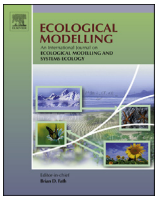
Ecological Modelling 313 (2015) 29–40

Contents lists available at ScienceDirect

Ecological Modelling

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



Incorporating food-web parameter uncertainty into Ecopath-derived ecological network indicators

Vanessa Guesnet[a], Géraldine Lassalle[a,*], Aurélie Chaalali[b,1], Kelly Kearney[c], Blanche Saint-Béat[d], Battle Karimi[e], Boutheina Grami[f], Samuele Tecchio[b], Nathalie Niquil[b], Jérémy Lobry[a]

[a] IRSTEA, UR EABX, Aquatic Ecosystems and Global Changes, 50 avenue de Verdun, 33612 Cestas cedex, France
[b] CNRS, UMR 7208 BOREA, Université de Caen Basse-Normandie, Esplanade de la Paix, CS 14032, 14032 Caen cedex 5, France
[c] Cooperative Institute for Marine and Atmospheric Studies, University of Miami Rosenstiel School of Marine and Atmospheric Science, NOAA Atlantic Oceanographic and Meteorological Laboratory, 4301 Rickenbacker Causeway, Miami, FL 33149, United States
[d] Littoral Environnement et Sociétés, UMR 7266 CNRS-Université de La Rochelle, 2 rue Olympe de Gouges, 17042 La Rochelle cedex, France
[e] UMR 6249 Laboratoire Chrono-Environnement, Pôle Universitaire du Pays de Montbéliard, 4 place Tharradin, BP 71427, 25211 Montbeliard cedex, France
[f] Laboratoire de Cytologie Végétale et Phytoplanctonologie, Département des Sciences de la Vie, Faculté des Sciences de Bizerte, Université de Carthage, Zarzouna, Bizerte, Tunisia

ARTICLE INFO

Article history:
Received 19 February 2015
Received in revised form 29 May 2015
Accepted 30 May 2015

Keywords:
Ecopath with Ecosim
Ecosystem models
Network analysis
Parameter uncertainty
Comparative studies

ABSTRACT

Ecological network analysis (ENA) provides numerous ecosystem level indices offering a valuable approach to compare and categorize the ecological structure and function of ecosystems. The inclusion of ENA methods in Ecopath with Ecosim (EwE) has insured their continued contribution to ecosystem-based management. In EwE, ENA-derived ecological conclusions are currently based on single values of ENA indices calculated from a unique input flow matrix. Here, we document an easy-to-use routine that allows EwE users to incorporate uncertainty in EwE input data into the calculation of ENA indices. This routine, named ENAtool, is a suite of Matlab functions that performs three main steps: (1) import of an existing Ecopath model and its associated parameter uncertainty values in the form of uncertainty intervals into Matlab; (2) generation of an ensemble of Ecopath models with the same structure as the original, and with parameter values varying based on the prescribed uncertainty limits; and (3) calculation of a set of 13 ENA indices for each ensemble member (one set of flow values) and of summary statistics across the whole ensemble. This novel routine offers the opportunity to calculate ENA indices ranges and confidence intervals, and thus to perform quantitative data analyses. An application of ENAtool on a pre-existing Ecopath model of the Bay of Biscay continental shelf is presented, with a focus on the robustness of previously published ENA-based ecological traits of this ecosystem when the newly introduced uncertainty values are added. We also describe the sensitivity of the ENAtool results to both the number of ensemble members used and to the uncertainty interval set around each input parameter. Ecological conclusions derived from EwE, particularly those regarding the comparison of structural and functional elements for a range of ecosystem types or the assessment of ecosystem properties along gradients of environmental conditions or anthropogenic disturbances, will gain in statistical interpretability.

