INTRODUCTION

Size-based approaches to aquatic ecosystems and fisheries science: a symposium in honour of Rob Peters

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Abstract: This special issue honours Rob Peters' outstanding contributions to the field of aquatic ecology. It focuses on the size spectrum approach — in which individual organisms, rather than species, are the most basic biological unit — and highlights applications of this approach to fisheries management. The 21 papers in this issue cover three subject areas: (*i*) the use of size spectra to characterize variation in community structure, (*ii*) the development of size-based models of ecosystem dynamics to address fisheries questions, and (*iii*) applications of size-based theory to examine the consequences of variation in predator–prey size relationships, body size – trophic level relationships, and body size – life history relationships. The empirical studies herein demonstrate the utility of size spectra as indicators of population or community structure and for detecting impacts associated with environmental change. Future research focused on refining size-based sampling methods, standardizing metrics and analytical methods, understanding model sensitivity to the underlying assumptions, and comparative studies across ecosystems will enhance our ability to reliably interpret changes in size spectrum characteristics, thus facilitating their use as indicators of ecological change.

Résumé : Le présent numéro spécial souligne la contribution exceptionnelle de Rob Peters au domaine de l'écologie aquatique. Il se penche sur l'approche axée sur les spectres de tailles, selon laquelle l'individu, plutôt que l'espèce, constitue l'unité biologique la plus fondamentale, et il présente des applications de cette approche de gestion des pêches. Les vingt et un articles qu'il renferme couvrent trois grands secteurs d'étude, à savoir (*i*) l'utilisation des spectres de tailles pour caractériser les variations de la structure de communautés, (*ii*) le développement de modèles basés sur la taille de la dynamique des écosystèmes pour examiner des questions touchant aux ressources halieutiques, et (*iii*) des applications de la théorie basée sur la taille pour examiner les conséquences des variations des relations de la taille des prédateurs et proies, des relations entre la taille du corps et le niveau trophique et des relations entre la taille du corps et le cycle biologique. Les études empiriques présentées démontrent l'utilité des spectres de tailles comme indicateurs de la structure des populations ou des communautés et pour détecter les impacts associés aux modifications de l'environnement. Des travaux de recherche futurs visant le raffinement des méthodes d'échantillonnage basées sur la taille, la normalisation des paramètres et méthodes analytiques, la compréhension de la sensibilité des modèles aux hypothèses sous-jacentes et des études comparatives de différents écosystèmes accroîtront la capacité d'interpréter de manière fiable les variations des caractéristiques des spectres de tailles, en facilitant ainsi l'utilisation comme indicateurs de changements écologiques. [Traduit par la Rédaction]

Introduction

> "… size has a remarkably great influence on the organization of animal communities" (Elton 1927)

Body size is the most conspicuous trait of living organisms, varying over 20 orders of magnitude in mass across taxa from bacteria to whales or sequoias and very often over 10 orders of magnitude within a single ecosystem (Woodward et al. 2005; Andersen et al. 2016a). It has long been recognized to correlate with many important physiological and ecological processes (Elton 1927; Kleiber 1932; Thompson 1942; Schmidt-Nielsen 1984; Brown et al. 2004), with relationships that follow well-defined scaling rules represented by power functions, conveniently expressed as straight lines in double logarithmic plots. These relationships have been observed and compiled over decades in the scientific literature, of which the book by Rob Peters (1983), *The Ecological Implications of Body Size*, is a landmark. This volume has encouraged much further work that sought to (*i*) refine our understanding of size-based patterns with additional data and (or)

statistical techniques (e.g., Savage et al. 2004; Barnes et al. 2010; Yvon-Durocher et al. 2011), (*ii*) explain these patterns from more basic principles (e.g., West et al. 1997; Kozlowski and Weiner 1997; Glazier 2014), and (*iii*) predict the consequences for processes at higher levels of organization such as the dynamics and structure of food webs (e.g., Petchey et al. 2008; Brose et al. 2016) and even global patterns and processes including marine diversity (Reuman et al. 2014) and productivity (Jennings and Collingridge 2015).

