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Migration Ecology of North Atlantic Humpback Whales

Mapping Movements throughout the Annual Cycle

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Summary

Animal migration is a fascinating natural phenomenon where large numbers of animals embark on long-distance journeys, seeking out favorable environmental conditions and prey throughout the annual cycle. During their journeys, migrating animals play essential roles in a range of ecosystems and in human economies and cultures. Documenting the movement patterns of migrating animals is essential for understanding ecosystem processes and assessing the threats of a changing climate and anthropogenic disturbance. Whether migrating animals are capable of responding to ecosystem changes and their vulnerability to anthropogenic stressors are important questions in a rapidly changing world. However, studying migrating animals throughout their annual movements is logistically challenging, leading to knowledge gaps in some species' migration patterns and the mechanisms driving them, especially in the vast and dynamic ocean environment.

In this thesis, a range of techniques was used to fill major knowledge gaps in humpback whale (*Megaptera novaeangliae*) movement patterns and migration ecology in the North Atlantic Ocean. The main objectives were (1) to document the movements of North Atlantic humpback whales throughout the annual cycle, with a particular focus on the Northeast Atlantic and reproductive females, (2) to study the migration strategies of these animals, and (3) to provide novel insights into the annual budgeting of energy during humpback whale migration.

This thesis contains the description of a fully tracked annual migration of a pregnant female humpback whale, which demonstrated connectivity between three Northeast Atlantic feeding grounds (Barents Sea, Norway, Iceland) within the same season. Our results show that whales can adapt their migration speed to compensate for time spent foraging during winter while successfully providing for a calf. This work offered detailed insights into the movements of a mother-calf pair throughout the entire migration and suggested that the energetic cost of one of the longest documented mammalian migrations may be higher than in other humpback whale populations.

In the second paper, we described the seasonality and spatial development of a foraging site in the northern Norwegian fjords during winter, using photo-identification. A female-biased sex ratio and high return rates to this area demonstrate that this site has become an important part of the annual cycle predominantly for female humpback whales in the Northeast Atlantic. Our results confirmed the connectivity between the Barents Sea feeding ground and the Norwegian winter feeding aggregation. Finally, we provided the first estimates of pregnancy rates for Northeast Atlantic humpback whales.

We then compiled a basin-wide dataset of humpback whale movement from satellite telemetry collected over the last two decades. We identified six distinct migration strategies humpback whales use during their long migration between high latitude foraging grounds and the tropical breeding ground. Migration distance explained only 23% of the variation in these migration strategies, which highlights the enormous variability of migration strategies within foraging sites. We documented for the first time that some animals migrated toward the breeding grounds but spent no time in the area before returning northward. This work presented movement patterns inferred from satellite telemetry in all known foraging grounds of the North Atlantic and the main breeding ground in the West Indies.

In conclusion, this thesis revealed important novel information on the space use of North Atlantic humpback whales throughout the year and the specific behaviors and habitat use of reproductive females. The included papers presented crucial knowledge regarding the migration ecology of Northeast Atlantic humpback whales, their unusual annual schedules, the connectivity between different areas of the foraging grounds, and their specific migration strategies and energetic requirements. This information can inform ecosystem management and assessment of the species’ conservation status. The presented movement patterns are a valuable reference for future changes caused by continued climate change and increasing anthropogenic use of the ocean.

List of included papers

I: Kettemer, L.E., Rikardsen, A. H., Biuw, E.M., Broms, F., Mul, E., & Blanchet, M. A. (2022). Round-trip migration and energy budget of a breeding female humpback whale in the Northeast Atlantic. *PloS ONE*, *17*(5), e0268355.

II: Kettemer, L.E., Ramm, T., Broms, F., Biuw, E.M., Blanchet, M.A., Bourgeon, S., Dubourg, P., Ellendersen, A.C.J., Horaud, M., Kershaw, J., Miller, P.J.O., Øien, N., Pallin, L.J., Rikardsen, A. H. (202X). Don't Mind if I Do - Arctic humpback whales respond to winter foraging opportunities before migration (accepted in *Royal Society Open Science*).

III: Kettemer, L.E., Biuw, E.M., Blanchet, M.A., Clapham, P.J., Ferguson, S.H., Fossette, S., Heide-Jørgensen, M.P., Kennedy, A., Laidre, K.L., Lawson, J., Lefort, K., Matthews, C.J.D., Nourani, E., Øien, N., Robbins, J., Vély, M., Víkingsson, G.A., Zerbini, A.N., Rikardsen, A.H., (202X). From the Arctic to the Tropics - Mapping humpback whale migrations across the North Atlantic (manuscript)

Contributions

	Paper I	**Paper II**	**Paper III**
Concept and idea	**LEK**, AHR,	**LEK,** FB, AHR	**LEK**, AHR, MPH, AZ
Study design and methods	**LEK**, EMB, MB, AHR, EM	**LEK**, TR, FB, SB, LP	**LEK**, EN, EMB, AHR, MB, AZ
Data gathering and/or laboratory work	**LEK**, EM, AHR	**LEK**, TR, FB, AHR, MB, NO, SB, AE, PM, JK, MH, PD	**LEK**, AHR, NO, MPH, MV, AK, JR, SF, SHF, CM, JL, KL, KrL, GAV, PC, NO
Analysis and interpretation	**LEK**, MB, AHR, EMB	**LEK**, LP, JK, TR	**LEK**, EN, EMB, AHR, MB, AZ
Manuscript preparation (with additional input from all coauthors)	**LEK**, MB, AHR, EMB, EM	**LEK**, TR, AHR, EMB, MB	**LEK**, EMB, MB, AHR, AZ

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1 Introduction

Animal movement is a foundational aspect of ecology that shapes patterns of biodiversity in many ecosystems of the world. These emergent biodiversity patterns are underpinned by individuals and groups of animals completing the complex tasks of finding resources, avoiding risks, and moving efficiently through their respective landscapes (Dingle and Drake, 2007). One of the most impressive feats of animal movement is the migrations that highly mobile animals undertake across often large distances. Migration is a ubiquitous phenomenon across animal taxa that allows animals to take advantage of spatially and seasonally separate favorable habitats or resources, including food, breeding opportunities, and shelter throughout the year (Dingle and Drake, 2007; Chapman *et al.*, 2014). Migration can be considered the directed movement between home ranges, within which animals move on smaller temporal and spatial scales (Figure 1), although many variations of this definition exist in the literature (Dingle and Drake, 2007). Migration occurs across vastly different temporal and spatial scales: plankton exhibit diurnal vertical movements, birds,

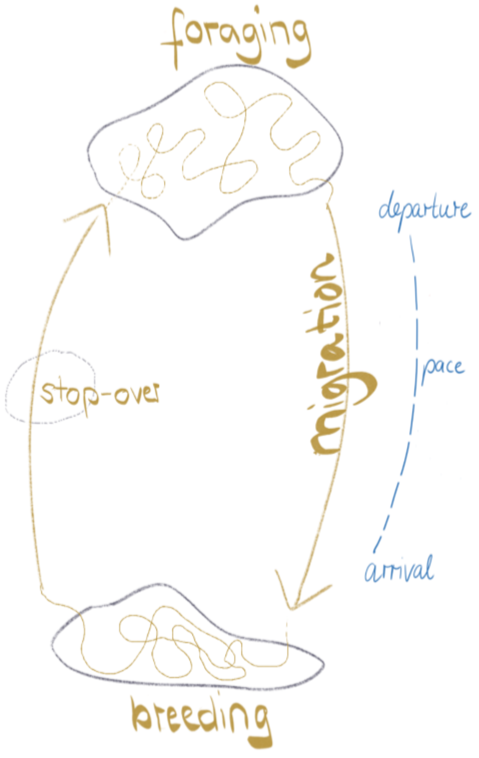

Figure 1 Schematic representation of a return migration between geographically and seasonally separate foraging and breeding areas, within which animals move in a less directed manner. During the migration, departure time, migration pace, and arrival time, as well as the use of potential stop-over areas, are important determinants of migration characteristics.

and whales undertake long-distance annual migrations, monarch butterflies engage in multi-generational migrations, and salmon and sea turtle hatchlings embark on once-in-a-lifetime journeys.

No matter the scale, the seasonal movements of large numbers of insects, birds, fish, or mammals play crucial roles in global ecosystems (Roman and McCarthy, 2010; Bauer and Hoye, 2014; Olds *et al.*, 2016). Animal migrants act as vectors between ecosystems, transporting nutrients, diseases, and parasites across vast spatial scales (Altizer, Bartel and Han, 2011; Bauer and Hoye, 2014). While they occupy their seasonal habitats, they usually occur in great numbers, acting as important predators and heavily impacting nutrient transfer throughout the system (Lundberg and Moberg, 2003). Whales do so, for example, by fertilizing the ocean via defecation (Roman and McCarthy, 2010; Roman *et al.*, 2014), and migrating salmon transport nutrients from the open ocean to forest ecosystems as they migrate up streams to spawn (Helfield and Naiman, 2001). Animal migrants are also important for human economies and nutrition (e.g., herring, salmon, whales, locusts) and hold significant cultural value globally (Shuter *et al.*, 2011). Given the vital role of migration in global ecosystems, describing migration patterns and understanding the mechanisms underlying the phenomenon on an individual and population level is an important challenge in ecology (Bowlin *et al.*, 2010).

A range of methods can be used to document the movements of animal migrants throughout the annual cycle. Mark-recapture methods, genetics, and, more recently, biotelemetry each provide valuable insights into movement patterns across scales. However, the migration patterns of many species are still unknown, making it challenging to identify mechanisms underlying migration patterns and factors affecting migrating animal populations. As a first step toward conserving migratory species, the seasonality of their movements, spatial corridors, and habitats must be defined (Webster *et al.*, 2002; Seidler *et al.*, 2015; Hays *et al.*, 2019). Information from movement data collected by satellite can then be linked to the energetic budgets on an individual (Braithwaite, Meeuwig and Hipsey, 2015) and then population level (Dunlop *et al.*, 2021; Pirotta, 2022). Energetic budget models can be used to assess the impact of anthropogenic disturbance and climate change on migratory species (van der Hoop, Corkeron and Moore, 2017; Pirotta, Mangel, *et al.*, 2018).

To understand the mechanisms that drive migration patterns, we can assess observed patterns in the context of energetic and reproductive outcomes. Optimal migration theory was developed to understand trade-offs associated with migratory decisions on an individual level using optimality principles (Alerstam, 2011). To survive and reproduce successfully, animal migrants must maximize fuel intake and limit energetic costs throughout migration. A migrating individual can optimize its movements either to minimize the locomotion costs by reducing the pace of migration or by minimizing the migration duration, which saves on daily metabolic costs (Hedenström and Alerstam, 1995). Many migrants are long-lived capital breeders that decouple the breeding and foraging season, and balancing their energy budget throughout the year is of unique importance for their fitness (Evans and Bearhop, 2022). Migratory decisions are constrained by species-specific qualities (e.g., locomotion mode), an individual’s annual energetic needs, and life-stage-specific requirements (Avgar, Street and Fryxell, 2014). Individual differences in learning and experience also contribute to observed differences in migration patterns (Fayet, 2020). For example, site fidelity is thought to inhibit, to some degree, the adaptation to changed conditions (Matthiopoulos, Harwood and Thomas, 2005; Abrahms *et al.*, 2021). External factors, such as density effects (Mysterud *et al.*, 2011), prey dynamics (Szesciorka *et al.*, 2020), and environmental conditions (Shaw, 2016), also modulate the conditions under which animals have to optimize migratory decisions.

Matching movements to the occurrence of resources in the seasonal cycle (phenology), and reproductive needs, is another primary constraint of animal migration (Alerstam and Bäckman, 2018). To successfully match their movements to the occurrence of resources, migrants rely on the predictability of prey occurrence and environmental conditions (Alerstam, Hedenström and Åkesson, 2003; Avgar, Street and Fryxell, 2014). On smaller scales, the heterogeneous distribution of resources, especially in patchy and dynamic marine environments, means that animals are inherently adapted to be able to respond to natural fluctuations in resources, but this ability is specific to a species’ behavioral and energetic potential (Fleming *et al.*, 2016; Abrahms *et al.*, 2018, 2021; Shuert *et al.*, 2023). Identifying plasticity in migratory behavior is a priority in understanding potential responses to disturbance and changes in environmental conditions (Lindström *et al.*, 2014; Silber *et al.*, 2017).

Climatic change or anthropogenic impacts can disrupt the balance of animal movements with their environment, leading to a mismatch between resources and the animals that need them. Changes in migratory timing in response to changes in, for example, the timing of spring onset are now well documented to affect marine systems (Anderson *et al.*, 2013; Ramp *et al.*, 2015; Descamps *et al.*, 2017). For marine vertebrates, direct physiological effects and changes in the predator-prey relationship are predicted to be most common outcomes of climate change (Sydeman *et al.*, 2015), resulting in altered distributions (Silber *et al.*, 2017) and migration phenology (Ramp *et al.*, 2015). In addition to these changes, marine migrants face habitat alterations, from increasing human use of the oceans, including coastal development, ship traffic and pollution (Avila, Kaschner and Dormann, 2018).

While their movements may provide them the opportunity to escape certain conditions at some time during the year, migratory species are, for the same reason, exposed to a variety of potentially harmful human impacts across the range of their movements (Lascelles *et al.*, 2014). Migratory species, therefore, present unique challenges to management and conservation since they cross and inhabit a range of different countries' economic zones and often spend much of their time in areas outside of national jurisdiction (Harrison *et al.*, 2018; Dunn *et al.*, 2019; Hays *et al.*, 2019). Understanding the population structure and exchange based on movements is essential for designing effective management, conservation interventions, and monitoring programs (Lascelles *et al.*, 2014; Clapham and Zerbini, 2015).

2 Study species

Humpback whales (*Megaptera Novaeangliae*) undertake one of the most enigmatic animal migrations. Like many other species of baleen whales (Mysticetes), they migrate thousands of kilometers between breeding and foraging areas (Brown, 1957). Humpback whales are capital migrants, *sensu* Evans and Bearhop (2022), that decouple the foraging and breeding season almost entirely. In contrast, income migrants continue foraging as they migrate (Evans and Bearhop, 2022). As generalist predators, they feed on krill (*Euphausiacea*) or small forage fish, including herring (*Clupea harengus*), capelin (*Mallotus villosus*), and sand lance (*Ammodytes* spp.), at high latitudes of all ocean basins during the productive season (Chittleborough, 1953). Rorqual whales (balaenopterids) forage via a mechanism termed lunge diving. This highly costly filter feeding mode requires high densities of prey on the feeding grounds to be effective in energy acquisition (Goldbogen *et al.*, 2011). Rorqual whales are uniquely adapted to migrating extremely long distances because of this efficient mode of foraging at high prey densities, large capacity for fat storage, and efficient mode of transport due to their size (Hein, Hou and Gillooly, 2012), adaptations that release them from some constraints other migrants experience. However, the upper bounds of baleen whale migration capabilities continue to be an active area of research.

Humpback whales breed at low latitudes in areas delineated by the 21°C thermocline (Rasmussen *et al.*, 2007). Patterns in migration timing and routes vary with sex, age, and reproductive stage as they are mediated by differing energetic and habitat requirements (Dawbin, 1966; Lockyer, 1986; Brown *et al.*, 1995; Craig and Herman, 2000; Pallin, Baker, *et al.*, 2018; Bejder *et al.*, 2019). While males may aim to arrive early on breeding grounds to maximize access to mating opportunities and thus leave feeding grounds early in the season, pregnant females generally stay longest on feeding grounds to maximize energetic intake (Chittleborough, 1965; Dawbin, 1966; Pallin, Baker, *et al.*, 2018). Mother-calf pairs may choose migration routes near coastal areas where they can rest and nurse (Craig and Herman, 2000; Bejder *et al.*, 2019). Migration destinations to breeding and foraging grounds are thought to be stable and maternally directed, as calves remain with their mothers for their first migration during the first year (Clapham and Mayo, 1987; Baker *et al.*, 2013). As a result, site fidelity, or annual return rates to foraging grounds, are high (Clapham *et al.*, 1993; Herman *et al.*, 2011; Barendse *et al.*, 2013). Usually, humpback whales also exhibit site fidelity to breeding sites, but there have been exceptions that demonstrate some flexibility in this pattern. For example, some individual whales were observed to switch between breeding grounds in the North Atlantic (Stevick *et al.*, 2016).

The adaptive benefits of baleen whale migration have been vividly debated in the literature, with limited consensus (Pitman *et al.*, 2020). Potential candidates for the adaptive benefits of baleen whale migration include the energetic and growth benefits of warm water temperatures in breeding areas and predator avoidance benefits for calves (Corkeron and Connor, 1999; Clapham, 2017). It has also been proposed that warm water provides benefits for adult whales during a season in which prey densities are below the threshold at which foraging strategies are energetically efficient (Brodie, 1975; Kshatriya and Blake, 1988), although more recent work suggests that warm waters present a thermoregulation challenge, rather than benefits, for highly insulated whale bodies (Ryg *et al.*, 1993). Most recently, the need for epidermal molting in warm waters was proposed as a possible driver of migrations (Pitman *et al.*, 2020). Molting requires increased blood flow to the outer skin layers which would cause excessive heat loss in cold waters, with potential secondary benefits to calf growth and survival (Pitman *et al.*, 2020). The reasons likely remain debated partly due to a lack of knowledge on the links between whale behaviors, the associated energetic costs and benefits, and reproductive outcomes mediated by energy budgeting of different behaviors through the annual cycle.

Like all great whales, humpback whale populations have been decimated during the era of industrial whaling (Stevick *et al.*, 2003; Pallin, Baker, *et al.*, 2018; Zerbini *et al.*, 2019). In contrast to some other baleen whale species, humpback whales have been remarkably successful at recovering their population sizes and, as a result, are no longer listed as endangered across much of their range, with some notable exceptions, including, in the North Atlantic, the CVI population segment (Cooke, 2018). Climate change and increasing anthropogenic use of the ocean and its resources pose new challenges to recovering large whale populations (Avila, Kaschner and Dormann, 2018; Nelms *et al.*, 2021). For example, a decline in the reproductive success of West Atlantic and Northeast Pacific humpback whales was linked to climate-mediated changes in the food web (Kershaw *et al.*, 2020; Gabriele *et al.*, 2022). However, humpback whales are often considered relatively resilient to stressors due to their flexibility in prey choice and habitat preferences (Fleming *et al.*, 2016; Moore and Reeves, 2018; Moore *et al.*, 2019). Some humpback whale populations and other baleen whales have already been observed to change their movement patterns temporally and spatially (Carroll *et al.*, 2014; Ramp *et al.*, 2015). However, the impact of direct anthropogenic stressors acting in concert with such changes can lead to compounding effects (Maxwell *et al.*, 2013; Halpern *et al.*, 2015). Humpback whales face mortality and stress from entanglements in fishing gear, ship strikes, and pollution, including noise (Dunlop, 2019; Sprogis, Videsen and Madsen, 2020), plastic (Garcia-Garin *et al.*, 2021), and chemical pollutants (Elfes *et al.*, 2010; Sala *et al.*, 2022). While these factors affect the individual, they can affect reproductive success, survival, and eventually, population viability (E. Pirotta *et al.*, 2019; Dunlop *et al.*, 2021; Torres *et al.*, 2022).

Establishing a baseline understanding of migrating animals' spatial and temporal distributions, movement paths, reproductive rates, and ecosystem roles is paramount to assessing potential changes in their population status (Lascelles *et al.*, 2014; Avila, Kaschner and Dormann, 2018; Nelms *et al.*, 2021). Humpback whales form crucial links in food webs locally, turning over large amounts of biomass into nutrients, thereby increasing production (Roman *et al.*, 2014; Blanchet *et al.*, 2019). Their movements link across geography transporting biomass between ecosystems from the poles to the (sub-) tropics. Their sinking bodies provide crucial nutrients to specialized benthic communities (Lundberg and Moberg, 2003; Smith, Roman and Nation, 2019).

Humpback whales forage at high latitudes to take advantage of seasonally high productivity during summer and fall in specific areas, with high maternally directed site fidelity (Clapham and Mayo, 1987). Six largely distinct foraging sites are described in the North Atlantic (Figure 2), located in Norway (including the Barents Sea, Norwegian Sea, and coastal northern Norway), Iceland, Atlantic Canada (including the Gulf of St. Lawrence and Newfoundland-Labrador), the Gulf of Maine (USA), and Greenland (Katona and Beard, 1990; Smith *et al.*, 1999; Stevick *et al.*, 2006). Two known breeding grounds are described in the North Atlantic: The West Indies, an island chain in the Caribbean Sea, and the Cape Verde Islands, off the coast of Mauretania and Senegal (Figure 2). Information on the seasonality and duration of the feeding season has been documented traditionally from photo-identification studies, which also provided knowledge on the connectivity between breeding and feeding grounds, and whaling records (Chittleborough, 1965; Dawbin, 1966; Clapham and Mayo, 1987).

Figure 2 Schematic overview of the feeding grounds in the North Atlantic in brown: The Gulf of Maine, Atlantic Canada, Greenland, Iceland, Barents Sea/Norway. The breeding grounds, Cape Verde Islands and West Indies, are shown in blue.

While humpback whales from across the North Atlantic travel to the West Indies, recent evidence is mounting that the western and eastern parts of the population are distinct based on their behavior, i.e., distribution in time and space in this region (Jones, 2018; Stevick *et al.*, 2018). Northeast Atlantic whales are more likely to be re-sighted in the Lesser Antilles, which include Dominica and Guadeloupe (Stevick *et al.*, 2018). The breeding season is thought to peak in April, ca. six weeks later than the breeding season in the more northwestern Greater Antilles. The Greater Antilles are much better researched, including the well-documented Dominican Republic and protected Silver and Navidad Bank breeding areas. Recently, acoustic monitoring has provided more detailed information on the seasonality of habitat use in the West Indies, showing that individuals continue to be present well into May in the Greater Antilles (Heenehan *et al.*, 2019).

The CVI breeding ground, in contrast, is occupied by a much smaller number of humpback whales during March and April and has received considerably less research attention until recently. This area is thought to be dominated by Northeast Atlantic whales, predominantly sighted in Norway during winter (Wenzel *et al.*, 2020). The two breeding areas, West Indies and CVI, appear to be genetically and behaviorally distinct population segments that mix on the northeast foraging grounds (Jones, 2018; Gabualdi *et al.*, 2023), with some exchange due to individual whales that use both breeding grounds in different years (Stevick *et al.*, 2016).

3 Objectives

The principal aim of this work was to improve our understanding of humpback whale migration ecology and their distribution throughout the annual cycle in the North Atlantic. In collaboration with my coauthors, I analyzed a comprehensive dataset of humpback whale movement data from satellite telemetry in conjunction with photo identification, hormone and genetic profiling, and bioenergetic models.

The specific objectives were to:

1) Document the movements of North Atlantic humpback whales throughout the annual cycle, with a particular focus on the Northeast Atlantic and reproductive females (paper 1, 2, 3)

2) Document different migration strategies (pathways, phenology, and migration pace) and how they relate to sex, reproductive state, and feeding ground origin (paper 1, 2, 3)

3) Assess the energetic demands and trade-offs associated with humpback whale migration from the Northeast Atlantic (paper 1).

4 Analytical approaches

To address the objectives defined for this thesis, we used a range of tools that provide insights into humpback whale migrations across multiple scales. In papers 1 and 3, we used satellite telemetry, which provides individual-level detailed movement information on the annual and ocean-basin-scale. Based on the telemetry data in paper 1, we used a bioenergetic model to quantify the energetic cost of migration for a humpback whale in the Northeast Atlantic. In paper 2, a large sample of photo-identification and hormone and genetic screening of biopsy material obtained over a decade was analyzed to describe the demographic parameters of one specific feeding area in the Northeast Atlantic. In paper 3, we collated telemetry data from over 200 humpback whales and two decades to assess the variability in migration strategies and movement patterns across their range in the North Atlantic Ocean. In the following, I outline the general principles of the main methods used in this thesis.

Telemetry data

In papers 1 and 3, we used satellite telemetry as a basis to assess the movements and behaviors of humpback whales across the North Atlantic. Biotelemetry has emerged as a crucial tool in ecology and conservation, and ongoing technological advances mean it is now widely available (Cooke, 2008; Hussey *et al.*, 2015). The most used satellite technology in the marine realm is based on the Argos system. Argos is a global system of satellites maintained by the company CLS (www.cls-telemetry.com). Transdermal Argos satellite tags developed for large baleen whales (SPOT or SPLASH tags from www.wildlifecomputers.com) were deployed on humpback whales using an air-powered rifle from small motorboats. Tags were deployed between 2014 and 2019 in coastal fjords of northern Norway during the winter and during a cruise in September 2018 in the Barents Sea, in the waters east of Svalbard.

We further collated, harmonized, and cleaned Argos satellite telemetry data from collaborators across the North Atlantic region during two decades from all other foraging grounds of the North Atlantic and the common breeding ground in the West Indies. These collaborators followed the above-outlined procedure, but some data from experimental deployments using other types of tags were included in Paper 3 (Heide-Jørgensen and Laidre, 2015).

Because satellite signals cannot travel through water, Argos tags send a unique identifier or small package of data to a single satellite within the short time air-breathing animals breathe at the surface. A location is determined based on the known trajectory of the Argos satellite and the Doppler shift between two subsequent signals by triangulation (Hooten *et al.*, 2017). While these benefits make Argos suitable for tracking large marine vertebrates over long distances, the uncertainty around locations tends to be large, ranging from hundreds to thousands of meters. These errors were classified with categorical error classes for each location until 2007, with each error class associated with a specific uncertainty estimate (defined by CLS). Since 2011, a multi-model Kalman filter algorithm has been used to estimate error ellipses around the provided location, providing error ellipses for all valid locations. This method accounts for the anisotropic nature of the errors caused by the polar orbit of Argos satellites (Hooten *et al.*, 2017). Processing raw location information also relies on previous locations to improve accuracy, and the uncertainty around individual locations is influenced by weather conditions, the location of the animal and the satellites, and animal behavior because the type of movement impacts the frequency and duration of surfacing events.

Given these limitations of raw location data obtained from the Argos system, the data must be further processed. Simple filters on maximum swim speeds and spikes in turning angles (Freitas *et al.*, 2008) can identify erroneous location fixes. State-space models have become instrumental in obtaining reliable estimates of an animal’s movement and space use (Patterson *et al.*, 2008). State space models consider the uncertainty estimates around provided locations and movement process models (Mcclintock *et al.*, 2015) to reconstruct a most-likely movement path based on the raw data. Continuous-time state-space models employ a random or correlated random walk, and regularized locations can be sampled from this path (Jonsen *et al.*, 2020). In this thesis, we used a continuous-time state space model to reconstruct a most likely movement path from raw satellite locations with either error ellipses or categorical quality information (Jonsen and Patterson, 2020).

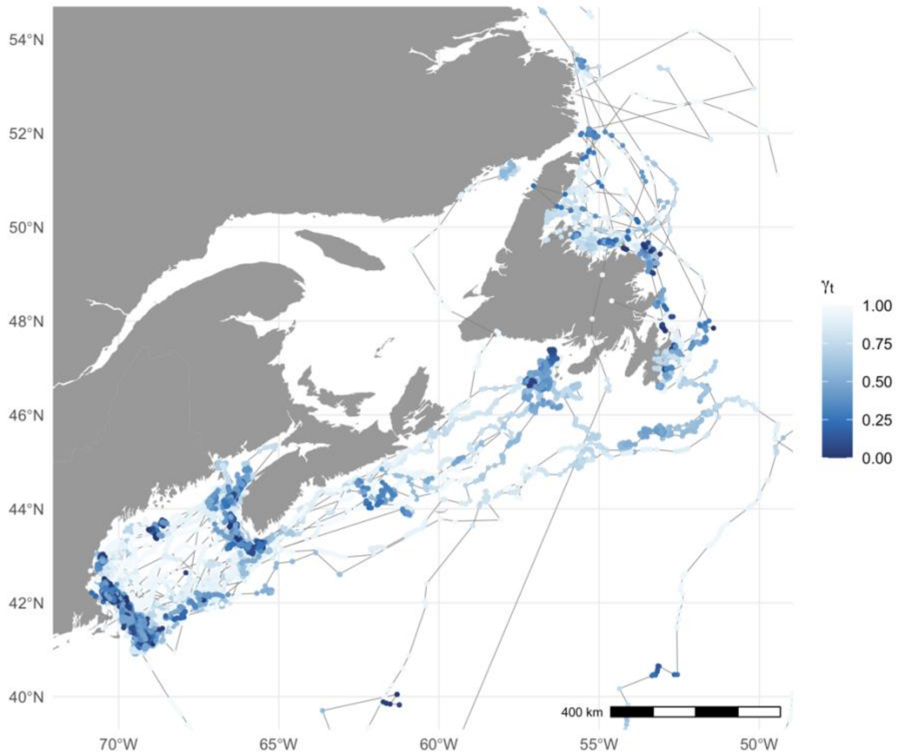

Figure 3 Example of movement persistence modeled from satellite telemetry data in the Gulf of Maine and Atlantic Canada foraging grounds. Dark blue indicates low movement persistence (indicative of ARS), and light blue indicates high persistence or transiting movements.

We obtained a regularized set of locations an animal has likely used over time from the state-space model. We can infer underlying behavioral modes based on this most likely movement path (Jonsen *et al.*, 2019). This method relies on the movement speed of an animal (step length between locations), the turning angles between successive locations, and the degree of autocorrelation of these parameters along the path (movement persistence, γ, Figure 3). Movement persistence varies between 0-1 and indicates the autocorrelation between successive speeds and turning angles along the path (Jonsen *et al.*, 2019; Jonsen and Patterson, 2020). These parameters indicate types of behaviors, for example, 'area restricted search behavior' (ARS), which is generalized as localized movement with varying turning angles and low autocorrelation, representative of, for example, foraging, search behavior, or resting (Tinbergen, Impekoven and Franck, 1967). In contrast, if an animal is transiting or migrating, speed and turning angles may be highly correlated as an animal maintains movement direction and speed.

Bioenergetic modeling

Due to their highly mobile nature and size, we cannot directly measure most physiological parameters for large cetaceans, particularly over long timescales, and distances. In paper 1, we used a bioenergetic model calibrated for humpback whales. This model allowed me to estimate the cost of migration based on the swim speed estimated from Argos location data. The energy required to overcome the drag a typical whale would experience while swimming at a given speed is estimated as the cost of transport in addition to a metabolic cost estimate per day (Fish, 1996; Braithwaite, Meeuwig and Hipsey, 2015). The parameters for this model require knowledge of the kinematics of movement and body shape of a whale. These parameters are difficult to obtain and must be estimated for large whales, so they are associated with some uncertainties. To allow for comparisons to earlier studies, we maintained the same parameter values (Braithwaite, Meeuwig and Hipsey, 2015; Riekkola *et al.*, 2020). In the model, static parameters include the wetted surface area, body mass, drag coefficient, propulsive efficiency, aerobic efficiency, the ratio of active to passive drag, and the density of seawater. Swim speed is then varied dynamically according to swim speed estimated from telemetry data along regularly sampled steps of the reconstructed movement path. This gives the instantaneous cost of swimming at a given speed per second (in Watts), which is multiplied by the seconds in a day and added to an estimate of the basal metabolic rate, representing the energy required for physiological processes, resulting in the total energetic cost per day.

Photographic identification

Mark-recapture techniques are a traditional tool used to understand population dynamics across space and time when direct observation of the entire life cycle is difficult or impossible. In paper 2, we used this method to describe the connectivity between different foraging areas, describe the seasonality of the foraging aggregations, and investigate return rates for individual animals. Artificial markings, such as ringing, tagging, or color markings, can be used to identify individuals in different regions and across seasons (Hammond, 2009). In some cases, natural individual markings are present, making the artificial tagging of individuals superfluous. Humpback whales have individually recognizable and stable markings in their ventral flukes' coloring and ridge patterns (Katona and Whitehead, 1981). These natural markings allow researchers to follow individual whales' movements across entire ocean basins and decades of movement using repeated photographic identification (Hammond 2009; Herman *et al.*, 2011). This method also allows citizen scientists, tourists, and dedicated individuals out on the water and along coastlines to contribute data, which substantially increases the availability of photographic material (Peres dos Santos *et al.*, 2022; Cheeseman *et al.*, 2023). The natural markings on humpback whale flukes can be assessed by eye, given sufficient picture quality (Friday *et al.*, 2000). These methods can yield information on spatiotemporal movement patterns and demographic parameters such as reproductive success and population abundance (Ramp *et al.*, 2010; Kershaw *et al.*, 2020). As such, photo-id studies are indispensable for studying the population dynamics of wide-ranging animals such as baleen whales (Cheeseman *et al.*, 2023).

Hormone screening

Assessing population health based on photographic identification requires long-term effort and the presence of researchers or the public near whale aggregations to be feasible (Herman *et al.*, 2011). When whales aggregate in remote areas, such as the Northeast Atlantic, photographic material is often insufficient for such long-term studies. Physiological parameters obtained from tissue samples can be used to assess individuals' health and reproductive status to infer population health (Clark, 2013). Hormone levels can provide detailed insights into an animal's health and life cycle status. Recently, methods have been developed to measure sex hormones (testosterone and progesterone) to assess the reproductive biology of large whales (Kellar, 2008; Vu *et al.*, 2015). The method is becoming a popular tool to monitor the population health of baleen whales since it allows for the collection of large numbers of biopsy samples even in remote areas with limited logistical support because these hormones are relatively accessible in the outer blubber layer and stable once frozen at -20°C (Pallin et al. 2023).

