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2011

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Citation for published version (APA):

Hartvig, M. (2011). *Food Web Ecology -- individual life-histories and ecological processes shape complex communities*. [Doctoral Thesis (compilation)]. Department of Biology, Lund University.

Total number of authors:

1

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Food Web Ecology

- individual life-histories and ecological processes
shape complex communities

Abstract

This thesis sets out a food web framework for size-structured populations. The framework enables an ecological approach to food web modelling as the individual life-history from birth, through maturation, and ultimately death is explicitly resolved with the use of bioenergetics based on individual body size. Each population resolves size-structure through a size-spectrum containing the individual abundance as a continuous function of body size. Individuals select prey items of a suitable size, which can be popularised as “big ones eat smaller ones”. This allows individuals to change diet throughout life (life-history omnivory). In the framework individual food consumption leads to growth in body size and allocation to reproduction, which drives the population dynamics as opposed to instantaneous population increase in unstructured food web models. Paper I introduces the framework and shows how a simple realistic parametrisation is possible when a trait-based species characterisation is used. An analytical approximation of the food web framework is derived, and validated through comparison with dynamic simulations. Paper II extends the dynamic framework by also considering space, and demonstrates how large food webs can be formed through sequential community assembly. The resulting communities resemble the topology of natural food webs as well as complying with empirical data on diversity and biomass distributions – demonstrating that individual-level food encounter and prey-selection from the rule “big ones eat smaller ones” lead to complex and realistic food webs. Paper III uses the analytical solution of the framework to show the conditions under which the many-small-eggs strategy of the fishes is a viable strategy. Paper IV utilises the trait-based species description to show that coexisting species pairs involved in intraguild predation exist for all resource levels. The model thus explains empirically observed coexistence at high resource levels contrary to contemporary theoretical models. Paper V demonstrates how harvesting initiates a trophic cascade that may propagate both downwards and upwards in trophic levels, and that the harvesting pattern may influence whether or not trophic cascades are empirically detected. In Paper VI the analytical solution is used to provide a theoretical understanding of empirically observed relationships between natural mortality, growth, and production rates.

Keywords: food web, community ecology, community assembly, size-structure, life-history omnivory, ontogeny, trophic interactions, trait based model, topology, emergent organisation, size-spectrum

Food Web Ecology

– individual life-histories and ecological processes
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Martin Hartvig

Akademisk avhandling, som för avläggande av filosofie doktorsexamen vid naturvetenskapliga fakulteten vid Lunds Universitet, kommer att offentligen försvaras i Blå Hallen, Ekologihuset, Sölvegatan 37, fredagen den 29 april 2011, klockan 10.00.

Fakultetens opponent: Owen Petchey, Professor, Institute of Evolutionary Biology and Environmental Studies, University of Zurich, Switzerland.

Avhandlingen kommer att försvaras på engelska.

Doctoral thesis
Department of Biology
Lund University, Sweden, 2011

A doctoral thesis at a university in Sweden is produced either as a monograph or as a collection of papers. In the latter case, the introductory part constitutes the formal thesis, which summarizes the accompanying papers. These have either already been published or are manuscripts at various stages (in press, submitted or ms).

Doctoral thesis
Graduate Programme in Theoretical Ecology
Department of Biology, Faculty of Science
Lund University, Sweden, 2011

The main part of the work presented in this thesis was performed at the Department of Theoretical Ecology, which ceased to exist on December 31, 2010, due to a merging of all departments involved in biology at Lund University, Sweden.

Hartvig, M. (2011). Food Web Ecology – individual life-histories and ecological processes shape complex communities. Doctoral thesis. Department of Biology, Lund University, Lund, Sweden.

ISBN: 978-91-7473-080-7

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Printed by: Tryckeriet i E-huset, Lund, Sweden, 2011

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Food Web Ecology

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It is interesting to contemplate an entangled bank, clothed with many plants of many kinds, with birds singing on the bushes, with various insects flitting about, and with worms crawling through the damp earth, and to reflect that these elaborately constructed forms, so different from each other, and dependent on each other in so complex a manner, have all been produced by laws acting around us.

Darwin (1859)

Introduction

When I contemplate nature I image ecological relationships between individuals rather than between species. Interactions among species is a theoretical abstraction, which indeed is useful, but we should always remember that inter- and intra-species interactions are an emergent result of individual-level interactions. In this thesis I set out a foundation for a theoretical examination of food webs from the individual level. As I will return to later most of the ideas I propose are not new, but I will put the many ideas together into one synthesised food web framework that can be used to generate and test hypotheses. Only when considering the ecological processes that make up food webs can we test hypotheses in a trustworthy manner.

Community ecology has been termed a ‘mess’ (Lawton, 1999), but a recent synthesis has cleaned up this mess by realising: “*At the most general level, patterns in the composition and diversity of species – the subject matter of community ecology – are influenced by only four classes of process: selection, drift, speciation, and dispersal. Selection represents deterministic fitness differences among species, drift represents stochastic changes in species abundance, speciation creates new species, and dispersal is the movement of organisms across space.*” (Vellend, 2010). My

main focus in this thesis is on selection: I demonstrate that individual-level processes drive population dynamics, which ultimately select which species that survive the struggles and which species that will go extinct. Secondly, I focus on a simplified description of dispersal processes, as individuals only interact with individuals encountered in the spatial landscape. Thirdly, I allow communities to form as a consequence of new species invading from an external pool of species, which may be regarded both as dispersal from surrounding communities, as well as a speciation process that creates new species. The process drift, which can drive population dynamics off the deterministically determined route set by ‘selection’ is not considered.

Individuals may engage in different interactions as predation, mutualism, competition, and parasitism, but this thesis focuses solely on trophic interactions and their derived interaction types as apparent competition. This is not to say that such other interaction types are not important, but merely a restriction enforced by my limited abilities.

I stress the importance of individual-level ecology in food webs, as I put emphasis on the life-history of individuals and how their diet changes throughout life due to size dependent food selection. Communities are assembled through sequential arrival of new species. By assuming that individuals only considers relative prey size when selecting prey, I demonstrate that the emergent food web structure that connect species resembles natural food webs. I thus show that individual-level processes lead to complex and realistic food webs – or in other words: the complexity in Darwin’s entangled bank is the result of individual interactions and their growth and reproduction that drives population dynamics.

Objectives

The objectives of this thesis are:

1. To develop a food web framework that is driven by individual-level processes.
2. To show that model communities resemble natural communities.
3. To demonstrate the utility of the framework by giving theoretical explanations to empirically observed phenomena.

Overview

This thesis consists of six papers (Fig. 1). In Paper I the food web framework is developed, and a simple parametrisation is achieved through a trait-based species description. Additionally it is shown that simple assumptions allow an analytical solution of the framework, which is validated against dynamic simulations. Paper II extends the framework by including a spatial distribution of the individuals within each population. Sequential community assembly is used to generate large food webs, which are validated against structure in natural food webs as well distributions of biomass and diversity in natural communities. Paper II thus contributes to

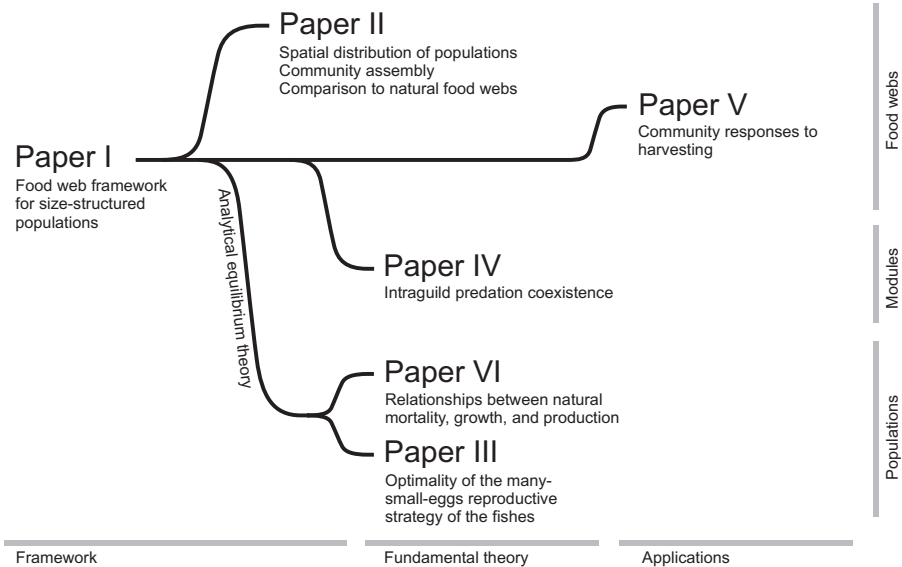


Fig. 1: Relation between the the six papers that constitutes this thesis. Paper I and II develops the food web framework. Papers II-IV and VI use the framework to establish fundamental theory at different levels of organisation: population, modules, and food web level. Paper V applies the framework to examine how communities as a whole react to harvesting.

fundamental theory, as it enables an understanding of the individual-level processes that shape and maintain structure in natural communities.

Fundamental theory is advanced further in paper IV, which uses the framework to examine the scope for coexistence in intraguild predation modules. Contrary to previous theoretical approaches, the framework finds that coexistence is possible at high resource levels in accordance with empirical evidence. Paper III and VI utilises the analytical solutions of the framework to find the conditions under which the many-small-eggs strategy of the fishes is optimal (Paper III), and to link empirically observed relationships of mortality, growth, and production to individual-level parameters (Paper VI).

Paper V employs the framework to examine the system-level response of fishing, and demonstrates that trophic cascades induced by fishing may propagate both upward and downwards in trophic level. Additionally it is shown that fishing pattern can mask the trophic effects of harvesting, whereby the cascade is not empirically detectable. This application shows directly that a system-level approach should be taken in e.g. management of marine fisheries, as fishing pattern can be used to avoid substantial changes in the biomass composition across trophic levels, which may have severe consequences that in worst case leads to species extinctions.

The models in this thesis are parameterised for fish communities, as these constitute a common and widespread system type, where species have a large size difference between offspring and adult. Clearly, in such populations individual body size is important as metabolic requirements and diet differ greatly between life-stages.

The presented framework is however not limited to aquatic systems, but may be reparameterised for less strongly size-structured systems as well (Paper I).

The introductory part of the thesis (*Food Web Ecology*) discusses the components needed to construct the food web framework in separate sections, and ends up demonstrating how individual-level processes lead to large and complex food webs along with a discussion of the framework. The introduction thus predominantly treats Paper I and II. The discussion of the utility of the framework and the remaining papers are included in *Summary of papers* (pp. 33). All papers are available in the back of the thesis (pp. 53).

Ecology of population dynamics

Population dynamics in food web models are predominantly described with classic Lotka-Volterra conservation equations (Box 1), where the species' interaction coefficients often are replaced with non-linear functional responses representing the effect that an upper limit exists to the per capita consumption of prey (Holling, 1959; Jeschke et al., 2002). Similarly the intrinsic growth rate for resources is often replaced with functions incorporating logistic or semi-chemostatic growth (Verhulst, 1838; Gurney et al., 1990; Persson et al., 1998).

Parameter values in Lotka-Volterra systems stem from several processes that are aggregated, and are thus difficult to interpret and parameterise. To overcome this Yodzis and Innes (1992) developed a bioenergetic approach to population dynamics, where each species is assigned a characteristic body mass, and allometric scaling of metabolism is used to express maximum per capita energy intake rates and losses.

Irrespective of whether Lotka-Volterra systems are posed in an energetic or abstract form they are based on two fundamental assumptions of predation leading to instantaneous 1) production of offspring, and 2) mortality. The latter assumption is in correspondence with nature, whereas the first makes a drastic simplification of the organisms' life-history. Instantaneous offspring production may be justified as a separation of time-scales, where dynamics of the population are perceived on a slow time-scale (e.g. annual) and reproduction on a faster scale (e.g. inter-annual). However, if the premature life-stages are of similar or longer duration than the time-scale of population dynamics that justification becomes problematic, as the next generation is not determined by the current offspring generation (e.g. overlapping generations). Secondly, for many types of organisms the ecology of offspring and juveniles differ greatly from the ecology of adults. Aquatic ecosystems provide a very pronounced and widespread example of this, as fish offspring arrive at a low trophic level and grow through multiple trophic levels before reaching maturation (Werner and Gilliam, 1984). During this journey, from the milligram range and up to up to several kilogram, fish change diet (and enemies!) and consequently exhibit life-history omnivory in their preying on different trophic levels in different life-stages (Pimm and Rice, 1987).

To resolve ecological characteristics of individuals in different life-stages within a population a structured modelling approach is needed. In this thesis I use a contin-

uous representation of the body size composition within each population. $N_i(m, t)$ is the size-spectrum (body size composition) of a population, and for size-structured populations the appropriate conservation equation is the McKendrick-von Foerster equation that ensures that changes in abundance density at size m is determined by somatic growth and mortality (Box 1). The reproductive output from mature individuals enters as a flux of offspring into the smallest life-stage (Fig. 2).

The fundamental assumptions underlying this approach is that consumption leads to 1) instantaneous uptake of energy that are allocated into somatic growth and reproduction (depending on maturation status), 2) continuous production of new immature offspring of size m_{0i} , and 3) instantaneous mortality. These assumptions are ecologically reasonable compared to the assumptions of Lotka-Volterra, as

Box 1: Population dynamics

LOTKA-VOLTERRA (Lotka, 1925; Volterra, 1926):

$$\frac{dN_i}{dt} = N_i \left(b_i + \sum_j a_{ij} N_j \right), \quad (1)$$

is a conservation equation for unstructured populations $N_i(t)$ having intrinsic per capita growth rate b_i , and per capita effect a_{ij} from species j on its per capita growth rate. Resources are typically modelled with $b_i > 0$, whereas a constant mortality term ($b_i < 0$) often is included on consumers (representing mortality sources not explicitly resolved by the model).

Fundamental assumptions: Consumption leads to instantaneous 1) production of mature offspring, and 2) mortality.

MCKENDRICK-VON FOERSTER (McKendrick, 1926; von Foerster, 1959):

$$\frac{\partial N_i}{\partial t} + \frac{\partial}{\partial m} (g_i N_i) = -\mu_i N_i, \quad (2)$$

is a conservation equation for structured populations $N_i(m, t)$. $N_i(m, t)dm$ is the density of individuals in the mass range $[m; m + dm]$. Individuals change body size through somatic growth $g_i(m, N, t)$ and experience mortality $\mu_i(m, N, t)$, which both depend on the abundance and size distributions of other species $N(m, t)$. Reproduction from all mature individuals enters through the boundary condition as a flux of offspring in the smallest life-stage m_{0i} : $g_i(m_{0i}, t)N_i(m_{0i}, t) = R_i(t)$.

Fundamental assumptions: Consumption leads to 1) instantaneous somatic growth and allocation of energy to reproduction (depending on maturation status), 2) continuous production of new immature offspring of size m_{0i} , and 3) instantaneous mortality.

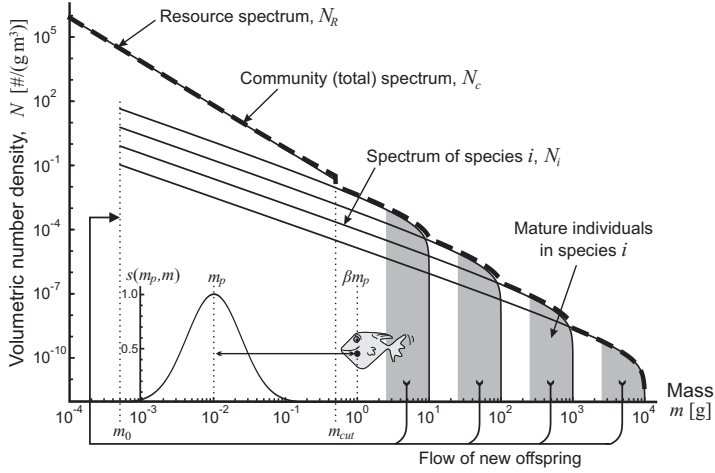


Fig. 2: Illustration of the food web model (Paper I): resource spectrum (with cut-off m_{cut}) and four species size-spectra with different sizes at maturation m_* ($m_* = 2.5, 25, 250,$ and 2500 g) having offspring of size m_0 . Shaded regions mark mature individuals from maturation size m_* to maximum asymptotic size M . The sum of all spectra gives the community spectrum. Inset shows how individuals feed on smaller prey using a feeding kernel with a preferred preferred predator-prey mass ratio β .

the physiological and chemical processes governing energy uptake and growth clearly occur much faster than population dynamics. That consumption leads to a continuous production of immature offspring is also reasonable if population dynamics is perceived on a time-scale similar to the duration between reproductive events of mature individuals (e.g. annual). Whereas Lotka-Volterra models assume all individuals of a population to be identical the McKendrick-von Foerster approach only assume individuals of size m within a population to be identical.

The size-structured framework in this thesis provides an individual-level approach to food web modelling, as it explicitly resolves the entire life-history of individuals from birth, through reproduction, maturation, and ultimately death (Fig. 2; Paper I). The McKendrick-von Foerster equation enables the scaling from individual-level life-history to population level dynamics.

The framework can be perceived as a dynamic version of equilibrium size-spectrum theory (Andersen and Beyer, 2006) extended to account for individual-level reproduction. Paper I validates the equilibrium assumptions through comparison with the full dynamic model. The framework is conceptually similar to physiologically structured models (Andersen and Ursin, 1977; Metz and Diekmann, 1986; de Roos and Persson, 2001), and as these based on individual-level processes. The contribution of this thesis is to introduce a generic species description through the use of traits in the parametrisation, which renders the developed framework useful as a size-structured food web framework (Paper I).

Life-history and individual-level processes

You begin life as an offspring, and ultimately you end up dead. In between you consume food, grow in body size, and engage in reproduction to pass your genes on to the next generation. A bioenergetic model turns consumption of prey biomass into individual growth and reproduction if the individual has matured (Box 2; Paper I; Kitchell and Stewart, 1977; Kooijman, 2000).

Perhaps one of the most important discoveries that has enabled an individual-level energetic basis for population dynamics is the discovery of a $3/4$ allometric scaling of metabolism (Kleiber, 1947). This has led to the development of models for universal scaling laws (West et al., 1997; Banavar et al., 1999), along with critique of these (e.g. Kozłowski and Konarzewski, 2005). Analyses of empirical data demonstrate that no universal $3/4$ scaling law exist for metabolism, as the exact scaling exponent vary across taxa and metabolic states (White et al., 2007). It is however worthwhile noting the similarities of scaling within taxa (Peters, 1983), as well as the similarity of the mass-specific metabolism across taxa (Makarieva et al., 2008). More important than the precise value of the scaling exponent is that additional individual- and population-level processes as maximum consumption, locomotion rates, and mortality can be described with allometric functions of body size that are often related to the allometry of metabolism (Peters, 1983; Woodward et al., 2005; Marquet et al., 2005).

Body mass the ideal currency for modelling the life-history of individuals, since the size-structured approach with the McKendrick-von Foerster equation allows a continuous representation of body size, and because individual-level processes can be described with allometric functions.

In the developed food web framework the community spectrum is the sum of all species spectra along with a resource spectrum, which represents food items from lower trophic levels than the resolved species (Fig. 2; Paper I). The biotic environment an individual experiences is given by the community spectrum, which contains food items as well as enemies which may consume the individual. Food is encountered with a search rate that increases with body size (Ware, 1978), and individuals have a maximum consumption rate which scales similarly to metabolism (Jobling, 1994). Metabolism is covered with highest priority, after which a fraction of the acquired energy is used for growth, and the remaining for reproduction. Individuals naturally do not invest in reproduction before size at maturation m_* is reached, and the degree to which adults should invest in reproduction can be found from ecological requirements, and validated from ecological patterns (Paper I). The resulting reproductive allocation function implies a trade-off between m_* and the mass-specific reproduction: large sized m_* species may escape predation mortality by growing to large body sizes where mortality is less pronounced, or a high mass-specific allocation to reproduction may be achieved at the cost of experiencing larger adult predation mortality due to a smaller m_* (Charnov et al., 2001).

Mortality is simple to model, as it is a matter of bookkeeping: what is eaten is removed from the community spectrum. Individuals are exposed to a starvation

mortality if consumption cannot cover metabolic cost. Mortality from other sources than predation and starvation is assumed constant within species and inversely proportional to generation time (Peters, 1983), and assures that the largest individuals in the model experiences mortality. Paper V additionally addresses mortality stemming from harvesting.

The bioenergetic processes growth and reproduction, as well as the emergent property of mortality, drives the intra- and inter species population dynamics in the McKendrick-von Foerster equation (Box 1). Unification of life-history and individual-level processes in a population model is used in Paper III to find the conditions under which the many-small-eggs strategy of the fishes is optimal. In Paper VI the unification is used to explain empirically observed relationships between natural mortality, growth, and production.

Box 2: Bioenergetics

The maximum amount of food an individual can consume is hm^n , resulting in the acquired energy:

$$E_i(m) = \alpha f_i(m)hm^n - km^p, \quad (3)$$

where α is assimilation efficiency, and km^p metabolic losses. $f_i(m)hm^n$ corresponds to an individual-level Holling type II functional response, and $f_i(m)$ is denoted the feeding level determining the degree of satiation ($f \in [0; 1]$):

$$f_i(m) = \frac{\varepsilon_i(m)}{\varepsilon_i(m) + hm^n}, \quad (4)$$

determined by the amount of encountered food:

$$\varepsilon_i(m) = v(m) \sum_j \int \alpha_{ij}(x_i - x_j, m, m_p) N_j(m_p) m_p dm_p, \quad (5)$$

which is given by the individual interaction coefficient α_{ij} and search volume $v(m) = \gamma m^q$, which is an increasing function of body size (Ware, 1978).

