

Individual based modeling of North Atlantic common minke whale (*Balaenoptera acutorostrata*) migratory and foraging behaviour in the Nordic Seas

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In loving memory of my parents, Amy, my grandparents, Aunt Claudette, and Grommit. The love and support they have given me continues to allow me to accomplish the things I do today.

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Abstract

The North Atlantic common minke whale (*Balaenoptera Acutorostrata*) is an abundant, top-level marine predator in the Nordic Seas and Barents Sea ecosystems whose large-scale migratory and foraging behaviors are widely unknown. Understanding these behaviors may offer important insight into their life-history and management-unit structuring as defined by the International Whaling Commission. Existing modeling do not incorporate spatially-explicit movements of individual minkes, limiting our ability to investigate their large-scale behaviors. In this study, an individual based model (IBM) for minke whales is developed as an extension of the NORWECOM.E2E ecosystem model to identify behaviors that may contribute to minke distribution in the Nordic Seas. The energetic reward of both their use of migration within predominant currents and four large-scale foraging strategies are investigated.

First, the effect on minke migration from ocean circulation and migration path selection are tested by running simulations with variation in activation of currents and paths (into and out of the Nordic Seas) along the Norwegian coast, the Norwegian Sea center, and the Greenland coast. Simulations are then run with variation in foraging strategies: random-walk, migration only, and periodic searching for maximum prey density with either random-walk or migration along the route determined to be optimal. NORWECOM.E2E model output of Norwegian spring-spawning herring, blue whiting, and mackerel are used as prey-fields. The optimal migration route is found to be in along the Norwegian coast and out through the Norwegian Sea center, with mean migration durations of 24.611 ± 0.051 d and 24.997 ± 0.041 d. Foraging that incorporates migration and 10 d periods of maximum prey density searching is found to have the highest foraging efficiency index (2.381 ± 0.435). Random-walk movement with maximum prey density searching had similarly high index (2.256 ± 0.444), along with an increase in mean individual whale movement of $14.159 \text{ km d}^{-1} \text{ whale}^{-1}$.

The development of a minke IBM is an important addition of a high-level predator in Nordic Seas and Barents Sea modeling efforts, and the results from this study could have implications for minke population structuring and success in these areas. With migration throughout the Nordic Seas being energetically viable, interaction between whales categorized as separate sub-stocks could be possible. As an unvalidated model with key improvements necessary, further development of individual based modeling of minkes with more dynamic data is encouraged.

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Chapter 1

Introduction

1.1 Statement of Purpose

With an estimated population of 108140 whales (CV 0.23) in the Nordic Seas and Barents Sea (Bøthun *et al.*, 2009), the North Atlantic common minke whale (*Balaenoptera Acutorostrata*) plays an important role as a top-level marine predator in its ecosystem. It has been estimated to consume approximately 1.8×10^6 tonnes to 2.2×10^6 tonnes (CI 95 %) of fish per annum based on previous population estimates (Folkow, 2000), and has a distribution throughout the entire Nordic Seas and Barents Sea (Glover *et al.*, 2010). Portions of this population are known to be year-long residents while others are thought to perform seasonal migrations into and out of the Nordic Seas to as far south as $10^{\circ}09'N$ in the North Atlantic (Folkow and Blix, 1991). It is has also been a target species for whaling since the 1920s (Horwood, 1990), and it is currently commercially hunted by Norway and Iceland. Despite its critical position in the ecosystem and existing human interactions, little is known about the North Atlantic common minke whales' large-scale migratory and foraging behaviors - behaviors that have been linked to reproduction and feeding success in whales (Bradford *et al.*, 2006; Whitehead, 1996).

Only relatively recently have spatially-explicit models been developed to study such behavior for cetaceans at an individual level - most notably for endangered species like the blue whale (*Balaenoptera musculus*; Bailey *et al.*, 2009) and the dusky dolphin (*Lagenorhynchus obscurus*; Srinivasan, 2009). Despite such work, modeling efforts involving minkes have so far been limited to small-scale foraging models (Smout and Lindstrom, 2007), area-structured trophic-interaction models (such as MULTSPEC, Bogstad *et al.*, 1997; ECO-PATH, Song and Zhang, 2014; and Atlantis, Hansen, 2014), GAM distribution models (Murase *et al.*, 2006; Skern-Mauritzen *et al.*, 2011), and abundance estimation models (Bravington and Hedley, 2010; Bøthun *et al.*, 2009).

Ecosystem models like ECOPATH and Atlantis, with a trophic mass-balance focus (Fulton *et al.*, 2004; Pauly *et al.*, 2000), do not encompass the individual movements of species within their defined habitat blocks and can therefore not be used for analyzing the effect of movement processes on migration timing and predator-prey interactions. Incorporating discrete movement in individual based models (IBM)s is an approach, as was implemented with grey seals (*Halichoerus grypus*) by Austin *et al.* (2004), which provides quantitative methods for analyzing such processes.

The Norwegian Ecological Model System (NORWECOM) is an end-to-end ecosystem model that includes coupling between physical processes (implemented using the ROMS ocean model), chemical process, and biological interactions (Aksnes *et al.*, 1995; Skogen and S iland, 1998; Skogen *et al.*, 1995). Higher trophic levels have been recently incorporated as IBM modules, such as pelagic fish (Utne and Huse, 2012) and *Calinus finnmarchicus* (Hj ollo *et al.*, 2012), each with discrete movement of the species and validated with field data. The modeling system is modularized, allowing flexible use of the model's components and varying grid systems. The newest developments of NORWECOM.E2E uses a polar stereographic grid system, whereas the recent study by Utne and Huse (2012), with validated pelagic fish IBMs, was developed on a rectangular grid system (Figure 1.1; red grid). The latest NORWECOM.E2E modeling area spans the North Atlantic and arctic regions (Figure 1.1; blue grid), covering all potential summer migration and feeding areas of the North Atlantic common minke whale. Pelagic fish species within the model are known prey species of the minke whale, including: Norwegian spring spawning (NSS) herring (*Clupea harengus*; Haug *et al.*, 2002), blue whiting (*Micromesistius poutassou*; V ikingsson *et al.*, 2014), and Northeast Atlantic (NEA) mackerel (*Scomber scombrus*; Olsen and Holst, 2001). With these prey fields, a minke IBM that quantifies individual movements of minkes can be developed to assess the effectiveness of prey strategies potentially used by them during their summer feeding months and presumed summer migration.

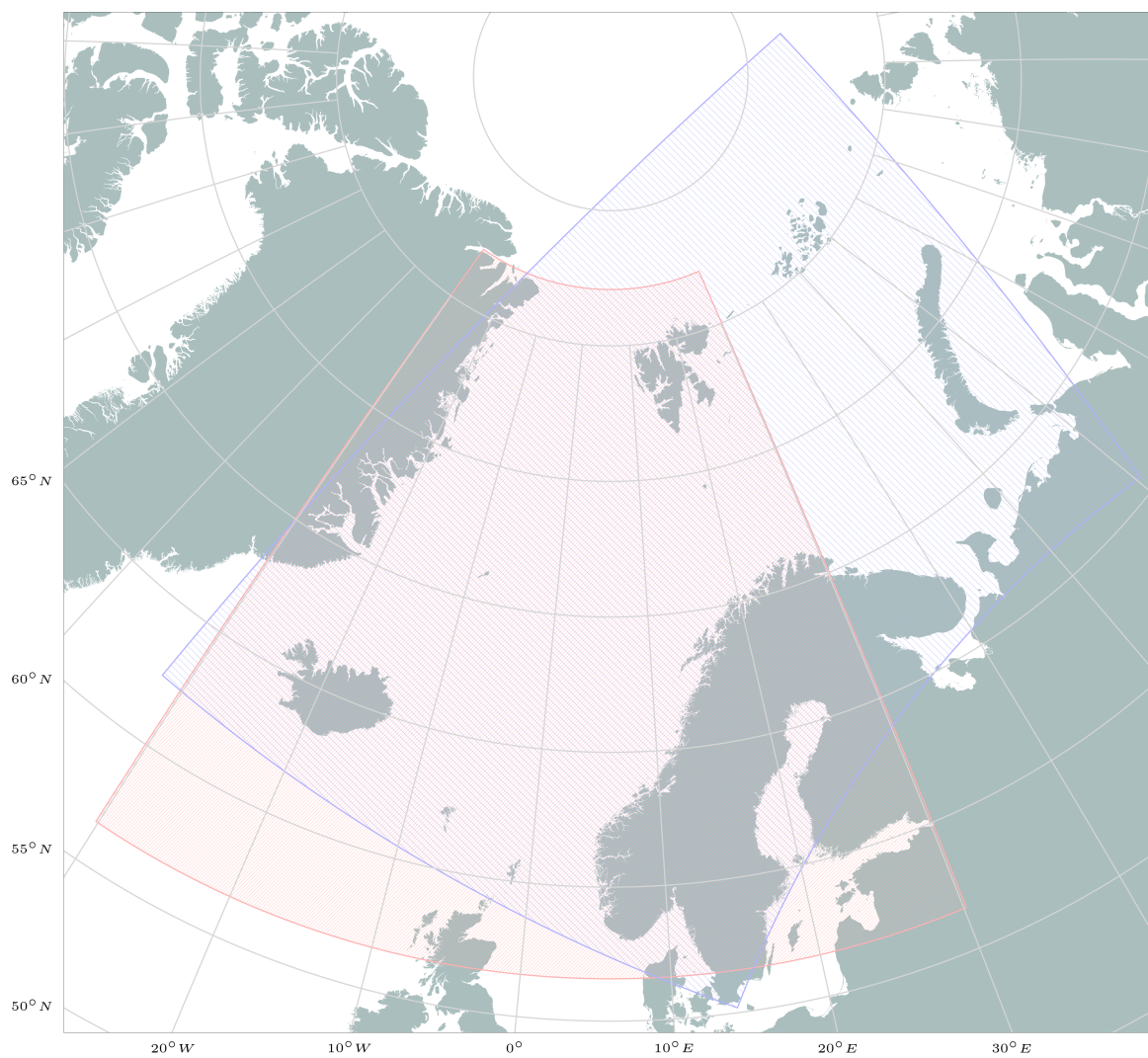


Figure 1.1: NORWECOM model grid areas. Rectangular NORWECOM.E2E grid area used by [Utne and Huse \(2012\)](#) (red-hatched area) and NORWECOM.E2E polar stereographic grid area used for recent developments (blue-hatched area).

1.2 Overview

The Nordic Seas are characterized by strong surface current systems that move large volumes of water - the most prominent being the East Greenland Current (EGC) and the Norwegian Coastal Current (NCC) that is encompassed in the Norwegian Atlantic Current (NwAC). The EGC transports roughly 3 Sv in surface flows, originating along the northern coast of Greenland flowing south with speeds between 20 cm s^{-1} and 30 cm s^{-1} through the Denmark Strait (Foldvik *et al.*, 1988). On the eastern boundary of the Nordic Seas, the NCC transports 1.8 Sv northward along the Norwegian coast from the Atlantic water introduced along the southern Norwegian coast and the Faroe-Shetland ridge, moving at a mean annual speed of 34.1 cm s^{-1} in the surface layer (Skagseth *et al.*, 2011). West of the NCC, smaller mean annual velocities have been observed in the NwAC, between 17.6 cm s^{-1} and 23.2 cm s^{-1} (Orvik *et al.*, 2001), moving predominantly northward. The entire current system of this area can be seen in Figure 1.2 from the modeling study of Skogen *et al.* (2007).

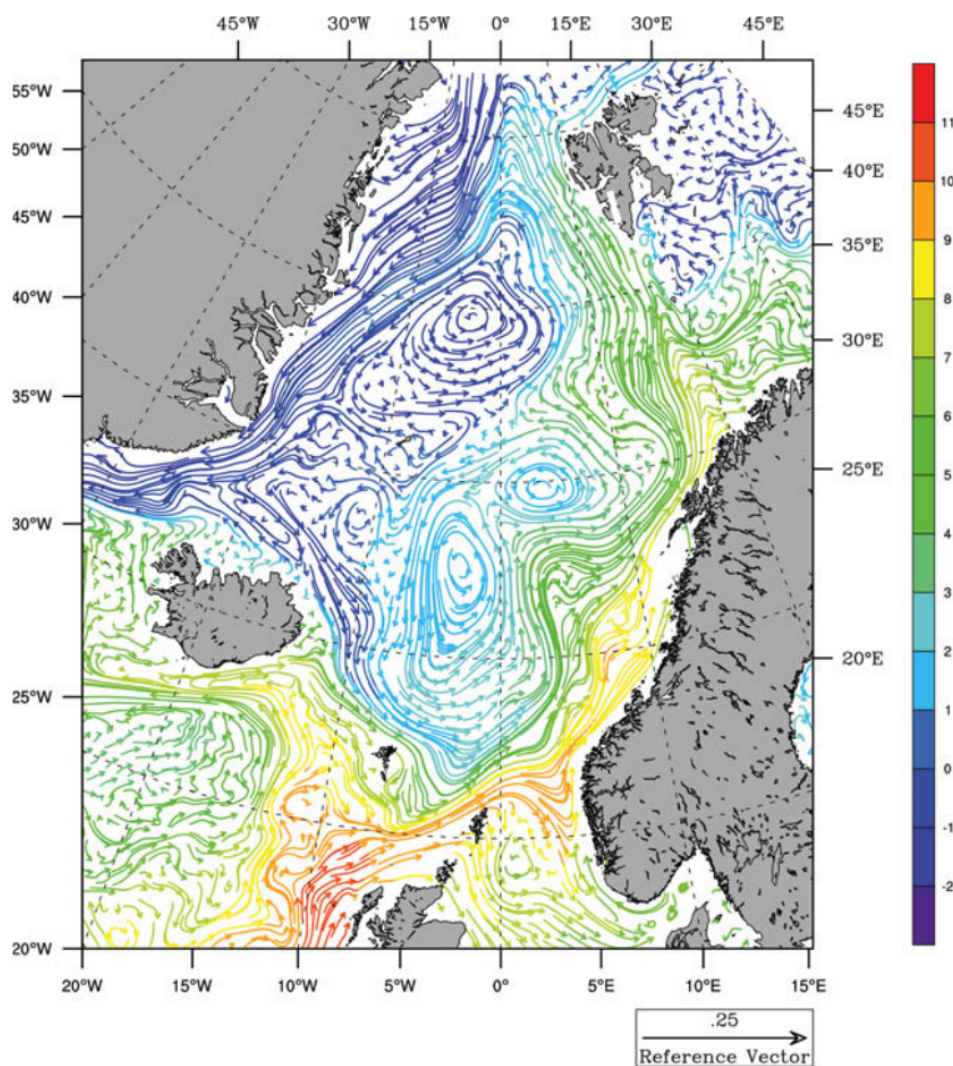


Figure 1.2: NORWECOM modeled mean temperature and currents between December and March, 1995 at a depth of 20 m (Skogen *et al.*, 2007). This year experienced a high NAO index, as was experienced in 1998.

In a study by Heide-Jorgensen *et al.* (2001), two minke whales were marked with satellite tags for a combined total of 78 days. The maximum mean travel speed for one whale was 3.2 km h^{-1} (approximately 88.9 cm s^{-1}), which is over 250 % of the annual mean velocity the NCC reported by Skagseth *et al.* (2011), and it is nearly 300 % of the maximum velocity of the EGC (Foldvik *et al.*, 1988). This is approximately the same swimming speed found by Blix and Folkow (1995) using radio transmitters and visual observations of dive times to be metabolically optimal for minke whales.

While some minkes are believed to migrate, any migration paths that might be used by them can only be inferred through knowledge of the above current systems and static observations made by sightings. Management areas determined by the International Whaling Commission, shown in Figure 1.3, have been surveyed at regular intervals since 1993 (Bøthun *et al.*, 2009; Skaug *et al.*, 2004). These surveys have illustrated a wide pelagic distribution, apart from aggregation at known feeding areas like fronts and shelf slopes (Doniol-

Valcroze *et al.*, 2007; Skern-Mauritzen *et al.*, 2011). The timing of these possible migrations is also unknown, but has been estimated to be approximately between April and October based on observations of increased stranding numbers in the British Isles (Evans, 1993; Pierce *et al.*, 2004), which is assumed to be the migration period in the bioenergetic study by Blix and Folkow (1995).

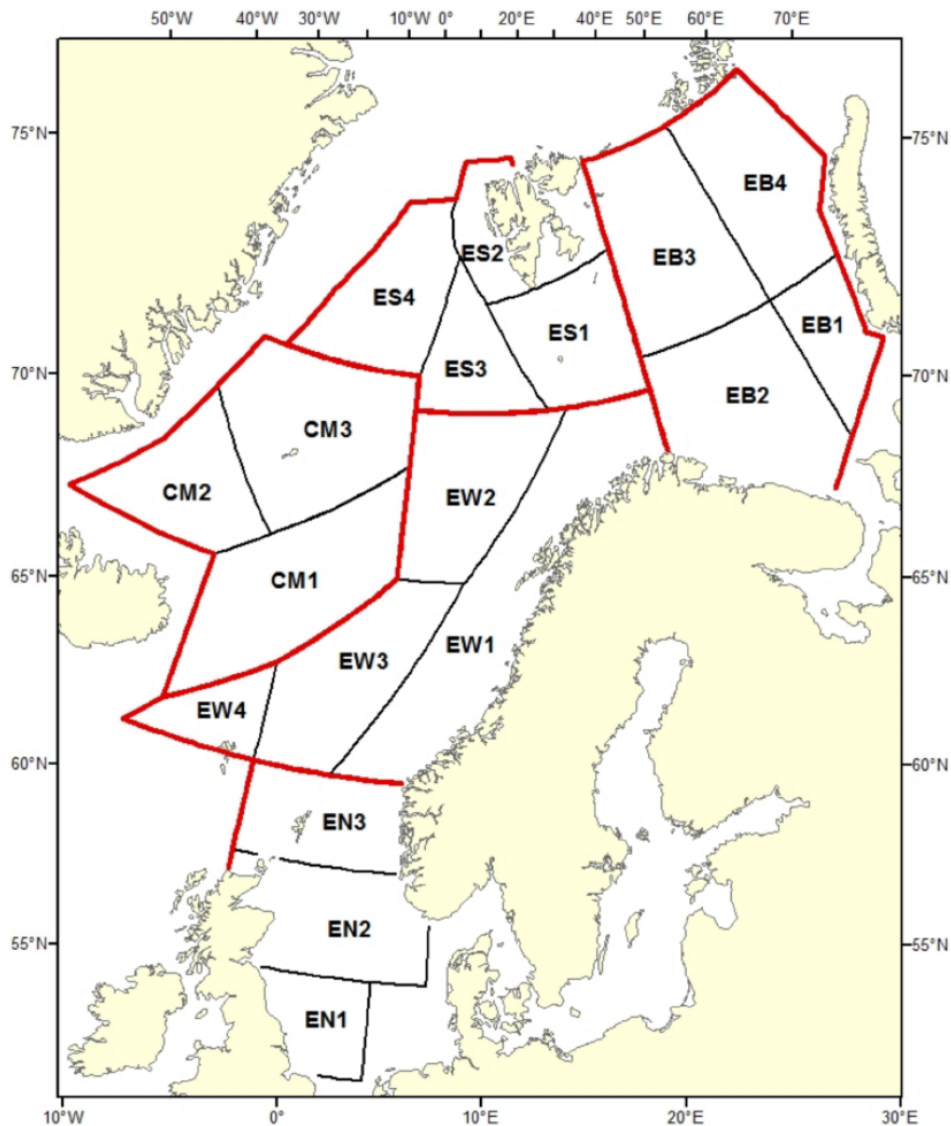


Figure 1.3: Small Management Areas with subdivided block structure developed during the 2008-2013 Norwegian sightings survey cycle (Øien, 2013)

This pelagic distribution of minke whales across the Nordic Seas could be the result of migration, foraging, or some combination of the two. It is a common assumption in modeling studies of marine predators that their movements are some form of a random walk strategy, like Correlated Random Walk and Lévy flight movements (Austin *et al.*, 2004; Papastamatiou *et al.*, 2013), but large movements of whales to and from feeding areas are often direct with routes exhibiting a consistent pattern (Horton *et al.*, 2011; Silva *et al.*, 2013).

However minke whales arrive at feeding areas, localized foraging behavior of minke whales has been better observed. Piatt and Methven (1992) have described minke

whales in Witless Bay, Newfoundland, Canada to display a significant threshold foraging response behavior when preying on capelin (*Mallotus villosus*), abandoning their prey efforts when density of their prey fell below a threshold level (proposed to be between 100 m to 1000 m by [Friedlaender et al., 2009](#)). Known as predator-prey interaction stability, where preying pressure is equal to prey availability, it is found to improve when prey densities are at levels where the response of the predator is near its threshold of pursuing or leaving its prey and when prey distribution is more aggregated ([Hassell and May, 1974](#)). This predictive behavior could potentially be used by minke whales in combination with migratory movements to areas of higher productivity, as has been seen in other baleen whales ([Silva et al., 2013](#)).

In this study, a minke IBM is developed to extend the NORWECOM.E2E model with an important marine predator in the Nordic Seas and Barents Sea ecosystems and to have a spatially-explicit IBM that may be used to investigate the large-scale movement behaviors of minke whales, otherwise not possible with a trophic mass-balance focussed ecosystem model. The questions that will be investigated in this study include: (1) if migrating in the direction of predominant ocean circulation patterns in the Nordic Seas is rewarding for the North Atlantic common minke whale, and (2) if it is energetically advantageous for minke whales to combine migratory movement with periodic searches for highest prey density compared to strategies that incorporate only random-walk foraging, strictly migratory movement, or random-walk movement with periodic maximum prey density searching.

Chapter 2

Methodology

2.1 NORWECOM

The minke IBM is developed within the NORWECOM.E2E modularized model framework. This IBM does not have feedback into NORWECOM.E2E via predation of whales on their prey field, as the only validated pelagic fish data are available from a previous development of NORWECOM.E2E (Utne and Huse, 2012) and are loaded as static prey fields. These data are loaded after having been re-gridded to the polar stereographic grid system (described below) used by the current development of NORWECOM.E2E and the minke IBM developed in this study. The minke IBM performs movements of the whales with each NORWECOM.E2E day-step after the physical forcing is loaded and the chemical and lower-trophic biological modules have been run. Besides providing the framework to run the minke IBM, the only NORWECOM.E2E process that affects minkes is their movement by ocean circulation at the end of each day-step (Figure 2.1). The prey fishes reproduction, mortality, bioenergetic processes, and movement by ocean circulation are reflected in their daily change in biomass and position, which are output from the previous NORWECOM.E2E development simulation that incorporated these processes. For a flowchart of module interactions in the NORWECOM.E2E framework, including the minke IBM module, see Appendix 6.A.1.

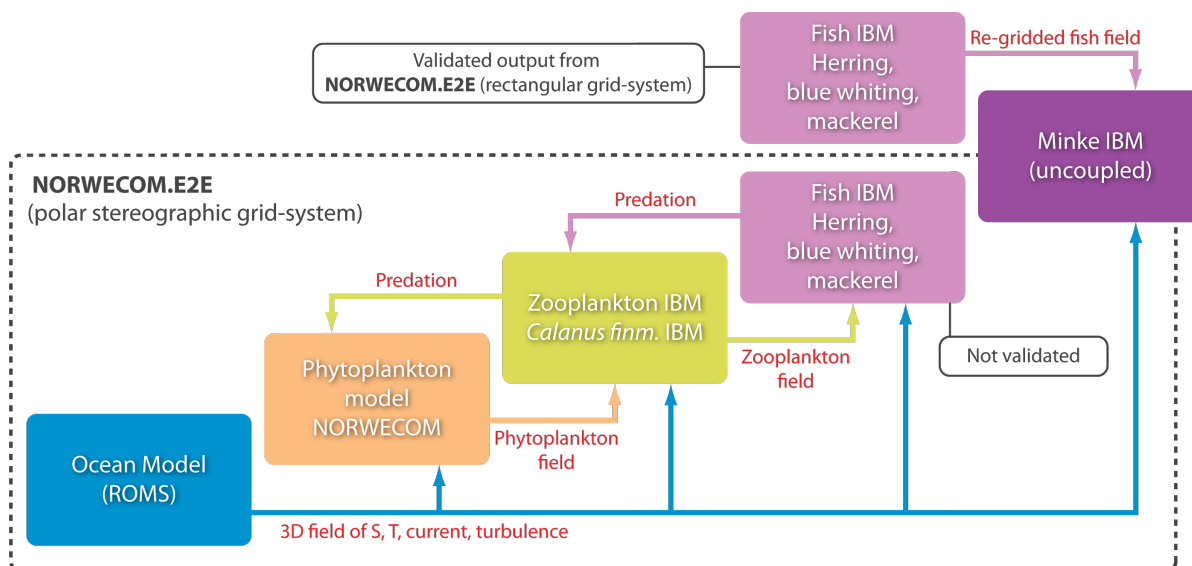


Figure 2.1: NORWECOM.E2E environment with minke IBM module and static prey field loading (adapted from Hjøllø *et al.*, 2012)

2.2 Minke IBM

2.2.1 Assumptions

With the prey fields imported to NORWECOM.E2E and unable to be depleted, the whales' bioenergetic response to preying has been simplified by assuming the same energetic requirement, consumption, and speed for the entire whale population. The daily energetic requirement of minkes described by Blix and Folkow (1995) of $80 \text{ kJ kg}^{-1} \text{ d}^{-1}$ is used, assuming a mean population weight of $4000 \text{ kg whale}^{-1}$. Stomach capacity of each whale is set to the mean capacity of all age groups (189.1 kg) reported by Tamura and Konishi (2014). The point value for swimming speed of adult minkes of 2.7 km h^{-1} is used for both migratory and foraging swimming speeds, which is consistent with observations of minkes exhibiting both behaviors (Heide-Jorgensen *et al.*, 2001). Mean energy content of NSS herring (6.2 kJ kg^{-1}) and blue whiting (4.2 kJ kg^{-1}) have been taken from their seasonal energetic values reported by Pedersen and Hislop (2001) for quarters 2, 3, and 4. With no energy content values available in the literature for NEA mackerel, the value for herring is used. Whales are assumed to move and feed at the surface (0 m). Competition between individuals is ignored, as are the interactions of other high-level predators, which are absent from the model.

2.2.2 Movement

For all simulations, whales enter and exit the model at a independently assigned dates, move within the grid area using a foraging strategy described below while encountering prey. The only attributes differing between whales

are their entry and exit dates (set at the start of the simulation), and the amount of fish they encounter.

Entry dates and exit dates are randomly generated within 5σ of a normally distributed date range, centered at 15 April for entry dates and 15 September for exit dates. The exit date is set one month earlier than their predicted exit date from the Nordic seas to account for the approximate 1 month travel time out of the model area (see section 1.2). Prior to each day-step, whales are activated if their entry day into the model is greater than or equal to the active simulation day, and they are deactivated if their return day has passed and have reached their exit position. If the whale is activated, their position and biomass of each prey encountered is written to file before the whales are moved for the active simulation day. See Figure 2.2 for a diagram of the minke IBM's general sequence for one whale over a day-step and Appendix 6.A.1 for the general movement routine that calls all foraging strategies.

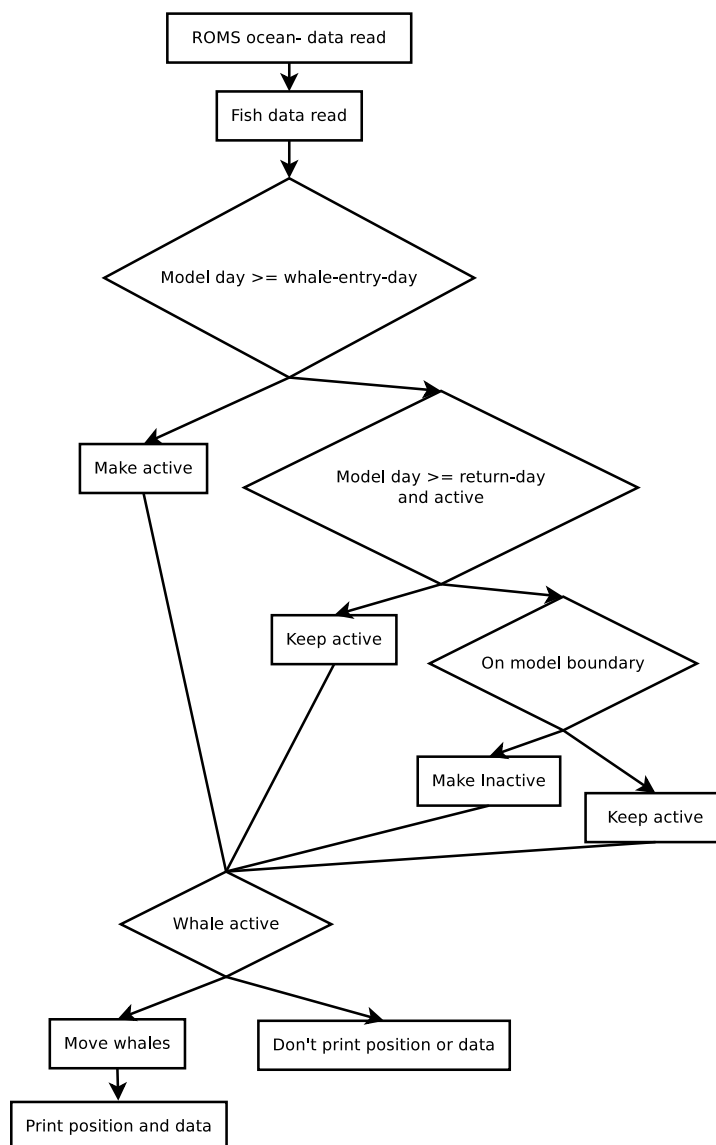


Figure 2.2: General minke IBM model process flow-chart.

