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Multi-agent simulation of benthic foraminifera response to annual variability of feeding fluxes

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ABSTRACT

In this work we describe a novel simulation model of foraminifera and their microhabitat. The simulations reported here are focused on the response of foraminiferal populations to environmental feeding fluxes. The experiments allowed to calibrate the model and to simulate realistic population patterns known from culture experiments, as well as from oceanographic and paleoecologic studies. Variability of annual food flux has a direct impact on productivity of foraminifera: population sizes closely follow the intensity of constant and seasonal food fluxes in both scenarios. This correlation between the food influx and population size is interpreted as the consequence of changing the carrying capacity of the system. Seasonal pulses of particulate organic matter enhance the population size which is represented by a higher number of fossilized shells. Our model offers a flexible experimental design to run sophisticated *in silico* experiments. This approach reveals a novel methodology for testing sensitivity of fossil and recent foraminiferal assemblages to environmental changes. Furthermore, it facilitates predictive applications for monitoring studies based on simulation of various scenarios.

1. Introduction

This work introduces a multi-agent simulation model of Foraminifera and their microhabitat (Fig. 1). Artificial life methodology [1,2] is employed to develop an *in silico* software model that is continuously improved and calibrated for reconstruction and prediction of various short- and long-term processes of foraminifera, including their behavior (Fig. 2), population dynamics, life-history strategies, energy flow, as well as selected evolutionary phenomena.

Foraminifera are ideal model organisms often used for testing paleoecological and evolutionary hypotheses (e.g. [3,4]). They are single-celled eukaryotes that populate marine benthic and pelagic zones throughout the world [5–7]. Foraminifera have an extraordinary fossil record at least since the Cambrian (500 million years ago) [8,7]. Most foraminifers produce diverse shells, covering their soft cells. Foraminifera with spheroidal (globular) chambers that belong to the class Globothalamea [9] represent the main focus of our investigations.

This study follows morphogenetic models developed to simulate diverse patterns of foraminiferal shells that grow by successive additions of chambers [10–12]. It extends these models to agent population models by introducing foraminiferal behavior, energy flow, and life cycles for realistic simulations of population dynamics and evolutionary processes (see [13–15] for further explanation of the eVolutus project).

Benthic foraminifera mainly feed on particulate organic matter (POM), thus they are strongly dependent on POM availability in time and space [6,7,16,17]. Seasonality (e.g., nutrient availability, light and temperature) is the most conspicuous temporal variability that influences POM flux. The POM flux and its variability have a direct impact on distribution, life history strategies, reproduction, and population dynamics of foraminifera [18,6,17].

A life span in foraminifera ranges from a few weeks to a few years [19,18]. Although life cycles with three generations are frequent in benthic foraminifera, a typical life cycle is characterized by an alternation of two modes of reproduction: sexual (in the haploid generation) and asexual (in the diploid generation) [19] (Fig. 3). This life cycle helps foraminifera adjust to variable environmental conditions by generating diverse and flexible life history strategies [6].

The main objectives of this study include: (1) defining and calibration of model parameters; (2) designing and running feeding experiments that test a response of foraminiferal life cycles to

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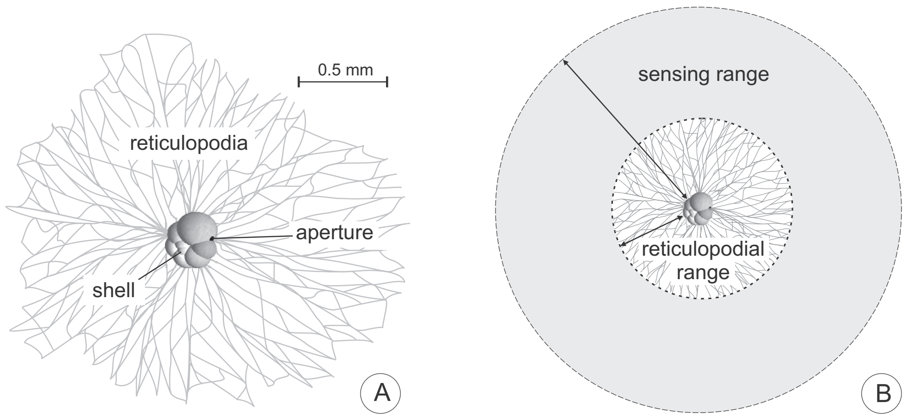

Fig. 1. A foraminifer with its reticulopodia. (A) A single individual with extended reticulopodia during searching and feeding behavior. (B) A model of an agent with the circular reticulopodia range surrounded by the chemotactic sensing range.

