UiT The Arctic University of Norway

Faculty of Bioscience, Fisheries and Economics
Institute of Artic and Marine Biology

The influence of prey distribution on marine top predator movements

Emma F. Vogel

A dissertation for the degree of Philosophiae Doctor – September 2023

Cover photo: Emma Vogel

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“The more clearly we can focus our attention on the wonders and realities of the universe about us, the less taste we shall have for destruction”

~Rachel Carson

Supervisors

Professor Audun Håvard Rikardsen

Department of Arctic and Marine Biology
Faculty of Biosciences, Fisheries and Economics
UiT – The Arctic University of Norway
9037 Tromsø, Norway

Dr. Marie-Anne Blanchet

Terestrial Ecology and Sea Birds, Norwegian Polar Institute
Fram Centre, 9007 Tromsø, Norway

Department of Arctic and Marine Biology
Faculty of Biosciences, Fisheries and Economics
UiT – The Arctic University of Norway
9037 Tromsø, Norway

Dr. Erik Martin Biuw

Marine Mammal Research Group, Institute of Marine Research
Fram Centre, 9007 Tromsø, Norway

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Table of Contents

Summary

Predation requires spatial and temporal co-occurrence of predators and their prey. Interactions between marine top predators and their prey fundamentally influence ecosystem structure and energy transfer. Marine top predators, such as killer whales (*Orcinus orca*) and humpback whales (*Megaptera novaeangliae*), have been suggested as key sentinels for ecosystem health because they play pivotal roles in shaping marine food webs and exhibit clear responses to ecosystem changes. Since top predator movements are rarely influenced by any natural predators, they serve as excellent model species for the study of predator-prey interactions. Importantly, their movements can reveal information about predator-prey interactions that would otherwise be challenging to observe, since they primarily occur underwater and out of sight. Biotelemetry can help overcome these limitations by remotely revealing multidimensional marine predator movements over monthly to yearly timescales. In the three papers comprising this thesis, the movements of two top predators, killer whales and humpback whales, were examined to investigate the influence of three corresponding prey types on their movements within the Norwegian and Barents Seas: herring (*Clupea harengus*), harbour seals (*Phoca vitulina*) and capelin (*Mallotus villosus*).

Paper I explored how the movements of a highly flexible generalist top predator may be influenced by patchy prey density distributions. Specifically, Norwegian spring spawning herring densities were paired with satellite telemetry data from 29 killer whales recorded during winter and spring in 2015-2019. Herring densities were estimated from direct acoustic-trawl survey observations, which is distinct from previous studies using indirect prey distribution proxies, and from a fully coupled ecosystem model. Results demonstrate that killer whales follow herring for hundreds of kilometres along the coast of Norway from their northern inshore overwintering areas to more southern offshore spawning grounds on the continental shelf. All whales altered their movements to be more restricted when herring density increased, consistent with area-restricted searching, although individuals exhibited this in different amounts. This suggests that killer whales alter their behaviour in response to herring biomass distribution patterns by reducing their speed and directionality in areas with elevated relative herring density on the Norwegian Shelf. Consequently, killer whale distributions may be expected to change concurrently with herring distributions and densities in future. These findings can serve as a baseline for future comparative studies and for potentially identifying previously unknown areas of high herring density, which could be used to inform future herring survey designs.

Paper II compared the movements of two killer whales identified to feed on seals with six fish-eating individuals between 2015-2021, with the aim of differentiating their movements

according to their prey. Prey choice history of each whale was assessed using photo-identification together with $\delta^{13}C$ and $\delta^{15}N$ stable isotope analysis prior to tagging. Three related movement differences were found to differentiate the two groups: (1) differences in routes taken; (2) differences in their distances to the shore, and (3) differences in the proportion of movements directed towards or away from known harbour seal haul-out areas. These differences might reflect individual prey specialization, or alternatively prey switching. Regardless, the findings in this paper demonstrate how the movements of these generalist predators can be differentiated by their unique prey characteristics. This highlights that killer whales optimise their seasonal foraging strategies according to their preferred prey after leaving the northern fjords. Importantly, the presumed seal-eating killer whales tagged in this study took a unique coastal route through the Lofoten Archipelago rather than following herring offshore, contrary to previously-recorded killer whale movements associated with herring in this region. This finding could be used for targeted killer whale tagging of presumed seal-eating killer whales in future studies.

Paper III further explores the influence of patchy prey distribution on generalist predators, by pairing lateral and vertical movement data from ten satellite-tagged humpback whales in the Barents Sea in 2018 with concurrent capelin surface and vertical density estimates. Mixed effect modelling indicated that these predators exhibited characteristic area-restricted search behaviours where prey density was the highest. Whale dive depth was also found to be positively correlated with diurnal and seasonal variations in the vertical distribution of capelin. This confirmed that in addition to whales foraging in regions of high prey density, they also target the densest shoals of targeted prey on a vertical scale. These findings imply that capelin density directly influences humpback whale movements, emphasizing the importance of directly measuring prey density for a deeper understanding of marine predator-prey dynamics. Together, the main findings of this thesis revealed novel interactions between marine top predators, killer whales and humpback whales, and their corresponding prey species, herring, harbour seals, and capelin, in the Norwegian and Barents Seas. The presumed prey-switching behaviours recorded by both top predators in these regions demonstrates a complexity in predator-prey interactions that should be accounted for in ecosystem models. These findings present opportunities for future studies to connect prey distribution with the unique predator-prey movements identified here with actual observed predation events by employing finer-scale biologging tags. Considering the rapid climate-driven marine ecosystem changes in the Arctic both currently and in the near-future, these findings underscore the need for understanding the degree of flexibility generalist marine top predators have in response to changing prey distributions.

List of papers

Paper I: Vogel, E.F., Biuw, M., Blanchet, M.A., Jonsen, I.D., Mul, E., Johnsen, E., Hjøllo, S.S., Olsen, M.T., Dietz, R. and Rikardsen, A., (2021). Killer whale movements on the Norwegian shelf are associated with herring density. *Marine Ecology Progress Series*, *665*, 217-231.

Paper II: Vogel, E.F., Rikardsen, A., Blanchet, M.A., Blevin, P. and Biuw, M., (*In revision*). Norwegian killer whale movements reflect their different prey types. *Polar Research.*

Paper III: Vogel, E.F., Skalmerud, S., Biuw, M., Blanchet, M.A., Kleivane, L., Skaret, G., Øien, N. and Rikardsen, A.H. (2023). Foraging movements of humpback whales relate to the lateral and vertical distribution of capelin in the Barents Sea. *Frontiers in Marine Science, Volume* 10, 1254761.

Contributions/roles	**Paper I**	**Paper II**	**Paper III**
Concept and idea	**EFV**, MB, MAB, AHR	**EFV**, MB, PB, AHR	**EFV**, SS, MB, AHR
Study design and methods	**EFV**, MB, MAB, AHR	**EFV**, MB, AHR	**EFV**, MB, SS, AHR, SG
Data gathering and interpretation	**EFV**, MB, MAB, AHR, EM, MTO, RD, IDJ, SSH	**EFV**, MB, MAB AHR	**EFV**, SS, MB, MAB, SG, AHR, LK, NØ
Method development	**EFV**, MB, MAB, IDJ, SSH	**EFV**, MB, PB, AHR, MAB	**EFV**, MB, SS, MAB, AHR, SG,
Manuscript preparation	**EFV**	**EFV**	**EFV**

EFV= Vogel, E.F.
MB= Biuw, M.
MAB= Blanchet, M.-A
IDJ= Jonsen, I.D.
EM= Mul, E.
EJ= Johnsen, E.
SSH= Hjøllo, S.S.
MTO= Olsen, M.T.
RD= Dietz, R
AHR= Rikardsen, A.H.
PB= Belvin, P.
SG= Skaret, G.
SS= Skalmerud, S.
NØ= Øien, N.
LK= Kleivane, L.

Abbreviations

ARS – Area restricted search
NSS – Norwegian spring spawning (herring)
NASC – Nautical area scattering coefficient
EDSU – Elementary distance sampling unit
PSU – Primary sampling unit
INLA – Integrated nested Laplace approximation
TMB – Template model builder
GRF – Gaussian random field
SPDE – Stochastic partial differential equation
QFASA – Quantitative fatty acid signature analysis

1 Introduction

Why study top predator-prey relationships?

Predation plays a fundamental role in ecosystem structure and dynamics, prey populations and species viability (Schmitz et al., 2010). Predation shapes ecosystems by increasing prey mortality rates and by regulating the dynamics of lower trophic levels (Soule et al., 2005; Wootton and Emmerson, 2005; Walsh and Reznick, 2008). Many marine top predators are considered to be sentinel species, as they play pivotal roles in shaping marine food webs, are sensitive to anthropogenic influences on the environment, and are highly mobile, exhibiting clear responses to changes in their ecosystems (Fossi and Panti, 2017; Hazen et al., 2019). Given these criteria, cetaceans, such as killer whales and humpback whales are exemplar marine sentinels, making them excellent study or model species to examine both ecosystem health and predator-prey relationships.

The influence of predators on their ecosystem may vary according to their prey species and the flexibility of their diet both at the population and the individual level. Prey can also influence predator abundance, distribution, phenology and behaviour, and therefore also their impact on the ecosystem. The complex and interconnected nature of marine ecosystems makes it difficult to identify movements specifically reflecting predation. However, the movements of top predators like humpback whales, and in particular apex top predators such as killer whales, are ideally suited to studying predation because their movements are rarely influenced by themselves avoiding predation.

Understanding variability in predator foraging behaviour both at the individual- and population-level is key to predicting their responses to ecosystem changes. Yet, the underlying influences and effects of predation are some of the most challenging ecological processes to study (Lennox et al., 2022). Furthermore, changes in marine predator distributions and movement patterns are projected due to intensifying anthropogenic pressures and climate change (Niella et al 2020, Niella et al 2022, Anderson et al 2013). Therefore, studying how, why and where predators overlap and interact with their prey is fundamental to understanding these changes at the ecosystem and global scale.

Box 1: Optimal foraging theory

Since predator movements are influenced by prey choice, abundance and distribution, optimal foraging theory can be used to explain and predict predator movements (Thums et al., 2011; Womble et al., 2014; Goldbogen et al., 2015; Bestley et al., 2015; Joy et al., 2015; Hays et al., 2016;). Optimal foraging theory is an economic model used to assess the performance of individual predator choices and proposes that animals will adopt efficient foraging strategies that enhance their net energy gain (MacArthur and Pianka, 1966; Pyke et al., 1977). This involves maximizing food intake while minimizing the energetic cost linked to consuming a certain amount of energy from prey. Given that more successful and profitable foragers will have higher reproductive fitness (Hedenström and Alerstam, 1997; Houston and McNamara, 2014), it is beneficial for animals to forage in a way that maximizes their energy gain by spending more time in areas that are more energetically profitable than others (Stephen and Krebs, 1986). Marginal value theory suggests that an animal will target a patch of prey until it is no longer profitable for them, i.e., once their energy intake rate equals or drops below the average capture rate (Charnov, 1976). Accordingly, a predator will seek out areas with high prey densities to maximise the energy efficiently of its feeding, as predicted by optimal foraging theory (MacArthur and Pianka, 1966). This means an individual will spend longer on average foraging within denser, higher-quality prey patches than in sparser, lower-quality prey patches (Charnov, 1976; Watanabe et al., 2014). If multiple prey types are available, optimal foraging (and therefore prey choice) may also be influenced by the energy content of available prey. For example, a low density but high-quality food source may be more optimal than a high density, low-quality food source (Pyke and Stephens, 2019).

Predator movements influenced by prey characteristics

The behaviour and movements of marine predators are ultimately influenced by the distribution, availability, abundance, and behaviour of their prey (Womble et al., 2014; Goldbogen et al., 2015; Hays et al., 2016, Lennox et al., 2023). Prey species density and variability can span different spatiotemporal scales according to environmental and species characteristics (Benoit-Bird et al., 2013). So-called ‘patchy prey’ is distributed in dense aggregate patches, such as shoals of fish, whereas other prey can be more dispersed and discrete, such as seals. Spatiotemporal distributions of prey reflect the highly heterogeneous nature of the marine environment (Boyd, 1996; Sims et al., 2008; Bestley et al., 2010). This creates an ever-evolving challenge for marine predators to locate suitable prey (Goldsworthy et al., 2010). Some predators can make informed foraging decisions across short distances through sensory cues related to resource abundance and distribution (Sims and Quayle, 1998). Similarly, predators may be aware of and use historical patterns in seasonal and geographical prey distributions and previous foraging success (Bradshaw et al., 2004; Biuw et al., 2009; Iorio-Merlo et al., 2022). In order to optimize foraging success, predators typically track and follow prey movements and migrations by navigating through dynamic prey patterns and heterogeneous environments (Russell et al., 1992). Therefore, prey distribution significantly impacts predator fitness and performance (Tiselius et al., 1993; Boyd, 1996; Fauchald et al., 2000). Marine predators respond to changes in prey distribution by modifying both their horizontal and vertical movements (Thums et al., 2011, Bestley et al., 2015, Joy et al. 2015). Predator success hinges on overlapping both spatially and temporally (Fretwell and Lucas, 1970; Krebs, 1978). Prey distribution, however, is not the only characteristic that influences a predator's ability to locate prey and forage successfully. Efficient predator foraging is also influenced by prey abundance, patch density, and the spatial scales of aggregated patches (Lasker, 1975; Milne et al., 1989; Tiselius et al., 1993; Beyer, 1995; Boyd, 1996; Leising, 2001). The distribution of prey not only significantly impacts foraging success but also effects the energetic costs associated with foraging behaviour, and therefore overall predator performance (Tiselius et al., 1993; Boyd, 1996). Understanding predator behaviour and distribution therefore requires assessment of their prey in terms of costs and benefits to the predator (Fretwell and Lucas, 1970).

Identifying predator foraging behaviour

Identifying predator foraging behaviours (both temporally and spatially) is a key first step in understanding resource distribution within the ecosystem (Goldsworthy et al., 2010), since the way in which a predator traverses through its environment often reflects various characteristics of their targeted prey (Womble et al., 2014; Goldbogen et al., 2015; Hays et al., 2016; Vogel et al., 2021). For free-ranging foragers, behaviours like prey searching and exploiting prey patches are frequently discerned by comparing animals' spatial movement against predictions derived from ecological and foraging theories. When predators forage, their surface movements frequently reflect area-restricted search (ARS) behaviour within prey patches (Kareiva and Odell, 1987: Witteveen et al., 2008; Hazen et al., 2009; Silva et al., 2013), which is characterized by decreased speeds and increased turning rates (Jonsen et al., 2005; Breed et al., 2009; McClintock et al., 2012).

Box 2: Differentiating predator movements and behaviours

Predator movements and behaviour are distinct but interconnected aspects of animal ecology, each contributing to our understanding of how predators interact with their environments and their prey.

Predator movements:

Marine predator movements refer to the physical displacements of a predator within its habitat. The various ways in which animals relocate from one place to another, known as animal movement, play a vital role in ecological processes, leading to the emergence of the field known as movement ecology (Nathan et al., 2008). Movement is the outcome of diverse animal behaviours in terms of spatial displacement and thus it has a significant influence on shaping populations, communities, ecosystems, and evolution (Baker, 1978; Swingland and Greenwood, 1986; Dingle, 1996; Natan et al., 2008). Broader population movement patterns have traditionally been inferred through opportunistic observations of groups of animals (e.g. whaling records; Townsend, 1935), and for some species, the use of natural markings to identify and coarsely track the movements of individuals, such as the unique fluke prints of humpback whales (Hammond, 1990). Recent advances in animal telemetry and biologging have revealed and allowed us to quantify marine animal movements directly and somewhat continuously, thus allowing for more detailed analysis. Predator movements provide valuable information about spatial distribution, migration routes, home ranges, and habitat utilization. They reveal where predators travel, when they move, and how far they roam. Movements can offer insights into aspects such as daily activity patterns, navigation, and responses to environmental cues.

Predator behaviour:

Predator behaviour, however, encompasses a broader spectrum which includes movements but also extends to other activities, interactions, and responses to stimuli (Breed and Moore, 2021). Predator movements are a subset of predator behaviour. While movements focus on the physical aspect of how predators traverse their habitats and how long they remain in an area, movements do not inherently inform on behaviour. Rather, behaviour must either be inferred or directly observed (Fryxell et al., 2008; Brown et a., 2013). Behaviour encompasses a wider range of activities that reflect the predator's role in the ecosystem and its

Box 2: Differentiating predator movements and behaviours (continued)

interactions with both abiotic and biotic factors, including prey. Behavioural studies often delve into the decision-making processes, strategies, and tactics predators use to locate, capture, and consume prey. Analysing predator behaviour provides insights into ecological roles, energy acquisition, and the ecological impact of predators on their ecosystems.

Understanding animal movement requires consideration of their internal state (Nathan et al., 2008; Gurarie et al., 2016). An animal's movements are highly intricate and shaped by how they respond to the environment around them. Animal movement data (surface relocations) alone are frequently used to make behavioural inferences (Blackwell, 2003: Morales et al., 2004; Jonsen et al., 2005; Gurarie et al., 2009; McClintock et al., 2012; Fleming et al., 2015). However, these can sometimes lead to misleading results (McClintock et al., 2013; Bentley et al., 2016; McClintock et al., 2017). Integrating predator movement data with detailed environmental and biologging data (e.g., bathymetry, prey distribution, accelerometer, heart rate and depth data) can aide in further understanding predator behaviours and their divers (McClintock et al., 2017), allowing researchers to construct a more comprehensive picture of how predators function within their ecosystems.

Differentiating between generalist and specialist predator behaviour

Differentiating prey preference versus food availability remains a fundamental challenge for understanding the feeding behaviours of wild animals. For generalist feeders, it is often unclear whether foraging choices reflect prey preferences, or simply prey availability at a specific time and place (Krahn et al., 2008; de Bryun et al., 2013). While optimal foraging theory predicts individual predator behaviours, the impact of individual predation behaviour on the wider predator population and surrounding ecosystem dynamics remains relatively unexplored (Frølich et al., 2022). Generalist predator populations are typically comprised of sub-populations often displaying a spectrum of foraging specialties and prey preferences (Bolnick et al., 2003; Durban and Pitman, 2012; Ford and Ellis, 2014). This often leads to populations composed of individual specialists (Bolnick et al., 2003). In theory, evolutionary selection will favour diet and foraging specializations, since specialists typically employ more efficient foraging strategies than their generalist counterparts (MacArthur and Pianka, 1966; Stephens and Krebs, 1986; Futuyma and Moreno, 1988; Ford and Ellis, 2014). Specialisms may reflect the local prey availability or individual preferences and may vary seasonally (Jourdain et al., 2020b). If multiple types of prey are available, optimal foraging may also be influenced by the energy content of available prey (and therefore prey choice). For example, a low density but high-quality food source may be the optimal choice, as compared to a high density but low-quality food source (Pyke and Stephens, 2019). Since the movements of predators are influenced by prey choice, as well as by prey abundance and distribution, optimal foraging theory can therefore be used to explain and predict predator movements (Thums et al., 2011; Womble et al., 2014, Goldbogen et al., 2015, Hays et al., 2016; Bestley et al., 2015, Joy et al., 2015).

Predators utilising a diverse range of prey choices can be explained through optical foraging theory (MacArthur and Pianka, 1966), which extends to a multitude of ecological systems (Sih and Christensen, 2001) and provides a valuable framework for understanding the fundamental mechanisms driving predator decision-making. In accordance with optimal foraging theory, predators choose their prey based on the availability of food and the energy yield from different dietary options. This theory operates on the assumption of stable prey populations and aids in predicting instances when predators adhere to their preferred prey. Furthermore, the theory acknowledges that if an alternative food source is available that does not compromise the predator's energy intake, astute predators will also exploit this option (Stephens and Krebs, 1986).

Challenges in observing prey distributions

Describing the influence of patchy prey distributions on top predators such as killer whales and humpback whales poses a fundamental challenge in marine ecology (Levin, 1992; Benoit-Bird et al., 2013; Chave, 2013). The heterogeneous, multi-dimensional nature of predator-prey interactions coupled with the difficulty in obtaining direct observations in the vast ocean poses challenges to observing prey distributions and their influence on predator movements (Fauchald et al., 2000; Nicol et al., 2013; Young et al., 2015). Many previous studies investigating marine predator movements instead correlate changes in predator behaviours to indirect proxies of prey distribution. Consequently, investigating predator–prey relationships using directly-observed prey density distributions is rare in marine studies (Pendleton et al., 2020). This can be achieved through pairing biotelemetry with prey data.

Box 3: Differentiating biotelemetry and biologging

Electronic tracking of wild animals has enabled researchers to remotely observe and understand their movements, behaviours, and surrounding environments that are otherwise difficult to observe (Hussey et al., 2015; Kays et al., 2015; Hays et al., 2016; Lennox et al., 2017). Generally, there are two main categories of electronic tags used for animal tracking: *transmitting* tags and *logging* tags (Cooke et al., 2021).

Transmitting tags, or *biotelemetry,* collect and then transmit data to external receiving stations (Harcourt et al., 2019), and therefore do not need to be recovered. Biotelemetry tags transmit messages that can be used to estimate locations across large spatial and temporal scales. There are many types of telemetry tags (e.g., acoustic, VHF, radio, satellite, Fastloc-GPS), some of which can also transmit behavioural information, such as dive depth and duration. Satellite telemetry connection requires connection through air and depends on satellites being within the line of sight of the tags, effectively limiting the range of communication as a function of satellite altitude and orbit. Satellite telemetry is a suitable tool for studying cetaceans since they regularly must come to the surface to breath. Logging tags, or *biologging*, on the other hand, are archival, collect data onboard, often at higher resolution (e.g., high-resolution accelerometers recoding at >300 Hz) then transmitters, although these tags must be later recovered to receive the data (Rutz and Hays, 2009).

Cetaceans are a particularly challenging group to study, given their high level of mobility (some species migrating over entire oceans) and the limited time they spend at the surface. Satellite transmitting biotelemetry devices are a viable solution to both of these challenges (Fedak et al., 2002; Harcourt et al., 2019). Despite limited bandwidth resulting in relatively low-resolution movement data, satellite telemetry is an excellent method for revealing the longer-term and more offshore movements and behaviours of large marine megafauna (Hart and Hyrenbach, 2009), and is the tracking method used throughout this thesis. These movements would be difficult, if not impossible to observe using traditional observation-based methods.

Researchers must consider the biological questions they are interested in, as well as the capabilities and limitations of each respective tag type of tag in order to choose the tool best suited for their research.

Electronic animal tracking

Analyzing animal movement patterns across space and time can provide insights into their foraging strategies (Charnov, 1976; Weimerskirch et al., 2005; Doniol-Valcroze et al., 2011; Reluga and Shaw, 2015). Traditionally, marine predator movements and behaviours have been broadly studied through the analysis of stomach contents, fecal or tissue samples and opportunistic visual observations (Carroll et al., 2019; Lübcker et al., 2021; Remili et al., 2021; Takahashi et al., 2022). Studying specific movement patterns of marine animals can be challenging, seeing as they spend most of their time below the surface of the water and out of sight of researchers. Biotelemetry and biologging techniques can be used to remotely study the multidimensional overlap between predators and prey, revealing their difficult to observe behaviours.

Pairing biotelemetry with observed prey data is rare (Pendleton et al., 2020), but can further these approaches by observing actual behaviours rather than the outcomes of successful predation. This data pairing is essential for understanding how predators adapt their movements and foraging in response to fluctuations in prey distribution and density (Benoit-Bird et al., 2013). Fine-scale biologging studies have been conducted examining marine predator foraging behaviours over hourly to daily timescales in relation to actual prey characteristics using animal-borne biologging video/cameras and accelerometers tags (Davis et al., 1999; Watanabe and Takahashi, 2013; Carroll et al., 2014; Viviant et al., 2014; Volpov et al., 2015; Watanabe et al., 2019; Del Caño et al., 2021) or biologging accelerometer-only tags and separate simultaneously-collected acoustic prey distribution information (Burrows et al., 2016; Reidy et al., 2023). Despite their coarser resolution, longer-term satellite telemetry tracking studies have rarely been paired with observed prey distributions to investigate how these behaviours evolve over weekly to monthly timescales.

The acquisition of vast volumes of animal movement data, through satellite tracking, has now become feasible on an unprecedented scale and level of intricacy. Moreover, this data can be correlated with similarly advancing remotely sensed or modelled environmental information (Kays et al., 2015). Furthermore, biologging techniques (including accelerometers, audio and video recording devices) offer direct insights into certain physiological aspects (such as heart rate; Czapanskiy et al., 2022), as well as social elements (such as foraging and interactions with fellow conspecifics (Matika et al., 2022; Clayton et al., 2023)). These observations can contextualize animal movements (Wilmers et al., 2015). The integration of movement patterns with their corresponding contextual factors has facilitated a deeper detailed understanding of foraging behaviour.

The principle aim of this thesis is to use satellite tracking data of killer whales and humpback whales, combined with available prey resource data, to investigate how prey directly influences the movement of marine predators. To achieve this, the objectives of the thesis are as follows:

- To explore whether Norwegian killer whales follow the migration of spring spawning herring to their southern spawning grounds (**Paper I**).
- To examine how the movements of killer whales observed to feed on pinnipeds differ from those who feed on herring (**Paper II**).
- To determine the influence of Barents Sea caplin's multidimensional distribution on humpback whale horizontal and vertical movements (**Paper III**).

The schematic below illustrates how various types of whale data were linked with specific prey covariates in order to answer these three main objectives (Figure 1).

