

Review

From Bacteria to Whales:
Using Functional Size Spectra
to Model Marine Ecosystems

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Size-based ecosystem modeling is emerging as a powerful way to assess ecosystem-level impacts of human- and environment-driven changes from individual-level processes. These models have evolved as mechanistic explanations for observed regular patterns of abundance across the marine size spectrum hypothesized to hold from bacteria to whales. Fifty years since the first size spectrum measurements, we ask how far have we come? Although recent modeling studies capture an impressive range of sizes, complexity, and real-world applications, ecosystem coverage is still only partial. We describe how this can be overcome by unifying functional traits with size spectra (which we call functional size spectra) and highlight the key knowledge gaps that need to be filled to model ecosystems from bacteria to whales.

Size Matters for Individuals to Ecosystems

Ecosystems are under pressure from human activities and environmental change. These changes in marine systems manifest at different levels of biological organization, from individuals to ecosystems, with consequences for a range of services to society. Models are needed to understand and predict how ecosystems are changing in response to these pressures and to help ecosystem-based management promote recovery and prevent further degradation.

Body size has been described as the ‘master trait’, setting the pace of life by dictating processes such as metabolism, respiration, development, movement, and constraining the role of an individual in its food web [1–3]. Species-based food web models traditionally represent species as nodes either irrespective of their body size or using an average population-level body size to determine food web interactions [4]. However, over the past decade there has been rapid development of size-based ecosystem models that focus on how individual size governs feeding interactions and biological rates, originally ignoring species identity. This powerful approach gives rise to emergent distributions of biomass, abundance, and production of organisms and is now being applied in a wide range of environments, most notably in the global ocean [5–8]. Although primarily developed for aquatic communities and ecosystems, this perspective has also influenced recent developments to model all life on Earth [9,10].

The field of size-based ecosystem modeling is rooted in 50 years of the empirical **size spectrum** (see [Glossary](#)). It stems from observations of equal biomass of plankton in logarithmic body mass bins (which equates to declining abundance of individuals with body size), famously hypothesized by Sheldon and colleagues to hold ‘from bacteria to whales’ [11]. The general approach traces even further back, to Elton’s ‘pyramids of numbers’ in the 1920s

Trends

Size-based ecosystem models have proliferated in the past 10 years.

They are a general and powerful approach to modeling ecosystem structure and function

Great progress has been made toward modeling ecosystems from bacteria to whales.

Unifying models across scales and confronting models with data are now the key needs

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[1,12]. Since Sheldon's hypothesis, observed size spectra have shown a remarkable regularity in shape and slope across a range of ecosystems [13] and communities, including those from the open ocean [14,15], sea bottom [16,17], coasts [18], freshwater [19], and even land [20,21]. Sheldon's call for a solid theoretical foundation to explain this regularity prompted the development of mathematical models and size spectrum theory [13,22].

Fifty years on from Sheldon's first empirical spectra, and 90 years since Elton set the stage for size spectra with the introduction of **ecological pyramids**, we revisit Sheldon's vision and ask how far have we come? Can we now robustly model the size spectrum from bacteria to whales? We begin by explaining the different types of size-based models, how they scale individual processes to predict ecosystem properties, and how they are being applied across the size spectrum to answer real-world problems. We find that the vision to span sizes of bacteria to whales has largely been realized, but that total ecosystem coverage is not yet complete. To model the entire ecosystem under human exploitation and environmental change, we argue that we must unify size spectra with other **functional traits** to advance size-based ecosystem models. We discuss four future research priorities to help achieve this.

How to Model the Community Size Spectrum?

Over the past five decades, a diverse range of models has emerged that focuses on how individual-level size-based processes give rise to community size spectra, primarily in the marine environment (Figure 1). Here, we provide a road map for these different approaches, with a focus on models developed over the past decade.

Static Models

The simplest models to predict the size spectrum are based on assumptions about the mean ratio of predator to prey sizes and the metabolic scaling of consumption and/or turnover rates with body size. The first of these focused on broad predator and prey groupings or trophic levels and assumed an average size for each group to infer a community **predator: prey mass ratio** (PPMR) [23,24]. More recently, stable isotope analysis has been used to derive trophic level–body size relationships across individuals within size classes to improve estimates of mean PPMRs and predict the scaling of abundance and biomass with body mass [12,25]. These models, typically predict biomass **size spectrum slopes** of 0 or steeper (and -1 or steeper for the abundance spectrum). Using primary production as inputs, these simple macroecological models can be used to estimate marine consumer biomass and productivity in the global ocean in the absence of fishing [5,26]. They have also been used to assess the contribution of fish to the marine inorganic carbon cycle [27,28]. Because they do not have explicit mortality terms, assessing the impacts of fishing involves snapshot comparisons between predicted unexploited and observed exploited size spectra [29].

Individual-Based Models

In reality, the size spectrum is an emergent property of many individual-level processes: feeding, growing, dying, reproducing, and moving in space and time. These processes are stochastic and can be represented through the use of individual-based models (IBMs), which describe a set of rules and events that affect individuals. IBMs focusing on the processes of size-based predation driving growth and death have been used to model the community size spectrum and produce emergent size spectra that are broadly consistent with the Sheldon expectation of an abundance size spectrum slope of -1 when taken as an average across many stochastic realizations [9,30]. More detailed IBMs have introduced greater complexity through representation of species-specific or functional traits and, to accommodate this, use cohorts or groups of individuals as agents to predict emergent size spectra [9,30]. A powerful use of IBMs formulated with stochastic size-based processes has been to derive simpler **size spectrum models** (SSMs) that capture the processes of an average individual based purely on

Glossary

Ecological pyramids: graphs of relative abundance or biomass across trophic levels in ecological communities [1].

