Canadian Journal of Fisheries and Aquatic Sciences
Journal canadien des sciences halieutiques et aquatiques

The theoretical foundations for size spectrum models of fish communities

Journal:	<i>Canadian Journal of Fisheries and Aquatic Sciences</i>
Manuscript ID	cjfas-2015-0230.R2
Manuscript Type:	Review
Date Submitted by the Author:	16-Nov-2015
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Keyword:	MARINE < Environment/Habitat, COMMUNITIES < General, ECOSYSTEMS < General, MODELS < General

1 **The theoretical foundations for size spectrum models of fish**
2 **communities**

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9
10 **Abstract**

11 Size spectrum models have emerged from 40 years of basic research on how body size
12 determines individual physiology and structures marine communities. They are based
13 on commonly accepted assumptions and have a low parameter set, which make them
14 easy to deploy for strategic ecosystem oriented impact assessment of fisheries. We
15 describe the fundamental concepts in size-based models about food encounter and the
16 bioenergetics budget of individuals. Within the general framework three model types
17 have emerged that differs in their degree of complexity: the food-web, the trait-based
18 and the community model. We demonstrate the differences between the models
19 through examples of their response to fishing and their dynamic behavior. We review
20 implementations of size spectrum models and describe important variations concerning
21 the functional response, whether growth is food-dependent or fixed, and the density-
22 dependence imposed on the system. Finally we discuss challenges and promising
23 directions.

24
25 **Key words:** Ecosystem approach, food-web, ecosystem based fisheries management

26 Introduction

27 Marine community models range from the original Lotka-Volterra differential equations
28 to extremely complicated end-to-end simulations (Plagányi 2007; Fulton et al. 2011). In
29 the middle of the range we find size spectrum models. Size spectrum models use body
30 size of individuals to represent the entire fish community as a size distribution. The
31 reliance of body size simplify the description of predator-prey interactions, individual
32 physiology and vulnerability to fishing gear. This paper highlights one of the important
33 advantages of the size spectrum approach: a well-founded and unifying mechanistic
34 basis allowing for great explanatory power and parsimonious use of data.

35

36 Size spectrum models are relevant to fisheries science in the context of the ecosystem
37 approach to fisheries management (Pikitch et al. 2004). While single-species stock
38 assessments and impact assessment will continue to be important management tools,
39 they need to be supplemented by strategic impact assessments at the level of the
40 ecosystem. Such impact assessments assist the development and implementation of
41 strategic long-term management goals for the ecosystem, e.g., how should fishing
42 pressure be distributed over the entire ecosystem? How do we balance exploitation of
43 competing fisheries such as forage fisheries and consumer fisheries? How do we
44 maximize the yield (of biomass or wealth) of the entire ecosystem while minimizing risk
45 of failure or impoverish components of the system under environmental change? To
46 answer these questions, we need to quantitatively understand the relationship between
47 fishing practice (what, when and how much) and the abundance of species and sizes of
48 organisms throughout the community.

49

50 Size spectrum models are especially suited to these questions because they resolve the
51 most important aspects of fish life history and trophic ecology. A key characteristic of fish is
52 that individuals grow through several orders of magnitude in body size through their

life. This, combined with the strong relationship between body-size and trophic niche (Barnes et al. 2008; Gilliam et al. 2011), means that individuals change their trophic niche throughout ontogeny (Werner and Gilliam 1984). Such ontogenetic trophic niche shifts makes it difficult to apply the conventional food-web approach, where each species is described by a single metric (abundance or biomass) and a specific trophic level, to fish communities. The relation between body size and trophic niche has prompted the hypothesis that individual body size (rather than species identity) is the primary determinant of community structure (Jennings et al. 2001).

Size spectrum models are based upon the long tradition in ecology of recognizing body size as a central trait to describe individuals (Elton 1927; Haldane 1928; Andersen et al. 2016a) because it correlates strongly with: metabolism (Kleiber 1932; Winberg 1956, Brown et al. 2004), predator-prey relations (Ursin 1973; Barnes et al. 2008), encounter rates (Acuña et al. 2011), functional responses (Rall et al. 2012), reproductive effort, and other vital rates (Peters 1983). For application to fisheries, body size furthermore is an excellent descriptor of mesh-size regulations and characterizes the value of a catch (Andersen et al. 2015). Finally, distributions of abundance vs. size show a remarkable regularity (Sheldon and Prakash 1972; Sheldon et al. 1977; Boudreau and Dickie 1992) and deviations from this regularity has been used to characterize ecosystem level impact of fishing (Rice and Gislason 1996; Daan et al. 2005). The size spectrum modeling paradigm promises a “charmingly simple” (Pope et al. 2006) set of tools with a low to intermediate complexity that can be readily deployed for a given system and provide quantitative information about the ecosystem impact of fishing (Collie et al. 2014). This makes it possible to apply the models in situations where more complex but also data-demanding end-to-end models cannot be employed either because of lack of data or manpower to calibrate and run them.

The various types of size spectrum model can be viewed as different developments of the same core concepts. We review the common basic concepts behind size spectrum models focusing on models that describe an entire fish community. Among them we recognize three broad classes of decreasing levels of complexity. Most complex are the 'food-web' models, so called because they explicitly represent individual populations with species-specific energy budget parameters and prey preferences, thereby quantifying a network of trophic interactions as an explicit food-web. These are simplified into the 'trait-based' models by reducing differences among the populations to a single continuous variable representing a trait (usually maturation size) and simplifying prey selection to a fixed predator-prey body size ratio. Further simplification produces the 'community' size spectrum models, so called because they ignore differences among populations thereby representing the community as a single population of interacting individuals that differ only in their body-size. We explain how the simpler models can be derived from the more complex, starting from the food-web and ending with the community model. Further we develop analytical "equilibrium" solutions to the models. We illustrate the models' behavior, in particular their response to fishing, and finally discuss challenges and open issues for further development.

Concepts underlying size spectrum models

Size spectrum models are founded on three common concepts: First, biomass (and equivalent energy) is conserved, enabling accountancy of energy flows at the community level based on individual level processes. Second, trophic interactions are the main determinant of community structure and these are foremost determined by predator-prey size ratios. Third, the energy budget of an individual is allometrically linked to body size, so that body size can be used as a key identifier of organisms and their interactions with the community. The three main ecological processes for any organism are growth, reproduction and mortality and all three can be linked to body

size in this modeling framework. This simplification has great strategic value as it enables ecological measures such as production rate and size structure (which are important for ecosystem based fisheries management) to be derived from relatively little and accessible data about physiology and life history invariants. The equations for the models used in the examples to follow are provided in Table 1 and parameters in Table 2.

