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Review

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

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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 gain 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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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

Table 1
Modelling the community size-spectrum: historical references; recent trends in the development of models; new directions of research. From a conceptual representation (CR) of marine ecosystems to a tool for strategic management (SM).

Key topics	Main references
History	
Modelling the biomass distribution (CR):	a balance between population growth and metabolic loss (Platt and Denman, 1978; Silvert and Platt, 1978)
	a predation driven biomass transfer (Thiebaux and Dickie, 1992)
	a biomass balance controlled by birth and predation (Zhou and Huntley, 1997; Benoît and Rochet, 2004)
Developments	
Modelling significant processes (CR):	representation of individual bioenergetic and maturation (Hartvig et al., 2011; Maury and Poggiale, 2013)
	representation of intrinsic, starvation and ageing mortalities (Maury et al., 2007a; Blanchard et al., 2009)
Modelling environmental drivers (CR):	representation of resource (Maury et al., 2007a; Blanchard et al., 2009; Hartvig et al., 2011)
	representation of temperature (Maury et al., 2007a; Guiet et al., 2016)
Modelling diversity (CR):	representation of functional groups diversity (Blanchard et al., 2009; Maury, 2010)
	representation of traits diversity (Andersen and Beyer, 2006; Hartvig et al., 2011; Maury and Poggiale, 2013)
	representation of the food web structure (Blanchard et al., 2014; Scott et al., 2014)
Directions	
Understanding community stability (CR):	individuals' role on community stability (Datta et al., 2010; Plank, 2012; Zhang et al., 2013)
	species' role on community stability (Zhang et al., 2013; Maury and Poggiale, 2013)
Understanding community dynamics (CR):	individuals' role on community dynamic (Zhou, 2006)
	environmental variability and community dynamic (Maury et al., 2007b; Maury and Poggiale, 2013)
Understanding community functioning (CR):	spectrum models as test-bed for significant process testing (Andersen et al., 2008; Hartvig and Andersen, 2013)
	community structure explains individual's properties (Andersen et al., 2009a,b)
	community level characterizations of diversity (Maury and Poggiale, 2013; Reuman et al., 2014)
Managing ecosystems (SM):	community spectrum as indicator (Jennings and Blanchard, 2004; Houle et al., 2012)
	spectrum models as test-bed for fishing strategy testing (Andersen and Pedersen, 2009; Shephard et al., 2012)
Modelling full ecosystems (SM):	spectrum models for ecosystem-based management (Blanchard et al., 2014; Jacobsen et al., 2016)
	spectrum models for climatic projections (Blanchard et al., 2012; Merino et al., 2012; Woodworth-Jefcoats et al., 2013)
	global ecosystem models (Maury, 2010; Carozza et al., 2016)

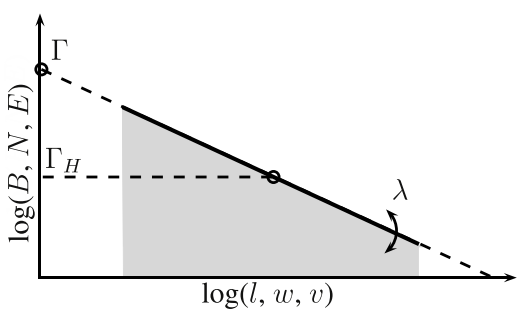

Fig. 1. Linear community size-spectrum: λ, slope; Γ, intercept; Γ_H, midpoint height.

Table 2
Slope λ values depending on ecosystems metrics. Expressed as a function of the slope λ_1 or λ_2 of the normalized abundance spectrum. For a $\ll$ Sheldon $\gg$ biomass spectrum of slope 0, $\lambda_1 \simeq 2$ and $\lambda_2 \simeq 6$ (Andersen et al., 2015; Sprules and Barth, 2015).

	$w \propto v$	$l \propto v^{1/3}$
Abundance N (normalized)	$-\lambda_1$	$-\lambda_2$
Biomass B ($B = Nw$) (normalized)	$-\lambda_1 + 1$	$-\lambda_2 + 3$
Energy E ($E \propto B$) (normalized)	$-\lambda_1 + 1$	$-\lambda_2 + 3$
Abundance N	$-\lambda_1 + 1$	$-\lambda_2 + 1$
Biomass B ($B = Nw$)	$-\lambda_1 + 2$	$-\lambda_2 + 4$
Energy E ($E \propto B$)	$-\lambda_1 + 2$	$-\lambda_2 + 4$

robust measure to detect the impact of fishing (Bianchi et al., 2000; Shin and Cury, 2001; Fulton et al., 2004). It can also be impacted by environmental variations. As far as we know observed effects of the environment concern plankton communities (San Martin et al., 2006; Yvon-Durocher et al., 2011), for fish communities only numerical experiments suggest a link between the slope of the community size-spectrum and environmental conditions (Guiet et al., 2016). It is explained by the length of the trophic chain sustained in a given ecosystem.

The intercept Γ ultimately refers to the level of richness of an ecosystem. It is a stronger indicator of the impact of the environment. For example, poor oligotrophic regions show small values of their intercept compared to rich eutrophic environments. This second property of the community size-spectrum links ecosystems total biomass to primary production over large scales (Boudreau and Dickie, 1992). In order to avoid the correlation between intercept and slope, Daan et al. (2005) prefer the definition of a midpoint size class and chose the midpoint heights Γ_H rather than intercepts to determine the level of richness of ecosystems (see Fig. 1). For instance, it avoids the statistical artefact of an increasing intercept as the slope declines.

