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EcoTroph: Modelling marine ecosystem functioning and impact of fishing

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ABSTRACT

EcoTroph (ET) is a model articulated around the idea that the functioning of aquatic ecosystems may be viewed as a biomass flow moving from lower to higher trophic levels, due to predation and ontogenetic processes. Thus, we show that the ecosystem biomass present at a given trophic level may be estimated from two simple equations, one describing biomass flow, the other their kinetics (which quantifies the velocity of biomass transfers towards top predators). The flow kinetic of prey partly depends on the abundance of their predators, and a top-down equation expressing this is included in the model. Based on these relationships, we simulated the impact on a virtual ecosystem of various exploitation patterns. Specifically, we show that the EcoTroph approach is able to mimic the effects of increased fishing effort on ecosystem biomass expected from theory. Particularly, the model exhibits complex patterns observed in field data, notably cascading effects and 'fishing down the food web'. EcoTroph also provides diagnostic tools for examining the relationships between catch and fishing effort at the ecosystem scale and the effects of strong top-down controls and fast-flow kinetics on ecosystems resilience. Finally, a dynamic version of the model is derived from the steady-state version, thus allowing simulations of time series of ecosystem biomass and catches. Using this dynamic model, we explore the propagation of environmental variability in the food web, and illustrated how exploitation can induce a decrease of ecosystem stability. The potential for applying EcoTroph to specific ecosystems, based on field data, and similarities between EcoTroph and Ecopath with Ecosim (EwE) are finally discussed.

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1. Introduction

One of the first approaches, pioneered by Elton (1927) and Lindeman (1942) for describing aquatic ecosystem, was to assign the individual numbers or biomass or the biological production by its component species onto integer trophic levels (TLs), and thus represent the ecosystem as a pyramid of number, biomass or production. This approach, which differentiated between primary producers and detritus (TL = 1), first-order consumers (TL = 2), second-order consumer (TL = 3), etc., was dominant until the early 1970s, and served, for example, as a major structuring element of the International Biological Program (Golley, 1993).

This approach was sharply criticized by Rigler (1975), who pointed out that most aquatic animals feed at more than one trophic level, and that, therefore, TLs cannot be used to structure ecosystem data (see also Cousin, 1985). Thus, he suggested, trophic levels were only conceptual entities, not parameters that could be derived from empirical data. This critique was devastatingly effective, and for a while, the TL concept faded from view. However, in the same year that Rigler's critique appeared, Odum and Heald (1975) published an alternative to trophic-levels-as-a-concept, i.e., fractional trophic level. These can be estimated from different types of empirical data (see e.g., Kline and Pauly, 1998), and which hence, by Rigler's own criteria, have as legitimate a place in ecology as, for example, sea surface temperature.

The emergence of Ecopath as a widely used approach and software for modelling aquatic ecosystems (Polovina, 1984; Christensen and Pauly, 1992), contributed in a major way to the resurgence of trophic levels, especially as they were not an input to Ecopath, but an output, i.e., parameters that were estimated by Ecopath. And, as the use of Ecopath spread worldwide, so did the trophic level concept (Pauly et al., 2000). Two other developments also contributed to increasing familiarity with trophic levels. One is the emergence of FishBase (Froese and Pauly, 2000), the online database on fish, covering all fish species in the world (over 30,000), and which present estimates of trophic levels for nearly half of these species. The other is the demonstration of the worldwide occurrence of the phenomenon now widely known as 'fishing down marine food webs' (Pauly et al., 1998).

Here, we present EcoTroph as a trophic-level based ecosystem modelling approach which makes full use on the conceptual advances heralded by Odum and Heald (1975). This approach is not

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an elaboration (i.e., complexification) of previous food web modelling effort, nor does it aim to replace more comprehensive (and often more complex) models. On the contrary, EcoTroph results from attempts to simplify trophic modelling. Within the family of tropho-dynamic models, it may be regarded as constituting an ultimate stage, wherein species as such disappear behind trophic levels. EcotTroph thus may be seen as providing an oversimplified, but useful caricature, thereby offering another interpretation of available data, and another view of ecosystems.

After publication of a first version of a trophic-level based model (Gascuel, 2005), an in-depth comparison, equation by equation, with the well-established Ecopath with Ecosim model revealed inconsistencies in its formulation. This applied particularly to the implementation of top-down control, and to the catch equation, which was made compatible with standard formulations. Additionally, simulations based on parameters of flow kinetics were updated using a recently published empirical model (Gascuel et al., 2008a).

This paper thus presents a new version of the trophic-level based model, from now called EcoTroph. We also aim to assess the ability of the model to mimic the generic rules which appear to regulate the functioning of marine ecosystems, with emphasis on the impact of fishing. In a first step, the general principles and assumptions of the model are presented, and their mathematical formulations are detailed. Then, we show that the model is an efficient theoretical tool to build generic relationships between parameters (for instance between fishing effort and catch, or ecosystem biomass) and that it gives a consistent representation of the trophic functioning of ecosystems. The model is then used to analyse the impact of fishing on ecosystem biomass given various exploitation patterns and to explore the propagation of environmental variability in the food web. The sensitivity of the model to input parameters is also explored. Practical use of EcoTroph for case studies is briefly discussed in the last section, where we also present EcoTroph as a module of EwE (vers. 6).

