Modeling implications of food resource aggregation on animal migration phenology

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Abstract

The distribution of poikilotherms is determined by the thermal structure of the marine environment that they are exposed to. Recent research has indicated that changes in migration phenology of beluga whales in the Arctic are triggered by changes in the thermal structure of the marine environment in their summering area. If sea temperatures reflect the spatial distribution of food resources, then changes in the thermal regime will affect how homogeneous or clumped food is distributed. We explore, by individual-based modelling, the hypothesis that changes in migration phenology are not necessarily or exclusively triggered by changes in food abundance, but also by changes in the spatial aggregation of food. We found that the level of food aggregation can significantly affect the relationship between the timing of the start of migration to the winter grounds and the total prey capture of individuals. Our approach strongly indicates that changes in the spatial distribution of food resources should be considered for understanding and quantitatively predicting changes in the phenology of animal migration.

Introduction

The distribution of food resources through the oceans is spatially and temporally affected by physical processes (Pakhomov et al. 1994; Hunt et al. 1999; Pollard et al. 2002). The dynamic features of such processes like oceanographic fronts, eddies, and upwellings locally increase biological productivity and aggregate prey species, (e.g., Fiedler and Bernard 1987; Podesta et al. 1993), leading to the development of localized food webs (Olson and Backus 1985; Mann and Lazier 1991). Most marine apex predators have an energetic advantage to feed on dense, patchily distributed aggregations of schooling prey (e.g., Goldbogen et al. 2011) and therefore respond to environmental heterogeneity using different movement strategies (Mueller et al. 2008; Mueller and Fagan 2008). Migration, defined as a round-trip journey between discrete favorable home ranges (Sinclair 1983; Fryxell and Sinclair 1988), is one of these strategies. However, apart from the movement itself, the timing of migration is of crucial importance for a temporal synchrony between aggregated food resources and predators to enable efficient foraging (e.g., Visser et al. 2011).

Currently, as with many other ecological processes, animal migration phenology is affected by climate change (Hughes 2000; Walther et al. 2002; Parmesan 2006; Rosenzweig et al. 2008). Although such effects on the timing of migration are becoming well documented (e.g., Both et al. 2005), the factors determining such changes

are still poorly understood. In the ocean, warming of waters tends to enhance thermal stratification and more generally to modify the dynamics of physical processes (e.g., Sarmiento et al. 2004), which in turn affects local productivity (Behrenfeld et al. 2006) and consequently the aggregation of prey organisms. This might change the spatial distribution of prey in foraging areas; so that predators would have to adjust their migration timing to match the best feeding conditions (e.g., Learmonth et al. 2006). However, the mechanisms through which physical forcing, primary productivity, aggregations of prey, and migratory predators are linked, remain unclear.

One reason for this is that ecological drivers of migration used to be notoriously difficult to investigate in natural systems. This has changed with the recent improvements of biotelemetry technologies and satellite remote sensing which strongly improved our ability to collect detailed environmental and movement data. Moreover, individual-based modeling has also advanced over the last decade and is increasingly used to develop models that can mimic the dynamics of organisms and populations in their environments and forecast their response under environmental change (Railsback and Harvey 2002; Grimm et al. 2005; Stillman and Goss-Custard 2010; Grimm and Railsback 2012).

The Arctic appears to be particularly vulnerable to climate change (Walsh 2008). Previous studies reveal trends of decreasing sea-ice extent in the Arctic Ocean coincident with global warming (Maslanik et al. 1996). Such changes are expected to affect the whole polar ecosystem, and especially marine predators, such as beluga whales, which occupy top trophic positions and as such incorporate cascading effects of disturbance on other trophic levels. The beluga whale, a medium sized, ice-adapted odontocete, is the most abundant of the arctic cetaceans. Although several populations of this species reside in the same locale all year round (Moore et al. 2000), others undertake seasonal migrations of varying extents (Lesage and Kingsley 1998; Richard et al. 2001). The diet has not been well described for every population, but it is strongly assumed to include both capelin *Mallotus villosus* and Arctic cod *Boreogadus saida*, which are important components of Arctic marine food webs and form dense aggregations during the open-water season (Welch et al. 1993; Kelley et al. 2010).

In the context of global warming, habitat change is particularly critical when a species is highly specialized in its resource use. Although beluga whales are feeding generalists, they remain vulnerable to climate-induced food web cascades that may be triggered by rapid shifts in environmental conditions (Hansen et al. 2003). Thus, there is a certain urgency in understanding how the migratory patterns of populations will change as they are most likely to be affected by environmental change in the Arctic.

A recent study showed that the eastern Hudson Bay (EHB) population (Canada) undertakes migration in fall to reach the Labrador coasts in winter (Bailleul et al. 2012). This study highlighted that the summer foraging movement and the date of migration to the winter grounds of individuals from this endangered population were related to the thermal structure of the summer area. As water temperatures affect the physiology and therefore the distribution of ectotherms, like fish preys of beluga whales, the study hypothesized that the thermal structure of the area reflects the potential spatial distribution of prey. Consequently, the study suggested that changes in migration phenology are not necessarily or exclusively triggered by changes in food abundance, but also by changes in the spatial distribution of food. The warming in the Arctic is expected to modify the thermal structure of sea waters, which could result in changes in how homogeneous or clumped food is distributed. The study also hypothesized that such changes could affect the foraging efficiency of beluga whales strongly enough to cause changes in migration phenology (Bailleul et al. 2012).

