



Simulating individual-based movement in dynamic environments



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ABSTRACT

The accuracy of spatially-explicit individual-based models (IBMs) often depends on the realistic simulation of the movement of organisms, which is especially challenging when movement cues (e.g., environmental conditions; prey and predator abundances) vary in time and space. A number of approaches or sub-models have been developed for simulating movement in IBMs. We evaluated four movement sub-models (restricted-area search, kinesis, event-based, and run and tumble) in a spatially-explicit cohort IBM in which the prey and predators were both dynamic (varying across cells and over time) and responsive to the dynamics of the cohort individuals. Movement, growth, and mortality were simulated every 25 min for 30 12-h days (single generation) on a 2.7×2.7 km² grid with 625 m² cells, and egg production was calculated based on weight and survival of individuals at the end of 30 days. We based the cohort model on small pelagic coastal fish, and the prey was based on zooplankton and the predators based on a typical piscivorous fish. Movement sub-models were calibrated with a genetic algorithm in dynamic and static versions of the prey and predator-defined environments. Prey and predator fields were fixed in the static environment; in the dynamic environment, prey density was reduced based on consumption and predators actively sought out cohort individuals. Static-trained sub-models were then tested in the dynamic environments and vice versa. The four movement sub-models were successfully trained and performed reasonably well in terms of egg production (a measure of individual fitness) when trained and tested in the same type of environment. However, the type of environment affected calibration success, and static-trained models did not perform well when tested in dynamic environments because cohort individuals moved in response to both prey and predator cues rather than primarily avoiding fixed-in-space high mortality cells. Use of movement sub-models in IBMs should carefully consider how the conditions assumed for calibration relates to the dynamic conditions the model will be used to address.

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1. Introduction

Individual-based models (IBMs) are becoming increasingly popular, and many are spatially-explicit with dynamic environmental conditions (DeAngelis and Mooij, 2005; Grimm et al., 2005; Filatova et al., 2013). The accuracy of simulations often depends on realistic movement of organisms, which is especially challenging when movement cues (often related to environmental conditions) vary in time and space. The resolution of spatially-explicit models has been increasing as finer resolution environmental and movement data become available (Myers et al., 2006; Mills et al., 2007; Schick

et al., 2008; Neumann et al., 2015), more detailed physical-chemical models can be solved that generate environmental inputs (Allen et al., 2007; Soufflet et al., 2016), and management issues have required spatially-detailed predictions (Lindenmayer and Fischer, 2013; Guisan et al., 2013; Peterson et al., 2013; Hofmann and Gaines, 2008). One of the major challenges in spatially-explicit individual-based modeling is how to represent the movement behaviors and decisions of individuals.

Models that include representation of dynamic environments, particularly in aquatic systems where the fluid nature of water strongly affects the biological community, are also becoming more common as methods have advanced for coupling physical and biological models. For example, Goodwin et al. (2006) simulated the passage of migrating fish around hydroelectric dams using hydrodynamic movement cues generated from a physical model. Fiksen et al. (2007) simulated the dispersal of larval cod based on their vertical position and the current patterns predicted by a general cir-

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ulation model, and Huse and Ellingsen (2008) predicted changes in capelin migration patterns in response to climate change using a model that coupled a biophysical model of the Barents Sea with an IBM of the capelin population. Another way spatially-explicit IBMs can incorporate dynamic environments is in multi-species modeling, where the behavior of one model individual affects the conditions perceived by its prey, predators, and competitors. Sable (2007) developed an IBM of a six fish species tidal marsh community to assess the effects of hypoxia, and Campbell et al. (2011) evaluated the effects of the spatial arrangement of artificial reefs on a three species reef fish community in the northern Gulf of Mexico. Throughout this paper, we focus on behavioral movement of fish, and so cite fish-related papers and use terms like swimming speed and assess fitness of individuals with egg production based on a typical fish fecundity by weight relationship. However, our methods are easily generalized such that the methods and results apply to variety of taxa and to other movement algorithms.

Modeling movement is challenging because we rarely understand the mechanisms that fish and other organisms use to perceive and respond to their environment (Nathan et al., 2008; Demšar et al., 2015). Movement is even more challenging in models with dynamic environments because the spatial distribution of movement cues varies from one time step to the next. Feedback mechanisms further complicate movement simulation in dynamic environments. Feedback mechanisms (e.g., predators chase their prey; crowding depletes prey) cause the distribution of movement cues to change in time and space in response to movement decisions of the individuals. In this situation, the environment can not only vary in time and space, but also in response to the local activities of individuals and thus to the state of the population.