The size spectrum

The size spectrum represents abundance or biomass of individuals as a function of their body size. In this context 'body size' usually means body mass because it is the natural metric to formulate an energy budget.

Three size spectrum representations are common in the literature (Sprules and Barth, this issue; Andersen and Beyer 2006; Rossberg 2012): the abundance density spectrum, the biomass density spectrum and the "Sheldon" biomass spectrum. The abundance density spectrum $N(w)$ represents the number of individuals in the body mass range from w_1 to w_2 as $\int_{w_1}^{w_2} N(w) dw$, and here it is referred to as the size spectrum for brevity. It can be constructed from observations by dividing the total number of individuals in a size class by the width of the size class and therefore has dimensions of numbers per mass (often referred to as the "normalized size spectrum"; Sprules and Barth, this issue). The biomass density spectrum is constructed from the abundance density spectrum by multiplying with body mass $N(w)w$ (dimensions biomass per mass). The "Sheldon" biomass spectrum (Sheldon and Parsons 1967) is the biomass in logarithmically wide classes, i.e., the biomass in the range w to cw where c is a constant larger than one determining the width of the size class. For example, the "octave" bin used by Sheldon implies $c = 2$, and normal log10 base implies $c = 10$. If we assume that the abundance density spectrum follows a power-law $N(w) = \kappa w^\lambda$ within the class then

the biomass spectrum can be found as:

$$B_{\log}(w) = \int_w^{cw} N(\omega) \omega \, d\omega = \kappa \frac{c^{2+\lambda} - 1}{2 + \lambda} w^{2+\lambda} \propto w^2 N(w),$$

where ω is a dummy variable for the integration. All terms except $w^{2+\lambda}$ are independent of size, hence the biomass spectrum is proportional to the number density spectrum multiplied by the body mass squared. For mathematical analyses the density spectra are convenient because integrals over these give the abundance and biomass. For presentation purposes the Sheldon biomass representation $w^2 N(w)$ is convenient because, at the community level, it shows how the biomass of prey is distributed with size (assuming that the size range of preferred prey is constant), and on a species level it is proportional to the cohort biomass.

Conservation equation

The size spectrum is calculated by considering a balance between mortality and growth at all body sizes (w). Individuals flow into size classes via somatic growth whilst some are lost to natural and fisheries mortality. This balance is formalized by the McKendrick-von Foerster equation (see Silvert and Platt (1978) for a derivation):

$$\frac{\partial N_i(w)}{\partial t} + \frac{\partial g_i(w) N_i(w)}{\partial w} = -\mu_i(w) N_i(w), \quad (1)$$

where $g_i(w)$ is the growth rate (mass per time) and $\mu_i(w)$ the mortality (per time), and $N_i(w)$ is the size spectrum of species i . Thus eq. (1) scales from individual-level processes of growth and mortality to the population-level size spectrum. Recruitment from the population flows into the size spectrum at the smallest body size (typically the egg size) w_0 . This is represented as a boundary condition:

$$g_i(w_0)N_i(w_0) = R_i, \quad (2)$$

where R_i is the recruitment (number of recruits or eggs per time). The above two equations are mathematical formalizations of a mass balance, and can be thought of as the size-based version of classic survivor analysis used in age-based models.

The following outlines the central assumptions in the models about how growth g_i , mortality μ_i and reproduction (recruitment) R_i , are calculated. With the partial exception of recruitment these are all calculated from individual level processes of predator-prey encounter and a bioenergetic budget (Figure 1).

The Andersen-Ursin encounter model

The key process in the models is predator-prey encounters between individuals governed by a formalization of the general rule, bigger fish eat smaller fish (Andersen and Ursin 1977). Individuals prefer prey a certain fraction smaller than themselves (M1, Table 1) (Ursin 1973). The clearance rate (dimensions time⁻¹) is an increasing function of body size (larger fish clear a larger volume of water for prey per time than small fish) (M2). The combination of preference, clearance rate and prey abundance specifies the food encounter rate (M3, biomass per time). Intake upon encounter ("satiation") is represented with a type II functional response (M5) as the "feeding level" $f_i(w)$, i.e., the ratio between consumption and maximum consumption (M4) (dimensionless number between 0 and 1).

Individual energy budget

The energy budget describes how consumed food is used for maintenance, activity, growth and reproduction. Consumed food is assimilated and first used for standard

metabolism, widely recognized to be an allometric function of body mass: $k_s w^p$. Juvenile individuals use the remaining available energy for growth, while mature individuals apportion the energy between growth and reproduction (M6-M8). The exact specification of allocation of energy between growth and reproduction is not crucial. The one used here ensures that when the feeding level is constant, size-at-age curves resembles a von Bertalanffy curve and the gonado-somatic is independent of body size (Hartvig et al. 2011).

Reproduction and recruitment

Reproduction and recruitment represent the reproductive output from the entire population. The reproductive output $R_{p,i}$ (numbers per time; M9) is discounted by a reproductive efficiency ϵ to represent losses due to egg mortality and spawning effort, and used to calculate the recruitment R_i . Within this context, recruitment refers to the rate of production of new individuals from the fertilized egg stage, but it could be done at a later stage if properly discounted (Andersen and Beyer 2015). Ideally the recruitment is equal to the reproductive output, but many models apply a stock recruitment relationship (M10). The density dependence imposed by the stock recruitment relationship avoids the competitive exclusion between species that otherwise tends to occur (Hartvig and Andersen 2013). The stock-recruitment relationship contains two essential parameters: the “slope” parameter that specifies recruitment at low population sizes and the maximum recruitment that specifies the population carrying capacity. The slope parameter is given directly by the egg production of the population (Andersen and Beyer 2015), but the maximum recruitment has to be specified separately. This parameter represents all effects on the population that are not explicitly represented in the model, such as limitations due to juvenile habitat size that is known to limit some marine populations (Rijnsdorp and Leeuwen

1992). The maximum recruitment and possibly the recruitment efficiency are key parameters for calibrating a model to data from real fish stocks (see discussion).

Mortality

Three categories of mortality are recognized. First, predation mortality (M13) emerges from the trophic dynamics within the system; second, intrinsic or background mortality (M12) is usually represented as an allometric function of asymptotic size (Brown et al. 2004), though starvation mortality can be explicitly added (e.g., Hartvig et al. 2011); third, exogenous sources of mortality (especially fishing) are often added.