Functional trait: a measurable property of an individual organism, sometimes aggregated to the species-level, that influences its ecological role or performance.

McKendrick–von Foerster equation: continuous first-order partial differential equation that models changes in abundance at size or age through time. Originally implemented for age-structured dynamics, it was later applied to the size spectrum and subsequently adapted to model fluxes of food-dependent growth and mortality by representing size-based predator and prey interactions through the use of a distribution of preferred predator-prey mass ratios.

Predator prey mass ratio (PPMR): ratio of predator to prey mass measured at the individual level. At the community level, PPMR is the average mass of predators at trophic level n divided by the average mass of their prey at trophic level $n-1$. Observed PPMR from dietary data is referred to as realized. In contrast, models are parameterized with preferred PPMRs, which are used in combination with prey size availability and predator search rates to predict realized diets.

Size spectrum: the size distribution of all individuals in a community or ecosystem according to numerical abundance (abundance size spectrum) or biomass (biomass size spectrum) (y axis) across size classes (x axis) typically on log axes. A normalized size spectrum converts the biomasses or abundances to densities by dividing them by the width of the size classes.

Size-spectrum models: deterministic continuous time models that explicitly predict changes in the size spectrum through time, starting with size-based, individual-level mechanistic processes. Different levels of complexity can be represented in size spectrum models. Community SSMs only consider differences in size, ignoring differences between species. The community size spectrum can be derived from the trait-based and food-web models by integrating over all trait classes or summing over

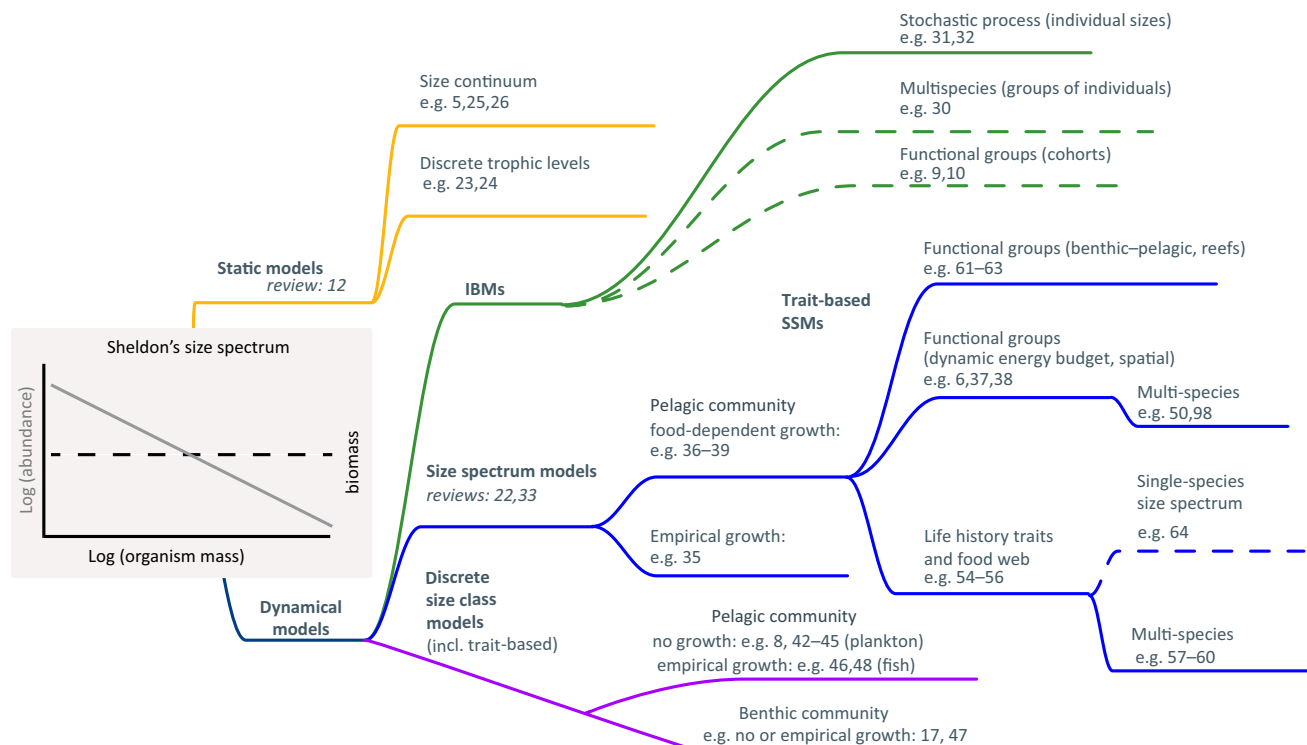
size and to assess how well these capture the mean across many stochastic realizations [31,32].