The role of body size is especially relevant in aquatic ecosystems, where the flows of energy and matter are strongly dependent on size relationships between individual predators and prey (Hildrew et al. 2007). This general finding has promoted a simple and unifying perspective, within the emerging domains of metabolic ecology and macroecology (Brown et al. 2004; Reuman et al. 2008), linking size-based processes at the individual level to regularly observed patterns of body size distributions at the level of ecosystems, the so-called "size spectra" (Sheldon et al. 1972; Kerr and Dickie 2001). It in turn has motivated an increasing use
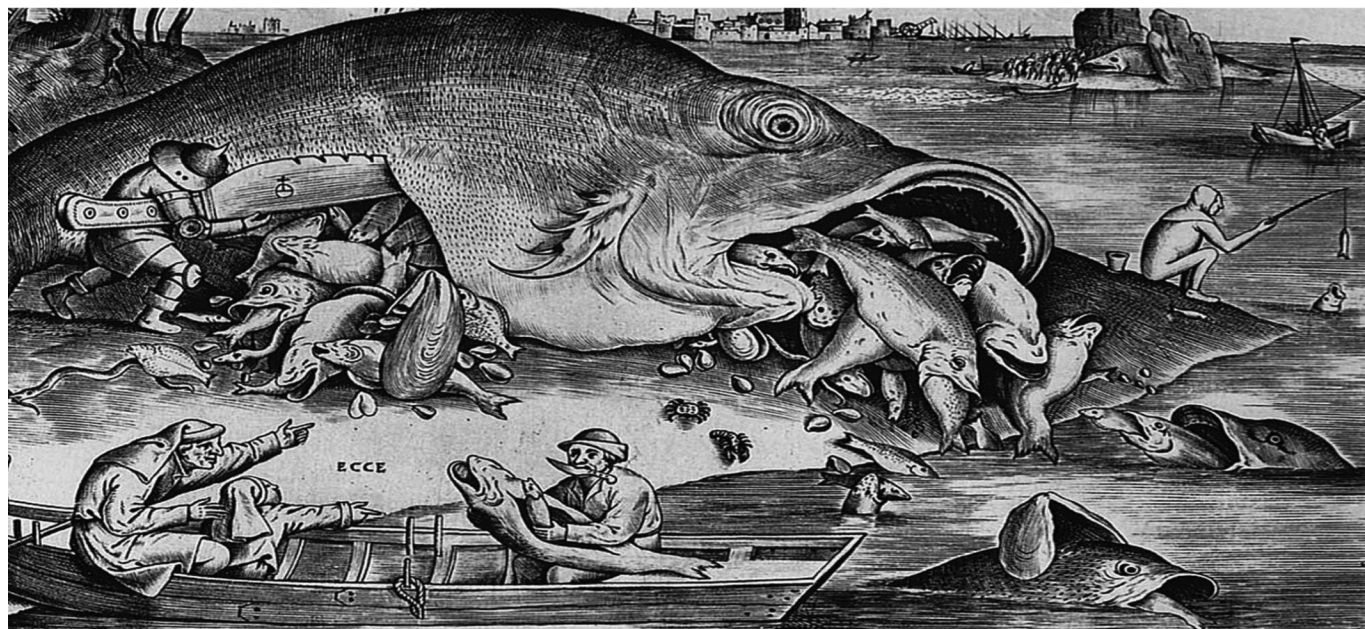
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Fig. 1. "Big fish eat little fish", by Pieter van der Heyden (1556).

of size distributions as indicators of ecosystem structure and functioning (e.g., Sprules and Munawar 1986; Daan et al. 2005; Petchey and Belgrano 2010; Trebilco et al. 2015), which is further justified by the fact that the same ecological processes shaping the size spectrum can be affected by environmental factors such as temperature and anthropogenic disturbances — especially fishing — in predictable ways (e.g., Rice and Gislason 1996; Blanchard et al. 2005; Dossena et al. 2012). Another important justification comes from theory linking these macroecological (or "static") approaches to dynamical approaches and demonstrating that the commonly observed pattern of a near linear size spectrum — as represented in a double-logarithmic plot of density versus size (see Sprules and Barth 2016, fig. 2) — emerges as the equilibrium or long-term average of ecosystem dynamics with size-structured predator–prey interactions (Benoît and Rochet 2004; Law et al. 2009; Datta et al. 2010).