Resource

The resource spectrum $N_R(w)$ represents food other than fish. The resource is needed for the smallest individuals who are not yet large enough to be piscivorous but it can represent any kind of food: a single size-group of small zooplankton prey species, a size spectrum of zooplankton prey (as in Fig. 1), or a size distribution including larger prey, e.g. benthic production. The resource can be constant, in which case the growth rate of small fish is fixed, or it can be modeled dynamically, e.g., as a semi-chemostat (M14). The semi-chemostat formulation is convenient because it leads to a very stable dynamics of the resource. Using logistic growth results in a more pronounced dynamical response of the resource which translate into stronger dynamics of the fish part of the model (de Roos et al. 2008).

Models types

We now briefly describe how these common concepts are used to create size spectrum models at three levels of complexity and demonstrate an approximate analytical solution for the equilibrium.

Food-web model

In the food-web model, the processes M1 – M15 are instantiated with all parameters from Table 2 being species specific (either representing identified species or hypothetical ones matching relevant criteria), but in practice some parameters are usually cross-species constants, such as the exponents n , p and q . Populations, thus identified as different species, interact through predator-prey relations with interaction strengths specified by an interaction matrix, which represents a combination of species-specific preferences and encounter probabilities. This matrix could be populated with empirical interaction coefficients derived from stomach content analyses, spatial overlap (Blanchard et al. 2014), or it may represent hypothetical distributions -- random and uniform (everything eats everything else) interaction networks are popular hypotheses. A fully specified food-web model has 14 parameters for each species, plus an interaction matrix, so for k species the total is up to $3 + 14k + k^2$ parameters.

Trait-based model

The trait-based model represents differences among species only by the governing trait of asymptotic size (Pope et al. 2006). This assumes that the most important trait is the asymptotic size (or, equivalently, size at maturation), which embodies a trade-off between reproductive output and asymptotic size. The trait-based model is conceptually derived from the food-web model by assuming that all parameters in Table 2 are cross-species constants and by using theoretical arguments to determine $R_{\max}$ as a function of W (appendix A). Feeding interaction are solely determined by individual size. The solution is the trait size spectrum $N(w, W)$ (dimensions numbers per mass per asymptotic mass) describing the joint distribution of individual and asymptotic sizes (Andersen and Beyer 2006). In numerical implementations the asymptotic size axis is discretized, typically into logarithmic 'bins' grouping species in asymptotic size classes. In practice, the results of the trait-based model are effectively independent of the

number of simulated asymptotic size classes once this number is greater than 10. The trait-based model is specified with the 18 parameters in Table 2.

Community model

The community model ignores all differences between species and only considers differences in size (Benoît and Rochet 2004). It can be derived from the trait-based and food-web models by integrating over all trait-classes or summing over species (Zhang et al. 2012):

$$N_c(w) = \int_w^{\infty} N(w, W) dW = \sum_{i=1} N_i(w).$$

The integral only runs from w because asymptotic size groups with $w < W$ does not contribute to the community spectrum at size w . The community model only resolves the ‘community spectrum’ $N_c(w)$. Substantial consequences arise because this model is unable to represent maturation, reproduction and recruitment. The energy budget (M6-M8) is simplified such that growth is solely available energy multiplied by an “average growth efficiency” derived from equilibrium theory (M7b; Appendix A). Because energetic losses to reproduction are not explicitly accounted for, the model will not reproduce von Bertalanffy growth. Further, most implementations in the literature use just a linear functional response, ignore standard metabolism and use a fixed resource (Table 3), however, these simplifications are not significant for the community model. In its most comprehensive form, the community model requires only 11 parameters (less without the functional response and with fixed resource).

Equilibrium solutions

Analytical solutions to the trait-based model can be derived under the assumption that the feeding level is constant $f(w) = f_0$ and that the spectrum is infinitely long, i.e. $w_0 = 0$ and $\max(W) = \infty$ (Andersen and Beyer 2006; Hartvig et al. 2011). This results in an ‘equilibrium community spectrum’:

$$N_c(w) = \frac{1}{\Phi} \frac{f_0}{1 - f_0} \frac{h}{\gamma} w^{n-2-q} \quad (3)$$

with $\Phi = \sqrt{2\pi}\sigma\beta^{q-n}\exp[(q-n)^2\sigma^2/2]$. The scaling exponent $n - 2 - q \approx -2.05$ is in accordance with observations (Boudreau and Dickie 1992). The equilibrium solution for each species spectrum is:

$$N(w, W) \propto \kappa W^{2n-q-3+a} w^{-n-a} \left[1 - \left(\frac{w}{W}\right)^{1-n}\right]^{a/(1-n)} \quad (4)$$

with the “physiological mortality” a given in (M17). This result is used to calculate expected scaling solutions to predation mortality, the scaling of maximum recruitment with asymptotic size used in the trait-based models, and the average growth efficiency in the community model (Appendix A). Note that the solution in eq. (4) does not fulfill the boundary condition (M9); the total reproductive output calculated from (4) will lead to a life-time reproductive output larger than 1 and increasing with asymptotic size (discussed in Hartvig et al. 2011 and Rossberg 2012). This discrepancy has to be resolved by density-dependent effects within each population not accounted for in (4), and it has been used to relate the slope parameter in stock-recruitments relationship to asymptotic size (Andersen and Beyer 2015). In the dynamical models the emergent physiological mortality depends on asymptotic size, with smaller species having a smaller a than larger (Hartvig et al. 2011), in accordance with empirical measurements of how mortality depends on asymptotic size (Gislason et al. 2010). Even though (4) is

not an exact solution of the entire model, it is still a useful approximation, as demonstrated by its ability to resolve species diversity (Reuman et al. 2014).

The equilibrium results all rely on the metabolic assumption inherent in the functional response where consumption is proportional to w^n . If a functional response is not used the solution for the exponent of the community spectrum will differ from eq. (3). In particular it will not depend on the metabolic exponent n , but rather on the preferred predator-prey mass ratio β (Benoît and Rochet 2004; Datta et al. 2010; Rossberg 2012). Such solutions will result in consumption rates that do not follow metabolic scaling.

Parameters

Parameters are either determined from knowledge about the specific species (for the food-web model), or from cross-species investigations of life-history invariants (Table 2; see Hartvig et al. (2011), App E. for a detailed discussion). The relatively small set of parameter facilitates formal investigations of model behavior under varying parameter values (Thorpe et al. 2015; Zhang et al. 2015).

