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An assessment of the trophic structure of the Bay of Biscay continental shelf food web: Comparing estimates derived from an ecosystem model and isotopic data

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ABSTRACT

Comparing outputs of ecosystem models with estimates derived from experimental and observational approaches is important in creating valuable feedback for model construction, analyses and validation. Stable isotopes and mass-balanced trophic models are well-known and widely used as approximations to describe the structure of food webs, but their consistency has not been properly established as attempts to compare these methods remain scarce. Model construction is a data-consuming step, meaning independent sets for validation are rare. Trophic linkages in the French continental shelf of the Bay of Biscay food webs were recently investigated using both methodologies. Trophic levels for mono-specific compartments representing small pelagic fish and marine mammals and multi-species functional groups corresponding to demersal fish and cephalopods, derived from modelling, were compared with trophic levels calculated from independent carbon and nitrogen isotope ratios. Estimates of the trophic niche width of those species, or groups of species, were compared between these two approaches as well. A significant and close-to-one positive ($r^2_{Spearman} = 0.72$, n = 16, $p < 0.0001$) correlation was found between trophic levels estimated by Ecopath modelling and those derived from isotopic signatures. Differences between estimates were particularly low for mono-specific compartments. No clear relationship existed between indices of trophic niche width derived from both methods. Given the wide recognition of trophic levels as a useful concept in ecosystem-based fisheries management, propositions were made to further combine these two approaches.

1. Introduction

Validation of a model corresponds to a demonstration that, within its domain of applicability, it possesses a satisfactory range of accuracy consistent with the intended applications (e.g. Rykiel, 1996). The most classical validation process used with dynamic or predictive models, i.e. simulations, takes the form of a statistical assessment of "goodness-of-fit" between predicted values and the observed data not used in the model development, e.g. ecological niche models with the distribution of a single species (mostly presence/absence data) (Araujo et al., 2005) or, recently, ecosystem classes (Roberts and Hamann, 2012) as the dependent variables. This step does not guarantee that the scientific basis of a model and its internal structure correspond to actual processes or to the cause-effect relationships operating in the real system. However, it can confer a sufficient degree of belief in or credibility to a model to justify its use for research and decision making.

In the growing context of ecosystem-based fisheries management (EBFM) (Garcia et al., 2003; Pikitch et al., 2004), ecosystem models have increasingly been used for forecasting and management purposes (Plagànyi, 2007). They range from extended single-species models incorporating additional inter-specific interactions, e.g. the SeaStar model for the Norwegian herring (Tjelmeland and Lindstrøm, 2005), to complex whole ecosystem models describing all trophic levels (*TLs*) in the ecosystem, e.g. Ecopath with Ecosim (EwE) (Christensen and Walters, 2004; Christensen et al., 2008) or Linear Inverse Modelling (LIM) (Grami et al., 2011; Legendre and Niquil, 2013) for mass-balanced temporally integrated food web models or Atlantis for spatially explicit bio-geochemical end-to-end ecosystem models (Fulton et al., 2004). Given the potentially high complexity of models used for decision making (Fulton et al., 2003), statistical methods evaluating whether models make reasonable predictions regarding the trophic impacts of fisheries, and of other anthropogenic pressures,

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on ecosystems are still being progressed and are therefore not routinely applied (Christensen and Walters, 2004; Fulton et al., 2011).

Considering the widely used EwE modelling approach (Morissette, 2007), Ecosim dynamic simulations can be validated by assessing their ability to reproduce "reasonably well" the past patterns of change in relative abundance, or catch of major species, by computing a statistical measure of "goodness-of-fit" to these historical data (Pauly et al., 2000; Piroddi et al., 2010). Nevertheless, this critical step requires that independent time series of effort, biomass and catch data for the major species are available at the spatio-temporal scale of interest and incorporating marked trends. Comparing Ecopath model outputs to independent data as a method for evaluating a model's capabilities has increasingly focused on trophic level (*TL*) estimates (e.g. Kline and Pauly, 1998; Pauly et al., 1998b; Dame and Christian, 2008; Nilsen et al., 2008; Navarro et al., 2011). A radically different approach, stable isotope analysis (SIA), is becoming standard practice for describing trophic interactions in natural systems (Peterson and Fry, 1987; Post, 2002; Bouillon et al., 2011; Miller et al., 2011). Carbon and nitrogen stable isotope ratios, in particular, have been effectively proven to be a valuable source of dietary information when feeding is too difficult to observe. Examples of SIA performed on most representative species of a given ecosystem, from primary producers to top predators, are more and more prevalent in the scientific literature (Davenport and Bax, 2002; Lavoie et al., 2010; Papiol et al., 2012).

