Ecological Modelling 222 (2011) 3002–3010

Contents lists available at ScienceDirect

Ecological Modelling

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

Dynamic model of Lake Chozas (León, NW Spain)—Decrease in eco-exergy from clear to turbid phase due to introduction of exotic crayfish

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ARTICLE INFO

Article history:
Available online 24 May 2011

Keywords:
Eco-exergy
Entropy
Dynamic model
Phosphorus cycle
Procambarus clarkii
Lake Chozas

ABSTRACT

We developed a dynamic model of the phosphorus cycle in Lake Chozas, a small shallow water body in León (NW Spain). The calibrated model simulated seasonal dynamics of phosphorus concentrations in major components of the lake's ecological network before and after 1997, the year when an invasive allochthonous crustacean, the Louisiana red swamp crayfish (*Procambarus clarkii*), was introduced into the lake. The shift from clean to turbid phase, due to grazing by crayfish on submerged vegetation, caused a gradual decrease in eco-exergy, reflecting an increase in entropy, related to breakdown of ecosystem internal equilibria. This case study verifies the hypothesis of Marchi et al. (2010) that, after an initial relatively stable state, the allochthonous species may cause an increase in entropy indicating perturbation of the ecosystem.

1. Introduction

Lake Chozas is a small shallow-water body (volume 17,551 m^3; maximum depth 1.8 m) in León (NW Spain). It is surrounded by small areas of meadow wetlands which host a major nesting colony of lapwings.

The first limnological study of the lake, as an example of oligotrophic wetland with abundant aquatic vegetation, was made by Fernández-Aláez (1984). Since 1994, the lake has been regularly monitored. Plant cover did not vary significantly in Lake Chozas from 1984 to 1996, with 95% of the bottom covered by a varied community of macrophytes (Fernández-Aláez et al., 1984, 1999a). Loss of vegetation was recorded in 1997, when there was a sharp reduction in mean submerged vegetation density, although different species of macrophytes were affected differently (Fernández-Aláez et al., 2002). Destruction of the habitat of aquatic plants altered the trophic web of the lake, with serious loss of biodiversity and breakdown of submerged vegetation control mechanisms (Rodríguez et al., 2005).

Crayfish are major herbivores in lakes (Lodge et al., 1998), suggesting that they may determine a shift from clear to turbid conditions in some wetlands (Harper et al., 1990). In the case of Lake Chozas, benthivory by crayfish led to decomposition of submerged vegetation and sharply increased nutrient load, due to intense bioturbation of sediment. The resulting eutrophication and high concentrations of organic detritus increased turbidity. Resuspension of sediment by wind in the absence of vegetation also favoured a cascade of mechanisms reinforcing water turbidity (Rodríguez et al., 2003). As already mentioned, eutrophication was due to introduction and expansion of an exotic species, the Louisiana red swamp crayfish, *Procambarus clarkii* (Girard, 1852), as well as to alterations in food availability and refuge. This decapod crustacean of the cambaridae family is native to NE Mexico and central southern USA (specifically Louisiana), and was introduced into Spain in 1974 for aquaculture (Gutiérrez-Yurrita and Montes, 1999). Its high tolerance to changes in abiotic conditions, as well as its life-style, rapid population development and ability to acquire food are all evidence of its ecological flexibility, making it an invasive species and earning it the name of "killer shrimp". It adapts much more readily than Mediterranean indigenous river crayfish and therefore tends to replace other species, becoming the strongest link in the ecological chain (Gherardi and Holdich, 1999).

Zhang et al. (2003) have shown that a structurally dynamic change from dominance of submerged vegetation to dominance of phytoplankton takes place by increase of the phosphorus concentration. Introduction of crayfish entails decomposition of submerged vegetation, transferring the nutrients stored in the plants to the water phase, which explains the increased growth of phytoplankton. Introduction of crayfish should therefore be expected to show the structurally dynamic change described by

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0304-3800/$ – see front matter. Published by Elsevier B.V.
doi:10.1016/j.ecolmodel.2011.04.016

Zhang et al. (2003). A model of Lake Chozas was developed to demonstrate and follow the structural changes caused by introduction of crayfish. An ecological model was appropriate because it captures the structural changes of the entire lake ecosystem. The model also made it possible to follow the development of eco-exergy. Marchi et al. (2010) proposed that a possible reaction to structural changes would be increasing entropy, which would correspond to a decrease in eco-exergy. A model could therefore be used to test this hypothesis.

Marchi et al. (2010) stated that after an initial relatively stable state, the effects of allochthonous species on an ecosystem may manifest in three different ways:

(a) increased entropy and ecosystem perturbation,
(b) integration of the species into the ecosystem and its ecological network by adaptation to new conditions, and
(c) addition of new links, relations and diversity to the ecosystem by the species, decreasing entropy.

In line with this idea, we postulated that after 1997 Lake Chozas exemplified (a), since the decrease in density of certain species led to loss of information stored in the biomass and in the genetic heritage of these organisms. To test this assumption, we developed a calibrated dynamic model embodying eco-exergy, to verify whether an ecosystem perturbed by an alien species, in this case *P. clarkii*, showed a decrease in eco-exergy, which corresponds to an increase in entropy. The model represented the phosphorus cycle in sediment and the water column of Lake Chozas, based on the assumption that phosphorus was the limiting factor for eutrophication (phytoplankton growth) in the system.