Implementation

Size spectrum models may be simulated with “Mizer”, a reference implementation in R (Scott et al. 2014), or with the matlab code (see online supplementary). For the food-web model we have used the parameterization for the North Sea (Blanchard et al. 2014), which uses $n = 2/3$ as is customary in the fisheries literature. For the trait-based and community models we have used $n = 3/4$ to conform with “metabolic” theory (West et al. 2001). The results are qualitatively sensitive to the value of n as long as it is changed in all the relationships in Table 1. The community model has been implemented as a trait-based model with a single trait group having a very large asymptotic size. As the individuals in the trait group mature their growth rate declines (Fig. 2d). In this way the

average growth in the community model corresponds to the average growth in a trait-based model. Our implementation avoids the need for an additional senescent mortality for the largest individuals as is common practice (Law et al. 2009; Rochet and Benoît 2012).

All simulations are set up with 100 logarithmically spaced grid points on the mass axis, with the first grid point set to egg size w_0 . Each simulation was run with a time step of 0.25 year until convergence (Appendix B).

Example simulations

All three models predict size spectra, growth rates and mortality (Figure 2). In the absence of fishing and top predators the largest size groups ($w > 10$ kg) are superabundant, i.e., that part of the spectrum is greater than predicted by the equilibrium solution. This is most pronounced in the food-web model, and could be changed by increasing the background mortality Z_0 . The superabundance results in higher predation mortality on medium-sized individuals, which triggers a trophic cascade and associated changes in growth and mortality of smaller individuals (Andersen and Pedersen 2010).

Responses to fishing

The behavior of the models is illustrated by examining the response of the time-averaged solution to fishing and their dynamical behavior. Fishing using size-selective gear is represented by adding a fishing mortality that depends on body size, and possibly also asymptotic size or species. We illustrate fishing through two scenarios: a) community-wide fishing on all species with a trawl-type selectivity pattern having 50% selectivity at $0.05W$, and b) a bottom-up perturbation where forage fishery is removed from scenario (a) simulated by setting fishing mortality zero on all species with $W <$

200 g in the food-web and trait-based models and on individuals with $w < 200$ g in the community model (Figure 3). In scenario (a) (community wide fishing) the reduction of large individuals induces a trophic cascade throughout the community seen as a wave in the size spectrum. When forage fishing is removed (b), the food-web and trait-based models predict an increase of forage fish but relatively modest effects on the rest of the community. The forage fish have a higher biomass than in the unfished situation due to the partial release from predation by higher trophic levels caused by fishing. The response of the community model is different: it predicts a decline in the size-range where fishing is removed, while the effects on the rest of the community are weak, as in the other models. This difference in the community models stems from its inability to represent fishing (or, in this case, absence of fishing) on specific species or life histories, but only on body sizes. This result emphasizes the importance of representing individual populations in fisheries applications. The two scenarios illustrates the relative importance of mortality and growth to mediate trophic cascades: in scenario (a) the trophic cascade is mainly mediated by changes in predation mortality, which leads to a strong cascade. In scenario (b) increases in forage fish abundance has two effects with opposite consequences: 1) it increases growth rates of larger individuals, but 2) it also increases competition between juvenile individuals of larger species and forage fish leading to decreased growth rates. The end result is a modest trophic cascade (Houle et al. 2013; Jacobsen et al. 2015). The importance of competition between forage fish and juvenile predatory fish in real ecosystems could be analyzed by comparing stomach contents of forage fish and juvenile predatory fish. In summary: the food-web and trait-based models predict similar response to selective fishing, while the community model fails to resolve effects on different populations.

Dynamic solutions

The community model also differs from the food-web and trait-based model in dynamical behavior, i.e., how the solution varies over time. All models tend to be unstable (oscillate over time) if the trophic overlap is small. The trophic overlap is determined by the ratio between the width of the size preference function, σ , and the predator-prey size ratio $\log(\beta)$: the smaller the value of $\sigma/\log(\beta)$, the smaller the trophic overlap, and the more unstable the solution becomes (larger oscillations) (Datta et al. 2011; Zhang et al. 2012) (Figure 4). Oscillations in the trait-based models are fairly modest, but the community model is prone to unrealistically strong non-linear dynamics: the solution varies by up to 10 orders of magnitude (Figure 4b and d). This means that some parts of the spectrum alternate between being completely devoid of fish and being fully populated. It is therefore evident that the non-linear properties of the community model are fundamentally different from the models with life-history diversity, such as the trait-based models or a food-web model. Even if the community model is made linearly stable with a high trophic overlap or a diffusion term (Datta et al., 2011), the strong dynamical response will still be present if the model is perturbed away from the equilibrium. This should be kept in mind if the model is used to simulate the dynamical behavior of marine ecosystems (Zhang et al. 2012; Rossberg 2013 p. 273).

Challenges and open issues

Size spectrum models distinguish themselves from unstructured models by resolving individual body size as a continuous state variable (body size). To what extent do individual body size and species identity determine the ecological outcomes of community dynamics? The thrust of size spectrum modeling has become an emphasis on the former, whilst unstructured models have emphasized the latter. Some size spectrum models represent species interactions, and some attempts have been made to find a common understanding between the two perspectives. Notably, a food-web model with implicit representation of intra-species size structure was obtained (Rossberg and

Farnsworth 2011) to (indirectly) describe interactions among species of different sizes. The importance of explicitly resolving the size-structure of species, or where it can safely be ignored, is context dependent so requires specific and systematic exploration (Jacobsen et al. 2015; Woodworth-Jefcoats et al. 2015).

An important difference between implementations of size spectrum models is whether growth is fixed or food-dependent (Table 3). Fixing growth simplifies model setup and calibration. It is justified by the modest variations in growth observed in marine species. Fixing growth, however, has consequences which should be considered when the model is calibrated and results are interpreted. A model with fixed growth will still resolve trophic cascades mediated by mortality, but it will not resolve competition, which is crucial to describe the phenomenon of overcompensation (De Roos and Persson 2002) and may be important to understand the response of the spectrum to, e.g. fishing on 'forage' species (Houle et al. 2013; Jacobsen et al. 2015). More importantly, without food-dependent growth, the mass balancing between growth and predation mortality is broken. This requires that care is taken in the setup to ensure that predation mortalities are in the correct range by adjusting the "other food" compartment (Thorpe et al. 2015). Having too low predation mortalities (as in Hall et al. 2006; Worm et al. 2009; Rochet et al. 2011) will result in a model that is essentially a set of weakly coupled single-species models thus defying the purpose of a multi-species model.