Acquired energy is used for a mixture of growth:

$$g_i(m) = [1 - \psi_i(m, m_*)]E_i(m), \quad (6)$$

and production of m_{0i} sized offspring:

$$R_i = \frac{\epsilon_i}{m_{0i}} \int N_i(m) \psi_i(m, m_*) E_i(m) dm, \quad (7)$$

where ϵ_i is an efficiency, and $\psi_i(m, m_*) \in [0; 1]$ the level to which an individual invests in reproduction, which switches from zero at size at maturation m_* . The precise form of $\psi_i(m, m_*)$ is determined in Paper I.

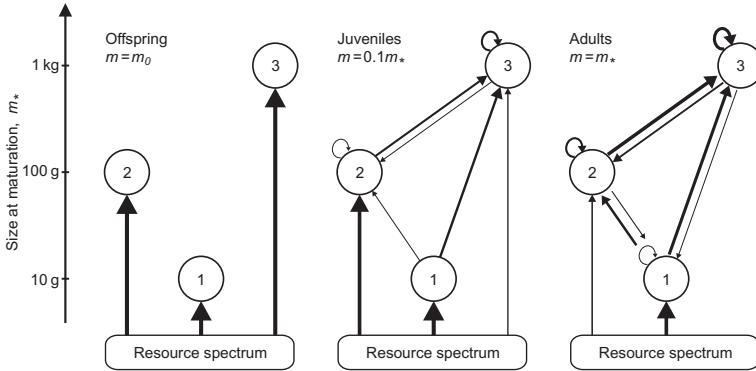


Fig. 3: Individuals engage in different trophic relationships depending on their life-stage. The potential strengths of the individual trophic interactions are denoted with the thicknesses of the arrows. Offspring of equal size from different species populations eat similar resources (left). Juvenile individuals from small body sized species continue to feed on small resources, whereas juveniles of larger body size in other species populations may start eating from higher trophic levels (middle). This pattern continues till individuals reach their highest trophic position in adulthood (right). As individuals grow in size they feed on increasingly larger food items, which additionally increases the potential for cannibalism (left to right). The effective species-level food web structures is the sum of the interactions occurring at all life-stages, and corresponds to putting the three illustrations on top of each other.

Trophic interactions at the individual level

In this thesis I assume that individuals do not care about species identity when selecting prey, and show that the empirically observed species-level interaction patterns emerge as a consequence of individual interactions.

In the animal kingdom it is a general pattern that predators are larger than their prey (Warren and Lawton, 1987; Cohen et al., 1993; Brose et al., 2006a; Barnes et al., 2010), which justifies incorporating the prey selection rule “big ones eat smaller ones”. The specific size-selective feeding kernel used in this thesis assumes that predators have a preferred predator-prey mass ratio (Box 3, Fig. 2, inset), which is e.g. supported by stomach analyses (Ursin, 1973, 1974).

Through using the “big ones eat smaller ones” rule Fig. 3 demonstrates how individuals’ trophic relationships change throughout life: offspring eat small resources, juveniles eat larger items, and individuals reach their highest trophic position in the adult stage, where the largest prey items are targeted. The depicted interaction strengths are the potential maximum strengths determined by size-dependent feeding. The species-level trophic interaction pattern is the product of the trophic interactions of all individuals in the population.

A trivial requirement for a trophic interaction to occur is that the prey and predator encounter each other in the spatial landscape. In Paper II it is assumed that each population has a spatial distribution, and as home range is an increasing function of body size (Kramer and Chapman, 1999; Haskell et al., 2002; Jetz et al., 2004) large individuals span a larger fraction of space compared to smaller individuals. From

Box 3: Individual interactions

SPATIAL CONSTRAINTS: The possibility that a m sized predator (from species i) co-occur with a m_p sized prey (species j) is given by their spatial overlap (Paper II):

$$\Omega(x_i - x_j, m, m_p) = \frac{\exp\left(\frac{-(x_i - x_j)^2}{2[\sigma_x(m)^2 + \sigma_x(m_p)^2]}\right)}{\sqrt{2\pi[\sigma_x(m)^2 + \sigma_x(m_p)^2]}}, \quad (8)$$

where home range $\sigma_x(m)$ is an increasing function of body size mimicking that large individuals cover a larger fraction of the spatial landscape. Individuals are most likely to meet each other if they have identical centre of their spatial distribution, $x_i = x_j$, where the probability is $\Omega_{ij} = 1/\sqrt{2\pi[\sigma_x(m)^2 + \sigma_x(m_p)^2]}$. The principle is illustrated in Fig. 4.

FEEDING KERNEL: Individuals within a species have a preferred predator-prey mass ratio β_i :

$$s_i(m, m_p) = \exp\left[-\left(\ln\left(\frac{\beta_i m_p}{m}\right)\right)^2 / (2\sigma^2)\right], \quad (9)$$

meaning that predators are optimal at capturing prey of size m/β_i where $s_i(m, m/\beta_i) = 1$. The bell-shaped feeding kernel is a log-normal function with width σ . The bell-shaped relationship caricatures that a predator may not be fast enough to capture prey larger than m/β_i , and that it may have visual/physical problems detecting/handling smaller prey items. The feeding kernel is depicted in Fig. 2 (inset).

ADDITIONAL TRAITS: If prey is assumed to possess a set of vulnerability traits \bar{V} (spines, hiding capability, etc.), and predators a set of foraging traits \bar{F} (length of teeth, search strategy, etc.) the resulting interaction strength can reflect the match through:

$$a_{ij} = \exp\left(\sum_k \nu_k |V_k - F_k|\right), \quad (10)$$

where ν_k is the importance of trait type k . If traits are perfectly matching ($V_k = F_k$) a full interaction of $a_{ij} = 1$ is possible.

THE INTERACTION COEFFICIENT α_{ij} between individuals is the product of Ω_{ij} , s_i , and a_{ij} , and it enters (5) when calculating encountered food (Box 2). An interaction coefficient to a prey of optimal size, and to which the predator is fully adapted to ($a_{ij} = 1$), is limited in strength by Ω_{ij} , which is strictly smaller than 1 due to the spatial spread of populations. The actual flow of energy from interactions is given by the search volume and the level of satiation of the predator (Box 2).

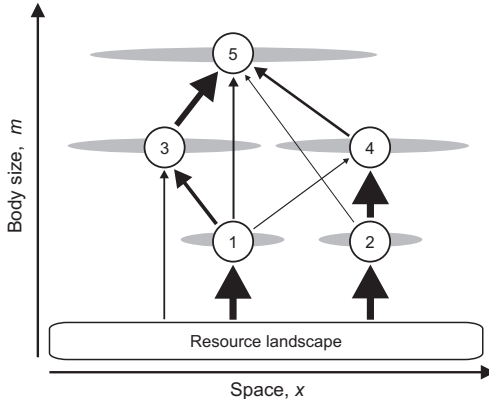


Fig. 4: The role of space and body size on individual-level interaction strengths. Each node contains individuals of size m from a species population. Species are assumed to have identical preferred predator-prey mass ratios $\beta_i = \beta$, and nodes are placed with a vertical distance corresponding to β . Home range is an increasing function of body size, such that large individuals cover larger parts of space (grey area). Individual interactions decrease in strength when a) body size difference between individuals increase (e.g. nodes 4-2 vs. 5-1), or b) the spatial overlap between the interacting populations decrease (e.g. nodes 5-3 vs. 5-4).

the spatial overlap of the interacting populations a spatial interaction coefficient is calculated. Populations with large spatial overlap can have many individual-level interactions, whereas populations with a minor overlap only will have few interactions between individuals from the two populations. Fig. 4 demonstrates how both spatial constraints and size-dependent feeding shape interaction strengths between individuals of different sizes.

Additional traits beyond preferred predator-prey mass ratio matters in determining interaction strengths. These traits may be incorporated as a set of vulnerability and foraging traits as in the framework by Rossberg et al. (2010). Vulnerability traits could be armour, spines, poison production, or refugee seeking for protection against predators, whereas foraging traits could be teeth, strong check muscles, or chemical sensing to pursue and attack prey. The potential interaction strength is given by the degree to which the predators traits match those of the prey (Box 3). If the prey has body armour and hides in a refuge, the predator may need chemical sensing to locate the prey as well as strong check muscles and teeth to attack the prey.

A recent analysis of functional responses of centipedes and spiders feeding on fruit flies and springtails showed that body size is more important than species identity to quantify interaction strengths (Rall et al., 2011). This may justify exclusion of vulnerability and foraging traits when species identity is assumed to account for these traits. Consequently these traits are not included in the framework of this thesis. It would however be interesting to implement vulnerability and foraging traits, and examine how they affect the resulting community structure when their importance is varied.

The effective individual-level interaction coefficient is given by the product of the

different interaction kernels (Box 3), and enters the bioenergetics when calculating the amount of food an individual of a given size encounter (Box 2).

Trait-based species description

Traits are physiological, morphological, and ecological characteristics of a species. Characterising species from a set of traits opposed to a set of species-specific parameters reduces parameter richness considerably in models, and enables a more general analysis of multi-species systems, where the role of the different species can be interpreted more easily due to the information contained in the traits.

A species defined by a set of traits may formally be regarded as a ‘functional species’ as it represents all species that share the set of traits. Consequently functional species represent many taxonomic species when only a single trait is used to characterise a species, whereas there may be a one-to-one correspondence when more traits are included.

Species-specific parameter sets can be avoided or reduced with body size scaling of parameters, as this allows parametrisation from cross-species analyses (Peters, 1983). This approach has e.g. enabled the construction of a dynamic food web model of 29 species in the Benguela ecosystem, where many of the species-specific parameters were not available (Yodzis, 1998).

Species are only characterised by the trait size at maturation m_* in Papers I and III-VI, whereas preferred predator-prey mass ratio β_i and the centre of the spatial distribution of the population x_i additionally are used in Paper II. When species are characterised only by m_* it is not possible to construct size-structured dynamic communities with more than three species (Supplementary). To overcome this limitation random species couplings are employed in Paper I. If species have equal $\beta_i = \beta$ higher trophic levels of communities are only rarely occupied, whereas diversity in β_i strategies enables a stable energy supply from low to high trophic levels, which enables high trophic level species more easily (Paper II). Body size is not a species trait in the models, but an individual-level trait used to describe the individual life-history. Body size and the trait m_* is used to obtain species neutral parameters through cross species analyses (Paper I): individual-level metabolism is e.g. given by body mass, whereas the mass-specific allocation to reproduction depends on a species m_* (Paper III; Gunderson, 1997).

Food webs

Classical food webs describe the trophic relationships between species in a community, and can be represented by matrices and network diagrams (example in Fig. 6). Two variants exist: 1) Binary food webs that describe the topological layout through assigning matrix element A_{ij} the value ‘1’ if i eats j and ‘0’ if not. 2) Flow based webs where A_{ij} represents the interaction strength of i to j independent of the abundances of both species.

An inherent problem with the classical food web concept is that it considers interactions to occur at the species- contrary to at the individual level. This means that all individuals in a population are treated equal, and that differences in diet between e.g. offspring and adults are not resolved.

This thesis resolves this problem by including individual-level interaction kernels, which ensures that a trophic interaction between two individuals only can occur if the individuals co-occur in space, and if the prey has a suitable size. The interaction kernel enters the size-structured modelling approach in the prey encounter model (Box 2), contrary to directly in the population dynamics through a_{ij} in the unstructured Lotka-Volterra approach (Box 1).

Topological models

The topological structure of natural food webs are non-random as they exhibit patterns of self-organisation: the frequency distribution of links can be described by power laws (Montoya and Solé, 2002). It is of fundamental interest to understand these topologies, and how they vary from system to system, as models have to be able to reproduce the structure of natural food webs.

Contemporary research in food web topology focuses solely on binary food webs, and to enable comparison of topologies several properties are used, ranging from simple properties like connectance and fraction of cannibals, to more complex properties as mean chain lengths and clustering coefficients (for more details see Dunne, 2009).

Development of models that can reproduce the topological properties of natural webs has been a major achievement. The most widely used method to generate model topologies of natural food webs is the niche model (Williams and Martinez, 2000) belonging to a class of purely statistical phenomenological models that at least take desired number of species and connectance as input parameters (Cohen and Newman, 1985; Williams and Martinez, 2000; Cattin et al., 2004; Allesina et al., 2008). Recently more process driven approaches involving phylogenetic correlations (Rossberg et al., 2006) or foraging theory (Beckerman et al., 2006; Petchey et al., 2008) have been introduced; both approaches have connectance as an emergent property, while several input parameters are tuned using optimisation to provide a best fit to empiric webs.

A future challenge in topological food web research is to obtain models that also explain the link strengths contained in the flow-based food web description (Berlow et al., 2004; Wootton and Emmerson, 2005).

Dynamic food web models

Natural food webs are dynamical systems as predator-prey interactions and reproduction cause fluctuations in population abundances. To make predictive models for natural systems the topology thus have to be linked with population dynamics. The most challenging problem in this respect is stability, which is related to what makes species within a food web coexist (see McCann (2000) for details).

Research in dynamic food webs took off when May (1972) showed that linear stability becomes increasingly unlikely for increasing species richness or complexity (number of links per species). This was in direct conflict with the prevailing viewpoint that complexity would increase stability as consumers would have alternative food sources when species are lost in the system (Odum, 1953; MacArthur, 1955; Elton, 1958). Shocks from the discovery by May (1972) are still present today, which is surprising considering that it was early on shown that natural food webs are more likely to be stable than the random food webs considered by May (Yodzis, 1981).

Mainly two properties of empirical food webs have been found to be important in mediating stability: 1) weak links in the food web that dampen oscillations in population abundances (McCann et al., 1998; Neutel et al., 2002), and 2) the topological structure the food web (Yodzis, 1981).

Most links in natural food webs are found to be weak (Paine, 1992; de Ruiter et al., 1995; Wootton, 1997), and weak links may result from allometry in interaction strengths (Brose et al., 2006b). Species at high trophic levels tend to be more mobile in space, and can thus couple spatially separated channels that transfer energy from lower trophic levels – a property which has been shown to have a stabilising effect (McCann et al., 2005; Rooney et al., 2006). If an extra requirement of weak interactions is added these results actually fit well into the classical idea that complexity in energetic pathways buffers against dramatic changes in population abundances (Odum, 1953; MacArthur, 1955; Elton, 1958), suggesting that the current understanding of food web stability is not fundamentally different from the starting point.

The topology of a food web has a pronounced effect on stability as dynamic models, that receive a binary food web as input, show much higher degree of species persistence when realistic contrary to random food webs are used (Martinez et al., 2006). Recently it was found, that reduction of biomass flows with allometric interaction strengths does not have a stabilising effect on random networks, meaning that the topology of the web is important to enable mediation of stability from weak links (Kartascheff et al., 2010).

In addition to topology and link strengths Kondoh (2003) has shown that adaptivity in feeding links promotes stability, as predators then target the most abundant species. The adaptive process occurs at a faster timescale than populations dynamics. Prey switching can be modelled without recourse to multiple timescales by including the effect in the functional response (van Leeuwen et al., 2007).

Early dynamic models considered community modules, which can be subunits of whole networks or appear on their own in nature (Holt, 1997). Large food webs consisting of multiple modules can be stable if: 1) the individual modules are persistent on their own, or 2) the food web structure itself stabilise modules that cannot persist in isolation (e.g. Kondoh, 2008). Paper IV considers the community module ‘intraguild predation’ and shows, contrary to previous theoretical results, that it may persist on its own even at high resource levels.

Current approaches

Two approaches are used for combining food web topology and dynamic models. At present the most widely used approach is to generate a food web structure with a topological model, often the niche model, and use it as an input to the dynamic model that is simulated forward in time where some of the initial species are lost (Kondoh, 2003; Williams and Martinez, 2004; Brose et al., 2006b). The alternative to this top-down approach is to assemble communities using a bottom-up method where species-diversity build up over time as a consequence of sequential assembly and/or evolution (Paper II; Loeuille and Loreau, 2005; Rossberg et al., 2008; Zhang et al., 2011).

Table 1 compares current dynamic frameworks that have been evaluated against natural food webs. Common for the approaches is that they build on the energetic approach by Yodzis and Innes (1992). Bottom-up approaches have the advantage that they are useful for studies where the topology changes, whereas no straightforward methods exist in the top-down approach to e.g. determine the trophic relations of an alien species that tries invading a food web. Trophic interactions occur at the individual level, and this can only be handled if the size-structure of the populations is resolved in the model. Rossberg et al. (2008) and Paper II perform the most extensive comparisons to natural systems as e.g. biomass distributions are compared in addition to topological properties. Parameters in Loeuille and Loreau (2005) are difficult to determine from empirical data compared to the other approaches. Rossberg et al. (2008) contains many parameters, where some can be estimated while other require model calibration to enable realistic communities. In comparison all parameters in the models by Brose-Williams-Martinez and Paper II can be estimated from ecological data and processes. Some of the model frameworks rely on interference competition or prey switching to obtain large and stable communities.

Table 1: Comparison of dynamic food web frameworks. See text for descriptions of framework and criteria for comparison.

	Brose, Williams, Martinez	Loeuille & Loreau	Rossberg et al.	Paper II
Emergent topology		✓	✓	✓
Resolves size-structure				✓
Validated empirically	(✓)†	✓	✓	✓
Easy to parameterise	✓			✓
Performs without:				
interference competition	✓		✓	✓
prey switching		✓		✓

†This model has not been compared with empirical webs, but Martinez et al. (2006) compared some model web properties with the niche-model (Williams and Martinez, 2000).

These processes definitely occur in nature, but especially the relative importance of interference is difficult to assess from data. Models that can produce large and stable food webs without recourse to additional stabilising processes are preferred due to their simplicity (cf. Hypothesis testing).

Emergent topology from individual interactions

The framework in this thesis considers trophic interactions at the individual level. Individual interaction strength depends on the spatial overlap between the predator and prey populations, and the size of the prey relative to the predator individual (Paper II). Interactions at species-level in the model thus emerges as the product of all interactions that the individuals within the species are involved in.

Communities are assembled by sequentially allowing a new random species to invade from a low initial biomass, and simulating the model forward in time whereby population dynamics will either push the species to extinction or allow establishment (Post and Pimm, 1983; Drake, 1990; Law, 1999). Species, which are characterised by the traits size at maturation m_* , preferred predator-prey mass ratio β_i , and location x_i , are drawn randomly by selecting (m_*, β_i, x_i) from random distributions. The first species enters an environment comprised only by resources, and subsequent successful invasions either augment the community or cause community reconfigurations, where some of the resident species are excluded. After about a thousand invasion attempts the number of species reaches a plateau around which species richness fluctuates when additional species invade (Paper II).

Fig. 5 shows an example of a community that results from community assembly. The carrying capacity of resources is constant across the spatial landscape, and the resource dynamics at each point in space is described with semi-chemostatic growth (Paper II). Consequently only individuals that are closely located in space will compete for resources – which species that compete for resources can be seen in Fig. 6. All individuals irrespective of species identity consume only resources in the earliest life-stages, but between 10^{-2} g and 1 g individuals start consuming other species as the resources become too small (cf. Fig. 2). The example clearly illustrates how the individual-level prey-encounter model naturally leads to ontogenetic niche shifts when individuals grow in size. The frequency distribution of different prey in the stomach of an individual is the product of prey abundances and interaction interaction strength. It is noted that individuals engage in many weak interactions with other species, and that cannibalism never is the dominating food source even though a species naturally always has the largest spatial overlap with its own population. The reason for this is two-fold: 1) species have similar total biomass irrespective of m_* (Paper II), but as small sized m_* species have their biomass distributed over a more narrow size range they offer a higher biomass for larger predators, and 2) species richness is a decreasing function of m_* , which additionally increases the total biomass offered by species with small m_* .

Stability in the model may be mediated through spatiality in at least three manners: 1) space reduces the intensity of resource competition among species, 2) as

only the overlapping part of populations can interact space assists in enforcing weak links, and 3) large mobile predators couple spatially separated energy channels (McCann et al., 2005). Additionally differences in preferred predator-prey mass ratios β_i of species at different locations result in varying transfer speeds of energy from low to high trophic levels – an asymmetry that has been shown to contribute to stability (Rooney et al., 2006). Differences in β_i also enable higher trophic level species more easily, as the different β_i secures a more steady energy supply to high trophic level species.

From a species perspective the many different weak links in different life-stages may be hypothesised to mediate coexistence as well, which however is contradicted by a recent study by Rudolf and Lafferty (2011) that showed that ontogenetic niche shifts reduces the persistence of species in food webs. Their description of individual life-history omnivory is however extremely simplified, and it would be interesting to test the role of niche shifts on stability in the current framework that accounts realistically for the relevant processes.