Little is known about the humpback whales foraging in Northeast Atlantic waters, especially in the remote Barents Sea and coastal Norway. We, therefore, aimed to establish the first estimates of the pregnancy rate in this population to help identify whether movement patterns in this subset of the population are distinct by sex and reproductive status. In paper 2, we used progesterone measured in biopsy samples of humpback whales from the Barents Sea and Norwegian fjords to determine the reproductive status of female humpback whales. Tissue biopsies were collected over multiple years in northern Norway and in one year in the northern Barents Sea. We extracted hormones using a protocol established for humpback whales (Kellar, 2008; Clark *et al.*, 2016; Pallin, Robbins, *et al.*, 2018) and measured the progesterone level in the outer blubber layer. Subsequently, the likelihood of pregnancy was established based on a model calibrated with known pregnancies in other populations (Pallin, Baker, *et al.*, 2018; Kershaw *et al.*, 2020). To increase the available sample size, we also used additional data from collaborators who had used a slightly different hormone extraction method. This allowed us to assess whether deviations in the laboratory methods were comparable, which can be an important consideration for future studies. The presented progesterone levels will also be valuable to inform our understanding of the development of hormone levels throughout gestation and the annual cycle since this is the first study to present progesterone values from the winter months, relatively late in the gestation period.

5 Summary of the main findings

In this thesis, I aimed to fill gaps in the existing knowledge by describing the space use of humpback whales in the North Atlantic throughout the year and identifying their migratory patterns. This essential information has been fragmented so far due to the logistical difficulties of sampling and instrumenting large mobile animals inhabiting remote areas such as the Arctic and their long-distance movements across the open ocean. The included papers addressed gaps in our understanding of humpback whales' individual and population-level movement patterns by using satellite telemetry data, photographic identification, and hormonal and genetic screening of tissue samples. This work also explored the migration ecology of humpback whales in the North Atlantic across different scales, from assessing the detailed movements and energetic expenditure of one individual throughout an annual cycle and migration to quantifying the demographic structure of the Northeast Atlantic foraging grounds, to an exploration of the diverse migration strategies of humpback whales from this area and the whole North Atlantic.

In paper 1, we started at the scale of one single individual (Figure 4, panel 1). We assessed its migration route and timing, migration pace and which factors affected it, space use throughout the year, and the estimated energetic cost of this extremely long migration (ca. 18 000 km both ways). In this first paper, we demonstrated that Northeast Atlantic humpback whales can follow an unusual annual schedule, connect multiple foraging grounds in the Northeast Atlantic, modulate speed according to this routine, and might give birth outside known breeding grounds on the way to their destination. These results illustrate the capabilities of humpback whales to push the boundaries of long-distance migrations. Using data from one individual with a complete migration track and additional knowledge on its successful reproduction event, we were able to provide a highly magnified window into the life of the elusive Northeast Atlantic humpback whales and discuss gaps in bioenergetic models as they have been developed for humpback whales.

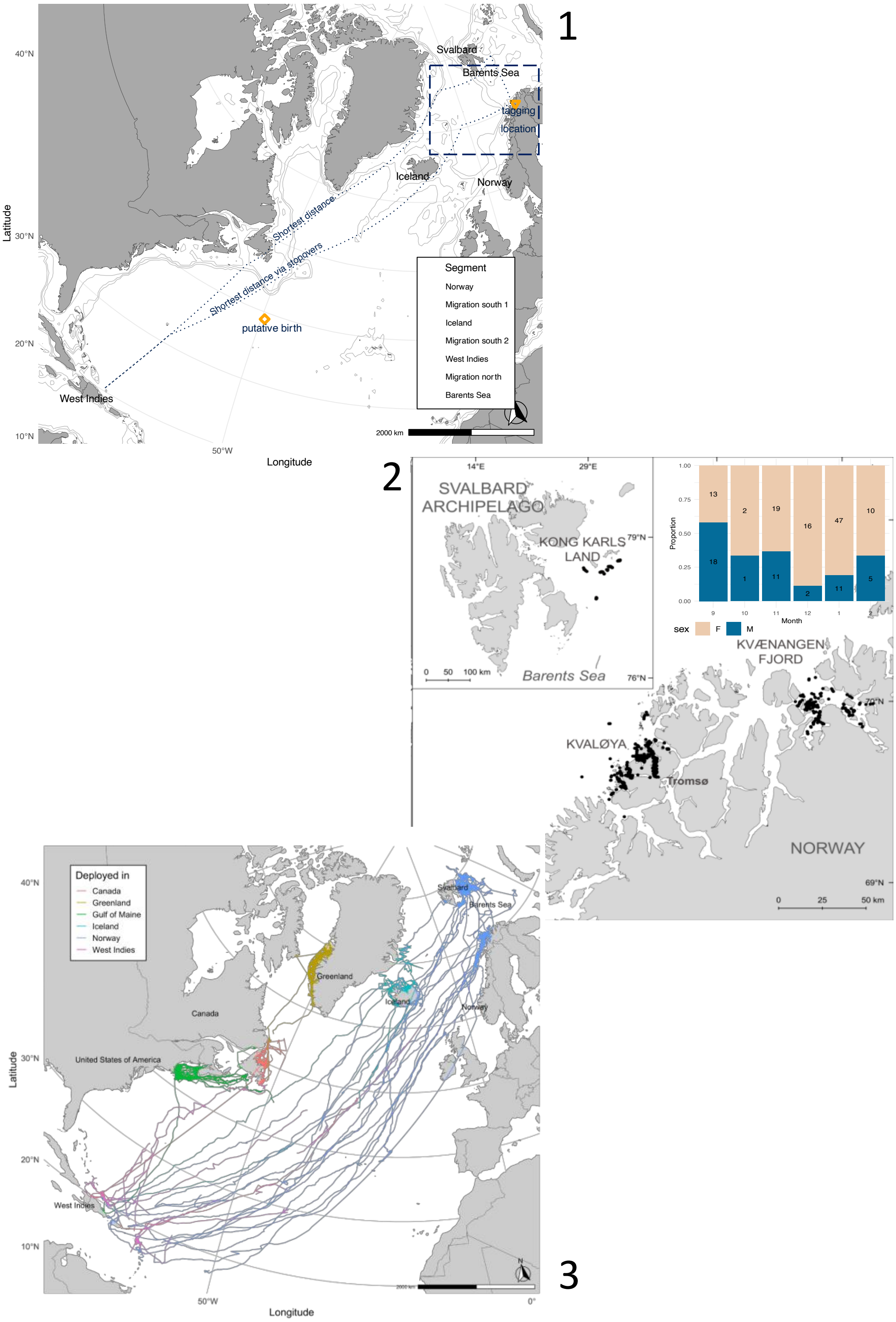

Figure 4 This thesis investigated the movement ecology of North Atlantic humpback whales on different scales. ***(1)*** *Paper 1 included data on one individual through one annual cycle,* ***(2)*** *paper 2 provided information on the demographics of hundreds of individuals over a decade, and* ***(3)*** *paper 3 included telemetry data from >200 individuals across the North Atlantic basin over two decades.*

As a second step, we provided novel information on the spatiotemporal distribution of Northeast Atlantic humpback whales, this time using a larger window of focus, specifically the Barents Sea and fjord systems of northern Norway (Figure 4, panel 2). We described the demographics of the Northeast Atlantic feeding ground using photographic matching and genetic and hormone screening of biopsy materials. We also established evidence for the connectivity between the Barents Sea and the fjord systems of northern Norway. The results provided a detailed description of the geographical distribution of whales each year since humpback whales started visiting northern Norway in 2010 and the first published description of the establishment of this foraging site. We showed that individual whales return at remarkably high rates to northern Norwegian fjord systems and identified a female bias in this area and higher rates of pregnancy in contrast to the Barents Sea. Until the end of this study in 2019, 866 individuals had been recorded. Overall, this study demonstrated that humpback whales in the Northeast Atlantic could respond to shifts in herring distribution and used this resource excessively throughout winter. Notably, the site seems valuable to females who continue to feed late in the season. The study also complements paper 1 by providing further evidence of the annual routines of Northeast Atlantic humpback whales and the first estimates of pregnancy rates for this population.

Eventually, we used an even broader perspective and considered the migration strategies of humpback whales using satellite telemetry data spanning the entire North Atlantic and two decades (Figure 4, panel 3). Paper 3 presented an overview of the current state of knowledge on the spatiotemporal distribution of humpback whales in the North Atlantic as documented by satellite telemetry data. A primary aim was to collate and standardize this data as a comprehensive overview, since the dataset included some published but many so far unpublished satellite tracks. We identified six different migration strategies across foraging grounds of the Barents Sea, northern Norwegian fjords, and Iceland. These strategies differed mainly in migration timing (Figure 5) and pace. The diversity of within-site strategies was remarkable, and this demonstrates the extent to which individuals can modulate their migrations, likely optimizing their movements to various external and internal drivers. Most notably, we identified a previously unknown migration tactic in which Northeast Atlantic whales return towards foraging grounds before ever reaching the described breeding ground area or spending substantial time there. This provides an important hint as to the constraints and trade-offs under which humpback whales undertake this long-distance migration. We proposed that this ‘returning early’ behavior could represent a carry-over effect from time constraints of the annual cycle or be related to life-history stage of the animals. This can help us further understand the reasons for baleen whale migrations by providing an unexpected example of migratory behavior.

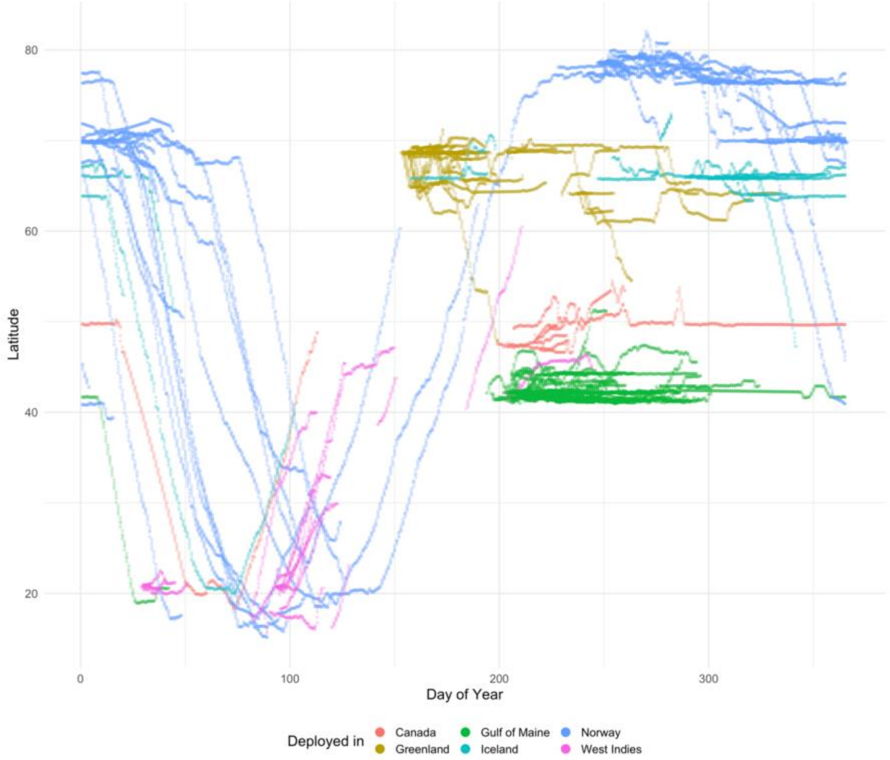

Figure 5 The variability of migration timing in individuals, as indicated by latitudinal changes in their location for each day of the year, tracked from various feeding grounds in paper 3.

In conclusion, this thesis revealed important novel information on the space use of North Atlantic humpback whales throughout the year and the specific behaviors and habitat use of reproductive females. Crucial knowledge regarding the migration ecology of Northeast Atlantic humpback whales, their unusual annual schedules, the connectivity between different areas of the foraging ground, and their specific migration strategies and energetic requirements were presented. This information will be crucial in ecosystem management and important as documentation of a baseline condition in a changing ocean. The presented results can also be informative for future studies on baleen whale migration behavior and the trade-offs associated with very long migration distances.

This thesis includes the following main insights:

1. Connectivity between foraging grounds in the Northeast Atlantic throughout the seasonal cycle
2. Full annual documentation of the movements of a pregnant female
3. Indication for breeding activities outside breeding grounds
4. A female bias on the northern Norwegian winter feeding ground
5. A first assessment of the pregnancy rates of Northeast Atlantic humpback whales
6. A comparison of migration strategies across a latitudinal gradient of migration distances; including a novel migration strategy
7. An overview of movement data collected over two decades in the North Atlantic

In the following, I will first outline some notable limitations of my work, then discuss specific aspects of this work in the context of migration ecology and suggest directions for future research.

6 Limitations

Gaps in the available telemetry data

Although we collated and analyzed a large satellite telemetry dataset in this thesis, there were some notable gaps in the available data. First, we tagged many individuals in the northern Barents Sea and Norway, but we could not capture any migrations to the CVI breeding area. The behavior of whales migrating to the CVI remains poorly documented. We have few insights into their migrations apart from a general understanding of the connectivity and general timing of their whereabouts in Norway and CVI based on recent efforts in collecting photo-identification material (Wenzel *et al.*, 2009, 2020), and genetic estimates of their level of interchange with the general population of the North Atlantic (Palsbøll *et al.*, 1995; Ruegg *et al.*, 2013). However, the expected divide in migration pathways would be around British waters, and photo identification suggests strong connectivity between those areas and CVI, with the highest number of matches from the Norwegian coastal feeding ground to the CVI (Broms, 2015; Jones, 2018). The CVI is a small and endangered part of the population (Wenzel *et al.*, 2020) and constitutes a separate population segment in the North Atlantic (Jones, 2018; Gabualdi *et al.*, 2023). If the migration corridor of these animals were more coastal in the southern part of the migration, it would cross many exclusive economic zones, with high amounts of fishery and other infrastructure around Europe (Halpern *et al.*, 2015), exposing these whales to many potential threats along their migrations. Future studies are required to understand such risks along their migration routes. Additional work should address whether their behavior is unique in terms of movements and seasonality on northern feeding grounds so that appropriate conservation measures can be undertaken that ensure the protection of whales belonging to this small population segment on their feeding ground, where they interact with fisheries, tourism, shipping and infrastructure for the petroleum industry (Mul, 2020).

Furthermore, due to logistical constraints, sampling and telemetry deployments in the Barents Sea/Svalbard area were restricted to one year, and most of the photo-identification effort was also conducted during the same cruise. Although this kind of bias in effort is common in telemetry studies (Hamilton *et al.*, 2021), it is important to acknowledge that it may introduce biases in the interpretation of the data. Migration data was also only fragmented in the western basin, despite decades of humpback whale tracking. However, a dedicated study would find sufficient data in paper 3 to assess the migration ecology of the Gulf of Maine humpback whales in more detail, perhaps in conjunction with simulated trajectories based on known departure and arrival time frames, which are well documented in this area.

Uncertainties in pregnancy rates

Due to limited sample sizes, the pregnancy rates we established in paper 2 were not robust enough to infer population health or changes in pregnancy rates over time. Nevertheless, these first pregnancy rate estimates will provide a baseline for future assessments. Large sample sizes, consistently obtained over a longer period, can provide valuable insights into the movement patterns of pregnant females, their foraging success, and thus population health (e.g., Pallin et al. (2018; 2023). Alternatively, long-term observational studies can be conducted to assess the rate at which females return with calves (calving rate), as demonstrated, for example, in Atlantic Canada (Herman *et al.*, 2011; Kershaw *et al.*, 2020). These kinds of studies require sustained funding and large teams and are logistically demanding in terms of sampling and laboratory work. Alternative measures of population health, e.g., estimated body condition from unmanned aerial vehicles (UAV) and photogrammetry, can be used, although to be useful, they have to be included in monitoring schemes (Aoki *et al.*, 2021; Bierlich *et al.*, 2022; Torres *et al.*, 2022).

Uncertainties and assumptions in the bioenergetic model

In paper 1, we used a bioenergetic model to quantify the energetic cost of humpback whale migration in the Northeast Atlantic. This drag-based approach to assessing the cost of transport requires swim speeds to be estimated over a time frame that can be varied but is limited by the accuracy of the biotelemetry location data. In paper 1, for example, we used a step length of 6 hours. Swim speeds rely on the estimated distance swum by the animal between two locations as a straight line and, as such, cannot account for any tortuosity or variability of speed between the two locations. This estimated swim speed, therefore, always includes uncertainties. Recently, movement models became available that can simulate a range of trajectories for each set of locations, therefore providing a confidence interval around the speed estimate (Noonan *et al.*, 2019).

Swimmers can also modulate their behavior to optimize locomotion costs, e.g., by varying their dive patterns and the depth at which they swim, so some effect of this variability in blubber layer thickness and, thus, buoyancy and body shape may be behaviorally offset (Nousek McGregor, 2010; Arce *et al.*, 2019). For example, diving at a certain minimum depth will avoid additional costs caused by interactions between the animal body and the water surface; at approximately three times an animal's body 'height' wave drag becomes negligible (Blake, 2009). However, this might incur additional costs due to having to overcome buoyancy to dive. Furthermore, swimmers and flyers continue to move forward after the cessation of propulsive activity ('stroke'); by using this 'glide' phase, a stroke-and-glide movement pattern can save up to 32% energy compared to constant-stroke movement (Ribak, Weihs and Arad, 2005). During this glide period, the animal can also save energy by reducing additional drag incurred when moving the body during stroke, a phenomenon well documented in pinnipeds (Biuw *et al.*, 2003; Aoki *et al.*, 2011). These behavioral modifications were not accounted for in our model. However, as described above, the limited precision in the estimation of animal movement speeds from telemetry data, especially from error-prone Argos satellite telemetry, inherently smoothes over smaller-scale movement processes. However, this method can still provide a rough estimate of the costs of movement over long time scales, i.e., months.

Some parameters used to estimate the energetic cost of movement in humpback whales in paper 1 have traditionally been estimated based on studies from other species or dead animals (Braithwaite, Meeuwig and Hipsey, 2015). Recent advances in technology and their application to large whales increasingly allow for more precise estimates of swimming and foraging kinematics, as well as morphometrics, such as the surface area of an animal. For example, the drag coefficient can now be estimated from the oscillation of high-frequency suction cup tags in conjunction with biophysical modeling exercises (Gough *et al.*, 2021), and surface area can be estimated from UAV and photogrammetry (Christiansen *et al.*, 2016). Nonetheless, we decided to maintain traditional parameter spaces to make our results comparable to previous studies from other regions and because updated parameters are still being validated (Zhang *et al.*, 2023). A dedicated work assessing the sensitivity of the bioenergetic model to changes in the used parameter space would provide a more precise assessment of the trade-offs that humpback whales face while making movement decisions. Such work could make more robust statements on whether humpback whales use time or energy-optimizing strategies during migration. Such a sensitivity analysis could also improve our understanding of the performance of older parameter estimates against recently refined measurements and how these changes might influence past interpretations of bioenergetic models.

General limitations of the drag-based approach to bioenergetic modeling include that some parameters change over time, even if they are taken accurately during tag deployment (Aoki *et al.*, 2021). These include, for example, the thickness of the blubber layer, which influences the cost of locomotion in free-ranging marine mammals since it determines the animal's buoyancy (Aoki *et al.*, 2011) and influences body shape by varying the drag coefficient. Many baleen whales are capital breeders and thus naturally vary their blubber layer thickness throughout the annual cycle by building up fat reserves during the foraging season and consuming it when they fast during migration and lactation in the breeding season. Whether or not an animal is pregnant will also influence the drag by modulating the circumference and shape through abdominal distension, altering the finesse ratio by ~ 3 - 4% throughout gestation (Nousek McGregor, 2010; Christiansen *et al.*, 2016), a factor that will change throughout gestation and with changing body condition as stored fat is used to nurture the calf (Christiansen *et al.*, 2014).

Missing baseline knowledge in the Northeast Atlantic

Limited knowledge of the historical distributions and seasonal movement of humpback whales in the Northeast Atlantic makes it challenging to understand whether movement patterns are already changing in response to climate change and increased anthropogenic pressures in the oceans during the last decades. Accounts from early whalers describe that humpback whales were present in the Northeast Atlantic during the winter and moved through the Norwegian and Barents Sea in the progression of the season (Hjort, 1902; Ingebrigtsen, 1929). It thus seems possible that Northeast Atlantic humpback whales always had an 'unusual' annual schedule compared to animals from other areas. The formative studies for our understanding of humpback whale migration patterns stem from other areas, particularly the southern Ocean (Chittleborough, 1958; Dawbin, 1966). Knowledge on past movement patterns in the Northeast Atlantic is fragmented. There is also limited knowledge on humpback whale movements during recent decades, i.e., while the population was recovering. We therefore lack an understanding of how movement patterns might have changed with simultaneously occurring ecosystem changes or fluctuations, including climate change impacts in the Barents Sea and fluctuating distribution patterns of prey species, despite efforts from extensive surveys in the last decades and, more recently, acoustic monitoring (Øien, 2009; Løviknes *et al.*, 2021; Aniceto *et al.*, 2022). These knowledge gaps limit our understanding of how each factor impacts the whale distribution patterns observed since photo-id effort increased and biotelemetry deployments were initiated. Is the winter foraging activity related to population recovery and density effects, possibly in conjunction with environmental changes in the core foraging area? Have Northeast Atlantic humpback whales always displayed this 'unusual' annual routine, and are we only starting to see this with more available data? Or is this annual routine a result of some of these changes in conjunction? While we can say that humpback whales followed the herring into different fjord wintering areas (paper 2), we cannot make definitive statements on these questions. Most likely, the phenomenon is driven by a combination of these factors, and I discuss some of them in more depth in the perspective and conclusion section.

7 Perspective and Conclusion

Spatiotemporal distribution on North Atlantic foraging grounds

The results presented in this thesis support the idea of a more or less continuous foraging area and season of the Northeast Atlantic humpback whales throughout the Norwegian and Barents Seas, as had been suggested by studies based on historical whaling data (Ingebrigtsen, 1929) and ecosystem surveys (Øien, 2009). Previous studies also considered the foraging area as a continuous region, including the Norwegian Sea, with known foraging hotspots around Jan Mayen and Bear Island, and the Barents Sea, including the area around Svalbard (Stevick *et al.*, 2006). For example, the movement patterns of the individual tracked in paper 1 confirm that animals start foraging around Bear Island upon returning from breeding grounds and then continue towards the Barents Sea as the season progresses. Multiple individuals used the known foraging area around Bear Island. The movement data presented in paper 3 also suggests that some of the winter sightings in Iceland can be attributed to this area being along the migration pathway of individuals foraging in the northern Norwegian and Barents Sea and the fjords of northern Norway.

We further presented evidence that continuing to forage in Norway after a precluded season in the Barents Sea is a common strategy among Northeast Atlantic humpback whales (papers 1 and 2). However, in paper 3, we also showed that many individuals headed directly south on their migration after foraging in the Barents Sea until the end of the fall and sometimes continued foraging even into winter in the Barents Sea. Our results also showed that upon leaving known foraging grounds in coastal northern Norway, some animals continued to show ARS-like movements while moving southward along the Norwegian coast and in coastal areas of Iceland (paper 3). In conjunction, these observations confirm that the foraging season lasts not only through the winter in Norwegian fjords but also longer than previously assumed in the Barents Sea (although the observations were restricted to one particular year), and even continues after animals leave the Norwegian fjords (paper 3). This is a much later foraging season than previously assumed, based on knowledge from other feeding grounds and surveys in the Northeast Atlantic (Øien, 2009; Bengtsson, Lydersen and Kovacs, 2022). Much previous knowledge on humpback whale migrations stems from other, better documented, foraging grounds, e.g., in the Gulf of Maine, and our results indicate that Northeast Atlantic humpback whales have a different annual schedule, as suggested earlier (Smith and Pike, 2009).

Due to their costly foraging mode, the distribution and density of prey patches are important key determinants of the foraging efficiency of baleen whales and, consequently, their energetic balance throughout the year (Goldbogen *et al.*, 2011). A visual comparison among the movements in the foraging areas in paper 3 indicated that animals spent transiting between foraging patches within the foraging sites might be different. This could be due to differences in prey species or prey distributions and could also be related to the geographic characteristics of each foraging ground. For example, foraging activity in the Barents Sea occurs over a wide shelf area, where prey distribution could be more ephemeral than, for example, in the Gulf of Maine, which is constrained by the coastline and shows distinct foraging hotspots. If whales forage in fjord systems, such as coastal Norway and Iceland, prey may be more densely aggregated or prey patches less dispersed across space. Therefore, the energy gain in these different foraging areas could be different, which could affect movement patterns, either within feeding grounds or in the timing of the following migrations. Future studies would be needed to understand the differences of migration patterns of humpback whales across the North Atlantic in the context of environmental conditions on their respective foraging grounds. For example, in the Northeast Atlantic, previous studies have attempted to assess how whale movements are related to prey fields from surveys (Skern-Mauritzen *et al.*, 2011; Nøttestad *et al.*, 2015), and the data presented here provides an opportunity for a more detailed look at such relationships (Vogel *et al.*, 2021). Since telemetry and biopsy data collection is expensive and logistically challenging, efforts to share and collate are crucial for advancing our understanding of the movement ecology of large marine migrants. Collaboration and open data practices will become ever more urgent to assess the potential effects of ecosystem changes on movement dynamics.

Winter whales in northern Norwegian fjords – a novel phenomenon?

An interesting question raised but not answered in this thesis is: Does the seasonal occurrence of humpback whales during winter in northern Norwegian fjords reflect a change in the migration phenology of Northeast Atlantic humpback whales, or have humpback whales only changed their spatial distribution during the winter? Further, why, and how have humpback whales re-established their presence in the area after a 100-year absence?

Multiple factors should be considered in conjunction: 1. A general lack of reliable data on this population's historical spatiotemporal distribution and movements 2. A population collapse of humpback whales due to over-harvesting. 3. A collapse and changes in the distribution of NSS herring and other prey within the last decades. 4. Simultaneous changes in the Arctic and subarctic ecosystems. I will discuss these reasons in the following.

(1) Historical whaling observations document that humpback whales were present along the northern Norwegian coast during winters more than 100 years ago, but apparently in much lower numbers than documented in paper 2 (Ingebrigtsen, 1929). After this, various sighting surveys provided information on the distribution of humpback whales in the Norwegian Sea (Øien, 2009), but these were unable to document movements throughout the year. Further, the breeding ground areas to which Northeast Atlantic humpback whales predominantly migrate historically received less research attention (Kennedy and Clapham, 2017). This precludes knowledge on whether Northeast Atlantic humpback whales have changed their migration phenology in the last decades.

(2) The disappearance of large whales from many areas, has been documented worldwide, and in some areas, whales are starting to return (Jackson *et al.*, 2020; Keen *et al.*, 2021a; Herr, 2022). A loss of cultural memory can break down patterns of migration in over-harvested populations, a mechanism suggested to have prevented the re-occupation of extirpated areas in baleen whales, and recovery of this behavior can take generations (Clapham, Aguilar and Hatch, 2008; Jesmer *et al.*, 2018). In addition, density effects in migratory and resource-discovery processes are a well-established phenomenon in which higher abundances increase the likelihood of exploratory movements that can lead to the discovery of new habitats (Mysterud *et al.*, 2011). For example, in partial migrants, where migration is a plastic trait, more animals migrate in years of higher population abundance (Nilsson *et al.*, 2006). It is, therefore, reasonable to assume that population density effects and loss of

knowledge after exploitation could partly explain why whales were not present in this area since they were observed 100 years ago (Ingebrigtsen, 1929).

(3) Since whales have recovered from exploitation to larger population sizes, the distribution of NSS herring, on which they feed in northern Norway, has changed multiple times (Dragesund, Johannessen and Ulltang, 1997). Before the recent observation of whale foraging in northern Norway (paper 2), herring wintering distribution was concentrated in the fjord systems of Tysfjord – Vestfjord. This area is further south and further inland than the fjord systems in which humpback whales are now observed. Whales might therefore have been less likely 'discover' this herring stock while searching for prey.

(4) The foraging area in the Barents Sea has been undergoing drastic changes due to rapid climate change (Johannesen *et al.*, 2012). Seasonal dynamics and distributions of sea ice and water masses have led to shifts in prey species and their predators' movements (Bengtsson, Lydersen and Kovacs, 2022). Humpback whales using this area as a foraging ground are thought to be flexible in their prey choices and might have shifted their habitat use in recent years in response throughout the Norwegian Sea (Løviknes *et al.*, 2021). Furthermore, increased whale densities on the foraging ground (Barents Sea) might have led to increased resource competition and therefore the necessity for whales to explore resources outside of this core foraging area.

While I cannot provide an answer to the questions of 'if' and 'why' in this thesis, I will speculate further on the 'how', i.e., potential behavioral processes behind the emergence of this winter foraging site, in a later section (potential social mechanisms of adaptation) since this evokes relevant questions regarding the behavioral ecology of humpback whales.

Migration ecology of North Atlantic humpback whales

Variability in migration strategies

My findings provide further evidence that humpback whales on their breeding migrations can modulate migratory schedules at an individual level as part of their migration strategy. This was evident in the various migration schedules presented in paper 3 (Figure 5). How this affects the energetic balance of these whales throughout the year, and what the underlying reasons are (external or internal), needs further investigation. Recent work on the energetic budgets of migratory baleen whales indicates that the energetic cost of migration is low relative to average or good foraging seasons. In years of poor foraging success, however, the cost of migration could be detrimentally expensive relative to the energy gain during the foraging season (Gough, 2022). These results lend more support to the idea that some animals might forego migrations during some years, which is of particular relevance to animals having to cover very long distances and has been repeatedly suggested for Northeast Atlantic humpback whales as a possible tactic (Smith and Pike, 2009; Kennedy *et al.*, 2014; Kennedy and Clapham, 2017). However, we demonstrated that animals can alternatively limit their time spent on the breeding grounds (paper 3) and modulate migration speed (paper 1). While we provided an initial estimate of the energetic cost of this long migration under a 'high migration speed' scenario in paper 1, the energetic outcome of the various strategies documented in paper 3 should be investigated in more depth using bioenergetic models (E. Pirotta *et al.*, 2019). This work could also be extended by simulating additional migration tracks for foraging grounds that currently have little or no migration data available. Higher-resolution movement data (e.g., from suction cup tags) from the different foraging grounds could be integrated to understand variations in foraging success in relation to migration strategies.

In paper 3, we found that some individuals completed the migration but spent no or very limited time on the breeding grounds. This strategy has, to my knowledge, not been observed in other humpback whale migrations. Limiting time on breeding grounds could be a valuable tactic that results from time constraints after extensive time spent foraging late in the season and covering very long migration distances. It is also possible, that some individuals are unable to accumulate sufficient energetic reserves for this migration. This surprising migration strategy evokes questions on the role and adaptive benefits of migration. While the potential benefits of baleen whale migration continue to be debated, the most recent suggestions focus on the potential benefits of reaching warm temperatures, with 21°C temperature delineating breeding grounds (Rasmussen *et al.*, 2007), for epidermal molt, or the sloughing of skin cells (Pitman *et al.*, 2020). Animals from various reproductive groups returned before spending any substantial time in the breeding areas (paper 3), which could indicate that reaching warm-enough temperatures for a short time fulfills the annual requirements of epidermal molt. Males, non-pregnant females, and females with failed pregnancies could constitute this sample. Another reason for this tactic could be that these whales had already precluded mating during their approach to the area. Singing, and therefore potential mating, is increasingly documented at high latitudes (Kowarski *et al.*, 2018; Magnúsdóttir and Lim, 2019; Aniceto *et al.*, 2022), providing more evidence for potential breeding behaviors northward of breeding areas.

The specific requirements of reproductive females

We considered the life-stage specific requirements of humpback whales in the Northeast Atlantic in each paper, with a particular focus on females during gestation (papers 1 and 2). We know that humpback whales have differing habitat requirements and timing of their movements depending on their sex and reproductive state (Brown *et al.*, 1995; Herman *et al.*, 2011). Females are known to show habitat preferences during migration in other regions, for example, by migrating closer to shore and seeking out sheltered areas for nursing (Félix and Guzmán, 2014; Bejder *et al.*, 2019). However, the movements of mother-calf pairs outside the breeding grounds, especially during migration, and their potentially specific requirements remain cryptic in many areas. Some recent studies detailed the behavior of mother-calf pairs on feeding grounds, where short-term high-resolution data provided insights into their small-scale interactions (Félix and Botero-Acosta, 2011; Bejder *et al.*, 2019; Tackaberry *et al.*, 2020). We assessed the movements of an individual pregnant female in paper 1, detailing that whale mothers from the Northeast Atlantic use the foraging ground in northern Norway extensively and even spent time on the Icelandic shelf after leaving this core foraging area in February. In paper 2, we provided more support for the idea that northern Norway is particularly important for females by demonstrating a female-biased sex ratio at the same site during the winter. This result is in line with the expectation that females and pregnant females stay longest on foraging grounds, and results from whaling data obtained in the Northeast Atlantic (Ingebrigtsen, 1929; Dawbin, 1966). This is the first work addressing the habitat requirements or migration patterns of female humpback whales in this region and the first to estimate pregnancy rates. Hormones extracted from males in our sample for paper 2 were shared with collaborators and will be used to assess male reproductive biology using testosterone levels. Because obtaining tissue samples from free-ranging cetaceans is challenging, other methods, such as observational catalogs of calving rates and measurements of body condition from UAV, can be alternative or complimentary tools to study the reproductive success of large whale populations. Information on the sex and reproductive state of individuals in a habitat such as the fjords of northern Norway could inform management. In this area, reproductively active females spend extensive time foraging and might therefore be particularly sensitive to disturbance.

Energetic cost of migrations

In paper 1, we estimated the energetic cost of a complete annual migration based on an existing bioenergetic model calibrated for humpback whales (Braithwaite, Meeuwig and Hipsey, 2015; Riekkola *et al.*, 2020). We used the same parameter space as these previous studies to allow for comparisons to results obtained in other areas. However, the importance of an improved calibration of this model emerged. The relative contribution of different parameters determines the importance of the cost of transport relative to the basal metabolic rate. Therefore, the calibration of this model affects the interpretation of model results and the ecological questions being addressed with these models. These questions include, for example: Are longer migrations more costly even if whales adapt the migration speed? Will detours or increased migration distances have deleterious effects on whales? What is the effect of years of poor feeding conditions on the annual energetic budget of a whale?