A number of approaches have been developed for simulating movement in IBMs. These approaches make different assumptions about how organisms perceive and respond to their environment and use different mathematics to predict movement responses. Restricted-area search assumes individuals are able to evaluate all cells within a defined area and identify the cell with the highest quality habitat (Railsback et al., 1999; Giske et al., 2003; Haas et al., 2004). Artificial neural networks (ANNs) use information about the current location, past experience, and other cues to determine directional velocities (Huse and Giske, 1998; Huse and Ellingsen 2008). Run and tumble divides the movement into running, where individuals move in a constant direction, and tumbling, where individuals randomly select a new swimming direction (Humphries et al., 2010; Loboschewsky et al., unpublished manuscript).

Correlated random walks are a common approach for simulating movement where a random turning angle and swimming speed are selected at each time step from defined probability distributions. Random walks can direct movement without considering environmental cues or they can adjust behavior (angle and swimming speed) based on environmental information (Codling et al., 2008). Kinesis is a random walk approach that continuously adjusts turning angle and swimming speed distributions based on current environmental cues (Humston et al., 2000, 2004). Event-based movement allows for switching among multiple discrete random walk behaviors (or other user defined behaviors) based on current and recently experienced environmental cues (Anderson, 2002; Goodwin et al., 2006).

Dynamic environments in spatially-explicit IBMs can be either externally forced or dependent on the state of population of interest. Many coupled models use the output of hydrodynamic and water quality models as inputs to an IBM, which is then run separately (Goodwin et al., 2006; Fiksen et al., 2007; Huse and Ellingsen, 2008). In this case, individuals in a particular cell at a particular time will always experience the same conditions defined by the output from the physical model (e.g., temperature). In other cases, models have been developed in which the environmental condi-

tions also respond to the dynamics of the population of interest. For example, allowing for depletion of prey in cells due to crowding and for predators to aggregate on groups of individuals resulting in dynamic prey and predator fields that respond to the movements of the individuals. In multi-species IBMs, the prey and predator fields can themselves be modeled with their own movement approaches (Campbell et al., 2011; Rose et al., 2015). In dynamic environments with feedbacks, an individual's behavior affects its exposure to prey, competitors, and predators, which in turn, affects the prey, competitor, and predator dynamics.

In this paper, we evaluate four movement sub-models (restricted-area search, kinesis, event-based, and run and tumble) in a spatially-explicit cohort IBM in which the prey and predators are both dynamic (vary across cells and over time) and responsive to the dynamics of the cohort individuals. We very roughly based the cohort model on a small pelagic fish, and thus the prey was based on zooplankton and the predators on a typical piscivorous fish. We used egg production as a measure of fitness, and the terms swimming speed and swimming angle to describe movement. However, the cohort model was relatively general and the analysis and results also apply to other (non-swimming) taxa with fitness measures other than egg production that move in 2-dimensional space.

The analysis approach was to train the four sub-models using a genetic algorithm (GA) in dynamic and static versions of the prey and predator-defined environments, and then to test the trained sub-models in the other type of environment. We examined egg production, weight, abundance, the mean cell quality experienced, and trajectory measures of individuals to evaluate sub-model performance. Sub-models were trained in the dynamic environment and tested in the static environment, and trained in the static environment and tested in the dynamic environment. We conclude with a discussion of the movement patterns generated by each sub-model, and recommendations for future application of these sub-models in applied population and community IBMs.

2. Methods

2.1. Model overview

The individual-based cohort model followed the growth, mortality, and movement of individuals on a 2.7 km × 2.7 km spatial grid of 625 m² square cells. We simulated growth, mortality, and movement for 3000 super-individuals every 25 min for a 30 day generation with 12 h days. Cells are referred to by the x-dimension (column number, *c*) and y-dimension (row number, *r*); continuous locations of individuals are in meters in the *x* and *y* dimensions from the origin located at the lower left corner. Individuals moved in continuous space and were mapped to cells, which were each associated with a prey biomass and number of predators in the cell. Individual growth was a function of the prey biomass in its cell, and mortality was determined by the number of predators in the cell as well as individual length. Movement was made modular so that the four different movement sub-models could be used interchangeably. The cohort model and the GA used to calibrate the movement sub-models were coded in Fortran 90.

The cohort model used a super-individual approach (Scheffer et al., 1995) to simulate both the individuals in the cohort and the predators. A super-individual is a model individual worth some number of actual individuals with identical characteristics. Use of super-individuals allows for simulation of a fixed number of model individuals (fixed array sizes) and for simulation of high mortality. In a true individual-based approach, when an individual dies, it is removed from the simulation. With super-individuals, all model individuals remain in the simulation, but their worth is decreased to represent mortality effects.

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