Empirical studies of freshwater ecosystems nuanced the linear spectra assumption with the observation of dome-shaped structures where levels of biomass deviate from the expected values (Boudreau and Dickie, 1992; Sprules and Goyke, 1994). Considered to be stable features Thiebaux and Dickie (1993) suggested that the domes correspond to different trophic groups. The community level spectrum remains nevertheless good enough to represent the biomass distribution at ecosystem scale.

2.2. Modelling the biomass distribution

As a subset of physiologically structured models, the community size-spectrum models link the biomass size-distribution B (or N, or E) of the community to s (l, w or v), with individual level processes. For doing so, they usually rely on the predation-driven biomass transfer from a prey of size s_j to a larger predator of size s_i (Fig. 2a). Biologic matter $P(s_i, s_j)$ (expressed in term of B, N or E) eaten by predators at s_i from preys at s_j is turned into growth of the predator $G(s_i) = \alpha P(s_i, s_j) - M(s_i)$, after removing maintenance needs $M(s_i)$, and accounting for the yield α of the conversion of preyed matter into predators tissues (Andersen and Beyer, 2006; Maury et al., 2007a). Predators s_i are also potential preys for larger predators of size s_k, thus propagating this individual based process from the smaller to the larger individuals in the community. Disregarding

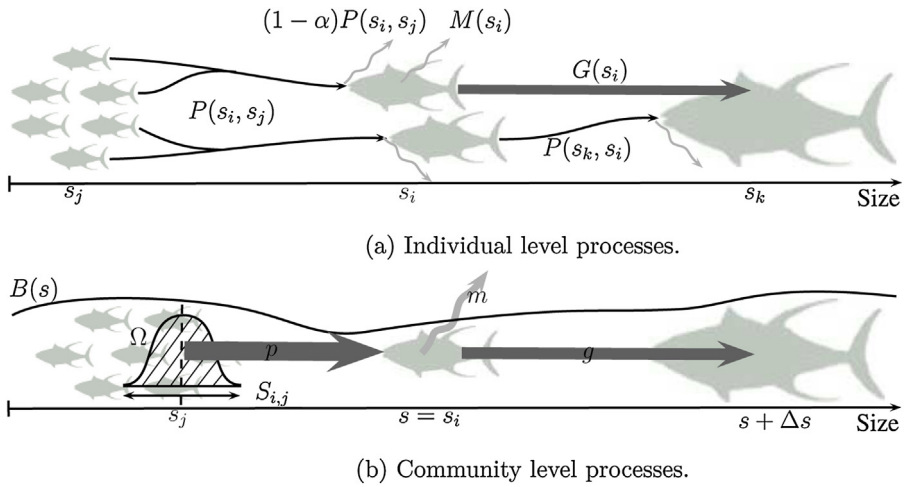

Fig. 2. Size selective predation drives the flow of energy in marine ecosystems at individual and community levels: black arrows represent biomass fluxe and grey arrows biomass dissipation.

species, the community level biomass density distribution B (or N or E) emerges summing the biomass density associated to all individuals at sizes s_i, s_j, s_k and so on along s.

Integrated at the community level, these individual level processes lead to a flux of abundance N from size s to size $s+\Delta s$ that is mediated by predation and growth (Fig. 2b). Predation p is controlled by a prey selection function Ω characterized by the mean predator-prey size ratio s_i/s_j and the width of prey selectivity $S_{i,j}$, namely the range of prey of size s_j available to a predator of size s_i. Predation fuels maintenance m and growth g. The dynamics of the abundance distribution is usually represented combining and advection term representing growth and a sink term μ accounting for predation induced mortality and other types of mortality:

$$\frac{\partial N}{\partial t} = -\frac{\partial gN}{\partial s} - \mu N \tag{1}$$

This equation is well-known in population ecology as the McKendrick von Foerster equation (M'Kendrick, 1925; Foerster, 1959), expressed in size instead of age. The McKendrick von Foerster equation is at the core of continuous community size-spectrum models (Arino et al., 2004; Benoît and Rochet, 2004; Blanchard et al., 2009; Hartvig et al., 2011). Other biological processes have been added to this equation, such as reproduction as boundary condition, or various types of mortalities such as disease, ageing, starvation or fishing. However, only the relationship between predation p, individual growth g and maintenance m explains the regularity of the spectrum.

Based on the individual and community levels representations, two theoretical explanations are suggested to explain the regularity of the slope λ. They are labelled by Rossberg (2012) as the ≪ oligotrophic ≫ and the ≪ eutrophic ≫ regimes. In the ≪ oligotrophic ≫ regime, the encountered food compensates the metabolism and the slope is determined by the allometric exponents of encountered food (p) and metabolic requirement ($g+r$) (Andersen and Beyer, 2006). In the ≪ eutrophic ≫ regime, the food available is not limiting and the slope is determined by the balance between growth of predators (g) and the mortality they inflict on their prey (p) (Benoît and Rochet, 2004).