To explore the hypothesis that aggregations of food resources affect the foraging efficiency of beluga whales and cause changes in their timing of migration, we used remotely sensed data from Bailleul et al. (2012) and we developed an individual-based model (IBM). While a link between variation in food abundance and migration phenology is strongly expected, here we explore changes in spatial distribution of food as a potential driver of the timing of the start of migration. Since there are no data on foraging efficiency of beluga whales, we instead used pattern-oriented modeling to validate the model, that is, we checked whether it was capable of reproducing movement patterns observed in the field.

Our ultimate aim was to advance our understanding of animal migration and to increase our capacity to conserve migratory systems under the threat of climate-driven environmental change. Based on the example of beluga whales, we identified an environmental factor influencing migratory animals that so far has not been considered, but might be crucial for many species and regions.

Methods

Field study

From a field study conducted between 2002 and 2004, we observed that EHB beluga whales seasonally commuted between two main different environments, the shallow estuaries of the EHB in summer and the deep Labrador Sea in winter (Fig. S1) (Bailleul et al. 2012). The individuals are present in the summer grounds from late May (Lewis et al. 2009) to October/November, while they

occupy the winter grounds during the rest of the year. In summer, individuals, equipped with satellite transmitters, have shown increased foraging activity in the month prior to migration. The increased foraging was illustrated by changes in diving behavior and movement strategies, defined as aggregated and dispersed. Each strategy was related to the thermal structure of the bay and to the timing for fall migration (Bailleul et al. 2012). All the individuals tracked, left the EHB around 3 months after the start of monitoring, and spent around 5 months in the winter areas. All transmitters stopped functioning after 8 months, preventing documentation of the spring migration.

Model description

Our model IRAMA (Implications of food Resources' Aggregation on Migratory Animals) was implemented according to the observations resulting from the field study described above. Its description follows the ODD (Overview, Design concepts, Detail) protocol for describing IBMs (Grimm et al. 2006, 2010). The model and its analyses were implemented in R (R Development Core Team 2011). The R code of the model is available in the (Fig. S2).

Purpose

The purpose of IRAMA is to investigate the relationship between the spatial aggregation of food resources, the foraging efficiency of Arctic beluga whales, and the potential changes in their timing of migration. The foraging efficiency is quantified by the total prey capture of individuals confronted with different spatial distributions of food resources. Both summer and winter conditions are likely to drive the fall migration phenology. Thus, the model explores whether it is more beneficial, in terms of total prey capture, to remain longer within the summer area or to leave earlier for the winter area. Based on the movements of individuals observed in the field, only spatial patterns of resources within the summer habitat varied in the model, while the spatial pattern of resources in winter was fixed.

Entities, state variables, and scales

The set of state variables characterizing both beluga whales and their environment is listed in Table 1. Space is represented explicitly for the summer domain. Horizontally, the region consists of 250×250 square grid cells of 1 km² each, corresponding to 62,500 km² (Table 2). Boundary conditions are closed: if a beluga's movement step goes beyond the borders of the model world, the individual is forced to turn back. One time step in the model represents 1 hour. To match the field observations, the model runs over an 8-month period

Table 1. Details of beluga and resources state variables in the model.

State variable	Unit	Explanation
Summer domain		
Beluga		
Current location	km	x and y coordinates of a beluga (coordinates are relative to the grid of resources)
Resource in view	–	Resource value viewed by a beluga, given its current location
Moving speed	m/sec	Horizontal or vertical speed varying between each location
Diving depth	m	Maximum diving depth reach by a beluga at each location (=z coordinate)
Diving duration	sec	Diving duration related to maximum diving depth
Capture	–	Logical variable indicating whether a beluga catch a prey
Resources		
Location	km	x and y coordinates of the centre of grid cells
Value	–	Resource value within a grid cell corresponding to a fraction of the global abundance
Degree of aggregation	–	Value indicating the level of resources aggregation
Winter domain		
Beluga		
Moving speed	km/h	
Diving depth	m	cf above
Diving duration	sec	
Capture	–	

including foraging in the summer domain, which never exceeds 3 months, and foraging in the winter domain.

Ideally, start of migration, that is, transition between summer and winter domain, would be triggered by the beluga whale's adaptive decision, which is based on its energy demands and the efficiency of its foraging in the summer domain and the potential benefit expected in the winter domain. However, data for representing this decision do not yet exist. We therefore imposed the time spent in the summer domain over a wide range (between 0 and 2184 h i.e., 3 months), with the remaining time of the simulation period spent in the winter area. This allows us to compare the consequences of different starting dates of migration. Note that resource levels are constant during one simulation, which means that resources depletion is not considered in the model.