The use of models of size spectrum dynamics to understand the behaviour of aquatic ecosystems and their response to fisheries has also increased in importance, especially in the last 10 years. These models differ from traditional food-web approaches by explicitly representing body size variation within populations and (or) communities through continuous distributions (Hartvig et al. 2011; Scott et al. 2014). This is relevant for aquatic systems in which individuals, most notably fish, undergo extensive ontogenetic changes in size and ecological function. The intermediate level of complexity and the conceptual simplicity of these models make them complementary alternatives to currently more popular models used for developing an ecosystem-based approach to fisheries, e.g., *Ecopath* with *Ecosim* (*EwE*; Christensen and Walters 2004) and *Atlantis* (Fulton et al. 2011).

With the objective of bringing together people working on these emerging research areas in aquatic ecology and fisheries, we organized a symposium on size-based approaches at the 144th meeting of the American Fisheries Society, held in August 2014 in Quebec City, Canada. This symposium was funded by the Canadian Network of Aquatic Ecosystem Services (CNAES-NSERC) and is dedicated to Rob Peters because of his outstanding contributions to the field. This special issue of 21 original papers comes from that symposium: 63 scientists report new research on hundreds of freshwater ecosystems spread across four continents (Europe, Africa, North America, and South America) and several

marine ecosystems from both the Atlantic Ocean and the Pacific Ocean. This set of studies emphasizes the size spectrum approach, with individual organisms as the most basic unit instead of species, and highlights applications to fisheries management. This emphasis sets it apart from earlier collections with a body-size focus (e.g., Hildrew et al. 2007; Blanchard 2011; Belgrano and Reiss 2011).

We have grouped the papers into three subject areas, based on the approach to analyzing and (or) modeling size-based data: (*i*) a review and set of original studies that assess the ability of size spectrum descriptors to characterize and explain empirical variation in ecosystem structure; (*ii*) a review and a set of original papers that develop size-based models of ecosystem dynamics and use them to address questions related to fisheries management; and (*iii*) a more diverse set of papers that focuses on extensions of the theory that underpins the work in the first two sections, addressing specifically predator–prey size relationships, body size – trophic level relationships, and body size – life history relationships.

(*i*) Size spectrum as an indicator of ecosystem structure

The linear size spectrum is an attractive representation of aquatic ecosystems because (*i*) it consists of just two parameters, the size spectrum slope, which measures the relative frequency of small versus large organisms in the ecosystem, and the intercept (or height), which measures the overall abundance of organisms in the system, (*ii*) it has theoretical support and thus can be used to make inferences about individual-level attributes such as average predator–prey mass ratio, trophic transfer efficiency, size-selective mortality, and (or) the allometry of foraging rates, and (*iii*) it is a purely functional, taxon-free representation that is relatively easy to sample and to estimate statistically. Sprules and Barth (2016) review the history of the size spectrum approach in ecology and its theoretical foundations and applications. They provide a useful guide on how to sample, estimate, and interpret size spectra data for researchers interested in applying this approach to their own work. They also make recommendations for standardizing size-based ecological studies to avoid common pitfalls and to make future cross-system comparisons more meaningful.