For all strategies, whales are stepped in increments of 15 km (D_{step}) toward their destination position until the maximum daily travel distance has been reached. This distance is used to prevent issues with movement onto land and out of the grid area by the whales, and it is set to be within the minimum vertical and horizontal resolution of all grid-cells in the grid (approximately 16 km). All whales are initialized with the same speed and are thus assumed to have the same maximum distance for movement in a 24 h day-step period of 64 km. For all simulations, this is the maximum distance the whales are permitted to move in a single day-step (D_{max}).

The distance to the destination position (determined by the strategy in use) is the magnitude of the vector between the current position and the destination position, which is found by the difference in latitude and longitude between the two positions. These differences are converted to meters at the latitude of the current position (Equation 2.1):

$$Q_{lat} = \left(\frac{60'_{lat}}{1^\circ_{lat}} \right) \left(\frac{1852m}{1^\circ_{lat}} \right) \quad (2.1)$$

$$Q_{lon} = \left(\frac{60'_{lon}}{1^\circ_{lon}} \right) \left(\frac{1852m}{1^\circ_{lon}} \right) \cos(\theta_{lat}) \quad (2.2)$$

Q_{lat}	Ratio of meters to 1°latitude ($m1^\circ_{lat-1}$)
Q_{lon}	Ratio of meters to 1°longitude ($m1^\circ_{lon-1}$)
θ_{lat}	Current latitude of whale ($^\circ_{lat}$)

Whales are moved incrementally by D_{step} until D_{max} is reached. The distance to the destination position is checked before each step, and if less than the D_{step} , they are then moved the remaining distance to the destination. Randomness in each movement is generated by adding a random distance component between -15 km and 15 km (i.e. $\pm D_{step}$) multiplied by a factoring variable (R_{mov}) used to control the degree of randomness in the movement. An R_{mov} value of 0.0 results in direct movement between the origin and destination positions. With increasing R_{mov} , longitudinal and latitudinal variation around the destination position is produced, which results in dispersion and movement distances that may be less than D_{max} . The general movement calculation is shown in (Equation 2.3):

$$\Delta D_{lon} = Q_{lon} |Lon_2 - Lon_1| \quad (2.3)$$

$$\Delta D_{lat} = Q_{lon} |Lat_2 - Lat_1| \quad (2.4)$$

$$D_{dest} = \sqrt{(\Delta D_{lon})^2 + (\Delta D_{lat})^2} \quad (2.5)$$

$$\Delta D_{lon-mov} = \Delta D_{lon} \left(\frac{D_{mov}}{D_{dest}} \right) + D_{rand} R_{mov} \quad (2.6)$$

$$\Delta D_{lat-mov} = \Delta D_{lat} \left(\frac{D_{mov}}{D_{dest}} \right) + D_{rand} R_{mov} \quad (2.7)$$

ΔD_{lon}	Longitudinal distance between current and destination position (m)
ΔD_{lat}	Latitudinal distance between current and destination position (m)
Lon_1	Longitude of current position ($^{\circ}lon$)
Lon_2	Longitude of destination position ($^{\circ}lon$)
Lat_1	Latitude of current position ($^{\circ}lat$)
Lat_2	Latitude of destination position ($^{\circ}lat$)
D_{rand}	Randomly generated distance to move (m)
R_{mov}	Assigned randomness factor
D_{mov}	Movement step distance or distance remaining to destination (m)
D_{dest}	Distance from origin to destination position (m)
$\Delta D_{lon-mov}$	Longitudinal distance from current and next position (m)
$\Delta D_{lat-mov}$	Latitudinal distance from current and next position (m)

The whales' destination positions are determined at the start of each day-step by one of the foraging strategies described below. For each simulation, one foraging strategy is assigned to the entire population. If moving to a randomly selected position or maximum fish density position the whale stops once this position is reached, whether or not D_{max} has been reached. At the end of the whales movement, whales are moved by the modeled hydrography if it has been enabled for that simulation.

Once a whale is at their destination position for the active day, the surface current velocity from the grid-cell containing the their origin position is used to move them via the currents. This is done through use of an existing NORWECOM routine. The biomass of any prey species present in the cell containing the whale's final position are recorded.

To avoid difficulties experienced with the movement of whales to a position off the grid during a simulation, an offset buffer of 5 grid-cells set around the perimeter of the grid is used to confine their movement (red dashed line shown on Figure 2.3B).

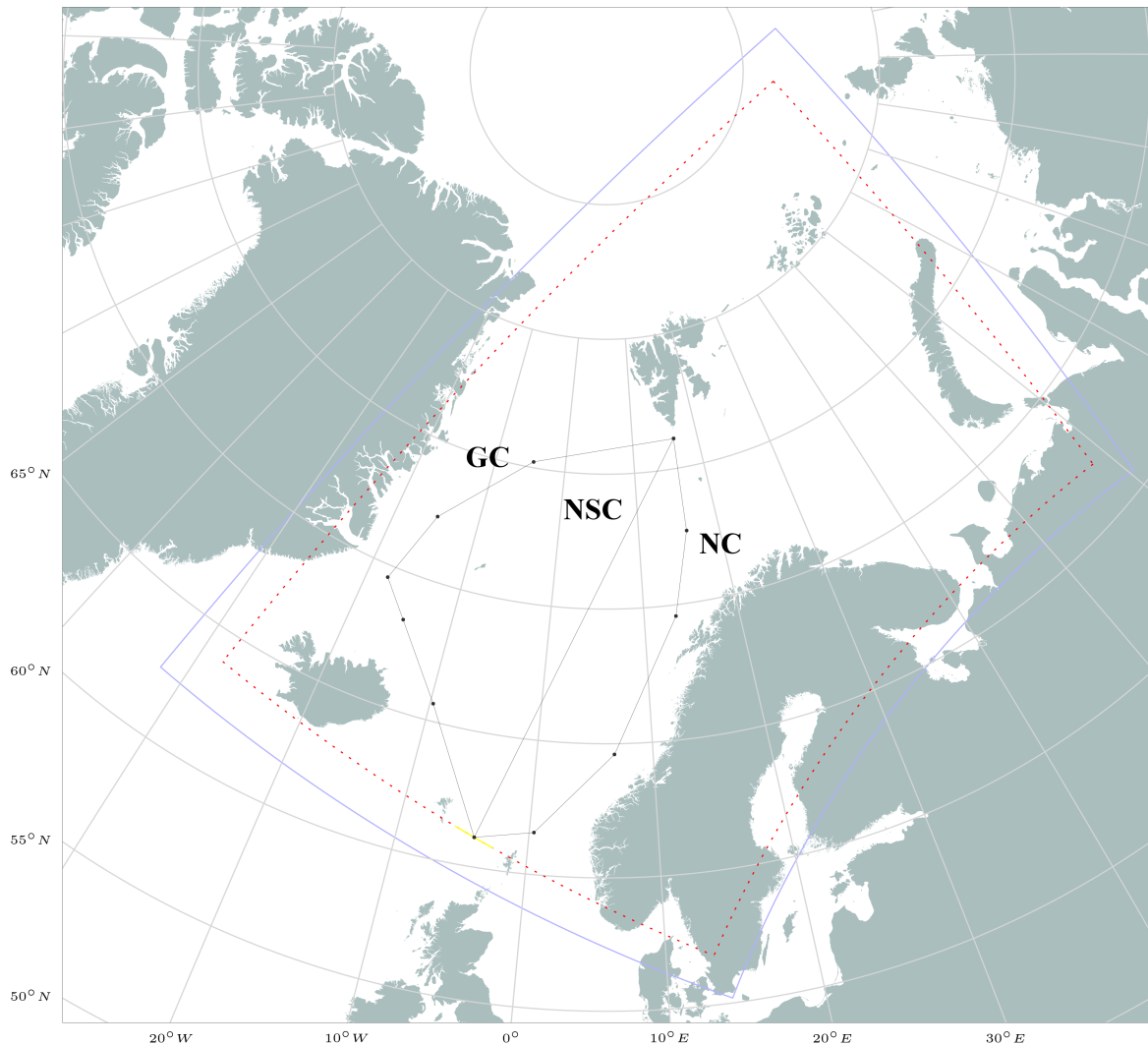


Figure 2.3: Minke IBM grid area and attributes. NORWECOM.E2E grid area (blue solid line) with minke whale movement offset area (red dashed line), whale entry and exit area (yellow solid line), IWC small management area for the Norwegian Sea (solid red polygon), and Minke IBM migration paths: Norwegian Sea Center (NSC), Norwegian Coast (NC), and Greenland Coast (GC).

2.2.2.1 Study Area

The modelling area is a truncation of the full NORWECOM.E2E polar stereographic grid, covering approximately 8.4×10^6 km² of the Nordic Seas region including the northern North Sea, Norwegian Sea, Barents Sea, Greenland Sea, Iceland Sea, and Irminger Sea (Figure 2.3). It ranges latitudinally between 86.84748°N and 55.29657°N and longitudinally between 31.77648°W and 109.93210°E. The grid corner-points are as follows: 109.93210°E, 83.64842°N; 31.77648°W, 62.55577°N; 60.26522°E, 65.71642°N; and 14.04101°E, 55.2966°N. This model region covers the key areas known to encompass the summer distribution of North Atlantic common minke whales.

2.2.2.2 Migration path selection

Three migratory paths are visually determined from the visualization of the modeled Nordic Seas current system by [Skogen *et al.* \(2007\)](#) for the year 1996, which has a similar North Atlantic Oscillation index ([Rigor *et al.*, 2002](#)) and can be expected to have a similar seasonal current system ([Skogen *et al.*, 2007](#)). The paths selected for migration into and out of the model area are as follows: the Norwegian Sea center (NSC), the Norwegian coast (NC), and the Greenland coast (GC). An adequate number of geodesic positions are taken from areas within these general regions to allow the path to lie within areas of highest velocity having 1 and 6 waypoint positions (Figure 2.3B).

Unique positions for entering and exiting the grid areas are randomly generated for each whale at model runtime along the entry and exit boundary, between -6.5°W and -2.5°W , in the region of the Faroe-Shetland ridge boundary, (Figure 2.3B). All in-migration paths terminate at the same arbitrarily chosen position in the vicinity of known feeding areas around Bear Island, Spitsbergen ($76.10399277^{\circ}\text{N}$, $16.34683488^{\circ}\text{E}$), ([Skaug *et al.*, 2004](#)).

2.2.2.3 Homing

While using the homing (HM) strategy whales are moved D_{max} along the migration path waypoints. With each step towards the destination position (i.e. the next waypoint), the proximity of the whale's present position is checked to see if it is within 0.1 grid-cell-width (approximately 1.5 m) of the destination waypoint. If within this distance, the destination is updated to the next waypoint in the migration path array, and the whale's movement is stopped for that day-step.

If the simulation date is greater than or equal to a whale's return date, the homing array is updated from in-path waypoints to out-path waypoints. The updating of homing positions is performed at the start of each day-step regardless of the foraging strategy, as all strategies will switch to homing once the whale's return date is reached in order to move them from the model area. If a whale's current position is south of the next return waypoint, its next homing position is updated to the nearest waypoint position south of its current position. Figure 2.4 shows the sequence of model events for the HM strategy, with the model code presented in Appendix 6.A.1.

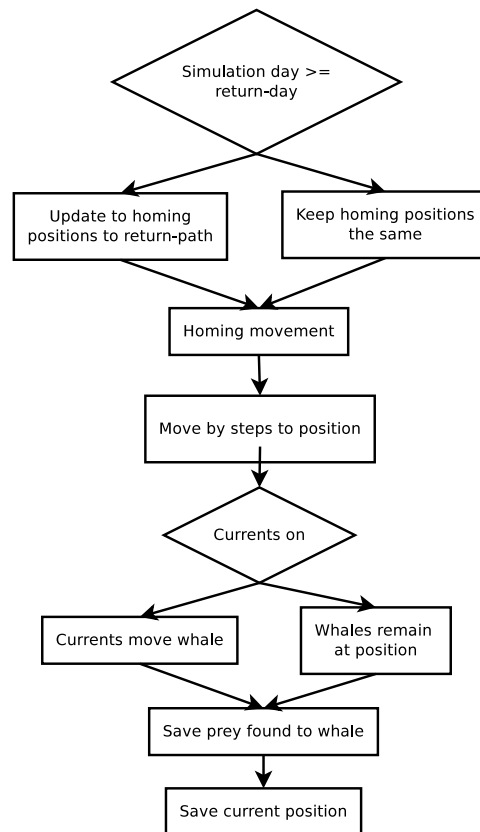


Figure 2.4: Homing (HM) strategy process flowchart.

2.2.2.4 Random-walk

The random-walk (**RW**) foraging routine selects a random destination position at the start of each day-step for the whale to move towards, in the step increments described above, until D_{max} is reached. From the whale's origin position, a position is randomly selected within 5 grid-cell positions from the origin position. Once selected, the position is checked to be within the grid-offset boundary. If it is not within the grid-offset, another position is selected until a valid position is found.

Once the active simulation day is the randomly generated for a whales to begin its return migration, the whales begins using the HM strategy and moves toward their next out-path homing waypoint, with the final point being their exit location. Figure 2.5 shows the sequence of model events for the RW strategy, with the model code presented in Appendix 6.A.1.

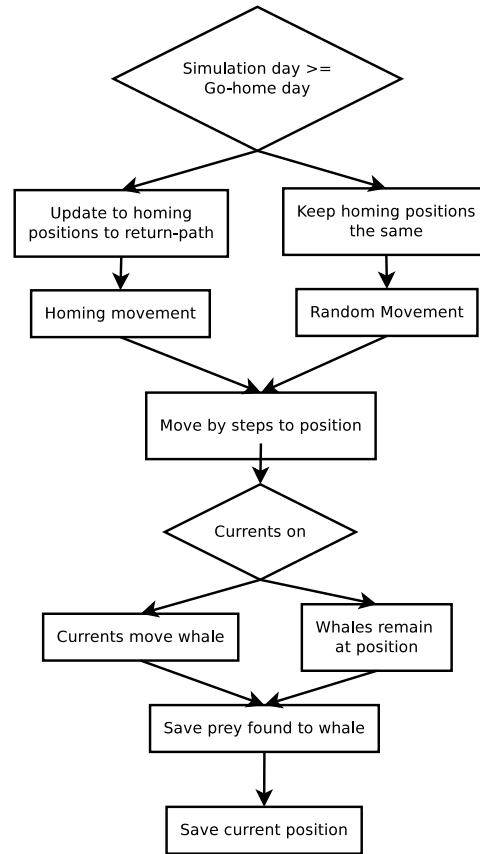


Figure 2.5: Random (RM) strategy process flowchart.

2.2.2.5 Maximum fish density searching

The maximum prey density search (MPDS) foraging strategy searches the whales prey detection area (all adjacent cells within 1 grid-cell from the present position) for the cell with the maximum biomass of their preferred prey, moving the whales toward the center of the grid-cell with the highest density. This detection area is larger than the 1000 m detection radius suggested by [Friedlaender *et al.* \(2009\)](#), as the grid resolution and prey biomass distribution, being evenly distributed over the grid-cell, do not allow for searching to be performed within such a detection limit. The maximum number of feeding days of the whales (d_{fmax}) is parameterized to restrict them to a limited feeding period before they travel via the RW or HM strategy.

At model run-time whales are initialized with a number of days they have been on feeding (d_{feed}) and a number of days they have traveled between feedings (d_{trav}), both of which are initialized at model run-time to 0.0 for all whales in the population. When prey is detected in a whale's detection field, it moves to the center of the grid-cell with the maximum prey-density, and d_{feed} is increased by one. Whales are moved to the maximum densities in the order of preferred prey. For example, if all prey are detected in the detection area, the whale is moved to the location of the first prey preference. If only the second and third prey preferences are present, the whale will be moved to the second

prey preference grid-cell-center. Once d_{fmax} maximum is reached, or there are no fish found by the end of one day-step (and a series of movement-steps), the whales move by the assigned movement routine for that simulation, and the travel period value is increased by one.

The whales are considered to be “well fed” when d_{fmax} is reached and the d_{tmax} has not yet been reached. The MPDS density search movement first checks that the whales are well fed at the start of each day-step. If well fed, the whale is moves via RW or HM as described above. If not well fed, the detection area is evaluated for presence of prey within its prey detection field.

While the whale is not well fed, and no prey is detected, the whale will be stepped towards the randomly selected position or next homing position until D_{max} is reached. At the start of each step, the whale will search the detection area for prey presence. Figure 6.1 shows the sequence of model events for the MPDS-R and MPDS-H strategies, with the model code presented in Appendix 6.A.1.

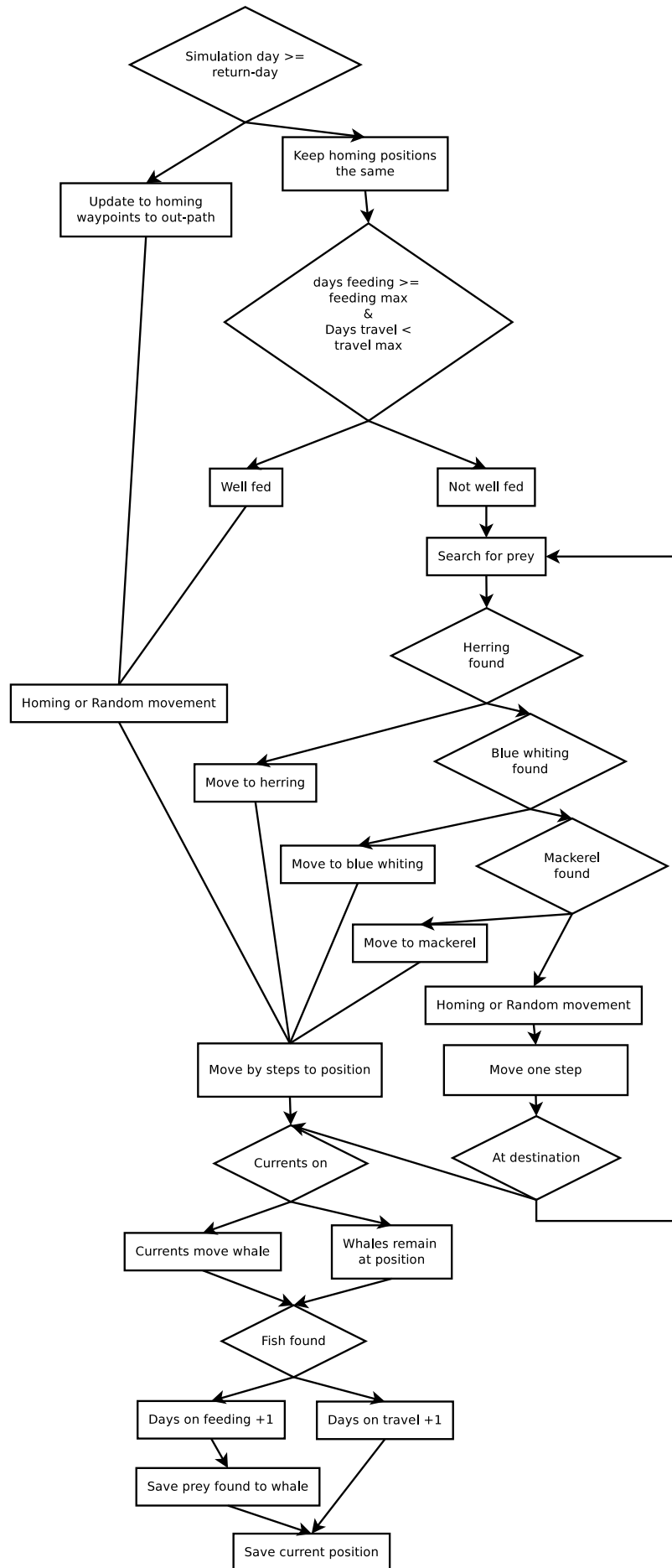


Figure 2.6: Maximum prey density search (MPDS) strategy process flowchart.

2.3 Prey field pre-processing

The recent developments of the NSS herring, blue whiting, and NEA mackerel IBMs have not been validated, so model output will be used from the study by [Utne and Huse \(2012\)](#), which has been validated and used a rectangular grid system. As the new development of NORWECOM.E2E uses a polar stereographic grid system, this output will be re-gridded and used as static prey fields, meaning there will be no effect of prey depletion from predation on the prey field. The originating rectangular grid system has a horizontal resolution that is much greater between latitudes (5 km and 20 km, approximately) than the newer polar stereographic grid system (between 16 km and 25 km, approximately), (Figure 2.3A). For each of prey species in the year 1998, the rectangular gridded values of total number of fish per grid-cell are re-gridded to a corresponding polar stereographic grid-cell with the smallest calculated distance from the originating cell's position. Distances are calculated using the inverse transformation method of the *pyproj.Geod* library (version 1.9.3) ([Whitaker, 2014](#)).

These values of total fish per grid-cell (fish cell⁻¹) are then converted to units of biomass per grid-cell (kg cell⁻¹). Biomass per unit area is derived by multiplying the fish number per unit area by the average weight for the fish species and the ratio between the area of the originating grid-cell and the area of the nearest polar stereographic grid-cell (Equation 2.8). Weighted averages of adult size classes for the associated simulation year are used for NSS herring (0.222 171 kg), blue whiting (0.074 574 kg), and NEA herring (0.233 105 kg) from annual survey data by the Havforskningssinstituttet (herring and blue whiting, [ICES, 2007b](#); mackerel, [ICES, 2007a](#)).

$$B_{e2e} = N_{species} W_{species} \left(\frac{A_{e2e}}{A_{2010}} \right) \quad (2.8)$$

B_{e2e}	NORWECOM.E2E gridded biomass (kgm^2)
$N_{species}$	Number of fish per NORWECOM 2010 grid cell (<i>fishnumber</i>)
$W_{species}$	Weight of fish species being re-gridded (kg)
A_{e2e}	Area of destination NORWECOM.E2E grid cell (m^2)
A_{2010}	Area of origin NORWECOM 2010 grid cell (m^2)

The re-gridded data for all prey species vary temporally in their distribution and density for the year 1998 (Figures 2.7- 2.9).

At the beginning of April, herring are distributed off the Norwegian coast roughly between 60° N and 65° N, with an approximate longitudinal spread of 10°, and a maximum biomass-density of $1.02838 \times 10^5 \text{ kg m}^{-2}$ north of 65° N and east of 10° W. The area of distribution extends in area in July (with density decreasing) and position moving both northward and westward with a linear boundary appearing at its northwestern border (approximately from 70° N to 80° N and 10° W to 10° E). Densities increased along this border in August, with a large portion of the biomass returning to an overwintering location near the Norwegian coast in September. By November, the distribution is contracting tightly to coastal overwintering locations between 67° N and 70° N, approximately, with a maximum density of $2.834723 \times 10^6 \text{ kg cell}^{-1}$.

Blue whiting is more widely distributed than herring at the start of April, with two large aggregations, spanning approximately from 60° to 70° N and 10° W to 20° E, with a density of $2.1344 \times 10^4 \text{ kg/m}^2$ at the most densely populated cell. In May, the density aggregates are along a thin front in the southern region of its April distribution, increasing in density to $4.8685 \times 10^4 \text{ kg m}^{-2}$. They expand again in June and July, with portions of the population beginning to aggregate near the Norwegian coast. Densities begin increasing in September at coastal overwintering locations near 65° N and 10° E, with a maximum of $9.5333 \times 10^4 \text{ kg cell}^{-1}$ reached by November.

Mackerel are not distributed in the Nordic Seas until the beginning of July, covering a much smaller longitudinal area compared to herring and blue whiting, from approximately 5° W to 5° E and 63° N to 67°, and they had a density maximum of $1.11230 \times 10^5 \text{ kg cell}^{-1}$. Their distribution extends to 70° N in August before expanding and moving just north of 60°N in September. In October, the distribution latitudinally flattened between, 60° N and 63° N, and it expands between 20° W and 15° E, approximately. The maximum local density is seen in October at $1.78458 \text{ kg cell}^{-1}$.

The overlap of the distributions (primarily herring and blue whiting) occurs primarily between 0° longitude to 20° E and 65° N to 70°. From May to September, the distribution of herring extends exclusively beyond the overlap area to the north and west and to the east along the southern Norwegian coast. Blue whiting is distributed beyond the overlap area for the duration of the simulation to the south and east from 0° longitude to the southern Icelandic coast.

With all fish distributions, the boundary areas of fish distributions appear scattered with presence of fish transient and dispersed. Throughout the distributions, there are select cells that remain absent of fish for the duration of the simulations at varying latitudes and longitudes (Figures 2.7- 2.10).

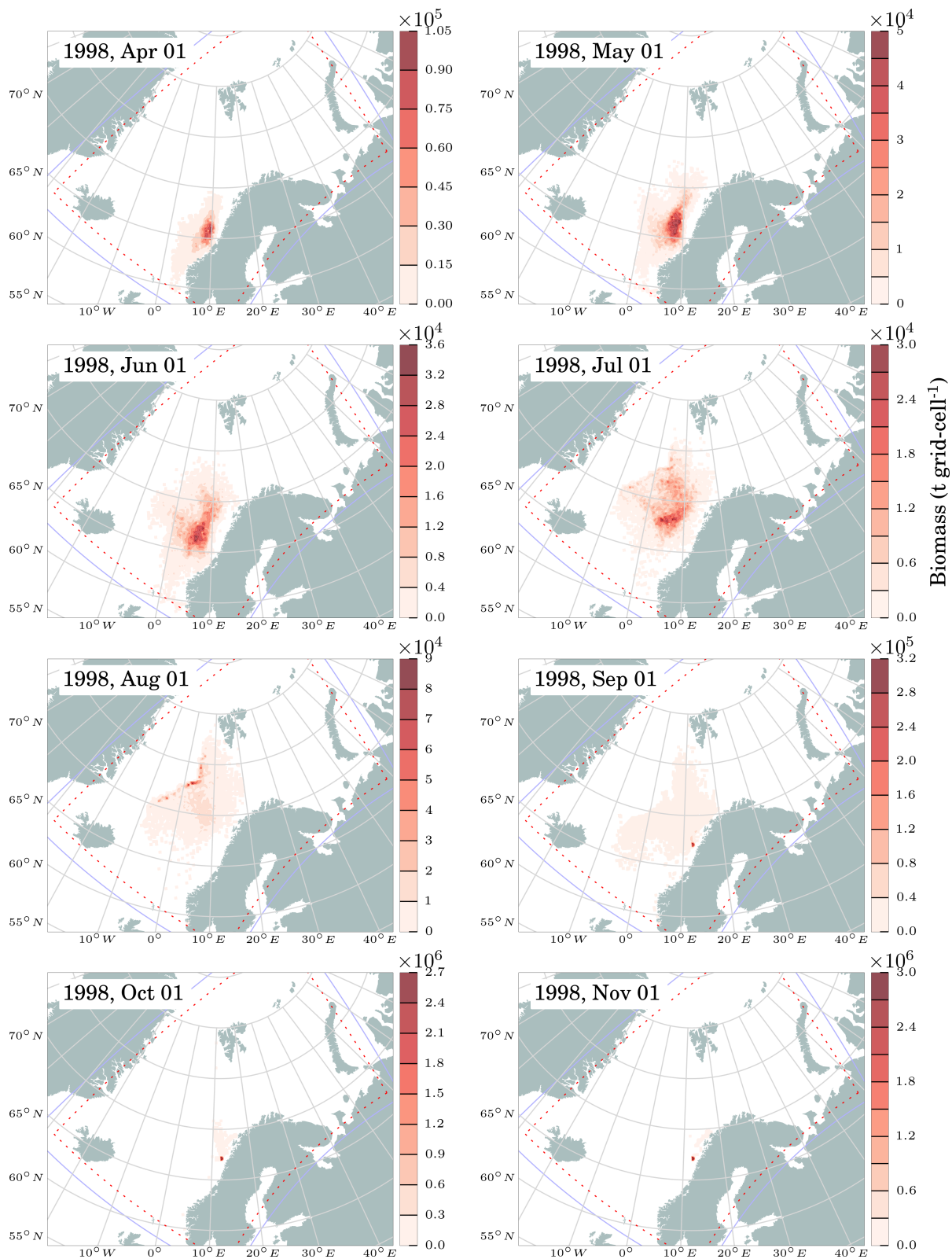


Figure 2.7: Average biomass densities of herring for the year 1998, reprojected from output of the NORWECOM 2010 rectangulargrid to the NORWECOM.E2E polar stereographic grid.