Process overview and scheduling

Beluga whales move, dive, and capture prey in response to resource values encountered at their current location,

Table 2. Overview and explanation of input parameters and initial values used in the model.

Parameter	Unit	Description	Values
Related to the summer environment			
Resources abundance	–	Number of entities within the domain	20,000
Aggregation levels	–	Values of resources aggregation tested	0, 5, 10,25, 50, 100, 200,300
Simulation domain	km²	A squared domain within resources are placed and beluga can move	250 × 250
Resources location	km	The *x* and *y* coordinates of a resource entity	Random
Timing			
Total simulation time	h	Total period over which model calculations take place	5088
Simulation time step	h	Period over which the model states are re-calculated	1
Related to beluga			
Moving speed	km/h	Maximum swimming or diving speed reachable by individuals	3
Beluga location summer	km	Initial *x* and *y* coordinates of a beluga in summer	Random
Diving depth summer	m	Maximum depth reachable by beluga in summer	200
Diving depth winter	m	Maximum depth reachable by beluga in winter	800
Diving duration summer	sec	Maximum duration in summer	600
Diving duration winter	sec	Maximum duration in winter	1200

which determines the orientation and speed of horizontal movement and the characteristics of dives. While beluga whales' movements were based on theoretical movements of foraging animals, dive parameters and prey captures were determined from underlying data given by the field study (Bailleul et al. 2012). The model's schedule is depicted in Fig. 1 and described in the following; names of the corresponding submodels are given in parentheses and described in detail below, in the ODD section "Submodels".

Depending on the resource values sensed at its current location (Sense), a beluga moves horizontally or dives. Horizontal movement is either a correlated random walk for low resource levels (Move1) or a random walk for high resource levels (Move2). Dives have a strong probability to be short and shallow (<20 m) when resource level is low (Dive1), whereas they are mainly deep (> 20 m) and long when this level is high (Dive2). In

both Dive1 and Dive2, food can be captured only when diving depth exceeds 20 m (Capture).

Design concepts

The movement path and the resulting total number of captures of individual whale *emerge* from their behavioral response to different resource levels. Beluga whales *adapt* their behavior according to their currently sensed resource level. In order to make their adaptive decisions on moving and diving, each beluga whale has to *sense* the resource value found at its position. When encountering high resource levels, the animal implicitly *predicts* that resources are aggregated so that turning to a random walk with increased turning angle and decreased swimming speed should increase foraging success. Model individuals do not have a *memory* and do not *learn*. *Stochasticity* is introduced in the model using random initial locations of beluga whales within the summer area and by randomly determining the structure of the resource distributions. Likewise, the choice of movement directions and speed during a dive includes stochastic elements. In addition to individual movement paths, each individual's total prey capture at the end of the whole simulation duration (i.e., 5088 h or 8 months) was *observed*.

Initialization

Resources were distributed and aggregated through the summer area using the function GaussRF (R Development Core Team 2011) according to the chosen level of aggregation (Table 2). This distribution was fixed for a certain simulation run, but chosen anew for each repetition using the same level of aggregation (Fig. 2). One beluga whale at a time was placed at a random initial location, with a randomly chosen direction of movement (Fig. 2); thus, 250 beluga whales were simulated for each parameter combination.

Submodel sense

A beluga whale first evaluates the resource value at its current position (grid cell). Based on the optimal foraging theory (McArthur and Pianka 1966), we defined two types of movement according to the resource value sensed. Thus, depending on the resource value, the individual proceeds to move or dive: if the value sensed is below a threshold, defined as the mean of resource values of all grid cells of the domain, plus the standard deviation, the individual proceeds to Move1, otherwise to Move2. The submodel Move2 is only used in summer.

Submodel move summer

Move1 corresponds to a correlated random walk where the turning angle is selected from a normal distribution centered at the previous direction and with a standard deviation of $\pi/8$ radians, while the swimming speed (km/h) is selected from a (truncated) normal distribution with mean = 2 and standard deviation = 0.5. For Move2, beluga whales adopt a simple random walk and increase the range of possible turning angles (uniform distribution ranging between 0 and 2π radians) and decrease their speed (normal distribution with mean = 0.5 and standard deviation of 0.3). For both Move1 and Move2, the maximum speed is set to 3 m/sec according to the field data (Bailleul et al. 2012).

Submodel dive summer

At each new location, beluga whales dive. Characteristics of dives, that is, depth and duration, are determined by probabilities related to the resource value sensed. When the sensed resource value is below the threshold (see Submodel sense), Dive1 is used: A maximum depth between 0 and 200 m is determined according to the probability:

