixed effect model. Left: Increase in distance between the centroids of foraging patches visited during consecutive trips in response to the thermocline depth encountered during a trip. Right: Difference between males and females in the distance travelled between consecutive foraging patches. In both plots raw data are displayed in black and model predictions in red.*

Discussion

In this study, I used long-term data on the movement of harbour seal to assess temporal changes in distribution in the Moray Firth (Scotland) and the inter-individual variability of foraging behaviour within the population. I have shown that seal distribution remained consistent over the last 30 years, and slight differences observed between the two long-term time periods (1989-2009 *vs* 2014-2017) could be explained by individual variation of seals tagged. Similarly, I did not detect any apparent differences in population level distribution between the pre- and post-breeding season. Changes in female's foraging area size, during the pre-breeding season, indicate that more subtle changes were occurring at the individual level. I then focussed the analysis on the more recent data, and assessed the number, size and repeatability of foraging patches used by individuals over time. The total foraging area used by a seal increased with the number of distinct patches, but the size of individual patches was independent of the number of patches used by an individual. To quantify the repeatability of individual foraging behaviour I used the overlap of ARS locations distribution between consecutive months, two week periods and trips. I found that the foraging areas used were highly repeatable at all three temporal scales investigated, but repeatability decreased with the number of foraging patches used. Finally, I assessed whether sexual, seasonal or environmental factors influenced seals repeatability. Females during the pre-breeding season were significantly more repeatable and used a smaller foraging area than males. When assessed at the foraging trip scale, seal site fidelity during consecutive trips was influenced by the level of water stratification indicated by the thermocline depth.

The results of the habitat models showed that harbour seal occurrence was associated with habitat characteristics, such as water depth, distance to the nearest haul-out and sediment type. These results agree with previous research done on this population (Bailey *et al.* 2014; Carter *et al.* 2022). Bathymetry and distance to the haul-out site are two common drivers of harbour seals distribution around the UK (Carter *et al.* 2022) and in other parts of their range (Grigg *et al.* 2012; Blanchet *et al.* 2014). However, the association with other environmental features can be more variable between populations or colonies (Huon *et al.* 2021; Carter *et al.* 2022). For example, the association with seabed slope was retained in all the final models for this population, but it was not found to be important in other parts of the UK (Carter *et al.* 2022) and it showed an opposite relationship to other populations experiencing different environments (Blanchet *et al.* 2014). Recent studies have also suggested the use of more complex descriptions of seabed morphology which future studies should investigate for this population (Wyles *et al.* 2022). Furthermore, in contrast to Carter *et al.* (2022) results, I found an influence of sediment type on harbour seal occurrence, with a preference for muddy sand substrate in three out of four models. These differences in results may arise from discrepancies in sediment type classification or summary of sediment type over different grid sizes, this study used a 4 x 4 km grid, while Carter *et al.* (2022) used 5 x 5 km.

Predator distribution is generally assumed to be associated with suitable habitat for key prey species (Tollit *et al.* 1998; Bailey *et al.* 2014). Although probability of sandeel occurrence (Langton *et al.* 2021) was retained in all models, I only found a relationship with the covariate in the model with the most recent GPS data. This could be explained by the fact that sandeels are an important prey species for harbour seals, but early studies found that this population had a seasonal (Pierce *et al.* 1991) and inter-annual (Thompson *et al.* 1997) variation in diet, with clupeids and gadoids as other important prey species (Tollit *et al.* 1997). While, recent studies have confirmed the utmost importance of sandeels in the diet of harbour seals in the Moray Firth (Wilson & Hammond 2019), which would support the relationship found between sandeel probability and seal occurrence. Furthermore, it could be hypothesised that the reason why the covariate did not display a strong influence is the spatial scale at which sandeel probability was summarised. The data from Langton *et al.* (2021) was available at a 200 meters resolution, but to be included in the model it was summarised at a 4 x 4 km resolution, which could have caused the loss of some smaller localised hotspots used by the seals. The spatial and temporal scale at which data are being analysed has often influenced the ability of identifying predator-prey association in the wild (Fauchald & Tveraa 2003; Wakefield *et al.* 2009). Future studies should assess the spatial association of harbour seals with sandeel probability of occurrence at a finer-spatial scale.

The comparison between the predictions of the probability of seal occurrence between 1989-2009 and 2014-2017 indicated, that despite an overall agreement, some areas were used differently in the two time period, notably the areas surrounding the Smith Bank. This sand bank is found in the north-east of the Moray Firth and is known to be important for many marine predators (Mudge & Crooke 1986; Thompson *et al.* 2015; Risch *et al.* 2019; Williamson *et al.* 2022). However, by exploring the number of individuals using each cell, I showed that those areas were only used by a small number of tagged individuals. This suggests that the differences observed may have been due to variability in movement patterns between the individuals tagged in the two time periods, rather than a shift in population distribution. Individual variability in movement patterns within populations has been previously described in pinnipeds (Austin *et al.* 2004), and it has been highlighted as a challenge for conservation measures and management plans (Cooke 2008) as it may limit the population level inference that can be drawn from biologging data (Lindberg & Walker 2007; Hebblewhite & Haydon 2010). Thus, quantifying and characterising such variability, as done here, provides important information to contextualise the overall population distribution observed. Finally, population level inference should be done in consideration of the individuals sampled and the possibility that these may not be a representative sample, as outlined by the STRANGE framework (Webster & Rutz 2020). In this study, seals were tagged while haul-out on land, thus individuals that haul-out more frequently or spend more time hauling out may have a higher chance to be caught (Thompson *et al.* 1989; Cunningham *et al.* 2009). To remove any behavioural change caused by the deployment of the tag, the first week of data post tag deployment was removed from the analysis.

The data used in this study have been collected prior to the construction of two offshore windfarms currently operating on the Smith Bank (Benhemma-Le Gall *et al.* 2021). There is evidence of windfarms having a reef effect that leads to an increase of predator occurrence in the surrounding areas (Scheidat *et al.* 2011; Russell *et al.* 2014). For example, harbour and grey seals (*Halichoerus grypus*) had a higher probability of displaying foraging behaviour in proximity to offshore structures (Russell *et al.* 2014). Thus, future studies should focus on assessing changes in distribution and movement patterns in response to the presence of these offshore windfarms, and whether it will become a point of attraction for this population. The inter-individual variability observed will be necessary to contextualise any future changes observed. Especially, to account for the fact that differences in movement patterns may affect how individuals are exposed to threats (Thiers *et al.* 2014) and their ability to cope with changes in their environment (Patrick & Weimerskirch 2014).

Despite evidence for a seasonal variation in diet (Pierce *et al.* 1991; Tollit & Thompson 1996) and movement (Sharples *et al.* 2012), harbour seal probability of occurrence in the pre- and post-breeding season was consistent with individuals using most of the areas available to them. In contrast to other studies on pinnipeds (Allegue *et al.* 2022), there was no apparent seasonal change in their distribution. On the other hand, the lack of changes in at-sea distribution agrees with the lack of seasonal patterns in fidelity to haul-out sites observed in this population (Cordes & Thompson 2015). Furthermore, predators might be adjusting other behavioural patterns to those of their prey, such as their diving behaviour (Elliott *et al.* 2008; Jessopp *et al.* 2013b) or diel pattern (Schreer *et al.* 2001; Biuw *et al.* 2010; Blanchet *et al.* 2015) while maintaining a similar spatial distribution. Especially in both seasons the area around the headland near the Dornoch Firth was consistently used by between 20 and 40 percent of the individuals tagged. The slight change in the number of individuals using the area east of Tarbat Ness during the post-breeding season, confirms observations from previous studies on harbour seals seasonal distribution in the Moray Firth, which used a much smaller sample size (Thompson *et al.* 1996).

The importance of the waters surrounding the headland in the Dornoch Firth was already described by Bailey *et al.* (2014), who highlighted that the static and dynamic environmental conditions of this areas created a profitable foraging patch for this predator (Zamon 2001; Cox *et al.* 2018a). Except for this apparent hotspot, there was high inter-individual variability between the areas used in the two seasons. Further research is needed to investigate the link between diet composition and habitat association, and possibly to explore individual specializations of foraging strategies. Previous studies on diet composition relied on the analysis of faecal samples (Tollit & Thompson 1996; Tollit *et al.* 1998), while advances in biologgers now allow to collect information on prey species captured at sea (Goulet *et al.* 2019; Yoshino *et al.* 2020), generating more accurate individual based data.

To allow integration of data from multiple biologger types, a state-space model was used to estimate daily average locations accounting for the difference in error structure between the devices (Bailey *et al.* 2014). Models based on daily averages lack the temporal scale to capture localised changes in movement such as seals performing ARS behaviour (Bailey *et al.* 2014). Therefore, to focus the analysis on harbour seal foraging behaviour, I analysed only the GPS data, which were collected at a finer-temporal scale and with a higher accuracy (Costa *et al.* 2010b). These were then used in a Hidden Markov Model, which classified seal movement into transit and ARS behaviour to infer foraging areas (Dragon *et al.* 2012; van Beest *et al.* 2019).

Evidence shows that some marine predators can be highly repeatable at monthly, seasonal or yearly scales (Arthur *et al.* 2015; Wakefield *et al.* 2015). While others, such as McHuron *et al.* (2018), showed that individual California sea lions (*Zalophus californianus)* were quite repeatable over consecutive trips, but repeatability decreased at longer temporal scales. I found that harbour seals were highly repeatable in the foraging patches visited over time at a monthly, fortnightly and trip-by-trip scale. Camprasse *et al.* (2017) suggested that the temporal scale at which foraging behaviour is repeatable may depend on whether predators are benthic or pelagic foragers, as the former could be exploiting more predictable resources. This might explain the differences observed between our results and the ones by McHuron *et al.* (2018), where sea lions displayed a mixture of foraging strategies (shallow, epipelagic, benthic and deep-diving - McHuron *et al.* 2016), while harbour seals in this study area are mostly benthic foragers (Tollit *et al.* 1998). Given the challenges of re-deploying biologgers on the same individuals harbour seals, I focussed my analysis within breeding seasons. However, unintentionally five individual seals were tagged in different (two) or similar (three) seasons in two different years. The comparison of the foraging areas used in the two time periods showed a high repeatability between and across seasons. Furthermore, the comparison between the observed and null distribution showed that individuals were highly repeatable but different from others, suggesting that seals in this population show some degree of specialization. Given that personality traits and foraging strategies may have consequences on individual fitness (Patrick & Weimerskirch 2014), future research should focus on assessing the impact of different foraging strategies on individual fitness and reproductive success (Derango & Schwarz 2021).

My results on factors influencing repeatability show that, during the pre-breeding period, females were significantly more consistent and used a smaller foraging area than males. Sexual differences in foraging behaviour between males and females in this population have been described in relation to trip duration and foraging ranges during the pre-breeding season (Thompson *et al.* 1998). Furthermore, similarly to the results found here, Blanchet *et al.* (2014) studying harbour seals in Svalbard observed that males and females were more similar between September and December, and then diverged in home range size and total distance swum from January. Authors hypothesised that differences may arise from changes in sex-related dietary preferences, but no data were available to test this hypothesis. Furthermore, this observation was based on a very small sample size and differences were assessed on a monthly basis rather than in relation to the breeding season as done here.

This study shows that both as a population and as individuals, the seals of the Moray Firth have consistently used the same areas over time and remain associated with similar habitat features. Recent studies on harbour seal habitat preference around the coasts of the UK assessed seal association with static and dynamic environmental features, such as sea surface temperature, water column stratification and spatial variation in stratification (Carter *et al.* 2022). Results found that spatial variation in water column stratification was a significant predictor for harbour seals in the Moray Firth, with seals targeting more stratified waters. In Carter *et al.* (2022), environmental variables were derived from remote sensed data, while in this study, I have used data collected from the biologgers deployed on the seals to obtain in situ measurements of the conditions encountered by the animals. Then, I assessed if dynamic environmental variables influenced their site fidelity. I found that the depth of the thermocline significantly influenced how far apart foraging patches were during consecutive trips. Specifically, I observed an increase in distance between consecutive foraging areas visited in response to a deeper thermocline depth encountered, suggesting that once seals encountered more mixed waters, they changed foraging area in the subsequent trip. By using in situ measurements of water temperature, I was able to show that dynamic environmental variables may not just influence the overall distribution (Carter *et al.* 2022), but shape movement decisions at a much finer-scale. There is evidence that water mass properties, such as sea surface temperature, have significant influence on the occurrence and initiation of foraging behaviour of other phocids (Bestley *et al.* 2013; Nowak *et al.* 2020). Furthermore, the formation of the thermocline can particularly influence prey distribution in the water column (Baumgartner & Mate 2003) and it has been found to influence fur seals diving depth (Kuhn 2011) and little penguins (*Eudyptula minor*) foraging efficiency (Pelletier *et al.* 2012). Here, I showed that on top of influencing predator at-sea behaviour, environmental conditions influence predator movement decisions over consecutive trips.

In conclusion, in this study I have shown the importance of collecting environmental data at the spatial and temporal scale experienced by the predator (Biuw *et al.* 2007; Boehme *et al.* 2008). These data provided new insights on how the environment shapes predator behaviour, potentially allowing these to be incorporated into movement models (Patterson *et al.* 2009) to investigate the role of environmental variables at finer temporal scales or to describe differences between the conditions through which predators swim compared to where they decide to forage. Furthermore, quantifying behavioural repeatability and plasticity will be critical to understand how individuals cope in a changing environment (McHuron *et al.* 2018). This is particularly relevant in the context of an individual memory and ability to acquire new information. Central place foragers have the recognized ability to use memory to return to previously visited foraging patches, and recent studies have shown how they can integrate this knowledge with current prey encounters to inform behavioural decisions (Iorio-Merlo *et al.* 2022). Here, I showed that predators can also incorporate information at another temporal scale and use the experience on a foraging trip to influence where they will forage next. Finally, understanding the inter-individual variability in distribution, and which factors are affecting it, is critical to contextualise apparent changes in distribution when these are used to assess the impacts of anthropogenic disturbances (Bailey *et al.* 2014; Russell *et al.* 2016).

Supplementary material

Table S2.1 – Details of the harbour seals tracked in the study.

Table S2.2 – Sediment type occurrence in the 4x4km grid over the study area.

Table S2.3 – Candidate GAMs for model averaging for the time period between 1989-2009 and 2014-2017.

Table S2.4 – Results candidate GAMs with data from 1989 to 2009.

Table S2.5 – Results candidate GAMs with data from 2014 to 2017.

Table S2.6 – Candidate GAMs for model averaging for the pre- and post-breeding season.

Table S2.7 – Results candidate GAMs with data from the pre-breeding season.

Table S2.8- Results candidate GAMs with data from the post-breeding season. – Table reporting the Bhattacharyya's affinity values used in the repeatability analysis.

Figure S2.1 – Comparison of 50% and 95% utilization distributions.

Figure S2.2 – Seal tracks from GPS data.

Figure S2.3 – GAM covariates influence on seal probability of occurrence between 1989 -2009.

Figure S2.4 – GAM covariates influence on seal probability of occurrence between 2014 -2017.

Figure S2.5 – GAM covariates influence on seal probability of occurrence during the pre-breeding season.

Figure S2.6 – GAM covariates influence on seal probability of occurrence during the post-breeding season.

Figure S2.7 – HMM step length and angle distributions, and validation plots.

Figure S2.8 – 95% utilization distribution and overlap of foraging area for the 5 seals that were tagged in multiple years.

Table S2.1. *Details on harbour seals tracked in the Moray Firth Scotland between 1989 and 2017 used in the study. Table report information on the sex, weight, type of biologger deployed, start and end time of the data, days for which the tag recorded data, and during which season the seal was tagged (pre- vs post-breeding).*

Deployment year	Tag ID	Sex	Weight (kg)	Data type	Data start	Data end	Days	Season
1989	108	F	79	VHF	31/05/1989	29/07/1989	60	Pre-breeding
1989	100	F	90	VHF	01/06/1989	29/07/1989	59	Pre-breeding
1989	101	F	94	VHF	01/06/1989	29/07/1989	59	Pre-breeding
1989	102	F	90	VHF	01/06/1989	29/07/1989	59	Pre-breeding
1989	103	F	74	VHF	01/06/1989	08/07/1989	38	Pre-breeding
1989	107	F	90	VHF	01/06/1989	29/07/1989	59	Pre-breeding
1989	70	F	59	VHF	30/10/1989	30/11/1989	32	Post-breeding
1989	140	M	73	VHF	30/10/1989	06/02/1990	100	Post-breeding
1989	131	M	66	VHF	31/10/1989	18/01/1990	80	Post-breeding
1989	132	M	78	VHF	31/10/1989	06/02/1990	99	Post-breeding
1989	133	F	66	VHF	31/10/1989	06/02/1990	99	Post-breeding
1991	179	M	56	VHF	28/05/1991	05/07/1991	39	Pre-breeding
1991	180	M	85	VHF	28/05/1991	31/07/1991	65	Pre-breeding
1991	181	M	58	VHF	28/05/1991	29/06/1991	33	Pre-breeding
1991	183	M	56	VHF	28/05/1991	06/07/1991	40	Pre-breeding
1991	184	M	82	VHF	28/05/1991	27/07/1991	61	Pre-breeding
1991	185	M	57	VHF	28/05/1991	08/07/1991	42	Pre-breeding
1991	193	M	56	VHF	28/05/1991	06/07/1991	40	Pre-breeding

Deployment year	Tag ID	Sex	Weight (kg)	Data type	Data start	Data end	Days	Season
1991	194	M	88	VHF	28/05/1991	23/07/1991	57	Pre-breeding
1991	198	M	88	VHF	28/05/1991	17/07/1991	51	Pre-breeding
1991	199	F	95	VHF	03/06/1991	31/07/1991	59	Pre-breeding
2004	43861	M	78	SRDL	29/09/2004	16/11/2004	49	Post-breeding
2004	43866	M	78	SRDL	29/09/2004	09/12/2004	72	Post-breeding
2004	43867	M	77	SRDL	29/09/2004	02/04/2005	186	Post-breeding
2004	43864	F	60	SRDL	16/10/2004	13/03/2005	149	Post-breeding
2004	43868	M	68	SRDL	16/10/2004	14/03/2005	150	Post-breeding
2005	33185	F	71	SRDL	05/03/2005	23/05/2005	80	Pre-breeding
2005	33257	M	70	SRDL	05/03/2005	06/04/2005	33	Pre-breeding
2005	33869	F	79	SRDL	05/03/2005	28/07/2005	146	Pre-breeding
2005	33255	F	80	SRDL	06/03/2005	23/06/2005	110	Pre-breeding
2005	33843	M	88	SRDL	06/03/2005	13/07/2005	130	Pre-breeding
2007	26629	F	61	SRDL	01/03/2007	13/06/2007	105	Pre-breeding
2009	44281081	F	82	GPS-GSM	14/04/2009	07/06/2009	55	Pre-breeding
2009	44494740	F	61	GPS-GSM	14/04/2009	19/07/2009	97	Pre-breeding
2009	44671242	F	82	GPS-GSM	14/04/2009	17/07/2009	95	Pre-breeding
2009	44542657	F	78	GPS-GSM	14/04/2009	26/07/2009	104	Pre-breeding
2009	44671246	F	81	GPS-GSM	14/04/2009	22/08/2009	131	Pre-breeding
2014	12915	F	85	GPS-GSM	28/09/2014	04/02/2015	129	Post-breeding
2014	13115	M	71	GPS-GSM	29/09/2014	05/02/2015	129	Post-breeding

Deployment year	Tag ID	Sex	Weight (kg)	Data type	Data start	Data end	Days	Season
2014	13212	F	71	GPS-GSM	29/09/2014	13/02/2015	137	Post-breeding
2014	12922	F	64	GPS-GSM	29/09/2014	16/01/2015	109	Post-breeding
2014	13207	F	64	GPS-GSM	28/09/2014	18/01/2015	112	Post-breeding
2014	13214	M	63	GPS-GSM	28/09/2014	22/03/2015	175	Post-breeding
2014	12919	M	92	GPS-GSM	29/09/2014	23/10/2014	24	Post-breeding
2014	13208	M	48	GPS-GSM	28/09/2014	21/01/2015	115	Post-breeding
2014	12921	F	59	GPS-GSM	28/09/2014	23/01/2015	117	Post-breeding
2014	13209	M	71	GPS-GSM	29/09/2014	19/01/2015	112	Post-breeding
2014	13210	F	55	GPS-GSM	28/09/2014	23/01/2015	117	Post-breeding
2014	13213	M	53	GPS-GSM	29/09/2014	18/01/2015	111	Post-breeding
2015	13120	F	83	GPS-GSM	27/02/2015	13/07/2015	136	Pre-breeding
2015	13282	M	83	GPS-GSM	23/02/2015	23/05/2015	89	Pre-breeding
2015	13314	F	72	GPS-GSM	25/02/2015	16/07/2015	141	Pre-breeding
2015	13313	M	95	GPS-GSM	25/02/2015	11/05/2015	75	Pre-breeding
2015	13203	F	86	GPS-GSM	25/02/2015	19/07/2015	144	Pre-breeding
2015	13286	F	94	GPS-GSM	25/02/2015	04/07/2015	129	Pre-breeding
2015	13284	M	91	GPS-GSM	26/02/2015	11/06/2015	105	Pre-breeding
2015	13255	M	64	GPS-GSM	23/02/2015	19/06/2015	116	Pre-breeding
2015	13316	M	76	GPS-GSM	26/02/2015	16/06/2015	110	Pre-breeding
2015	13204	M	101	GPS-GSM	27/02/2015	08/07/2015	131	Pre-breeding
2015	13318	F	73	GPS-GSM	27/02/2015	27/06/2015	120	Pre-breeding

Deployment year	Tag ID	Sex	Weight (kg)	Data type	Data start	Data end	Days	Season
2015	13322	F	90	GPS-GSM	25/02/2015	26/06/2015	121	Pre-breeding
2015	13320	F	94	GPS-GSM	26/02/2015	04/07/2015	128	Pre-breeding
2017	14426	F	80	GPS-GSM	08/03/2017	03/06/2017	87	Pre-breeding
2017	14429	F	90	GPS-GSM	04/03/2017	09/07/2017	127	Pre-breeding
2017	14430	F	87	GPS-GSM	04/03/2017	29/06/2017	117	Pre-breeding
2017	14466	F	77	GPS-GSM	06/03/2017	22/07/2017	138	Pre-breeding
2017	14427	F	88	GPS-GSM	06/03/2017	23/04/2017	48	Pre-breeding
2017	14434	F	81	GPS-GSM	06/03/2017	10/07/2017	126	Pre-breeding
2017	14470	M	86	GPS-GSM	18/02/2017	12/05/2017	83	Pre-breeding
2017	14468	F	90	GPS-GSM	04/03/2017	24/07/2017	142	Pre-breeding
2017	14433	F	82	GPS-GSM	15/02/2017	30/05/2017	104	Pre-breeding
2017	14439	M	97	GPS-GSM	17/02/2017	01/07/2017	134	Pre-breeding
2017	14438	M	92	GPS-GSM	19/02/2017	15/06/2017	116	Pre-breeding
2017	14478	F	96	GPS-GSM	19/02/2017	14/06/2017	115	Pre-breeding
2017	14424	M	88	GPS-GSM	19/02/2017	11/06/2017	112	Pre-breeding
2017	14461	F	91	GPS-GSM	15/02/2017	28/06/2017	133	Pre-breeding
2017	14467	M	89	GPS-GSM	17/02/2017	14/06/2017	117	Pre-breeding
2017	14471	M	82	GPS-GSM	15/02/2017	25/06/2017	130	Pre-breeding
2017	14437	F	104	GPS-GSM	19/02/2017	24/06/2017	125	Pre-breeding
2017	14460	M	90	GPS-GSM	15/02/2017	07/05/2017	81	Pre-breeding
2017	14464	F	86	GPS-GSM	07/03/2017	10/07/2017	125	Pre-breeding

Deployment year	Tag ID	Sex	Weight (kg)	Data type	Data start	Data end	Days	Season
2017	14463	F	79	GPS-GSM	04/03/2017	30/05/2017	87	Pre-breeding
2017	14462	F	83	GPS-GSM	19/02/2017	07/07/2017	138	Pre-breeding
2017	14207	M	105	GPS-GSM	18/02/2017	14/06/2017	116	Pre-breeding
2017	14436	F	66	GPS-GSM	04/03/2017	20/06/2017	108	Pre-breeding
2017	14472	M	88	GPS-GSM	18/02/2017	22/04/2017	63	Pre-breeding
2017	14479	F	67	GPS-GSM	04/03/2017	10/06/2017	98	Pre-breeding
2017	14477	F	73	GPS-GSM	19/02/2017	26/05/2017	96	Pre-breeding
2017	14474	F	73	GPS-GSM	19/02/2017	16/06/2017	117	Pre-breeding
2017	14428	M	85	GPS-GSM	18/02/2017	10/05/2017	81	Pre-breeding
2017	14473	F	74	GPS-GSM	16/02/2017	28/05/2017	101	Pre-breeding
2017	14432	M	115	GPS-GSM	05/03/2017	13/06/2017	100	Pre-breeding
2017	14431	F	88	GPS-GSM	17/02/2017	07/06/2017	110	Pre-breeding

Table S2.2. *Sediment type occurrence in the 4x4 km grid over the study area.*

Sediment type	Grid cells
Sand	294
Gravelly sand	195
Muddy sand	162
Sandy gravel	98
Sandy mud	11
Gravel	7

Table S2.3. *Summary information of the candidate models used for model averaging for the probability of harbour seal occurrence during the time period between 1989 and 2009, and the time period between 2014 and 2017. Specifically, degrees of freedom (df), log-likelihood (Log-Link), Akaike's Information Criterion corrected for small sample size (AICc), difference between AIC values (Delta) and model weight (Weight). Covariates included in the model were: square-root of water depth, square root of seabed slope, distance to the nearest haul-out, probability of sandeel occurrence and sediment type.*

Model	Covariates	df	Log-Link	AICc	Delta	Weight
1989 - 2009						
1	s(Bathymetry) + s(Slope) + s(Distance to nearest haul-out) + Sediment type	15.70	-288.12	608.37	0.00	0.50
2	s(Bathymetry) + s(Slope) + s(Distance to nearest haul-out) + s(Sandeel probability) + Sediment type	15.70	-288.12	608.37	0.00	0.50
2014 - 2017						
1	s(Distance to nearest haul-out) + s(Bathymetry) + Sediment type	9.32	-188.35	395.61	0.00	0.32
2	s(Distance to nearest haul-out) + s(Sandeel probability) + s(Bathymetry) + Sediment type	11.85	-186.02	396.16	0.55	0.24
3	s(Bathymetry) + s(Slope) + s(Distance to nearest haul-out) + s(Sandeel probability) + Sediment type	12.56	-185.29	396.18	0.57	0.24
4	s(Distance to nearest haul-out) + s(Slope) + s(Bathymetry) + Sediment type	10.60	-187.47	396.49	0.88	0.20

Table S2.4 *Results of the candidate GAMs for probability of harbour seals occurrence during the time period between 1989 and 2009 (see Table S2.3), in relation to square-root of water depth, square root of seabed slope, distance to the nearest haul-out, sandeel probability and sediment type (reference level: sand). Table reports estimates and standard error (Std Error) for the parametric coefficients, estimated degrees of freedom (edf) a measure of complexity of model term and χ2 the effect of the term on the model output for smoother covariates. Indication of model fit reported as total deviance explained and adjusted* R^2.

Predictors	**Model 1**				**Model 2**			
	Estimate	**Std Error**	**EDF**	**χ2**	**Estimate**	**Std. Error**	**EDF**	**χ2**
Intercept	-1.77	0.26			-1.77	0.26		
Sediment - Gravelly sand	-0.03	0.28			-0.03	0.28		
Muddy sand or sandy mud	0.63	0.37			0.63	0.37		
Gravel or sandy gravel	-0.94	0.32			-0.94	0.32		
s(Depth)			4.43	79.88			4.43	79.87
s(Slope)			0.96	19.50			0.96	19.50
s(Haulout Distance)			4.56	17.91			4.56	17.91
s(Sandeel Probability)							0.00	0.00
Observations	731				731			
Deviance explained	36.8%				36.8%			
R^2	0.39				0.39			

Table S2.5. *Results of the candidate GAMs for probability of harbour seals occurrence during the time period between 2014 and 2017 (see Table S2.3), in relation to square-root of water depth, square root of seabed slope, distance to the nearest haul-out, sandeel probability and sediment type (reference level: sand). Table reports estimates and standard error (Std Error) for the parametric coefficients, estimated degrees of freedom (edf) a measure of complexity of model term and χ2 the effect of the term on the model output for smoother covariates. Indication of model fit reported as total deviance explained and adjusted* R^2.

Predictors	**Model 1**				**Model 2**				**Model 3**				**Model 4**			
	Est	**Std Err**	**EDF**	**χ2**	**Est**	**Std Err**	**EDF**	**χ2**	**Est**	**Std Err**	**EDF**	**χ2**	**Est**	**Std Err**	**EDF**	**χ2**
Intercept	-3.18	0.36			-3.19	0.36			-3.18	0.36			-3.18	0.36		
Sediment - Gravelly sand	-0.47	0.40			-0.62	0.42			-0.62	0.42			-0.48	0.40		
Muddy sand or sandy mud	2.05	0.47			2.14	0.46			-2.15	0.47			2.07	0.47		
Gravel or sandy gravel	-1.00	0.40			-0.99	0.40			-0.92	0.41			-0.89	0.41		
s(Depth)			3.69	53.55			3.39	38.07			3.31	36.12			3.56	48.23
s(Slope)											0.55	1.06			0.63	1.56
s(Haulout Distance)			1.11	42.03			1.11	41.31			1.11	41.06			1.12	42.21
s(Sandeel Probability)							1.83	4.07			1.85	3.83				
Observations	731				731				731				731			
Deviance explained	50.5%				51.1%				51.3%				50.7%			
R^2	0.552				0.528				0.528				0.523			

Table S2.6. *Summary information of the candidate models used for model averaging for the probability of harbour seal occurrence during the pre- and post-breeding period. Specifically, degrees of freedom (df), log-likelihood (Log-Link), Akaike's Information Criterion corrected for small sample size (AICc), difference between AIC values (Delta) and model weight (Weight). Covariates included in the model were: square-root of water depth, square root of seabed slope, distance to the nearest haul-out, probability of sandeel occurrence and sediment type.*

Model	Covariates	df	Log-Link	AICc	Delta	Weight
Pre-breeding season						
1	s(Bathymetry) + s(Slope) + s(Distance to nearest haul-out) + Sediment type	15.17	-267.91	566.85	0.00	0.5
2	s(Bathymetry) + s(Slope) + s(Distance to nearest haul-out) + s(Sandeel probability) + Sediment type	15.17	-267.91	566.85	0.00	0.5
Post-breeding season						
1	s(Bathymetry) + s(Slope) + s(Distance to nearest haul-out) + Sediment type	10.28	-274.46	569.8	0.00	0.5
2	s(Bathymetry) + s(Slope) + s(Distance to nearest haul-out) + s(Sandeel probability) + Sediment type	10.28	-274.46	569.8	0.00	0.5

Table S2.7. *Results of the candidate GAMs for probability of harbour seals occurrence during pre-breeding period (see Table S2.6), in relation to square-root of water depth, square root of seabed slope, distance to the nearest haul-out, sandeel probability and sediment type (reference level: sand). Table reports estimates and standard error (Std Error) for the parametric coefficients, estimated degrees of freedom (edf) a measure of complexity of model term and χ2 the effect of the term on the model output for smoother covariates. Indication of model fit reported as total deviance explained and adjusted* R^2.

Predictors	**Model 1**				**Model 2**			
	Estimate	**Std Error**	**EDF**	**χ2**	**Estimate**	**Std. Error**	**EDF**	**χ2**
Intercept	-2.12	0.26			-2.12	0.26		
Sediment - Gravelly sand	0.12	0.31			0.12	0.31		
Muddy sand or sandy mud	2.06	0.45			2.06	0.45		
Gravel or sandy gravel	-0.54	0.35			-0.54	0.35		
s(Depth)			4.45	61.06			4.45	61.05
s(Slope)			0.94	12.37			0.94	12.37
s(Haulout Distance)			3.69	24.61			3.69	24.61
s(Sandeel Probability)							0.00	0.00
Observations	731				731			
Deviance explained	38.4%				38.4%			
R^2	0.404				0.404			

Table S2.8. *Results of the candidate GAMs for probability of harbour seals occurrence during post-breeding period (see Table S2.6), in relation to square-root of water depth, square root of seabed slope, distance to the nearest haul-out, sandeel probability and sediment type (reference level: sand). Table reports estimates and standard error (Std Error) for the parametric coefficients, estimated degrees of freedom (edf) a measure of complexity of model term and χ2 the effect of the term on the model output for smoother covariates. Indication of model fit reported as total deviance explained and adjusted* R^2*.*

Predictors	**Model 1**				**Model 2**			
	Estimate	**Std Error**	**EDF**	**χ2**	**Estimate**	**Std. Error**	**EDF**	**χ2**
Intercept	-2.13	0.25			-2.13	0.25		
Sediment - Gravelly sand	0.10	0.29			0.10	0.29		
Muddy sand or sandy mud	0.99	0.36			0.99	0.36		
Gravel or sandy gravel	-0.77	0.34			-0.77	0.34		
s(Depth)			3.66	68.27			3.66	68.27
s(Slope)			0.95	15.78			0.95	15.78
s(Haulout Distance)			0.92	6.88			0.92	6.88
s(Sandeel Probability)							0.00	0.00
Observations	731				731			
Deviance explained	33.5%				33.5%			
R^2	0.369				0.369			

Table S2.9. *Table reporting the Bhattacharyya's affinity value indicating the spatial overlap of foraging patches visited over consecutive months, biweekly periods and foraging trips, followed by details on the sex of the individual and in which season it was tagged (pre- vs post-breeding).*

PTT	Seal ID	Monthly overlap	Biweekly overlap	Trip-by-trip overlap	Sex	Season
12915	13	0.65	0.77	0.69	F	Post-breeding
14426	14	0.88	0.86	0.88	F	Pre-breeding
14429	30	0.71	0.77	0.84	F	Pre-breeding
13120	42	0.44	0.68	0.78	F	Post-breeding
14430	53	0.60	0.66	0.57	F	Pre-breeding
14466	56	0.79	0.78	0.89	F	Pre-breeding
14427	59	0.92	0.87	0.75	F	Pre-breeding
14434	63	0.87	0.90	0.89	F	Pre-breeding
13282	72	0.67	0.88	0.92	M	Pre-breeding
14470	72	0.62	0.82	0.80	M	Pre-breeding
14468	75	0.77	0.62	0.72	F	Pre-breeding
13314	76	0.85	0.83	0.85	F	Pre-breeding
14433	81	0.88	0.84	0.68	F	Pre-breeding
14439	86	0.54	0.32	0.73	M	Pre-breeding
13115	90	0.83	0.81	0.77	M	Post-breeding
14438	90	0.45	0.61	0.60	M	Pre-breeding
13313	99	0.66	0.61	0.50	M	Pre-breeding
13203	105	0.79	0.84	0.90	F	Post-breeding
13212	127	0.77	0.74	0.78	F	Post-breeding
13286	158	0.66	0.73	0.81	F	Pre-breeding

PTT	Seal ID	Monthly overlap	Biweekly overlap	Trip-by-trip overlap	Sex	Season
14478	158	0.90	0.87	0.80	F	Pre-breeding
14424	169	0.54	0.49	0.63	M	Pre-breeding
14461	174	0.92	0.90	0.90	F	Pre-breeding
14467	178	0.75	0.23	0.65	M	Pre-breeding
14471	191	0.23	0.72	0.68	M	Pre-breeding
14437	216	0.83	0.91	0.86	F	Pre-breeding
14460	219	0.71	0.00	0.83	M	Pre-breeding
13284	230	0.25	0.23	0.36	M	Pre-breeding
12922	242	0.65	0.69	0.60	F	Post-breeding
14464	242	0.87	0.88	0.87	F	Pre-breeding
14463	250	0.89	0.88	0.91	F	Pre-breeding
13207	253	0.62	0.78	0.78	F	Post-breeding
13214	260	0.34	0.34	0.37	M	Post-breeding
13255	264	0.59	0.47	0.59	M	Pre-breeding
14462	268	0.66	0.76	0.73	F	Pre-breeding
13316	270	0.66	0.63	0.57	M	Pre-breeding
14207	272	0.65	0.49	0.85	M	Pre-breeding
13208	274	0.73	0.72	0.70	M	Post-breeding
14436	276	0.87	0.86	0.89	F	Pre-breeding
14472	280	0.82	0.90	0.92	M	Pre-breeding
14479	283	0.84	0.85	0.91	F	Pre-breeding
14477	285	0.40	0.88	0.87	F	Pre-breeding
12921	294	0.55	0.47	0.75	F	Post-breeding

PTT	Seal ID	Monthly overlap	Biweekly overlap	Trip-by-trip overlap	Sex	Season
13209	307	0.73	0.83	0.75	M	Post-breeding
14474	314	0.76	0.70	0.75	F	Pre-breeding
13210	317	0.69	0.79	0.52	F	Post-breeding
13213	322	0.79	0.65	0.62	M	Post-breeding
14428	331	0.32	0.81	0.82	M	Pre-breeding
14473	337	0.79	0.81	0.78	F	Pre-breeding
13204	338	0.18	0.29	0.90	M	Post-breeding
13318	341	0.67	0.69	0.86	F	Pre-breeding
14432	376	0.93	0.92	0.93	M	Pre-breeding
13322	383	0.76	0.86	0.88	F	Pre-breeding
13320	384	0.65	0.60	0.24	F	Pre-breeding
14431	384	0.86	0.86	0.89	F	Pre-breeding