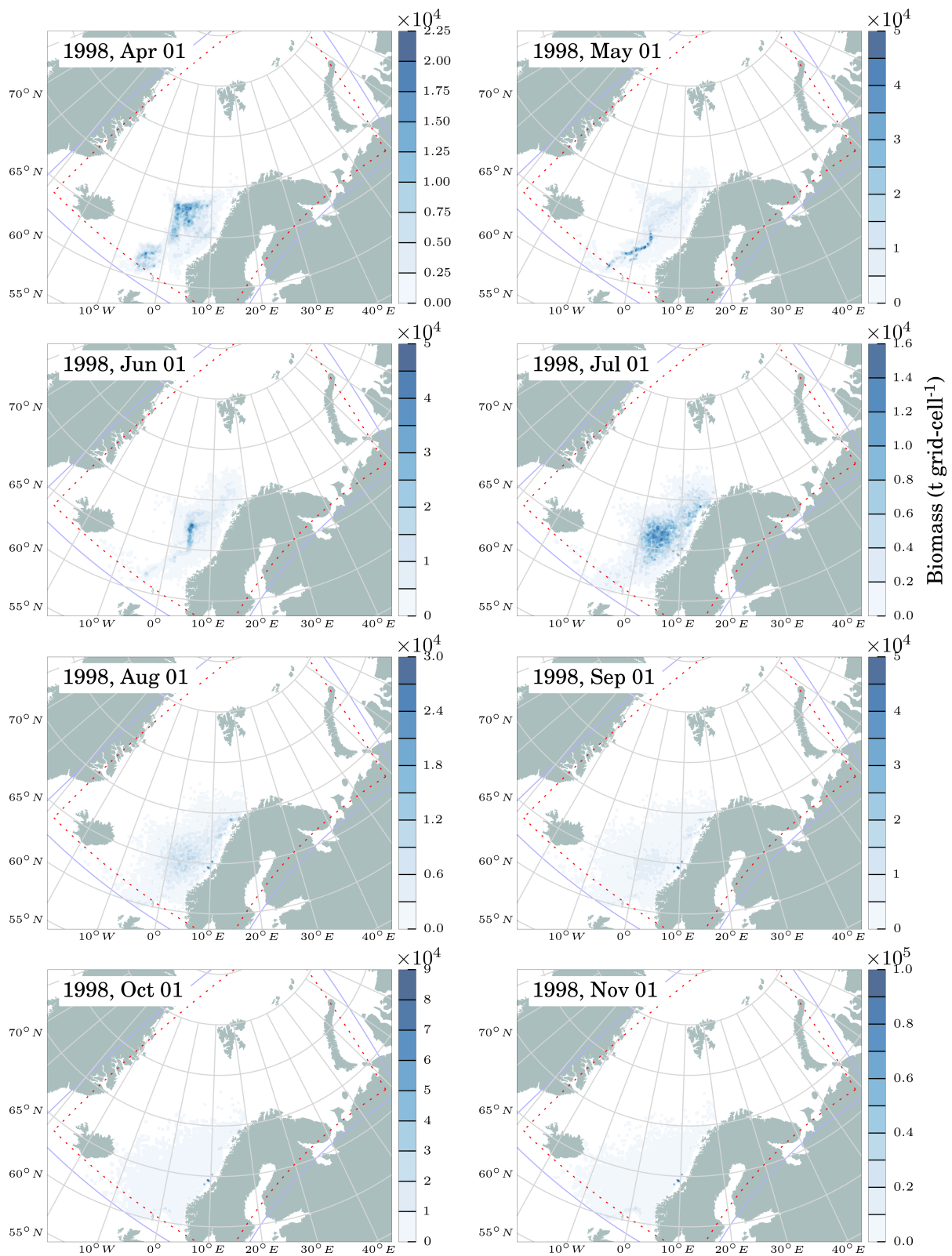


Figure 2.8: Average biomass densities of blue whiting for the year 1998, reprojected from output of the NORWECOM 2010 rectangulargrid to the NORWECOM.E2E polar stereographic grid.

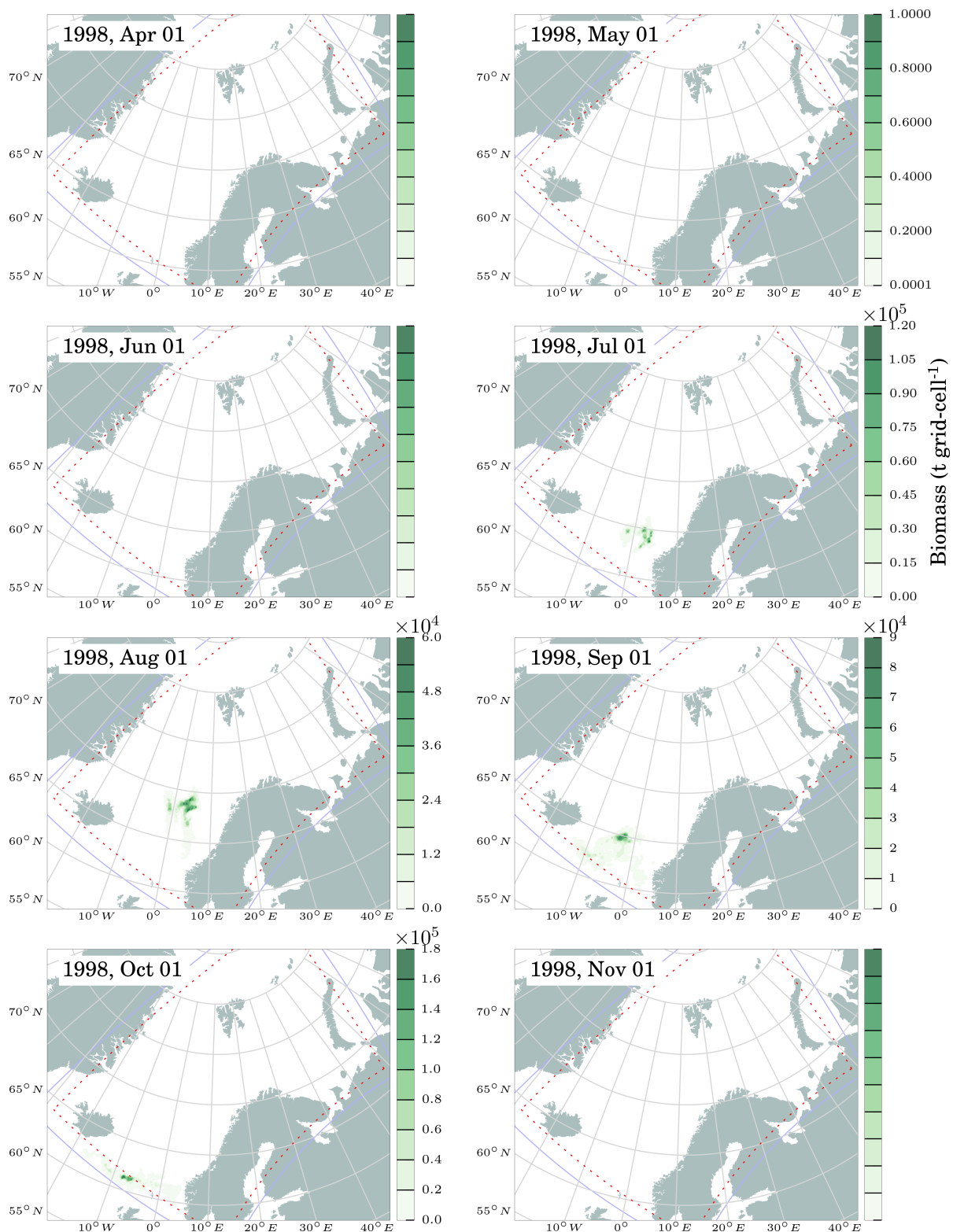


Figure 2.9: Average biomass densities of mackerel for the year 1998, reprojected from output of the NORWECOM 2010 rectangular grid to the NORWECOM.E2E polar stereographic grid.

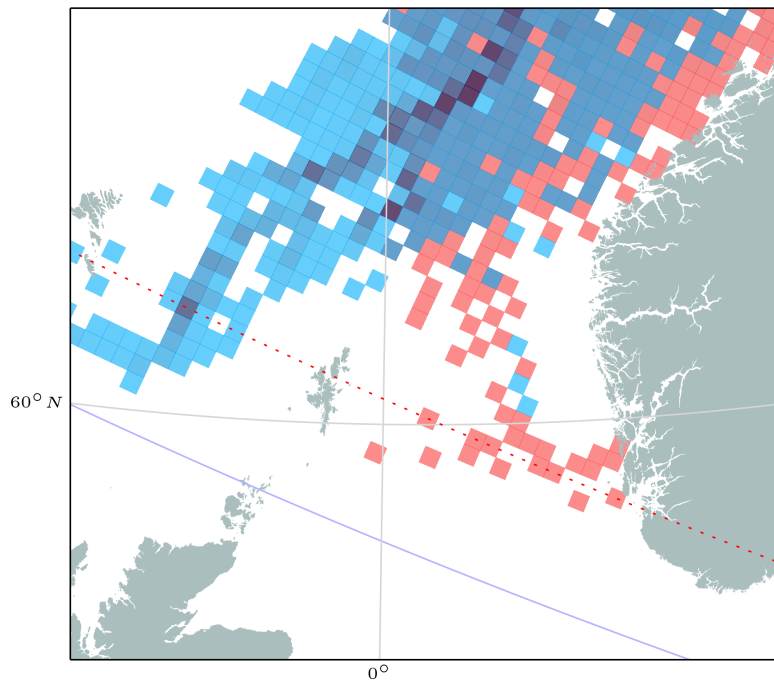


Figure 2.10: Gridded herring and blue whiting distributions near the southern Norwegian coast on 01 May, 1998. The light blue solid line marks the model grid area, with the red dashed line marking the offset boundary containing the whale movement. The relative densities of each species are shown in shades of red (herring) and blue (blue whiting).

2.4 Simulation data post-processing

2.4.1 Erroneous movement: Off-grid and landings

Without an intelligent path searching algorithm implemented to navigate around bodies of land, along with the large distances minke whales are capable of moving in a single day, it is possible for whales to cross land. In addition, the algorithms used in the NORWECOM.E2E model to transform geodesic coordinates to grid coordinates sometimes result in incorrect grid coordinates (i.e. off the model grid), causing a programmatic error. To prevent problems from moving off grid or analysis errors with whales that have moved over land, a flag is applied to each whale that experiences either, and it is removed from the model or analysis. A total of whales from the population who have landed or moved off-grid is recorded and is to be considered for interpretation of the results.

2.4.2 Migration-time, distance, and speed calculations

Individual whale migration times for each in-period and out-period are averaged to obtain a mean travel time for the population. The in-period is determined for each whale as the time between the day they entered the model and the day at which they have reached a position within 0.3° latitude and longitude (or nearer) to the feeding location off Bear Island. The exit migration is defined as being the period after a whale's return migration date and it is located 0.3° latitude and longitude (or further) away from the feeding location, lasting until the day they reach their exit position on the model boundary.

Using daily whale position output, values for change in position between day-steps are calculated for each whale, including movement by currents, using the *pyproj.Geod* library (version 1.9.3) ([Whitaker, 2014](#)) as described in the software documentation ([Whitaker, 2006](#)). Hourly speed of the whales (m h^{-1}) is then derived from this distance value by dividing the distance by 24 h. Daily speeds of all whales are averaged across both in and out-migration periods to give a mean speed of the population.

2.4.3 Encounter rate and foraging efficiency calculations

A prey encounter is considered to be a non-zero biomass value in the grid-cell containing each whale's final position during a day-step. There is a maximum of three possible encounters per day per whale if all three prey species are present in the cell containing their final position in a day-step. The sum of all encounters for each prey species is made, and it is divided by the total number of encounters to yield the percentage of total encounters for each of the prey species. The number of encounters per whale ($N_e \text{ whale}^{-1}$) is the ratio of the total number of encounters and the number of whales simulated (i.e. not landed or moved off-grid).

The foraging efficiency (Eff) of minke is determined to be the ratio of a derived value of energy intake to an assumed daily expenditure of energy. It is assumed that the whales will consume their full consumption capacity (189.1 kg) of their highest order preferred prey encountered. This weight is converted to units of energy (kJ) using Equation 2.9 through multiplying it by the average unit energy per unit weight of that species (kJ kg^{-1}). This value is then divided by the product of their daily energetic requirement ($80 \text{ kJ kg}^{-1} \text{ d}^{-1}$) and the assumed average minke weight ($4000 \text{ kg whale}^{-1}$) to yield the foraging efficiency (Equation 2.9). The mean of all whales' Eff values is taken to get the mean daily efficiency of the population (Eff_{pop}). When $Eff_{pop} = 1$, the populations energetic intake is equal to its energy requirement.

$$E_{cons} = V_{whale} E_{prey} W_{prey} \quad (2.9)$$

$$Eff_{whale} = \frac{E_{cons}}{(E_{req} W_{whale})} \quad (2.10)$$

$$Eff_{pop} = \frac{Eff_{whale_1} + \dots + Eff_{whale_n}}{n} \quad (2.11)$$

E_{cons}	Daily energy consumed by individual whale (kJ)
V_{whale}	Volume of consumption per whale (kg whale^{-1})
E_{prey}	Energy content of prey (kJ kg^{-1})
W_{prey}	Weight of whale (kg)
Eff_{whale}	Foraging efficiency of individual whale
E_{req}	Daily energy expenditure by individual whale ($\text{kJ whale}^{-1} \text{ kg}^{-1}$)
W_{whale}	Weight of whale (kg)
Eff_{pop}	Mean foraging efficiency of the population
n	Number of whales in population

2.5 Simulations

2.5.1 Overview

Simulations are performed using a representative population of 1000 whales and performed over daily time-steps for the year 1998. Fish prey fields for NSS herring, blue whiting, and NEA mackerel are pre-processed from the NORWECOM.E2E rectangular grid system to polar stereographic grid system on which the minke IBM has been implemented (see section 2.3). Only one prey preference ordering is used for the scope of this study: (1) NSS herring, (2) blue whiting, and (3) NEA mackerel. Herring is set to be the primary preferred prey as it has been commonly found to be the primary preference of minkes (Olsen and Holst, 2001). The ordering of blue whiting and herring is arbitrarily chosen. Swimming speed of all whales is set to a constant 2.7 km h^{-1} (see section 2.2.1).

The simulations are run in a sequence such that the results of each section are used to inform the next. First a population adequate in size to produce the smallest SEM for daily means of whale speed and foraging efficiency is determined. The effect of currents is assessed by running a simulation with the currents on and with the currents off. With the effect of currents decided, simulations with variations in the three pre-determined migration paths are run to determine the most plausible and rewarding path for migration and foraging. Then, simulations using the described foraging strategies are run, so that derived values of foraging efficiency may be compared. For a detailed summary of simulation parameterization, see Table 2.1.

Table 2.1: Simulation configurations. The following strategies are referred to: random-walk (**RW**), homing (**HM**), maximum prey density search with random-walk (**MPDS-R**), and with homing (**MPDS-H**). Migration paths used are the Norwegian Sea center (**NSC**), the Norwegian coast (**NC**), and the Greenland coast (**GC**). R_{mov} is the randomness in movement between origin and destination positions, and d_{fmax} is the maximum number of days whales may feed before traveling

	Simulation	Strategy	Population (N ^o whales)	In path	Out path	Currents	R_{mov}	d_{fmax} (days)
Population	1	HM	100	NC	NSC	on	0.0	2
	2	HM	1000	NC	NSC	on	0.0	2
	3	HM	10000	NC	NSC	on	0.0	2
Currents	2	HM	1000	NC	NSC	on	0.0	2
	4	HM	1000	NC	NSC	off	0.0	2
Migration	5	HM	1000	NSC	NSC	on	0.0	2
	6	HM	1000	NSC	NC	on	0.0	2
	2	HM	1000	NC	NSC	on	0.0	2
	7	HM	1000	NC	GC	on	0.0	2
	8	HM	1000	GC	NC	on	0.0	2
Foraging	9	RW1	1000	NC	NSC	on	0.0	2
	10	RW2	1000	NC	NSC	on	0.9	2
	2	HM1	1000	NC	NSC	on	0.0	2
	11	HM2	1000	NC	NSC	on	0.9	2
	12	MPDS-R1	1000	NC	NSC	on	0.0	2
	13	MPDS-R2	1000	NC	NSC	on	0.9	2
	14	MPDS-R3	1000	NC	NSC	on	1.8	2
	15	MPDS-R4	1000	NC	NSC	on	0.0	6
	16	MPDS-R5	1000	NC	NSC	on	0.0	10
	17	MPDS-R6	1000	NC	NSC	on	0.0	2000
	18	MPDS-H1	1000	NC	NSC	on	0.0	2
	19	MPDS-H2	1000	NC	NSC	on	0.9	2
	20	MPDS-H3	1000	NC	NSC	on	1.8	2
21	MPDS-H4	1000	NC	NSC	on	0.0	6	
22	MPDS-H5	1000	NC	NSC	on	0.0	10	
23	MPDS-H6	1000	NC	NSC	on	0.0	2000	

2.5.2 Population size

For all simulations, the whales are configured to use the HM strategy with no randomness in their movements ($R_{mov} = 0.0$) between waypoints, and they are arbitrarily configured to migrate in along the NC path and out along the NSC path, as it is only the SEM of the population's speed and foraging efficiency that will be evaluated (Table 2.1). The maximum number of feeding days (d_{feed}) is set to 2 days, but it is not applicable to the HM strategy.

Simulations with four minke population sizes are run to find an adequate population size for SEM comparisons efficiency: 100, 1000, and 10000 (Table 2.1). To properly compare the SEM of the different simulations, it is necessary for the data to be normally distributed. This is determined using the *scypi.stats library* (Jones *et al.*, 2001), using multiple K-tests on a sample data-set for all common probability distribution types as described by Dietrich (2012). With normally distributed data confirmed, the smallest population simulated with an adequately small standard error of the mean will be used for subsequent simulations.

2.5.3 Currents

Two simulations are run for evaluating the effects of currents on the movement of the whales following the same general configuration as the population size simulations (i.e. NC as the in-path, NSC as the out-path, HM as the strategy, and $R_{mov} = 0.0$), along with using the optimal population size current configurations (Table 2.1). The first simulation is run with the currents activated, altering the whales' final positions for each day-step. Currents are then deactivated for the second simulation, so the mean speed of the population may be observed without the effect of the currents.

2.5.4 Migration

With the population size determined, and the effect of currents known, variations in-migration path selection are tested with five permutations of path configurations. All whales are configured to use homing destination selection movement (HM) without randomness in their movements between positions ($R_{mov} = 0.0$). The maximum number of feeding days (d_{fmax}) is set to 2 days for all simulations, which does not have an effect in the homing strategy.

The following are the in-path and out-path configurations for of the migration simulations (Table 2.4.2):

1. In: Norwegian Sea Center (NSC); Out: Norwegian Sea Center (NSC)
2. In: Norwegian Sea Center (NSC); Out: Norwegian Coast (NC)
3. In: Norwegian Coast (NC); Out: Norwegian Sea Center (NSC)
4. In: Norwegian Coast (NC); Out: Greenland Coast (GC)
5. In: Greenland Coast (GC); Out: Norwegian Coast (NC)

Mean migration times and speed of the population for in-periods and out-periods along these path configurations are calculated for comparisons (see section 2.4.2).

2.5.5 Foraging

The most rewarding migration configuration is used for foraging simulations using various parameterizations of the previously defined strategies: RW, HM, MPDS with random-walk, and MPDS with homing (Table 2.1).

Two simulations are run using the RW strategy and two using the HM. The first simulation for both strategies is run with R_{mov} set to 0, and the second simulations for both strategies is run with R_{mov} set to 0.9. For all simulations the maximum number of feeding days (d_{fmax}) is set to 2 days, which does not have an effect with either strategy.

For both the MPDS-R foraging strategy, as well as the MPDS-H, there are six simulations run with variations in R_{mov} and d_{feed} . The first three are run with R_{mov} set to 0.0, 0.9, and 1.8, respectively, and with d_{fmax} set to 2 days. The last three simulations are run with R_{mov} set to 0.0, and with d_{fmax} set to 2, 6, and 10, respectively. The maximum number of travel days, d_{tmax} , is set to 2 days. Varying values of R_{mov} and d_{fmax} are arbitrarily chosen to evaluate the effect of these parameters on foraging efficiency. The d_{tmax} value is chosen based on observations with preliminary model runs where whales were observed to travel too quickly to summer feeding regions with higher values (according to the assumptions on migration previously stated). The R_{mov} values are chosen arbitrarily due to there being no prior studies that give clear indication towards the level of randomness in minke whale movement or duration of their feeding periods.

Chapter 3

Results

3.1 Simulations

All standard error of the mean (SEM) values are reported with a confidence interval (CI) of 95 %.

3.1.1 Population Size

The daily mean of population speed and foraging efficiency varied little, with much higher variation in the SEM, highest between simulations with a population of 100 and 1000 (Figure 3.1; Table 3.1). The mean speed of the population during migration periods with SEM for populations of 100, 1000, and 10000 were: $3.08 \pm 0.18 \text{ km h}^{-1}$, $3.10 \pm 0.05 \text{ km h}^{-1}$, $3.07 \pm 0.02 \text{ km h}^{-1}$, respectively. Mean values of foraging efficiency with SEMs were as follows: 2.04 ± 0.29 , 2.03 ± 0.09 , and 2.05 ± 0.03 .

Computation time for processing datasets from simulations with a population size of 10000 was found to be exceedingly high and prohibitive for the volume of simulations necessary for the this study.

Whales flagged for moving beyond the model grid boundaries increased with an increase in population size. There were 1.000 whales flagged as off-grid for the population of 100, 13 for the population of 1000, and 151 for the population of 10000.

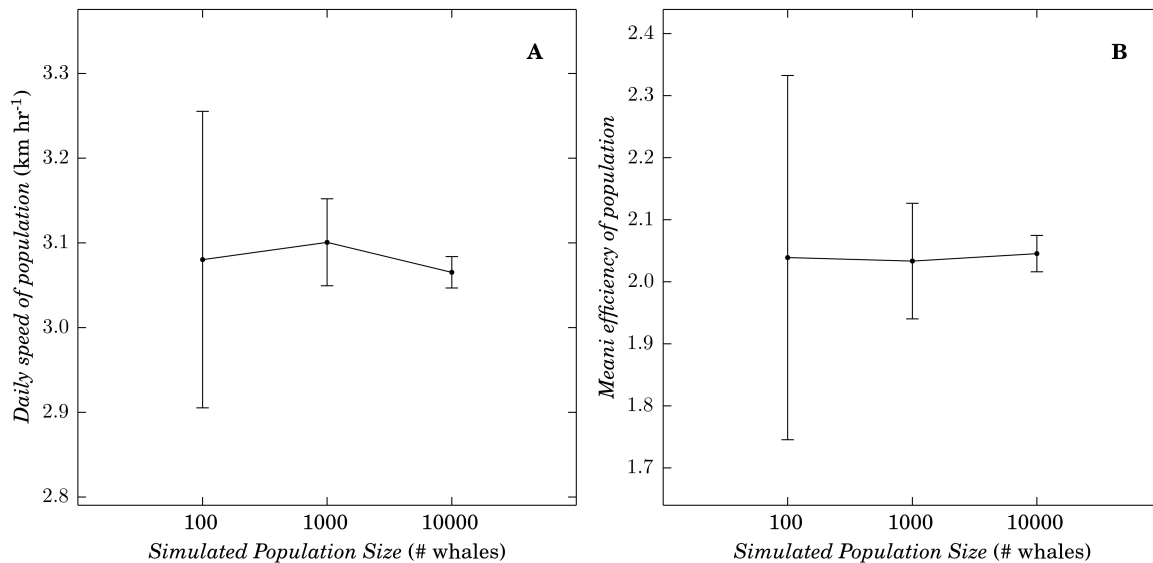


Figure 3.1: Daily mean speed and foraging efficiency with varying population sizes. **A** Daily mean speed of population **B** Daily mean preying efficiency. Simulations are run with the following population sizes: 100, 1000, and 10000 whales. Error bars indicate the range of standard error of the mean (CI 95%).

3.1.2 Currents

The mean speed of the population was higher for the simulation with currents activated $3.195 \pm 0.028 \text{ km h}^{-1}$ than that with it deactivated $3.133 \pm 0.002 \text{ km h}^{-1}$, and there is no overlap of the SEM between the two (Figure 3.2A; Table 3.1). Daily maximum speeds of individual whales within the population with currents activated varied between approximately 5.5 km h^{-1} and 0 km h^{-1} for both migration periods (Figure 3.8). When currents were deactivated individual speeds varied between approximately 2.9 km h^{-1} and 3.1 km h^{-1} (Figure 3.4).

Travel-time differences were greatest for the in migration periods of the current simulations, varying between $24.53 \pm 0.05 \text{ km h}^{-1}$ for the activated current simulation and $26.78 \pm 0.05 \text{ km h}^{-1}$ for the deactivated simulation (Figure 3.2B). With about 2% change in mean population speed between the current simulations, there is an approximate 8% decrease in travel-time during the in-migration period (along the NC path) and an approximate 4% increase during the out-migration period (along the NSC path).

There were 13 whales that experienced erroneous movement out of the model grid boundaries for each of the simulations with currents activated.

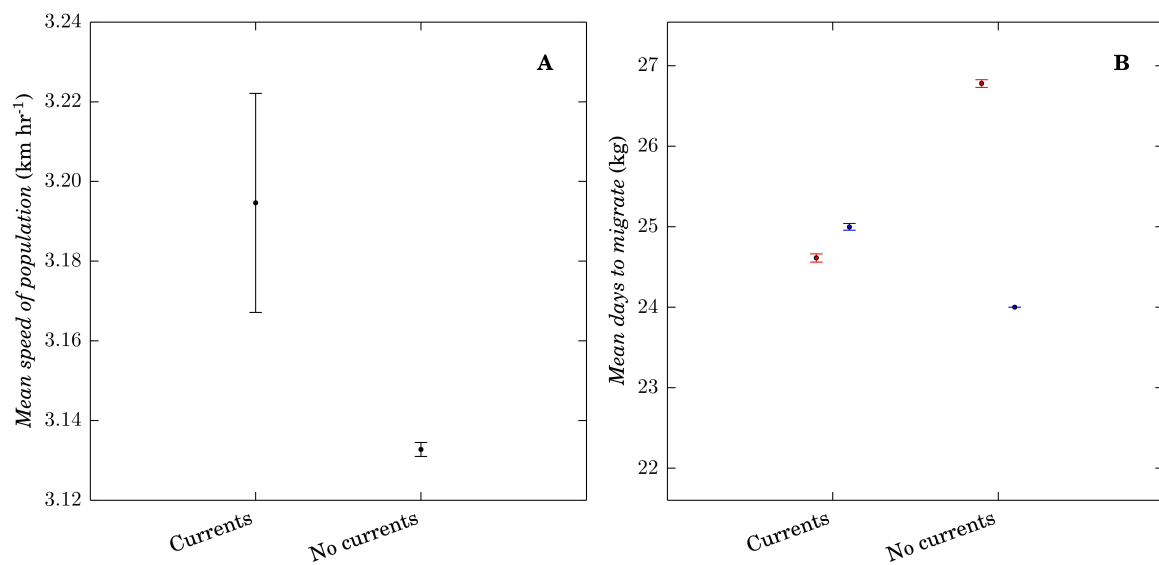


Figure 3.2: **A** Mean days to migrate and **B** mean migration speeds with variation in current configuration. Error bars indicate the range of standard error of the mean (CI 95%). All simulations follow the NC into the model area and the NSC out of the model area. The first simulation is run with currents activated and no movement of whales to a layer identified as having a current direction nearest to the movement of the whales. The second simulation is run with currents deactivated.

Table 3.1: Mean migration periods and speed of the population with number of erroneous movements. The in and out-periods are the number of days whales spend migrating to and from the Bear Island feeding location. Speed is the mean speed of the population over both migration periods. Whales whose movements went off the model grid are counted as "off-grid", and whales whose movement crossed land are counted as "landed". Whales are removed from all analysis if they experienced either erroneous movement. The standard error of the mean (SEM) is presented with a CI of 95%.

