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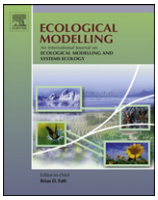

An inverse model for the analysis of the Venice lagoon food web

D. Brigolin[a,*], C. Savenkoff[b], M. Zucchetta[a], F. Pranovi[a], P. Franzoi[a], P. Torricelli[a], R. Pastres[a]

[a] *Department of Environmental Sciences, Informatics and Statistics, Università Ca' Foscari Venezia, Dorsoduro 2137, 30123 Venezia, Italy*
[b] *Pêches et Océans Canada, Institut Maurice-Lamontagne, 850 route de la Mer, Mont-Joli, Québec G5H 3Z4, Canada*

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ABSTRACT

A steady-state model of the Venice lagoon food web was constructed, based on a comprehensive set of data, which were collected in the years 2001–2005. Energy flows were estimated by means of an inverse methodology of constrained optimization based on the Minimum Norm criterion, i.e. on the minimization of both the sum of squares of the residuals and of the sum of squares of energy flows. The solution was constrained by a set inequalities, which were derived from general eco-physiological knowledge and site specific data on energy flows. The trophic network was represented by thirty-two nodes, including single-species compartments for the species of high economical or ecological relevance. Mass balance equations were weighted, in order to obtain meaningful results in presence of large differences, up to 5 orders of magnitude, among biomasses. A perturbation technique was applied, with the purpose of reducing the risk of finding solutions heavily affected by the set of constraints and of obtaining a more robust representation of the energy flows. The main patterns of energy flow are consistent with those obtained in previous attempts at modelling the Venice lagoon food web. Micro- and macro-phytobenthos account for the largest fraction of the primary production. Energy is then transferred towards higher trophic levels by means of two main pathways: the recycling of dead biomass through the detritus compartment and the direct consumption by grazers. The first pathway is the most important and accounts for approximately two/thirds of the energy transferred to the second trophic level.

1. Introduction

In spite of the increasing anthropic pressure (Veneto Region Statistics Database, 2010, http://statistica.regione.veneto.it), the Venice lagoon ecosystem is still supporting diverse human activities, such as tourism, harbour, fishery, which can be regarded as "ecosystem services" (sensu Costanza et al., 1997). Preserving this "natural capital", represents a huge management challenge, since, at present, the sediment export is not compensated by the inputs coming from the tributaries and the atmospheric downfall. As a result, the existence of typical habitats, such as salt marshes, mud flats, etc., is being severely threatened: as an example, in the last 60 years, 40% of the salt marshes has disappeared (Venice Water Authority, 2010), many secondary canals are being progressively filled, and the depth of flat shallow areas is, in general, increasing. In order to invert this trend, the Venice Water Authority is designing a comprehensive restoration plan, which includes the reconstruction of the main morphological structures and the protection of the existing ones. Within this context, it is mandatory to understand how such interventions could affect the whole ecosystem functioning. A class of models widely used for this purpose are steady state food web models, which are often applied to coastal ecosystems to quantify mass and energy fluxes associated with trophic interactions between different compartments of a food web (Belgrano et al., 2005). These models generate a snapshot of the trophic network at one moment in time, which is consistent with the set of input data. However, they can be subsequently used for understanding how the ecosystem would respond to changes in the external fluxes, such as fishery export, or internal ones, such as organic matter sedimentation and resuspension. Food web models have been already applied to the Venice lagoon ecosystem. Carrer and Opitz (1999) first developed a 16-compartments network to study the ecosystem of a specific site of the lagoon, and then Carrer et al. (2000) simplified this model to 12-compartments and coupled it with a bioaccumulation model for an ecotoxicological study. Libralato et al. (2002) implemented a 27-compartments model which was applied to two different lagoon habitats, and was recently coupled with a biogeochemical model, in an attempt to achieve an end-to-end representation of the ecosystem dynamics (Libralato and Solidoro, 2009). The same food-web model was adapted by Pranovi et al. (2003) to study the impacts of clam dredging on the lagoon ecosystem. However, all these modelling attempts were based on data sets collected in the 1990s, when the ecosystem was shifting from a condition of severe eutrophication and massive presence of macroalgae to a mesotrophic condition. Furthermore, the rapid increase of fishery activity targeting the

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[*] Corresponding author.
E-mail address: brigo@unive.it (D. Brigolin).

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bivalve *Ruditapes philippinarum* in the 1990s, was changing the sedimentation–resuspension pattern in some areas of the lagoon.

In order to detect the effect of these changes on the ecosystem structure and functioning, a new and more comprehensive data set was assembled (see Appendix A), which can be mostly referred to the year 2003. Such data set allowed the identification and modelling of the fluxes among a higher number of compartments, thirty-two, including the main target species of the artisanal fishery and some species with key ecological role.

The food web model was constructed using a method belonging to the class of so-called Inverse Model, IM (Vézina and Platt, 1988), according to which the trophic network is balanced, under a set of constraints, on the basis of an objective least-squares criterion for the minimization of the residuals, i.e. of the differences between the left hands and the right hands of the steady-state mass balance equations. IM have been widely used in ecosystem modelling during the last years, as they allow one to consistently estimate a large number of unknown flows from a relatively small number of observations (Leguerrier et al., 2003; Vézina et al., 2004; Savenkoff et al., 2007a,b) concerning standing biomasses, diets and flows.