Size-based models have been characterized as "highly unrealistic" and being based on "unrealistic and even contradictory assumptions" (Froese et al. 2015; Andersen et al. 2016b). We hope to have made it clear that the basic assumptions are realistic and internally consistent. Nevertheless, while the size-based models have matured to a degree where they can be applied to make impact assessments of fishing on marine ecosystems, they still face challenges related to density-dependence, life-history trade-

offs, termination at the large body sizes end, calibration procedure, and numerical implementation, which must be confronted: each will be briefly discussed.

Density dependence

All food-web models of real ecosystems, i.e. with specific species, require some form of density dependent regulation of the abundance of each species to avoid competitive exclusion. Not much is known about the exact mechanism of the regulation and how different mechanisms affect model results. The size based interactions and trait differences among species in size spectrum models provide insufficient niche differentiation to avoid competitive exclusion (Hartvig and Andersen 2013). Additional niche differentiation may be represented by a random species-specific interaction matrix, which can support coexistence (Hartvig 2011; Hartvig et al. 2011). Other commonly used mechanisms are (Table 3): stock-recruitment relationships; fixed recruitment; predator-dependent functional responses, whereby intake depends on the density of competitors as well as prey (also used in Ecosim) (Abrams 2014); and prey switching (Maury and Poggiale 2013), whereby rare prey are not attacked (leading to an emergent type III functional response). Which of these mechanisms is the most correct representation of effects in real ecosystem is currently unknown: stock-recruitment relations and fixed recruitment are in line with standard practice in fisheries science, but have little theoretical support; predator-dependent functional responses and prey switching certainly occur to some extent, but the understanding is currently too weak to make general statements of the strength of the processes. Within structured models, such as size spectrum models, the type of density dependent regulation may have a profound impact on the solution, both the size spectrum of the individual species and the relative abundances of species (compare Fig. 4 in Maury and Poggiale (2013) with Figure 2B). As an example, we tested the prediction from the trait-based model against empirical observations by comparing the asymptotic size distribution with observations

from three trawl surveys in the North Sea (Daan et al. 2005) (Figure 5). Even though the comparison does not reject the modeled distribution, more comparisons with similar data from other systems are needed to build confidence in the predicted asymptotic size distributions.

In addition to ensuring coexistence of species, the imposed density dependence also acts as a carrying capacity. In the food-web model the carrying capacity ($R_{\max}$) is found by calibrating to observed biomasses. The trait-based model, however, relies on theoretical results from the equilibrium theory. That theory compares favorably to the calibrated results (Figure 6). Nevertheless, the use of a stock-recruitment relationship is unsatisfactory as it introduces a dominating external regulation on the biomass of species. This may bias the response time of community size structure (Fung et al. 2013), which is of interest in conservation. Further, the stock-recruitment relationship means that a large amount of spawned biomass is simply lost to unspecified density-dependent processes. The stock-recruitment relationship therefore breaks the mass-balancing which is carefully observed in the other processes in the model (Persson et al. 2014). Since there is no generally accepted solution to the problem of maintaining coexistence, results should be interpreted in light of the assumptions used to represent density dependent regulation. It must be emphasized that this problem is common to all food-web models and not unique to size spectrum models.

Traits and trade-offs

The trait-based model assumes that the most important trait is the asymptotic size. Fish, however, vary in other traits than asymptotic size. The questions are then: which other trait(s) should be included in a model to represent observed variation? And how can suitable trade-offs be formulated and parameterized? An obvious trait is activity. Increased activity causes higher prey encounter rates (higher value of the clearance rate

constant, γ). On the other hand, higher activity results in increased metabolic rates and increased vulnerability due to higher exposure to predators. It is possible that inclusion of an activity trait would make it possible to distinguish sedentary from active species with the same asymptotic size, such as anglerfish and scombroids. Such a trait may not solve the problem of competitive exclusion because it does not lead to sufficient niche differentiation. A trait which would lead to niche differentiation could be related to habitat (Hartvig 2011; Zhang et al. 2013), i.e., pelagic vs. benthic (Blanchard et al. 2011). In both cases more theoretical investigations are needed but also empirical work to establish and parameterize the trade-offs.

Closure of the spectrum at large body sizes

An overlooked issue is the termination (closure) of the model spectrum at the largest body sizes. Closure is usually achieved (rather arbitrarily) by choosing a maximum body size and enforcing some background mortality to kill off the largest individuals. However, the size of this mortality clearly influences the results, in particular in the unfished situation. In the simulations presented here (Figure 2), this background mortality is relatively low, leading to the superabundance of large individuals compared to the equilibrium solution. However, we do not know the real abundance of the largest individuals in an unfished system, because most systems are heavily perturbed. Further, what is the theoretical largest size of a fish? Why are teleost fish not larger than a few hundred kg? There is no physiological mechanism in the model to limit the asymptotic size, and current theoretical understanding can only guess at an answer to this question (Freedman and Noakes 2002; Andersen et al. 2008; Andersen et al. 2016a). A satisfactory theoretical understanding of the factors limiting the upper size of fish is needed to bolster the consistency of the models.

Calibration to real systems

Size based models can be calibrated to real ecosystems, for instance on the scale of a continental shelf (in smaller systems immigration / emigration violate the assumed population closure). In the trait-based models calibration is achieved by varying some of the crucial parameters, such as the growth rate parameter h and the carrying capacity of the resource to reproduce observed average growth rates of individuals and ecosystem level catch rates of the fishery (Pope et al. 2006; Kolding et al. 2015). The next level of sophistication is to match modeled species to known species characteristics (Jacobsen et al. 2015), and further to include a species interaction matrix (Hall et al. 2006; Blanchard et al. 2014). In these cases the biomass of each species has to be calibrated by adjusting $R_{\max}$. Another important parameter that hitherto has been ignored is the reproductive efficiency ϵ . This parameter represents egg survival, which is likely to vary substantially between species. Introducing yet another calibration parameter, however, requires more data. Currently, the calibration methods applied are statistically simple. A more sophisticated approach acknowledges uncertainty by creating an ensemble of plausible models, requiring them to fulfill general criteria (Thorpe et al. 2015). A possible future direction could be introduction of a full statistical framework where distributions of parameter values are derived from observations of biomasses and stomach content by maximizing a likelihood function (Lewy and Vinther 2004; Spence et al. 2015). Finally, it should be kept in mind that even though a model may be well calibrated to current situations there is no guarantee that it will reliably predict the future.