	Simulation	Strategy	In-path	Out-path	In-period (days)	SEM (days)	Out-period (days)	SEM (days)	Speed (km hr ⁻¹)	SEM (km hr ⁻¹)	Off-grid (whales)	Landed (whales)
Population	1	HM	NC	NSC	24.525	0.049	24.970	0.038	3.198	0.087	1	0
	2	HM	NC	NSC	24.611	0.051	24.997	0.041	3.195	0.028	13	0
	3	HM	NC	NSC	24.589	0.052	24.949	0.042	3.199	0.009	151	0
Currents	2	HM	NC	NSC	24.611	0.051	24.997	0.041	3.195	0.028	13	0
	4	HM	NC	NSC	26.778	0.048	24.000	0.000	3.133	0.002	0	0
Migration	5	HM	NSC	NSC	22.363	0.032	24.929	0.041	3.160	0.019	0	0
	6	HM	NSC	NC	22.363	0.032	29.734	0.057	3.024	0.028	0	0
	2	HM	NC	NSC	24.611	0.051	24.997	0.041	3.195	0.028	13	0
	7	HM	NC	GC	24.612	0.051	30.481	0.058	3.327	0.025	13	3
	8	HM	GC	NC	33.285	0.044	29.760	0.055	2.911	0.021	0	0
Foraging	9	RW1	NC	NSC	60.211	0.507	102.377	0.608	2.652	0.061	3	364
	10	RW2	NC	NSC	60.462	0.482	102.312	0.598	2.587	0.081	13	516
	2	HM1	NC	NSC	24.611	0.051	24.997	0.041	3.195	0.028	13	0
	11	HM2	NC	NSC	25.672	0.098	25.755	0.102	3.201	0.057	66	11
	12	MPDS-R1	NC	NSC	60.941	0.539	99.322	0.529	1.721	0.148	91	676
	13	MPDS-R2	NC	NSC	59.902	0.476	97.865	0.546	1.730	0.197	146	742
	14	MPDS-R3	NC	NSC	59.970	0.537	99.576	0.540	1.874	0.410	460	594
	15	MPDS-R4	NC	NSC	60.844	0.587	94.938	0.377	1.259	0.360	214	779
	16	MPDS-R5	NC	NSC	64.500	0.458	92.667	0.228	1.062	0.749	251	793
	17	MPDS-R6	NC	NSC	60.500	0.403	94.000	0.062	0.805	1.099	390	747
	18	MPDS-H1	NC	NSC	44.855	0.139	27.814	0.079	2.376	0.085	15	114
	19	MPDS-H2	NC	NSC	47.960	0.246	35.853	0.232	2.271	0.103	120	181
	20	MPDS-H3	NC	NSC	58.961	0.467	90.529	0.467	2.061	0.275	337	561
21	MPDS-H4	NC	NSC	59.852	0.459	68.965	0.852	1.611	0.127	14	560	
22	MPDS-H5	NC	NSC	66.875	0.069	105.646	0.355	1.284	0.365	16	936	
23	MPDS-H6	NC	NSC	54.365	0.277	92.397	0.492	0.697	0.155	53	892	

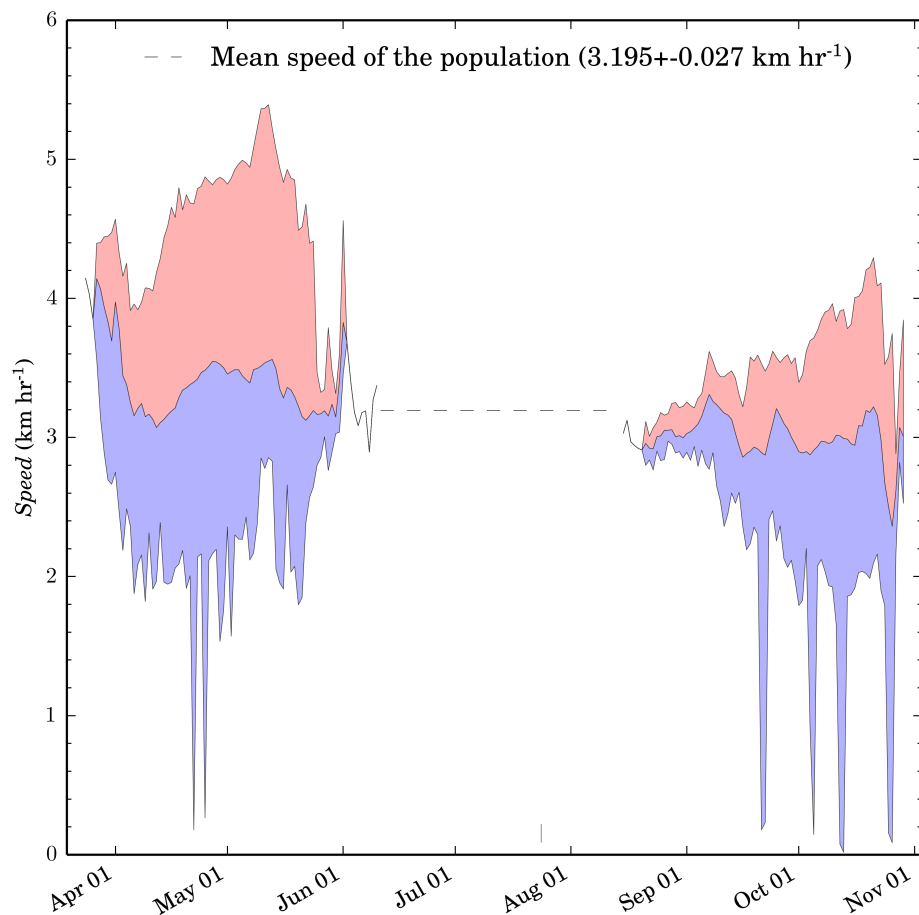


Figure 3.3: Daily mean speed of population with daily maximum and minimum individual whale speeds (in-path: NC; out-path: NSC). The line above the red-shaded area is the speed of the fastest individual in the population with the daily mean speed of population as the line between the red and blue-shaded areas. The line below the blue-shaded area is the speed of the slowest individual in the population. Position data within $\pm 0.3^\circ$ longitude and latitude of the summer feeding position have been filtered, so they do not affect mean values and to improve visualization. Standard error of the mean (SEM) is presented (CI 95%)

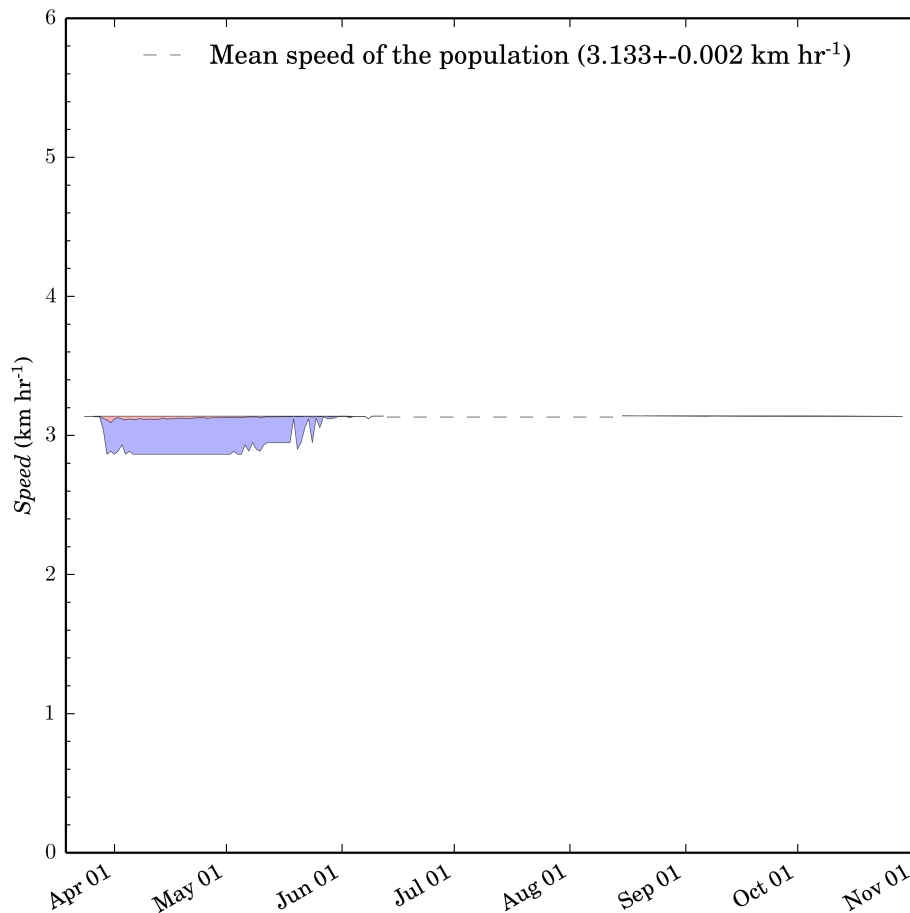


Figure 3.4: Daily mean speed of population with daily maximum and minimum individual whale speeds (in-path: NC; out-path: NSC). The line above the red-shaded area is the speed of the fastest individual in the population with the daily mean speed of population as the line between the red and blue-shaded areas. The line below the blue-shaded area is the speed of the slowest individual in the population. Position data within $\pm 0.3^\circ$ longitude and latitude of the summer feeding position have been filtered, so they do not affect mean values and to improve visualization. Standard error of the mean (SEM) is presented (CI 95%)

3.1.3 Migration

Migration durations varied with changes in migration paths and direction (in or out of the model area along those paths) (Table 3.1). The configuration with the shortest total migration periods were seen when whales migrated either in or out along the Norwegian Sea Center (NSC) path, with a migration periods of 22.363 ± 0.032 days and 24.929 ± 0.041 days, respectively (Figure 3.5A). The next shortest migration period to the NSC in-migration was the in-migration along the NC (22.363 ± 0.032 days). The longest period occurred with migration along the GC (33.285 ± 0.044 days), followed by the out-migration along the GC (30.479 ± 0.058 days).

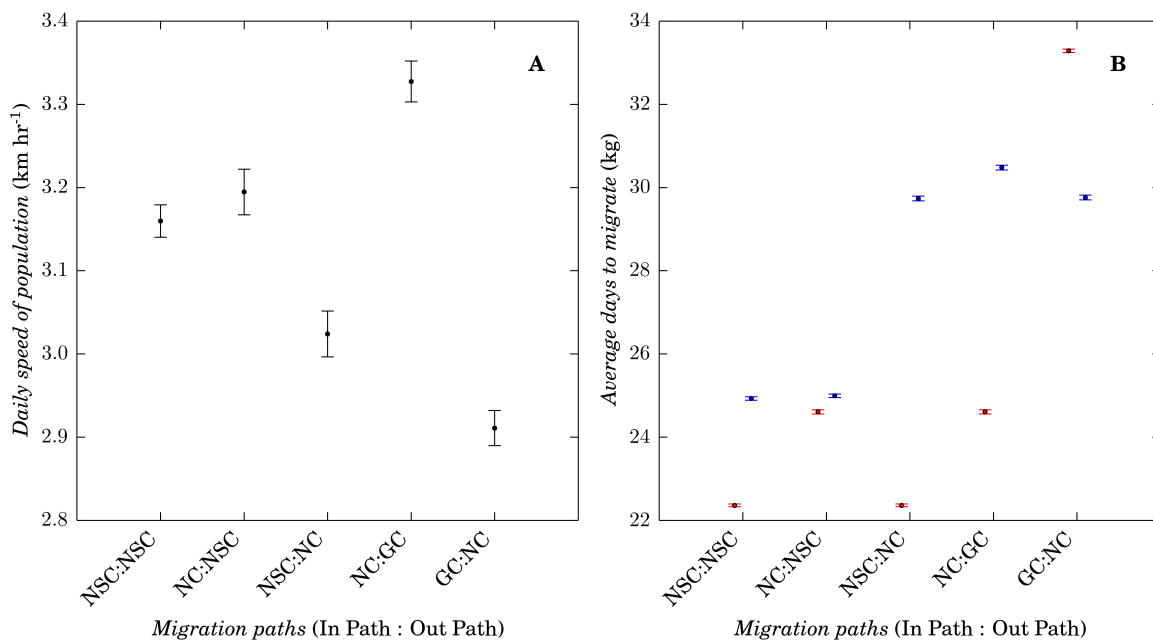


Figure 3.5: **A** Mean days to migrate and **B** mean daily migration speeds of populations along varying migration paths. Error bars indicate the range of standard error of the mean (CI 95%). Simulation migration paths are as follows: Norwegian Sea Center (NSC), Norwegian Coast (NC), and Greenland Coast (GC).

The mean daily speed of the population for in and out-migration periods differed between all migration path configurations (Table 3.1). The fastest mean speed ($3.327 \pm 0.025 \text{ km h}^{-1}$) was seen with the NC for in-migration and the GC for out-migration (Figure 3.5B). Conversely, the slowest speed ($2.911 \pm 0.021 \text{ km h}^{-1}$) occurred with the GC followed in and the NC out. The second highest mean speed ($3.195 \pm 0.028 \text{ km h}^{-1}$) was with the NC for in-migration and the NSC followed out. The configuration with the fastest migration periods used the NSC for in and out migration, had a speed of $3.160 \pm 0.019 \text{ km h}^{-1}$.

Maximum and minimum speeds of individual whales, as well as the daily mean speed of the population, were erratic for all simulations with occasional large peaks in minima and maxima (Figures 3.6- 3.10). The maximum speeds of individuals were greatest with migration in along the NC and out along the GC (5.393 km h^{-1}), (Figure 3.9), followed closely by that with migration in on the NC and out through the NSC (5.363 km h^{-1}), (Figures 3.8). The lowest maximum individual whale speed was 4.287 km h^{-1} with in-migration on the GC and out along the NC (Figure 3.10). The maximum individual whale speed (4.562 km h^{-1}) was from the simulation having migration in and out through the NSC (Figure 3.6).

Erroneous movement of whales out of the model grid-boundaries were experienced during the simulation with the NC as the in-path and NSC as the out-path (13 off-grid) and the simulation with the NC as the in-path and the GC as the out-path (13 off-grid and 3 landed), (Table 3.1).

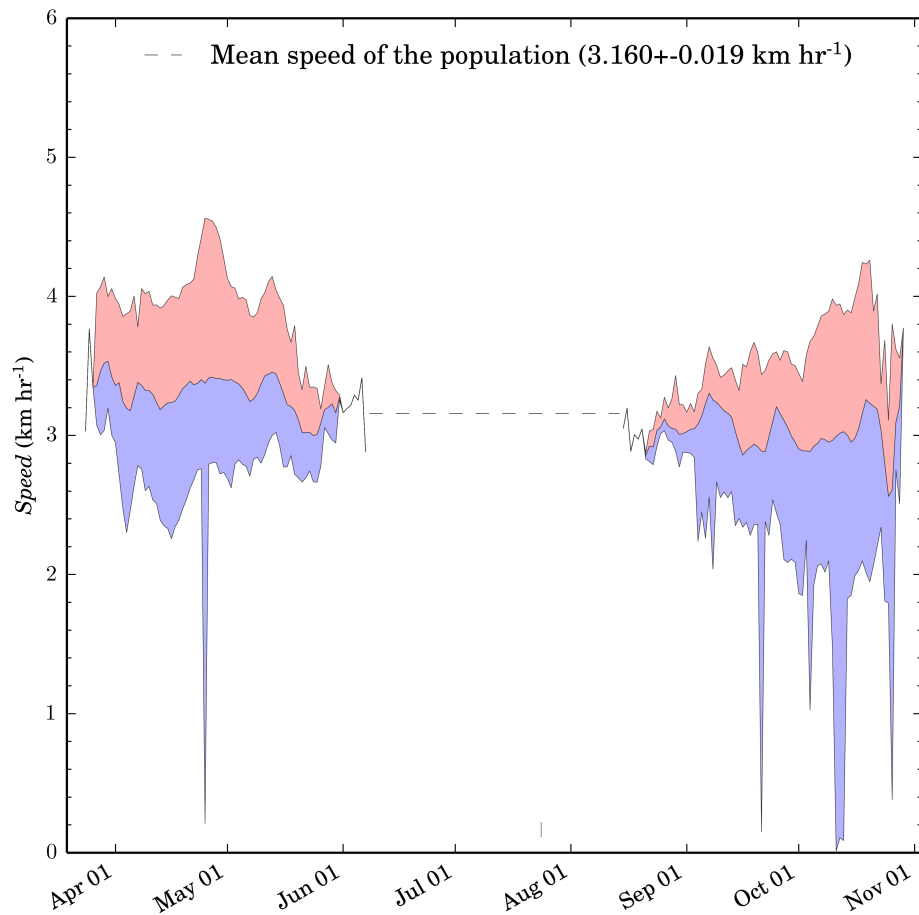


Figure 3.6: Daily mean speed of population with daily maximum and minimum individual whale speeds (in-path: NSC; out-path: NSC). The line above the red-shaded area is the speed of the fastest individual in the population with the daily mean speed of population as the line between the red and blue-shaded areas. The line below the blue-shaded area is the speed of the slowest individual in the population. Position data within $\pm 0.3^\circ$ longitude and latitude of the summer feeding position have been filtered, so they do not affect mean values and to improve visualization. Standard error of the mean (SEM) is presented (CI 95%)

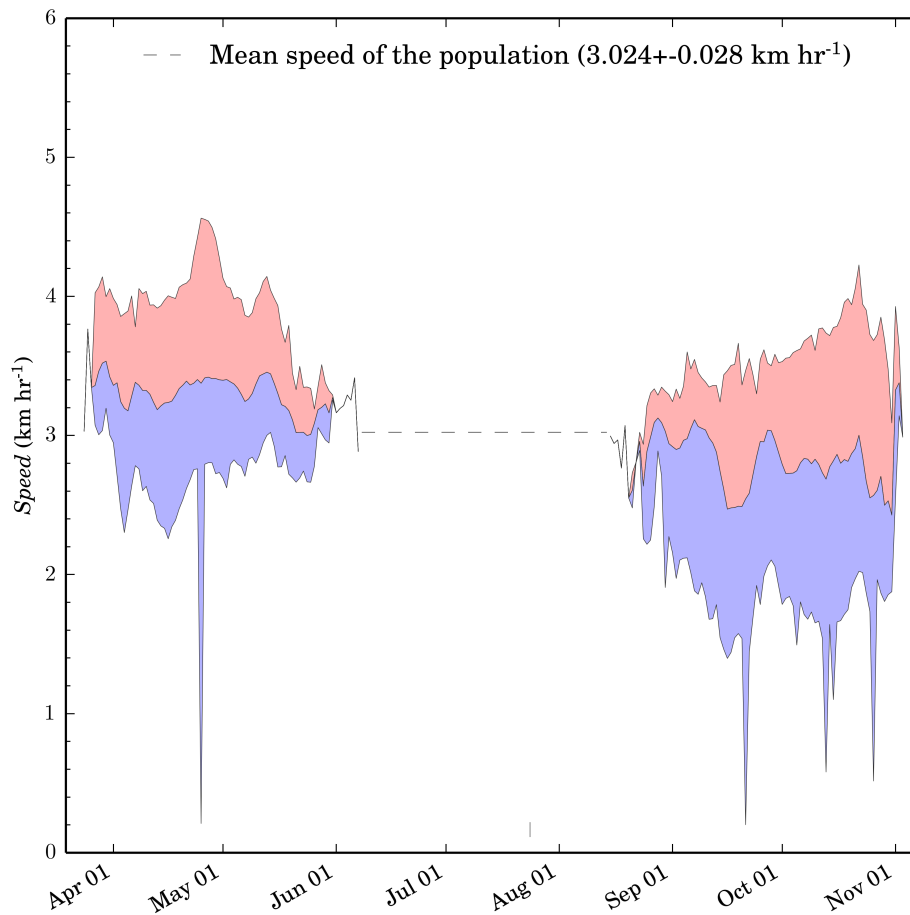


Figure 3.7: Daily mean speed of population with daily maximum and minimum individual whale speeds (in-path: NSC; out-path: NC). The line above the red-shaded area is the speed of the fastest individual in the population with the daily mean speed of population as the line between the red and blue-shaded areas. The line below the blue-shaded area is the speed of the slowest individual in the population. Position data within $\pm 0.3^\circ$ longitude and latitude of the summer feeding position have been filtered, so they do not affect mean values and to improve visualization. Standard error of the mean (SEM) is presented (CI 95%)

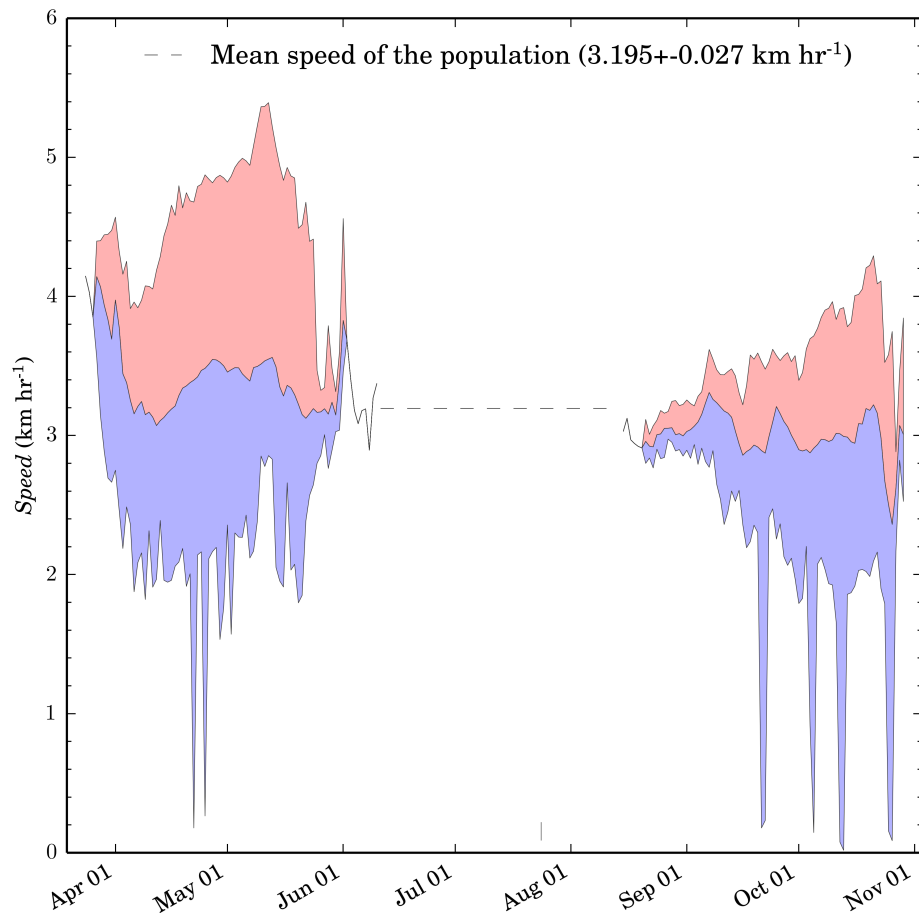


Figure 3.8: Daily mean speed of population with daily maximum and minimum individual whale speeds (in-path: NC; out-path: NSC). The line above the red-shaded area is the speed of the fastest individual in the population with the daily mean speed of population as the line between the red and blue-shaded areas. The line below the blue-shaded area is the speed of the slowest individual in the population. Position data within $\pm 0.3^\circ$ longitude and latitude of the summer feeding position have been filtered, so they do not affect mean values and to improve visualization. Standard error of the mean (SEM) is presented (CI 95%)

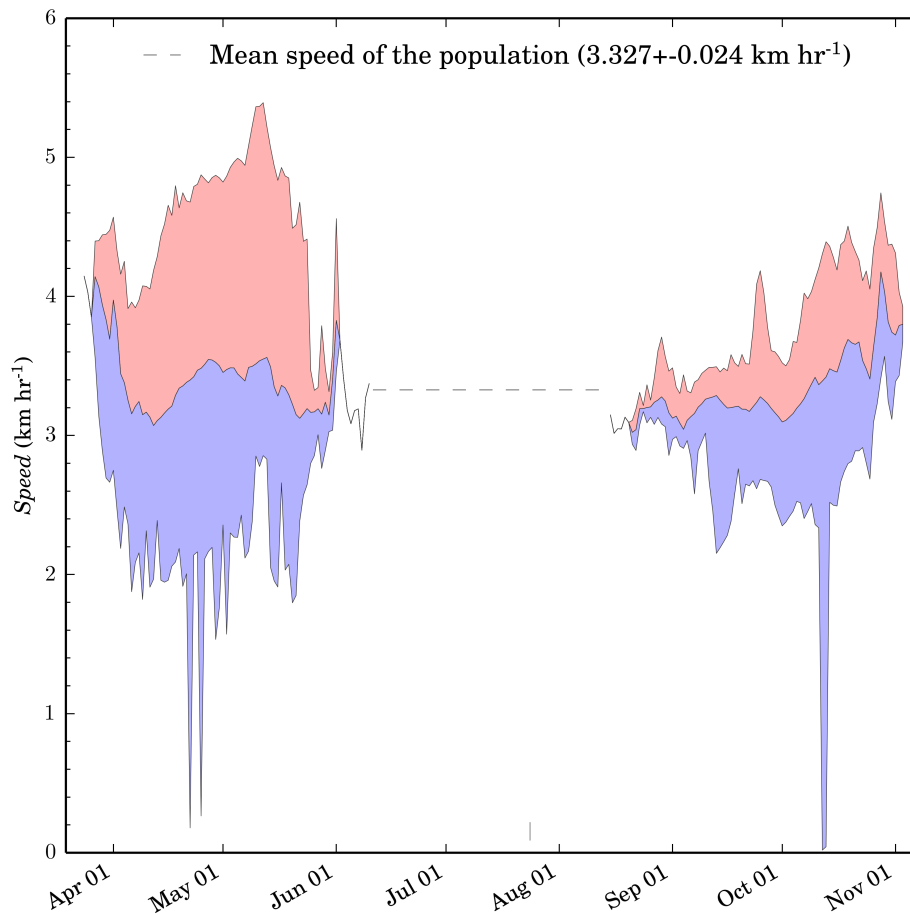


Figure 3.9: Daily mean speed of population with daily maximum and minimum individual whale speeds (in-path: NC; out-path: GC). The line above the red-shaded area is the speed of the fastest individual in the population with the daily mean speed of population as the line between the red and blue-shaded areas. The line below the blue-shaded area is the speed of the slowest individual in the population. Position data within $\pm 0.3^\circ$ longitude and latitude of the summer feeding position have been filtered, so they do not affect mean values and to improve visualization. Standard error of the mean (SEM) is presented (CI 95%)

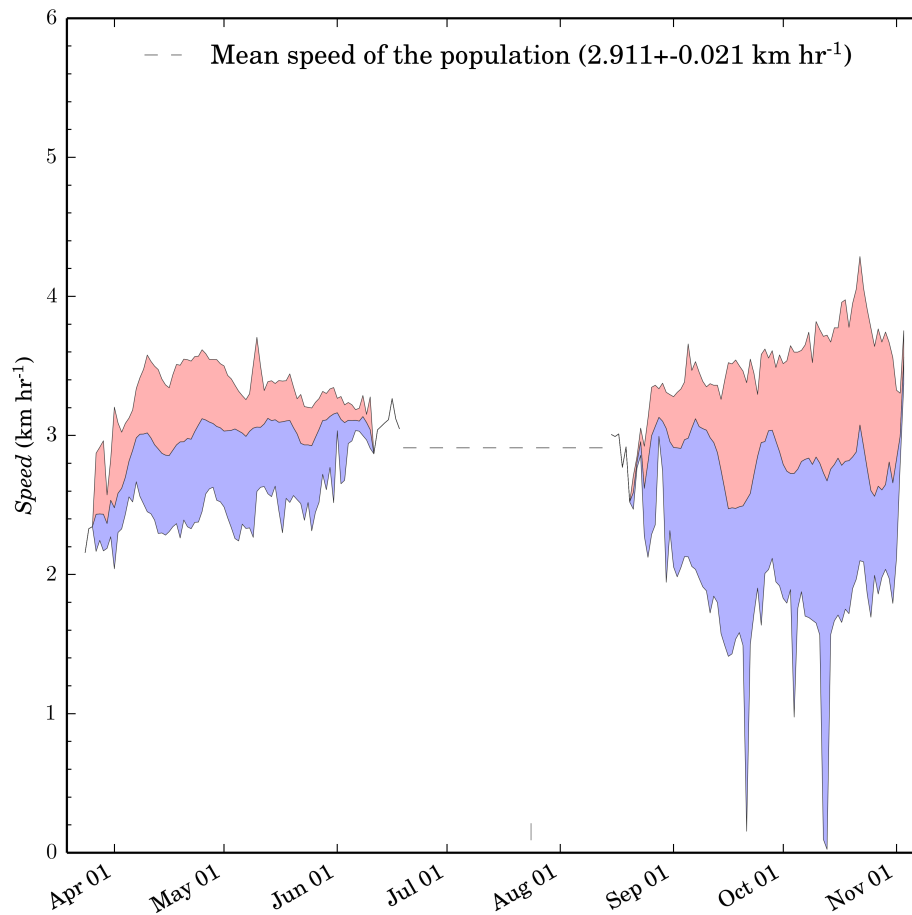


Figure 3.10: Daily mean speed of population with daily maximum and minimum individual whale speeds (in-path: GC; out-path: NC). The line above the red-shaded area is the speed of the fastest individual in the population with the daily mean speed of population as the line between the red and blue-shaded areas. The line below the blue-shaded area is the speed of the slowest individual in the population. Position data within $\pm 0.3^\circ$ longitude and latitude of the summer feeding position have been filtered, so they do not affect mean values and to improve visualization. Standard error of the mean (SEM) is presented (CI 95%)

3.1.4 Foraging

3.1.4.1 Foraging Efficiency

Foraging efficiency ranged between 0.586 ± 0.312 (MPDS-H6) and 2.381 ± 0.435 (MPDS-H5) for all simulations (Table 3.2). An increase in R_{mov} resulted in a small decrease in efficiency for both RW and HM foraging strategies, while relatively small increases in efficiency were seen with an increased R_{mov} for MPDS strategies (Figure 3.11). Within each foraging strategy, the simulations with variation in R_{mov} had means with overlapping SEMs (Table 3.2; Figure 3.11).