Longer migrations seem more costly than shorter migrations, even though whales can increase the migration speed to reduce the duration of migration (Riekkola *et al.*, 2020).

Recent work also demonstrated the importance of successful foraging seasons to offset the energetic costs of migration (Gough, 2022). Therefore, the relative balance between foraging energy intake and expenditure during the migration is a crucial factor in the energy balance throughout the annual cycle (Gough, 2022), meaning that whales with longer migrations may be very sensitive to reduced foraging success and disturbance during the foraging season. While bioenergetic models will always provide an approximation of the true cost of animal movements, our results indicated that it was crucially important to understand the relative importance of the cost of transport, which varies with swim speed and the physiological state of the whale, in comparison to the cost of daily maintenance. This relative cost will influence our inferences on whether faster migrations are most optimal (time optimizers) and how individual whales might optimize their migration strategy to conserve energy. This knowledge is important in delineating the potential effects of changing conditions on the foraging grounds and during migrations.

The effects of disturbance from anthropogenic activities have been found to be highly context-dependent (Pirotta *et al.*, 2021), so if animals are, for example, foraging and exposed to a stressor such as noise, the stressor has a higher impact on their energetic balance than if they had been resting at the time. If the stressor occurred in a poor-forage year, the effects might have a proportionally much larger effect on survival. Comparing foraging success in more detail across foraging areas and linking the dataset presented here with higher-resolution data from tag deployments on the foraging grounds can accurately assess foraging success and energy expenditure during the foraging season (Aoki *et al.*, 2021; Bierlich *et al.*, 2022) would create a more comprehensive picture of the variation in the annual energy budgets across humpback whales' distributional range in the North Atlantic.

Optimal migration in humpback whales

Optimal migration theory is a useful framework for understanding the trade-offs associated with migration on an individual and population level (Alerstam, 2011). The theoretical concepts were established and widely used in the study of bird migrations (Alerstam and Hedenström, 1998). Optimality concepts were first employed in the context of animal migration by researchers studying flight mechanics, aerodynamics, and physiology (Alerstam and Hedenström, 1998). In recent decades, an explosion of knowledge has enabled increasingly complex considerations and opened new perspectives (Alerstam and Hedenström, 1998; Alerstam, Hedenström and Åkesson, 2003). While there are some differences between the original concepts and their application to marine mammal migrations, the same concepts can be considered to understand the adaptive benefits of baleen whale migrations and the constraints under which they migrate (Braithwaite, Meeuwig and Hipsey, 2015). For example, unlike birds, whales can store large amounts of fat and still move efficiently, although buoyancy effects might have some influence on their cost of transport (Nousek McGregor, 2010). Instead, rorqual whales are, for example, constrained by the high cost of foraging, which requires high prey densities to be efficient (Goldbogen *et al.*, 2011; Gough, 2022).

In contrast to birds and pinnipeds, baleen whales are theoretically able to give birth and nurse their young anywhere and do not need to match the timing of birth as precisely as land-based breeders. We provide an example of this in paper 1. Due to the high potential for fat storage, whales can thus decouple the use of breeding habitats from lactation more easily. However, they must optimize their migration speed to balance resting, nursing, and transport vs. basal metabolic costs while matching their arrival to resource abundance on the foraging grounds (paper 1). Braithwaite and coauthors (2015) found that the optimal migration strategy in humpback whales depends on the timing of movements to seasonal prey availability and suggested an optimal migration speed. Optimal time allocation is a crucial consideration in optimal migration theory, but such predictions are sensitive to the calibration of the bioenergetic model and depend on ecosystem phenology. In paper 1, we found that this energetic model would benefit from further refinement to make robust assessments on whether humpback whales optimize their migrations for time or energy savings (discussed above). Future studies could build on this work and conduct further modeling and simulation exercises to understand the strategies for optimal migration in humpback whales based on our results in paper 1 and using the collated dataset and information in paper 3. Such a study could also include aspects of phenology in the different foraging sites.

Extensions of the energetic model

As an extension of the energetic model we used in paper 1, which assessed the migration cost of an individual, others have established modeling frameworks to understand the relationship between migration decisions and energetic outcomes (Pirotta, Mangel, *et al.*, 2018) and can be further developed to simulate the ecological implications of disturbance on a population level (Pirotta, Booth, *et al.*, 2018; Dunlop *et al.*, 2021). Such dynamic variable state-space models integrate physiology and movement decisions with environmental conditions and then link outcomes of different strategies to the survival and reproductive success on a population level. In one such study applied to baleen whales, individual migration decisions were primarily determined by fat reserves, future reproductive needs, and time constraints throughout the annual cycle (E. Pirotta *et al.*, 2019). Using simulations, Pirotta and coauthors also explored the energetic envelope of the movement decisions, and their results emphasized a high potential for variability between individuals, something we also documented for North Atlantic humpback whales in paper 3. Notably, the timing and location of birth can be critical in these models since they determine the cost of lactation and the timing of critical energetic demand of the mother. This or similar models could be adapted to humpback whales in the North Atlantic, as an extension of the work presented in this thesis (Pirotta, 2022). The novel migration strategies we documented in paper 3 (early return from breeding migration) also open highly relevant questions about the energetic condition of such animals and their ability to accumulate sufficient reserves for migration which should be addressed in the future. Such work would allow an assessment of the risk of anthropogenic activities and improve predictions on the effects of climatic change on humpback whales across the North Atlantic.

Conservation implications

The spatiotemporal distributions of animals can determine which threats they are exposed to (Stepanuk, 2021). Although studying the conservation of humpback whales was not an explicit aim of this thesis, the presented results will be informative for future management assessments and for population assessments conducted by the International Whaling Commission. While the pressures of human activities are highest in coastal waters (Kron, 2012; Avila, Kaschner and Dormann, 2018), high-seas migration routes may also expose whales to encountering fisheries and shipping (V. Pirotta *et al.*, 2019), and these effects tend to be poorly documented and quantified because they occur in remote areas. Since females seem over-represented in northern Norway (paper 2), they might experience higher rates of disturbance than whales foraging exclusively in the Barents Sea because anthropogenic impacts are concentrated in coastal areas (Kron, 2012; Mul, 2020). The Norwegian fjord systems have a higher degree of overlap with anthropogenic activities, particularly from fisheries, tourism interactions, and shipping (Mul, 2020). Due to the high energetic costs of reproduction in mammals (Oftedal, 1997; Christiansen *et al.*, 2016) and the added constraints of accounting for the requirements of a smaller accompanying calf, the energetic balance and movements of female humpback whales are likely more constrained in comparison to non-reproducing females or males (Braithwaite, Meeuwig and Hipsey, 2015). This information is essential in a population health context and should be considered in ecosystem management frameworks for this region. To effectively inform management, long-term sampling schemes of either body condition, or pregnancy rates, should be included in official monitoring programs. Closer monitoring of the effects of disturbance, particularly entanglements in fishing gear and interactions with whale-watching tourism, should be established in northern Norway, given that pregnant females and animals from the small population segment in CVI use this area.

During their migrations, Northeast Atlantic humpback whales spend much of their time traveling through the high seas ecosystem (papers 1 and 3). The results in papers 1 and 3 suggest that birth or breeding activities might occur outside the delineated breeding areas. The breeding area is at least partly within protected areas managed for impacts on marine mammals, for example, the Sanctuary for Marine Mammals of the Dominican Republic (Mattila *et al.*, 1989). Derville and coauthors (2019) also noted a surprising independence of mother and calf pairs of sheltered waters in Oceania. If it is true and turns out to be a common phenomenon that Northeast Atlantic whales give birth outside the West Indies breeding ground, this may lead to differential exposure to anthropogenic activities in contrast to whales migrating in the western basin, who can access breeding ground areas with less effort and under fewer time constraints. Notably, some Northeast Atlantic whales passed through the area of a newly established high-seas marine protected area during their migration (NACES MPA, https://www.ospar.org). Recently, the Intergovernmental Conference on Marine Biodiversity of Areas Beyond National Jurisdiction has also, after decades of negotiations, agreed on a treaty on the protection of high seas habitat in 2023. The movements and habitat use of humpback whales in relation to these areas should be examined in more detail.

Humpback whale migrations in a changing ocean

Migration phenology under climate change

Long-distance migrants are considered vulnerable to climate change, as the habitats to which their movements are attuned in time and space may shift at different rates (Anderson *et al.*, 2013; Kubelka *et al.*, 2022). In addition, some of the predictability on which migrating animals base their movement decisions may become unreliable as accurate predictors of foraging conditions, leading to mismatches of movement and resources. While the impacts of climate change were not explicitly addressed in this thesis, the presented results provide important baseline information, and some of the observed patterns open questions about the future of humpback whale migrations. Since telemetry was first employed on humpback whales, many animals have changed their migrations due to climate change (Ramp *et al.*, 2015; Davidson *et al.*, 2020). Humpback whales have been documented to shift their annual schedules and arrive earlier, for example, on the Gulf of Maine feeding grounds (Pendleton *et al.*, 2022). Whales in Atlantic Canada shifted their arrival date by one day per year due to rising sea surface temperatures and earlier ice-break up (Ramp *et al.*, 2015), and the duration of the breeding season has expanded by one month in the Eastern Pacific (Avila *et al.*, 2020). This indicates that external cues play a role in the decision-making of migration timing in humpback whales, as has been demonstrated for blue whales (Oestreich *et al.*, 2022). However, the large variability in departure timing demonstrates that migration timing emerges from an interplay between internal and external cues, as expected for humpback whales, given the staggered migration schedules of different groups (Chittleborough, 1965).

Photoperiod and temperature are recognized as universal migration cues (Bauer *et al.*, 2011). However, in northern Norway, internal state and prey availability appear to override such cues, given the large variability of departure timing (papers 1, 2, 3). Since phenological shifts in humpback whale migration have occurred over a timeframe shorter than an individual whale's average lifespan, it appears that individuals can adjust the migration phenology throughout their lifetime (Ramp *et al.*, 2015; Pendleton *et al.*, 2022). The migration tracks from which we derived migration strategies in paper 3 were primarily collected in recent years, as opposed to movement data on the foraging grounds. Thus, temporal trends in this dataset are unlikely to be detectable. For example, humpback whales have used the coastal Norwegian fjords to forage on herring since ca. 2010 (Jourdain and Vongraven, 2017). However, the data collated in paper 3 provides an opportunity for future work to understand the differences in phenology between the various foraging areas in more detail, i.e., which cues might the movements be related to, and how might the phenology have changed throughout the two decades of data included in this dataset.

Are humpback whales resilient to climate change?

While migratory animals experience challenges in changing ecosystems (Wilcove and Wikelski, 2008), humpback whales are sometimes considered one of the potential 'winners' of climate change. The species is considered 'resilient,' following, e.g., Moore and Reeves (2018), based on their robust population size after recovery from exploitation, their large spatial distribution, behavioral plasticity, and overall population health. Humpback whales score high in this resiliency range because they are generalist predators able to switch between different prey types occurring in different areas, despite their general philopatry to migration routes and foraging grounds (Moore and Reeves, 2018). However, it is unclear whether North Atlantic humpback whales have reached historical abundance after exploitation due to uncertainties in estimating historical abundance estimates (Ruegg *et al.*, 2013).

As a seasonal migrant, humpback whales only visit polar regions during the productive season, are not directly ice-associated, and may thus benefit from extended periods of sea-ice free seas, leading to extended foraging seasons and spatially increased habitat, potentially increased productivity, or availability of prey species such as northward shifting fish stocks. The results in paper 2 suggest that Northeast Atlantic humpback whales responded to changes in the spatial distribution of herring. However, how far this response requires changes in the annual schedules is uncertain due to the limited data on their previous temporal migration patterns. Whether spatially, temporally, or both, changes in distribution patterns provide challenges for traditional static ecosystem management and conservation (Atwell, O’Neal and Ketterson, 2011; Ingman *et al.*, 2021). While endemic Arctic species score significantly lower on the resiliency framework and prioritizing the management and conservation of these species is crucial, seasonal migrants also face anthropogenic impacts that accumulate over their large range movement and across the annual cycle (Lascelles *et al.*, 2014).

Potential social mechanisms of adaptation

Our results in paper 2 demonstrated that whales foraged on herring in Norwegian fjord systems in increasing numbers over the study duration, returning year after year at high rates. Given this growth in numbers of whales and the high return rates of individuals to this area (paper 2), a social learning component could be a plausible explanation for the increased whale abundance in fjords of northern Norway. Social learning can help spread innovative adaptations to changing conditions through the population (Teitelbaum *et al.*, 2016), and humpback whale social aggregations might drive population structuring (Clapham and Zerbini, 2015; Wray, Keen and O'Mahony, 2021). Baleen whale migration routes are thought to be a learned trait, via matrilineally transmitted knowledge (Baker *et al.*, 2013). Although humpback whales live in fission-fusion societies, there is some evidence that they form long-term bonds with specific individuals (Wray, Keen and O'Mahony, 2021), a mechanism that may enhance social learning (Aikens *et al.*, 2022). Social cues are increasingly being recognized as a crucial component of migratory decisions. For example, collective sensing helps to salmon and blue whales move accurately in accordance with environmental cues, thus shaping phenology (Berdahl, Westley and Quinn, 2017; Oestreich *et al.*, 2022).

Baleen whales are re-occupying historical habitats, slowly increasing their presence there over time, for example, fin whales in specific fjords of Canadian British Columbia and the Southern Ocean, and Southern Right whales in the Southern Ocean (Carroll *et al.*, 2014; Jackson *et al.*, 2020; Keen *et al.*, 2021b; Herr, 2022). Baleen whales' ability to recover lost areas of their historical distribution may in part be driven by social learning mechanisms, indicating how important such processes can be for conservation and movement ecology. Northern Norway could provide an interesting case study for future research that aims to address how far social learning plays a role in baleen whale movement processes. Since social learning and animal culture could provide important mechanisms for adaptation to changes in environmental conditions (Brakes *et al.*, 2021), these questions are not only of value to basic research but have important implications for the conservation of migratory species in an age of ecosystem change and as such deserves more research attention.

Conclusion

The results presented in this thesis fill major knowledge gaps in our understanding of the distributions of North Atlantic humpback whales. By investigating different scales, we have, for the first time, gained a clear picture of the year-round movements of Northeast Atlantic humpback whales, including their migration patterns. Notably, we have examined their movement dynamics in the fall and winter, as well as the demographic composition of the recently established winter foraging site in fjords of northern Norway, along with an assessment of the differences in movements between various demographic groups.

The work included in this thesis highlights the variability in migration strategies, offering novel insights into the pacing of migrations and carry-over effects between migration stages. Additionally, we have estimated the energetic cost of one of the longest mammalian migrations. The impressive example of the unusually timed migration of the Northeast Atlantic humpback whales showcases our continuously evolving understanding of the ecology of marine migrants. We also provided an overview of movement patterns across all feeding grounds by collating satellite telemetry data from over 200 individuals over two decades. Documenting humpback whale movement patterns in space and time provides essential information for ecosystem management.

Overall, this thesis opened exciting avenues for future research and laid a strong foundation for understanding North Atlantic humpback whale migrations. It also offers valuable insights for the study of baleen whale migration in general.

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PAPER I

Round-trip migration and energy budget of a breeding female humpback whale in the Northeast Atlantic.

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RESEARCH ARTICLE

Round-trip migration and energy budget of a breeding female humpback whale in the Northeast Atlantic

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Abstract

In the northern hemisphere, humpback whales (*Megaptera novaeangliae)* typically migrate between summer/autumn feeding grounds at high latitudes, and specific winter/spring breeding grounds at low latitudes. Northeast Atlantic (NEA) humpback whales for instance forage in the Barents Sea and breed either in the West Indies, or the Cape Verde Islands, undertaking the longest recorded mammalian migration (~ 9 000 km). However, in the past decade hundreds of individuals have been observed foraging on herring during the winter in fjord systems along the northern Norwegian coast, with unknown consequences to their migration phenology, breeding behavior and energy budgets. Here we present the first complete migration track (321 days, January 8th, 2019—December 6th, 2019) of a humpback whale, a pregnant female that was equipped with a satellite tag in northern Norway. We show that whales can use foraging grounds in the NEA (Barents Sea, coastal Norway, and Iceland) sequentially within the same migration cycle, foraging in the Barents Sea in summer/fall and in coastal Norway and Iceland in winter. The migration speed was fast ($1.6\ ms^{-1}$), likely to account for the long migration distance (18 300 km) and long foraging season, but varied throughout the migration, presumably in response to the calf's needs after its birth. The energetic cost of this migration was higher than for individuals belonging to other populations. Our results indicate that large whales can modulate their migration speed to balance foraging opportunities with migration phenology, even for the longest migrations and under the added constraint of reproduction.

Introduction

In many animal taxa, migration is a crucial behavior that allows organisms to match their life history requirements to environmental variability in space and time [1]. In many cases, feeding and breeding areas are geographically separated, sometimes by substantial distances. In

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response, some long-range migrants have developed a capital breeding strategy, where they fast while in suitable breeding areas and accumulate energy reserves at suitable feeding grounds [2, 3]. The survival and reproductive success of capital breeders therefore relies on maximizing energy gain on feeding grounds and minimizing energy expenditure, to cover fasting periods of migration and reproduction. Because the amount of energy available to a capital breeder is fixed during the feeding period, capital breeders need to optimally match migrations to external conditions and internal state (e.g., prey availability and pregnancy, [3–5]). This requires careful budgeting of energy over the annual and life cycle [3, 4]. While there is currently no way to obtain continuous data on energy expenditure of free-ranging large cetaceans over their annual cycle, bioenergetic models can be used to estimate energy expenditure. Long-term individual tracking data provides information (such as movement speed) to parameterize these models [4, 6, 7].

Humpback whales (*Megaptera novaeangliae)* undertake the longest migrations of all mammals. In the northern hemisphere, they typically migrate from summer and fall feeding grounds at high latitudes to winter breeding grounds in specific tropical areas delineated by warm water temperatures [8, 9]. In the Northeast Atlantic (NEA), humpback whales forage in the Barents Sea and adjacent waters [10, 11], around Iceland [12] and Greenland [13], and then migrate to breeding grounds in the West Indies [14, 15] or the Cape Verde Islands [15, 16]. The distance between the Barents Sea and the West Indies represents the longest migration route of any humpback whale population (a great circle distance of ~ 9 000 km vs. 8 461 documented by [9]). Northwest Atlantic humpback whales also migrate to the West Indies from Newfoundland-Labrador, the Gulf of St. Lawrence, or the Gulf of Maine [15, 17–19], a distance up to 5 000 km. As a result of this long migration distance, NEA humpback whales may face high energetic constraints compared to whales migrating elsewhere. However, until now, no tracking data following NEA humpback whales on their migration has been available.

During the last decade, hundreds of humpback whales have been observed in specific fjord systems of northern Norway during winter (main season November–January [20–23]). Here, the whales feed on large aggregations of Norwegian Spring Spawning herring (*Clupea harengus*) that have overwintered in these fjord systems in this period [20, 22]. While within-season photographic matches have been reported between coastal Norway and the Cape Verde Islands [21], it remains unclear whether whales feeding in coastal Norway during the winter also migrate to breeding grounds in the West Indies within the same season. Given the traditional view of humpback whale migration phenology, feeding during the winter may present a shifted or extended feeding season, which may exacerbate the existing constraints of covering the long distance to breeding grounds and matching the timing of the reproductive season. However, since Norway lies between the Barents Sea and breeding grounds, feeding there may allow individuals to accumulate additional energy reserves prior to migration to increase breeding success [23]. While pregnant humpback whales commonly maximize the time spent on feeding grounds and leave later than other groups [24–26], this may present a critical trade-off if they must reach suitable waters prior to the end of gestation, for instance if early calf survival is influenced by water temperature or the availability of sheltered waters [9, 27].

Here, we present the first tracking data of a full round-trip migration for a humpback whale. The female was tagged at the feeding area in coastal northern Norway in January. Because the whale was observed without a calf when tagged, and then observed again with a calf upon its return to the same area in the following season, we had the unique opportunity to examine the round-trip migration covering late pregnancy, calving and lactation. We aimed to 1) describe the migration phenology and migration pathway through the NEA, 2) describe the movement characteristics of a female during pregnancy and lactation, and 3) estimate the energetic cost of this migration.

Materials & methods

Tag deployment and data pre-processing

We deployed a transdermal Argos satellite tag (SPOT-303, size: 300mm x 24mm, www.wildlifecomputers.com) on a female humpback whale on the winter feeding grounds in coastal northern Norway (Kvænangen fjord, January 8th, 2019, Fig 1). The tag was deployed from a 26-ft open rigid-hull inflatable boat using an Aerial Rocket Tag System launcher (LKARTS- Norway) from about eight meters distance. Tagging procedures were approved by the Norwegian Food Safety Authorities (Mattilsynet) under permit FOTS-ID 14135. We programmed the tag to send 16 transmissions/hour for the first 100 days, then 14 transmissions/hour for the following 30 days and then 12 transmissions/hour for the next 90 days. After 220 days, the tag sent 80 transmissions per day for the rest of the deployment. The sighting history of this individual was extracted from the North Norwegian Humpback Whale Catalogue (NNHWC, [28]) by matching photographs of its fluke (sighting history in S1 Table in S1 File). Sightings on the 2nd and 14th November 2019 confirmed the presence of a calf (Fig 2). All numerical and statistical analyses were performed using R software version 4.0.3 [29].

Because migration speed was one of the key parameters used in our analyses, the raw Argos locations were projected to an azimuthal equidistant projection centered on the middle of the track (45˚N, 20˚W) to best conserve distances between locations across the latitudinal range. Extreme outlier positions were then removed using a speed, angle and distance filter (max speed: 9 ms^{-1}, `sda()` function of the trip package, version 1.7.1, [32] based on [33]). All positions with quality class Z were removed. The filtered locations were then used to reconstruct the most likely path using a continuous time state-space model from the foieGras package using `fit_ssm()` in version 0.6–9 [34–36]. This model assumes an underlying correlated random walk process considers the error ellipse estimates around the original locations provided by CLS-Argos (S1 Fig in S1 File), and the most likely movement path and its associated uncertainty estimates are returned. We sampled locations along the predicted path at 6-hourly intervals, which were then used throughout our further analyses.

We also calculated the movement persistence, γ, between successive locations, which is the autocorrelation in speed and directionality for each step [35], using `fit_mpm()` in foieGras. Movement persistence characterizes a continuous behavioral mode, ranging from meandering movements associated with area restricted search behaviors (ARS, $\gamma = 0$) to directed movement ($\gamma = 1$) usually associated with transit. Switches in γ therefore indicate changes in behavioral mode, e.g., between migration and residence. To identify start and end dates of migration, we conducted a segmentation analysis on γ, using the “Lavielle” method, `lavielle()` within adehabitatLT, version 0.3.25 [37–39].

To identify the calving date, we carried out the same analysis using speed as the parameter. Based on gestation duration, the whale would have given birth in the first months after leaving the feeding grounds, so we limited this analysis to the southbound leg of the migration. We assumed two different behavioral states (pre- and post-birth) distinguished by the difference in swim speed between pregnancy and lactation (i.e., accompanying a neonate calf).

To assess whether the whale deviated from the shortest possible path to the breeding grounds, we calculated the least cost path through water between the mean latitude and longitude of feeding and breeding locations, constraining the path to water depth > 10m (obtained from [30]), using the `lc.dist()` function in marmap, version 1.0.4 [40]. Two resulting alternative shortest distances are given between the feeding ground and breeding ground: either directly or via the observed stopovers (Fig 1).

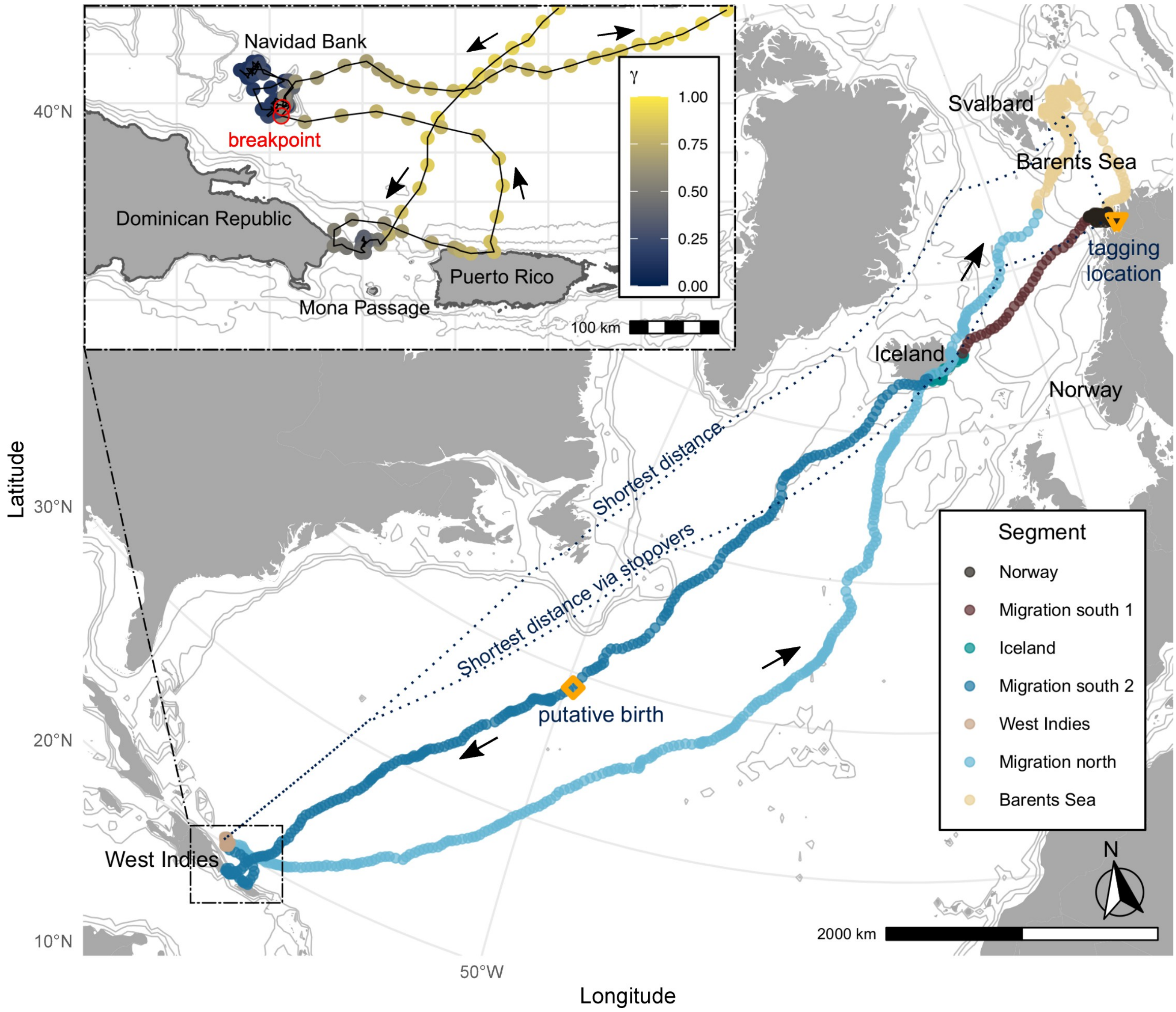

Fig 1. Full migration track of a pregnant female humpback whale in the Northeastern Atlantic. Locations from predicted path colored by the different migration segments. Tagging location is indicated by an orange triangle and the putative location of birth is indicated by an orange square. The inset shows movements on the breeding grounds, colored by movement persistence, yellow indicating directional travel, and blue indicating meandering movement. Arrows show the direction of movement. Dotted blue lines in the main map indicate the shortest possible distances through water. Contour lines show the 200 m, 1000 m, and 2000 m bathymetric isolines (data from [30] for the main map and [31] for the inset). Landmass data was obtained from naturalearth.

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Energetic model

We estimated the energetic cost of this migration using a bioenergetic model that estimates the energy required for an animal to cover 1) its basic energy requirements (basal metabolic rate, BMR) and 2) the cost of overcoming the drag forces associated with moving its body through water at a given speed (cost of transport, $E_{COT,}$ based on [41]). The model parameters (Table 1) are described in [6] and [7]. We estimated BMR using the Kleiber allometric

Fig 2. Photographs from deployment and resighting with calf. Left: Fluke and tag position at time of deployment (January 8th, 2019). Right: First re-sighting the following season, the individual accompanied by calf (November 2nd, 2019) with the tag still in place. Photo: A. Rikardsen.

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equation of BMR in relation to body mass in kcal day^{-1} [42]:

$$BMR = 4186.8\,[70M^{0.75}] \qquad \text{(Eq 1)}$$

where M is body mass (kg). We assumed a body mass of 30 000 kg for a 13 m female (in accordance with [6, 43]). We multiply by 4186.8 to convert to Joule day^{-1} and then multiply by the migration duration (in days) which gives the metabolic maintenance cost (Joule).

The energetic cost of transport E_{COT} is calculated as:

$$E_{COT} = \left(\frac{\lambda}{2\varepsilon_A \varepsilon_P}\right)\rho S C_d V^3 \qquad \text{(Eq 2)}$$

Here, the aerobic efficiency ε_A describes how efficiently metabolic energy is converted to mechanical work by the muscles, and ε_P is the propulsive efficiency describing how efficiently mechanical work is converted to forward motion [44]. The C_d term is the drag coefficient, ρ is the density of water (kg m^{-3}) and S is the wetted surface area of the whale (m^2). The ratio of active to passive drag, λ, accounts for the fact that active body movements and posture changes change how drag forces act on a body moving through a medium [41]. Finally, V is the speed of the animal through water (ms^{-1}), estimated from displacement between predicted locations.

Table 1. Parameters, units and values used to calculate the energetic cost of migration. Parameter estimates were chosen in accordance with [6, 7].

PARAMETER	UNIT	VALUE	SOURCE
C_D	Drag coefficient	0.003	[6]
S	Wetted surface (m^2)	0.054 $M^{0.696}$	[45]
M	Mass (kg)	30 000	[43]
E_P	Propulsive efficiency	0.8	[46]
E_A	Aerobic efficiency	0.2	[46]
λ	Ratio of active to passive drag	0.7	[41]
P	Density of seawater (kg m^{-3})	1 027	Standard for seawater
V	Swim speed (ms^{-1})	dynamic	Displacement between locations, constant for each 6-hour step

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Eq (2) gives the instantaneous power required to overcome drag (in Watt, or Joule s^{-1}) at a given speed. Our data consists of interpolated positions at 6-hour intervals, providing swim speed estimates for each of these intervals. To convert the instantaneous power (Eq 2) to the energy expenditure required to swim at this speed for the duration of each interval, we therefore multiply it by the timestep duration (i.e., 6 hours). To obtain an estimate of the daily cost of transport, we then sum every set of four 6-hour estimates. We then calculated the total energetic cost of migration as the sum of estimated metabolic maintenance cost and cost of transport (E_{COT}), for the duration of the round-trip (139 travelling days, 14 days along Iceland and 17 days on breeding grounds).

Because we use swim speed to estimate the energy requirements of migration it is important to account for the way ocean currents may assist or impede movements, i.e., how much of the observed displacement is due to movement by the whale itself. We estimated speed over ground from the geodesic distance between consecutive predicted locations using geodist() in the geodist package [37]. We then corrected speed over ground for ocean surface currents to obtain estimated swim speed through water. We used the nearest available record of surface current from a coupled atmosphere-land-ocean-sea ice model at quarter-degree spatial and hourly temporal resolution [47] (S1 Fig in S1 File). The ocean current data were prepared by the UK Met Office, Exeter, UK and made available online by E.U. Copernicus Marine Service Information [48]. We extracted the *u* and *v* current vectors nearest to each observed whale location in time and space. We followed [49] using `windSupport()` in the package windR [50] (accessed 15.02.2021). Speeds presented throughout the manuscript refer to speed through water (current- corrected swim speeds). We classified each location during the migration as either resting ($< = 0.5ms^{-1}$) or transiting ($> 0.5ms^{-1}$ in accordance with [6]). Summary statistics are given as medians and 25th and 75th quantiles (Q_{25}-Q_{75}), unless otherwise stated.

Results

We satellite tracked a female humpback whale for 321 days (January 8th, 2019 –December 6th, 2019) from the fjords of northern Norway to the West Indies and back to the same Norwegian fjord (November 2019), via the Barents Sea (Fig 1). The whale was last photographed in the same fjord on January 2nd, 2020. Previous photographic records from the North Norwegian Humpback Whale Catalogue (NNHWC) show that it was present on the Norwegian coastal feeding grounds also during the 2013/14 and 2014/15 winter seasons (NNHWC, S1 Table in S1 File). We identified seven segments in the track which corresponded to changes in the movement persistence mean: 1. Norway, 2. Transit to Iceland ("migration south 1"), 3. Iceland, 4. Transit to breeding grounds ("migration south 2"), 5. West Indies, 6. Transit to feeding grounds ("migration north"), 7. Barents Sea and Norway (Fig 1). The breakpoints between segments identified departure and arrival times (dashed lines Fig 3).