2. Eco-exergy and entropy

Exergy is defined as the amount of work that a system can perform by coming to thermodynamic equilibrium with its environment (Jørgensen, 1982, 1992a,b, 1997b, 1999a). It reflects how self-organized ecological systems develop by keeping their state as far as possible from thermodynamic equilibrium.

Biological processes use captured energy (input) for respiration and to stay far from thermodynamic equilibrium, that is, to maintain a low-entropy, high exergy state with respect to their environment and thermodynamic equilibrium (Jørgensen, 2007). Indeed, entropy is a measure of a system's inability to perform useful work; thus, as the entropy of a system increases, its available energy (also called useful work or exergy) decreases. The second law of thermodynamics states that the total entropy (exergy) of a system must always increase (decrease). As the system approaches thermodynamic equilibrium, its entropy reaches a maximum. In this final state of maximum entropy, the system has zero exergy or no potential for work. An event may create complexity and order, decreasing entropy and increasing information and biodiversity, or it may reduce complexity, order, information and biodiversity (Marchettini et al., 2008).

In the present study we used eco-exergy (exergy applied to ecological systems) to map the complexity and order of Lake Chozas before and after the biological invasion. Eco-exergy is a measure of energy quality and provides an easier interpretation of ecological processes than entropy. It represents ecosystem changes well, because unlike entropy, it is not bound to heat variations, which are difficult to quantify in complex systems such as ecosystems. Entropy is an enigma of thermodynamics because it embodies time irreversibility, quality and information, all properties that give it a central position in biology and ecology (Tiezzi, 2006).

Like entropy, the eco-exergy of an ecosystem cannot be calculated exactly, since it is impossible to measure concentrations of all components and quantify all contributing factors precisely. However, the biomass of major ecosystem components can be estimated and eco-exergy can therefore be computed by Eq. (1):

$$\text{Exergy} = RT\sum_i \left[C_i \quad \ln\left(\frac{C_i}{C_i^{\text{eq}}}\right) + (C_i - C_i^{\text{eq}})\right] \tag{1}$$

where R is the gas constant, T ambient temperature, C_i and C_i^{eq} concentrations of ecosystem component i in the current state and at thermodynamic equilibrium, respectively (Jørgensen, 2008). Jørgensen (1997b) also proposed a relative exergy index, Ex:

$$\text{Ex} = \sum_{i=1}^{n} \beta_i C_i \tag{2}$$

where C_i is the concentration of ecosystem component i $(1, \ldots, n)$ (for example, the biomass of a taxonomic or functional group) in the ecosystem, and β_i is a weighting factor, related to the information stored in the biomass. β-values are closely correlated with the free energy of the information embodied in organisms (Jørgensen et al., 2010a). If $i = 1$ represents detritus, $\beta = 1$ corresponds to detritus, in other words β-values are normalized with respect to detritus. Since 1 mg of detritus contains 18.7 J, multiplying exergy by 18.7 according to Eq. (2), we obtain eco-exergy in J m^{-3} when C_i is in mg m^{-3}.

$\beta_i \equiv \ln \quad C_i/C_i^{\text{eq}}$ has been calculated for various organisms, based on the number of non-nonsense genes coding the amino acid sequences of enzymes. Enzymes determine the life processes of organisms (Jørgensen et al., 2005). In any case, eco-exergy can provide an interpretation of the natural trend of ecosystems and is a good indicator of ecosystem services and sustainability (Jørgensen, 2010b). Thermodynamics-based goal functions, like eco-exergy and entropy, express the degree of energy dissipation or disorder of a system, and are therefore interesting tools to study the impacts of invasive species on ecosystems, highlighting time variations in stored information. The aim of this article was to quantify the change in complexity of Lake Chozas resulting from introduction and proliferation of *P. clarkii*, using eco-exergy.

3. Materials and methods

3.1. Model

A dynamic model of the phosphorus cycle, based on 1996–1997 monitoring data, was developed for Lake Chozas using the programme STELLA (version 8.1.4). The state variables, forcing functions and processes used in the model are shown in Fig. 1. The model had two layers (water and sediment) and state variables were in mg P m^{-3} for both layers. The water data was used directly and the sediment data was converted from mg P m^{-2} to mg P m^{-3} by assuming an active layer of sediment 0.1 m deep. Symbols and related units are illustrated in Table 1. The model had eight state variables related to phosphorus concentrations, because P was assumed a limiting factor for the lake ecosystem. They were: phosphorus in phytoplankton (PA), zooplankton (PZ), sediment (PESed), sediment pore water (P_I), submerged plants (Psp), detritus (P_Det) and exotic crayfish (P_crayfish), as well as soluble reactive phosphate in the water column (PS).

The model was applied to two scenarios:

1. pre-1997, before introduction of the crayfish, when water quality was oligotrophic, and
2. post-1997, when the effects of the crayfish on the indigenous community of the lake had begun to manifest.