Using the RW foraging strategy, the highest efficiency value (2.069 ± 0.117) occurred with an R_{mov} of 0.0 (Table 3.2). Foraging efficiency of the population does not drop below 1.000 for the duration of the simulation, with two extended periods below the mean efficiency occurring at the beginning of May and in early October (Figure 3.12B).

The HW strategy also had a maximum foraging efficiency (0.652 ± 0.081) with an R_{mov} of 0.9, but much lower than both RW simulations (Table 3.2). While HM foraging efficiency of the population is higher than RW in late April and early October, there is a sharp decline in May with an extended period of zero efficiency until a spike in late August followed by a steep incline in September (Figure 3.15B).

For both MPDS strategies the MPDS-H5 strategy, with d_{fmax} set to 6 days, had the highest foraging efficiency of the population (2.382 ± 0.435), which was the largest value for all simulations (Table 3.2). The maximum efficiency value from the MPDS-R simulations (2.256 ± 0.444) was with MPDS-R3 having an R_{mov} of 1.8. The lowest value from each was with a d_{fmax} of 2000 (continuous feeding): MPDS-R6 (0.934 ± 1.830) and MPDS-H6 (0.586 ± 0.312). The MPDS-R3 strategy had a foraging efficiency continuously above an efficiency of 1.000 with more variability from April to July when compared to the latter half of the feeding period (Figure 3.18B). In the MPDS-H5 simulation, there were peak periods of foraging efficiency higher than seen with MPDS-H3 (e.g. 01 July to 01 August); though, there were also drop in efficiency below 1.000 in mid-May and early September (Figure 3.21B).

3.1.4.2 Prey Encounter

The ratio between encounters for each prey species and the total number of prey encounters was consistent for each foraging strategy (Table 3.2). For all simulations, blue whiting had the highest rates of encounter, followed by herring, then mackerel.

With the RW strategy, the percentage of total encounters for all prey species varied less than 1% between both simulations, RW1 ($R_{mov} = 0.0$) and RW2 ($R_{mov} = 0.9$). The total encounters per whale were equal for both of the RW foraging simulations (Table: 3.2). Blue whiting encounters begin early in the

simulation, with encounters of herring offset by approximately one month, and mackerel encounters beginning 01 June (Figure 3.12A). Herring encounters peak at the end of May, gradually decreasing until August, with another small peak in September. Blue whiting encounters are consistent throughout the feeding period, except for a small low in early May. Mackerel encounters are low compared to blue whiting and herring, occurring between June and October.

The HM strategy saw even less variation in the change of encounter composition with an increase in R_{mov} from 0.0 to 0.9 having no more than $\pm 0.6\%$ change for each species. Though blue whiting encounters are less than 0.4% different from the RW strategy for blue whiting encounter rates, there is a decrease in mackerel encounters of approximately 6.5% and an equivalent increase in herring encounter composition. Total encounters per whale decreased by 0.49 encounters with the increase in R_{mov} (Table 3.2). The simulation with the highest foraging efficiency, HM1, both herring and blue whiting have peaks in their encounter rates at the end of April, steeply increasing before and steeply decreasing after these peaks (Figure 3.15A). Two brief peaks of herring encounters then occur in early July, followed by another two in mid-August. After the last herring peak in August, there is a smaller and more sustained herring encounter by the population, with a delay of several days before a sustained encounter of blue whiting occurs of equal magnitude to the encounter around May. Mackerel is encountered beginning mid September to late November.

Encountered prey composition of the MPDS-R strategy varied within 2% in response to changes in R_{mov} , with larger increases in herring (0.39%, $R_{mov} = 0.9$) and mackerel (0.44%, $R_{mov} = 1.8$). The MPDS-R strategy experienced decreases herring and mackerel encounters and an increase in blue whiting encounter with increases in d_{fmax} . With an increase in R_{mov} , the MPDS-H strategy had a small decrease in herring encounters (0.11%, $R_{mov} = 0.9$) and increase in mackerel encounters (0.12%, $R_{mov} = 0.9$) followed by an increase in herring (3.25%, $R_{mov} = 1.8$) and mackerel (0.05%, $R_{mov} = 1.8$). For both MPDS-R and MPDS-H strategies, the number of encounters increase with and increase in R_{mov} and decreased with an increase in d_{fmax} (Table: 3.2). The monthly trend in time-of-encounter for the three prey species is similar for the RW and MPDS-R3 strategies with MPDS-R3 having more noise in the daily encounters (Figure 3.18A); whereas, the MPDS-H5 prey encounters were consistent throughout the simulation, as compared to HM1 (Figure 3.21A). Blue whiting encounters peak in approximate 10 day intervals through April and May, reaching a period of sustained encounters from early June until early August. This is followed by a low period with another smaller sustained period peaking in early October. Herring encounters with the MPDS-R5 strategy begin mid-April with less pronounced peaks across multiple days. The encounters with MPDS-R5 are continuous and have high daily-variability until decreasing in late August. The lowest prey encounters for both MPDS strategies were with a d_{fmax} of 2000 (an unlimited feeding maximum), with 54.50 encounters whale⁻¹ (MPDS-R6) and 27.54 encounters whale⁻¹ (MPDS-H6).

3.1.4.3 Distribution

The total spatial coverage of the population using the RW1 strategy extends from the Norwegian coast to the Greenland Coast and arctic ice edge, with track densities decreasing with distance away from the whale entry boundary (Figure 3.13). The population is most densely aggregated immediately following entry to the model (April to May) and the distribution gradually expands with time in all directions from the entry boundary (Figure 3.14). Following the return date of 15 September, the spatial distribution of the population remains more widely distributed as the population begins exiting the model.

Track-lines from the HM1 strategy simulation are tightly grouped along the NC path with whales dispersing between waypoints (Figure 3.16). Following the return date, whales gradually distribute along the path, exiting across the entire exit boundary. By 01 April, the first whale to enter the model is located at approximately 66° N and 8° E, with the entire NC path distributed with whales in tight groupings by early May (Figure 3.17). The entire population is located at the Bear Island feeding location in early July and begin to migrate back out in early September. Whales are extended across the entire NSC by early October. In November, the entire population has exited the model area.

The MPDS-R3 strategy had densest coverage east of 8° W to the Norwegian coast and from southern model boundary offset to 67° N (Figure 3.19). Sparse tracks extended beyond this area up to 72° N and west to 20° west, with an aggregation of movements west of Jan Mayen and some rounding the east coast of Iceland. Whale distribution was most dense in early May, which then dispersed in all directions in August, with few individuals in the Iceland and Greenland Seas (Figure 3.20). By September, there are two whales that have reached the western Barents Sea, with a distribution found along the entire Norwegian coast, spreading throughout the Norwegian sea to the Iceland and Greenland Seas. Some whales remained at 70° N at the start of October, and most of the population was out of the model with the remainder occupying the southern Norwegian Sea. All whales had exited by early November.

Whale tracks for the MPDS-H5 strategy resembled that of H1, covering the same regions but with wider coverage along the NC in-migration path, particularly around 65° N and north of 70° N (Figure 3.23). Movements were less sequential over-time for MPDS-H5 than compared to H1, with a large aggregation collectively following the Norwegian coast, from early May to early August (Figure 3.22). In early September, the population has begun reaching the Bear Island feeding location, with a larger latitudinal spread and one whale at approximately 62° N and 1° W. By early October, the bulk of the population extends the entire NSC path from the Bear Island feeding location to the exit boundary, with several whales still remaining in the easter Norwegian Sea north of 35° N, and all whales exited by early November.

Distributions of the least efficient MPDS strategies, MPDS-R6 and MPDS-H6, were both concentrated in a small region on the southern coast of Norway. The MPDS-R6 distribution ranged between approximately 4.4° W and 5.2° E, and did not move north of 62° N for the entire simulation (Figure 3.24A). The MPDS-H6 distribution similarly ranged between approximately 4.5° W and 4.5° E, also remaining below 62° N (Figure 3.24B).

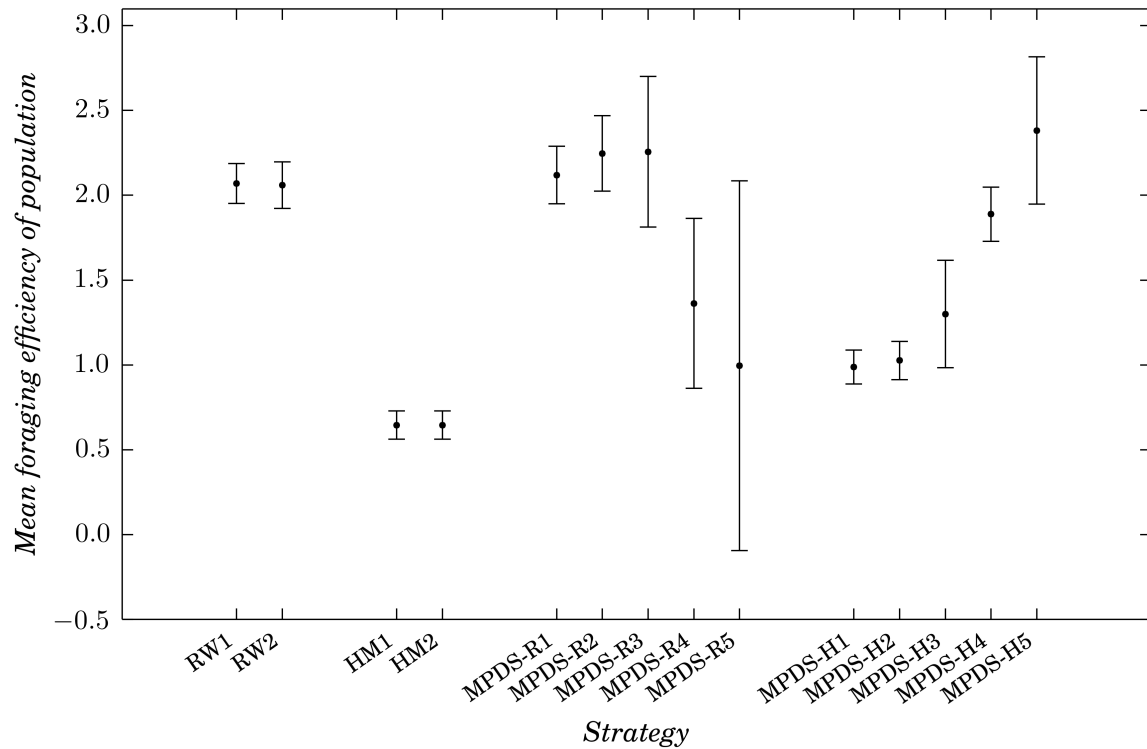


Figure 3.11: Mean preying efficiency of simulations with changes in foraging strategy, randomness in movement between daily destinations (R_{mov}), and number of days on feeding between travelling (d_{feed}).

Table 3.2: Percentage of total prey encounters by prey species, total prey encounters per whale, mean daily movement of whales, and mean foraging efficiency of the population. Whales may have up to three encounters per day if all species are present. Total encounters are divided by the final number of whales in the simulation after whales with erroneous movement are removed. Mean daily movement is the mean distance moved by one whale in the population during a day-step. Eff_{pop} is the mean foraging efficiency of the population. The standard error of the mean (SEM) is presented with a CI of 95%

	Simulation	Strategy	Herring (%)	Blue whiting (%)	Mackerel (%)	Encounters (Nb whale ⁻¹)	Movement (km day ⁻¹)	SEM (km day ⁻¹)	Eff_{pop}	SEM
Population	1	HM	39.75	58.97	1.27	50.82	76.743	2.078	0.650	0.256
	2	HM	39.73	59.07	1.20	50.94	76.671	0.664	0.652	0.081
	3	HM	39.74	59.07	1.19	50.98	76.772	0.209	0.652	0.026
Currents	2	HM	39.73	59.07	1.20	50.94	76.671	0.664	0.652	0.081
	4	HM	37.11	61.75	1.14	51.59	75.186	0.042	0.637	0.079
Migration	5	HM	33.68	64.81	1.52	38.93	75.837	0.467	0.545	0.073
	6	HM	32.38	65.81	1.81	47.50	72.577	0.664	0.616	0.076
	2	HM	39.73	59.07	1.20	50.94	76.671	0.664	0.652	0.081
	7	HM	46.78	52.94	0.29	39.48	79.859	0.591	0.477	0.074
	8	HM	27.24	69.98	2.78	30.51	69.861	0.507	0.410	0.063
Foraging	9	RW1	33.28	59.03	7.69	158.23	63.652	1.454	2.069	0.117
	10	RW2	33.73	58.17	8.10	158.23	62.100	1.952	2.059	0.137
	2	HM1	39.73	59.07	1.20	50.94	76.671	0.664	0.652	0.081
	11	HM2	39.14	59.45	1.41	50.45	76.827	1.371	0.646	0.083
	12	MPDS-R1	23.36	67.99	8.65	159.58	41.300	3.542	2.119	0.170
	13	MPDS-R2	24.84	66.07	9.09	170.92	41.509	4.731	2.246	0.222
	14	MPDS-R3	24.45	64.58	10.96	176.33	44.983	9.829	2.256	0.444
	15	MPDS-R4	22.52	72.03	5.45	87.16	30.206	8.633	1.363	0.500
	16	MPDS-R5	21.70	74.45	3.85	60.67	25.485	17.980	0.995	1.089
	17	MPDS-R6	17.43	80.73	1.83	54.50	19.309	26.373	0.934	1.830
	18	MPDS-H1	40.46	58.84	0.69	79.04	57.031	2.029	0.988	0.100
	19	MPDS-H2	40.35	58.84	0.81	82.27	54.515	2.465	1.026	0.112
	20	MPDS-H3	43.71	55.55	0.74	104.43	49.466	6.604	1.300	0.316
21	MPDS-H4	47.06	52.58	0.37	147.90	38.656	3.053	1.888	0.160	
22	MPDS-H5	47.58	52.18	0.24	190.56	30.824	8.758	2.381	0.435	
23	MPDS-H6	59.25	39.19	1.56	27.54	16.734	3.731	0.586	0.312	

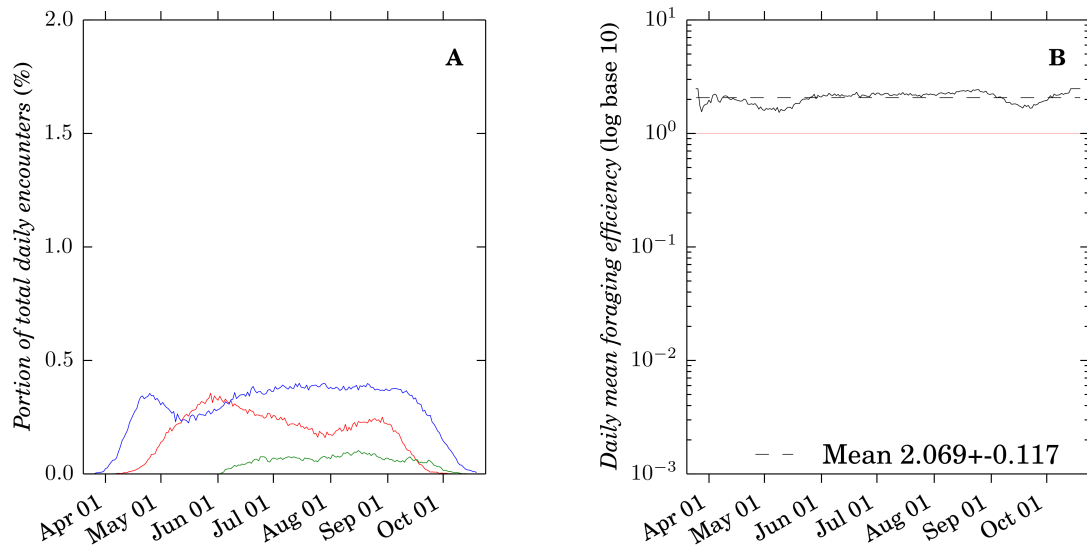


Figure 3.12: Daily prey encounter rates by prey type and daily energy efficiency of the population using the RW strategy; $R_{mov} = 0.0$; $d_{fmax} = 2$. **A** Percent of daily prey encounters of the population by type: herring (red line), blue whiting (blue line), and mackerel (green line). **B** Daily mean energy efficiency of the population (Eff_{pop}) with SEM (CI 95%). The solid red line marks $Eff_{pop} = 1.000$.

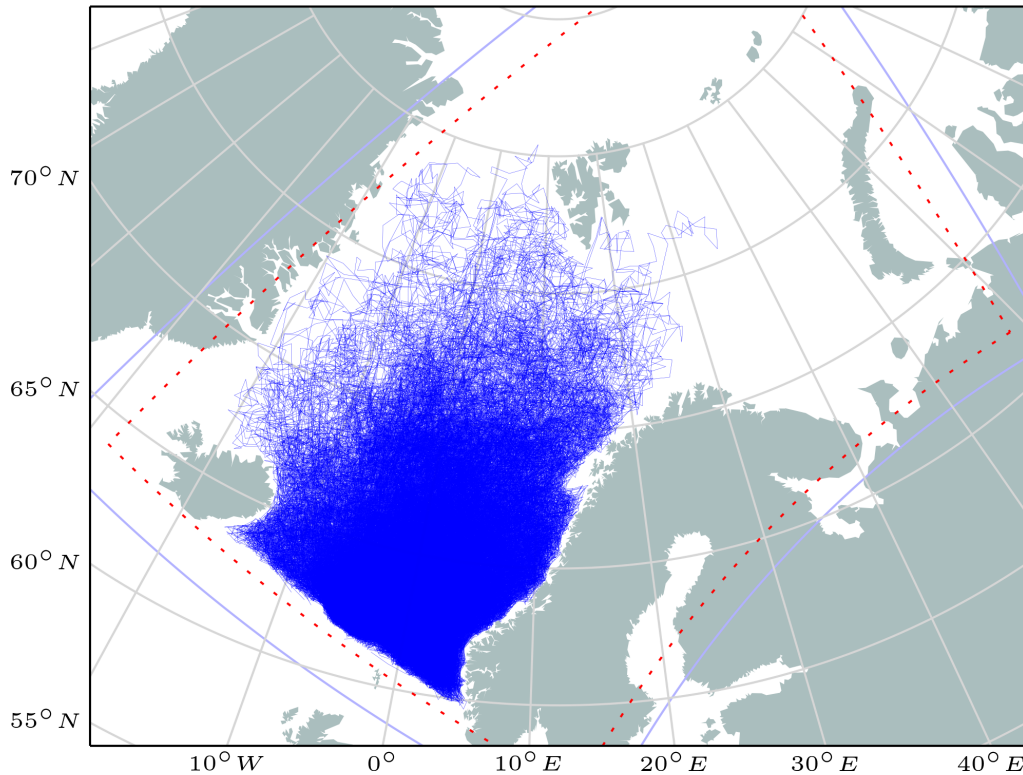


Figure 3.13: Minke population track-lines for the simulation year 1998 using the RW strategy; $R_{mov} = 0.0$; $d_{fmax} = 2$. The light blue solid line marks the model grid area, with the red dashed line marking the offset boundary containing the whale movement. Dark blue lines are drawn along tracklines of individual whales.

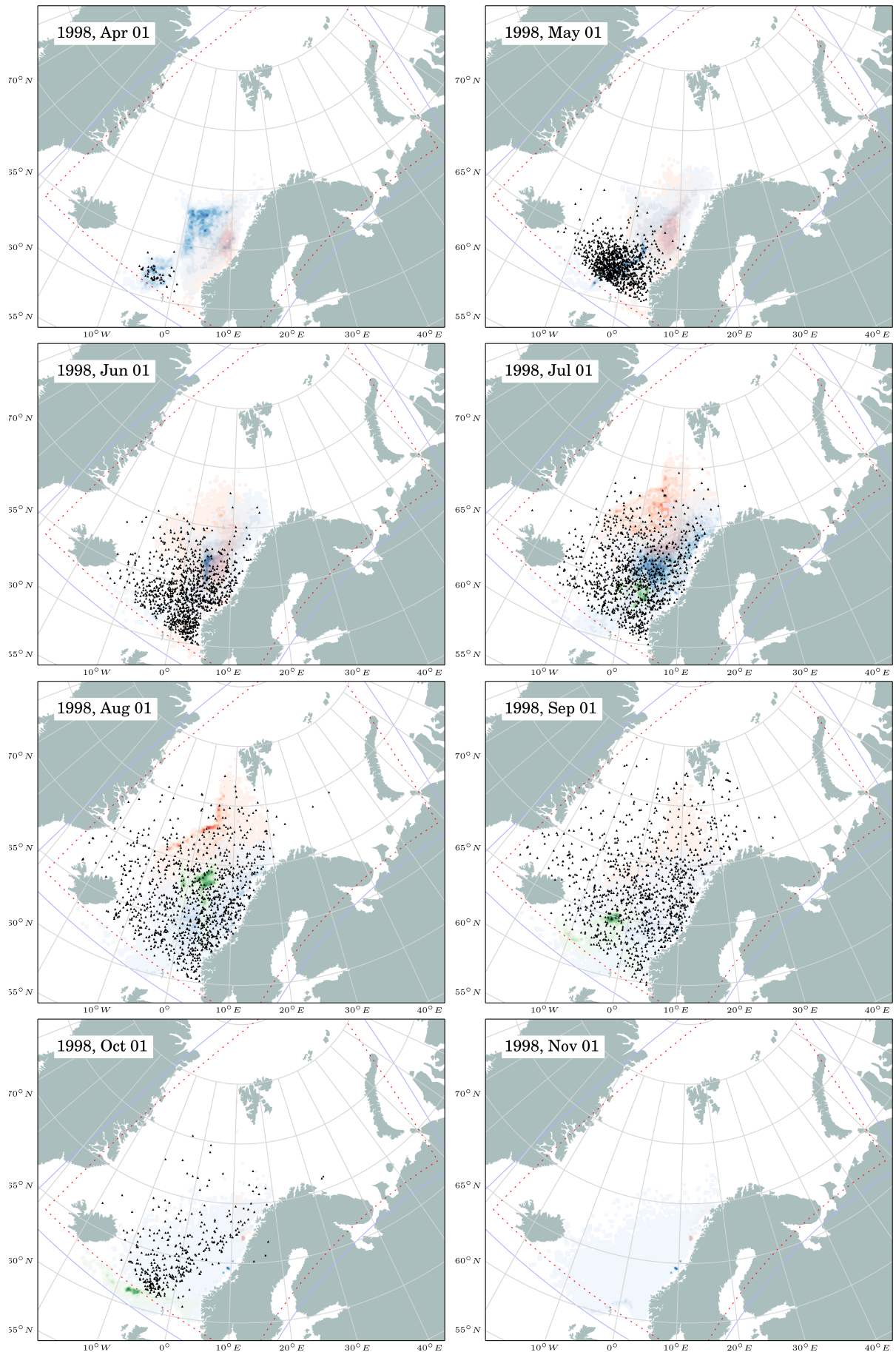


Figure 3.14: Monthly distribution of simulated whales using the RW strategy; $R_{mov} = 0.0$; $df_{max} = 2$. Whales shown as black triangles. Herring distribution is shown in shades of red, blue whiting in shades of blue, and mackerel in shades of green. The model area is bound by a solid blue line with the offset containing whale movement shown as a dashed red line.

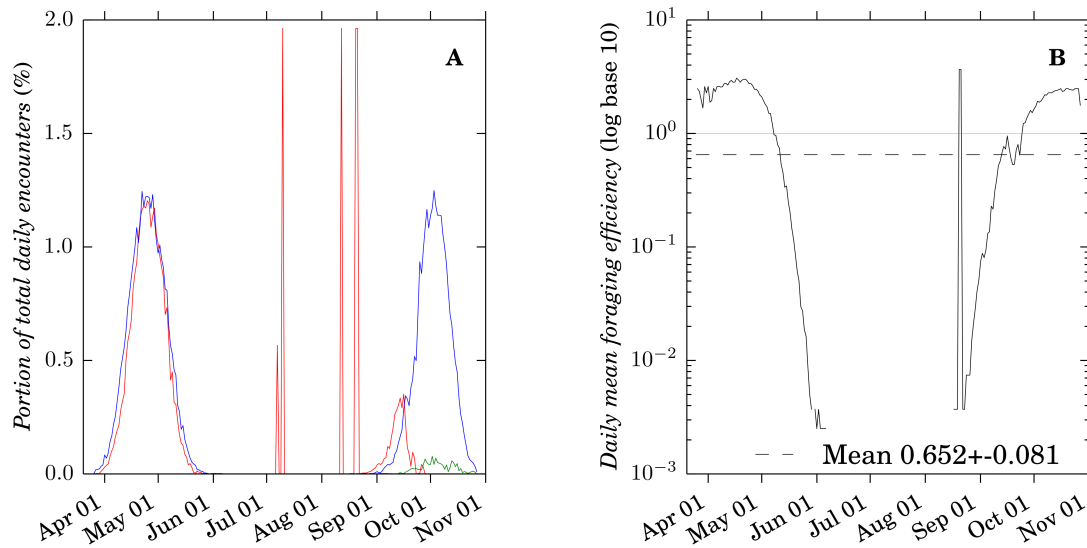


Figure 3.15: Daily prey encounter rates by prey type and daily energy efficiency of the population using the HM strategy; $R_{mov} = 0.0$; $d_{fmax} = 2$. **A** Percent of daily prey encounters of the population by type: herring (red line), blue whiting (blue line), and mackerel (green line). **B** Daily mean energy efficiency of the population (Eff_{pop}) with SEM (CI 95%). The solid red line marks $Eff_{pop} = 1.000$.

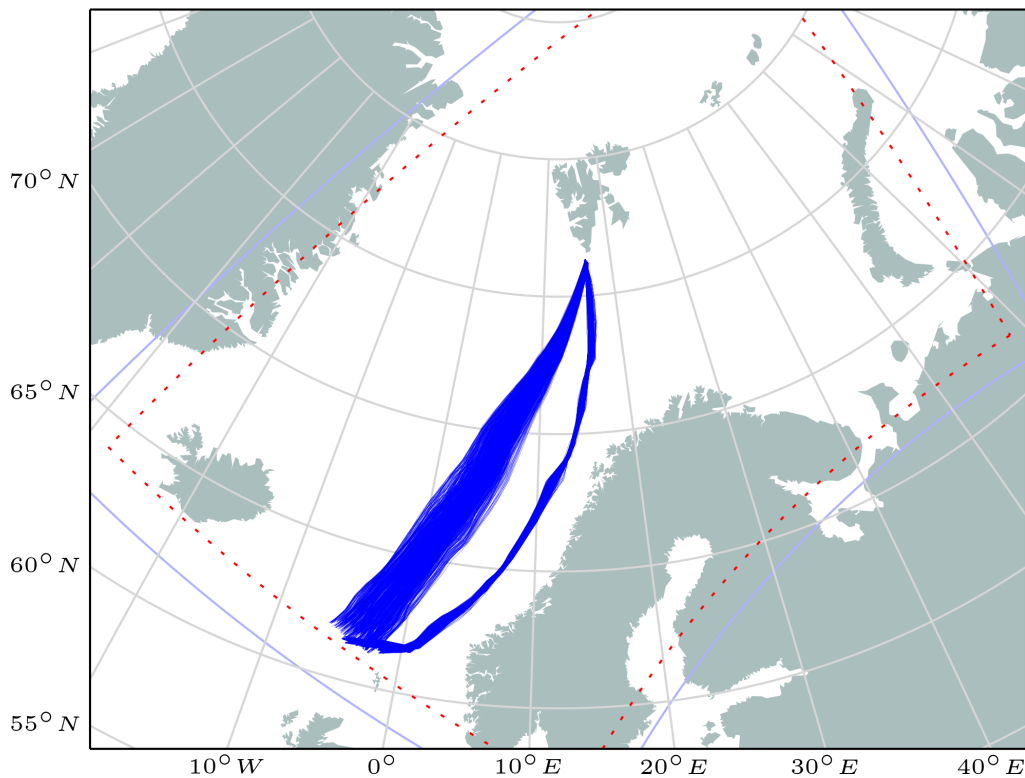


Figure 3.16: Minke population track-lines for the simulation year 1998 using the HM strategy; $R_{mov} = 0.0$; $d_{fmax} = 2$. The light blue solid line marks the model grid area, with the red dashed line marking the offset boundary containing the whale movement. Dark blue lines are drawn along tracklines of individual whales.