Before presenting the main findings of this thesis (Chapter 4), the thesis will include a description of the study areas (Chapter 2.1) and study species (Chapter 2.2). Next, the methods are described (Chapter 3), including animal behaviour analysis (Chapter 3.1) and the sampling and modelling of prey fields (Chapter 3.3). The main findings of the three research studies and their implications are then discussed (Chapter 5). Suggestions of future research are presented in Chapter 6, followed by conclusions in Chapter 7.

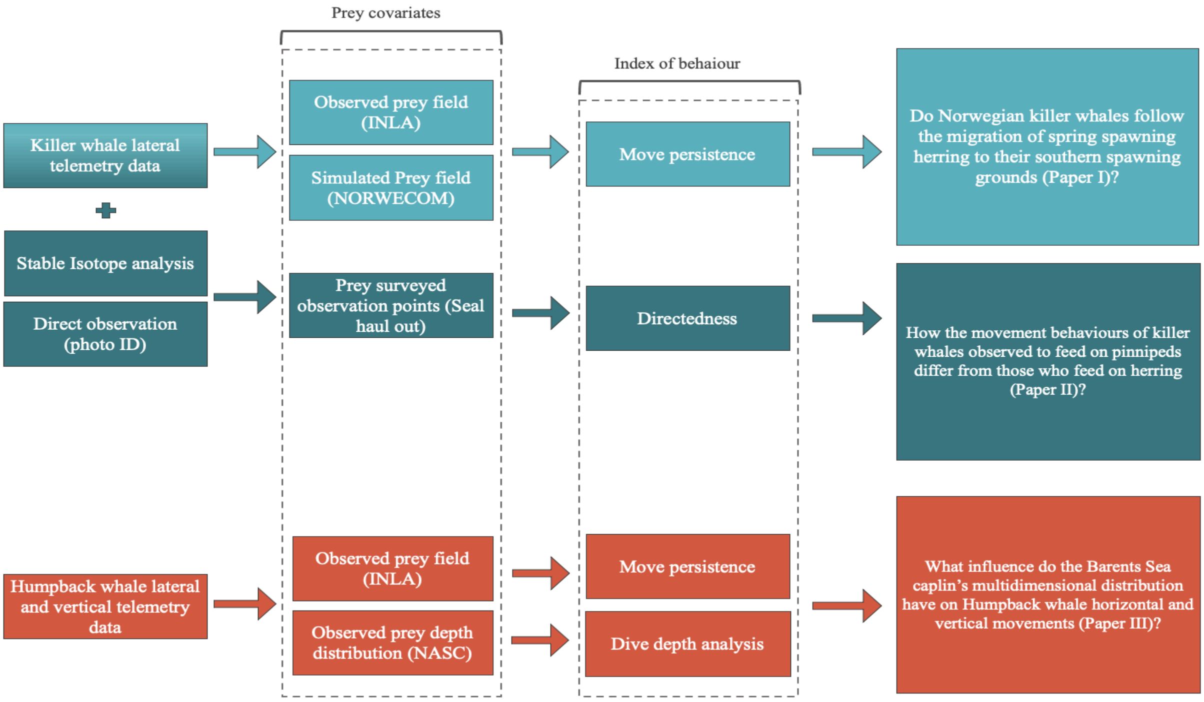

Figure 1. Schematic diagram illustrating how various types of whale data were linked with specific prey covariates in order to answer the three main objectives of this thesis.

2 Study area & species

2.1 Study areas

The northeast Atlantic (Figure 2) is regarded as a highly productive area, in particular the Norwegian Sea and Barents Seas (Sakshaug and Slagstad, 1991; Hamre, 1994; Sakshaug, 1997; Carmack and Wassmann, 2006; Raj et al., 2019). Some of the world's largest pelagic fish stocks are located in the Barents Sea and the Norwegian Sea, such as Norwegian spring spawning (NSS) herring (*Clupea harengus*), capelin (*Mallotus villosus*) and cod (*Gadus morhua*).These highly productive areas also support a large biomass of marine predators such as cetaceans, pinnipeds, seabirds, and large fishes (Hamre, 1994; Mauritzen et al., 2022). Baleen whales, such as humpback whales, have been increasingly observed in the summer and autumn in the northern Barents Sea, exploiting the abundant and growing prey stocks (Gjøsæter et al., 2009; van der Meeren and Prozorkevich, 2019; Leonard and Øien, 2020; Hamilton et al., 2021; Skern-Mauritzen et al., 2022). Predator foraging hotspots in the Barents Sea co-occur with the main summer feeding grounds for adult capelin feeding on krill (van der Meeren and Prozorkevich, 2019; Hamilton et al., 2021). Here, humpback whales have been assumed to feed mainly on herring, capelin, and krill (Løviknes et al., 2021). During the summer and autumn, northeast Atlantic humpback whales forage throughout the Norwegian and Barents Seas and around Iceland, mainly on capelin, and krill (Christensen et al., 1992; Leonard and Øien, 2020; Løviknes et al., 2021; Hamilton et al., 2021). At least some proportion of this humpback whale population also utilise abundant resources well into the winter season in the Norwegian Sea and along the Norwegian coast before commencing their annual breeding migrations southward (Kettemer et al., 2022).

The Norwegian Sea homes the overlapping feeding grounds of large pelagic fish stocks such as NSS herring, blue whiting and Northeast Atlantic mackerel (Nøttestad et al., 1996; Larsen et al., 1996; Kaartvedt, 2000). NSS herring are of particular interest for this thesis, since they are an important prey species for both humpback whales and killer whales, particularly in the winter. NSS herring densely aggregate in overwintering areas in the Norwegian Sea and around coastal northern Norway each year. However, the precise location of these areas varies, and is attributed to periodic shifts in their dominate age class (Dragesund et al., 1997). After overwintering, NSS herring migrate to their relatively static coastal spawning grounds spanning from Troms county down to southern Norway in the spring (Dragesund et al., 1997). While their breeding grounds are consistent, their migration routes are highly variable due to frequent shifts in their overwintering areas (Dragesund et al., 1997; Huse et al., 2010; Toresen et al., 2019).

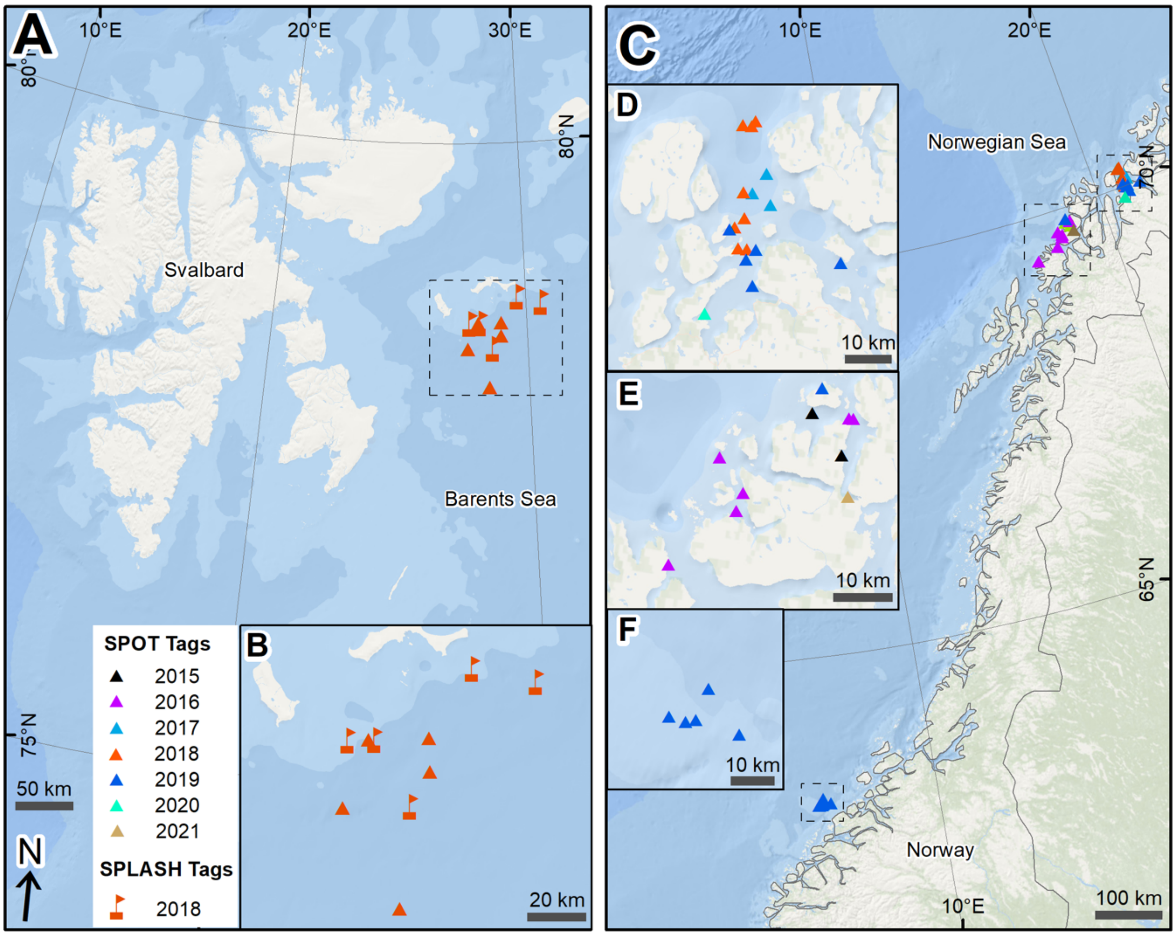

Figure 2. Maps of the study areas in this thesis: the Barents Sea (Panel A) and the Norwegian Sea (Panel C). Points, colored by tagging year, are shown in all panels indicating tagging sites of whales included in this thesis. Triangle points indicate SPOT tags and flagged points are SPLASH tags. All points in the Barents Sea (Panel A and Inset B) represent humpback whales. Points in Panel C represent tagging locations of killer whales, where insets D and E highlight whales that were tagged in Northern Norway near the NSS herring overwintering grounds, and inset F shows area off the coast of western Norway where killer whales were tagged around the NSS herring spawning.

2.2 Study species

2.2.1 Killer whales

Killer whales are widely distributed odontocetes that are considered generalist top predators at the species level. In some areas, local populations of killer whales remain generalist feeders, while other subpopulations can have very specialized diets (Durban and Pitman, 2012; Ford and Ellis, 2014; Foster, 2019), that may vary seasonally (Jourdain et al., 2020a). Specializations may only be beneficial in environments with a stable and predictable availability of the target prey, while a more generalist strategy may be favoured under variable conditions. Killer whales in Norwegian waters are thought to primarily feed on Norwegian spring-spawning (NSS) herring (Similä et al., 1996; Simila, 1997; Simon et al., 2007; Mul et al., 2020; Vogel et al., 2021). However, these whales have also been observed feeding on a wide variety of other prey types, such as harbour seals (*Phoca vitulina)*, salmon (*Salmo salar)*, mackerel (*Punctualis piscis)*, and lumpfish (*Cyclopterus lumpus)*, along the Norwegian coast (Similä et al., 1996, Foote et al., 2009; Vester and Hammerschmidt, 2013; Nøttestad et al., 2014; Vongraven and Bisther, 2014; Cosentino, 2015; Jourdain et al., 2017, 2020a, 2020b; Bories et al., 2021).

Unlike many other cetacean species that undertake seasonal migrations in response to critical life history stages, killer whales are thought to move primarily in search of feeding opportunities (Corkeron and Connor, 1999). These highly flexible marine predators utilize a diverse range of foraging strategies fine-tuned to the characteristics and specificities of their prey choice. For example, cooperative foraging tactics such as 'carousel feeding' can be used by some groups of killer whales targeting patchily-distributed pelagic fish. In this method, whales coordinate the herding shoals of fish together into more densely packed bait balls. They then push the bait balls to the surface and take turns stunning the fish with their tails (Similä and Ugarte, 1993). Killer whales exhibit similarly sophisticated yet strikingly different foraging techniques when targeting larger prey, such as seals and large baleen whales. Here, cooperative hunting typically takes place with smaller groups and much less exchange of vocalizations to avoid detection from their more sophisticated prey. An example of this kind of orchestrated pursuit is the cooperative hunting displayed by Antarctic killer whales specialized in hunting marine mammals, where groups of killer whales target seals hauled out on small ice flows. These whales create waves by rapidly swimming towards the targeted ice floe, in order to eventually wash the seal off the ice (Pitman and Durban, 2012).

2.2.2 Humpback whales

Humpback whales are cosmopolitan mysticetes that are considered generalist foragers. Humpback whales typically migrate annually between their high latitude foraging grounds and low latitude breeding grounds (Katona and Beard, 1990; Larsen et al., 1996; Smith et al., 1999;

Ryan et al., 2016). When foraging, rorqual whales like humpback whales require dense concentrations of prey to bulk filter-feed effectively, enabling the energy storage needed to support their long breeding migrations (Piatt and Methven, 1992; Hazen et al., 2009, 2015; van der Hoop et al., 2019). Humpback whales feed on a variety of small schooling fish (e.g., capelin, herring, mackerel, sandlance) and krill (Baker et al., 1985; Clapham and Palsbøll, 1997; Clapham, 2018; Meynecke et al., 2021). Humpback whales are generalist foragers that are patchy-prey obligates. These bulk filter-feeders need dense concentrations of prey to feed efficiently (Piatt and Methven, 1992; Hazen et al., 2009, 2015; van der Hoop et al., 2019) and possess specialized strategies adapted to do so. Being a generalist forager allows humpback whales to opportunistically switch their targeted prey as conditions vary to optimize efficiency (Fleming et al., 2016). Whilst in the Barents Sea, humpback whales have been assumed to feed mainly on herring, capelin and krill (Løviknes et al., 2021). Despite being patchy-prey obligates, they are nevertheless very much patch generalists who employ a wide range of specialized feeding techniques to efficiently capture their prey. During the summer and autumn, northeast Atlantic humpback whales forage throughout the Norwegian and Barents Seas and around Iceland (Christensen et al., 1992; Leonard and Øien, 2020; Hamilton et al., 2021), and at least some proportion of the population also make use of abundant resources well into the winter season (Kettemer et al., 2023).

2.2.3 Prey

2.2.3.1 Norwegian Spring Spawning Herring

Norwegian spring spawning (NSS) herring are a key prey fish species in the highly productive northeast Atlantic region, and accordingly, play a fundamental role in the predator-prey relationships within the Norwegian and Barents Seas ecosystems (Hamre, 1994). NSS herring exhibit extensive seasonal migrations between their wintering, spawning and feeding grounds (Huse et al., 2002). Dense concentrations of overwintering herring form in late Autumn, typically remaining in their wintering areas in and around the northern Norwegian fjords until mid-January when their spawning migration begins southward towards the continental shelf edge (Røttingen et al., 1994; Huse et al., 2010; Figure 3a). Herring migration pathways can differ both spatially and temporally between years (Huse et al., 2010). Similarly, the location of spawning and wintering grounds can also differ with each year. This spatiotemporal variability in herring overwintering and spawning distributions is thought to be influenced by the recruitment of dominant age classes into the adult stock (Huse et al., 2010). In addition to lateral movements between wintering and spawning grounds, herring also exhibit diel vertical migration in the water column, where they are typically observed concentrating at depth between dawn and dusk, then dispersing upward in the water column at night (Huse and Korneliussen, 2000). This diurnal pattern is expected to be correlated with daily changes in sun angle and is attributed to avoiding predation and to conserving energy (Huse and Korneliussen, 2000).

2.2.3.2 Harbour seals

Harbour seals (*Phoca vitulina*) are generalist predators with a broad coastal distribution in the Northern Hemisphere (Bigg, 1981; Lowry et al., 2001). They are opportunistic, central-place foragers that will feed on abundant and near-by prey, including herring (Olsen and Bjørge, 1995; Thomas et al., 2011). Harbour seals frequently haul out on land (Stevick et al., 2002) to rest, avoid predators, breed and molt (Sullivan, 1980; Da Silva and Terhune, 1988; Thompson, 1989; Thompson et al., 1994; Jemison and Kelly 2001), and typically live in groups of tens to some hundreds. Harbour seals are scattered along the entire Norwegian coast, far into the fjords, with particularly high densities around the Lofoten Islands and northern Norway (Figure 3b). The northernmost harbour seal population is located along the west coast of Svalbard (Figure 3b).

2.2.3.3 Capelin

Capelin are a schooling pelagic fish, known to conduct diel vertical migration (Gjøsæter, 1998; Hop and Gjøsæter, 2013). Capelin are an important food source for many meso- and top-predators throughout the north east Atlantic (Hamre, 1994). Specifically, capelin are an important prey species for northeast Atlantic-humpback whales, that target capelin while foraging in the Barents Sea in the summer and autumn (Løviknes et al., 2021). Capelin undertake diel vertical migrations, with a tendency to aggregate at deeper depths during the day and disperse towards the surface at night (Skaret et al., 2020; Fall et al., 2021). This pattern is believed to be linked to variations in light intensity. The tendency of capelin to undertake vertical migrations is attributed to following their primary prey, krill, which utilize diel vertical migration to evade visual predators. Similarly, capelin themselves likely also migrate to avoid their visual predators (Gjøsæter, 1998; Hop and Gjøsæter, 2013). During summer months, large shoals of adult capelin migrate to central and northern areas of the Barents Sea to feed (Dalpadado et al., 2012; Dalpadado and Mowbray, 2013; Figure 3c).

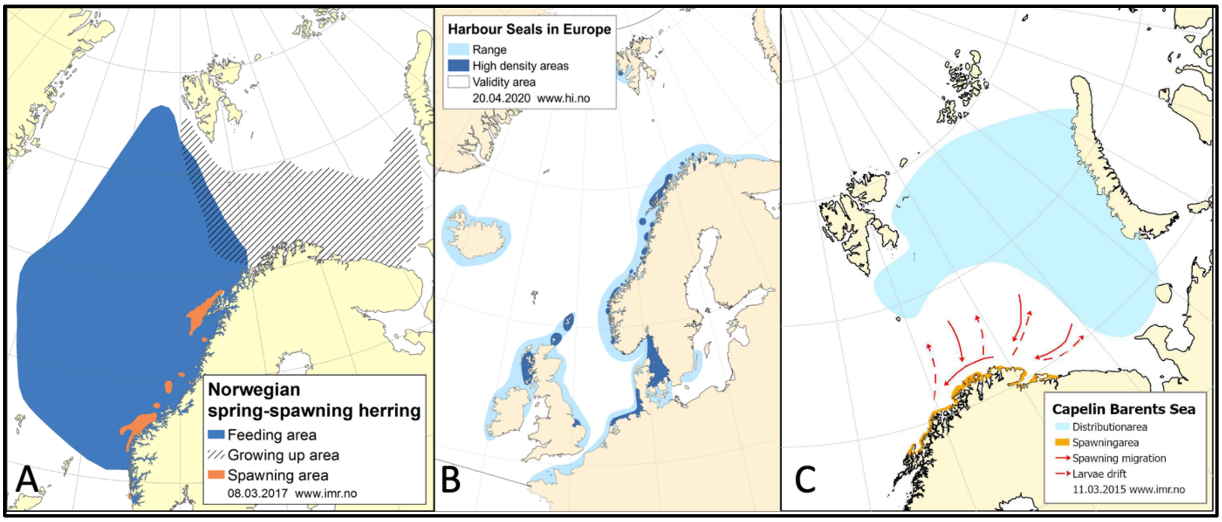

Figure 3. Maps showing distributions of NSS herring (Panel A), harbour seals (Panel B) and capelin (Panel C). Maps modified from www.imr.no.

3 Methods

3.1 Sampling of animal movement data

Animal-borne telemetry, a tracking method involving physically attaching a transmitting tag whose signal can be detected by satellites, has greatly aided our ability to study the movements of animals in the wild (Hays et al., 2016). This technique is able to uncover previously unknown habitats and associated movement patterns. One of the limitations of satellite telemetry is that information can only be relayed to satellites when the satellite is above the horizon, and when the path between the transmitter and satellite is unobstructed. Cetaceans are a particularly challenging group to study, given their high level of offshore mobility (some species migrating over entire oceans) and the limited time they spend at the surface (when they may have an unobstructed path to a satellite). Satellite telemetry is a viable solution for both of these obstacles because satellite can receive transmissions covering a large area and transmitters can rapidly relay information during the short intervals of time that whales spend on the surface (Fedak et al., 2002; Hart and Hyrenbach, 2009).

Between 2015-2021 33 killer whales and 10 humpback whales were equipped with subdermal SPOT or SPLASH wildlife computers satellite tags (Figure 2, Figure 4, and Figure 5). Subdermally-anchored satellite tags were deployed with an air-powered rifle on humpback whales (Figure 4 Panel A: tag placed below their dorsal fins), and on killer whales (Figure 4 Panel B: tags placed in the center of their dorsal fins) following best practices (Andrews et al., 2019).

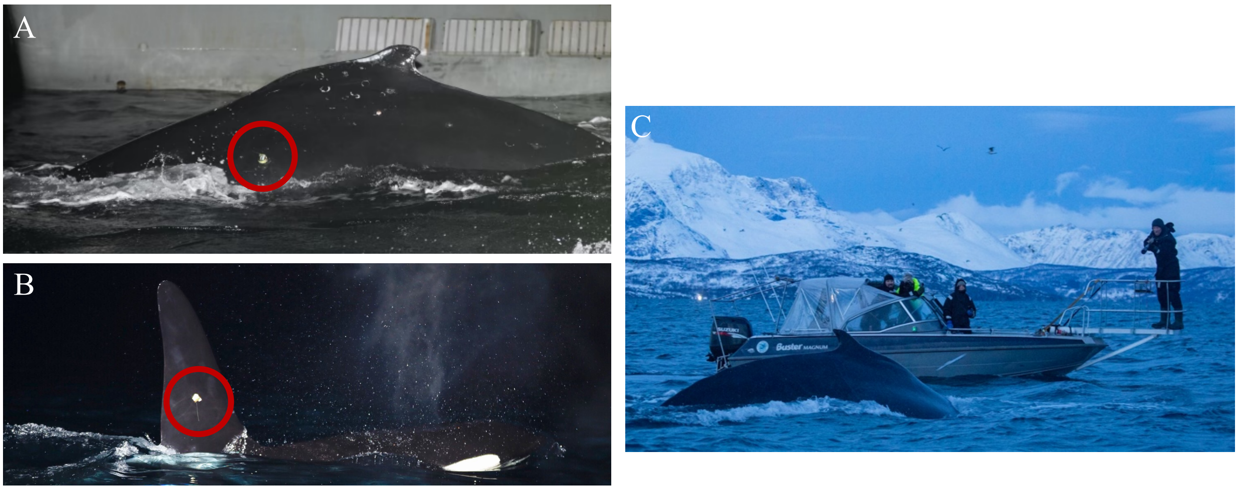

Figure 4. Subdermal satellite telemetry tag deployed on a humpback whale (Panel A), killer whale (Panel B). Panel C shows tagging procedures from boat.

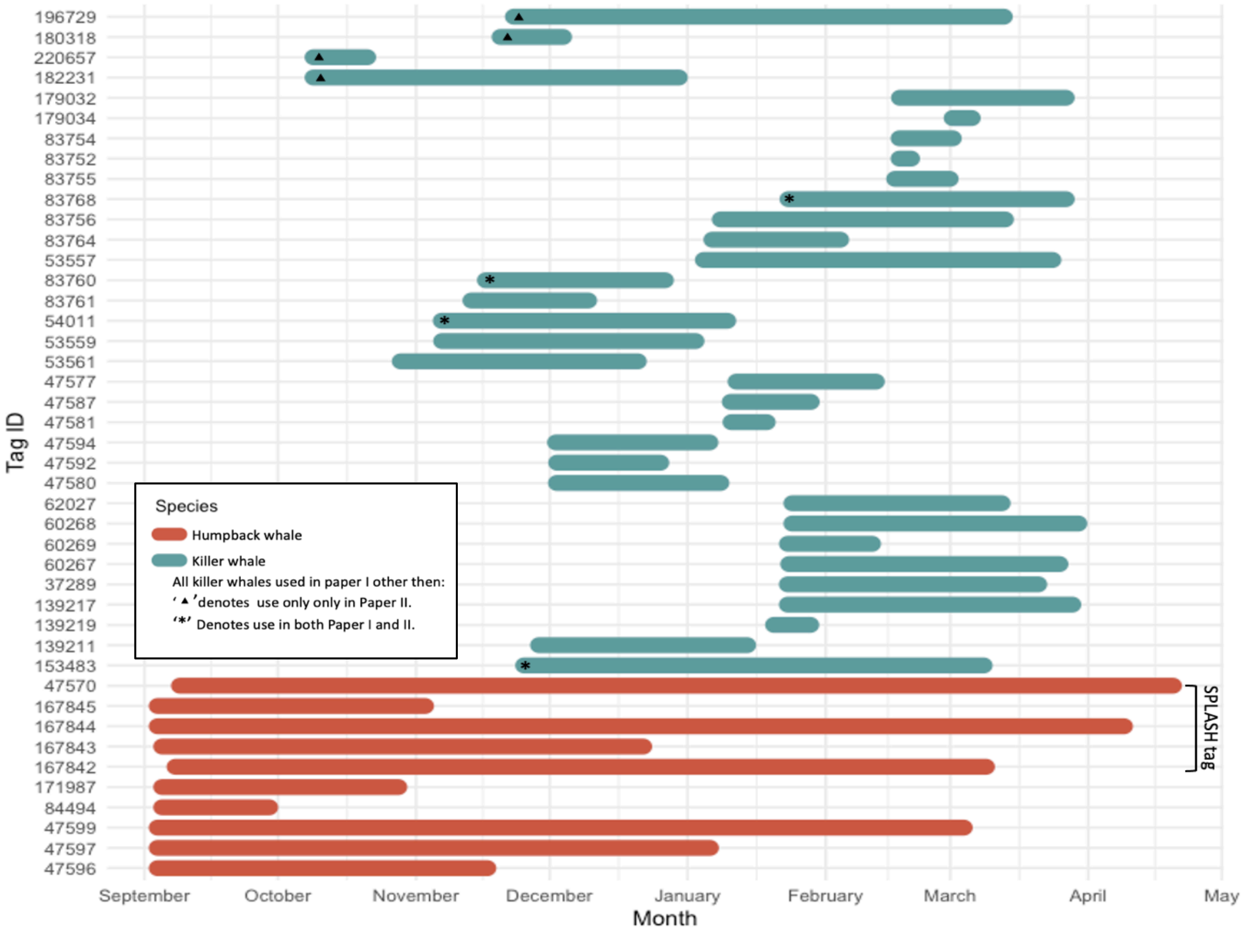

Figure 5. Tagging periods and retention times of Argos satellite tags from all data analysed in this thesis. Humpback whales and killer whales are represented in red and teal respectively. Note that tagging occurred between 2015-2021, but are plotted in this graph across the same Julian year to emphasize seasonality.