Numerical solution procedure

Gains in accuracy and speed of the numerical solution may be achieved by moving to more advanced methods. The standard method is a first-order semi-implicit upwind scheme that is simple to implement (Appendix B). The drawback of this method is that it has numerical diffusivity, is not very efficient, possibly inaccurate for dynamics, and is

unable to resolve “cohort cycles” (de Roos and Persson 2001) with discontinuities in the solution in the form of “shocks”. To move forward, we recommend looking in the rich literature from computational fluid mechanics for inspiration, in particular towards higher order finite-volume techniques with limiters, which maintains positivity of the solution (Zijlema 1996), or spectral methods (Rossberg 2012). Enhancements to the numerical scheme could be implemented to common benefit in the (open access) reference implementation “Mizer” (Scott et al. 2014).

Current and future applications

We have shown how size spectrum models can be used to simulate how fishing of one group of species affects the entire system and that is very difficult to achieve with alternative models. Despite several open issues in size-based modeling, as discussed above, the model framework has already shown its use to: illustrate how fishing drives trophic cascades (Andersen and Pedersen 2010), simulate the impact of rising temperatures (Maury et al. 2007; Pope et al. 2009), explore the potential impacts of climate change scenarios on fish production (Blanchard et al. 2012; Woodworth-Jefcoats et al. 2013; Barange et al. 2014; Lefort et al. 2014), describe the indirect effect of ecosystem recovery strategies (Andersen and Rice 2010), quantify the interaction between forage and consumer fishery fleets (Engelhard et al. 2013; Houle et al. 2013) or between fisheries and marine mammals (Houle et al. 2015), evaluate ecosystem fishing strategies and indicators (Houle et al. 2012; Blanchard et al. 2014; Jennings and Collingridge 2015; Spence et al. 2015; Thorpe et al. 2015), evaluate balanced harvesting (Rochet et al. 2011; Jacobsen et al. 2014; Law et al. 2014) and describe the ecosystem level yield (Worm et al. 2009; Andersen et al. 2015). Other obvious uses would be as operating models in management strategy evaluations, as the basis for bio-economic evaluations of fishing on the entire community (Andersen et al. 2015), and to further developing our basic understanding of fish community functioning. In our view, the

community model is best limited to theoretical work examining the steady-state solutions. The trait-based model can be quickly deployed in data-poor situations and makes a flexible tool for exploration of community-level fishery interactions. The food-web types of models are well suited to more specific fisheries questions where a higher level of species identity is needed than provided by the trait-based model. Besides these strategic applications, it is tempting to deploy size spectrum models for tactical ecosystem based management, e.g., for providing advice on specific species. We are reluctant to endorse such uses because we find the purely process-oriented framework too rigid to provide precise quantitative information on the species level. In conclusion: the small number of parameters, the low computational requirements and the solid mechanistically basis provide a framework of low to intermediate complexity, highly suited to the strategic impact assessment of pressures such as fishing and environmental change on marine ecosystems.

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597 **Acknowledgements**

598 We thank Julia L. Blanchard and Axel Rossberg for comments on the manuscript. This
 599 work was supported by the Centre for Ocean Life, a VKR Centre of Excellence supported
 600 by the Villum Foundation.

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- 869 *Methods Fluids* **22**: 619–641.
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874 Table 1. Governing equations of the full food-web model. Subscript "i" refers to species number.

Encounter and consumption

Prey size selection	$\phi\left(\frac{w_{\text{prey}}}{w}\right) = \exp\left[-\left(\ln\left(\frac{\beta_i w_{\text{prey}}}{w}\right)\right)^2 / (2\sigma_i^2)\right]$	M1
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Clearance rate	$V_i(w) = \gamma_i w^q \text{ with } \gamma_i = \frac{f_0 h_i \beta_i^{n-q}}{(1-f_0)\sqrt{2\pi}\kappa_r \sigma_i}$	M2
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Encountered food	$E_i(w) = V_i(w) \sum_j \theta_{ij} \int_0^\infty \phi\left(\frac{w_{\text{prey}}}{w}\right) N_j(w_{\text{prey}}) w_{\text{prey}} dw_{\text{prey}}$	M3
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Maximum consumption rate	$I_{\max,i}(w) = h_i w^n$	M4
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Feeding level	$f_i(w) = \frac{E_i(w)}{E_i(w) + I_{\max,i}(w)}$	M5
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Growth and reproduction

Maturation function	$\psi(w) = \left[1 + \left(\frac{w}{\eta_i W_i}\right)^{-10}\right]^{-1} \left(\frac{w}{W_i}\right)^{1-n}$	M6
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Somatic growth	$g_i(w) = (\alpha f_i(w) I_{\max,i} - k_i w^p)(1 - \psi(w))$	M7a
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	$g(w) = \bar{\epsilon}(\alpha f(w) I_{\max} - k w^p)(1 - \psi(w))$	M7b
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Egg production	$g_r(w) = (\alpha f_i(w) I_{\max,i} - k_i w^p) \psi(w)$	M8a
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	$g_r(w) = \bar{\epsilon}(\alpha f(w) I_{\max} - k w^p) \psi(w)$	M8b
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Boundary condition

Population egg production	$R_{p,i} = \frac{\varepsilon}{2w_0} \int_{w_0}^{W_i} N_i(w) g_r(w) dw$	M9
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Recruitment	$R_i = R_{\max,i} \frac{R_{p,i}}{R_{\max,i} + R_{p,i}}$	M10
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Boundary condition	$N_i(w_0) g(w_0) = R_i$	M11
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Mortality

Background mortality $\mu_0 = Z_0 W_i^z$ M12

Predation mortality $\mu_{p,i}(w_{\text{prey}}) = \sum_j \int_{w_0}^{W_j} \phi\left(\frac{w_{\text{prey}}}{w}\right) (1 - f_j(w)) V_j(w) \theta_{ij} N_j(w) dw$ M13

Resource spectrum

Population dynamics $\frac{dN_r(w)}{dt} = r_0 w^{n-1} (\kappa(w) - N_r(w)) - \mu_{p,r}(w) N_r(w)$ M14

Carrying capacity $\kappa(w) = \kappa_r w^{-\lambda}$ M15

Trait-based model

Maximum recruitment $R_{\text{max},i} = \kappa_R \kappa (\alpha f_0 h w_0^n - k_s w_0^p) W_i^{2n-q-3+a} w_0^{-n-a} \Delta W_i$ M16