SSMs

SSMs are dynamic deterministic models that explicitly predict changes in the size spectrum through time, starting with size-based, individual-level mechanistic processes (see [22,33] for reviews). At the core of this modeling approach is the **McKendrick von Foerster (MF) partial differential equation** that is modified to represent a distribution of sizes rather than ages. The first dynamic size spectrum models represented open-water (pelagic) systems, focusing on how gains through growth and losses through respiration or predation propagated along the size spectrum through time [34,35]. SSMs proliferated following a pivotal study that resolved the food-dependent growth and mortality component, provided an analytic solution to the size spectrum slope, as well as demonstrating how it changed with fishing [36]. SSMs track the changing abundance of individuals at size through time as a function of fluxes due to growth and mortality with a renewal term at smallest sizes that represents the birth rate of new offspring. Feeding rates are a consequence of size-dependent prey availability, encounter rates, and ontogenetic changes in the preferred prey size and range (Box 1). Prey size selection is specified from the distribution of the preferred PPMR. SSMs have been extended to include more detailed processes such as energy allocation to reproduction, spatial processes, and seasonality [37–40]. In the absence of any fishing, SSMs produce abundance size spectrum slopes close to -1 , conforming to Sheldon's conjecture of near equal biomass across logarithmically binned body mass classes. In contrast to the static scaling models, predicted size spectra from SSMs on a log-log plot can exhibit nonlinear patterns such as truncation at

species. Trait-based SSMs represent differences among species through the strict use of functional traits (e.g., offspring, maturation, and asymptotic sizes) rather than species groups.

Slope of the size spectrum: the slope of a straight line fitted through the size spectrum on a log-log plot, which is also the exponent from a power law fit to the size spectrum on linear axes. A slope of $b=0$ of the biomass size spectrum conforms to Sheldon's [11] original conjecture that biomass is distributed equally across logarithmically binned size classes which equates to a slope of $b-1$ for the biomass density size spectrum (normalized by dividing by size class widths). Similarly, the abundance size spectrum slope is $b-1$ and $b-2$ when it is an abundance density (by dividing by size class widths).



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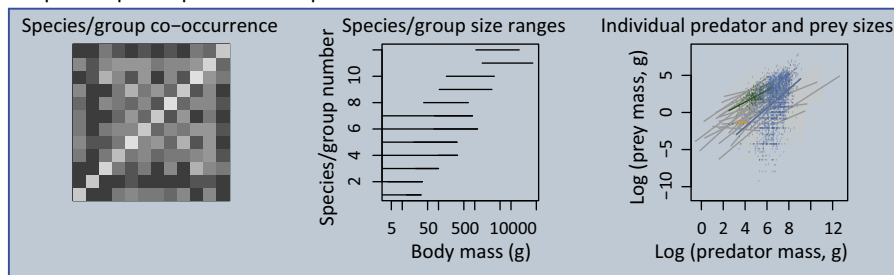
Figure 1. How to Model the Size Spectrum? Taxonomy of the different types of approaches that have been used to model the community size spectrum, highlighting key references and reviews (italics). An expanded reference list for each model type is given in the Supplemental Information. Abbreviations: IBM, individual-based model; SSM, size spectrum model.

Box 1. How Can Ecological Data Inform SSMs?

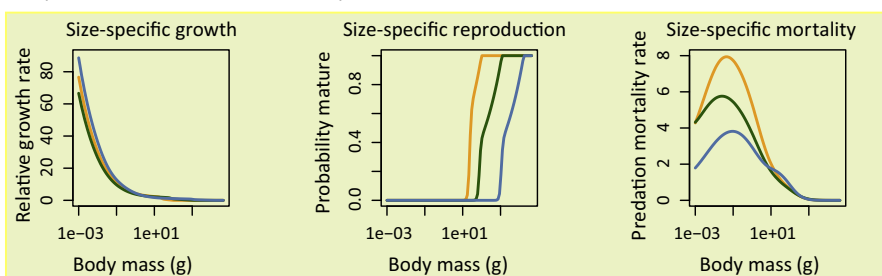
SSMs scale individual-level processes up to ecosystem structure and dynamics. Here, we illustrate in three steps how species and size-specific data can be used to develop a multispecies or functional size spectrum models (Figure 1).

Step 1. First, species-specific and individual-level data that can be used to parameterize SSMs include: spatial or habitat co-occurrences of species; groups or size classes (example data from [52,57]); information on offspring, adult and asymptotic sizes (example data from [3]); and individual-level PPMRs (data from [96]). Three contrasting species, embedded within the community size spectrum, are shown in orange, green, and blue. Step 2. Once parameterized, an SSM can be set up using an initial size spectrum at the first time step [52]. At each time step, species- and size-specific rates of feeding and energy allocation into maturation are calculated. These are then used to predict individual food-dependent, size-specific growth, mortality, and reproductive rates. Growth and mortality rates determine the fluxes of abundance in and out of each size, and new offspring enter the size spectrum of each species at its smallest size. Step 3. Because the growth, mortality, and reproduction depend on the abundance of predators and prey in each time step, the predicted changes in abundance at size through time are solved numerically by looping through time steps until an equilibrium is reached. The numerical density (N) at body mass (w) for each group or species is summed across all groups to give the normalized size spectrum. These are outputted at each time step along with predicted changes in size-specific growth, reproduction, and mortality rates. Changes in the size spectrum slopes can be calculated by fitting, at each time step, a straight line through the predicted size spectrum if plotted on a log-log plot or alternatively by fitting a power law if estimating exponents. Predicted changes in individual level (Step 2) and population and community level (Step 3) properties can then be confronted with empirical data for comparison or repeating the above process in conjunction with a statistical procedure to formally estimate parameters and their uncertainty (Box 3).