The ecosystem assessed in the present work was the well-studied French part of the Bay of Biscay continental shelf. Firstly, the mass-balanced model (Lassalle et al., 2011) was evaluated through comparing *TLs* calculated using this model with *TLs* estimated from independent carbon and nitrogen isotope data (Chouvelon et al., 2012a,b). The extent of the validation data for our current study was relatively unique as it incorporated all predators in a large ecosystem, with the exception of seabirds. Predators conventionally refer to organisms with $TLs \geqslant 3.5$. *TL* can be defined as a dimensionless index defining how much above the primary producer's level (or level 1) an organism feeds on average (Odum and Heald, 1972). Secondly, the cross-comparison realized in this study was further extended to indices of the trophic niche width, providing information about the diversity of resource types consumed by a consumer. For the first time in this type of comparative study, a Bayesian metric based on a standard ellipse was used on isotopic data to estimate the niche breadth (Jackson et al., 2011). This potential method of ecosystem model validation was then discussed in the context of defining indicators of ecosystem health and impacts of fisheries on ecosystems. Finally, propositions were made for a routine that could be added to Ecopath to generalize this validation step.

2. Materials and methods

2.1. Study area

The Bay of Biscay is a very large bay opening onto the North-East Atlantic Ocean, located from 1 to 10°W and from 43 to 48°N (Fig. 1). The continental shelf covers over 220,000 km^2 along the French coast, extending more than 200 km offshore in the north of the Bay but only 10 km in the south. Two main river plumes, i.e. the Loire and the Gironde, influence its hydrological structure (Planque et al., 2004; Puillat et al., 2004). The Bay of Biscay also presents a vast oceanic domain and a continental slope indented by numerous canyons (Koutsikopoulos and Le Cann, 1996). These physical and hydrological features greatly influence phytoplankton dynamics and, as a consequence, the whole composition, organization and functioning of the food web (Varela, 1996). Overall, the Bay of Biscay supports a rich fauna including many protected species, e.g. marine mammals, seabirds, sharks and rays, and is subjected to numerous anthropogenic activities such as important fisheries (Lorance et al., 2009; OSPAR, 2010).

2.2. Mass-balanced ecosystem model

Ecopath with Ecosim is a tool for analysing organic matter and energy flows within a steady-state/static mass-balanced snapshot of the system (Ecopath) and/or a time dynamic simulation module (Ecosim) (Christensen and Walters, 2004; Christensen et al., 2008). Originally proposed by Polovina (1984), the Ecopath model has been combined with routines for network analysis (Ulanowicz, 1986). A detailed description of the main equations of the Ecopath model is described in the first Supplementary material (see also www.ecopath.org).

2.2.1. TLs and omnivory index in Ecopath

TL was first defined as an integer identifying the trophic position of organisms within food webs (Lindeman, 1942) and was later modified to be fractional (Odum and Heald, 1975). Routinely, a *TL* was defined as 1 for producers that obtained all of their energy from photosynthesis and detritus that are considered as dead organic matter. For consumers, a *TL* of 1 + [the weighted average of the preys' *TL*] was set. Following this approach, a consumer eating 40% plants (with $TL = 1$) and 60% herbivores (with $TL = 2$) will have a *TL* of $1 + [0.4{\cdot}1 + 0.6{\cdot}2] = 2.6$. *TL*, as a dimensionless index, can be formulated as follows:

$$TL_i = 1 + \sum_{j=1}^{n} DC_{ij} \times TL_j \tag{1}$$

where i is the predator of prey j, DC_{ij} is the fraction of prey j in the diet of predator i and TL_j is the trophic level of prey j.

The omnivory index (*OI*) is calculated as the variance of the *TL* of a consumer's prey groups and is dimensionless (Pauly et al., 1993). A parallel was made with the variance in mathematics calculated by taking the sum of squared differences from the mean and dividing by the number of observations minus one. It measures the variability of *TLs* on which a group of species feed but does not represent the variability of prey within a *TL* (i.e. TL_j in Eqs. (1) and (2) already corresponded to average values) nor the variability in feeding behaviour between individual predators. When the *OI* value is zero, the consumer in question is specialized, i.e. it feeds on a single prey group. A large value indicates that the consumer feeds on prey groups characterized by a large range of *TLs*, and thus shows a more generalist strategy:

$$OI_i = \sum_{j=1}^{n} (TL_j - (TL_i - 1))^2 \times DC_{ij} \tag{2}$$

where the contribution of each prey j to the variance of the consumer i is a proportion of the fraction of the prey j in the diet of the consumer i (DC_{ij}). The square root of the *OI* is the standard deviation (*SD*) of estimates of *TLs* (Christensen and Pauly, 1992; Gascuel et al., 2009).

For species that migrate to/from the study area for part of the year, it is possible to take into account their migratory behaviour by setting, in the diet composition matrix, the diet import proportion to the fraction of time spent outside the system. Imports were not considered in the calculation of *TLs* (Marta Coll, pers. comm.). Ecopath by definition assigns a *TL* of 1 to detritus. Fishery discards were considered as dead material and were also given a *TL* of 1. These assumptions regarding the composition and *TL* of detrital components should be considered when interpreting *TL* and *OI* estimates (Burns, 1989; Nilsen et al., 2008).