



Incorporation of diet information derived from Bayesian stable isotope mixing models into mass-balanced marine ecosystem models: A case study from the Marennes-Oléron Estuary, France



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ABSTRACT

We investigated the use of output from Bayesian stable isotope mixing models as constraints for a linear inverse food web model of a temperate intertidal seagrass system in the Marennes-Oléron Bay, France. Linear inverse modeling (LIM) is a technique that estimates a complete network of flows in an under-determined system using a combination of site-specific data and relevant literature data. This estimation of complete flow networks of food webs in marine ecosystems is becoming more recognized for its utility in understanding ecosystem functioning. However, diets and consumption rates of organisms are often difficult or impossible to accurately and reliably measure in the field, resulting in a large amount of uncertainty in the magnitude of consumption flows and resource partitioning in ecosystems. In order to address this issue, this study utilized stable isotope data to help aid in estimating these unknown flows. $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ isotope data of consumers and producers in the Marennes-Oléron seagrass system was used in Bayesian mixing models. The output of these mixing models was then translated as inequality constraints (minimum and maximum of relative diet contributions) into an inverse analysis model of the seagrass ecosystem. The objective of this study was to investigate how the addition of diet information gained from the stable isotope mixing models would help constrain a linear inverse food web model. In order to investigate this, two inverse food web models were built to track the flow of carbon through the seagrass food web on an annual basis, with units of $\text{mgC m}^{-2} \text{d}^{-1}$. The first model (Traditional LIM) included all available data, with the exception of the diet constraints formed from the stable isotope mixing models. The second model (Isotope LIM) was identical to the Traditional LIM, but included the Bayesian mixing model diet constraints. Both models were identical in structure, and intended to model the same Marennes-Oléron intertidal seagrass bed. Each model consisted of 27 compartments (24 living and 3 detrital) and 175 flows. Comparisons between the outputs of the models showed the addition of the Bayesian mixing model-derived isotopic diet constraints further constrained the solution range of all food web flows on average by 26%. Flows that were directly affected by an isotopic diet constraint were 45% further constrained on average. These results showed that incorporation of the isotope information resulted in a more constrained food web model, and demonstrated the benefit of utilizing multi-tracer stable isotope information in ecosystem models.

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1. Introduction

Current ecological questions are often complex in nature, requiring a holistic perspective in order to adequately address the

multitude of variables and relationships. There is thus an ever-increasing pressure on ecologists to address these questions at the ecosystem scale. Quantitative food web models, representing partial or whole ecosystem flux networks, are a promising methodology to address ecological questions (Finn and Leschine, 1980; Christian et al., 2009; Leslie and McLeod, 2007). These models are able to simultaneously explore effects of environmental changes on ecosystem structure and function, as well as emergent properties such as system dependencies, recycling, and efficiencies (Niquil et al., 2012). Banašek-Richter et al. (2004) showed that ecosystem

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descriptors based on quantified systems models are more accurate than their qualitative counterparts. Estimation of complete flux networks of food webs in marine ecosystems is recognized for its utility to understand ecosystem functioning (Niquil et al., 2012). However, many components of ecosystem models are understood conceptually, but difficult or impossible to measure in the field, and therefore must be estimated (Niquil et al., 1998; van Oevelen et al., 2010; Vezina and Platt, 1988).

Inverse analysis is a powerful quantitative modeling method for estimating unmeasured components in ecosystem structures and has been widely used for this reason in food web modeling (Breed et al., 2004; Daniels et al., 2006; Degré et al., 2006; Donali et al., 1999; Eldridge et al., 2005; Eldridge and Jackson, 1993; Grami et al., 2008, 2011; Jackson and Eldridge, 1992; Kones et al., 2009; Leguerrier et al., 2003, 2007; Niquil et al., 1998, 2006). It has become commonly referred to as linear inverse modeling (LIM). Similarly to ECOPATH with ECOSIM (Christensen and Pauly, 1992; Pauly, 2000; Walters et al., 1997), LIM produces a static, mass-balanced, temporally integrated snapshot of the complete food web. Recent methodological advances have resulted in moving from models being solved with a single objective function (frequently a minimization function, (Vezina and Platt, 1988), to utilizing stochastic Markov Chain Monte Carlo methods to produce probability distributions of model results (LIM-MCMC) (Kones et al., 2006, 2009; Van den Meersche et al., 2009; van Oevelen et al., 2010). This technique avoids underestimates in both the size and complexity of the modeled food web as a result of the parsimony principle (Johnson et al., 2009; Kones et al., 2006). A more thorough review on the subject is covered by Niquil et al. (2012). Few applied studies have made use of recent methodological advances in this field, despite the relevance to informing conservation and environmental management decisions (Christian et al., 2009).