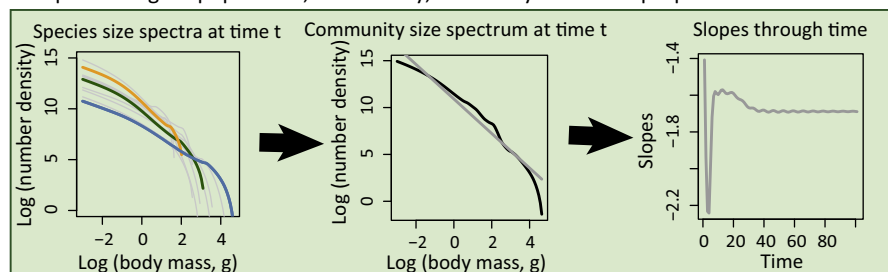
Step 1: Empirical patterns and parameters



Step 2: Predicted individual-level processes



Step 3: Emergent population, community, and ecosystem-level properties



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Figure 1. Example Showing Three Steps for Building an SSM That Involve Linking Empirical Patterns (Step 1) to Individual (Step 2) and Population and Community Level Predictions (Step 3).

the largest body masses and time-varying oscillations that propagate through the size spectrum (travelling waves) [31,41].

Discrete Size Class Models

SSMs focus on size-dependent predation as the key process linking growth, death, and reproduction. However, processes other than predation, such as nutrient uptake and intake rates of filter feeders can be modeled as size dependent processes. For instance, nutrient uptake scales with cell size for phytoplankton [42], and this has been used to model nutrient and light fixation and thus photosynthesis by unicellular phytoplankton [43]. These models usually include discrete size classes where changes in abundance through time are from birth and death processes and where individuals do not grow in size (similar to a species-based allometric food web model) [8,44,45]. For organisms that do grow in size (e.g., fish and benthic invertebrates), discrete size class models often use empirical growth relationships [46–48], based on the assumption that growth is not strongly food dependent; contrary to the assumptions of most (but not all, e.g., [35,49]) SSMs where both growth and predation are linked to size-based feeding.

Trait-Based SSMs: Including Other Functional Traits

Perhaps the biggest leap in the development of SSMs has involved blurring the distinction with species-based food web models. Trait-based SSMs resolve species-specific traits through asymptotic maximum size and size at maturation, and allow species-specific interactions [50–52]. Even with this added layer of complexity, these models predict an overall community size spectrum that is consistent with simpler models, but also provide a size spectrum for each species (Box 1). This advance makes SSMs similar to physiologically structured population models but capable of resolving the complexity of food web models through the use of traits [4,50,51,53]. Increasing trait diversity in the SSMs has the effect of stabilizing complex ecological communities [54–56]. Multispecies extensions of the trait-based model have enabled real-world ecosystem applications in combination with extensive species-specific trait data for parameterization [57–60] (Box 1). Although trait-based models have so far focused on fish communities they also include a background resource size spectrum, which implicitly represents the plankton community as a series of discrete size classes that do not grow in body size [51] and thus are partial representations of ecosystems.

Despite the ubiquity of size-based processes in pelagic ecosystems, not all processes and communities are size based. SSMs have moved beyond pure pelagic communities and towards greater ecosystem coverage by representing different communities and functional groups; some of which are not size structured [61,62]. The benthic community receives much of its energy flow directly from detritus fall (sinking rates are size based) from the pelagic ecosystem, but once there, the widely flexible scavengers can feed on both pelagic and benthic components. However, intake rates of filter feeders and scavengers still scale with body size. The latter can still be modeled with SSMs, but by relaxing the prey size selection assumption where individuals of different sizes compete for a shared unstructured resource [61]. For example, on coral reefs, large herbivorous fishes compete in a size-based manner for non-size based resources such as macroalgae [63]. Dynamic size spectra of organisms that share energy in this way tend to have shallower and more variable size spectra than those that follow ‘big eat small’ rules. The use of functional groups can help to resolve size-dependent spatial movement and habitat use embedded in SSMs [7,38,39]. For example, [38] breaks the pelagic ecosystem into epipelagic, mesopelagic, and migratory communities, and includes both vertical and horizontal movement of individuals, which affects their vulnerability to predation. Habitat structural complexity and size-dependent hiding is an important feature that affects prey vulnerability on coral reefs and influences emergent predictions of size spectra that are consistent with observations across a gradient of habitat complexity [63].

