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Simple models for studying complex spatiotemporal patterns of animal behavior

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ABSTRACT

Minimal mathematical models able to explain complex patterns of animal behavior are essential parts of simulation systems describing large-scale spatiotemporal dynamics of trophic communities, particularly those with wide-ranging species, such as occur in pelagic environments. We present results obtained with three different modelling approaches: (*i*) an individual-based model of animal spatial behavior; (*ii*) a continuous taxis-diffusion-reaction system of partial-difference equations; (*iii*) a 'hybrid' approach combining the individual-based algorithm of organism movements with explicit description of decay and diffusion of the movement stimuli. Though the models are based on extremely simple rules, they all allow description of spatial movements of animals in a predator–prey system within a closed habitat, reproducing some typical patterns of the pursuit-evasion behavior observed in natural populations. In all three models, at each spatial position the animal movements are determined by local conditions only, so the pattern of collective behavior emerges due to self-organization. The movement velocities of animals are proportional to the density gradients of specific cues emitted by individuals of the antagonistic species (pheromones, exometabolites or mechanical waves of the media, e.g., sound). These cues play a role of taxis stimuli: prey attract predators, while predators repel prey. Depending on the nature and the properties of the movement stimulus we propose using either a simplified individual-based model, a continuous taxis pursuit-evasion system, or a little more detailed 'hybrid' approach that combines simulation of the individual movements with the continuous model describing diffusion and decay of the stimuli in an explicit way. These can be used to improve movement models for many species, including large marine predators.

1. Introduction

Mathematical models of spatiotemporal dynamics of trophic communities are effective and indispensable tools allowing researchers to analyze a variety of biological, behavioral, climatic and hydrological processes that determine the complex dynamics of marine ecosystems. Solving the problems of harvest control, of natural resource management, of monitoring species invasion, of protecting the endangered endemic animals requires deep understanding of the underlying processes that cause the emergence of the spatial patterns in the communities of interacting species. Climatic changes, in particular, the observed trends of global warming (Huang et al., 2015), increase the significance of the theoretical modelling studies that help scientists to explain and forecast the response of migrating species to spatial variation in ocean productivity (Hobday et al., 2013, 2015; Dell et al., 2015; Young et al., 2015). Due to strong observed and projected trends in environmental factors, statistical models cannot give a reliable prognosis of the ecosystem development. Models that reflect mechanisms of ecological and behavioral processes will be much more useful in predicting the impact of climate change on harvested and/or vulnerable species (Plagányi et al., 2011). Stressing the importance of developing new approaches to modelling spatial movements of large marine predators, Boschetti and Vanderklift (2015) noted that a better understanding of the animal foraging behavior improves density estimates and provides more accurate information for decision-making.

Along with the detailed simulation systems describing large marine ecosystems in great detail (Dragon et al., 2015; Lehodey et al., 2015; Senina et al., 2015), simple, so-called 'minimal' or

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'conceptual' theoretical models capable of reproducing complex dynamics observed in the natural communities play a highly important role in applied ecological studies (Medvinsky et al., 2001; Petrovskii and Li, 2005; Tyutyunov et al., 2007). In seeking the minimal description of the ecological problem, researchers must test alternative theories that explain a given observation and are commensurate with the complexity of the problem. The simplest and the most general model will be potentially more robust in practical applications (Ginzburg and Colyvan, 2004).

A clear and justified mathematical description should be used for every process that governs the dynamics of the ecosystem being studied: species reproduction, mortality, passive and active migrations, feeding, growth, etc. Ideally, this will ensure that assembly of the simulation system of any complexity consists of simple, sensible, and empirically proven model elements. If any element fails, we must not complicate the simulation model just to procure a desired result, but rather, we must modify or revise the theory. Eventually, if thorough quantitative validation of the more complicated modelling tools built for ecosystem management is impossible or difficult, qualitative validation of the basic models ensures their reliability. Therefore, building simple minimal models of ecological processes is an extremely useful task for both theory and practice. Such simple minimal models have been developed for a range of purposes over recent decades (Accolla et al., 2015; Couzin, 2002; Edelstein-Keshet et al., 1998; Okubo et al., 1977; Parrish et al., 2002; Pitcher et al., 1993; Tsyganov et al., 2004; Tyutyunov et al., 2007, 2008, 2009, 2013).