Note that besides the continuous size-spectrum formulation (Eq. (1)) other formulations exist to compute the community size-spectrum. Also based on individual bioenergetics, they can be summarized as size resolved food webs, for plankton communities in particular (Moloney and Field, 1991; Poulin and Franks, 2010), or size-resolved life history models (Shin and Cury, 2001; Hall et al., 2006; Pope et al., 2006). The first category accounts for the predation-driven biomass transfer from preys to predators but does not account for individuals' growth in size during life history. Individuals in a size class always remain in this size class. The second category represents explicitly the growth of populations or species, parameterized using empirically derived life history traits (e.g. growth rates, fecundity, etc). It disregards mass and energy conservation. In this paper we focus on continuous size-spectrum models.

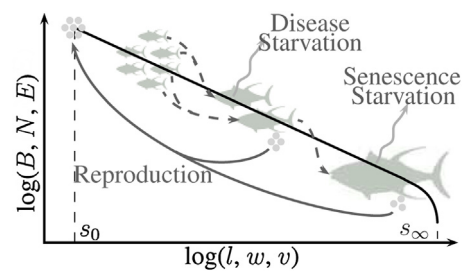

Fig. 3. Additional processes of the community size-spectrum besides predation-driven growth: black arrows represent biomass fluxes in the community and grey arrows represent dissipation and losses.

2.3. Modelling significant processes

Further to the basic biomass balance which accounts for individual's growth, respiration and death by predation, other processes have been introduced to increase the model's realism or close the mass budget (Fig. 3). These processes can impact the stability of community spectra (see Section 3.1), they can be related to the slope λ, its intercept Γ (height Γ_H), or affect the sensitivity of the spectrum to environment or fishing.

Arino et al. (2004) and Maury et al. (2007a) introduced reproduction in the boundary condition formulation at the smaller size end of the spectrum s_0 in fish communities (see Fig. 3). In Maury et al. (2007a), part of the biomass preyed is diverted from growth and maintenance to be invested into the reproduction of offspring that is re-injected into the size-spectrum at the initial size s_0. With such a resource-dependent reproduction, the model links the intercept Γ (height Γ_H) to food-resources. Developments of trait based size-spectrum models (see Section 2.5) completed this representation by considering that only adults larger than a species-dependent size threshold can contribute to reproduction (Hartvig et al., 2011;

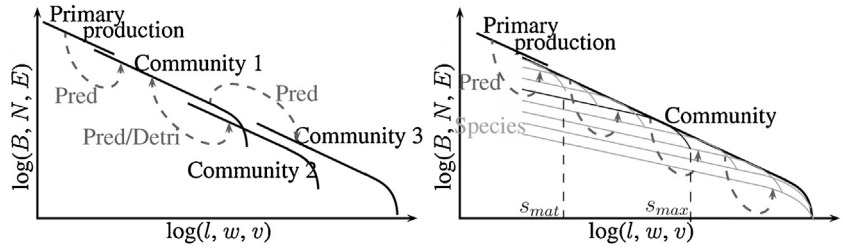

Fig. 4. Representation of diversity with community size-spectrum models: functional community diversity (left); trait-based community spectrum (right).

Maury and Poggiale, 2013). These formulations can be associated with a starvation mortality limiting the development on the community spectrum when maintenance, growth and/or reproduction needs cannot be supported with available resources (Maury et al., 2007a). Thus, community size-spectrum models can account for the trade-off between reproduction, growth and development that individuals are facing when resources are limited.

Toward large size classes s_∞, senescence mortality or predation by super predators out of the spectrum are used to close it (Fig. 3). In spectrum models it avoids the unrealistic case of unbounded spectra since the range of sizes in real ecosystems are obviously bounded. Introduced for their ecological realism these processes are independent of life histories except for the DEB-derived ageing mortality in Maury and Poggiale (2013). They may have a strong impact on community size-spectra slopes λ and intercepts Γ (height Γ_H). Besides a mortality to close the spectrum, a background mortality accounting for disease or other hazard source can be distributed throughout the spectrum. It has been shown to enhance solution's stability (Plank, 2012).

Maury and Poggiale (2013) used the Dynamic Energy Budget theory (DEB, Kooijman, 2010) to fully account for individual's physiology in a community size-spectrum model. It introduces the role of reserves on community dynamic. The introduction of these reserves provides a buffer to perturbations when investigating the sensitivity of marine ecosystems to the environment.

Fig. 3, illustrates how reproduction, starvation and senescence (with or without background mortality such as disease) complete the community size-spectra theory. In the case of fish communities, these processes can be complemented by the addition of fishing as external stressor. An external size-selective mortality term is usually directly introduced in the governing Eq. (1) (Benoît and Rochet, 2004; Blanchard et al., 2009) to account for fishing.

2.4. Modelling environmental drivers

In marine ecosystems the regular biomass distribution of the spectrum (Fig. 1) spans up to 20 orders of magnitude in size from bacteria to fish. Over such a wide size range, organisms display many different reproduction strategies and feeding modes. Most recent studies in community size-spectrum modelling focus on fish communities, their spectrum is represented aligned with an external primary production spectrum or are simply constrained by a primary production pool serving as a food source for small fish sizes.