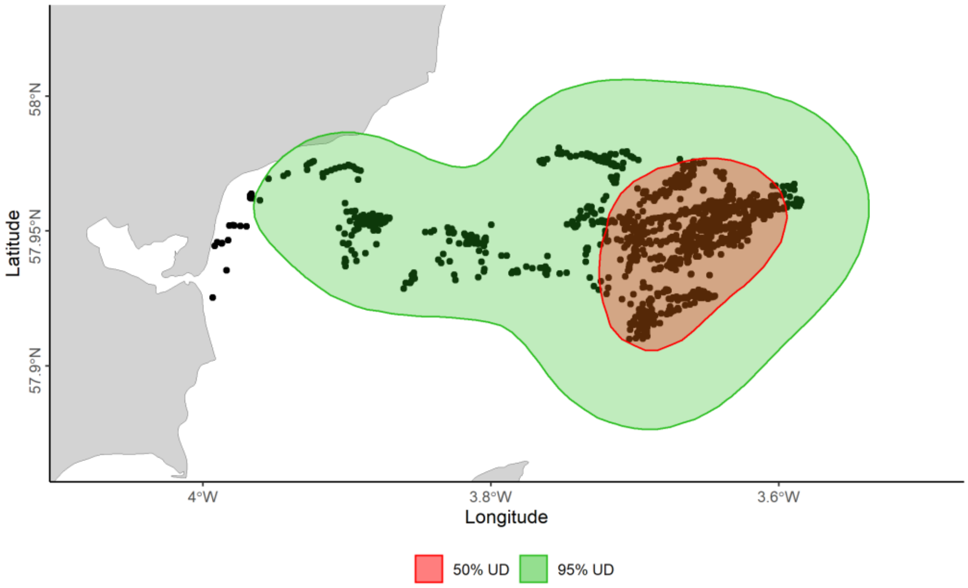

Figure S2.1. *Comparison between the 50% and 95% utilization distributions (UD) for all the locations classified as ARS for one individual.*

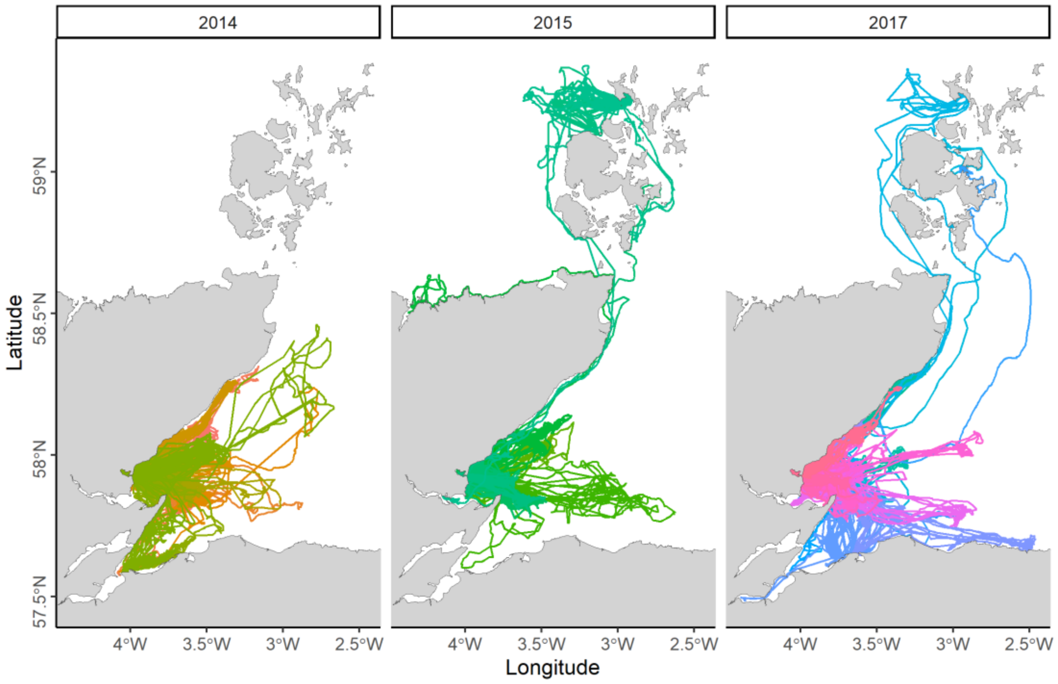

Figure S2.2. *Harbour seal GPS tracks reconstructed from all the GPS locations available across the three deployments of GPS Tags (September 2014 – February 2015, March – July 2015, and March – July 2017). Different colours represent different individuals (2014 = 12, 2015 = 13, 2017 = 31).*

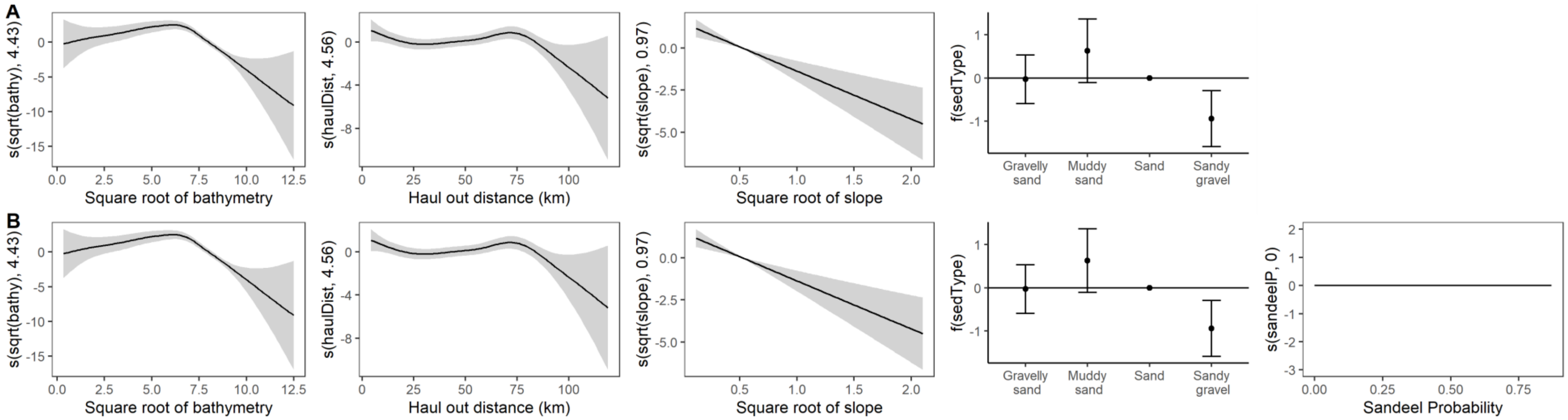

Figure S2.3. *GAM smoothing curves for square root of water depth (m), distance to the nearest haul-out sire (km), square root of seabed slope (degrees), probability of sandeel occurrence and parametric effect sediment type (reference level: sand) in relation to harbour seal occurrence between 1989 and 2009 for A) Model 1 and B) Model 2 (see Table S2.3).*

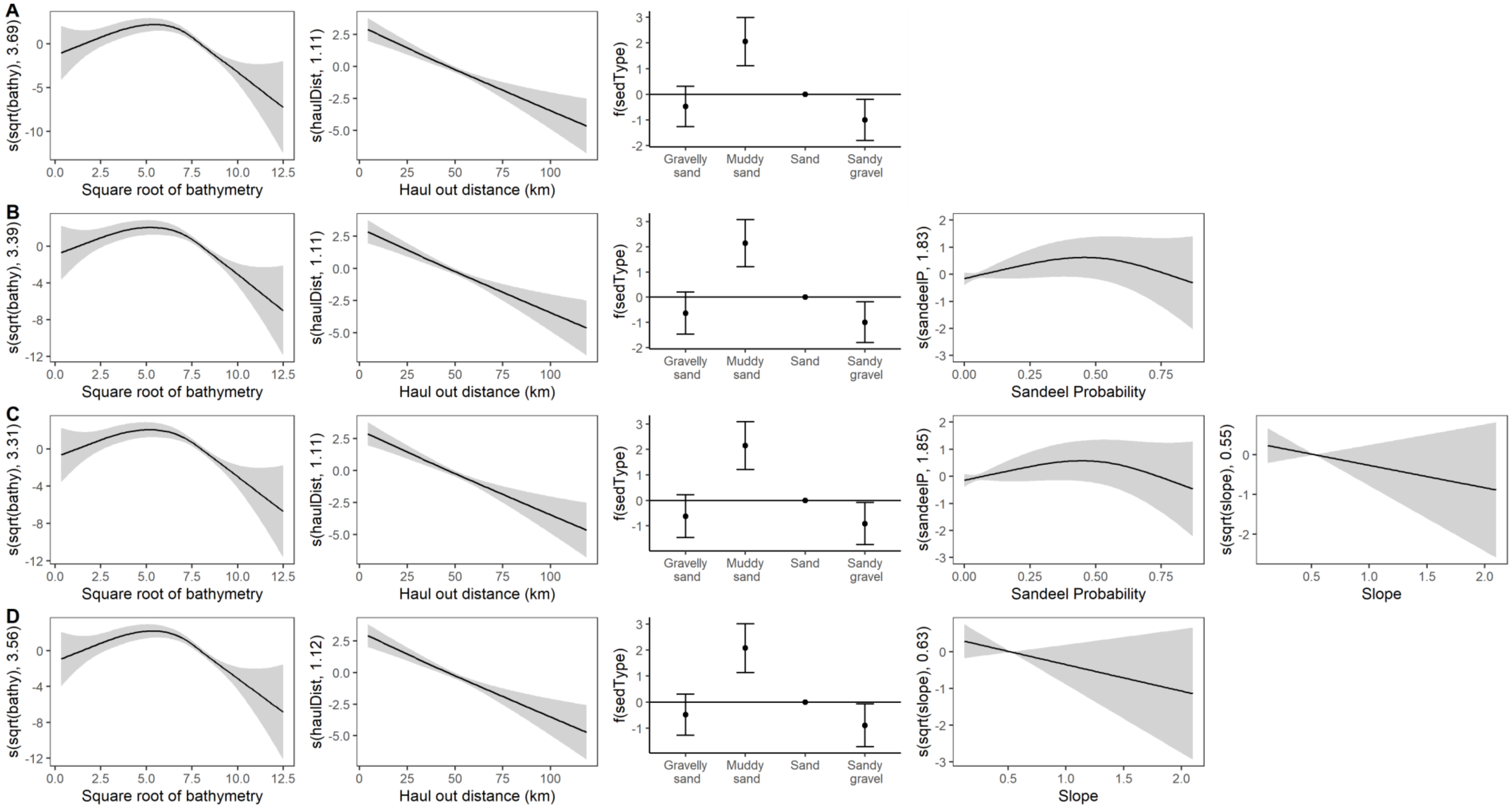

Figure S2.4. *GAM smoothing curves for square root of water depth (m), distance to the nearest haul-out sire (km), square root of seabed slope (degrees), probability of sandeel occurrence and parametric effect sediment type (reference level: sand) in relation to harbour seal occurrence between 2014 and 2017 for A) Model 1, B) Model 2, C) Model 3 and D) Model 4 (see Table S2.3).*

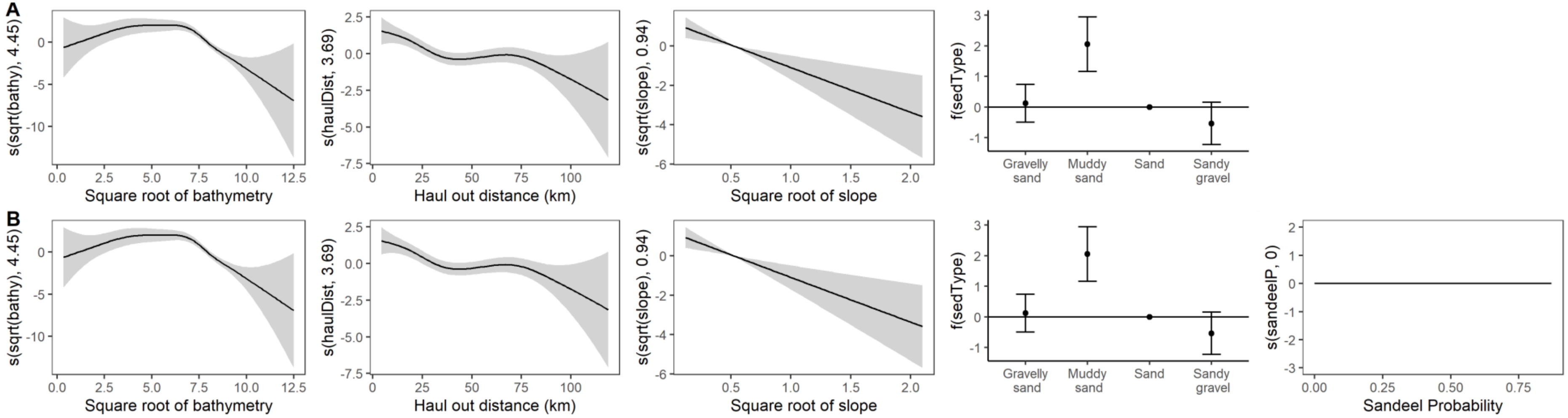

Figure S2.5. *GAM smoothing curves for square root of water depth (m), distance to the nearest haul-out sire (km), square root of seabed slope (degrees), probability of sandeel occurrence and parametric effect sediment type (reference level: sand) in relation to harbour seal occurrence between during the pre-breeding season for A) Model 1 and B) Model 2 (see Table S2.6).*

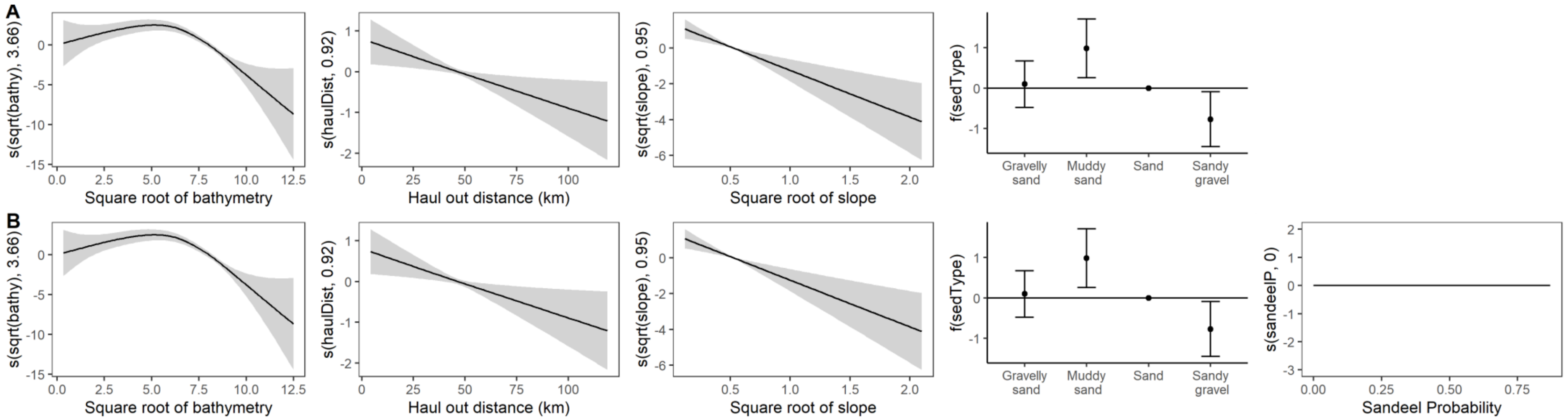

Figure S2.6. *GAM smoothing curves for square root of water depth (m), distance to the nearest haul-out sire (km), square root of seabed slope (degrees), probability of sandeel occurrence and parametric effect sediment type (reference level: sand) in relation to harbour seal occurrence between during the post-breeding season for A) Model 1 and B) Model 2 (see Table S2.6).*

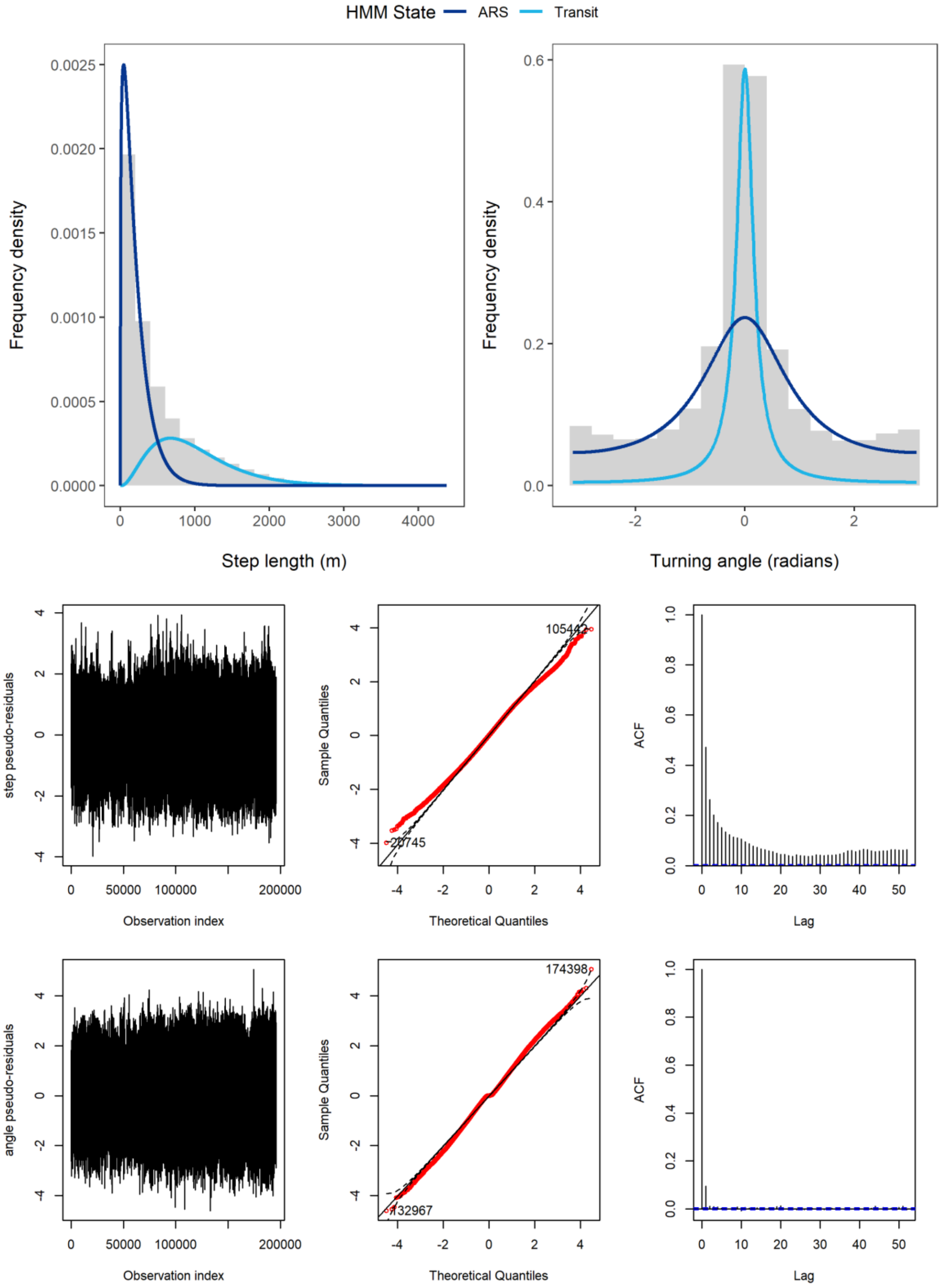

Figure S2.7. *In the top panel, state-dependent distributions of the step length and turning angle in the HMM. Below, model validation plots: time series, QQ-plots and ACF plots of pseudo-residuals (left to right).*

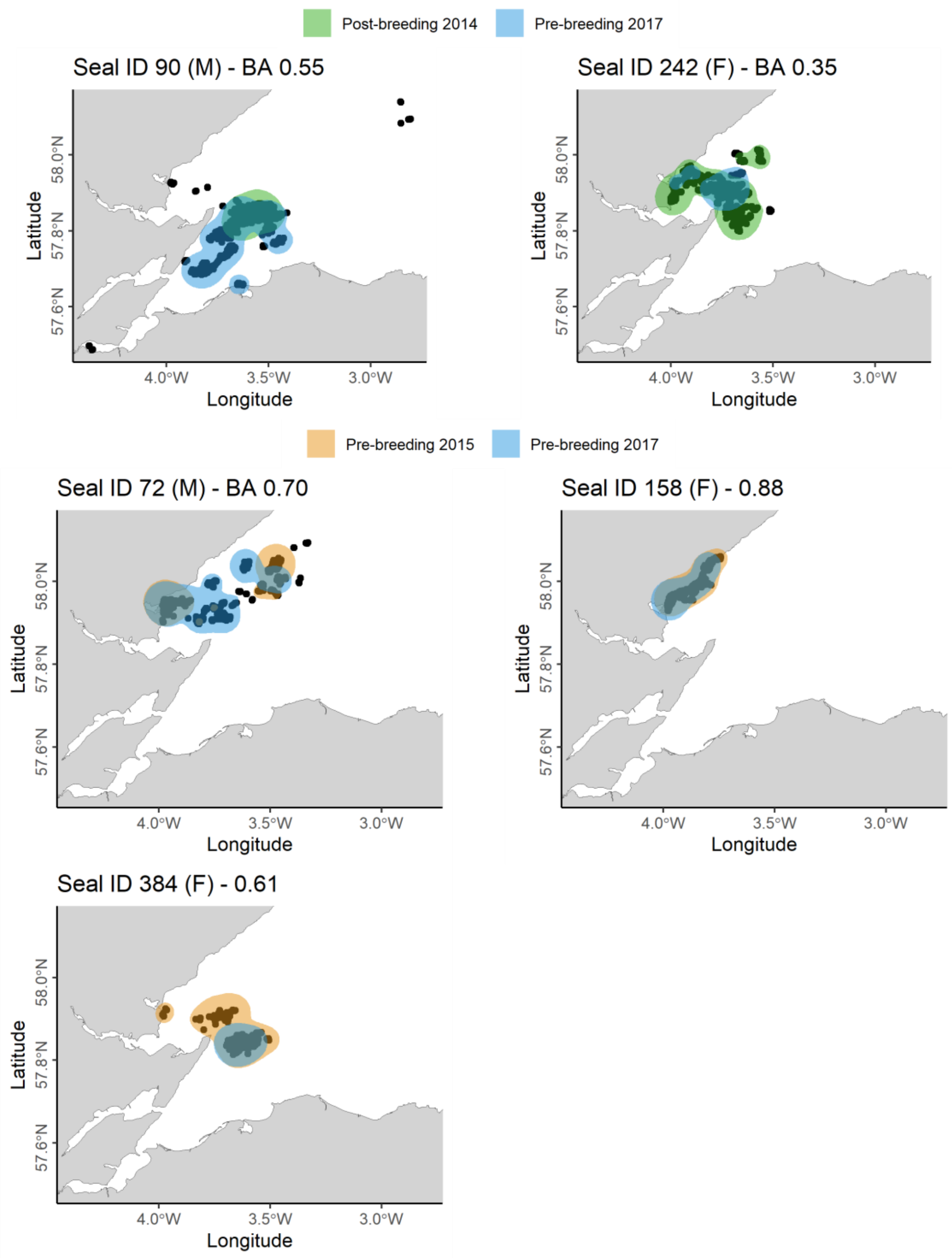

Figure S2.8. *Maps showing the 95% utilization distribution for the five seals that were tagged twice. Top panel shows two individuals that were tagged during the post-breeding season in 2014 and pre-breeding season in 2017. Bottom panel shows the three individuals that were tagged during the pre-breeding seasons in 2015 and 2017. At the top of each map there is the ID number of each seal, the sex of the individual and the Bhattacharyya's Affinity Index (BA), a measure of overlap between the distributions.*

Chapter 3

Predators integrate memory and perception of prey distributions in their movement and foraging behaviour

Chapter 3

Predators integrate memory and perception of prey distributions in their movement and foraging behaviour

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Abstract

Predators may acquire memory of productive foraging patches over time, giving rise to patterns of site fidelity to foraging locations. In turn, additional information will be acquired in subsequent visits, and memory updated over time. Therefore, predators are expected to use long-term, recent and current information to inform their movement decisions. This study aims to investigate whether the movement of a free-ranging predator is influenced by historic memory of good foraging patches and encounters with prey, and how its occurrence in those patches may be influenced, at a finer temporal scale, by more recent prey encounters. I used passive acoustic methods to collect data on the occurrence, movement and foraging behaviour of coastal bottlenose dolphins (*Tursiops truncatus*). Specifically, I assessed if dolphin direction of movement at the beginning of an encounter differed between sites located in well-known foraging hotspots compared to others, or in response to the presence of foraging calls. Then, I investigated if the probability of dolphins occurring in these hotspots varied in response to the proportion of time that foraging was detected in the previous 12, 24 and 36 hours. The variability in the direction from which dolphin clicks originated was used to infer differences in movement direction, with a high variability indicating area restricted search (ARS) behaviour. I used the range of directions from which dolphin clicks originated to infer ARS behaviour. I found that dolphins initiated ARS in response to both prey encounters and while within foraging hotspots. This suggests that both memory of good foraging areas and prey encounters led to the initiation of ARS behaviour. Furthermore, dolphins used their recent foraging experience, and possibly the predictability with which they encountered prey, to influence their occurrence at a foraging patch. This study illustrates how a free ranging predator used information on prey distribution acquired at different temporal scales to influence its movement decisions.

Introduction

There is growing evidence of predators' cognitive abilities and the role they play in foraging and movement decisions (Collett *et al.* 2013; Auger-Methe *et al.* 2016; Fagan *et al.* 2017). For example, cognitive mapping is a process used to associate spatial information with attributes of phenomena in an individual memory (Balda & Kamil 1992; Burt de Perera 2004; Bingman & Cheng 2005; Normand & Boesch 2009), such as, chimpanzees (*Pan troglodytes verus*) remembering the location of fruit trees (Normand & Boesch 2009). On the other hand, insects may use other processes such as path integration and landmarks maps (Dyer 1991; Webb 2019). The use of memory to return to previously successful foraging patches is a well-recognised strategy used to improve predator foraging efficiency (Berger-Tal & Bar-David 2015). Site-fidelity to long-term high quality foraging patches or predictable resources can provide fitness advantages to individuals (Bradshaw *et al.* 2004; Davoren 2013). Furthermore, memory plays a fundamental determining many other observed movement patterns such as migratory routes (Abrahms *et al.* 2019a) and home ranges (Spencer 2012). Nevertheless, it is recognised that predators should use a mixture of memory and random-search exploration to account for stochasticity in the environment (Boyer & Walsh 2010).

An individual's memory and knowledge of their environment can also be considered as a more dynamic process, where recent information is integrated with long-term memory to make future predictions (Martin-Ordas *et al.* 2010). Episodic memory by definition is the storage of temporally dated events and the temporal-spatial relations among these events (Tulving 1972). Many vertebrates have the ability to store information about previous experience by associating past events with specific sets of environmental conditions and locations, defined as episodic-like memory (Emery & Clayton 2004; Babb & Crystal 2006; Boyer & Walsh 2010; Jozet-Alves *et al.* 2013). For example, corvids have the ability to retain locations where they cached foods, but also associate it with the information on how perishable different resources are (Clayton & Dickinson 1999), while Risso's dolphin (*Grampus griseus*) used information on prey distributions collected while diving to plan their next dive (Arranz *et al.* 2018).

In predictable environments where sites have been identified as historically good foraging patches, predators should adopt a 'win-stay, lose-switch' strategy (Switzer 1993) where, for example, decisions are based on a recent successful or unsuccessful resource encounter (Ranc *et al.* 2021). This highlights an important distinction between cognitive maps and expectancies, with the former being long-term stable knowledge and the latter recently learned site-specific information (Spencer 2012). While long-term knowledge of good foraging areas may remain static over time, observed visitation or return rates to a site may be shaped by a predator's recent experience (Ranc *et al.* 2021).

Predators are also expected to adapt their behaviour to their current experience and external stimuli (Bell & Baum 2002; Iwata *et al.* 2015). Given that resources are heterogeneously distributed in the marine environment, ecological theories predict that predator movements should change upon encountering profitable prey (Kareiva & Odell 1987). Predators are predicted to remain in the same patch using area restricted search (ARS) behaviour as they have a higher probability of encountering more prey nearby (Benhamou 1992). Although there is evidence of predators initiating ARS in response to prey encounters (Hamer *et al.* 2009; Bailey *et al.* 2019), other studies have highlighted that memory may also drive this behaviour (Davoren *et al.* 2003; Weimerskirch *et al.* 2007; Thums *et al.* 2011), or that predators may use a combination of both (Iorio-Merlo et al. 2022). Predator searching strategy should then be determined by a mixture of historic, recent, and current information on prey distributions. Furthermore, most studies investigating predator's use of memory in their movements have focussed on central-place foragers and/or used biologging data to test their hypothesis (Regular *et al.* 2013; Merkle *et al.* 2014; Iorio-Merlo *et al.* 2022).

The bottlenose dolphin (*Tursiops truncatus*) population in the Northeast of Scotland has been studied extensively over the last two decades, using passive acoustics (Janik 2000b; Bailey *et al.* 2010) and long-term observations of recognisable individuals (Wilson *et al.* 1999; Cheney *et al.* 2019)**.** These studies have provided knowledge on their distribution (Wilson *et al.* 2004b; Cheney *et al.* 2013), habitat-use (Hastie *et al.* 2004; Pirotta *et al.* 2014) and foraging behaviour (Janik 2000a; Hastie *et al.* 2006). In particular, several studies have focussed on dolphin occurrence and behaviour in two deep-water channels that occur within the population's core range, Sutors and Chanonry (Hastie *et al.* 2004; Bailey & Thompson 2010). These two sites have been recognised for their importance as foraging areas, especially for dolphin feeding on *Salmonid spp.* (Hastie *et al.* 2004), although other areas within the Moray Firth also have a high probability of foraging call detections (Pirotta *et al.* 2014). However, detailed comparison of foraging activities between the channels and other areas is missing.

Passive acoustic monitoring (PAM) has recently been used to investigate dolphin occurrence within Sutors and Chanonry in relation to environmental cycles (Fernandez-Betelu *et al.* 2019). Findings suggest that dolphin occurrence was influenced by site-specific diel and tidal patterns. Although, some study systems can use passive acoustics to study animal movement by triangulating their locations (Stanistreet *et al.* 2013; Macaulay *et al.* 2017), most acoustic studies only provide information on marine mammal occurrence or vocal behaviour (e.g. occurrence - Bailey *et al.* 2010; foraging behaviour - Pirotta *et al.* 2014). Two previous studies of dolphin searching behaviour have used the duration of encounters around acoustic recorders to investigate whether dolphins engaged in ARS behaviour, finding initial support for the hypothesis that dolphins display ARS behaviour in relation to the detection of foraging calls (Bailey *et al.* 2019; Fernandez-Betelu *et al. in review* - Appendix). However, recently developed acoustic technologies can be used to triangulate the location of odontocete clicks to study their fine-scale movements (Macaulay *et al.* 2017). This method has already been applied to study fine-scale movement of harbour porpoises around underwater structures (Gillespie *et al.* 2020) and their responses to impulsive noise (Graham *et al. submitted*).

Given the recent evidence of episodic like memory in bottlenose dolphin (Davies *et al.* 2022), in this study, I used passive acoustic data to investigate how a free-ranging predator uses information on prey distribution at three different temporal scales. Specifically, I studied how dolphins were using (i) long-term memory and current prey encounters to adjust their fine-scale movements, and (ii) recent foraging experience to influence their residence time in foraging hotspots. I first confirmed that the two deep-water channels were indeed foraging hotspots for this population. Predators are expected to spend longer, and return more often, to profitable foraging areas compared to other locations that they transit through (Switzer 1993). I therefore compared the encounter duration and inter-encounter interval within each of the two hotspots and the rest of the study area. Then, given current and long-term use (Hastie *et al.* 2004; Bailey & Thompson 2010) of these channels by the resident population of dolphins (Cheney *et al.* 2014), I assumed that individual dolphins would have an historic memory of these two sites as profitable foraging areas. Thus, I used this information to test the hypothesis that both long-term memory of profitable foraging areas and prey encounters would influence initiation of ARS behaviour by a free-ranging predator (Iorio-Merlo *et al.* 2022). Compared to previous studies (Bailey *et al.* 2019), I used passive acoustic data (Gillespie *et al.* 2020; Graham *et al. submitted*) to investigate the direction of dolphins' fine-scale movements and make inferences about their searching behaviour. Encounters with prey were inferred from detected foraging calls (Janik 2000a; Pirotta *et al.* 2014). Dolphin movement was modelled in response to their presence in one of the historically profitable foraging patches and detections of foraging calls. Finally, I tested the hypothesis that dolphin occurrence at these sites would also be influenced by recent foraging experience in addition to their long-term knowledge of the foraging areas. Therefore, I modelled dolphin probability of occurrence at Sutors and Chanonry in response to the proportion of hours with foraging call detections in the previous 12, 24 and 36 hours.

Methods

Study site and acoustic data collection

This study was conducted within the inner Moray Firth (Scotland), a designated Special Area of Conservation (SAC) for its resident population of bottlenose dolphins (Cheney *et al.* 2014). Specifically, our study focussed in the area between the two deep-water channels, Sutors (57°41.41′N, 03°59.18′W) and Chanonry (57°5.14′N, 04°5.85′W) (Figure 3.1) where previous studies of temporal occurrence have been conducted (Fernandez-Betelu *et al.* 2019).

I used passive acoustic monitoring (PAM) devices to collect data on dolphin occurrence, movements and foraging behaviour. Specifically, a variety of PAM recorders were deployed at 13 selected locations between Sutors and Chanonry (Figure 3.1). I used the detection of echolocation clicks on different recorders to investigate dolphin occurrence, and I used the direction from which the clicks originated to infer their movements around the devices. In addition, dolphin foraging behaviour was identified using detections of foraging buzzes and bray calls (Janik 2000a; Pirotta *et al.* 2014). I used three types of device; echolocation detectors (CPODs), single channel broad band sound recorders (SoundTrap ST500) and directional hydrophone clusters (Graham *et al. submitted*). These were deployed at sampling sites for different periods of time depending upon recording capabilities (Figure 3.2). A SoundTrap ST500 and a CPOD were deployed at two longer-term sites (Figure 3.1) in May 2020, and recorded for the whole summer, while a directional hydrophone cluster and a CPOD were deployed at the short-term sites (Figure 3.1) and recorded data during the month of July 2020 (Figure 3.2). Devices were recovered using an ROV allowing for inspection of the condition of the mooring and the device.

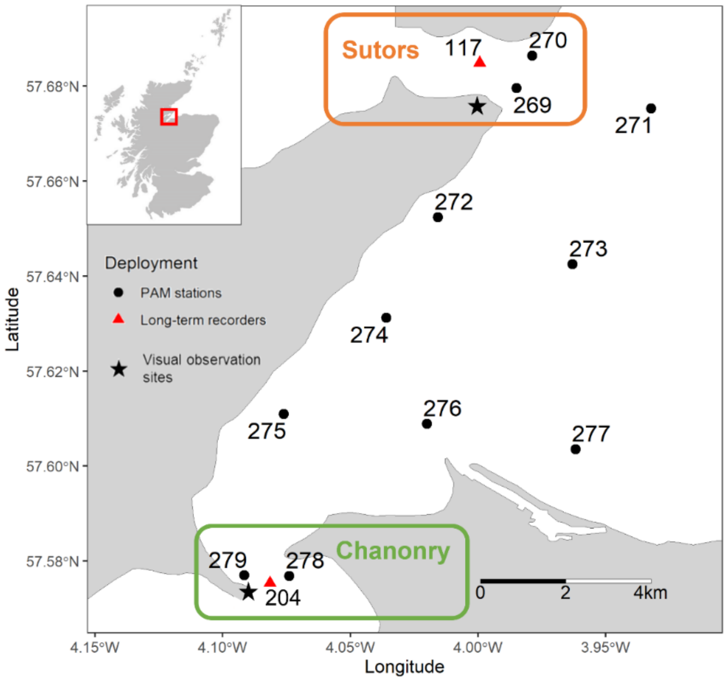

Figure 3.1. *Map of the study area with the locations where the sound recorders were deployed and where visual observations took place (black stars). A SoundTrap ST500 and a CPOD were deployed at the long-term sites (red triangles), while a directional hydrophone cluster and a CPOD were deployed at the short-term sites (black circles). The two deep-water channels Sutors and Chanonry are highlighted on the map.*

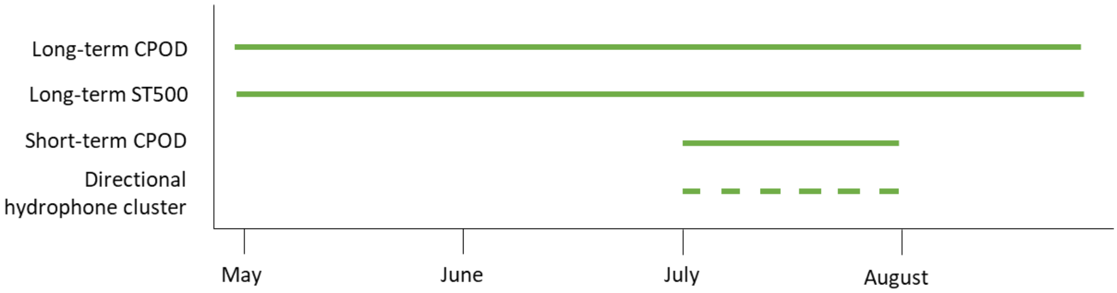

Figure 3.2. *Diagram showing the time periods in which passive acoustic devices were set to record between May and August 2020. Long-term CPOD, long-term ST500 and Short-term CPOD recorded continuously, while the directional hydrophone cluster recorded in a duty cycle of 24 hours out of 96 hours.*

CPODs

CPODs (Chelonia Ltd, UK) are odontocete echolocation detectors commonly used to study cetacean occurrence and distribution (Williamson *et al.* 2017; Fernandez-Betelu *et al.* 2019). These data loggers record the time of echolocation click detections occurring in the frequency range between 20 kHz to 160 kHz. CPODs record data continuously, and in this study, they recorded for up to 4 months at two long-term sites and for 1 month at short-term sites (Figure 3.1). At each location CPODs were moored using subsurface acoustic release, 2 meters away from the seabed, as described in Bailey *et al.* (2010).

Long-term SoundTraps

At each of the two long-term sites (Figure 3.1) a SoundTrap ST500 (Oceans Instruments) was deployed and set to record continuously on the high gain setting with a sample rate of 48 kHz**.** The SoundTrap at Sutors recorded for three months between May and July 2020 and the SoundTrap in Chanonry recorded for four months between May and August 2020. SoundTraps were deployed with the CPODs on subsurface moorings and recovered with an ROV.