In the only marine study of this section, Robinson and Baum (2016) present evidence for strong size structuring of trophic interactions in a minimally perturbed coral reef fish community: trophic position scaled positively with size both within and across species, and individual abundance declined consistently with size. In addition, the size spectra of two distinct trophic groups differed in a way that is consistent with predictions from metabolic theory: herbivorous fish, which share a common resource base, had a shallower size spectrum slope than the group of carnivorous fish, where frequent trophic transfers and their associated energy losses are expected to produce a steeper spectrum slope.

The distinction between two broad trophic groups is also the focus of Mehner et al. (2016), who compared prey fish and piscivorous fish in European lakes. They found no evidence that the prey size spectrum is affected by the piscivore spectrum; however, they did find a strong negative effect of prey fish density on the prey spectrum slope and a similar negative effect of predator fish density on the predator spectrum slope. This suggests that competition within feeding groups has a stronger influence on size structure than predation between them. In the same study system, Arranz et al. (2016) show that, within a species, density had a stronger influence on size structure than several environmental predictors: for six common fish species, higher population abundance was associated with steeper size spectra, smaller mean size, and lower size diversity.

Chu et al. (2016) use a suite of indicators to quantify community responses to environmental gradients and show that fish community size structure in Ontario lakes was best explained by a combination of both local and regional predictors and that CPUE of large-sized fish and the normalized length size spectrum were the community indicators most responsive to those predictors. This study also shows that angling pressure exerts a rather complex, nonmonotonic influence on community size structure in this large set of approximately 700 inland lakes.

Another important type of anthropogenic pressure is the change in natural land cover, which affects the local structure of aquatic habitats and disturbs the regional processes that ultimately determine species distributions. Benejam et al. (2016) show that, in subtropical Uruguayan streams, large-sized fish have been relatively favored in more impacted watersheds. These changes were associated with lower richness and the presence of large and tolerant species, highlighting how knowledge of species composition can deepen our understanding of variation in size structure.

The papers described above cover a variety of sampling methods such as gillnet sampling, electrofishing, and visual census. Hydroacoustic sampling is a promising alternative, as it tends to be less size selective, more cost effective, and less invasive than traditional catch methods. Wheeland and Rose (2016) explore the potential for hydroacoustics to estimate fish size spectra using Lac Du Bonnet, a reservoir in Manitoba, as a test system. They show that the method is effective when fish are not strongly aggregated and single individual targets are discernible in enough numbers. Estimated size spectra closely followed the linear model, with significant variation evident over the sampling season, between years and between locations within the reservoir. In Lake Opeongo, Ontario, de Kerckhove et al. (2016) detected temporal trends toward shallower fish size spectrum slopes from 2005 to 2009, accompanying the known decline in abundance of small-bodied fish in this period. Through a power analysis, they demonstrated that the size spectrum slope can be effective as an indicator of ecosystem change over relatively short time scales when compared with traditional aquatic indicators (e.g., fish abundance, individual growth rates) estimated from harvest-at-age sampling.

(ii) Size-based models of ecosystem dynamics: theory and applications

In the ecosystem approach to fisheries, understanding the dynamical feedbacks between ecosystem components, be they species or functional groups, is of fundamental importance (Plagányi 2007). However, modelling the dynamics of multiple interacting components is challenging, because the number of potential model parameters increases geometrically with system size. Fortunately, the realized set of parameter values can be greatly reduced by incorporating information on traits of individuals and (or) species, of which body size is the most noticeable. The role of body size in constraining rates and parameters of ecosystem models has been recognized in many studies using traditional food-web approaches (e.g., Yodzis and Innes 1992; Loeuille and Loreau 2005; Brose et al. 2016). Size also plays a key role in several other model types such as stage-structured (de Roos and Persson 2002), physiologically structured (van de Wolfshaar et al. 2006), and individual-based (Giacomini et al. 2013) models. Andersen et al. (2016b) review the class of dynamical size spectrum models that have recently gained importance in fisheries studies. The authors identify three major model categories (community, trait-based, food web) that have been proposed in the literature and that reflect a progressive increase in both complexity and the level of species-specific detail. The paper demonstrates the common theoretical underpinnings of these models, illustrates differences in their dynamical responses to fishing, and ends with a discussion on current challenges and directions for future work.