Limitations of SSMs

Despite the utility of SSMs, they have several limitations, some of which are inherent, and others are challenging and slowly being overcome. First, SSMs are not always well suited to address questions relating to single-species population dynamics, especially where food is unlimited and where predation mortality is less important – two key processes in SSMs. Many population dynamic models are applied to well-studied species, where parameter values for key processes and life stages are relatively well known, making SSMs unnecessary (although see [64] for their utility in data-poor cases). Second, when ontogenetic variation in body size is small (e.g., in seabirds [65]) simpler unstructured, stage-structured, or allometric models (that use a mean body size) are likely to be more appropriate than SSMs [4,66]. Third, SSMs have generally been applied at regional and larger spatial [57,67,68] scales, and might not be as appropriate at finer scales [33]. Many management-related questions need to be addressed on a local scale where the community dynamics might be well understood in terms of species and habitat interactions [69], and the size-dependent nature of these interactions are nuances rather than key drivers of the dynamics. Having said this, recent work has shown that output from a functional group SSM applied on coral reefs, where species-based food web descriptions were lacking, compared well with data at local scales [63]. The appropriate spatial scale for applying SSMs is still an open question and requires more detailed cross-scale tests of theory to resolve. Last, SSMs have focused on taxonomic subsets of the size spectrum (e.g., plankton and fish communities; Box 2) and therefore have only achieved partial ecosystem coverage so far. However, by bringing together different strands of size-based modeling this issue can be addressed. The functional size spectrum framework shown in Figure 2 builds upon the trait-based approach by combining alternative model structures (including non-size based ones) and could form the basis of size-based ecosystem models that resolve the dynamics of important microbial, plankton and nekton functional groups, all the way up to marine mammals and seabirds. We expand on this and other research opportunities below.

Beyond Bacteria to Whales: Future Research Directions for Size-Based Ecosystem Models

Despite SSMs not having been fully developed all the way from bacteria to whales, in many respects, the recent achievements of size-based models extend beyond Sheldon's initial vision for describing the size spectrum (Box 2). SSMs are being used to examine: spatial distributions of abundance [6], species interactions [57], diversity-stability links [55], eco-evolutionary processes [70], and consequences of human-induced and environmental change [68,71,72]. Here, we highlight four promising research innovations that will help us realize the full potential and wider generality of this approach for modeling whole ecosystems.

Beyond One Size Fits All: Unifying Models through Functional Traits

The simple rule of size-based prey selection has proven useful for understanding the structure and dynamics of communities but one size-based rule will not universally fit all organisms with life-history, morphology, habitat, and behavioral traits all affecting realized food web interactions [73]. For example, marine mammals illustrate how technological innovations enable different size-based strategies to maximize energy intake. Baleen plates and the ability to forage over large spatial scales (also dependent on large body size) allow baleen whales to feed down food chains and exploit highly productive but patchy plankton and nekton. Similarly, echolocation enables beaked whales to extend their prey detection range and forage selectively on larger, energetically richer, but more sparsely distributed prey compared to seals of similar body sizes that are constrained to forage on smaller but more predictably distributed prey [74]. Differences in size-based rules also apply to species of zooplankton (e.g., salps [75]), fish (e.g., sunfish), sharks (e.g., whale sharks [76]), and seabirds ([65]).

Box 2. How Are SSMs Models Being Used?

A synthesis of 75 papers published on since 2010 (Supplemental Information) illustrates that the different types of size-based models (Figure 1) collectively cover a size range of >20 orders of magnitude (Figure 1). However, there are no models that span this entire range (Supplemental Information). Only 13 of the 75 papers explicitly capture the dynamics of more than one functional group. Furthermore, none of the 75 papers resolve the size classes dominated by bacteria and none explicitly capture the dynamics of marine mammals or seabirds.

Fish and fisheries studies dominate both in terms of focal taxa and the characteristic size range (Figure 1A) covered by dynamic models, even though there are more plankton empirical studies (Figure 1B, see Supplemental Information). Of these studies, 44 studies have used SSMs and 37 of these have used them to investigate the ecosystem consequences of fishing intensity and selectivity, marine protected areas, climate change, patterns of biodiversity, and structural habitat loss (Figure 1C, Supplemental Information). These recent studies include real-ecosystem applications spanning from the global ocean [6] to local coral reefs [63]. Fishing applications are most numerous among these. Reductions in the empirical slopes of fish community size spectra have been attributed to the removal of large-bodied individuals (and release of their smaller prey) through fishing [97]. These features of exploited marine ecosystems have led to some of the key developments of dynamic SSMs to provide a theoretical framework for the use of size-based indicators to monitor the ecosystem effects of fishing [22]. From a conservation and management viewpoint, a key advantage of the size-based approach is that predictions can be compared to modeled unexploited size spectra under changing environmental conditions, rather than relying solely on historical baselines that may not be relevant under current or future environmental conditions [29]. The application of SSMs in this context can also include analysis of how several changing input variables – including primary production, temperature, and fishing mortality rates – affect predicted changes in abundance, biomass, production, slopes, or other outputs.