Directional hydrophone cluster

The directional hydrophone clusters are stainless-steel frames containing a 4-channel SoundTrap, either ST4300HF or ST4300 (Oceans Instruments), and four hydrophones arranged in a small tetrahedral array (Figure 3.3) (Graham *et al.*

submitted). These SoundTraps were set to record at 96 kHz in a duty cycle, recording 24 hours out of 96 hours during the month of July 2020. Each of these devices recorded data for almost 6 days before stopping due to battery limitations. At two locations (275 and 279, see Figure 3.1) one of the four channels did not record any data, so these sites were removed from any analyses requiring directional information. Furthermore, at one of these locations (275) the device was not upright upon recovery (observed from ROV) and hence was removed from all the analyses.

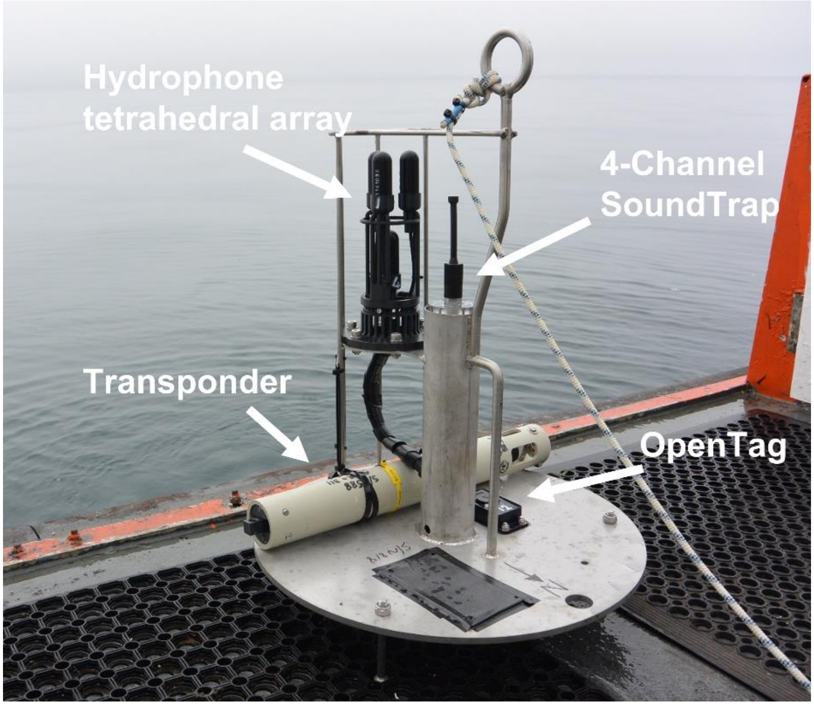

Figure 3.3. *Picture of the directional hydrophone cluster highlighting the main components mounted. The OpenTag was used to assess the cluster underwater position in relation to the seabed and the Transponder was used during the recovery to localise the cluster position.*

Acoustic data processing

CPOD data

Data collected by the CPODs were processed using the manufacturer's CPOD software (Chelonia Ltd, UK). Following the methods by Fernandez-Betelu *et al.* (2019), I only used click trains that were classified as High or Moderate Quality. The clicks detected by the CPODs deployed for the whole summer were used to determine dolphin foraging behaviour (see below) over longer timescales. The CPODs deployed with the directional hydrophone clusters were used to compare dolphin detections during days when the clusters were recording with days when they were not recording during July. I used a Mood's median test to compare number and duration of encounters. I applied a Bonferroni correction to account for multiple comparisons.

SoundTrap data

All sound files recorded by the 4-channel SoundTraps were processed using a PAMGUARD click detector (Gillespie *et al.* 2009). The detector was set to detect any sound above 10 dB in amplitude with no frequency filters. This allowed us to detect bottlenose dolphin echolocation clicks and boat engine noises that were used to estimate the underwater orientation of the directional hydrophone clusters (see Appendix 3A).

Bottlenose dolphin clicks were identified using a custom designed PAMGUARD click classifier (Gillespie *et al.* 2009) based on the classifier developed by Pirotta *et al.* (2014) for higher frequency recordings. Dolphin clicks were defined as clicks where the energy in the frequency band between 15 – 48 kHz was 10 dB greater than between 10-15 kHz, the mean frequency over the integration range 0-48 kHz was between 20 and 48 kHz, and the clicks had less than 10 zero-crossings and a maximum duration of 0.2 ms.

To minimise false detections, I further filtered the detected clicks for dolphin click trains. For a click train threshold, I used the upper-quartile inter-click-interval (ICI) between all the clicks classified by PAMGUARD as dolphin clicks. Thus, I retained only those clicks that were either followed or preceded by another click classified as dolphin within the threshold. Prior to all further analysis, dolphin clicks were time drift and orientation corrected (see details for the methods in Appendix 3A), and pitch and roll angle of the hydrophone cluster frame was checked to be within 10° from horizontal on the seabed. Finally, to split the click detections into encounters, I further filtered the data to retain only the minutes in which dolphin clicks were detected (i.e. dolphin detection positive minutes - DPMs). Exploration of the time intervals between DPMs was used to determine the threshold to be used to group dolphin click detections into encounters (Bailey *et al.* 2019). Only encounters longer than 1 minute were retained in the analysis (Bailey *et al.* 2019).

Dolphin foraging behaviour

I used dolphin foraging buzzes and bray calls as proxies for dolphin foraging behaviour during each encounter (Janik 2000a; Pirotta *et al.* 2014). To identify dolphin foraging buzzes I fitted separate Gaussian-mixture-models to the dolphin clicks detected by the long-term CPODs and by the directional hydrophone clusters (Pirotta *et al.* 2014). These models classified echolocation clicks based on their ICI, with echolocation buzzes being the group with the lowest ICI. Foraging buzzes in the long-term SoundTrap datasets could not be detected at the 48 kHz sampling frequency.

Bray calls were detected from long-term SoundTraps and the directional hydrophone clusters using a deep-learning automatic detector (Bergler *et al.* 2019). Using an adaptation of ORCA-SPOT (Bergler *et al.* 2019), a Convolutional Neural Network was trained to detect dolphin bray calls (Fernandez-Betelu *et al. in review* - Appendix). The detector was trained using recordings collected in the study area in 2018 and was demonstrated to have a 98.7% accuracy in bray calls detection (Fernandez-Betelu *et al. in review* - Appendix). Following analysis with the AI detector, bray detections were summarised as bray-positive-minutes. Furthermore, to remove possible false positive detections, only individual bray calls detections that were longer than 3 seconds were kept in the analysis.

Land-based visual data collection

During days that the directional hydrophone clusters were recording, land-based visual observations were carried out from two vantage points at Sutors and Chanonry (Figure 3.1). Observations were carried out during six out of seven recording days at Sutors and during every recording day at Chanonry. Observers spent on average 4 hours and 46 minutes at Sutors and 4 hours at Chanonry during daylight hours. At Sutors, observations were carried out from a vantage point on the South Sutor, roughly 90 meters above sea level (Figure S3.1), while at Chanonry observations were made from

Chanonry point on the beach (Figure S3.2). Both locations allowed visual observations of dolphins within the acoustic range of recording sites 270 and 269 in Sutors (Figure S3.1), and 279 and 278 in Chanonry (Figure S3.2). During observation periods, the date and time of dolphin sightings were recorded together with group size estimates. Encounters started when dolphins were first sighted and lasted until the animals left the field of view.

Foraging distribution in the Inner Moray Firth

I described the occurrence of foraging behaviour within the Inner Moray Firth using the data collected by the directional hydrophone clusters. First, I calculated the proportion of encounters in which foraging buzzes or bray calls were detected. Then, to assess whether the two channels are foraging hotspots in the area, I used a Mood's median test to assess if dolphins spent longer and occurred more often in the two channels compared to other locations. P-values adjusted with a Bonferroni correction were used to assess significance.

Influence of historic memory and prey encounters on movement

This analysis aimed at investigating whether dolphin movement was influenced by prey encounters or the historic memory of good foraging areas. In contrast to previous studies that used encounter duration to investigate dolphin ARS behaviour (Bailey *et al.* 2019), here I used movement data collected by the directional hydrophone clusters. Directions from which clicks originated during an encounter were used to infer dolphin movement (Figure 3.4). I assumed that, if dolphins were travelling through an area in a highly directional movement, clicks would originate from a less variable direction. On the other hand, if dolphins displayed ARS behaviour, clicks would be detected from a wider range of directions (Figure 3.4). To quantify the variability in click directions during an encounter I used the circular range of dolphin clicks bearings.

The circular range is a metric representing the shortest arc on the circle that contains all the data in a group (Mardia & Jupp 1999). In this dataset, it represents the spread of directions from which clicks originated during a specific amount of time (Figure 3.4). There was a positive relationship between the angular range and the duration of each encounter (Figure S3.3A). Therefore, to ensure that the response in movement observed was due to the influence of the covariates and not an artifact of the dolphins spending longer in one location, the circular range for click directions was calculated for the first 10 minutes of each encounter. This threshold was selected to have enough individual clicks to capture dolphin movements at the beginning of the encounter. Only encounters longer than 10 minutes were used in this analysis. Furthermore, to ensure that variation in angular bearing was not driven by the number of individuals present in an encounter, I used estimates of dolphin group size collected during the visual observations to investigate the relationship between angular range and group size using the acoustic encounters detected at sites (269, 270 and 278).

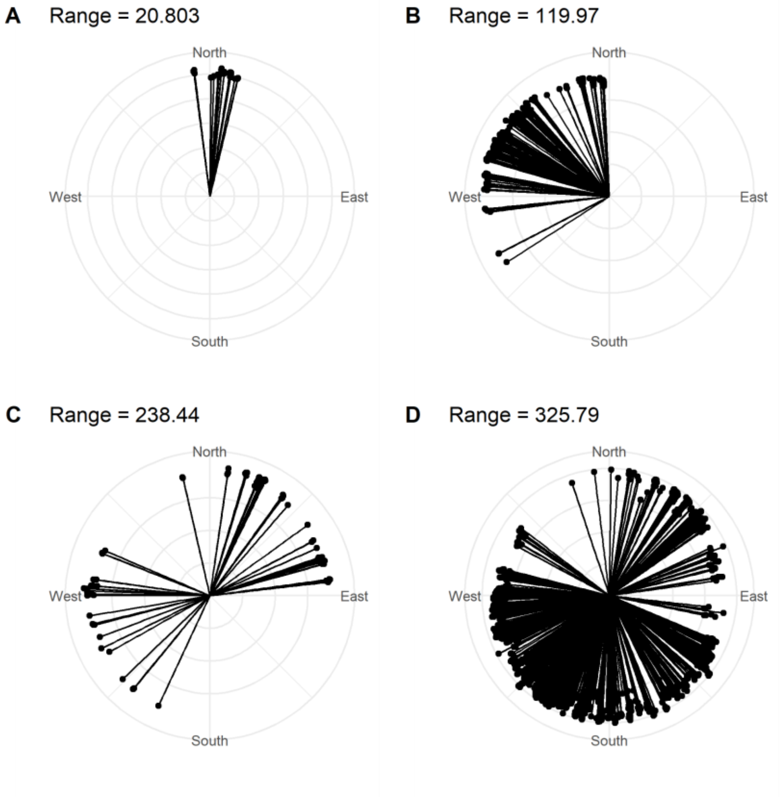

Figure 3.4. *Examples of distribution of dolphin click directions during four different encounters with the respective angular range value above.*

A linear mixed effect model was used to test the hypothesis that both prey encounter and occurrence within one of the two well-known foraging hotspots would influence their movement. Prey encounters were identified by the occurrence of either foraging buzzes (Pirotta *et al.* 2014) or bray calls (Janik 2000a) during the first 10 minutes of each encounter, and assigned a binary value representing the presence (1) or absence (0) of foraging calls. To test the influence of historic memory, a two level factor was included representing whether the encounter occurred in one of the channels (foraging hotspot) or any other area of the Inner Moray Firth (other). Prior to fitting the model, the response variable was transformed using a Box-Cox transformation to improve the model fit. Deployment location was included as a random effect. To determine the influence of both covariates I set up two models one with an additive effect and one with an interaction. Models were compared between them and with a null model using a likelihood ratio test within the *anova* function (Chambers & Hastie 1992) of the *stats* R package (R Core Team 2022).

Influence of recent foraging experience on occurrence at foraging hotspots

This analysis was used to test the influence of recent foraging experience, as an indication of expected prey distribution on predator occurrence. A binomial model (GLM) was used to assess the probability of dolphin occurrence in response to the proportion of foraging positive hours in previous fixed time scales. First, dolphin occurrence was defined using a binary value (0 and 1) representing the presence or absence of dolphin echolocation clicks in each hour recorded by the hydrophone clusters deployed in the two channels (locations: 269, 270, 278 and 279 - Figure 3.1). I used the proportion of foraging positive hours in the previous 12, 24 and 36 hours as a proxy for recent foraging experience. As the hydrophone clusters were duty cycled, to calculate the proportion of foraging hours, I used the presence of foraging buzzes and bray calls detected by the long-term CPODs and SoundTraps, respectively. Correlation of foraging positive hours determined by the two calls was explored using a Kendall correlation test. Significance of p-values was adjusted using a Bonferroni correction. Furthermore, I explored if there was a difference in the dolphin response in the two channels, by including channel (Sutors and Chanonry) as a factor in the model. Models were fitted using penalized quasi-likelihood estimation with the function *glmmPQL* in the *MASS* R package (Breslow & Clayton 1993; Bolker *et al.* 2009). This model was chosen as it allowed to account for the temporal autocorrelation structure in the response variable using a continuous autoregressive process (corCAR1). This choice of models meant that I was not able to compare models and hypothesis testing was limited to the *t* test statistics produced by model outputs.

All analyses were carried out in the statistical programme R v. 4.1.1 (R Core Team 2021). The linear mixed effect model was fitted using the *lme4* package (Bates *et al.* 2015). All the models were validated and checked using the functions available in the *dHARMA* package (Hartig 2021) or by graphical checking of residuals. Temporal autocorrelation in the data was checked using autocorrelation plots.

Results

Dolphin clicks detections and encounter definition

Bottlenose dolphins were detected throughout the summer in both channels (Figure 3.5A) and they were detected during almost all recording days at the short-term sites (Figure 3.5B).

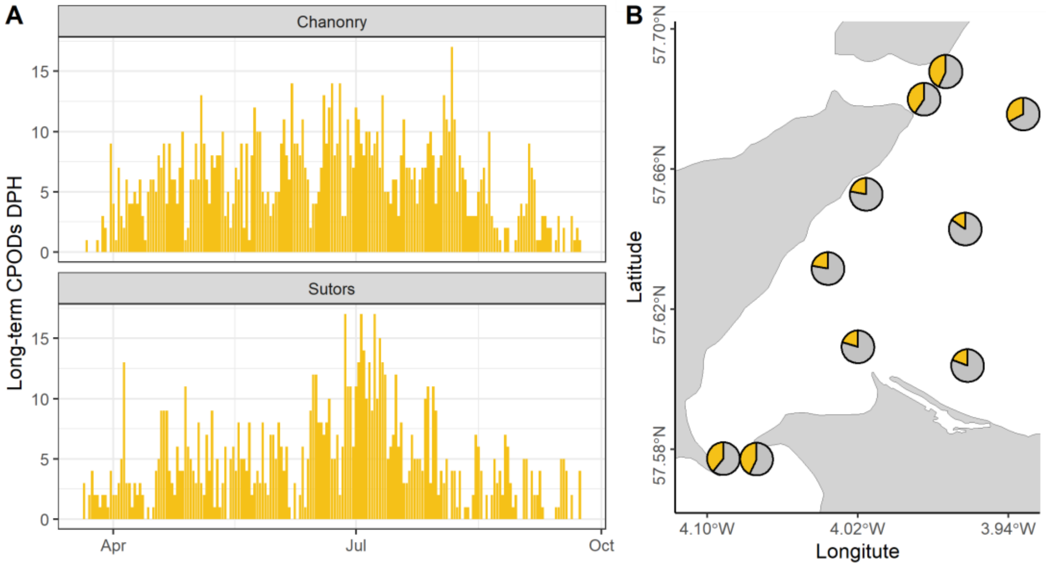

Figure 3.5. *A) Bottlenose dolphin detection positive hours per day as detected from the Long-term CPODs deployed in the two channels. B) Proportion of dolphin detection positive hours (in yellow) and hours with no detections (in grey), during the whole deployment as detected from the directional hydrophone clusters.*

I explored the inter-click-interval of the dolphin clicks detected by the directional hydrophone clusters at each location (Table S3.1) and used 0.3 milliseconds as a threshold to filter dolphin click trains. Based on the interval between DPMs (Table S3.2), I selected 10 minutes as the gap needed between detections to define a new encounter (Fernandez-Betelu *et al.* 2019). Based on the directional hydrophone cluster data, the mean number of encounters across location was 33 (±17) with some differences between locations (minimum number of encounters 15 at location 272 and maximum number of encounters 65 at location 270 - Figure 3.1).

Comparison of directional hydrophone cluster recording days and non-recording days for the month of July

The data collected by the CPODs deployed with the directional hydrophone clusters confirmed that the six recordings days were representative of dolphin occurrence during the month of July (Figure 3.6), with no significant difference in the daily number of encounters detected (*Mood's median:* z = 0.15, *corrected p-value* = 0.29) or their duration (*Mood's median:* z = 0.09, *p* = 1).

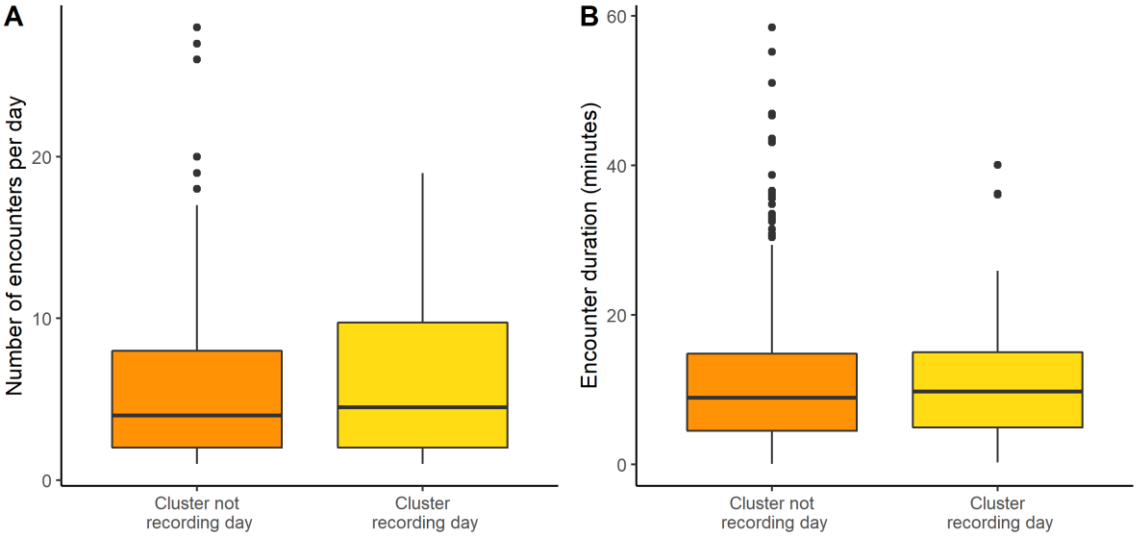

Figure 3.6. *Comparison of (A) the daily number of encounters and (B) their duration detected by the CPODs, during days in which the directional hydrophone clusters were recording and other days when the clusters were not recording during July. In both cases there was no significant difference.*

Dolphin foraging behaviour in the Inner Moray Firth

The two Gaussian-mixed-models fitted were both successful at grouping dolphin click ICIs in three categories, with the shortest ICI representing dolphin foraging buzzes. Dolphin foraging buzzes and bray calls were detected at all the locations, with some differences between sites (Figure 3.7).

There was a high return rate at all locations with an interval of on average 2.23 hours (± 2.8) between encounters. Although, dolphins did not return more frequently (*Mood's median:* z = -2.15, *corrected p-value = 0.06*) in the deep water channels, they significantly stayed longer (*Mood's median:* z = 4.65*, corrected p-value* = <0.001) in Sutors and Chanonry, compared to other locations in the Inner Moray Firth (Figure 3.8).

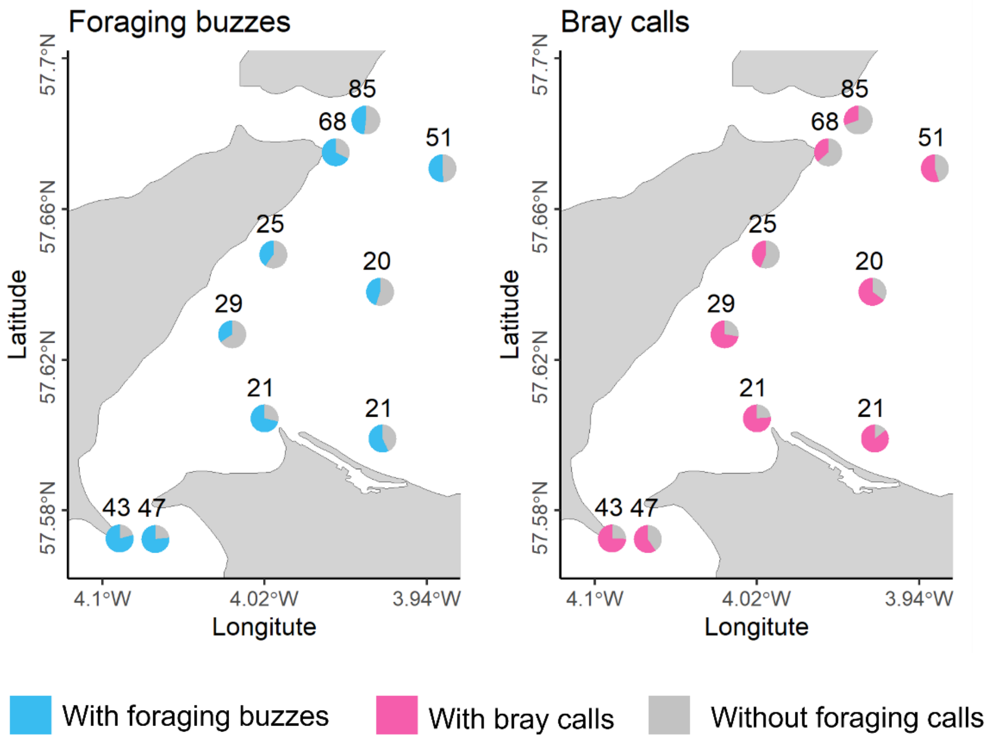

Figure 3.7. *Maps showing the proportion of bottlenose dolphin encounters with and without foraging calls detected by the directional hydrophone clusters. The number of encounters detected at each location is indicated above each pie-chart.*

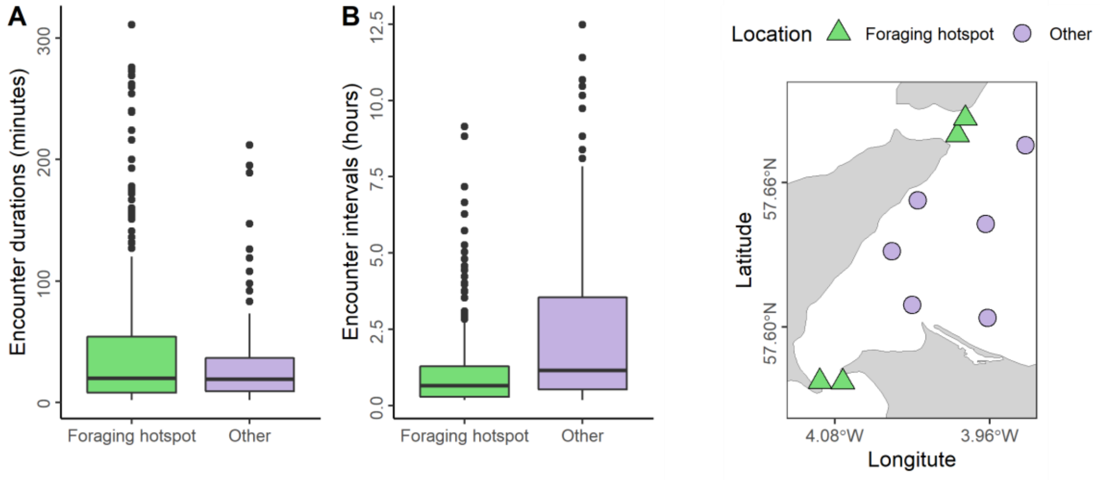

Figure 3.8. *Comparison of (A) encounter duration and (b) inter-encounter interval detected by the directional hydrophone clusters between the two deep water channels (Sutors and Chanonry) and the other locations within the Inner Moray Firth. Map showing the directional hydrophone cluster locations deployed within the channels (triangles) and in other locations (circles).*

Current experience and historic memory

I used the angular range of the directions from which dolphin clicks originated during the first 10 minutes of each encounter to infer whether dolphins were transiting or displaying ARS in the area surrounding the directional hydrophone clusters. Calculating the angular range using the clicks in the first 10 minutes better captured dolphin movement, in comparison to using a shorter threshold which underestimated the range in multiple encounters (Figure S3.4). Furthermore, the angular range in the first 10 minutes of each encounter was not correlated with the encounter duration (*Pearson: r*= 0.07, *p* = 0.24*, df* = 277 - Figure S3.3B) and could thus be used as an independent measure of dolphin searching behaviour. Moreover, to ensure that the angular range was not influenced by the size of a dolphin group, I explored the relationship between the number of individuals and the angular range for 29 encounters spread over three sites. There was no relationship (*Kendall: p = 0.61* - Figure S3.5) between the maximum number of individuals estimated during an encounter and the angular range of the dolphin clicks during the first 10 minutes of that encounter.

The results of the linear mixed effect model showed that both the presence of foraging calls and whether dolphins were in a foraging hotspot significantly influenced dolphin clicks angular range at the beginning of an encounter (Table 3.1). Specifically, both the detection of a foraging call (Figure 3.9A) and being in a hotspot (Figure 3.9B) significantly increased the angular range. The model selection supported the inclusion of both covariates but not their interaction (Table S3.3). The model marginal R^2 was 0.09 and the conditional R^2 was 0.15.

Table 3.1. *Linear mixed effect model result showing the significant influence of the presence of foraging calls in the first 10 minutes of the encounter and location (foraging hotspot vs. other) in the model with angular range as a response.*

Covariate	**Estimate**	**Std. Error**	**Df**	**p-value**
Intercept	10.59	0.92	1	**<0.001**
Foraging presence	2.51	0.63	1	**<0.001**
Location	-2.66	1.12	1	**0.018**

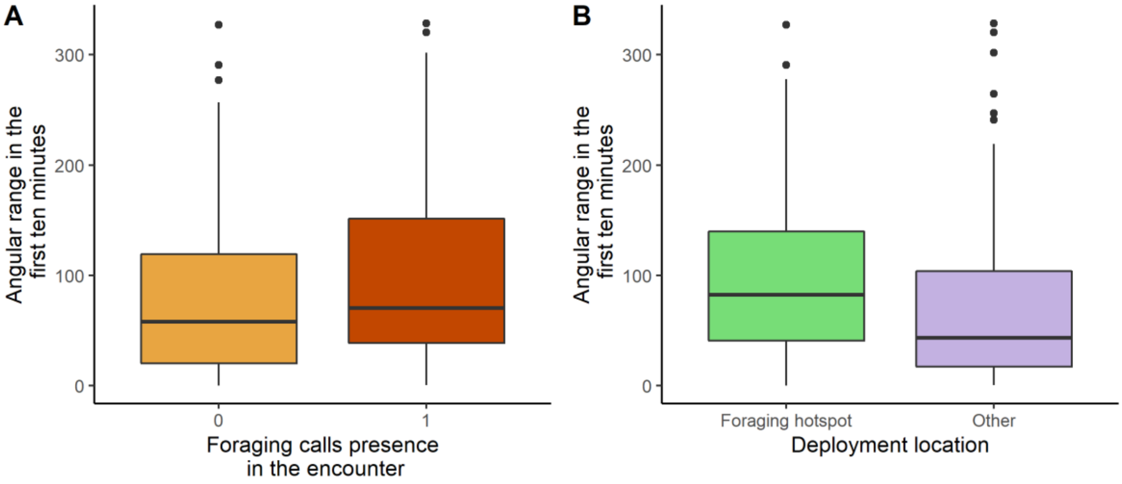

Figure 3.9. *Angular range during the first 10 minutes of each encounter in response to A) the presence of foraging calls (either foraging buzz or bray call) and B) whether the encounter occurred in foraging hotspots or any of the other deployment locations in the inner Moray Firth.*

Recent foraging experience

To investigate how recent foraging events would influence dolphin behaviour, separate generalized linear models were run for each time scale (12, 24 and 36 hours before) and for the two foraging calls. The proportion of hours with foraging buzzes and bray calls were found to be highly correlated at two timescales (Figure S3.6 - 12 hours *Kendall* z = 12.52, *adjusted p-value* = < 0.001, τ = 0.38, n = 608; 24 hours *Kendall* z = 5.91*, adjusted p-value* = < 0.001, τ = 0.17, n = 608), while at 36 hours covariates representing the two calls were included in the same model (*Kendall* z = 2.07, *adjusted p-value* = 0.17, τ = 0.06, n = 608).

The two models, looking at the effect of previous foraging behaviour at the shortest time scale, found that both foraging buzzes and bray calls significantly increased (Table 3.2 and Figure 3.10) the probability of dolphins occurring in either channel. Similar results were obtained with the models were covariates represented the proportion of foraging hours in the previous 24 hours (Table 3.2 and Figure 3.10). At the longest time scale, I was able to use as covariate the influence of previous foraging behaviour determined by foraging buzzes and bray calls together. At this time scale only bray calls were found to have a significant effect (Table 3.2 and Figure 3.10). Finally, in the models with bray calls at 12 and 24 hours, the model also found a significant difference of dolphin probability of occurrence in the two channels (Table 3.2), with a higher probability in Sutors (Figure 3.10).

***Table 3.2.** Probability of dolphin occurrence in the deep water channels in response to the proportion of hours with foraging buzzes and/or bray calls in the previous 12, 24 and 26 hours (specified in the Model column), and the channel in which dolphins were detected (either Sutors or Chanonry). Significance levels: *<0.05, **<0.01, ***<0.001*

Model	Parameters	Estimate	*t*	Conditional R^2 (marginal R^2)
Foraging buzzes - previous 12 hours	Intercept	0.32	1.85	0.06 (0.04)
	Foraging call	2.98	3.9 ***	
	Channel	-0.12	-0.71	
Bray calls – previous 12 hours	Intercept	-0.07	-0.29	0.05 (0.03)
	Foraging call	1.95	3.78 ***	
	Channel	0.5	2.53 *	
Foraging buzzes – previous 24 hours	Intercept	0.41	2.11 *	0.02 (0.02)
	Foraging call	2.29	2.55 *	
	Channel	-0.12	-0.66	
Bray calls – previous 24 hours	Intercept	-0.2	-0.57	0.03 (0.02)
	Foraging call	2.17	2.86 **	
	Channel	0.6	2.48 *	
Both calls – previous 36 hours	Intercept	-0.61	-1.4	0.06 (0.04)
	Bray call	2.23	2.1 *	
	Foraging buzz	2.45	1.96	
	Channel	0.43	1.09	

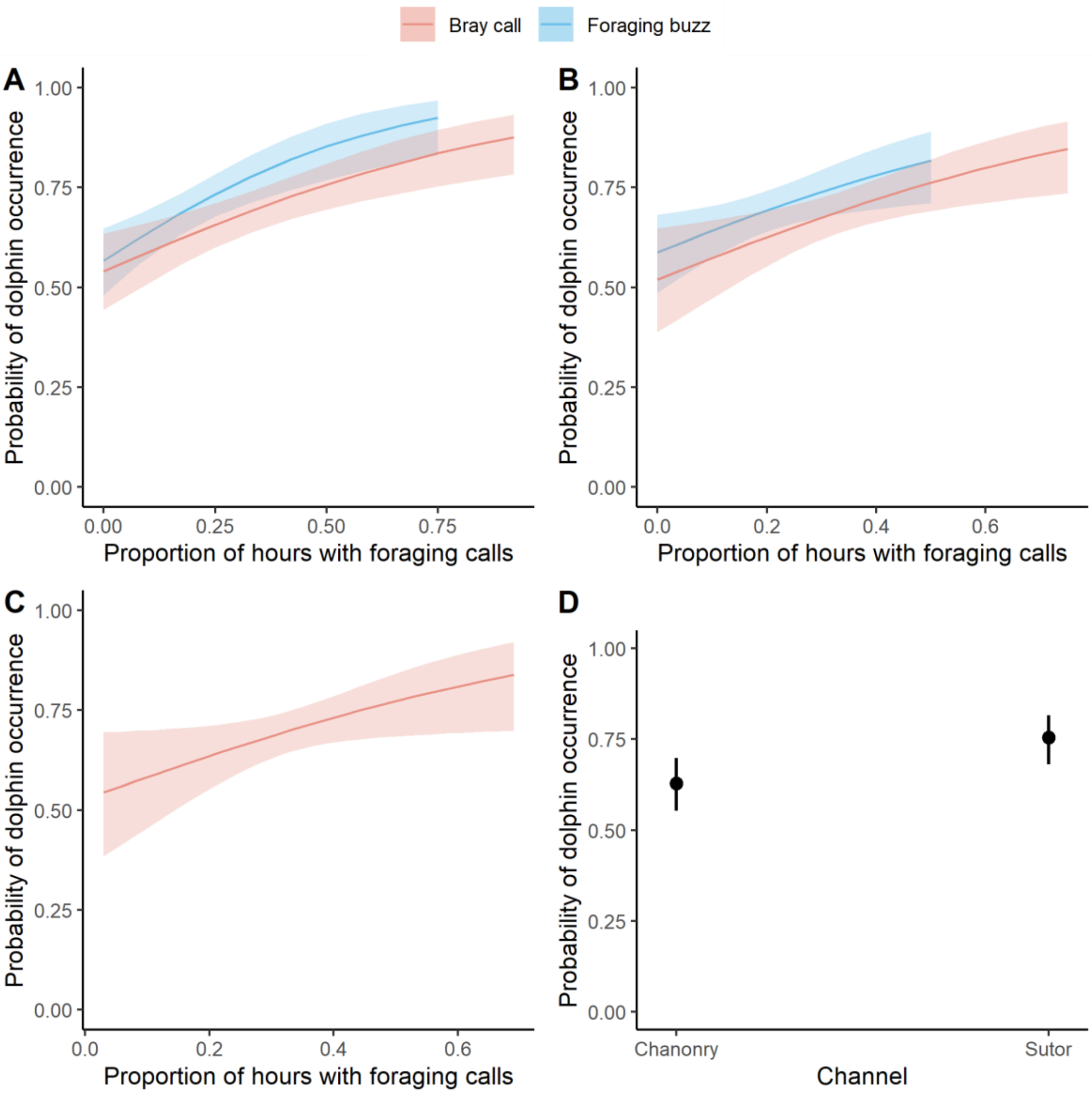

Figure 3.10. *Probability of dolphin occurrence in response to the proportion of hours with foraging buzzes and bray calls in the previous: A) 12 hours, B) 24 hours and C) 36 hours. D) Probability of dolphin occurrence in either channel, as estimated by the model with proportion of hours with bray calls in the previous 12 hours.*

Discussion

In this study, I present evidence that predators use information on current, recent and long-term knowledge of prey distribution in their movement decisions. Both prey encounters and being in historically high-quality foraging areas influenced predator fine-scale movements. In particular, I found that dolphins displayed ARS behaviour in the two deep-water channels independently from the presence of foraging calls at the beginning of an encounter, highlighting that possibly dolphins were changing behaviour in expectation of a higher probability of encountering prey (Thums *et al.* 2011; Iorio-Merlo *et al.* 2022). Furthermore, I found that predators used their recent foraging success, and possibly the predictability with which they were encountering prey, to influence their occurrence in a foraging patch (Ranc *et al.* 2021). Together these results indicate that predators integrate multiple sources of information on prey distribution to maximise their foraging output.

Previous studies of bottlenose dolphins have provided insight into how marine predators change behaviour in response to prey encounters (Bailey *et al.* 2019; Fernandez-Betelu *et al. in review* - Appendix). These studies have shown that, when foraging calls were detected during an encounter, dolphins stayed longer in the area. These studies used the time that dolphins spent within the detection ranges of a hydrophone as an indication of ARS. Here, I used variation in the direction from which dolphin clicks originated to infer dolphin movement and behaviour (Graham *et al. submitted*). In movement studies based on telemetry data, a high variability in turning angle has often been interpreted as an animal displaying ARS behaviour (Dragon *et al.* 2012). Here I showed a significant increase in circular range at the beginning of an encounter when foraging calls were detected, indicating that dolphins initiated ARS behaviour in response to encountering prey. These findings add to the evidence that free-ranging predators, like bottlenose dolphins, use ARS behaviour (Silva *et al.* 2013; Towner *et al.* 2016; Meese & Lowe 2020), and show that cetacean fine-scale ARS movement can be studied using passive acoustic data.

The dispersed hydrophone array deployed in this study allowed us to identify a complex network of foraging patches between two main foraging hotspots, Sutors and Chanonry (Hastie *et al.* 2006; Bailey & Thompson 2010). The higher number and extended duration of encounters in the two deep-water channels reinforced the importance of these two areas. However, the proportion of encounters with foraging behaviour was high in the whole Inner Moray Firth. The inter-encounter interval was low (mean encounter interval: 2.23 ± 2.8 hours) at all sites, possibly indicating that dolphins sampled the whole area in search for less predictable foraging opportunities

(Roth II & Lima 2007). Adopting a mixture of memory-driven and random search strategies has been suggested as an effective method for predators to maximise their foraging output (Boyer & Walsh 2010). This might be particularly true for free-ranging predators whose movements are not constrained by other physiological needs such as central place foragers which are required to return to resting sites on land (e.g. Cordes *et al.* 2011) or to nest sites for breeding (e.g. Shaffer *et al.* 2003).