One important aspect of any model application to fisheries management is to quantify model uncertainty. Although size spectrum models have been parameterized for real systems before (e.g., Blanchard et al. 2014), a formal statistical framework to fully explore available data and to quantify parameter and model uncertainty was lacking. Spence et al. (2016) devise a Bayesian approach to estimate uncertainty from data and parameters of a size spectrum model fitted to the North Sea fish community and its multispecies fisheries and show that their more sophisticated statistical procedure greatly improved model fit over previous estimation methods.

The North Sea fish community is also the focal empirical system in Datta and Blanchard (2016), who modify a size spectrum model calibrated to this system (Blanchard et al. 2014) and evaluate how including seasonality in the model alters its dynamics: seasonal variation in resource production and fish reproduction led to (i) higher temporal variability in all investigated community metrics, including the size spectrum slope, and (ii) lower overall fishing yield, indicating that current nonseasonal size spectrum models may overestimate yields in similar systems.

Using another modified size spectrum model, Canales et al. (2016) explore how changing plankton size structure affects the dynamics and coexistence of anchovy and sardine. They adapted the feeding kernel in the model to better represent the known differences between these species in both prey size selectivity and the ontogeny of feeding preferences and found that coexistence between the two species was only possible when large-sized plankton were available.

Dynamical size spectrum models are also applicable to freshwater systems. van Zwieten et al. (2016) use a trait-based size spectrum model to compare competing hypotheses explaining the successful invasion of Lake Victoria by Nile perch. Both the model and extensive empirical evidence favor the recently proposed depensation hypothesis that environmentally induced mortality on cichlids weakened their control on perch through size-structured predation on larvae and permitted perch to become dominant. A key support for their conclusions was that the observed changes in Nile perch size structures, which are consistent only with the depensation hypothesis, were explicitly and successfully predicted by their model.

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Applying a similar size spectrum model, Kolding et al. (2016) explore the possible consequences of fishing selectivity on the dynamics of fish communities in Lake Kariba in Africa. The model predictions and empirical data indicate that spreading the fishing effort over wider size ranges, as observed in the less controlled Zambian side of the lake, led to higher yields while preserving community structure. The authors call for a revaluation of current size restrictions embedded in many fisheries regulations, arguing that this would be particularly beneficial for inland fisheries in developing countries where fishing for food is the major objective.

An interesting contrast to this theme is made by McCann et al. (2016), who use a more traditional size-structured food web modelling approach and show that indiscriminate fishing (i.e., spreading fishing mortality uniformly across species and trophic positions) can lead to important losses of diversity despite increased productivity. By favoring small-sized, faster growing populations, intensive indiscriminate fisheries can increase yields but at the cost of reducing the ecosystem's adaptive capacity to buffer against environmental fluctuations. The authors discuss their findings in light of the Tonlé Sap fisheries in Cambodia, suggesting that its nearly indiscriminate fishing pattern could make it vulnerable to ongoing and future environmental changes.

The papers presented above add to a growing list of size-based model applications designed to assess the ecosystem effects of fishing or other perturbations. With an increasing number of alternative models available for this purpose, it is important to have a comprehensive understanding of their differences and commonalities so that informed management decisions can be made. Jacobsen et al. (2016) compare a trait-based size spectrum model to the widely used *EwE* model, both parameterized for the California Current system. The size-based model predicts maximum sustainable yields to occur at relatively higher fishing mortalities. In addition, the two models predict contrasting cascading effects of fishing, with *EwE* dominated by bottom-up effects and the size-based model dominated by top-down effects, which can be explained by their different emphases on intraspecific versus interspecific processes within a community.