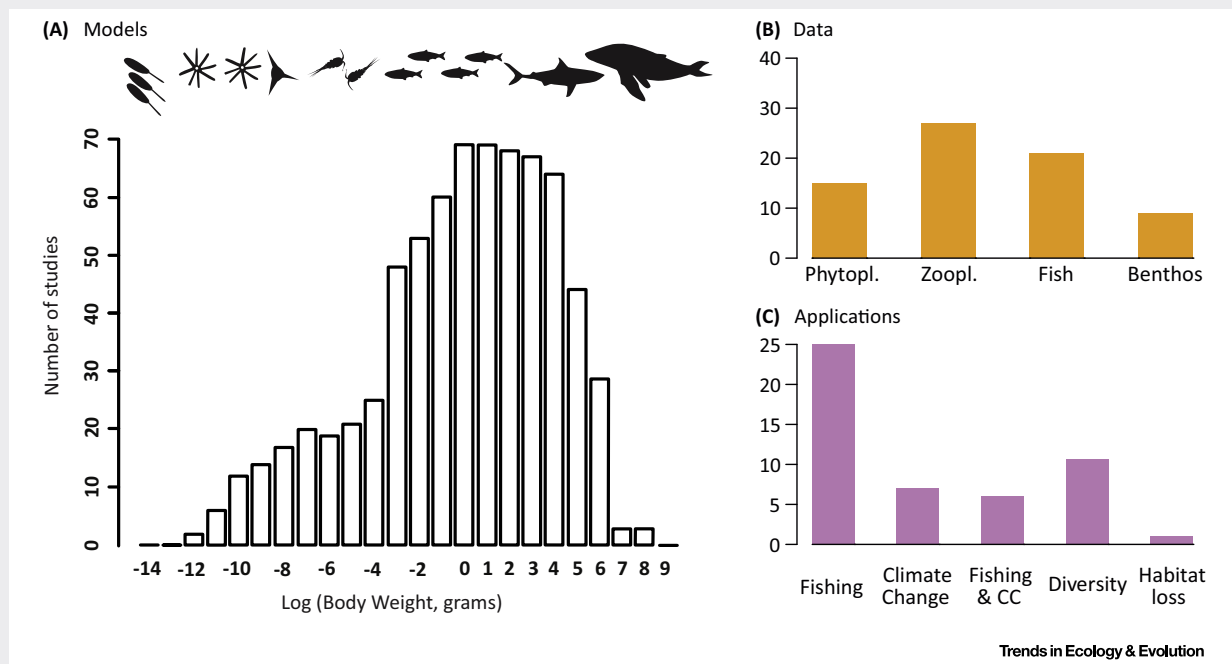
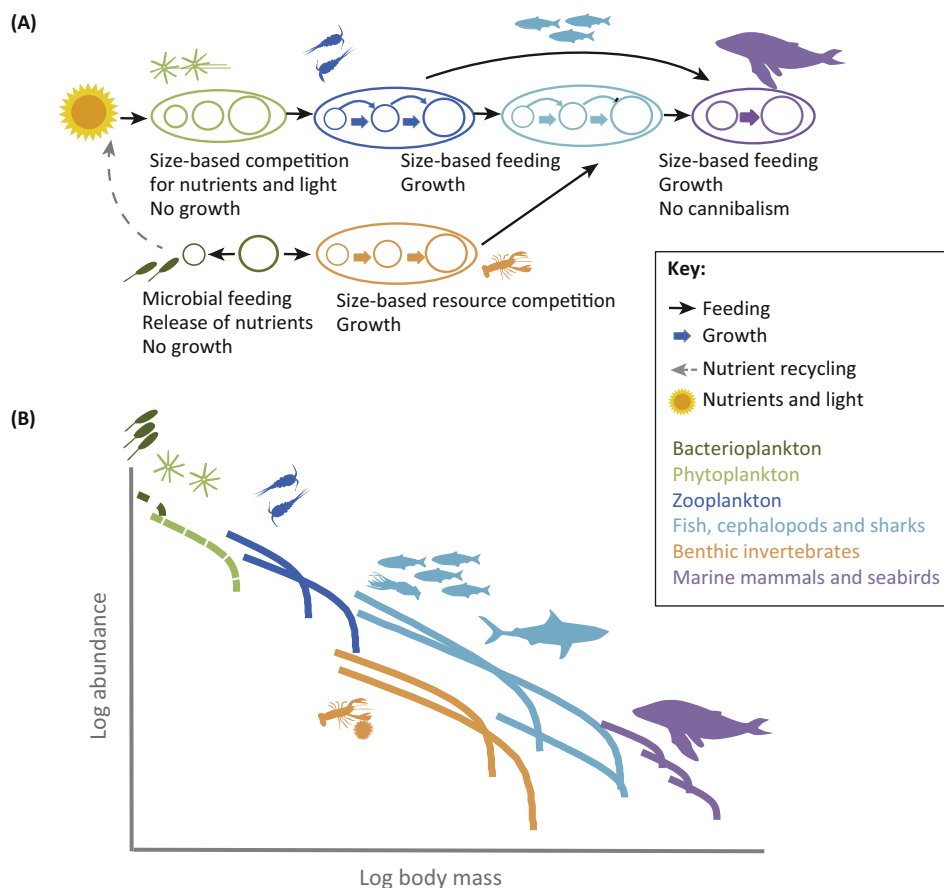


Figure 1. Synthesis of SSM Size Spectrum Studies Published in the Last 5 Years (details and keyword search terms are provided in the Supplemental Information). (A) Number of modeling studies that explicitly represent size classes spanning bacteria to whales. (B) Number of empirical size spectrum papers published for different focal communities. (C) Number of different types of size-based ecosystem model applications. Abbreviations: CC; climate change; Phytopl.; phytoplankton; Zoopl.; zooplankton.