The primary production spectrum (see Fig. 4) or pool constrains the intercept Γ (height Γ_H) of the fish spectrum and affects its dynamics. It sets the amount of resource available to smaller fish which feed on it, allowing their growth and indirectly fuelling the reproduction which defines the initial biomass level of the spectrum. It also sets the dynamic between resource and consumers with diverse coupling. Some models adopt a one way coupling, meaning that the resource remains constant and independent of grazing pressures (Blanchard et al., 2009). The growth of smaller fish is constant and has no effect on the dynamic of the community. Others account for the dynamic between resource and consumers with a logistic equation (Maury and Poggiale, 2013) or semi-chemostat formulation (Hartvig et al., 2011) for the variation of total primary production. Then the growth of smaller fish is variable and impacts the dynamic of the fish community spectrum. Alternatively to an external primary production spectrum or pool, Blanchard et al. (2009) represent the detritus flux in ecosystems and use it as source of food for a benthic community size-spectrum. Individuals feed on the detritus pool whose dynamic is controlled by the dead primary production and dead or egested mass generated by a pelagic community size-spectrum. The consideration of detritus closes the biomass budget in modelled ecosystems.

Note that the slope of the primary production's spectrum λ is usually fixed at a constant theoretical value (cf Table 2), though variations of the relative biomass of small and large primary producers have been shown to impact the production of fish communities. For instance, Woodworth-Jefcoats et al. (2013) suggest that the size structure of phytoplankton communities has a first order impact on the fish community size-spectrum.

The biomass spectrum exhibits a regular shape across ecosystems and different intercepts (heights) at distinct primary production levels, but also at distinct temperatures. Because it controls chemical reactions, temperature controls metabolic rates which underpin maintenance, growth or reproduction (Clarke and Johnston, 1999; Kooijman, 2010) as well as the functional responses to food density (Rall et al., 2012). Guiet et al. (2016) use the Arrhenius equation to correct feeding, metabolism and background mortality in a spectrum model. At constant resource level, with increasing temperature the spectrum intercept Γ (height Γ_H) globally decreases, with more or less variations on distinct temperature ranges. Their result is explained by the fact that, at a fixed resource level, the scaling with temperature of processes related to biomass assimilation (feeding) is weaker than the scaling of processes related to biomass loss and dissipation (mortality and metabolism). Therefore, with warming the increasing food assimilation on the resource fails to completely balance the increasing biomass loss and dissipation of the fish community. Many community size-spectrum models use the Arrhenius equation to account for the impact of temperature on the community size-spectrum (Maury et al., 2007a; Andersen and Pedersen, 2009; Blanchard et al., 2012; Merino et al., 2012; Woodworth-Jefcoats et al., 2013). In addition to the impact of temperature on communities' intercepts (heights), the impact of temperature on the speed of the energy flow within communities may affect other properties, such as their resilience to perturbations or the intensity of trophic cascades (Andersen and Pedersen, 2009).

In most applications, the role of temperature and resource are regarded as two independent drivers. However, with their BiOeconomic mArine Trophic Size-spectrum (BOATS) model, Carozza et al. (2016) attempt to link temperature variations to a change in the size structure of the resource spectrum. This coupling between resource and temperature is also indirectly introduced in models of the community size-spectrum applied to address climate and

fisheries issues and forced by outputs of coupled ocean and biogeochemistry models (Maury, 2010; Woodworth-Jefcoats et al., 2013). In these models, the size distribution of the resource on which the fish communities are feeding is represented by distinct compartments for small and large phytoplankton and eventually small zooplankton or detritus. However, in these models the retroaction of upper trophic levels is neglected, assuming the dominant role of biogeochemistry and disregarding the grazing mortality induced by small fish. The explicit representation of these feedbacks as well as the coupling of detritus into biogeochemical cycles is complex, biogeochemical and size-spectrum models being characterized by distinct significant time-steps and distinct vertical resolutions.

Finally, current models of the community spectrum essentially focus on the link between lower trophic levels, e.g., phytoplankton and zooplankton, eventually detritus and fish communities. They disregard other source of food such as macroalgaes, seagrass or mangroves which may locally have a strong impact. In addition, community size-spectrum models also often overlook the role of other environmental stressors such as the effect of acidification (Fabry et al., 2008) and oxygen limitation (Pörtner and Knust, 2007). New developments in these directions may be necessary.

2.5. Modelling diversity

Unlike species-based models, size-spectrum models disregard metabolic and physiological differences of the individuals having the same size. However, a sardine and a juvenile tuna are obviously very different despite their same size. The only dimension of biodiversity that is considered in standard size-spectrum models is body size, disregarding any other dimension possibly important in a functional perspective.

To overcome this weakness, some community size-spectrum formulations adopt a mixed compartment based and spectrum based approach, to represent functional groups diversity (Fig. 4). For instance, Blanchard et al. (2009) couples two community size-spectra, parameterized to represent pelagic and benthic communities, and interacting through size selective predation but also through the recycling of dead organic matter. This detrital pathway aliments benthic communities and is slow compared to the main energy pathway between the pelagic community and the primary producers. Accounting for non-predatory interactions in marine ecosystems, the approach revealed that ecosystem's resilience and function depends on the coupling's strength (Blanchard et al., 2011). Also accounting for functional groups diversity and for differences in energy pathways, the Apex Predators ECOSystem Model (APECOSM, Maury, 2010) focuses on the interaction between epipelagic, mesopelagic and migratory communities in the water column. The three spectra are linked through size-selective predation and they account for the biomass export to the deep sea by the diurnal cycle of migratory organisms.