3.2 Behavioural analyses

3.2.1 Lateral movements

Lateral movements associated with foraging encompass a spectrum of techniques, from stealthy stalking to high-speed pursuits, given that predators fine-tune their movements to account for the predation avoidant strategies of their prey (Jonsen et al., 2019). These lateral pursuits often involve intricate adjustments to optimize attack angles and minimize the chances of escape.

While movement can be observed simply through the visualisation of animal tracks, behavioural inferences require a method to identify and quantify movement patterns correlated with specific behaviours. This thesis characterizes whale movements using move persistence (γ_t ; Paper I and III), which is a continuous scale measure of the autocorrelation between successive displacements, accounting for variability in both speed and heading (Jonsen et al., 2019). Values range continuously between 0 and 1, where 0 designates highly variable movement typically in a restricted area associated with predation, and 1 denotes consistent and directed movement associated with transiting between prey patches (Jonsen et al., 2019). Unlike other discrete and somewhat arbitrary behavioural states (Breed et al., 2012; Auger-Méthé et al., 2017; Eisaguirre et al., 2019; Jonsen et al., 2019), the use of a continuous metric can reveal differences in movement between individuals.

3.2.2 Vertical movements

In the vertical plane, marine predators optimize their dive depths to overlap with and exploit prey across their different water depths (Wright et al., 2017). Many pelagic zooplankton and fish synchronously move up and down in the water column throughout a daily cycle, a process know as diel vertical migration (Haze, 2003). Accordingly, predators will optimize their daily movements to match that of their targeted prey species, enabling predators to intercept and capitalize on their movements (Womble et al., 2014). Therefore, the depth distribution of predators throughout the day should reflect that of their prey. This thesis examined how humpback vertical movements relate to vertical prey density (Paper II).

3.3 Sampling and modelling of prey fields

In Norway, there exists a long history of extensive ecosystem surveys focusing on collecting biological and acoustic data pertaining to commercially-important species. This thesis created interpolated prey fields from herring, capelin and harbour seal data collected between 2015 and 2019 (Figure 6). The Institute of Marine Research and associated collaborators have conducted the Barents Sea Ecosystem Survey annually for the last 20 years, providing unique detailed insights on the distribution of ecologically-significant pelagic fish like capelin. Similarly, the Norwegian spring spawning herring surveys have led to the collection of biological and acoustic herring data over the last 35 years. Harbour seals are also regularly surveyed along the Norwegian coast, and annual sub-area counting surveys since 1996 result in total Norwegian population estimates every 5 years.

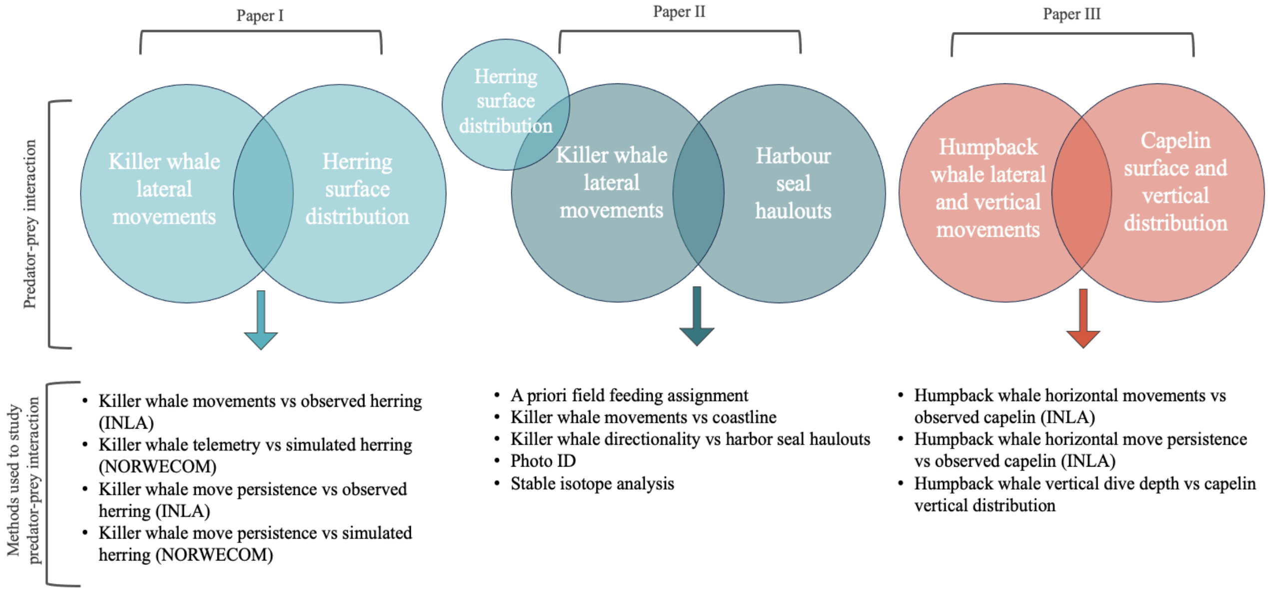

Figure 6. Schematic summary of the methods and scope of the three chapters in this thesis, where the intersections of the Venn diagrams represent the various predator prey relationships studied in each chapter using the methods outlined below.

3.3.1 Spatial field interpolation

Fleets of research vessels have been used to collect continuous acoustic data and biological data from trawl hauls by the Institute of Marine Research and collaborators for various specific species and/or ecosystem surveys. These surveys consist of acoustic echosounder data that is continuously collected along transects linking evenly-spaced grids of biological and abiotic sampling stations (Figure 7, panel A). Acoustic echosounder data is recorded using Simrad EK60 or EK80 equipment that has been calibrated according to established protocols (Demer et al., 2015). The echosounder data undergoes processing through the Large Scale Survey System software package (Korneliussen et al., 2006). Researchers on board the vessels are responsible for classifying and assigning acoustic backscattering to different biological categories, considering both acoustic signal characteristics and the biological data from the pelagic trawl catches. The resulting values reflecting acoustic density are recorded as the nautical area scattering coefficient (NASC; m^2/nmi^2) (Figure 7, panel B), with a horizontal resolution of 1 nautical mile and a vertical resolution of 10 meters (Johnsen et al., 2019). This estimate merges the acoustic data at a 1 nautical mile resolution (referred to as the Elementary Distance Sampling Unit; EDSU) with biological data from the nearest sampling station as Primary Sampling Unit (PSU) in this estimation process.

The vertically-integrated EDSU density estimates are then used to create an interpolated prey density surface, using the Integrated Nested Approximation model (INLA) and Template Model Builder (TMB) (Rue et al., 2009; Lindgren et al., 2011; Martins et al., 2013; Lindgren and Rue, 2015; Kristensen et al., 2016). Next, irregular triangulated meshes covering the entire survey region were created, where the mesh size is adapted to the sampling resolution such that areas with a denser number of data points are associated with smaller mesh sizes (Figure 7 panel C). A spatial interpolation model was developed in TMB, where unexplained variation in density is assumed to follow a Gaussian Random Field (GRF) process, and where spatial autocorrelation is governed by a Matérn function with parameters estimated by TMB. To model spatial point processes, TMB uses the stochastic partial differential equation (SPDE) approach originally implemented in INLA (Rue et al., 2009; Lindgren and Rue, 2015). To account for the barrier effect caused by the coastline, supporting barrier models were also employed, as described in Bakka et al. (2016, 2018, 2019). Together, these spatial point-process methods were used on the prey density point values along transects to interpolate relative prey density (Figure 7 panel D).

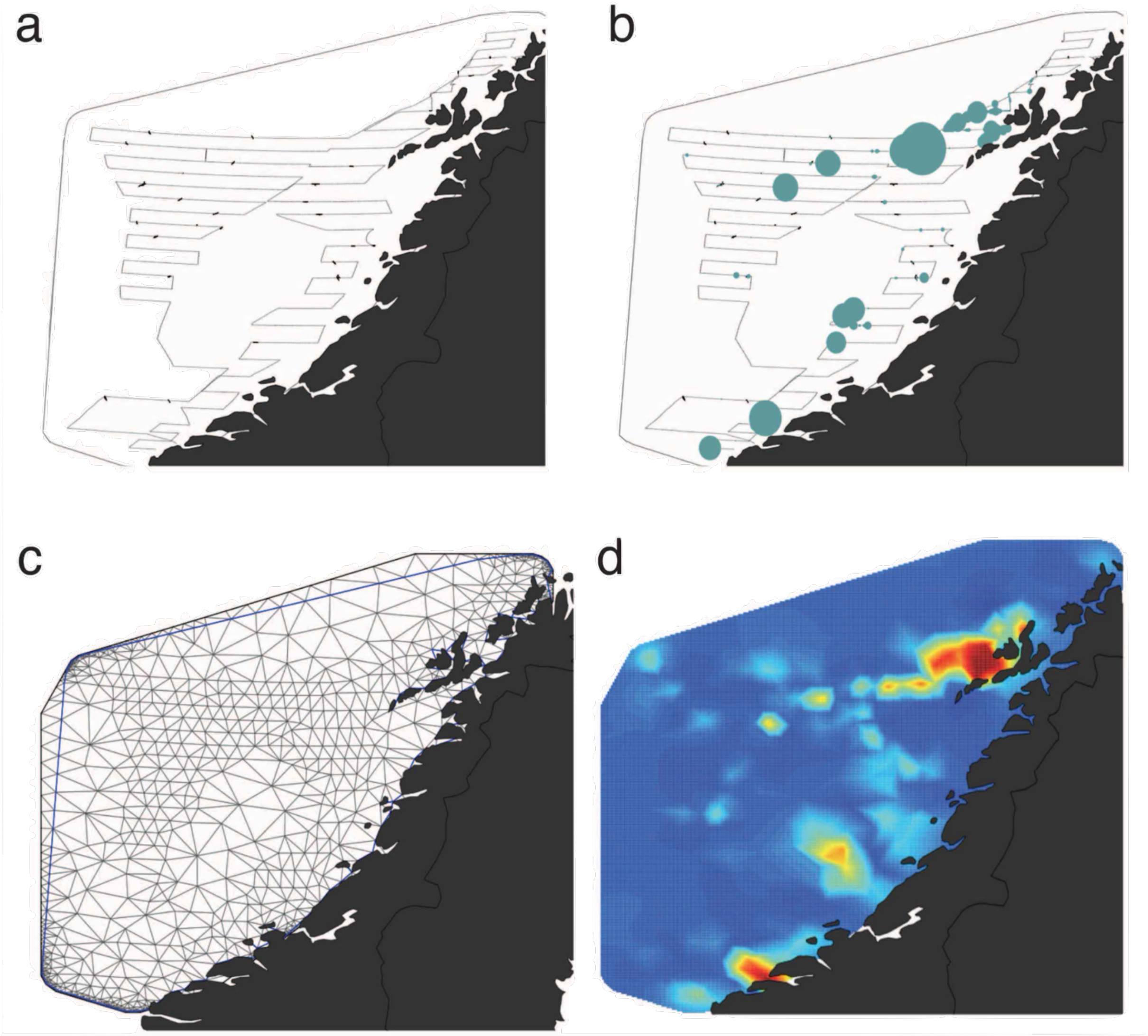

Figure 7. Example of steps to interpolate relative prey (herring) density along the Norwegian coast. Panel (a) depicts the paths of 2016 NSS herring survey vessels, which continuously collected NASC values as an indicator of herring distribution. Clusters of points along the path indicate biological trawl stations. Together with the NASC values, the biological data were used to characterize the herring spawning stock. In Panel (b) survey paths are shown together with teal circles proportional to the magnitude of NASC values. Panel (c) shows the adaptive triangular mesh for INLA extrapolations, which allows the INLA model to compensate for different survey track densities in the region. Panel (d) depicts the 2016 NSS relative herring biomass distribution generated by INLA. Red indicates areas of high relative biomass.

Box 3: Non-telemetric techniques of studying marine predator-prey interactions

For terrestrial predators, determining diet is achievable through directly observing feeding or foraging behaviours. However, when it comes to estimating the diets of marine mammals, researchers mainly utilise indirect methodologies, such as stomach and fecal content and chemical tissue analysis (Pierce and Boyle, 1991; Bowen and Siniff, 1999), since most of their lives (including feeding behaviours) take place below the surface and out of sight.

Stomach and fecal contents

Stomach and fecal content analysis are techniques for assessing the dietary habits of marine animals. However, obtaining stomach content data requires post-mortem analysis, which either involves animals being already deceased or necessitates sacrificing animals for examination. The examination of recovered hard parts (either within the digestive system or in fecal matter) such as bones and shells, provides insights into diet composition. Nevertheless, this method is constrained by the variable processes of prey digestion and retention within the predator's digestive system (Bowen and Iverson, 2013), which can influence the accuracy and completeness of the dietary information obtained from these remains. For example, this method also will not reflect soft organisms that the animal may have consumed. Genetic analysis of prey DNA recovered from stomachs and feces can indicate prey types, however currently it can only indicate presence-absence within the diet at this point and prey characteristics such as size are unclear (Deagle and Tollit, 2007).

Chemical analysis of tissue

The ratios of stable isotopes of carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) are often examined to learn about an individual's prior foraging habitats and trophic positions (Hobson, 1999; Newsome et al., 2007, 2010). The $\delta^{13}C$ of a predator tissue sample reflects the origin of food sources, indicating the sources of primary production in the food consumed by the marine mammals. Coastal ecosystems are typically characterized by higher $\delta^{13}C$ than offshore waters (Newsome et al., 2010; Søreide et al., 2006). $\delta^{15}N$ is commonly used as an indicator of the trophic level of a consumer (Hobson and Welch 1992; Hobson et al., 1994, 2002; Hobson, 1999; Kelly, 2000), owing to the stepwise enrichment from food source to consumer. Controlled diet experiments estimated the half-life rates in bottlenose dolphin (*Tursiops trucuntus*) skin to be 48 ± 19 days for nitrogen and 24 ± 8 days for carbon (Giménez et al., 2016).

Box 3: Non-telemetric ways of studying marine predator-prey interactions (continued)

While stable isotopes of carbon and nitrogen are valuable for addressing various ecological inquiries, they generally lack the capacity to offer quantitative assessments of diet species composition unless a predator feeds on just three prey species. In cases involving only two isotopes and more than three potential food sources, the system becomes underdetermined, leading to multiple possible solutions (Phillips and Gregg, 2001). In this thesis, stable isotope analysis of carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) were used to determine prior foraging behaviors of eight killer whales (paper II).

Fatty acid analysis is also a valuable method for studying marine mammal diets (Budge et al., 2006; Bowen and Iverson, 2013; Bories et al., 2021). By examining the unique fatty acid profiles in predator fat stores, derived from various prey, researchers can discern dietary habits over time. This involves identifying fatty acids in blubber or adipose tissue, indicating specific prey species consumed due to their distinct profiles. Quantitative Fatty Acid Signature Analysis (QFASA) quantifies prey contributions using prey fatty acid data, predator fat samples, and metabolic coefficients. While offering advantages like non-invasiveness and insights into long-term diets, challenges include accurate coefficient usage and metabolic variations. Used alongside stable isotope and stomach content analyses, fatty acid analysis enhances our understanding of marine mammal diets.

4 Main Findings

- **Killer whale movements change according to the herring density on the Norwegian shelf (Paper I).**
    - Killer whales follow Norwegian spring spawning (NSS) herring over long distances along the coast from their northern Norwegian inshore overwintering areas to more southernly offshore spawning grounds on the Norwegian continental shelf.
    - All whales changed from fast, directed, to slow, non-directed movement when herring density increased, although individual responses varied in magnitude.
    - Tagging data confirmed that after leaving the fjords, whales continue to feed on herring along the Norwegian shelf.
    - NSS herring constitute an important prey resource for at least some killer whales in the northeastern Atlantic, beyond the herring overwintering period, throughout the herring spawning migration.

- **Norwegian killer movements reflect their different prey types (Paper II).**
    - *Fish-eaters* appear to specialize on fish, whilst *seal-eaters* may switch opportunistically between fish and seals based on availability and preference.
    - Based on track routes, *seal-eaters* closely followed the coastline, whereas fish-eaters moved mostly offshore along the continental shelf.
    - Based on distance to the shore, *seal-eaters* remained on average closer to the shore than the *fish-eaters*.
    - *Seal-eaters* displayed more haul-out directed movements as compared to *fish-eaters*.
    - Tracking data can identify Norwegian killer whale movements thought to be associated with different prey types and therefore might reflect their varied and flexible foraging strategies.
    - Norwegian killer whales are opportunistic generalist foragers but exhibit some level of foraging flexibility, prey specialisation or preference.

- **Foraging movements of humpback whales reflect the lateral and vertical distribution of capelin in the Barents Sea (Paper III).**
    - Humpback whales consistently displayed reduced speed and directionality where capelin density was the highest.
    - Humpback whale movements showed no consistent relationships with sun elevation.
    - Humpback whale dive depth was positively correlated with diurnal and seasonal variations in the vertical distribution of capelin.
    - Whales target the densest shoals of capelin at a range of depths, throughout the day and night.
    - Overall, regions of high capelin density are important foraging grounds for humpback whales, highlighting the central role capelin plays in the Barents Sea marine ecosystem.

5 Discussion

Identifying behaviour in relation to prey fields

An important commonality highlighted across **papers I, II and III** is that predator movements associated with foraging behaviours are shaped by characteristics and distributions of their prey. While **paper I** focused on the influence of herring on killer whales and **paper III** examined the influence of capelin on humpback whales, both established that prey densities were negatively correlated with whale move persistence. Specifically, whales exhibited lower move persistence (reduced speeds and frequent turning) in areas where their presumed targeted prey was denser, and exhibited higher move persistence (transiting behaviour, high speed and more direct movements) values in areas with lower prey densities. This indicated, perhaps unsurprisingly, that both species of whale are more likely to exhibit restricted foraging behaviour in areas of high prey density, in agreement with previous observations recording similar area-restricted foraging by Weddell seals, Bottlenose and Common Dolphins (Mori et al., 2005; Bailey et al., 2019). Overall, this finding supports the conclusion that lateral marine predator behaviours are inherently interconnected with their foraging strategies (Bestley et al., 2015).

Paper II established that killer whales presumed to be foraging on seals did so closer to shore than herring feeding individuals, and consistently directed more of their movements towards known harbour seal haul-out areas. Presumably, this behaviour is optimized for encountering pinnipeds near their haul-outs. This finding goes beyond previous research that has demonstrated Norwegian killer whales predate on harbour seals as part of their diverse diets and foraging strategies (Jourdain et al., 2017, 2020b). Therefore, the key implication of these findings illustrate that that killer whales optimise movement and area-use strategies depending on their targeted prey species.

Paper III further examined predator-prey relationships by exploring the role of both lateral and vertical capelin density on humpback whale movements. This study showed that humpback whale dive depth is strongly correlated with capelin depth distribution throughout the day and night in the Barents Sea. This diurnal vertical pattern humpback whale diving behaviour reflects their adjustments in diving behaviour in response to capelin density distributions. This is supported by studies in Antarctic and North American waters showing that foraging humpback whales in other waters maximised their energetic gain by targeting the densest prey depth layers to optimise their energy efficiency (Goldbogen et al., 2008; Ware et al., 2011; Friedlaender et al., 2013, 2016; Burrows et al., 2016). Therefore, **Paper III** builds upon previous observations of diel vertical migration by demonstrating that this behaviour occurs consistently over at least monthly timescales, when most previous observations recorded only showed this over shorter (hourly to daily) temporal scales. In doing so, it delivers improvements in our understanding of how individual humpback whales optimize their daily depth use to match that of their targeted prey species. These findings highlight the importance of assessing the influence of prey density in the vertical dimension on other top predator movements, such as the relationship between herring density and killer whale movements.

Using light intensity inferred from sun angle as a proxy for predator depth use, both **papers I and III** found no clear relationship with move persistence at the population level. This finding was somewhat surprising because both herring and capelin are known to exhibit daily diel-vertical migrations, so whale dive depths, and therefore surface behaviour, might be expected to vary with light intensity (Huse and Korneliussen, 2000; Skaret et al., 2020; Fall et al., 2021). However, **paper III** revealed, using actual whale depth data, that humpback whales did in fact follow their prey throughout their diel-vertical migrations. The absence of any clear trend in horizontal movements in relation to sun angle, and by proxy daily changes in depth use, is unsurprising, considering recent pinniped studies have found that foraging behaviour derived solely from horizontal movement data cannot be used as proxies for vertical movements (Bestley et al., 2015; Carter et al., 2016). Therefore, the killer whales in **paper I** presumably similarly optimize their dive depths to follow the densest shoals of herring throughout the day and night, despite this not being reflected in their horizontal movements. These findings highlight the need for future studies of Norwegian killer whales foraging on herring using telemetry satellite tags that can record both lateral and vertical movements, like the SPASH tags used in **paper III**.

Overall, the key finding of **papers I, II and III** linking specific whale movement characteristics with higher prey densities has important implications for using top predator movements to identify previously undocumented prey concentrations or ‘hotspots’ of biodiversity and productivity in lesser surveyed areas (Biuw et al., 2017; Block et al., 2011; Hindell et al., 2011; Bestley et al., 2015). Additionally, this finding highlights the benefit of pairing predator movements with actual prey distribution fields to identify areas of high ecosystem productivity. Thus, the predators movements be used as indicators of prey distribution and movement.

Synthesising the movement responses of multiple species in high-productivity areas could be applied in future ecosystem models (Bestley et al., 2015).

Individual predator differences influenced by prey

While the overarching finding of paper I demonstrated that killer whale movements were more restricted in areas of higher herring density, indicating their movements broadly reflect their prey characteristics and distributions, tracks of individual whales also revealed more complex relationships. **Paper I** demonstrated that two killer whales, whose move persistence values reflected foraging on herring in herring spawning grounds, later left the herring spawning areas while herring was still abundant. Instead, these two individuals travelled northward into the Barents Sea towards Novaya Zemlya. While it remains unclear why these whales left the area of abundant herring, it is plausible that they may have switched to forage on other pelagic fish such as capelin or potentially other ice-obligate species such as seals. One implication of this finding is that by switching to other prey when herring is abundant, these individuals may have other prey preferences (Murdoch, 1969). The concept of prey switching involves changes in predator behaviour over time. This phenomenon is noticeable when a predator appears to favour one prey type over another, especially when the favoured prey is energetically less profitable over the more readily available prey (Murdoch, 1969). This necessitates knowledge of the prey community's composition and distribution within the predator's habitat (Murdoch, 1969; Oaten & Murdoch, 1975).

The prey switching behaviour in **paper I** was similarly observed in **paper II** through photo ID records which observed at least one of the killer whales foraging herring and hunting seal at the time of tagging. In **paper II,** the two field-identified *seal-eating* killer whales also took unique routes when compared to the *fish-eating* killer whales and in **paper I**. Importantly, this finding demonstrated that these whales took unique routes that were optimised for harbour seal foraging opportunities. This finding is consistent with recent research that recorded large dietary diversity of individual killer whales across the North Atlantic (Remili et al., 2023). Presumably, the unique northward paths taken by the two whales in **paper I** were also optimizing their movements for an alternative prey. However, further investigations are needed to determine prey type. Therefore, a key implication of these differences in individual whale movements recorded in these two papers is that there is individual complexity in foraging behaviour associated with generalist top predators that should be accounted for when modelling ecosystem dynamics (Shaw, 2020).

Individual variation often goes unexplored in studies that aggregate and average movement data (Franke et al., 2004). The differences in individual whale movements highlighted in **papers I and II** underscore the importance for mixed effect models allow and test for individual variation in responses to prey distributions and other environmental variables. **Paper III** showed that two of the tagged humpback whales did not exhibit restricted movements in areas of high capelin density, as indicated by their different slopes in the mixed effect models. This differs from the findings of **paper I**, which indicated that all killer whales responded the same way to changes in herring density. Specifically, the inclusion of individual intercept terms in the mixed effect model improved the fit, suggesting that there are individual differences in movement characteristics between these Norwegian killer whales. While age, sex and other demographic parameters often influence individual movements (Ketterson and Nolan, 1985; Quinn and Brodeur, 1991), other factors that are often more difficult to quantify, such as animal personality, must also be considered (Roche et al., 2016; Vanden et al., 2021). This is consistent with previous research which showed variation across different individual movements shown in mixed effect modelling can in part be attributed to individual personality (Magurran, 1993; Dall et al., 2004; Stamps, 2007). The inclusion of random slopes in **paper III** may reflect differences in the degree of generalist behaviour or prey preferences. These observations emphasise how not accounting for individual differences in movement limits our understanding of how individuals and groups interact with their environment and risks oversimplifying the intricate mechanisms underpinning species' responses to ecological cues and constraints (Shaw et al., 2020). Furthermore, quantifying individual movement responses to prey density is vital for understanding how individual predators, populations and their foraging strategies can adapt to environmental changes.