Physiological mortality $a = \frac{f_0 h}{\alpha f_0 h - k_s} \beta^{2n-q-1} \exp\left[\frac{(2n(q-1) - q^2 + 1)\sigma^2}{2}\right]$ M17

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879 *Table 2. Symbols and values of species-independent parameters in the trait-based and community models.*

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Symbol	Explanation	Value and unit ^a
w	Body weight	g
W	Asymptotic body weight	g
$N(w)$	Abundance density spectrum	numbers/gram ^b
β	Preferred predator-prey mass ratio	100 ^c
σ	Width of size preference	1.3 ^d
θ	Species preference	1
q	Exponent for clearance rate	0.8 ^e
f_0	Initial feeding level	0.6 ^f
α	Assimilation efficiency	0.6
h	Factor for maximum consumption	20 g ^{0.25} yr ⁻¹ g
n	Exponent for maximum consumption	$\frac{3}{4}$ ^h
k_s	Factor for standard metabolism	2.4 g ^{0.25} yr ⁻¹
p	Exponent for standard metabolism	$\frac{3}{4}$ ^h
η	Ratio between size at maturation and W	0.25 (0.01) ⁱ
κ_R	Constant for max. recruitment	1.7 ^g
ε	Efficiency of reproduction	0.1 ^j
w_0	Egg size	1 mg ^k
Z_0	Factor for background mortality	2 g ^{0.25} yr ⁻¹ l
z	Exponent for background mortality	-0.25 ^m
r_0	Resource productivity	4 g ^{0.25} yr ⁻¹ n
w_{cut}	Maximum size of resource	1 g ^o
κ_r	Resource carrying capacity	10 ¹² g ⁻¹ b, g

^aValues in parentheses refers to the community model

^bThe units of the abundance density spectrum could also be expressed as a concentration, i.e., as numbers/gram/volume or numbers/gram/area. In that case the units of the resource carrying capacity should also be changed accordingly. Further, the units of the clearance rate would become volume per time or area per time respectively.

^cUrsin 1973; Jennings et al. 2001.

^dUrsin (1973) finds $\sigma = 1$, but here σ is increased to represent cross-species variation. In the food-web model $\sigma = 1$ except if specific knowledge about a species exists.

^eAndersen and Beyer, 2006.

^fAssumes that fish in general are not satiated ($f_0 < 1$) while also have a significant surplus after assimilation and standard metabolism, i.e, larger than $k_s/(ah) = 0.2$. Setting f_0 in the middle of the range 0.2...1 gives 0.6. See also Hartvig et al. (2011), App. E.

^gAdjusted to give similar results to the North Sea model (Blanchard et al. 2014), despite the use of different exponent for n ; see text and Figure 2.

^hSee text.

ⁱBeverton, 1992.

^jAndersen and Beyer (2013). Note that this differs from the North Sea model (Blanchard et al. 2014), where a value of $\varepsilon = 1$ was used. This will (in the North Sea model) lead to overestimations of F_{msy} for individual species.

^kNeuheimer et al., 2015.

^lThis value leads to a background mortality on a 10 kg individual of 0.2 yr^{-1} . These individuals will have little predation mortality in the model, so background mortality is the largest part. See also discussion.

^mStandard “metabolic” assumption (Brown et al. 2004).

ⁿHartvig et al., 2011.

^oSet to include mesoplankton, such as shrimps.

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884 *Table 3* Implementations of size spectrum models. References are given to where a particular
 885 model was first formulated or calibrated to specific system, but not to applications of the models.
 886 The column “growth” refers to the functional response used to calculate growth rate.

Reference	Growth	Reproduction	Resource	Density dependence
<i>Food-web models</i>				
Hall et al. 2006, Rochet et al. 2011	Fixed	Fixed	N.a.	Stock-recruitment
Hartvig 2011, Hartvig et al. 2011	Type II	Dynamic	Dynamic	Emergent
Houle et al. 2012, Blanchard et al. 2014	Type II	Dynamic	Dynamic	Stock-recruitment
Rossberg et al. 2013	Type II	Dynamic	Dynamic	Emergent
<i>Trait-based models</i>				
Pope et al. 2006, 2009	Fixed	Fixed	N.a.	Stock-recruitment relationship
Andersen and Pedersen 2010	Type II	Fixed	Dynamic	Fixed recruitment
Houle et al. 2013; Jacobsen et al. 2014	Type II	Dynamic	Dynamic	Stock-recruitment relationship
Maury and Poggiale 2013	Type II	Dynamic	Dynamic	Switching
<i>Community models</i>				
Benoît and Rochet 2004; Blanchard et al. 2009; Law et al. 2009	Type I	N.a.	Fixed	Fixed boundary condition
(1)				
Blanchard et al. 2011	Type I &	Dynamic	Fixed	Fixed boundary

	II			condition
Maury et al. 2007	Type II	Dynamic	Dynamic	
This article	Type II	N.a.	Dynamic	Fixed boundary condition

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888 *(1) Note that Law et al. (2009) uses a slightly different conservation equation than the*
889 *other models.*

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893 Figure 1. Illustration of the size spectrum calculation of for a species (thin black line) from the perspective of
 894 an individual at a given size. All processes inside the oval around the fish are individual level processes, with
 895 dark grey arrows representing mass flows and the light grey arrow representing mortality losses. The scaling
 896 from individual level processes of growth, egg production and predation are facilitated by the McKendric-von
 897 Foerster equation (eq. 1) and the boundary condition (M11). The process is iterative with the size spectrum
 898 being needed to calculate the population-level measures of reproduction and recruitment. The numbers refer
 899 to the equations in Table 1.

Figure 2. Solutions of the community model (left column), the trait-based model (middle column), the North Sea food-web model (right column) and the equilibrium solution (dashed lines) in an un-fished situation as a function of body mass. Top: Biomass size spectra in the “Sheldon scaling” depicting biomass in log-spaced size groups, showing community spectrum (thick), background spectrum (thick grey), species spectra (thin grey) and the theoretic average spectrum from the equilibrium solution (dashed). Middle: growth rates (solid) compared to the maximum possible growth rate when fed ad libitum (dashed; for the food-web model this is an average over all species). Bottom: average predation mortality, (solid), for each species (grey) and from the equilibrium solution (dashed). Note that in the trait-based model all asymptotic size classes experience the same predation mortality since feeding is only based on size.