Stable isotopes are commonly used to study trophodynamics in ecosystems. Stable isotope analyses allow determination of food sources actually assimilated in the tissues of consumers over time, properly reflecting their trophodynamics depending on food source availability. Consumption rates are often difficult or impossible to accurately measure in the field, especially for smaller organisms, resulting in a large uncertainty in the magnitude of consumption flows and trophic resource partitioning in ecosystem models. Stable isotope data can be utilized to estimate these unmeasured flows (Navarro et al., 2011; van Oevelen et al., 2010). While the use of stable isotopes in diet studies has become standard practice (Moore and Semmens, 2008; Post, 2002), the integration of stable isotope data with whole food web network models has not been utilized frequently (Baeta et al., 2011; Navarro et al., 2011). The merits of this technique have been discussed recently in the literature (Navarro et al., 2011; van Oevelen et al., 2010).

Until now, only one stable isotopic marker ($\delta^{13}\text{C}$ or $\delta^{15}\text{N}$) at a time has been incorporated into inverse analysis models (Eldridge et al., 2005; Jackson and Eldridge, 1992; Oevelen et al., 2010; van Oevelen et al., 2006). Using two or more isotopic markers significantly increases model structure complexity and greatly increases model run time. This problem is compounded in situations where Monte Carlo methods are used to run the inverse analysis thousands of times (Kones et al., 2009; Niquil et al., 2012; van Oevelen et al., 2010). This has significant implications when attempting to add stable isotope information into food web models solved using the new linear inverse model-Markov chain Monte Carlo techniques (Kones et al., 2009; Niquil et al., 2012).

Therefore, the goal of this study was to find a way to incorporate information from multiple stable isotope elements (i.e., ^{13}C , ^{15}N , etc.) into food web models using the LIM-MCMC technique, with minimum added complexity. In order to do this, we used the R package SIAR (Stable Isotope Analysis in R; Parnell et al., 2010) to analyze Bayesian mixing models using $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ data

to estimate food source distributions of the compartments in an inverse food web model of an intertidal seagrass bed. This information was then integrated into the LIM-MCMC food web model. Results of this model were compared with a corresponding model of the same system that excluded the isotope information obtained with the SIAR mixing models in order to investigate the effects of the added stable isotope information.

2. Methods

2.1. Marennes-Oléron Bay study site and model data

The seagrass system studied was an intertidal *Zostera noltii* meadow located in Marennes-Oléron Bay, on the Atlantic coast of France ($45^{\circ}54' \text{ N}$, $1^{\circ}12' \text{ W}$) (Fig. 1). This is a semi-enclosed, macrotidal bay, which receives freshwater inputs from the Charente River ($15\text{--}500 \text{ m}^3 \text{ s}^{-1}$). The seagrass bed studied extends for 15 km along the eastern shore of Oléron Island, and is 1.5 km at its widest.

Primary producer biomass, benthic consumer biomass, and stable isotope data used in this model were obtained from (Lebreton et al., 2009, 2012). Sampling was conducted at two stations (a high flat station and a low flat station) in 2006 and 2007 (Fig. 1) and the results were averaged (Table 1). Each station was a homogeneous area of 100 m^2 parallel to the coastline, about 250 m from the upper and lower limits of the seagrass bed, respectively. The stations were each broken up into 100 plots of 1 m^2 for sampling. Both sampling sites were exposed at every low tide, with the higher in elevation of the two sites being exposed for 5 h longer on average (Lebreton et al., 2009). Average emersion times on the seagrass bed were computed for this study using bathymetric data and tidal measurements, and those processes (i.e., phytoplankton production, bird grazing, zooplankton grazing, etc.) affected by the tidal cycle were scaled accordingly in the food web model.

2.2. Linear inverse model (LIM-MCMC) formulation

Two inverse food web models were built to track the flow of carbon through the seagrass food web on an annual basis, with units of $\text{mgC m}^{-2} \text{ d}^{-1}$. The first model (Traditional LIM) included all available data, with the exception of the diet constraints formed from the stable isotope mixing models. The second LIM (Isotope LIM) was identical to the Traditional LIM, but included the SIAR diet constraints. Both models were identical in structure, and intended to model the same Marennes-Oléron intertidal seagrass bed.

First, an *a priori* topological model was formulated of the food web based on local expert knowledge and previous studies (Leguerrier et al., 2003, 2004), defining the compartments and all probable connections between them. All macrofaunal species sampled in the system were included which had a biomass of at least $0.05 \text{ g ash-free dry weight m}^{-2}$. This biomass threshold value resulted in 96.5% of the total measured biomass during sampling being included in the inverse food web model. The benthic and pelagic fauna of the system were parsed into compartments based on similarity of species-specific characteristics such as taxonomy, habitat, known feeding habits, known predators, and stable isotope ($\delta^{13}\text{C}$ and $\delta^{15}\text{N}$) values. Priority was placed on aggregating species into the compartments in such a way so as to balance between maintaining the true trophic complexity of the ecosystem versus the need to keep the model simple enough that solutions could be produced in a timely manner. As the complexity of the model scales exponentially with the number of compartments, some aggregation was necessary. However, loss in precision of stable isotope data due to aggregation of species with dissimilar signatures was considered to be undesirable for the mixing models, and was

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