Papers I and II established prey-dependent movement differences in killer whale foraging strategies for herring and harbour seals. This flexibility in foraging strategies is advantageous when considering ecosystem fluctuations and anthropogenic-driven climate changes (Sweeney and Jarzyna, 2022). For example, it is hypothesized that Norwegian killer whales may have diversified their diets to incorporate seals in response to the herring fisheries collapse in the 1970s (Jourdain et al., 2017; Andvik et al., 2020). The ability to flexibly adapt foraging strategies in response to environmental changes gives generalist foragers an obvious advantage when compared to strict specialists (Fisher et al., 2003; Munday, 2004; Clavel et al., 2011;

Prokopenko et al., 2023). Therefore, a key implication from **papers I and II** is that movement data can identify prey-specific foraging strategies for Norwegian killer whales.

6 Conclusions and future perspectives

This thesis has explored how prey directly influences the movement of humpback and killer whales using satellite tracking data from 2015 to 2021 combined with available resource data. The work has contributed new information regarding how predators specialise their movements to optimise foraging on specific prey, with implications for foraging flexibility, predator-prey interactions, and marine ecosystem management.

First, herring densities estimated from acoustic-trawl survey observations and a fully-coupled ecosystem model were used to study how the density of herring patches influences killer whale movements along the Norwegian Coast, finding that killer whales display more restricted movements in areas of higher herring density on the Norwegian Shelf. This reduction in speed and directionality in response to herring biomass distribution patterns is consistent with area-restricted searching. These findings gave insight into how killer whales alter their behaviour in response to changes in herring. The analysis suggests killer whale distributions may be expected to change concurrently with herring distributions and densities in future.

Next, killer whale movements along the Norwegian coast were analysed to assess whether the movements of harbour seal-eating individuals could be differentiated from those eating fish. Seal-eaters foraged closer to shore and more of their movements were directed towards known harbour seal haul-out areas, whereas fish-eaters foraged routinely further offshore after leaving the herring overwintering areas, following the offshore herring spawning migration pathway along the continental shelf. These findings indicated that killer whales optimise their seasonal foraging strategies according to their preferred prey characteristics. This could be used for targeted killer whale tagging of presumed seal-eating killer whales in future studies.

Finally, humpback whale tracks derived from satellite tags were analysed in conjunction with concurrent capelin density estimates to study the influence of lateral and vertical capelin density on humpback whale movements. This is the first time that both lateral and vertical humpback whale movements have been related to capelin distribution in the Barents Sea. Humpback whales were found to exhibit characteristic area-restricted search behaviours where capelin density was the highest, and to target the densest shoals of prey following diurnal variations in the vertical distribution of capelin. This highlighted that capelin density directly influences humpback whale movements, emphasizing the importance of directly measuring prey density for a deeper understanding of marine predator-prey dynamics.

High-resolution biologging studies of killer whales and humpback whales along the Norwegian coast and in the Barents Sea are warranted to collect direct observations of feeding using accelerometers and video loggers. This would enable direct estimations of foraging effort and to quantify consumption rates (Nichols et al., 2022), which are essential information for managing harvested species (such as herring, capelin, and harbor seals) while considering ecosystem health. Feeding observations could be used to validate the foraging behaviour inferred from the movement data analysed in this thesis. Ideally, double-tagging whale individuals with satellite telemetry tags and biologging tags would allow for cross-validation of their lateral movements by comparing periods of low move persistence with concurrent video and accelerometry data to verify whether foraging events occurred. Extended tagging efforts of Norwegian killer whales throughout the spring, summer and autumn are also needed to help inform their foraging behaviour throughout that part of the year, given the lack of data between April-October. The vast majority of Norwegian killer whale tagging efforts occur in the late autumn and winter, when the whales can predictably be observed near shore and in fjords foraging on herring. Since tag retention is around 42 ± 28 d (mean ± SD, n = 33), ranging from 3 to 110 days, little is known about the movements and distribution of these whales between May and September. Additional year-round tracking information will enable future analysis to examine their movements with various prey species distributions at different time periods throughout the year.

In conclusion, the work presented in this thesis found that whales move in predictable and definable ways in relation to their prey types and distributions. Understanding the influence of prey distribution on predator movements can be used to inform future prey survey design and uncover aspects of their life history traits that otherwise would be hard to observe and describe, such as identifying new overwintering areas. Such areas of high prey density are indicative of high concentrations or 'hotspots' of biodiversity, as well as commercially-important fish stocks, which can also be important top predator foraging areas. Knowledge of these ecologically-important foraging areas should be used to focus future management and conservation efforts, where many species can benefit concurrently (Hooker et al., 2011; Montevecchi et al., 2012; Allen and Singh, 2016; Carter et al., 2016). The escalating anthropogenic pressures of fishing, shipping, and coastal development combined with rapid climate-driven changes in the Arctic marine ecosystem are poised to trigger major shifts in the behaviours of marine predators and their prey (Anderson et al., 2013; Sydeman et al., 2015; Niella et al. 2020, 2022). Therefore, we need current observations of marine predator-prey movements, distributions and interactions (Hays et al., 2016). The results presented in this thesis are, therefore, timely and can serve as a much-needed baseline that will aid prediction of predator behavioural changes in response to potential shifts in prey abundance and distributions.

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Papers

Paper I
Killer whale movements on the Norwegian shelf are associated with herring density.

Emma F. Vogel, Martin Biuw, Marie-Anne Blanchet, Ian D. Jonsen, Evert Mul, Espen Johnsen,
Solfrid Sætre Hjøllo, Morten Tange Olsen, Rune Dietz, and Audun Rikardsen

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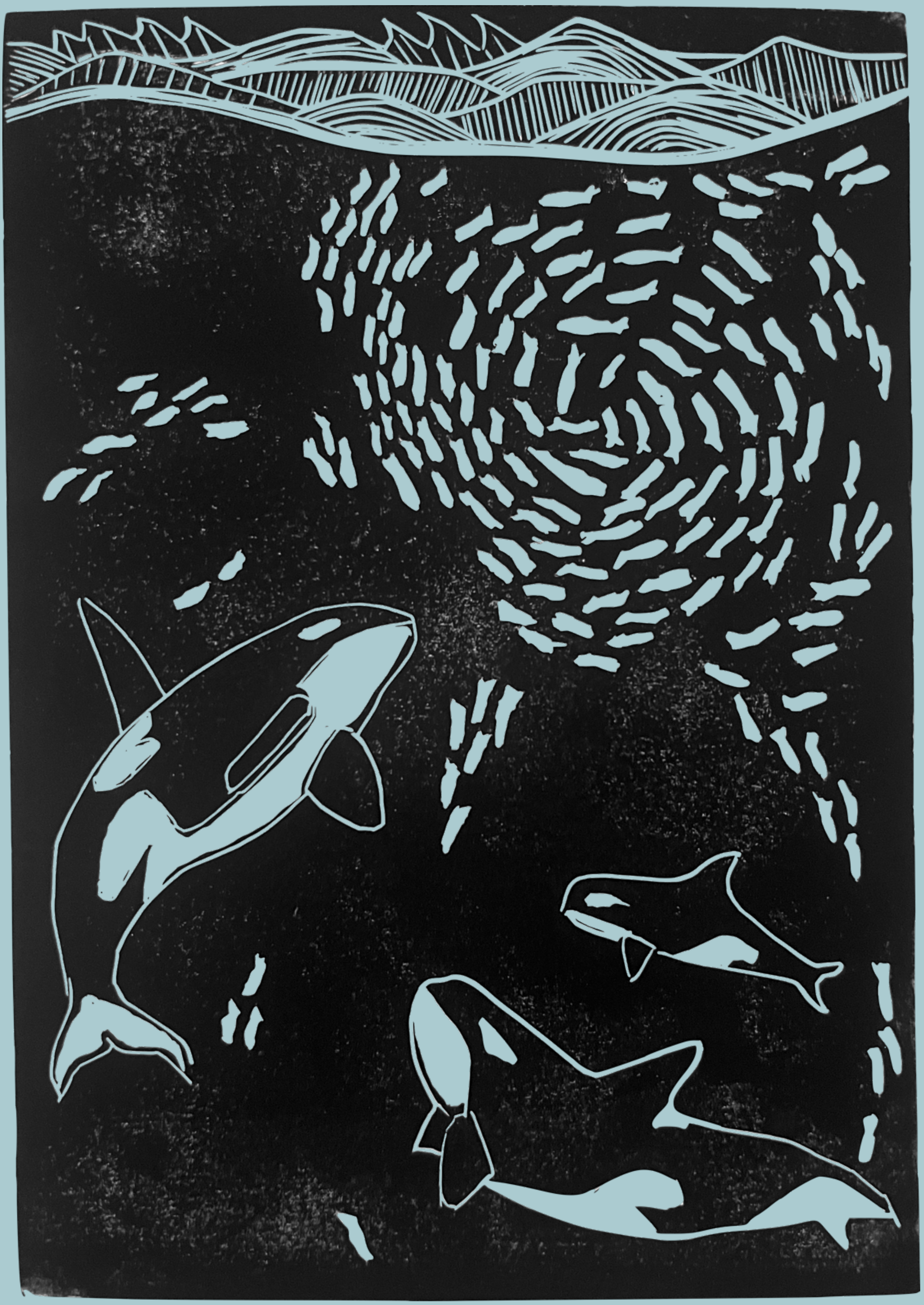

Paper II

Norwegian killer whale movements reflect their different prey types.

Emma F. Vogel, Audun Rikardsen, Marie-Anne Blanchet, Pierre Blevin, and Martin Biuw

In review.

Norwegian killer whale movements reflect their different prey types

Running head: Killer whale movements reflect prey selection.

Emma F. Vogel[1], Audun H. Rikardsen[1,2], Marie-Anne Blanchet[1,3], Pierre Blévin[4], Martin Biuw[5]

[1]UiT - The Arctic University of Norway, Faculty of Biosciences, Fisheries and Economics, 9037 Tromsø, Norway
[2] Norwegian Institute for Nature Research, Hjalmar Johansen gate 14, 9007 Tromsø, Norway
[3] Norwegian Polar Institute, Fram Centre, Tromsø 9296
[4]Akvaplan-niva AS, 9296 Tromsø, Norway
[5]Institute of Marine Research, FRAM—High North Research Centre for Climate and the Environment, 9007 Tromsø, Norway

Abstract

Norwegian killer whales are thought to be generalists that feed primarily on fish, but some individuals have been observed targeting pinnipeds. Field observations of foraging behaviours formed the basis of a priori classification as either *seal-eaters* or *fish-eaters*. Concurrent collection of photo identification and biopsies for stable isotope analysis were used to validate prey choice classification. We found through satellite tracking that whales classified as *seal-eaters* took different paths south after leaving the northern fjords seemingly optimized for pinniped predation. Specifically, we found that *seal-eaters* took paths that tightly followed the coastline remaining on average 6.9±10.7 km (mean ± sd, n= 315) from the coast, whereas *fish-eaters* moved offshore along the continental shelf traveling on average 45.1±30.2 km (n=1534) from the coast. We also found that *seal-eaters* displayed more harbour seal haul-out directed movements as compared to *fish-eaters* (p=0.001). As expected, our data suggests that the *fish-eaters* feed primarily on fish, whilst *seal-eaters* appear to opportunistically use diverse foraging strategies optimized for either fish or seals based on availability and preference. Our findings demonstrate that tracking data can inform on Norwegian killer whale movements associated with different prey types and selection.

KEYWORDS: Orcinus orca, prey diversification, stable isotopes, satellite tracking, seal, herring

1 INTRODUCTION

Killer whales, as a species, are generalist opportunistic foragers that feed on available prey in their local environment. Globally, over 150 species have been recorded as potential killer whale prey, including squid, fish, other marine mammals, and even seabirds (Foster, 2019). Generalist predator populations are typically comprised of sub-populations often displaying a spectrum of foraging specialties and prey preferences (Bolnick et al., 2003; Durban & Pitman, 2012; Ford & Ellis, 2014). This might reflect the local prey availability or individual preferences and may vary seasonally (Jourdain et al., 2020b). For example, killer whales of the Northeast Pacific are categorized in three distinct ecotypes: *residents*, specializing on fish and squid, *transients*, feeding solely on marine mammals, and *offshores* feeding on both bony and cartilaginous fishes (Bigg *et al.,* 1987; Ford et al., 2000). For a generalist feeder, it is often not clear if foraging choices reflect prey preferences, or simply prey availability at a specific time and place (Krahn et al., 2008; de Bryun et al., 2013). Differentiating between prey preference and food availability is a fundamental challenge for understanding the feeding behaviors of wild animals. Stomach contents and stable isotopes analysis have been used to examine killer whale dietary ecology (Ford et al. 1998; Wijnsma et al., 1999; Saulitis et al., 2000; Pitman & Ensor 2003; Jourdain et al., 2020b). Measured ratios of stable isotopes of carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) reflect both foraging habitats and trophic positions, respectively (Hobson, 1999; Newsome et al., 2007, 2010). The $\delta^{13}C$ of a predator reflects the origin of food sources, indicating the sources of primary production in the food consumed. Coastal ecosystems are typically characterized by higher $\delta^{13}C$ than offshore waters (Søreide et al., 2006; Newsome et al., 2010;). The $\delta^{15}N$ is commonly used as an indicator of the trophic level of a consumer (Hobson & Welch, 1992; Hobson et al., 1994; Hobson, 1999; Kelly, 2000; Hobson et al., 2002). Recent studies using $\delta^{13}C$ and $\delta^{15}N$ as dietary tracers highlighted differences in prey specialization (fish-eating vs seal-eating) in killer whale from Norway (Jourdain et al., 2020b; Bories et al., 2021). Specifically, Jourdain et al (2020b) found values of $\delta^{15}N$ were significantly higher (12.6 ± 0.3) amongst seal eaters than it was for *fish-eaters* (herring-eaters: 11.7 ± 0.2‰ and lumpfish-eaters:11.6 ± 0.2‰). A comparison of field observations, with the results of stomach content and stable isotopes analyses, can reveal either consistent prey choice or prey switching over time (Jourdain et al., 2020b). While these approaches can identify prey diversity, they often cannot differentiate between prey preference and either seasonal changes in prey availability and/or declining abundance of prey.

While much is known about how prey choice influences the movements of killer whales in the Antarctic and North Pacific, less is known about Norwegian killer whales (hereafter *NKWs*) behaviors (Pitman & Ensor, 2003; Andrews et al., 2008; Ford & Ellis, 2014; Reisinger et al., 2015; Ford, 1998). Field observations suggest that killer whales off the Norwegian coast feed almost exclusively on herring (*Clupea harengus*) (Similä et al., 1996; Similä, 1997; Simon et al., 2007; Mul et al., 2020; Vogel et al., 2021). However, recent investigations using stable isotopes ($\delta^{13}C$ and $\delta^{15}N$) and lipidomic fingerprints as dietary tracers indicate that NKWs feed on a wide spectrum of prey. Some individuals display specialization on fish while, others seem more flexible, feeding on both fish and marine mammals (Jourdain et al., 2020; Bories et al., 2021). Recent observations of NKWs preying upon harbour seals (*Phoca vitulina*) and other marine mammals, such as harbour porpoises (*Phocoena phocoena*) (Consentino, 2015; Jourdain et al., 2017, 2020b) are consistent with these dietary studies. Studies on NKWs have primarily been conducted in the winter, when they are readily found, associated with overwintering herring along the coast of Norway. Thus, the perception that NKWs primarily feed on herrings might be influenced by sampling bias (Jourdain et al., 2019; Lennox et al., 2022). Indeed, field studies conducted at other locations and periods reported NKWs feeding on a wide variety of prey items such as Atlantic salmon (*Salmo salar*), mackerel (*Scomber scombrus*), harbour porpoise (*Phocoena phocoena*), harbour seals (*Phoca vitulina*) and lumpfish (*Cyclopterus lumpus*) (Vester & Hammerschmidt, 2013; Nøttestad et al., 2014;

Vongraven & Bisther, 2014; Cosentino, 2015; Jourdain et al., 2017; Jourdain et al., 2019; Jourdain et al., 2020a). Similar observations of populations of killer whales broadening their diets have been reported in the Northeast Pacific (Hanson et al., 2021).

Unlike many other cetacean species that undertake seasonal migrations in response to critical life history stages, killer whales are thought to move primarily in search of feeding opportunities (Corkeron & Connor, 1999). Field observations (Jourdain et al.; 2017; Jourdain et al., 2019) and recent satellite-tag tracking studies (Mul et al., 2020; Vogel et al., 2021) show that NKWs persistently feed on overwintering herring, and frequently exhibit area-restricted foraging behaviors in dense herring aggregations along their offshore routes. Satellite tagging studies in the Antarctic have revealed similar localised foraging behaviors for fish eating killer whales (Andrews et al., 2008). Strikingly, Antarctic killer whales targeting pinnipeds (such as Antarctic type B) were found to display nomadic and far-ranging movements (Andrews et al., 2008). Similar nomadic movements have been described for NKWs based on opportunistic field observations of whales targeting seals, where individuals were occasionally observed transiting between seal colonies (Jourdain et al., 2017). A detailed satellite tracking study of the long-term continuous movement behavior of NKWs feeding on pinnipeds has not been reported. Tracking studies could help define how different prey might influence NKWs movements. Understanding the nuances of killer whale feeding behaviors can help us better understand population demographic trends (Tixier et al., 2017).

Here, we describe the movements of Norwegian killer whales equipped with satellite transmitters to determine if the movements of killer whales observed targeting seals differed from those targeting fish. We used photo-identification and stable isotopes ratio analysis of carbon and nitrogen ($\delta^{13}C$ and $\delta^{15}N$) to better understand if these differences were driven by prey preferences.

2 MATERIALS AND METHODS

2.2 Field work

Fieldwork took place in Troms County fjord areas (2015−2021) between October and January. Individual killer whales were *a priori* characterized as either *seal-eater* or *fish-eater* based on observed behaviours at the time of tagging. Specifically, putative seal foraging behaviours included direct observation of feeding on seals, as well as observations of fast and directed movements towards seals. In contrast, putative fish foraging behaviours included more tortuous movements concentrated in areas of overwintering herrings, as well as considering relative proximity to purse seine herring fishing boats (Mul et al., 2020).

Satellite tagging procedures and tag programming were performed as described in previous papers (Mul et al., 2019; Dietz et al., 2020; Vogel et al., 2021). In short, an Aerial Rocket Tagging System (ARTS, Kleivane et al., 2022), was used to deploy either SPOT5 or SPOT6 Limpet Argos transmitters (Wildlife Computers) onto the dorsal fin of killer whales. This placement maximised both tag retention and the accuracy of ARGOS positions (Mul et al., 2019). Tags were set to transmit 14−15 times every hour during the first 45 days, after which the transmission rate was reduced to 8−10 times per hour for the next 45 days, and finally 2-3 times per hour after 90 days. More detailed descriptions of tag programming can be found in Dietz et al. (2020). Following satellite tag deployment, whales were reapproached, and a 4 cm length and 0.5 cm large skin/blubber biopsy was subsequently collected also using the ARTS system. The skin was separated from the blubber in each biopsy sample and kept frozen at -20°C within few hours after sampling. In total, 13 killer whales were both tagged and biopsied. Photographs of the dorsal fins were acquired in cases where light and weather conditions allowed (n=2, ID 182231 and ID 22065). Sampling and tagging were conducted in accordance with FOTS permit (8165 and 24075).

2.3 Tag data processing and movement analysis

We used the pre-processed location data provided by Argos-CLS through their Kalman filter routine (Lopez et al., 2014). All further data processing and statistical analyses were performed using ‘R’ (version 3.6.1, R Core Team 2019). To compensate for the irregular nature of time series sampling using Argos positions, while accounting for the corresponding Argos location error, a continuous-time correlated random walk state-space model from the R package ‘foieGras’ (Jonsen & Patterson, 2019; Jonsen et al., 2020) was applied. Using this model, we estimated locations at 3 hr-intervals. Eight killer whales were tagged and biopsied concomitantly. Of the 13 whales that were tagged and biopsied concomitantly in this study, eight had tracking durations that were greater than 12 days, only these were included for further analysis. Among these eight whales, two were a priori categorised *seal-eaters* (Table 1, red rows; individual tag ID 182231 and ID 22065) and six as *fish-eaters* (Table 1; individual tag ID 54011, ID 83760, ID 83768, ID 153483, ID 180318, and ID 196729). Previously published satellite tag data from whales categorised as fish-eaters (n=25) was used to visualize and compare movements but are not detailed in this study. A detailed description of these whales has been previously published (Vogel et al., 2021).

One of the *fish-eaters* (ID 153483) was tagged and biopsied in the Kaldfjord area outside Tromsø in November 2015, when herring was still overwintering within this fjord. The rest of the *fish-eaters* (ID 54011, ID 83760, ID 83768, ID 180318, and ID 196729) were tagged and biopsied in 2018-2020 (November and January) further north in the Kvænangen fjord at a time when herring had established overwintering areas in this fjord. It is worth noting that around both Kaldfjord and Kvænangen fjord areas, seal haulout areas are also present. The whales designated as *seal-eaters* (ID 182231 and ID 22065) were both tagged and biopsied in the Kaldfjord area in October in 2019 and 2021. In these years, the herring had stopped using this area for overwintering.

The distance to the coast of each location was calculated using the ‘dist2land’ function in the R package ‘ggOceanMaps’ (Vihtakari et al., 2020).

It is not uncommon for NKWs to leave the herring overwintering areas within the northern fjords on transient round-trip offshore excursions (Van Ruiten, 2021). This behavior was hypothesized to be related to scouting for either alternative prey or more abundant prey patches. In this study we were primarily interested in determining the paths whales take after leaving the northern fjords and how prey preference might influence their paths. For this reason we only used tracking data occurring after each whale permanently left the northern fjords (i.e. without returning in that season). Fjord boundaries were determined using spatial data from the Fjord Catalog published by the Norwegian Ministry of Environment (Christensen, 2020) as previously described in Vogel et al. (2021). These truncated tracks are hereafter referred to as *out-of-fjord*.

The direction of whale travel between two consecutive points, the *heading*, was calculated using the “bearingRhumb” function from the “geosphere” R package (Hijmans, 2021). The locations of harbour seal *haul-outs* (n=93) were obtained from the time series of annual counting surveys along the Norwegian coast carried out by the Institute of Marine Research (https://www.hi.no/hi). We calculated the heading between each whale location and the closest seal haulout. Using these two bearings, the *whale heading* and the *heading to the nearest haul-out area*, we calculated the absolute difference between these two headings the *delta-bearing* (Δ-*bearing)*. Δ-*bearing* values ranged from 0° (directly towards the nearest haul-out) to 180° (directly away from the nearest haul-out). Here, we consider Δ-*bearing* values between 0° and 45° to indicate movements towards the nearest seal haul-out area, values between 135° and 180° to indicate whales moving away from the nearest haul-out area, and Δ-*bearing values* between 45° and 135° were considered non-directed. Delta-bearing values were also grouped into two categories: *haul-out directed,* (0°< Δ-*bearing* < 45° or 135°< Δ-*bearing*

< 180°) vs. *non-directed* (45°< Δ-*bearing* < 135°). While the inclusion of 135° - 180° as directed movements related to seal predation might seem counterintuitive, the reason why values between 0° - 45° and 135° - 180° are both considered directed is because these movements presumably reflect either specific movements towards a known haul-out area in search of seal prey or movements away from a that location after predation, or discovering the absence of prey at that location. The proportion of *haul-out directed* movements was calculated as the fraction of *haul-out directed* points divided by the sum of *haul-out directed* + *non-directed* points. Statistical comparisons between *seal-* and *fish-eaters* Δ-*bearing proportions* were calculated using a double-tailed two-proportion Z-test.

To test if the Δ-*bearing proportions* of the whales actually reflected the locations of the specific seal haul-outs, and not simply the coastline, we also calculated Δ-*bearing* in relation to 93 randomly generated points along the coast within the geographical limits of the distribution of the known haul-out areas. Points were randomly selected from the coastline defined by Natural Earth (https://www.naturalearthdata.com/). This detailed coastline includes both the Norwegian mainland as well as its offshore islands. We then followed the same protocol as explained prior for calculating Δ-*bearing* of each point, but this time in relation to these *random coastal points.*

2.4 Photo ID

Dorsal fin photographs were compared to the Catalogue of Norwegian killer whales 2007-2021 (Jourdain & Karoliussen, 2021), to determine if prior feeding history could be ascertained to support *a priori* categorization for dietary preferences of tracked individuals. Only the two a priori categorized *seal-eaters* were concurrently photographed, since they were the only whales tagged within daylight hours and prior to the complete onset of polar night.

