



Review

Modelling the community size-spectrum: recent developments and new directions



Jérôme Guiet^{a,b,*}, Jean-Christophe Poggiale^c, Olivier Maury^{a,b}

^a IRD (Institut de Recherche pour le Développement) – UMR 248 MARBEC, Av Jean Monnet CS 30171, 34203 Sète cedex, France

^b University of Cape Town, Dept. of Oceanography – International Lab. ICEMASA Private Bag X3, Rondebosch 7701, Cape Town, South Africa

^c University Aix-Marseille – UMR 7294 MIO – OCEANOMED – Bât. Méditerranée, LUMINY, 163 Avenue de Luminy, case 901, 13009 Marseille, France

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ABSTRACT

The regularity of the community size-spectrum, i.e., the fact that the total ecosystem biomass contained in logarithmically equal body size intervals remains constant, is a striking characteristic of marine ecosystems. Community size-spectrum models exploit this feature to represent marine ecosystems with two measures: the slope and the intercept (height) of the community spectrum. Size-spectrum models have gained popularity over time to model the properties of fish communities, whether to investigate the impact of fishing, or embedded into end-to-end models to investigate the impact of climate. We review the main features and state of the art developments in the domain of continuous size-spectrum models. The community spectrum emerges from a balance between size-selective predation, growth and biomass dissipation. Further to these basic components, reproduction and various causes of mortality have been introduced in recent studies to increase the model's realism or simply close the mass budget of the spectrum. These different processes affect the stability of the spectrum and affect the predictions of the size-spectrum models. A few models have also introduced a representation of life-history traits in the community size-spectrum. This allows accounting for the diversity of energy pathways in food webs and for the fact that metabolism is both size- and species-specific. The community-level metabolism therefore depends on the species composition of the community. The size-spectrum's regularity at the community level can serve as a conceptual basis for building theories of marine ecosystems' functioning. It is also used as indicator of anthropogenic and natural disturbances. The mechanistic nature of size-spectrum models as well as their simple and aggregated representation of complex systems makes them good candidates as a strategic management tool. For instance, for testing the impact of different fishing management actions or for projecting marine ecosystem's states under various climate change scenarios.

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* Corresponding author at: IRD (Institut de Recherche pour le Développement) – UMR 248 MARBEC, Av Jean Monnet CS 30171, 34203 Sète cedex, France.
E-mail address: jerome.guiet@ird.fr (J. Guiet).

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1. Introduction

Marine ecosystems encompass many physical, chemical and biological interactions, at different spatio-temporal scales and different organization levels. Various types of ecosystem models have been developed over the years, each focusing on different aspects of these ecosystems (Plagányi, 2007; FAO, 2008). For instance, individual based models fully account for life history as well as intra- and inter-specific interactions (Shin and Cury, 2001; DeAngelis and Mooij, 2005), while physiologically structured models link individual level processes to populations' energetics (Metz and Diekmann, 1986; De Roos and Persson, 2001). Yet other approaches only model target species and their evolution in a changing environment (Lehodey et al., 2008; Dueri et al., 2014), while food web models focus on trophic interactions between populations, species or functional groups (Christensen and Walters, 2004; Fulton et al., 2011). Formally, marine ecosystem models can be continuous or discrete, Lagrangian or Eulerian, individual based or formulated at the population level with an age or size structure, multi-agent systems or deterministic differential equations (Tuljapurkar and Caswell, 1997; Kot, 2001). This variety of formalisms reflects the complexity of marine ecosystems and the diversity of modelling objectives. Models are implemented to fulfil several objectives (FAO, 2008): from the conceptual description of ecosystems in order to understand processes; to the testing of long term management decision in order to inform and advice strategic planning; to the short-term tactical management advice.