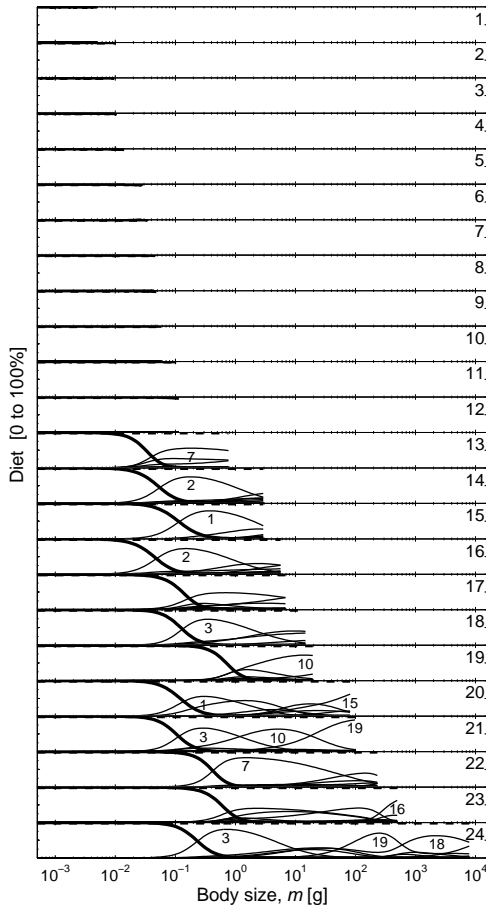


Fig. 5: Diet composition as a function of body mass m for each of 24 species within a community. Species are ordered from small to large m_* vertically. The smallest species only consume food from the resources (thick lines). Thin lines indicate diet from other species, and diets exceeding 50% are marked with the species number of the prey. The shown diet composition is the time-averaged composition.

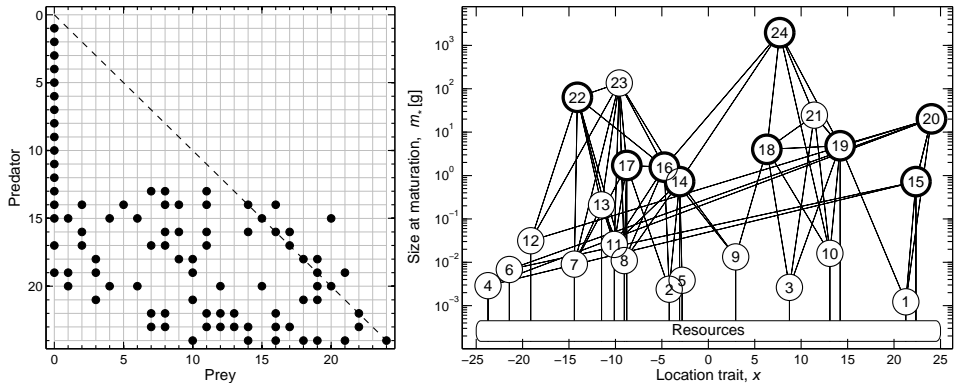


Fig. 6: Food web matrix (sorted by m_*) and network diagram. Species marked with thicker line widths are cannibalistic. The food web is obtained by sampling stomachs in individuals larger than $10^{-2}m_*$ in Fig. 5. A link to a prey is included if the prey constitutes more than 5% (link threshold) of the total diet in a sampled predator stomach.

The resulting interaction pattern seems complicated (Fig. 5), but it should be noted that it is only a result of spatial overlaps, size-dependent food selection, and relative abundances of prey populations. Paper I shows that e.g. the biomass distribution of the dynamic food web model can be approximated with an analytical solution of the food web framework, which can be obtained when species have identical preferred predator-prey mass ratios $\beta_i = \beta$, and the community spectrum, from which the individuals retrieve food and experience mortality, is assumed to follow a power law. The analytical approximation thus provides a baseline expectation of the results of complex food web simulations.

Measuring food web topology

When discussing problems associated with characterising natural systems with a species-level food web matrix Woodward et al. (2010) note: “*Whilst the concept of a food web is simple, their empirical representation is neither straightforward nor singular*”. Fig. 5 clearly illustrates this problem: To obtain a food web matrix from this model community one have to sample the community, and the topology of the matrix will depend on the sampling method. Fig. 6 shows how the resulting food web will look if all individuals from a certain fraction of their maturation size is sampled.

Paper II examines how the topological properties of the model webs vary depending on sampling method and link threshold. Paper II additionally compares the emergent organisation of food web structure, species diversity, abundance, and biomass distributions with empirical data. From the available data it is not possible to falsify the model webs as being representatives of natural food webs, as they resemble both topology and internal organisation of natural food webs.

Hypothesis testing

Empirical data are used for testing hypotheses. Collecting data for testing community level hypotheses is a time-consuming process that lasts several years. It is thus critical that the right kind of data is collected. Scientific progress in food webs has undergone paradigm shifts when problems with empirical data has been identified in the subsequent analysis process. The first generation of food webs suffered from too poor resolution and bias in sampling efforts across trophic levels, where the second problem persisted in a second generation of food webs (Martinez, 1991; Cohen et al., 1993; Dunne, 2009). At present it is recognised that to move our understanding of food webs forward a shift from binary to flow-based food web descriptions is needed, which calls for reliable and comparable methods for measuring interaction strengths (Berlow et al., 2004; Wootton and Emmerson, 2005). Additionally it is recognised that body size has to be incorporated into food webs such that the ecological characteristics of different life-stages are captured (Cohen et al., 2003; Woodward et al., 2010).

The framework in this thesis is based on individual-level processes, and may be analysed at multiple levels of organisation: 1) community level, 2) species level 3) trait level, and 4) the individual level. Thus one can sample everything from stomach contents to distribution of biomass across species, trophic levels, and body size. Analysing results obtained through sampling in the individual-based food web framework corresponds to the process of analysing results obtained through sampling in real ecosystems, with the exception that the model can be sampled without sampling errors and constraints on duration of fieldwork and budget. Realistic models are therefore valuable tools for testing hypotheses before embarking on large scale field work, as they can e.g. assist in designing experiments and determining which kind of data that will be needed in the subsequent analysis phase. Oppositely, it is critical that model builders interact with empirical ecologist to ensure, that their models utilises processes and parameters that can be quantified from ecological data.

Trustworthy models for testing hypotheses should be based on ecological processes as opposed to e.g. having food web structure as an input. Food webs are emergent properties, and models lacking a bottom-up approach for trophic interactions are not suitable for species invasion experiments where individual-based processes are needed to describe the trophic relations of the invading species. Models should additionally employ as few stabilising mechanisms as possible, as this allows assessment of the mechanisms importance once they are added.

Concluding remarks

The motivation for developing the current food web framework was that it should be possible to obtain realistic dynamic community models by including individual life-history and individual-level properties. Similarly Petchey et al. (2008) has the process-based motivation that it should be possible to use optimal foraging theory to obtain food web topologies that resemble natural webs. However, as Petchey et al.

(2008) use optimality to determine which prey species a predator species should interact with, the approach taken in this thesis is quite different: individuals ignore species identity and considers only relative prey size when targeting prey. The results of Paper II show, that when individual life-history is included in population dynamics a species-neutral prey encounter model leads to food web structures that are similar to natural webs. This raises an interesting question: To which degree are feeding patterns the result of adaptive processes, and to which degree are the patterns simply a reflection of morphological compatibility between prey and predator superimposed on the relative abundances of prey that are spatially available to the predator?

The current work can be considered as an advancement of the metabolic theory ecology (MTE, Brown et al., 2004) as the foundation is the energetics of metabolism and the goal is to explain ecological patterns at species- and community-level. Compared to the MTE framework the current approach can additionally explain diversity distributions, food web structure, and biomass structure within populations. This level of detail is achieved through a synthesis of several ecological approaches: life-history, individual-level bioenergetics and food encounter models, allometry, size-structured population dynamics, community assembly, and trait-based species definitions.

The approach taken in this thesis may serve as a starting point for a process based ecosystem model. Needed enhancements would be nutrient cycling through a more realistic nutrient based resource model, that is fed by nutrients from dead material, and an external energy source representing sunlight. Additionally ecological processes should depend on abiotic physical factors as temperature and salinity. Stoichiometry is known to affect species composition (Hall, 2009), and incorporating stoichiometric constraints into the bioenergetic processes should be considered, as this may assist in mediating food web stability as nutrients originate from different channels of varying strength.

In conclusion a food web framework that is driven by individual-level processes has been developed, and validated with empirical data on food web topology as well as empirical data on diversity and biomass distributions. It is worthwhile noting that no calibration of parameters has been performed, and that all model parameters are obtained from the literature. Conceptual simplicity has been obtained in the framework, without sacrificing ecological realism, rendering the approach useful to tackle important problems as e.g examining the consequences of species invasions (Elton, 1958) and extinctions (Borrvall et al., 2000; Lundberg et al., 2000) in large, complex, and realistic food webs.

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Food Web Ecology

Summary of papers

This thesis consists of six papers (Fig. 1, pp. 11), where Paper I defines a food web framework based on individual-level processes, and Paper II extends this framework by including a spatial distribution of individuals within a species. Papers II-VI demonstrate the utility of the framework by contributing to fundamental ecological theory (Paper II-IV and VI), and by applying the framework to examine community-level effects of commercial fishing (Paper V). This summary briefly summarises the six papers and discusses their main findings.

Food web framework

Paper I introduces a food web framework for size-structured populations. This enables an ecological approach to food web modelling as the individual life-history from birth, through maturation, and ultimately death is explicitly resolved with the use of individual-level bioenergetics. Individuals select prey items of a suitable size, which can be popularised as “big ones eat smaller ones”. This allows individuals to change diet throughout life (life-history omnivory) contrary to having a fixed diet. In the framework individual food consumption leads to growth in body size, and allocation to reproduction, which drives the population dynamics as opposed to instantaneous population increase in unstructured food web models. Use of allometry in the individual-level processes, and characterisation of species with the trait size at maturation m_* enables a species neutral parameter set – i.e. it does not include species-specific parameters. The model is parameterised for fish communities as these constitute a common and widespread system type where species have a large size difference between offspring and adult. Parametrisation for other taxa and system types is naturally possible. When species are characterised solely by the m_* trait it is not possible to obtain communities having more than three species (Supplementary). To overcome this we introduce randomly chosen coupling strengths between species. Size-dependent food selection still govern who-eats-whom, but the interactions strengths are reduced by the species couplings. This heterogeneity enables larger food webs, which are simulated and analysed at four levels of organisation: community level, species level, trait level, and individual level. We show that the food web model may be solved analytically when the community spectrum is assumed to follow a power law using a similar procedure as in equilibrium size-spectrum theory (Andersen and Beyer, 2006), but obtain slightly different results as we explicitly account for standard metabolism. The analytical solution provides a baseline expectation of the results of complex food web simulations, and agrees well with the simulations of the full model.

Paper II extends the food web framework by assuming that populations are spatially distributed. In addition to m_* the traits used to characterise a species

are extended to include also preferred predator-prey mass ratio β_i , and the centre of the populations' spatial distribution x_i . The extra traits eliminates the need for the random species couplings. Differences in β_i allow individuals of equal size from different species population to utilise slightly different niches, which assist in enabling species diversity. Having different β_i also enables high trophic level species more easily, as the different β_i species constitute channels that secure a more steady energy supply to high trophic level species. Spatiality contributes to food web stability, as it 1) reduces the intensity of resource competition among species, 2) weakens the possible interaction strengths since only the overlapping part of populations can interact (McCann et al., 1998), and 3) large more mobile individuals couple spatially separated 'channels' that transfer energy from low to high trophic levels (McCann et al., 2005) – these channels may be constituted by different β_i species meaning that they transfer energy with varying speed, which can increase stability further (Rooney et al., 2006). Large food webs are formed through sequential community assembly.

Comparison with natural systems

Assembled model communities are compared with natural food webs, and it is found that both their topology and internal organisation of diversity and biomass distributions comply with empirical data (Paper II). This demonstrates that individual-level food encounter and prey-selection from the rule 'big ones eat smaller ones' leads to complex and realistic food webs.

A food web is said to be interval if the species can be ordered such that the food web matrix have adjacent connections in all rows simultaneously (Cohen, 1977). Natural food webs are close to interval (Stouffer et al., 2006), which has been hypothesised to be the result of a one-dimensional niche space (Cohen, 1977) where body size has been shown to account for a significant degree of the observed intervality (Zook et al., 2011). Recently the one-dimensional hypothesis has been challenged as non-intervality has been shown to be most pronounced at intermediate dimensionality, and that the degree of non-intervality hereafter is a decreasing function of dimensionality (Rossberg et al., 2010).

Non-intervality of the model webs in this thesis is within the range observed in natural food webs (Paper II). The degree of non-intervality in empirical food webs have previously been ascribed to phylogenetic correlations (Cattin et al., 2004), whereas Paper II and Fig. 6 demonstrates that observed diet discontinuities additionally can stem from the spatial organisation of the community. This hypothesis could be tested by comparing species diets across communities that have a similar species composition, but differences in internal spatial distribution of species.

Application: The many-small-eggs strategy of the fishes

Paper III uses the analytical solution of the framework (Paper I) to examine the viability of the many-small-eggs reproductive strategy of the fishes. The viability is examined by calculating the lifetime reproductive success as a function of asymptotic

body size, which is compared to the number of offspring needed to sustain the population. This reveals that both lower and upper limits to asymptotic size exist, beyond which the lifetime reproductive success is too low to support the population. The upper limit is quite high, meaning that lifetime reproductive success effectively is an increasing function for the relevant range of asymptotic sizes. The lower limit suggests, that the reason why predominantly smaller fishes turn to parental care is, that the reduction in mortality is absolutely crucial, contrary to the case in larger species, to the feasibility of their reproductive strategy.

Application: Understanding intraguild-predation

Intraguild predation (IGP) is a form of omnivory where a predator competes for a shared resource with a consumer while also preying on the consumer (Polis et al., 1989). The feeding relations of an individual often change during ontogeny, and IGP may emerge as a consequence of this life-history omnivory: species, which change body size and diet throughout ontogeny, may compete for a shared resource in early life-stages, and predate on the competitor in the adult life-stage (Werner and Gilliam, 1984; Mylius et al., 2001). As IGP naturally emerges in the size-structured framework it is ideal for making a general analysis of IGP.

Paper IV resolves the discrepancy between empirical data and theory in IGP: theory predicts that consumers and predators involved in IGP can only coexist at intermediate resource levels, as the predator will exclude the consumer at high resource levels (and vice versa at low resource levels, Holt and Polis, 1997; Mylius et al., 2001), which stands in striking contrast to empirical studies showing that IGP coexistence occurs at high resource level as well as being a widespread interaction type (Arim and Marquet, 2004; Amarasekare, 2008). Paper IV agrees with earlier theoretical models in the respect that a given species pair only can coexist in a finite resource range, but through examination of the trait space spanned by the consumer and predator Paper IV demonstrates that coexisting species pairs can be found for all resource levels. Such an examination is not feasible with the typical species-based approach, as the parameter space that needs to be examined for coexistence is high-dimensional.

Large food webs may be constituted by several interconnected community modules as IGP (Holt, 1997). Large food webs can be stable if: 1) the individual modules are stable on their own, or 2) the food web structure itself stabilises modules that cannot persist in isolation (e.g. Kondoh, 2008). Paper IV demonstrates that the IGP module can persist on its own, suggesting that it may assist in maintaining species richness when it is embedded in a food web.

Application: Linking fisheries science with community ecology

In Paper IV we use the analytical solution of the framework to combine fisheries science and community ecology. The study provides a theoretical understanding of empirically observed relationships between natural mortality, growth, and production rates. More specifically we relate the von Bertalanffy growth constant K to

asymptotic body size and show that natural mortality and productivity are proportional to K . The derivation of productivity, along with the derivation of growth and trophic efficiency by Andersen et al. (2009), provide a complete link between energetic descriptions of communities (Lindeman, 1942) and analytical size-spectrum theory (Paper I; Andersen and Beyer, 2006).

Application: Community-level effects of fishing

Paper V employs the size-structured framework to examine community-level effects of fishing. We find that the response of the community goes beyond the trophic range targeted by the fishery, as the harvesting initiates a trophic cascade that may propagate both downwards and upwards in trophic levels. Fishing mostly causes a reduction in biomass in the fished range, but the overall size spectrum slope do not change. Empirical detections of slope changes do however appear, as such studies base the estimation of spectrum slope on data from the fished range (Shin et al., 2005). If ecosystem-wide fishing is employed (fishing on most size groups) the biomass is seen to respond both positively and negatively in different trophic ranges, and the signature of the trophic cascade is less pronounced. Harvesting effects on upper trophic levels can still be devastating with ecosystem-wide fishing, but the response of the ecosystem as a whole may be less drastic in terms of reconfiguration of biomass distribution across trophic levels – suggesting that exploitation pattern may affect whether trophic cascades are empirically detected. This additionally suggests that ecosystem-level fishing patterns should be considered in management to avoid substantial changes in the biomass composition across trophic levels, which may have severe consequences that in worst case can lead to species extinctions. A recent study uses the model of this study to investigate the effects of rebuilding plans of exploited communities (Andersen and Rice, 2010).

Paper V employs stock-recruitment relationships to avoid problems of food web stability while maintaining minimal model complexity. In the full model stock-recruitment is an emergent property, and it would be interesting to reexamine the effects of harvesting in the model communities resulting from Paper II.

Final remarks

It is worthwhile noting that no calibration of parameters is employed in the modelling framework, and that all model parameters are obtained from the literature (Paper I). The framework thus provides an easy method of generating large and complex communities that share properties with empirical food webs (Paper II).

Paper III-VI employs the framework from Paper I and clearly demonstrates the utility of the framework by contributing to the understanding of a wide range of problems: 1) the life-history of the fishes, 2) the presence of IGP at high resource levels in nature, 3) providing a theoretical underpinning of empirical relationships in fisheries science, and 4) providing insight to indirect community-level effects of commercial fishing.

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Supplementary

Assembly of food webs with m_* species

In the model from paper IV a species is solely defined by the trait size at maturation, m_* . This can be considered a minimum model of a food web with size-structured species populations. In the model individuals of a species grow during ontogeny and utilise increasingly larger resource items (cf. Fig. 2, pp. 14). How many species can coexist on the continuum of resources provided by the resource spectrum? One hypothesis is that only one species should be able to persist on the resource, and another is that the intricate trophic interactions, that depend on the size composition of the resource spectrum and the competing species, would allow several species to coexist. If the second hypothesis is true: how many species can coexist?

To examine this I allow one species to invade the pristine system constituted by the resource spectrum (Fig. S1.A, parameters from paper I and IV are used). When the species invades the fitness landscape changes, and allows larger species to invade as the newly established species provides larger food items (S1.B). As the system builds up large portions of the fitness landscape remains positive, indicating that additional invasions are possible (S1.B-D1). In other words: the system does not enter an evolutionary stable endpoint as the fitness landscape remains open (positive). Additional invasions cause extinctions of residents, and communities with more than three species are rarely encountered (Fig. S2). If the resource spectrum is shortened, or if the resource level is decreased, then only two smaller species can

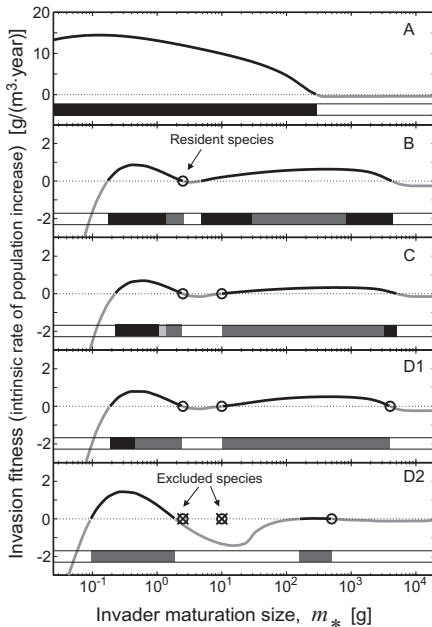


Fig. S1: Invasion fitness landscapes for the initial buildup of a community having (A) no species, (B) one resident; $m_1^* = 2.5$ g, (C) two residents; m_1^* and $m_2^* = 10$ g, (D) three residents; m_1^* , m_2^* , and $m_{D1}^* = 4$ kg, and (D2) one resident; $m_{D2}^* = 500$ g. Under each landscape it is denoted whether invasion by a species with a given m_* leads to coexistence (black), exclusion of one of the resident species (dark grey), exclusion of one of the resident species and the invader (light gray), or if the invader cannot invade (white).

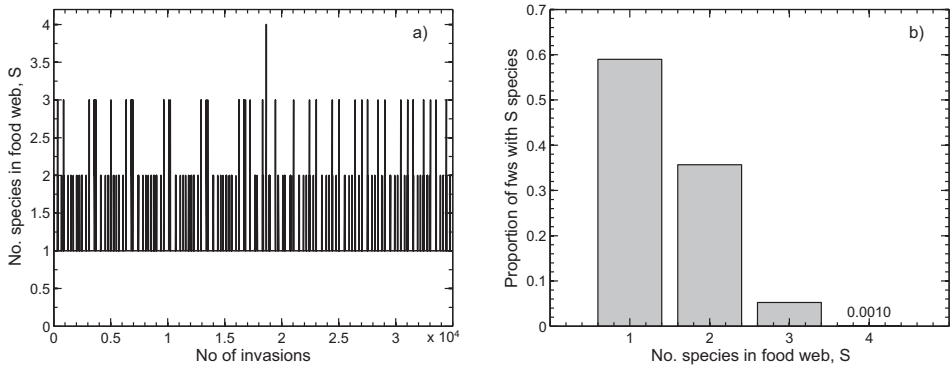


Fig. S2: Assembly from randomly selected m_* species. a) Community build-up (35,000 invasion attempts), and b) community size distribution (produced from 1026 stable food webs, average community size: 1.46).

coexist. Numerous experiments (not shown) have been performed where more than three species were rarely encountered if the preferred predator-prey mass ratio was not reduced substantially. In conclusion: a maximum of three species defined solely by m_* are expected to coexist on the resource spectrum.

