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Modeling the direct and indirect effects of copper on phytoplankton–zooplankton interactions

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ABSTRACT

Predicting the effects of pollution at the community level is difficult because of the complex impacts of ecosystem dynamics and properties. To predict the effects of copper on a plant-herbivore interaction in a freshwater ecosystem, we built a model that focuses on the interaction between an alga, *Scenedesmus* sp., and a herbivore, *Daphnia* sp. The model assumes logistic growth for *Scenedesmus* and a type II functional response for *Daphnia*. Internal copper concentrations in *Scenedesmus* and *Daphnia* are calculated using a biodynamic model. We include two types of direct effects of copper on *Scenedesmus* and *Daphnia* that results from hormesis: a deficiency effect at low concentration and a toxic effect at high concentration. We perform a numerical analysis to predict the combined effects of copper and nutrient enrichment on the *Scenedesmus*–*Daphnia* interaction. Results show three types of outcomes depending on copper concentration. First, low ($4\,\mu g\,L^{-1}$) and high ($50\,\mu g\,L^{-1}$) copper concentrations cause deficiency and toxicity, respectively, leading to the extinction of all populations; for less extreme concentrations (between 4 and $5\,\mu g\,L^{-1}$ and between 16.5 and $50\,\mu g\,L^{-1}$), only the consumer population becomes extinct. The two populations survive with intermediate concentrations. Second, when population dynamics present oscillations, copper has a stabilizing effect and reduces or suppresses oscillations. Third, copper, on account of its stabilizing effect, opposes the destabilizing effect of nutrient enrichment. Our model shows that (1) *Daphnia* is affected by copper at lower concentrations when community interactions are taken into account than when analyzed alone, and (2) counterintuitive effects may arise from the interaction between copper pollution and nutrient enrichment. Our model also suggests that single-value parameters such as NOEC and LOEC, which do not take community interactions into account to characterize pollutants effects, are unable to determine pollutant effects in complex ecosystems. More generally, our model underscores the importance of ecosystem-scale studies to predict the effects of pollutants.

1. Introduction

Laboratory tests used to assess the toxicology of chemicals are mostly based on single species tests. Typically, the effects of chemicals are assessed with a model species, and several parameters describing the toxicological effects for an external concentration are calculated (NOEC, LC_{50}, LD_{50}, etc.). These parameters reflect the toxicological effects of a chemical on a species in the laboratory; such an organism-centered approach (Villeneuve and Garcia-Reyero, 2011) considers only the direct effects (Strauss, 1991). However, estimating toxicological effects on an ecosystem is more challenging because of the complex impacts of ecosystem dynamics and properties (Fleeger et al., 2003). For instance, Lampert et al. (1989) tested the effects of the herbicide atrazine on some aquatic systems. Laboratory tests on *Daphnia* showed an effect with an effective concentration of $2\,mg\,L^{-1}$, while tests on a food chain system with *Daphnia* and algae showed a significant reduction in *Daphnia* population growth at $0.1\,mg\,L^{-1}$. A third test conducted in enclosure experiments with natural communities showed responses to atrazine concentrations between 0.1 and $1\,\mu g\,L^{-1}$. These experiments show that indirect effects can be greater than direct effects (Lampert et al., 1989) and that standard laboratory tests do not reveal the indirect effects of pollution at the community level. In addition to indirect effects, studying the effects of pollutants on ecosystems requires the consideration of the organisms' internal concentration, which varies with trophic level, as well as the pollution from multiple contaminants. As a consequence, predicting the effects of pollution at the community level is a complex issue. Therefore, studying pollutant effects with ecosystem-centered approaches is the focus of the new paradigm

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of the ecological risk assessment (Villeneuve and Garcia-Reyero, 2011).

Mathematical modeling has already proved a useful tool to help predict the effects of a pollutant at the population (Manyin and Rowe, 2008) and ecosystem (Traas et al., 1998; Trudel and Rasmussen, 2001; Van den Brink et al., 2006) levels in a few cases. Although food web models have been applied to the study of persistent organic pollutants such as PCBs, introducing more ecological thinking into the analyses of contaminant effects still represents a major challenge (Campfens and MacKay, 1997; Scharler et al., 2005).

In this article, we build a model designed to predict the effects of copper on an important plant-herbivore interaction in freshwater ecosystems. As a receptor of urban wastewater, industrial and mine effluents, agricultural runoff, and atmospheric pollution, aquatic ecosystems are prone to copper pollution (Jørgensen, 2010; Nriagu, 1979). Copper is an essential element of life (Mertz, 1981) as it enters the composition of numerous enzymes. A low internal concentration may induce deficiency effects (Bossuyt and Janssen, 2003). However, single-species tests in the laboratory showed that copper is highly toxic at high concentrations (Clements et al., 1992). Copper has negative impacts on primary producers, microorganisms, invertebrates, fish, and amphibians (ATSDR, 1990; WHO, 1998).

In this article, we examine the copper effects on the interaction between algae and *Daphnia* sp. for several reasons. First, this interaction plays a key role in the dynamics of many freshwater ecosystems (McCauley and Murdoch, 1987; McCauley et al., 1988) and it is commonly used as a model system in ecology and ecotoxicology. Algae and *Daphnia* are frequently used in toxicology tests on isolated populations (Reynolds, 2011) as well as in standard ecotoxicological tests, for instance, for water quality monitoring. Although our model focuses on a specific prey-predator interaction, it is representative of communities with strong trophic interactions (Berlow et al., 1999, 2004), as is generally the case in freshwater ecosystems (Shurin et al., 2006).