The movement analysis revealed a significant difference in dolphin behaviour within and outside the two deep-water channels. Predators can acquire memory of their environment and the distribution of their prey to help them target good foraging areas in the future (Arthur *et al.* 2015; Votier *et al.* 2017; Collet & Weimerskirch 2020). I hypothesised that the changes in dolphin behaviour within the two channels occurred in anticipation of a higher probability of encountering prey. Changes in behaviour due to expectation of resources has been suggested to explain the initiation of ARS behaviour of southern elephant seals (*Mirounga leonina*) (Thums et al. 2011) and of harbour seals (*Phoca vitulina*) (Iorio-Merlo *et al.* 2022). However similar predictions have not been tested on cetacean species.

Furthermore, the model selection did not support the inclusion of the interaction between the two covariates, suggesting that dolphins were changing their behaviour within the channels independently from the presence of foraging calls. These two deep-water channels in the Inner Moray Firth have been studied for several decades and are recognized as two key foraging hotspots for this population (Hastie *et al.* 2004). It has been hypothesised that dolphin's use of these channels is due to their topographic and oceanographic characteristics, which lead to the formation of tidal fronts (Bailey & Thompson 2010). The association of marine predators with oceanographic features such as these is due to their influence on prey availability and accessibility (Davoren 2013; Boyd *et al.* 2015). For example, Jones *et al.* (2014) found that the occurrence of harbour porpoises was strongly associated with strong tidal flow. Furthermore, given that the same individuals have been seen using these areas over decades (Cheney *et al.* 2014), I assumed that this population would have a long-term memory and knowledge of these profitable foraging hotspots. However, passive acoustic data, as used in this study, cannot be used to infer individual behaviour. It could be hypothesised that in a highly social species like the bottlenose dolphin, knowledge may be shared between individuals and from mother to calves, reinforcing a similar pattern of use within the population and through time (Wild *et al.* 2019).

Recent experience of foraging success or failure can influence the fine scale return rate of predators to foraging patches (Ranc *et al.* 2021). Study of predator return-rates, in this study, was limited by the inability to identify individuals from passive acoustic data. However, this population displays high site fidelity to both deep-water channels (Fernandez-Betelu *et al.* 2019), and our data suggest a high rate of occurrence at both sites. Thus, I investigated how recent foraging experience and short-term memory of foraging success might influence the occurrence of dolphins at these foraging patches. I found a positive relationship between the proportion of hours with foraging calls detections and the probability of dolphins occurring in both channels at all time scales. Thus, recent successful foraging experience led to a higher probability of dolphins occurring in either site, possibly in response to a higher probability of finding more prey items. At the longest temporal scale, I was able to model the two foraging calls. The results showed that when in the same model only the proportion of hours with bray calls was significant. While detections of foraging buzzes may indicate dolphins foraging with a variety of prey, bray calls are associated with feeding events on Salmonid *spp. (Janik 2000a)*. Salmonids are among the largest prey species that bottlenose dolphins feed on (Santos *et al.* 2001), which might suggest that at longer temporal scale only memories that might lead to higher rewards are retained.

When predators forage for predictable resources, they should adopt a ‘win-stay, lose-switch’ strategy to take advantage of continuous prey availability (Switzer 1993). In fact, evidence for this behaviour has not been found for pelagic marine predators foraging on more variable resources (Weimerskirch *et al.* 2005). In this study, an increase in dolphin occurrence could have also resulted from multiple groups of dolphins using the site consecutively to take advantage of increased prey availability. Although I was not able to account for this limitation, long-term photo-identification studies in these channels (unpublished data) confirm that the same individuals are consistently observed using both channels during the summer months. Predator occurrence within foraging patches might also be influenced by rates of prey depletion and regeneration or changes in prey anti-predatory and vigilance behaviour (Berger-Tal & Bar-David 2015). Thus, the information relevant to predators might be related not only to the presence or absence of prey, but also to prey behaviour (Laundre 2010). Thus, future studies should focus not just on characterizing prey presence at these sites, but also prey behaviour in relation to the predator occurrence and foraging.

These results show that although the two foraging hotspots are known to be predictable foraging patches, the frequency with which dolphins actually encounter prey might determine their occurrence at a finer temporal scale. Previous studies of the effect of prey predictability at this scale have focussed on experimental work using feeding stations in terrestrial systems (Millon *et al.* 2008; Monsarrat *et al.* 2013; Janson 2016). Capturing prey and predator dynamics at a similar temporal scale in the marine environment can prove challenging, thus I used detections of foraging calls as a proxy to identify prey encounters. However, the use of foraging calls as proxies comes with limitations, most importantly that the actual presence of prey cannot be verified, and some vocalizations may represent other behaviours. For example, dolphins may use echolocation buzzes both in foraging and social contexts (Herzing 1996; Martin *et al.* 2019). Moreover, foraging proxies may only indicate that predators attempted to capture prey, such as salmon, and do not necessarily indicate successful prey capture. Future studies may investigate further the relationship between bray call rate and visual observation of successful salmon capture. Furthermore, future studies should also aim to collect simultaneous data on dolphin behaviour and salmon occurrence, first to verify the relationship between bray call detections and salmon occurrence, and second to test the hypothesis that differences in salmon encounter predictability drives patterns of dolphin occurrence in the two channels.

Previous studies have found memory to be relevant to predators over either the short-term, for example days (Carroll *et al.* 2018; Ranc *et al.* 2021) or long-term, at monthly or yearly scales (Bradshaw *et al.* 2004; Merkle *et al.* 2014). Here, I showed that dolphins are most likely integrating information at different temporal scales to inform their movement and foraging decisions. Finding resources is one of the main drivers of animal movement, making the understanding of the rules underpinning such decisions fundamental for the comprehension of animal behaviour, their distribution and habitat use pattern (Mueller & Fagan 2008; Fagan *et al.* 2017). This study adds to the evidence that predators are neither omniscient nor naïve, and their imperfect knowledge of their environment needs to be accounted for in individual based models that inform conservation (Spencer 2012).

Supplementary material

Table S3.1 – Summary of inter-click interval of PAMGUARD classified clicks at each location.

Table S3.2 – Summary of inter-DPM interval at each location for encounter definition.

Figure S3.1 – Aerial picture of the Sutors channel.

Figure S3.2 – Aerial picture of the Chanonry channel.

Figure S3.3 – Relationship between angular range and encounter duration.

Figure S3.4 – Relationship between angular range calculated in the first 5 and 10 minutes of an encounter.

Figure S3.5– Relationship between the number of individuals during and encounter and the angular range in the first 10 minutes of an encounter.

Figure S3.6 - Relationship between the proportion of hours with foraging buzzes and bray calls in the previous 12, 24 and 36 hours.

Appendix 3A – Directional hydrophones cluster time drift and orientation correction Details on the steps taken to correct time drift on directional hydrophone cluster and to estimate the orientation correction factor for the cluster underwater orientation.

Table S3.1. *Summary table of the inter-click-interval in seconds between all the clicks classified as dolphin clicks by the PAMGUARD classifier. The table reports the upper, 95th and 99th quartile. These values were used to determine a suitable threshold to define dolphin click trains.*

Site	uq	q95	q99
269	0.435	9.420	51.739
270	0.423	15.120	99.292
271	0.321	11.066	75.065
272	0.191	11.490	155.763
273	0.306	15.250	167.466
274	0.291	46.773	1028.500
276	0.253	5.810	34.265
277	0.361	14.980	180.933
278	0.344	9.780	53.141
279	0.296	4.591	22.936

Table S3.2. *Summary table of the interval in minutes between dolphin detection positive minutes at each location. The table reports the upper, 95th and 99th quartile. These values were used to determine a suitable threshold to define different encounters.*

Site	uq	q95	q99
269	1	7.00	63.79
270	2	10.00	61.54
271	2	12.00	172.40
272	2	44.00	319.73
273	2	37.45	529.06
274	3	27.20	406.79
276	1	5.05	187.38
277	2	9.70	206.04
278	1	3.90	30.38
279	1	3.00	36.24

Table S3.3. *Results of the model selection anova analysis. Models were compared using likelihood ratio test. Dolphin probability of occurrence was modelled in response to the presence of foraging calls in the first 10 minutes of the encounter and location (foraging hotspot vs.other). Each model also included the hydrophone deployment*

Model	AIC	BIC	Log-lik	DF	p-value
~ Foraging presence * Location	1,717.6	1742.1	-862.61		
~ Foraging presence + Location	1,717.0	1735.1	-853.49	2	<0.001
~ 1	1,731.2	1742.1	-852.81	1	0.24

Figure S3.1. *Aerial picture of the Sutors channel with highlighted the visual observation advantage point (star), and the deployment locations of passive acoustic devices visible from the advantage point (circles).*

Figure S3.2. *Aerial picture of the Chanonry channel with highlighted the visual observation advantage point (star), and the deployment locations of passive acoustic devices visible from the advantage point (circles).*

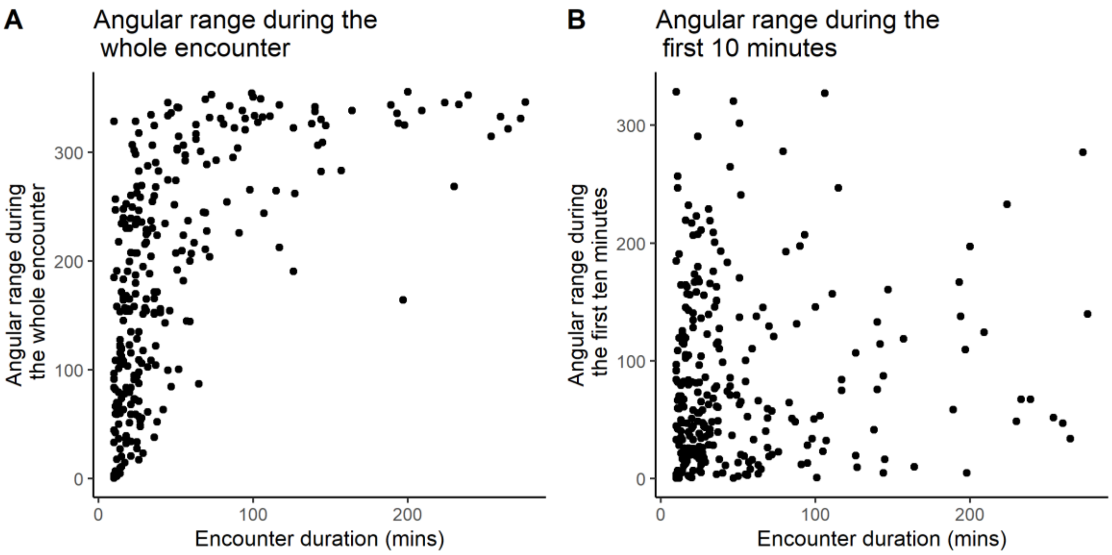

Figure S3.3. *A) Relationship between the bearing range during the whole encounter and the encounter duration - Pearson correlation r = 0.6, p = < 0.001, df = 277 . B) Relationship between the bearing range during the first 10 minutes of the encounter and encounter duration – Pearson correlation r = 0.07, p = 0.23, df = 277.*

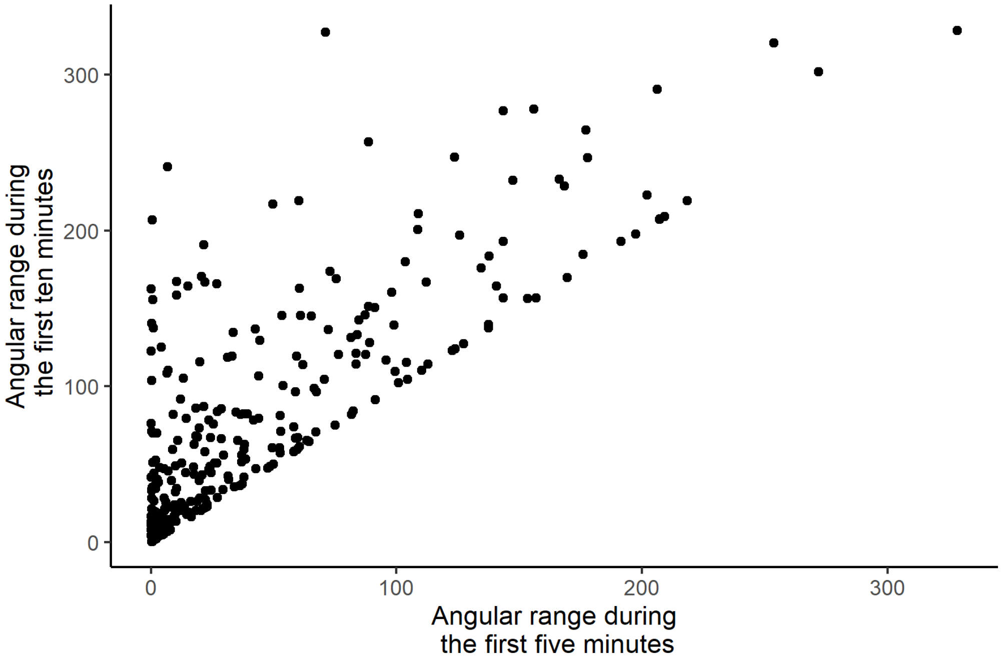

Figure S3.4. *Relationship between the angular range calculated using the clicks detected in the first five and ten minutes of each encounter.*

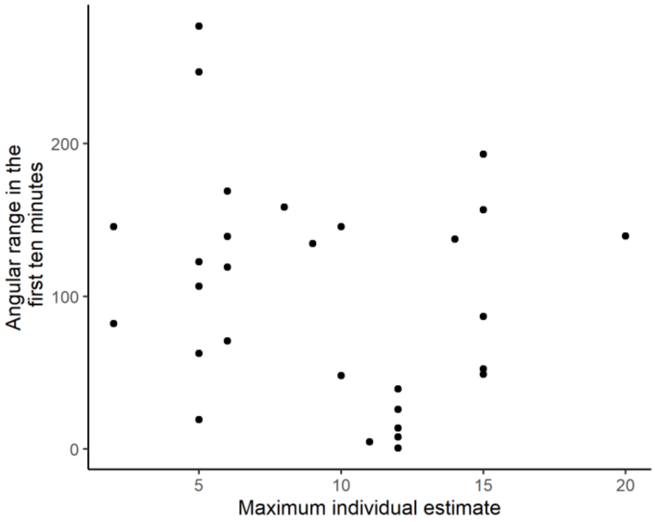

Figure S3.5. *Relationship between the maximum number of individuals during an encounter estimated by visual observations and the angular range during the first ten minutes at three locations (269, 270 and 278). Kendall correlation t=-0.52, p = 0.061.*

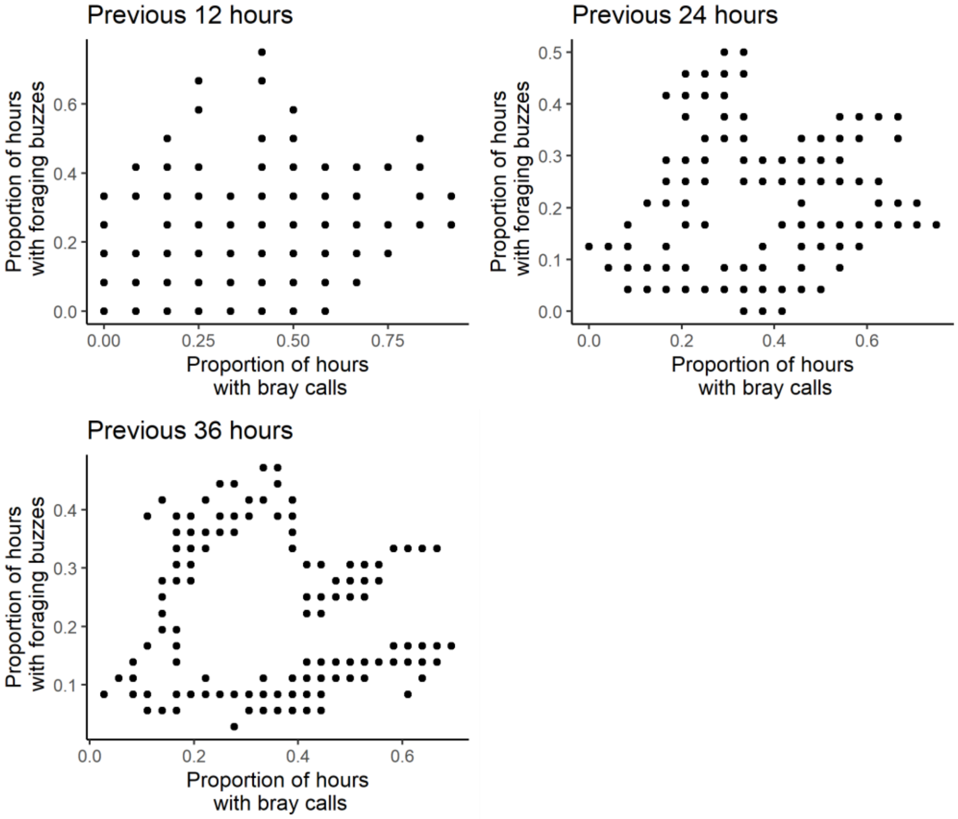

Figure S3.6. *Relationship between the proportion of hours with foraging buzzes and bray calls calculated for each hour recorded on the directional hydrophone clusters deployed in Sutors and Chanonry in the previous 12, 24 and 36 hours. Proportion of foraging hours were defined using the data from the long-term CPOD and long-term SoundTrap for buzzes and bray calls respectively.*

Appendix 3A. Directional hydrophone cluster time drift and orientation correction

Directional hydrophone cluster time drift

Time drift on each directional hydrophone cluster was corrected using an artificial sound produced with two metal rods 20 meters away from each cluster, for twelve times, during the recording period. SoundTraps recordings were inspected visually and aurally in Raven (K. Lisa Yang Center for Conservation Bioacoustics 2019) where the artificial sound could be identified (Figure A3.1). Time drift was estimated using the time difference between when the sound was produced and when it was recorded by the SoundTrap. An initial exploration of the time difference revealed that there were two different drifting patterns depending on the SoundTrap model, ST4300 or ST4300HF (Figure A3.2). However, during each recording day (24 hours periods) the SoundTraps were drifting consistently (Figure A3.2). Thus, to estimate a correction factor over the 24 hours period I used two linear regression models, one for each SoundTrap model (Figure A3.2). The predicted values of the two linear models were extracted and applied as a time correction factor to the data.

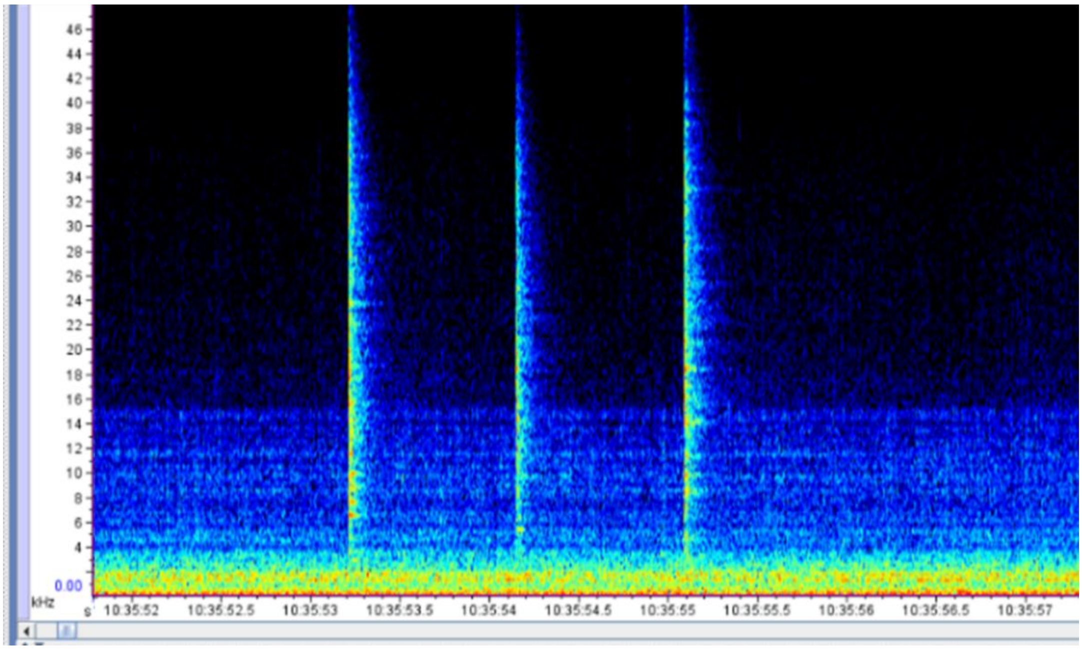

Figure A3.1. *Example of the Raven spectrogram view of the sound produced by the two metal rods.*

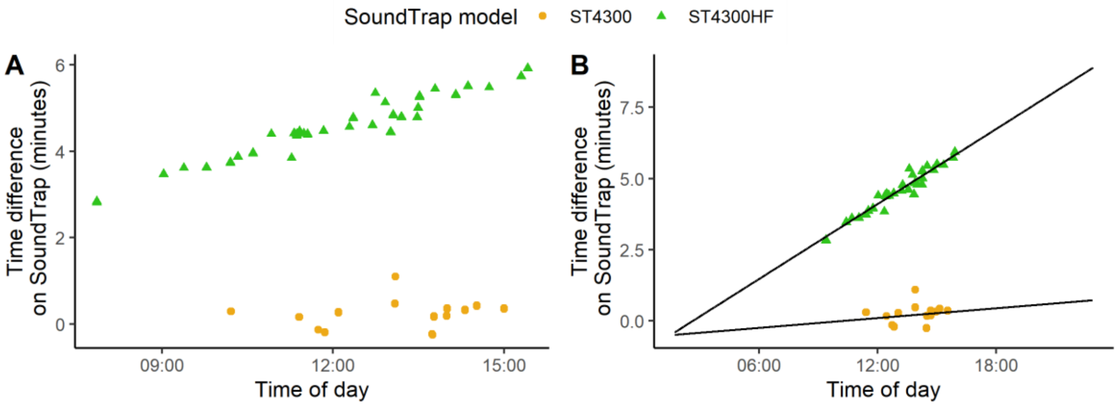

Figure A3.2. *A) Time difference between the time at which the metallic noise was produced and the time at which it was recorded on the SoundTrap, during the day. B) Predicted output of the linear models for the two models of SoundTraps used.*

Directional hydrophone cluster orientation correction

To study dolphin movement, I used PAMGUARD to calculate the horizontal angle to each click detected on the directional hydrophone cluster (Macaulay *et al.* 2017; Gillespie *et al.* 2020). However, in order to represent true directional bearings, these needed to be corrected for the underwater orientation of each directional hydrophone cluster. First, I used the data from the OpenTag attached to the base of the frame (Figure 3.3) to ensure, that the frame was horizontal on the seabed surface. Then, I was able to determine the devices orientation using a grid-search analysis on the theoretical and observed angles towards a boat engine noise, while the boat was moving around the clusters. Three orientation tests were performed, on three different days, during which the boat travelled around each directional hydrophone cluster three times at roughly 20 meters distance. During the orientation test the boat GPS was recording the boat location every second, allowing me to estimate the real bearing between the cluster and the boat. After all the clicks were time corrected, I extracted the clicks detected during the orientation tests and calculated a median bearing per second to match the time scale of the boat GPS (Figure A3.3-A). To find the correction factor for each location, I ran 359 simulations of the detected bearings by rotating the bearings by one degree at each simulation. I used a grid-search approach to find the best matching simulated bearings (Figure A3.3-B) to the true bearing towards the boat (Figure A3.3-C) calculating at each simulation the difference between the observed and the true bearings. The number of degrees that the bearings were rotated by, in the simulation with the lowest Chi-square value, was used as a correction factor for all the clicks from that cluster.

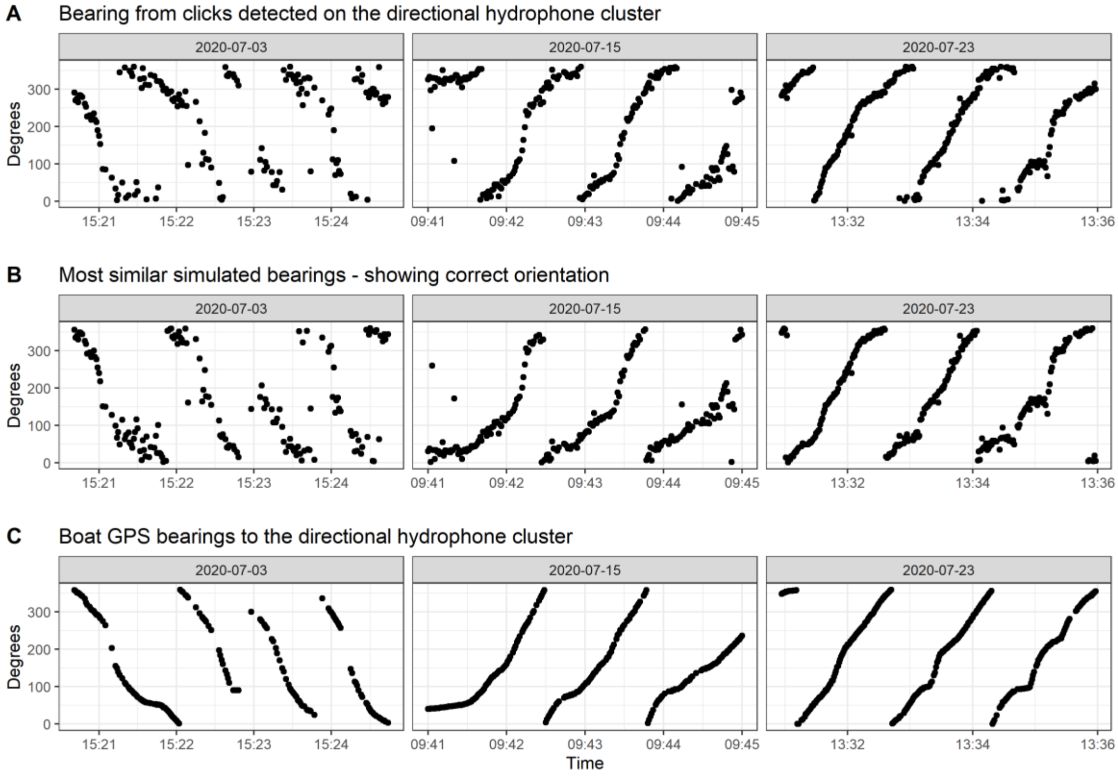

Figure A3.3. *Orientation correction process: A) Median bearing per second of the clicks detected by PAMGUARD during the three orientation tests. B) Median bearing per second of the simulation that scored the lowest difference between the observed bearing and the true bearing towards the boat. C) Calculated bearing between the boat GPS location and the hydrophone cluster deployment location per second during the three orientation tests.*

Chapter 4

Prey encounters and spatial memory influence use of foraging patches in a marine central place forager

Chapter 4

Prey encounters and spatial memory influence use of foraging patches in a marine central place forager[1]

Abstract

Given the patchiness and long-term predictability of marine resources, memory of high-quality foraging grounds is expected to provide fitness advantages for central place foragers. However, it remains challenging to characterise how marine predators integrate memory with recent prey encounters to adjust fine-scale movement and use of foraging patches. Here, I used two months of movement data from harbour seals (*Phoca vitulina*) to quantify the repeatability in foraging patches as a proxy for memory. I then integrated these data into analyses of fine-scale movement and underwater behaviour to test how both spatial memory and prey encounter rates influenced the seals' area restricted search (ARS) behaviour. Specifically, I used one month's GPS data from 29 individuals to build spatial memory maps of searched areas, and archived accelerometery data from a subset of five individuals to detect prey catch attempts, a proxy for prey encounters. Individuals were highly consistent in the areas they visited over two consecutive months. Hidden Markov Models showed that both spatial memory and prey encounters increased the probability of seals initiating ARS. These results provide evidence that predators use memory to adjust their fine scale movement and this ability should be accounted for in movement models.

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[1] This chapter has been published as: Iorio-Merlo, V., Graham, I.M., Hewitt, R.C., Pirotta, E., Aarts, G., Hastie, G.D. & Thompson, P.M. (2022). Prey encounters and spatial memory influence use of foraging patches in a marine central place forager. Proceeding of the Royal Society B, DOI: 10.1098/rspb.2021.2261.

Introduction

Whilst key aspects of predator movements can be explained by theoretical search strategies (Sims *et al.* 2006), it is recognised that factors such as cognitive and perceptual abilities may also influence movement patterns (Sims *et al.* 2006; Auger-Methe *et al.* 2016; Fagan *et al.* 2017). Predator movements can be characterised into different modes (e.g. oriented vs. non-oriented, exploratory vs. area restricted search), with switches between these modes characterising temporal and spatial variation in foraging effort (Fagan *et al.* 2019). Area restricted search (ARS) movement is widely recognised as a strategy by which predators concentrate their search activity in areas rich in resources (Kareiva & Odell 1987; Benhamou 1992). Specifically, predators are expected to decrease their speed and increase turning angles upon encountering prey, thereby increasing time spent in areas where the probability of encountering further prey items is high (Schoener 1971; Kareiva & Odell 1987; Ward & Saltz 1994). Thus, an increase in prey encounters has been hypothesised to drive the initiation of ARS behaviour (Hamer *et al.* 2009; Bailey *et al.* 2019). However, prey encounters are often highly stochastic, and since most predators have well-developed cognitive and sensory abilities, they are also expected to use other information sources to initiate ARS (Davoren *et al.* 2003; Thums *et al.* 2011; Auger-Methe *et al.* 2016).

Many terrestrial and marine species display site fidelity to foraging and breeding locations, supporting their ability to store information on habitat quality (Gonzalez-Gomez & Vasquez 2006; Cordes *et al.* 2011; Cameron *et al.* 2020). Furthermore, mechanistic movement models that include spatial memory can successfully replicate observed patterns of site fidelity (Van Moorter *et al.* 2009; Nabe-Nielsen *et al.* 2013). Given the patchiness and high spatio-temporal predictability of marine resources, site fidelity and memory of foraging grounds is hypothesised to provide fitness advantages over an individual's lifespan (Bradshaw *et al.* 2004; Arthur *et al.* 2015; Abrahms *et al.* 2019a). In particular, animals may use spatial memory to target patches of resources outside their perceptual ranges (Weimerskirch *et al.* 2007; Wakefield *et al.* 2015; Fagan *et al.* 2017). For example, black-browed albatrosses (*Thalassarche melanophris*) targeted areas of < 1 km^2 where they had previously encountered fishing vessels, despite these being > 100 km from their colony (Collet & Weimerskirch 2020). Predators may thus use spatial memory to identify foraging areas, within which they then focus searching activity using ARS movement (Regular *et al.* 2013).

Previous studies considering both memory and the influence of prey encounters on searching strategies are based either on terrestrial systems (Merkle *et al.* 2014; Schlagel *et al.* 2017) or simulations (Mueller & Fagan 2008; Schlägel *et al.* 2014; Bracis *et al.* 2018). Despite evidence of marine predators returning to foraging grounds (Davoren *et al.* 2003; Thums *et al.* 2011; Meese & Lowe 2020), it is only recently that advances in biologging and acoustic technologies have provided finer resolution data to empirically test the effect of prey-encounter events on marine mammal and seabird movements (Iwata *et al.* 2015; Bailey *et al.* 2019). To date, I am aware of no study that has directly explored how marine predators combine longer-term spatial memory and contemporary prey encounters to adjust their fine-scale movements.

Here, I used movement data from biologgers deployed on coastal harbour seals (*Phoca vitulina*) to test the influence of both spatial memory and prey encounters, and their interaction, on ARS behaviour in this central place forager (Orians & Pearson 1979). First, movement data were used to classify seal activities at sea (Dragon *et al.* 2012). To provide initial support that seals have memory of foraging areas, I explored individual repeatability of foraging patches over two consecutive months. As a proxy for memory, data on the seal's activities were used to build spatial memory maps representing the areas in which seals concentrated their searching effort over a one month period. For a subset of animals, I then used fine-scale accelerometer data (Ydesen *et al.* 2014; Cox *et al.* 2018b), to infer prey encounter events while the animal was diving. Finally, I fitted two Hidden Markov Models (HMM) (Langrock *et al.* 2012) to test whether spatial memory alone, or in combination with prey encounters, increased the probability of an animal initiating ARS behaviour during a foraging trip.

Methods

Case study species and data collection

Harbour seals are central place foragers inhabiting temperate coastal waters (Thompson *et al.* 2019). During February and March 2017, thirty-one adult harbour seals (11 Males and 20 Females) were captured and tagged in Loch Fleet, NE Scotland (57.935° N, 4.042° W) (see Cordes *et al.* 2011 for background on the study site and population). Seal capture and handling occurred in accordance with the Home Office Licence issued to the Sea Mammal Research Unit (Licence No. 192CBD9F) with local licence approval from the University of St Andrews Animal Welfare and Ethics Committee. Fastloc GPS-GSM phone tags (Sea Mammal Research Unit Instrumentation, University of St Andrews, UK) were attached to the pelage at the back of the neck, using the capture and handling methods detailed in Russell *et al.* (2016). Tags were equipped with a GPS (Global Positioning System) receiver, wet-dry sensor, and pressure sensor, providing geo-referenced summaries of activity and diving patterns via the GSM (Global System from Mobile communication) phone network (McConnell *et al.* 2004). Tags also collected tri-axial accelerometer data that were archived onboard, subject to digital storage limitations, but not relayed through the GSM network due to the volume of data from the high sampling frequencies used. Tags from a subset of five individuals were subsequently recovered on the shore after tags detached during the moult, allowing archived tri-axial accelerometer data to be downloaded.

Tags were programmed to record GPS information every time a seal surfaced. However, due to variation in satellite availability, this resulted in an irregular time series. On average, locations were recorded every 15 minutes. When the wet-dry sensor determined that the animal was at sea, the pressure sensor also recorded depth. Below a depth threshold of 1.5 m, time-depth data were recorded every 4 seconds and stored in the tags. Dives were summarised using depth bins at 23 equally spaced time points throughout the dives. For each dive, the maximum diving depth, duration, and time-depth summary were transmitted through the GSM network. The tri-axial accelerometer measured the *g*-force at a frequency of 12.5 Hz. Because the accelerometers were not calibrated prior to release, a post-hoc calibration was applied to the data, described in detail in Appendix 4A. Next, a box-moving average (window width of 12 Hz) of each of the three axes was calculated. These smoothed values represent an approximation for the gravitational component, which can be used to derive the pitch angle. Finally, these smoothed estimates were subtracted from the measured raw *g*-forces to obtain the dynamic or specific acceleration, which can be used to determine prey capture attempts (Shepard *et al.* 2008).

Identification of ARS behaviour

I fitted a total of three HMMs (Table 4.1) to classify at-sea activities and to build spatial memory maps of searched areas (Model 1), to assess the influence of memory alone on all individuals (Model 2), and to assess the simultaneous influence of spatial memory and prey encounters on the subset of five individuals for which accelerometer data were available (Model 3). All models were fitted using the momentuHMM package (McClintock & Michelot 2018).

To ensure the analysis focussed on central place foraging trips, I selected round-trips from and to the same haul-out site location, which were a) > 12 hours and b) included locations that were > 2 km from the haul-out site. This avoided the inclusion of shorter periods in the water which typically represent resting near intertidal haul-out sites (Thompson *et al.* 1998; Cordes *et al.* 2011).

I used batches of five dives as the unit of analysis to avoid potential numerical problems in estimating the maximum likelihood and extreme residual autocorrelation associated with a dive-by-dive analysis (van Beest *et al.* 2019). The mean dive cycle (i.e. dive and subsequent period at surface, a dive being the time spent below 1.5 m depth) was 4.46 (± 6.68) minutes, and the 90th percentile of the time interval between GPS locations was 25 minutes. Dive locations were estimated by linearly interpolating between the GPS positions using the manufacturer software. However, due to gaps in the GPS datasets there might be uncertainty around some dive locations (Appendix 4B - Figure B4.1). Therefore, in the analyses I only used batches of five dives that were associated with at least one raw GPS location (for more details see Appendix B).

Table 4.1. *Overview of the three HMMs, showing the number of individuals included in the model, the time period for which movement data were used, the covariates that were included in the model to assess the influence on the transition probabilities and a summary of the objectives and what was the output used for.*

Model	# of individuals	Time period	Covariates	Objective and output
Model 1	31	February – June	None	• Identification of ARS locations to be used in the repeatability analysis • Spatial memory maps with the proportion of dive batches spent searching for the month of April and a month prior to the beginning of the accelerometer data
Model 2	29	May	• Spatial memory of ARS behaviour in April.	• Test the influence of memory on the transition probability between ARS and Transit
Model 3	5	April – May - June	• Spatial memory of ARS behaviour during the month prior to the beginning of the accelerometer data • Mean number of prey encounters per dive in each dive batch	• Test the influence of memory and prey encounters on the transition probability between ARS and Transit

Seal activities at sea were classified into two behavioural states using an HMM based on the step length and turning angle between consecutive dive batches (see below). The two states are assumed to represent transit and ARS movement, which are characterised by long directional displacement or short tortuous movement, respectively (McClintock *et al.* 2013). I calculated the step length and turning angle between the locations of the first dive of each batch and assumed these observations resulted from state-dependent gamma and wrapped Cauchy distributions (McClintock *et al.* 2017), respectively. Following the methodology described by Russell *et al.* (2015) and Carter *et al.* (2020), if any dive batch was not associated with a raw GPS location, the step length and turning angle were set to 'not available' (NA) (Langrock *et al.* 2012); thus, the state was assigned solely based on the Markov property (for more details see Appendix 4B). Finally, I selected the initial values of the parameters using the estimates from the model with the lowest AIC score among 50 iterations with randomly selected initial values. The most likely state sequence given the final model was decoded using the Viterbi algorithm (Zucchini & MacDonald 2009).