However, even in compartment-based size-spectrum formulations, the functional role of biodiversity remains largely eluded as they do not resolve the metabolic differences of distinct species of the same size. To fill this gap, the most recent developments in community size-spectrum models attempt to account mechanistically for the role of species diversity with the introduction of trait-based formulations (Hartvig et al., 2011; Maury and Poggiale, 2013). These formulations resolve the biomass advection (Eq. (1)) not at the community level but at the level of trait defined species. Instead of solving a single community spectrum, they solve the McKenrick von Foerster equation for a potentially large set of functionally different species. The community dynamics emerges as the sum of each species contributions and interactions (Fig. 4). Transposing at the species level the general and simple parameterization of original size-spectrum formulated at the community level, trait-based approaches differentiate species by their maturation size s_{mat} (Hartvig et al., 2011) or by their maximum length s_{max} (Maury and Poggiale, 2013). Both measures are indeed scaling with metabolism in a number of ways (e.g. Kooijman (2010)). The species spectra are coupled by the size-selective predation so that each species can potentially eat organisms of every species. Considering a diversity of traits allows multiple energy pathways and it impacts the stability of the community spectrum (Zhang et al., 2013). It also allows the representation of trade-offs between species spectra when perturbed by environment or fishing. Note that to ensure the coexistence between species spectra, a random coupling between predator and prey species had to be introduced (Hartvig et al., 2011), or the inclusion of schooling that prevents small species to be fully depleted by large predator species (Maury and Poggiale, 2013). The definition of additional traits such as habitat traits may be the next step to model species-diversified communities maintaining the coexistence (Hartvig and Andersen, 2013).

Finally, some approaches go beyond generic trait-based representations by parameterizing explicitly species spectra to represent a particular set of species in a given ecosystem (see Blanchard et al., 2014; Spence et al., 2015 or the model Mizer, Scott et al. (2014)). These models which can be described as size-spectrum based food web models are better suited than the trait-based model for studies where a level of taxonomic identity is required.

2.6. Advantages and disadvantages of the size-spectrum formulation

With size-spectrum models, the complexity of aquatic ecosystems is aggregated using organism's size as the only structuring trait, and eventually species' size with trait based formulations. They disregard the role of taxonomic diversity on life history or behaviour. On the other side, food web models or other specifically disaggregated approaches (e.g. Plagányi, 2007) are structured according to taxonomic identity or functional groups. They allow the explicit representation of the role of biodiversity. In this context, size-spectrum models have both advantages and disadvantages.

On the advantages side, size-spectrum models focus on emergent properties at the level of ecosystems. They rest on synthetic parameterization of a few key governing processes and avoid the caveat of over-parameterization that is associated to the explicit representation of specific traits and intra-specific interactions that species-based food web models require. Synthesizing the complexity of marine ecosystems at the specific level, they are convenient for large scale studies to analyse the impacts of climate and/or fishing on ecosystems biomass (Blanchard et al., 2012; Woodworth-Jefcoats et al., 2013; Lefort et al., 2015; Le Mézo et al., 2016). Moreover, while the empirical determination of all the interactions or energy pathways in marine ecosystems would be a colossal task, the easily measured biomass size-spectrum provides a consistent starting point to develop theories of the functioning of marine ecosystems. In a nutshell, community size-spectrum models allow overriding the gaps of our empirical knowledge at the species level.

On the disadvantages side, size-spectrum models are expressed at the community level. They are obviously not appropriate to address species-specific dynamics, though they have sometimes been used to provide the biotic environment in which target species evolve (Maury, 2010). Community size-spectrum models generally disregard the role of taxonomic diversity, but recent developments attempt to tackle this issue (Section 2.5, Scott et al. (2014), Blanchard et al. (2014)). This generality makes them especially difficult to compare to observations. Finally the regularity of the community size-spectrum appears over large spatial and temporal scales. This makes it difficult to use it to reproduce local systems where imports and exports are important.

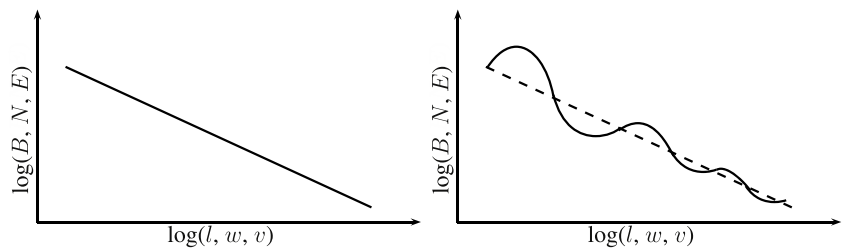

Fig. 5. Dynamic of the community size-spectrum: steady spectrum (left); oscillating solutions (right).