Exotic phenomena

When examining the assembly process (Fig. S1) one notices a peculiar scenario: the invader can initially invade (positive fitness landscape), but this invasion causes a re-configuration of the community resulting in exclusion of one resident and the invader (Fig. S3). This phenomena is known as 'resident strikes back', as the biomass from the invader allows the resident to reach an alternative attractor through changing its size-spectrum composition (Fig. S4; Mylius and Diekmann, 2001). Thus: invasion does not necessarily imply fixation, meaning that one have to turn to simulations to be sure of the outcome of a potentially feasible invasion.

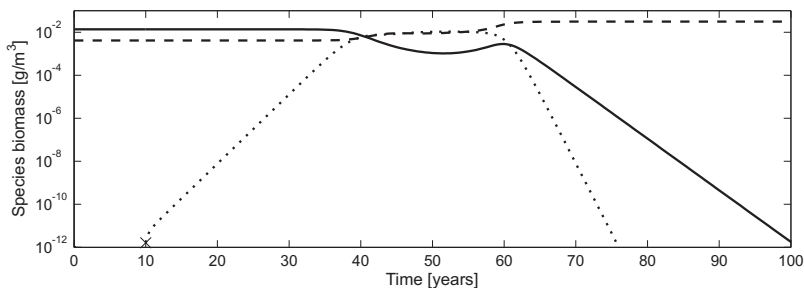


Fig. S3: Example of invader induced attractor shift (IIAS). Time evolution of the biomass of two residents ($m_1^* = 2.5$ g solid, and $m_2^* = 10$ g dashed lines), where an invader ($m_I^* = 1.5$ g, dotted line) invades and causes a reconfiguration of the community.

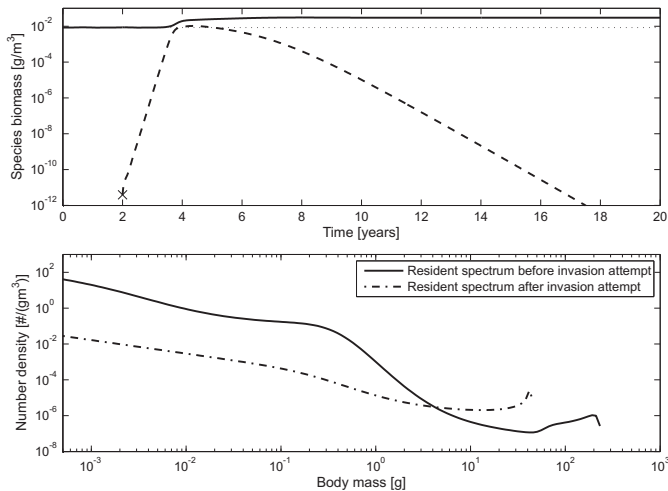


Fig. S4: Example of IIAS or 'resident strikes back' with one resident species ($m_* = 55$ g). Upper plot: time evolution of biomass for resident (solid line) and invader ($m_* = 5$ g, dashed line). Lower plot: size-spectrum of the resident before (solid line), and after the invasion attempt (dash-dotted line).

Alternative stable states (Fig. S5) are briefly examined in paper IV to obtain a qualitative description of different coexistence states. The two species coexistence diagram in paper IV, may be enhanced to include the outcome in the cases where coexistence is not possible. Such a diagram (Fig. S6) resembles pairwise invasibility plots (PIPs) used in evolutionary ecology (van Tienderen and de Jong, 1986). I term these plots pairwise invasion diagrams (PIDs), as they show the outcome of the invasion rather than whether the invader can initially invade. Obtained PIDs (Fig. S6) show that regions where invader induced attractor shift occurs are not widespread, and can thus be considered an exotic phenomena.

PIDs are similar to PIPs, and can thus be used to predict the direction of evo-

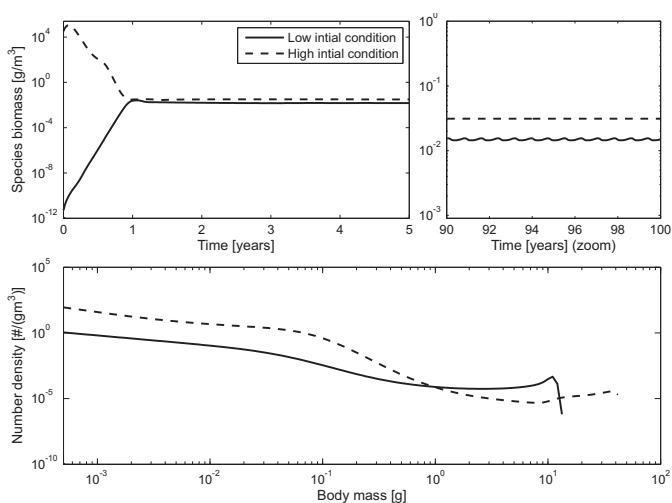


Fig. S5: Example of an alternative stable state ($m_* = 10$ g). Through invasion in small numbers the 'normal' state is reached (solid line), and introduction in high numbers allows the species to reach an alternative stable state (dashed line). Upper plot: time evolution of the species' biomass. Lower plot: size-spectra for the two states.

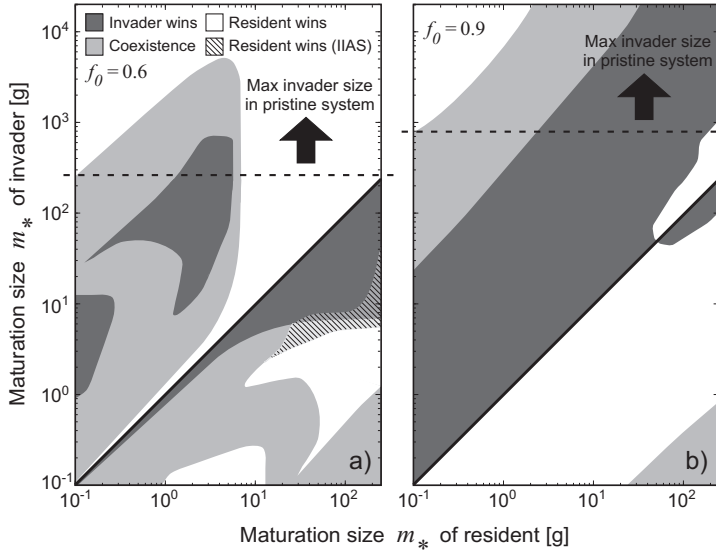


Fig. S6: Pairwise invasion diagrams (PIDs) showing the outcome of an invasion into a system having one resident species. a) PID for medium resource level ($f_0 = 0.6$), and b) high resource level ($f_0 = 0.9$). PIDs show regions of co-existence (light grey), where invader excludes the resident (dark grey), where invasion is impossible (white), and where IIAS are present (hatched). The dashed line shows the maximum invader size that can invade a pristine community.

lution. In the case of medium resource level (Fig. S6.a) a single species will evolve towards smaller size at maturation m_* , as mutant (invader having a m_* close to the resident) invasions will replace the resident when the mutant's m_* is smaller than the resident's m_* . In resource-rich environments (Fig. S6.b) small residents will evolve towards larger m_* , and large residents will evolve towards smaller m_* ; at a size around 50 g the species reaches a singular point, where evolution can either come to a halt or cause speciation (Geritz et al., 1998).

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Popular scientific summaries

Food Web Ecology

Martin Hartvig, Lund University, 2011

Popular scientific summary of doctoral thesis

Individuals shape complex food webs in nature

A food web is a network diagram that describes which species that eat each other in nature. Such networks in marine environments e.g. show that cod eat herring, sprat, and sandeel – and that these eat numerous other species. Understanding of these relationships is a fundamental scientific problem, which can be used to assess the consequences for the stocks when we e.g. fish cod for New Years eve, herring for the Christmas table, and sandeel for animal feed.

When diving into the ocean you are quickly overwhelmed by complexity. A cod is not just a cod. There is small cod, large cod, and cod larvae, which are tiny cods that have just hatched from their eggs. The larvae eat copepod eggs, the smaller cods feast on crustacea on the ocean floor, and the larger cods pursue smaller fish as sandeel, sprat, and herring.

To understand this complexity we have to consider the individuals instead of species as more systematic patterns then emerge: small individuals eat small prey, and large individuals eat large prey.

When individuals reach adulthood they start reproduction. The difference between “small” and “large” species is that they reach adulthood at different body sizes. Herring reach the adult stage at a small size, where growth stops as energy is spend on reproduction instead of growth. Correspondingly, this happens at a larger body size for cod.

From the simple rule ‘big ones eat smaller ones’ we have formulated a mathematical model of individuals’ life-history and their food intake from the larvae stage, through the juvenile stage, to the adult stage, where they start reproducing and thus contributes to their species population (Paper I). This conceptually simple model results in food webs that resembles natural food webs, allowing us to conclude that complex natural food webs result from simple individual-level interactions (Paper II).

Fish has a peculiar reproductive strategy, as they produce many small eggs that are left alone from the beginning. This stands in striking contrast to mammals, who produce few larger offspring which they care for. With the use of the mathematical model we show that the strategy of the fishes is advantageous for them, but that a lower boundary of adult body size exists, below which the strategy becomes problematic (Paper III). Eggs cannot be arbitrarily small, which renders the many-small-eggs strategy disadvantageous to e.g. the stickleback, as the size of the eggs and the stickleback itself prohibits production of many eggs. To compensate for this the stickleback has evolved parental care as the mammals: The male stickleback builds a nest, where the female spawns, after which the males guards the nest till

the eggs hatch. By doing this the stickleback reduces mortality for the population as a compensation for the missing eggs.

In nature species compete for food. If two species share prey, the one which is best at capturing prey will outcompete the other. If one of the species has a larger adult body size the large one can eat the smaller one, while they compete for food in the early life-stages. The two species can only coexist if the smaller one is better at capturing food in the early life-stages. This constellation is termed 'intraguild predation', and in nature it occurs in environments with both low and high productivity. Our model explains coexistence in both environments (Paper IV), whereas contemporary models fail to describe the coexistence in high productivity environments.

Fisheries biologists use a set of numbers as e.g. natural mortality, which is the mortality not stemming from fishing, to assess how many tonnes of fish that can be harvested without damaging the stock. Our model can be used to relate these numbers to individual-level processes, which allows estimation of natural mortality from fish consumption and body size (Paper VI). This increases the confidence to the assessment models, as the numbers used for the model can be cross-checked using different methods.

Models used in stock assessment are predominantly based on management of single stocks, meaning that they cannot manage ecosystems as a whole. Using our mathematical model we show how marine ecosystems respond when multiple species are fished intensively (Paper V). By adjusting the fishing level on large and small species it is possible to avoid reconfiguration where some species reach a higher biomass while other species experiences a reduction of biomass, which renders them vulnerable to extinction.

In addition of providing an understanding of how natural ecosystems are organised, the model developed in this thesis can also be used to establish models for multi-species fisheries, which may help ensure future presence of cod for New Year, and herring that can be washed down with snaps at Christmas.

Food Web Ecology

Martin Hartvig, Lund Universitet, 2011

Populärvetenskaplig sammanfattning av doktorsavhandling

Individer formar komplexa födovävar i naturen

En födoväv är ett diagram som beskriver vilka arter som äter vilka i naturen. I sådana diagram ser man till exempel att torsk livnär sig på sill, skarpsill och tobis och att dessa i sin tur livnär sig på ett otal andra arter. Att förstå sådana sammanhang i naturen är dels ett grundläggande vetenskapligt problem och dels nödvändigt för att förstå vilka konsekvenser det kan få för olika fiskbestånd när vi till exempel fiskar torsk till nyårsmiddagen, sill till julbordet eller tobis till djurfoder.

Om man dyker blir man snabbt överväldigad av komplexiteten i havet. En torsk är inte bara en torsk. Det finns liten torsk, stor torsk och torsklarver som är pyttesmå torskar som just har kommit ut ur äggen. Larverna äter ägg från vattenloppor, små torskar äter kräftdjur från havsbotten och större torsk försöker få fatt i mindre fiskar som tobis, skarpsill och sill.

För att förstå denna komplexitet måste man betrakta individer snarare än arter då mer systematiska sammanhang synliggörs: små individer äter små byten och stora individer äter stora byten.

När de enskilda individerna blir könsmogna börjar de reproducera sig. Skillnaden mellan "små" och "stora" arter är att de blir könsmogna vid olika storlekar. Sillen blir könsmogen vid små storlekar vilket gör att de slutar växa, till följd av att energin används till reproduktion i stället för tillväxt. Motsvarande könsmognas torsk först vid större storlekar.

Med utgångspunkt i den enkla regeln att 'stora äter små' har vi formulerat en matematisk modell av individers livshistoria och födointag från larvstadiet, via ungfiskstadiet till vuxenstadiet, där de reproducerar sig och bidrar till hela artens population (Artikel I). Denna konceptuellt enkla modell visar sig kunna reproducera födovävar som liknar födovävar vi ser i naturen. Därav drar vi slutsatsen att naturens komplexa nätverk är ett resultat av interaktioner på individnivå (Artikel II).

Fisk har en säregen reproduktionsstrategi eftersom de producerar många små ägg som måste klara sig själva från början. Detta i kontrast till exempelvis däggdjur som får ungar i mindre antal men som tas omhand bättre. Genom att använda den matematiska modellen visar vi att fiskens strategi är fördelaktig, men att det finns en gräns för hur liten kroppsstorlek en art kan ha utan denna strategi blir problematisk (Artikel III). Det finns gränser för hur små äggen kan vara och på grund av detta är strategin med många små ägg inte fördelaktig för exempelvis spiggen eftersom storleken på äggen och kroppsstorlek gör att den inte kan producera tillräckligt med ägg. För att kompensera för detta har spiggen anpassat sig evolutionärt till att ta hand om sina ägg precis som däggdjuren: Han-spiggen bygger ett bo där honan

lägger äggen och sedan vaktar hannen äggen tills de kläcker. På detta sätt reducerar spiggen dödligheten för populationen som kompensation för lägre äggproduktion.

I naturen konkurrerar arter om föda. Om två arter livnär sig från samma byte kommer den som är bäst att fånga och utnyttja bytet att konkurrera ut den andra. Om den ena arten har en större kroppsstorlek än den andra, kan de två arterna konkurrera om föda i tidiga livsstadier, medan den större arten kan äta av den mindre arten i senare livsstadier. De två arterna kan samexistera om den mindre arten är bättre än den större på att utnyttja födan i tidiga livsstadier. En sådan konstellation kallas för 'intraguild predation' och återfinns i naturen i miljöer med både hög och låg näringsstillgång. Vår modell kan förklara denna typ av samexistens i bägge dessa typer av miljöer (Artikel IV). Andra modeller kan bara förklara samexistensen i näringsfattiga miljöer däremot.

Fiskeribiologer utnyttjar ett antal mått för att utforma skötselplaner som berör hur många ton fisk som kan fiskas utan att överutnyttja bestånden. Ett sådant mått är exempelvis naturlig dödlighet, det vill säga sådan dödlighet som inte beror på fiske. Vår modell kan användas för att relatera sådana mått till processer på individnivå så att exempelvis den naturliga dödligheten kan beräknas från fiskens födointag eller kroppsstorlek (Artikel VI). Detta ökar trovärdigheten i de modeller som används i fiskerivården eftersom de måtten modellen utnyttjar kan kontrolleras med olika metoder.

De modeller som används inom fiskerivården är i stor utsträckning baserade på att man har en separat modell för varje art sig, men ingen modell för hela ekosystemet. Med vår matematiska modeller visar vi hur marina ekosystemen påverkas när flera olika arter fiskas intensivt samtidigt (Artikel V). För att anpassa fisket på stor och liten fisk arter kan man undvika att bestånden hos vissa arter växer explosionsartat medan andra riskerar att dö ut.

Modellen som studeras i denna avhandling har med andra ord flera tillämpningsområden. Dels kan den användas för att besvara grundläggande frågor om hur naturen fungerar, och dels kan den inspirera till utveckling av ekosystembaserade modeller till anpassning av fisket på olika arter, så att vi även i framtiden kan ha torsk på nyårsafton och sill till julsnapsen.

Food Web Ecology

Martin Hartvig, Lund Universitet, 2011

Populærvidenskabeligt resumé af Ph.D.-afhandling

Individer former komplekse fødenetværk i naturen

Et fødenetværk er et diagram, der beskriver hvilke arter der spiser hinanden i naturen. I sådanne diagrammer ser man f.eks. at havets torsk spiser sild, brisling, og tobis – og disse et utal af andre arter. At forstå sådanne sammenhænge i naturen er et helt grundliggende videnskabeligt problem, som kan bruges til at forstå hvilke konsekvenser det kan få for bestandene, når vi f.eks. fisker torsk op til nytårsbordet, sild til julebordet, eller tobiser til brug i dyrefoder.

Hvis man dykker ned i havet, bliver man hurtigt overvældet af kompleksiteten. En torsk er ikke bare en torsk. Der findes små torsk, store torsk og torskelarver, som er bittesmå torsk der lige er kommet ud af deres æg. Larverne spiser vandloppeæg, de små torsk guffer krebsdyr fra havbunden, og de større torsk vil forsøge at få fat i mindre fisk som tobis, brisling, eller sild.

For at forstå denne kompleksitet er vi nødt til at betragte individer fremfor arter, da mere systematiske sammenhænge så kommer til syne: små individer spiser små byttedyr, og store individer spiser store byttedyr.

Når de enkelte individer bliver voksne begynder de at reproducere sig. Forskellen mellem “små” og “store” arter er, at de bliver voksne ved forskellige størrelser. Silden bliver voksen ved en lille størrelse, hvor væksten stopper fordi energien bruges på reproduktion i stedet for vækst. Tilsvarende sker dette først ved en større størrelse for torsken.

Med udgangspunkt i den simple regel at ‘de store spiser de små’ har vi formuleret en matematisk model af individens livshistorie og fødeindtag fra larvestadiet, via ungfiskstadiet, til voksenstadiet, hvor de reproducerer sig og bidrager til den samlede artspopulation (Artikel I). Denne konceptuelt simple model viser sig at resultere i fødenetværk mellem arter som ligner de fødenetværk vi ser i naturen, hvormed vi kan konkludere at naturens komplekse netværk er resultatet af simple interaktioner på individniveau (Artikel II).

Fisk har en speciel reproduktionsstrategi, da de producerer mange små æg, som må klare sig selv fra begyndelsen. Dette står i skærende kontrast til blandt andet pattedyr, som får et lille antal større unger de passer godt på. Ved at anvende den matematiske model viser vi at fiskenes strategi er fordelagtig for dem, men at der findes en grænse for, hvor lille en voksenkropsstørrelse en art kan have før strategien bliver problematisk (Artikel III). Der findes grænser for hvor små æg kan være, og pga. af dette er strategien med mange små æg ikke fordelagtig for f.eks. hundestejlen, da størrelsen af æggene og dens egen kropsstørrelse gør, at den ikke kan producere nok æg. For at kompensere for dette har hundestejlen tilpasset sig evolutionært ved at udvikle forældrepleje som ved pattedyr: Han-hundestejlen bygger en

rede, hvor hunnen lægger æggene, og hannen holder vagt til de klækker. På denne måde reducerer hundestejlen dødeligheden for populationen som kompensation for de manglende æg.

I naturen er der konkurrence om føden mellem arter. Hvis to arter har samme byttedyr, vil den art der er bedst til at fange og udnytte byttet på sigt udkonkurrere den anden. Hvis den ene art har større kropsstørrelse end den anden, kan de to arter konkurrere for føde i tidlige livsstadier, hvorimod den store art kan spise den lille art i senere livsstadier. De to arter kan kun sameksistere hvis den lille er bedre end den store til at udnytte fødegrundlaget i det tidlige livsstadie. I naturen findes denne konstellation, som kaldes 'intraguild predation', i miljøer med både lavt og højt næringsniveau. Vores model kan forklare denne sameksistens i begge miljøer (Artikel IV), hvorimod nuværende modeller ikke kan forklare sameksistensen i næringsrige miljøer.

Fiskeribiologer benytter sig af en række parametre, som f.eks. den naturlige dødelighed, som er den dødelighed der ikke skyldes fiskeri, til at lave forvaltningsplaner for hvor mange tons fisk der kan fiskes op uden at bestanden lider overlast. Vores model kan bruges til at relatere disse parametre til processer på individniveau, så den naturlige dødelighed f.eks. kan beregnes ud fra fisks fødeindtag og kropsstørrelse (Artikel VI). Dette øger tilliden til de modeller der anvendes i forvaltningen, da de parametre der benyttes til modellen kan krydstjekkes med forskellige metoder.

De modeller der benyttes til fiskeriforvaltning er i vid udstrækning baseret på, at man har en separat model for hver art, hvorfor de ikke kan bruges til økosystembaseret forvaltning. Med vores matematiske model viser vi hvordan det påvirker marine økosystemer, når der fiskes intensivt på forskellige arter samtidigt (Artikel V). Ved at justere fiskeriindsatsen på store og små arter kan man undgå at nogle arter får en meget stor population, mens andre får deres population reduceret til et niveau, hvor de kommer i fare for at uddø.

Den model som udvikles i denne afhandling kan altså ikke alene bruges til at forstå hvorfor naturen ser ud som den gør. Den udgør også et udgangspunkt for økosystembaseret forvaltning, så vi i fremtiden fortsat kan spise torsk til nytår og sild til julesnapsen.