This method leads to select a unique solution, i.e. a well defined set of flows, out of the space of potential solutions by means of a constrained optimization, based on a minimum-norm principle. IM allows one to combine compartmental mass balance equations, with data equations and eco-physiological constraints on the energy flows (inequalities) (Savenkoff et al., 2004): the latter can be defined on the basis of the general literature and of site-specific knowledge concerning the functioning of a given ecosystem. Therefore, IM presents the additional advantage of obtaining, from a mechanistic model, estimates of energy flows among compartments which are consistent with both general ecological principles and site specific knowledge concerning, for example, dietary preferences, fishery landings etc. Furthermore, the use of a completely specified and repeatable protocol, which assures that there is a one-to-one correspondence between the set of input data and constraints and the model output, allows one to implement Monte Carlo based methods for the assessment of the robustness of the solutions and for the estimation of the uncertainty of key outputs, in relation to that of a specified subset of input data (Savenkoff et al., 2007a).

In this study, the IM was used for constructing a mass balance model for the ecosystem of the Venice lagoon, with the specific objectives of:

(i) characterizing the structure and functioning of the lagoon food web in the year 2003 and comparing it with previous lagoon food web models, in order to detect trends in the ecosystem evolution;
(ii) investigating the role of the organic detritus in sustaining the ecosystem productivity and fishery.

2. Materials and methods

The IM developed within this work seeks the solution to the inverse problem by means of an objective method for constrained optimization, based on the minimum-norm principle. This method was initially adapted from physical sciences by Vézina and Platt (1988) for the reconstruction of planktonic food webs. Savenkoff et al. (2004, 2007a) extended it to the whole ecosystem network. Details on the solution algorithm are reported in Vézina and Platt (1988) and Savenkoff et al. (2004). This section focuses on equations and constraints used within the present work, which differ slightly from those employed in previous studies (Savenkoff et al., 2004, 2007a). The model structure and its parameterization are described in detail in the next section.

In order to estimate unknown flows, IM combines mass balance equations with: (i) data equations and (ii) constraints on the flows, expressed as inequalities. The mass balance equations specify that, for each compartment, the sum of inflows is balanced by the sum of outflows, a net change in the biomass variable, ΔB_i and a residual term, ε. No change in biomass, $\Delta B_i = 0$, during the studied time period was assumed (steady-state assumption). Production was assumed equal to the biomass lost to fishing, predation, natural mortality other than predation, hereafter termed other mortality causes, and net migration (migration out of or into the study area, food intake of predators that are not part of the system, etc.). Other mortality causes could include other natural causes of death such as disease or could reflect unsuspected processes occurring in the ecosystem, such as misreported catch, unsuspected migration or other processes not accounted for in the model (Savenkoff et al., 2004). The mass balance equations computed through the optimization algorithm has not to be exactly balanced, that is, the sum of the inputs and outputs for each compartment does not necessarily equal zero. The differences are termed residuals, and are represented by the error term ε. Residuals are assumed to be randomly and independently distributed with uniform variance (Vézina and Platt, 1988). The general mass balance equation for individual compartments can be written as:

$$\begin{aligned}&\text{Consumption} - \text{respiration} - \text{egestion} - \text{fishing mortality}\\&\quad - \text{predation} - \text{other mortality} - \text{net migration} = 0 + \varepsilon \qquad (1)\end{aligned}$$

Data equations may also be used for fixing the value of certain flows or combinations of flows: in our application, for example, data equations were used for specifying fishery landings and a sub-set of diet coefficients. Data equations are treated by the constrained optimization method as mass-balances equations: therefore a solution is sought which minimizes the sum of squares of the residuals between input data and model output.

In general, field data do not allow one to completely specify all flows. As a result, the system of equations is underdetermined, since the number of flows to be solved largely exceeded the number of independent mass balance relations. In order to obtain a solution which is consistent with general eco-physiological knowledge and site-specific information about feeding preferences, a set of additional constraints can be defined (Savenkoff et al., 2004). As an example, flows must be positive and ratios of flows should fall within certain ranges to satisfy basic metabolic efficiencies of assimilation and growth.

Furthermore, the constrained optimization was performed using the weighting scheme proposed in Vézina and Savenkoff (1999), according to which data equations and unknown flows are multiplied by the inverse of the variances as the weights for energy balance (Appendixes B and C). The use of weights limits the influence of compartments with high energy stocks on the solution. Therefore, it is particularly useful when the food web is likely to include compartments with very different biomasses.

2.1. Random perturbations of input data

In many food web studies only one steady-state solution is computed, and uncertainty cannot be considered in the subsequent interpretation of the results (Bundy, 2005; Morissette et al., 2009). Within this work the solution's robustness to uncertainty in input data was assessed based on the random perturbation methodology proposed by Savenkoff et al. (2007a). A sub-set of input data was considered in this analysis, namely the fishery landings for the main target species. Each nominal value for landings, x_i, was replaced by a "synthetic" input data, $x_i + r_n \mathrm{SD}_i$, where r_n is a real number randomly chose between −1 and 1, assuming an uniform distribution.