$$P(depth) = 1/\exp(0.06 \times depth) \quad (1)$$

and dive duration is sampled between the minimum duration, which is calculated for a round trip between the surface and the maximum depth while swimming at full speed (3 m s^{-1}), and the maximum duration (here fixed
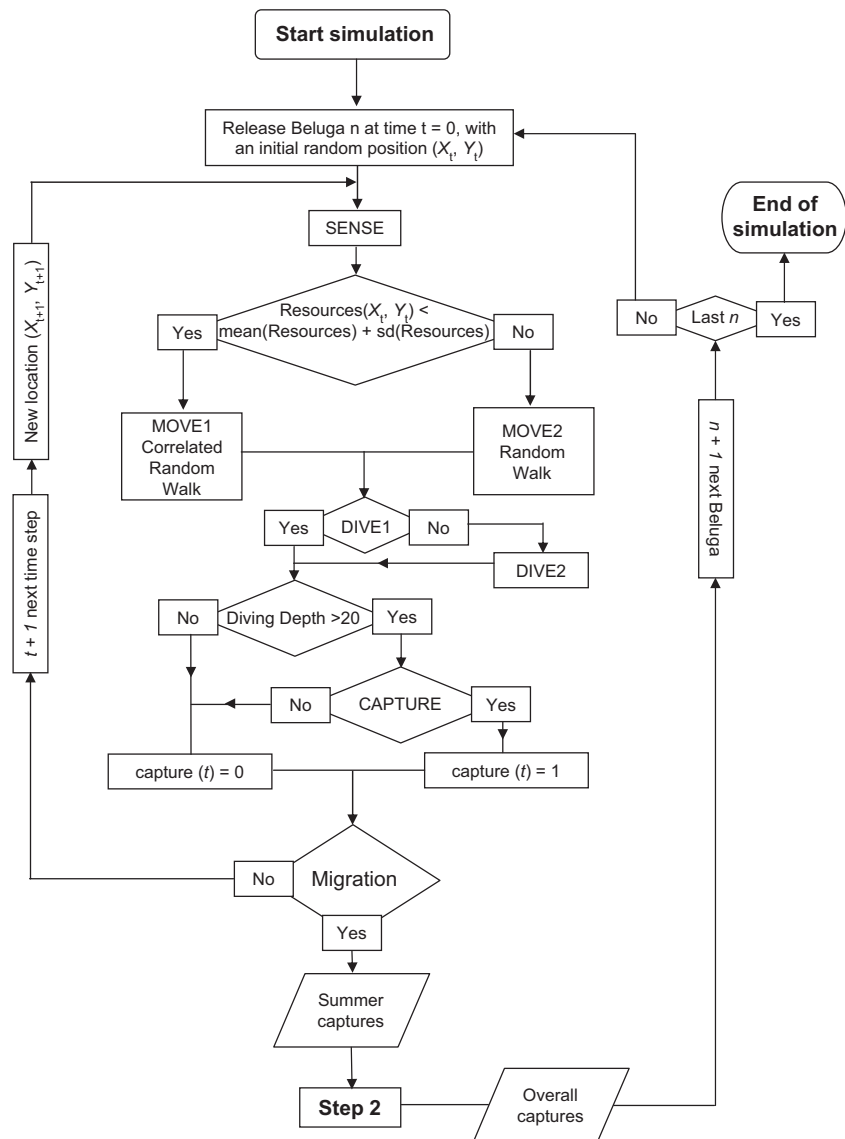

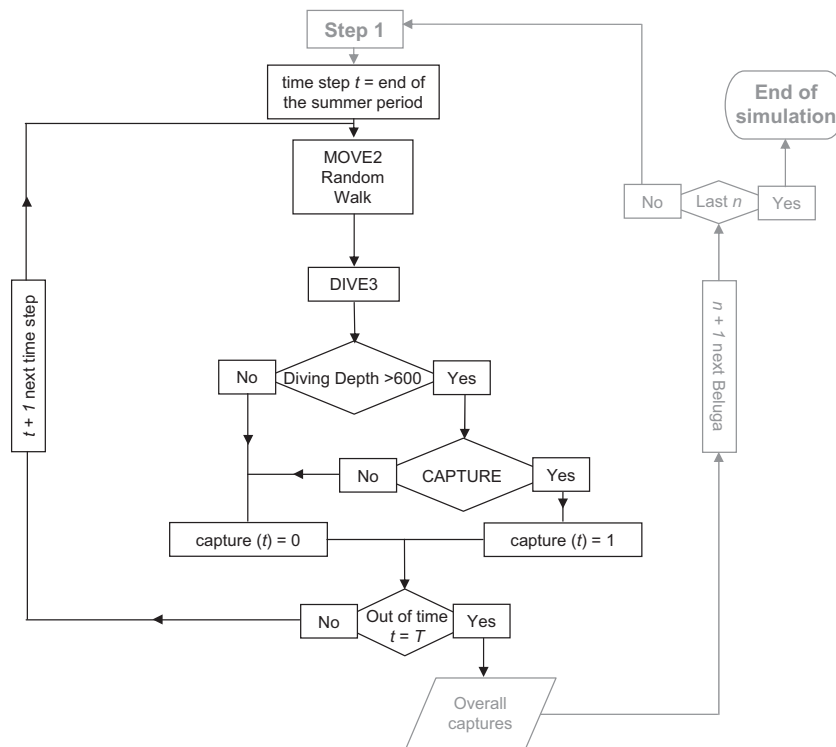**Figure 1.** Flow chart representing the different steps of the model and the general process.