These differences are not exceptions, but rather demonstrate that one size does not necessarily fit all. Most organisms have a distribution of prey size preference bounded by a minimum and maximum size [1]. In SSMs, as long as the size preference is known, then the feeding function can be adapted for different types of feeding [59,77]. This is powerful; it means that a size spectrum framework becomes more generalizable through greater flexibility in these functional traits. Even organisms such as parasites can be represented as they follow a ‘reverse size rule’ that means they feed on larger organisms but still have a minimum and maximum size for hosts [78].

Currently, there is limited cross-fertilization between plankton-focused and higher trophic level size-based models, but realistic coupling to plankton is recognized as a key uncertainty in higher trophic level models [5]. For these higher trophic level models, plankton dynamics are



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Figure 2. Functional Size Spectrum: An Illustration Applied to a Conceptual Marine Ecosystem from Bacteria to Whales. (A) Stylized size-structured ecosystem model emphasizing different processes across the size spectrum. Larger circles are used to illustrate relative changes in size within functional groups. Black arrows illustrate the presence of feeding within and across groups but do not show the full extent of the many feeding links present in size spectrum models. Thick colored arrows represent growth in size. (B) Hypothetical emergent size spectra for the same types of functional groups shown in A but here represented via life history traits depicted by differences in offspring and adult asymptotic sizes [3].

usually assumed to be: (i) static [36]; (ii) modeled as a discrete size classes (without fluxes of growth through the size spectrum) [79]; or (iii) externally forced [6,72,80]. Externally forced plankton inputs are often derived from satellite estimates [5] or coarsely size-structured Earth systems or regional biogeochemical models [49], rather than being explicitly linked to phytoplankton and zooplankton size spectrum dynamics [81] or emerging plankton trait-based models [82]. To improve ecosystem coverage and feedbacks, there is much scope for better integration of dynamic SSMS already in use in different parts of the size spectrum.

Formulating ecosystem models as functional size spectra overcomes some of the limitations of purely size- or species-based approaches and also has other advantages. First, most components are likely to have some features that are size dependent. For example, although seabirds and seals do not have large variation in individual sizes they still exert strong prey size selectivity on fish communities [59], and have search and intake rates that scale with body size. Second, size- and trait-based parameterization of food webs can help to constrain parameters and reduce uncertainty in complex models (Box 3). A functional size spectrum approach also has the potential to be expanded to some terrestrial food webs, where interest in individual

Box 3. Predicting Ecosystem Structure and Function in an Era of Rapid Change: Managing Uncertainty

Data are needed to parameterize and test SSMs to apply them to real ecosystems and assess how accurate their predictions of ecosystem structure and function are (Box 1). Because SSMs are computationally inexpensive relative to more complex ecosystem models, there could be scope for the development of SSMs as real-time observational models. Predictions from models could be combined with data collected at different scales or organizational levels ranging from individual growth rates, tagging data, species or community biomass, and abundance or large fisheries catches [57,72,98]. More research on the level of complexity needed to accurately capture ecosystem function and dynamics without inflating uncertainty is needed.

Models have been confronted by data in different ways: qualitative comparisons with size spectrum slopes from the relevant part of the size spectrum and more quantitative assessment of models by calibrating and fitting them to data. Calibrating the model with earlier observations and then assessing model skill by comparing time-series of predictions with later observations is an approach that is being used for size spectrum modeling [57,58,60].

Uncertainty also comes from our imperfect knowledge about what drives the structure of ecosystems. This is especially critical in ecosystem models, where different models make different assumptions and prioritize species identity over size (or vice versa) in how individuals interact. Model intercomparisons [99,100] enable these approaches to be considered in a wider context and such broad uncertainties are being tackled through their use as part of ecosystem model ensembles. Tools to formally integrate data and assess parameter uncertainty are beginning to be used in conjunction with SSMs and data. One advantage of the Bayesian framework is that it can account for the effects of parameter and observational uncertainty on model outputs, by presenting these outputs probabilistically. This allows a more informed assessment of the uncertainty and associated risk of using modeled outcomes for management decisions and for identification of which sources of uncertainty matter the most [48,56,60]. The latter is particularly useful for prioritizing data needs.

body size distributions has increased in recent years [83,84], and where the manner in which individual-level processes scale up to ecosystems is beginning to be explored [9].

Beyond Slopes: Testing Predictions with Observed Size Spectra

Clearly, SSMs have come a long way, but do we actually have the data to assess whether or not they can predict abundance and biomass all the way from bacteria to whales in an integrated fashion? While empirical size spectra studies are numerous (for reviews, see [13,84]), a key limitation of SSMs is that model skill assessment is difficult across the entire ecosystem. This is because technology has limited data collection to taxonomically defined communities or habitats due to the challenges of a huge variety of sampling platforms to observe bacteria and plankton (bottle samples, small nets, and optical counters), fish (trawls and acoustics), mammals (visual or acoustics), reefs (visual census), and benthos (grabs and cores). It is clear that we need better integration of whole ecosystem data and models, from accurate representation of underlying individual processes to more detailed tests of their predictions.