2.5 Stable Isotopes Analysis

SIA analyses were conducted in freeze-dried skin samples (n=8). An accurate amount (1.5-2.0 mg) of sample were weighed into tin cups and placed in a Flash EA connected to a Delta V Advantage Thermo Scientific Continuous Flow Mass Spectrometer (Thermo Scientific, Bremen, Germany) were the values of $\delta^{13}C$ and $\delta^{15}N$, weight % of N and C were determined. Lipid-extracted samples were used to determine $\delta^{13}C$ to control for the low $\delta^{13}C$ found in the lipid fraction of an organism that can lead to bias (Yurkowski et al., 2015; Jourdain et al., 2020), whereas $\delta^{15}N$ values were obtained from non-lipid-extracted samples due to the unpredictable changes in $\delta^{15}N$ values of cetacean skin following lipid extraction (Lesage et al., 2010; Ryan et al., 2012; Jourdain et al., 2020). Lipids were removed by using a solution of 7% methanol in dichloromethane. The accuracy and precision of $\delta^{13}C$ and $\delta^{15}N$ analyses were measured by replicate analysis of B2155 Protein Reference material from (Elemental Microanalysis Ltd, Great Britain) plotted on the calibration line made from the results of analyses of USGS64 and USGS66 Glycine reference material from United States Geological Survey. On average, the values for B2155 for these analyses were $\delta^{15}N_{AIR}$ = 6.07‰ ± 0.18 and $\delta^{13}C_{VPDB}$= -27.11‰ ± 0.05, while the certified values of the reference material B2155 were $\delta^{15}N_{AIR}$= 5.94‰ ± 0.08 and $\delta^{13}C_{VPDB}$:-26.98‰ ± 0.13.

3 RESULTS

3.1 Killer whale movements

In this study, both *seal-eaters* (ID 182231 and ID 220657*,* Figure 1) and all *fish-eaters (*ID 54011, ID 83760, ID 83768, ID 153483, ID 180318, and ID 196729; Figure 1 panel B, light green points) eventually travelled south, albeit following different paths (supplemental Figure 1). Upon tagging in October 2021, *seal-eater* ID 220657 (purple) subsequently began its coastal southward route (Figure 1). In contrast, the other *seal-eater* (ID 182231, pink), tagged in October 2019, first moved north to a fjord associated with herring overwintering and remained near there for an additional two months before traveling south. While *seal-eater* ID 182231 was in this fjord that was known to be associated with overwintering herring, it moved differently than the other *fish-eating* whales who exhibited typical herring associated restricted movements towards the centre of the fjords. In contrast *seal-eater* ID 182231 frequently travelled close to the perimeter of the fjords (supplemental Figure 1). During this time, killer whale ID 182231 was also observed taking an offshore excursion northwest out of the fjords. It next travelled northeast along the coastline before returning to the fjord it was tagged in (Figure 1 and supplemental Figure 1). This whale was photographed feeding on herring (photo not included). *Seal-eater* (ID 182231, pink) began its southern coastal route in early December. After leaving the herring overwintering areas, all *fish-eaters* initially headed offshore, west of Lofoten and Vesterålen, broadly following the known herring spawning migration paths (see Vogel at al., 2021 for details). The route taken by the six *fish-eaters* in this study (Figure 1 panel B, light green dots), were similar to routes taken by the 25 killer whales (described in detail in Vogel et al., 2021) that were all also a priori categorised as *fish-eaters* (Compare light green and grey points in Figure 1 B). The *seal-eaters* followed a coastal path southward, staying typically within 6.9 ± 10.7 km (mean ± sd, n= 315, max= 79.7 km) from the shore (Figure 2), while the six *fish-eaters* were routinely further offshore (45.1 ± 30.2 km, n=1534, max= 156.18 km). *Seal-eaters* generally explored fjords along their predominantly southward route (see tracks in Figure 1 panel A), and are the only whales tagged by our group to have been observed traveling in-between Lofoten/Vesterålen islands and the mainland (Figure 1).

A significant fraction of the two *seal-eater's* movements were seal haul-out directed, (Fig 3 panel A, green circles). The fraction of haul-out directed movements for *seal-eater* ID 182231 and ID 220657 was 0.55 (n=211) and 0.51 (n=102) respectively. On average, the fraction of haul-out directed movements for both *seal-eaters* was 0.53. The six *fish-eaters* had a mean fraction of haul-out directed movements of 0.43 (n=1528 directed points; ranging from

0.34 - 0.48). The differences in the fraction of haul-out directed movements between *seal-* and *fish*-eaters, while small, was statistically significant (Z-test; P-value = 0.001, χ^2= 10.573; Fig 3 panel B). These results indicate that the movements of the *seal-eaters,* either towards or away from the nearest seal haul-out*,* were more frequently directed than the *fish-eaters*.

In contrast, when randomly generated coastal points (Figure 3 panel A, yellow circles) were substituted for seal haul-out areas, a difference between the *seal-* and *fish-eaters* was not observed (Figure 3 panel B). The fraction of *randomly generated coastal points* directed movements for *seal-eater* ID 182231 and ID 220657 was 0.50 (n=211) and 0.51 (n=102) respectively. On average*,* the fraction of *randomly generated coastal points* directed movements for the *seal-eaters and fish-eaters* was respectively 0.50 (*n*=313) and 0.44 (*n*=1528, ranging from 0.26 - 0.54). These proportions were not statistically different (Z-test; P-value = 0.073, χ^2=3.205; Fig 3 panel B). These results indicate that there was no significant difference in directional movements between *seal-* and *fish-eaters* relative to the *randomly generated coastal points*.

3.3 Photo ID

Only one whale (*ID 220657*) was successfully matched to a known individual (NKW-702) in the catalogue (Jourdain & Karoliussen, 2021). Based on photographic associations with other conspecifics, it was determined that this whale is a member of a group with an observed history of feeding on both *fish* and *seals* (pers comm. Jourdain). There was no match to the photo-ID of the other putative *seal-eater*, *ID* 182231, in this database.

3.4 Stable Isotopes Analysis

The highest δ^{15}N value (13.78‰, Table 1) was measured in one of the a priori categorized *seal-eaters* (ID182231). Note that as mentioned above, this whales photo-ID had not match in the catalogue. In contrast, we found a lower δ^{15}N value (12.04‰, Table 1) for the second a *seal-eater* (ID 220657). Note that this whales photo-ID revealed a prior history of feeding on both seal and herring. This individual had a δ^{15}N ratio slightly below the reported values for seal-eating killer whales in Jourdain et al., 2020 (12.6 ± 0.3‰). The δ^{15}N values of the six whales a priori designated as *fish-eaters* (11.7 ± 0.35‰) were, on average, in line with values reported for herring-eating killer whales in Jourdain et al. 2020 (11.7 ± 0.2 ‰).

4 DISCUSSION

Based on our *a priori* classifications as either *seal-eaters* or *fish-eaters*, our tracking results indicate that these two groupings of whales take different paths, seemingly optimized for their preferred prey, after leaving the northern fjords. To the best of our knowledge, this study is the first to describe satellite tracks of Norwegian killer whales thought to be foraging on seals along the Norwegian coast. Our classification was further supported by δ^{15}N signatures and prior photo-ID history, when available. Together with our tracking data, these data suggest that the *fish-eaters* appear to specialize on fish, whilst *seal-eaters* may opportunistically use diverse foraging strategies optimized for fish and seals based on availability and preference. While all whales eventually travelled in a southernly direction after leaving the northern fjords where the tagging was conducted, *fish-eaters* continued to follow the offshore herring spawning migration pathway along the continental shelf off the Norwegian coast, and their movements appear to respond to local herring aggregations (Hjøllo et al., 2012; Utne et al., 2012; Slotte et al., 2016; Vogel et al., 2021; Salthaug et al., 2022). In contrast, *seal-eaters* closely followed the coast, seemingly targeting known harbour seal haul-outs.

The offshore southward movements of *fish-eaters* were expected, as they reflected the movements and distributions of herring when they migrate south to their offshore spring spawning grounds (Dragesund et al., 1997). In contrast, the *seal-eaters* followed a coast-hugging path, traversing shallow coastal waters that are typically associated with harbour seal habitats (Nilssen et al., 2010). Seals tend to remain close to their coastal haul-outs throughout the year (Carter et al., 2020). Thus, we speculate that the coastal paths taken by the *seal-eaters* were optimized for preying on pinnipeds near their haul-outs. This might also explain their southernly travel direction, since most of the known seal haul-outs are south of the whales' tagging locations. Nonetheless, prior to leaving the fjords, *seal-eater* ID 182231 was photographed near herring fishing boats. Furthermore, tracking data for *seal-eater* ID 182231 indicated that prior to leaving of the northern fjords for the final time of the season (the criteria for inclusion for analysis in this study), was observed taking an offshore excursion out of the fjords, presumably to feed on offshore pelagic fish.

We found two aspects of movement that differentiated the *fish-eaters and seal-eaters*: (1) differences in the route taken as reflected by their average distance from shore, and (2) differences in the proportion of directed movements towards or away from known harbour seal haul-out areas. These differences might reflect individual prey specialization (i.e., fish vs. seals), preference or diversifying feeding strategies. In our previous studies we also found evidence consistent with prey switching behavior among NKWs (Dietz et al., 2020; Vogel et al., 2021). In these studies, all individuals followed offshore herring aggregations (Vogel et al., 2021), but two individuals later deviate from the herring aggregations and switch to migrate northwards into the Northeastern Barents Sea, likely in search of alternative prey along the marginal ice zone (Dietz et al., 2020).

The movement patterns of the *seal-* and *fish*-eaters were strikingly different, suggesting these groups utilised different foraging strategies, at least on a seasonal basis. We found that the *seal-eaters* (as compared to the *fish-eaters*) had a slightly higher propensity for directed movements relative to seal haul-out areas. This difference was not observed for the negative control using *randomly generated coastal points.* Thus, while a coastal route might improve the chances of encountering a seal, a coastal route directed towards seal haulout areas would further enhance the efficiency of that strategy. Since the fractions of directed movements towards the randomly generated coastal points were similar to those of haulout directed points for the *fish-eater* and for one *seal-eater* (ID 220657), it suggests that *seal-eater* ID 182231 drives the difference between haulout-directed and random. This is consistent with the stable isotope data for this individual indicating that it was feeding at a higher trophic level. Regardless, the low number of seal-eaters in this study warrants caution in interpreting these results.

We cannot rule out the possibility that the whales designated as *seal-eaters* in our study could have also been feeding on porpoises. Norwegian killer whales have been observed to also feed on harbour porpoises (Consentino, 2015), and harbour porpoises, like harbour seals, are known to be a costal species whose spatial distributions frequently overlap in Norwegian waters (Bjørge & Øien, 1996; Consentino, 2015). Additionally, foraging on porpoises would also result in elevated $\delta^{15}N$ ratios. The combination of stable isotopes analysis, photo-ID records and visual observations (some of the most reliable methods for understanding individual killer whale diet) suggests that the *seal-eaters* in this study were generalists primarily preying on pinnipeds, but occasionally also preying on fish. While one *seal-eater* (ID 182231) had an isotopic signature consistent with feeding at a high trophic level 4–7 weeks prior to tagging, the second *seal-eater* (ID 220657*)* had a lower $\delta^{15}N$ ratio indicative of feeding at an intermediate trophic level, likely reflecting a mixed diet. Interindividual variations in $\delta^{15}N$ are not surprising since the proportion of marine mammal prey items in the diet of NKWs is known to vary considerably between individuals and across seasons (Jourdain et al., 2020). This whale is also consistent with its photo-ID records, suggesting that ID 220657 is part of a group that has been known to prey upon both seals and fish (Pers. comm. Jourdain). Although

ID 182231 was observed pursuing seals at the time of tagging and had a very clear $\delta^{15}N$ indicative of high trophic level feeding, it is likely that this individual also utilised a range of foraging strategies, since it remained near the main herring overwintering fjords for two months, and was observed feeding on herring like the *fish-eaters* in this study. Although not included in the formal analysis of this study since these movements occurred before the whale left the fjords for the season (see methods), it was noted that that the in-fjord movements of *seal-eater* ID 182231 appeared to differ subtly from than the typical *fish-eaters* in fjord movements. Specifically, this individual sometimes seemed to closely follow the perimeter of the fjords, presumably searching the edges for seals, while *fish-eaters,* in contrast, had more tortuous and concentrated movements associated with herring predation.

Prey switching between fish and pinnipeds might reflect diverse feeding strategies influenced by the relative abundance and availability of prey types. It could also result from individual prey preferences. Demonstrating prey preference is challenging because it requires establishing predation on a specific species despite the availability and abundance of an alternate prey type. Since the availability of different prey types will vary seasonally and geographically, this type of information can potentially be leveraged to identify a prey preference. Both *seal-eaters* in this study were tagged in October, while the whales categorized as *fish-eaters* were tagged between November and January. Thus, it is important to consider seasonal variations in herring abundance when attempting to differentiate between a prey preference for pinnipeds versus diversifying feeding strategies due to a diminished abundance of herring. *Seal-eater* ID 220657 left the fjords in October at the very onset the herring overwintering aggregation. Thus, it is possible herring may have been at a relatively low concentrations when this dividual left the fjords, making it is unclear if this individual had a preference for seals. In contrast, *seal-eater* (ID 182231) which was also tagged in October, remained in the northern fjords for an additional two months presumably feeding on high concentrations herring. In early December, when herring was still abundant, this whale began its southward coastal journey thought to be optimised for seal predation. Displaying movements associated with seal predation when herring was still abundant suggests that *seal-eater* (ID 182231) has an apparent preference for seals.

One possible criticism of our study is the low sample size (n=2) of a priori categorised *seal-eating* whales. With only two individuals in this category, the statistical power of our observations is limited. Nonetheless, the two *seal-eating* individuals in our study took clearly unique paths, presumably optimised for seal predation, as compared to the more commonly studied Norwegian *fish-eating* killer whales. Future tagging efforts should prioritise *seal-eating* Norwegian killer whales to increase the statistical power of the observations reported here. Additionally, it should be noted that the validity of the discrete characterisation of Northeast Atlantic killer whales has been questioned (Foote, 2022). Our tracking, SIA and photo-ID results support recent studies that Norwegian killer whales are opportunistic generalists with varying degrees of prey preference and specialization (Jourdain et al., 2020). Nonetheless, our movement results based on a priori categorization suggests some level of prey specialisation or preference exists. Future long-term studies investigating the diversity of feeding strategies are needed to reconcile our observations. Regardless, we conclude that the characterisation of these whales as being either *seal-eaters* or *fish-eaters* has some value, but should only be considered a reflection of their current prey selection (with as of yet an undetermined duration), rather than a fixed specialisation.

In conclusion, horizontal movements and spatial use acquired using satellite telemetry can be used for providing additional evidence for prey preference, and may be specifically useful to differentiate individuals targeting fish from those targeting pinnipeds. While killer whales have been observed and photographed along the Norwegian coast, between the Lofoten and Versterålen archipelagos and the mainland, the *seal-eating* killer whale satellite tracking information presented in this study is the first to document the tracks and movement behaviours of these mixed-diet whales as they leave the northern herring overwintering areas and travel southward. Using satellite tracking, we identified geographical areas along the Norwegian coast that were uniquely used by killer whales targeting seals. Although based on only two individuals, it is striking how similar the unique coastal routes were for the *seal-eaters*. This area could be targeted in future tagging studies to balance against past *fish-eater* bias. Furthermore, predation at higher trophic levels (i.e., seals) is associated with greater exposure to toxic pollutants (Andvik et al., 2020; Andvik et al., 2021; Remili et al., 2022). It is therefore important to assess the proportion of the population that target high trophic level prey, specifically, to understand the frequency, seasonality, and geographical occurrence of Norwegian killer whales prey selection so that the drivers of this behavior can be identified.

Author Contributions

Emma F. Vogel: Conceptualization; data curation; formal analysis; investigation; methodology; Visualization; writing – original draft; writing – review and editing. **Audun H. Rikardsen**: Conceptualization; investigation; project administration; supervision; writing – review and editing. **Marie-Anne Blanchet**: Formal analysis; supervision; writing – review and editing. **Pierre Blévin**: Investigation; methodology; writing – review and editing. **Martin Biuw**: Formal analysis; supervision; writing – review and editing.

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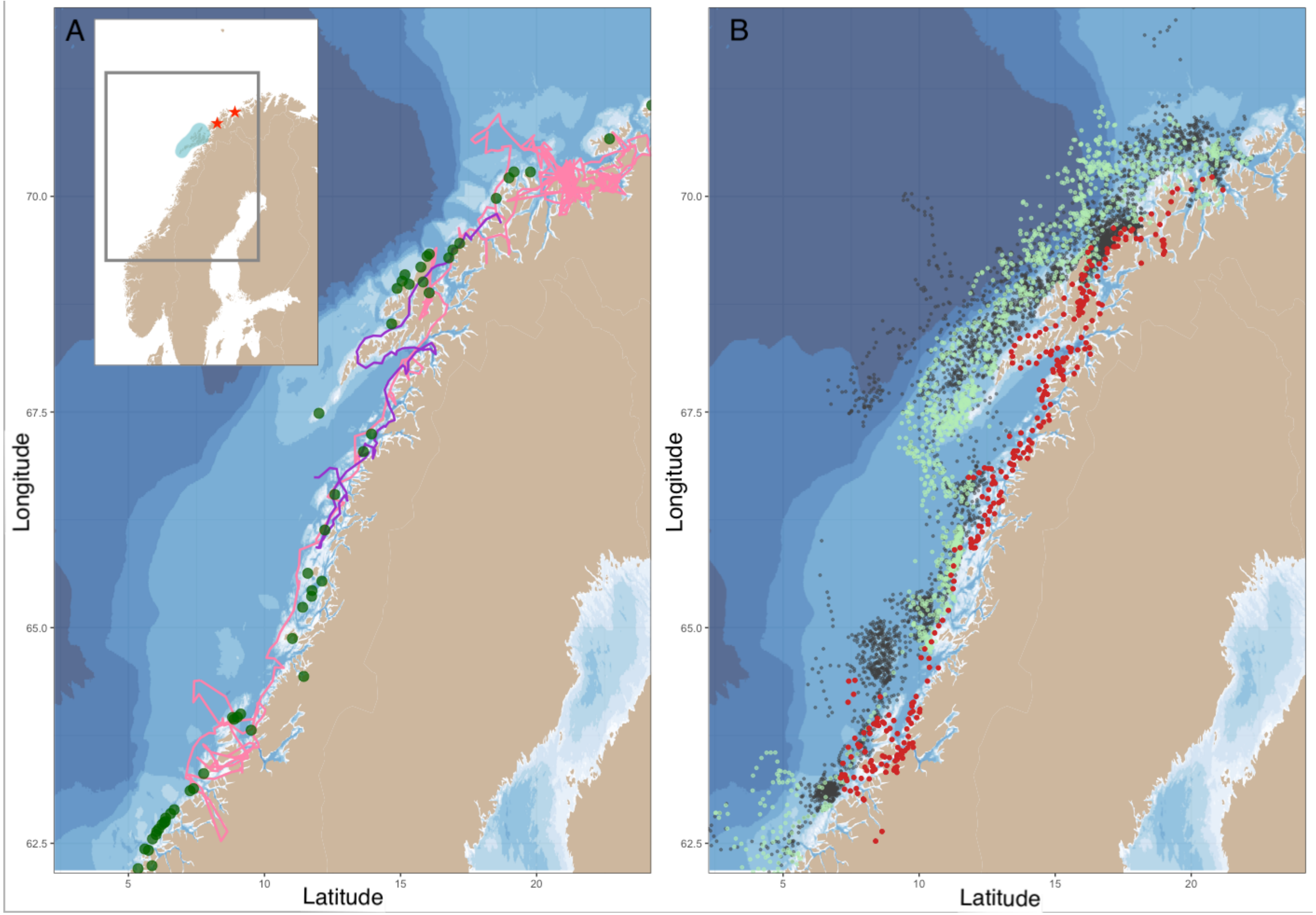
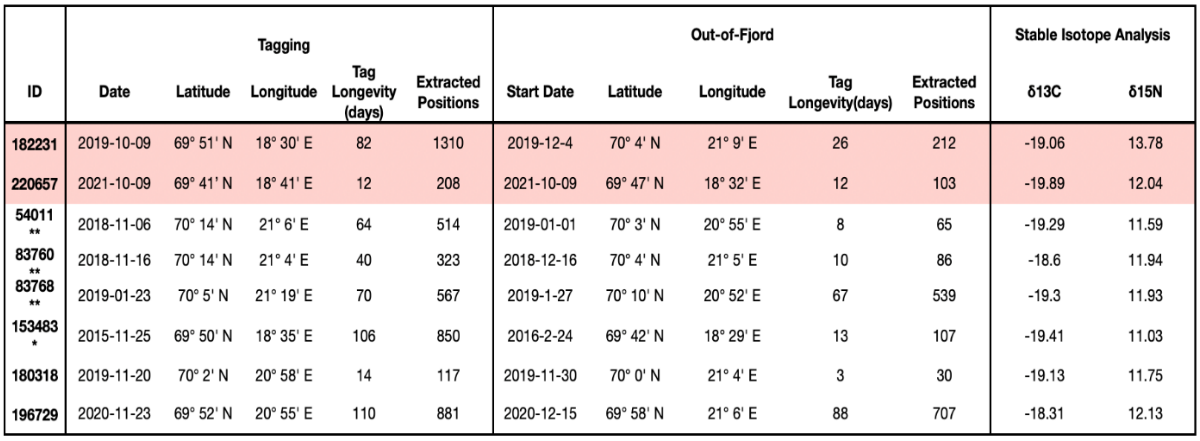


Figure 1 Panel A shows the full reconstructed paths (pink (ID 182231) and purple (ID 220657) lines) of seal-eaters. Dark green circles in panel A indicate locations of known harbour seal haul-outs. Panel B shows locations of the six fish-eaters (light green) and the two seal-eaters (red) after they left the northern fjords where they were tagged. This data is superimposed over data points from 25 additional killer whale tracks (grey dots) previously described in Vogel et al 2021. These whales have a similar distribution to the six fish eating whales, but are distinct from our two seal eating individuals. Lofoten and Versterålen indicated by teal shading in panel A inset. Tagging locations within Northern Norwegian fjords indicated with red stars in panel A inset. Bathymetry is depicted in blues where deeper water is indicated by darker blues and shallower is lighter blues.

Table 1 Tagging information from 8 killer whales tagged and biopsied between 2015 and 2021 utilized in this study. 'Tagging' represents initial tag deployments, biopsying locations and time. 'Out-of-Fjord' represents the portion of the track out after each whale left the Northern fjords where they were tagged. Note that the number of extracted positions are the raw ARGOS positions. * indicates that tracking data were concurrently used by Dietz et al. (2020) and Vogel et al (2021); ** indicates that data were concurrently used by Mul et al. (2020) and Vogel et al (2021.) Red shading indicates whales that were a priori categorised as *seal-eating*, all others were categorised as *fish-eaters*. Isotopic values refer to $\delta^{13}C$ and $\delta^{15}N$ from skin samples.



	Tagging					**Out-of-Fjord**					**Stable Isotope Analysis**	
ID	**Date**	**Latitude**	**Longitude**	**Tag Longevity (days)**	**Extracted Positions**	**Start Date**	**Latitude**	**Longitude**	**Tag Longevity(days)**	**Extracted Positions**	**δ13C**	**δ15N**
182231	2019-10-09	69° 51' N	18° 30' E	82	1310	2019-12-4	70° 4' N	21° 9' E	26	212	-19.06	13.78
220657	2021-10-09	69° 41' N	18° 41' E	12	208	2021-10-09	69° 47' N	18° 32' E	12	103	-19.89	12.04
54011 **	2018-11-06	70° 14' N	21° 6' E	64	514	2019-01-01	70° 3' N	20° 55' E	8	65	-19.29	11.59
83760 **	2018-11-16	70° 14' N	21° 4' E	40	323	2018-12-16	70° 4' N	21° 5' E	10	86	-18.6	11.94
83768 **	2019-01-23	70° 5' N	21° 19' E	70	567	2019-1-27	70° 10' N	20° 52' E	67	539	-19.3	11.93
153483 *	2015-11-25	69° 50' N	18° 35' E	106	850	2016-2-24	69° 42' N	18° 29' E	13	107	-19.41	11.03
180318	2019-11-20	70° 2' N	20° 58' E	14	117	2019-11-30	70° 0' N	21° 4' E	3	30	-19.13	11.75
196729	2020-11-23	69° 52' N	20° 55' E	110	881	2020-12-15	69° 58' N	21° 6' E	88	707	-18.31	12.13

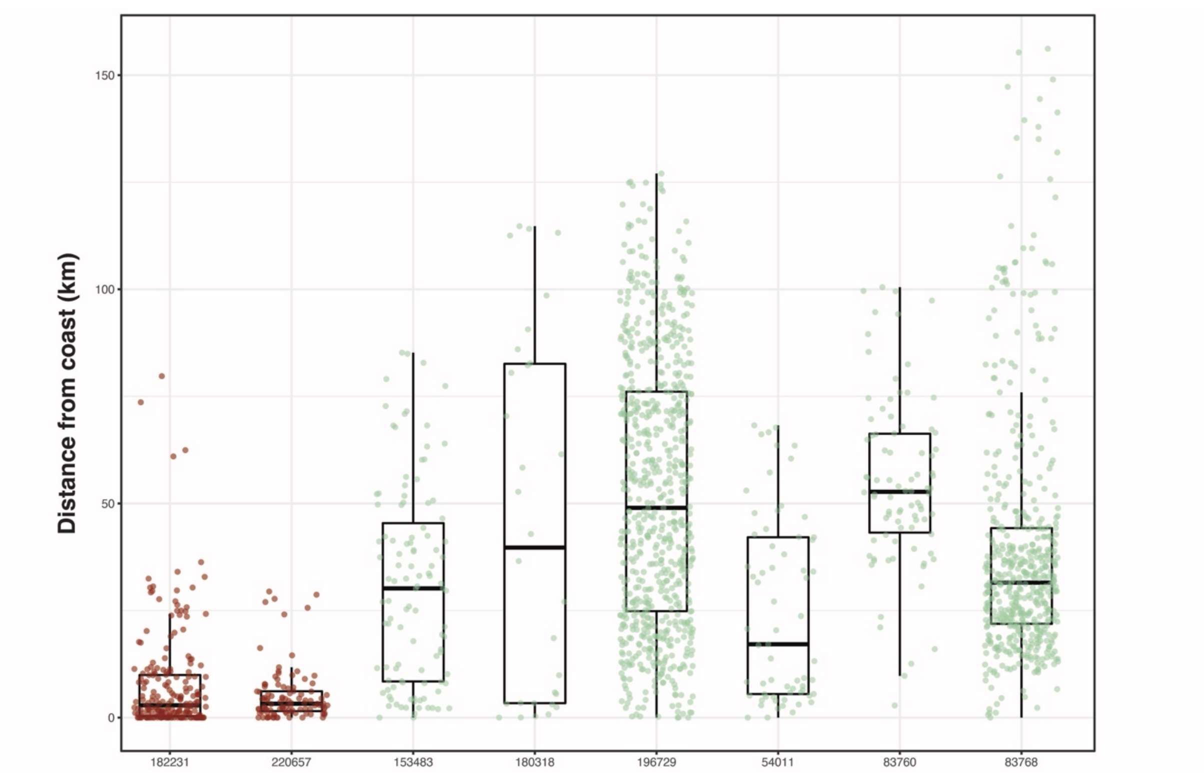


Figure 2 Box plots of distance from the coast for individual whales. Individual tracking points for *seal-eaters* are shown in red, whereas *fish-eaters* are shown in green.