2. Method

2.1. General principle: modelling ecosystem functioning as a trophic flow

The trophic level of an organism or the mean trophic level of a population is defined as:

$$\tau_i = 1 + \sum_j (D_{ij} \cdot \tau_j) \quad (1)$$

where D_{ij} is the proportion of the prey *j* in the diet of consumer *i*, and τ_j is the mean trophic level of the prey, with the trophic level of primary producers and detritus being conventionally set equal to unity. Thus, trophic level emerges from the diet of individuals. It constitutes a state variable characterizing each unit of biomass in an ecosystem and defining its position within the food web.

The first key point of EcoTroph is that it deals with the continuous distribution of the biomass occurring in an ecosystem, as a function of trophic levels (Fig. 1). Biomass enters the food web at trophic level 1, as generated by the photosynthetic activity of the primary producers, and recycling by the microbial loop. With the exception of semi-autotrophic organisms with small biomasses in some ecosystems (e.g. coral polyps, tridacnid clams), there is usually no biomass between trophic levels 1 and 2. Herbivorous and detritivorous are at trophic level 2. Then, at trophic levels higher than 2, the biomass is distributed along a continuum of trophic level values. Some trophic levels may contain more or less biomass, but the variability of the diet of the different consumers of an ecosystem should result in all trophic levels being 'occupied'.

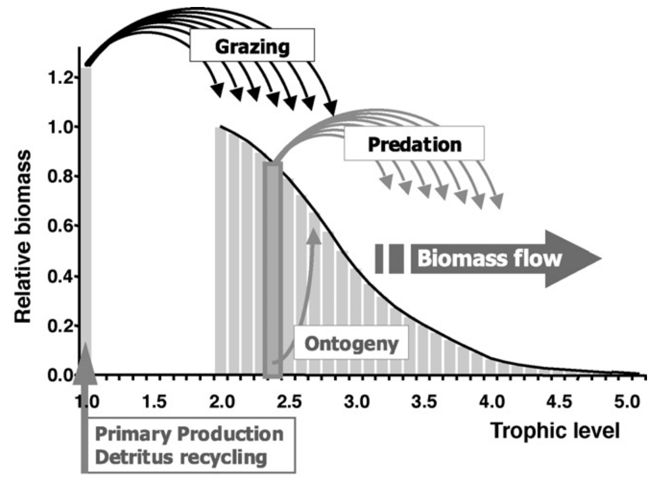

Fig. 1. Diagram of the trophic functioning of an ecosystem: theoretical distribution of the biomass by trophic level and trophic transfers processes, given an arbitrary input of biomass (fixed equal to 1 for TL = 2).

As a consequence, the EcoTroph equations are based on a continuous approach and the model aims to simulate the state variable $B(t, \tau)$, i.e., the density of biomass occurring in the ecosystem at time *t*, at trophic level τ (see notations in Table 1). Firstly, we present a steady-state version of the model, wherein the state variable is $B(\tau)$, i.e., the distribution of the ecosystem biomass by trophic level. In a second step we will move to a dynamic version of EcoTroph referring to time.

A discrete approximation of the continuous distribution is used for mathematical simplification and visual representation. Thus, the distribution of the ecosystem biomass is split into fractional classes (see Fig. 1). Conventionally, we consider trophic classes of $\Delta\tau = 0.1$ trophic level, from trophic level 2, corresponding to first-order consumers, to trophic level 5, sufficient to cover all top predators likely to occur in marine systems (Pauly et al., 1998; Cortés, 1999). Thus, the state variable becomes $B\tau$, the biomass in the $[\tau, \tau + \Delta\tau]$ trophic class. The resulting bivariate graph (B_τ as a function of τ) represents a key aspect of ecosystem functioning and constitutes what is called a 'biomass trophic spectrum' (Gascuel et al., 2005).

The second key idea of EcoTroph is that the trophic functioning of marine ecosystems can be modelled as a continuous flow of biomass surging up the food web, from lower to higher trophic levels. All of the organic particles start in the food web with photosynthesis or detritus recycling at trophic level 1. From there, they move up more or less rapidly in the food web, jumping for each predation event to a trophic level, which is defined by the mean diet of the predator. The fate of a given particle is thus characterized by continuous processes (ontogenic changes in trophic levels) and abrupt jumps (of 1 TL on average) caused by predation. Few particles reach the highest trophic levels, and most will stop long before that, due to non-predation mortality, excretion or respiration. But the particles that move up in the food web constitute a biomass flow which has to be considered as a whole. All particles jointly have a wide range of trajectories whose mean is a continuous curve. Thus, using a continuous model is not an approximation of the discrete trajectories; it is the mean process itself, expressed as biomass flow (see Gascuel et al., 2008a).

2.2. Biomass and flow equations

2.2.1. Biomass equation

In flux physics, quantities related to a flow of liquid, moving for instance in a canal, are linked by the following equation

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