The whale left the Norwegian fjords on February 7th, 2019, to the east coast of Iceland, where it spent 15 days before continuing the southward migration on March 1st (Fig 3). It was present on known breeding grounds from mid-April to mid-May. After its return to the NEA, the feeding season lasted between late July and late October 2019 in the Barents Sea, and between early November and at least until the last sighting on January 6th, 2020, in the Norwegian fjords (> 5 months). We found that using the stopovers in Norway and Iceland increased the shortest possible distance between feeding and breeding grounds by 7.5% to 9 071 km (Fig 1). The cumulative distance of the observed migration path was 18 500 km, split between 9500 km on the 68-day southward migration (coastal Norway–West Indies) and 9000 km on the 71-day northward migration (West Indies–Barents Sea). The whale deviated from the shortest

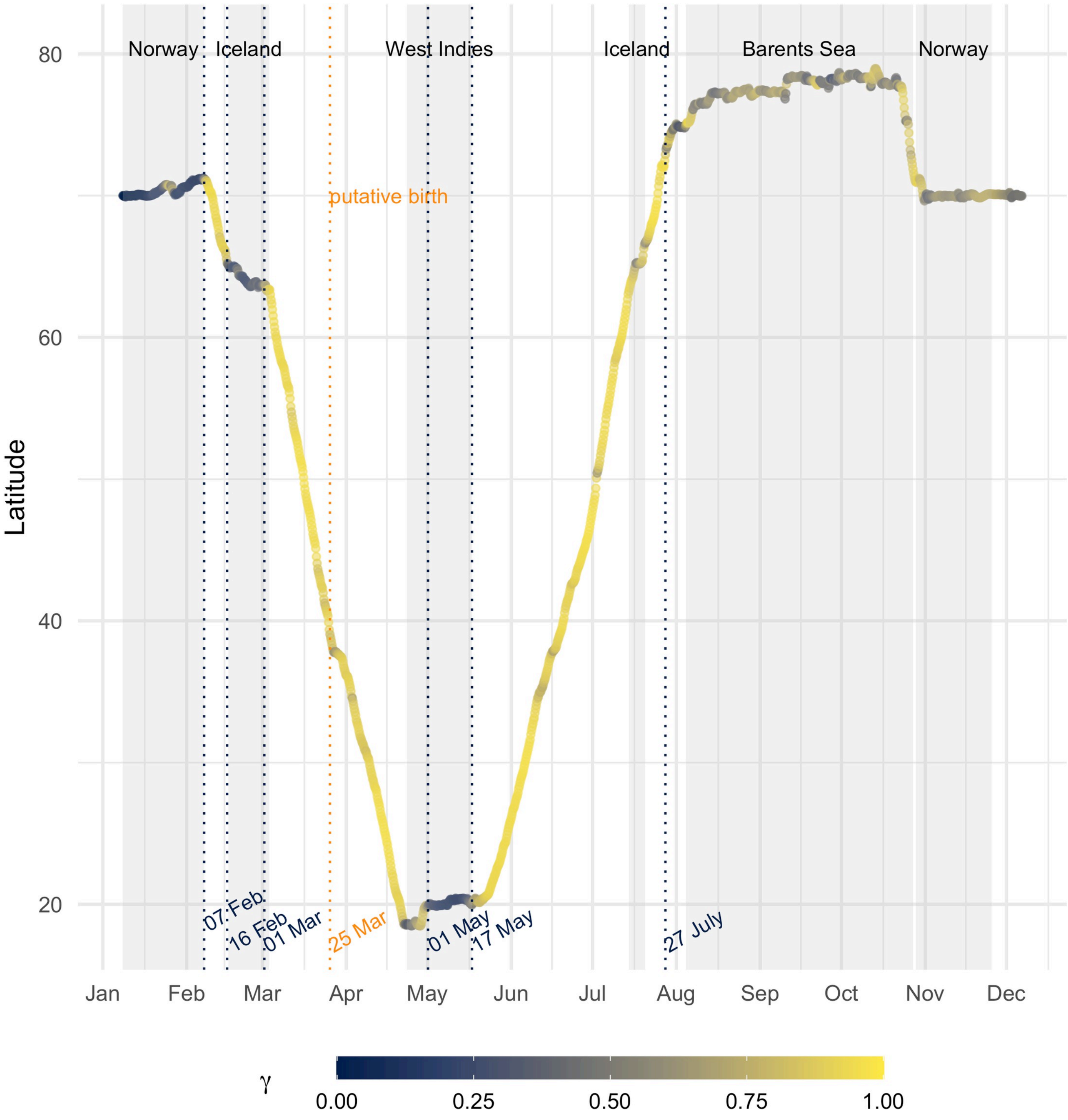

Fig 3. Migration and movement persistence. Migration of the whale as indicated by the change of latitude over time with movement persistence, γ, at the respective location shown in color (0–1). Background shading indicates when the whale was observed over the continental shelf (water depth < 200 m [32]). The time spent on shelf regions are associated with low γ in dark blue indicative of area restricted search behavior, while high γ in yellow indicates transit. The blue dotted lines indicate the break points based on changes in mean movement persistence.

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path and followed different paths during the southward and northward migration, with the northward path further to the east (Fig 1).

Based on the segmentation, we define migration as the part of the track between coastal Norway until switching to low movement persistence south of the Barents Sea. During this migration, 139 days were classified as transiting (speed: 1.5 ms^{-1}, Q_{25}-Q_{75}: 1.1–1.8) and 31 days as stationary at stopover areas in Iceland and on the breeding ground in the West Indies (Fig 3). Migration speed was fastest in the first migration segment ("migration south 1", Norway to Iceland: 1.9 ms^{-1}, Q_{25}-Q_{75}: 1.7–2.2, Fig 4). We detected a breakpoint, i.e., a change in mean speed, during the second migration segment ("migration south 2") from Iceland to the West Indies. This was associated with a shift in median speed from 1.7 ms^{-1} (Q_{25}-Q_{75}: 1.4–2.1) to 1.3 ms^{-1} (Q_{25}-Q_{75}: 0.8–1.6, Fig 4). After an initial sharp decline and short period (24 hours) of very slow speeds (< 0.5 ms^{-1}), speeds increased again but remained lower than during the early migration (Fig 4). This suggests that calving occurred just after crossing the Gulf Stream/ North Atlantic Current at 39°N 49°W, on March 25th (Fig 1) in sea surface temperature around 18°C. Most resting (< = 0.5 m/s) occurred after this date (Fig 4, red circles). During the northward migration median speed was 1.5 ms^{-1} (Q_{25}-Q_{75}: 1.1–1.8). Therefore, median speed prior to the putative calving date was overall faster (pre-calving: 1.8 ms^{-1}, Q_{25}-Q_{75}: 1.5–

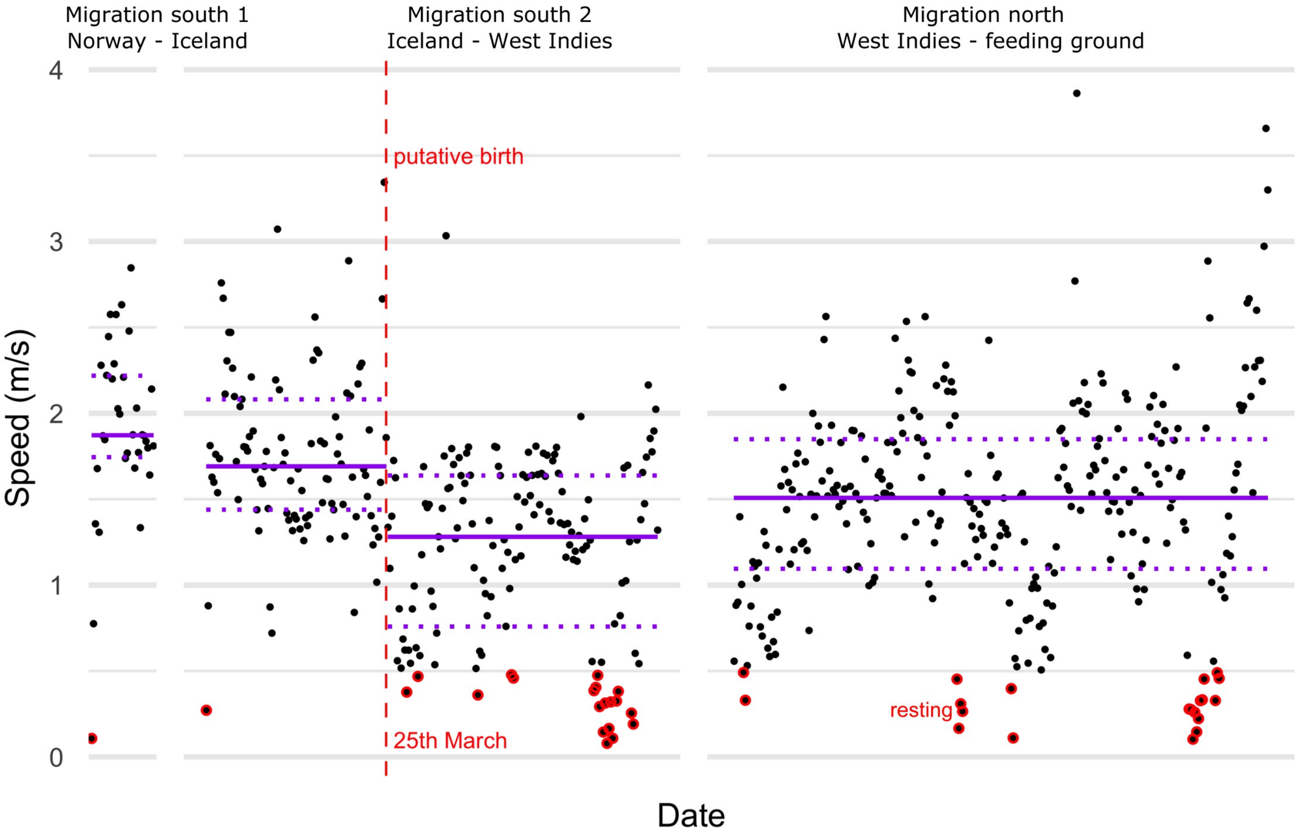

Fig 4. Speed during the migration segments. Chronological from left to right: Norway–Iceland, Iceland–West Indies, West Indies–Barents Sea. Segmentation based on movement persistence. The dotted red line indicates the putative time of calving based on a segmentation analysis of the "southward migration 2" segment, which was associated with a change in median speed from 1.7 ms^{-1} to 1.3 ms^{-1} (horizontal lines indicate median speed and dotted lines the respective first and third quartiles).

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2.1) than when the whale was presumably traveling with her calf (post-calving: 1.4 ms^{-1}, Q_{25}-Q_{75}: 1.0–1.7, Fig 4).

The mother-calf pair reached Mona Passage (between Puerto Rico and Hispanola) on April 21st and then moved between coastal areas of the Dominican Republic and the north coast of Puerto Rico until April 28th (Fig 1). For ~ 3 days, the pair seemed to be resting (speed < 0.5 ms^{-1}) but the end of southward migration (i.e., a breakpoint associated with a shift in mean movement persistence) was only detected after the pair transited to Navidad Bank on May 1st (Figs 1 and 3). They remained there until initiating the northward migration on May 17th. On the northward migration, the mother-calf pair passed close to the Iceland coast but continued moving north. The end of migration was detected on July 27th, south of the Barents Sea (73˚N, 9˚E, Figs 1 and 3). After ~3 months they proceeded towards the Norwegian coast (October 23rd), where they arrived in early November.

Using the bioenergetic model, we estimated the total cost of the round-trip migration (from coastal Norway to the Barents Sea) to be 142 030 megajoule (MJ), 28 360 MJ allocated to cost of transport and 113 670 MJ to maintenance metabolism (Table 2). This total estimate includes energetic expenditure for 170 days (coastal Norway–Barents Sea), of which 139 days were spent actively transiting ("migration south 1", "migration south 2", "migration north") and 31 days stationary on stopovers in Iceland (14 days) and on the breeding ground in Navidad Bank (17 days). We also present a theoretical cost at lower migration speeds (as reported in previous studies, 0.9 m s^{-1} and 1.1 m s^{-1}) in S2 Table in S1 File. The whale was likely lactating for 124 out of the 170 days, given the putative calving date.

Discussion

We present the longest and first fully recorded round-trip migration of a humpback whale, and the first satellite track of an individual from the Northeast Atlantic (NEA). While earlier studies have provided key insights into humpback whale movement and migrations in many other regions, these studies have only mapped migrations one way, due to the limited longevity of tag deployments. Most studies tracked humpback whales from breeding grounds and in one published case from feeding grounds [7, 19, 51–53]. We show connectivity between three known NEA feeding grounds, describe the phenology of this migration, and provide new detailed information on the movements of a mother-calf pair. We were also able to estimate

Table 2. Energetic cost of migration.

PARAMETER	A) FULL MIGRATION INCL. ICELAND AND BREEDING GROUNDS	B) NORTHWARD MIGRATION
DURATION (days)	170 (transiting: 139)	71
DISTANCE (km)	18 500	9 000
MEDIAN SWIM SPEED (ms^{-1}± IQR)	1.3 ± 1.2 (transiting: 1.6 ± 0.7)	1.5 ± 0.8
E DAY^{-1} (MJ Day^{-1})	834	867
E_{COT} (MJ)	28 360	14 309
METABOLIC MAINTENANCE (MJ)	113 670	47 738
E_{TOTAL} (MJ)	142 030	62 047

Energetic cost of migration for **A)** a full migration for a female traveling with a calf from Norway to West Indies, including a stopover in Iceland, **B)** values for the northward migration, from West Indies breeding grounds to the start of foraging behavior south of Barents Sea feeding grounds. Values presented are migration days, kilometers traveled (km, as measured along the track), the energetic cost of transport (E_{COT}), the cost per day, metabolic maintenance (total BMR expenditure) and the total energetic cost (sum of E_{COT} and metabolic maintenance). Energetic costs are presented in megajoule (MJ).

https://doi.org/10.1371/journal.pone.0268355.t002 the most likely location and timing of calving during the southward migration and show how this affected the whale's migration speed. This track provided unique empirical data to estimate the energetic requirements of this migration route. It therefore allowed us to explore the trade-offs associated with allocating time between feeding, breeding, and migration throughout the annual cycle.

We demonstrate that humpback whales can use several NEA feeding grounds (the Barents Sea, coastal northern Norway, Iceland) and migrate to the West Indies to give birth within the same annual cycle. The connectivity between these feeding grounds in the NEA has been sporadically documented by photographic matches between Iceland and the Norwegian coast [54], between the Barents Sea and Iceland [Broms, pers. communication], and between the Barents Sea and the Norwegian coast [23]. Sequential use of these three areas within one annual cycle had not been recorded prior to this study. The tracked individual foraged in northern Norway until early February, and likely for two additional weeks in Iceland [12]. Humpback whale winter feeding aggregations have previously been described from Iceland [55] and Alaska [56], and at least some of the observed individuals migrate at the end of this feeding season. Only a fraction of the whales feeding in the Barents Sea are observed at the coast of northern Norway in the winter [11, 23]. Many of these have been observed in several seasons, suggesting there may be an individual preference for this feeding strategy [23]. The remainder of the population may travel directly from the Barents Sea to breeding grounds, or continue feeding offshore where they are less easily observed, as there is also high herring biomass offshore in the winters.

The whale left Norway on February 7th, slightly later than other whales, as most leave between December and late January [23]. In other regions, pregnant females also remain up to two months longer on the feeding grounds compared to other groups [24–26], presumably to cover the substantial additional cost of pregnancy and lactation [57, 58]. Females can maximize their calf's chances of survival by providing sufficient energy and resources both during pregnancy and subsequent lactation [59, 60]. This strategy may increase reproductive success of the mother if it is successfully employed across years [24, 57, 61].

The female appeared to be able to partly compensate for the late departure from feeding grounds by increasing its overall travel speed during transit, thus arriving towards the end of, but still within, the breeding season of NEA humpback whales [15]. Whales from the NEA exhibit a later breeding season in the West Indies (February–May) than whales from the Northwest Atlantic. This may be due to their longer migratory distance [15, 62], or different seasonality of feeding. Based on this difference in breeding season and their spatial use of the West Indies, NEA humpback whales might form a behaviorally distinct population segment [15]. Most NEA humpback whales are sighted in the east of the West Indies [15], but the tracked individual frequented areas predominantly associated with Northwest Atlantic humpback whales further west (Dominican Republic, incl. Navidad Bank). Whale presence in the Dominican Republic peaks in February and early March, with few sightings in April [63], but our data substantiates recent evidence from acoustic monitoring that the season in this area lasts until the end of May [64].

Calving occurred during the southward migration, ~35 days before the female reached the breeding grounds. Calving is generally expected in calm, shallow coastal or bank waters [65–69] and not in exposed oceanic waters. However, the observed changes in movement (i.e., from fast to very slow movement followed by a period of continuous movement at reduced speed) are consistent with the behavior reported from earlier observations of calving events [65, 66, 70]. Newborn calves have been documented outside of the described main breeding grounds elsewhere [26, 71] and historical whaling records from Norway include records of late-stage pregnancies in Norwegian waters during winter and spring [72], also indicating humpback whales from this region might give birth shortly after these observations were made, likely outside breeding grounds [73]. This indicates that shallow waters are not crucial for neonates immediately after birth, but that perhaps water temperatures may need to be above some critical value [9]. It may also reflect that maximizing maternal energy intake in productive waters is more important to calf survival than a birth in shallow, warm breeding grounds.

The overall migration speed (1.5 ms^{-1}) was faster than documented for humpback whale migrations in most other regions and varied throughout the migration. Speed was highest during pregnancy early in the migration (1.7–1.9 ms^{-1}) and remained relatively high during nursing (1.4 ms^{-1}). Previously reported average migration speeds obtained from satellite tracks ranged between 0.9 ms^{-1} [7] and 1.63 ms^{-1} [52], the fastest being reported from the only other available tracking study covering the migration from feeding to breeding grounds [52]. Whales satellite tagged on the West Indies breeding ground and heading towards the NEA were also slightly faster compared to those heading to western feeding grounds, presumably due to their longer migration distance (1.25 ms^{-1} [19]). None of these studies accounted for ocean currents, but speed was overall only slightly influenced by currents (mean absolute difference between speed through water and speed over ground 0.07 ms^{-1}, S2 Fig in S1 File). The fast migration speed may be a response to time constraints in reaching the breeding grounds given 1) the long distance between Norway and the West Indies, 2) the late departure from Norway at the end of the winter and 3) the additional stopover in Iceland. Elephant seals for example also increase migration speed to precisely time their arrival to breeding grounds where they give birth [5], and our data indicate this may be the case in humpback whales.

While fast migration speeds may be expected for NEA humpback whales, nursing whales are generally expected to migrate slower than those traveling without calves (0.86–1 ms^{-1} [6, 68, 74]). Although the present female adjusted her speed when traveling with the calf, the migration speed still exceeded previous estimates of theoretical optimal migration speed estimated for nursing humpback whales for similarly long migrations (1.1 ms^{-1} for ~ 8 500 km one-way [6]). After the putative calving, swim speeds decreased, and more days were spent resting. However, we identified fewer resting days compared to what has been previously reported as optimal for energy conservation, calf growth and milk transfer rates (14% compared to 27% [6]). Routine swim speeds for baleen whales, i.e., the speed at which animals swim most efficiently based on physical adaptations, seem to converge around 2 ms^{-1} during transiting movements on feeding grounds [75, 76]. Swim speeds slower than 2 ms^{-1} observed from tracking data may therefore be due to resting periods between swimming bouts not resolved at 6-hourly resolution.

In other regions, lactating humpback whale females choose migration routes close to coastlines and spend time in sheltered areas to rest and nurse [68, 77]. In contrast, the migration of NEA whales occurs almost entirely on the high seas. Therefore, mother-calf pairs may have different resting/energy conservation strategies. Reduced resting time and faster swim speeds can lead to a loss of milk and increased energetic demands of the calf, increasing the energetic cost to the mother beyond that solely caused by higher costs of transport at higher swim speed [6]. Because we cannot reliably quantify this effect (but see [6]), we did not include the cost of lactation and gestation. Therefore, the total energy expended by the mother during migration will be higher than reported.

The fast migration speed and long distance resulted in a high energetic cost of this migration, compared to e.g., lactating females migrating 0.6 ms^{-1} slower and ~ half the distance from Australia to the Southern Ocean [7]. However, the fast migration speed reduced the time required to complete the distance (70 compared to a mean of 62 days reported by [7]). This means that some of the additional cost caused by fast speeds was offset by reducing maintenance costs, compared to if the migration duration had been extended by slower swim speed. If the whale in this study had migrated at a slower speed during the northward migration, e.g., the theoretical optimal migration speed reported by [6] (1.1 ms^{-1}) or the average swim speed of mother-calf pairs reported by [7] (0.9 ms^{-1}), its arrival to the feeding ground would have been delayed (24 or 45 days, respectively). While reducing the cost of transport, this would have caused the whale to miss part of the feeding season and would have incurred higher maintenance costs for each additional day of migration. Migration strategies available to whales feeding throughout the winter in Norway may therefore be to 1) travel fast, spend time on breeding grounds (as we observe), 2) travel slowly and reduce time on breeding grounds or 3) travel slowly and start feeding later in the year (e.g., mid-August/mid-September).

Obtaining reliable measurements of biomechanical parameters and travel speeds is challenging for large marine vertebrates, so bioenergetic models such as the one presented here, rely on a range of assumptions and approximations [6, 78]. While parameter values in the model are averages of estimates, true values are likely variable between individuals and over time (due to differences in mass, condition, surface area, gaits, appendage morphometrics, behavioral patterns). For example, we use a fixed value for the drag coefficient (C_d) which has been estimated by previous studies. Substantial uncertainty exists around this value for most species, including humpback whales ([6] but see [76] and [79]), and it also varies with many of the same factors mentioned above. Similarly, BMR cannot be directly measured for large free-ranging marine animals, and there is disagreement on the relationship between size and metabolic cost for large animals [80, 81], so we rely on estimates based on allometry. Since both C_d and BMR are central parameters in this model, our estimates are only rough indicators. Importantly, changing the values for BMR and C_d in the bioenergetic model may lead to a shift in the relative importance of maintenance cost vs. transport cost, i.e., the importance for a whale to minimize metabolic cost (by decreasing the duration of migration) vs. minimizing transport cost incurred from movement (by decreasing speed). By using the same parameters as previous studies, we can ascertain that the relative cost of this migration is larger than that reported previously [7], but the magnitude of the increase cannot be determined with certainty.

Additional uncertainties exist regarding the energetic costs of mother-calf pair movement and how these scale with speed, since calves swim directly at their mothers' side, thereby changing the mothers' drag profile and their own [82]. While optimal swim speeds seem to be largely independent of size across the range examined in a recent study (minke whales—blue whales [75]), calves have less muscular power and lower lung capacity than adults [83]. Therefore, calf requirements and swim speed likely determine resting periods and overall migration speed. Furthermore, animals likely swim at a depth where additional wave drag produced at the air/water interface is minimized (e.g., ~12 m for large baleen whales) [84]. Ocean current speed at depth may differ to current speed at the surface. As the tag used in this study did not collect dive information, we assumed that the whale swims at an optimized depth most of the time, avoiding additional wave effects at the surface, and that the ocean current effects experienced can be approximated by surface currents (0–5 meters depth).

The behavioral choice observed in this study (i.e., longer feeding season and faster migration speed), and the resulting higher energetic cost, indicates a trade-off between benefits incurred from spending time on the breeding grounds with the calf (e.g., optimized nursing and growth, predator avoidance summarized in [27, 67]) and resting during migration, as well as the need to return to high latitudes in time to feed and replenish energy reserves. However, there is limited knowledge on the seasonality of humpback whale occurrence in the Barents Sea, limited to periods of survey and observer effort in the area. A better understanding of this seasonality is required within the context of ongoing ecosystem changes [85]. It is unclear whether the winter feeding in coastal Norway presents a supplemental nutritional opportunity for whales or compensation for poor foraging success during the summer/autumn. Recent growth in the NEA humpback whale population [11] and food-web changes in the Barents Sea [86] may have led to a reduction in foraging success, which could be compensated for during the winter, given the high herring biomass in Norwegian waters. Increased competition due to changes in the prey base and concomitant whale population recovery has been proposed as a cause for humpback whales to feed during winter in the Pacific [85, 87]. Low prey availability on the main feeding grounds may also cause Southern Ocean humpback whales to seek out supplemental feeding opportunities [53, 74], and ecosystem changes may have caused a reduction in foraging and reproductive success in Northwest Atlantic humpback whales [88].

Conclusion

We confirm that a successful breeding migration can take place after a winter feeding season in Norwegian fjords within the same season, and that NEA feeding grounds can be used sequentially throughout the year. Breeding humpback whale females can seemingly compensate for the long feeding season by increasing migration speed, successfully balancing it with the associated energetic costs, calf requirements and the phenology of feeding opportunities throughout the annual cycle. These findings demonstrate how individual behavioral choices can allow a whale to successfully balance energetic levels throughout the annual cycle, allowing it to adjust its movements to local prey availability. A better understanding the energetic requirements of this migration will allow researchers, managers, and policy makers to consider the needs of these top predators in ecosystem-based fisheries management, and to assess the potential impacts of increasing anthropogenic activities in the Arctic. Our results may facilitate future studies on the sensitivity of this northern population to a rapidly changing Arctic ecosystem and provide new insights in humpback whale migration ecology in the NEA and in general.

Supporting information

S1 File. Contains S1 and S2 Tables and S1 and S2 Figs.
(DOCX)

S1 Data. Contains date-time, corrected speed, movement persistence, and distance between all relocations estimated from the reconstructed path.
(CSV)

S2 Data. Daily latitude and longitude of the reconstructed path.
(CSV)

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PAPER II

Don’t mind if I do – Arctic humpback whales respond to winter foraging opportunities before migration.

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Don't mind if I do - Arctic humpback whales respond to winter foraging opportunities before migration

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Abstract

Migration patterns are fundamentally linked to the spatiotemporal distributions of prey. How migrating animals can respond to changes in their prey distribution and abundance remains largely unclear. During the last decade, humpback whales (Megaptera novaeangliae) used specific winter foraging sites in fjords of northern Norway, outside of their main summer foraging season, to feed on herring that started overwintering in the area. We used photographic matching to show that whales sighted during summer in the Barents Sea foraged in northern Norway from late October to February, staying up to three months and showing high inter-annual return rates (up to 82%). The number of identified whales in northern Norway totaled 866 individuals by 2019. Genetic sexing and hormone profiling in both areas demonstrate a female bias in northern Norway and suggests higher proportions of pregnancy in northern Norway. This may indicate that the fjord-based winter feeding is important for pregnant females before migration. Our results suggest that humpback whales can respond to foraging opportunities along their migration pathways, in some cases by continuing their feeding season well into winter. This provides an important reminder to implement dynamic ecosystem management that can account for changes in the spatiotemporal distribution of migrating marine mammals.

Introduction

The spatiotemporal distribution of prey resources is considered foundational to animal movement. Seasonal migrants, in particular, rely on predictably occurring resources to fuel their year-round energy demands (Abrahms et al., 2019; Evans & Bearhop, 2022). However, ecosystems undergo changes at multiple scales as a result of natural variability, anthropogenic drivers, or a combination of these. For example, cyclical changes can occur naturally on decadal scales or interannually (e.g. fluctuations in ice cover and prey distributions), and anthropogenically caused alterations can be sudden (e.g., construction projects), or gradual (e.g., climate change or pollution). Such variability in the physical environment can cause changes that cascade through the food web, resulting in shifts in the timing and spatial distribution of prey aggregations important to seasonal predators (Descamps et al., 2017; Meredith et al., 2019; Pallin et al., 2023; Shaw, 2016). In response to these types of environmental variability, migratory species may have to modify their spatiotemporal distribution and movement patterns, but the extent to which they can do so successfully is unclear (Davidson et al., 2020; Lascelles et al., 2014; Shaw, 2016).

Marine predators are generally experts in locating resources in patchy and dynamic marine environments, so they might be able to respond to interannually changing prey distributions (Benson et al., 2002; Neumann, 2001). However, animals undertaking long-distance migrations rely on learned information to inform their movements and time it to match resource peaks. Baleen whales, for example, show strong culturally transmitted philopatry to foraging and breeding grounds (Barendse et al., 2013) and likely base their movements on memory of past resource distributions (Abrahms et al., 2019). Both humpback whales (*Megaptera novaeangliae*) and fin whales (*Balaenoptera physalus*) have changed the timing of their migrations in response to earlier sea ice break up in the Gulf of St Lawrence over a 30-year period (Ramp et al., 2015). Additionally, changes in the migratory timing of humpback, blue (*Balaenoptera musculus*), and gray (*Eschrichtius robustus*) whales off California have been hypothesized to be driven by local oceanography, regional upwelling, and basin-scale climate conditions (Ingman et al., 2021). Some recovering baleen whale populations are also re-populating historical foraging grounds decades after they had nearly been extirpated from over-exploitation (Calderan et al., 2020; Keen et al., 2021).

When such changes in the phenology or distribution of migratory animals are observed, secondary effects on other parts of the annual cycle of migratory animals are expected (Davidson et al., 2020; Pendleton et al., 2022). However, these secondary effects are difficult to detect and may impact population vital rates, so it is important to consider them in context of the annual cycle to assess potential long-term effects (Marra et al., 2015). Furthermore, dynamically changing spatiotemporal patterns of movement pose challenges to the management and monitoring of highly mobile animals (Lascelles et al., 2014). It is therefore essential to describe the habitat use of migratory animals throughout the annual cycle and to integrate this knowledge into an ecosystem management framework (Pendleton et al., 2022). This is particularly important where sensitive parts of a population, such as pregnant or nursing females, aggregate and in coastal regions where overlap with human activity is concentrated (Avila et al., 2018; Bejder et al., 2019; Dunlop et al., 2021).

During the last decade, humpback whales in the North Atlantic have started to aggregate in fjord systems of northern Norway during the winters (between November and February), hereafter referred to as 'northern Norway' (Jourdain & Vongraven, 2017). Here, they forage extensively on Norwegian spring-spawning (NSS) herring that shifted their wintering distribution into these areas (Aoki et al., 2021; ICES, 2019; Vogel et al., 2021). This shift resulted in a dense and energy-rich prey resource along the migratory path of humpback whales (Jourdain & Vongraven, 2017; Kettemer et al., 2022). NSS herring have shifted their wintering distribution regularly in the past (Dragesund et al., 1997), a phenomenon thought to be related to the stock's age structure, potentially acting in conjunction with environmental changes (Huse et al., 2010; ICES, 2019). Northeast Atlantic humpback whales generally forage throughout the Norwegian and Barents Seas during summer and autumn (Christensen et al., 1992; Hamilton et al., 2021; Leonard & Øien, 2020) and migrate to breeding grounds in the West Indies (Stevick et al., 2018) and Cape Verde Islands (Wenzel et al., 2020), where most of them are observed in March - April and April - May, respectively. During the era of commercial whaling in the Northeast Atlantic (1881 - 1904), humpback whales were caught off northern Norway in areas occupied by forage fish during the winter (Christensen et al., 1992; Ingebrigtsen, 1929; Kramvig et al., 2016). No substantial numbers of humpback whales have been observed in the fjords since then, especially not during wintertime, apart from occasional sightings of humpback whales by fishing and whale watching vessels, which are common throughout Norwegian waters at most times of the year.

This novel or re-established foraging site appears to represent additional foraging opportunities for humpback whales after the presumed main summer foraging season, before their long southward migration towards tropical breeding grounds. Recent satellite tracking data and photographic matches have confirmed that animals observed during winter in northern Norway can still migrate to the breeding grounds during the same year (Kettemer et al., 2022; Wenzel et al., 2020). However, no studies have quantified the connectivity between the Barents Sea and northern Norway, described the duration and spatial distribution of the foraging aggregation in northern Norway, or assessed whether the demographic composition in both feeding areas differs. The importance of northern Norway as a foraging opportunity for various demographic groups of humpback whales and the population should thus be explored in detail, given that the foraging season in northern Norway occurs unusually late in the year compared to the foraging seasons of humpback whales elsewhere.

In this study, we aimed to describe the foraging aggregation within the context of the Northeast Atlantic humpback whales' annual cycle, its demographic composition, and spatiotemporal distribution. To this end, we used photographic ID matching to (1) quantify the connectivity between the Barents Sea and northern Norway, (2) establish the duration and geographic distribution of the foraging area in northern Norway, and (3) to assess the return rate of individual whales that foraged in the fjords of northern Norway both within and between years. Finally, we used genetic and hormone screening of biopsy samples to (4) quantify the sex ratio and pregnancy rate of humpback whales in the Barents Sea and northern Norway.

Materials and Methods

Study site and data collection

We collected photo-identification data and biopsies in several fjords of northern Norway and waters of the Barents Sea surrounding the Svalbard Archipelago (Figure 1). Northern Norway is not affected by sea ice during the winters, as it is characterized by warm North Atlantic water. The sea ice edge occurred around the Svalbard Archipelago during the peak of sea ice coverage in April between 2005- 2018 (see e.g., (Hamilton et al., 2021)), and the area is generally free of ice between June and December. The North Norwegian Humpback Whale Catalogue (NNHWC) was established in 2010 when humpback whales started aggregating in northern Norway during the late autumn and winter. From hereon we refer to 'summer' as the foraging season spanning June to September, and 'winter' as the foraging season from October to February. The study sites included waters around Andøya (2010 to 2012), Kvaløya (2012 to 2017), and Kvænangen (2017 to 2019) (Figure 1). Photographic sampling was conducted using small vessels and was dictated by weather and light conditions. During the polar night (December-January), sampling was usually restricted to a few hours around midday. However, on some sampling trips, a flash system allowed sampling to continue in low-light conditions. The sampling effort differed between years and study sites (Table 1). The public and other research organizations also submitted pictures, and an interactive online web portal for the submission of fluke photographs was established in 2015 (hvalid.no) and active until 2017, after which data collection continued with the existing network of contributors.