Acknowledgements

First, and definitely foremost, I wish to thank my collaborator Ken H. Andersen. Tak for alle vores diskussioner ved whiteboardet (også dem hvor jeg altid skulle være på tværs), tak for de motiverende samtaler, og tak for de mange ting du har lært mig.

Secondly, I want to thank all my fellow students who have made the work zone a friend zone as well. Florian, I probably spent most time discussing with you – however, I do not think we've ever had the time to discuss our research. Jacob, det var skojigt att prata skit och food webs med dig – hoppas att vi snart kan jobba tillsammans igen, eller grilla i solsken. Mikael, at diskutere økologi (med lystfiskeri i baghovedet) og videnskabsteori satte det hele i perspektiv. Carlos (MRDR-R), compadre, you really turned every workday into something positive. Christina og Mie, tak for vores mange samtaler og diskussioner. To the Venezuela crew, thanks for an unforgettable journey (and for waking me up at 4am to go birding)! Lars, tak for din kritiske sans. Jakob, tak for at du også var dansk lystfisker i Lund. Lai, thanks for the mathematical angle. Rikke, Jane, Karen og Marc: tak for kaffe!

Ulrich Brose, Axel Rossberg, Björn Rall, Richard Law, Owen Petchey, and Ulf Dieckmann: thank you for motivating and fun research stays. Stays that have helped keeping up the motivation when sitting home alone in the office thinking about why we do science. LEM guys: going to Ukraine was an experience I would not have been without! FishACE guys: thanks for some super workshops – even though the food at times actually was too good! Åke, drinking bear, eating olives, and going to Hungarian outdoor bathes is the way to do science. To all of my coauthors: Thanks for the things you've learned me. To everybody in Sizemic: thank you for caring about size. To the people at the Umeå and CPH workshop: thank you for your enthusiasm about size-structure. To my reviewers: thanks for your patience, and for trying to teach me scientific writing.

To everybody in my department: thanks for fika, innebandy, lunch, late night swimming, religious hotels, and unforgettable departmental days! Per och Jörgen, tack for de teoretiske diskussioner. Niclas, min ormforskarkollega: tack for trevlig forskning och samarbetet på fiskeriekologikursen. Jonas och Anders N: det samma gäller for er. To everybody at DTU Aqua: thanks for your hospitality and for including me as one of your own.

Dr. Jostein Starrfelt: I find the yearly meetings on synthesis at the Centre for Theoretical Reality and Reality inspiring, siempre!

Kære venner og familie. Tak for at I er der! Tak for jeres venskab, forståelse, snakkerier, gode middage, lange gåture, kaffe, torsdagsøl og øl, hentning og pasning af Alma, Berlin, træning, diskussioner, og fisketure. Och er på Albogatan: Tack for en äventyrlig tid i Lund! Team Greenland: Thanks for a fishing adventure that I think about almost every single day!

Mette og Alma, I er mine piger, og det er Jer jeg elsker. Alma, jeg er taknemmelig for at du ikke giver en hujende fis for mit arbejde. Mette, tak for din overbærenhed, støtte og kærlighed – uden dig kunne dette slet ikke lade sig gøre!

Included papers

This thesis is based on the following papers:

- I** Hartvig, M., Andersen, K.H., and Beyer, J.E. 2011. Food web framework for size-structured populations. *Journal of Theoretical Biology*, 272(1):113–122. **55**
M.H. and K.H.A. planned the study. M.H. did the analysis. All authors discussed the results. M.H. wrote the paper with help from KHA and JEB.
- II** Hartvig, M. 2011. Ecological processes yield complex and realistic food webs. *Manuscript*. **73**
M.H. designed the study, did the analysis, and wrote the manuscript.
- III** Andersen, K.H., Beyer, J.E., Pedersen*, M., Andersen, N.G., and Gislason, H. 2008. Life-history constraints on the success of the many small eggs reproductive strategy. *Theoretical Population Biology*, 73(4):490–497. **101**
K.H.A., J.E.B., and M.P. planned the study, and did the analysis. All authors discussed the results. K.H.A. wrote the paper with help from the coauthors.
- IV** Hartvig, M. and Andersen, K.H. 2011. Widespread coexistence in size-structured intraguild predation systems with life-history omnivory. *Submitted*. **111**
Both authors planned the study, did the analysis, and discussed the results. M.H. wrote the paper with help from K.H.A.
- V** Andersen, K.H., and Pedersen*, M. 2010. Damped trophic cascades driven by fishing in model marine ecosystems. *Proc. R. Soc. B*, 277(1682):795–802. **127**
Both authors planned the study and discussed the results. K.H.A. did the analysis. K.H.A. wrote the paper with help from M.P.
- VI** Andersen, K.H., Farnsworth, K. D., Pedersen*, M., Gislason, H., and Beyer, J.E. 2009. How community ecology links natural mortality, growth, and production of fish populations. *ICES Journal of Marine Science*, 66(9):1978–1984. **137**
K.H.A., K.D.F., and M.P. planned the study, and did the analysis. All authors discussed the results. K.H.A. wrote the paper with help from the coauthors.

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*Before January 2010 Martin Hartvig (M.H.) was named Martin Pedersen (M.P.). His family changed family name when his daughter was named.

Food web framework for size-structured populations

Paper I

Appeared in:

Hartvig, M., Andersen, K.H., and Beyer, J.E. 2011. Food web framework for size-structured populations. *Journal of Theoretical Biology*, 272(1):113-122.

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Food web framework for size-structured populations

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ARTICLE INFO

Article history:

Received 22 September 2010

Received in revised form

2 December 2010

Accepted 4 December 2010

Available online 10 December 2010

Keywords:

Community ecology

Trait based model

Life-history omnivory

Ontogeny

Size-spectrum

ABSTRACT

We synthesise traditional unstructured food webs, allometric body size scaling, trait-based modelling, and physiologically structured modelling to provide a novel and ecologically relevant tool for size-structured food webs. The framework allows food web models to include ontogenetic growth and life-history omnivory at the individual level by resolving the population structure of each species as a size-spectrum. Each species is characterised by the trait 'size at maturation', and all model parameters are made species independent through scaling with individual body size and size at maturation. Parameter values are determined from cross-species analysis of fish communities as life-history omnivory is widespread in aquatic systems, but may be reparameterised for other systems. An ensemble of food webs is generated and the resulting communities are analysed at four levels of organisation: community level, species level, trait level, and individual level. The model may be solved analytically by assuming that the community spectrum follows a power law. The analytical solution provides a baseline expectation of the results of complex food web simulations, and agrees well with the predictions of the full model on biomass distribution as a function of individual size, biomass distribution as a function of size at maturation, and relation between predator-prey mass ratio of preferred and eaten food. The full model additionally predicts the diversity distribution as a function of size at maturation.

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1. Introduction

Food webs are typically modelled using unstructured species populations based on generalised Lotka–Volterra equations. This unstructured formulation ignores individual life-history by assigning a fixed trophic position to all individuals within a species. In aquatic ecosystems this assumption is violated as fish offspring reside at a low trophic level and grow during ontogeny through multiple trophic levels before reaching maturation (Werner and Gilliam, 1984). Along this journey, from the milligram range and up to several kilogram, fish change diet (as well as enemies) and consequently exhibit life-history omnivory through preying on different trophic levels in different life-stages (Pimm and Rice, 1987). Thus the assignment of a unique trophic level and role (resource, consumer, predator, etc.) for species in unstructured models is incompatible with systems where ontogenetic growth and life-history omnivory are pronounced. In the cases where trophic level of individuals within a species is positively correlated with body size (Jennings et al., 2002), individual size may be used as a proxy for trophic level. Models may therefore account for ontogenetic growth and life-history omnivory by resolving the size-structure within each species.

A general framework for large food webs that includes the size-structure for all species must fulfil a set of requirements. It should: (1) be generic in the sense that large species-specific parameter sets are not necessary, (2) be based on mechanistic physiological individual-level processes, where parameters represent measurable biological quantities, (3) resolve food dependent growth of individuals (Werner and Gilliam, 1984), (4) be practically solvable for species-rich systems over many generations, and (5) comply with empirical data on size-structured communities. In this work we develop a food web framework complying with these requirements by resolving the life-history of individuals within species by a continuous size-spectrum. We parameterise the model for aquatic systems as an example of a size-structured community with widespread life-history omnivory, but the framework may be parameterised for other system types (cf. Discussion). In fish communities the most prominent empirical patterns, which the model framework should comply with, are that individuals exhibit biphasic growth (Lester et al., 2004), and the Sheldon community spectrum. Sheldon et al. (1972) hypothesised that the community biomass spectrum, from bacteria to whales, as a function of body mass is close to constant. Empiric studies later showed that the biomass for fish indeed is close to constant or slightly declining as a function of body mass (Ursin, 1982; Boudreau and Dickie, 1992) with the complication that heavily fished systems have a steeper decline in biomass (Jennings et al., 2002; Daan et al., 2005).

The importance of resolving ontogenetic growth and life-history omnivory has long been realised in fisheries science, where

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mechanistic individual-level size-structured food web models of fish communities were pioneered (Andersen and Ursin, 1977). Independently, the physiologically structured population model (PSPM) framework (Metz and Diekmann, 1986; de Roos and Persson, 2001) has been developed in the field of ecology. While providing the ecological realism needed for a size-structured food web framework these approaches typically rely on large species-dependent parameter sets, which must be reduced for the approaches to be useful as generic frameworks.

Reduction to species-independent parameter sets has been achieved in unstructured models of interacting populations by scaling of physiological and demographic rates with body size (Yodzis and Innes, 1992). By using body size as a trait this approach has resulted in several simple generic food web models for unstructured populations (Loeuille and Loreau, 2005; Virgo et al., 2006; Brose et al., 2006b; Lewis and Law, 2007).

In this work we combine the two approaches into one unified framework: We (1) use a physiological based description of individual life-history, and (2) use a single trait (size at maturation) to characterise each species while using trait and body size scaling to get one condensed species-independent parameter set. All processes are based on descriptions at the level of individuals, and interaction strengths among individuals are dynamic through the prescription of size-dependent food selection. This leads to a realised effective food web structure which depends on the emergent size-spectrum composition of all species. In this manner we synthesise a general framework that in a conceptually simple yet ecologically realistic way can be used to model food webs where the life cycle of individuals in each species is explicitly modelled from birth to reproduction and death.

Our primary objective is the formulation and parameterisation of the food web framework. Food webs generated by unstructured food web models may be analysed at the community level in terms of distributions of biomass across species and trophic levels. Trait-based size-structured food webs allow a more detailed analysis of the community level as well as enabling analysis on three additional levels of organisation: (1) at the community level, i.e., the distribution of total biomass as a function of body size of individuals regardless of their species identity, and the distribution of biomass and diversity as a function of the trait size at maturation, (2) at the species level, i.e., distribution of biomass as a function of size within a given species, (3) at the trait level, which in the case of a single trait equals the species level, and (4) at the individual level, i.e., distribution of size of food in the stomachs. Due to this added complexity of size-structured food webs, our secondary objective is to illustrate diversity and biomass distributions at different levels of organisation. To this end we generate an ensemble of food webs and analyse them in terms of distributions of average community size-spectra, species size-spectra, trait biomass distributions, and trait diversity distributions. Finally, we develop an analytical solution of the model framework, basically by assuming that the community spectrum follows a power law (equilibrium size-spectrum theory, EQT). All distributions, except the diversity distribution, may be calculated from EQT, and we demonstrate general accordance between EQT and the results from the full food web simulations. The accordance between EQT and the food web simulations validates the simplifying assumptions behind EQT. EQT provides a “null-solution” to the size- and trait-distributions which may be used as a baseline expectation of the results of large size-structured food web simulations.

2. Food web model

The model is based on a description of the processes of food encounter, growth, reproduction, and mortality at the level of an

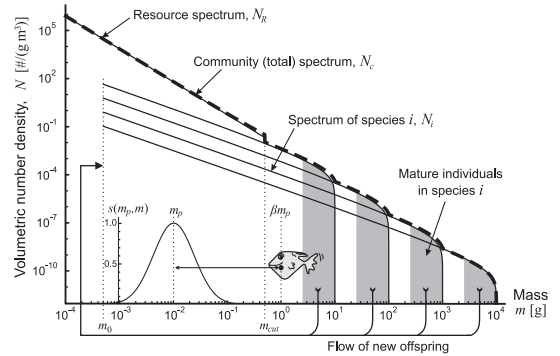


Fig. 1. Illustration of the community model: resource spectrum (with cut-off m_{cut}) and four species size-spectra ($m_* = 2.5, 25, 250,$ and 2500 g) having offspring of size m_0 . Shaded regions mark the spawning stock from maturation size m_* to maximum asymptotic size M . The sum of all spectra gives the community spectrum (dashed). The spectra shown are the steady-state solutions from Andersen and Beyer (2006). Inset shows how individuals feed on smaller prey using a feeding kernel with a preferred PPMR of β .

individual with body mass m (Fig. 1). The model is based on two central assumptions: (1) Prey selection is determined at the individual level where individual predators select prey from the rule “big individuals eat smaller individuals”, and at the species level through introduction of species-specific size-independent coupling strengths (Andersen and Ursin, 1977; Werner and Gilliam, 1984; Emmerson and Raffaelli, 2004). (2) In addition to species-specific coupling strengths, species identity is characterised by a single trait: size at maturation m_* . Interactions among individuals are described by a food encounter process which leads to consumption by predators and mortality on their prey. Food consumption leads to growth in body mass, and when an individual reaches size at maturation m_* it starts allocating energy for reproduction, as well as producing new offspring. Thus the model encapsulates the life-cycle of individuals from birth to maturity and death.

Population dynamics of species i is obtained from individual growth $g_i(m)$ and mortality $\mu_i(m)$ by solving the number conservation equation (McKendrick, 1926; von Foerster, 1959):

$$\frac{\partial N_i}{\partial t} + \frac{\partial}{\partial m} (g_i N_i) = -\mu_i N_i. \tag{1}$$

The population structure of species i is described by the size-spectrum $N_i(m, t)$, denoted $N_i(m)$ to ease notation. The size-spectrum represents the volumetric abundance density distribution of individuals such that $N_i(m) dm$ is the number of individuals per unit volume in the mass range $[m; m + dm]$. Similarly $B_i(m) = m N_i(m)$ denotes the biomass spectrum (biomass density distribution), and $B_i(m) dm$ the biomass per unit volume in the range $[m; m + dm]$. The sum of all species’ size-spectra plus a resource spectrum $N_R(m)$ is the community spectrum (Fig. 1):

$$N_c(m) = N_R(m) + \sum_i N_i(m). \tag{2}$$

The community spectrum represents the entire biotic environment providing individuals with food (from smaller individuals) as well as their predation risk from larger individuals. To include species-specific preferences each species i has its own experienced community spectrum:

$$N_{i,c}(m) = \theta_{i,R} N_R(m) + \sum_j \theta_{i,j} N_j(m), \tag{3}$$

where $\theta_{i,j} \in [0; 1]$ is the coupling strength of species i to species j . Coupling strengths are independent of body size (cf. Discussion)

since size-dependent food intake is described with a feeding kernel (below).

2.1. Food consumption

The consumption of food by an individual depends on the available food from the experienced community spectrum, on the volume searched per time, and on its functional response. The consumed food is assimilated and used to cover respiratory costs. Remaining available energy is used for somatic growth by immature individuals and for a combination of somatic growth and reproduction by mature individuals.

We incorporate the rule of “big ones eat smaller ones” by assuming that predators have a preferred predator–prey mass ratio (PPMR). This assumption is inspired by stomach analyses of marine fish (Ursin, 1973, 1974), and supported by stable isotope analyses (Jennings et al., 2001). The feeding kernel describing the size preference for prey is prescribed with a normalised log-normal function (Fig. 1, Ursin, 1973):

$$s(m_p, m) = \exp \left[- \left(\ln \left(\frac{\beta m_p}{m} \right) \right)^2 / (2\sigma^2) \right], \tag{4}$$

where m_p is prey mass, m predator mass, β the preferred PPMR, and σ the width of the function. The food available (mass per volume) for a predator of size m

$$\phi_i(m) = \int m_p N_i(m_p) s(m_p, m) dm_p. \tag{5}$$

Encountered food (mass per time) is the available food multiplied by the volumetric search rate $v(m) = \gamma m^q$, where q is a positive exponent signifying that larger individuals search a larger volume per unit time (Ware, 1978). Satiation is described using a feeding level (number between 0 and 1, Kitchell and Stewart, 1977; Andersen and Ursin, 1977):

$$f_i(m) = \frac{v(m)\phi_i(m)}{v(m)\phi_i(m) + hm^n}, \tag{6}$$

where hm^n is the maximum food intake. Feeding level times hm^n corresponds to a type II functional response.

2.2. Somatic growth

Ingested food $f(m)hm^n$ is assimilated with an efficiency α accounting for waste products and specific dynamic action. From the assimilated energy an individual has to pay the metabolic costs of standard metabolism and activity, km^p . Thus the energy available for growth and reproduction is

$$E_i(m) = \alpha f_i(m)hm^n - km^p. \tag{7}$$

Of the available energy a fraction $\psi(m, m_*)$ is used for reproduction, and the rest for somatic growth:

$$g_i(m, m_*) = \begin{cases} (1 - \psi(m, m_*))E_i(m) & E_i(m) > 0 \\ 0 & \text{otherwise.} \end{cases} \tag{8}$$

If the intake is insufficient to cover respiratory costs ($E_i(m) < 0$) growth is halted. Body size does not shrink when costs cannot be covered, instead starving individuals are exposed to a starvation mortality (see Section 2.4). The maximum asymptotic size M an individual can obtain is reached when all available energy is used for reproduction ($\psi(M, m_*) = 1$).

2.3. Reproduction

In order to generate growth trajectories with biphasic growth the allocation rule $\psi(m, m_*)$ has to change smoothly from 0 around

size at maturation to 1 at the theoretical maximum asymptotic size M . The allocation rule $\psi(m, m_*)$ is derived using two requirements: (1) that the size of gonads is proportional to individual mass (Blueweiss et al., 1978) and (2) that size at maturation is proportional to asymptotic size (Beverton, 1992; Froese and Binohlan, 2000; He and Stewart, 2001). To obtain an analytical solution as to how individuals allocate available energy to growth and reproduction we assume that the allocation rule is based on a constant feeding level \bar{f} . Requiring allocation to reproduction to be proportional to individual mass, $\psi(m, m_*)\bar{E}(m) = k_r m$, gives $\psi(m, m_*) = k_r m / \bar{E}(m)$, where $\bar{E}(m) = \alpha \bar{f} h m^n - km^p$ denotes the available energy when feeding level is constant. The factor k_r is found by the second requirement through $\psi(M, m_*) = 1 : k_r = \bar{E}(M) / M$ where $M = m_* / \eta_*$. The allocation can thus be described as

$$\psi(m, m_*) = \left[1 + \left(\frac{m}{m_*} \right)^{-u} \right]^{-1} \frac{\bar{E}(m_*/\eta_*)}{\bar{E}(m)} \frac{m}{m_* / \eta_*}, \tag{9}$$

where the term in the square brackets is a smooth step function switching from zero to one around the size at maturation (u determines transition width).

The exponents of maximum consumption and standard metabolism are close to equal (cf. Appendix E and Discussion). In the limit of $n=p$ the available energy for growth and reproduction becomes $\bar{E}(m) = hm^n$ where $h = \alpha \bar{f} h - k$. This gives: $\psi(m, m_*) = [1 + (m/m_*)^{-u}]^{-1} (\eta_* m / m_*)^{1-n}$, meaning that the juvenile growth pattern is $g = hm^n$ whereas adults grow according to $g = hm^n - h(m_*/\eta_*)^{n-1}m$. Thus the growth model is a biphasic growth model where adults follow von Bertalanffy growth curves as advocated by Lester et al. (2004).

The total flux of offspring is found by integrating the energy allocated to reproduction $\psi(m, m_*)E_i(m)$ over all individual sizes:

$$R_i = \frac{\varepsilon}{2m_0} \int N_i(m) \psi(m, m_*) E_i(m) dm, \tag{10}$$

where m_0 is the egg size, ε the efficiency of offspring production (Appendix C), and $1/2$ takes into account that only females spawn (assuming equal sex distribution). Reproduction determines the lower boundary condition of (1) for the size-spectrum of the species:

$$g_i(m_0, m_*) N_i(m_0) = R_i. \tag{11}$$

2.4. Mortality

The mortality rate $\mu(m)$ of an individual has three sources: predation mortality $\mu_p(m)$, starvation mortality $\mu_s(m)$, and a small constant background mortality $\mu_b(m_*)$. The background mortality is needed to ensure that the largest individuals in the community also experience mortality as they are not predated upon by any individuals from the community spectrum.

Predation mortality is calculated such that all that is eaten translates into predation mortalities on the ingested prey individuals (Appendix A):

$$\mu_{p,i}(m_p) = \sum_j \int s(m_p, m) (1 - f_j(m)) v(m) \theta_{j,i} N_j(m) dm. \tag{12}$$

When food supply does not cover metabolic requirements km^p starvation mortality kicks in. Starvation mortality is proportional to the energy deficiency $km^p - \alpha f hm^n$, and inversely proportional to lipid reserves, which are assumed proportional to body mass:

$$\mu_s(m) = \begin{cases} 0 & E_i(m) > 0 \\ -E_i(m) / \xi m & \text{otherwise} \end{cases}. \tag{13}$$

Mortality from other sources than predation and starvation is assumed constant within a species and inversely proportional to

generation time (Peters, 1983):

$$\mu_b = \mu_0 m_*^{n-1}. \quad (14)$$

2.5. Resource spectrum

The resource spectrum $N_R(m)$ represents food items which are needed for the smallest individuals (smaller than βm_0). The dynamics of each size group in the resource spectrum is described using semi-chemostatic growth:

$$\frac{\partial N_R(m,t)}{\partial t} = r_0 m^{p-1} [\kappa m^{-\lambda} - N_R(m,t)] - \mu_p(m) N_R(m,t), \quad (15)$$

where $r_0 m^{p-1}$ is the population regeneration rate (Fenchel, 1974; Savage et al., 2004) and $\kappa m^{-\lambda}$ the carrying capacity. We prefer semi-chemostatic to logistic growth since planktonic resources rebuild from depletion locally due to both population growth and invasions.

