Ecological Modelling 320 (2016) 213–230

Contents lists available at ScienceDirect

Ecological Modelling

journal homepage: www.elsevier.com/locate/ecolmodel

Mechanistic modelling of daphnid-algae dynamics within a laboratory microcosm

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ARTICLE INFO

Article history:
Received 13 February 2015
Received in revised form
14 September 2015
Accepted 22 September 2015

Keywords:
Bayesian inference
Species interactions
Model-guided experiments
Daphnia magna
Pseudokirchneriella subcapitata

ABSTRACT

Our study describes the functioning of a 2-L laboratory microcosm of two species, daphnids (*Daphnia magna*) and microalgae (*Pseudokirchneriella subcapitata*), in two abiotic phases (water column and sediment). We modelled the dynamics of both species and their interactions using a mechanistic model based on coupled ordinary differential equations. The main processes occurring in this two-species microcosm were thus formalised, including growth and settling of algae and growth, survival and grazing of daphnids. We estimated model parameters by Bayesian inference, using simultaneously all data from multiple experiments specifically conducted for this study. Two types of model verifications were performed: (1) internal verification to validate model structure and parameter estimation method using all data simultaneously; and (2) external verification to validate the ability of the model to be applied under new sediment conditions. For all parameters, we obtained biologically realistic values and reasonable uncertainties. The first verification step allowed us to confirm the modelled processes and the benefits of our parameter estimation method. The second one confirmed the ability of the model to describe microcosm functioning under different abiotic conditions. This innovative combination of mechanistic modelling and model-guided experiments revealed successful to understand the algae-daphnid microcosm functioning. This approach appears promising and can be applied to various issues in the ecological and ecotoxicological fields.

1. Introduction

Interactions between species strongly influence ecosystem functioning and are therefore widely studied. For instance, species interactions can underlie processes such as spatial segregation (Costa et al., 2008) or exotic-native species dynamics (Söderbäck, 1994). Many studies have explored the impacts of several stress factors on trophic relationships: climatic variations (Sutherst et al., 2007), diet and temperature (Farjana et al., 2012), infection (Lin et al., 2014), chemical stress factor (Ham et al., 1995; Taylor et al., 1995; Turner et al., 2000) or habitat disturbance (Pathikonda et al., 2009).

Today, several experimental devices are commonly used to study ecosystem functioning and species interactions. Laboratory microcosms are both realistic and reproducible (Daam and Van den Brink, 2007). Moreover, many ecological and biochemical interactions and processes can occur within microcosms, that may involve multiple species and abiotic compartments, for example water and sediment. In addition, microcosms may be useful for predicting the states of real aquatic ecosystems (Benton et al., 2007; Cadotte et al., 2005). Microcosms allow to address various issues in aquatic ecology or ecotoxicology. For instance, several climate warming effects have been investigated (McKee et al., 2002). In ecotoxicology, microcosms have been used to examine the functional responses of communities to chemical stress factors (Bone et al., 2012; Brinke et al., 2010; Clément and Zaid, 2004; Clément et al., 2005; Faupel et al., 2012). However, the inherent complexity of microcosms, due to both biotic and abiotic interactions, leads to confounding factors that do not always ensure a good understanding of responses.

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http://dx.doi.org/10.1016/j.ecolmodel.2015.09.020
0304-3800/

To address this issue, several mechanistic dynamic models have been developed to describe the ecological interactions and physiological processes occurring within such ecosystems. When the processes occurring in the functioning of a microcosm are modelled, parameters included in the model can be estimated using experimental data. Several types of data can be used (for example number of individuals, species biomass or reproduction data), each one representing different processes. The submodels related to each process can be parametrized independently of each other, if all types of data cannot be managed together. However this method may cause problems. First, potential correlations between parameters that are not estimated simultaneously are not taken into account. Secondly, information about a given process can be provided by data which are not directly related to this process. Thus, information may lack and parameter estimations can be less precise when all data are not used simultaneously for the statistical inference. Bayesian inference allows the use of multiple types of data, collected at different scales, as well as the estimation of all the parameters simultaneously (Billoir et al., 2008). This method provided benefits in several ecology fields. For instance, animal densities (Gopalaswamy et al., 2012) or parentage of individuals (Hadfield et al., 2006) were investigated with more precision by combining different types of behavioural, spatial and genetic data. In species abundance studies, Bayesian inference allowed handling the inherent difficulties of abundance data modelling in a hierarchical framework (Moore and Barlow, 2011).

We aim here at modelling in an integrated way the processes involved in a two-species microcosm using data from experiments specifically designed for this purpose. We also intend to verify the robustness of both our model and parameter estimation method that implies to use all data simultaneously within a Bayesian framework. For that, we used here a reduced version of an original microcosm (Clément and Cadier, 1998) with only two species interacting. We chose two model organisms, microalgae (*Pseudokirchneriella subcapitata*) and daphnids (*Daphnia magna*), linked by a trophic relationship.