1. Introduction

Marine ecosystems are affected by climate change (Beaugrand, 2004; Hoegh-Guldberg and Bruno, 2010) and by other natural or human-caused disturbances (Pauly et al., 1998; Borja et al., 2010). Ecosystem models are useful to get a better understanding of the structure and function of a system and for predicting how it may change over time when facing single or multiple pressures (Plagànyi, 2007). Ecopath with Ecosim (EwE) is a widely used modelling approach to represent marine food webs (Polovina, 1984; Christensen and Walters, 2004; Christensen et al., 2008). Since its

---

* Corresponding author. Tel.: +33 5 57 89 08 02.
E-mail addresses: vanessa.guesnet@yahoo.fr (V. Guesnet), geraldine.lassalle@irstea.fr, geraldinelassalle2@hotmail.com (G. Lassalle), aurelie.chaalali@gmail.com (A. Chaalali), kkearney@rsmas.miami.edu (K. Kearney), blanche.saintbeat@gmail.com (B. Saint-Béat), karimi.battle@gmail.com (B. Karimi), grami.boutheina@gmail.com (B. Grami), samuele.tecchio@unicaen.fr (S. Tecchio), nathalie.niquil@unicaen.fr (N. Niquil), jeremy.lobry@irstea.fr (J. Lobry).

[1] Present address: IFREMER, Unité Écologie et Modèles pour l'Halieutique, Route de l'Ile d'Yeu, BP 21105, 44311 Nantes cedex 03, France.

http://dx.doi.org/10.1016/j.ecolmodel.2015.05.036

development in the early 1980s, about 400 EwE models representing a wide variety of ecosystems worldwide have been published (Colléter et al., 2013a,b). Coupling EwE models to Ecological Network Analysis (ENA; Ulanowicz, 1986) was proposed as a relevant method to estimate energy flows and to characterize emergent properties of food webs, i.e. characteristics not directly observable that can only be detected by analysis of within-system interactions (Christensen and Pauly, 1992). ENA is a suite of tools that include input–output analysis, trophic structure analysis, pathway analysis, biogeochemical cycle analysis, and information analysis (Dame and Christian, 2006; Borrett and Lau, 2014). The main challenge for ENA is to capture the properties of entire food web in terms of a limited number of indices. In the scope of the European Marine Strategic Framework Directive (MSFD; http://ec.europa.eu; Directive 2008/56/EC), the EU Member States have to report on the environmental status of the seas under their jurisdiction and to work on achieving "Good Environmental Status" (GES) using food-web indicators as one possible metric. In this direction, nine food-web indicators are currently under evaluation as potential indicators of GES; the Ecological Network Analysis indices are among these candidate indicators (Rombouts et al., 2013; Niquil et al., 2014).

The EwE network analysis plugin has been employed in many instances, notably to study the stability of ecosystems and their response to perturbations (Patricio et al., 2006; Lobry et al., 2008; Baeta et al., 2011; Selleslagh et al., 2012) or, more recently, to assess the dynamical food-web reorganization and redirection of energy flow pathways under environmental changes (Tomczak et al., 2013). Nonetheless, these holistic conclusions relied on single values of ENA indices which were derived from a single input data matrix with no specified uncertainty. Moreover, the ecological interpretation of these single values mostly relies on non-statistical comparisons with values obtained for ecosystems of the same type. Given that data uncertainties may translate to uncertainties in model outputs (e.g. Niiranen et al., 2012), it is generally agreed that important scientific questions should be scrutinized with as many models as possible (Fulton, 2010; Gårdmark et al., 2012). One method of incorporating uncertainty into Ecopath model analysis is to use an ensemble parameterization technique, building several Ecopath models each representing a potential manifestation of a food web and falling within the uncertainty ranges of the observed data (Aydin et al., 2007; Kearney, 2012). This approach results in distributions of parameters rather than specific values, while still meeting basic thermodynamic requirements. Kearney et al. (2012) provided a suite of Matlab functions to construct such a distribution of parameters based on an Ecopath model and its data pedigree, i.e. a quantification of the parameter certainty tied to the parameter's origin. In this study, we extend the Kearney et al. (2012) code for generating this type of ensemble to feed into calculations of ENA indices. This work will allow parameter uncertainty to be incorporated into model-derived ENA indices, and will also improve interpretation of these indices by allowing statistical analyses. When overhauling the EwE source code between the release of EwE versions 5 and 6, the EwE developers chose not to continue support of the Ecoranger module, which had allowed users to explore parameter uncertainty ranges in a Bayesian context (Christensen et al., 2005). The code presented in this paper now offers an alternative method for analyzing this uncertainty.