Spatial memory of foraging patches

Searching areas were defined using the locations of dive batches that were classified as ARS by Model 1. To quantify how consistently seals visited the same areas over time, I calculated the spatial overlap between searched areas visited during two consecutive months (Arthur *et al.* 2015); here, April and May. Kernel utilization distributions (UD) for each of the two months were calculated using the adehabitatHR package (Calenge 2006) using a grid size of 500 m by 500 m. The most appropriate kernel bandwidth was estimated using the First-Passage-Time method described in Lascelles *et al.* (2016). Overlap between 50% UD was estimated using the Bhattacharyya's affinity (BA) index (Bhattacharyya 1943), where 0 indicates no overlap and 1 identical distributions. To compare the observed overlap with a null distribution of BA values, I used a pairwise comparison to calculate the overlap between a seal's UD in May with the UD in April of another randomly selected individual.

As a proxy for spatial memory, I built memory grids using the proportion of dive batches classified as ARS by Model 1, in a 1 x 1 km grid over the study area. Two sets of memory grids were built to be used in Model 2 and Model 3, respectively (Table 4.1). I first created a set of spatial memory grids representing the individual's ARS behaviour during the previous month of the data included in Model 2 (Table 4.1). Then I created a second set of grids representing the areas used during one month prior to data included in Model 3 (Table 4.1). Due to the differences in accelerometer data availability between individuals (Table 4.2) the month used to build the spatial memory grid for each of these five individuals varied.

Table 4.2. *Summary data for the five individuals whose tags were recovered, including start and end dates and the number of trips included in each model. Start and end date under Model 3 represent the time for which accelerometer data were available for each individual. For the three pregnant females, I only used trips that occurred before the animals gave birth.*

Seal ID	Sex	Weight (Kg)	Length (cm)	Pregnancy status	Dives with prey encounters	Total prey encounters	Model 1 memory map		Model 3		
							Start date	# trips	Start date	End date	# trips
90	M	92.2	149	/	2,785	16,277	2017-04-15	11	2017-05-17	2017-06-13	6
158	F	96.4	144	Yes	10,051	46,085	2017-03-27	21	2017-04-28	2017-06-10	17
242	F	86.2	138	Yes	5,598	19,707	2017-04-22	13	2017-05-23	2017-06-04	5
283	F	66.8	129	Yes	2,466	18,968	2017-04-29	26	2017-05-31	2017-06-10	8
285	F	73.2	134	No	8,263	45,053	2017-03-17	11	2017-04-18	2017-05-22	10

Prey encounters

I inferred prey encounter events from the accelerometer data while animals were at sea. In coastal waters, harbour seals most frequently dive to the seabed and perform U-shaped dives through all phases of their foraging trips (Tollit *et al.* 1998; Vance *et al.* 2021). Therefore, I used accelerometery data to detect prey encounters during the bottom phase of each of these dives (Vance *et al.* 2021), characterised as the period when seals were within 20% of the maximum dive depth (Bailleul *et al.* 2008).

I used two different methodologies to detect prey encounters. First, I identified sudden peaks in dynamic acceleration resulting from rapid head and body movements (Viviant *et al.* 2010; Guinet *et al.* 2014; Cox *et al.* 2018b). This method has been validated with captive harbour seals and was able to identify prey capture attempts (Ydesen *et al.* 2014; Cox *et al.* 2018b). I calculated the standard deviation in dynamic acceleration over a moving window of 1.5 s for each axis and used a k-means cluster analysis to group the standard deviation values into two activity states, “high” and “low”. I assumed an animal made a prey capture attempt, and thus encountered a prey item, when its activity was determined to be “high” on all three axes (Viviant *et al.* 2010; Guinet *et al.* 2014; Cox *et al.* 2018b). Second, I identified changes in body pitch angle, which have been used as indicators of the more subtle movements that harbour seals may use to catch benthic prey in shallow coastal waters (Brasseur *et al.* 2012). The pitch angle was calculated based on the estimated gravitational component of the measured *g*-forces (Cox *et al.* 2018b). I calculated the differences between peaks and troughs in the time series of body pitch angle during each dive. Prey capture attempts were identified when a change in pitch angle greater than 20° occurred within a window of 5 seconds (Brasseur *et al.* 2012). As these two methodologies have not previously been used together, I assessed whether the identified foraging attempts derived from the two methods (i.e. bursts in dynamic acceleration and drops in body pitch angle) occurred at the same time. To avoid counting the same event twice, I then calculated the total number of prey encounter events in each dive by summing the number of independent attempts detected by either method.

Assessing the drivers of ARS behaviour

To assess which factors influenced the initiation of ARS behaviour, I ran two separate models Model 2 and Model 3 (Table 4.1). Model 2 was based on foraging trips occurring in May and included the spatial memory grids of the seals' activities during the month of April as covariates on the transition probabilities between transit and ARS state (Leos-Barajas *et al.* 2016). In Model 3, I included the spatial memory grid of activities during the month prior to the beginning of the accelerometer data and the mean number of prey encounters per dive in each dive batch as covariates (see 'Identification of ARS behaviour'). Note that although five individuals were represented in both models, the memory grids differed between models (see 'Spatial memory of foraging patches section'). After assessing the correlation between the two covariates, I investigated both their additive effect and the effect of an interaction between the two. To assess the influence of each covariate, I fitted the models including both covariates or each covariate separately and ranked them based on AIC and BIC (Burnham & Anderson 2002). Covariates were retained in the model if their inclusion reduced the information criteria by at least 2 units (Burnham & Anderson 2002).

Results

Between February and July 2017, each of the thirty-one tagged seals performed on average 44 foraging trips, which extended across the NE of Scotland (Figure 4.1A). Foraging trips lasted on average 38.65 hours (± 34.79 hours), with the longest trip performed by a male lasting 6.36 days. There was large inter-individual variation in at-sea distribution (Figure 4.1A). However, the ranging patterns and characteristics of the trips of the five individuals for which accelerometer data were available fell within the range of all tagged individuals (Figure 4.1B, Table S4.1).

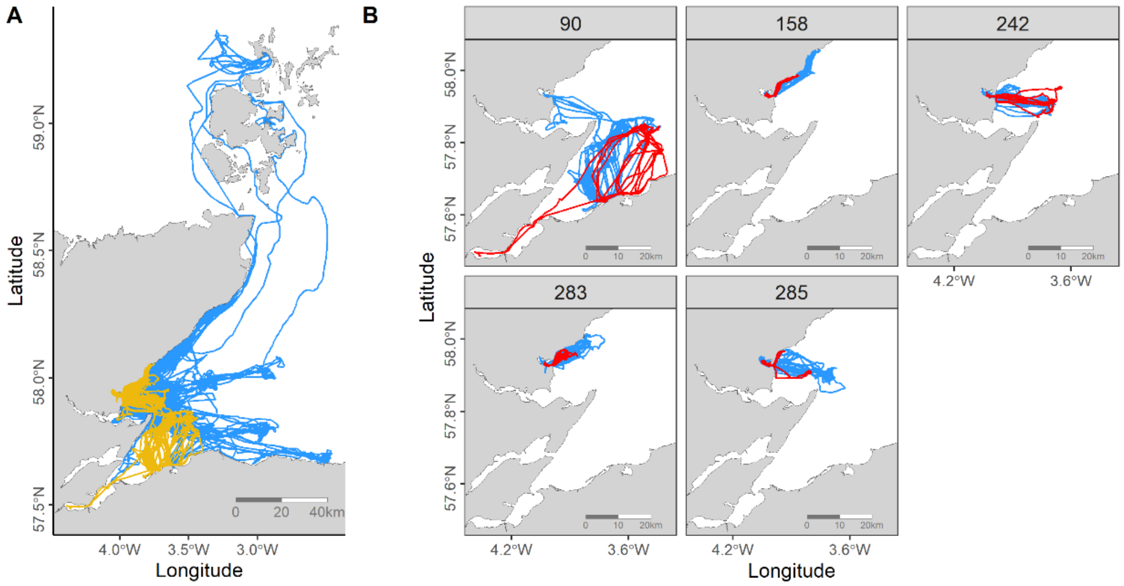

Figure 4.1. *A) Maps displaying the movements of the 31 tagged harbour seals in the Moray Firth (Scotland), showing data from the five retrieved tags in yellow. B) Tracks of the five focal seals where tags were recovered. The trips with accelerometer data that were included in the analysis are highlighted in red (Model 3), while the time period before and after is shown in blue.*

Memory of foraging patches

The first HMM (Model 1) assigned the dive batches into two states: state 1 (step length: 1026.98 m ± 193.83 m, angle: $\mu = 0$, $\gamma = 0.80$) and state 2 (step length: 587.81 m ± 172.48 m, angle: $\mu = 0$, $\gamma = 0.027$) (Figure S4.1). Based upon the combination of short step length and low concentration (i.e. high variability) in turning angle, state 2 was assumed to represent ARS behaviour.

I was able to compare the areas animals visited in May with those visited in April for 29 seals (two tags stopped recording during May). On average these seals performed 10 (± 5.61) foraging trips in each month. I found 5.57 km to be the most appropriate *h* smoothing value to calculate individual's 50% UD (Figure S4.2). Individuals were highly consistent in the areas they visited in April and May (Table S4.2, Figure 4.2), showing much higher overlap than the null distribution (Figure 4.2). From the output of Model 1, dive batches classified as state 2 were used to create the spatial memory grids to be used as covariates in Model 2 and Model 3 (e.g. Figure 4.3B).

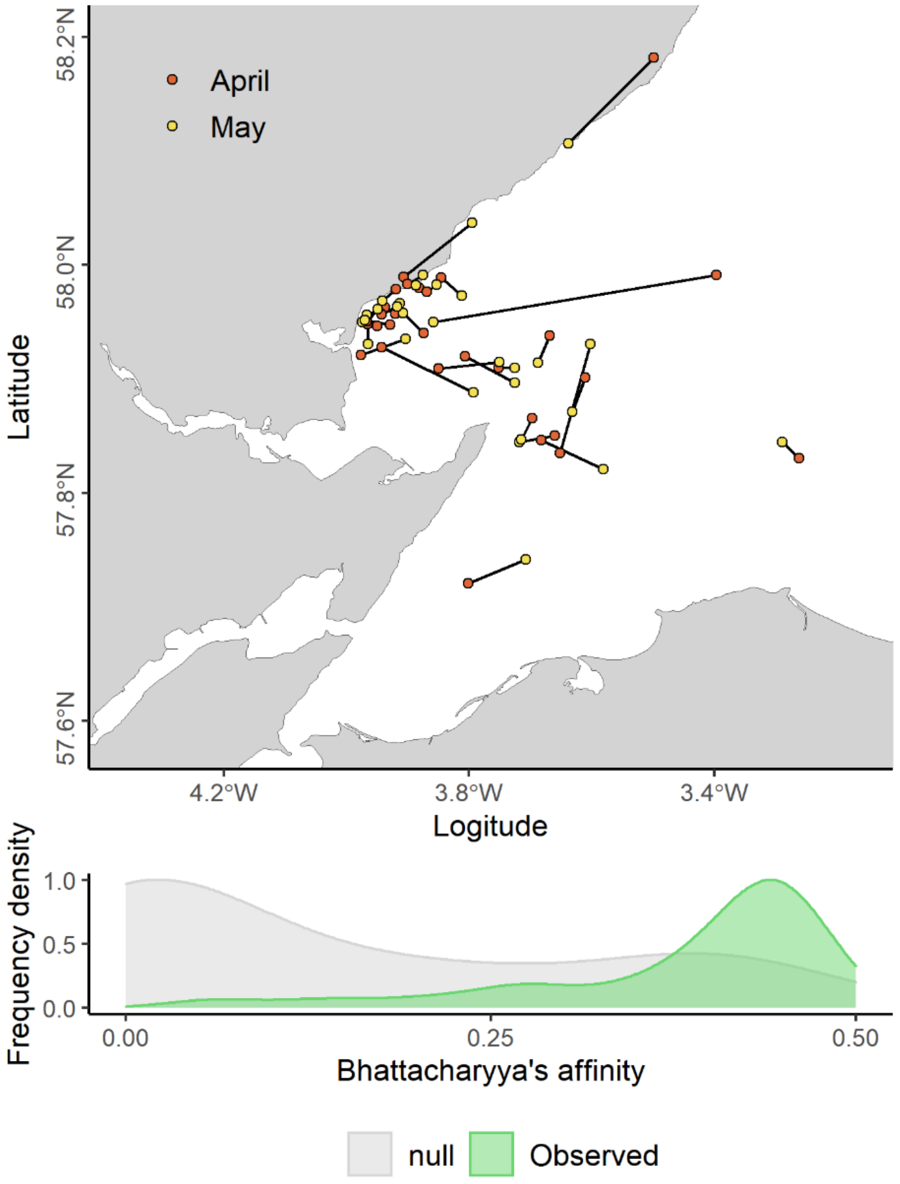

Figure 4.2. *Top: Centroid location of the areas animals searched in April (red) in relation to the centroid location of the ones visited in May (yellow) for 29 individuals. Bottom: Frequency distribution of the observed overlap (green) of an individual's searched areas in consecutive month, estimated using Bhattacharyya's affinity index, and the null distribution of Bhattacharyya's affinity values from the overlap with the areas searched by another randomly selected individual.*

Detection of prey encounters

Prey encounters were detected in all 51 foraging trips for which I had accelerometer data (Table 4.2, Figure 4.3A). Within each of these trips, 69.45% of dives had at least one prey encounter identified by one of the two methods. In total, 51,586 encounters were identified from peaks in acceleration and 78,441 encounters were identified from changes in body pitch angle towards the seabed (Figure 4.4). Of these, only 981 events (0.008% of the total attempts identified) overlapped in time, possibly suggesting that the methods had identified the same event. There was inter-individual variability in the detection of prey encounters by the two methods (Figure S4.3).

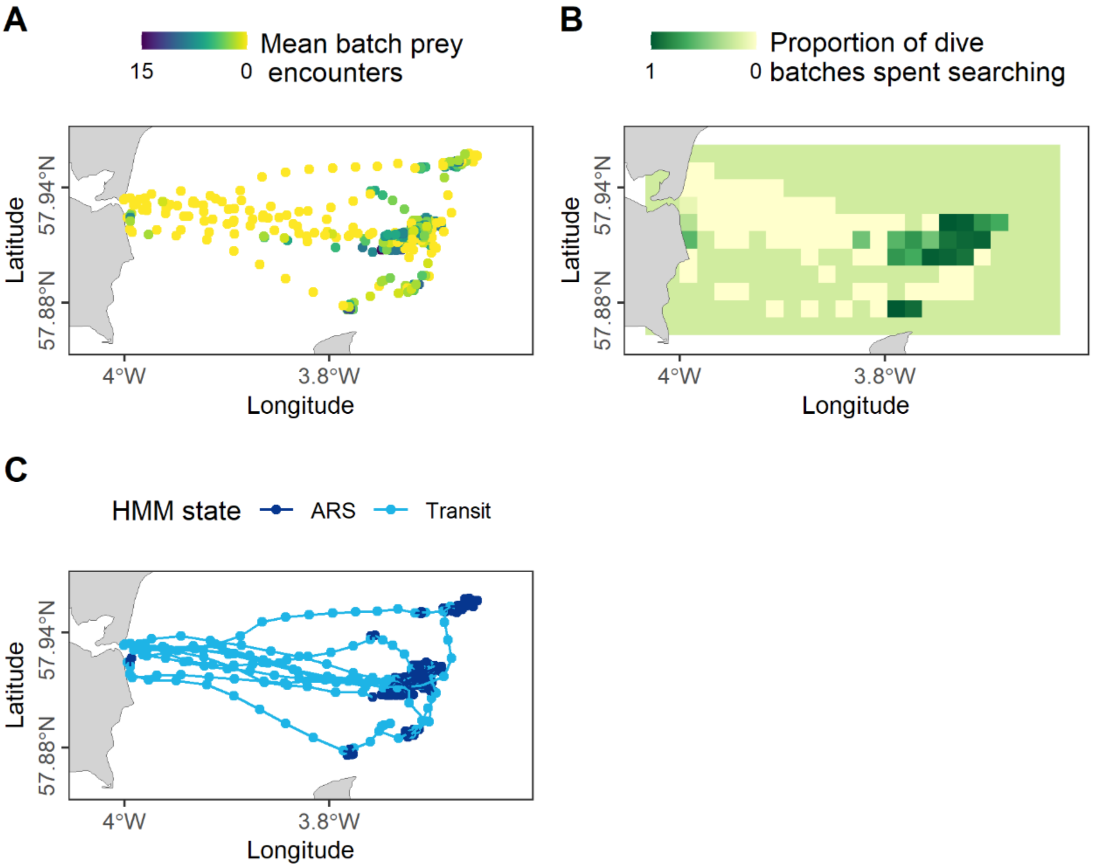

Figure 4.3. *Example of the spatial variation in prey encounters and proxy for spatial memory in relation to the behavioural state classification of Model 3 for the foraging trips of seal 242. A) Locations of dive batches, colour-coded by the mean number of prey encounters per dive batch. B) Memory grid, showing the proportion of dive batches classified as ARS by Model 1 in each grid cell during the month prior to the trips in Model 3. C) Tracks of the trips used in Model 3, colour-coded by the decoded HMM state. Missing parts of the tracks are due to unreliable dive batches (see Appendix 4B).*

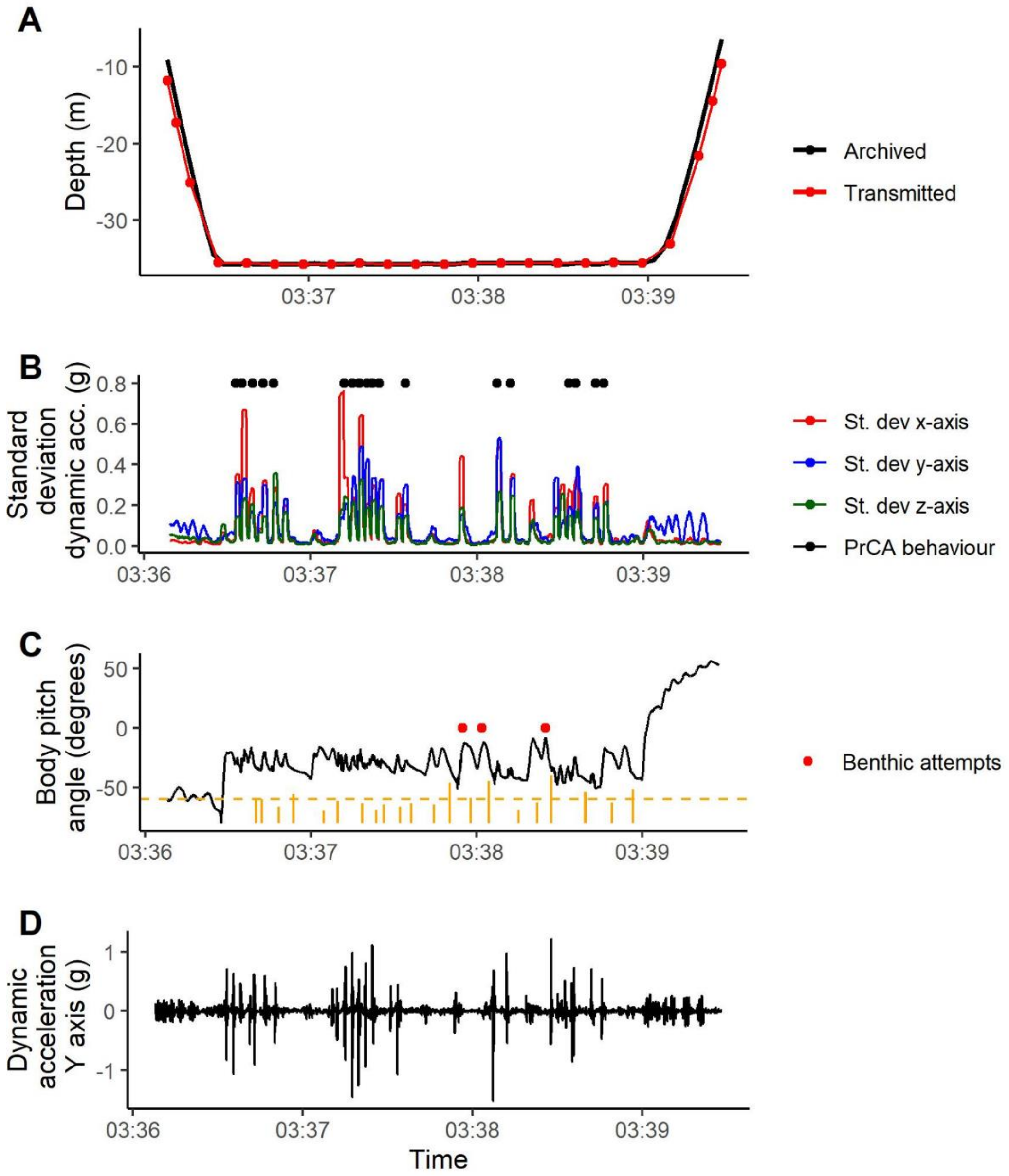

Figure 4.4. *Example of data collected by the GPS-GSM tag during one dive. From top to bottom: A) Time-depth profile reconstructed from the archived data in the tag (black), recorded every 4 seconds, and from the 23 depth bins transmitted through the GSM network (red). B) Standard deviation of the acceleration recorded by the accelerometer on all the three axes. Black circles along the top highlight prey catch attempts recorded when all three axes were above a specified threshold. C) Time series of body pitch angle calculated from the raw accelerometer data. Yellow lines at the bottom of the plot show the magnitude of changes in body pitch angle, as identified by the time-series analysis. The dotted yellow line marks the 20° threshold which was considered indicative of a potential prey catch attempt. Changes in body pitch angle above the threshold that occurred in less than 5 seconds are indicated with red circles as benthic attempts. D) Lateral acceleration recorded by the accelerometer showing flipper stroke amplitudes and rate.*

Drivers of ARS behaviour

The second model (Model 2) assigned dive batches during foraging trips occurring in May into two behavioural states: (i) the first was characterised by long step length and small turning angle (step: 1049.335 m ± 556.832, angle: $\mu = 0$, $\gamma = 0.826$), which I assumed represents an animal transiting; (ii) the second was characterised by short step length and large turning angle (step: 207.162 m ± 181.983, angle: $\mu = 0$, $\gamma = 0.424$), which I assumed represents ARS behaviour (Figure S4.4). Both model selection criteria supported the inclusion of spatial memory, based on seal movements in April, as a covariate in the model (Table 4.3). The proportion of foraging batches spent searching in the same area during the previous month increased an individual's probability of initiating ARS behaviour (Figure 4.5 – Model 2).

Table 4.3. *Comparison of the models based on AIC and BIC, with all covariates and removing one variable at a time for both Model 2 and Model 3. The memory covariate represents the number of dive batches spent searching in a grid cell during the previous month, and prey encounters indicates the mean number of catch attempts per dive for each batch.*

Model 2	**Log-Likelihood**	**AIC**	**BIC**	**Δ AIC**	**Δ BIC**
With memory	-164,875	329,759	329,848	0	0
Without memory	-165,000	330,017	330,090	258	242
Model 3	**Log-Likelihood**	**AIC**	**BIC**	**Δ AIC**	**Δ BIC**
Memory + Prey encounters	-26,816	53,657	53,739	0	0
Memory * Prey encounters	-26,814	53,657	53,751	0	12
Without memory	-26,845	53,780	53,781	54	41
Without prey encounters	-26,882	53,909	53,910	129	116

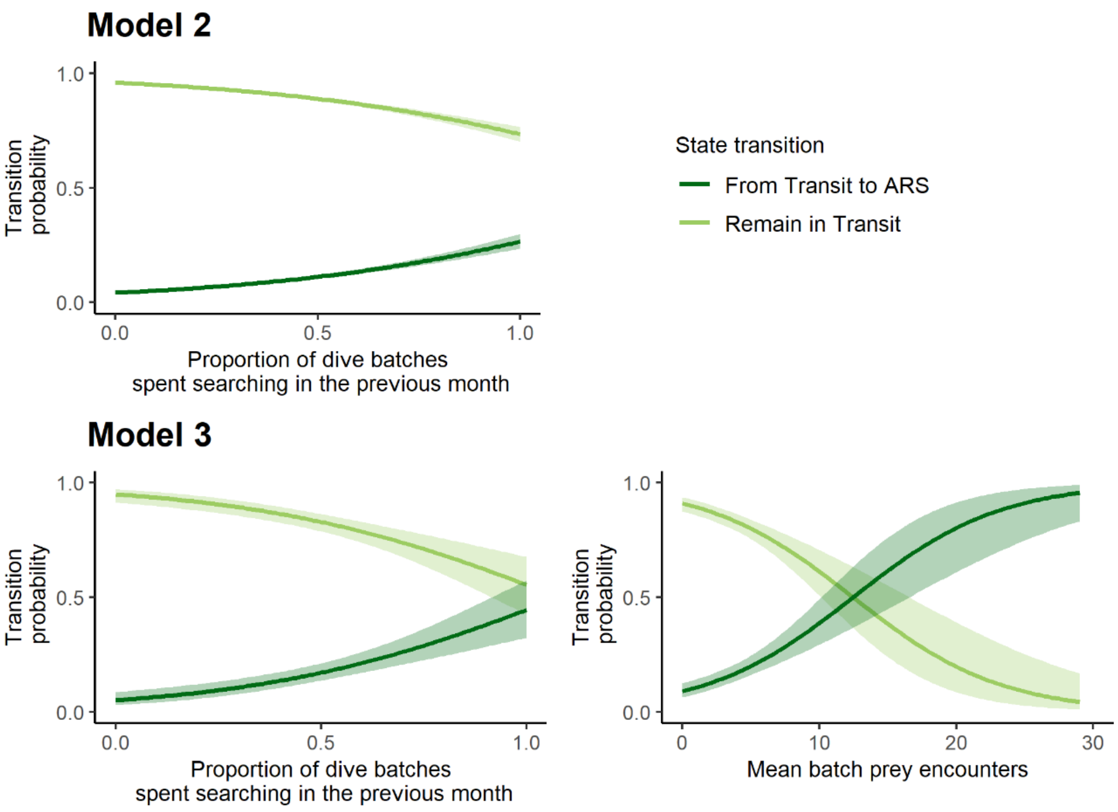

Figure 4.5. *Transition probability (mean and 95% CI) of remaining in a transit state or switching to an ARS state for the covariates included in Model 2 and Model 3. Model 2: Influence of proportion of dive batches spent searching in the previous month (proxy for spatial memory) on the 29 individuals included in Model 2. Model 3: (left) Influence of proportion of dive batches spent searching in the previous month on the five individuals included in Model 3. (right) Influence of the mean batch prey encounters on the five individuals included in Model 3.*

Model 3 assigned movement between the dive batches into a Transit state (step: 893.543 m ± 623.451, angle: μ = 0, γ=0.827) and an ARS state (step: 164.869 m ± 150.729, angle: μ = 0, γ = 0.397) (Figure 4.3C and Figure S4.5). I found no correlation (*Kendall* τ = 0.14) between the prey encounters detected and the memory maps of the ARS behaviour during the previous month (Figure S4.6). Based upon the HMM output, the seals spent 27.35% (± 9.22%) of the dive batches transiting, and 57.27% (± 21.68%) in ARS behaviour, while 15.98% (± 15.72%) of the dive batches could not be classified due to a lack of GPS locations. Both model selection criteria suggested that including prey encounter events and a proxy for memory of previous ARS movement (i.e. the proportion of dive batches spent searching in the area) improved the model (Table 4.3). The BIC score suggested no significant improvement in the model by including an interaction between the two covariates (Table 4.3). The discrepancy observed between the model selection criteria on the inclusion of the interaction is due to the BIC favouring simpler model (Ward 2008). Model 3 showed that the probability of an individual initiating ARS behaviour was associated with prey encounters and areas where individuals spent time searching before (Figure 4.5 – Model 3). Finally, the variation I observed in mean prey encounters per batch during times classified as ARS shows that animals spent time actively searching within the foraging patch (Figure 4.6).

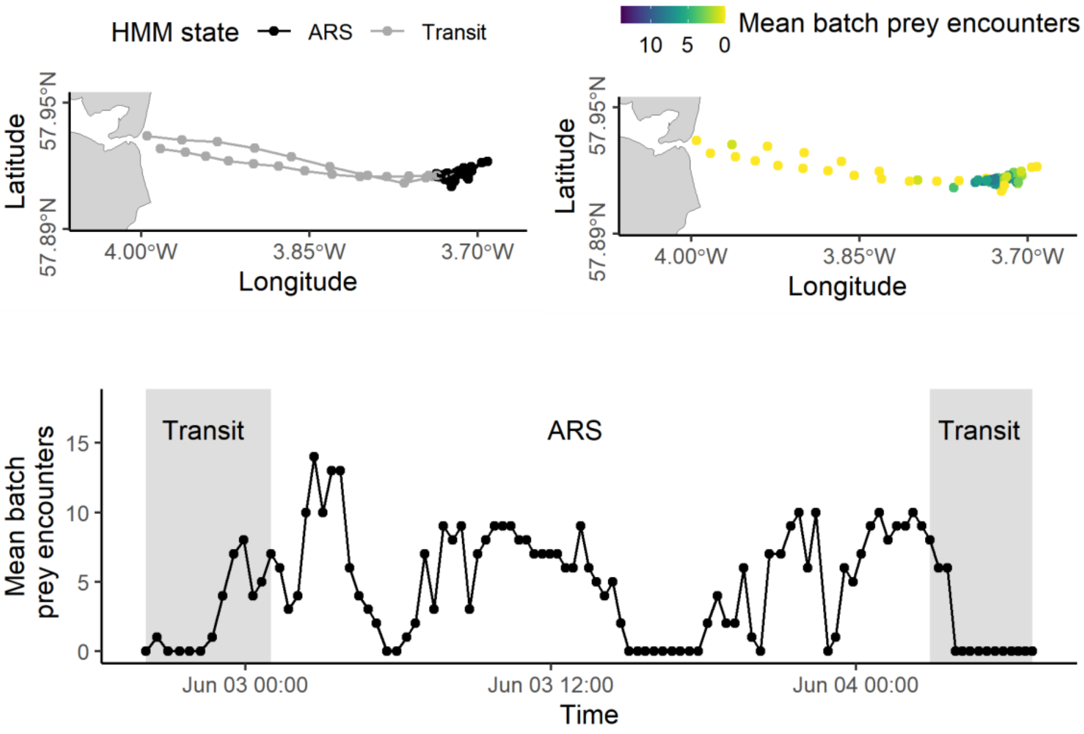

Figure 4.6. *Variability in prey encounters during foraging trip 128 for seal 242. The top two panels show the trip colour-coded by the state assigned by Model 3 (left) and the mean number of prey encounters per dive batch (right). The bottom panel show the variability of mean batch prey encounters during the foraging trip. Shaded areas highlight the parts of the trip that were classified as Transit. Observed variability in prey encounters within the ARS period indicates that ARS includes periods of searching (with zero prey encounters).*

Discussion

Understanding the drivers of animal movement and foraging behaviour remains a central topic in movement ecology (Holyoak *et al.* 2008; Hays *et al.* 2016). I found that individuals repeatedly used the same areas over time, which supports the reliance on spatial memory by predators to return to previously visited foraging grounds (Cordes *et al.* 2011). Therefore, I explored how marine predators use information both within and outside their perceptual ranges to adjust their behaviour and movement, showing that both memory and prey encounters influenced animals' foraging decisions (Kareiva & Odell 1987; Thums *et al.* 2011). Specifically, this model shows that encountering prey and having memory of searched areas coincide with an increased probability of an individual initiating ARS behaviour.

It is challenging to quantify the distribution and variability of prey encounters at scales that are relevant to marine predators (e.g. Davoren 2013; Yoshino *et al.* 2020). I overcame this challenge by using animal-borne accelerometer data to identify prey catch attempts, which can be used as a proxy for prey encounters (Ydesen *et al.* 2014). As predators may adapt prey capture strategies according to prey size or type (Hocking *et al.* 2014; Hocking *et al.* 2016), I used two previously defined proxies for prey catch attempts. Using either methodology alone would have reduced detections by 60% (Viviant *et al.* 2010) and 40% (Brasseur *et al.* 2012), respectively. The number of prey encounters showed a positive relationship with the probability of seals initiating searching behaviour. These findings provide support for the hypothesis that predators increase their residence time in foraging patches where encounter success is high (Stephens & Krebs 1986). However, individual residence times could increase either due to longer search time between prey encounters or higher prey capture rate and handling time. While I was unable to make inferences about foraging success and handling times from accelerometer data alone, this may be possible in the future using auxiliary sensors (Volpov *et al.* 2015; Goulet *et al.* 2019).

Previous studies have also found that predators adjust their foraging behaviour to the density of resources encountered (Mori *et al.* 2007). For example, prey capture rate of double-crested cormorants (*Phalacrocorax auritus*) was a good indicator of prey density (Enstipp *et al.* 2007). Similarly, blue whales (*Balaenoptera musculus*) adjusted the number of feeding lunges per dive to krill density (Hazen *et al.* 2015). The results of this study show a similar positive relationship, with a higher probability of transitioning to ARS when more prey encounters occurred. This further suggests that predators might be using the number of prey encounters to assess the profitability of the foraging patch. Therefore, I hypothesise that the probability of initiating ARS behaviour is indeed indicative of the quality of the foraging site.

Many marine central place foragers repeatedly move between and return to terrestrial breeding and resting sites (Naves *et al.* 2006; Cordes & Thompson 2013) and foraging areas (Augé *et al.* 2014; Wakefield *et al.* 2015; Collet & Weimerskirch 2020). It is increasingly recognised that individual foraging decisions are modified by the memory of previous experience in different foraging areas (Bracis *et al.* 2015). In the results, I showed that the seals displayed a high level of repeatability in the areas they searched for prey in over the span of two months. In contrast, previous research on repeatability in otariids found little overlap of foraging areas between trips within a year (Arthur *et al.* 2015). Furthermore, this dataset was not limited to a specific sex or life-history class (e.g. lactating females only as in Call *et al.* 2008; Arthur *et al.* 2015), but included both sexes, as well as pregnant and non-pregnant females. The observed repeatability in this study seems to be a common trait shared across sexes. All seals tagged in this study were adults, for which a higher repeatability is expected compared to young individuals (Grecian *et al.* 2018).

Given that individuals in this population showed high repeatability of searched areas used, I tested whether memory influenced fine-scale movement decisions by including spatial memory in the Hidden Markov Model. I found that the probability of initiating ARS behaviour was linked with individuals' spatial memory. Similarly, Thums *et al.* (2011) found that southern elephant seals (*Mirounga leonina*) had a high probability of engaging in ARS behaviour along the shelf edge, independent of prey capture attempts recorded while diving. In this study, individuals changed their behaviour in anticipation of profitable foraging areas. The differences observed between Model 2 (with data from 31 individuals) and Model 3 (with data from 5 individuals) could indicate individual differences in the importance of memory which should be investigated further. This analysis assessed the influence of spatial memory associated with a 1 x 1 km grid without making any assumptions about what features the animals might be using to recognize the areas (Thums *et al.* 2011) or which cues they might be following to return to these areas (Reynolds *et al.* 2015).

Short- and long-term memory of encountered resources can also vary through the lifetime of an individual, with acquisition of new information and memory decay over time (Fagan *et al.* 2013). In this study, I compared multiple foraging trips occurring over consecutive months, building upon earlier studies that have investigated the role of memory over a series of dives or paired trips (Iwata *et al.* 2015; Votier *et al.* 2017). This analysis focussed on two months in spring/summer, future research should aim to extend this approach to explore the role of memory over longer temporal scales using movement data across different seasons (Thompson *et al.* 1996; Sharples *et al.* 2012). For example, seasonal changes in prey distribution might affect the foraging areas targeted by individuals, causing a mismatch between the areas visited in consecutive months and the persistence of memory at longer time scales (Lesage *et al.* 2004). Comparison of the movements of individuals during similar time periods in different years would be needed to observe long-term memory-driven behaviour (Arthur *et al.* 2015; Wakefield *et al.* 2015). Spatial and temporal information on prey distribution is also needed to understand how memory of prey patches may vary within or between years.

Having prior knowledge on prey distribution can be particularly useful for predators that feed on cryptic prey species with low encounter rates. In this case, predators should adopt a Bayesian foraging strategy, whereby historic prey encounters are used as prior information that is updated while encountering prey (McNamara *et al.* 2006; Biernaskie *et al.* 2009). In this study predators appeared to adjust their movement in response to both prior knowledge and current experience to initiate ARS. However, the same drivers could also influence predators patch departure (Marshall *et al.* 2013); the Marginal Value Theorem predicts that foragers should only leave a patch and switch back to transit movement when intake rate drops below the average intake rate of the entire area (Charnov 1976). Here, I was only able to incorporate archival accelerometery data from the subset of tags that were recovered. However, with improvements in on-board processing (Cox *et al.* 2018b), data on prey encounters can now be accessed in near real-time with the associated GPS data, allowing these models to be tested over ecologically relevant spatial and temporal scales.

In conclusion, this study gives new insights into another driver of ARS behaviour. These findings provide empirical evidence that predators use other information, such as spatial memory, to guide movement decisions and to initiate ARS behaviour. Previous studies showed that predators responded to their recent prey encounters, but this was insufficient to fully explain observed movement patterns (Bracis *et al.* 2015; Auger-Methe *et al.* 2016). The ability of predators to memorise the distribution of predictable resources has been predicted to have evolved to cope with environmental variability and to maximise their long-term energy intake (Bradshaw *et al.* 2004; Polansky *et al.* 2015; Abrahms *et al.* 2019a). These results reinforce the importance of accounting for this ability within movement models (Nabe-Nielsen *et al.* 2013; Liukkonen *et al.* 2018).

Additional information

Ethics

All research activities were conducted under the Home Office Licence issued to the Sea Mammal Research Unit (Licence No. 192CBD9F) with local licence approval from the University of St Andrews Animal Welfare and Ethics Committee.

Data accessibility

All data are available from the Dryad Digital Repository https://doi.org/10.5061/dryad.6q573n601 (Iorio-Merlo *et al.* 2021) and all processing codes are available in the GitHub Repository (github.com/virginiaIorio/Drivers-of-seal-ARS-behaviour).

Author's contributions

V.I-M.: conceptualization, methodology, formal analysis, writing – original draft, visualization. I.M.G.: conceptualization, writing – review and editing, supervision, investigation, data curation. R.C.H.: investigation. G.A.: methodology, writing – review and editing. E.P.: methodology, formal analysis, writing – review and editing. G.D.H.: investigation, writing – review and editing. P.M.T.**:** conceptualization, writing – review and editing, supervision, project administration, funding.