Figure 1. Continued.

to 600 s as no dive duration within the summer area exceed this value in the field):

$$Minimum\ duration = (maximum\ depth \times 2)/maximum\ speed \quad (2)$$

Dive duration is sampled according to the probability:

$$P(duration) = 1/\exp((1/depth) \times duration) \quad (3)$$

when the resource value is above the threshold, Dive2 is used. Dive2 is characterized by the same ranges as Dive1, but $P(depth)$ is here selected from a normal distribution with mean = 50 and standard deviation = 20, whereas $P(duration)$ remains identical to equation (3).

Submodels move and dive winter

In winter, only Move2 is used. However, movement does not actually affect the individual's location, which is no longer considered. For the winter period, we used the submodel Dive3: a maximum depth is sampled between 0 and 800 m and following the probability $P(depth)$, which is selected from a normal distribution with mean = 50 and standard deviation = 20. Dive duration is sampled between the minimum duration (see eq. 2) and the maximum duration (here fixed to 1200 sec) according to the probability $P(duration)$ (see eq. 3).

Submodel capture

Prey capture potentially occurs when diving depth exceeds 20 m in Dive1 and Dive2 and 600 m in Dive3. The probability to capture a prey in a diving event is related to the dive duration. For a given depth, the longer the dive duration, the higher the probability to capture a prey.

$$P(capture) = dive\ duration/maximum\ duration \quad (4)$$

Comparison to field observations

We evaluated the model's ability to reproduce spatial patterns of movements observed in the field during the 2002 to 2004 seasons (Bailleul et al. 2012). In this field study, it has been shown that spatial scales of individuals' movements were related to the thermal structure of the study area. It has been hypothesized that the thermal structure of the environment reflected the spatial distribution of prey and therefore that movements of beluga whales were related to prey distribution. Consequently, we analyzed 50 simulated tracks for each level of prey aggregation using the first-passage time (FPT) method to have a measure of the simulated spatial scales of individuals' movements (Fauchald and Tveraa 2003). Such measures were then
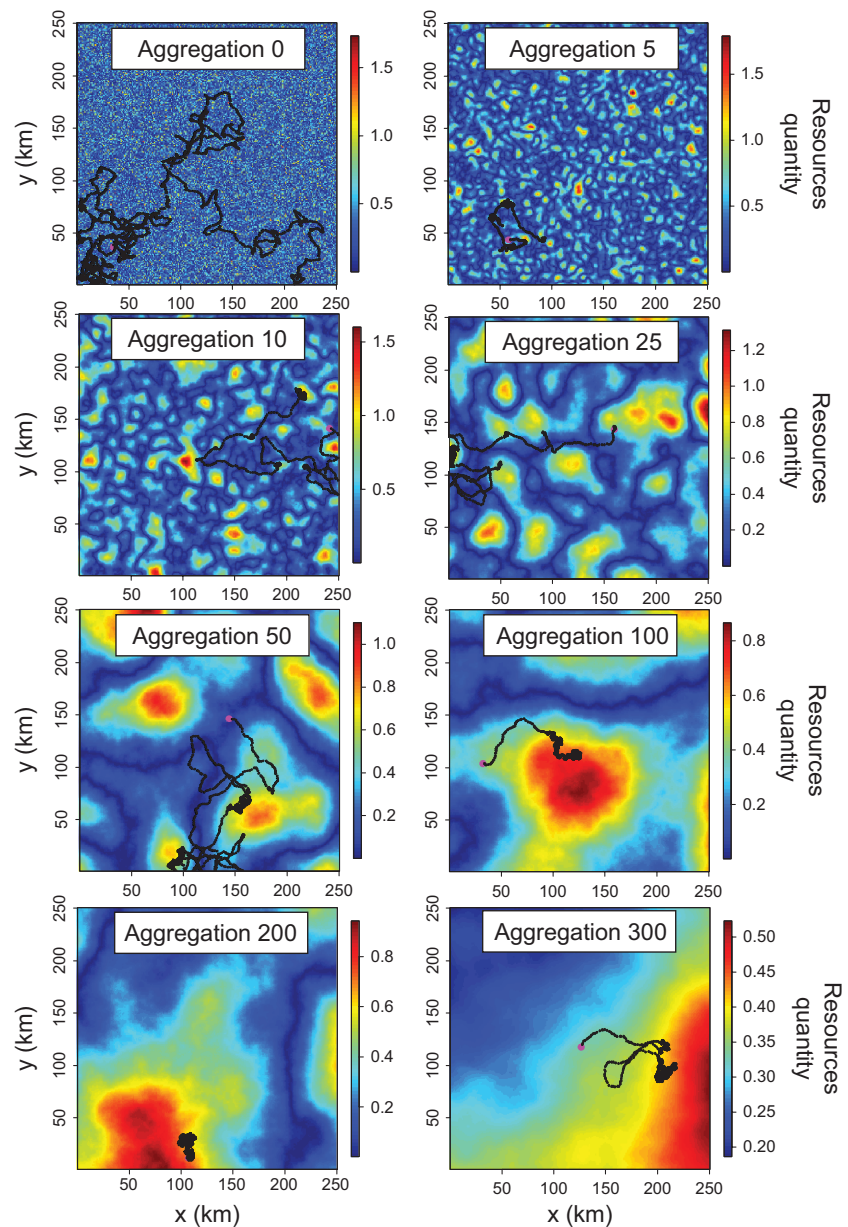
Figure 2. Simulated summer spatial domain represented for one individual (of 250) for each level of resources aggregation tested. In every cases, the abundance of resources is fixed to 20,000. Black dots illustrate the locations and the movement of individuals. The pink dots mark the random initial location of each simulation

compared to those obtained from field data by the same method (see Bailleul et al. 2012).