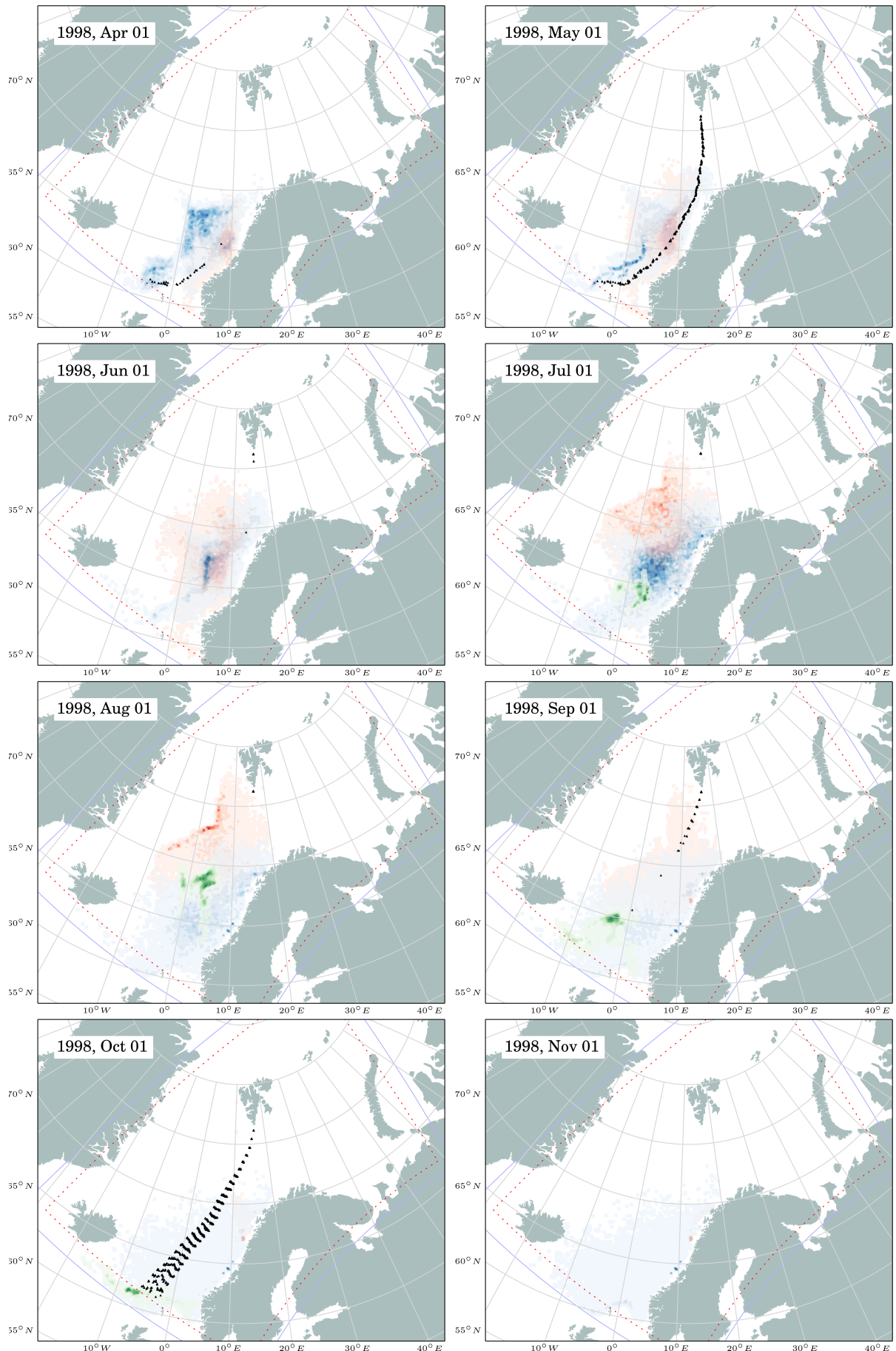


Figure 3.17: Monthly distribution of simulated whales using the HM strategy; $R_{mov} = 0.0$; $d_{fmax} = 2$. Whales shown as black triangles. Herring distribution is shown in shades of red, blue whiting in shades of blue, and mackerel in shades of green. The model area is bound by a solid blue line with the offset containing whale movement shown as a dashed red line.

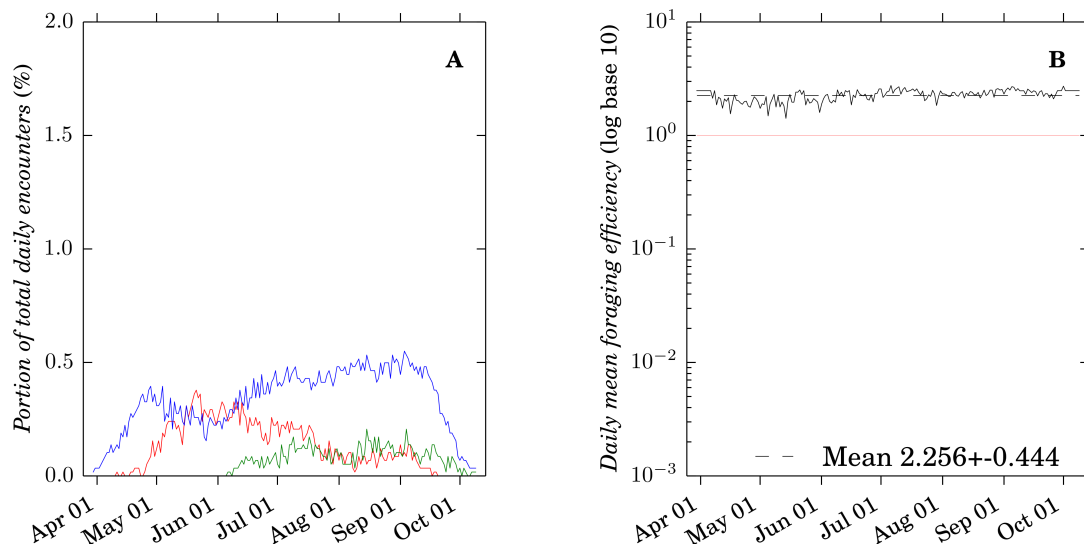


Figure 3.18: Daily prey encounter rates by prey type and daily energy efficiency of the population using the MPDS-R strategy; $R_{mov} = 1.8$; $d_{fmax} = 2$. **A** Percent of daily prey encounters of the population by type: herring (red line), blue whiting (blue line), and mackerel (green line). **B** Daily mean energy efficiency of the population (Eff_{pop}) with SEM (CI 95%). The solid red line marks $Eff_{pop} = 1.000$.

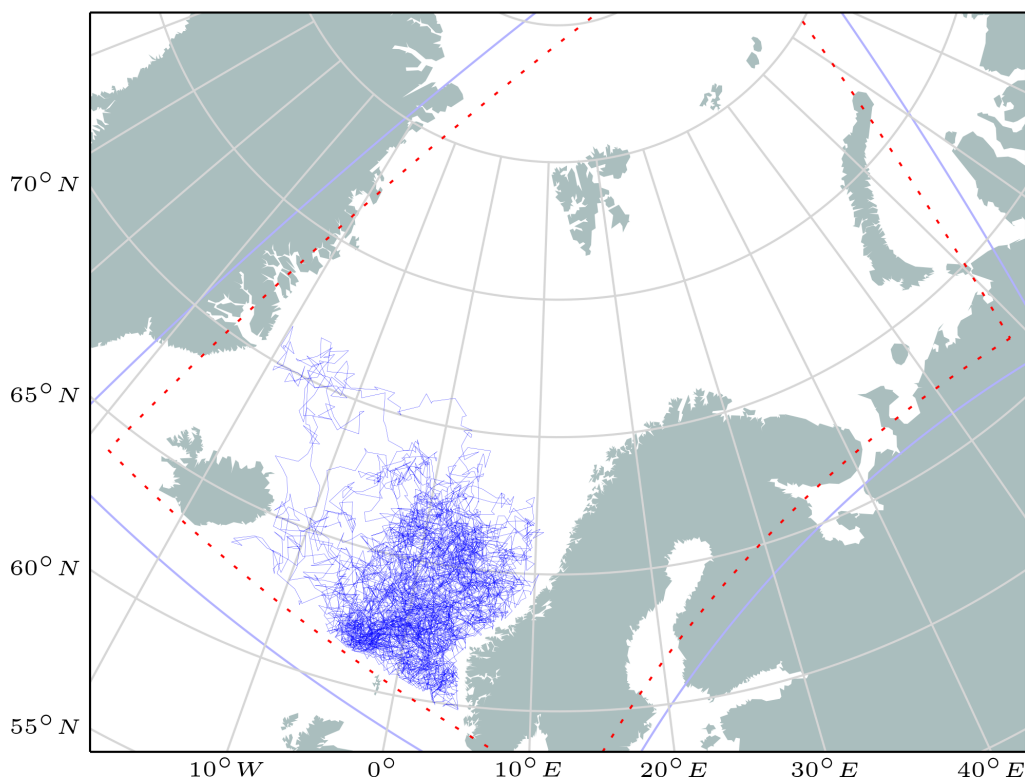


Figure 3.19: Minke population track-lines for the simulation year 1998 using the MPDS-R strategy; $R_{mov} = 1.8$; $d_{fmax} = 2$. The light blue solid line marks the model grid area, with the red dashed line marking the offset boundary containing the whale movement. Dark blue lines are drawn along tracklines of individual whales.

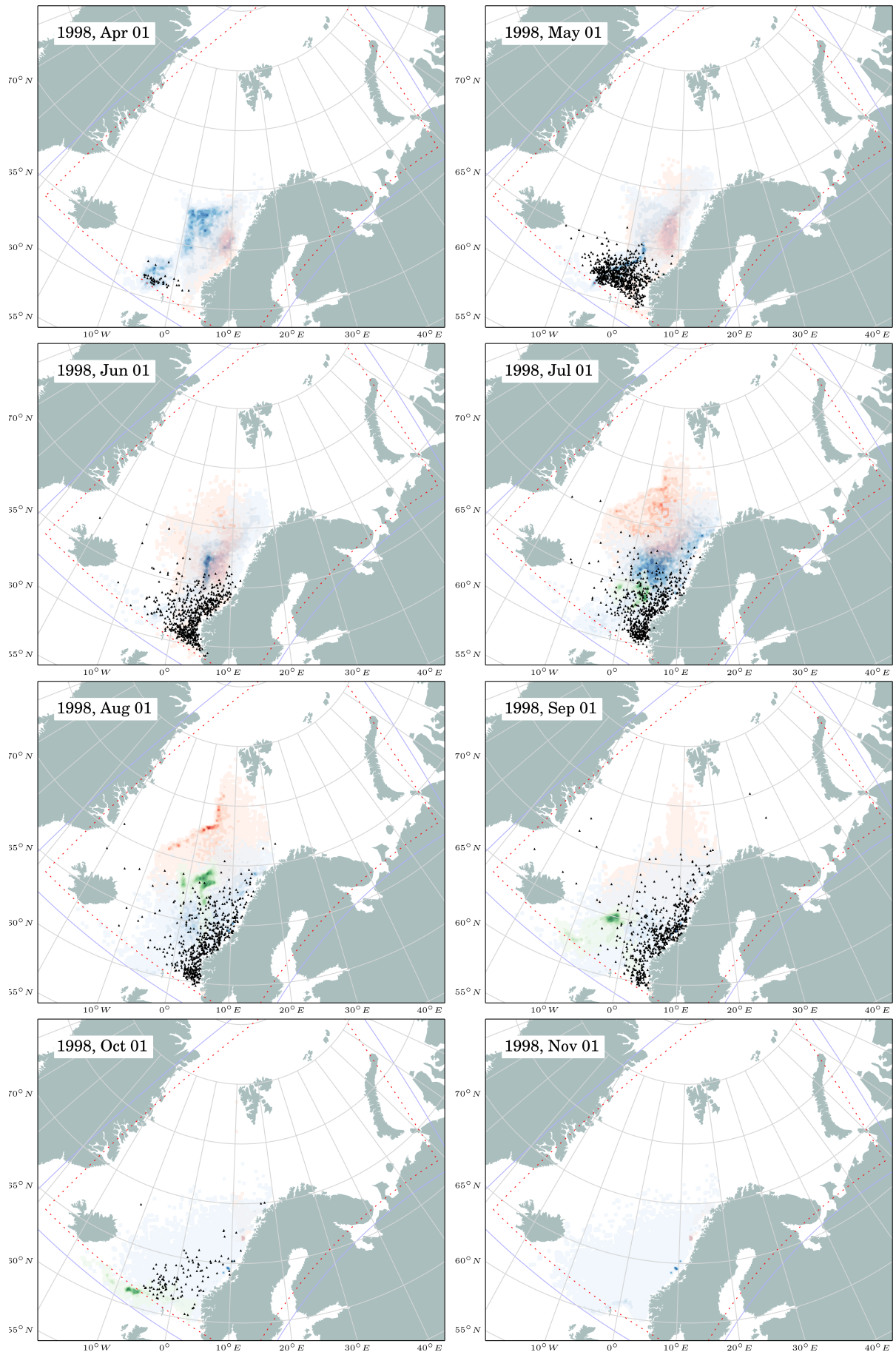


Figure 3.20: Monthly distribution of simulated whales using the MPDS-R strategy; $R_{mov} = 1.8$; $df_{max} = 2$. Whales shown as black triangles. Herring distribution is shown in shades of red, blue whiting in shades of blue, and mackerel in shades of green. The model area is bound by a solid blue line with the offset containing whale movement shown as a dashed red line.

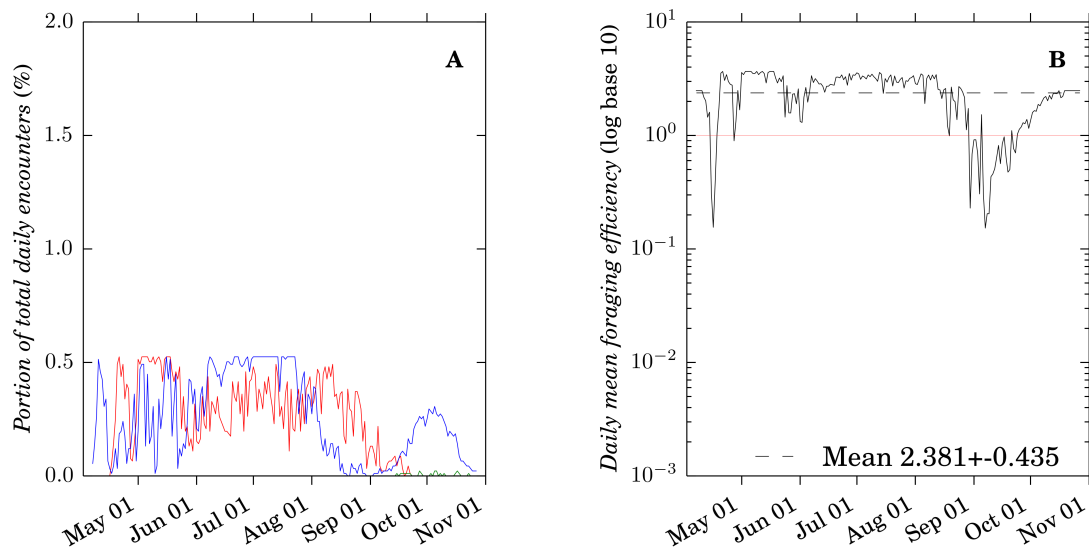


Figure 3.21: Daily prey encounter rates by prey type and daily energy efficiency of the population using the MPDS-H strategy; $R_{mov} = 0.0$; $d_{fmax} = 10$. **A** Percent of daily prey encounters of the population by type: herring (red line), blue whiting (blue line), and mackerel (green line). **B** Daily mean energy efficiency of the population (Eff_{pop}) with SEM (CI 95%). The solid red line marks $Eff_{pop} = 1.000$.

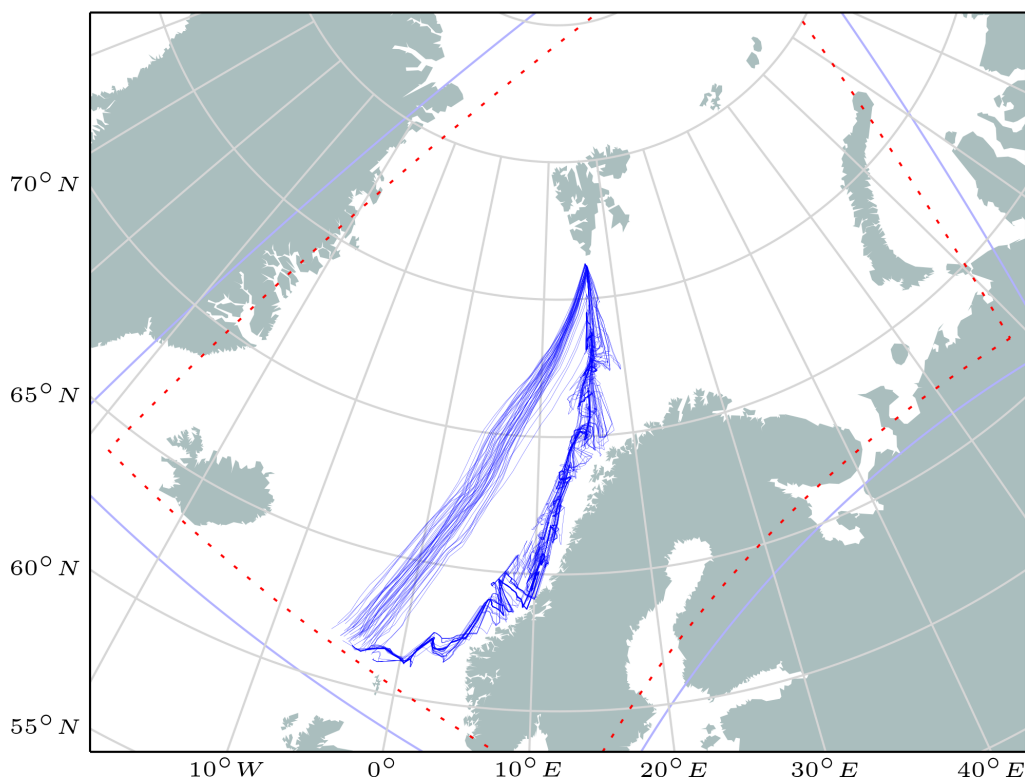


Figure 3.22: Minke population track-lines for the simulation year 1998 using the MPDS-H strategy; $R_{mov} = 0.0$; $d_{fmax} = 10$. The light blue solid line marks the model grid area, with the red dashed line marking the offset boundary containing the whale movement. Dark blue lines are drawn along tracklines of individual whales.

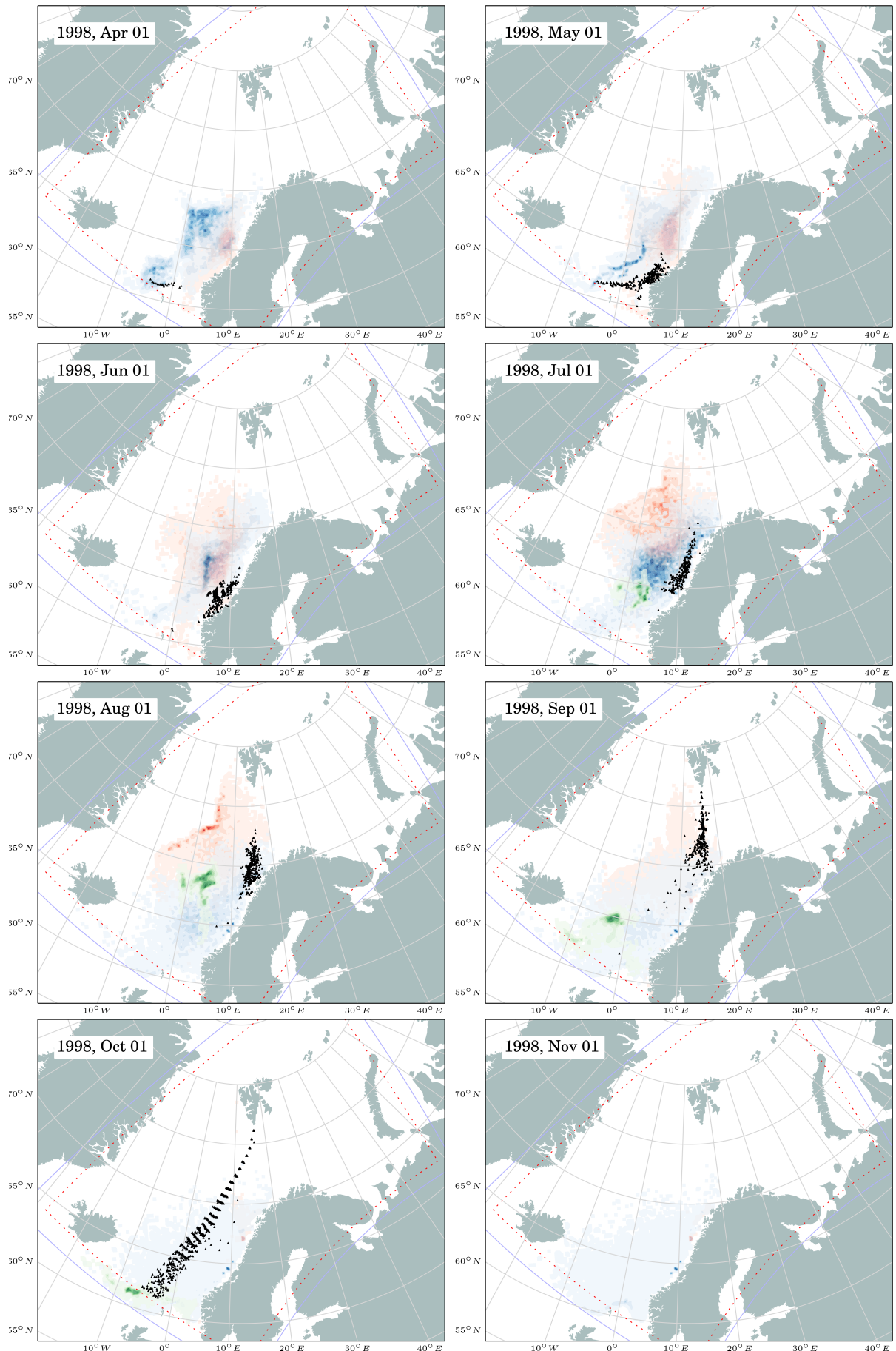


Figure 3.23: Monthly distribution of simulated whales using the MPDS-H strategy; $R_{mov} = 0.0$; $d_{fmax} = 10$. Whales shown as black triangles. Herring distribution is shown in shades of red, blue whiting in shades of blue, and mackerel in shades of green. The model area is bound by a solid blue line with the offset containing whale movement shown as a dashed red line.

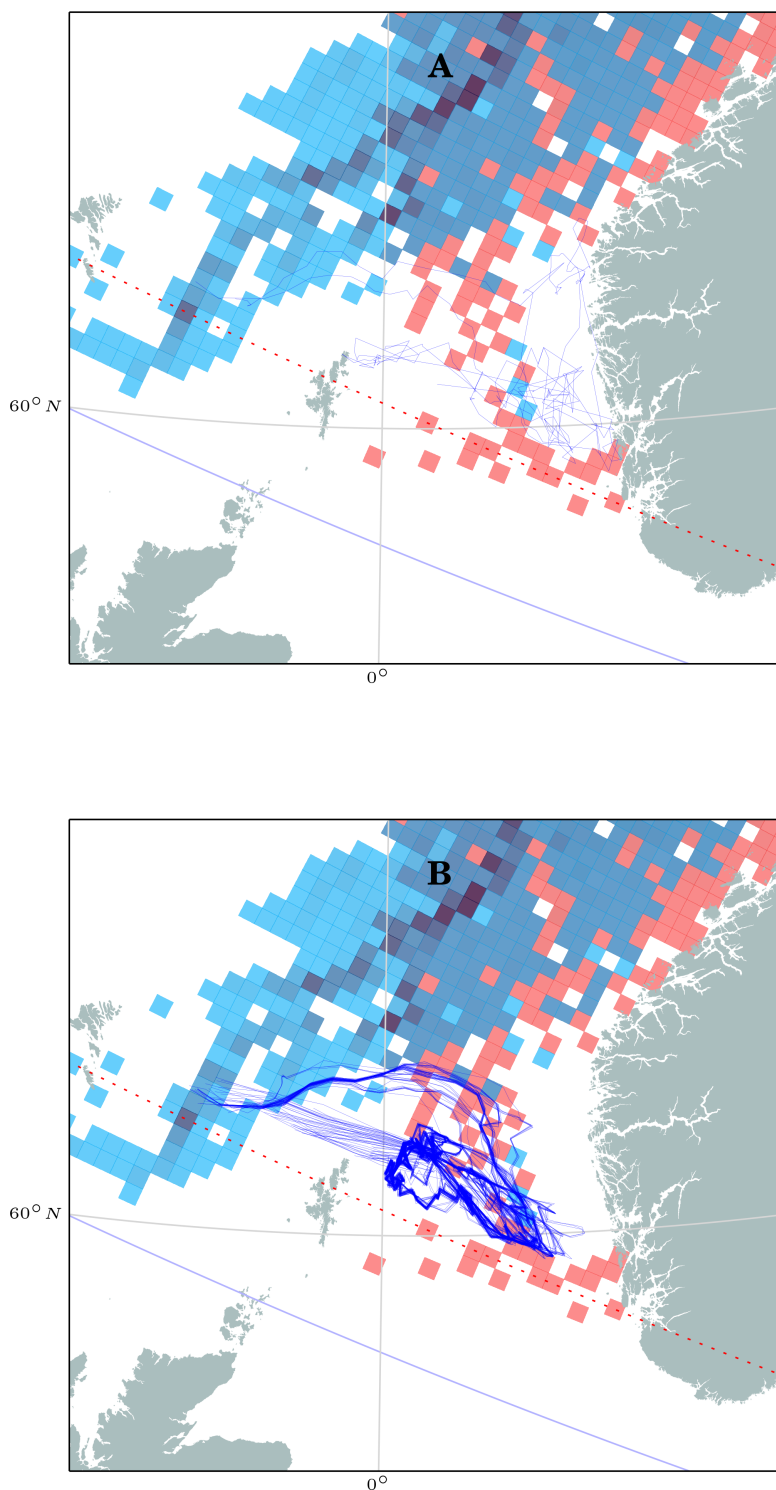


Figure 3.24: Minke population track-lines for the simulation year 1998 using the **A** MPDS-H5 and **B** MPDS-H6 strategies; $R_{mov} = 0.0$; $d_{feed} = 2000$. The light blue solid line marks the model grid area, with the red dashed line marking the offset boundary containing the whale movement. Dark blue lines are drawn along tracklines of individual whales. Gridded fish distributions are shown for 01 May, 1998. The species present on this day are herring (red grid-cells) and blue whiting (blue grid-cells).

Chapter 4

Discussion

4.1 Simulation evaluation

4.1.1 Currents

The effect of predominant currents on whale movement in the NC and NSC corresponds to the relative difference in current magnitudes between these two areas, as depicted by (Orvik *et al.*, 2001; Skagseth *et al.*, 2011). While point values presented by Skagseth *et al.* (2011) and Orvik *et al.* (2001) describe the Norwegian Coastal Current as being roughly 1.5 to 2 times greater in velocity than the Norwegian Atlantic Current, the mean speed of the whales ($3.195 \pm 0.028 \text{ km h}^{-1}$ with currents on; Table 3.1) is large compared to the speed of both currents (34.1 cm s^{-1} or 1.23 km h^{-1} for the NCC; Skagseth *et al.*, 2011), leaving the signal from currents in the whales' speed less pronounced.