From the 3rd to the 11th of September 2018, a research cruise was conducted in cooperation between the Institute of Marine Research (IMR, Bergen, Norway) and UiT - The Arctic University of Norway (UiT, Tromsø, Norway), surveying the northern Barents Sea, east of the Svalbard archipelago close to the island group of Kong Karls Land (Figure 1). We chose the timing and area based on information on humpback whale occurrence from prior annual joint Norwegian/Russian ecosystem surveys in the Barents Sea and adjacent waters (IMR, Norway/PINRO, Russia). When humpback whales were sighted, a small boat was launched to allow closer approaches. We took fluke photographs from both the small boat and the larger research vessel using DSLR cameras. In addition to this cruise, photographs from incidental humpback whale encounters around Svalbard, and the Barents Sea were submitted by various contributors (2012 to 2019), mostly nature-tourism expedition vessels that typically spend multiple weeks around Svalbard and Franz Josef Land, and to a smaller extent research cruises not targeted at marine mammals).

We took biopsies from either the fluke or flank of each individual from small open boats (20-26ft) using an airgun (ARTS launching system, LKARTS-Norway) to deploy a floating arrow with a 4 or 6 cm long sterile stainless steel biopsy tip (CetaDart, DK). Depending on the shooting distance, usually about 4-20 meters, the shooting pressure was between 6-10 bars.

Sampling procedures were approved by the Norwegian Food Safety Authorities (Mattilsynet), under permits FOTS-ID 14135 and FOTS-ID 8165. We collected skin (N = 169) and blubber samples (N = 112) from humpback whales between 2011 - 2019 in the Troms area of northern Norway, and during September 2018 in the northern Barents Sea. Samples were stored at -20°C in either tin foil or glass vials (blubber) or 96% EtOH (skin).

Photo-identification

We identified individual humpback whales using the unique pigmentation pattern on their ventral flukes (Katona & Whitehead, 1981) and created sighting histories from re-identifications of photo-identified whales. Intervals between an individual's first and last sightings within a season indicate the minimum length of stay during the season. We calculated the annual return rate, a measure of site fidelity on a population level, as

Table 1. Table of effort-based photo ID sampling and non-effort-based data collection for each location within the northern Norwegian fjords (2010/11 to 2018/19). Sampling was mainly conducted by UiT and the founder of the NNHWC (effort-based). Other records (non-effort-based) represent days in which various contributors submitted fluke identification photographs. The period depicts the first and last humpback whale fluke capture in a season, with days indicating the duration between them, indicative of minimum season duration.

	Andøya		**Kvaløya**		**Kvænangen**			
Winter season	Survey effort (days)	Other records (days)	Survey effort (days)	Other records (days)	Survey effort (days)	Other records (days)	Period	Days
2010/11	2	1					27 Dec- 19 Jan	23
2011/12	1	3	2				06 Dec- 29 Jan	54
2012/13		15	19	25			03 Nov- 11 Feb	100
2013/14		33	22	35			07 Nov- 06 Feb	91
2014/15		14	39	44			28 Oct- 15 Feb	110
2015/16		12	29	51			29 Oct- 24 Feb	118
2016/17			18	27		5	23 Oct- 24 Jan	93
2017/18					10	5	10 Nov- 13 Jan	64
2018/19					28	26	26 Oct- 28 Jan	94
Total	**3**	**78**	**129**	**182**	**38**	**36**		**747**
Mean	**1.5**	**13**	**21.5**	**36.4**	**19**	**12**		**83**

the number of photographically recaptured individuals in a given year divided by the total number of individuals sighted in that year (Clapham et al., 1993).

Individual sighting histories for this study relied on 3677 sightings of 1169 unique humpback whales documented in the NNHWC between 2010 and 2019. The catalog covers a latitudinal range from 67^{o} to 80^{o} N. It contains sighting records of individual humpback whales throughout the year, with summer sightings mainly from the Barents Sea and winter sightings from northern Norway (Figure 1). In northern Norway, we collected fluke photographs of 866 individual humpback whales, 856 (98.9%) of these during the winter. Most (54.7%) photographs were collected during dedicated sampling conducted between October and February, while remaining photos were contributed by third parties, including all summer sightings (1%).

Over nine years of study, we conducted 170 days of dedicated photo-identification survey effort, with considerably less effort during the first two winters (Table 1). The average annual sampling effort across all winter seasons was 17 days (± 13.1) and 23.6 days (± 9.4), excluding the first two seasons. We identified 342 individual whales in the Barents Sea, with most identification photographs (95%) obtained during a research cruise in September 2018. Other collaborators submitted fluke photographs from incidental humpback whale encounters between 2012 and 2019.

Sex determination

We determined the sex of individuals using skin samples (Bérubé & Palsbøll, 1996), using the odontocete oligonucleotide primer set, ZFYX0582F, ZFY0767R and ZFX0923R, which showed clear bands on the gel electrophoresis. As a control, samples from four killer whales (*Orcinus orca*) of known sex (two males and two females) were used in every PCR reaction. After initial testing, primer concentrations were optimized to 1 µl of 10 µM for the Y primer-set (ZFYX0582F/ZFY0767R) and 0.5 µl of 5 µM for the X primer-set (ZFYX0582F/ZFX0923R).

Resampling rate in biopsy material

To estimate the within-season recapture rate in our dataset, we conducted a relatedness analysis on a subset of the samples for which genetic sequences were available (N= 107). We used NGSrelate v2 (Hanghøj et al., 2019) to calculate the coefficients of relatedness, based on genotype likelihoods calculated with ANGSD v.v0.935-53-gf475f10 (Korneliussen et al., 2014). See S2 Text in supporting information for more details.

Progesterone concentrations and pregnancy status

We used progesterone concentrations as a proxy for pregnancy status and extracted the progesterone from blubber samples as described in (Kershaw et al., 2020; Pallin et al., 2018), with minor adjustments to the method. See S1 Text and S3 Table in supporting information for more details. Progesterone was measured in 82 female blubber samples and 19 male control samples. Blubber samples taken from flukes were excluded since they usually do not contain enough blubber to conduct the analysis and may have different fat and hormone profiles leading to potential misclassifications.

We quantified progesterone concentrations using two commercially available progesterone enzyme immunoassays (EIA; Enzo Life Sciences, kit ADI-900-011, and ELISA; DRG International Inc. EIA-1561), see S1 Text and S3 Table in supporting information for more details on the difference between the two methods. The dried hormone extract was re-suspended in 1ml phosphate buffered saline (pH 7.5) containing 1% bovine serum albumin, vortexed, and then kept samples at -20°C. The EIA and ELISA kits we used have 100% reactivity with progesterone; the detection limit is between 15 - 500 pg ml^1 and 0 - 40 ng ml^1, respectively, based on the standard curves. Two additional standard dilutions were added to lower the detection limit of the EIA standard curve to 3.81 pg ml^1. We ran samples blind and in duplicate and re-ran samples that fell outside the detection limit at varying dilutions. The progesterone EIA's inter-assay coefficient of variation (COV) and intra-assay COV ranged from 2.7 - 8.3% and 4.9 - 7.6%, respectively. The mean inter-assay COV was 14.7% for the EI, and the mean intra-assay COV was 5.2% for the ELISA. Progesterone values are reported as nanograms per gram of blubber (ng g^1). We repeated the extraction and measurements for a subset of the blubber samples, in which case we report the averaged resulting progesterone level and ran multiple samples at several dilutions.

We assigned pregnancy status based on blubber progesterone concentrations using previously established models developed from female humpback whales of known pregnancy status from the Gulf of Maine and the Gulf of St Lawrence (Kershaw et al., 2020; Pallin et al., 2018). Previous studies successfully applied this modeling approach to other populations (e.g., Western Antarctic Peninsula (Pallin et al., 2018), Oceania (Riekkola et al., 2018)). Pregnancy rates were determined as the number of pregnant females divided by the total number of assayed females for years in which at least five samples were available, i.e., in which sample size allowed for reasonably robust estimation.

Statistical analysis

We checked whether the sex ratio deviated significantly from parity (1:1) for each region (northern Norway in winter, Barents Sea in summer) using a two-tailed exact binomial test for the Barents Sea, and one-tailed test for Norway. We then tested whether the pregnancy rate differed between the summer (samples obtained in June and September) and winter season (samples obtained between October and February in northern Norway), using a Chi-squared test of independence. Quasi-binomial Generalised Linear Models (GLMs) were used to investigate variation in annual pregnancy rates between 2011 and 2018, and over the feeding season between June and February, using a “logit” link function to take into account overdispersion in the pregnancy rate data. Given the limited and variable biopsy sample sizes and the variability in pregnancy rate estimates, it was important to consider these data in the context of their power to detect significant changes over time. The power of the GLMs was estimated using the pwr.f2.test function in the pwr package (R version 3.6.2 (R Core Team, 2019)). The power to detect a trend in the pregnancy rate over the 8-year study period was 17.4%, and the power to detect a trend through the feeding season was 6.08%. Thus, the variability in pregnancy rate estimates makes the detection of significant temporal trends unlikely. A significance threshold of $p < 0.05$ was used to determine significance in all statistical tests. Results are presented as mean ± standard deviation, unless otherwise noted.

Results

Photographic collections

In northern Norway, the total number of photo-identified humpback whales per winter season ranged from a minimum of six individuals in the first year off Andøya (2010) to a maximum of 408 individuals in the 2015/16 season off Kvaløya (Figure 3 and S1 Table in supporting information). The peak in sightings occurred between November and January. The cumulative curve of identifications began to plateau after the winter of 2015/16 but showed a slight increase in 2018/19 in Kvænangen (Figure 3). In the Barents Sea, we registered humpback whale sightings from May to September, although most were photographed in September 2018. In total, we found five between-season re-sightings in the Barents Sea.

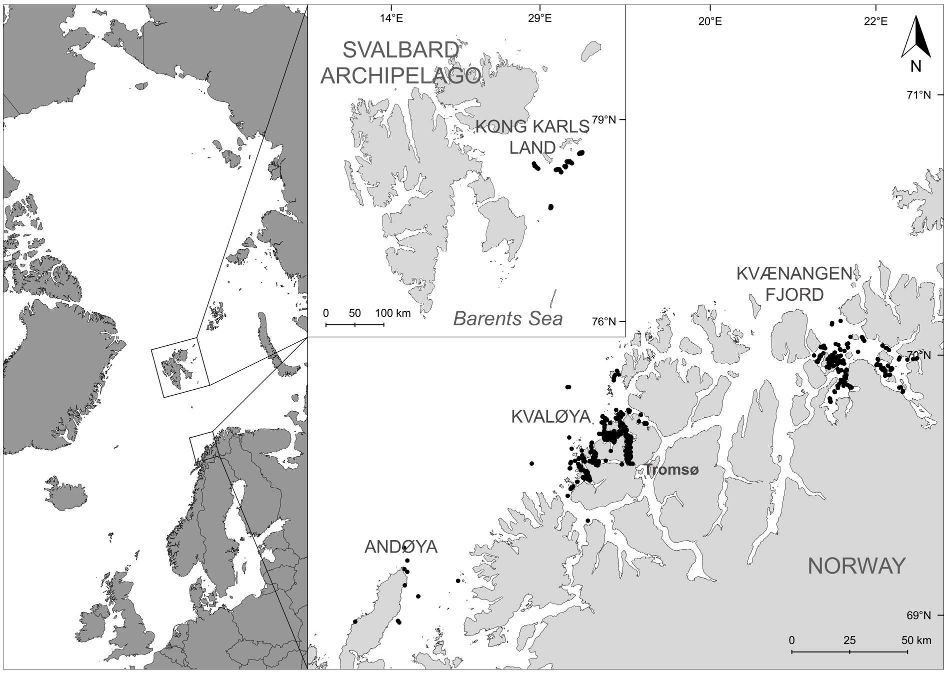

Figure 1. Left panel shows the Svalbard Archipelago with black dots close to Kong Karls Land representing GPS locations of photographic records of humpback whales (*Megaptera novaeangliae*). The inset shows the three main locations (Andøya, Kvaløya, and Kvænangen fjord) of the northern Norwegian foraging area. Not all pictures were submitted with GPS locations, those without are not included in the figures.

Connectivity between Barents Sea and Norway

We matched 39 individual humpback whales sighted during summer in the Barents Sea to northern Norway during the winter (Figure 2). One individual was photographed in two different summers in the Barents Sea and subsequently re-sighted off northern Norway during winter both these years. 17 matches of 16 individuals occurred within the same year (Figure 2), showing that individuals transitioned between Barents Sea and northern Norway in the succession of one foraging season. Most of the re-sightings were first recorded in northern Norway in the end of November (S2 Table in supporting information).

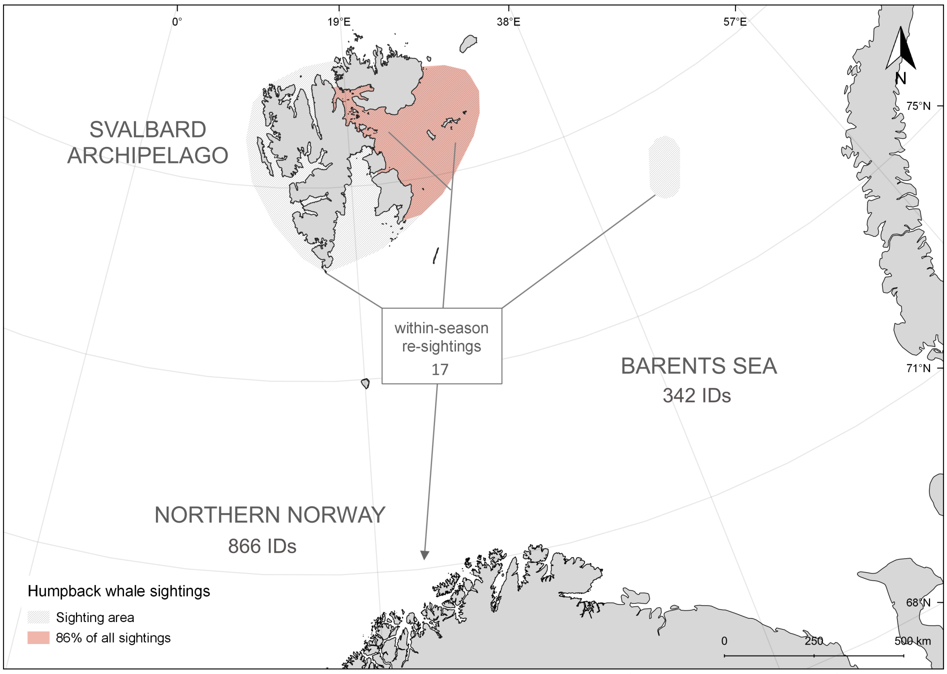

Figure 2. Map of the sampling area in the Barents Sea (in grey and orange) with the number of identified individuals in the Barents Sea (including the Svalbard Archipelago) and northern Norway, respectively, and the number of within-season matches between those two areas. The beginning of grey lines indicate first sighting locations within the Barents Sea of the individuals that were subsequently re-sighted in northern Norway. 86% of all humpback whale IDs in the Barents Sea were collected in the orange-shaded area.

Site fidelity in northern Norway

Between the winter of 2010/11 and 2018/19, we photo-identified 866 individual humpback whales in northern Norway (Figure 3). The majority (53.4%, N = 457) returned in two or more winters. Most of these whales were seen in two (N = 202), three (N = 131) or four (N = 83) different years. The longest period over which an individual was re-sighted was seven years. Re-sightings between seasons occurred most frequently in sequential years (69.4%), followed by two-year intervals (20.6%) (Figure 4). Until the winter of 2013/14, new fluke captures accounted for more than 70% of the total number of whales identified in a season. In all following winters, the number of re-sightings was higher than first captures, on average 70.9% (± 10.5) (Figure 3).

The annual return rate, a measure of population-level site-fidelity, progressively increased until a peak in the 2016/17 season (the final winter season off Kvaløya, 81.8%; Figure 4), decreasing to 70 and 79% during the following two winter seasons (2017/18, 2018/19) in Kvænangen. 43.2% of the whales were seen more than once within a season. The time interval between within-season re-sightings ranged from a minimum of 2 days to a maximum of 15 weeks, on average 27.5 days (± 11.5; Figure 3). More than half the whales identified across the nine years of study were re-sighted, with 27% returning to feed for more than three years, most often in sequential years. In the winter of 2016/17, considerably fewer humpback whales were encountered around Kvaløya, and the first individuals were sighted in Kvænangen fjord. In the consecutive winter, the fjords around Kvaløya were deserted, and the feeding activity had shifted to Kvænangen fjord.

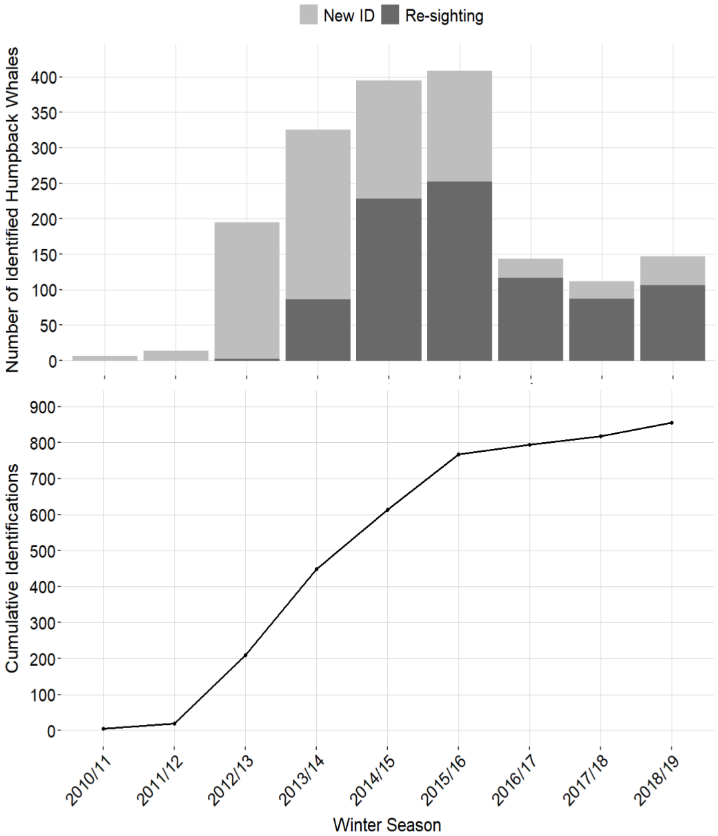

Figure 3. Upper panel: Total number of individual humpback whales (*Megaptera novaeangliae*) photo-identified each winter season in northern Norway between 2010 and 2019. Light grey shading indicates newly identified individuals, and dark grey shading indicates re-sights of previously identified individuals. Lower panel: Discovery curve illustrating the trend in the cumulative number of individual photo-identified humpback whales during winter in northern Norway (2010/11 -2018/19).

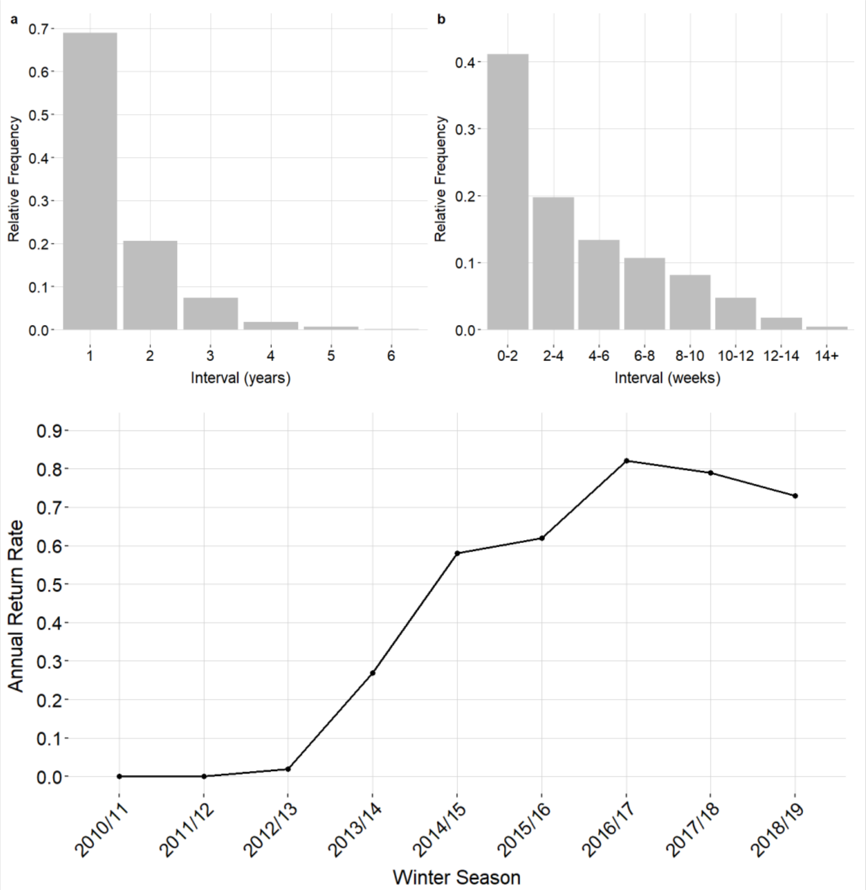

Figure 4. Upper panel: (a) Between season re-sighting intervals (b) within-season re-sighting intervals of humpback whales (*Megaptera novaeangliae*) in northern Norway (2012/13 to 2018/19). Lower panel: Annual return rate of humpback whales to northern Norway (2010/11 to 2018/19).

Resampling rate in biopsy material

A relatedness analysis based on a subset of the samples for which genetic sequences were available (107 individuals) indicated that no individuals were biopsied repeatedly within the same season (coefficients of relatedness <1; S4 Table in supporting information).

Sex ratio

The sex ratio in the Barents Sea was 1.4 (18M:13F, N= 31) and in northern Norway 0.6 (48M:76F, N= 124). No significant deviation from parity was found for the Barents Sea sample (p = 0.473), but the sex ratio differed significantly from parity in northern Norway with a bias in favor of females (p = 0.007). The sex ratio in northern Norway differed significantly between years in our sample ($X^2 = 12.9$, p = 0.019). In years with low sample sizes (2011/12, 2017/18) the ratio of males in the sample was higher. The sex ratio did not differ significantly between months throughout the winter season ($X^2 = 3.2$, p = 0.571; S1 Figure in supporting information).

Pregnancy rate

All but three of the females for which blubber samples were available (N= 82) were successfully assigned a reproductive status (i.e., pregnant or non-pregnant) by the reference model (with 99.9% confidence), and all male controls (N= 19) were correctly classified as non-pregnant.

Table 2. Numbers of female humpback whales assessed for progesterone levels and pregnancy rates in the Barents Sea and northern Norway by area and season. The pregnancy rate (pregnant females/all assayed females) is reported for months with at least five samples.

Area	Season	Females	Pregnant	Not pregnant	Pregnancy rate (%)
northern Norway	June 2011	2	1	1	-
	June 2012	7	1	6	14
Barents Sea	September 2018	10	2	8	20
northern Norway	Winter 2013 / 2014	7	2	5	29
	Winter 2015 / 2016	12	1	11	8
	Winter 2016 / 2017	9	5	4	56
	Winter 2017 / 2018	2	0	2	-
	Winter 2018 / 2019	30	14	16	47
Total		**79**	**26**	**53**	

All progesterone concentrations are reported in S3 Table in supporting information. The pregnancy rate was low in the summer (22% northern Norway in June, 20% Barents Sea in September 2018) and higher (median = 38%, 25th quantile = 24%, 75th quantile = 49%) during winter in northern Norway when pooled over all years (Table 2). However, the difference between the Barents Sea and northern Norway in 2018/19 (20% vs. 47%) was not statistically significant ($X^2 = 2$, p = 1). Rates in winter varied across years between 8 - 56% (Table 2). During the winter season, the pregnancy rate declined after a peak in December (73%), to 26% in January and 17% in February (Table 3). Due to the limited sample size and high variance, the power to detect a relationship in the pregnancy rate over winters in the eight-year study period was low (17.4%), and over the months during the feeding season even lower (6.1%). Thus, the variability in pregnancy rate estimates makes the detection of significant temporal trends unlikely.

Table 3. Numbers of female humpback whales assessed for progesterone levels and pregnancy rates in the Barents Sea and northern Norway by area and month. The pregnancy rate (pregnant females/all assayed females) is reported for months with at least five samples.

Area	Month	Females	Pregnant	Not pregnant	Pregnancy rate (%)
Northern Norway	June	9	2	7	22
Barents Sea	September	10	2	8	20
Northern Norway	October	2	0	2	-
	November	14	6	8	43
	December	11	8	3	73
	January	27	7	20	26
	February	6	1	5	17
Total		**79**	**26**	**53**	

Discussion

Within-season matches between the Barents Sea and northern Norway confirm that some Northeast Atlantic humpback whales continued their foraging season in fjord systems of northern Norway. Studies on other humpback whale feeding grounds have shown that females generally leave feeding grounds later than males resulting in a female bias late in the foraging season (Barendse et al., 2013; Dawbin, 1966; Pallin et al., 2018), consistent with our observation of a female bias in northern Norway but not the Barents Sea. Per our expectations, the pregnancy rate estimated during winter in northern Norway was higher than in June and September, indicating that pregnant animals may indeed be more likely than the general population to maximize their energy intake by continuing their foraging season in northern Norway. An increase in pregnancy rates in the temporal progression of the foraging season was also observed in other areas (Pallin et al., 2018); summer 59%, autumn 72%), a pattern consistent with knowledge obtained from whaling data (Dawbin, 1966).

The establishment of the foraging site in northern Norway coincided with dense herring concentrations in the area since 2010 (documented in detail since 2015 by e.g., (ICES, 2019)). During the overwintering period between October and February, the NSS-herring spawning stock can use separate areas concurrently including near and offshore waters (Huse et al., 2010), and fishing vessels reported that individual humpback whales foraged further offshore in previous years. Before 2010, the overwintering distribution of this herring stock was concentrated in fjords further south, and humpback whales were not present at this site (Jourdain & Vongraven, 2017). Shifts in NSS-herring overwintering distribution have occurred repeatedly and are most likely related to changes in the stock's age structure mediated by oceanographic conditions and fishing pressure (Dragesund et al., 1997; Huse et al., 2010). Since humpback whales established the northern Norway winter foraging aggregation in 2010, NSS-herring slightly shifted their distribution northward within the fjord systems until 2019, followed by a corresponding shift in whale distribution. The high annual return rate, comparable to main feeding grounds in other areas (Calambokidis et al., 1996; Clapham et al., 1993; Ramp et al., 2010), indicates that foraging in northern Norway has become an important part of the annual routine for some Northeast Atlantic humpback whales. Since the feeding activity is coupled to herring overwintering distribution, future shifts in the whales' winter distribution can be expected as the herring stock changes its migration patterns and overwintering areas.

Information on the migration phenology of Northeast Atlantic humpback whales remains sparse due to the logistic challenges involved in surveying the Barents Sea region. Therefore, the duration of the summer foraging season is unknown. Our sighting data from the Barents Sea confirm that the area east of the Svalbard archipelago is an important foraging ground for humpback whales in late summer/autumn. This supports previous evidence from annual ecosystem surveys, whaling records, and tracking data (Hamilton et al., 2021; Nøttestad et al., 2015; van der Meeren & Prozorkevich, 2018). Tracking data from 2018 indicates that whales initiated migration from the Barents Sea between October and December in 2018, the same year most sightings and all biopsies were collected in the Barents Sea (Hamilton et al., 2021).

Within-season resighting patterns in northern Norway show that most whales stayed longer than two weeks, many for about one month and some up to three months. This should be considered a minimum estimate, as whales might arrive before their first sighting or stay after the last recorded sighting. In the North Pacific, groups of humpback whales have also been observed foraging on herring during some periods of the winter, however, this seems to be representing smaller numbers of whales than in the present study (Straley et al., 1995; Straley et al., 2018). In Iceland, humpback whales have also been reported throughout the year (Magnúsdóttir & Lim, 2019). The humpback whale aggregation in northern Norway is to our knowledge the largest, longest-lasting, and most stable documented winter foraging aggregation.

Photographic matching to the breeding grounds in the West Indies (Stevick et al., 2018), along with a recently recorded round-trip migration by a female humpback whale (Kettemer et al., 2022) and unpublished tracking data show that many animals migrate to breeding areas after foraging in northern Norway during the winter. However, pregnant females delaying their migration until late in the season may give birth along the migration route despite increasing their migration speed (Kettemer et al., 2022), indicating carry-over effects from the long foraging season into the next stages of migration

Our results provide a first indication that pregnant females might preferentially visit northern Norway as a continuation of the feeding season in the Barents Sea. When we restricted the analysis to the one year for which we had sampled the Barents Sea and northern Norway, small sample sizes however meant that our analysis lacked statistical power to conclude this with certainty. We could not confirm that pregnant females remained the longest in northern Norway. However, the statistical power to detect temporal trends in our data was low. One explanation for the lower pregnancy rates at the end of the season (January/February) may be that not all humpback whales complete migrations every year. Juvenile individuals and resting females for whom the cost and risks outweigh the benefits of migration may therefore dominate the sample towards the end of the season. This might contribute to lower pregnancy rates among females sampled, as well as an increase in the proportion of males in February.

Monitoring pregnancy rates over time can indicate population health and growth rates, provided that the sample sizes are sufficient (Kershaw et al., 2020; Pallin et al., 2018). Our estimate of the variation in pregnancy rate between years is likely not sufficiently robust to infer trends in reproductive rates, due to the low number of samples in some years. Overall, the pregnancy rate in summer and winter was lower than those reported on other foraging grounds. On other humpback whale feeding grounds, pregnancy rates were reported to be higher, for example, 57% in the Southern Ocean (Riekkola et al., 2018), 58% (36-86%) in the Western Antarctic Peninsula (Pallin et al., 2018), 19 - 48% in the North Pacific (Clark et al., 2016), and 25% - 63% in the northwest Atlantic (Kershaw et al., 2020). Previous pregnancy rate assessments in North Atlantic humpback whales did not detect an increase in blubber progesterone concentrations between females sampled early and late in the season (Kershaw et al., 2020; Aoki et al, 2021), so this is likely not the sole driver of the increase. The variability between years reported here was similarly high in those other studies. Pregnancy rate estimates present a minimum of true rates, as they usually include immature females. Pregnancy rates sampled at different times of the gestation period may vary, e.g., be inflated by subsequently aborted/reabsorbed pregnancies when sampled early (Pallin et al., 2018; Riekkola et al., 2018). However, the large effect size of the difference in pregnancy rates during summer vs. winter in our results was indicative of a true difference. Recent work shows that pregnancy rates are tightly linked to fluctuations in prey availability in the Antarctic, North Pacific and North Atlantic (Cartwright et al., 2019; Gabriele et al., 2022; Kershaw et al., 2020; Pallin et al., 2023). Further studies should assess whether low pregnancy rates here may indicate slowing population growth following recovery from exploitation (Leonard & Øien, 2020) and resulting population density effects in a recovering population of Northeast Atlantic humpback whales foraging in the Barents Sea, or poor nutritional status due to changing environmental conditions and prey availability as is the case for humpback whales in other areas (Cartwright et al., 2019; Gabriele et al., 2022; Pallin et al., 2023).

Rapid and fundamental ecosystem changes in the Barents Sea associated with warming, sea ice loss, and increased inflow of Atlantic waters have impacted a core foraging habitat of humpback whales (Hamilton et al., 2021; Johannesen et al., 2012). Further south in the Norwegian Sea, sightings of humpback whales have been less common during summers in 2009 - 2012 in contrast to the years 2006 - 2007, indicating a northward shift of foraging activity or changing migration timing on their northward journeys (Nøttestad et al., 2015). In general, humpback whale populations have shown remarkable recovery after historical exploitation (Cartwright et al., 2019; Pallin et al., 2018; Straley et al., 2009; Zerbini et al., 2019). Yet, their reproductive success is tightly coupled to prey availability (Pallin et al., 2023), and humpback whale populations in the Northwest Atlantic and North Pacific have been experiencing declining calving rates, likely due to ecosystem shifts mediated by climate change (Cartwright et al., 2019; Kershaw et al., 2020).

In the case of Northeast Atlantic humpback whales, herring superabundance events inside fjord systems provided a feeding opportunity outside of the presumed core feeding season, but along whales' distributional range or migratory paths. The recent shift of herring distribution may have made this resource more accessible to whales since it now occurs closer to migratory routes (Kettemer et al., 2022) and might be more densely aggregated in fjord systems, in contrast to wintering areas herring occupied during the last decades (Huse et al., 2010; ICES, 2019). Northern Norway could be considered a spatial continuation of the foraging area in the Barents Sea, potentially extending the duration of the foraging season, or a stopover after the commencement of southward migration from the Barents Sea. As Northeast Atlantic humpback whales recover to historical abundance (Leonard & Øien, 2020), density-dependent resource competition in the Barents Sea might play a role in changed distribution patterns. Increased whale abundances, potentially in conjunction with ecosystem changes, might lead to increased resource competition and more exploratory foraging movements outside of the main foraging areas.

As generalist predators, humpback whales are thought to be adaptable to changes in their prey distribution and abundance, relative to other baleen whale species. However, they certainly will not be able to respond to all kinds of changes in the structure of prey fields, as has been documented in other areas (Gabriele et al., 2022; Kershaw et al., 2020; Pallin et al., 2023). It is further unclear how late-season foraging, as documented in this study, affects the annual cycle of Northeast Atlantic humpback whales. Since migratory species rely on habitats that are spread over vast distances and multiple jurisdictions, managing these habitats becomes an international responsibility. Dynamic management of ocean and coastal ecosystems that can account for changes in spatiotemporal distributions is a challenging but necessary task for the future that requires concerted efforts from multiple actors and potential protection during migration in areas beyond national jurisdiction (Lascelles et al., 2014). Climate change is projected to severely impact population vital rates and alter distributions of top predators on longer time scales (Descamps et al., 2017; Meyer-Gutbrod et al., 2015; Moore et al., 2019; Seyboth et al., 2016). Therefore, continued monitoring of the pregnancy or calving rate in this population is warranted as the ecosystems of the Barents and Norwegian seas shifts to a new ecological state (Hamilton et al., 2021; Johannesen et al., 2012). Knowledge of year-round distributions and critical habitat, especially during potentially vulnerable periods such as pregnancy, are essential for mitigating adverse effects of human activities on top predators (Lascelles et al., 2014).