While there is consistency in the prediction of steady state size spectrum slopes across several models, both modeled and observed size spectra can exhibit nonlinear patterns. Different hypotheses have been proposed to explain lumpy (nonlinear) patterns in size spectra, including habitat complexity [63,85], omnivory [86], smaller PPMR, and narrower range of prey sizes [41], and dynamic seasonal or longer-term cycles [40,77]. Dynamic oscillations (travelling waves) have been shown to arise due to changes in parameters (such as PPMR) or through perturbations such as size-selective fishing [62,71,87] or bottom-up disturbances [62,88] that affect the stability of size spectrum. Temporal variation around a time-averaged size spectrum can have important consequences for ecosystem services, such as fisheries stability. In contrast, individuals hiding in size-structured refugia, such as coral reef crevices [63], produce lumpy size spectra that are beneficial for survival rather than evidence of oscillations or instability. Empirical examples show lumpy zooplankton size spectra in productive coastal eddies result in older and larger larval fish due to increased food availability and hence survival [89]. Under different environmental conditions, it is likely that there are multiple causes of nonlinear patterns and

variability in the size spectra that emerge at different time and space scales, but these have yet to be tested in a systematic and inclusive way.

Beyond Fixed Traits: Extinctions, Invasions, and Evolution

A fundamental area of ecological research involves understanding how the loss of a species affects biodiversity throughout the food web [4]. Although early SSMs ignored species identity and were viewed as too simple to represent biodiversity, recent work suggests that SSMs could hold considerable promise in biodiversity research. In addition to representing functional diversity (species, traits, and functional groups), SSMs have been extended to explain patterns in size-based diversity (diversity size spectrum; [90]). From these models, empirically observed macroecological patterns such as species richness versus body mass emerge. Whether or not this theory holds across different types of ecosystems warrants investigation.

Coexistence and persistence of different species and functional groups is affected by how density dependence and competition are incorporated into models [91]. Changes in phenotypic and genotypic plasticity also affect coexistence, and have recently been incorporated into SSMs examining species invasions, community assembly, and adaptive dynamics [70]. Given the large redistribution of species under climate change, advances that enable species composition and traits to change and evolve provide a framework for exploring the emergence and evolution of novel communities and trait distributions.

Beyond Fishing and Warming: Multiple Stressors and Their Interactions

A key strength of applied SSMs has been the ability to test joint and marginal effects of fishing and climate change on the size spectrum. In terms of fishing, until recently, human–natural ecosystem interactions have involved simplified representations of fishing as an impact by including a size and gear and/or species-dependent mortality term. The role of economic and behavioral drivers such as the technological development of fisheries, affecting the efficiency to catch fish, is beginning to be tackled through more detailed consideration of the two-way feedbacks between humans and size-structured ecosystems [49,92].

Two of the biggest missing stressors in the context of climate and environmental change include effects of acidification and disease outbreaks. Given the expected incidence of acidification and disease outbreaks under global warming, we need a better understanding of how these stressors operate at the individual level before incorporating them in SSMs. Incorporating a wider range of stressors into the size-spectrum modeling framework could enable initial assessments of cumulative ecosystem impacts to be made, as well as better integration with empirical size spectrum studies where stressors such as temperature, nutrients, pollution, and pH have been studied across gradients in natural and controlled experimental aquatic ecosystems [93,94]. Development of theory in this area could focus on understanding physiological mechanisms controlling size-dependence of performance and stress responses and, in the case of disease, susceptibility and immunity. A first step could be to combine modeled experimental and observational systems to test hypotheses of multiple stressors.

Concluding Remarks

Size-based community and ecosystem models are being applied to a wide range of ecosystems to investigate structure and function, biogeochemical cycles, as well as the impacts of climate change, habitat loss, and fishing but there are still Outstanding Questions. Nevertheless, Sheldon's vision of considering the marine pelagic ecosystem from bacteria to whales has motivated 50 years of both empirical and modeling work on size spectra. His vision has largely been realized, and expanded; we have SSMs that go from sizes of phytoplankton to whales, and even include benthic systems. However, other key components of marine ecosystems

Outstanding Questions

How can functional traits be used to improve the representation of the microbial loop, parasites, plankton, marine mammals, and benthic communities?

What are the most important traits that confer ecosystem stability?

How well does the output from SSMs agree with data on the structure, function, and dynamics of ecosystems?

How can we confront SSMs with observed size spectrum data to test different hypotheses that could explain nonlinearity?

How can we best represent phenotypic and genotypic plasticity in SSMs?

How can we model changes in species composition for exploring extinction, invasions, and evolution of novel communities?

How do we include impacts of acidification and disease epidemics in SSMs?

How do we best include multiple stressor interactions in SSMs?

have either not yet been tackled or are only superficially treated. The roles of bacteria and viruses in the microbial loop, which lead to nutrient recycling and enhance trophic efficiency in the food web, has yet to be integrated into SSMs. Furthermore, diseases and parasites, which are increasingly recognized as important components of marine systems [95], have not yet been tackled. Finally, the largest animals, the baleen whales, which feed on much smaller animals than themselves, have only been implicitly represented in SSMs so far (but, see [9]).

By using functional size spectra and trait-based approaches, we have the tools needed to model whole ecosystems. Although early models ignored species identity, SSMs can now capture species traits and functional groups, suggesting that further development and unification of approaches across the size spectrum is likely to result in a wider range of ecosystem and biodiversity applications in the near future. By showing the diverse applications and emerging approaches that allow us to tackle the entire ecosystem, we hope this review stimulates wider consideration of size spectrum models in ecology.

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