3. Models of the community size-spectrum as conceptual tools (Table 1, Directions)

3.1. Understanding community stability

Models of the community size-spectrum provide a conceptual representation of marine ecosystems allowing their better understanding, starting with the analysis of their stability. Size-spectrum models often exhibit transient or oscillating solutions (Arino et al., 2004; Benoît and Rochet, 2004), as illustrated Fig. 5. These oscillations correspond to a well-known characteristic of predator-prey models (Lotka, 1925; Volterra, 1928) that few empirical experiments reveal in real systems (Fussmann et al., 2000; Beninca et al., 2008). Such oscillations are however poorly documented along the biomass size-spectrum in actual marine ecosystems, because of insufficient sampling, or because of their convolution with the effects of environmental variability at different frequency.

To investigate these oscillations along the size-spectrum, Law et al. (2009) as well as Datta et al. (2010) developed an individual-centred stochastic model of the predation and growth process. In order to better account for the randomness of predatory interactions, this so called jump-growth model allows two predators of a same size s_i to grow differently when they each ingest a prey of size $s_j < s_i$. A cohort of predators at s will be spread on $[s + \Delta s - \delta_1, s + \Delta s + \delta_1]$ after growth (δ_1 illustrates the variability of growth due to the variability of the predation success). The McKendrick von Foerster equation (Eq. (1)) is a first order approximation of the jump growth model. Valid close to the steady state, the equation loses its correctness for non-equilibrium solutions (Datta et al., 2010). The addition of a diffusion term accounting for the cohort spread is suggested to be a better second order approximation of the jump-growth model in this case (Benoît and Rochet, 2004; Datta et al., 2010), and it also tends to stabilize the modelled spectra.

In reality, various processes are susceptible to stabilize community size-spectra. First, Plank and Law (2012) and Plank (2012) show using the jump-growth model that decreasing the predator-prey size ratio s_i/s_j and widening prey selectivity $S_{i,j}$ have important stabilizing roles. A small, close to unity, predator-prey size ratio s_i/s_j is stabilizing. Disregarding the shape of the selectivity function (a Gaussian curve or the convolution of two sigmoidal curves for instance), a spread selectivity (large $S_{i,j}$) also stabilizes the size-spectrum. Ecologically, it implies that increased connectance (selectivity width) and increased food chain length (small predator-prey size ratio) enhance stability. Second, density-independent processes have also been shown to be stabilizing. Capitán and Delius (2010) used an approach similar to the jump-growth formulation to demonstrate the stabilizing role of maintenance respiration and continuous reproduction. Finally, the introduction of biodiversity in size-spectrum models (Zhang et al., 2013, see Section 2.5) appears to be stabilizing as well. Trait-based size-spectrum models represent the diversity of size-dependent growth rates of individuals belonging to different species. Individuals in the same food environment do not grow at the same speed because they do not all belong to the same species. Like in the jump-growth model, they therefore lead to a dispersion phenomenon along the size dimension.

The inclusion of traits is however not sufficient to fully stabilize size-spectrum models (e.g. Zhang et al., 2013) and the potential stabilizing role of other stabilizing processes have to be investigated. In this perspective, Maury and Poggiale (2013) proposed that schooling could exert such a stabilizing effect on the community size-spectrum. According to Maury (2016), schools are indeed density-dependent and they only appear when populations are abundant, increasing the predatory mortality and limiting individuals growth. This density-dependent phenomenon would strongly stabilize marine ecosystems and the associated size-spectrum. Finally, biomass size-spectra characterize regional ecosystems and aggregate spatially heterogeneous biomass distributions. However, spatial interactions and spatial refuges are other stabilizing processes (Janssen et al., 2007) that may be worth incorporating in spectrum models.

3.2. Understanding community dynamic

Besides dynamic oscillations exhibited by unstable spectra, the dynamic response to perturbations of the community size-spectrum is another property which can be investigated with spectrum models. First, Pope et al. (1994) described a seasonal dynamic with a large wave of biomass propagating from small to large individuals while fading. The wave represents seasonal variations of resource which propagate up the size-spectrum. This study actually doesn't study the mechanisms of this dynamic but assume it to set an environment in which individuals develop. Mainly Zhou (2006) formalizes the dynamic response of the perturbed dynamic size-spectrum. It is described by the propagation of waves driven by individuals growth, dumped by mortalities and spreading while they propagate away from the source (see Fig. 5 right). Maury et al. (2007b) also investigate the dynamic of the spectrum in upper trophic levels when forced by oscillations of resource or temperature. Waves of biomass propagate through the spectrum but amplify up to a resonant range before they fade. It is explained by different characteristic times (the time to reach a given size) between small individuals which grow and die quickly compared to large individuals. At different sizes individuals track the oscillations of resource more or less closely.

These different models of the dynamic of the size-spectrum however rely on the community level spectrum representation. They disregard the important role of species diversity. Different species with different growth speed and different sensitivities to variations of their environment will propagate perturbations differently. For instance, clear waves propagation may be observed along species spectra, at the community level the signal may not be as clear since species waves could be out of phase or cancel each other. Trait-based size-spectrum models increase the complexity of the biomass spectrum representation but provide different

possible energy pathways in communities which may strongly affects dynamic solutions.

Note that the analysis of the dynamic of the size-spectrum should be accompanied by the improvement of the numerical schemes used to solve the dynamic of size-spectra. They should avoid an excessive numerical diffusion.