Conclusion

Our results suggest that winter foraging on fjord-based herring is a strategy that is preferentially used by female humpback whales in northern Norway. Our findings suggest that this strategy has become an important annual event for humpback whales, contingent on herring overwintering in these fjords. The population of humpback whales in the Northeast Atlantic is recovering from historical exploitation, while the ecosystem in which they forage is undergoing rapid changes. The establishment of this foraging site is evidence of humpback whales' ability to respond flexibly to prey resources along their migratory pathways, with potential effects on their migration timing that need further investigation. Monitoring the potential anthropogenic impacts on migratory species as their distributions respond to changing environmental conditions, with special attention to core foraging areas, will be important to ensure adverse impacts can be recognized and addressed. In particular, if many of the whales visiting northern Norway during winter are either pregnant or are part of the endangered population segment that migrates to the Cape Verde breeding ground, potential impacts of the shipping and fishing industries should be priorities for ecosystem management. Future work should also aim to understand how this additional foraging opportunity impacts the overall reproductive performance and annual schedules of individual whales, and how this ultimately may affect population dynamics.

supporting information

S1 Figure

Sex ratio by month Sex ratio among humpback whales (*Megaptera novaeangliae*) sampled in the Barents Sea and northern Norway.

S1 Table

Overview of photographic identification for each winter season in northern Norway Individuals identified, cumulative identifications, new individuals, re-sighted individuals, annual return rate and within-season re-sightings.

S2 Table

Re-sighted individuals between the Barents Sea and northern Norway. Sightings-ID, sighting locations and dates for individuals sighted both in the Barents Sea and northern Norway.

S3 Table

Table of all progesterone values and model results. Model results and progesterone levels for all samples run, including results of the subset of samples extracted with both methods for comparison.

S1 Text

Comparison of extraction methods Details on the difference between the two different extractions used for progesterone analysis.

S2 Text

Relatedness methods Detailed methods for within-season re-sampling assessment using rxy.

S4 Table

Pairwise coefficients of relatedness matrix Resulting pairwise relatedness coefficients for a subset of individuals.

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Supporting Information

Figure S1 Sex ratio by month. Sex ratio among humpback whales (*Megaptera novaeangliae*) sampled in the Barents Sea and northern Norway.

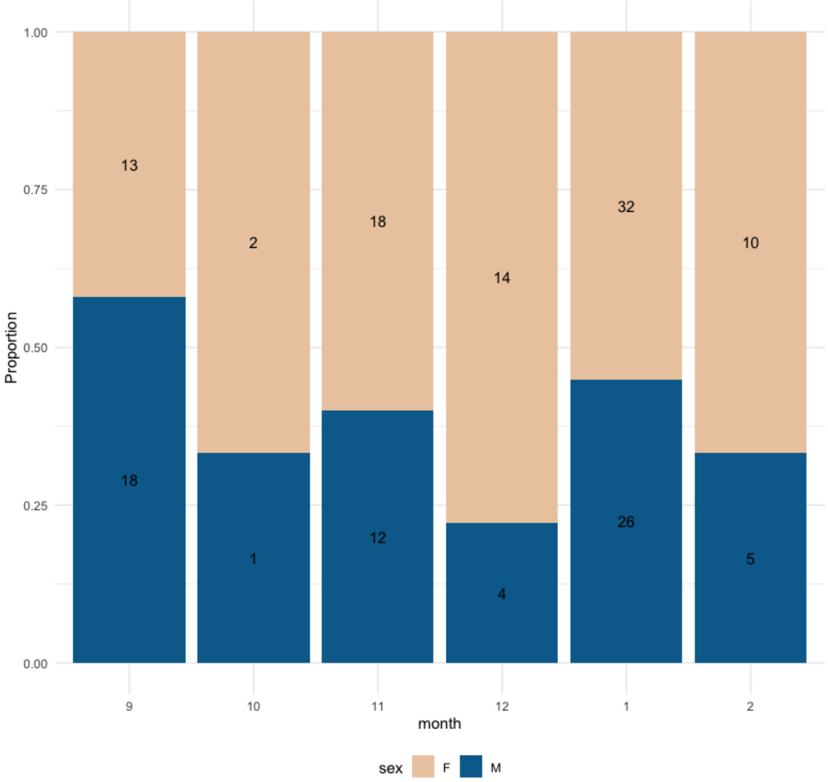

Table S1 Overview of photographic identification for each winter season in coastal Norway. Individuals identified, cumulative identifications, new individuals, re-sighted individuals, annual return rate and within-season re-sightings.

Year	**2010/11**	**2011/12**	**2012/13**	**2013/14**	**2014/15**	**2015/16**	**2016/17**	**2017/18**	**2018/19**
Total no. of identified individuals/year	6	13	194	325	394	408	143	111	146
Cumulative identifications	6	19	210	448	613	768	794	817	856
No. of new individuals/year	6	13	191	238	165	155	26	23	39
No. of re-sighted individuals/year	0	0	3	87	229	253	117	88	107
Annual return (%)	0	0	2	27	58	62	82	79	73
No. of within-season re-sights	0	0	51	117	192	180	71	45	83

Table S2 Re-sighted individuals between the Barents Sea and northern Norway. Sightings-ID, sighting locations and dates for individuals sighted both in the Barents Sea and Norway.

ID	summer feeding location	summer sighting date (m/d/y)	winter feeding location	winter first sighting	winter last sighting
NNHWC-117	NE-Svalbard	7/19/12	Kvaløya	12/9/12	1/2/13
NNHWC-138	NE-Svalbard	8/25/12	Kvaøya	12/24/12	12/4/12
NNHWC-139	NE-Svalbard	8/25/12	Kvaøya	11/27/12	
NNHWC-156	NE-Svalbard	9/8/18	Skjervøy	10/28/18	12/19/18
NNHWC-193	Hinlopen Strait	7/12/13	Kvaløya	12/2/13	
NNHWC-286	NE-Svalbard	9/8/18	Skjervøy	11/13/18	1/4/19
NNHWC-286	Border to Russia	8/8/15	Kvaløya	11/17/15	
NNHWC-295	Hinlopen Strait	7/7/14	Kvaløya	11/16/14	01.12.1014
NNHWC-344	NE-Svalbard	9/5/18	Skjervøy	12/17/18	
NNHWC-387	Hinlopen Strait	7/7/14	Kvaløya	12/21/14	
NNHWC-471	Hornsund	8/28/18	Skjervøy	1/9/19	
NNHWC-567	Border to Russia	8/8/15	Kvaløya	11/30/15	12/2/15
NNHWC-609	NE-Svalbard	9/5/18	Skjervøy	12/18/18	1/9/19
NNHWC-698	NE-Svalbard	9/3/18	Skjervøy	11/16/18	12/11/18
T2-73	NE-Svalbard	9/5/18	Skjervøy	11/14/18	11/15/18
T3-18	NE-Svalbard	9/4/18	Skjervøy	12/21/18	
TT2-29	NE-Svalbard	9/9/18	Skjervøy	12/31/18	

Table S3 All progesterone values and model results. Model results and progesterone levels for all samples run, including results of the subset of samples extracted with both methods for comparison.

Table_S3

Sample	Extraction	Year	Date	P4	log(P4)	Preg	Pregnant	Month	Season	Notes	Probabil	Hi	Hi Correct	Low	Low Correct	Control (Male)	Re-extract
Mnova16002	2016.01.024	2016	1/13/2016	0.956803476	-0.019177256	0	No	1	15/16	Coastal Norway	2.22E-16	2.22E-16	0.00E+00	2.22E-16	0.00E+00		
2016.01.019		2016	2/6/2016	1.311666243	0.117823342	0	No	2	15/16	Coastal Norway	2.22E-16	2.22E-16	0.00E+00	2.22E-16	0.00E+00		
Mnova16003	2016.01.008	2016	2/1/2016	0.557348336	-0.253873291	0	No	2	15/16	Coastal Norway	2.22E-16	2.22E-16	0.00E+00	2.22E-16	0.00E+00		
Mnova16006	2016.01.011	2016	2/1/2016	0.593032505	-0.226921502	0	No	2	15/16	Coastal Norway	2.22E-16	2.22E-16	0.00E+00	2.22E-16	0.00E+00		
Mnova16010	2016.01.015	2016	2/6/2016	198.8373512	2.298497969	1	Yes	2	15/16	Coastal Norway	1	1	0.00E+00	1	0.00E+00		
Mnova16012	2016.01.017	2016	2/6/2016	0.622019928	-0.206195702	0	No	2	15/16	Coastal Norway	2.22E-16	2.22E-16	0.00E+00	2.22E-16	0.00E+00		
Mnova16014	2016.01.019	2016	2/6/2016	0.652813886	-0.185210617	0	No	2	15/16	Coastal Norway	2.22E-16	2.22E-16	0.00E+00	2.22E-16	0.00E+00		
Mnova16016	2016.01.021	2016	2/20/2016	0.69174374	-0.160054762	0	No	2	15/16	Coastal Norway	2.22E-16	2.22E-16	0.00E+00	2.22E-16	0.00E+00		
2016.01.006		2016	11/7/2016	102.6236327	2.011247384	1	Yes	11	16/17	Coastal Norway	1	1	0.00E+00	1	0.00E+00		
2016.01.001		2016	12/31/2016	127.6640883	2.106068748	1	Yes	12	16/17	Coastal Norway	1	1	0.00E+00	1	0.00E+00		
2017.01.007		2017	1/4/2017	1.10359132	0.042808276	0	No	1	16/17	Coastal Norway	2.22E-16	2.22E-16	0.00E+00	2.22E-16	0.00E+00	1	
2017.01.008		2017	1/4/2017	1.315398485	0.119057337	0	No	1	16/17	Coastal Norway	2.22E-16	2.22E-16	0.00E+00	2.22E-16	0.00E+00		
2017.01.010		2017	1/15/2017	164.7148019	2.216732628	1	Yes	1	16/17	Coastal Norway	1.00E+00	1.00E+00	0.00E+00	1.00E+00	0.00E+00		
2017.01.011		2017	1/13/2017	1.201915112	0.079873796	0	No	1	16/17	Coastal Norway	2.22E-16	2.22E-16	0.00E+00	2.22E-16	0.00E+00	1	
2017.01.012		2017	1/13/2017	0.578473709	-0.237716375	0	No	1	16/17	Coastal Norway	2.22E-16	2.22E-16	0.00E+00	2.22E-16	0.00E+00		
2017.01.015		2017	1/11/2017	6.773915265	0.83083976	0	No	1	16/17	Coastal Norway	2.47E-15	1.81E-06	1.81E-06	2.22E-16	2.25E-15		
2017.01.001		2017	11/14/2017	0.706203896	-0.151069891	0	No	11	17/18	Coastal Norway	2.22E-16	2.22E-16	0.00E+00	2.22E-16	0.00E+00	1	
2017.01.005		2017	11/14/2017	0.417354288	-0.379495121	0	No	11	17/18	Coastal Norway	2.22E-16	2.22E-16	0.00E+00	2.22E-16	0.00E+00		
2017.01.006		2017	11/14/2017	0.843229911	-0.074053997	0	No	11	17/18	Coastal Norway	2.22E-16	2.22E-16	0.00E+00	2.22E-16	0.00E+00	1	
2018.01.001		2018	9/4/2018	0.718404075	-0.143631213	0	No	9	18	Barents Sea	2.22E-16	2.22E-16	0.00E+00	2.22E-16	0.00E+00		
2018.01.002		2018	9/4/2018	1.109227287	0.045020544	0	No	9	18	Barents Sea	2.22E-16	2.22E-16	0.00E+00	2.22E-16	0.00E+00		
2018.01.003		2018	9/4/2018	303.7914581	2.482575558	1	Yes	9	18	Barents Sea	1	1	0.00E+00	1	0.00E+00		
2018.01.004		2018	9/4/2018	194.7449783	2.289466268	1	Yes	9	18	Barents Sea	1	1	0.00E+00	1	0.00E+00		
2018.01.005		2018	9/4/2018	0.882724529	-0.054174805	0	No	9	18	Barents Sea	2.22E-16	2.22E-16	0.00E+00	2.22E-16	0.00E+00	1	
2018.01.009		2018	9/7/2018	0.312042263	-0.505786581	0	No	9	18	Barents Sea	2.22E-16	2.22E-16	0.00E+00	2.22E-16	0.00E+00		
2018.01.015		2018	9/7/2018	0.372677288	-0.428667073	0	No	9	18	Barents Sea	2.22E-16	2.22E-16	0.00E+00	2.22E-16	0.00E+00	1	
2018.01.016		2018	9/7/2018	0.486273738	-0.313119185	0	No	9	18	Barents Sea	2.22E-16	2.22E-16	0.00E+00	2.22E-16	0.00E+00	1	
2018.01.017		2018	9/8/2018	0.437398231	-0.359122978	0	No	9	18	Barents Sea	2.22E-16	2.22E-16	0.00E+00	2.22E-16	0.00E+00		
2018.01.018		2018	9/8/2018	0.482736622	-0.316289753	0	No	9	18	Barents Sea	2.22E-16	2.22E-16	0.00E+00	2.22E-16	0.00E+00		
2018.01.020		2018	9/8/2018	0.32306122	-0.490715171	0	No	9	18	Barents Sea	2.22E-16	2.22E-16	0.00E+00	2.22E-16	0.00E+00	1	
2018.01.022		2018	9/9/2018	0.324596969	-0.48865554	0	No	9	18	Barents Sea	2.22E-16	2.22E-16	0.00E+00	2.22E-16	0.00E+00		
2018.01.023		2018	9/9/2018	0.168455488	-0.773514836	0	No	9	18	Barents Sea	2.22E-16	2.22E-16	0.00E+00	2.22E-16	0.00E+00	1	
2018.01.026		2018	9/9/2018	0.20848949	-0.680915833	0	No	9	18	Barents Sea	2.22E-16	2.22E-16	0.00E+00	2.22E-16	0.00E+00		
2018.01.028		2018	9/9/2018	0.567278686	-0.246203534	0	No	9	18	Barents Sea	2.22E-16	2.22E-16	0.00E+00	2.22E-16	0.00E+00		
2018.01.032		2018	10/26/2018	0.520011923	-0.283986699	0	No	10	18/19	Coastal Norway	2.22E-16	2.22E-16	0.00E+00	2.22E-16	0.00E+00		
2018.01.033		2018	10/26/2018	0.609093895	-0.215315753	0	No	10	18/19	Coastal Norway	2.22E-16	2.22E-16	0.00E+00	2.22E-16	0.00E+00		
2018.01.038		2018	11/6/2018	347.9784932	2.541552403	1	Yes	11	18/19	Coastal Norway	1	1	0.00E+00	1	0.00E+00		
2018.01.039	Mnova18059	2018	11/6/2018	0.91413743	-0.038988508	0	No	11	18/19	Coastal Norway	2.22E-16	2.22E-16	0.00E+00	2.22E-16	0.00E+00		
2018.01.040	Mnova18060	2018	11/6/2018	0.456686488	-0.340381838	0	No	11	18/19	Coastal Norway	2.22E-16	2.22E-16	0.00E+00	2.22E-16	0.00E+00		
2018.01.041		2018	11/6/2018	0.510225088	-0.292238191	0	No	11	18/19	Coastal Norway	2.22E-16	2.22E-16	0.00E+00	2.22E-16	0.00E+00		
2018.01.043	Mnova18063	2018	11/7/2018	1.843337596	0.265604881	0	No	11	18/19	Coastal Norway	2.22E-16	2.22E-16	0.00E+00	2.22E-16	0.00E+00	1	
2018.01.044	Mnova18064	2018	11/7/2018	79.58533376	1.900833042	1	Yes	11	18/19	Coastal Norway	1.00E+00	1.00E+00	0.00E+00	1.00E+00	0.00E+00		
2018.01.045		2018	11/7/2018	153.6396624	2.186503344	1	Yes	11	18/19	Coastal Norway	1.00E+00	1.00E+00	0.00E+00	1.00E+00	0.00E+00		
2018.01.046		2018	11/7/2018	1.933410686	0.286324115	0	No	11	18/19	Coastal Norway	2.22E-16	2.22E-16	0.00E+00	2.22E-16	0.00E+00	1	
2018.01.047		2018	11/7/2018	261.1418481	2.416876473	1	Yes	11	18/19	Coastal Norway	1.00E+00	1.00E+00	0.00E+00	1.00E+00	0.00E+00		
2018.01.048		2018	11/13/2018	0.655320773	-0.183546065	0	No	11	18/19	Coastal Norway	2.22E-16	2.22E-16	0.00E+00	2.22E-16	0.00E+00		
2018.01.049		2018	11/13/2018	0.383548177	-0.416180077	0	No	11	18/19	Coastal Norway	2.22E-16	2.22E-16	0.00E+00	2.22E-16	0.00E+00		
2018.01.051		2018	11/15/2018	872.4925177	2.940761711	1	Yes	11	18/19	Coastal Norway	1	1	0.00E+00	1	0.00E+00		
2018.01.053	Mnova18072	2018	12/2/2018	190.3375529	2.279524482	1	Yes	12	18/19	Coastal Norway	1	1	0.00E+00	1	0.00E+00		
2018.01.054	Mnova18073	2018	12/2/2018	0.811878619	-0.090508896	0	No	12	18/19	Coastal Norway	2.22E-16	2.22E-16	0.00E+00	2.22E-16	0.00E+00		
2018.01.057		2018	12/4/2018	136.0270604	2.133625313	1	Yes	12	18/19	Coastal Norway	1	1	0.00E+00	1	0.00E+00		
2018.01.058		2018	12/4/2018	106.6856462	2.028105992	1	Yes	12	18/19	Coastal Norway	1	1	0.00E+00	1	0.00E+00		
2018.01.059		2018	12/4/2018	0.925390389	-0.033675016	0	No	12	18/19	Coastal Norway	2.22E-16	2.22E-16	0.00E+00	2.22E-16	0.00E+00		
2018.01.060		2018	12/4/2018	84.05189925	1.924547531	1	Yes	12	18/19	Coastal Norway	1	1	0.00E+00	1	0.00E+00		

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2018.01.061		2018	12/4/2018	0.259553442	-0.585773208	0	No	12	18/19	Coastal Norway	2.22E-16	2.22E-16	0.00E+00	2.22E-16	0.00E+00		
2018.01.063		2018	12/4/2018	287.296901	2.458330941	1	Yes	12	18/19	Coastal Norway	1	1	0.00E+00	1	0.00E+00		
2019.01.001		2019	1/8/2019	196.0461137	2.292358237	1	Yes	1	18/19	Coastal Norway	1	1	0.00E+00	1	0.00E+00		
2019.01.002		2019	1/8/2019	97.59533626	1.989429065	1	Yes	1	18/19	Coastal Norway	1	1	0.00E+00	1	0.00E+00		
2019.01.003		2019	1/8/2019	0.317329908	-0.498488995	0	No	1	18/19	Coastal Norway	2.22E-16	2.22E-16	0.00E+00	2.22E-16	0.00E+00		
2019.01.004		2019	1/9/2019	0.844003815	-0.07365559	0	No	1	18/19	Coastal Norway	2.22E-16	2.22E-16	0.00E+00	2.22E-16	0.00E+00		
2019.01.005		2019	1/9/2019	322.5546217	2.508603269	1	Yes	1	18/19	Coastal Norway	1	1	0.00E+00	1	0.00E+00		
2019.01.008		2019	1/9/2019	1.582404165	0.199317417	0	No	1	18/19	Coastal Norway	2.22E-16	2.22E-16	0.00E+00	2.22E-16	0.00E+00	1	
2019.01.009		2019	1/19/2019	260.4045613	2.415648587	1	Yes	1	18/19	Coastal Norway	1	1	0.00E+00	1	0.00E+00		
2019.01.014		2019	1/19/2019	0.961315948	-0.017133853	0	No	1	18/19	Coastal Norway	2.22E-16	2.22E-16	0.00E+00	2.22E-16	0.00E+00		
2019.01.016		2019	1/23/2019	0.503806297	-0.297736409	0	No	1	18/19	Coastal Norway	2.22E-16	2.22E-16	0.00E+00	2.22E-16	0.00E+00		
2019.01.017		2019	1/24/2019	0.372110462	-0.42932812	0	No	1	18/19	Coastal Norway	2.22E-16	2.22E-16	0.00E+00	2.22E-16	0.00E+00		
2019.01.019	Mnova18050	2019	1/24/2019	0.545209432	-0.263436639	0	No	1	18/19	Coastal Norway	2.22E-16	2.22E-16	0.00E+00	2.22E-16	0.00E+00		
o135		2011	6/6/11	30.78			Yes			Coastal Norway							extracted in Scotland
o335		2011	6/15/11	3.64			No			Coastal Norway							extracted in Scotland
o335		2012	1/21/12	3.42			No			Coastal Norway						1	extracted in Scotland
o435		2012	1/21/12	3.27			No			Coastal Norway						1	extracted in Scotland
o335		2012	6/13/12	3.49			No			Coastal Norway							extracted in Scotland
o435		2012	6/13/12	3.23			No			Coastal Norway							extracted in Scotland
o735		2012	6/18/12	3.42			No			Coastal Norway							extracted in Scotland
o635		2012	6/18/12	15.67			Yes			Coastal Norway							extracted in Scotland
o935		2012	6/25/12	3.63			No			Coastal Norway							extracted in Scotland
1035		2012	6/25/12	6.67			Uncertain			Coastal Norway							extracted in Scotland
1235		2012	6/29/12	3.49			No			Coastal Norway							extracted in Scotland
1135		2012	6/29/12	4.93			No			Coastal Norway							extracted in Scotland
o135		2013	11/29/13	3.53			No			Coastal Norway							extracted in Scotland
o735		2013	12/6/13	10.46			Yes			Coastal Norway							extracted in Scotland
1035		2013	12/7/13	12.31			Yes			Coastal Norway							extracted in Scotland
o135		2014	1/26/14	3.6			No			Coastal Norway							extracted in Scotland
o235		2014	1/26/14	3.52			No			Coastal Norway							extracted in Scotland
o635		2014	1/31/14	3.47			No			Coastal Norway							extracted in Scotland
o735		2014	1/31/14	3.39			No			Coastal Norway							extracted in Scotland
LK-Mn-04		2016	1/20/16	3.42			No			Coastal Norway							extracted in Scotland
CH-Mn-05		2016	1/21/16	2.56			No			Coastal Norway							extracted in Scotland
LK-Mn-07		2016	1/24/16	2.6			No			Coastal Norway							extracted in Scotland
LK-Mn-09		2016	1/25/16	2.65			No			Coastal Norway							extracted in Scotland
CH-Mn-10		2016	1/26/16	2.72			No			Coastal Norway							extracted in Scotland
MW-Mn-05		2017	1/22/17	8.64			Uncertain			Coastal Norway							extracted in Scotland
LK-Mn-04		2017	1/22/17	30.76			Yes			Coastal Norway							extracted in Scotland
LK-Mn-03		2017	1/22/17	2.84			No			Coastal Norway							extracted in Scotland
MB-Mn-07		2017	1/26/17	23.77			Yes			Coastal Norway							extracted in Scotland
1035		2013	12.07.2013	39.48	1.64	1	Yes	7	2013	Coastal Norway	1	1	0	1	0		sample from Scotland, re-extracted in Tromsø
o135		2011	06.06.2011	240.22	2.38	1	Yes	6	2011	Coastal Norway	1	1	0	1	0		sample from Scotland, re-extracted in Tromsø
o135		2011	06.06.2011	124.98	2.1	1	Yes	6	2011	Coastal Norway	1	1	0	1	0		sample from Scotland, re-extracted in Tromsø
LK-Mn-04		2017	22.01.2017	111.66	2.05	1	Yes	1	2016/17	Coastal Norway	1	1	0	1	0		sample from Scotland, re-extracted in Tromsø
LK-Mn-04		2017	22.01.2017	53.78	1.73	1	Yes	1	2016/17	Coastal Norway	1	1	0	1	0		sample from Scotland, re-extracted in Tromsø
MB-Mn-07		2017	26.01.2017	162.44	2.21	1	Yes	1	2016/17	Coastal Norway	1	1	0	1	0		sample from Scotland, re-extracted in Tromsø
MB-Mn-07		2017	26.01.2017	188.58	2.28	1	Yes	1	2016/17	Coastal Norway	1	1	0	1	0		sample from Scotland, re-extracted in Tromsø
o135		2014	26.01.2014	4.32	0.64	0	No	1	2013/14	Coastal Norway	2.22E-16	1.33E-14	0	2.22E-16	0.00E+00		sample from Scotland, re-extracted in Tromsø
o335		2012	13.06.2012	4.97	0.7	0	No	6	2012	Coastal Norway	2.22E-16	5.03E-12	0	2.22E-16	0.00E+00		sample from Scotland, re-extracted in Tromsø
o735		2012	18.06.2012	2.42	0.38	0	No	6	2012	Coastal Norway	2.22E-16	2.22E-16	0	2.22E-16	0.00E+00		sample from Scotland, re-extracted in Tromsø
o635		2012	18.06.2012	94.09	1.97	1	Yes	6	2012	Coastal Norway	1	1	0	1	0.00E+00		sample from Scotland, re-extracted in Tromsø
o935		2012	25.06.2012	1.89	0.28	0	No	6	2012	Coastal Norway	2.22E-16	2.22E-16	0	2.22E-16	0.00E+00		sample from Scotland, re-extracted in Tromsø
1235		2012	29.06.2012	16.96	1.23	NA	Undetermined	6	2012	Coastal Norway	0.999991739	1	8.26E-06	0.665298176	0.334693563		sample from Scotland, re-extracted in Tromsø
o235		2014	26.01.2014	1.67	0.22	0	No	1	2013/14	Coastal Norway	2.22E-16	2.22E-16	0	2.22E-16	0.00E+00		sample from Scotland, re-extracted in Tromsø

Text S1 Details and comparison of extraction methods. Details on the methods and differences between the two different extractions used for progesterone analysis.

We thawed frozen blubber samples at room temperature and homogenized them seven times for 40 sec at 5000 rpm, using a Precellys 24 tissue homogenizer, and cooled samples on ice between intervals. We rinsed the resulting homogenates using a series of solvent washes, removed tissue debris, collected the supernatants, and evaporated the samples using pressurized air. We stopped evaporation when a thin solvent coating was left to prevent complete desiccation and potential oxidation of the residue. A subset of samples was homogenized manually before the same tissue debris removal, and solvent washes and extracts were dried down under nitrogen.

We pooled results from two slightly different extraction and quantification methods, so we confirmed that the results were comparable by repeating extraction and pregnancy assignment of a subset of samples (N = 13) using both methods. While progesterone levels differed, the same pregnancy status was assigned for all 13 of these individuals, and therefore we included all samples in the pregnancy rate analyses. We repeated the extraction and measurements for a subset of the blubber samples, in which case we report the averaged resulting progesterone level, and ran multiple samples at several dilutions.

The mean progesterone concentration for pregnant individuals was 224.4 ± 173.6 nanogram per gram of blubber (ng g^{-1} P4) (NO 221.7 ± 182.2; BS 194.7 ± 7), ranging between 79.6 (194.7 BS) and 872.5 (303.8 BS). Using the other method (marked as “Scotland” in Table S3), pregnant female concentrations were 20.6 on average and ranged from 10.5-30.8. The mean concentration for non-pregnant females was 0.7 ± 0.3 ng.g-1 (NO 0.7 ± 0.3; BS 0.52 ± 0.3), ranging between 0.3 and 6.8 (0.2 - 1.1 BS); and 3.3 on average with a range from 2.6-4.9.

Text S2 Relatedness methods. Detailed methods for within-season re-sampling assessment using r_{xy}

To look for potential re-sampling individuals within sampling season, 107 genomes were sequenced at low coverage using an Illumina HiSeq4000 platform (Novogene, Hong Kong). The 1,781,057,402 paired-end reads obtained were mapped to the available humpback whale reference genome (GenBank assembly accession: GCA_004329385.1). NGSRelate v2 which allows to calculate pairwise relatedness (r) between two individuals x and y using identity by descent have been used. As input for NGSrelate, genotype likelihoods (GL) of the dataset were calculated from the mapped bam files using ANGSD v0.935-53-gf475f10. The following filtering options were used: minimum mapping and base quality of 15 (-minmapQ and -minQ 15);

calculate genotype likelihoods using model from SAMtools (-GL 1); output binary genotype likelihoods (-doGlf 3); infer major and minor alleles using GL (-doMajorMinor 1); calculate per site frequencies using a fixed major and minor allele (-doMaf 1); only include SNPs with a p-value less than 1 × 10–6 (-SNP_pval 1e-6), and a minimum minor allele frequency of 0.01 (-minmaf 0.01). The number of sites used between pairwise comparisons to calculate relatedness (r_{xy}) ranged from 14829 to 28014.

Table S4: Pairwise coefficients of relatedness matrix Resulting pairwise relatedness coefficients for a subset of individuals.