Figure 3. Response to fishing on the community for the North Sea food-web model (grey), the trait-based model (solid black) and the community model (dashed black). Size spectra are shown relative to the unfished size spectra from Figure 2. a) Response to fishing all species with a trawl-type selectivity pattern. Selection on each species starts at $0.05W$ and the fishing mortality is 0.5 yr^{-1} . In the community model all individuals larger than 10 g are fished. b) Changes to the fished community in panel a) when forage fishing is removed, i.e. fishing on species with an asymptotic size smaller than 200 g (or individuals smaller than 200 g for the community model).

Figure 4. Illustration of the time-dependent solution in the community model (two left-most columns) and the trait-based model (right-most column). Top row: average biomass spectra (solid) and range of variation (grey patch). Bottom row: the phase-plane between a prey of 10 g and a predator with a size one predator-prey mass larger ($\beta 10$ g) illustrated with vertical dashed lines in the top row. Left column: community model with width of size preference $\sigma = 1.3$. Middle column: community model with $\sigma = 1$. Right column: trait-based model with $\sigma = 1$. Other parameters as in Figs. 2 and 3, except that the largest size of the organisms is 1000 kg.

Figure 5. Asymptotic weight spectrum (extended Sheldon hypothesis), showing total numbers of individuals in logarithmically spaced asymptotic weight groups in an unfished (grey) and fished situation (black) from the trait-based model. The simulation results are compared to data from three different trawl surveys (Daan et al. 2005). It is assumed that the trawl surveys only retain individuals larger than 10 cm.

Figure 6. Maximum recruitment, R_{max} , for the North Sea model (circles) and the trait-based model with log-spaced asymptotic size groups (line) and with asymptotic size groups with the same asymptotic sizes as in the North Sea model (crosses).

Appendices for: The theoretical foundations for size spectrum models of fish communities

Appendix A: derivations of equilibrium solutions

The predation mortality can be derived from the community spectrum (eq. 3) (Andersen and Beyer 2006):

$$\mu_p = aAw^{n-1}, \quad (A1)$$

where $A = \alpha f_0 h - k_s$ and a is the physiological mortality (M16). Mortality scales with exponent $n - 1 \approx -0.25$ in accordance with empirical observations (McGurk 1986).

Maximum recruitment

The maximum recruitment in the trait-based model is calculated using the equilibrium solution $N(w_0)$ from (eq. 2). This solution provides a prediction for the relative abundance of species depending on their asymptotic size. The recruitment needed to support this abundance of individuals at size w_0 is given by the boundary condition (M11):

$$R_{\max,i} = \kappa_R g(w_0) N(w_0, W_i) \Delta W_i$$

where $\Delta W_i = \sqrt{W_i/W_{i-1}}$ is the spacing between asymptotic size groups, which is needed to come from the joint size and asymptotic size distribution in (1) to the size distribution (without asymptotic size) needed for the boundary condition. Inserting expressions for growth and abundance at size w_0 and assuming that $w_0 \ll W$ leads to the approximation in (M16). The dimensionless constant κ_R determines the strength of early-life density dependent regulation imposed by the stock-recruitment relationship by setting the ratio between $R_{\max}$ and κ . This free parameter effectively determines the ratio between piscivory and planktivory among the smallest fish: a higher value of κ_R

leads to a more abundant fish spectrum compared to the resource spectrum, and thus a higher the level of piscivory (Houle et al. 2013). For the simulations presented here, κ_R has been manually regulated to ensure that the predation mortality of 1 g individuals is on the order of 3 year^{-1} (Figure 2). If κ_R is very large, piscivorous mortality is high and early-life density dependent regulation is small, leading to competitive exclusion between the species groups until only two species are left, a small and a large species (Hartvig and Andersen 2013).

Average growth efficiency

For an individual at the asymptotic size the growth rate is zero and the growth efficiency is zero, while a juvenile uses all available energy for growth. The average growth efficiency used in the community model represents the distribution of growth efficiencies between individuals with the same size (Andersen et al. 2009). It can be calculated simply from the conservation equation at steady state:

$$\frac{dgN_c}{dw} = -\mu_p N_c$$

Inserting the description of growth in the community models as $g(w) = \bar{\alpha}Aw^n$ and the mortality from (A1) gives the average growth efficiency:

$$\bar{\alpha} = \frac{a}{2 + q - 2n} \approx 0.51$$

The entire distribution of the growth efficiency is derived in Zhang et al. (2012).

Appendix B: numerical solution procedure

The solution is discretized on a logarithmic grid starting with the first grid point w_1 set to the egg size w_0 , and the following grid points as $w_j = Cw_{j-1}$, for $j > 1$. The “expansion factor” $C > 1$ determines the number of grid points. For each species i , the growth and mortality are calculated using the previous time-step’s solution, $g_{i,j}^t$ and $\mu_{i,j}^t$, with t being the time step, at all grid points j .

The discretization scheme is first-order implicit for the time derivative and first-order upwind for the mass-derivative:

$$\frac{N_{i,j}^{t+1} - N_{i,j}^t}{\Delta t} + \frac{g_{i,j}^t N_{i,j}^{t+1} - g_{i,j-1}^t N_{i,j-1}^{t+1}}{\Delta w_j} = -\mu_{i,j}^t N_{i,j}^{t+1}$$

with $\Delta w_j = w_j - w_{j-1}$. This may be rewritten by collecting terms of N :

$$N_{i,j-1}^{t+1} \left(-\frac{\Delta t}{\Delta w_j} g_{i,j-1}^t \right) + N_{i,j}^{t+1} \left(1 + \frac{\Delta t}{\Delta w_j} g_{i,j}^t + \mu_{i,j}^t \right) = N_{i,j}^t,$$

which by naming the terms in the two parentheses $A_{i,j}$ and $B_{i,j}$ becomes:

$$N_{i,j-1}^{t+1} A_{i,j} + N_{i,j}^{t+1} B_{i,j} = N_{i,j}^t.$$

This may be rewritten as an explicit expression for $N_{i,j}^{t+1}$:

$$N_{i,j}^{t+1} = \frac{N_{i,j}^t - A_{i,j} N_{i,j-1}^{t+1}}{B_{i,j}},$$

which can be solved as an iteration once the spectrum in the first grid cell, $N_{i,1}^{t+1}$, is known. This found using the boundary condition eq. (2) to give

$$N_{i,1}^{t+1} = N_{i,1}^t + \frac{\Delta t}{\Delta w_1} R_i.$$

The equilibrium solution converges when more than 100 grid points are used (Figure B1).

Figure B1: Influence of the number of grid points on the solution of the trait-based model at equilibrium. A) The value of the Large Fish Indicator; B) the predation mortality of individuals with a size of 10 g.

References for Appendices

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