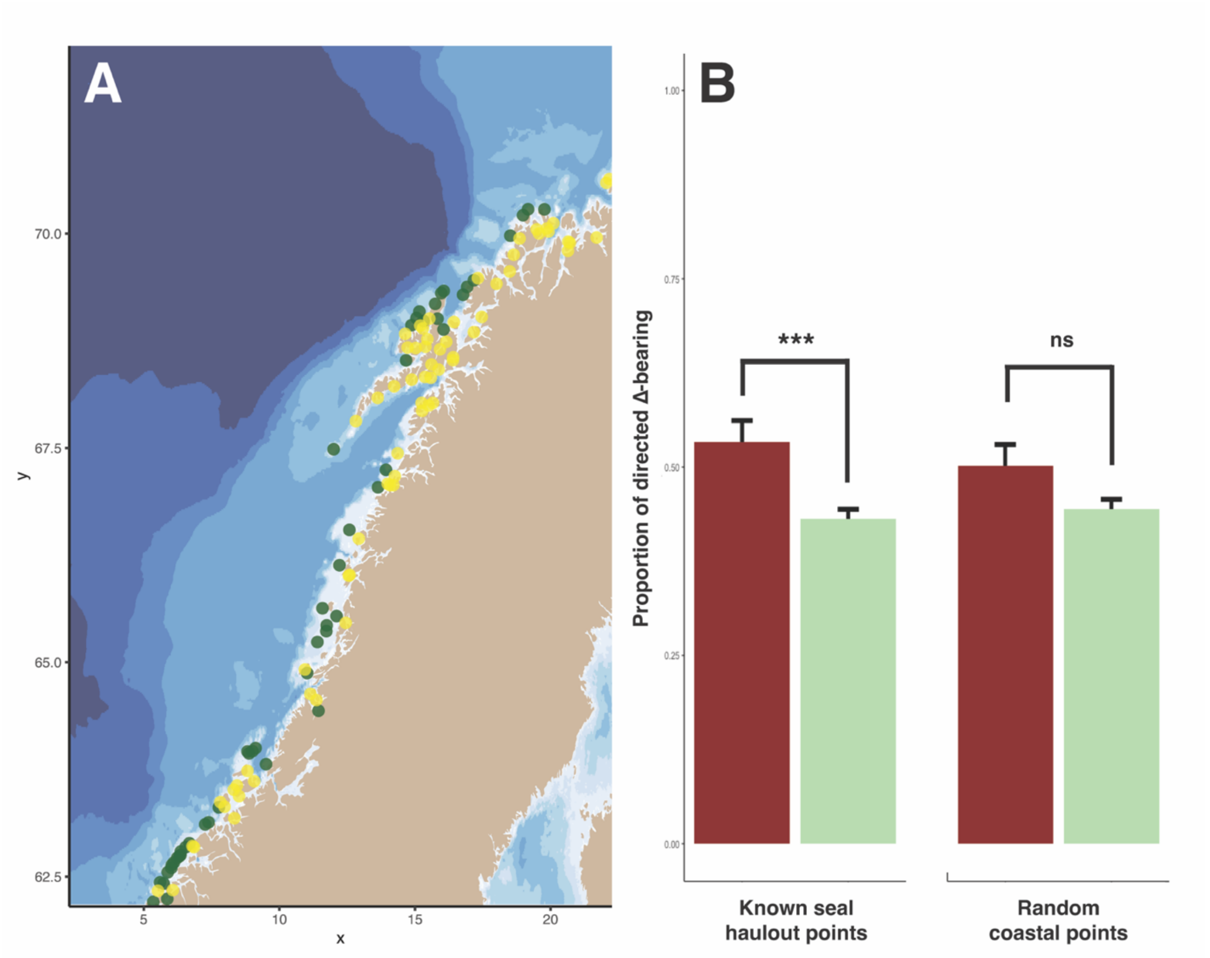
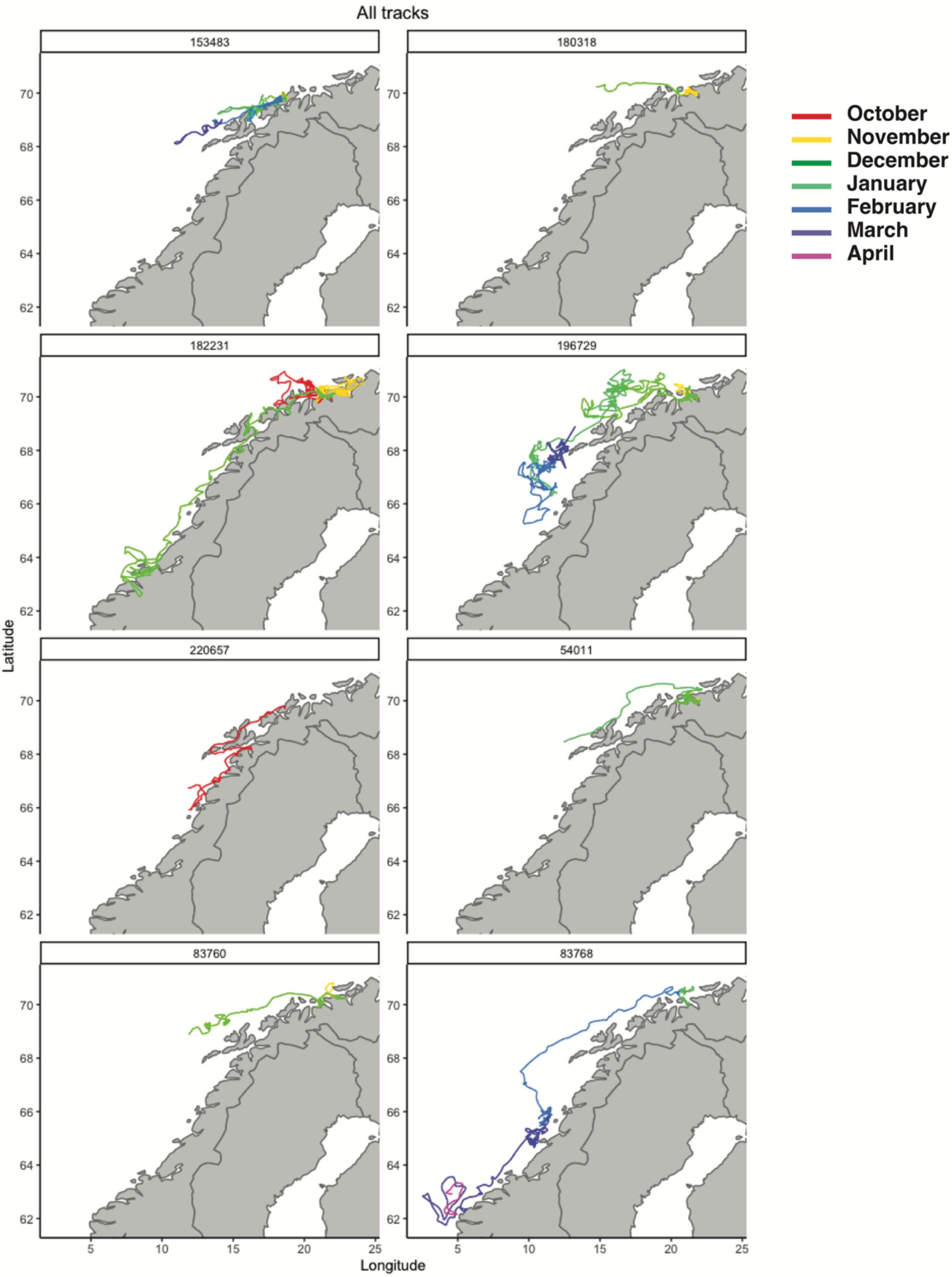


Figure 3 Map depicting known seal haul-out areas (green circles) and randomly generated coastal points (yellow circles) along the Norwegian Coast (Panel A). Panel B shows a bar graph of the proportions of directed Δ-bearing to either nearest known seal haul-out (left) or nearest randomly generated coastal point (right). Bars are colored by putative feeding grouping where red indicates *seal-eating* and light green indicates *fish-eating*. Results from the two double-tailed two-proportion Z-test indicated by black brackets, where '***' indicate a significant p-value of 0.001 and 'ns' indicates a non-significant p-value of 0.073.



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715 Supplemental Figure 1 Panels shows the reconstructed full paths of all eight whales included in the study. Unique
716 individual whale IDs are on top of each map and paths are coloured by month. ID 182231 and ID 220657 are the
717 two *seal-eaters.*

718

Paper III

Foraging movements of humpback whales relate to the lateral and vertical distribution of capelin in the Barents Sea.

Emma F. Vogel, Stine Skalmerud, Martin Biuw, Marie-Anne Blanchet, Lars Kleivane, Georg Skaret, Nils Øien, and Audun Rikardsen

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EDITED BY
Molly E. Lutcavage,
University of Massachusetts Boston,
United States

REVIEWED BY
Robert Schick,
Duke University, United States
Uffe Høgsbro Thygesen,
Technical University of Denmark, Denmark

*CORRESPONDENCE
Emma F. Vogel
emma.vogel@uit.no

†PRESENT ADDRESS
Marie-Anne Blanchet,
Terrestrial økologi og sjøfugl, Norwegian Polar Institute FRAM –High North Research Centre for Climate and the Environment, Tromsø, Norway

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Foraging movements of humpback whales relate to the lateral and vertical distribution of capelin in the Barents Sea

Emma F. Vogel[1]*, Stine Skalmerud[1], Martin Biuw[2], Marie-Anne Blanchet[1,3]†, Lars Kleivane[3], Georg Skaret[2], Nils Øien[2] and Audun Rikardsen[1]

[1]Faculty of Biosciences, Fisheries and Economics, The Arctic University of Norway, Tromsø, Norway, [2]Institute of Marine Research, Framsenteret (FRAM) – High North Research Centre for Climate and the Environment, Tromsø, Norway, [3]Terrestrial økologi og sjøfugl, Norwegian Polar Institute, FRAM – High North Research Centre for Climate and the Environment, Tromsø, Norway

Understanding how individual animals modulate their behaviour and movement patterns in response to environmental variability plays a central role in behavioural ecology. Marine mammal tracking studies typically use physical environmental characteristics that vary, and/or proxies of prey distribution, to explain predator movements. Studies linking predator movements and the actual distributions of prey are rare. Here we analysed satellite tag data from ten humpback whales in the Barents Sea (north-east Atlantic) to examine how their spatial movement and dive patterns are influenced by the geographic and vertical distribution of capelin, which is a key prey species for humpback whales. We used capelin density estimates based on direct observations from a trawl-acoustic survey and sun elevation to explore the drivers of changes in movement patterns. We found that the humpback whales' exhibited characteristic area restricted search movement where capelin density was the highest. While horizontal movements showed both positive and negative individual relationships with sun elevation, humpback whale dive depth was positively correlated with diurnal variations in the vertical distribution of capelin. This suggests that in addition to whales foraging in regions of high capelin density, they also target the densest shoals of capelin at a range of depths, throughout the day and night. Overall, our findings suggest that regions of high capelin density are important foraging grounds for humpback whales, highlighting the central role capelin plays in the Barents Sea marine ecosystem.

KEYWORDS

humpback, movement, capelin (*Mallotus villosus*), behaviour, predator-prey, telemetry, Barents Sea

1 Introduction

The distribution, availability, abundance, and type of prey strongly influences the behaviour of marine predators (Womble et al., 2014; Goldbogen et al., 2015; Hays et al., 2016). Marine predators may adapt both their horizontal and vertical movements in response to changes in patchy prey distribution to optimise their foraging efficiency3 (Boyd 1996; Sims et al., 2008; Bestley et al., 2010; Thums et al., 2011; Bestley et al., 2015; Joy et al., 2015). Optimal foraging theory predicts that predators should concentrate their efforts on high prey density patches while minimising the transit time between prey patches to maximise their net energy gain and ultimately their fitness (Hedenström and Alerstam 1997; Houston and McNamara 2014). During foraging, marine predators commonly exhibit area-restricted search (ARS) behaviour, characterised by reduced speeds and increased turning rates to remain within a prey patch (Kareiva and Odell 1987; Witteveen et al., 2008; Hazen et al., 2009; Jonsen et al., 2005; Breed et al., 2009; McClintock et al., 2012; Silva et al., 2013). In contrast, movement associated with transit displays consistent and elevated speeds with lower turning rates (Fauchald and Tveraa 2003). When prey density declines in a particular area, predators may either leave in search of another high-density patch, or switch to alternate prey species (Murdoch 1969; Van Baalen et al., 2001; Vogel et al., 2021). Therefore, movement analysis of predators can be linked to areas of high prey density.

The humpback whale (*Megaptera novaeangliae*) is a cosmopolitan species, with several distinct stocks identified around the world (Gulland, 1966; Stone et al., 1990; Baker et al., 1993; Rasmussen et al., 2007). Humpback whales typically migrate yearly between high latitude feeding areas and low latitude breeding grounds (Clapham, 2009). Their main feeding grounds are generally nutrient rich waters, where their diet consists of a variety of patchily distributed prey including fish, krill, copepods, and squid (Baker et al., 1985; Clapham and Palsbøll, 1997; Clapham, 2009; Meynecke et al., 2021).

The northeast Atlantic is regarded as a highly productive area, in particular the Barents Sea (Sakshaug and Slagstad, 1991; Sakshaug, 1997; Carmack and Wassmann, 2006). This area has some of the world's largest pelagic fish stocks, such as Norwegian spring-spawning herring (*Clupea harengus*), capelin (*Mallotus villosus*) and cod (*Gadus morhua*). Northeast Arctic cod and haddock are the largest stocks of these species in the world (Hop and Gjøsæter, 2013; Hansen et al., 2019; Johannesen et al., 2019). The high productivity of this area also supports a large biomass of marine predators such as cetaceans, pinnipeds, seabirds and large fishes (Skern-Mauritzen et al., 2022). Marine predators are frequently observed in these productive waters exploiting the abundant prey resources (Gjøsæter et al., 2009; van der Meeren and Prozorkevich, 2019; Hamilton et al., 2021; Skern-Mauritzen et al., 2022). During the summer and autumn, northeast Atlantic humpback whales forage throughout the Norwegian and Barents Seas and around Iceland (Christensen et al., 1992; Leonard and Øien, 2020; Hamilton et al., 2021), and at least some proportion of the population also make use of abundant resources well into the winter season (Kettemer et al., 2022).

In the Barents Sea, humpback whales have been assumed to feed mainly on herring, capelin, and krill (Løviknes et al., 2021). In the last decades, an increase of humpback whales and other baleen whales in the northern Barents Sea has been attributed to growing fish stocks (Leonard and Øien, 2020). More generally, feeding hotspot areas in the Barents Sea for several marine mammal species overlap with the main feeding ground for adult capelin feeding on krill (van der Meeren and Prozorkevich, 2019; Hamilton et al., 2021). During summer months, shoals of capelin migrate to central and northern areas of the Barents Sea to feed, primarily on copepods and krill (Dalpadado et al., 2012; Dalpadado and Mowbray, 2013). While in these summer feeding grounds, capelin undertake diel vertical migrations, with a tendency to aggregate at deeper depths during the day and disperse towards the surface at night (Dalpadado and Mowbray, 2013; Skaret et al., 2020 Fall et al., 2021). This pattern is believed to be linked to variations in light intensity. The tendency of capelin to undertake vertical migrations is attributed to following their primary prey, krill, which utilise diel vertical migration to evade visual predators. Similarly, capelin themselves likely also migrate to avoid their visual predators (Gjøsæter, 1998; Hop and Gjøsæter, 2013).

Two feeding modes are generally observed for humpback whales: ram feeding and lunge feeding (Goldbogen et al., 2013). Ram feeding is characterised by whales swimming through dense prey schools at constant, slow speeds with their mouths open, forcing water through their exposed baleen plates (Goldbogen et al., 2013). Lunging, on the other hand, is characterised by whales engulfing a large volume of prey-filled water at high speed, thereafter, filtering the water out with their mouths closed (Goldbogen et al., 2013). Feeding can occur at the surface, in shallow waters, and/or at depth and at the bottom (Jurasz and Jurasz, 1979; Ware et al., 2011; Ware et al., 2014; Mastick et al., 2022). While little is known about how humpback whales locate and track prey patches, presumably they use multiple senses, such as visual, auditory, and olfactory. They may also use memory of previously visited areas, rely on cues from conspecifics or anthropogenic cues such as the presence of fishing vessels.

One common limitation of previous marine mammal predator-prey telemetry-based studies is that they use indirect proxies of prey distribution. In this study we are able to examine the links between predator movements and the distribution of a key prey resource, capelin. Moreover, we account for horizontal movements (*c.f.* Vogel et al., 2021), as well as for vertical movements of whales in relation to their prey. The main objective of this study is to assess the degree to which northeast Atlantic humpback whale diving behaviour and spatial distribution is influenced by the spatial and vertical distribution of capelin in the Barents Sea using satellite telemetry and large-scale acoustic survey data. Our study aims to investigate: (1) the association between Barents Sea capelin distribution and both horizontal and vertical movements of humpback whales, (2) whether diel variations in light levels influence the horizontal movement behaviour of humpback whales, (3) how diel variations in humpback whale diving correlates with capelin vertical distribution and (4) the presence of individual variation in the behavioural responses of whales to capelin density.

2 Materials and methods

2.1 Study site

Tagging (Figure 1A) was conducted between the 4th and 9th of September 2018 as part of a collaborative research cruise conducted between the University of Tromsø and Institute of Marine Research (IMR) within the Barents Sea, just east of Svalbard. The choice timing and location of tagging efforts was informed by previous humpback whale sightings data collected from prior annual Joint Norwegian/Russian ecosystem surveys in the Barents Sea and adjacent waters (van der Meeren and Prozorkevich, 2019). Tagging took place concurrently with the annual joint Barents Sea Norwegian/Russian ecosystem cruise (between August and October 2018) that was conducting its acoustic and biological surveying for capelin in the same area (dashed line, Figure 1A).

2.2 Tagging methods

Ten subdermally-anchored satellite tags (5 SPOT-303 tags and 5 SPLASH-302 tags, Wildlife Computers, Redmond, WA) were deployed using an Aerial Rocket Tagging System (ARTS, Kleivane et al., 2022) following best tagging practices described by Andrews et al. (2019). Specifically, whales were slowly approached and tagged from a 20 ft open rigid inflatable boat. Tags were placed below the dorsal fin and were sterilised with 70% ethanol before deployment. When possible, photographs of the flukes were taken, enabling identification of the individual whales and ensuring that the same individual was not tagged twice. Tagging was approved by the Norwegian Food Safety Authority (Mattilsynet) under permit FOTS ID 14135 2017/279575.

The five deployed SPOT tags provided transmissions used to drive estimates of geographic position using the doppler-shift of the signals received by Argos satellite receivers, as described at https://www.argos-system.org. These tags were programmed to send ~15 transmissions per hour for the first four months, then reduce to 12 transmissions per hour for the following three months, before finally reducing to 80 transmission per day until their batteries failed or the tag was lost. This programming schedule allowed for high temporal resolution data early in the tagging period and then coarser data later to prolong battery life in cases when tags remained attached for longer periods than expected. The five SPLASH tags similarly transmitted horizontal position data, whilst additionally recording information on the diving behaviour of the tagged animal. These tags were programmed to transmit 400 data transmissions per day, in order to receive as much behavioural dive information as possible during the main period of interest, i.e. the summer feeding season.

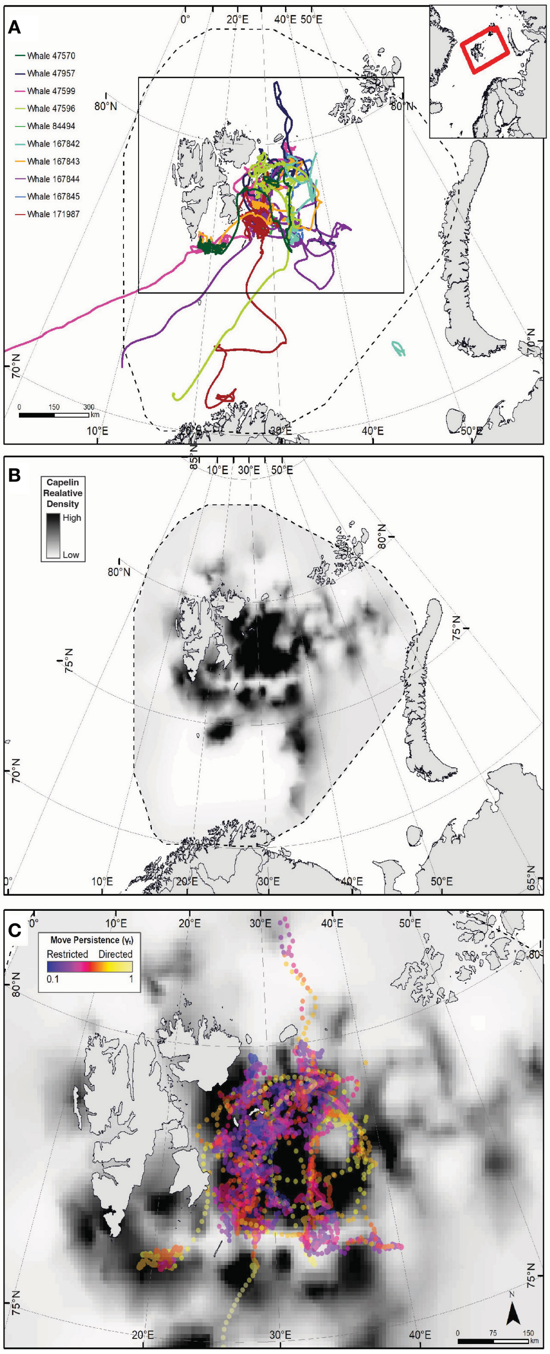

FIGURE 1
Tracks from 10 humpback whales (at 3-hr time interval steps) instrumented in the northern Barents Sea in September 2018 **(A)**. Dashed line in **(A, B)** show the spatial extant of the capelin modelled density. Red Box in inset indicates the spatial frame of **(A, B)**. **(B)** depicts the 2018 modelled relative capelin density distribution. Dark black indicates areas of higher relative density. **(C)** shows relative density of capelin with humpback whale move persistence (γ_t) estimate points between September 4th 2018 and October 31st overlaid, where yellow points indicate high γ_t (i.e. transiting behaviour) and dark purples indicate low γ_t (i.e. restricted foraging behaviour).

2.3 Tag data processing

Tag location data were pre-processed by Argos-CLS using their Kalman filter (Lopez et al., 2014). All subsequent data processing and statistical analyses were carried out using the R programming language (version 4.2.2, R Core Team, 2022). A continuous-time correlated random walk state-space model (CRW) implemented in the 'fit_ssm' function in the 'aniMove' R package (Jonsen et al., 2023) was used to estimate the most probable paths taken by each whale (Jonsen et al., 2019; Jonsen et al., 2020; Jonsen et al., 2023). Specifically, the CRW represents the most likely path an animal took based on the pre-filtered ARGOS position estimates by converting the non-uniform time series to a regularised path (Johnson et al., 2008), accounting for location uncertainty and temporally-irregular transmissions (Jonsen et al., 2005). This model enabled us to estimate whale positions while accounting for location uncertainty at regularised 3-hour intervals. Substantial gaps in tracking data can present challenges when fitting these types of models, such as unreliable predictions during these periods of data absence. To mitigate this issue, whale tracks containing a gap greater than 1 week were split prior to CRW modelling and further statistical analysis. A split-track segment was included in subsequent analyses only if it had at least 20 consecutive raw data points and there was at least one position each day.

2.4 Humpback whale movements

2.4.1 Horizontal movements-move persistence (γ_t)

Move persistence (γ_t) is a behavioural index that considers autocorrelation between consecutive movements of animal track locations and accounts for changes across both speed and heading (Jonsen et al., 2019). This continuous metric ranges from 0, indicating highly tortuous movements typically within a restricted area, associated with e.g. searching or foraging, to 1, representing consistent movements in terms of both directionality and speed (Jonsen et al., 2019). We selected move persistence as our metric of humpback whale horizontal movement behaviour, because it provides a continuous scale that allows for subtle difference in movement behaviour, rather than defining somewhat arbitrary discrete behavioural states (Breed et al., 2012; Auger-Méthé et al., 2017; Eisaguirre et al., 2019; Jonsen et al., 2019). The 'fit_mpm' function in the 'aniMotum' R package (Jonsen et al., 2023) was used to estimate pooled move persistence from the location data.