2015/2016

M16004 M16006 M16007 M16008 M16009 M16010 M16011 M16013 M16014 M16015 M16016 M16017 M16018 M16019 M16020

M16021 M16022 M16023 0.413 0.311 0.263 0.442 0.382 0.423 0.447 0.374 0.434 0.433 0.423 0.326 0.436 0.398 0.456 0.458 0.436 0.425

M16003 0.331 0.292 0.383 0.367 0.361 0.328 0.389 0.342 0.365 0.326 0.318 0.360 0.331 0.389 0.383 0.360 0.345 **M16004** 0.375 0.338 0.331

0.344 0.313 0.311 0.292 0.300 0.295 0.363 0.291 0.293 0.278 0.303 0.270 0.284 **M16006** 0.296 0.312 0.312 0.194 0.191 0.199 0.252 0.225

0.364 0.211 0.241 0.247 0.229 0.221 0.184 **M16007** 0.410 0.397 0.413 0.336 0.399 0.414 0.407 0.341 0.404 0.361 0.390 0.418 0.401 0.402

M16008 0.417 0.385 0.348 0.380 0.386 0.390 0.349 0.379 0.364 0.363 0.367 0.355 0.373 **M16009**

0.431 0.346 0.388 0.376 0.392 0.360 0.408 0.375 0.384 0.395 0.377 0.383 **M16010**

0.393 0.470 0.423 0.496 0.295 0.472 0.419 0.463 0.493 0.451 0.464 **M16011**

0.401 0.364 0.385 0.282 0.393 0.341 0.364 0.398 0.371 0.391 **M16013**

0.458 0.500 0.311 0.441 0.442 0.443 0.463 0.444 0.458 **M16014**

0.468 0.331 0.397 0.434 0.447 0.455 0.444 0.424 **M16015**

0.287 0.444 0.423 0.457 0.460 0.459 0.468 **M16016**

0.265 0.292 0.279 0.285 0.269 0.288 **M16017**

0.429 0.460 0.447 0.459 0.460 **M16018**

0.455 0.420 0.430 0.427 **M16019**

0.464 0.497 0.464 **M16020**

0.482 0.450 **M16021**

0.544 **M16022**

2016/2017

M16002 M16024 M16025 M16026 M16027 M16028 M16029 M17007 M17008 M17010 M17011 M17012

M17013 M17014 M17015 0.431 0.278 0.385 0.407 0.379 0.372 0.331 0.380 0.413 0.416 0.332 0.374 0.304 0.359

0.381 **M16001** 0.232 0.434 0.445 0.454 0.374 0.305 0.422 0.423 0.437 0.301 0.364 0.270 0.376 0.436 **M16002**

0.161 0.156 0.167 0.336 0.391 0.148 0.177 0.149 0.391 0.217 0.398 0.138 0.149 **M16024** 0.471 0.487 0.303 0.257

0.489 0.476 0.499 0.210 0.368 0.179 0.437 0.525 **M16025** 0.435 0.314 0.256 0.469 0.482 0.461 0.236 0.372 0.194

0.409 0.478 **M16026**

0.311 0.254 0.461 0.490 0.442 0.217 0.382 0.208 0.430 0.478 **M16027**

0.362 0.302 0.318 0.305 0.367 0.326 0.332 0.266 0.301 **M16028**

0.253 0.274 0.268 0.364 0.306 0.387 0.251 0.262 **M16029**

0.450 0.439 0.265 0.395 0.234 0.454 0.474 **M17007**
0.449 0.250 0.372 0.216 0.445 0.486 **M17008**
0.241 0.383 0.191 0.415 0.461 **M17010**
0.274 0.386 0.226 0.226 **M17011**
0.283 0.369 0.400 **M17012**
0.219 0.196 **M17013**
0.481 **M17014**

2017/2018

M17002 M17004 M17005 M17006 M17009
0.466 0.469 0.485 0.465 0.442 **M17001**
0.452 0.489 0.475 0.426 **M17002**
0.422 0.418 0.442 **M17004**
0.475 0.388 **M17005**
0.419 **M17006**

2018/2019

M18033 M18034 M18035 M18036 M18037 M18038 M18039 M18040 M18041 M18042 M18043 M18044 M18045 M18046 M18047 M18048 M18049 M18051 M18052 M18053 M18054 M18055 M18056 M18058 M18061 M18065 M18066 M18067 M18068 M18069 M18070 M18071 M18074 M18075 M18076 M18077
M18078 M18079 M18080 M18081 M18082 0.221 0.484 0.485 0.504 0.489 0.386 0.487 0.532 0.474 0.475 0.463 0.332 0.398 0.477 0.497 0.210 0.467 0.490 0.217 0.259 0.487 0.243 0.125 0.140 0.235 0.544 0.317 0.398 0.389 0.352 0.404 0.477 0.322 0.278 0.495 0.434 0.474 0.428 0.468 0.394 0.463 **M18001** 0.253 0.243 0.261
0.250 0.269 0.234 0.244 0.233 0.257 0.241 0.340 0.294 0.178 0.247 0.400 0.257 0.253 0.402 0.413 0.217 0.384 0.368 0.356 0.379 0.221 0.356 0.322 0.306 0.403 0.317 0.233 0.382 0.434 0.290 0.308 0.290 0.299 0.266 0.315 0.252 **M18033** 0.635 0.505 0.491 0.384 0.463 0.489 0.466 0.460 0.454 0.373 0.424 0.449 0.499 0.244 0.450
0.476 0.243 0.264 0.442 0.264 0.136 0.157 0.250 0.505 0.341 0.424 0.404 0.340 0.419 0.440 0.321 0.285 0.479 0.413 0.443 0.415 0.465 0.431 0.495 **M18034** 0.509 0.493 0.393 0.470 0.505 0.463 0.457 0.452 0.361 0.421 0.473 0.520 0.234 0.451 0.485 0.240 0.256 0.452 0.248 0.126 0.157 0.238 0.524 0.312 0.426 0.387 0.342 0.420
0.455 0.318 0.292 0.484 0.394 0.449 0.413 0.465 0.427 0.504 **M18035** 0.477 0.376 0.473 0.525 0.476 0.506 0.467 0.372 0.421 0.458 0.523 0.255 0.475 0.514 0.256 0.264 0.457 0.256 0.132 0.142 0.254 0.527 0.319 0.429 0.413 0.371 0.423 0.476 0.345 0.296 0.480 0.407 0.451 0.438 0.457 0.409 0.473 **M18036** 0.370 0.484 0.502
0.464 0.449 0.471 0.351 0.457 0.461 0.498 0.212 0.448 0.493 0.232 0.258 0.443 0.247 0.152 0.140 0.233 0.513 0.324 0.419 0.391 0.352 0.388 0.481 0.326 0.273 0.481 0.449 0.447 0.440 0.463 0.406 0.475 **M18037** 0.393 0.393 0.381 0.391 0.382 0.341 0.374 0.372 0.359 0.273 0.376 0.410 0.272 0.298 0.360 0.301 0.202 0.218 0.284
0.390 0.316 0.353 0.367 0.310 0.329 0.374 0.335 0.316 0.367 0.361 0.368 0.350 0.347 0.349 0.383 **M18038** 0.478 0.493 0.500 0.497 0.379 0.422 0.467 0.499 0.204 0.463 0.481 0.213 0.261 0.464 0.284 0.127 0.126 0.237 0.473 0.343 0.399 0.407 0.322 0.381 0.489 0.326 0.270 0.482 0.391 0.430 0.424 0.431 0.384 0.460 **M18039**
0.496 0.484 0.474 0.356 0.423 0.465 0.514 0.219 0.484 0.527 0.214 0.262 0.455 0.251 0.147 0.162 0.256 0.515 0.321 0.420 0.410 0.352 0.421 0.496 0.351 0.285 0.499 0.431 0.454 0.422 0.480 0.422 0.498 **M18040** 0.493 0.482 0.372 0.409 0.506 0.488 0.218 0.497 0.480 0.219 0.250 0.473 0.265 0.131 0.125 0.239 0.478 0.321 0.412
0.389 0.336 0.395 0.505 0.341 0.287 0.500 0.411 0.435 0.410 0.454 0.395 0.450 **M18041** 0.468 0.388 0.425 0.450 0.481 0.231 0.473 0.486 0.233 0.245 0.464 0.275 0.150 0.136 0.233 0.467 0.352 0.411 0.390 0.356 0.401 0.477 0.336 0.308 0.462 0.395 0.442 0.413 0.439 0.400 0.459 **M18042** 0.360 0.423 0.454 0.488 0.204 0.475
0.495 0.215 0.238 0.461 0.263 0.123 0.127 0.235 0.469 0.304 0.387 0.369 0.334 0.381 0.481 0.317 0.276 0.450 0.396 0.423 0.432 0.441 0.399 0.465 **M18043**
0.378 0.283 0.368 0.330 0.367 0.360 0.332 0.338 0.316 0.354 0.286 0.260 0.326 0.327 0.394 0.387 0.391 0.326 0.404 0.356 0.327 0.347 0.366 0.352 0.387 0.384 0.338 0.391 0.370 **M18044**
0.352 0.447 0.259 0.413 0.444 0.273 0.286 0.365 0.300 0.201 0.192 0.277 0.405 0.356 0.419 0.401 0.349 0.399 0.398 0.334 0.301 0.389 0.412 0.413 0.405 0.398 0.411 0.402 **M18045**
0.504 0.177 0.466 0.463 0.168 0.216 0.478 0.190 0.096 0.109 0.197 0.521 0.256 0.351 0.338 0.311 0.341 0.485 0.280 0.229 0.476 0.362 0.385 0.355 0.416 0.339 0.441 **M18046**
0.215 0.480 0.489 0.228 0.242 0.477 0.245 0.103 0.122 0.211 0.539 0.327 0.421 0.371 0.369 0.414 0.473 0.346 0.278 0.481 0.416 0.437 0.431 0.495 0.427 0.495 **M18047**
0.213 0.207 0.411 0.400 0.194 0.381 0.382 0.414 0.394 0.211 0.344 0.294 0.291 0.313 0.285 0.190 0.327 0.398 0.264 0.265 0.269 0.266 0.206 0.300 0.230 **M18048**
0.544 0.231 0.268 0.464 0.269 0.151 0.141 0.249 0.472 0.344 0.421 0.393 0.372 0.405 0.482 0.350 0.304 0.489 0.429 0.450 0.445 0.468 0.405 0.456 **M18049**
0.225 0.263 0.451 0.250 0.128 0.128 0.256 0.508 0.329 0.429 0.417 0.359 0.417 0.468 0.326 0.283 0.474 0.436 0.474 0.443 0.465 0.415 0.480 **M18051**
0.401 0.216 0.388 0.361 0.380 0.390 0.208 0.327 0.302 0.284 0.351 0.282 0.215 0.343 0.401 0.245 0.276 0.263 0.282 0.247 0.294 0.259 **M18052**
0.246 0.406 0.357 0.380 0.398 0.245 0.320 0.317 0.313 0.364 0.317 0.248 0.350 0.413 0.284 0.305 0.298 0.296 0.263 0.320 0.275 **M18053**
0.254 0.120 0.116 0.209 0.508 0.310 0.369 0.340 0.337 0.366 0.500 0.327 0.281 0.415 0.402 0.433 0.379 0.458 0.391 0.455 **M18054**
0.370 0.356 0.355 0.224 0.347 0.315 0.307 0.328 0.306 0.273 0.321 0.382 0.259 0.289 0.285 0.282 0.269 0.320 0.252 **M18055**
0.408 0.361 0.097 0.305 0.222 0.224 0.255 0.212 0.193 0.265 0.337 0.169 0.198 0.175 0.189 0.135 0.213 0.142 **M18056**
0.362 0.133 0.290 0.197 0.201 0.266 0.211 0.145 0.281 0.356 0.203 0.219 0.168 0.214 0.147 0.225 0.176 **M18058**
0.216 0.319 0.315 0.384 0.310 0.311 0.219 0.302 0.380 0.252 0.260 0.282 0.300 0.242 0.283 0.241 **M18061**
0.302 0.390 0.374 0.343 0.386 0.467 0.334 0.256 0.477 0.426 0.465 0.397 0.499 0.398 0.485 **M18065**
0.400 0.368 0.325 0.381 0.319 0.345 0.368 0.335 0.355 0.377 0.368 0.326 0.378 0.334 **M18066**
0.429 0.362 0.418 0.407 0.350 0.334 0.433 0.418 0.441 0.427 0.416 0.428 0.410 **M18067**
0.328 0.420 0.379 0.314 0.310 0.412 0.370 0.427 0.424 0.371 0.397 0.396 **M18068**
0.351 0.330 0.496 0.398 0.369 0.358 0.359 0.378 0.346 0.354 0.362 **M18069**
0.382 0.314 0.352 0.417 0.418 0.427 0.431 0.414 0.425 0.420 **M18070**
0.329 0.291 0.449 0.396 0.416 0.389 0.455 0.380 0.447 **M18071**
0.398 0.348 0.357 0.354 0.337 0.350 0.346 0.334 **M18074**
0.318 0.325 0.323 0.327 0.298 0.346 0.299 **M18075**
0.436 0.445 0.419 0.459 0.439 0.484 **M18076**
0.442 0.395 0.449 0.431 0.421 **M18077**
0.430 0.437 0.415 0.440 **M18078**
0.409 0.424 0.425 **M18079**
0.428 0.474 **M18080**
0.550 **M18081**

S2009

M18003 M18004 M18005 M18006 M18007 M18008 M18009 M18010 M18011 M18012 M18013 M18014 M18015 M18016 M18018 M18019 M18028 M18029

M18030 M18031 0.202 0.464 0.452 0.464 0.433 0.467 0.459 0.461 0.488 0.463 0.492 0.473 0.514 0.475 0.463 0.273 0.480 0.458 0.464 0.435 **M18002** 0.183

0.217 0.200 0.277 0.215 0.218 0.160 0.174 0.226 0.234 0.217 0.214 0.218 0.203 0.341 0.251 0.229 0.206 0.245 **M18003** 0.462 0.443 0.415 0.479 0.459 0.465

0.449 0.462 0.455 0.442 0.458 0.474 0.495 0.263 0.461 0.481 0.452 0.450 **M18004** 0.423 0.387 0.450 0.442 0.418 0.470 0.440 0.444 0.422 0.457 0.466 0.460

0.308 0.445 0.450 0.450 0.463 **M18005** 0.399 0.467 0.454 0.397 0.466 0.465 0.450 0.472 0.441 0.440 0.431 0.316 0.450 0.430 0.456 0.415 **M18006** 0.441 0.441

0.374 0.429 0.432 0.453 0.444 0.440 0.451 0.415 0.344 0.448 0.425 0.415 0.406 **M18007** 0.492 0.414 0.479 0.502 0.482 0.486 0.484 0.479 0.488 0.303 0.472

0.473 0.469 0.458 **M18008**

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0.409 0.444 0.421 0.455 0.411 0.411 0.447 0.215 0.420 0.436 0.412 0.409 **M18010**

0.480 0.473 0.456 0.492 0.484 0.459 0.303 0.471 0.437 0.468 0.432 **M18011**

0.481 0.503 0.499 0.470 0.481 0.284 0.463 0.464 0.464 0.465 **M18012**

0.492 0.485 0.473 0.470 0.305 0.507 0.479 0.456 0.436 **M18013**

0.471 0.453 0.453 0.287 0.471 0.465 0.476 0.416 **M18014**

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0.534 0.476 0.439 **M18028**

0.461 0.464 **M18029**

0.430 **M18030**

PAPER III

From the Arctic to the Tropics- Mapping humpback whale migrations across the North Atlantic

Kettemer, L. E., Rikardsen, A. H., Biuw, E. M., Blanchet, M. A., Clapham, P. J., Ferguson, S. H., Fossette, S., Heide-Jørgensen, M. P., Kennedy, A., Laidre, K. L., Lawson, J., Lefort, K., Matthews, C. J. D., Nourani, E., Øien, N., Robbins, J., Vély, M., Víkingsson, G. A., Zerbini, A. N.

manuscript

From the Arctic to the Tropics –

Mapping humpback whale migrations across the North Atlantic

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Abstract

Humpback whales (*Megaptera novaeangliae*) occur in all ocean basins and have shown remarkable recovery across most of their range after the end of industrial whaling. However, a lack of comprehensive understanding regarding their movement patterns across ocean basins hinders population viability assessments and our understanding of their responses to climate change and anthropogenic threats. In the North Atlantic, humpback whales migrate vastly disparate distances between northern and polar foraging grounds in the eastern and western basin to tropical breeding ground. In this study, we compiled over two decades of satellite telemetry data from >200 individual humpback whales across the North Atlantic. We assessed spatiotemporal movement patterns on major foraging grounds and the main breeding ground and during the migrations. We identified six migratory strategies based on migration pace (speed and tortuosity) and phenology (the timing of migration departure and arrival). Migration distance only explained 23% of the observed variation in migratory strategies, suggesting that whales migrating from the same foraging ground latitude employ different strategies. Some whales that occupied northern Norway during the winter returned early from breeding grounds or initiated a return migration before reaching the core breeding area. This indicates that long winter foraging seasons might affect the following migration phases in humpback whales, or that stays on the breeding ground are not a required stage of the annual cycle. Our results will facilitate basin-wide assessments of the North Atlantic population of humpback whales, provide essential information for ecosystem management and will guide research efforts in the future.

Introduction

Populations of large whales are recovering from industrial whaling. At the same time, they are facing new challenges from increasing anthropogenic impacts; including ship strikes, entanglement in fishing gear, noise pollution and climate change (Tulloch *et al.*, 2019; Nelms *et al.*, 2021). Due to their highly mobile and long-lived lifestyles, many of the large whales use a wide range of habitats across ocean basins. This makes them notoriously difficult to monitor, while knowledge on their spatiotemporal movement patterns is fragmented in most areas and mostly stems from whaling data, photographic identifications (photo-ID) and sighting surveys. A lack of baseline knowledge on large whale migration ecology still impedes our understanding of how large whales might respond to climatic changes and anthropogenic threats, in particularly if they inhabit areas that are far from coastlines or in remote regions, or during their offshore migrations (Lascelles *et al.*, 2014; Silber *et al.*, 2017).

Humpback whales (*Megaptera novaeangliae*) occur in all ocean basins worldwide, and like many baleen whales they undertake annual migrations between summer high latitude feeding grounds and tropical breeding areas during winter and spring (Clapham and Mead, 1999). In their foraging areas, they are subject to sometimes rapidly changing ecosystems, and during migration they cross vast expanses of the high seas (Stevick *et al.*, 2006; Kettemer, Rikardsen, *et al.*, 2022; Pallin *et al.*, 2023). After the end of industrial whaling, humpback whales have shown remarkable recovery across most of their range, including in the Southern Ocean (Pallin *et al.*, 2018), the North Pacific and the North Atlantic (Stevick *et al.*, 2003; Leonard and Øien, 2020). However, recent evidence indicates that ecosystem shifts on some foraging grounds are now negatively affecting reproductive success, for example in the western North Atlantic(Kershaw *et al.*, 2020), and North Pacific populations (Cartwright *et al.*, 2019; Gabriele *et al.*, 2022). Several studies have also reported changes in the migration timing of this species, but the outcome of these changes on the population are unknown (Ramp *et al.*, 2015; Avila *et al.*, 2020; Gosby *et al.*, 2022; Pendleton *et al.*, 2022).

In the North Atlantic, photo-ID studies have shown that humpback whales migrate from several largely discrete feeding grounds to a common tropical breeding ground in the West Indies (Stevick *et al.*, 2006). Some individuals in the eastern basin also migrate to a smaller breeding ground in the Cape Verde islands (Wenzel *et al.*, 2020). Knowledge of humpback whale movements is traditionally obtained from whaling data, sighting surveys and photographic matching of their fluke patterns (Chittleborough, 1965; Clapham and Mayo, 1987; Øien, 2009). In the last two decades, local satellite telemetry efforts have provided data and insights into movements on foraging grounds of this species in the North Atlantic (Dietz *et al.*, 2002; Robbins *et al.*, 2013; Heide-Jørgensen and Laidre, 2015; Hamilton *et al.*, 2021) and to a lesser extent in the West Indies breeding area (Kennedy *et al.*, 2014). However, there is a limited understanding of the connectivity between foraging grounds (Ryan *et al.*, 2016; Kettemer, Ramm, *et al.*, 2022; Kettemer, Rikardsen, *et al.*, 2022) and a definite lack of data detailing the migrations to breeding grounds.

Migration distances between breeding and feeding areas vary greatly for humpback whales from different foraging grounds in Greenland, Canada, the Gulf of Maine, Iceland and Norway, ranging between 2.500 and 9.000 km one way. In the last decade, humpback whales also established a winter foraging ground in fjord systems of northern Norway, highlighting that whales can respond to changes in local food distribution by modulating their migration and feeding patterns (Kettemer, Ramm, *et al.*, 2022). These differences in migration timing and distances could mean that animals from different sides of the basin have different energetic costs and risks associated with migration (Riekkola *et al.*, 2020). Such risks include differential exposure to pollutant levels, risks of ship strikes or bycatch risk (Elfes *et al.*, 2010; Hitchcock *et al.*, 2019; Stepanuk, 2021). Differences in migration patterns can reflect variations in trade-offs associated with costs and risks or different environmental conditions that affect how an individual can optimize the fitness outcome of migration (Alerstam, 2011; Braithwaite, Meeuwig and Hipsey, 2015). These differences may also be linked to potentially distinct population segments if behaviors are consistently different and lead to a lack of spatiotemporal overlap on the breeding ground (Stevick *et al.*, 2018; Wenzel *et al.*, 2020).

Generally, demographic variations in terms of migration characteristics, such as departure timing and route selection are well known for many baleen whale species, based on photo-ID and sighting surveys, genetic profiling and whaling data (Chittleborough, 1965; Dawbin, 1966; Craig and Herman, 2000; Pallin *et al.*, 2018). However, an individual's migration strategy emerges from a set of migration characteristics through the annual cycle (Alerstam, 2011). This can only be assessed with continuous information from the same individual, for example as can be gained from satellite telemetry (Phillips *et al.*, 2017; Abrahms *et al.*, 2018). Optimal migration theory (Alerstam, 2011) posits that individuals optimize their migration strategies in regard to their energetic balance and resource use, and these strategies are known to mediate the survival success of an individual depending on environmental conditions (Abrahms *et al.*, 2018; Torres *et al.*, 2022). Variation of migration strategies on a population level provides resilience to environmental changes by spreading the risk of mismatched movements (Freshwater *et al.*, 2019).

Here we use 20 years of satellite telemetry data from humpback whales in the North Atlantic basin to document their movement patterns and their seasonal use of the oceanscape. We (i) aimed to assess whether animals from different foraging grounds use distinct migration strategies related to the large variation in migration distances they must cover, and (ii) to explore the variability of strategies among individuals from the same feeding area. Finally, we aimed to (iii) update information on the spatiotemporal distribution and movements within different foraging grounds, as well as the connectivity between these different areas, and movements in the West Indies breeding ground based on two decades of satellite telemetry campaigns.

Methods

We use satellite telemetry data of humpback whales instrumented around the North Atlantic (Table 1), including the five known distinct foraging grounds; the Gulf of Maine in the United States and Canada, Atlantic Canada including the Gulf of St. Lawrence and Newfoundland/Labrador, the west coast of Greenland, Iceland, summer feeding grounds in the Barents Sea and winter feeding grounds in fjord systems in northern Norway. Additionally, we also used telemetry data from one of the breeding grounds, the Greater and Lesser Antilles of the West Indies Island chain (Table 1). In total, we used satellite telemetry data collected from 206 individual humpback whales over a 20-year period between 2002 and 2021. The deployments documented 24 southward migration tracks, defined as when the whales left the known feeding grounds and had a directed southward movement towards the breeding grounds (Table 2). Eight of these were also tracked when returning northward after spending time on the breeding grounds. In addition, 11 northward tracks from tags deployed in the West Indies were available in addition to the documented northward movements of animals instrumented on foraging grounds.

Most campaigns used subdermal Argos tags (SPOT303, SPOT305 or SPLASH, www. wildlifecomputers.com), deployed via air-powered rifles from small boats. In some earlier years, experimental tag types were deployed, specifically, SPLASH SWING tags in Greenland, for details see (Dietz *et al.*, 2002; Laidre *et al.*, 2010; Heide-Jørgensen and Laidre, 2015), and the tag types have been slightly modified over the duration of some telemetry campaigns, e.g., in the Gulf of Maine and Greenland. Some contributors collected information on the sex of tracked individuals, either from long-term observations (Gulf of Maine) or from genetic profiling of biopsy samples (Kettemer, Ramm, *et al.*, 2022). In some cases, pregnancy or other reproductive status was assessed with a progesterone level analysis, see details in Kettemer et al. (2022). Known pregnancy status is indicated in Table 2.

Telemetry data

All analyses were conducted in R v. 4.2.1 (R Core Team, 2020). We removed Argos- classified Z locations (those for which the location process failed) and employed a filter on speed (max 8 ms^{-1}) and spikes in turning angles using the *argosfilter* package (Freitas *et al.*, 2008). We removed locations individual outliers not captured in that process manually, for example, where large gaps (> 48 hours) occurred within the first 5 and last 5 locations of the track, respectively since these cause model fitting problems (for more information on data quality see in supporting material Figures S1 and S2).

From the filtered raw locations, we estimated a most likely path using a random walk using the *aniMotum* package (Jonsen and Patterson, 2020), accounting for the Argos quality classification (lc) of each location (either lc quality or error ellipses, estimated by CLS- Argos). As this is required for the model fitting, we projected the locations to an azimuthal equidistant projection centered on the middle of the North Atlantic (45°N, 20°W). We then sampled a set of locations along each animal’s path at 6-hour intervals. We removed individuals with fewer than 15 locations (N= 5) and obtained converged models for 196 individuals. To represent distribution data from all individuals, we established a grid of hexagonal cells for each of the deployment areas (defined by a 100% minimum convex polygon) and counted the number of filtered locations per cell (~ $10km^2$). For converged tracks, we then estimated a movement persistence parameter based on the autocorrelation of speed and turning angles between subsequent location intervals (*aniMotum* package). Movement persistence is continuous and varies between 0 and 1: a value of 0 indicates localized, area-restricted searching movements, while a value of 1 indicates transiting movements.

In total, we successfully reconstructed tracks of 196 humpback whales, from the five feeding areas and one breeding ground over 17 years of satellite telemetry deployments (Figure 1A). The spatial distribution of all locations collected within the foraging grounds and in the breeding ground, including locations of 10 animals for which tracks were not successfully modeled (206) are shown in Figure 1 B. The median track duration for modeled tracks varied between 20 and 48 days (between the different deployment locations, Table 1).

Table 1 Summary of deployments for each deployment region.

Deployment area	Number of tags	First deployment	Last deployment	Last Transmission	Med. Duration	Max duration	Med. N Locations	Med. Locations per day	Sum tracking days
Canada	7	2018-07	2019-08	2019-09	22 days	279 days	119	7	410 days
Greenland	46	2002-08	2013-10	2013-10	20 days	104 days	188	10	1130 days
Gulf of Maine	67	2011-07	2018-08	2019-02	32 days	192 days	422	15	2655 days
Iceland	25	2003-09	2021-09	2021-10	22 days	153 days	297	14	773 days
Norway	37	2011-08	2019-01	2019-12	48 days	332 days	981	24	2797 days
West Indies	19	2008-01	2019-04	2019-05	19 days	56 days	75	6	385 days

Migration characteristics

To identify tracks that captured migratory movements, we selected individuals with locations on the high seas (i.e., outside of any exclusive economic zone (EEZ), or that showed a continuous and persistent change in latitude, because telemetry campaigns usually operate in nearshore areas within EEZs, and thus can be used to distinguish between animals that remained locally around deployment areas and those that left these areas. EEZ and high seas regions were obtained from shape files provided by Marine Regions (https://www.marineregions.org/eez). To estimate departure timing, we first established a kernel density 90% home range contour for each of the feeding ground areas using the *adehabitatHR* package (Calenge, 2006), based on locations of animals that did not show migration behavior. For each individual identified as a migratory whale, we then identified the first location outside of this area that was followed by at least 5 locations outside of this range. In cases where animals were foraging outside of this core area, we manually confirmed the last time they left the area and used the first location outside of the area as the estimated departure time if it was followed by persistent change in latitude.

We estimated movement speed by calculating the geodesic distance between relocations sampled along the reconstructed path. To estimate arrival dates for individuals whose migration was not fully captured (i.e., those whose tags ceased operating) we multiplied the average speed during the observed track with the distance traveled from the last available location's latitude, on average by the other animals successfully tracked to the breeding ground (defined as reaching 19°N) from the same deployment area. When animals did not reach 19°N but northward movement was captured in the data, the date of the southernmost location was considered the arrival date. Migration characteristics estimated based on incomplete tracks are italicized in Table 2 and individuals marked with an asterisk.

The tortuosity of each path was calculated as the sum of distances between relocations (path length) divided by the Euclidean distance between the start and end of the migration (i.e., the first and last locations estimated during the migration track). Where tracks contained gaps in the raw data larger than 2 days during migration, we estimated departure timing and speed based on the reconstructed track: in this case, we used interpolated locations along a straight line between the last observed locations before the track was interrupted and the locations received once data transmission was re-established.

Migration strategies

To assess the presence of distinct migration strategies, we conducted a principal components analysis (PCA) based on the following characteristics: departure time (as day of the year, centered on the summer solstice (June 21st as day 1) to ensure that December and January departure times are treated as similar in the analysis), observed or projected arrival time (as day of the year), median movement speed (in ms^{-1}), variation in movement speed (as the interquartile range of speed), resting locations relative to migration locations (the number of relocations with speed < 0.5 ms^{-1} divided by the number of collected locations during migration), and tortuosity of the migration path. We removed from the PCA analysis individuals with large gaps (> 2 days) during the migration that affected tortuosity and speed estimates, resulting in 21 individuals being included in the PCA. PCA is a commonly used dimension reduction method for multivariate datasets with a range of potentially correlated predictor variables. During the process, new axes (principal components) are constructed such that each new axis explains successively less of the overall variation in the dataset. Based on this PCA, we used a cluster analysis (k-means) to identify groups of individuals that exhibited similar characteristics and then assessed whether variability in the first two principal components corresponded to different migration distances with a linear model (migration distance ~ PCA1 + PCA2).

Results

We were able to track the southward breeding migration of 24 whales instrumented at the foraging grounds. Of these, 10 tracks represented full migrations, meaning that they were tracked all the way from deployment locations at their feeding area and all the way to the breeding area. Of the 24 whales, 6 (2 full migrations) were instrumented in the northern Barents Sea, 11 (5 full migrations) animals in the fjords of northern Norway, 5 (1 full migration) animals off Iceland, and one each from the Gulf of Maine and Canada (both full migrations) (Figure 1**A**). For whales instrumented at the breeding grounds, the northward migration was documented for 11 individuals, representing two deployment locations in the West Indies breeding ground (Figure 1**A**). For animals instrumented in the West Indies, destinations could not be conclusively determined. Additionally, we were also able to track the northward migration of 8 individuals instrumented on the feeding grounds, reached the West Indies breeding grounds and initiated their northward migration before the tag was lost.

Table 2 Migration characteristics for 24 individuals tracked on their southward migration towards tropical waters. First latitude denotes the latitude at which the tag was deployed, Departure date is the day on which an animal was considered to have left the foraging area; Arrival date is the day on which an animal was considered to have arrived to the West Indies breeding ground, either observed or projected; Resting is the number of locations where speed < 0.5 ms^{-1} relative to the number of observed migration days tracked for this individual, and Tortuosity is the tortuosity of the track as the length of the track divided by the Euclidean distance between the start and end of migration. Characteristics inferred for incomplete tracks are italicized, and these individuals are marked with an asterisk. Animals that began their northward migration before reaching the breeding ground area, or spent less than a day there, are shaded in gray. Females assessed for pregnancy by hormonal screening are marked with either + (pregnant) or - (not-pregnant). Cluster indicates which migration strategy cluster the individual was assigned to in the k-means clustering on the PCA, individuals removed from the PCA for data quality reasons are marked with -.

PTT	**First Latitude**	**Departure date**	**Med. speed**	**IQR speed**	**Resting**	**Tortuosity**	**Arrival date**	**Migration days**	**Incomplete track**	**Sex (preg.)**	**Cluster**
Gulf of Maine											
111869	43	09-Jan	1.87	0.54	0.00	1.08	25-Jan	15.83		f	2
Canada											
175037	48	29-Aug	-	0.73	-	-	*18-Feb*	-	*		-
Iceland											
50687	64	02-Feb	1.89	0.24	0.03	1.01	*06-Jun*	*124.16*	*		5
60007	66	30-Jan	1.59	0.95	0.00	1.09	*01-Jun*	*121.42*	*		3
60012	66	12-Jan	1.65	1.26	0.00	1.02	*02-May*	*110.10*	*		3
93117	66	25-Dec	1.31	1.09	0.19	1.17	26-Feb	63.00			1
37282	66	19-Nov	1.46	0.37	0.00	1.03	*16-Feb*	*88.63*	*		2
mean	65.60		1.58	0.78	0.04	1.06		101.46			
Norway											
110822	69	27-Jan	1.06	1.39	0.28	1.09	*01-May*	*95.23*	*		6
166142	70	23-Jan	1.00	0.86	0.52	1.28	30-Apr	96.88		m	4
166143	70	08-Jan	1.01	0.64	0.70	1.14	*17-Apr*	*99.24*	*	f -	4
166148	70	28-Jan	1.72	0.51	0.00	1.04	*20-Jun*	*143.04*	*	f +	5
166149	70	20-Feb	1.43	1.30	0.17	1.25	*21-May*	*90.35*	*	f -	6
166150	70	19-Jan	1.05	0.71	0.74	1.28	02-May	103.25		f +	4
47598	70	22-Feb	1.66	0.99	0.06	1.10	18-Apr	55.62		f -	3
83274	70	30-Dec	1.94	0.61	0.02	1.11	*24-Feb*	*55.74*	*	m	1
83278	70	09-Feb	1.45	0.97	0.10	1.11	20-Apr	70.50		f +	3
83287	70	23-Jan	1.65	0.81	0.06	1.07	24-Mar	60.25		f +	1
83271	70	25-Jan	1.85	0.57	0.00	1.11	*23-Mar*	*56.58*	*	m	1
mean	69.91		1.44	0.85	0.24	1.14		84.24			
Barents Sea											
110820	76	24-Nov	1.50	1.01	0.06	1.32	*06-Mar*	*102.98*	*		4
140099	77	17-Sep	1.02	0.82	0.19	1.29	*06-Jan*	*111.52*	*		-
47570	77	10-Dec	1.10	0.98	3.14	1.18	16-Mar	96.25		m	4
167844	79	11-Jan	1.29	0.99	0.12	1.25	*11-Apr*	*90.63*	*	f +	-
47597	79	16-Nov	1.06	1.10	2.22	1.21	*23-Feb*	*98.92*	*		4
47599	79	17-Jan	1.60	0.90	0.05	1.12	19-Mar	61.25		m	1
mean	77.83		1.26	0.97	0.96	1.23		93.59			

Migration strategies

The migration characteristics of 24 individuals are summarized in Table 2, asterisks denote an incomplete track, and characteristics estimated based on those are italicized. All characteristics are based on regularly sampled locations along reconstructed paths at 6-hour intervals. Departure timing from foraging areas varied from August to the end of February, while the arrival timing to the West Indies varied between January 07 and May 02 (up to May 31 for incomplete tracks) (Table 2). Median migration speed varied among individuals (1 -1.9 ms^{-1}), as did the inter quartile range of speed (IQR speed: 0.2 – 1.5). The duration of the migration was shortest for one individual from the Gulf of Maine (16 days) and varied from 55 to 103 (143 for incomplete tracks) for whales from the eastern basin (Table 2). The migration track tortuosity varied between 1.01 and 1.32.

Whales instrumented in Iceland departed at various times between November 19th and February 2nd and migrated on average for 101 days at 1.58 ms^{-1}. The only complete trajectory reached the breeding ground in mid-February and incomplete tracks were projected to arrive between mid-February and early June. Individuals from Norway did not migrate before December 30th but generally later (January 8th – February 22nd), as they were instrumented during the winter. These animals only arrived at the breeding ground after April 17th, one individual was projected to arrive not until June 20th. Migration speed was 1.44 ms^{-1} and 84 migration days on average from Norway. From the Barents Sea, individuals departed between September 17th and January 17th, most after mid-November. Arrival time to the breeding ground was observed in mid-March for two individuals and projected to occur between February 23rd and April 11th for incomplete trajectories. The mean migration duration was 94 days at 1.26 ms^{-1}.

Whales from the eastern foraging grounds used a broad area for migration, spanning the entire width of the basin above ~ 56°N, and between 51°W and 19°W at around 45°N, converging slightly as whales approached the West Indies (Figure 1). Multiple individuals exhibited periods of localized ARS movements also after departing from foraging grounds, as evidenced by short sections of lower values of movement persistence during migration and increased track tortuosity (Figure 1 and Figure 3). This occurred mainly in coastal areas, along the Norwegian coast, around Iceland, and close to the Scottish Outer Hebrides, but also in one instance in open waters north of the Azores (Figure 3).

At least four individuals initiated their northward return migrations before reaching the breeding grounds or returned almost immediately upon their arrival to the breeding area; one additional individual also started moving northward but the data transmission ceased soon after (Figure 1, Table 2). The migration speed of these whales varied between 1 and 1.7 ms^{-1}, departure timing from the foraging ground was between December 10 and February 22, and arrival to the general breeding ground area (or the initiation of northward movement) occurred between March 16 and May 02. Three of these individuals were assigned to cluster 4, and one into cluster 3 (Table 2). This included two males, one pregnant and one non-pregnant female, all migrating from Norway or the Barents Sea (Table 2).

In the PCA on southward migration characteristics, the first two principal components explained 89% of the observed variance among the 6 included migration characteristics from 21 individuals (Table 3). The first principal component explained 71% and mainly represented variation in median speed (0.52), relative resting (-0.49), and tortuosity (-0.45). The second principal component explained 19%, mainly representing arrival date (0.62) as well as departure day (0.50) (Figure 4, panel B). We identified six distinct clusters in this PCA (Figure 4, panel C). Departure dates and arrival dates were highly positively correlated but neither appeared to influence migration speed substantially (Figure 4, panels A and B). As expected, median speed was negatively correlated with track tortuosity and the relative number of resting days (Figure 4, panels A and B).