(*iii*) Body size variation: cause and consequence of ecosystem processes

Much of the size-based theory discussed in the previous sections relies on simplifying assumptions regarding body size variation. In particular, the distribution of life history traits (e.g., maturation and asymptotic sizes) and the distribution of prey size preferences relative to predator size (i.e., the feeding kernel) are structured as constant model inputs. In reality, these traits are interdependent variables that can change with a variety of processes at the behavioral, physiological, ecological, and evolutionary levels. Internally driven changes in these variables may have significant effects on overall model dynamics that have yet to be fully explored. The papers in this section of the symposium explore some aspects of this issue.

Juanes (2016) documents complexities in the predator–prey size relationship, a fundamental aspect of all size-structured food-web theories (Reuman et al. 2008; Andersen et al. 2016*b*). He analyzed body lengths of predators and prey from a large marine dataset and found many of the patterns (e.g., increasing average and range of prey sizes with increasing predator size) that are assumed by size-based models. However, his analysis also revealed a tendency for trophic niche breadth to increase with size in larval fish and a strong tendency for it to decrease with size in adults. These findings show that developmental processes affect predator–prey relationships in food webs in ways that could influence community dynamics and structure.

A related concept to the predator–prey size ratio is the predator's body size – trophic level relationship (STLR). A linear and positive STLR is expected to result from a fixed predator–prey size ratio and is required for the maintenance of a linear spectrum (Chang et al. 2014). However, for large-sized predators, high individual metabolic demand prevents the persistence of populations feeding on high trophic levels, and the result is a negative STLR (Arim et al. 2007). The paper by Arim et al. (2016) extends the previous model of Arim et al. (2007) to the metacommunity scale and shows that the energetic limitation on trophic level can be modified by spatial connections between local communities: populations living in more central communities receive a higher influx of immigrants through random dispersal and thus can maintain relatively higher trophic levels.

Changes in predator–prey size relationships can be influential also for life history, as they define the relative energetic costs and benefits of foraging. Shuter et al. (2016) use a bioenergetic approach to combine optimal foraging and life history models and predict the reactions norms of maturation age and size, as well as asymptotic size, to variation in predator–prey mass ratio (PPMR). Their predictions match qualitatively the observed life history variation of lake trout in Lake Opeongo, Ontario, across a time series of almost 80 years with a fourfold change in PPMR after a forage fish species (cisco) was introduced in the lake. The theory that they propose provides a framework for phenotypic plasticity in size-structured models that is consistent with optimal life history principles.

In contrast to the bottom-up focus of Shuter et al. (2016), DeLong and Walsh (2016) focus on the top-down effects of changing predation risk on life history traits, particularly maximum body size and growth rate. They use the simple supply–demand (SD) model (which postulates that the optimal life history strategy is to grow up to a size at which metabolic demand matches the rate of environmental resource supply) and show that it can predict the qualitative diversity of responses to predation risk that have reported in the literature and that are reinforced by the authors' own empirical analyses.

Finally, life history traits are important determinants of species vulnerability to changes in habitat quality or availability. As maximum body size is a good predictor of many other aspects of life history, it is also expected to be a predictor of differences in species' responses to habitat loss. van der Lee and Koops (2016) use a matrix population modelling approach, parameterized using published allometric relationships between several life history attributes, to show that species with smaller maximum sizes tend to be demographically more sensitive to habitat loss, especially in preadult stages. The sustainable harvest rates for smaller species were also found to be more sensitive to habitat loss, although larger species were more sensitive to fishing mortality per se.

Concluding remarks

The extensive empirical studies presented in this symposium have shown that the size spectrum slope is an informative indicator of the state of communities or populations and can be used to detect significant impacts associated with environmental change. The statistical "power" of these indices, and hence their ability to identify change, hinges on refinements of both sampling protocols and sampling methods. Papers in this symposium have quantified (*i*) changes in spectra parameters between systems, (*ii*) their levels of variability within systems, and (*iii*) the utility of new sampling approaches, particularly hydroacoustic sampling, to parameter estimation. Further work in all these areas should provide significant advances in both sampling design and sampling gear, with the objective of increasing the power of size-based statistics to detect real change and hence improve the utility of spectra parameters as general ecological indicators. Also, standardization of methods and metrics will greatly facilitate collaboration among researchers working on freshwater and marine systems around the world. Increased collaboration will promote

comparative studies across systems, thus facilitating understanding of how the general constraints that metabolic scaling imposes on aquatic ecosystems are expressed in different systems with different spatial structures and environmental characteristics. Such comparative studies will provide valuable insights into how to reliably interpret changes in size spectrum characteristics and thus facilitate their use as indicators of ecological change.