Supplementary material

Table S4.1 – Summary of data available for the 31 seals tagged in 2017.

Table S4.2 – Number of trips used in the Utilization Distributions and Bhattacharyya's affinity values.

Figure S4.1 – Model 1 step length and angle distributions, and validation plots.

Figure S4.2 – Selection of smoothing parameter *h* for kernel utilization distributions.

Figure S4.3 – Proportion of dives for each individual with and without prey catch attempts.

Figure S4.4 – Model 2 step length and angle distributions, and validation plots.

Figure S4.5 – Model 3 step length and angle distributions, and validation plots.

Figure S4.6 – Relationship between spatial memory values and mean batch prey encounters.

Appendix 4A. Post-hoc correction of accelerometer data
Details of the process used to post-hoc calibrate the accelerometer data

Appendix 4B. Missing GPS locations in momentuHMM
Details on the processed used to remove dive batches from the HMM when GPS data were not available and how it affects the model output.

Table S4.1. *Summary table of the data available for the 31 harbour seals tagged in 2017. The five seals, for which accelerometer data were available, are highlighted at the top of the table.*

ID	Sex	First trip start	Last trip end	Number of foraging trips	Mean trip duration (hours)
90	M	2017-02-28 10:35:08	2017-06-13 16:21:12	20	70.35 (± 43.908)
158	F	2017-02-28 20:08:04	2017-06-12 17:00:32	56	27.79 (± 13.983)
242	F	2017-03-16 09:43:20	2017-06-10 15:44:40	32	42.22 (± 21.178)
283	F	2017-03-12 06:11:12	2017-06-10 18:01:40	64	26.78 (± 16.291)
285	F	2017-03-06 12:06:52	2017-05-26 06:00:36	39	30.59 (± 20.359)
14	F	2017-03-17 12:29:40	2017-06-01 14:46:20	49	29.08 (± 13.591)
30	F	2017-03-13 07:10:20	2017-06-17 08:42:00	39	41.38 (± 20.792)
53	F	2017-03-13 23:04:20	2017-06-11 07:54:08	20	83.67 (± 70.034)
56	F	2017-03-15 20:43:08	2017-07-21 18:29:44	74	29.22 (± 21.426)
59	F	2017-03-14 10:27:36	2017-04-22 11:16:20	12	58.78 (± 27.234)
63	F	2017-03-15 10:55:48	2017-07-09 15:43:12	69	27.11 (± 17.534)
72	M	2017-02-28 21:17:40	2017-05-10 15:38:44	34	27.35 (± 17.250)
75	F	2017-03-20 13:30:28	2017-07-19 09:15:52	32	60.03 (± 44.197)
81	F	2017-02-23 20:12:24	2017-05-27 05:47:12	33	34.81 (± 19.817)
86	M	2017-02-27 22:47:16	2017-07-01 08:17:44	41	44.64 (± 58.795)
169	M	2017-02-27 08:40:08	2017-06-09 14:42:08	48	35.24 (± 36.441)

ID	Sex	First trip start	Last trip end	Number of foraging trips	Mean trip duration (hours)
174	F	2017-02-23 03:15:32	2017-06-25 16:31:36	53	29.41 (± 17.790)
178	M	2017-03-08 00:00:52	2017-06-12 17:24:24	22	50.78 (± 64.907)
191	M	2017-03-12 09:41:16	2017-06-24 16:37:32	28	56.20 (± 69.005)
216	F	2017-03-01 10:12:40	2017-06-17 05:31:04	26	66.18 (± 54.136)
219	M	2017-02-23 19:37:36	2017-05-06 15:15:44	18	25.45 (± 10.741)
250	F	2017-03-12 09:09:12	2017-05-29 04:26:56	42	30.14 (± 15.674)
268	F	2017-02-27 21:26:08	2017-07-04 00:27:40	61	35.99 (± 31.158)
272	M	2017-02-27 22:56:36	2017-06-11 16:03:12	17	74.76 (± 60.732)
276	F	2017-03-13 09:36:32	2017-06-18 12:21:16	30	52.76 (± 34.713)
280	M	2017-02-28 20:07:48	2017-04-21 10:51:28	18	43.45 (± 33.365)
314	F	2017-02-27 09:13:52	2017-06-09 05:54:28	58	28.49 (± 14.261)
331	M	2017-03-01 10:44:04	2017-05-09 14:23:36	29	38.24 (± 21.998)
337	F	2017-02-24 07:28:32	2017-05-25 06:16:44	39	32.58 (± 16.792)
376	M	2017-03-16 09:42:36	2017-06-12 03:16:40	30	20.52 (± 9.396)
384	M	2017-02-28 18:07:00	2017-06-01 15:50:44	30	50.93 (± 28.921)

Table S4.2. *The number of trips used in the utilization distribution analysis for each seal in each month, and Bhattacharyya's affinity values indicating the spatial overlap of foraging patches visited in April and May.*

Seal ID	# Trips in April	# Trips in May	50% BA overlap	95% BA overlap
14	18	22	0.444	0.922
30	13	11	0.357	0.848
53	8	6	0.385	0.896
56	21	17	0.377	0.842
63	21	18	0.442	0.930
72	16	5	0.422	0.916
75	6	6	0.411	0.898
81	15	2	0.461	0.932
86	12	7	0.202	0.604
90	9	7	0.136	0.596
158	20	19	0.453	0.931
169	13	19	0.274	0.822
174	14	14	0.408	0.911
178	7	8	0.453	0.918
191	4	15	0.253	0.643
216	6	3	0.451	0.859
219	4	3	0.061	0.843
242	11	11	0.470	0.928
250	18	14	0.464	0.938
268	21	14	0.288	0.735
272	3	6	0.335	0.660

Seal ID	# Trips in April	# Trips in May	50% BA overlap	95% BA overlap
276	9	10	0.448	0.883
283	24	23	0.442	0.929
285	15	3	0.452	0.897
314	16	16	0.427	0.930
331	15	5	0.401	0.872
337	13	10	0.435	0.894
376	14	6	0.487	0.946
384	12	11	0.437	0.902

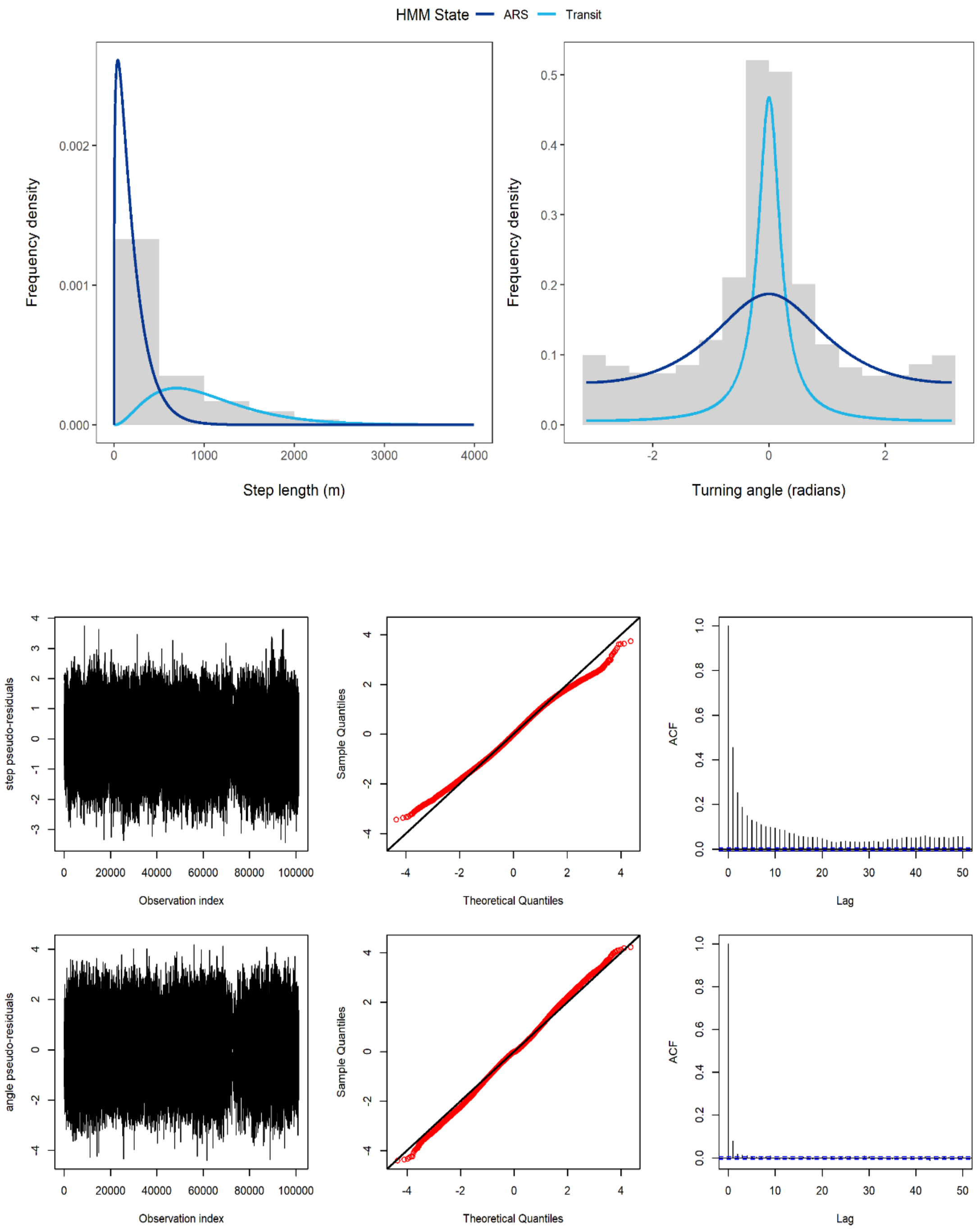

Figure S4.1. *In the top panel, state-dependent distributions of the step length and turning angle in the model fitted to build the memory grid (Model 1). Below, model validation plots: time series, QQ-plots and ACF plots of pseudo-residuals (left to right).*

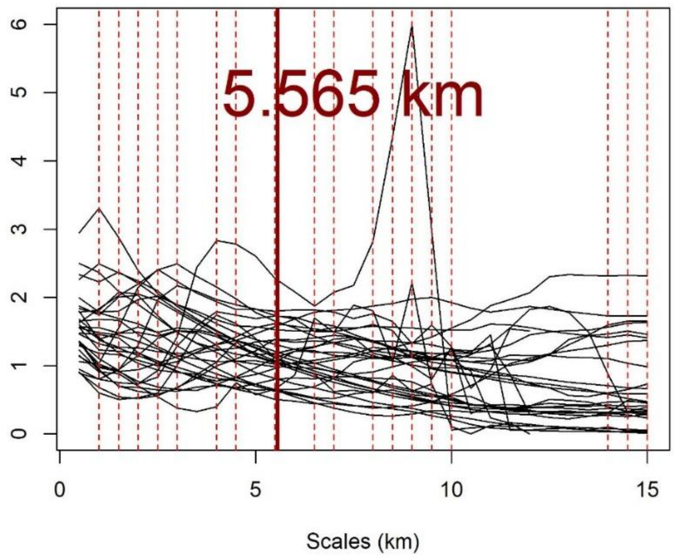

Figure S4.2. Identification of most appropriate smoothing parameter h for the calculation of kernel utilization distribution. Following the methods in Lascelles et al. (2016). The black lines represent the log variance in First Passage Time at various scales for each individual seal. The red dotted line shows the peak ARS scale for each individual, assessed from 0 to 15 km at 500 m intervals. The solid red line shows the average ARS scale across individual, which was used as the kernel smoothing factor.

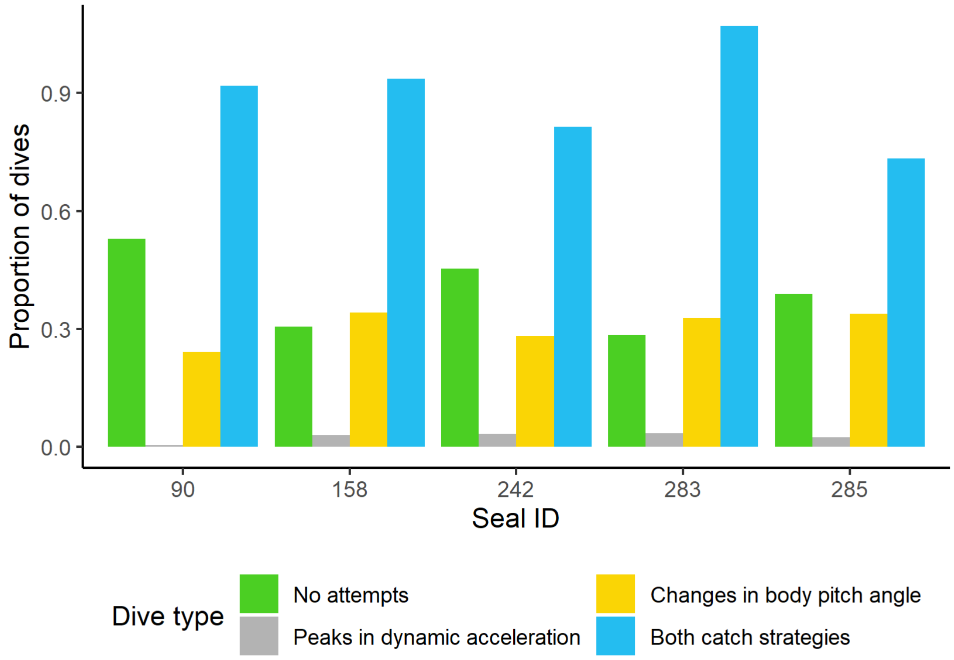

Figure S4.3. *Proportion of dives in which I detected prey catch attempts with the method by Viviant et al. (2010) only (Peaks in dynamic acceleration), with the method by Brasseur et al. (2012) only (Changes in body pitch), or with both methods, and the proportion of dives in which no attempt was detected, for each seal.*

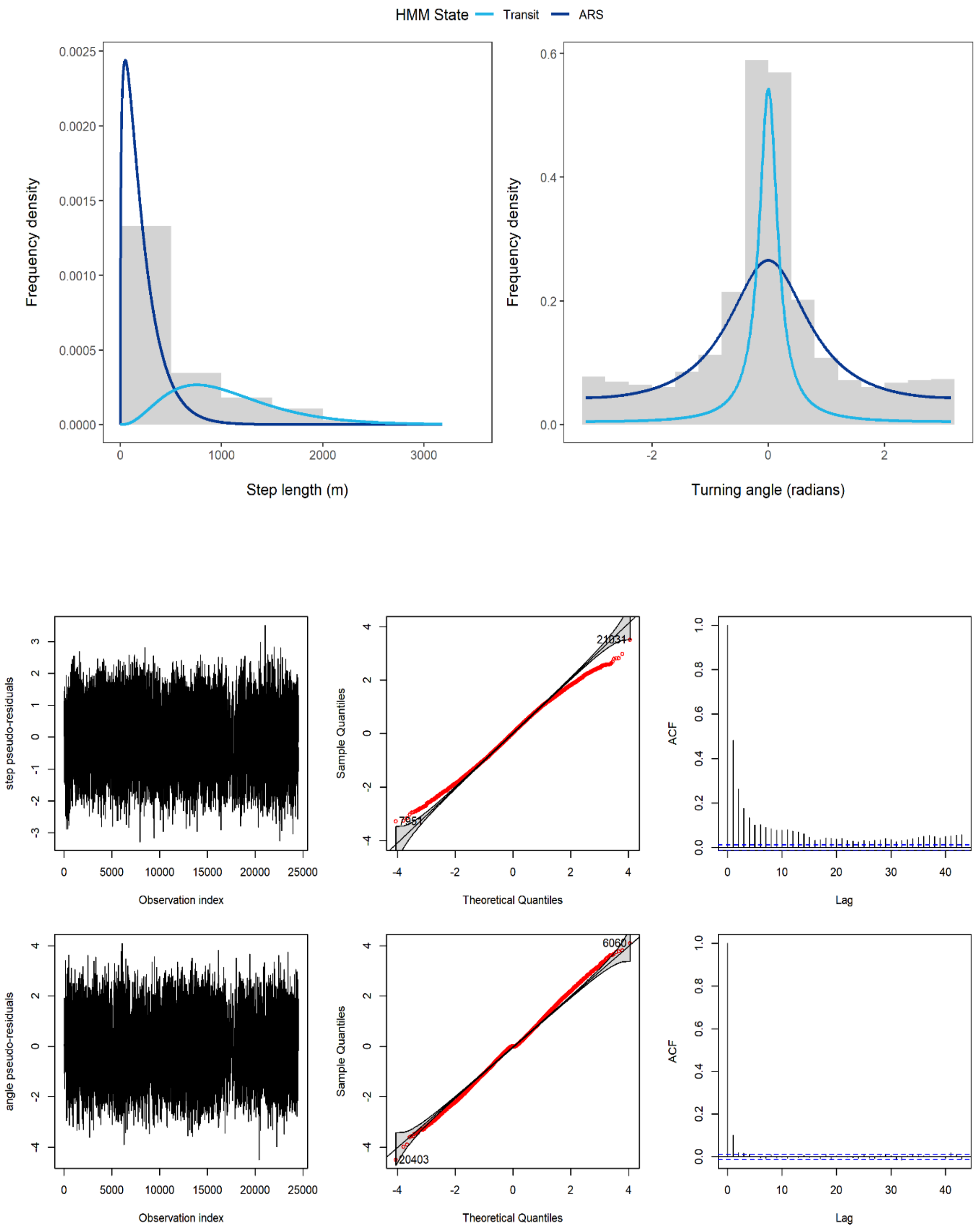

Figure S4.4. *In the top panel, state-dependent distributions of the step length and turning angle in the model fitted to assess the influence of spatial memory (Model 2). Below, model validation plots: time series, QQ-plots and ACF plots of pseudo-residuals (left to right).*

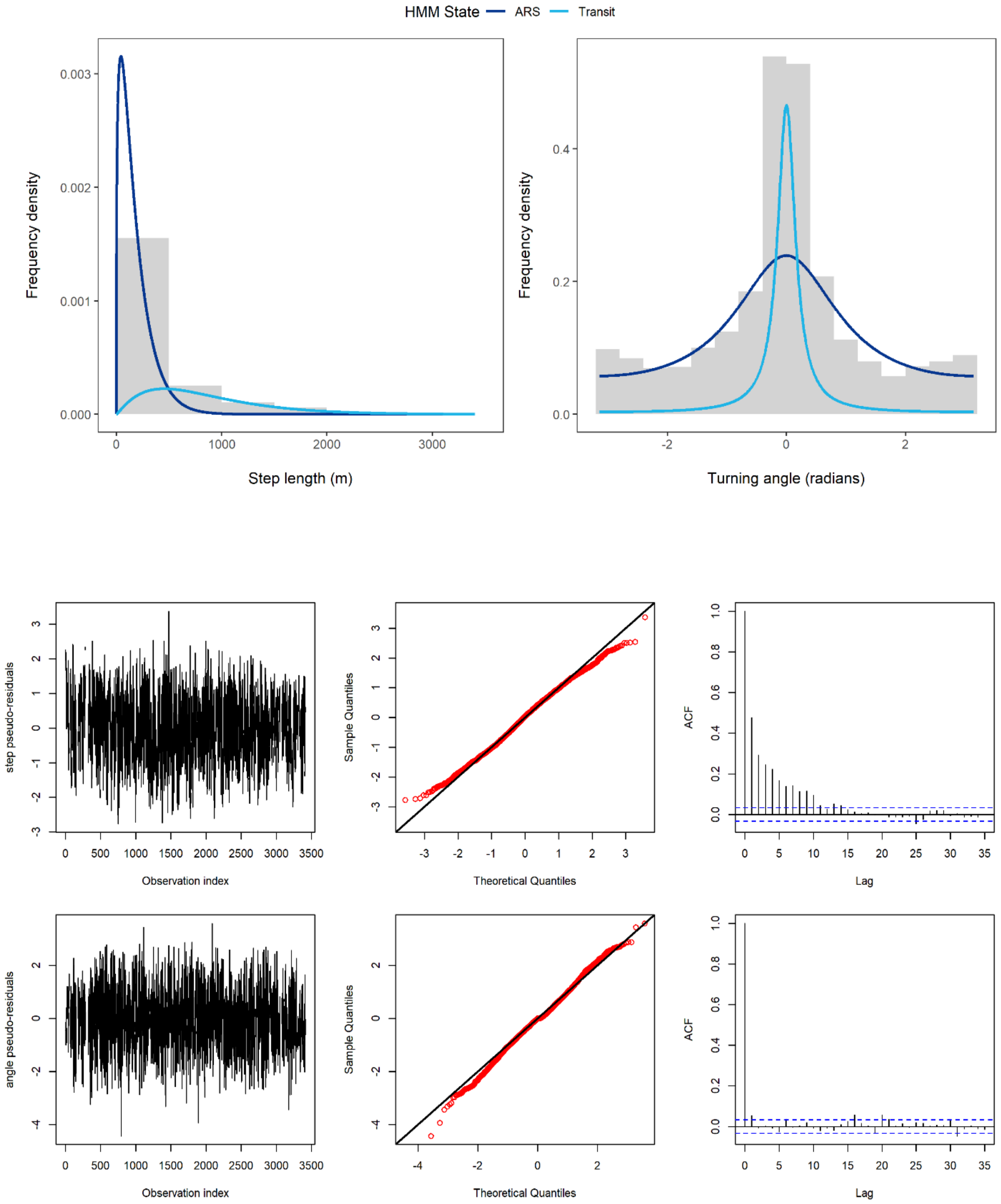

Figure S4.5. *In the top panel, state-dependent distributions of the step length and turning angle in Model 3. Below, model validation plots: time series, QQ-plots and ACF plots of pseudo-residuals (left to right).*

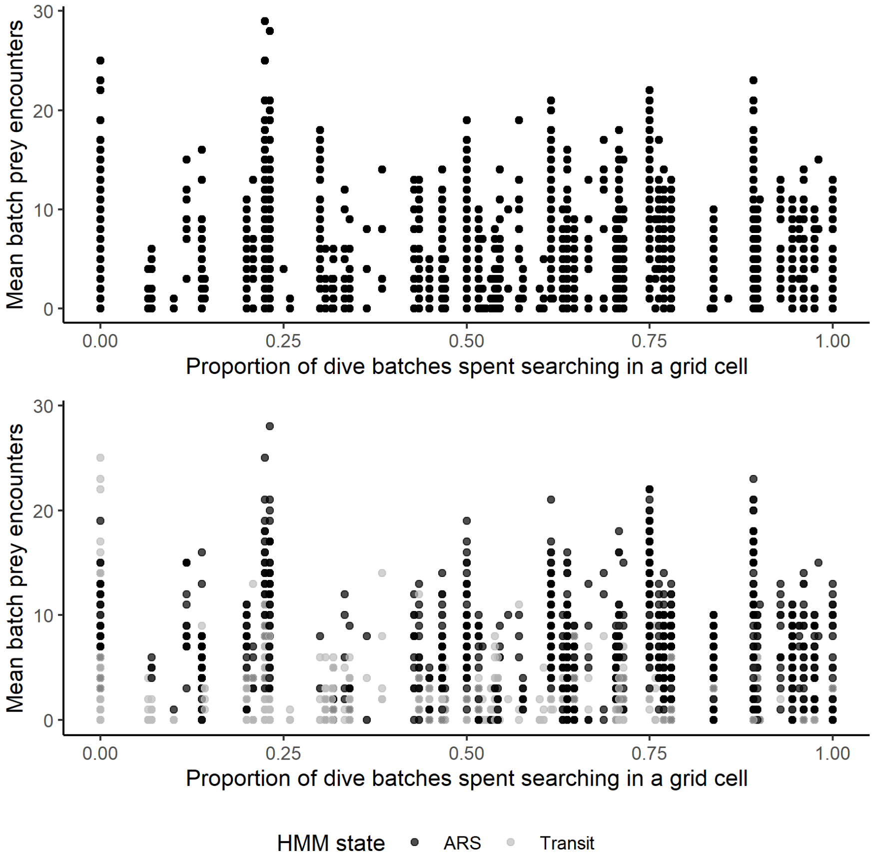

Figure S4.6. *The top panel shows the relationship between the mean batch prey encounters and the proxy for memory (proportion of dive batches spent searching in a grid cell), the two covariates included in Model 3. Each point represents a dive batch. The plot shows the dive batches from the five individuals included in Model 3. The bottom panel shows the relationship between the two covariates in Model 3 colour coded by the the two HMM states.*

Appendix 4A. Post-hoc correction of accelerometry data

Accelerometers are supposed to measure *g*-forces which, for stationary conditions, should have a total gravitational force F_g equal to 1*g,*

$$F_g=\sqrt{{X_S}^2+{Y_S}^2+{Z_S}^2}=1 \qquad \text{Eq. S1}$$

where X_S, Y_S and Z_S are the stationary forces of all three axis (Figure A4.1). However, most accelerometers, including ADXL345 had a systematic bias (i.e. offset) and scale effect, and this may even vary due to temperature and voltage variability.

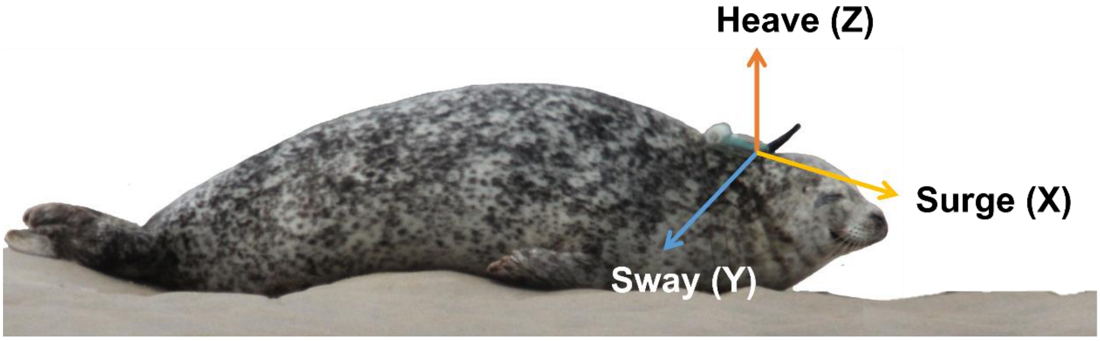

Figure A4.1. *Diagram showing the tag accelerometer axis relative to the seal.*

For each seal, first 1 second segments were selected from the accelerometry data stable, where the sum of the standard deviations of each axis (X, Y & Z) was small (i.e. <1% quantile). For these stable 1s segments, the average values of each of the three axes were classified into bins between +0.9 and -0.9g, at 0.1g intervals (i.e. 19 bins). For each day, the 1s segment with the lowest variability (i.e. lowest sum of standard deviations) was selected from each bin. This resulted in a relatively small table, with very stable segments, but with diverse values for X, Y and Z, that could be used for the post-hoc calibration.

Without error in the accelerometer measurements, and assuming that there was no dynamic acceleration during these stable segments, the total g-force value should be equal to 1*g* (Eq. S1). With error in the measurements, the observed accelerometers measurements need to be corrected: $X= \beta_{X,0}+ \beta_{X,1}\cdot\hat{X}$, $Y= \beta_{Y,0}+ \beta_{Y,1}\cdot\hat{Y}$ and $Z= \beta_{Z,0}+ \beta_{Z,1}\cdot\hat{Z}$, where $\hat{X}$,$\hat{Y}$ and $\hat{Z}$ are the measured g-forces in the three orthogonal axes, and β_0 and

β_1 are the unknown offset and scale factors, respectively. To estimate the parameters β, the least-squares were used, where the following function was minimized.

$$\sum\left(1-\sqrt{\left(\beta_{X,0}+\left(\beta_{X,1}+1\right)*X\right)^2+\left(\beta_{Y,0}+\left(\beta_{Y,1}+1\right)*Y\right)^2+\left(\beta_{Z,0}+\left(\beta_{Z,1}+1\right)*Z\right)^2}\right)^2 \qquad \text{Eq. S2}$$

Adding 1 to the scaling parameters (β_1) in eq. S2 ensured that the parameter estimates of both the scale and offset were close to 0, which improved convergence of the optimization. The optimization was achieved using non-linear least square (function *nls* of the r-package *stats* v3.4.3), where the response variable was set to 1 for all data points and the square root part of eq. S2 was defined as the formula. The estimated parameters β_0 and β_1 can be subsequently used to recalculate the surge (X), heave (Z), and sway (Y) axis.

Scale and offset parameter estimates

The magnitudes and the standard error of the bias (both scale and offset parameters) for each of the five accelerometers are presented in Table A4.1. These parameters were used to recalculate the three axes. The estimates of the offset and scaling parameters of the axis were small, except for $\beta_{Z,0}$, the offset of the Z-axis. This implies that the correction is especially noticeable in the heave dimension. If not corrected, the estimated gravitational component would be quite different from 1.

Table A4.1. *Mean parameter estimates for the offset and scaling in all three dimensions and the standard error (between brackets). The columns represent the ids of the accelerometers (ADXL345 – analog devices incl.) deployed on five harbour seals. Estimates >0.1 are shown in bold.*

Parameter	**14438**	**14464**	**14477**	**14478**	**14479**
$\beta_{X,0}$	-0.0526 (0.00111)	-0.0482 (0.00138)	-0.0841 (0.00234)	0.04363 (0.00155)	-0.0464 (0.00144)
$\beta_{X,1}$	0.0276 (0.00185)	0.0374 (0.00197)	0.0619 (0.00386)	0.02281 (0.00226)	0.0457 (0.00208)
$\beta_{Y,0}$	0.0384 (0.00050)	0.03224 (0.00075)	0.0387 (0.00060)	0.03466 (0.00076)	0.0273 (0.00071)
$\beta_{Y,1}$	0.0201 (0.00063)	0.02447 (0.00095)	0.0233 (0.00075)	0.02442 (0.00098)	0.0431 (0.00108)
$\beta_{Z,0}$	**0.1085 (0.00055)**	**0.14510 (**0.00073**)**	**0.2333** (0.00087)	**0.12496** (0.00072)	0.0830 (0.00057)
$\beta_{Z,1}$	0.0291 (0.00072)	0.01411 (0.00093)	0.0001 (0.00121)	0.02479 (0.00095)	0.0267 (0.00077)

Appendix 4B. Missing GPS locations in momentuHMM

Biologgers deployed on harbour seals in this study were set to record a GPS location every time a seal surfaced. However, due to variation in satellite availability, this resulted in an irregular time series, with a mean interval between GPS locations of 15 minutes. Dive locations are obtained by interpolation between GPS locations, causing dives to be placed along straight lines when there are large gaps between GPS locations (e.g. Figure B4.1).

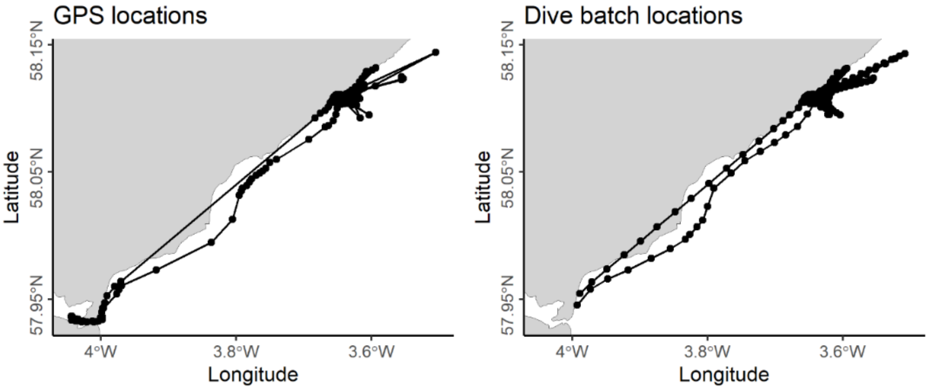

Figure B4.1. *Comparison of GPS data available for one foraging trip (left panel) with the interpolated locations of the dive batches used in the model (right panel).*

Following the methodology described by Russell et al. (2015) and Carter et al. (2020), I considered 'unreliable' dive batches to be those that are not associated with an accurate raw GPS locations. The mean dive cycle was 4.46 minutes and the 90th percentile of the time interval between GPS locations was 25 minutes. Thus, I considered 'unreliable' all dive batches longer than 25 minutes that did not contain a raw GPS location, and dive batches shorter than 25 minutes where the dive batches immediately before or after did not contain a raw GPS location. However, these dive batches were not excluded from the analysis. Instead, for all unreliable dive batches, the step length and turning angle were set to 'not available' (NA) (Langrock et al. 2012); and thus the state was assigned solely based on the Markov property. Setting the step length and turning angle to NA for the 'unreliable' locations ensured that state assignments were not unduly influenced by highly directional dive batches that occur along straight interpolated tracks corresponding to gaps in the GPS data (Figure B4.2).

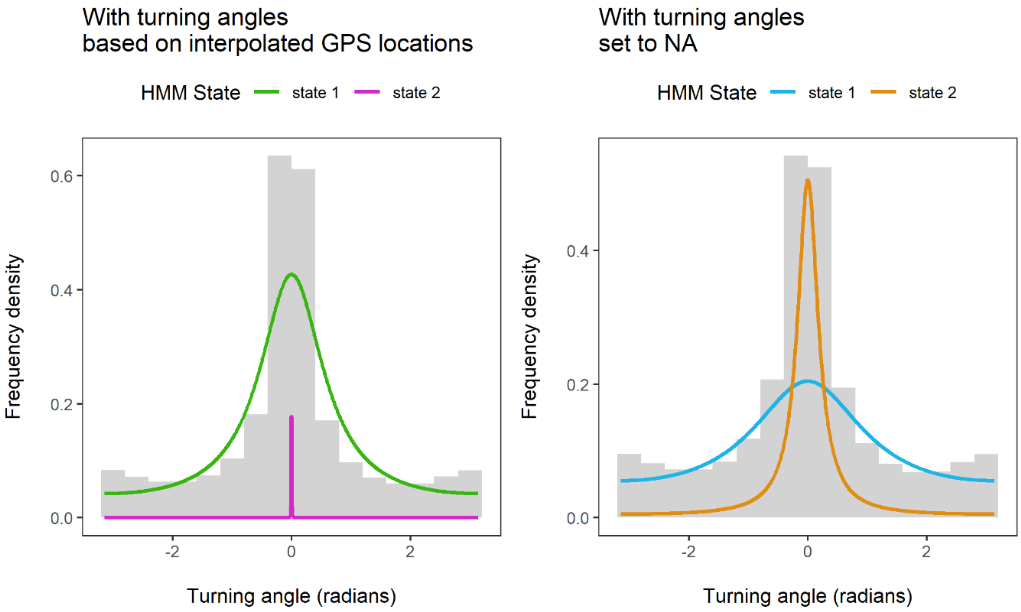

Figure B4.2. *The turning angle distribution for the two states in Model 1 when unreliable locations use step length and turning angles based on interpolated GPS data (left panel) and when the step length and turning angle of unreliable locations are set to "NA" (right panel).*

As shown in Figure B4.2, when unreliable locations use step length and turning angles based on interpolated GPS data, one of the HMM states capture their high directionality (i.e. no variation around 0). This leads to all other locations being assigned to the other state (Figure B4.3).

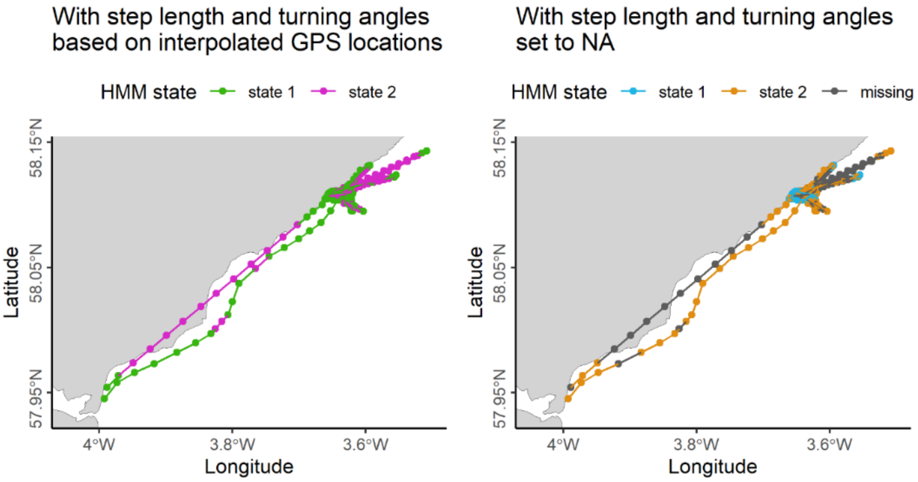

Figure B4.3. *Foraging trips with dive batches colour-coded by their assigned HMM state, when modelled using the step length and turning angle based on interpolated GPS data for unreliable locations (left) or setting them to NA (right). The missing locations in the right panel represent unreliable locations for which the step and turning angle were set to NA.*

Chapter 5

General discussion

Chapter 5

General discussion

Understanding the drivers of animal movement is an active area of research in movement ecology with many unanswered questions on the role that prey distribution, the physical environment and predator cognitive abilities play in predator movement decisions (Hays *et al.* 2016). As this knowledge is critical to underpin conservation and management plans for marine megafauna (Hyrenbach *et al.* 2000; Shillinger *et al.* 2008; Fraser *et al.* 2018; Hays *et al.* 2019), this thesis aimed at contributing towards a better understanding of these drivers of predator movement and foraging behaviour.

General knowledge on species ecology and population distribution is critical for the interpretation of movement patterns and informing questions about specific drivers (e.g. Regular *et al.* 2013). Marine megafauna in the Moray Firth have been studied for the last three decades (Thompson & Miller 1990; Hammond & Thompson 1991), building the knowledge needed to contextualise predator behaviour and to test specific hypothesis about drivers of predator occurrence, movement and foraging behaviour. Specifically, in this thesis, I investigated the role of inter-individual variability in explaining the temporal variation of population distribution (Chapter 2). Then, I quantified individual repeatability of foraging areas (Chapter 2 and 4), and how this was influenced by individual characteristics and environmental factors (Chapter 2). Finally, I assessed the influence of prey encounter and memory on predator initiation of area restricted search (ARS) behaviour (Chapter 3 and 4), and of prey predictability on predator occurrence at a foraging hotspots (Chapter 3).