With the advent of ecosystem-based management of marine ecosystems (FAO, 2008; Fogarty, 2013), models are now expected to account for the complex interactions between species at ecosystem scale while unravelling the relationships between drivers, pressures and resulting states. In order to fulfil these expectations, marine ecosystem models may become increasingly complex and may depend on an increasing number of parameters. Therefore, compromises are necessary in order to keep models' complexity and associated uncertainties in a manageable domain, finding a « sweet spot » between over simplification and over excessive complexity (Collie et al., 2016). Among the variety of marine ecosystem models, size-spectrum models appear as a promising alternative for such ecosystem-based approach (Jennings and Brander, 2010; Giacomini et al., 2016).

Sheldon et al. (1972) first made the observation that ecosystem biomass remains approximately constant when summed within logarithmically equal body mass intervals, from bacteria to whales. It triggered the definition of the size-spectrum, the distribution of biomass or abundance as a function of individuals' mass or size on a log–log scale. The observation of Sheldon et al. (1972) inspired several pioneering studies that have set the bases needed for developing a quantitative theory of ecosystem size-spectrum (See Table 1, History). In the meantime empirical observations of this spectrum multiplied for plankton communities (Sprules and Munawar, 1986; Heath, 1995; San Martin et al., 2006) as well as fish communities (Rice and Gislason, 1996; Bianchi et al., 2000). Recently, the spectrum theory has experienced a rejuvenated and growing interest for modelling energy flux and ecosystems dynamics at higher trophic levels while keeping a reasonable model complexity. It has been subject to important

developments around various key topics (see Table 1, Developments and Directions).

Based on the recent literature (Table 1), this review discusses the developments and new directions in community size-spectrum modelling. We underline the main features of the size-spectrum representation and its central mechanisms: the balance between growth, maintenance and size-selective predation. We describe the latest improvements of spectrum models and discuss their advantages and disadvantages. Finally, we review the modern challenges and potential applications of the size-spectrum approach, particularly in the context of an ecosystem-based management of marine ecosystems (Jacobsen et al., 2016; Blanchard et al., 2014), or for global predictions of climate change impacts (Maury, 2010). Along other reviews on the biomass size-spectrum (Sprules and Barth, 2015) and its modelling (Andersen et al., 2015), we here underline the diverse trends in size-spectrum modelling, from a conceptual description of ecosystems to a tool in a strategic management context.

2. Modelling the community size-spectrum (Table 1, History and Developments)

2.1. Size structure and community size-spectrum in marine ecosystems

Size is a major structuring trait of aquatic ecosystems and fish communities. Size heavily influences organisms' movement (Bainbridge, 1958; Ware, 1978), predation (Cohen et al., 1993; Lundvall et al., 1999; Scharf et al., 2000), growth, mortality and reproduction (Peters, 1986; Marquet et al., 2005; Woodward et al., 2005). All along their life cycle fishes pass through several trophic levels that are well correlated to their size (Jennings et al., 2001; Trebilco et al., 2013).

The structuring role of size in marine ecosystems is evident at the community level, with the emergence of the community size-spectrum. It is defined as the biomass distribution B , or abundance N , or energy E , as a function of individuals length l , or weight w , or volume v , in a log–log space. This definition is inspired by the observation of the « Sheldon » biomass spectrum, namely the observation of an approximate constant biomass in logarithmically constant biomass intervals Sheldon et al. (1972). Empiricists and modellers now adopt multiple definitions, with various combinations of B or N or E versus l or w or v , with or without normalization of the biomass B , abundance N and energy E distributions (Andersen et al., 2015; Sprules and Barth, 2015). The community size-spectrum summarizes complex biological and ecological processes with a simple distribution. Linear or quasi-linear in logarithmic scale, it can be described by its slope λ and intercept Γ (or height Γ_H) (Fig. 1).

The slope λ of the community size-spectrum can take different values depending on the quantities considered (B or N or E versus l or w or v , with or without normalization, see Table 2). But it is considered as an invariant property of unexploited ecosystems emerging from the scaling of individual level processes. Variations around the linear slope can be used as indicators of marine ecosystems health. For instance, departure from a linear shape is a

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