2.4.2 Vertical movements

SPLASH tags were programmed to optimise data collection for behavioural dive data. The tags recorded maximum dive depth, dive duration, dive start- and end-time for dives that were ≥15 meters deep and ≥2 minutes in duration. Like the horizontal position data, this data was also transmitted using Argos satellite receivers.

2.5 Capelin density

Continuous acoustic data and biological data from trawl hauls were collected as part of the joint Russian/Norwegian annual Barents Sea ecosystem survey (Eriksen et al., 2018) between August and October 2018. The data were used to map the relative density of capelin in the Barents Sea where the 10 whales were tagged. Using a fleet of research vessels, the survey is designed to visit an equally-spaced station grid with 35 nautical miles between each station, where the ships collect trawl data, and other abiotic data. The vessels survey along transects connecting the stations, and additional transects between the station grid in the areas where most capelin is expected (van der Meeren and Prozorkevich, 2019). The vessels continuously sample acoustic echosounder data along the transects using SIMRAD EK60 or EK80 equipment calibrated according to standard procedures (Demer et al., 2015). The echosounder data were processed using the Large Scale Survey System software package as outlined by Korneliussen et al. (2006). The classification and allocation of acoustic backscattering to biological categories was done by experts on board using a combination of acoustic signal characteristics and pelagic trawl catches, and with 'capelin' as a target category. The resulting acoustic density values were stored by category as nautical area scattering coefficient (NASC; m^2/nmi^2) (Maclennan et al., 2002) with a horizontal resolution of 1 nautical mile and a vertical resolution of 10 m. The abundance estimate of capelin used for assessment purposes is made in StoX (Johnsen et al., 2019), and combines the acoustic data at the resolution of 1 nautical miles (Elementary Distance Sampling Unit; EDSU) with biological data within a given pre-defined stratum using transects as Primary Sampling Unit (PSU). We used the R-package 'RstoX' (Holmin, 2019; Johnsen et al., 2019) to link the per-stratum biological data to acoustic data to obtain capelin density as biomass per EDSU.

Based on the vertically integrated EDSU density estimates from the above analysis, we created an interpolated capelin density surface, using the Integrated Nested Approximation model (INLA) and Template Model Builder (TMB) frameworks as implemented in the 'INLA' and 'sdmTMB' packages (Rue et al., 2009; Lindgren et al., 2011; Martins et al., 2013; Lindgren and Rue 2015; Kristensen et al., 2016; Anderson et al., 2022). Here, we used the INLA functionality to create irregular triangulated meshes covering the entire survey region, where the mesh size is adapted to the sampling resolution such that areas with denser number of data points are associated with smaller mesh sizes. We then developed a spatial interpolation model in TMB, where unexplained variation in density is assumed to follow a Gaussian Random Field (GRF) process, and where spatial autocorrelation is governed by a Matérn function with parameters estimated by TMB. To model spatial point processes, TMB uses the stochastic partial differential equation (SPDE) approach originally implemented in INLA (Rue et al., 2009; Lindgren and Rue, 2015). To account for the barrier effect caused by Svalbard's coastline, supporting barrier models were employed, as described in Bakka et al. (2016, 2018, 2019). Together, these spatial point-process methods were used on the capelin density point values along transects to interpolate relative capelin density as described previously in Vogel et al. (2021). We assumed that the NASC-derived density values follow a negative binomial distribution. The resulting interpolated surface is thus assumed to represent the overall spatial capelin distribution throughout the entire the survey period (September – October), as well as the entire vertical water column. Hereafter we refer to the resulting interpolated density surface as the 'relative capelin density field'.

2.6 Capelin density whale interactions

2.6.1 Horizontal interactions

To investigate how changes in time-varying move persistence (γ_t) calculated based on the whales' three hrs-interpolated locations are influenced by environmental variables and how these relationships may vary between individuals, we used mixed-effect modelling using the 'mpmm' package in R (Auger-Méthé et al., 2017; Jonsen et al., 2019; Jonsen et al., 2020). Specifically, we examined two environmental variables potentially correlated with humpback whale horizontal movements: (1) horizontal capelin density and (2) sun angle (as a proxy for light intensity), which is thought to be correlated with vertical distribution of capelin (Gjøsæter, 1998; Mowbray, 2002). Light intensity was included to examine whether whales preferentially forage in lower light levels when capelin is closer to the surface, compared to when the capelin move down through the water column when light levels are higher. Based on the location and time of each whale track coordinate along each movement trajectory, a corresponding relative capelin biomass value was extracted from the relative capelin density field. Tracking points that occurred outside of this field were excluded from the analyses. Additionally, only tracking points that occurred in September or October 2018 were used in this study which overlapped with the capelin survey. Sun angle values were calculated for every point along each humpback whale trajectory based on their recorded location and time using the 'solarpos' function from the 'maptools' R package (Bivand and Lewin-Koh, 2021).

We modelled γ_t as a function of various combinations of the explanatory variables and random effects structures:

$$\mathrm{logit}(\gamma_t) = \rho_t + \alpha_t + (\rho_t + \alpha_t | \, \mathrm{id})$$

This equation allows for nine possible model permutations (Table 1) for how the two environmental explanatory variables (relative capelin density and sun angle) might influence whales move persistence. Fixed effects are represented by capelin density (ρ_t) and sun angle (α_t), and terms in parentheses indicate random slopes, with individual whale identifiers (id) representing random intercepts to assess the extent to which relationships may differ among individuals (see Jonsen et al., 2019 for further details). The models were ranked based on changes in Akaike's information criterion (ΔAIC) and likelihood ratio (ΔLR).

2.6.2 Vertical interactions

To further investigate how humpback whale movements were influenced by the spatial characteristics of capelin, we also compared the five whales with dive data records (Table 2) to NASC-derived capelin density within the capelin acoustic survey area (Figure 1A, dashed line). Only dive data occurring between September 4th 2018 (first day of tagging) and October 31st 2018 were used for dive analysis. The calculated vertical capelin distribution (at 10-meter depth resolution) was derived from the acoustic NASC values collected from the capelin survey, regardless of geographic location within the survey area, and was segmented by time of day. To do this, we first calculated 25th, 50th and 75th quantiles of humpback whale dive depths by hour using the 'quantile' function from the 'qgam' package (Fasiolo et al., 2017). We then calculated the mean NASC value of each 10m depth cell per hour. Using these depth bin averages, we calculated the weighted 25th, 50th and 75th quantiles for the capelin data using the 'Quantile' function from the 'DescTools' package (Signorell, 2023). Since quantile capelin data are a function of the NASC measurements, the mean NASC values per cell were used to weight the capelin centre of mass values.

To compare the whale dive depth with the weighted capelin depth, a Pearson's product-moment correlation test was performed on the hourly 50% quantile (median) values of both datasets. A linear regression model was used with the 'lm' function from the 'stats' package (R Core Team, 2022), using the 50% quantile of the humpback whale dive depths by hour as the response variable and the weighted 50% quantile of capelin depth by hour as the predictor variable.

TABLE 1 Ranked list of mixed-effect models based on changes in Akaike's information criterion (ΔAIC) and likelihood ratios (ΔLR).

Model Formula	df	ΔAIC	ΔLR
~ capelin density + sun angle + (capelin density + sun angle | id)	**10**	**154012.85**	**153992.85**
~ capelin density + sun angle + (sun angle | id)	7	1.14	7.14
~ sun angle + (sun angle | id)	7	13.89	19.89
~ capelin density + sun angle + (1 id)	5	37.17	47.17
~ capelin density + sun angle + (capelin density | id)	7	39.88	45.88
~ sun angle + (1 | id)	5	52.75	62.75
~ capelin density + (1 | id)	5	75.49	85.49
~ capelin density + (capelin density | id)	7	77.34	83.34
~ 1 + (1|id)	5	102.00	112.00

The highest ranked model is shown in bold and has corresponding absolute AIC and LC values shown, all others are relative ΔAIC and ΔLR to these values.

TABLE 2 Tag summary statistics.

ID	Tag type	Tagging date	Tagging location	Last day of transmission	Tag duration (days)	Total Interpolated Positions	Extracted positions between tagging and October 31st 2018
47596	Spot	4/9/2018	78°36'N 29° 00'E	17/11/2018	74	685	460
47597	Spot	4/9/2018	78°24'N 27°42'E	6/1/2019	124	1094	460
47599	Spot	4/9/2018	78°06'N 28°30'E	4/3/2019	181	1683	460
84494	Spot	5/9/2018	78°36'N 28°06'E	29/9/2018	24	191	191
171987	Spot	5/9/2018	78°30'N 29°00'E	28/10/2018	53	614	460
167842	Splash	8/9/2018	78°45'N 30°39'E	9/3/2019	161	437	148
167843	Splash	5/9/2018	78°36'N 28°12'E	22/12/2018	108	847	452
167844	Splash	4/9/2018	78°36'N 27°48'E	9/4/2019	217	1052	458
167845	Splash	4/9/2018	78°24'N 28°42'E	3/11/2018	60	470	459
47570	Splash	9/9/2018	78°48'N 29°42'E	20/4/2019	223	727	421

The number of interpolated positions between tagging date and October 31st is the number of positions used to link whale behaviour and capelin density.

3 Results

3.1 Humpback whale tag performance

Tag duration was generally longer for Splash tags (60-223 days, mean=152, sd=55, n=5) than for Spot tags (24 –181 days, mean=92, sd=55, n=5) (Table 2). The period all ten whales were tracked within the area (Figure 1; Supplemental Figure 1) covered by the capelin surveys between tagging date and October 31st ranged from 19 to 58 days (mean=50, sd=14). This gave a total of 208 whale-days of spatial overlap between capelin survey data and whale tracking data between tagging date and October 31st that were used for subsequent capelin-humpback whale horizontal interaction analysis.

3.2 Horizontal humpback whale movements and distribution

The tracks of all ten whales exhibited highly clustered, tortuous movement patterns east of Svalbard on the Spitsbergen, Great and Central Banks (Figure 1A; Supplemental Figure 2), also reflected in clusters of low move persistence (Figure 1C), indicative of area-restricted search (ARS).

3.3 Vertical humpback behaviour

The Splash tags recorded 13,530 humpback whale dives in total (ranging from 120 for 5701 per individual), where 10,692 of the dives occurred during the capelin survey period (Table 3; Figure 2). Supplemental Figure 3 shows all recorded dives over a 5-month period for the 5 individuals tagged with Splash tags. A clear diurnal pattern can be seen is September and October (representing 79% of all dives recorded). A diurnal pattern was not observed in November, December, and January. Average dive depth across the full tracks of all individuals was 110 ± 80 meters, and average dive duration was 6 ± 3 minutes. Overall average dive depth between tagging and October 31st and within the survey area was 110 ± 78 meters, and average dive duration was 5 ± 2 minutes. The maximum recorded dive depth for an individual whale between tagging and October 31st was 352 meters.

The 50th quantile of hourly humpback dive depths displays a clear diurnal pattern (Figure 2). On average, the whales dove deeper in the daytime between 06:00 and 13:00, and shallower at night between 16:00 and 00:00, with the intermediate hours spent shifting gradually.

3.4 Capelin-Humpback whale interactions

3.4.1 Horizontal interactions

There is a clear spatial co-occurrence between low move persistence areas of humpback whales and high capelin density patches (Figure 1D). On average, move persistence was inversely influenced by capelin biomass and sun angle (Table 3). The most parsimonious model, $\text{logit}(\gamma_t) = \rho_t + \alpha_t + (\rho_t + \alpha_t \mid \text{id})$, included random intercept and slope terms, suggesting that there are individual differences in overall movement characteristics between whales. On average, humpback whales tended to exhibit restricted movements in areas of high capelin densities, suggesting foraging behaviour (Figure 3A). All but two of the whales (ID 167845, and to a lesser degree, ID 167843, Supplemental Figure 4) responded this same way to changes in capelin biomass. The relationship between

TABLE 3 Diving information from Splash satellite tags deployed on five individual humpback whales.

ID	n dives	Mean dive depth (meters)	σ dive depth (meters)	Max dive depth (meters)	Mean Dive duration (min)	σ Dive duration (min)	Max dive duration (min)
167842	75	106.66	83.82	319.75	8.31	7.09	43.47
167843	3260	111.94	74.43	327.75	5.13	2.20	14.70
167844	3848	112.57	80.16	351.75	5.93	2.65	20.73
167845	2839	110.88	80.97	335.75	5.19	2.40	18.67
47570	670	94.72	77.15	343.75	4.25	1.88	12.57

Table summarises dives that were conducted between tagging date and October 31st 2018. ID numbers are given by the tag manufacturer.

move persistence and sun angle was highly variable between individuals (Figure 3B), with seven individuals showing negative relationships while three had positive relationships. This suggests that humpback whales generally exhibit low move persistence when in high capelin density areas, whereas their relationship with sun angle is highly individual. The second ranked model logit $(\gamma_t) = \rho_t + \alpha_t + (\alpha_t \mid \text{id})$, was also considered based on its ΔAIC (<1.14) and its small LR values, as well as the belief that using AIC based rankings frequently selects for the most complex models (Wagenmakers and Farrell, 2004). This model considers capelin density as only influencing random intercepts, whilst sun angle was both random intercept and slope terms (Supplemental Figure 5). This model

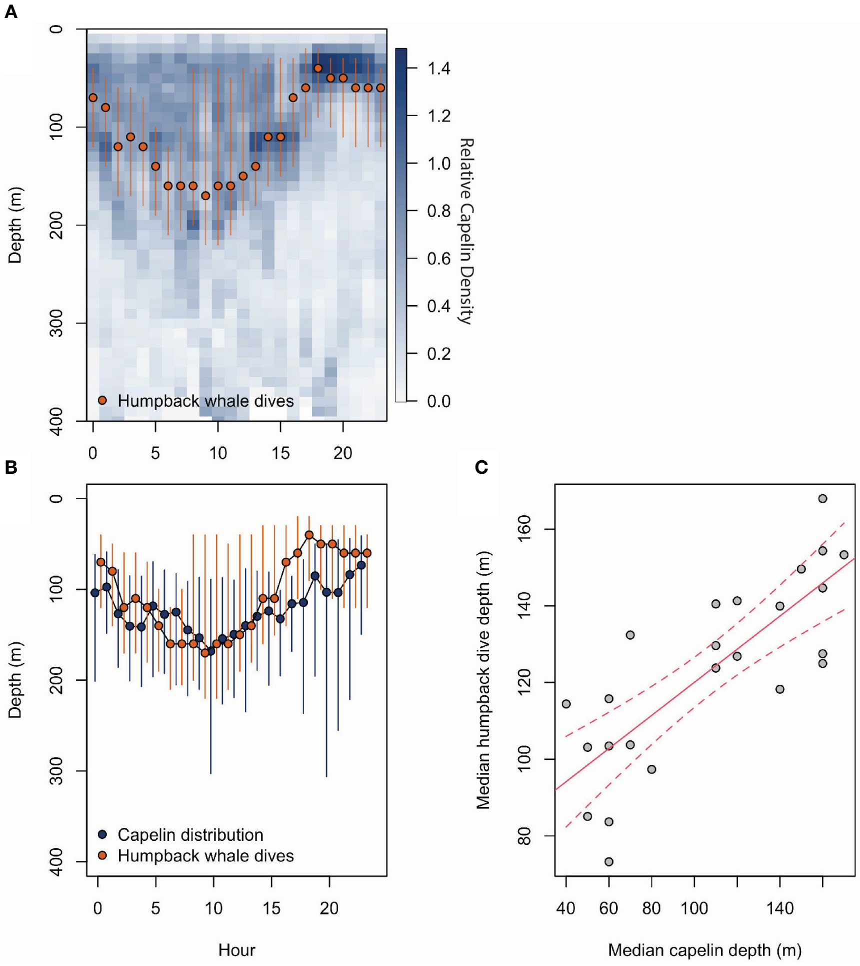

FIGURE 2
(A) shows relative capelin density throughout the water column and throughout the day from the IMR/PINRO Barents Sea Ecosystem Acoustic survey for capelin. The log transformed NASC values taken throughout the water column give a capelin density at 10 m depth bins. Here, dark blues indicate high relative capelin density and light blue indicate low relative capelin density. Superimposed over the capelin density is red points (representing median) and lines (representing 25-75% quantiles) of humpback dive depths. **(B)** again shows humpback whale dive depth median and 25%-75% quantiles in red with the same centre of mass capelin distribution in dark blue. Only dive data occurring between September 4th 2018 (first day of tagging) and October 31st 2018 were used because they overlapped temporally with the capelin survey. **(C)** shows the results from a linear regression model in red, with capelin median depth as the predictor and median humpback whale dive depth is the response variable.

indicated that all whales responded this same way to changes in capelin density, however whales respond individually to changes in sun angle, suggesting no clear relationship at the population level.

3.4.2 Vertical interactions

We found a strong positive linear relationship between whale dive depth and capelin distribution (adjusted $r^2 = 0.6086$, $p = 4.21e\text{-}06$, Figure 2). This suggests that humpback whale dive depth increases with capelin depth.

4 Discussion

Humpback whales broadly follow the spatial distribution and vertical movements of capelin when on the summer feeding grounds in the Barents Sea. Reduced speed and directionality of horizontal movements within areas of high capelin density strongly suggest that humpback whales target high-density capelin areas. Past ecosystem surveys, opportunistic sightings, and whaling records have all indicated that the area east of the Svalbard archipelago is an important foraging ground for northeast Atlantic humpback whales during late summer and fall (Nøttestad et al., 2015; van der Meeren and Prozorkevich, 2018; Hamilton et al., 2021). In addition, Ressler et al. (2015) found, based on visual whale sightings and echosounder caplin data, that humpback whale distribution correlated with the acoustic estimates of capelin. Through the use of satellite tracking, our study expanded on Ressler et al. (2015) by correlating individual humpback whale movement behaviour with capelin density. This supports the hypothesis that capelin are either (A) directly a key prey species for humpback whales during the late summer in the Barents Sea, or (B) that capelin and humpbacks target the same prey species, such as copepods and krill. Regardless of whether either or both of these hypotheses are true, our finding of humpback whales foraging movements being influenced by changes in capelin density distribution supports the strong link between humpback whales and capelin.

In addition to the strong negative relationship between capelin biomass and move persistence, our most parsimonious model also suggested that light intensity influenced the movement behaviour of humpback whales. Overall, the negative relationship between light intensity and whale move persistence suggests that whales display area-restricted foraging behaviour at higher sun intensities. This could reflect the whales diving deeper during the day to reach the capelin that migrate to the deep when light intensities are stronger (Dalpadado and Mowbray, 2013; Skaret et al., 2020; Fall et al.,

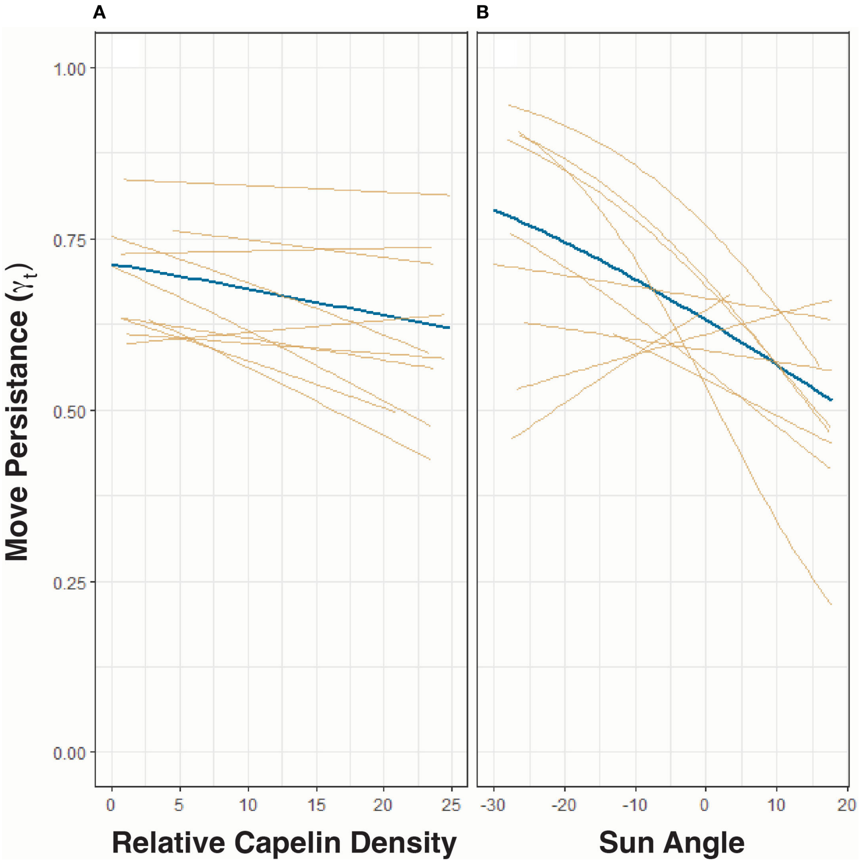

FIGURE 3
Most parsimonious model from mixed effect analysis of the relationship between humpback whale move persistence (γ_t) and relative capelin density **(A)** and sun angle (light intensity, **(B)**. Fixed effects are depicted in blue and random effects in yellow. As per the most parsimonious model [$\text{logit}(\gamma_t) = \rho_t + \alpha_t + (\rho_t + \alpha_t \text{id})$] in Table 2, both panels allow for random intercepts and random slopes.

2021), and therefore the whales have restricted surface behaviours. However, the substantial variability in the individual responses to light intensity suggests that this relationship is not uniform across individuals and may simply be a spurious artifact. For example, this individual variability could be due to the variations across both tag retention time and the amount of time each whale spent within the geographical limits of the capelin surveys in the Barents Sea. Furthermore, seeing as in the summer, light is consistently intense (high sun angle) in the Barents Sea due to its high latitude. Some whales stayed in this northern foraging area throughout the polar night until as late as January, well after the sun has ceased to rise over the horizon. It is plausible that the 3 h reconstructed step intervals used in this study might not provide sufficient temporal resolution to detect variations in the horizontal whale movements caused by capelin diel vertical migrations (Postlethwaite and Dennis, 2013). Similarly, the vertical migrations of capelin in the water column only influence the dive depth patterns of humpback whales, and not their horizontal movements (or at least not at this resolution). This is consistent with our finding of whale depths consistently following the capelin depths throughout the day and night. This explanation agrees with recent pinniped studies that suggesting that both vertical and horizontal movements need to be considered when examining seal foraging (Bestley et al., 2015; Carter et al., 2016). Fine-scale studies of humpback whale diving behaviour in other regions (e.g. Friedlaender et al., 2013) have found strong diel variations in their dive behaviours relating to variations to their prey and its relationship to light.

We also showed a strong positive correlation between whale dive depth and vertical capelin distribution. During the capelin survey period, August-October, capelin were found concentrating at the surface at night and moving deeper during the day. Correspondingly, humpback whale dive depths (between September and October) also showed a diurnal vertical pattern matching the capelin distribution. This diel vertical pattern in humpback whale diving behaviour likely reflects feeding on the densest patches of capelin, suggesting that humpback whales adjust their diving behaviour in response to capelin density distributions in the water column. Our findings are consistent with previous studies showing that foraging humpback whales in other waters maximised their energetic gain by targeting the densest prey depth layers to optimise their energy efficiency (Goldbogen et al., 2008; Ware et al., 2011; Friedlaender et al., 2013; Burrows et al., 2016; Friedlaender et al., 2016). Our results also suggest that humpback whales may feed throughout the day and night, which may help explain the complex relationship between horizontal move persistence and sun angle. The diurnal pattern of whale dive depth observed in September and October was not observed in November, December, or January. This might be expected since the attenuation of diurnal diving patterns in other polar marine mammals has been observed in winter (Biuw et al., 2010). Furthermore, since the number of dives recorded in November, December and January were limited, and only represented 21% of the total dive data, it is possible that the limited number of dives was insufficient to statistically reveal any underlying dive depth patterns.

While our results suggest a strong correlation between capelin distribution and humpback whale movements, it should be noted that there are differences in the spatial and temporal coverage of these datasets that might inadvertently introduce bias. The capelin biomass density field is based on directly measured NASC-derived capelin density that was limited to the geographical range covered by the acoustic surveys. To accommodate this, we limited our analyses to use only humpback whale location points that fell within the survey region. Furthermore, since the annual Barents Sea ecosystem cruise that collected the capelin data used in this study was conducted between August and October 2018, our INLA analysis represents a static image of capelin density for this time-period. In contrast, our whale satellite tagging data sometimes extended for time periods past this period, and typically with higher temporal resolution. For this reason, the whale movement data used in our analysis, either horizontal or vertical, was truncated to only include data that matched both the geographic and temporal constraints of the capelin survey data. Our capelin density distribution models a static spatial distribution over the survey area, and our mixed-effects modelling assumes that this static distribution is representative of the capelin distribution over this time period. While the broad-scale spatial distribution of capelin is believed to remain relatively stable over the summer and fall months, we cannot discount the possibility of variations resulting from fine-scale physical and biological oceanic dynamics that might occur. These variations could potentially influence whale movements. Nonetheless, the fact that we observed correlations between our static capelin distribution and our dynamic whale horizontal movements suggest that our static image captures the key aspects of the capelin distribution during this period, and therefore provides valuable information about predator-prey interactions. Similar analyses have previously found good agreement between herring distribution and killer whale move movement patterns in the Norwegian Sea (Vogel et al., 2021).