Drivers of movement and foraging behaviour

Theoretical models of simple searching strategies have often tried to describe predator movement observed in the wild (Sims *et al.* 2008; Humphries *et al.* 2010), in particular in relation to ARS behaviour (Weimerskirch *et al.* 2007; Auger-Methe *et al.* 2016). However, these sometimes fell short of fully capturing observed movement patterns (James *et al.* 2011; Nabe-Nielsen *et al.* 2013). Given that marine megafauna have highly developed cognitive abilities (Boyer & Walsh 2010; Auger-Methe *et al.* 2016; Collet & Weimerskirch 2020), memory has been suggested as one of the missing factors needed to explain these natural patterns (Sims *et al.* 2006; Weimerskirch *et al.* 2007). In this thesis, I showed that metrics that represented spatial memory influenced the initiation of ARS behaviour for both a free-ranging predator and a central place forager (Chapter 3 and 4).

Memory is a highly complex behaviour that must be simplified to be integrated into quantitative models (Fagan *et al.* 2013). Here, I used memory metrics that represented areas where individuals had previously foraged. In Chapter 3, I assumed that bottlenose dolphins (*Tursiops truncatus*) found in the Inner Moray Firth have historic memory of deep-water channels as profitable foraging areas. The same individuals have been observed in this area over many years (Cheney *et al.* 2013; Cheney *et al.* 2014), and these channels are considered foraging hotspots (Hastie *et al.* 2004). Thus, I assumed that the population would have a collective memory of prey distribution in the area, in particular at these two locations. On the other hand, in Chapter 4, I created individual spatial memory maps representing the areas in which individuals had previously spent time searching for prey, as a way to quantify memory. In the two chapters, models revealed that both predators were more likely to display, or initiate, ARS behaviour in response to these memory metrics. Thus, I interpreted these results in terms of predators adjusting their fine-scale movement in response to expectation of a higher probability of encountering prey (Thums *et al.* 2011).

The metrics used to represent memory were based on where predators had displayed searching and foraging behaviour before, without making assumptions about which features an individual would remember, or which cues they used to return to these sites. Questions still remain on how individuals are able to return to known areas especially in oceanic environment (Bonadonna *et al.* 2003). Seabirds may use odour maps to orientate themselves (Reynolds *et al.* 2015), and benthic species might be using bathymetric features (Mattern *et al.* 2007; Knox *et al.* 2018). However, high return rate to the same areas has also been found in highly pelagic species (Bradshaw *et al.* 2004). Furthermore, site fidelity to specific areas has been used to support the idea that marine megafauna have memory of previously visited areas (Davoren *et al.* 2003; Votier *et al.* 2017; Abrahms *et al.* 2019a). In Chapter 2 and 4, I used overlap of harbour seals (*Phoca vitulina*) foraging areas between consecutive time periods to show that individuals consistently used the same areas, further indicating that seals use memory to target known foraging patches.

There is also evidence from previous research on mammals and seabirds that movement patterns vary with age, and individuals become more directed in their movement and efficient in their searching behaviour over time (Laidre *et al.* 2004; Riotte-Lambert & Weimerskirch 2013; Carter *et al.* 2020). Thus, it is expected that adult individuals have memory and knowledge of prey distribution in the area they inhabit. All the seals tagged in the Moray Firth were adults (Chapter 2 and 4). Although there is no confirmation that dolphins detected by the hydrophones were adults (Chapter 3), calves up to three years old are observed with their mother (Grellier *et al.* 2003). Therefore, it is reasonable to assume that all individuals studied in this thesis were adults, or with adults, and thus had some previous knowledge on their environment. However, investigating the ontogeny of memory remains a challenging topic. Studies that have attempted to approach the topic have focussed on the movement behaviour of juvenile seabirds (Riotte-Lambert & Weimerskirch 2013; Grecian *et al.* 2018) or seals (McConnell *et al.* 2002; Carter *et al.* 2020). Findings suggested that individuals became more efficient over time in their movement and it was suggested that, for example, the long period of immaturity for seabirds was to allow individuals to become more efficient foragers prior to becoming active breeders (Riotte-Lambert & Weimerskirch 2013).

Memory is only valuable to predators in environments where resources are heterogeneously distributed (Spiegel *et al.* 2017) and have some spatio-temporal predictability (Fagan *et al.* 2013). Across the results found in this thesis, evidence emerged that environmental and prey predictability is a key driver of predator movement (Chapter 2, 3 and 4). At a fine scale, seals used the thermocline depth to inform decisions on foraging areas between consecutive trips (Chapter 2). Water column stratification has been recognised as an important feature for predictable prey aggregation across shelf seas (Cox *et al.* 2018a). While, at larger spatial scales interactions between ocean currents and topographic features created profitable foraging areas for the seals (Chapter 2) and tidal mixing fronts in the deep water channels for the dolphins (Chapter 3). Core harbour seal distribution areas were associated with locations around the headland near the Dornoch Firth (Thompson *et al.* 1996), and it has been suggested that the combination of dynamic environmental processes and the topography of this area creates a predictable profitable foraging patch (Bailey *et al.* 2014). Dynamic environmental features, such as these, are particularly important for predators as they may influence prey availability and accessibility (Ropert-Coudert *et al.* 2009; Bertrand *et al.* 2014; Boyd *et al.* 2015), as it has been hypothesised to explain the association of the dolphins with tidal mixing fronts in the deep-water channel (Bailey & Thompson 2010).

Investigating the association of predators and dynamic environmental features is particularly important to understand how these relationships may change in the future, especially in relation to climate change (Hazen *et al.* 2013a; Rutterford *et al.* 2015). The increase in storms and climatic events caused by climate change will affect many of these dynamic processes, for example thermal fronts and water column stratification (Behrenfeld *et al.* 2006; Cai *et al.* 2014). Disruption of predictable dynamic environmental processes have been shown to have significant effects on population demographics of many seabird species (Thompson & Ollason 2001; Ropert-Coudert *et al.* 2009; Chambers *et al.* 2011; Cleasby *et al.* 2017). Thus, movement studies investigating the link between predator foraging behaviour and dynamic environmental processes are critical to inform marine protected areas and dynamic ocean management plans (Maxwell *et al.* 2015; Abrahms *et al.* 2019b; Gilmour *et al.* 2022). Although this bottlenose dolphin population has been protected through the establishment of a Special Area of Conservation (SAC) (Wilson *et al.* 1997), many of the areas used by the dolphins are still widely impacted by commercial and recreational shipping traffic (Merchant *et al.* 2014; Pirotta *et al.* 2015a). Thus, identifying dolphin foraging patterns and habitat use within the Moray Firth is important to support the management and monitoring of this population.

Environmental processes and prey distribution are the main drivers of predator movement; however, it is challenging to disentangle the tight link between them (Hays *et al.* 2016). In Chapter 3 and 4, prey encounters were a significant driver of predator initiation of ARS behaviour. These results agree with predictions that, in highly heterogenous environments, predators should initiate ARS behaviour when encountering prey as they will have a higher probability of encountering more nearby (Kareiva & Odell 1987). However, I found that the seal probability of initiating ARS was positively associated with the number of prey encounters (Chapter 4), suggesting that predators may not just respond to individual prey items, but to the overall quality of the patch encountered (Enstipp *et al.* 2007; Hazen *et al.* 2015). Furthermore, at times, seals initiated ARS behaviour in response to prey encounters independently of the spatial memory metrics (Chapter 4) and I found a high proportion of dolphin encounters with foraging calls within and outside foraging hotspots (Chapter 3). These observations suggest that these predators may use a mixture of memory-driven and random search strategies to take advantage of more opportunistic foraging events (Boyer & Walsh 2010).

Collecting prey data at scales relevant to predators is still a challenge in foraging ecology (Wakefield *et al.* 2009; Carroll *et al.* 2017). Here, I used foraging proxies to detect prey encounter events. Detections of foraging calls were used to identify times in which dolphins encountered prey (Chapter 3) (Janik 2000a; Pirotta *et al.* 2014), while changes in body movement and acceleration were used to detect prey encounters while seals were diving (Chapter 4) (Viviant *et al.* 2010; Brasseur *et al.* 2012). In both studies, using different signals (e.g. foraging buzzes and bray calls, or changes in acceleration and body pitch angle) allowed me to capture dolphins displaying different responses to prey predictability (Chapter 3) and seal inter-individual variability in foraging behaviour (Chapter 4). In particular, the inter-individual variability of movement patterns observed in Chapter 2, led to the hypothesis that individuals in this population may display some level of foraging strategy specialization. The variability observed in the use of different catch strategies between the five seals (Chapter 4), for which accelerometer data were available, would support this hypothesis.

Although, foraging proxies are widely used to infer foraging behaviour and have brought new insights into predator underwater behaviour, they come with limitations (Kuhn *et al.* 2009a). For example, proxies may lead to misinterpretation of signals, if they have not been validated through visual observation (e.g. as in Ydesen *et al.* 2014), or they may represent multiple behaviours (e.g. foraging echolocation buzz and social buzz - Herzing 1996; Martin *et al.* 2019). Other limitations are that proxies, such as those used here, do not allow for inference on foraging success rate or validation of prey presence. To overcome these limitations in biologging studies, stomach temperature sensors to detect feeding events have been used (Kuhn & Costa 2006), or successful captures have been observed from other image sensors (Watanabe & Takahashi 2013). Furthermore, data on prey distribution, such as those collected using echosounders or cameras, can verify presence and identify species of prey encountered (Goulet *et al.* 2019; Yoshino *et al.* 2020). Future research could further investigate the relationship between acoustic signals and successful feeding events. For example, dolphins foraging on salmon are often observed bringing prey to the surface (Janik 2000a; Hastie *et al.* 2006). Thus, contemporary visual observation and acoustic recordings could be used to investigate the relationship between bray call production rate and salmon successful captures.

Obtaining independent data on prey distribution would have been necessary to test the hypothesis suggested in Chapter 3 on dolphins using predictability of prey encounters to influence their occurrence at foraging hotspots. In particular, two different patterns were observed in Sutors and Chanonry in response to the detection of bray calls. Exploration of the day-to-day variability of bray detections in the two channels showed a different pattern of occurrence, with bray calls detected in almost every hour in which the dolphins were present at Chanonry. This might suggest a difference in the predictability with which dolphins were encountering salmon in the two channels. However, this difference could also be due to changes in detection probability of bray calls between the two channels. Thus, collecting independent data on the occurrence of salmon in the two areas would first elucidate whether detections of bray calls match salmon occurrence in the channels. Second, data on salmon occurrence would also provide information on their presence at times when dolphins were not in the areas, and thus confirm whether salmon occurrence was indeed predictable or whether dolphins are responding to other environmental patterns (Fernandez-Betelu *et al.* 2019) or prey anti-predatory behaviour (Laundre 2010; Berger-Tal & Bar-David 2015). Given the evidence that predators associate with predictable resources (Weimerskirch 2007; Davoren 2013; Hazen *et al.* 2013b), understanding the temporal scale at which this association is occurring could be important for dynamic management plans (Jacox *et al.* 2020; Ortuño Crespo *et al.* 2020). Even though in this area the dolphins are already protected by the established SAC, these results may inform conservation management plans for this species in other area of their distribution.

Inference of foraging activity from ARS behaviour has been a widely applied method in movement studies (Fauchald & Tveraa 2003; Barraquand & Benhamou 2008; Boyd *et al.* 2014; Bennison *et al.* 2018). However, the combination of accelerometer and movement data, allowed the finer-scale association between spatial movement and prey encounters to be explored (Thums *et al.* 2011; Watanabe & Takahashi 2013; Iwata *et al.* 2015). In Chapter 4, there was variation in the number of prey catch attempts during periods classified as ARS by the Hidden Markov Model. This variation was interpreted as seals displaying active searching of prey during ARS times. These data also show that considering all those time periods classified as ARS as active foraging would have led to an overestimate of the time spent actively foraging, and thus caution is needed in the interpretation of activity budgets (McClintock *et al.* 2013). Furthermore, previous studies investigating cetacean fine-scale searching behaviour have used encounter duration to infer ARS around single static devices (Bailey *et al.* 2019) or group of devices (Fernandez-Betelu *et al. in review* - Appendix). As hydrophone arrays can be used to track cetacean species and re-construct their movement (Stanistreet *et al.* 2013; Macaulay *et al.* 2017), in Chapter 3 I used independent acoustic recorders to study the fine-scale movement of dolphins. In the results, I showed a positive relationship between the encounter duration and the variation in angular range detected, with encounters longer than 50 or 60 minutes recording clicks from all directions around the device. This could support the use of encounter duration, in the absence of fine-scale movement data, to infer ARS behaviour, as it shows that dolphins were using all the area available around the device during longer encounters and did not just transit through. Identification of areas where predators display searching behaviour is particularly important to identify important foraging areas (Augé *et al.* 2014; Hindell *et al.* 2016).

Populations as a cumulative sum of its individuals

Understanding and describing inter-individual variability within a population is particularly important in the context of conservation and management (Cooke 2008; Merrick & Koprowski 2017) as this variability increases the challenges associated with estimating population level inference (Bolnick *et al.* 2003; Gutowsky *et al.* 2015), and individuals may be exposed to different threats (Thiers *et al.* 2014; Patrick *et al.* 2015).

In Chapter 2, the inter-individual variability observed between the seals showed that differences in distribution over time were not necessarily due to a population distribution shift, but rather due to the differences in movement patterns between the individuals tagged. Assessments of changes in population distribution and abundance over time have been used to investigate shifts in distribution (Peschko *et al.* 2016) that might occur in response to climate change (e.g. Hazen *et al.* 2013a). Since the last deployment of biologgers in the Moray Firth, two offshore wind farms have been built within the species range (Benhemma-Le Gall *et al.* 2021). Thus, movement data prior to the construction could be used as a baseline to assess any shift in distribution. However, many habitat use and association models make the assumption that individuals are ecologically equivalent (Bolnick *et al.* 2003). This would allow to draw general conclusions on population distribution which can be useful for conservation and management plans (Hebblewhite & Haydon 2010; Reisinger *et al.* 2018), but individuals may respond differently to their environment violating the equivalence assumption (Thiers *et al.* 2014; Patrick *et al.* 2015). For example, given the inter-individual variability observed in this study, it is possible that the few individuals that travelled to the Smith Bank for foraging could have been disproportionally impacted by the windfarm construction compared to the majority of individuals that only used more inshore areas.

Statistical methods have been developed to account for the inter-individual variation within model structure allowing to estimate both population level inferences, while allowing individuals to respond independently (Gillies *et al.* 2006; Aarts *et al.* 2008). For example, Aarts *et al.* (2008) showed how individual grey seals (*Halichoerus grypus*) responded to environmental variables in comparison to the population mean response. Application of these methods are particularly useful where assessing individual level responses, or when preserving inter-individual variability is a conservation concern (Lesmerises & St-Laurent 2017). Future studies could elucidate the inter-individual variability observed in this population further by applying a framework similar to Aarts *et al.* (2008) to these data and explore individual level responses to environmental variables. However, studies analysing data within frameworks that account for inter-individual variability are often constrained by the sample size available (Beyer *et al.* 2010). In general, biologging studies are often limited by the number of individual tags that can be deployed, or restricted by the project timescale (Hebblewhite & Haydon 2010; Bogdanova *et al.* 2014). Thus, when possible, long-term studies should quantify temporal variation in distribution, and within population variation, to support interpretation of results when extensive datasets are not available (Phillips *et al.* 2007; Bogdanova *et al.* 2014; Hindell *et al.* 2017). For example, conclusions from the results in this thesis could be extended to other populations of harbour seals for which long-term at-sea distribution data are not available (eg. Blanchet *et al.* 2014).

In spite of the high inter-individual variability, there were a few locations within, and just outside, the Dornoch Firth that were used by a large proportion of the individuals tagged, and they remained consistently used over time (Thompson *et al.* 1996). However, limited data are available on the fine-scale prey distribution in the Moray Firth (Tollit & Thompson 1996; Greenstreet *et al.* 1998). Future studies should focus on characterizing prey occurrence and distribution in this relatively small area, but important for a high proportion of seals in this population. Understanding how prey distribution and availability varies at key foraging sites may help in the future to explain seal population dynamics (Wilson & Hammond 2019; Gallagher *et al.* 2022).

Agent-Based (or individual-based) Models (ABM) are a useful tool to simulate individual movement while accounting for individual variation in a population (Railsback & Grimm 2019). They allow for explicit modelling of individual movement in real landscape and management scenarios (Nabe-Nielsen *et al.* 2018; Chudzinska *et al.* 2021). However, these models require knowledge on the species ecology and movement in order to re-create natural patterns. For example, acquisition and decay of memory over time were required in order to re-create harbour porpoise (*Phocoena phocoena*) home range behaviour (Nabe-Nielsen *et al.* 2013). Harbour seal movement data, similar to those presented in this thesis, have been used to underpin the development of an ABM (Chudzinska *et al.* 2021). The model was able to successfully re-create the seal central place foraging behaviour and many of the trip characteristics. Although the model was able to capture some inter-individual variability, quantifying this variability, as done in this thesis, could inform the future development of this model. For example, results in this thesis showed changes in repeatability between the sexes and in relation to the breeding season, and differences were found in foraging strategies in relation to the number of foraging patches and size of foraging area used. Capturing all these natural patterns may be important as ABMs can be used to explore the impacts of multiple stressors on individual movement and physiology (Nabe-Nielsen *et al.* 2018).

In contrast to biologging studies which face the challenge of drawing population level inference from individual data, it is challenging to identify individuals from passive acoustic methods. Many marine mammal species are highly vocal which has facilitated research studying their occurrence (Mellinger *et al.* 2007; Zimmer 2011) and movement (Risch *et al.* 2014; Gillespie *et al.* 2020) using analysis of their vocalizations. However, many of the calls used to detect marine mammals are shared among the population (Garland *et al.* 2011; King & Janik 2015), making the study of individual challenging from such passive acoustic data. Only very few studies tracking animal movement using an array of hydrophones have been able to count multiple individuals through detection of simultaneous detections that were coming from different directions (Wiggins *et al.* 2012; Stanistreet *et al.* 2013; Helble *et al.* 2015; Hendricks *et al.* 2021). However, delphinids such as the bottlenose dolphins produce an individual stereotypical call unique to each individual, defined as a signature whistle (Janik & Sayigh 2013). Signature whistles offer a unique opportunity to detect the occurrence and movement of specific individuals using a less intrusive method than biologging. Furthermore, signature whistles have been used in mark-recapture studies to estimate population size, yielding similar estimates to those reached with photo-identification (Longden *et al.* 2020). Thus, detections of individual signature whistles over large acoustic arrays could be used in future to characterise individual home ranges and movements (Heupel *et al.* 2004; Heupel *et al.* 2006) or social structure (Papastamatiou *et al.* 2020). Limitations remain before this method can be widely applied as processing audio data and identifying signature whistles is a time consuming manual process (Kriesell *et al.* 2014). Moreover, data collected on individual movement using passive acoustic methods will be constrained by the deployment range of the hydrophone array, and thus would not necessarily be able to provide the same spatial extent of biologging data. However, such data would have helped to overcome one of the limitations of the analysis in Chapter 3, where I was unable to control for different individuals being present over consecutive encounters. Developments of automatic detectors using artificial intelligence may make these data available in the future (Bergler *et al.* 2019).

Implications of population and individual repeatability and variability for conservation

Behavioural repeatability, or consistency, has been observed across many taxa (Patrick *et al.* 2013; Jacoby *et al.* 2014; McHuron *et al.* 2018). It represents the persistence in time of individual specialization or preferences (Bell *et al.* 2009), and it has often been studied in the context of foraging behaviour (Bradshaw *et al.* 2004; Arthur *et al.* 2015; Wakefield *et al.* 2015; Cecere *et al.* 2020). In this thesis, I have focussed on predator repeatability of foraging areas used over time. Marine predators in the Moray Firth displayed a high degree of population and individual repeatability (Chapter 2 and 3).

Data collected in Chapter 3 reinforced the importance of Sutors and Chanonry as foraging hotspots (Hastie *et al.* 2004; Bailey & Thompson 2009), but also showed that dolphins displayed foraging behaviour in all the other locations where hydrophones where deployed (Pirotta *et al.* 2014). Thus, these results further highlight the importance of the whole Inner Moray Firth as a foraging area for this population within which some areas remain heavily used. However, this area only represents a portion of the whole population range. Photo-identification studies used to estimate population size and demographic parameters (Wilson *et al.* 1997; Cheney *et al.* 2014; Cheney *et al.* 2019), have also shown that there might have been an expansion in the range of bottlenose dolphin distribution in the Moray Firth (Wilson *et al.* 2004b). Furthermore, in more recent years, individuals moving between the Moray Firth SAC and the Firth of Forth have highlighted that the exchange between these two areas may occur more often than previously thought (Arso Civil *et al.* 2019). International collaborations and data exchange has now enabled the identification of larger-scale movements in this population, with individuals being identified along the east and south coast of England and Ireland (unpublished data), in Denmark and the Netherlands (Hoekendijk *et al.* 2021). Thus, although dolphins consistently used foraging areas in the Inner Moray Firth, their movements extend much further. Furthermore, similarly to the inter-individual variability observed in the seal movement patterns, photo-identification data have shown individual differences in dolphin movement and distribution (Pirotta *et al.* 2015b). For example, individual dolphins consistently used only parts of their range, while others moved between the Moray Firth and Tayside and Fife area during the summer months or between years (Quick *et al.* 2014). Such large displacements and changes in distribution highlight the challenges faced by conservation measure when protecting highly-mobile predators.

At a large temporal scale, the integration of over 30 years of biologging data collected on harbour seals showed that the core areas of distribution remained stable across decades. Central place foragers, such as the harbour seals are often protected by conservation measures at coastal breeding sites (Cordes *et al.* 2011). However, they can also be vulnerable to disturbance at-sea (Russell *et al.* 2016; Thompson *et al.* 2019). Analysis of long-term datasets, as done here, can highlight areas used consistently over time by a high proportion of the population. Furthermore, at an individual level, I found that harbour seals inhabiting the Moray Firth were highly repeatable in the foraging area they visited over time. The combination of high repeatability of foraging areas and the inter-individual variability observed in prey catching strategies, may further support that individuals within this population display some level of foraging specialization, and future studies should investigate this further.

The individuals tagged in this study belong to a population that has been monitored through a long-term individual based study using photo-ID (Cordes & Thompson 2013). These data have been used to monitor abundance, fidelity to haul-out sites, adult survival and fecundity (Cordes & Thompson 2014, 2015). The combination of life history information and individual movement at-sea could be used to investigate the success and consequences of foraging strategies and their long-term consequence on the population. Some subpopulations of harbour seals around the UK are declining, in the Moray Firth following a period of decline, the population has become more stable (Thompson *et al.* 2019). In particular, population studies have highlighted that in the Moray Firth survival of young individuals and low pupping success might have caused the initial population decline, but that breeding success still remains highly variable (Cordes & Thompson 2013; Matthiopoulos *et al.* 2014). Thus, understanding the possible connection between female reproductive success and their foraging strategies and repeatability (Patrick & Weimerskirch 2017; Grecian *et al.* 2019) could provide greater understanding of harbour seal population dynamics in the Moray Firth and around the UK.

Long-term repeatability and association with a specific foraging area is thought to have evolved in response to environmental variability (Bradshaw *et al.* 2004; Abrahms *et al.* 2019a). However, long-term site fidelity of marine predators to specific foraging areas (Baylis *et al.* 2012; Wakefield *et al.* 2015), and low level of flexibility observed in response to disturbance (Vander Zanden *et al.* 2016; Cardona *et al.* 2017), raises concerns on the long-term consequence of behavioural repeatability, as this may impact individual vulnerability to disturbance and climate change (Bolnick *et al.* 2003). Thus, it is important that conservation measures accounts for individual differences and the proportion of the population that might be affected. ABMs capturing and representing inter-individual variability and repeatability in movement patterns could be used specifically to assess individual consequences in the context of disturbance to investigate how individuals might be differentially impacted. Furthermore, as suggested by Chudzinska *et al.* (2021), ABMs like AgentSeal in combination with other tools, such as interim Population Consequences of Disturbance (iPCOD) could be used to estimate the long-term population consequences of disturbance (King *et al.* 2015). Finally, it has to be noted that other species of marine predators have displayed a high level of behavioural plasticity in their foraging behaviour (Camprasse *et al.* 2017), thus assessment of population level repeatability or flexibility should be one of the first steps required to contextualise animal responses.

Conclusions

In conclusion, this thesis aimed at improving our understanding on the drivers of marine predator movement patterns. It provided evidence that predators integrate information at multiple temporal scales and both within and outside their perceptual ranges to inform their decisions. In particular, it highlighted the key role played by resource distribution, and its predictability, in shaping predator ARS behaviour and occurrence. It also contributed empirical evidence that both a free-ranging predator and a central place forager used a combination of memory-driven and opportunistic strategies to maximise their foraging outcomes. Furthermore, it showed that individual differences in movement and foraging decision shaped the overall population distribution, and such differences may play a key role in understanding population resilience to disturbance. This thesis contributed to knowledge that can be applied to the conservation and management of marine predators, particularly emphasizing the importance of accounting for the inter-individual variability and intra-individual repeatability in population distribution assessments.

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Appendix

Other work co-authored during the PhD

Appendix

Fernandez-Betelu *et al.* (*in review*). Variation in foraging activity influences area-restricted search behaviour by bottlenose dolphins[2]

Abstract

Area-restricted search (ARS) behaviour is commonly used to characterise spatio-temporal variation in foraging activity of predators, but evidence of the drivers underlying this behaviour in marine systems is sparse. Advances in underwater sound recording techniques and automated processing of acoustic data now provide opportunities to investigate these questions where species use different vocalisations when encountering prey. Here, we used passive acoustics to investigate drivers of ARS behaviour in a population of dolphins, to determine if residency in key foraging areas increased following encounters with prey. Analyses were based on two independent proxies of foraging: echolocation buzzes (widely used as foraging proxies), and bray calls (vocalizations linked to salmon predation attempts). Echolocation buzzes were extracted from echolocation data loggers and bray calls from broadband recordings by a convolutional neural network (CNN). We found a strong positive relationship between the duration of encounters and the frequency of both foraging proxies, supporting the theory that bottlenose dolphins engage in ARS behaviour in response to higher prey encounter rates. This study provides empirical evidence for one driver of ARS behaviour and demonstrates the potential for applying passive acoustic monitoring in combination with deep learning-based techniques to investigate the behaviour of vocal animals.

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[2] Fernandez-Betelu, O., Iorio-Merlo, V., Graham, I.M., Cheney, B.J., Prentice, S.M., Xi Cheng, R. & Thompson, P.M., (*in review* - Appendix). Variation in foraging activity influences area-restricted search behaviour by bottlenose dolphins. *Royal Society Open Science.*

Introduction

Predators are expected to adjust their movements in response to prey distribution by remaining in areas rich in prey resources (Pyke 1984). Increasing turning rates and decreasing displacement distance can be used to identify periods of area-restricted search (ARS) behaviour, which are likely to occur in response to higher prey availability (Kareiva and Odell 1987). Given the heterogenous distribution of resources, predators that engage in ARS behaviour are predicted to increase their residency time in the vicinity of encountered prey (Benhamou 1992; Torres et al. 2017). For many marine predators, identification of ARS within tracks of tagged individuals has been critical for characterising spatio-temporal variation in foraging activity (Carter et al. 2016; Cox et al. 2018). However, ascertaining the drivers of ARS behaviour remains challenging in marine predators, due to the difficulties of empirically linking movement patterns to feeding events at sea (Weimerskirch et al. 2007; Watanabe and Takahashi 2013; Lidgard et al. 2014).

For animals that use distinct vocalisations when searching for and encountering prey, drivers of ARS behaviour may be investigated using passive acoustic techniques (Bailey et al. 2019). Bottlenose dolphins produce many different vocalizations, several of which are directly linked to foraging (Jones et al. 2019). For instance, like many other cetaceans, they produce echolocation buzzes, groups of echolocation clicks emitted at a high repetition rate, when they close in on prey (Wisniewska et al. 2014). To investigate the drivers of dolphin ARS behaviour, Bailey et al. (2019) modelled patterns of echolocation clicks, based on recordings from single echolocation data loggers, and characterised the variation in dolphin occurrence in relation to the presence of echolocation buzzes. As predicted, the probability of dolphins leaving areas around each device decreased with a higher proportion of foraging activity early in the encounter. However, contrary to expectations on ARS behaviour, animals were more likely to leave the area when there was a high proportion of foraging activity later in the encounter. To explain this inconsistency, Bailey et al. (2019) hypothesised that the restricted range of single echolocation data loggers (< 1000 m; Roberts & Read 2015) may not capture entire periods of ARS behaviour within each foraging patch. Further, to correct the underestimation of foraging activity from single acoustic recorders caused by the directional nature of echolocation clicks (Au et al. 2012), Bailey et al. (2019) based their results on modelled echolocation buzzes instead of vocalizations detected by the recorders. Therefore, omnidirectional cues for quantifying encounters with prey, coupled with broader arrays of passive acoustic devices may provide more powerful tests of this hypothesis.

In addition to echolocation buzzes, bottlenose dolphins produce bray calls, low frequency (< 2 kHz) omnidirectional vocalizations specifically associated with attempts to capture salmonids (Janik 2000). Echolocation data loggers can be deployed for periods of several months and the resulting data routinely processed to identify periods of occurrence and foraging activity (Nuuttila et al. 2013; Pirotta et al. 2014). However, the collection and analysis of long-term data on variation in broadband vocalisations, such as bray calls, have been constrained both by the capacity and longevity of underwater sound recorders and the need for manual analysis (Mellinger et al. 2007; King and Janik 2015). These constraints are now being overcome by the availability of relatively low-cost archival sound recorders (Malinka et al. 2018; Longden et al. 2020) and the development of automatic detectors based on deep learning techniques (Mac Aodha et al. 2018; Bergler et al. 2019; Shiu et al. 2020).

Here, we build upon the approach by Bailey et al. (2019) to investigate drivers of ARS behaviour in another population of bottlenose dolphins, by testing whether their residency time increased in response to foraging. Instead of single acoustic devices, we deployed arrays of echolocation data loggers and broadband sound recorders to characterise both occurrence and foraging activity within two known foraging areas (Hastie et al. 2004). We used two different proxies for foraging: (1) echolocation buzzes, identified by modelling echolocation inter-click intervals (Pirotta et al. 2014); and (2) bray calls, automatically detected using deep learning techniques, building upon the methodology of Bergler et al. (2019). We hypothesised that dolphins would remain longer within each of these foraging areas when the detection rates of foraging proxies within the encounter increased.

Material and methods

Study Area

This study was conducted in two narrow channels within the Moray Firth Special Area of Conservation (SAC), NE Scotland: Sutors (57o 41.41’N, 03o 59.18’W) and Chanonry (57o 5.14’N, 04o 5.85’W; Figure 1). During summer months, these two channels are intensively used by the resident population of bottlenose dolphins that occurs along the east coast of Scotland (Wilson, Thompson, and Hammond 1997; Hastie et al. 2003; Cheney et al. 2013). In Sutors, the highest concentration of sightings occurs at the eastern entrance of the channel (Wilson, Thompson, and Hammond 1997; Hastie, Wilson, and Thompson 2003). In Chanonry, dolphin density is higher in the northern part (Bailey and Thompson 2009), but foraging behaviour occurs in a relatively small area (0.3 km radius) next to the western promontory of the channel (Bailey and Thompson 2006). Visual observations have previously shown that both Sutors and Chanonry narrows are foraging hotspots (Hastie et al. 2004) where dolphins exhibit ARS behaviour (Bailey and Thompson 2006).

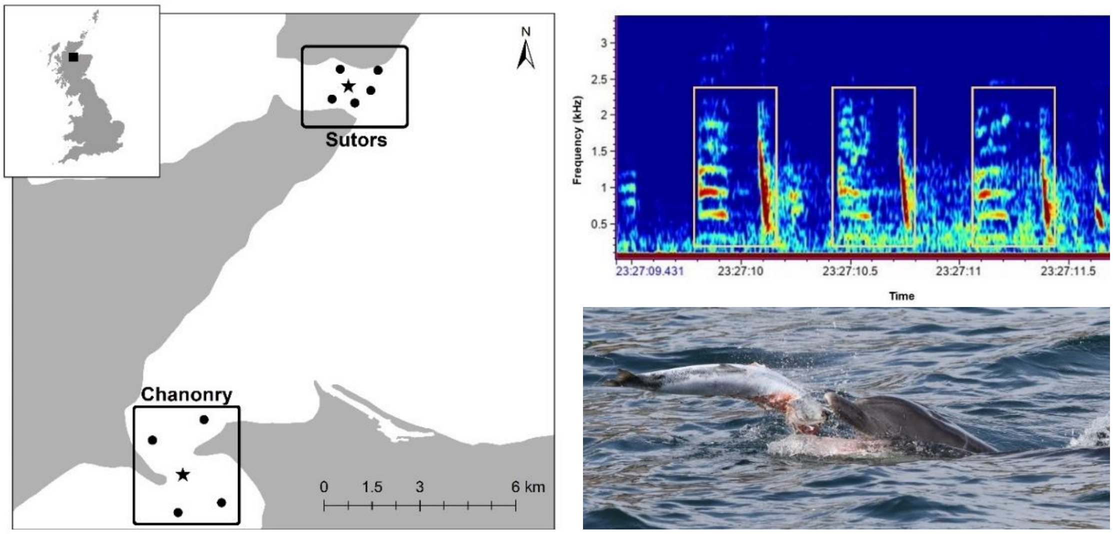

Figure 1. *Left: Map showing the passive acoustic monitoring arrays deployed at Sutors and Chanonry in NE Scotland including CPOD (●) and CPOD+SoundTrap (★) locations. Top right: Example of spectrogram (Raven Pro 1.6) with three bray calls annotated with yellow boxes. Bottom right: Bottlenose dolphin feeding on Atlantic salmon at Sutors. Photo by Dr B. Cheney - © Lighthouse Field Station, University of Aberdeen.*

Acoustic deployments

Between May and September 2018, echolocation data loggers (CPODs; Chelonia Ltd, UK) were deployed 2 m above the seabed to record continuously at six sites within Sutors and five sites within Chanonry (Figure 1). Arrays were designed to maximize the detection of echolocating dolphins within each site. Between June and September, a single broadband recorder (SoundTrap ST300HF; Ocean Instruments, NZ) was also deployed at the mooring in the middle of each array and was duty-cycled to record 50 % of the time (10 minutes every 20 minutes) at a sampling rate of 48 kHz.

Encounter definition

We used the manufacturer's custom software (www.chelonia.co.uk) to extract echolocation click detections and, following the manufacturer's guidelines, we only included dolphin clicks classified as High and Moderate quality. Using a similar approach applied by Bailey et al. (2019), unique dolphin encounters within each site were defined based on the interval between echolocation clicks detected by the CPODs. Specifically, a dolphin encounter was defined as a group of echolocation clicks, detected by any CPOD in the array, containing no gaps longer than the 95th quartile of the time gap distribution between click detection positive minutes. This threshold was calculated using data from Sutors because this location had the highest number of echolocation click detections. All the click detections from Sutors CPOD array were pulled together and all minutes containing at least one dolphin click were extracted. The distribution of time intervals between these detection positive minutes was investigated and the 95th quartile of the distribution was calculated. This 95th quartile was then used as a threshold to divide echolocation click detections into separate dolphin encounters in Sutors and Chanonry.

Detection of foraging behaviour

After grouping echolocation click detections by CPOD array, echolocation buzzes were identified by modelling the inter-click interval with a Gaussian mixture model (Pirotta et al. 2014). Bray calls were identified using DOLPHIN-SPOT, a deep convolutional neural network (CNN) based bray detector following the methodology of Bergler et al. (2019). DOLPHIN-SPOT produces an output that divides audio recordings into segments of variable length and labels them as bray call positive or negative (details in Supplementary Material 1 – DOLPHIN-SPOT).

Statistical analysis

To investigate whether dolphins remained longer in the area when foraging activity increased, we modelled dolphin encounter duration (decimal minutes) as a function of the proportion of foraging positive minutes within the encounter. Foraging positive minutes were defined as minutes with more than 5 echolocation buzzes or with at least one segment labelled as bray call positive. Since tides affect the occurrence of dolphins in Chanonry but not in Sutors (Fernandez-Betelu et al. 2019), channel (Sutors/Chanonry) and tidal stage in mid-encounter (Flood-High-Ebb-Low) were also included as explanatory variables. We used generalized linear models (GLM), with a gamma distribution. The link function was chosen between the identity and log link functions based on the lowest Akaike Information Criterion (AIC; Sakamoto, Ishiguro, and Kitagawa 1986). Due to differences in CPOD and SoundTrap deployment durations, two datasets were created for echolocation buzzes and bray calls respectively, and they were analysed in separate models. Models were assessed following a stepwise exclusion of variables using the variation in AIC (ΔAIC), starting from the models including all explanatory variables and all possible interactions. The model with the lowest AIC value was considered the most parsimonious and best approximating model (Burnham and Anderson 2002). We checked autocorrelation in residuals using autocorrelation plots (ACF). To match the SoundTrap 10-minutes duty-cycle, only encounters longer than 10 minutes were retained in the echolocation buzz dataset. Similarly, the bray call dataset only considered dolphin encounters with at least 10 minutes of SoundTrap recording.

We used the statistical program R v.4.1.2 in all the analyses (R Core Team 2021). Model assumptions were verified through visual inspection of the residual plots (Queen, Quinn, and Keough 2002) and using the R package performance (Lüdecke et al. 2021).

Results

Dolphin vocalisations were detected every day throughout the 17-week study period for an average of 5.3 hours/day at Sutors and 3.6 hours/day at Chanonry.

The distribution of time gaps between successive dolphin echolocation click detections ranged from 1 to 1581 min (26.35 h) in Sutors, the 95th quartile being 8 min. The threshold to divide echolocation detections into distinct encounters was rounded up to 10 min to be consistent with previous studies (Carlstrom 2005; Philpott et al. 2007; Todd et al. 2009; Wang et al. 2015; Fernandez-Betelu et al. 2019). Therefore, we defined a dolphin encounter as a group of click trains, detected by any CPOD in the array, containing no gaps longer than 10 minutes.