With currents deactivated, the average speed of the population was consistently higher than the parameterized speed (2.7 km h^{-1}) (Figure 3.4). This difference is thought to be the result of an inaccuracy in interpolation within the NORWECOM.E2E routine used to transform geodesic whale coordinates to grid coordinates for each movement. The variability in the population's mean speed during the in-migration period of the deactivated current simulation is likely the combined result of this coordinate transformation error and the method of waypoint selection (described in section 2.2.2.3). If some whales are stopping short of their maximum daily travel distance, having reached a waypoint, the daily minimum speed of the population will be consistently lower, while the maximum daily individual speed should be constant along a path with no intermediate waypoints such as the NSC.

4.1.2 Migration

The effect of current systems was most pronounced when alternating the direction whale movement along the NC and GC paths (Table 3.1). With an

estimated population of 108140 whales (Bøthun *et al.*, 2009), the approximate 8 day difference in travel days would amount to an additional expenditure of 2.768×10^{11} kJ for the population (based on the expenditure value from Blix and Folkow, 1995) or an equivalent of 4.465×10^4 t of herring (using Equation 2.8 and the averaged energy value for herring derived from values presented by Pedersen and Hislop, 2001).

Migration times to the feeding location off Bear Island are shorter along the NSC path compared to the NC; however, daily individual speed maxima and minima indicate a large degree of variability experienced due to currents along the NC compared to the NSC (Figure 3.8). Despite paths being routed through areas of highest current velocity, these are linear best-guesses, which do not reflect local variability in current speed and direction that could result in some individuals occasionally moving through counter-productive eddies. If whales were to use these systems to their benefit, they would presumably also avoid localized flows that would not aid their movement. The maxima seen in daily individual speed and mean speed of the population for the NC are much larger than the NSC (as an in-path; Table 3.1). This could potentially be maintained for the entire population if they were to navigate the current system more intelligently. Given the mean population speed and patterns in individual speeds from this path configuration, along with increased encounters of herring and a higher foraging efficiency, the NC is expected to be the more rewarding in-migration path for minke.

While the GC may be the migration out-path yielding the highest travel speeds, this path is mostly absent of prey species used in this study for the simulation year (Figures 2.7- 2.9). Despite other prey known to minke in this area (Neve, 2000), they could potentially still use this pathway without feeding if they were to fast following their summer feeding similar to Humpback whales (*Megaptera novaeanglia*), as observed by Bentley (1963).

Though a feasible migration path, the additional distance of the GC path, compared to the direct NSC path, adds roughly 5.5 d to the mean out-period for the population. Humpbacks are also shown to follow direct routes to breeding grounds during their migration after feeding (Paterson, 1991), which may be expected with minke. The NSC yielded the shortest migration-period of all out-paths, which is the most direct path the whales could take to their exit locations (Table 3.1).

4.1.3 Foraging

The RW strategy was the most rewarding strategy not incorporating maximum density searching, and attained a mean efficiency higher than all MPDS-H and simulations with the exception of MPDS-H5 (where d_{feed} was set to 10 d). This high efficiency, more than twice the level of balanced energy consumption and use (i.e. $E_{ff_{pop}} = 1.000$), appears to be due to the wide area coverage and a dispersal timing that coincides with prey dispersed having higher concentrations in the south from April to July, with wider distributions in August and

September (Figure 3.14). The higher encounter rate of mackerel also suggests this, as the distribution of mackerel did not extend as far north as both herring and blue whiting.

Movement of the HM1 strategy population went very quickly to the presumed feeding area and through the prey field, and it had the lowest prey encounters and efficiency for all strategies (with the exception of MPDS-H6). The HM1 simulation population (with $R_{mov} = 0$) had direct movement at the maximum travel distances for each day-step, gaining slightly higher efficiency by reaching the herring distribution located nearer to shore and the NC path (Figure 3.17). Despite having more dispersed movement with a higher R_{mov} , the HM2 population traveled slower along the NC, and the portion of the population migrating later experienced lower herring encounters and a lower efficiency due to blue whiting having a lower energy content than herring (Pedersen and Hislop, 2001).

The MPDS strategies both benefited from increases in R_{mov} resulting in more dispersed distributions, and their populations remained in lower latitudes with slower movement northward, yielding higher encounters. Whereas, the effect of increasing d_{fmax} was negatively rewarding for MPDS-R simulations and positively rewarding for MPDS-H simulations. For MPDS-R simulations, increases in d_{fmax} caused larger numbers of the population to be restricted to areas near the southern Norwegian coast with only their preferred prey of herring present, which the maximum density searching had led them to follow upon entering the model area. Increasing d_{fmax} in MPDS-H simulations from 2 d to 6 d and 10 d allowed the population to follow prey densities after having moved to higher latitudes, with each increase in feeding period yielding higher encounters and efficiency. The MPDS-R6 and MPDS-H6 populations (with $d_{fmax} = 2000$) followed herring towards the southern Norwegian coast where only herring was present. As prey distribution is less homogeneous in this area, the lack of other prey left less opportunity for encounters, with herring only intermittently available. MPDS-R6 appears to be slightly more efficient than MPDS-H6 due to more disperse movements in this area while MPDS-H6 whales would aggregate into the same low-encounter region while traveling towards a shared homing waypoint when no prey is present (Figures 3.24A and B).

Based on the above observations, a depleting prey field would likely pose a greater reduction in efficiency for strategies that incorporate random-walk. Despite setting a threshold at which whales decide to abandon prey areas, both MPDS-R and RW would be disadvantaged similarly in that the whales would return to areas already visited. It has been shown with random-walk foraging that prey decreases exponentially in areas where foragers return after prior depletion without restriction (Schoener, 1971), while discriminating against areas previously foraged likely results in saved time and energy (Baum, 1987). Though MPDS-R and MPDS-H strategies have the ability to follow a patch until a threshold density is reached, MPDS-H would move the whales along a predicted path into new prey regions, where MPDS-R would allow the possibility of revisiting previous foraged areas until an adequate density is found.

Despite the efficiency of MPDS-5 being seemingly close to that of MPDS-R3, there were extended periods of low efficiency for MPDS-H5 in May while migrating along low fish density areas, and from August to October when portions of the population were located at the Bear Island feeding location (Figure 3.21B). In addition, overall travel distances for MPDS-R were comparatively higher than MPDS-H, which suggests that a more sophisticated bioenergetic model, with a direct metabolic response to movement, would yield lower efficiencies for MPDS-R. Both of these factors support MPDS-H5 as being the most rewarding strategy.

Other studies have found marine predators to perform migratory movements with periods of foraging where they seek density patches. In a study by [Sims et al. \(2006\)](#), satellite tracked basking sharks were 90% more effective at finding areas of high zooplankton concentration using directed movements and area restricted search (ARS) when prey patches were found and then compared to simulated sharks using a random-walk foraging strategy. The tagging study by [Silva et al. \(2013\)](#) also identifies similar behavior in both blue and fin whales, which are closely related members of minke in the *Balaenoptera* family, who perform large-scale migrations with periods of ARS at various intervals (Figure 4.1).

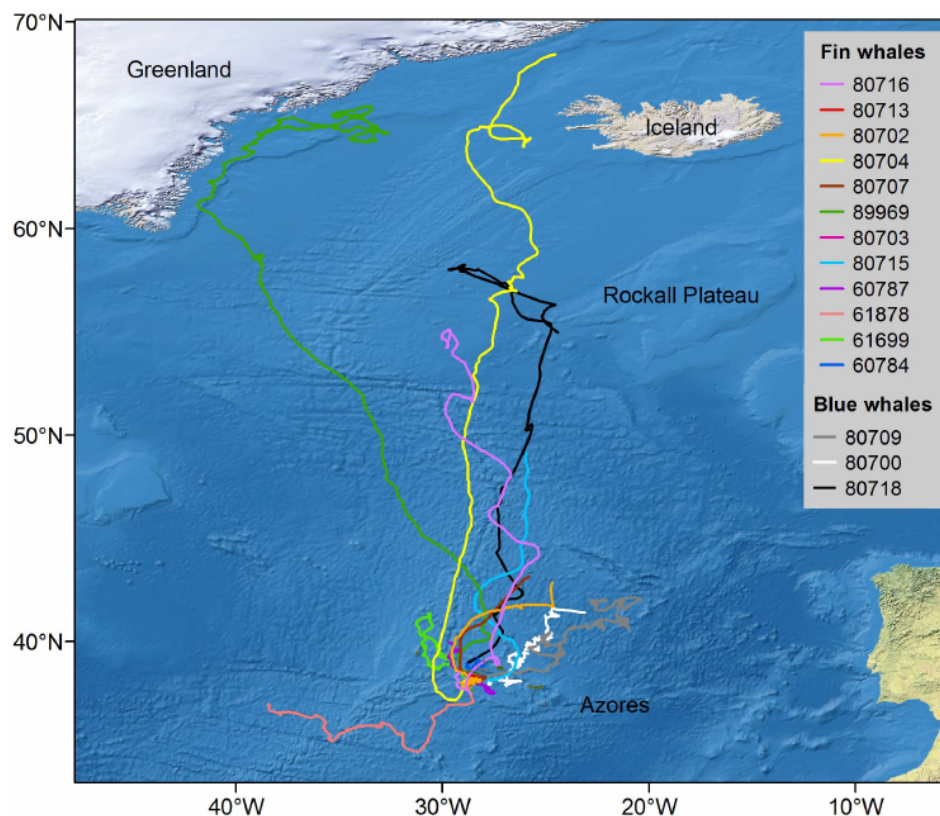


Figure 4.1: Tracks derived from ARGOS satellite positions of blue and fin whales using a hierarchical switching state-space model (Taken from [Silva et al., 2013](#)).

4.1.4 Further improvements

Means of migration period, speed and efficiency are useful for comparisons of migration and foraging strategies; however, the range of associated SEM values are not sufficient to statistically differentiate them, which was a result of insufficient an sample size. An additional reduction in sample size occurred due to movement of whales off the model grid and over land, and in some cases, nearly the entire population moved off-grid or over land (e.g. MPDS-R6 and MPDS-H6) reducing the sample size to a few individuals.

This erroneous movement could be addressed by implementing a method for navigation around land obstacles and by working strictly within the grid coordinate system, rather than performing transformations from geodesic coordinates. A recent example of intelligent path searching is given by [Almeida \(2013\)](#), using Dijkstra's algorithm ([Dijkstra, 1959](#)) to navigate simulated humpback migrations through a gridded current field to compare their movements to tracks obtained from satellite-tagged humpbacks. Movements off the model grid would not be possible if movement routines were to be based solely on the grid coordinate system, which would avoid the need for interpolation until output positions are generated. Combining these improvements with simulations that have much larger population sizes (and computation times) would allow for smaller error in the means to better differentiate the simulation success.

Along with correcting these errors, general improvements to the model build and optimization of the characterizations of minke and their interaction with the ecosystem are necessary. Calibration of resulting distributions to annual sighting-surveys could be done to further determine if the model is simulating minke movements realistically, for example, a root mean square deviation (RMDS), which was used by [Utne and Huse \(2012\)](#) for validation of the fish distributions used as prey fields in this study. A more advanced bioenergetic model could be implemented that encompasses attributes of mortality, reproduction, sex, and maturity, as well as natural variability amongst all ascribed attributes, rather than point values. Changes in R_{mov} and d_{fmax} feeding duration had a notable effect on model results, but optimal values for these and other parameters, such as d_{tmax} and order of prey preference could still be determined.

Chapter 5

Conclusion

The first spatially-explicit individual based model for minke whales was developed in this study and has been used to provide insight into the effect of predominant circulation patterns on possible minke migrations, as well as the energetic reward for minkes to use predictive foraging behavior. These large-scale behaviors were tested in a series of simulations with variation in minke migratory paths and foraging strategies. Migratory paths that followed areas of maximum velocity and coincided with the direction of whale movement were found to dramatically enhance the migration speed of minkes, and trends in individual whale speeds and available prey suggest that migration into Nordic seas along the Norwegian Coastal Current would be most rewarding with the best exit-route directly through the central Norwegian sea. Using a simplistic bioenergetic model, the foraging strategy incorporating migration and allowing for periodic feedings of 10 d was the most energetically rewarding. From these findings, it is both (1) more rewarding for North Atlantic common minke whales to migrate in the direction of predominant ocean circulation patterns in the Nordic Seas, and (2) more energetically advantageous for minkes to combine migratory movement with periodic searches for highest prey density compared to random-walk foraging, strictly migratory movement, or random-walk with periodic maximum prey density searching.

Understanding the movements of minkes in the Nordic Seas will assist in determining existing stock-structure, important for selection of appropriate management units (Frank and Brickman, 2000). With sub-stock structure of minkes remaining uncertain and disputed (Donovan, 1991), the results of this study suggest that individuals migrating along the Norwegian coast, Spitsbergen, and Barents Sea may energetically benefit from returning through the central Norwegian Sea, an area thought by some to have a distinct sub-stock of minkes found along the NC and Barents Sea (Andersen *et al.*, 2003; Born *et al.*, 2003), which could allow for interaction between these sub-stock if they exist. Humpbacks have been known to migrate directly against prevalent currents (Horton *et al.*, 2011), so it could not be considered unlikely for minkes given their comparatively high swimming efficiency (Blix and Folkow, 1995), which could suggest more isolation between sub-stocks.

Random-walk foraging experienced similarly high foraging reward to MPDS

strategies, which is in contradiction to previous studies on large marine predators. The non-depleting prey field used herein is expected to particularly increase efficiency of these strategies, which could be further examined following implementation of an intelligent path searching routine and optimization of the model parameters. The success of predictive foraging with prey-density searching foraging supports by the findings of [Silva *et al.* \(2013\)](#) who observed both blue and fin whales following long migrations with periods of area restricted search foraging.

Gathering more dynamic data would be immensely helpful for the further investigation of minke movement and spatial distribution. Satellite tagging studies of blue whales ([Bailey *et al.*, 2009](#)) have yielded tracks lasting more than 500 d, and logging of interactions between individuals is now possible through peer-to-peer tagging technology ([Holland *et al.*, 2009](#)). Such position data could be used to calibrate theoretical movements from the minke IBM to modeled movements fit by tagging data as has been done in recent studies ([Bailey *et al.*, 2009](#); [Papastamatiou *et al.*, 2013](#)).

The minke IBM has provided a new method for investigating the movements of North Atlantic common minke whales, and with it, useful methods for visualization of spatial data have been developed to facilitate model development and data interpretation (Appendix 6.B). In addition, this model can be extended to implement other cetacean species into the NORWECOM.E2E model, and there is a broad range of applications to these tools may be applied. With further development and more dynamic data, great potential exists for answering difficult questions surrounding the life-history, management, and conservation of minkes and other cetaceans.

Chapter 6

Appendices

Appendix 6.A Minke IBM Movement Routines

The minke module is composed of four Fortran modules called within NORWECOM.E2E (Figure 6.1). All files total 1944 lines of Fortran code. Code from the general movement routine was adapted from Kjell Utnes pelagic fish movement routine [Utne and Huse \(2012\)](#).

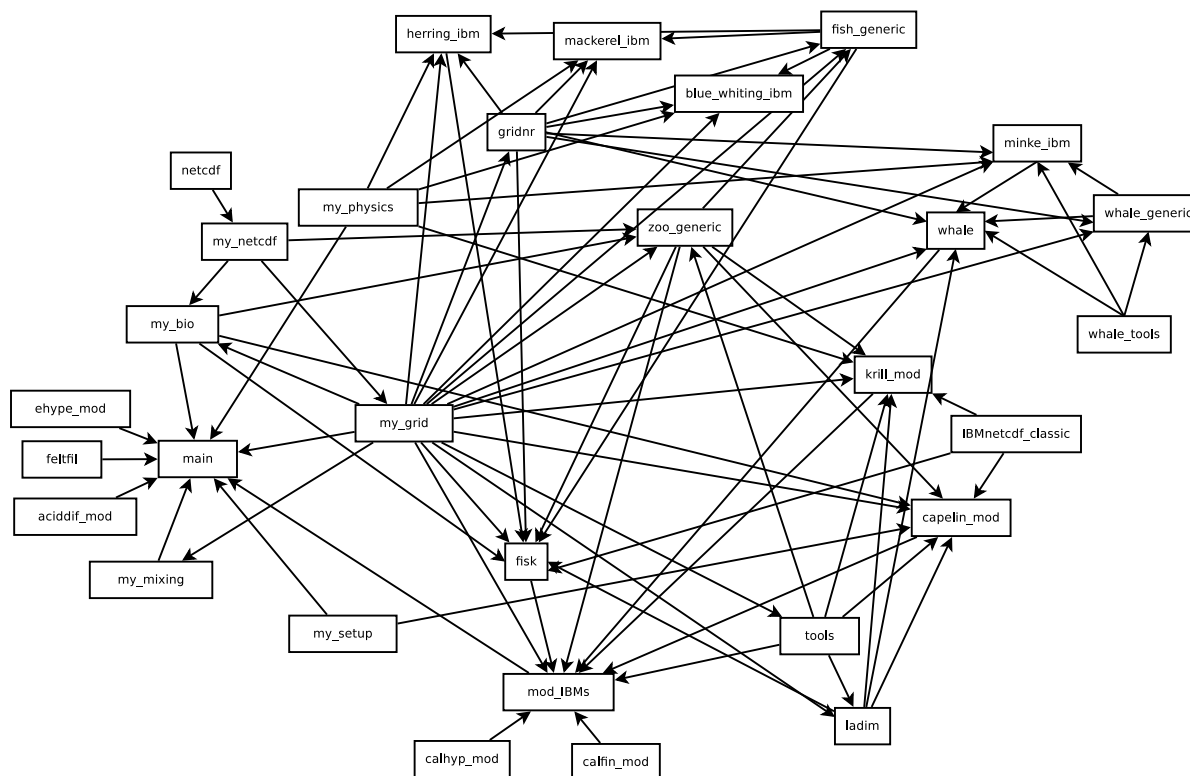


Figure 6.1: NORWECOM.E2E module environment with minke IBM (top-right)

6.A.1 Movement routines

```

1  !-----!
2  ! Main whale movement routine !
3  !-----!
4
5  subroutine move_whales(stock, ndate, hr, bw, mk)
6
7
8  ! Movement routine for whales
9  ! modified from ownmovfish() in fish_generic.F90
10
11 use my_grid , only : latit, longit, parea, fsm, im, jm, depth_zz
12 use mod_gridint ! with update bilin_inv routine
13 use my_physics, only : t
14 use minke
15 use ladim
16
17 implicit none
18

```



```

19  ! Whale class object
20  class(whale_ibm), intent(inout) :: stock ! whale stock class instance
21  ! Iterators and numbers
22  integer :: i ! whale individual iterator
23  real :: random_num ! temp random number variable
24  ! Time parameters
25  integer :: daynr ! current integer day of 365 day year
26  integer :: ndate(5) ! current integer date array
27  integer :: year ! current integer year
28  integer :: month ! current integer month
29  integer :: day ! current integer day
30  ! Prey data arrays
31  real, dimension(im, jm) :: bw ! grid biomass - blue whiting
32  real, dimension(im, jm) :: hr ! grid biomass - herring
33  real, dimension(im, jm) :: mk ! grid biomass - mackerel
34  ! Check land
35  integer :: ec(9) = (/0,2,0,0,-2,-2,-2, 0,0/) ! TODO
36  integer :: nc(9) = (/0,2,0,2, 2, 0,-2,-2,0/) !
37  ! Movement parameters
38  real :: dist_max ! Max daily swimming dist based on speed
39  real :: dlon_m ! change in lon/ypos in meters
40  real :: dlat_m ! change in lat/xpos in meters
41  real :: m_lon ! meters in one degree longitude
42  real :: m_lat ! meters in one degree latitude
43  ! Position parameters
44  real :: curr_lon ! decimal longitude position - current
45  real :: curr_lat ! decimal latitude position - current
46  real :: lon ! current check lon
47  real :: lat ! current check lat
48  real :: curr_pos(2) ! grid index position output from ll2grd()
49  real :: curr_xpos ! decimal grid index position - current
50  real :: curr_ypos ! decimal grid index position - current
51  real :: curr_zpos ! decimal grid index position - current
52  real :: last_xpos ! decimal grid index position - current
53  real :: last_ypos ! decimal grid index position - current
54  real :: new_lon ! decimal longitude position - current
55  real :: new_lat ! decimal latitude position - current
56  real :: new_pos(2) ! decimal grid index of new position
57  real :: new_xpos ! decimal grid index position - new
58  real :: new_ypos ! decimal grid index position - new
59  real :: rand_xpos ! decimal grid index position - random-walk
60  real :: rand_ypos ! decimal grid index position - random-walk
61  real :: dest_xpos ! decimal grid index position - destination
62  real :: dest_ypos ! decimal grid index position - destination
63  real :: hom_xpos ! decimal grid index position - homing
64  real :: hom_ypos ! decimal grid index position - homing
65  integer :: hom_idx ! homing array index position
66  ! Random-walk
67  real :: random_angle ! random walk heading
68  ! Prey search
69  logical :: prey_found ! bool - .true. = prey found via prey search
70  logical :: well_fed ! bool - .true. = max feeding reached
71  real :: p1_zpos ! decimal grid index position - current
72  real :: p2_zpos ! decimal grid index position - current
73  real :: p3_zpos ! decimal grid index position - current
74  logical :: p1_inrange ! bool - .true. = in feeding range
75  logical :: p2_inrange ! bool - .true. = in feeding range
76  logical :: p3_inrange ! bool - .true. = in feeding range

```

```

77  real :: p1_thresh      ! biomass threshold to enter feeding movement
78  real :: p2_thresh      ! biomass threshold to enter feeding movement
79  real :: p3_thresh      ! biomass threshold to enter feeding movement
80  real :: fishmax_idx(2) ! grid index position of max fish density - ll2grd()
81  integer :: x_min       ! xpos of prey detection range to west
82  integer :: x_max       ! xpos of prey detection range to east
83  integer :: y_min       ! ypos of prey detection range to north
84  integer :: y_max       ! ypos of prey detection range to south
85  integer :: di          ! index distance in i (y) dir for prey search
86  integer :: dj          ! index distance in j (x) dir for prey search
87
88
89  print *, 'move whales'
90
91  ! Assign integer date values from ndate
92  year  = ndate(1)
93  month = ndate(2)
94  day   = ndate(3)
95  daynr = daynumber(year, month, day)
96
97  ! Prey preference and strategy configuration
98  ! p1,p2,p3 arrays allocated in whale.F90>whale_ibm
99  select case (p1_id)
100     case(0)
101         p1 = hr
102         p1_zpos = hr_zpos
103         p1_thresh = hr_thresh
104     case(1)
105         p1 = bw
106         p1_zpos = bw_zpos
107         p1_thresh = bw_thresh
108     case(2)
109         p1 = mk
110         p1_zpos = mk_zpos
111         p1_thresh = mk_thresh
112  endselect
113
114  select case (p2_id)
115     case(0)
116         p2 = hr
117         p2_zpos = hr_zpos
118         p2_thresh = hr_thresh
119     case(1)
120         p2 = bw
121         p2_zpos = bw_zpos
122         p2_thresh = bw_thresh
123     case(2)
124         p2 = mk
125         p2_zpos = mk_zpos
126         p2_thresh = mk_thresh
127  endselect
128
129  select case (p3_id)
130     case(0)
131         p3 = hr
132         p3_zpos = hr_zpos
133         p3_thresh = hr_thresh
134     case(1)

```

```

135     p3 = bw
136     p3_zpos = bw_zpos
137     p3_thresh = bw_thresh
138     case(2)
139     p3 = mk
140     p3_zpos = mk_zpos
141     p3_thresh = mk_thresh
142 endselect
143
144 ! Start movement routine
145 !-----
146 print *, 'Start movement routines'
147
148 ! Loop through populations to move
149 do i=1,stock%pop
150
151     ! Get decimal grid index position of whale
152     curr_xpos = stock%whale(i)%xpos
153     curr_ypos = stock%whale(i)%ypos
154     curr_zpos = stock%whale(i)%zpos
155
156     if (stock%whale(i)%active.eq..true.) then
157
158         ! Convert decimal grid index positions to lon/lat
159         curr_lon = grd2ll(longit,curr_xpos,curr_ypos)
160         curr_lat = grd2ll(latit,curr_xpos,curr_ypos)
161
162         ! change migration course by date and position
163         if (feed_only_on == .true.) stock%whale(i)%migday2 = 365
164
165         if (daynr >= stock%whale(i)%migday2 .and. &
166             stock%whale(i)%goinghome == .false.) then
167             call update_homing(stock, i, daynr)
168         endif
169
170         hom_xpos = stock%whale(i)%hom_idx
171
172         ! Determine max meters whale can swim in 24hrs
173         dist_max = stock%whale(i)%sspeed*24. ! speed(m/hr)*hrs/day
174
175         ! Set distance whales may move each iteration until max daily dist
176         dist_step = 15000.0 ! just below minimum vert/horiz grid resolution
177
178         ! Set distance traveled and prey encountered to zero
179         stock%whale(i)%dist_trav = 0
180         dist_trav = 0
181         p1_found = 0
182         p2_found = 0
183         p3_found = 0
184         stock%whale(i)%p1_found = 0
185         stock%whale(i)%p2_found = 0
186         stock%whale(i)%p3_found = 0
187
188         ! Random walk
189         !-----
190         if (prey_strategy.eq.0) then
191
192             last_xpos = curr_xpos

```

```

193     last_ypos = curr_ypos
194
195     !slice must be larger than dist_step, else big loop
196     if (daynr < stock%whale(i)%migday2) then
197
198         call move_random(new_xpos, new_ypos, curr_xpos,curr_ypos)
199         rand_xpos = new_xpos
200         rand_ypos = new_ypos
201
202         do while (dist_trav <= dist_max)
203
204             ! Check if at new position
205             if (newpos_exit(curr_xpos, curr_ypos, &
206                 rand_xpos, rand_ypos) == .true.) exit
207
208             call move_newpos(rand_xpos,rand_ypos,curr_xpos,curr_ypos, &
209                 dist_trav, &!dist_step, &
210                 p1_found, p2_found, p3_found, stock, i)
211
212             if (curr_xpos < grid_offset .or. &
213                 curr_ypos < grid_offset .or. &
214                 curr_xpos > im-grid_offset .or. &
215                 curr_ypos > jm-grid_offset) then
216                 curr_xpos = last_xpos
217                 curr_ypos = last_ypos
218             exit
219         endif
220
221         ! TODO call check_land(curr_xpos, curr_ypos)
222     enddo ! dist stepping
223
224     elseif (daynr >= stock%whale(i)%migday2) then
225         do while (dist_trav <= dist_max)
226             ! Move to next homing position if homing reached
227             ! return path used should only have exit position (all -999)
228
229             call next_homing(stock%whale(i)%hom_xpos, &
230                 stock%whale(i)%hom_ypos, &
231                 stock%whale(i)%hom_idx, &
232                 curr_xpos, curr_ypos)
233
234             new_xpos = stock%whale(i)%hom_xpos(stock%whale(i)%hom_idx)
235             new_ypos = stock%whale(i)%hom_ypos(stock%whale(i)%hom_idx)
236
237             ! Check if at new position and at end of homing path
238             if (homing_exit(stock, i, curr_xpos, curr_ypos, &
239                 new_xpos, new_ypos) == .true.) exit
240
241             if (curr_xpos < grid_offset .or. &
242                 curr_ypos < grid_offset .or. &
243                 curr_xpos > im-grid_offset .or. &
244                 curr_ypos > jm-grid_offset) then
245                 stock%whale(i)%active = .false.
246             exit
247         endif
248
249         call move_newpos(new_xpos,new_ypos,curr_xpos,curr_ypos, &
250             dist_trav, &!dist_step, &

```

```

251         p1_found, p2_found, p3_found, stock, i)
252
253         ! TODO call check_land(curr_xpos, curr_ypos)
254
255     enddo ! dist stepping
256
257     if (opt_depth_on == .true.) then
258         call optimal_uv_current(depth_max, stock%whale(i)%xpos, &
259             stock%whale(i)%ypos, &
260             curr_xpos, curr_ypos, curr_zpos, &
261             idx_tmp)
262     else
263         curr_zpos = hom_zpos
264     endif
265
266 endif
267
268 if (currents_on.eq..true.) then
269     ! Move whale via currents at optimal depth at final position
270     call hormov_whale(curr_xpos, curr_ypos, curr_zpos)
271 endif
272 !endif
273
274 endif ! random-walk only
275
276
277 ! Homing only
278 !-----
279 if (prey_strategy.eq.1) then
280     !print *, 'homing strategy'
281     do while (dist_trav <= dist_max)
282
283         ! Move to next homing position if homing reached
284         call next_homing(stock%whale(i)%hom_xpos, &
285             stock%whale(i)%hom_ypos, &
286             stock%whale(i)%hom_idx, curr_xpos, curr_ypos)
287
288         new_xpos = stock%whale(i)%hom_xpos(stock%whale(i)%hom_idx)
289         new_ypos = stock%whale(i)%hom_ypos(stock%whale(i)%hom_idx)
290
291         ! Check if at new position and at end of homing path
292         if (homing_exit(stock, i, curr_xpos, curr_ypos, &
293             new_xpos, new_ypos) == .true.) exit
294
295         ! Returns position 'dist_max' distance towards homing position
296         call move_newpos(new_xpos, new_ypos, curr_xpos, curr_ypos, &
297             dist_trav, &!dist_step, &
298             p1_found, p2_found, p3_found, stock, i)
299     enddo ! dist stepping
300
301     ! Find index for depth with optimal current speed for movement
302     if (opt_depth_on == .true.) then
303         call optimal_uv_current(depth_max, stock%whale(i)%xpos, &
304             stock%whale(i)%ypos, &
305             curr_xpos, curr_ypos, curr_zpos, &
306             idx_tmp)
307     else
308         curr_zpos = hom_zpos

