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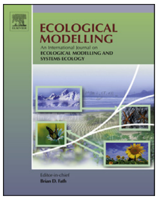

The power of hybrid modelling: An example from aquatic ecosystems

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ABSTRACT

Planktonic communities in ponds and lakes show a high annual dynamic controlled by biotic interactions, nutrients and weather. In recent years, there has been an increase in demand for realistic and accurate lake models to improve ecological management of water bodies and to answer ecotoxicological questions in aquatic risk assessment. Most existing aquatic models are either ecosystem models aimed at describing the overall ecosystem dynamics, but which are incapable of including individual life-cycles and plasticity, or very detailed and realistic individual-based models lacking an appropriate level of environmental complexity. To reconcile these concepts, we present here a modelling approach using an individual-based population model (IBM), integrated within an ecosystem lake model, to link responses at the individual and population levels. We combine an IBM for *Daphnia magna* (IDamP) and a complex biogeochemical lake model (StoLaM), to create the DaLaM (*Daphnia* Lake Model). We use DaLaM to predict population dynamics of *D. magna* and phytoplankton within a simplified, daphnid-dominated food web under field conditions. In DaLaM, relevant variable environmental conditions such as underwater light climate, water temperature, turbulence, and nutrient availability are realistically simulated forced by weather conditions. For model testing we used data from aquatic mesocosm field studies exhibiting variable nutrient and weather conditions and lasting from several months to 2 years. DaLaM gave improved predictions of the overall population patterns of daphnids and phytoplankton in the mesocosms in contrast to its separate submodels. This study is an example of successfully merging individual-based population models with dynamic ecosystem models utilising the accuracy of the former and the dynamic environment of the latter to simulate more realistic field populations.

1. Introduction

In recent years, there has been an increase in demand for realistic and accurate lake models, which are able to address anthropogenic stress factors such as eutrophication and ecotoxicologically relevant pollution, for use in lake management (Jørgensen, 2010; Mooij et al., 2010) and ecotoxicological risk assessment (Galic et al., 2010). Aquatic ecosystems are regulated by a multitude of biological interactions occurring between different trophic levels, known as bottom-up and top-down processes (McQueen et al., 1989). Among these processes, the interactions between primary producers and zooplankton grazers are key processes in pelagic freshwater food webs (Perhar et al., 2013; Persson et al., 2007; Zhao et al., 2008). Modelling these fundamental interactions requires knowledge about relevant factors such as weather conditions and nutrient dynamics controlling phytoplankton biomass and species-specific dynamics of the grazing population.

Several models integrating hydrodynamics and ecological processes have been developed (Jørgensen, 2010) to account for the dynamic physical properties of lakes (e.g., temperature, light and turbulence in the water column) and their variation with meteorological forces (e.g., Bruce et al., 2006; Mooij et al., 2010; Zhao et al., 2008).

In aquatic ecosystem models, nutrient dependency of primary and secondary producers is often described by detailed nutrient cycles (Mooij et al., 2010). Model realism can additionally

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be improved by integrating the concept of ecological stoichiometry (Sterner and Elser, 2002), which deals with the relative ratio of carbon and multiple chemical elements (mostly nitrogen and phosphorus) in food web interactions (Elser and Urabe, 1999). The stoichiometric concept distinguishes between mostly homeostatically regulated consumers and autotrophic organisms with variable nutrient content due to their ability for nutrient storage (Sterner and Elser, 2002). Constant C:N:P stoichiometry of herbivorous organisms can be maintained only by modifying their growth corresponding to the most constraining element in the diet as per Liebig's "law of the minimum" (Andersen et al., 2004). Phytoplankton as autotrophic organisms often have lower nutrient contents compared to the needs of herbivorous consumers (Sterner and Elser, 2002), frequently leading to an imbalance in the C:N:P stoichiometry between food and consumers. This can affect the population dynamics of consumers, e.g. a direct limitation of the growth rates of herbivorous organisms by the lack of nutrients (Urabe and Watanabe, 1992). In addition, the rate of consumer-driven nutrient recycling via excretion of surplus nutrients influences the nutrient content and growth of phytoplankton. Sterner and Elser (2002) pointed out that a combination of predator-prey interactions with biogeochemical-controlled conditions in explicit stoichiometric models leads to a more realistic representation of these processes. Both food quantity and food quality for herbivore consumers have a significant impact on the development of zooplankton and phytoplankton populations.