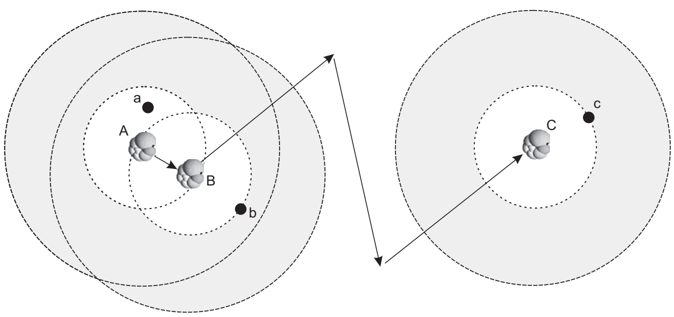

Fig. 2. A model of foraminiferal behavior that represents searching, sensing, feeding, and movement activities. When a food particle (a) falls into the white reticulopodia range of (A), it is collected and eaten. When a food particle (b) is within the gray sensing range of (A), a foraminifer has to move towards food. The particle is collected if the external limit of reticulopodia can reach it (B). When there is no food available, a foraminifer starts moving in a random direction, periodically changing directions (C). This strategy allows collecting particles (c) that are initially outside of both ranges.

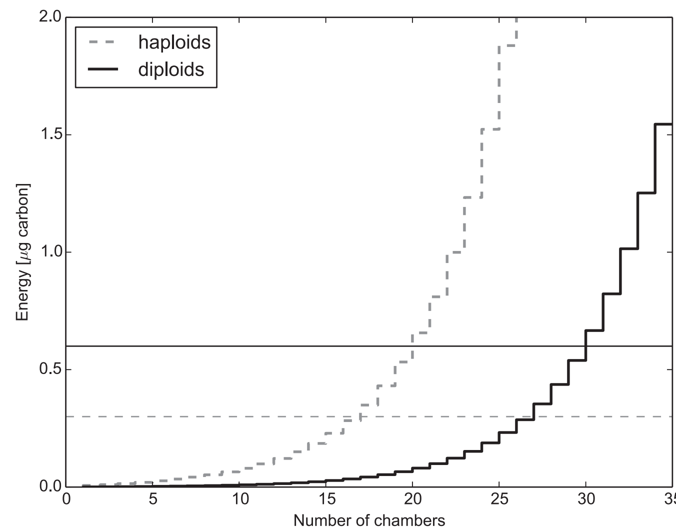

Fig. 4. The maximal amount of energy that can be stored by a simulated individual with the given number of chambers. Horizontal lines are the maturation checkpoints of haploids and diploids.

variability of feeding fluxes. We test the flexibility of such life strategies to aseasonal vs. seasonal organic matter fluxes.

1.1. Simulation software

For simulation experiments we use Framsticks [20,21], a highly configurable and versatile simulation toolkit. This software environment has been earlier used for modeling complex collective systems, autonomous agents, and evolutionary and co-evolutionary processes. It allows for an arbitrary number of genetic encodings and their hierarchy [22,23] and two modes of mechanical simulation (accurate rigid body and approximate elastic body)

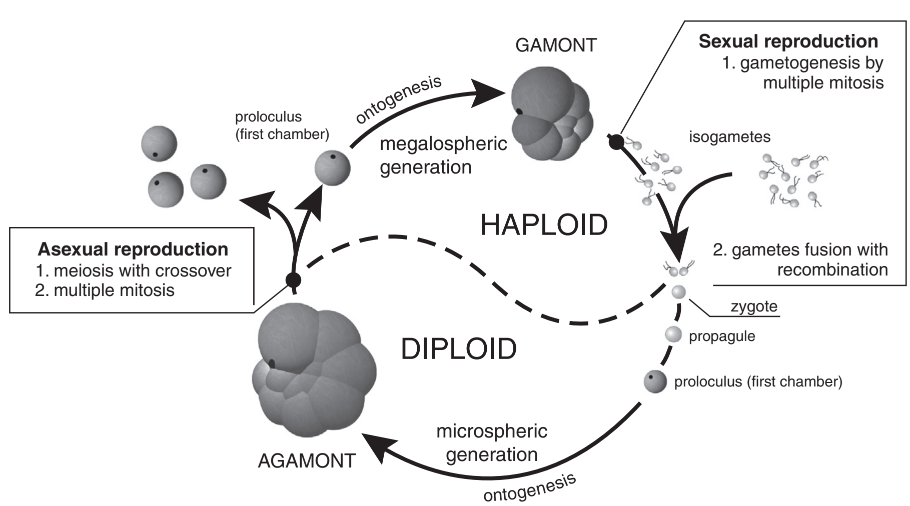

Fig. 3. Benthic foraminifera life cycle with bimorphic generations and two reproduction modes (modified after [19]). This cycle is introduced into the presented model.