```

```

309     endif
310
311     if (currents_on.eq..true.) then
312         ! Move whale via currents at optimal depth at final position
313         call hormov_whale(curr_xpos,curr_ypos,curr_zpos)
314     endif
315
316     if (curr_check.eq..true. .and. i==5) then
317         lon = grd2ll(longit, curr_xpos, curr_ypos)
318         lat = grd2ll(latit, curr_xpos, curr_ypos)
319     endif
320
321     endif ! homing only
322
323
324     ! Maximum prey density (+ random walk & + homing)
325     !-----
326     if (prey_strategy.eq.2 .or. prey_strategy.eq.3) then
327
328         ! Determine if hungry or should travel
329         !-----
330         if (mov_feed_on == .true.) then
331             if (stock%whale(i)%days_feeding >= feeding_max .and. &
332                 stock%whale(i)%days_travel >= travel_max) then
333                 well_fed = .false.
334                 stock%whale(i)%days_feeding = 0
335                 stock%whale(i)%days_travel = 0
336             elseif (stock%whale(i)%days_feeding >= feeding_max .and. &
337                 stock%whale(i)%days_travel < travel_max) then
338                 well_fed = .true.
339             elseif (stock%whale(i)%days_feeding < feeding_max .and. &
340                 stock%whale(i)%days_travel < travel_max) then
341                 well_fed = .false.
342             elseif (stock%whale(i)%days_feeding < feeding_max .and. &
343                 stock%whale(i)%days_travel >= travel_max) then
344                 well_fed = .false.
345             endif
346         else
347             well_fed = .false.
348         endif
349
350         ! Set destination position when no fish are present
351         !-----
352
353         ! Max Density Prey Search + Random walk
354         if (prey_strategy.eq.2) then
355
356             call move_random(rand_xpos, rand_ypos, curr_xpos,curr_ypos)
357
358             ! Max Density Prey Search + homing
359             elseif (prey_strategy.eq.3) then
360
361                 ! TODO just a placeholder for reference, pos would be set later
362                 ! again along with a next homing pos check
363                 new_xpos = stock%whale(i)%hom_xpos(stock%whale(i)%hom_idx)
364                 new_ypos = stock%whale(i)%hom_ypos(stock%whale(i)%hom_idx)
365
366             endif ! homing / random-walk

```

```

367
368     p1_inrange = .false.
369     p2_inrange = .false.
370     p3_inrange = .false.
371
372     ! Move whales step-wise until desitnation position
373     !-----
374     do while (dist_trav <= dist_max .and. p1_inrange==.false. &
375              .and. p2_inrange==.false. &
376              .and. p3_inrange==.false. )
377
378         ! If whales are under feeding requirement, look for prey
379         if (well_fed == .false. .and. daynr < stock%whale(i)%migday2) then
380
381             ! whale search radius
382             di = 1
383             dj = 1
384
385             call slice_idxns(curr_xpos, curr_ypos, di, dj, x_max, x_min, &
386                            y_max, y_min, &
387                            grid_offset)
388
389             ! Determine if which prey species are in prey detection range
390             if (maxval(p1(x_min:x_max,y_min:y_max)).gt.p1_thresh) then
391                 p1_inrange = .true.
392             endif
393             if (maxval(p2(x_min:x_max,y_min:y_max)).gt.p2_thresh) then
394                 p2_inrange = .true.
395             endif
396             if (maxval(p3(x_min:x_max,y_min:y_max)).gt.p3_thresh) then
397                 p3_inrange = .true.
398             endif
399
400         endif ! well fed
401
402         ! Choose destination based on location
403         !-----
404         if (p1_inrange == .true. .or. p2_inrange == .true. &
405            .or. p3_inrange == .true. ) then
406
407             ! Set index of new pos depending on presence of preferred prey
408             if (p1_inrange.eq..true.) then
409                 print *, 'max density - p1'
410
411                 ! Set depth to p1 avg depth
412                 curr_zpos = p1_zpos
413
414                 fishmax_idx = maxloc(p1(x_min:x_max, y_min:y_max))
415                 new_xpos = fishmax_idx(1) + x_min ! new lon position index
416                 new_ypos = fishmax_idx(2) + y_min ! new lat position index
417
418                 prey_found = .true.
419
420             elseif (p2_inrange.eq..true.) then
421                 print *, 'max density - p2'
422
423                 ! Set depth to p2 avg depth
424                 curr_zpos = p2_zpos

```

```

425
426     fishmax_idx = maxloc(p1(x_min:x_max, y_min:y_max))
427     new_xpos = fishmax_idx(1) + x_min ! new lon position index
428     new_ypos = fishmax_idx(2) + y_min ! new lat position index
429
430     prey_found = .true.
431
432 elseif (p3_inrange.eq..true.) then
433     print *, 'max density - p3'
434
435     ! Set depth to p3 avg depth
436     curr_zpos = p3_zpos
437
438     fishmax_idx = maxloc(p1(x_min:x_max, y_min:y_max))
439     new_xpos = fishmax_idx(1) + x_min ! new lon position index
440     new_ypos = fishmax_idx(2) + y_min ! new lat position index
441
442     prey_found = .true.
443
444 endif ! end prey-preference/homing selection
445
446 ! Check if at new position
447 if (newpos_exit(curr_xpos, curr_ypos, &
448             new_xpos, new_ypos) == .true.) exit
449
450 call move_newpos(new_xpos, new_ypos, curr_xpos,curr_ypos, &
451             dist_trav, &!dist_step, &
452             p1_found, p2_found, p3_found, stock, i)
453
454 else ! prey not in range (or well fed)
455     ! Use Random-walk destination
456     if (prey_strategy.eq.2 .and. daynr < stock%whale(i)%migday2) then
457
458         last_xpos = curr_xpos
459         last_ypos = curr_ypos
460
461         ! TODO call random pos selector above to not pick new
462         ! random pos with each dist-step iterations
463         new_xpos = rand_xpos
464         new_ypos = rand_ypos
465
466         ! Check if at new position
467         if (newpos_exit(curr_xpos, curr_ypos, &
468             new_xpos, new_ypos) == .true.) exit
469
470         call move_newpos(new_xpos, new_ypos, curr_xpos,curr_ypos, &
471             dist_trav, &!dist_step, &
472             p1_found, p2_found, p3_found, stock, i)
473
474         if (curr_xpos < grid_offset .or. curr_ypos < grid_offset .or. &
475             curr_xpos > im-grid_offset .or. curr_ypos > jm-grid_offset) then
476             curr_xpos = last_xpos
477             curr_ypos = last_ypos
478             !stock%whale(i)%active = .false.
479             exit
480         endif
481
482     ! Use homing destination

```



```

483     else!if (prey_strategy.eq.3) then
484         ! Move to next homing position if homing reached
485         call next_homing(stock%whale(i)%hom_xpos, &
486                       stock%whale(i)%hom_ypos, &
487                       stock%whale(i)%hom_idx, curr_xpos, curr_ypos)
488
489         new_xpos = stock%whale(i)%hom_xpos(stock%whale(i)%hom_idx)
490         new_ypos = stock%whale(i)%hom_ypos(stock%whale(i)%hom_idx)
491
492         ! Check if at new position and at end of homing path
493         if (homing_exit(stock, i, curr_xpos, curr_ypos, &
494                   new_xpos, new_ypos) == .true.) exit
495         if (curr_xpos < grid_offset .or. curr_ypos < grid_offset .or. &
496             curr_xpos > im-grid_offset .or. curr_ypos > jm-grid_offset) then
497             stock%whale(i)%active = .false.
498         exit
499         endif
500
501         ! Homing
502         if (opt_depth_on == .true.) then
503             ! Find index for depth with optimal current speed for movement
504             call optimal_uv_current(depth_max, stock%whale(i)%xpos, &
505                                   stock%whale(i)%ypos, &
506                                   curr_xpos, curr_ypos, curr_zpos, &
507                                   idx_tmp)
508         else
509             curr_zpos = hom_zpos
510         endif
511
512         call move_newpos(new_xpos, new_ypos, curr_xpos, curr_ypos, &
513                       dist_trav, &!dist_step, &
514                       p1_found, p2_found, p3_found, stock, i)
515
516         endif ! homing or random selection
517
518         endif ! move-to-fish or homing/random selection
519
520     enddo ! dist stepping prey search
521
522     ! Move whales with currents
523     !-----
524     if (currents_on.eq..true.) then
525         ! Move whale via currents at optimal depth at final position
526         call hormov_whale(curr_xpos, curr_ypos, curr_zpos)
527     endif
528
529     ! Set feeding, and travel between feeding counts
530     !-----
531     if (prey_found == .false.) then
532         stock%whale(i)%days_travel = stock%whale(i)%days_travel + 1
533     elseif (prey_found == .true.) then
534         stock%whale(i)%days_feeding = stock%whale(i)%days_feeding + 1
535     endif
536
537 endif ! end max prey density + homing
538
539
540     ! Finished moving, assign values to whale

```

```

541      !-----
542
543      stock%whale(i)%xpos = curr_xpos
544      stock%whale(i)%ypos = curr_ypos
545      stock%whale(i)%zpos = curr_zpos
546
547      ! Add encountered fish and distance traveled to whale object
548      stock%whale(i)%p1_found = p1_found
549      stock%whale(i)%p2_found = p2_found
550      stock%whale(i)%p3_found = p3_found
551
552      stock%whale(i)%dist_trav = dist_trav
553
554      endif ! if check for whale active status
555
556      enddo ! Loop through populations to move
557
558      endsubroutine move_whales
559
560
561      !-----!
562      ! Random movement !
563      !-----!
564
565      subroutine move_random(new_xpos, new_ypos, curr_xpos, curr_ypos)
566
567      use minke
568
569      logical :: valid_position ! true = new_xpos/ypos on grid
570      real    :: curr_xpos     ! decimal grid index position - current
571      real    :: curr_ypos     ! decimal grid index position - current
572      real    :: new_xpos      ! decimal grid index position - new
573      real    :: new_ypos      ! decimal grid index position - new
574      real    :: random_num    ! decimal random number from 0-1
575      integer :: x_min         ! xpos of range to west
576      integer :: x_max         ! xpos of range to east
577      integer :: y_min         ! ypos of range to north
578      integer :: y_max         ! ypos of range to south
579      integer :: di            ! index distance in i (y)
580      integer :: dj            ! index distance in j (x)
581
582      ! Bounding cells around position to search for new position
583      di = 5
584      dj = 5
585
586      call slice_idxs(curr_xpos, curr_ypos, di, dj, x_max, x_min, &
587                  y_max, y_min, &
588                  grid_offset)
589
590      ! Calculate new random position until it is off-land/on-grid
591      valid_position = .false.
592
593      do while (valid_position.eq..false.)
594          ! Get new random xpos < 1 grid cell away
595          call random_number(random_num)
596          new_xpos = ((x_max-x_min)*random_num)+x_min
597
598          ! Get new random ypos < 1 grid cell away

```

```

599     call random_number(random_num)
600     new_ypos = ((y_max-y_min)*random_num)+y_min
601
602     ! if resulting indices are not -999.0 or on land, proceed to move
603     ! otherwise, loop is performed until reasonable heading is picked
604     if (new_xpos < grid_offset .or. new_ypos < grid_offset .or. &
605         new_xpos > im-grid_offset .or. new_ypos > jm-grid_offset .or. &
606         fsm(nint(new_xpos),nint(new_ypos)) < 0.5) then
607         valid_position = .false.
608     else
609         valid_position = .true.
610     endif
611 enddo ! end valid position
612
613 endsubroutine move_random
614
615
616 !-----!
617 ! General movement routine (Also used for homing) !
618 !-----!
619
620 subroutine move_newpos(dest_xpos, dest_ypos, curr_xpos, curr_ypos, &
621                       dist_trav, &!dist_mov, &
622                       p1_found, p2_found, p3_found, stock, iter)
623
624 use my_grid , only : latit,longit,im,jm
625 use mod_gridint ! with updated bilin_inv routine
626
627 class(whale_ibm), intent(inout) :: stock ! whale stock class instance
628 integer :: iter
629 real :: random_num ! temp random number variable
630 real :: dlon_m ! change in lon/ypos in meters
631 real :: dlat_m ! change in lon/ypos in meters
632 real :: m_lon ! meters in one degree longitude
633 real :: m_lat ! meters in one degree latitude
634 real :: ve ! difference between homing pos and pos in m
635 real :: vn ! difference between homing pos and pos in m
636 real :: scalar ! scalar of homing diff (ie. dist/vector)
637
638 real :: dest_lon ! decimal lon of destination position
639 real :: dest_lat ! decimal lat of destination position
640 real :: dest_xpos ! decimal grid index of destination position - lon
641 real :: dest_ypos ! decimal grid index of destination position - lat
642
643 real :: curr_lon ! decimal lon position - current
644 real :: curr_lat ! decimal lat position - current
645 real :: curr_xpos ! decimal grid index of current position - lon
646 real :: curr_ypos ! decimal grid index of current position - lat
647
648 real :: new_lon ! decimal lon position - new
649 real :: new_lat ! decimal lat position - new
650 real :: new_xpos ! decimal grid index of current position - lon
651 real :: new_ypos ! decimal grid index of current position - lat
652 real :: new_pos(2) ! decimal grid index of new position
653
654 real :: dist_dest ! distance from current to destination position
655 real :: dist_mov ! Max daily swimming dist based on speed
656 real :: dist_trav ! total distance traveled in daystep

```

```

657
658 real :: p1_found      ! sum of prey1 biomass encountered
659 real :: p2_found      ! sum of prey2 biomass encountered
660 real :: p3_found      ! sum of prey3 biomass encountered
661
662 logical :: valid_pos ! boolean to shorten distance
663
664 real :: t4,t4a,t4b
665
666 ! Cacluate current lat/lon position of individual
667 dest_lon = grd2ll(longit, dest_xpos, dest_ypos)
668 dest_lat = grd2ll(latit, dest_xpos, dest_ypos)
669
670 ! Cacluate current lat/lon position of individual
671 curr_lon = grd2ll(longit, curr_xpos, curr_ypos)
672 curr_lat = grd2ll(latit, curr_xpos, curr_ypos)
673
674 ! Calculate meters per degree lat/lon for current position
675 m_lat = 60 * 1852 ! meters / degree latitude
676 m_lon = 60 * 1852 * cosd(curr_lat) ! meters / degree longitude
677
678 ! Calculate distance between homing position and current position
679 ve = abs(dest_lon-curr_lon) * m_lon ! meters
680 vn = abs(dest_lat-curr_lat) * m_lat ! meters
681 dist_dest = geodist(curr_lon, curr_lat, dest_lon, dest_lat)
682
683 dist_mov = dist_step
684
685 ! Set scalar = 1 if dist traveled eq or gt total dist to homing pos
686 if (dist_mov.lt.dist_dest) then
687     scalar = dist_mov/dist_dest
688 else
689     scalar = 1.
690     dist_mov = dist_dest
691 endif
692
693 call random_number(random_num)
694 if(curr_lon.gt.dest_lon) then
695     dlon_m = -(ve * scalar) + &
696     ((random_num-0.5)*(random_mov*2*dist_mov))
697 else
698     dlon_m = (ve * scalar) + &
699     ((random_num-0.5)*(random_mov*2*dist_mov))
700 endif
701
702 ! Calculate latitudinal change towards homing position
703 call random_number(random_num)
704 if(curr_lat.gt.dest_lat) then
705     dlat_m = -(vn * scalar) + &
706     ((random_num-0.5)*(random_mov*2*dist_mov))
707 else
708     dlat_m = (vn * scalar) + &
709     ((random_num-0.5)*(random_mov*2*dist_mov))
710 endif
711
712 !endsubroutine calc_lonlat_delta
713
714 ! Update position for movement towards homing position

```

```
715   ! convert dlon_m to deg from meters
716   new_lon = curr_lon + (dlon_m/m_lon)
717   ! convert dlat_m to deg from meters
718   new_lat = curr_lat + (dlat_m/m_lat)
719
720   new_pos = ll2grd(new_lon, new_lat, longit, latit, im, jm)
721   new_xpos = new_pos(1)
722   new_ypos = new_pos(2)
723
724   ! if new position is off-grid move to nearest gridcell+offset
725   if (new_xpos < grid_offset .or. &
726       new_ypos < grid_offset .or. &
727       new_xpos > im-grid_offset .or. &
728       new_ypos > jm-grid_offset) then
729     valid_pos = .false.
730   else
731     valid_pos = .true.
732     if (fsm(nint(new_xpos), nint(new_ypos)) < 0.5) then
733       stock%whale(iter)%active = .false.
734     endif
735   endif
736
737   curr_xpos = new_xpos
738   curr_ypos = new_ypos
739
740   ! Sum distance traveled before next iteration,
741   ! as displacement may be lower
742   p1_found = p1_found + p1(nint(curr_xpos), nint(curr_ypos))
743   p2_found = p2_found + p2(nint(curr_xpos), nint(curr_ypos))
744   p3_found = p3_found + p3(nint(curr_xpos), nint(curr_ypos))
745
746   dist_trav = dist_trav + dist_mov
747
748   endsubroutine move_newpos
```

Appendix 6.B Python Video Visualization

The following routine was developed to visualize the movement of whales on the model grid in relation to the movement of prey species, which was critical to the model's development. It uses the python *Animate* library from the *matplotlib* in combination with the cartographic plotting library *Basemap* and the *pcolormesh()* method from the *matplotlib* library to do this. Many of the data management and plotting tools developed for this project took comparable amounts of time and were comparably innovative, but this was by far the most helpful for coding the model. A total of 7042 lines of Python (for post-processing and visualization) were written, and while not a very descriptive metric, speaks to the amount of work involved.

```

1 def plot_norwecom(fig, ax, map_prop, plt_prop, plt_ext, g2_plons, g2_plats,
2                 sa_plons=None, sa_plats=None, plot_data=False, res='1'):
3     '''Plots the model study area with polygons and animated data'''
4
5     class UpdateMapData(object):
6
7         def __init__(self, ax, map_object, grid_lons, grid_lats,
8                     pt_data, pt_dates, pt_num):
9
10            self.ax      = ax
11            self.m       = map_object
12            self.lons    = grid_lons
13            self.lats    = grid_lats
14            self.pt_data = pt_data
15            self.pt_dates_str = pt_dates
16
17            if pts_on == False:
18                t0 = datetime.datetime(plt_year, 01, 01)
19                self.dates = np.empty(365, dtype=object)
20                for i in range(365):
21                    self.dates[i] = t0 + datetime.timedelta(days=i)
22            elif pts_on == True:
23                self.dates = np.empty(len(self.pt_dates_str), dtype=object)
24
25                for i in range(len(self.pt_dates_str)):
26                    self.dates[i] = datetime.datetime.strptime(self.pt_dates_str[i],
27                                                                '%Y-%m-%d')
28
29                self.pt_num = pt_num
30
31                # create image artist object for animation
32                x,y = self.m(0,0)
33
34                # animation point global list
35                self.pts_dots = [[] for i in range(pt_num)]
36
37                for z in range(self.pt_num):
38                    self.pts_dots[z] = m.plot(x,y, 'ro', markersize=2,
39                                              markeredgewidth=0.0)[0]
40
41            self.f_num = len(self.dates)
42            self.a_range = 500

```



```

101                                     norm=hr_norm, cmap = hr_cmap,
102                                     edgecolor='None')
103
104     self.bw_quad = self.ax.pcolormesh(psi_x, psi_y, self.fill_data,
105                                     alpha=0.6,
106                                     norm=bw_norm, cmap = bw_cmap,
107                                     edgecolor='None')
108
109     self.mk_quad = self.ax.pcolormesh(psi_x, psi_y, self.fill_data,
110                                     alpha=0.6,
111                                     norm=mk_norm, cmap = mk_cmap,
112                                     edgecolor='None')
113
114     if barbs_on == True:
115         ydim, xdim = self.lons.shape
116         self.uv_fill = np.zeros((ydim,xdim))
117         x, y = self.m(self.lons, self.lats)
118         self.barbs = m.quiver(x,y,self.uv_fill,self.uv_fill,
119                              cmap=plt.cm.jet)
120
121     def init(self):
122         '''erases previously animated data in last step'''
123
124         if pts_on == True:
125             # Init whale position points
126             for z in range(self.pt_num):
127                 self.pts_dots[z].set_data([], [])
128                 #self.pts_imgs[z].xytext = (0, 0)
129
130             # Init date label
131             self.date_label.set_text('')
132
133         if quads_on == True:
134             # Init fish pcolormesh data
135             self.hr_quad.set_array(np.array([]))
136             self.bw_quad.set_array(np.array([]))
137             self.mk_quad.set_array(np.asarray([]))
138
139         if barbs_on == True:
140             # Init UV barbs
141             self.barbs.set_UVC(np.array([]),np.array([]))
142
143         # return elements to be removed from plot with each frame
144         if (pts_on == True) & (quads_on == True) & (barbs_on == True):
145             return self.pts_dots, self.date_label, self.bw_quad, \
146                    self.hr_quad, self.mk_quad, self.barbs,
147         elif (pts_on == True) & (quads_on == False) & (barbs_on == True):
148             return self.pts_dots, self.date_label, self.barbs,
149         elif (pts_on == True) & (quads_on == True) & (barbs_on == False):
150             return self.pts_dots, self.date_label, self.bw_quad, \
151                    self.hr_quad, self.mk_quad
152         elif (pts_on == True) & (quads_on == False) & (barbs_on == False):
153             return self.pts_dots, self.date_label,
154         elif (pts_on == False) & (quads_on == False) & (barbs_on == True):
155             return self.date_label, self.barbs,
156         elif (pts_on == False) & (quads_on == True) & (barbs_on == False):
157             return self.date_label, self.bw_quad, self.hr_quad, \
158                    self.mk_quad

```



```

159
160     def __call__(self, i):
161         '''sets new values to animate with each step'''
162
163         print 'animation frame: {0:3d}'.format(i,)
164
165         if pts_on == True:
166             lonlat_idx = self.pt_data.date==self.pt_dates_str[i]
167             pt_lons = self.pt_data.lons[lonlat_idx].values
168             pt_lats = self.pt_data.lats[lonlat_idx].values
169
170             # Set position data for points
171             for z in range(len(pt_lons)):
172                 x, y = self.m(pt_lons[z],pt_lats[z])
173                 self.pts_dots[z].set_data(x, y)
174
175             for z in range(len(pt_lons), self.pt_num,1):
176                 self.pts_dots[z].set_data([], [])
177
178             # Create date string and set label data
179             yday = self.dates[i].timetuple().tm_yday
180             date_str = self.dates[i].strftime('%Y, %b %d')
181             print_str = '%s (%3d)' % (date_str, yday)
182             self.date_label.set_text(print_str)
183
184         if quads_on == True:
185             # Set data for pcolormesh() arrays
186             date = self.dates[i]
187             hr_data = hr_data_yr['data'][hr_data_yr['date']==self.dates[i]]
188             bw_data = bw_data_yr['data'][bw_data_yr['date']==self.dates[i]]
189             mk_data = mk_data_yr['data'][mk_data_yr['date']==self.dates[i]]
190             # Mask zero values and ravel to 1d array
191             hr_data = np.ma.masked_array(hr_data, hr_data<1).ravel()
192             bw_data = np.ma.masked_array(bw_data, bw_data<1).ravel()
193             mk_data = np.ma.masked_array(mk_data, mk_data<1).ravel()
194             # Set data array to quad objects
195             self.hr_quad.set_array(hr_data)
196             self.bw_quad.set_array(bw_data)
197             self.mk_quad.set_array(mk_data)
198
199         if barbs_on == True:
200             # Barbs
201             u,v = get_uv(self.dates[i].strftime('%Y-%m-%d'), barb_depth)
202             self.barbs.set_UVC(u,v)
203
204         if save_frames == True:
205             year = self.dates[i].year
206             save_date = datetime.datetime(year,9,1)
207             curr_date = self.dates[i]
208             if save_date == curr_date:
209                 save_figs(fig, plt_prop, plt_ext, meta, i)
210
211
212         if (pts_on == True) & (quads_on == True) & (barbs_on == True):
213             return self.pts_dots, self.date_label, self.bw_quad, \
214                 self.hr_quad, self.mk_quad, self.barbs,
215         elif (pts_on == True) & (quads_on == False) & (barbs_on == True):
216             return self.pts_dots, self.date_label, self.barbs,

```

```

217         elif (pts_on == True) & (quads_on == True) & (barbs_on == False):
218             return self.pts_dots, self.date_label, self.bw_quad, \
219                    self.hr_quad, self.mk_quad
220         elif (pts_on == True) & (quads_on == False) & (barbs_on == False):
221             return self.pts_dots, self.date_label,
222         elif (pts_on == False) & (quads_on == False) & (barbs_on == True):
223             return self.date_label, self.barbs,
224         elif (pts_on == False) & (quads_on == True) & (barbs_on == False):
225             return self.date_label, self.bw_quad, self.hr_quad, self.mk_quad
226
227
228     # Define ellipsoid object for distance measurements
229     #~~~~~
230     g = pyproj.Geod(ellps='WGS84') # Use WGS84 ellipsoid
231     r_equator = g.a # earth's radius at equator
232     r_poles = g.b # earth's radius through poles
233
234     # Map dimensions
235     #~~~~~
236     # Whole Norwecom Area
237     lon0 = 10.0
238     lat0 = 73.5
239     map_width = 4200000
240     map_height = 4200000
241     # Study Area
242     lon0 = -1.0
243     lat0 = 69.5
244     map_width = 2200000
245     map_height = 2700000
246
247     # Basemap projection
248     #~~~~~
249     m = Basemap(width=map_prop['width'],height=map_prop['height'],
250               rsphere=(r_equator, r_poles),\
251               resolution=res, projection='laea',\
252               lat_ts=map_prop['lat0'],\
253               lat_0=map_prop['lat0'],lon_0=map_prop['lon0'], ax=ax)
254
255     # Draw parallels and meridians
256     #~~~~~
257     m.drawparallels(np.arange(-80.,81.,5.), labels=[1,0,0,0], fontsize=10,
258                   linewidth=0.5, dashes=(None,None), color='#d6d6d6')
259
260     m.drawmeridians(np.arange(-180.,181.,10.), labels=[0,0,0,1], fontsize=10,
261                   linewidth=0.5, dashes=(None,None), color='#d6d6d6')
262
263     m.drawmapboundary(fill_color=map_colors['water'])
264
265     m.fillcontinents(color=map_colors['land'], lake_color=map_colors['land'])
266
267     # Print Plot Information
268     #~~~~~
269     print '\nPlot Information'
270     print '-----'
271     print "Map lat/lon center: ",lat0,lon0
272     print "Map height/width: ",map_width,map_height
273
274     # Animate Data

```

```
275 #~~~~~
276 if plot_data == True:
277     print '\nBegin processing data animation...'
278
279     ud = UpdateMapData(ax, m, g2_lons, g2_lats, whale_data,
280                       pt_dates, whale_num)
281
282     anim = animation.FuncAnimation(fig, ud, init_func=ud.init,
283                                   frames=ud.f_num, blit=False)
284
285     if quads_on == True:
286         print 'colorbars off'
287
288     # Draw Polygons
289     #~~~~~
290     draw_g2_poly(ax, m, g2_lons, g2_lats, grid_lines=False, hatch_on=False)
291     plot_tools.plot_buffer(ax, m, g2_lons, g2_lats, 'red', g2_offset)
292
293     # Save animation if present
294     if plot_data == True:
295         out_date = meta['date_run'].strftime('%Y-%m-%d_%H%M%S')
296         out_dir = './figures/videos/'
297         minke_outfile = 'minke_movement_'+ out_date + \
298                       '_svn'+meta['svn']+ \
299                       '_pop'+meta['population']+ \
300                       '_spd'+meta['speed']+ \
301                       '_in'+meta['in_path']+ \
302                       '_out'+meta['out_path']+ \
303                       '_str'+meta['strategy']+ \
304                       '.mp4'
305
306         fig.set_size_inches(4,4)
307         dpi = 600
308         writer = animation.writers['ffmpeg'](fps=5)
309
310         anim.save(out_dir+minke_outfile, writer=writer, dpi=dpi)
311
312         plt.show()
313
314 return
```


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