2.6. Derivation of parameters

Each species is characterised by a single trait, size at maturation m_* , and a species-independent parameter set is achieved through scaling with body size m and m_* . The model is parameterised for marine ecosystems using cross-species analyses of fish communities (Appendix E and Table 1).

The constant γ for the volumetric search rate is difficult to assess (Appendix E). However, since the feeding level $f(m)$ of small individuals is determined solely by the amount of encountered food from the resource spectrum, we may use *initial feeding level* f_0 as a physiological measure of food encounter; f_0 is defined as the feeding level resulting from a resource spectrum at carrying capacity. The initial feeding level is used as a control parameter for food availability (enrichment), through which the value of γ can be calculated (Appendix D):

$$\gamma_i(f_0) = \frac{f_0 h \beta^{2-\lambda}}{(1-f_0) \sqrt{2\pi} \theta_{i,R} \kappa \sigma}, \quad (16)$$

where it is noted that γ will be species dependent if species have different coupling strengths to the resources.

Table 1
Default parameter values for a temperature of 10 °C (Appendix E).

Symbol	Value	Units	Parameter
Individual growth			
f_0	0.6	–	Initial feeding level
α	0.6	–	Assimilation efficiency
h	85	g^{-1-n}/year	Maximum food intake
n	0.75	–	Exponent for max. food intake
k	10	g^{-1-p}/year	Standard metabolism and activity
p	0.75	–	Exponent of standard metabolism
β	100	–	Preferred PPMR
σ	1	–	Width of feeding kernel
q	0.8	–	Exponent for search volume
Reproduction			
m_0	0.5	mg	Offspring mass
η_*	0.25	–	m_* relative to asymptotic mass M
ε	0.1	–	Efficiency of offspring production
u	10	–	Width of maturation transition
Mortality			
ξ	0.1	–	Fraction of energy reserves
μ_0	0.84	g^{-1-n}/year	Background mortality
Resource spectrum			
κ	5×10^{-3}	$g^{-\lambda-1}/m^3$	Magnitude of resource spectrum
λ	$2-n+q$	–	Slope of resource spectrum
r_0	4	g^{-1-p}/year	Regeneration rate of resources
m_{cut}	0.5	g	Upper limit of resource spectrum

A *critical feeding level* f_c can be formulated as the feeding level where all assimilated food is used for metabolic costs (using values from Table 1):

$$f_c = \frac{k}{\alpha h} m^{p-n} = \frac{k}{\alpha h} \approx 0.2. \quad (17)$$

Individuals can only grow and reproduce if $f > f_c$. Assuming that individuals experience an average feeding level \bar{f} , the growth (8) of juveniles is $g = h m^n$ (for $n=p$). The parameter $h = \alpha h \bar{f} - k$ can be estimated through the relation between observed von Bertalanffy growth rate and asymptotic size yielding $h \approx 10 g^{0.25}/\text{year}$ (Andersen et al., 2008). This allows an estimation of the expected average feeding level of individuals in the field (Table 1):

$$\bar{f} = \frac{h+k}{\alpha h} \approx 0.4, \quad (18)$$

i.e., around twice the critical feeding level. As the initial feeding level f_0 is calculated from a resource spectrum at carrying capacity, the realised feeding level in the model will be smaller than f_0 . A value of $f_0 = 0.6$ was seen to give realised feeding levels around 0.4.

3. Methods

Stable food webs are constructed using the full dynamic food web model with random coupling strengths $\theta_{i,j}$. For each run, 30 species are assigned with m_* evenly distributed on a logarithmic size axis ($m_* \in [0.25 \text{ g}; 20 \text{ kg}]$), random $\theta_{i,j}$ matrices (mean 0.5), and a common $\theta_{i,R} = 0.5$ coupling to the resource spectrum. Numerical integration is performed by standard finite-difference techniques (Appendix G). Food webs are simulated in 10 consecutive intervals covering 300 years each, where species with a biomass less than $10^{-30} \text{ g}/m^3$ are eliminated after each interval. To eliminate food webs that still have not reached the final state each community is integrated for additional 500 years and discarded if any species has an absolute population growth rate larger than 1 logarithmic decade per 100 years. To ensure that each food web in the final ensemble spans multiple trophic levels we only retain food webs where at least one species has m_* larger than 2.5 kg. For statistics we use the mean of the last 250 years of the simulation with time steps saved in 0.1 year increments. In this manner 204 food webs having a total number of 1016 species were collected. Each web contained between 2 and 9 species with a mean of 4.98 species.

We analyse the generated food webs in terms of distributions of average community size-spectrum, species size-spectra, trait biomass distributions, and trait diversity distributions. Additionally we demonstrate the importance of distinguishing between what an individual prefers to eat and what is actually ingested (i.e., found in its stomach) by showing how emerging PPMRs vary with food availability and differ from preferred PPMRs.

An approximate steady-state solution to the food web model which neglects the dynamics of reproduction can be found using two assumptions: (1) all species consume food and experience mortality from a scaling community size-spectrum $N_c = \kappa_c m^{-\lambda}$, and (2) constant feeding level \bar{f} , which implies equal species coupling strengths $\theta_{i,j} = \bar{\theta}$. Whereas the food webs in the full model are based on a discrete set of m_* , the analytical solution considers m_* as a continuous distribution. The procedure for deriving the analytical solution is similar to the derivation of equilibrium size-spectrum theory (Andersen and Beyer, 2006), but the results are slightly different as standard metabolism is taken explicitly into account here. The food encountered by an individual is found using assumption (1): $v(m)\phi(m) = \gamma m^q \int N_c s(m_p, m) m_p dm_p \propto m^{2-\lambda+q}$. The feeding level is calculated from (6), and the requirement that it is constant (assumption 2) leads to a constraint on the exponent of the community spectrum: $\lambda = 2 + q - n$. Feeding with a constant feeding level generates a predation mortality of $\mu_p = \alpha_p m^{n-1}$ (Appendix A).

The size-spectrum of juvenile individuals is found as the steady-state solution of (1) using the above predation mortality and $g = hm^n$ (cf. Eq. (F.1)): $N(m, m_*) = \kappa(m_*)m^{-n-a}$, where $a = \alpha_p/h$ is the physiological level of predation (Beyer, 1989; Andersen and Beyer, 2006), which can be calculated as $a \approx \bar{f}/(\bar{f}-f_c)\beta^{2n-q-1}/\alpha = 0.86$ (Appendix B). The constant $\kappa(m_*)$ is found from the requirement that the sum of all species spectra should equal the community spectrum. Assuming a continuum of species the requirement can be written as $\int N(m, m_*) dm_* = N_c(m)$ which leads to $\kappa(m_*) \propto m_*^{2n-q-3+a}$ (Fig. 1). This approximate solution of the model will be referred to as equilibrium size-spectrum theory (EQT), and it will be compared to the output of the complete dynamic food web model.

In dynamic models, as in nature, the lifetime reproductive success (fitness) has to be $R_0 = 1$ for all coexisting species. Since EQT does not consider the boundary condition (11) lifetime reproductive success becomes a function of size at maturation: $R_0 \propto m_*^{1-a}$ (Andersen et al., 2008). One solution to making R_0 independent of m_* is to set $a=1$, but that breaks the above employed mass balance between growth and mortality used to calculate a . Due to the $R_0 \neq 1$ inconsistency in EQT we have a specific focus on the realised values of a when comparing food web simulations with EQT predictions. To examine how the regulation of R_0 occurs in the full food web model R_0 is split into two factors: (1) the probability of surviving to become adult and (2) lifetime reproduction per adult (Appendix F):

$$p_{m_0 \rightarrow m} = \frac{N(m)g(m, m_*)}{N(m_0)g(m_0, m_*)}, \tag{19}$$

$$R_{\text{adult}}(m_*) = \int_{m_*}^M p_{m_* \rightarrow m} \frac{\psi(m, m_*)E(m)}{g(m, m_*)} dm. \tag{20}$$

Survival probabilities and reproductive outputs in the food web simulations are compared with EQT predictions, which are calculated by inserting the EQT size-spectra into (19) and (20). Juvenile growth is $g \propto m^n$, which gives $p_{m_0 \rightarrow m} \propto m_*^{-n-a}m^n = m_*^{-a}$ and $R_{\text{adult}} \propto m_*$.

4. Model predictions

4.1. Growth trajectories

In unstructured models fluctuations are manifested as oscillations in the biomass of species, whereas the oscillations in structured models stem from oscillations in the size-spectrum

composition. Such oscillations give rise to fluctuating feeding levels as individuals encounter different levels of food in different life-stages (Fig. 2a). Variations in feeding levels between species and as a function of individual size lead to different emergent growth trajectories (Fig. 2b). The growth trajectories roughly follow the biphasic growth curve that is obtained if the feeding level is assumed to be constant.

4.2. Biomass structure

By pooling species from each food web into logarithmic evenly distributed m_* groups, and summing the size-spectra in each group, a size-spectrum is obtained for each m_* group. Next, the average of m_* groups across all food webs is performed to produce the average size-spectra of a m_* group (Fig. 3). Average community biomass spectrum $N_c(m)m$ follows the EQT prediction of a slope of $1+q-n=1.05$, meaning that the biomass in logarithmically evenly sized size-groups, $\int_{m_*}^{cm_*} N_c(m)m dm$, is a slightly declining function of body mass. The community spectrum oscillates around the EQT prediction due to a trophic cascade initiated by a superabundance of the largest predators which do not experience any predation mortality (Andersen and Pedersen, 2010). The peaks of the oscillating pattern are roughly spaced by the preferred PPMR. Biomass density within species is constant until individuals reach the end of the resource spectrum, and larger individuals, ≥ 0.1 g, have a biomass spectrum slope flatter than that of the community spectrum (Fig. 3). Thus, in contrast to EQT, the dynamic model produces species size-spectra that cannot be described as power laws. The number of small individuals is inversely related to size at maturation. The scaling of offspring abundance can be calculated using EQT as $N_0 \propto \int_{m_*}^{cm_*} \kappa(m'_*) dm'_* \propto m_*^{2n-q-2+a}$, which fits the simulated results well for $a=1$ (Fig. 3, inset).

The distribution of species biomass as a function of m_* can be calculated from EQT as

$$B(m_*) = \int_{m_*}^{cm_*} \int_{m_0}^M N(m, m'_*)m dm dm'_* \propto m_*^{n-q}. \tag{21}$$

As n and q are almost equal the biomass distribution $B(m_*)$ as a function of m_* is almost constant. This result is also borne out by the dynamical simulations (Fig. 4a) with some variation due to uneven species distribution along the m_* axis: peaks occur in species diversity separated by the preferred PPMR β (Fig. 4b).

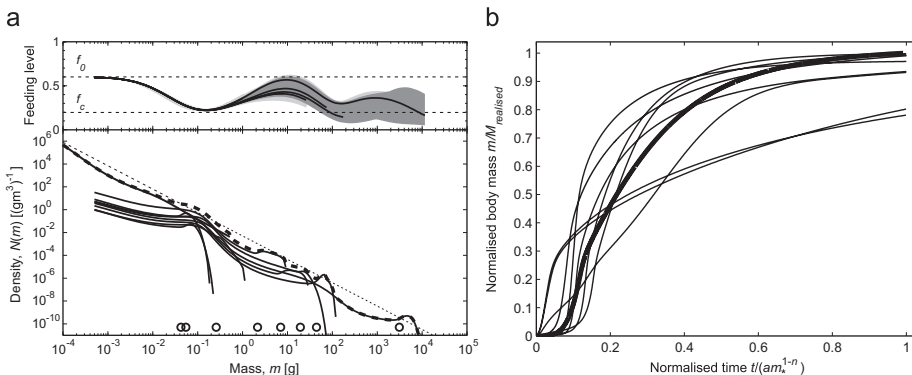


Fig. 2. Example of an eight species cyclic state. (a) Top: feeding levels of the species along with the min/max (light grey) and the 25%/75% (dark grey) percentile values of the time-series. Dashed lines indicate initial f_0 and critical f_c feeding level. Bottom: the time-average of the resource and species spectra along with the community spectra (thick dashed). The idealised community spectrum $\kappa_c m^{-2}$ (thin dashed) and the species maturation sizes m_* (circles). (b) Time averaged growth curves for the species (thin lines) along with the biphasic growth curve (8) for a fixed feeding level that equals 75% of the time and size averaged feeding level experienced by the species (thick line). Growth curves are normalised with realised asymptotic size (y-axis) and generation time (x-axis) to enable comparison.

4.3. PPMR and feeding level

The realised mean PPMR can be derived when prey concentrations are known: $\mathcal{N}(m_p)s(m_p, m)$ is the prey size distribution encountered by a m sized predator. Mean prey size encountered by a m sized predator is $\int_0^\infty m_p \mathcal{N}(m_p)s(m_p, m) dm_p / \int_0^\infty \mathcal{N}(m_p)s(m_p, m) dm_p$. The realised mean PPMR is calculated as the predator size m divided by the mean prey size:

$$PPMR(m) = \frac{m \int_0^\infty \mathcal{N}(m_p)s(m_p, m) dm_p}{\int_0^\infty m_p \mathcal{N}(m_p)s(m_p, m) dm_p} \tag{22}$$

Realised mean PPMR is always larger than the preferred PPMR β , due to higher abundance of smaller prey items (Fig. 5a). The realised mean PPMR calculated from EQT (using $\mathcal{N} \propto m_p^{-\lambda}$) is $\exp((\lambda-3/2)\sigma^2)\beta \approx 1.7\beta$. Realised PPMR from the simulations oscillate around this value due to the fluctuations in the community spectrum (Fig. 3).

As individuals grow to a size larger than βm_0 they switch from eating food in the resource spectrum to feeding on other species.

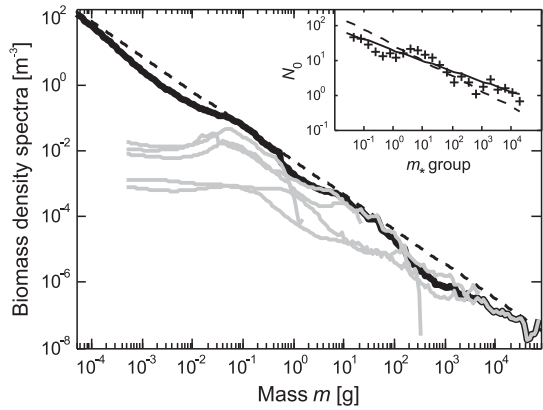


Fig. 3. Mean species biomass spectra (grey lines) when species are divided into five logarithmic evenly distributed m_* groups. Also shown is the total mean community biomass spectrum (thick line), and the EQT community biomass spectrum $\kappa_c m^{-a}$ (dashed). Inset shows how offspring abundance (N_0) scales with m_* (data pooled in 25 log groups). Expected EQT scaling of N_0 is shown for $a=0.86$ (dashed) and $a=1$ (solid).

This leads to a decrease in the feeding level from $f_0=0.6$ to about 0.45. The oscillations in feeding level increase in magnitude as body size increases due to larger fluctuations in prey availability (Fig. 5b). Many large individuals periodically have a feeding level below the critical feeding level f_c (where starvation kicks in) since prey items in the preferred size range become scarce, which results in ingestion of smaller food items and therefore increasing PPMR.

4.4. Reproduction and survival

Lifetime adult reproduction calculated from the simulated food webs fit the EQT prediction since it scales linearly with m_* (Fig. 6b). The probability of surviving to a given size is independent of m_* , as the survival curves of the different m_* groups lie on top of one another (Fig. 6a). Survival to m_* scales inversely with m_* (i.e., $a=1$, crosses in Fig. 6a), which ensures that R_0 is constant. However, if the $a=1$ scaling of survival to m_* is extrapolated to m_0 it is seen that it does not intersect $p_{m_0 \rightarrow m_0} = 1$. Instead the survival curves change slope between m_0 and around 10^{-1} g where predation mortality starts to dominate due to an abundance of fish individuals in the same order of magnitude as the resource spectrum, which is intensified by reduced growth stemming from food competition (Fig. 3). In summary survival does not scale with m_*^{-a} as predicted by EQT. Instead adult survival scales with m_*^{-1} (i.e., $a=1$) whereas individuals smaller than ≈ 0.1 g have a higher survival (i.e., a smaller scaling exponent).

5. Discussion

We have developed a generic food web framework suitable for analysing systems of interacting size-structured populations. The framework increases ecological realism compared to traditional unstructured food web models by explicitly resolving the whole life-history of individuals, but maintains simplicity by describing species with only one trait: maturation size m_* . Remaining parameters are made species independent through inter- and intraspecies scaling with m_* and body mass m . The productivity of the system is characterised by one parameter, the initial feeding level f_0 . Feeding behaviour is assumed to be determined by a feeding kernel with a fixed preferred PPMR (big individuals eat small individuals), multiplied by a species-specific coupling strength.

Only characterising the life-history and feeding preference of individuals of a species by body mass m and trait m_* is clearly a

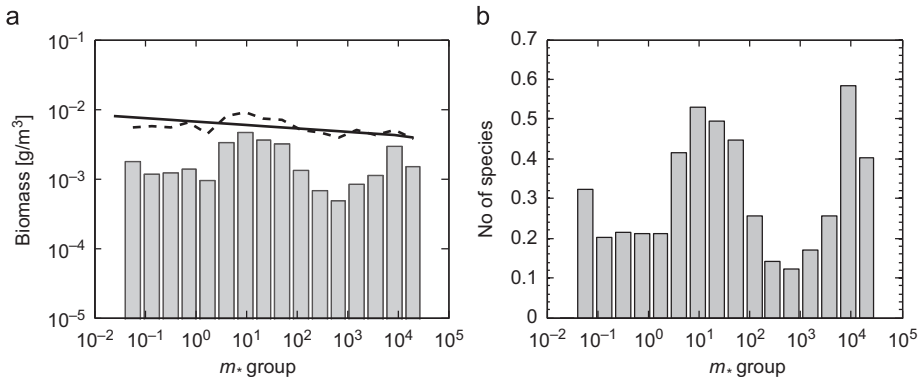


Fig. 4. (a) Distribution of biomass in different m_* groups. The expected distribution $B(m_*) \propto m_*^{-q}$ is illustrated with the solid line. Dashed line shows biomass per species (bar values divided with bar values in (b)). (b) Mean no. of species as a function of m_* . Species are pooled into 16 logarithmic groups.

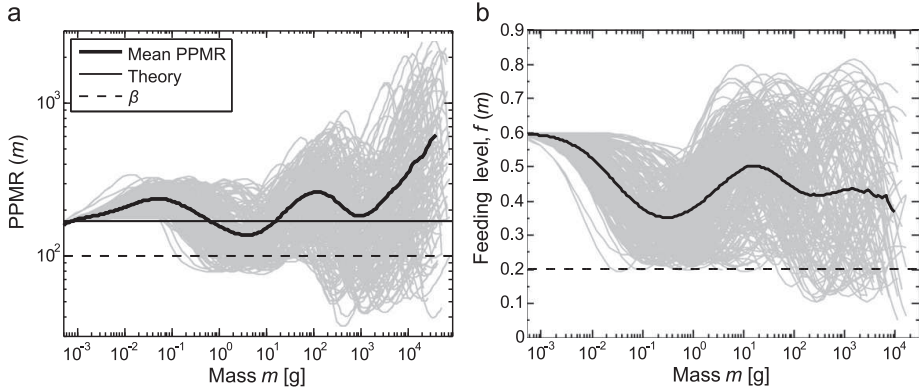


Fig. 5. (a) Realised PPMR from each food web (grey), mean realised PPMR across all simulations (thick black), realised PPMR prediction from equilibrium theory (thin black), and preferred PPMR β (thin dashed). (b) Feeding level for each species (grey), and mean feeding level (thick black).

simplification, but contemporary knowledge suggests that a large part of the individual bioenergetics related to growth (Peters, 1983) and reproduction (Blueweiss et al., 1978) indeed can be described by such scaling. Additionally it is well-known that predators often outsize their prey (Brose et al., 2006a) which justifies the use of the generalisation “big ones eat small ones”.

5.1. Model architecture

The model was parameterised from cross-species analyses of fish communities, since aquatic systems constitute a group of strongly size-structured ecosystems. Other less strongly size-structured taxa can be modelled as well through reparameterisation and by allowing each species to have its own offspring size $m_{0,i}$. Additionally, the description of how available energy is divided between growth and reproduction may have to be reformulated since animals in other taxa may exhibit determinate growth. Determinate growth can be modelled simply by replacing the allocation function (9) with only the part within the square brackets.