Our comparison of whale depth movements and capelin depth distribution also involves certain assumptions related to the spatial and temporal distributions of capelin that again might inadvertently introduce bias. For this comparison, we aggregated all the capelin depth data, regardless of location, to create a matrix of capelin density as a function of depth over time. Similarly, our whale depth data was aggregated within the survey region, to reveal whale depth use as a function of time of the day. This analysis does not consider the possibility that the depth uses of capelin and whales might differ geographically over the survey area. Regardless, the strong correlation between whale and capelin hourly depth suggests that their depth uses were relatively stable across the survey region, and again provides insight into the humpback whale-capelin predator prey interactions. The vertical movements of diving air-breathing animals almost certainly influence their horizontal behaviour, and a horizontal movement model would therefore most likely be improved by inclusion of such vertical information (Bestley et al., 2015; McClintock et al., 2017). However, in this study, only half of the whales were tagged with Splash tags (n=5) that provided both horizontal and vertical movement information. While this limited sample size is likely be sufficient for providing an indication of the relationship between the vertical diving behaviour and the vertical prey distribution, these data were too sparse for developing and fitting a complex three-dimensional model. For this reason, we analysed the horizontal and vertical movement and prey distribution data separately. A comparative study of three-dimensional whale movement in relation to the three-dimensional distribution of their prey might add further insight into whale predator prey behaviour. Future studies using only Splash tags are warranted to explore this multidimensional analysis.

This study presents direct evidence of the influence capelin density has on humpback whale movements in the Barents Sea, without relying on prey proxies. It highlights the direct relationship between prey and predator movements, emphasizing the importance of measuring prey density for a deeper understanding of marine predator-prey dynamics. This study also provides a timepoint against which future changes in humpback whale foraging behaviour and responses to environmental changes can be assessed.

Data availability statement

The raw data supporting the conclusions of this article will be made available by the authors, without undue reservation.

Ethics statement

The animal study was approved by the Norwegian Food Safety Authority 123 (Mattilsynet) under permit FOTS ID 14135 2017/279575. The study was conducted in accordance with the local legislation and institutional requirements.

Author contributions

EV: Conceptualization, Data curation, Formal Analysis, Investigation, Methodology, Validation, Visualization, Writing – original draft, Writing – review & editing. SS: Data curation, Formal Analysis, Investigation, Writing – original draft. MB: Conceptualization, Investigation, Methodology, Supervision, Validation, Visualization, Writing – review & editing. M-AB: Formal Analysis, Investigation, Supervision, Writing – review & editing. LK: Data curation, Writing – review & editing. GS: Methodology, Validation, Writing – review & editing, Investigation. NØ: Data curation, Writing – review & editing. AR: Conceptualization, Funding acquisition, Investigation, Resources, Supervision, Writing – review & editing.

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Conflict of interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

Publisher’s note

Supplementary material

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fmars.2023.1254761/full#supplementary-material

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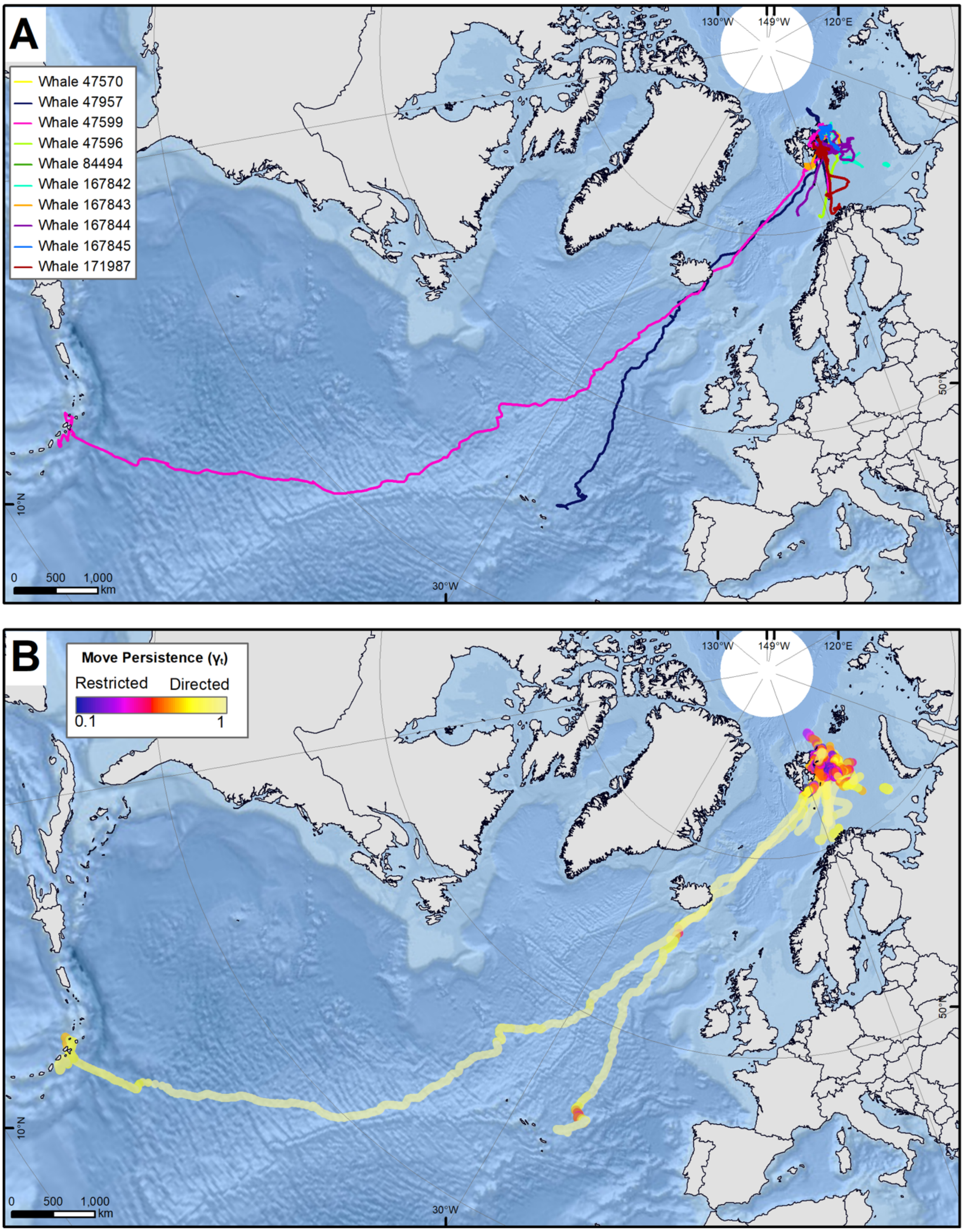
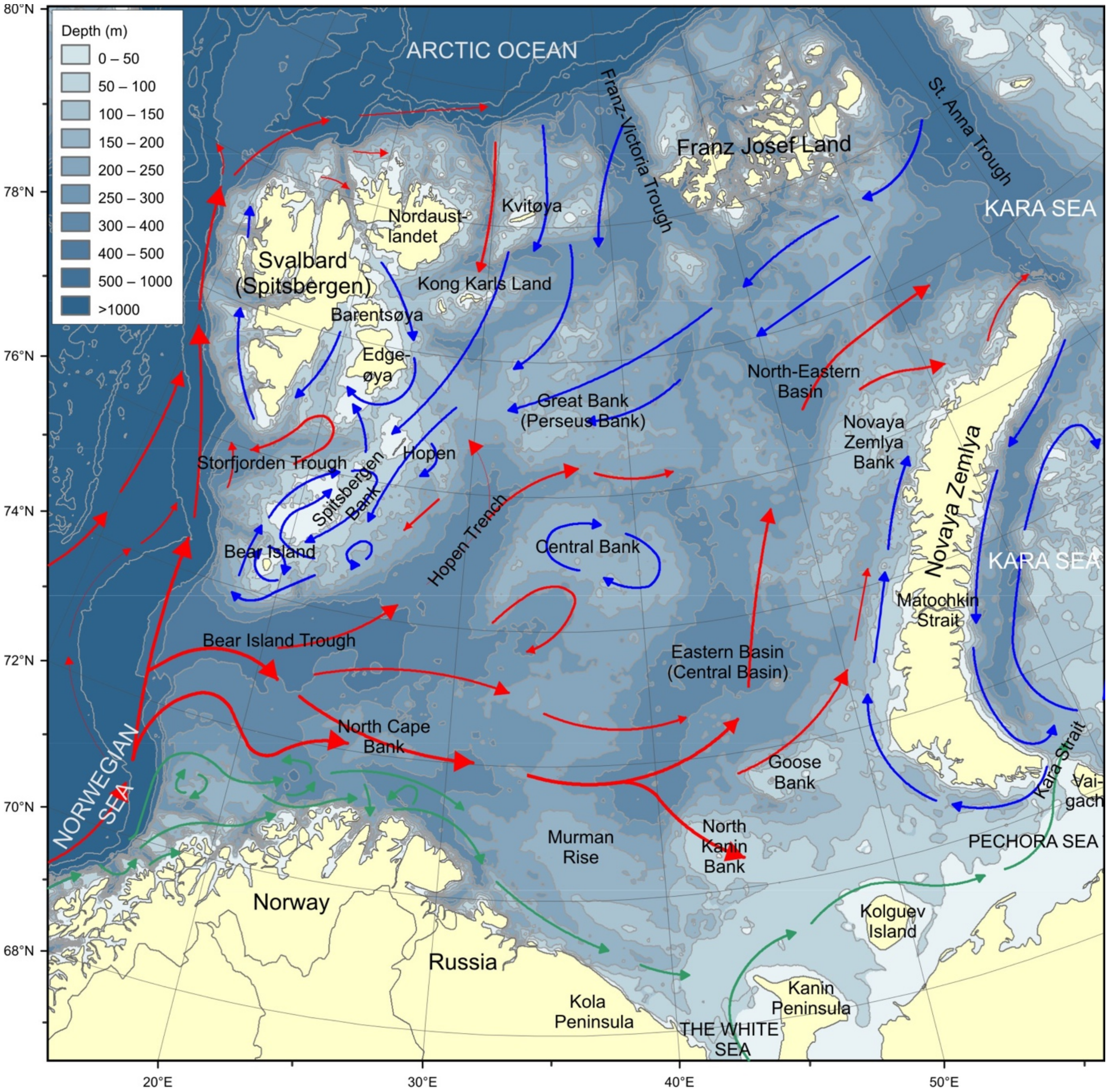
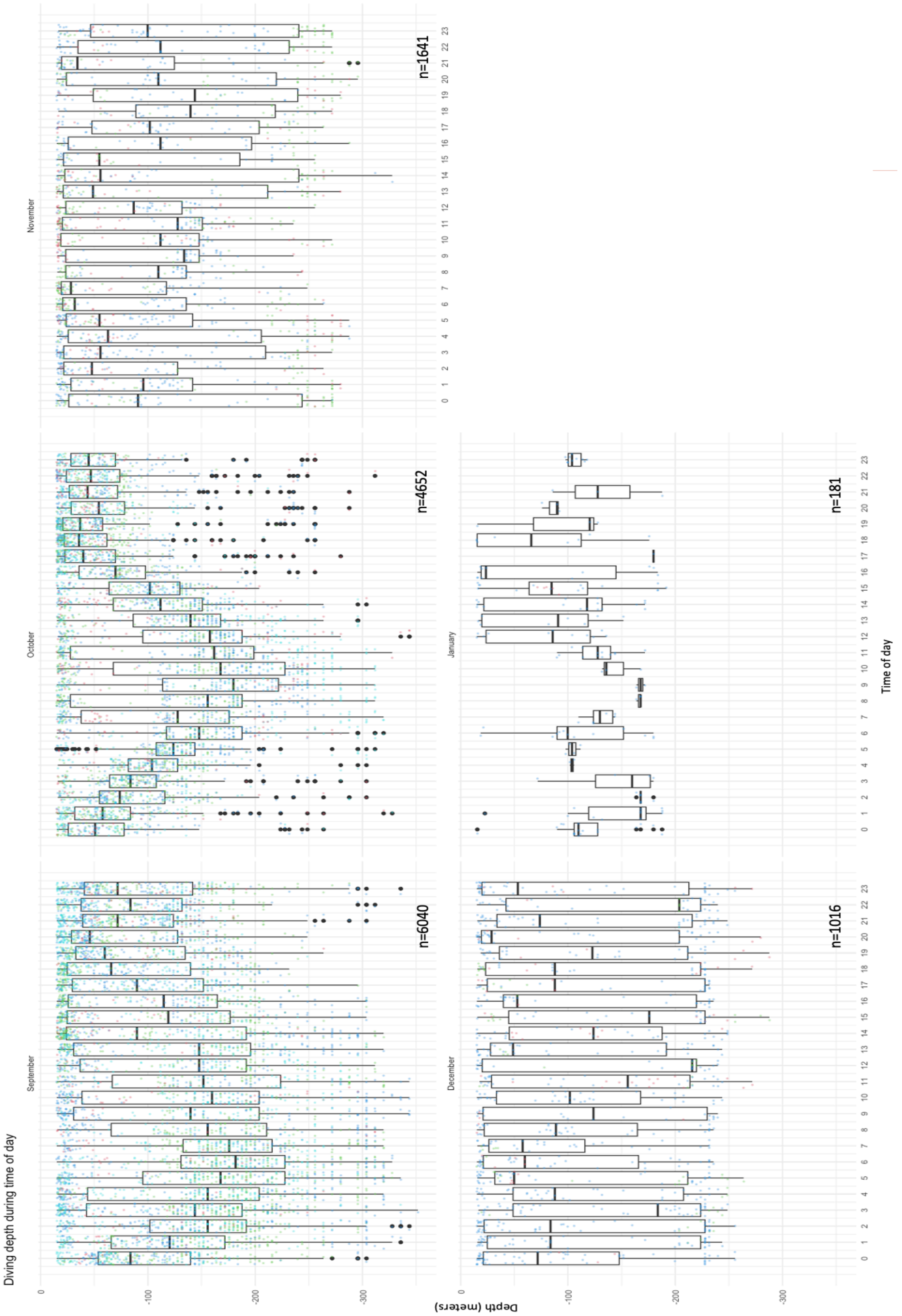


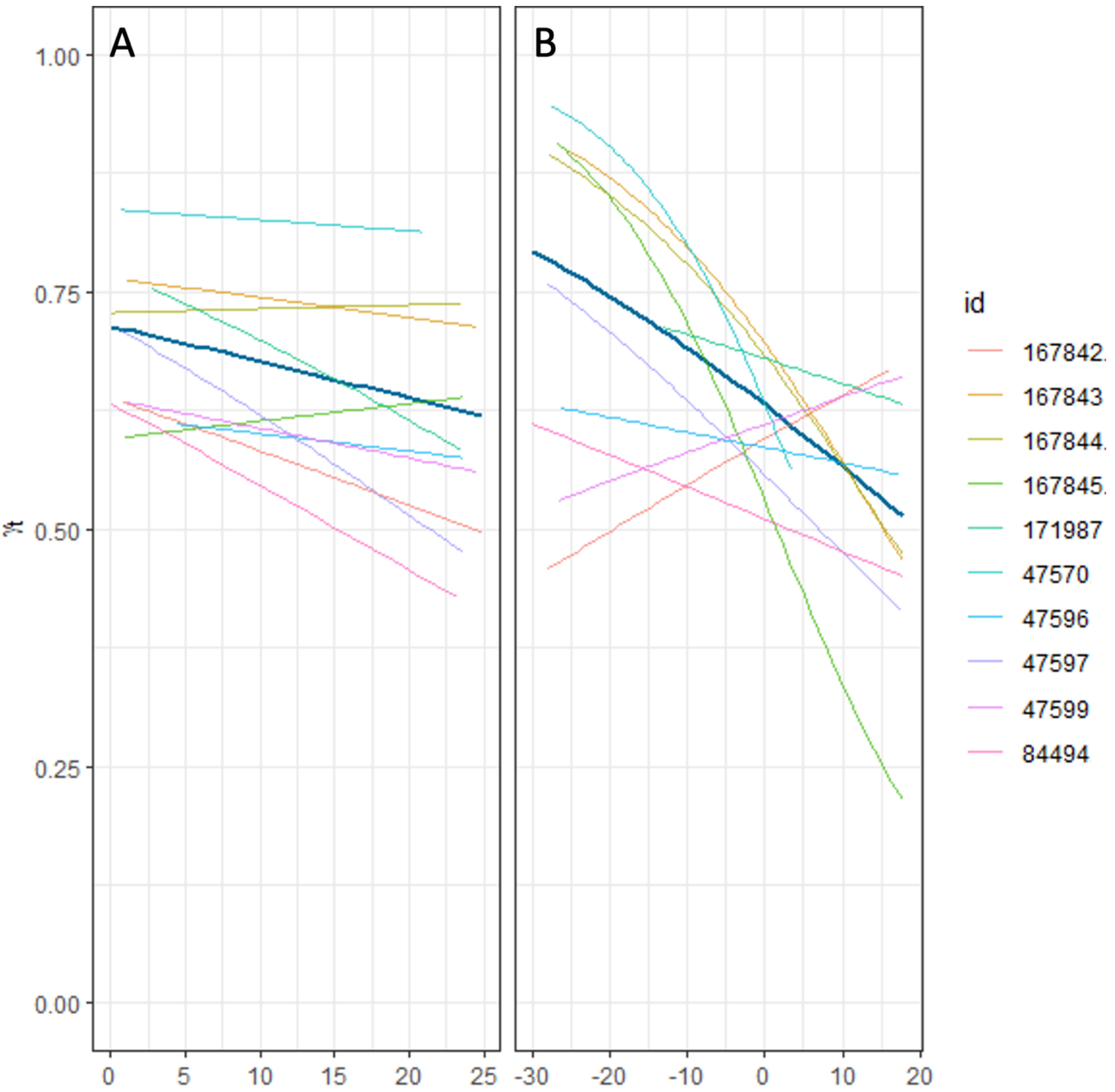
Supplementary Figure 1 Humpback whale CRW tracks from 10 whales tagged (5 Spot tags, 5 Splash tags) tagged in the northern Barents Sea tagged in the beginning of September 2018 shown in panel A. Two individuals (ID and ID) tags continued transmitting signals throughout their southward migration to towards their respective breeding grounds. Panel B humpback whale move persistence (γ_t) estimates overlaid, where yellow points indicate high γt (i.e. transiting behaviour) and pink/purples indicate low γ_t (i.e. restricted foraging behaviour).



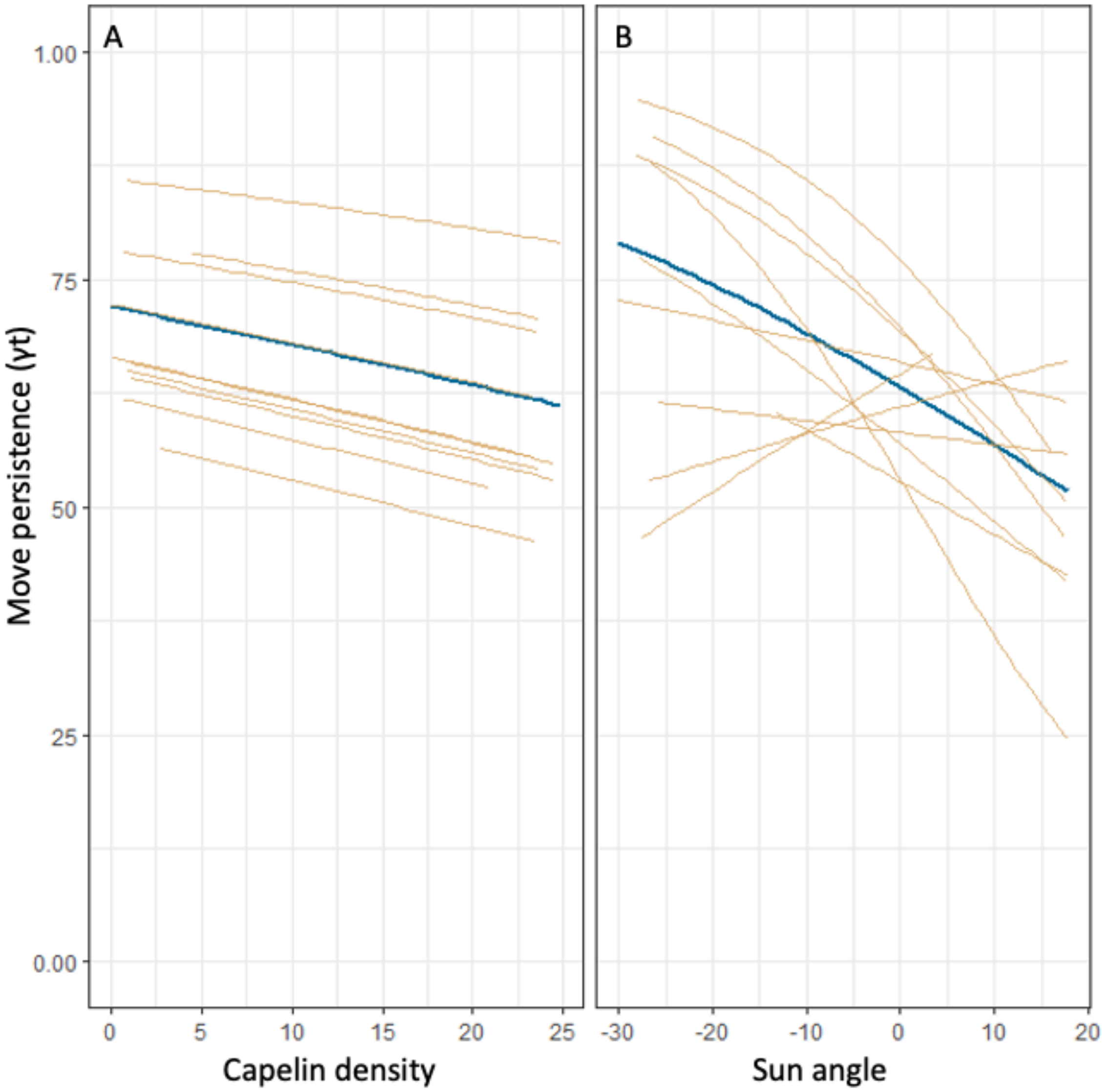
Supplemental Figure 2 Map of the Barents Sea with seafloor topography and main ocean currents, where red arrows indicate Atlantic currents, blue arrows indicate Arctic currents and green indicate coastal currents. (Reproduced from https://www.hi.no/hi/temasider/hav-og-kyst/hav-kyst-og-fjord/barentshavet).



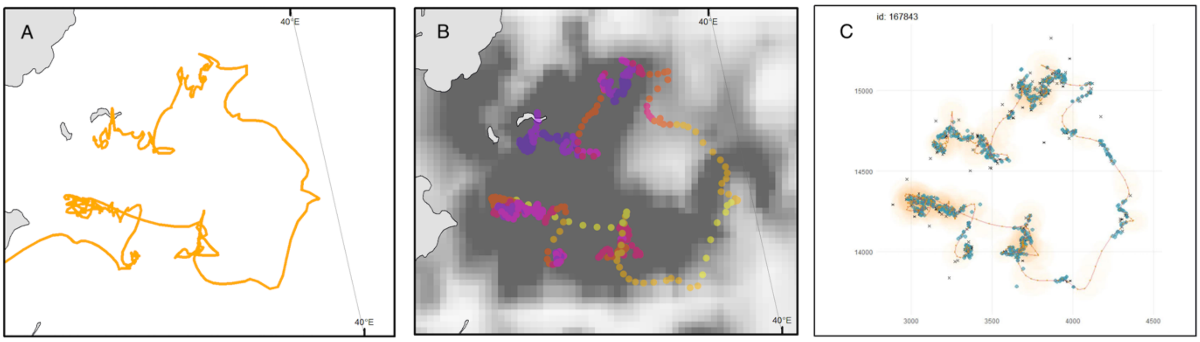
Supplemental Figure 3 Boxplots of humpback (n=5) dive depths recorded by Splash tags and parsed by hour of the day and by month. Colored points are superimposed over the box plots to indicate each actual dive depth measurements and are colored by individual ID. Only dive depth data occurring in September and October were used in our correlation analysis with vertical capelin distribution.



Supplemental Figure 4 Most parsimonious model (logit(γ_t) = $\rho_t + \alpha_t + (\rho_t + \alpha_t \mid \text{id})$) from mixed effect analysis of the relationship between humpback whale move persistence (γ_t) and (A) relative capelin density and (B) light intensity (sun angle) in table 3. Here both panels allow for random intercepts and slopes. Fixed effects are represented by the bold dark blue line, while random effect lines are colored by whale ID and indicates that 167845, and to a lesser degree 167843, are the only whales with a differing relationship with change in capelin biomass.



Supplemental Figure 5 Second ranked model (logit(γ_t) = $\rho_t + \alpha_t + (\alpha_t \mid id)$) from mixed effect analysis of the relationship between humpback whale move persistence (γ_t) and (A) relative capelin density and (B) light intensity (sun angle) from table 3. Here both panels allow for random intercepts, while only panel B allows for random slopes. Fixed effects are represented by the bold dark blue line, while random effect lines are yellow.



Supplemental Figure 6 Track from exemplar humpback whale ID 167845 (at 3-hr time interval steps) instrumented in the northern Barents Sea in September 2018 (panel A). Panel B shows relative density of capelin with humpback whale move persistence (γ_t) estimate points between September 4th 2018- and October 31st overlaid, where yellow points indicate high γ_t (i.e. transiting behaviour) and dark purples indicate low γ_t (i.e. restricted foraging behaviour). Dark black indicates areas of higher relative density. Panel C shows the same track showing the raw ARGOS points (blue points), modeled state space model CRW points (small orange points along orange line), as well as the location uncertainty (light orange 95% confidence ellipses). X is indicated points excluded from SSM due to poor data quality.