We first describe how laboratory microcosm experiments of the daphnid-algae system were conducted. Then, we describe the development of the mechanistic model based on ordinary differential equations (ODE) using the Overview, Design concepts and Details (ODD) protocol (Grimm et al., 2010). We also present how parameters were estimated using Bayesian inference and the model verifications we performed using different datasets. Finally, we discuss our results and propose some model improvements and perspectives on the use of both model and method.

2. Experiments

2.1. Microcosm preparation

The microcosm design used in our study was based on that developed by Clément and Cadier (Clément and Cadier, 1998), which was first used in chronic toxicity bioassays and as a diagnostic of urban discharge (Cauzzi, 2007; Clément and Zaid, 2004; Clément et al., 2005, 2014; Triffault-Bouchet et al., 2005; Verrhiest et al., 2001). The originally developed microcosm was composed of five species. In this study, we reduced it to two species, algae and daphnids, but we preserved the original protocol.

Laboratory experiments were conducted at LEHNA (ENTPE, Vaulx-en-Velin, France). Microcosm preparation (with the exception of the sediment) was identical for all experiments. Two litres of synthetic water were poured into cylindrical glass beakers following the addition of the sediment (when present). Synthetic water (pH = 7.7, hardness = 60 mg $CaCO_3$/L, $[P] = 0.1$ mg/L, $[N] = 1.31$ mg/L) was prepared according to Clément et al. (2014). To achieve microbiological stabilisation in the sediment, the microcosms were conditioned for seven days in the dark before the introduction of algae and daphnids (Verrhiest et al., 2002). At this point, the systems were gently aerated (using sterile glass Pasteur pipets connected to an aquarium air pump) to ensure an oxygen concentration above 80% of saturation. Microcosms were maintained at a constant temperature ($20 \pm 2\,^{\circ}C$).

Four different experiments were conducted to collect data that would allow us to estimate our model parameters. Two additional experiments were subsequently conducted to verify our model. We describe each set of experiment below.

2.2. Experiments used for parameter estimation

In these experiments, artificial sediment (100 g of Fontainebleau sand, a simple silicate sand which is both a classic breeding sediment for benthic organisms and a classic control sediment for tests on contaminated sediment) was used.

2.2.1. Experiment 1: algae settling

Beakers were placed in the dark and wrapped in aluminium foil, so that algal growth was prevented and algal settling was enabled. At the start of the experiment (day 0), approximately $6 . 10^9$ cells of *P. subcapitata* were introduced into each of 6 microcosms. The algal density in the water column was measured every two or three days for two weeks by sampling 30 mL from the beaker. After homogenisation of the 30 mL, only 1 mL was retained to measure algal density with a particle counter (Coulter^®). The remaining 29 mL were returned to its original beaker. This first experiment allowed us to obtain the number of algal cells per beaker in the water column over time in each beaker (named afterwards $Ydark_1$, index 1 refers to the water column compartment).

2.2.2. Experiments 2–4: algae-daphnid interaction

The following three experiments were conducted using a total of 17 beakers: 12 of them contained only algae and 9 of them contained algae and daphnids. The purpose of these experiments was to compare algal density with and without daphnids. Daphnids were supposed fed ad libitum with algal cells.

Beakers containing 2 L of synthetic water and artificial sediment were placed under periodic illumination (2200 ± 200 lux at the top of each beaker delivered by 36 W daylight tubes (Mazda), 16 h per day). At the start of the experiment (day 0), $4 . 10^7$ cells of *P. subcapitata* were introduced into all beakers and 10 daphnids (*Daphnia magna* neonates aged 24 ± 12 h) were introduced into 9 of these beakers. All algae and daphnids had been bred in the laboratory following internal protocols (Clément et al., 2014). The duration of these experiments was 21 days. In all microcosms, algal density in the water column was measured every two to three days, as in the algae settling experiment. Total algal density was measured once a week: the water column of 6 beakers was thoroughly mixed and total algal density was measured using a hematocytometric (Thoma) cell, and therefore these measurements required sacrificing the corresponding beakers. Then, the algal density on the sediment was deduced by subtracting the algal density in the water column from the total algal density. The number of daphnids in each beaker was counted (after neonate removal if necessary) and their size measured (from the centre of the eye to the caudal base of spine) twice or thrice per week. Daphnids neonates were removed from the microcosm every two days, that is why reproduction was considered as an independent process in the microcosm functioning. From these experiments, we obtained four types of data: (i) the number of algal cells in the water column over time with (YD_1) and without daphnids (Y_1), (ii) the number of algal cells on the sediment over time with (YD_2) and without daphnids (Y_2), (iii) the number of surviving daphnids over time (W), and (iv) the