3.3. Understanding community functioning

The conceptual representation of marine ecosystems with size-spectrum models also allows the testing of significant processes structuring ecosystems. In this perspective, Andersen et al. (2008) use a size-spectrum model to investigate the benefit for fish to produce many small eggs as reproductive strategy. Trait-based formulations also allow the investigation of population interactions and the functional role of specific diversity. For instance, Hartvig and Andersen (2013) analyse the coexistence between species and linked it to maturation sizes and predator-prey size ratios. Depending on these parameters, the relationship between two species will be dominated by their competition or a state of ≪ trophic ladder ≫ where the second species develop based on the first one. With trait-based size-spectrum models other traits can be considered to test the conditions of species coexistence.

Linking the energy balance at individual level to the dynamic of communities with the so-called equilibrium size-spectrum theory (Andersen and Beyer, 2006), important ecological properties can also be derived from the spectrum features. For example Andersen and Pedersen (2009) relates trophic and average individual growth efficiencies to the spectrum slope λ. Fishing impacts the steepness of the spectrum and thus the trophic efficiency. With the same equilibrium theory, Andersen et al. (2009a) use the biomass spectrum to demonstrate the links between growth, predation and fish production.

Finally, extending the biomass distribution function of size s to the biomass distribution function of trait s_{max}, Reuman et al. (2014) developed a diversity spectrum of the species distribution in a spatially delineated assemblage. The community spectrum striking characteristic of regularity could therefore be extended to characterize species abundance distributions thus opening new perspectives for the study and modelling of marine ecosystems. Still on the subject of the characterization of the species distribution, Maury and Poggiale (2013) developed a function, $\Phi_s^{s_{max}}$, which expresses the relative contribution of each trait to the total energy content of the ecosystem. Since different species do not have the same metabolic parameters, it characterizes the differences of energy flow along the size s dimension. The trait distribution can be used as a metric of ecosystem biodiversity.

4. Models of the community size-spectrum as strategic tools (Table 1, Directions)

4.1. Managing ecosystems

Community spectra reflect ecological processes governing the energy flow. Anthropogenic and natural disturbances should be captured by variations of the community spectrum shape. For instance, it is recognized that fishing activities target the largest organisms in marine ecosystems and alter the slope of the community size-spectrum λ. The slope has been shown to be a consistent indicator of fishing pressure (Bianchi et al., 2000; Fulton et al., 2004; Shin et al., 2005). It can be considered for strategic management since its departure from the theoretical value without fishing (see Table 2) allows estimating the exploitation level of the system considered (Jennings and Blanchard, 2004). However, fishing pressures are not the only pressures on the community structure, using a trait-diversified community size-spectrum model Guiet et al. (2016) suggest various effects of natural stressors on the slope of the size-spectrum. Therefore, the use of the community spectrum slope as ecosystem indicator needs to be considered along other complementary indicators. Size-spectrum models can be used to test potential indicators, measuring for example their sensitivity to different fishing intensity and selectivity (Houle et al., 2012), thus providing information for management decisions.

Fishing being often size-selective, community size-spectrum models also provide a tool to test how fishing impacts ecosystems and thus provide strategic information. For example, recent studies suggest that spreading the fishing pressure over large portions of ecosystems, in term of size or species, may be ecologically less destructive than the highly selective fishing patterns that usually prevail. With their simple structure, size-spectrum models have been used to quantify the differences of both fishing approaches. Law et al. (2012) concluded that a spread fishing pressure increases productivity. In the same spirit, Rochet and Benoît (2012) used the stability properties of the community spectrum to investigate how the distinct fishing strategies impact the dynamic of the spectrum. Fishing globally amplifies oscillations and spread fishing mitigates them compared to selective fishing. Finally, Andersen and Pedersen (2009) use a size-spectrum model to test how the effects of fishing are propagated throughout communities. They observe that it depletes larger individuals and induces trophic cascades up and down in trophic levels, with a dampening of the cascade away from the target trophic level.

In addition of the impact of fishing on the size structure of fish communities, trait-based size-spectrum models also allow measuring the impact of fishing on species composition. For instance, Shephard et al. (2012) use a diversified spectrum model to show that fishing larger individuals shifts the specific structure toward the dominance of smaller species. When the specific structure is not affected, the removal of larger individuals can be balanced by the growth of smaller individuals which replace their larger conspecifics, but with a combined extinction of larger species the expected recovery time of communities may extend.

4.2. Modelling full ecosystems

Size-spectrum models represent the energy flux and ecosystems dynamics at higher trophic levels while keeping a reasonable model complexity. This intermediate complexity and a conceptual simplicity make size-spectrum models a complementary alternative to popular models such as Atlantis (Fulton et al., 2011) or Ecopath with Ecosym (Christensen and Walters, 2004), for developing and ecosystem-based approach to fisheries. Also the representation of ecosystems without taxonomic detail is an important characteristic of most spectrum models, size-spectrum models representing the food web structure of full ecosystems have however been already successfully parameterized and confronted to observations in the North Sea (Blanchard et al., 2014). But such kind of approach is in its infancy and a formal statistical framework needs to be developed so that it can be considered as useful for quantitative fisheries management (Spence et al., 2015). Alternatively, the diversification of modelling techniques in ecosystem-based management also offer the opportunity of comparison between techniques. For instance, Jacobsen et al. (2016) compared a size-spectrum model for fish communities and a food web model applied to the California Current fish community. Both methods show differences in their predictions which highlight how each model emphasizes distinct details of ecological processes. This provides a broader view of the possible behaviour of real ecosystems and allows a more nuanced use of ecosystems models to assist management decisions.