The proposed modelling framework is similar to physiologically structured models (Andersen and Ursin, 1977; Metz and Diekmann, 1986; de Roos and Persson, 2001), and as these based

on mechanistic individual-level processes. Our contribution is to employ a trait-based description of species identity, and a formulation of food preference which is split into a size- and a species-based contribution, which renders the developed framework useful as a generic food web framework. Recently the PSPM approach has been reduced to a stage-structured model which facilitates multi-species studies (de Roos et al., 2008a); however this is achieved at the cost of collapsing continuous size-structure to a discrete stage-structure. A first step towards multi-species PSPMs was carried out with an intra-guild predation model, which showed that obtaining species coexistence between two size-structured populations is a difficult task (van de Wolfshaar et al., 2006); a result which is probably due to insufficient ecological differentiation of the two species. In the proposed framework the trait maturation size provides a simple and logical way of representing ecological differentiation of species, whereas this differentiation in PSPMs is less clear due to large species-specific parameter sets. Additional ecological differentiation and heterogeneity are obtained by also including food web structure in the form of species coupling strengths.

An alternative approach to model a size-structured community is the community size-spectrum models (Silvert and Platt, 1980; Benoît and Rochet, 2004). In these models the community is

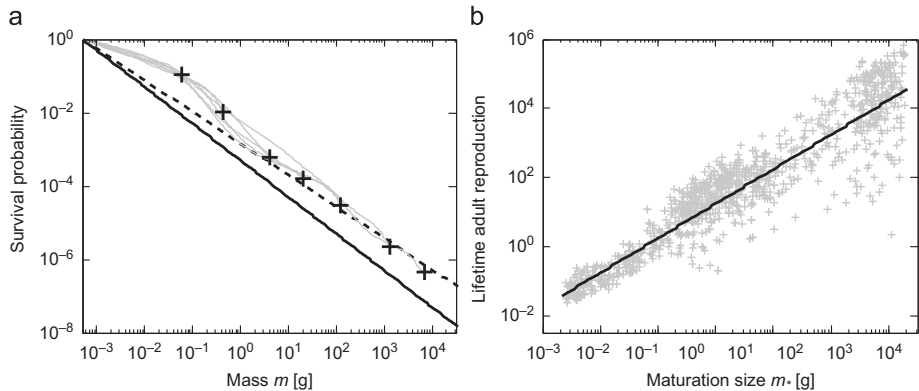


Fig. 6. The components of the expected lifetime reproductive output. (a) Probability of surviving to maturation size m_m (crosses) along with survival curves throughout life (grey lines) for data pooled into seven logarithmic groups. Expected $p \propto m_m^{-a}$ scaling from EQT is shown for $a=0.86$ (dashed) and $a=1$ (solid). (b) Lifetime adult reproduction for all species (crosses) along with EQT $R_{adult} \propto m_m$ expectation (line).

represented by a community size-spectrum of all individuals irrespective of species identity (Sheldon and Parsons, 1967). As with the physiologically structured models these are based on individual-level descriptions of life-history. The community spectrum approach has the drawback that species are not resolved, as all individuals are lumped together into one spectrum. Their advantage is their ability to make community-wide predictions with simple means (Blanchard et al., 2009) similarly to the mean-field theory in unstructured food webs (McKane et al., 2000; Wilson et al., 2003).

A central element in the model is the division of energy between somatic growth and reproduction through the allocation function $\psi(m, m_*)$. As in PSPMs our bioenergetic model is a net-production model where it is assumed that metabolic costs are covered with highest priority after which the remaining energy can be used for growth and reproduction. PSPMs are formulated either with one state variable: individual body weight (Kooijman and Metz, 1984; Claessen and de Roos, 2003), or with two state variables: somatic weight and reserve weight (de Roos and Persson, 2001). In the latter case energy is divided between the two states such that the ratio between the two state variables is aimed to be constant, and accumulated reserves are used for reproduction at the end of the growing season. In the case with only one state variable surplus energy is divided between somatic growth and reproduction with a fixed ratio (κ -rule). When using the κ -rule the maximum asymptotic size any species individual can obtain is M_+ where intake $\alpha hf(M_+)M_+^n$ equals the metabolic costs kM_+^p – meaning that all species would obtain the same asymptotic size if parameters are species independent as in our formulation. M_+ is very sensitive to the precise values of n and p , and they can therefore only be regarded as poor determinators for asymptotic size (Andersen et al., 2008). Our model deviates from the single-state PSPMs in this partitioning of energy, as we assume that mature individuals allocate an amount proportional to their body size for reproduction (Blueweiss et al., 1978), and that asymptotic size depends on the trait size at maturation (Beverton, 1992; Froese and Binohlan, 2000; He and Stewart, 2001). This ensures that the ratio between gonad size and somatic weight is constant within a species, which is similar to the partitioning rule used in two-state PSPMs. The allocation function is derived under the assumption of a constant feeding level throughout adult life. Even though the feeding level is assumed constant, the actual allocation still vary depending on the actual food availability, as $\psi(m, m_*)$ only determines the fraction of available energy allocated to reproduction. An alternative way to derive $\psi(m, m_*)$ is to let it depend on actual feeding levels. This assumption, however, would imply that individuals adjust their allocation to reproduction such that asymptotic size is always reached. This does not seem plausible as individuals in resource scarce environments probably obtain smaller maximum sizes, and therefore we find the most reasonable assumption to be that of a constant feeding level. The exponents n and p are close to equal in nature, and for $n=p$ the energy allocation function leads to biphasic growth where adults follow von Bertalanffy growth curves (Lester et al., 2004). We fixed the yearly mass-specific allocation to reproduction (yearly gonado-somatic index, GSI) to be independent of individual body size within a species. The obtained form of $\psi(m, m_*)$, however, yields a m_*^{-1} scaling of yearly GSI across species, which is consistent with empiric evidence (Gunderson, 1997). This means that the form of $\psi(m, m_*)$ implies a trade-off between m_* and the mass-specific reproduction: large m_* species can escape predation mortality via growth by paying the price of a lower mass-specific reproduction (Charnov et al., 2001). When the exponents n and p differ, growth will still be biphasic and adult growth curves will be similar to von Bertalanffy curves (see also Andersen and Pedersen, 2010). In conclusion the derived allocation rule leads to realistic growth patterns.

5.2. Food web structure

Food web structure is the most essential part of a food web model, and in principle two approaches can be taken to obtain a structure for a dynamic food web model: a top-down and a bottom-up approach.

The top-down method generates food web matrices from the desired number of species and connectance using a static model (stochastic phenomenological models: Cohen and Newman, 1985; Williams and Martinez, 2000; Cattin et al., 2004; Allesina et al., 2008, or more mechanistic approaches involving phylogenetic correlations (Rossberg et al., 2006) or foraging theory (Petchey et al., 2008)). Next, the food web matrix is used to drive a dynamic model, which is simulated forward in time where some of the initial species will go extinct, and the remaining species set can be used for analysis. Note that in addition to a decreased species richness in the final community other food web statistics as e.g. the final connectance may differ as well (Uchida and Drossel, 2007).

In the bottom-up approach link strengths are determined from ecological relations, such as a predator–prey feeding kernel: if the prey fits into a certain size range relative to the predator size, then interaction occurs between the nodes with a strength determined by the feeding kernel (Loeuille and Loreau, 2005; Virgo et al., 2006; Lewis and Law, 2007). Predator preferences depend, in addition to ecological characters, on evolutionary history and recent approaches add this component of phylogenetic correlations (Rossberg et al., 2008).

For size-structured food webs a top-down algorithm for generating realistic food web matrices does not exist. This is due to lack of data describing the three-dimensional interaction matrix – dimension one and two is respectively predator and prey identity as in the classic interaction matrix, and the third dimension is predator–prey body size. Thus one is confined to the bottom-up approach and/or random interaction matrices. In this study we use the bottom-up approach to prescribe interactions to obey the pattern of “big ones eat smaller ones”. Life-history omnivory (Pimm and Rice, 1987) is therefore naturally incorporated in size-structured food webs through the use of a feeding kernel. To obtain an ensemble of different communities we use the top-down approach of a classical two-dimensional predator–prey interaction matrix – that is we assume that regardless of size individuals within a species have equal potential maximum link strength (coupling strengths in our model) to another species. As no top-down method exists for generating this matrix we use random matrices. The actual link strength is the product of the coupling strength and the feeding kernel, meaning that link strengths indeed are dynamic as they depend on the size-structure of both prey and predator.

As we generate food webs from a fixed initial pool of only 30 species and use a random matrix as coupling matrix we only obtain small food webs (maximum: nine species). However, it should be noted that the number of resource species the resource spectrum represents is not included. To obtain larger food webs a larger species pool is needed along with a sequential assembly algorithm (Post and Pimm, 1983), and a better method for obtaining coupling strengths between species. Our primary interest in the food web analyses has been the size- and trait-structure of food webs with a finite number of species, and how these compare with EQT predictions, which are based on the premise of a continuum of species. The general correspondence with EQT indicates that the broad-scale patterns are relatively insensitive to how the species-specific coupling strengths (i.e. food web structure) are specified. Still, an interesting follow-up study would be focused on the coupling matrix structure, which may more generally be size-dependent, and how the effective food web structure that emerges

from the coupling strengths and feeding kernel compares with empiric food webs.

5.3. Community structure

We generated an ensemble of size-structured food webs and used averages over these to make general predictions of the structure of fish communities, in particular the size-structure of individual populations, and how these spectra “stack” to form the community size-spectrum. In accordance with EQT we find the community spectrum to scale with $\lambda = 2 + q - n \approx 2$ meaning that the distribution of biomass as a function of individual body size is close to constant when individuals are sorted into logarithmically evenly sized bins. This prediction means that the biomass of individuals between e.g. 1 and 10 g is the same as those present with body sizes between 1 and 10 kg, in accordance with the Sheldon hypothesis (Sheldon et al., 1972).

The distribution of biomass as a function of m_* is predicted to be almost independent of m_* in accordance with EQT. The result is reminiscent of the Sheldon hypothesis, and it can be formulated as an extension of the Sheldon hypothesis: “The total biomass of individuals ordered in logarithmically spaced groups of their maturation size is approximately constant”. This means that the total biomass of all species with m_* between 1 and 10 g is approximately the same as that of species with m_* within 1–10 kg. This prediction is a novel extension and could be tested by size-based field data. In contrast to EQT the dynamic framework also provides predictions on the distribution of the number of species as a function of m_* . Species tend to cluster in groups on the m_* axis separated by a distance corresponding to the preferred PPMR β . This clustering is partly a reflection of the use of a fixed value of β ; more diversity in feeding strategies (i.e. different β) would probably smoothen the species distribution as well as making the feeding level more constant.

The size-spectra of individual species do not to follow power laws as predicted by EQT since there is a change in spectrum slopes from small to medium sized individuals. This difference stems from different scaling relationships for the survival probability of small and large individuals. The less steep slope in survival for small individuals is due to a proportionally low mortality rate caused by their low abundance relative to similarly sized resource items. Incorporating mortality from the resource spectrum on the smallest individuals may thus result in a single survival probability scaling. The probability of surviving to m_* scale as m_*^{-a} for a physiological predation constant value of $a=1$, which is conflicting with the value $a=0.86$ predicted by EQT. The discrepancy about the value of a highlights an inconsistency within EQT: Enforcement of mass balance between growth and predation leads to $a=0.86$, while the reproductive boundary condition can only be fulfilled if $a=1$. The full food web simulations demonstrate that both the scaling of surviving to m_* and the scaling of the number of offspring are best predicted by a value of $a=1$. This indicates that when EQT predictions depend on a , the value $a=1$ should be used even though that breaks mass conservation in EQT.

Lastly we demonstrate that realised PPMRs (i.e. PPMRs based on ingested prey) emerge in the model. Average realised PPMR is always larger than the preferred PPMR β since smaller prey items are more abundant than larger ones. It is found that the realised PPMR is proportional to the preferred ratio (PPMR = 1.7β). Model predictions show that realised PPMR oscillates around this value due to fluctuations in the average community spectrum. PPMR displays large fluctuations with size demonstrating that determination of PPMR from single measurements is problematic due to high prey abundance sensitivity. Empirical findings show that realised PPMRs increase with body size (Barnes et al., 2010), but

one should be careful about concluding that the preferred PPMR (which we put into models) shares this size scaling, since relative abundances may cause the increase rather than actual behavioural prey preferences: even though we have a fixed preferred PPMR our model predicts that realised PPMR is an increasing function of body size.

5.4. Conclusion and outlook

The proposed food web framework increases ecological realism in food web models as it resolves the complete life-history of individuals by representing the size-structure of each species with a size-spectrum. More specifically the framework complies with five requirements of (cf. Introduction): (1) being generic with few parameters, (2) being mechanistic and utilising individual-level processes, (3) including food dependent growth, (4) being practically solvable for species-rich communities, and (5) complying with data on community structure and individual growth curves.

Trait-based size-structured food webs can be examined at four levels of organisation: at community level, at species level, at trait level, and at the individual level. We generated empirically testable hypotheses of mainly biomass distributions at different levels of organisation.

By assuming a power law community spectrum and a constant feeding level the full dynamic model can be simplified to an EQT model (Andersen and Beyer, 2006). Correspondence of predictions by EQT and the full model justifies the use of the simplifying assumptions. EQT is a powerful analytical tool that in a simple manner yields insight to e.g. the biomass distributions within and across species in size-structured food webs. However, as EQT assumes steady-state, the study of emerging effects, e.g. diversity and responses to perturbations, has to be conducted with the full model.

The PSPM framework has showed existence of alternative stable states where single populations can exist with different size-structure compositions (de Roos and Persson, 2002; Persson et al., 2007; de Roos et al., 2008b). It is an open question whether such alternative states become more widespread or if they disappear when more species interact with each other. This question is important since it tells whether such alternative states are expected to occur frequently or rarely in nature, and consequently whether exploitation can easily induce shifts between states. An important future challenge is thus to study the possibilities of multiple states in complex food webs – not only of single individual populations, but of the ecosystem as a whole. The proposed framework allows exactly this kind of studies since it provides a full ecologically realistic but conceptually simple model of size-structured ecosystems.

Natural future extensions of the model could be to allow the species coupling strengths to be size-dependent and make coupling strengths depend on vulnerability and forageability of prey and predators (Rossberg et al., 2008) as well as on the spatial overlaps of the interacting species. Adding this extra level of mechanistic realism would allow the framework to be useful for studying ecosystem consequences of spatial changes of species populations, which could be driven by climatic changes.

Acknowledgements

Niels Gerner Andersen is thanked for valuable discussions on bioenergetic models. M.H. was supported by the European Marie Curie Research Training Network FishACE (Fisheries-induced Adaptive Changes in Exploited Stocks) funded through the European Community's Sixth Framework Programme (Contract MRTN-CT-2004-005578). K.H.A. was supported by the EU seventh framework research projects MEECE and FACTS.

Appendix A. Supplementary information

Supplementary information associated with this article can be found in the online version at doi:10.1016/j.jtbi.2010.12.006.

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Appendix A-G (online)

Online appendices for Hartvig, M., et al., Food web framework for size-structured populations. *J. Theor. Biol.* (2011), doi:10.1016/j.jtbi.2010.12.006.

Appendix A. Derivation of predation mortality

Predators with a size between m and $m + dm$ have a food intake rate of $s(m_p, m)f(m)hm^n\theta N(m)dm$ for m_p sized prey. The total density of food available from all prey sizes to the predators in $[m; m + dm]$ is $\phi(m)$ (5), meaning that the mortality experienced by a m_p sized individual is:

$$\mu_{p,i}(m_p) = \sum_j \int \frac{s(m_p, m)f_j(m)hm^n\theta_{j,i}N_j(m)}{\phi_j(m)} dm. \quad (\text{A.1})$$

The maximum food intake may be expressed as a function of $f(m)$, $v(m)$, and $\phi(m)$ via (6), such that the predation mortality can be written as:

$$\mu_{p,i}(m_p) = \sum_j \int s(m_p, m)(1 - f_j(m))v(m)\theta_{j,i}N_j(m) dm. \quad (\text{A.2})$$

By using the EQT assumptions of constant feeding level and a power law community spectrum (cf. section 3) the mortality reduces to $\mu_p(m_p) = \bar{\theta}(1 - \bar{f}) \int s(m_p, m)v(m)\kappa_c m^{-\lambda} dm$, which can be solved analytically:

$$\mu_p(m_p) = \alpha_p m_p^{n-1}, \quad (\text{A.3})$$

where $\alpha_p = \bar{\theta}(1 - \bar{f})\sqrt{2\pi}\kappa_c\gamma\sigma\beta^{1+q-\lambda} \exp[\frac{1}{2}\sigma^2(1+q-\lambda)^2]$.

Appendix B. Available food and the physiological level of predation a

Using the EQT assumption of a power law community spectrum allows calculation of the available food density $\phi(m) = \bar{\theta} \int s(m_p, m)\kappa_c m_p^{-\lambda} m_p dm_p$:

$$\phi(m) = \alpha_\phi \bar{\theta} \kappa_c m^{2-\lambda}, \quad (\text{B.1})$$

where $\alpha_\phi = \sqrt{2\pi}\sigma\beta^{\lambda-2} \exp[\frac{1}{2}\sigma^2(2-\lambda)^2]$.

Using the EQT assumption of constant feeding level yielding $\lambda = 2 + q - n$ allows us to write $\bar{\theta}\kappa_c = \bar{f}h/(\alpha_\phi\gamma(1 - \bar{f}))$ by rearranging the expression of the feeding level (6). Using this and the definition of \bar{h} allows writing $\alpha_p = c(\bar{h} + k)\beta^{2n-q-1}/\alpha$ where $c = \exp[\frac{1}{2}\sigma^2((1+q-\lambda)^2 - (2-\lambda)^2)] = 1.03 \approx 1$. Ultimately using the definition of f_c allows writing the physiological level of predation $a = \alpha_p/\bar{h}$ as:

$$a = c \frac{\bar{f}}{\bar{f} - f_c} \beta^{2n-q-1} / \alpha. \quad (\text{B.2})$$

Appendix C. Calculating efficiency ε of offspring production

The efficiency of turning energy into offspring is denoted ε . It includes losses due to behavioural aspects, pre-hatching mortality, and that the energy contents in gonadic tissue is higher than in somatic tissue. It is a quantity that is difficult to measure, but for $n = p$ its value can be derived.

The energy (in units of mass) routed into reproduction (for $n = p$) is $\psi(m, m_*)\bar{h}m^n$ where $\bar{h} = \alpha\bar{f}h - k$. The energy of the produced offspring is then, $E_o(m) = \varepsilon\psi(m, m_*)\bar{h}m^n$:

$$E_o(m) = \varepsilon\bar{h}\eta_*^{1-n}m_*^{n-1}m. \quad (\text{C.1})$$

From Gunderson (1997) we have the yearly mass-specific allocation to reproduction:

$$\varrho(m_*) = \varrho_0\eta_*^{1-n}m_*^{n-1}, \quad (\text{C.2})$$

where $\varrho_0 = 1.2\text{g}^{1-n}/\text{year}$ is obtained using least sum of squares in fitting the curve to the data for oviparous fish in Gunderson (1997). Equalling (C.2) and E_o/m allow us to determine the efficiency of offspring production ε :

$$\varepsilon = \frac{\varrho_0}{\bar{h}} \approx 0.12. \quad (\text{C.3})$$

Appendix D. Setting the search rate prefactor γ from initial feeding level f_0

Food for the smallest individuals in the spectra will be supplied by the background spectrum. If we assume that the resource spectrum is at carrying capacity κ then an equilibrium initial feeding level f_0 for the small individuals can be calculated using (6).

Alternatively we may specify an initial feeding level f_0 and derive one other parameter. By solving the feeding level for γ by using the analytical solution for the density of food $\phi(m)$ (B.1) we find γ as a function of f_0 :

$$\gamma = \frac{f_0 h}{(1 - f_0) \alpha_\phi \theta_{i,R} \kappa} \approx \frac{f_0 h \beta^{2-\lambda}}{(1 - f_0) \sqrt{2\pi} \sigma \theta_{i,R} \kappa}. \quad (\text{D.1})$$

Appendix E. Parameter estimation

Individual growth: From Kitchell and Stewart (1977) we obtain an estimate of specific dynamic action on 15 % of food consumption, and conservative estimates of egestion and excretion on 15 % and 10 % respectively. This results in an assimilation efficiency of $\alpha = 0.6$.

The maximum intake scales with a 0.6–0.8 exponent, with $n = 0.75$ being an approximate average value (Jobling, 1994). Andersen and Riis-Vestergaard (2004) provides a length-based relationship for the maximum intake rate based on a whiting study adopted for saithe. Using $m = 0.01l^3$ (m in g and l in cm) (Peters, 1983), and an energy content of 5.8 kJ/g (fish) or 4.2 kJ/g (invertebrates) (Boudreau and Dickie, 1992) yields a prefactor h for the maximal food intake on $83 \text{ g}^{1-n}/\text{year}$ or $114 \text{ g}^{1-n}/\text{year}$ (at 10°C). These intake values overestimate the intake of large individuals since Andersen and Riis-Vestergaard (2004) use an intake exponent of 0.67 instead of $n = 0.75$. Due to this a value of $h = 85 \text{ g}^{1-n}/\text{year}$ is selected, which also provides reasonable fits to ‘cod-like’ growth curves ($m_* = 5 \text{ kg}$).