In the FPT method, each location of simulated tracks was associated with a circle of a fixed radius r. The time required for crossing the circle in the first passage (i.e., the FPT value) was calculated. The computational process was repeated for each location and for a range of r. Over the entire track, the variance among the FPT values (log transformed: see Fauchald and Tveraa 2003) was calculated as a function of r (Fig. S3). The radius corresponding to the maximum peak in variance indicated the most relevant scale, in km, of movement related to the food search effort.

Results

Relationship between resource aggregation, foraging efficiency, and timing of migration

The level of resource aggregation in summer significantly affects the relationship between the timing of migration and the overall prey capture of individuals. When resource aggregation is zero, the total prey capture of individuals is inversely related to the timing of the start of migration ($R^2 = 0.94$, $P < 0.001$) (Fig. 3A). Thus, later departures result in less prey. In contrast, this relation is reversed when prey is aggregated at moderate levels. At
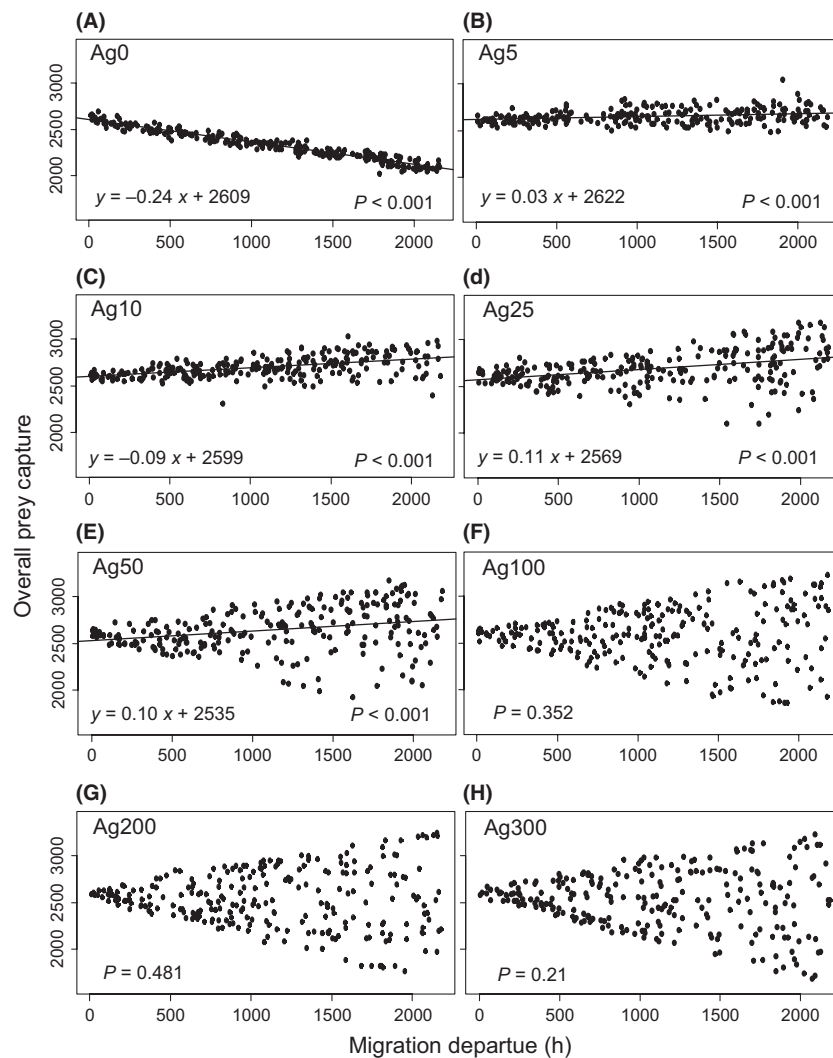
Figure 3. Relationships between the total prey capture (summer + winter) and the date of migration departure (i.e., the time spent within the summer domain) for each level of aggregation tested. Black lines represent linear regression curves. One black dot = one simulated individual.

levels of aggregation of 5–50, prolonged presence in the summer area results in a higher overall prey capture rate (Ag 5: $R^2 = 0.07$, $P < 0.001$; Ag 10: $R^2 = 0.25$, $P < 0.001$; Ag 25: $R^2 = 0.15$, $P < 0.001$, and Ag 50: $R^2 = 0.07$, $P < 0.001$) (Fig. 3B, C, D, E). For the higher levels (Ag 100, 200, and 300) the relationship is not significant (Fig. 3F, G, H). This may be due to increased individual variation observed at these higher levels of aggregation.