Although the dynamic carbon-nutrient stoichiometry of algae has long been known (e.g. Droop, 1974), the ecological stoichiometry for higher trophic levels has been rarely taken into account in complex ecosystem models (Jørgensen, 2010; Persson et al., 1999). In several simple strategic models, stoichiometric principles were considered for algae-herbivore interactions (e.g., Andersen, 1997; Diehl, 2007; Hessen and Bjerkeng, 1997; Loladze et al., 2000; Touratier et al., 2001), whereas only few lake models integrated stoichiometric principles (e.g., Perhar et al., 2013; Strauss, 2009; Zhao et al., 2008).

So while ecosystem models deal with nutrient dependencies and cycles, they ignore variability between individuals and adaptive strategies which can be very important for ecosystem dynamics (e.g. Grimm and Railsback, 2005). In contrast, individual-based population models (IBMs) have the potential to simulate the variability between individuals of the same population in terms of life history characteristics and how they change with environmental properties and adaption to different conditions (e.g. food availability, predation, temperature; Forbes et al., 2008; Preuss et al., 2009). The population properties in the IBMs (e.g., abundance, population growth rate, and age/size structure) emerge directly from the interaction of individuals with each other and their environment (Forbes et al., 2008; Grimm and Railsback, 2005). While the density dependence of interspecific interactions is already an important component of ecosystem models with unstructured populations, intraspecific effects such as crowding (Gergs et al., 2014; Preuss et al., 2009) or cannibalism (Strauss et al., 2016) as well as size selective predation (e.g. Gergs et al., 2013) can only be represented by structured population models. Life processes and food web interactions often vary depending on age, size, or developmental stage of the particular species. Among the structured population models, individual-based population models typically have the highest resolution in these properties, and are able to describe the population structure with respect to all these different properties simultaneously, based on tracking of each individual within a population (Cao et al., 2016). IBMs are particularly well-suited when ecotoxicological effect models such as toxicokinetic-toxicodynamic models are coupled with population models, since they can both simulate the individual accumulation of a toxin over time and are able to take into consideration different size-specific sensitivities (Gergs et al., 2015).

Hybrid modelling is a promising approach that integrates models with different scales and organisational levels to extend the questions a single model can deal with (Breckling et al., 2005). On the one hand, IBMs increase the potential of ecological models to describe complex interactions more precisely (Breckling et al., 2005), and on the other hand, ecosystem models can provide a more realistic environment for the individual-based population models. First examples of coupling IBMs to aquatic ecosystem models acting as dynamic environments are given in (Batchelder et al. (2002), vertical migration of copepods in marine upwelling systems) and (Makler-Pick et al. (2011), fish impact on lake food webs).

In this study we emphasized the realism of the modelled physical lake properties, the stoichiometric interactions within the food web, and the advantages of individual-based modelling of a grazer population, in providing realistic predictions of *Daphnia* population dynamics in the field. For this purpose we coupled two existing process-based ecological models: an individual-based population model for *Daphnia magna* (IDamP; Preuss et al., 2009) and a complex stoichiometric biogeochemical lake model (StoLaM; Strauss, 2009). The combination of both models is called DaLaM (*Daphnia* Lake Model) and is used in the present study to predict population dynamics of *D. magna* and phytoplankton in outdoor ponds under realistic weather and nutrient field conditions.

Our aim is to explore the feasibility of connecting IBMs to ecosystem models, and to see whether the predictive power of such hybrid models has been increased relative to the separate models, for extrapolating from individual-level endpoints observed in laboratory tests to populations-level responses in the field. To this end, we compared the use of structured and unstructured population models for *Daphnia* within an ecosystem model framework under similar conditions with reduced food web complexity.

2. Material and methods

2.1. Model description

DaLaM was constructed by combining the two existing, mechanistic models: IDamP and StoLaM. The model description follows the rationale of the ODD protocol (Grimm et al., 2006, 2010), but due to reasons of space limitation only a summary description of the most important elements is given in this chapter. A full ODD description of IDamP as well as a detailed description of StoLaM is provided in the Supplementary Information S1.

2.1.1. Purpose

The purpose of the DaLaM model is to predict population dynamics of *D. magna* under realistic and dynamic environmental field conditions, by considering algal growth in relation to nutrient resource dynamics as well as variable temperature and light conditions. The focus of developing DaLaM was not to include all the food web complexity of real ecosystems, but to capture their essential components relevant for a daphnid-dominated planktonic ecosystem while keeping the model robust and tractable.

The simulated environmental scenario in this paper is as follows: The type of waterbody is represented by aquatic mesocosms without inflow; the trophic state is mesotrophic to eutrophic depending on the sediment phosphorus release rates, and the weather conditions in Aachen, Germany, were used.

2.1.2. Entities, state variables and scales

A flow chart describing the relations between the individual submodels within DaLaM is shown in Fig. 1.