In this paper we consider only one particular process underlying spatiotemporal dynamics of marine population systems, namely the movement behavior causing animal aggregation. This is important as the spatial behavior of species is linked to their trophic relationships (e.g., Arditi et al., 2001; Tyutyunov et al., 2008; Willis, 2007, 2014). We consider three approaches to modelling the pursuit-evasion behavior of prey and predators: (*i*) individual-based models (IBM) of animal spatial behavior; (*ii*) continuous taxis-diffusion-reaction systems using partial-difference equations (PDEs); and (*iii*) 'hybrid' approaches combining the individual-based algorithm approach of organism movements with the explicit description of decay and diffusion of the movement stimuli. All these models are based on the common hypothesis of inertia: a delayed response of animals (both predator and prey species) to changing distribution of antagonistic species. We will demonstrate that though these models are based on extremely simple rules, due to this hypothesis they all produce quite complex realistic heterogeneous regimes under minimal modeling assumptions.

2. Statement of the problem

Spatial heterogeneity of population systems is highly dynamic. Formation of animal aggregations (i.e., swarming, schooling, etc.) occurs much faster than other key processes of population dynamics (Ritz et al., 2011), particularly as spatial aggregations occur at smaller spatial scales relative to the scale of environmental heterogeneity (Levin, 1992). Therefore, adequate models should demonstrate spatially inhomogeneous solutions induced only by the animals' spatial behavior. Neither the patchiness of environmental factors, nor population kinetics, i.e., birth/death demographic processes should play a crucial role in small-scale pattern formation. This is particularly true for highly developed pelagic species capable of active movements in space. Building adequate models for such species requires understanding of the mechanisms of the spatial movements of an animal being alone or within an aggregation. New approaches should be developed because most of the classical spatial population dynamics results were obtained during the second half of the 20th century on the basis of theoretical diffusion and taxis models and these models were primarily intended to describe microbiological and planktonic communities (Murray, 2003; Okubo and Levin, 2001). Direct transfer of these results to the modelling of larger species is fraught. Thus, practical needs for developing applied models of spatiotemporal dynamics of large ecosystems in changing environments raise new theoretical and methodological multidisciplinary problems at the intersection of ecology, ethology, mathematical modelling and cybernetics. One of the tasks is explaining the effects of self-organization observed in the populations of social animals such as schooling, swarming, flocking and synchronized behavioral responses to external signals and stimuli (e.g., Ritz et al., 2011).

Studying collective movements in fish populations, Pitcher and Parrish (1993) classified behavioral patterns and described typical examples of spatial configurations (flash expansion, ball, avoidance, herd, cruise, split, joinder, vacuole, hourglass, etc.), caused, in particular, by mutual attraction–repulsion interactions of prey and predators (see also Lee et al. (2006), Parrish et al. (2002) and Ritz (1991)). Such pursuit-evasion movements occur at much faster temporal scales than birth–death processes, and even faster than consumption of prey by predators because the predation efficiency (their ability to capture prey after an attack) may be quite low for some species, especially if prey exhibit active escape behavior to reduce the risk of predation (Lee et al., 2006; Ritz, 1991). The estimation of the proportion of successful attacks made for various species indicate that only few attacks performed by the predators pursuing their prey are successful (MacKenzie and Kiørboe, 1995; Hammerschlag et al., 2006; Roth and Lima, 2007).

3. The models

We first present in detail each of the three approaches that we suggest to use for modelling pursuit-evasion behavior in the predator-prey systems.

3.1. Individual-based model

An IBM is the most natural and intuitive way of modelling population dynamics (e.g., Huston et al., 1988). The individual-based approach describing a multi-agent system consisting of a finite number of members is especially effective for studying the behavior of animals at low abundance. Such models are highly useful for theoretical studies of various spatial phenomena in population dynamics. In particular, IBMs demonstrate that spatial heterogeneity can be a key factor altering the dynamics described by the classical (not resolved spatially) population models, which are, either explicitly or implicitly, based on the mass-action hypothesis borrowed from the chemical kinetics models (Tyutyunov et al., 2008; Accolla et al., 2015). IBM simulations are quite often used to unravel the mechanisms of the emergence of non-linear effects due to the spatial behavior of interacting animals, including such phenomena as patchiness of population distribution, density-dependent predation (e.g., predator interference) and the Allee effect (Cosner et al., 1999; Viscido et al., 2004; Ramanantoanina et al., 2011; Romanczuk and Schimansky-Geier, 2012; Tyutyunov et al., 2008, 2013; Harris and Blackwell, 2013; Accolla et al., 2015; Reuter et al., 2016; MacPherson and Gras, 2016). Additionally, taking into account the energy balance of interacting organisms opens new perspectives to building the realistic simulation models of spatiotemporal dynamics of biological systems (Maury and Poggiale, 2013; Politikos et al., 2015).

However, most of the individual-based models for collective behavior were subject to criticism (Katz et al., 2011; Romanczuk