Second, various direct effects of copper on algae and *Daphnia* sp. have been described, which allows us to accurately describe its effects on this particular plant-herbivore interaction.

The direct effects of copper on algae include the inhibition of photosynthesis (Havens, 1994), inhibition of growth (Fargasova et al., 1999; Fathi and El-Shahed, 2000; Yan and Pan, 2002), decreased concentrations of glucides, proteins, amino-acids (Fathi and El-Shahed, 2000), and chlorophyll (Fargasova et al., 1999) in algal cells, and decreased alkaline phosphatase activity (Fathi and El-Shahed, 2000). The direct effects of copper on *Daphnia* sp. life-history traits include a decrease in fecundity, survival, body length, weight, and carbon uptake, as well as a delay in maturation (Baird et al., 1991; Ingersoll and Winner, 1982; Knops et al., 2001; Koivisto et al., 1992; Winner and Farrell, 1976). Moreover, some behavioral responses of *Daphnia* to copper are known: their mobility decreases (Clement and Zald, 2004), while their swimming velocity, filtration rate, and ingestion rate are optimal for an intermediate copper range (Ferrando and Andreu, 1993; Untersteiner et al., 2003). These behavioral modifications may indirectly affect ecological interactions. For instance, the effect of copper on *Daphnia*'s mobility (Clement and Zald, 2004; Gutierrez et al., 2012; Sullivan et al., 1983) in turn affects its foraging behavior and ability to escape predators, and, ultimately, its prey and predator populations. Concerning *Scenedesmus*' behavior, copper reduces the colonies that they form in response to *Daphnia*'s predation (Lürling and Van Donk, 2000; Peña-Castro et al., 2004; Van Holthoon et al., 2003; Wu et al., 2013).

The study of copper effects is complicated by copper speciation and environmental factors. The response of each species' life-history trait—for instance, growth rate, predation, and mortality—varies greatly due to copper speciation (Van Veen et al., 2002). For example, the EC_{50} for *Daphnia* sp. can range from simple to twentyfold (Jørgensen, 2010). In addition, many environmental factors such as pH and CO_3^{2-}, Ca^{2+}, Mg^{2+}, Na^{+}, K^{+}, Cl^{-}, and SO_4^{2-} concentrations also modify responses to copper concentration (De Schamphelaere and Janssen, 2002). A few toxicity values can be determined for species-pollutant couples with the Biotic Ligand Model. This model allows the LD_{50} and EC_{50} to be determined for some species and pollutants as a function of variable environmental parameters (see Paquin et al., 2002 for an overview and De Schamphelaere and Janssen, 2002 for an example).

In this study, we use our model to analyze the effects of copper pollution on the *Scenedesmus*–*Daphnia* interaction. Nutrient enrichment has major destabilizing effects on prey-predator interactions, known as the paradox of enrichment (Rosenzweig, 1971). As freshwater ecosystems are often subject to nutrient enrichment, which is a major perturbation in aquatic ecosystems (Dudgeon et al., 2006; Sala et al., 2000), we also study the interaction between copper pollution and eutrophication.

2. Methods

2.1. Modeling freshwater ecosystems and copper effects

We consider a simple freshwater ecosystem consisting of two compartments, phytoplankton and zooplankton, with the genera *Scenedesmus* and *Daphnia* chosen as model organisms for these compartments. These genera include many species, but since the associated species have very similar life-history traits (McCauley et al., 1988), we do not distinguish them in our study. Moreover, all *Scenedesmus* species are approximately the same size, which is the main criterion for describing *Daphnia*'s size-based predation (Briand and McCauley, 1978; Burns, 1968; McCauley et al., 1988; Porter, 1973).

In freshwater environments, various phenomena of copper speciation have been described (Nomkoko et al., 2003; Van Veen et al., 2002). Moreover, the amount of bioavailable copper depends on many environmental parameters (Town and Filella, 2000). Among the various chemical forms toxic to freshwater organisms, it is widely acknowledged that copper toxicity is directly related to the concentration of free and bioavailable Cu^{2+} in water (Nomkoko et al., 2003; Van Veen et al., 2002). Therefore, we focus on this form in our study, referring to its concentration as copper concentration in water. Copper impacts on organisms may be either direct or indirect. Direct effects are due to copper bioconcentration in organisms through direct absorption (through skin or gills, or by drinking contaminated water) as well as its progressive accumulation in tissues, as copper excretion is weaker than copper absorption (ATSDR, 1990; WHO, 1998). Indirect effects occur through modifications to the densities and dynamics caused by the pollutant on the life-history traits of the concerned and related species.

2.2. Model

The model development follows several steps. We first model the *Scenedesmus*–*Daphnia* interaction without copper pollution. Next, we calculate the internal concentration of copper and analyze its effects on each species. Finally, we include its effects on model parameters to describe the *Scenedesmus*–*Daphnia* interaction in the presence of copper pollution. Our analysis relies on a classical community model that includes two variables, *Scenedesmus* and *Daphnia* densities.

2.2.1. Scenedesmus–Daphnia *interaction*

In a constant environment, *Scenedesmus* dynamics is assumed to be logistic (McCauley et al., 1988). The functional response of