At high levels, some individuals become very successful (high prey capture rate) whereas others are very unsuccessful (Fig. 4). This does not occur at lower levels of prey aggregation (Fig. 4). When considering successful individuals, they show the same relation as the individuals under moderate aggregation conditions: later departure results in more prey capture. Unsuccessful individuals must leave early to safeguard their prey intake. It should be noted that when taking all the individuals together

("successful" + "unsuccessful"), the highest captures are reached for a level of aggregation of 25.

Comparison to field observations

The evaluation of the model's ability to reproduce spatial patterns observed in the field indicated that spatial scales of movements were not significantly different between field observations of individuals dispersed through the summer area (mean scale = 156 ± 48 km) and simulations when resource aggregation was null (mean scale = 123 ± 51 km, t-test: $t = 1.62$, $P = 0.14$) (Fig. S4A). Likewise, no significant difference in spatial scales of movements were found between field observations of individuals aggregated through the summer area (mean scale = 55 ± 20 km) and simulations when the level of aggregation was 25 (mean scale = 41 ± 8 km, $t = 1.9$,
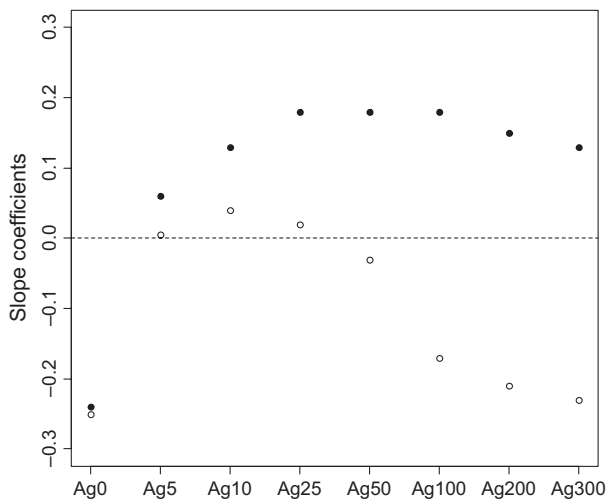
Figure 4. Slope coefficients of linear regression for "successful" (black dots) and "unsuccessful" (white dots) individuals (see text for details) between the total prey capture and the time spent in the summer area for every level of aggregation (Ag 0 to Ag 300).

$P = 0.08$) and 50 (mean scale = 54.5 ± 18.5 km, *t*-test: $t = 0.06$, $P = 0.95$) (Fig. S4B).

Discussion

In natural marine systems, migration can be governed by the seasonal aggregation of food, which leads to spatio-temporal matching between top marine predators and productive blooms and allows for highly efficient foraging (Croll et al. 2005; Doniol-Valcroze et al. 2007; Goldbogen et al. 2011). For instance, baleen whales migrate during the spring bloom in the North Atlantic and their presence at the feeding grounds matches the maximum production in the area, where they are able to efficiently locate the highest prey aggregations (Croll et al. 2005; Doniol-Valcroze et al. 2007; Goldbogen et al. 2011). In the Arctic, the seasonal sea-ice cover also creates conditions for a seasonal primary production bloom (Bluhm and Gradinger 2008), which favors the aggregation of copepod grazers and other zooplankton species and is attractive for species from higher trophic levels (Pershing et al. 2004; Bluhm and Gradinger 2008). In every case, spatiotemporal matching between top marine predators and productive blooms allows a highly efficient foraging (Croll et al. 2005; Doniol-Valcroze et al. 2007; Goldbogen et al. 2011).

However, climate change will affect the timing of primary production blooms (Visser et al. 2011) potentially leading to an asynchrony between the different levels of the trophic web, especially in the Arctic where the ongoing change is known to be exacerbated (Moritz et al. 2002). Thus, reduced sea-ice cover in the Arctic under effect of warming will result in a premature phytoplankton bloom,

with the potential to disrupt connectivity between phytoplankton and copepod grazers ascending from depth at specific times of the year (Hunt et al. 2002; Hansen et al. 2003; Bluhm and Gradinger 2008). Hypothetically, such a trophic decoupling could affect prey distribution, thereby reducing their spatial aggregation and consequently the foraging efficiency of beluga whales. This would lead to changes in the timing of migration.

The objective of this study was to explore whether changes in the spatial distribution of food resources alone can lead to changes in animal migration phenology. To achieve this, we developed the IBM IRAMA for an Arctic population of beluga whales. Although, some concepts in IRAMA were deliberately simplified, it was able to accurately describe the observed movements of beluga whales. Thus, we argue that the model, showing that the spatial distribution of food resources by itself may have an impact on the fall migration of beluga whales, is relevant to improve our understanding of factors possibly affecting migration of Arctic cetaceans.