To understand whether whales from the same breeding ground were grouped together in our clustering, we ran a linear model to predict migration distance using the first and second principal components (cluster assignment also shown in Table 2). We found that migration distance (as first latitude of the track, i.e., the foraging ground origin) explained 23% (adjusted R^2) of the variation in the first and second principal components and therefore migration strategies. Accordingly, the clusters did not closely correspond to foraging ground origin (Table 2). The mean characteristics for each identified strategy varied between the clusters as shown in Table 4.

Table 3 Results of the principal component analysis (PCA) of migration strategies for 21 individuals for which sufficient data were available (see Table 2). The columns show loadings of each variable on the first two principal components.

	PC1	**PC2**
Arrival yday	0.243	0.618
Departure Yday	0.381	0.497
Median Speed	0.521	-0.376
IQR speed	-0.278	0.429
Relative resting	-0.493	-0.118
Tortuosity	-0.453	0.181

Table 4 Average migration characteristics for each of the identified migration clusters based on a k-means cluster analysis of PCA results (component 1 and 2).

Cluster	First Latitude	Departure date (first, last)	Med. speed	IQR speed	Resting	Tortuosity	Arrival date (first, last)	Migration days	Sex (preg.)
1	71	25 Dec, 25 Jan	1.67	0.80	0.064	1.116	24-Feb, 24 Mar	59.36	m, f +
2	54.5	9 Jan, 19 Nov	1.67	0.46	0	1.055	25 Jan, 16 Feb	52.23	f
3	68	12 Jan, 22 Feb	1.59	1.04	0.04	1.08	18 Apr, 1 Jun	89.41	f-, f+
4	73.6	24 Nov, 23 Jan	1.12	0.88	1.23	1.235	23 Feb, 2 May	99.59	m, f+, f-
5	67	28 Jan, 2 Feb	1.80	0.38	0.02	1.03	6 Jun, 20 Jun	133.6	f +
6	69.5	27 Jan, 20 Feb	1.25	1.35	0.22	1.17	1 May, 21 May	92.79	f -

Movement within distinct feeding and breeding grounds

Whales instrumented in Greenland foraged mainly off the west coast of Greenland between June and November (2002 – 2013, Figure 2). The distribution shifted to the south-east as the season progressed, and the observed low movement persistence in both areas is consistent with foraging along the coast (Figure 3). One animal returned northward to Disko Bay (69°N 52°W) in November. Another individual transited to the Baffin Island coast of Canada and then returned to Greenlandic waters. Two individuals left the Greenlandic coast and transited to Canadian waters at the end of June and end of August, respectively.

In Canadian waters, whales were tracked within a region just north of Newfoundland between July and January (2018 – 2019). In the Gulf of Maine, whales were tracked between July and January (2009 – 2018). As the season progressed, animals in the Gulf of Maine moved northward, some into the Bay of Fundy, and in one case into the Gulf of St. Lawrence, and south of Nova Scotia (Figure 1). The spatial distribution of the movement persistence parameter indicated distinct locations of foraging, and also revealed transiting behavior between these apparent core foraging areas (Figure 3).

In the fjords of northern Norway, animals were present between late October and early February (2011 – 2019, Figure 2). The distribution shifted northward from year to year (2017- 2019). In 2017, whales occupied both more southern and northern fjords of Troms. In 2018 and 2019 most of the activity occurred in the more northerly fjord system. Nine individuals continued foraging just off the Norwegian coast, as far south as 67°N, after leaving the fjords for their southward migration to the tropics (Figure 3).

Animals instrumented in the northern Barents Sea remained in the area between July and January. One individual ventured as far north as 82°N, and another moved eastward towards

Russian waters in December and January (72°N 46°E). Some individuals appeared to transition towards coastal Norway as the season progressed (October and November, Figure 2 and Figure 3).

Whales instrumented in Iceland foraged in local waters around Iceland between June and January (2003 - 2019). In 2019 and 2021, four individuals were instrumented on the northwest coast of Iceland and transited to the east coast of Greenland (around 71°N 21°W and 68°N 22°W, Figure 1), where they spent multiple days in July, September, and October. Movement persistence was lower in these coastal areas than during the rest of migration, indicating ARS type movements indicative of prey searching, foraging or socializing. Another whale instrumented in the Barents Sea also utilized this area during September and October 2013, and also exhibited low movement persistence. Three whales transitioned from the northern to the southern coast of Iceland as the season progressed (October and November, Figure 2). Six whales instrumented in the Barents Sea and coastal Norway also spent time in Icelandic waters between November and March, during their southward migration. These individuals visited either the eastern or western coast of Iceland, respectively (Figure 2). One individual transited through Icelandic waters in July during its northward migration to the Barents Sea.

Whales instrumented in two locations in the Greater and Lesser Antilles in the West Indies breeding ground remained in the area for various periods of time between January and May (2008 – 2019, Figure 2). The departure time from breeding grounds varied between individuals, from February 2 to May 19. Whales instrumented in breeding grounds spent up to 3.5 weeks post-deployment within the West Indies.

Discussion

This study presents the first comprehensive overview of humpback whale migratory movements in the North Atlantic, as documented by satellite telemetry. Novel information on the movement patterns on all known foraging grounds, and in the common breeding ground in the West Indies. Humpback whales spent between 19 days migrating from the Gulf of Maine and between 55 and 104 days migrating from eastern basin foraging grounds. Departure time varied between August and February, and arrival timing to the West Indies was between January and May. Large variability in migration timing meant that while some animals were on their southward migration, others were already moving northward after their stay on breeding grounds. The area used for migration spanned the entire North Atlantic basin.

Six different migration strategies were characterized by differences in migration pace (speed and tortuosity) and phenology (migration departure and arrival time). Latitude of foraging only explained 23% of the variability in these two principal components, indicating that animals from the same foraging grounds use a wide variety of migration strategies. After foraging in Norway during the winter, multiple individuals did not reach the West Indies breeding ground or spent only few hours there before initiating their northward migration. Among these were pregnant females, non-pregnant females, and male. This indicates that either the individual circumstances did not make a stay in the breeding area a beneficial strategy, or that time constraints led animals to prioritize a timely return to foraging areas.

Movement patterns documented on the different foraging grounds generally confirmed previous documentations from photo-ID studies and sighting surveys. Frequently, individual whales moved between apparent foraging hotspots within distinct foraging sites, but we also highly that many transited between sites. For example, one individual instrumented in the Gulf of Maine transited into Canadian waters of the Bay of Fundy and three individuals instrumented in Iceland and the Barents Sea foraged on the Greenlandic shelf.

Movement on feeding and breeding grounds

Animals in all general foraging regions moved between different core foraging areas throughout the season. In Greenland, for example, animals moved southward along the coast. In the Gulf of Maine, animals moved northward into the Bay of Fundy, or, in one case, offshore. The spatial distribution of the movement persistence parameter on the foraging grounds identified areas of core foraging activity and areas within the foraging grounds that might represent movement corridors between food patches. This was most distinct in the Gulf of Maine. Such switches between core foraging sites most likely represents a response to ephemeral prey fields. We also documented exchanges between several distinct feeding sites by individuals from multiple areas. Examples included whales from Norway that passed by and used habitat in the east and west of Iceland, central-Norwegian and British waters, and Icelandic whales that used habitat along the eastern coast of Greenland. Whales from the western Greenland coast in some cases visited Canadian waters either during the foraging season, or possibly after initiating their southward migrations. There was also some exchange between the Gulf of Maine and Canadian waters up to the Nova Scotian coast and into the Gulf of St. Lawrence. This is consistent with previous evidence from photo-ID studies (Clapham *et al.*, 2003), and telemetry data adds detailed information on when this occurs. This type of dynamic information about individual movements and core foraging activity sites provides a valuable complement to traditional sighting and survey data, which generally only provide a snapshot at a specific time point. For example, some whales exhibited local movements with low movement persistence after leaving Norwegian fjords on their southward migrations. This highlights potentially important areas that were previously not described as key foraging areas. The time at which this occurred also reveals that whales continued foraging after the presumed end of the foraging season documented based on photo-ID (Kettemer, Ramm, *et al.*, 2022).

All individuals migrated to or toward the well-documented breeding ground in the West Indies. The time spent in the breeding area varied extensively between animals, while some spent no time or only a few hours in this area, others spent up to 3.5 weeks within the West Indies Island chain. The observed timing of the breeding season confirms acoustic monitoring data from the area, which had recently established humpback whale presence over longer time frames than previously documented from photo-ID (Heenehan *et al.*, 2019). This is not surprising given the temporal bias in research effort in the region, which historically tended to concentrate on the peak months of the winter breeding season (Stevick *et al.*, 2006; Kennedy and Clapham, 2017). The movements described here generally confirmed previous knowledge but highlighted the diversity in timing of the breeding season, and some movements between different areas within the breeding ground, for example between the Lesser Antilles and the Greater Antilles, confirming information gathered from photo-ID surveys (MacKay *et al.*, 2019). The high diversity in timing of the season and movements within the breeding ground likely contribute to maintaining gene flow between whales of the east and western basin, even as their core breeding seasons appear to differ in space and time. Collectively, whales utilized the waters of 14 different countries in the breeding grounds, often in succession throughout the season.

A high proportion of individuals from the Norwegian and Barents Sea feeding grounds are known from photo-ID to migrate to the Cape Verde Islands breeding grounds at least in some years (Broms, 2015; Wenzel *et al.*, 2020). There is so far no telemetry data from whales migrating to or from the Cape Verdes breeding ground. This distinct population segment has a much smaller estimated population and there is limited information on their migration routes or strategies (Wenzel *et al.*, 2020). These Cape Verde whales are considered to form a distinct breeding segment under the U.S. Endangered Species Act, and the small number of whales using this area are considered potentially sensitive and important to the overall population (Wenzel *et al.*, 2020). Future studies could use the range of migration characteristics from this study to inform simulations designed to infer possible migration routes and annual schedules of individuals migrating to the Cape Verde Islands until telemetry data have been collected that can provide detailed information about migrations to this smaller breeding ground.

Migration strategies.

Humpback whales exhibited a broad range of migration strategies in the North Atlantic. Using a principal component analysis, we identified six clusters of distinct migration strategies that were mostly explained by differences in migration pace (speed and tortuosity) and phenology (migration departure and arrival time). Latitude of the foraging ground, and therefore migration distance, only explained a small amount of the variability in the first two principal components. This highlights that animals from the same foraging grounds use a wide variety of migration strategies and that migration strategies might not primarily be constrained by migration distance. We provide new evidence that humpback whales can adopt a wide range of annual schedules, i.e., their migration timing south and north, and length of stay on the breeding and feeding grounds. For example, our results show that whales foraging in the Barents Sea can complete migrations to breeding grounds and back after a foraging season that lasted in some cases into January, much longer than previously documented. In cases where animals continued foraging in Norway in the winter before their southward migration, migration speed was not generally higher than for animals that left earlier, despite having to cover some of the longest migration distances of any humpback whales globally (Rasmussen *et al.*, 2007; Riekkola *et al.*, 2018; Modest *et al.*, 2021).

It is of particular interest to note that four animals from the Barents Sea/coastal Norway foraging grounds, for which we had complete trajectories including northward movement, remained in the breeding ground area less than a day or started their northward migration before even reaching the known breeding areas. All these individuals departed later than mid-December from the foraging ground; three migrated at a relatively slow speed of around 1 ms^{-1}, and only one migrated at a faster speed of 1.7 ms^{-1}. These individuals did not form a distinct cluster in our cluster analysis, likely because the duration of breeding ground attendance and northward migration were not included in the PCA. This behavior was observed in two males as well as a pregnant and a non-pregnant female. It is possible that a pregnancy detected from hormone analysis of samples collected prior to migration was aborted during migration, or that calves were born en-route but did not survive, potentially making a stay in breeding grounds no longer a beneficial strategy even for pregnant females. We did not assess age, and thus cannot exclude the possibility that the individuals were immature. Kettemer et al. (2022) provided a detailed account of the migration of one of the individuals included here, a pregnant female (id = 83278), that foraged in Norway during the winter and then in Iceland. This individual likely gave birth en-route and despite the extensive feeding season also spent time in the breeding grounds.

It further seems likely that males might encounter breeding opportunities on their migration as they approach breeding grounds, or that returning to foraging grounds is a greater priority than increasing breeding opportunities by spending more time in breeding grounds. For instance, animals in poor condition or juveniles could be expected to prioritize increased feeding opportunities and postpone breeding. To our knowledge, such patterns of delayed departure from feeding grounds, coupled with very short or no time spent at breeding grounds is not commonly observed in other migratory species. This observation raises questions about the definition of a breeding ground, as experienced by a whale, and might inform future studies into the reasons for baleen whale migrations. Overall, this might indicate that the migration schedule is constrained by a long foraging season, which can be offset by high migration speeds in some cases, see also Kettemer et al. (2022). One important question that arises is to what extent such variations in migration phenology are linked to reproductive status and body energy reserves.

Such carry-over effects, where conditions in one season affect the following season, are known to affect the survival of migratory animals (Bengtson Nash *et al.*, 2018; Imlay, Mann and Taylor, 2021). Such effects are thought to be an important determinant of the fitness of migrating animals (Norris *et al.*, 2004; Marra *et al.*, 2015; Gómez *et al.*, 2017). Carry-over effects are, however, difficult to observe and quantify. We provide some initial insights into how one migration characteristic (such as late departure timing from foraging grounds) might affect subsequent migratory phases (e.g., time on breeding grounds or increasing swim speed) in a baleen whale. There is very little published information on the migrations of humpback whales to breeding grounds (Modest *et al.*, 2021) and our study therefore fills an important knowledge gap for a substantial part of the North Atlantic humpback whale population. Unfortunately, insufficient migration data were available from the western foraging areas to compare migration strategies between the west and east of the North Atlantic basin in detail. Because of the large difference in migration distances, this is an important research topic that requires further attention. Nonetheless, insights from this study can be helpful in calibrating future research that requires information on the physiological and energetic envelope within which baleen whales undertake their migration, which will define their potential for adaptation. This kind of information is required in models that assess the effects of disturbance and climate change on migrating animals (Pirotta *et al.*, 2021; Pirotta, 2022).

Variations in migration timing is to be expected on a population level, and we show the broad range of migration timing in this system. Notably, migrations towards tropical waters by some whales occur at the same time as northward migrations by others. This difference in migratory timing likely emerges as a consequence of interactions between abiotic environmental cues (Freshwater *et al.*, 2019; Burnside *et al.*, 2021) and biotic factors, such as prey availability (Jones *et al.*, 2014) and internal state, including fat reserves and life history stage (Chittleborough, 1965; Gómez *et al.*, 2017). For humpback whales, sex and reproductive state influence migration strategy, with pregnant females remaining on foraging grounds longest and nursing whales choosing different routes to optimize calf survival (Craig and Herman, 2000; Félix and Guzmán, 2014; Pallin *et al.*, 2018; Modest *et al.*, 2021). While humpback whales generally show a high degree of fidelity to foraging grounds, some individuals may choose to vary their migration routes from year to year (Stevick *et al.*, 2016). Although this seems to be a rare occurrence, one individual in our study was first tracked from the foraging grounds in Canada but headed farther east than expected on its northward migration, possibly towards one of the eastern Atlantic foraging sites before the tag stopped transmitting. Diversity in migration strategies, particularly in phenology, can be an important factor in determining the resilience of a population to disturbance and ecosystem changes, as it provides the basis for a variety of responses to disturbance and the potential for adaptation to changing conditions (Armstrong *et al.*, 2016; Freshwater *et al.*, 2019).

If animals undertake migrations over vastly different distances (as occurs in the North Atlantic), this might make migrations more costly and result in potentially riskier migratory decisions. While it was previously documented that some humpback whales forage during the winter in Norway (Jourdain and Vongraven, 2017; Mul, 2020; Kettemer, Rikardsen, *et al.*, 2022), the variation in migration strategies as classified in our PCA was only explained to a small degree by migratory distance. Often, linear relationships between individually observed migration characteristics are reported and assessed because obtaining a larger set of characteristics is often logistically impossible, e.g., migratory distance vs. migration speed (Riekkola *et al.*, 2020; Modest *et al.*, 2021). These correlations often fail to identify clear relationships, possibly because they omit to account for preceding migratory decisions. Our results highlight that migratory scheduling and pace emerge from a complex set of migratory characteristics and showcase the large variability of strategies even within foraging grounds. However, the availability of data also constrained our analysis, e.g., we projected arrival dates based on the previously documented swim speed for trajectories that ceased to transmit before arrival to the breeding grounds. This introduced additional uncertainty into the analysis of migration strategies if animals are expected to increase movement speed as they approach breeding grounds.

Different migration distances have been shown to result in different energetic outcomes for humpback whales in other regions and there is some evidence that longer migration distances cause animals to migrate at higher speeds to maintain migration duration (Braithwaite, Meeuwig and Hipsey, 2015; Riekkola *et al.*, 2020; Gough, 2022). Further work is needed to investigate the relative importance of daily maintenance costs vs. the cost of increasing swim speeds (Kettemer, Rikardsen, *et al.*, 2022). For example, during years of poor forage, animals with tighter restrictions on phenology due to long migration distances might experience potentially more dangerous outcomes of changing conditions on foraging grounds, or poor foraging conditions during specific individual years (Gough, 2022). This might render parts of the population generally more susceptible to disturbance of any kind. Further, modeling based on information on the range of possible migration strategies collated here could provide insights for areas in which migration telemetry data are currently limited or unavailable (i.e., Gulf of Maine, Greenland, Canada, and the route from Norway to the Cape Verde Islands).

Conclusion

In this study, we present evidence revealing a high diversity in migration strategies among humpback whales in the North Atlantic, both between and within foraging areas. The substantial variation in migratory timing, utilization of various jurisdictions throughout the year, and extensive time spent on the high seas underscore the importance of considering spatial connectivity and the variability in spatiotemporal distributions of these highly mobile baleen whales. We also present novel information on humpback whales' space utilization in the Northeast Atlantic during the foraging and breeding season. Our findings provide evidence of foraging activity occurring outside of the core foraging areas, particularly southward of Norwegian fjord systems during the winter months. Moreover, movement patterns indicate the potential use of high-seas areas for breeding. It will be important to incorporate these factors into dynamic management frameworks and policy considerations to support efficient ecosystem management. Additionally, our work provides a valuable assessment of the available tracking data and the distribution of research efforts across the ocean basin. This evaluation should guide future deployments and research endeavors, ensuring effective allocation of resources and advancing our understanding of humpback whale behavior.

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Figures

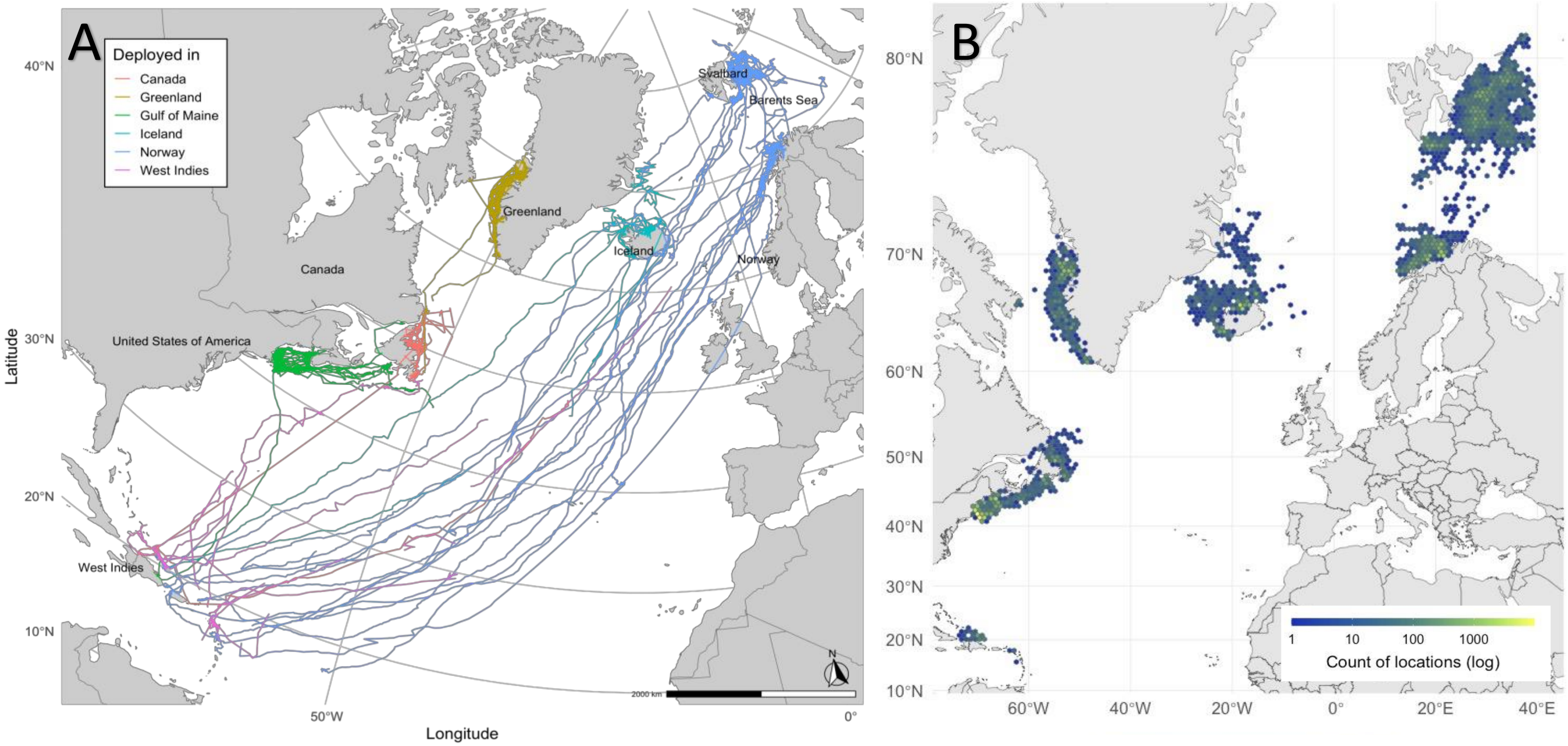

Figure 1 ***A*** *Map of successfully modeled humpback whale tracks (N= 196) data across the North Atlantic over two decades, deployed in the West Indies, Iceland, Norway, Greenland, Atlantic Canada and the Gulf of Maine, colored by deployment area. The tracks represent paths reconstructed using a state space model.* ***B*** *Geographic distribution of 201 humpback whale locations in a hexagonal grid of the 100% minimum convex polygon area for each area in which tags were deployed. The colors indicate the number of locations in each hexagonal grid of ca. 50 km^2 on a logarithmic scale.*

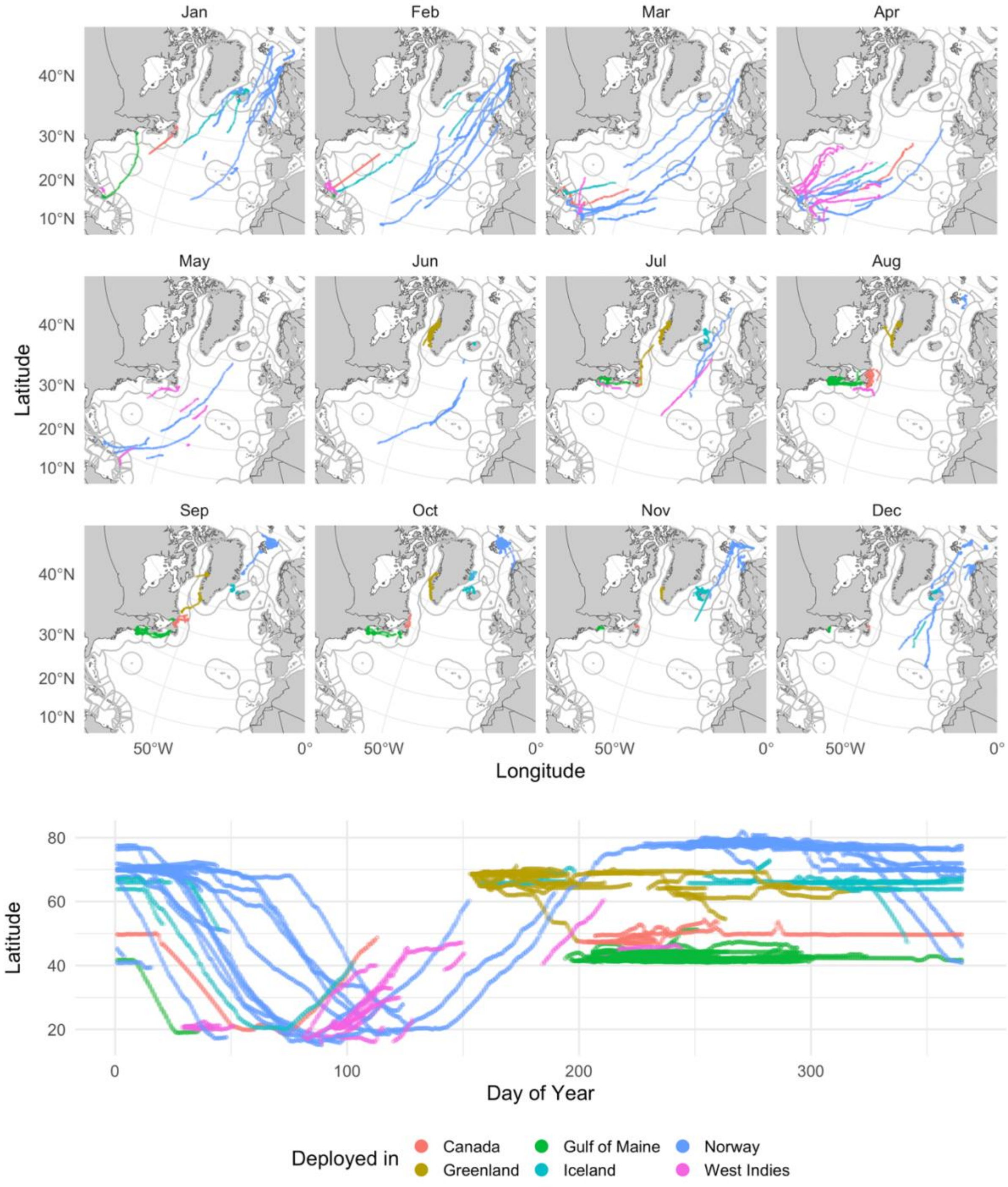

Figure 2 ***Upper panel*** *Seasonal distribution of humpback whale movements based on modeled tracks, split by month of the year. Colors indicate the area in which the tag was deployed. Grey lines indicate country EEZs.* ***Lower panel*** *Migratory movements throughout the year as the change in latitude over time (as day of the year, with day 0 = January 1st), colored by the area in which the tag was deployed.*

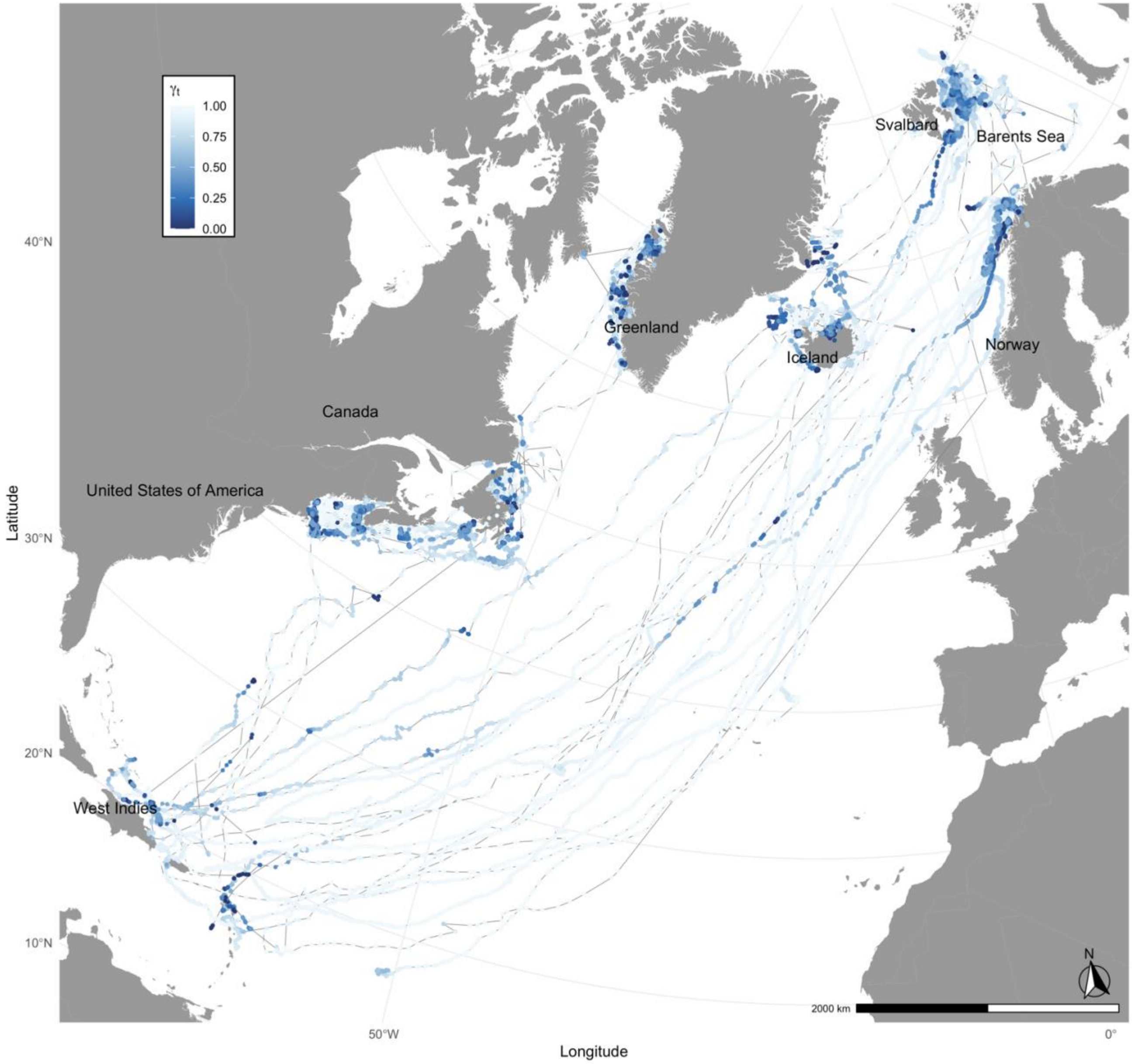

Figure 3 The color scale shows the movement persistence estimated for each predicted location along the modeled tracks, ranging from 0 (light blue) indicating meandering movements to 1 (dark blue) indicating directed movements.

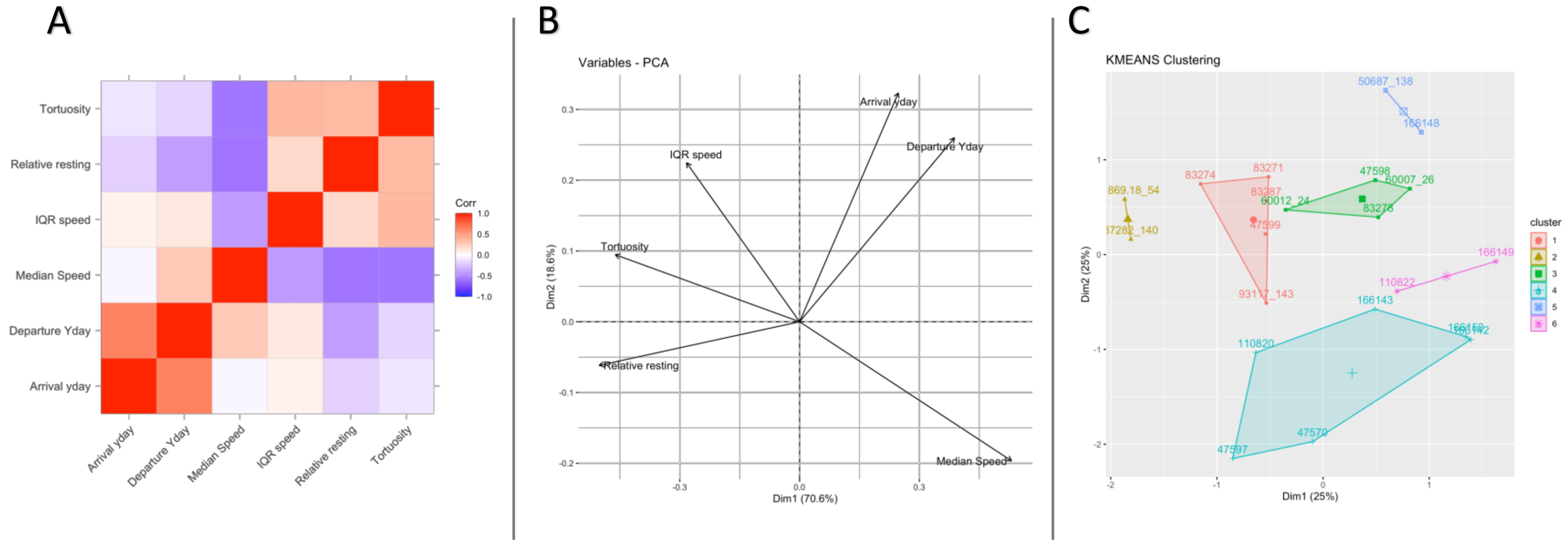

Figure 4 ***Panel A*** *shows the correlation matrix for the scaled variables included in the principal component analysis of migration strategies.* ***Panel B*** *shows the variable loadings on the first (x-axis) and second (y-axis) principal components. The migration strategies are indicated by departure timing (year day centered on the summer solstice), median speed, the variance of speed, (projected) arrival date, and resting locations (relative to total locations) during migration.* ***Panel C*** *shows the resulting cluster analysis with the ids from the 21 animals included in the PCA.*