The aim of this software development is to provide an easy-to-use routine to EwE users to generate a set of values for key ENA indices by explicitly taking into account uncertainty in model input data. To this end, two characteristics are identified as important: (i) a routine that can be called by a single line of Matlab code and can be run on all commonly used operating systems (recent Windows, Unix-based, and Mac platforms), independent of the EwE software versions used for the pre-existing ecosystem model construction and (ii) a routine based on formulas of ENA indices currently in use in the last version of the EwE software. The present work is also the opportunity to harmonize ENA indices calculations derived from two main approaches for constructing ecological flow networks, i.e. EwE and linear inverse modelling (LIM; Vézina and Platt, 1988). Different formulas for the same index exist in the scientific literature and correspond to different interpretations of the same idea. We demonstrate the use of this tool by applying it to a pre-existing Ecopath model of the Bay of Biscay continental shelf (Lassalle et al., 2011) for which data quality is already categorized using Pedigree scores (Lassalle et al., 2014). ENA indices distributions derived from the ENAtool routine are compared with previous point estimate values obtained with this Ecopath model to test for robustness of ENA-derived ecological conclusions. Finally, we test sensitivity of ENA indices distributions to the number of balanced ensemble members underlying their calculation and to the level of uncertainty applied to specific Ecopath model parameters.

2. Materials and methods

2.1. The Ecopath concept and equations

The Ecopath with Ecosim (EwE) modelling software enables the building and analysis of food-web models (Polovina, 1984; Christensen and Walters, 2004; Christensen et al., 2008). The full software package includes several modules (e.g. Ecopath, Ecosim, Ecospace) to explore food webs across both space and time. However, for this study, we will focus only on the Ecopath component, which calculates a static mass-balanced snapshot of the biomass and energy fluxes between functional groups in a food web. In this context, a functional group refers to a species or group of species that occupy a particular niche in the food web, and can range in resolution from a broad grouping (e.g. pelagic fish) to specific life stage of a species (e.g. juvenile herring). The Ecopath model calculation is based on two "master" equations. The first equation decomposes the production term of each functional group:

$$\begin{aligned}\text{Production} &= \text{fishery}\quad\text{catch} + \text{predation}\quad\text{mortality}\\ &\quad + \text{net}\quad\text{migration} + \text{biomass}\quad\text{accumulation}\\ &\quad + \text{other}\quad\text{mortality}\end{aligned}$$

"Other mortality" includes natural mortality factors such as mortality due to senescence and diseases.

The second equation describes the energy balance within each *functional* group:

$$\text{Consumption} = \text{production} + \text{respiration} + \text{unassimilated}\quad\text{food}$$

More formally, the two equations can be written as follows for *functional* group *i* and its predator *j*:

$$\begin{aligned} B_i \times \left(\frac{P}{B}\right)_i &= Y_i + \sum_j \left(B_j \times \left(\frac{Q}{B}\right)_j \times DC_{ij}\right)\\ &\quad + Ex_i + Bacc_i + B_i(1 - EE_i) \times \left(\frac{P}{B}\right)_i \end{aligned} \tag{1}$$

and

$$B_i \times \left(\frac{Q}{B}\right)_i = B_i \times \left(\frac{P}{B}\right)_i + R_i + U_i \tag{2}$$

where the main input parameters are biomass density (B, here in kg C km^{-2}), production rate (P/B, year^{-1}), consumption rate (Q/B, year^{-1}), proportion of i in the diet of j (DC_{ij}; DC = diet composition), net migration rate (Ex, year^{-1}), biomass accumulation ($Bacc$, year^{-1}), total catch (Y; $\text{kg C km}^{-2}\,\text{year}^{-1}$), respiration ($R$; $\text{kg C km}^{-2}\,\text{year}^{-1}$), amount of consumed food that is unassimilated