Implications of food Resources' Aggregation on Migratory Animals was intentionally designed as a simple representation of beluga whale migration. Our goal was not to provide realistic quantitative values of the total prey capture but rather to explore general trends resulting in different levels of resources aggregation. We are aware that food resource distribution in summer is unlikely to be the only force driving migration, but still, the spatial distribution of food resources is likely to contribute strongly and directly to seasonal and long-term biological abilities (e.g., survival, reproduction) of an organism (e.g., White 1978; Lindström 1999), which is why we focused on this aspect. Furthermore, a previous empirical study suggests that changes in the distribution of summer food resources led to a delayed departure for the migration to winter grounds for a population of beluga whales in the EHB (Bailleul et al. 2012). However, predation and unsuitable physical conditions within the winter habitat may also strongly influence the movement of migratory animals.

Model results suggest that, assuming fixed total amounts of food resources, the relationship between the total prey capture of individuals and the timing of migration to the winter grounds depends on the level of resource aggregation in summer. It is advantageous for all individuals to migrate earlier when resources are scattered during summer because the total prey capture decreases progressively with time spent in the summer area. Moreover, the low variability observed in this relationship suggests that all the individuals are affected in the same way. The results differ as soon as the resources are spatially aggregated so that individuals experience the same environment differently, as supported by the increasing ndividual variability

observed for every level of aggregation (from intermediate to high). We therefore distinguished "successful" and "unsuccessful" individuals. Successful individuals happen to find, by chance, patches with high resource levels in which they stay long enough to forage successfully. For these individuals, the longer they stay within their summer habitat, the more they capture prey, whatever the level of resources' aggregation. However, it should be noted that the more aggregated the resources, the lower the probability of finding by chance, a prey or a patch of prey. In that case, it is harder for the unsuccessful individuals to capture prey and therefore, they do not benefit from staying a long time within the summer area. At this stage, it appears that resource aggregation is not the only relevant parameter. Instead, the individuals' abilities in foraging behavior may be important for the understanding of migration processes. A first conclusion may be that when resources are aggregated either the individuals are efficient searchers so that they benefit from remaining for a long time within their summer habitat regardless of the level of resource aggregation, or they are not so they should leave the summer area early, especially when the level of resources aggregation is high.

Considering individuals as the main entity for this kind of approach is fundamental because it incorporates individual variability, which is inherent to all ecological systems. However, beluga whales are social animals living in groups from two to several 10 of individuals, or clans, governed according to a sexual or age-related segregation (Loseto et al. 2006). During the summer period, the largest pods consist of females accompanied by newborn calves and juveniles, while males tend to form smaller groups (Loseto et al. 2006). Previous studies have shown that foraging in groups can have benefits (Clark and Mangel 1986; Smith and Warburton 1992). An increase in foraging success could result from the synergistic effect of several individuals hunting together, by increasing prey encounters and capture rates, by decreasing the costs involved in the capture of large or difficult-to-handle prey, or by improving use of information in the presence of scarce, patchily distributed resources (Baird and Dill 1996). Therefore, interpreting model results for beluga whales at an individual level presents some limitations. For this species, the size and the composition of a group of individuals should be considered to more accurately describe the relationship between foraging efficiency and the timing of migration.

Other improvements can make our model more realistic. A more realistic environment could be implemented including resource depletion, or a more realistic energetic budget and different age stages could be considered. However, with the present state of knowledge, many of these would be based on uncertain values or hypothetical relations. We therefore advocate a targeted gathering of additional observations of this system, before envisaging model extensions. Especially, to explore how global climate change may affect important outcomes of animal migration, it is essential to further study how the environment affects animal physiology during migration and how animal physiology may influence the timing, scheduling, and extent of animal migration. Quantifying the metabolic consequences of behavioral, morphological, and physiological attributes of animal migration would provide insights into their effect on fitness and assess evolutionary strategies. This remains a stimulating challenge for future studies in ecology.

Acknowledgments

Conflict of Interest

None declared.

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Figure S1. One individual track (in red) through the Hudson Bay complex, obtained from telemetry. It illustrates the general pattern of belugas' movements in this area, with the summer residency area in the Eastern Hudson Bay (EHB) and the migration path until winter areas in the Labrador Sea (LS).

Figure S2. Detailed Code of the model IRAMA developed using the R language.

Figure S3: Examples of results induced by the first passage time (FPT) method. Four simulated tracks are presented on the left side for four different levels of resources aggregation (A) Ag0, (B) Ag5, (C) Ag50, (D) Ag300). The variance among the FPT values calculated as a function of *r* are presented on the right side. The radius corresponding to the maximum peak in variance (highlighted by a dash line) indicates the most relevant scale to differentiate Area Restricted Search (modeled by Move1) from the unidirectional movement (Move2).

Figure S4: Spatial scales (obtained with the FPT method) of simulated movements within the summer area compared to those observed in the field (A) when individuals are dispersed through the area and (B) when they are aggregated according to the level of resources aggregation. The absence of significant difference (ns) tends to validate the process of movement simulated in the model. *, **, and *** indicate significant differences with $P < 0.05$, $P < 0.01$ and $P < 0.001$ respectively.