Beside these examples of size-spectrum based food web models, size-spectrum models provide useful insights on the characteristics of ecosystems when the functional role of individuals and species is of bigger interest than their identity, especially on large scale. First, they allow compact representations of global-scale ecosystems at a reduced computational cost. Second, thanks to their mechanistic formulation, they adapt to various regional ecosystems configurations without the need for region-specific parameterization and allow projections of ecosystem states in future conditions without prescribing the food web structure. This is especially valuable for studying climate change impacts that are expected to trigger changes in oceans with no-analogues in the past. Coupled climate, biogeochemical, fish spectrum models are already applied to investigate the impact of climate, temperature and primary production, on fish production. Using such models, few studies attempted to investigate the convoluted effects of climate and fishing on large marine ecosystems (Blanchard et al., 2012), or in the Pacific (Woodworth-Jefcoats et al., 2013). Coupled with a bioeconomic model, a spectrum model was also applied to investigate the conditions that would allow fisheries and aquaculture to sustain current and increased fish consumption rates (Merino et al., 2012). The BOATS model also links all components of ecosystems from lower trophic levels to humans through an economic harvesting module (Carozza et al., 2016). Community size-spectrum models are tools to assess the impact of climate change on marine ecosystems services and to test global strategic management measures in a changing environment.

The APECOSM model Maury (2010) embed a continuous size-spectrum model of interactive epipelagic, mesopelagic and migratory communities into a spatially resolved advection-diffusion model accounting for the tridimensional transport of biomass by ocean currents and active swimming. APECOSM also considers the effects of food, temperature, oxygen and light on the behaviour of individuals. The model has been applied to investigate the bottom-up forcing of climate on fish communities (Lefort et al., 2015). Forced with a pre-industrial physical and biogeochemical environment the model has been applied to investigate the variability of the biomass spectrum at different individual's size (Le Mézo et al., 2016). It offers a strong basis for developing scenarios of the evolution of fish abundance in oceanic ecosystems.

5. Conclusion and perspectives

A wide range of marine ecosystem's models have been developed over the years and are presently available to the scientific community. Given the number of possible ways to look at the complexity of marine ecosystems, various objective-specific approaches coexist, all with advantages and disadvantages (Plagányi, 2007).

Continuous community size-spectrum models provide simple mechanistic representations of marine ecosystems (Benoît and Rochet, 2004; Andersen and Beyer, 2006; Maury et al., 2007a). They reduce the complexity of food webs and suggest the spectrum's slope and intercept (height) are useful for characterizing ecosystems' state. Size-spectrum models are particularly valid over large regions, in ecosystems where body size is the main driver of individuals' physiology and interactions, such as in pelagic ecosystems. However, in smaller regions the method seems to be also applicable with the emergence of size-spectrum based food web models.

The theory behind the community size-spectrum is now sufficiently developed to use size-spectrum models for testing ecological assumptions, for example regarding the impact of fishing (Houle et al., 2012; Rochet and Benoît, 2012), the efficiency of reproduction strategies (Andersen et al., 2008) or the impacts of environmental variability at various frequencies (Le Mézo et al., 2016). It is sufficiently developed to use size-spectrum models to assess the effects of climate change on marine ecosystem services (Blanchard et al., 2012; Merino et al., 2012; Woodworth-Jefcoats et al., 2013). The recent recognition that the structure of species diversity in communities exerts a strong influence on ecosystems' functioning, sensitivity to perturbations, and resilience (Blanchard et al., 2011), has spurred the development of trait-based models of community spectrum (Hartvig et al., 2011; Maury and Poggiale, 2013). However, despite this increasing complexity of models, few comparisons to empirical data have been conducted to date. The development of a size-based theory of marine ecosystems would certainly benefit from a better empirical validation. It may become possible with the recent determination of size-spectrum based food web models (Scott et al., 2014). For instance, Blanchard et al. (2014) already replicated realistic population, community structure and past responses to fishing with such multispecies size-spectrum model for the North Sea.

The size-spectrum models provide a baseline of ecosystems states and allow deconvoluting the effects of natural drivers from human induced perturbations and changes. Comparing theoretical spectrum values with empirical size-spectra provides insights on the health of ecosystems (Rice and Gislason, 1996; Bianchi et al., 2000). Size-spectrum models also provide tools to investigate *in silico* how environmental drivers alter the biomass flux from primary production to upper trophic levels (Maury et al., 2007b; Guiet et al., 2016). Embedded into ≪ end-to-end ≫ approaches, the mechanistic basis of size-spectrum models is well adapted to long-term projections of ecosystems to investigate oceans' future in different environmental and fishing context (Lefort et al., 2015; Carozza et al., 2016).

Size-spectrum models have evolved from conceptual representations of marine ecosystems. They now provide useful tools to test long term management decisions in order to inform and advice strategic planning. The use of spectrum models for tactical management remains out of reach. However, recent developments suggest a possible evolution in this direction (Spence et al., 2015).

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