Explicitly modelling size spectrum dynamics is considerably more complex than analyzing "static" empirical size spectrum data, which usually requires simple statistical approaches (e.g., linear regression). However, dynamical size spectrum models have become increasingly accessible, being used for a variety of applied questions as exemplified by several papers in this special issue. The development of modelling platforms and software packages such as *mizer* (Scott et al. 2014) will enable their widespread use by ecologists and fisheries scientists, as has happened with other ecosystem models such as *EwE*. With increasing availability of accessible software for a range of ecosystem models, it becomes both possible and desirable to adopt an ensemble modeling approach to strategic and tactical fisheries questions. By comparing the dynamics of variously structured ecosystem models (see Jacobsen et al. 2016) parameterized to a single system, a broader view of the behaviours possible for the real system will be achieved, and with this appreciation, a more nuanced and adaptable approach to management decisions will be realized.

Further development of size-based models demands continuing research to better understand the sensitivity of model predictions to fundamental model assumptions. These include but are not limited to some of the assumptions addressed in this special issue, specifically: (*i*) constant life histories, (*ii*) constant predator–prey size ratios, and (*iii*) constant allometric relationships. Another important point, already recognized in the ecological literature, is that size is a fundamental but insufficient trait to explain all aspects of ecosystem structure and dynamics (Williams et al. 2010; Hartvig et al. 2011; Rossberg 2013). This is reinforced by papers in this special issue that highlight important trait dimensions other than body size such as species-specific feeding preferences (Canales et al. 2016), parental care and larval survivorship (van Zwieten et al. 2016), spawning tactics (Datta and Blanchard 2016), and tolerances to environmental variables and perturbations (Benejam et al. 2016). These and other size-independent traits can be crucial for niche partitioning and the maintenance of coexistence in diverse aquatic communities (Hartvig and Andersen 2013). Stable coexistence has been achieved in multispecies size spectrum models through the addition of implicit niche partitioning and density-dependent factors, collectively represented by random matrices of feeding preferences or by stock–recruitment relationships (see the review by Andersen et al. (2016*b*) and the studies of Spence et al. (2016) and Datta and Blanchard (2016)). Nonetheless, a mechanistic inclusion of other traits can lead to important insights into the functioning of aquatic ecosystems and their responses to exploitation and would represent a natural extension of current size spectrum models.

Using size-based models is advantageous not only because size is an important determinant of ecological processes: such models make explicit predictions of changes in size distributions that can provide the critical information needed to distinguish between competing hypotheses regarding the causes of ecological change. The paper by van Zwieten et al. (2016) is one example: by making explicit predictions of temporal changes in the size distribution of Nile perch, their model focused attention on extensive data that had previously been overlooked, providing new evidence in favor of the depensation hypothesis (i.e., the collapse of haplochromine cichlids caused the upsurge of perch in Lake Victoria, not the other way round). Using size distributions in this manner highlights the usefulness of a pattern-oriented modelling approach in ecology (Grimm and Railsback 2012). This is especially relevant given the many reasonable hypotheses that can be proposed for

mechanisms underlying ecological phenomena. To distinguish the likely hypotheses from the possible, it is essential to contrast expected patterns of change in as many relevant data sets as are available. Size-based models expand the range of relevant data sets that can be used in this fashion and hence significantly extend our ability to extract reliable knowledge from observations on natural ecosystems.

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