Of the 2747 dolphin encounters recorded by CPODs, 1444 were longer than 10 minutes and 718 contained more than 10 minutes of SoundTrap broadband recordings (Table 1). In both datasets, encounters were significantly shorter at Chanonry than at Sutors (Echolocation buzz dataset: Kruskal-Wallis X2 = 43.3, df = 1, p < 0.001; Bray call dataset: Kruskal-Wallis X2 = 22.7, df = 1, p < 0.001; Table 1). No obvious seasonal trend in the duration of dolphin encounters was observed in either of the channels (Figure S2.1 in Supplementary Material 2).

Table 1. *Number of bottlenose dolphin encounters and median encounter duration in decimal minutes, including upper and lower quartiles. Number and median duration of encounters with and without foraging positive minutes (FPM).*

		Total encounters	**Median encounter duration (lower-upper quartile)**	**encounters without FPM (median encounter duration)**	**encounters with FPM (median encounter duration)**
Echolocation buzz dataset	*Sutors*	816	33.0 min (19.3 – 55.8 min)	26 (14.5 min)	790 (34.1 min)
	Chanonry	628	24.3 min (15.7 – 41.7 min)	58 (14.5 min)	570 (25.9 min)
Bray call dataset	*Sutors*	429	38.5 min (24.7 – 61.2 min)	118 (25.3 min)	311 (46.2 min)
	Chanonry	289	29.5 min (20.2 – 47.9 min)	69 (20.5 min)	220 (31.9 min)

Trained on 14% of the dataset, the CNN model detected bray calls in 20 10-minute unseen raw audio files with an accuracy of 98.7%, precision of 88.5% and false positive rate of 1% (see details in Supplementary Material 1). This model was then applied to the entire 2,436 h of broadband audio data set, where it automatically detected bray calls within 10,348 minutes (7% of the complete broadband dataset; Table 1).

As predicted from our hypothesis, dolphin encounters were longer when the proportion of foraging positive minutes was greater within the encounter. A positive trend was observed for both echolocation buzzes (Figure 2A) and bray calls (Figure 2B). The trend was weaker for bray calls than for echolocation buzzes and, overall, weaker in Chanonry compared to Sutors. For the echolocation buzz dataset, the most parsimonious model retained the interaction between (a) proportion of foraging positive minutes and channel (chisq = 16.8, df = 1, $p < 0.001$), (b) proportion of foraging positive minutes and tidal stage (chisq = 12.2, df = 3, $p < 0.01$) and (c) tidal stage and channel (chisq = 20.4, df = 3, $p < 0.001$). For the bray call dataset, the most parsimonious model retained the interaction between (a) foraging positive minutes and channel (chisq = 3.9, df = 1, $p < 0.05$) and (b) tidal stage and channel (chisq = 9.7, df = 3, $p < 0.05$; Supplementary material 2).

Discussion

ARS behaviour in marine predators is widely used as a proxy for encounters with heterogeneously distributed prey, however, empirical evidence for this relationship is sparse (Thums, Bradshaw, and Hindell 2011; Humphries et al. 2012; Bailey et al. 2019). Previous visual tracking at one of our study sites demonstrated that surface feeding events were more likely within areas that dolphins searched intensively (Bailey and Thompson 2006). Here, we showed that two different acoustic proxies for foraging were associated with longer bottlenose dolphin encounter duration within the two study sites.

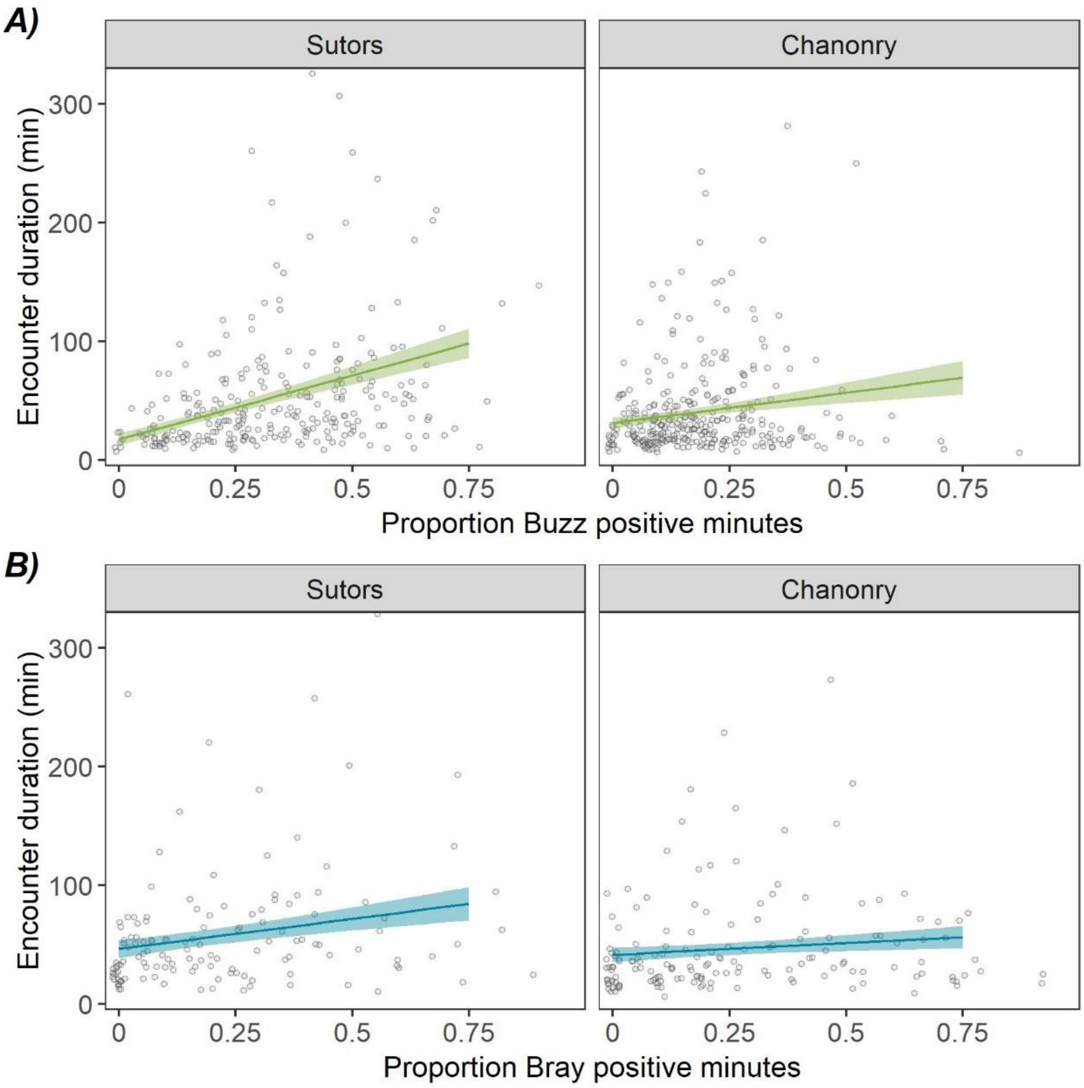

Figure 2. *Predicted dolphin encounter duration (minutes) in relation to the proportion of foraging positive minutes in the encounter for A) echolocation buzzes and B) bray calls divided by channel (Sutors: left; Chanonry: right) during flood. Shaded areas are the 95% confidence intervals. Plots include raw data (grey points).*

These results further support the theory that predators engage in ARS behaviour by increasing their residency time in an area after encountering prey (Kareiva and Odell 1987; Benhamou 1992; Hamer et al. 2009). In this study prey encounters were inferred by using the proportion of foraging positive minutes to link the encounter with the presence of prey. Previously, Bailey et al. (2019) found evidence of dolphins displaying ARS behaviour in response to foraging that occurred during the first third of an encounter but, unlike this study, not when considering foraging occurrence across the whole encounter. To overcome one of the limitations of Bailey et al.'s (2019) study, who deployed single recorders at four offshore study sites, we used arrays of recorders within two constrained (< 6 km^2) coastal areas where dolphins are known to forage regularly (Hastie et al. 2004; Bailey and Thompson 2006). Although, both studies used the detections of echolocation buzzes to infer foraging behaviour, here these were obtained through combined detections across each acoustic array, increasing the effective sampling area and the probability of detecting both echolocation buzzes and the full extent of the ARS behaviour. Differences in the results between these two studies may, therefore, have been caused by variation in design.

Bottlenose dolphins are selective opportunistic predators that feed on a variety of prey species, of varying quality (Wells and Scott 2009). Echolocation buzzes have not been linked to a specific prey and thus may represent encounters with various species. In contrast, to date, bray calls have only been associated with salmonid prey (Janik 2000; King and Janik 2015). Salmonids are among the largest prey species of these dolphins (Santos et al. 2001) and are known to influence behavioural patterns of these and other coastal marine mammals at a variety of scales (Lusseau et al. 2004).

The increase in dolphin encounter duration in relation to a higher proportion of bray positive minutes may be biased by the mechanics of capturing salmon. Due to the size of salmon, dolphins in the area are often seen regurgitating these fish repeatedly before swallowing them (B. Cheney, personal communication, June 2020), effectively increasing dolphin prey handling time. Therefore, dolphin encounters may be longer in response to successful feeding events. However, we could not disentangle the relative contribution of prey handling time to the observed increase in encounter duration because the average handling time for dolphins foraging on salmon is unknown. Further, the proportion of foraging minutes within each encounter may also be influenced by prey density within a patch and prey depletion rate (Watanabe, Ito, and Takahashi 2014; Hazen, Friedlaender, and Goldbogen 2015). Theory assumes that predators remain in a prey-rich patch until the density of prey decreases up to the point where the area is not profitable (Charnov 1976). Here, we showed that a high proportion of foraging positive minutes was linked to longer encounters, demonstrating that dolphins remain in prey-rich areas. Although, the relationship between bottlenose dolphin foraging call production rate and prey density is unknown, other predators have been found to adjust their behaviour to the density of their prey (Enstipp, Grémillet, and Jones 2007; Hazen, Friedlaender, and Goldbogen 2015). Future studies could investigate the rate of production of foraging calls within encounters to explore whether a decrease in foraging calls leads to patch departure. Our analyses showed a weaker correlation between encounter duration and foraging activity using bray calls than using echolocation buzzes (Figure 2). This is in contrast with the results found by Weimerskirch et al. (2007), where predators engaged in ARS behaviour only after capturing large prey items. Predator satiation is directly linked to prey size, and the level of satiation plays a major role in the behaviour of predators (Gill 2003). Therefore, one possible explanation for the dissimilarity between our study and the findings of Weimerskirch et al. (2007) is that dolphins may become satiated more quickly predating on salmonids than on smaller prey, leaving the area earlier. This weaker correlation between encounter duration and foraging using bray calls compared to echolocation buzzes could also be attributed to the differences in the methodology and data availability. Firstly, differences between these two vocalizations could be related to their detection range. CPODs detect echolocation clicks up to 1 km away (Roberts and Read 2015). There are no studies that estimate the detection range of bray calls but, like any other low frequency sound, they have the potential to travel longer distances. Although we increased the cumulative CPOD detection range by deploying arrays of devices, it is possible that the SoundTraps recorded some bray calls from dolphins located out of the detection range of the CPOD arrays. Alternatively, the weaker correlation between encounter duration and foraging using bray calls could have been caused by the duty-cycling of broadband recorders. Our CPODs recorded continuously, but SoundTraps were duty-cycled to record 50 % of the time, resulting in samples sizes for bray calls being smaller and biased towards longer encounters (Table 1). Further studies with continuous acoustic recordings and increased sample sizes, including visual observations, could explore potential differences in dolphin foraging behaviour linked to specific foraging vocalizations.

We found a positive correlation between encounter duration and proportion of time foraging within the encounter at both study sites, although the correlation was weaker in Chanonry than in Sutors (Figure 2). In coastal areas, the tidal cycle has a major effect on the distribution and behaviour of prey, which can shape predator foraging behaviour (Johnston, Thorne, and Read 2005; Hazen et al. 2009; Embling et al. 2012; Benjamins et al. 2015). While dolphin occurrence has not previously been linked to any tidal stage in Sutors, their occurrence increases during flood in Chanonry, and it has been hypothesised that this pattern may be related to cyclical changes in prey catchability, abundance, or behaviour (Fernandez-Betelu et al. 2019). One explanation for the weaker link between foraging activity and encounter duration in Chanonry is that predator-prey interactions may be associated with specific phases of the tidal cycle at this site. Further research to investigate variation in prey fields throughout the tidal cycle in the area would be required to test this hypothesis.

Similarly to previous passive acoustic studies, notably Bailey et al. (2019), our study used acoustic detections of foraging calls that could not be localised. These methods constrained our ability to study individual dolphin behaviour and thus our results represent dolphin groups. Furthermore, group size has the potential to influence both the proportion of foraging positive minutes and the duration of encounters. However, lack of localization and site- and context-dependent changes in dolphin vocalization rate limit the ability to infer group size from acoustic detections (Jones and Sayigh 2002; Luís, Couchinho, and dos Santos 2014). Arguably, dolphin encounters with a higher number of individuals could lead to higher vocalization rates. However, a previous study found that dolphin echolocation buzz rate decreased with group size (Martin et al. 2019). Geographical differences in the vocalization rate of dolphins linked to group size have also been found (Jones and Sayigh 2002) and site-specific information on our study population is lacking. Further research is required to investigate the link between dolphin vocalization rate and group size and their effect on encounter duration at these two sites. Nevertheless, in this study we showed that two different proxies for predator foraging behaviour led to similar conclusions about predator ARS behaviour.

Higher-endurance broadband recorders are now available, opening the potential to use new automated pattern recognition techniques to routinely extract distinct animal vocalizations from continuous long-term recordings (Romero-Mujalli et al. 2021; Ruff et al. 2021). These, in turn, could be used to explore other aspects of foraging theory, including investigating how patterns of bray call production within encounters affect decisions over when to leave prey patches (Charnov 1976). Furthermore, continuous long-term recordings could also be used to test whether foraging decisions are moderated by other factors that may affect the length of dolphin encounters, such as disturbance from boat traffic (Pirotta et al. 2015) or other anthropogenic stressors.

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Ethics

This was a non-invasive, acoustic observational study. No physical or behavioural interactions between the authors and any protected animal species occurred during this study. The deployment and recovery of passive acoustic devices was conducted under licences from Marine Scotland (No: 05594/15/0) and the Cromarty Firth Port Authority (L18/PoCF/03) using vessels with appropriate certification, accreditation, and endorsements.

Author contribution

OFB: data curation, conceptualization, methodology design, formal analysis, visualization, writing – original draft, funding acquisition. VIM: DOLPHIN-SPOT adaptation and training leader, data curation, conceptualization, writing – review and editing. IG: supervision, data curation, conceptualization, methodology design, writing – review and editing. BC: data curation, conceptualization, writing – review and editing. SP: DOLPHIN-SPOT adaptation and training, data curation, writing – review and editing.

RXC: DOLPHIN-SPOT adaptation and training, writing – review and editing. PT: supervision, conceptualization, writing – review and editing, project administration, funding acquisition.

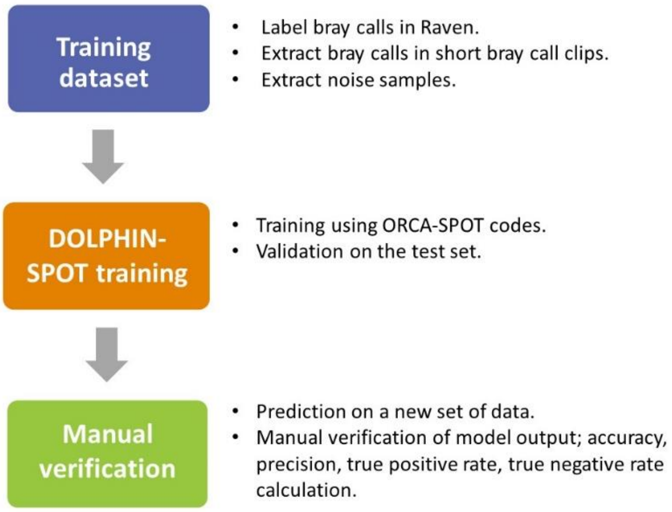
Data availability

The datasets and R Code supporting this study are available from the Dryad digital repository doi: 10.5061/dryad.djh9w0w1n.

Supplementary Material 1 – DOLPHIN-SPOT

DOLPHIN-SPOT

DOLPHIN-SPOT is a Convolutional Neural Network (CNN)-based dolphin bray call detector, following the methodology developed by Bergler et al. (2019). DOLPHIN-SPOT was trained on labelled bottlenose dolphins bray calls (Janik 2000) for automatic detection in broadband sound recordings. Here, we described the steps to train and validate the model and we also included the sensitivity and specificity metrics obtained during its validation (Figure S1.1).



- Label bray calls in Raven.
- Extract bray calls in short bray call clips.
- Extract noise samples.

- Training using ORCA-SPOT codes.
- Validation on the test set.

- Prediction on a new set of data.
- Manual verification of model output; accuracy, precision, true positive rate, true negative rate calculation.

Figure S1.1. *DOLPHIN-SPOT workflow including all the steps required for the training of the convoluted neural network (CNN).*

Methods

Training dataset

The training dataset was generated by processing 1767 h of broadband sound recordings from SoundTrap devices (ST300HF, Ocean Instruments, NZ; sampling rate 48 kHz). These devices were deployed at Sutors (57° 41.41'N, 03° 59.18'W) and Chanonry (57° 5.14'N, 04° 5.85'W), between May and September 2018. These two sites are intensively used by a population of bottlenose dolphins that produce a specific call, known as a bray call, when feeding on salmon (Janik 2000). These calls are low frequency (< 2 kHz) vocalizations that consist of two parts, a long multiband burst-call and a short tonal down-sweep (Janik 2000).

The automatic detector needed to be trained on labelled bray call clips and samples of the background noise (noise clips) as negative examples. Bray call and noise clips were extracted from longer sound recordings and were manually verified to include only dolphin bray calls and background noise respectively.

Bray call clips

Bray calls were manually annotated with Raven pro 1.6.1 software (K. Lisa Yang Center for Conservation Bioacoustics 2019) through visual inspection of the spectrograms (0 - 3.5 kHz, Hann window, window size 1,024, 85 % overlap). The start and end of the bray calls were annotated by drawing boxes using the manual selection tool. Bray calls were grouped under the same annotation box when calls occurred less than 2 seconds apart (Figure S1.2). Start and end time of each call, or group of calls, were used to extract the corresponding audio clips from the sound recording.

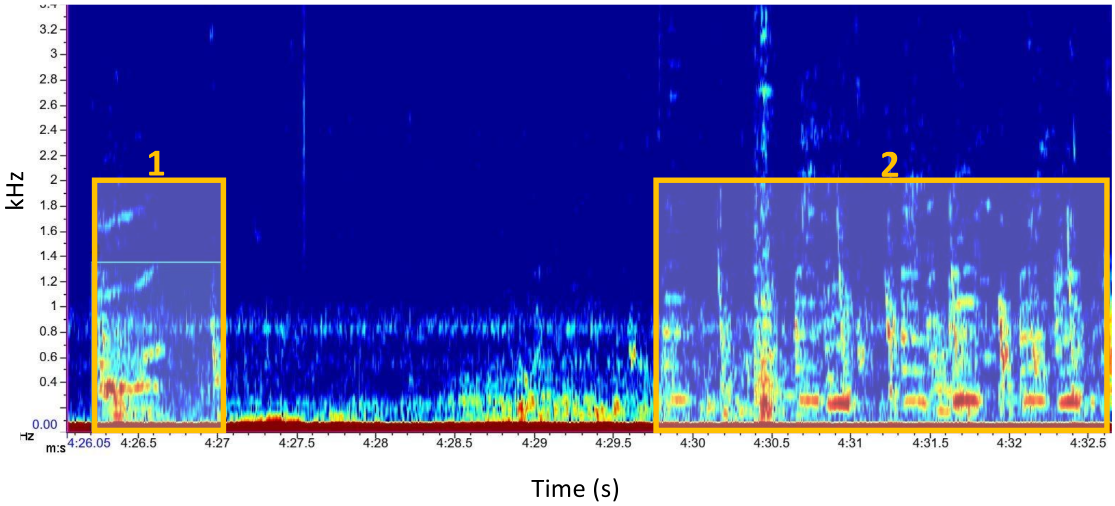


Figure S1.2. *Raven spectrogram including manual annotation examples: (1) single bray call annotation box and (2) grouped bray call annotation box (n brays < 2 seconds apart).*

Noise clips

There are often significantly more noises than animal vocalizations in continuous recordings. To handle such imbalance in the dataset, a lot more noise examples were included in the training data than the bray calls.

Our training dataset for the background noise was generated from a subsample of files in which bottlenose dolphins were absent. To determine dolphin presence, we pre-processed all the SoundTrap files using PAMGUARD (PAMGUARDBeta 2.01.03: Gillespie et al. 2008) and its whistle moan detector (Hann window, FFT Length 512 bins). Sound files, in which at least one whistle was detected, were discarded for the noise clip extraction, as we assumed it would indicate dolphin presence. To further minimise the possibilities of including any faint dolphin vocalizations in the noise clip dataset, files within a one-hour buffer around confirmed whistle detections were also discarded. Sound files without animal vocalizations were randomly subsampled to automatically extract distinct 2 seconds noise clips.

Noise augmentation was performed to obtain the largest possible variety of training variants in the noise clip dataset and improve the robustness of the model (see Bergler et al. 2019 for details on the noise augmentation process). Two thirds of the noise clips were used as negative examples, while the remaining third of the noise clips was used in the noise augmentation.

Final training dataset

A total of 31.5 h of audio files with dolphin vocalisations were analysed with Raven to manually annotate dolphin bray calls. The final dataset included 3,480 bray call clips (total duration 42.6 minutes). The raw audio dataset contained 781 h of sound recordings without dolphin whistles of which 220 h were randomly subsampled to automatically extract noise clips. A total number of 39,624 2-second noise clips were extracted and 13,208 were subsampled for the noise augmentation. Bray call and noise clips were further split into *training set* (70%), *validation set* (15%) and *test set* (15%).

DOLPHIN-SPOT Training and Prediction

The training of the model was carried out on a GPU node of a High-Performance Computer cluster (NVIDIA GeForce RTX 2080 Ti). Since most of the bray call energy occurs at low frequencies (< 2 kHz; Janik, 2000) we focused the training of the model on frequencies between 250 Hz and 4 kHz. The model was trained through iterations called epochs, during which it went through a training and a validation phase. We allowed a maximum of 200 epochs and the training was programmed to stop if the accuracy did not improve within 20 epochs. Following the selected ResNet-18 architecture by Bergler et al. (2019), we ran our model using ResNet18 with an initial convolution 7x7 kernel. These settings had the best balance between accuracy of results and speed of training. Noise augmentation and model training were implemented using PyTorch.

During the prediction process, DOLPHIN-SPOT divides broadband recordings into specified sliding windows (2.5 seconds) and assigns a probability that a given window contains at least one bray call. The algorithm then combines consecutive windows into segments of variable length with probabilities below or above a user-specified probability threshold. Finally, it transforms probabilities into a binary output and labels each segment as bray call positive or negative if the probability falls above or below the specified threshold. As the final output, DOLPHIN-SPOT produces annotation tables that include information on the beginning and end time of each segment and a binary variable describing the presence/absence of bray calls within a given segment. These annotation tables produced by DOLPHIN-SPOT can be directly uploaded to Raven.

DOLPHIN-SPOT Manual Verification

As suggested by Bergler et al. (2019) the trained model was verified on unseen data to test how robust it generalized. For the manual verification of the model, we randomly selected 20 10-minute audio files that had not been used in training. The audio files were processed using a sequence length of 2 seconds and a step size of 0.5 seconds. These resulted in a probability matrix that given 2-second segment included a "dolphin-bray". That probability was transformed into a binary variable (0: "noise", 1: "dolphin-bray") by specifying a probability threshold of >= 0.9. Model predictions for each of the 2-second segments were visually inspected in Raven and manually labelled as either true/false positive or true/false negative. Accuracy, precision, True Positive Rate (TPR) and False Positive Rate (FPR) metrics were then calculated.

Results

DOLPHIN-SPOT Training

The model required 78 hours and 148 epochs to be trained. The selected model achieved an accuracy of 98.1%, a precision of 97.7%, a true positive rate of 86.4 % and a false positive rate of 0.003%. During the automatic validation on the *test set*, the model achieved an accuracy of 99.0%, a precision of 98.7%, a True Positive Rate of 93.2% and a False Positive Rate of 0.02%.

DOLPHIN-SPOT Manual Verification

During the manual verification on 20 audio files, 5,983 2-second segments were visually inspected in Raven against the model predictions. Of these sections, 393 were true positive bray calls, while 51 were false positive and 26 false negative bray calls. These results led to 98.7% of accuracy, 88.5% precision, 93.7% True Positive Rate and 1% False Positive Rate (Figure S1.3).

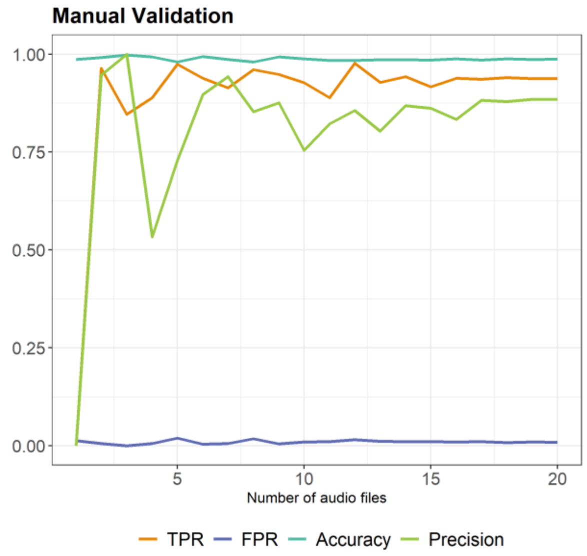


Figure S1.3. Sensitivity and specificity metrics obtained during the manual validation. Metrics were stable after analysing 17 audio files. TPR: True Positive Rate; FPR: False Positive Rate.

Supplementary Material 2

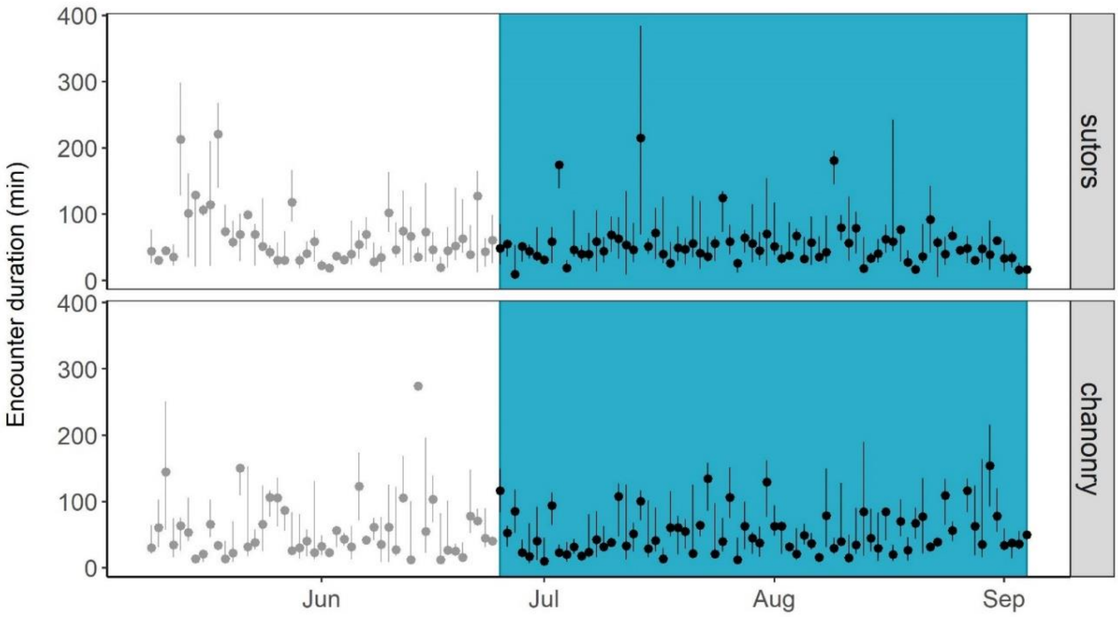


Figure S2.1. *Median dolphin encounter duration and inter-quartile ranges for the entire CPOD deployment (May-Sep 2018) and the SoundTrap deployment period (blue area) at each of the channels. Days with encounters included in the bray call dataset in black.*

Statistical analyses

Table S2.1: *Stepwise AIC selection process for echolocation buzz and bray call datasets. The starting model was a gamma distributed (identity link) generalised linear model: encounter duration ~ ProportionForagingPositiveMinutes * Channel * Tide. The most parsimonious model indicated by an asterisk*

Model	Explanatory Variables	df	AIC	ΔAIC
Echolocation Buzz Dataset				
1	BuzzProportion * Channel * Tide	17	13056.9	0.1
2	BuzzProportion + Channel + Tide + BuzzProportion:Channel + BuzzProportion:Tide + Channel:Tide	14	13056.8	0.0*
3	BuzzProportion + Channel + Tide+ BuzzProportion:Channel + Channel:Tide	11	13068.0	11.2
4	BuzzProportion + Channel + Tide + BuzzProportion:Channel	10	13087.3	30.5
5	BuzzProportion + Channel + Tide	7	13099.2	42.4
6	BuzzProportion + Tide	4	13097.3	40.5
7	BuzzProportion	3	13126.1	69.3
8	Null	2	13318.4	261.6
Bray call Dataset				
1	BrayProportion * Channel * Tide	17	6594.6	5.0
2	BrayProportion + Channel + Tide + BrayProportion:Channel + BrayProportion:Tide + Channel:Tide	14	6589.4	-0.2
3	BrayProportion + Channel + Tide + BrayProportion:Channel + Channel:Tide	11	6589.6	0.0*
4	BrayProportion + Channel + Tide + Channel:Tide	10	6593.1	3.5
5	BrayProportion + Channel + Tide	7	6600.3	10.7
6	BrayProportion + Channel	4	6621.4	31.8
7	BrayProportion	3	6640.8	51.2
8	Null	2	6678.7	89.1

Echolocation buzz dataset: most parsimonious model output

```
MODEL INFO:
Observations: 1444
Dependent Variable: Encounter.Duration
Type: Generalized linear model
  Family: Gamma
  Link function: identity

Standard errors: MLE
----------------------------------------------------------------------
                                               Est.    S.E.   t val.    p
------------------------------------------ -------- ------- -------- --
(Intercept)                                   24.89    2.57     9.68 0.00
BuzzProportion                                11.88   12.04     0.99 0.32
channelsutors                                 -0.70    3.40    -0.21 0.84
TideFlood                                      6.17    3.25     1.90 0.06
TideHigh                                      15.54    4.75     3.27 0.00
TideLow                                       -1.42    3.73    -0.38 0.70
BuzzProportion:channelsutors                  56.93   11.24     5.07 0.00
BuzzProportion:TideFlood                      39.14   13.73     2.85 0.00
BuzzProportion:TideHigh                      -15.07   16.21    -0.93 0.35
BuzzProportion:TideLow                        -5.12   15.21    -0.34 0.74
channelsutors:TideFlood                      -13.18    3.80    -3.47 0.00
channelsutors:TideHigh                       -19.07    4.93    -3.87 0.00
channelsutors:TideLow                         -3.24    4.36    -0.74 0.46
----------------------------------------------------------------------
```

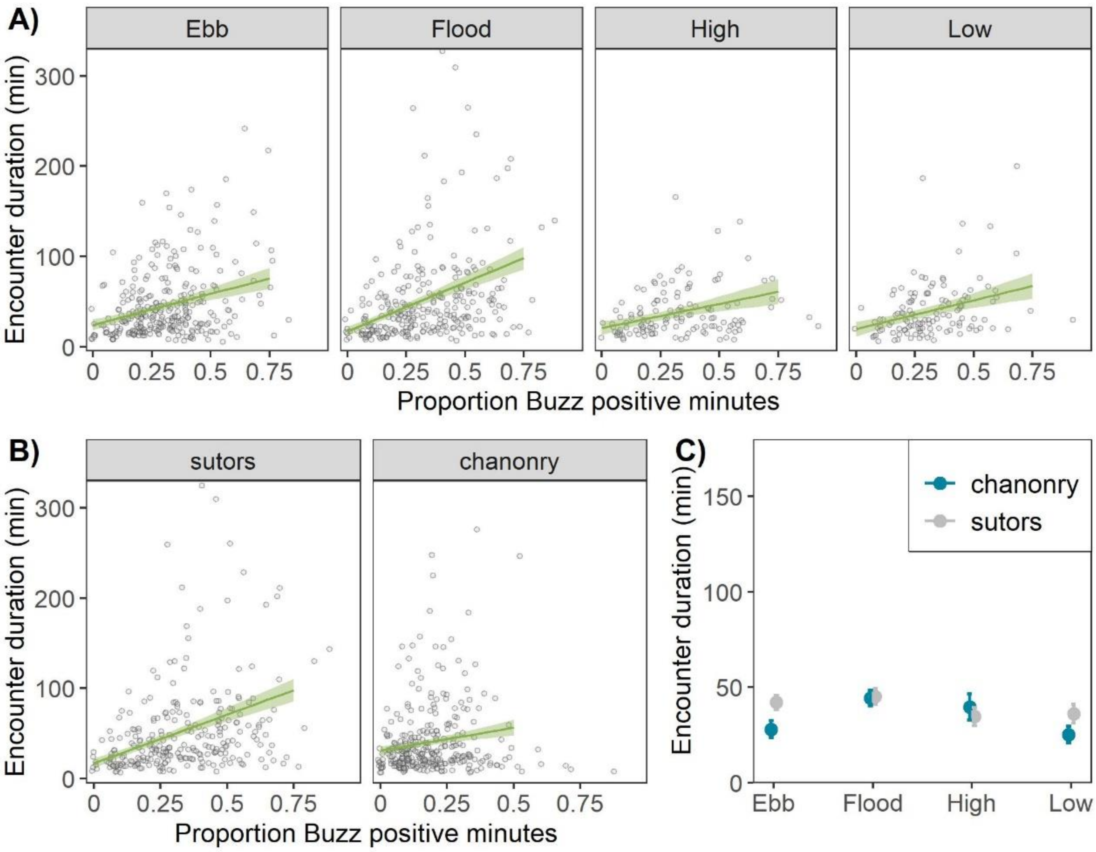


Figure S2.2: *Predicted dolphin encounter duration in relation to A) the proportion of buzz positive minutes by tidal stage at Sutors, (B) the proportion of buzz positive minutes by channel during flood, and C) tidal stage within channel, including raw data (grey points).*

Bray call dataset: most parsimonious model output

```
MODEL INFO:
Observations: 718
Dependent Variable: Encounter.Duration
Type: Generalized linear model
  Family: Gamma
  Link function: identity
```

```
Standard errors: MLE
-----------------------------------------------------------------------
                                               Est.     S.E.   t val.     p
------------------------------------------ -------- ------- -------- ---
(Intercept)                                   25.28     3.27     7.74   0.00
BrayProportion                                19.97     7.59     2.63   0.01
channelsutors                                 15.60     4.29     3.63   0.00
TideFlood                                     16.26     4.00     4.06   0.00
TideHigh                                      11.47     5.43     2.11   0.04
TideLow                                        0.56     4.38     0.13   0.90
BrayProportion:channelsutors                  30.77    13.00     2.37   0.02
channelsutors:TideFlood                      -10.63     5.87    -1.81   0.07
channelsutors:TideHigh                       -20.73     6.85    -3.03   0.00
channelsutors:TideLow                         -5.91     6.28    -0.94   0.35
-----------------------------------------------------------------------
```

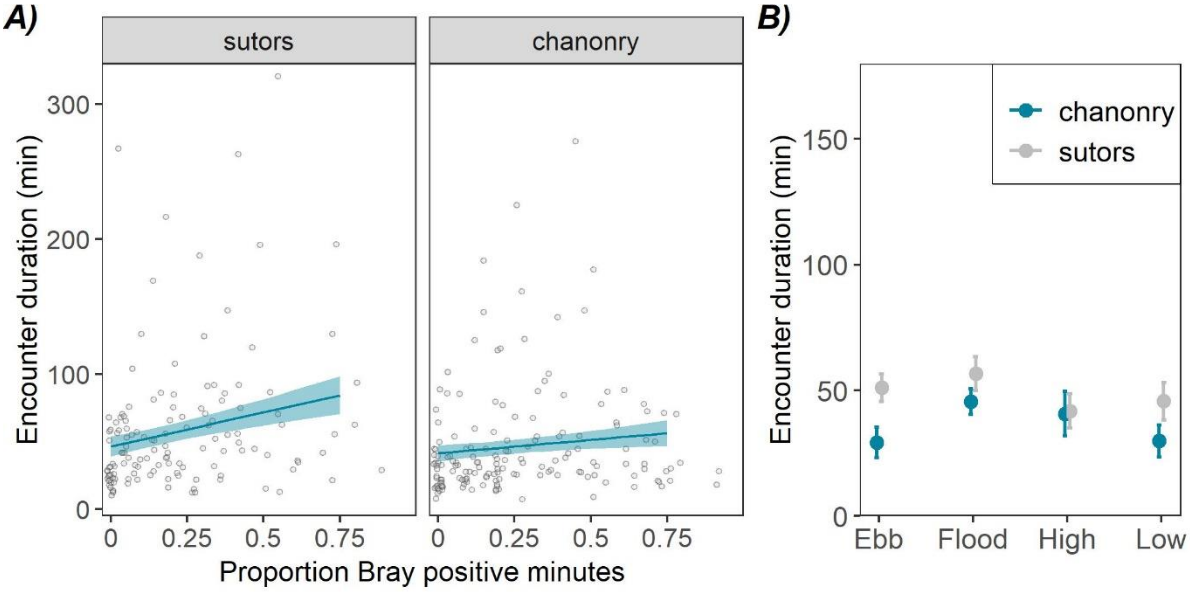


Figure S2.3: *Predicted dolphin encounter duration (minutes) in relation to A) the proportion of bray positive minutes within channel during flood, and B) tidal stage within channel, including raw data (grey points).*

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