The standard metabolism scaling exponent p for fish is slightly higher than for other taxa, around 0.8 from intra- and interspecies measurements (Winberg, 1956; Killen et al., 2007). For simplicity we assume $p = n$. The first term (acquired energy) in the growth model (8) is $\alpha f(m) h m^n$ where the feeding level $f(m)$ is a decreasing function of body size (see *Results*). This has the effect that even when $n = p$ is assumed the acquired energy term still effectively scale with a smaller exponent than the maintenance term km^p in accordance with the experimental data on food intake and standard metabolism. Furthermore it is noted that this clearly makes the individuals in each functional species non-neutral. The bioenergetic consequences of $n \neq p$ has been explored in detail by Andersen et al. (2008).

The prefactor for standard metabolism can from Peters (1983) be determined to $6.5 \text{ g}^{1-n}/\text{year}$ if the diet is composed of only invertebrates and $4.7 \text{ g}^{1-n}/\text{year}$ if all the energy is from fish. Both values were corrected to 10°C using $Q_{10} = 1.83$ (Clarke and Johnston, 1999). It is assumed that energy costs due to activity can be described with an activity multiplier on the standard metabolic rate. Estimations of activity costs are difficult to obtain, but activity multipliers are often reported in the range 1 to 3; e.g. 1.25 for North Sea cod (Hansson et al., 1996), 1.7 for dace (Trudel and Boisclair, 1996), and 1.44–3.27 for saithe (Andersen and Riis-Vestergaard, 2004) (however see also Rowan and Rasmussen (1996); He and Stewart (1997)). A reasonable value of the prefactor for the standard metabolism and activity costs is assumed to be $k = 10 \text{ g}^{1-n}/\text{year}$ corresponding to an activity multiplier in the range 1.5 to 2.1.

Food encounter: The preferred predator-prey mass ratio is set to $\beta = 100$ (Jennings et al., 2002) and the width of the selection function to $\sigma = 1$, which catches the general picture for at least cod and dab (Ursin, 1973). It should be noted that small organisms such as copepods have a larger σ of 3–4.5 (Ursin, 1974), but for simplicity and since focus is on species with rather large m_* the width σ will be held constant.

The exponent for swimming speed is $q = 0.8$ (Andersen and Beyer, 2006). The prefactor γ for the volumetric search rate is difficult to assess from the literature. An alternative approach is to determine it as a function of initial feeding level f_0 via (D.1). Experience with the model shows that feeding level is a decreasing function of body size. This means that it is sensible to use an initial feeding level f_0 that is larger than the expected average feeding level \bar{f} . In this study a default value of $f_0 = 0.6$ is used. This along with default parameters yields $\gamma = 0.8 \cdot 10^4 \text{ m}^3 \text{ g}^{-q}/\text{year}$ (Table 1). An alternative estimate of γ is possible by multiplying the prefactors for swimming speed (Ware, 1978) and swept reactive field area (reactive radius assumed equal to body length): $\gamma = 20.3 \cdot \pi \cdot 0.01^{-2/3} \text{ cm}^3 \text{ g}^{-q}/\text{s} \approx 4.3 \cdot 10^4 \text{ m}^3 \text{ g}^{-q}/\text{year}$, which indeed justifies the use of $f_0 = 0.6$.

Mortality: Realistic energy reserve sizes may be $\xi \in [5\%; 20\%]$, and in the present study $\xi = 0.1$ is used. A widely used background mortality for ‘cod-like’ $m_* = 5 \text{ kg}$ fishes is $\mu_b = 0.1 \text{ year}^{-1}$, which yields $\mu_0 = 0.84 \text{ g}^{1-n}/\text{year}$.

Reproduction: The efficiency of offspring production was not found in the literature. However, an analytical expression may be obtained (for $n = p$) by combining the calculation of yearly mass-specific allocation to reproduction from the bioenergetic model (Appendix C) with empirical measurements (Gunderson, 1997), which yields $\varepsilon = \varrho_0/h \approx 0.1$. The fraction of asymptotic size to mature at is $\eta_* = 0.25$ (Andersen et al., 2008). Offspring mass is $m_0 = 0.5$ mg which corresponds to an egg diameter of 1 mm (Wootton, 1979; Chambers, 1997).

Resource spectrum: The carrying capacity of the resource spectrum should equal the magnitude of the community spectrum: $\kappa m^{-\lambda}$, with an exponent $\lambda = 2 - n + q = 2.05$ (Andersen and Beyer, 2006). The magnitude of the resource spectrum is set to $\kappa = 5 \cdot 10^{-3} \text{ g}^{\lambda-1}/\text{m}^3$, which is comparable with findings from empirical studies (Rodriguez and Mullin, 1986). The constant for resource regeneration rate is $r_0 = 4 \text{ g}^{1-p}/\text{year}$ at 10°C (Savage et al., 2004). The cut-off of the resource spectrum is set to include mesoplankton, $m_{cut} = 0.5$ g.

Appendix F. Expected Lifetime Reproductive Success

The expected lifetime reproductive success can be split into two components: 1) the probability of surviving to become adult, and 2) lifetime reproduction per adult.

Appendix F.1. Survival probability

If we set $\frac{\partial N}{\partial t} = 0$ in (1) we may obtain the steady-state solution as:

$$N(m) = \frac{K(m_*)}{g(m, m_*)} \exp\left(-\int \frac{\mu(m)}{g(m, m_*)} dm\right), \quad (\text{F.1})$$

where $K(m_*)$ is the constant from the integration along m . We notice that the probability of surviving from size m_0 to size m is $p_{m_0 \rightarrow m} = \exp\left(-\int_{m_0}^m \frac{\mu(m')}{g(m', m_*)} dm'\right)$, which along with $p_{m_0 \rightarrow m_0} = 1$ allow us to write the survival probability as:

$$p_{m_0 \rightarrow m} = \frac{N(m)g(m, m_*)}{N(m_0)g(m_0, m_*)}. \quad (\text{F.2})$$

Appendix F.2. Lifetime adult reproduction

The amount of energy an adult belonging to a m_* population will spend on reproduction throughout its life is:

$$R_{life}(m_*) = \int_{t_*}^{\infty} p_{t_* \rightarrow t} \psi(m, m_*) E(m) dt,$$

where t_* is maturation age, and $\psi(m, m_*) E_i(m)$ the rate at which energy is allocated to reproduction. Noting that $g(m, m_*) = \frac{dm}{dt}$ allows us to write this as:

$$R_{life}(m_*) = \int_{m_*}^M p_{m_* \rightarrow m} \frac{\psi(m, m_*) E(m)}{g(m, m_*)} dm. \quad (\text{F.3})$$

Appendix G. Details of Numerical Methods

The model is in the form of a series of coupled partial-integro-differential equations (1), one for each species with the size preference function (4) being the integral kernel. The equations are of the first order in mass (i.e. hyperbolic) in which case shocks could be formed in the solutions. However the integral kernel smooths out any discontinuities and the equations can be solved effectively and accurately using a standard semi-implicit upwind finite-difference scheme for solving PDEs (Press et al., 1992). The McKendrick-von Foerster PDE (1) is discretised by calculating $g(m, m_*)$ and $\mu(m)$ explicitly and making the time update implicit, to yield:

$$\frac{N_w^{i+1} - N_w^i}{\Delta t} + \frac{g_w^i N_w^{i+1} - g_{w-1}^i N_{w-1}^{i+1}}{\Delta m_w} = -\mu_w^i N_w^{i+1}, \quad (\text{G.1})$$

where i denotes the time step, and w the grid index on the mass axis ($i, w \in \mathbb{N}^+$). First order approximations have been used for both the time and mass derivatives. The discretisation in mass is known as the upwind approximation since the derivative is calculated from w and $w - 1$, which is possible since the growth

function is non-negative. It is further noted that the ∂m approximation is semi-implicit since densities at time step $i + 1$ are used. Equation (G.1) may be written as:

$$N_w^{i+1} \underbrace{\left(-\frac{\Delta t}{\Delta w_w} g_{w-1}^i \right)}_{A_w} + N_w^{i+1} \underbrace{\left(1 + \frac{\Delta t}{\Delta w_w} g_w^i + \Delta t \mu_w^i \right)}_{B_w} = \underbrace{N_w^i}_{C_w}, \quad (\text{G.2})$$

which allows us to write an explicit solution for the density spectrum at the $i + 1$ time step:

$$N_w^{i+1} = \frac{C_w - A_w N_w^{i+1}}{B_w}, \quad (\text{G.3})$$

which can be solved iteratively since N_1^{i+1} is given by the boundary condition. The flux in the boundary $g(m_0, m_*)N(m_0, t)$ is equal to the reproduction flux of new recruits R (11) such that $g_0^i N_0^{i+1} = R$, which yields: $A_1 = 0$, and $C_1 = N_1^i + \frac{\Delta t}{\Delta m_1} R$.

This semi-implicit upwind scheme is very stable but diffusive. The third order QUICK (Quadratic Upwind Interpolation for Convective Kinematics) scheme along with the techniques by Zijlema (1996), which prevents overshooting problems introduced by the QUICK method, were used to check that numerical diffusion poses no problem for $\Delta t = 0.02$ years, and a m_w mass grid with 200 logarithmically evenly distributed points. To ensure stability the Courant condition (i.e. Press et al. (1992)):

$$\frac{|g_w^i| \Delta t}{\Delta m_w} \leq 1, \quad (\text{G.4})$$

is prudent to fulfill. The essence of the criterion is that Δt should be small enough not to allow individuals to skip any mass cells m_w during their growth trajectory.

The grid m_w spans the offspring size m_0 to 85 kg to include maturation sizes up to the order of 20 kg. The grid for the background spectrum ends at m_{cut} , and the lower limit should be low enough to ensure food items for the smallest individuals in the functional species, i.e. 3 decades lower than m_0 . Identical Δm_w is used for the background and species spectra to ease computations in the overlap $[m_0; m_{cut}]$.

To save computational time the ODEs for the background spectrum (15) are solved analytically. The solution at time $t_0 + \Delta t$ for the semi-chemostatic equation is:

$$N_R(m, t_0 + \Delta t) = K(m) - \left(K(m) - N_R(m, t_0) \right) e^{-[\tau_0 m^{p-1} + \mu_p(m)] \Delta t}, \quad (\text{G.5})$$

where $K(m) = \frac{r_0 m^{p-1} \kappa m^{-\lambda}}{r_0 m^{p-1} + \mu_p(m)}$ is the effective carrying capacity at resource size m .

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Ecological processes yield complex and realistic food webs

Paper II

Hartvig, M. 2011. Ecological processes yield complex and realistic food webs.
Manuscript.

Ecological processes yield complex and realistic food webs

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Abstract

A recent deterministic food web framework for size-structured populations is extended to explicitly resolve the spatial distribution of populations. Individuals in the size-structured populations select prey items of a suitable size relative to their own size, which allows individuals to change diet throughout life (life-history omnivory). Growth in body size and allocation to reproduction drives the population dynamics as opposed to instantaneous population increase in unstructured food web models.

Trophic interactions at the individual level can occur if prey has appropriate size, and if the predator and prey co-occur in space. Thus, as in nature, the resulting food web structure is the product of individual interactions.

Sequential community assembly leads to large, complex, and realistic communities: emergent organisation of food web structure, species diversity, abundance, and biomass resemble empirical data. Assembled communities demonstrate that non-intervality, which have previously been ascribed to phylogenetic correlations, additionally can stem from the spatial organisation in the community.

Individuals of different sizes within a population interact with different species, meaning that observed food web structure depends on which individuals that are targeted with the applied sampling method. Sampling in the model thus corresponds to sampling in nature. Several topological properties are found to be sensitive to the employed sampling methods, and abundance distributions are found to be more sensitive than biomass distributions.

Keywords: dynamic food webs, trait based model, community assembly, emergent organisation, trophic interaction, spatial interaction, ontogeny, size-structure, community ecology

Introduction

To predict the consequences of ecological perturbations trustworthy dynamic food web models are needed. The requirements to ‘trustworthy models’ are that they reproduce properties of the present and the past in accordance with empirical data from proven ecological processes. Ecological processes are of key importance as these are invariant of space and time and hence do not change when the environment or species compositions change. Higher level properties as e.g. food web structure

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needs to be emergent properties, as it is the ecological characteristics of an alien species, and not its original food web connections, that determines the faith of the invader and the impact on the invaded food web.

At present most dynamic food web models violate this requirement as they use food web structure as input to e.g. examine the degree of persistence, defined as the number of species in the initial web that is still present after simulating the dynamic system to its steady-state (e.g. Kondoh, 2003; Williams and Martinez, 2004b; Brose et al., 2006). In the model by Kondoh (2003) more flexibility is however allowed as the input matrix only determines potential links, and adaptive foraging is used to determine actual link strengths.

Two exceptions of dynamic food web models that have emergent food web structure that compares to natural webs have been published. Loeuille and Loreau (2005) used an evolutionary approach to obtain dynamic food webs, and showed that their model can be fitted to characterise some basic topological properties of natural food webs. Secondly Rossberg et al. (2008) developed a complex model where food webs emerge through evolution and invasion from surrounding communities, and performed a more rigorous empirical comparison of both food web structure and biomass distribution. Both approaches have the drawback that some parameters cannot be estimated directly from data, and the latter relies on parameter tuning, whereas it is difficult to control for which types of systems the first model will produce if it is not used as a fitting model.

To increase realism in the ecological processes I employ a physiologically structured model to enable a detailed individual-level account of the processes governing consumption, body growth, reproduction, and mortality, which ultimately drives population dynamics (Metz and Diekmann, 1986; de Roos and Persson, 2001). As the scope in this work is of a general nature a trait-based species description is employed contrary to using a species-specific parameter set (Hartvig et al., 2011). Communities are assembled using sequential assembly where the community gradually builds up and partly collapses with the introduction of new invading species (Post and Pimm, 1983; Drake, 1990). The model is conceptually simple, while including a high degree of ecological realism compared to earlier approaches. It relies solely on parameters that can be estimated from data. The emergent organisation in the assembled communities are validated with empirical data on food web structure, species diversity, abundance, and biomass distributions.

In the current work the effects of sampling method on food web structure, abundance and biomass distributions are examined. Some food web properties depend strongly on sampling methods. The same applies for abundance distributions, whereas biomass distributions are less sensitive. The model do not include evolutionary processes, nevertheless the assembled food webs are non-interval, which is a property of natural food webs that is typically ascribed to phylogenetic constraints (Cattin et al., 2004). The emergent food web structure suggests that non-intervality additionally may be the result of the spatial (or niche) organisation of species in a community – a hypotheses that can be tested empirically by comparing diet continuities of identical species in different food webs.

Community Model

Food web models typically assume species to be located at some fixed point in space, or the spatial overlap of two interacting species are somehow included in the interaction strength between the two species. I assume species to have their populations distributed in space. In the model food web structure emerges through the simple assumption that individual-level predator-prey interactions only can occur if the prey has appropriate size, and if the predator and prey have spatially overlapping populations. Fig. 1 shows how link strengths between individuals of different sizes vary depending on relative differences in body size, and the distance between the centre of the populations.

The model (Table 1) is based on a recent model (Hartvig et al., 2011) extended to include a representation of spatial structure. The entire life-history from birth, through maturation, reproduction, and ultimately death is explicitly resolved. A species is characterised by the traits: size at maturation m_* , its preferred predator-prey ratio β_i , and its central location x_i . The solution of the model is the continuous population structure of each species i represented in the form of a size-spectrum $N_i(m, t)$ at time t (denoted $N_i(m)$ for simplicity). $N_i(m)$ is the number density of individuals as a function of body mass m , and $N_i(m)dm$ is the number of individuals in the size range $[m, m+dm]$. The dynamics of the species' size-spectra is governed by a conservation equation (McKendrick, 1926; von Foerster, 1959) stating that changes in number density at size m is determined by somatic growth g_i and mortality μ_i :

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

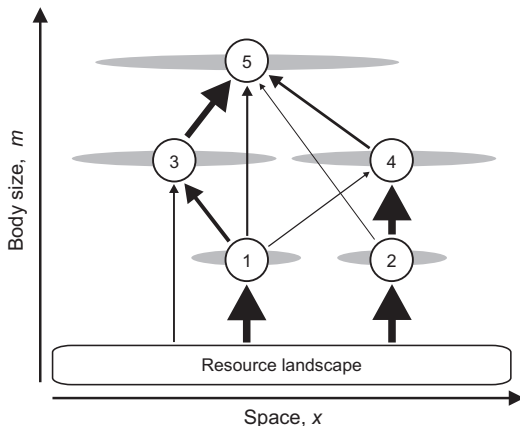


Figure 1: The role of space and body size on individual-level interaction strengths. Each node contains individuals of size m from a species population. Species are assumed to have identical preferred predator-prey mass ratios $\beta_i = \beta$, and nodes are placed with a vertical distance corresponding to β . Home range is an increasing function of body size, such that large individuals cover larger parts of space (grey area). Individual interactions decrease in strength when a) body size difference between individuals increase (e.g. nodes 4-2 vs. 5-1), or b) the spatial overlap between the interacting populations decrease (e.g. nodes 5-3 vs. 5-4).

Table 1: Model equations. m is individual mass, m_p is mass of a prey item, and m_* is maturation size. A species is characterised by (m_*, β_i, x_i) .

Community size-spectrum	$N_c(m) = \int N_R(m, x)dx + \sum_i N_i(m)$	(M1)
Volumetric search rate	$v(m) = \gamma m^q$	(M2)
Feeding kernel	$s_i(m, m_p) = \exp[-\ln^2(\beta_i m_p/m)/(2\sigma^2)]$	(M3)
Home range	$\sigma_x(m) = \sigma_{x,0} + \frac{1}{2} \log\left(\frac{m}{m_0}\right)$	(M4)
Spatial interaction kernel*	$\Omega(x_i - x_j, m, m_p) = \frac{1}{\sqrt{2\pi}[\sigma_x(m)^2 + \sigma_x(m_p)^2]} \exp\left(\frac{-(x_i - x_j)^2}{2[\sigma_x(m)^2 + \sigma_x(m_p)^2]}\right)$	(M5)
Encountered food	$\varepsilon_i(m) = v(m) \int \int s_i(m, m_p) \Omega_R(x_i - x, m) N_R(m_p, x) m_p dm_p dx + v(m) \sum_j \int s_i(m, m_p) \Omega(x_i - x_j, m, m_p) N_j(m_p) m_p dm_p$	(M6)
Feeding level	$f_i(m) = \varepsilon_i(m) / [\varepsilon_i(m) + h m^n]$	(M7)
Acquired energy	$E_i(m) = \alpha f_i(m) h m^n - k m^p$	(M8)
Allocation to reproduction	$\psi(m, m_*) = \left[1 + \left(\frac{m}{m_*}\right)^{-u}\right]^{-1} \left(\frac{m_* m}{m_*}\right)^{1-n} \quad \text{for } n = p^\dagger$	(M9)
Somatic growth	$g(m, m_*) = \begin{cases} [1 - \psi(m, m_*)] E_i(m) & E_i(m) > 0 \\ 0 & \text{otherwise} \end{cases}$	(M10)
Reproduction	$R_i = \frac{\epsilon}{2m_0} \int N_i(m) \psi(m, m_*) E_i(m) dm$	(M11)
Predation mortality	$\mu_{p,i}(m_p) = \sum_j \int s_j(m_p, m) [1 - f_j(m)] v(m) \Omega(x_j - x_i, m_p, m) N_j(m) dm$	(M12)
Starvation mortality	$\mu_{s,i}(m) = \begin{cases} 0 & E_i(m) > 0 \\ -E_i(m) / [\xi m] & \text{otherwise} \end{cases}$	(M13)
Background mortality	$\mu_b(m_*) = \mu_0 m_*^{n-1}$	(M14)
Resource dynamics	$\frac{\partial N_R(m, x)}{\partial t} = r_0 m^{p-1} [\kappa m^{-\lambda} - N_R(m, x)] - \mu_p(m) N_R(m, x)$	(M15)

*For resources $\Omega_R(x_i - x, m) = \Omega(x_i - x, m, \cdot)$ where $\sigma_x(m_p) = \sigma_{x,0}$ (Appendix A).

†See (Hartvig et al., 2011) for the equation governing the general case of $n \neq p$.

The biotic environment an individual experiences is given by the community spectrum $N_c(m)$, which contains food items needed to grow in size as well as enemies which may consume the individual. N_c is the sum of all species spectra and a resource spectrum, which represents additional smaller food items (M1).

Emerging interaction strengths and the spatial representation

Individuals search the biotic environment for food with a size-dependent volumetric search rate (M2). Prey items are selected with a size-selective feeding kernel, which enforces a preferred predator-prey mass ratio β_i (M3).

Offspring of size m_0 are produced at location x_i and have a spatial distribution width (home range) described by $\sigma_x(m_0)$. As individuals grow in size their home range $\sigma_x(m)$ increases.

A predator-prey interaction between two individuals may occur if 1) the two individuals are at the same spatial location, and 2) if the prey is of a suitable size. Interaction coefficients between individuals thus emerge from the feeding kernel and from a spatial interaction kernel.

Home range area is roughly proportional to body size (Kramer and Chapman, 1999; Haskell et al., 2002; Jetz et al., 2004) meaning that home range distance scales as $m^{1/2}$. As home range distance is a power law of body mass the spatial axis x is defined to represent $\log(\text{space})$. If offspring with size m_0 has spatial distribution

width $\sigma_{x,0}$ the distribution width for a m sized individual is:

$$\sigma_x(m) = \sigma_{x,0} + \frac{1}{2} \log \left(\frac{m}{m_0} \right). \quad (2)$$

The abundance density of individuals within a species is assumed to be normal distributed in space, such that species i has a density peak at x_i with width $\sigma_i(m)$. A species thus has the percentage $\mathcal{N}(x; x_i, \sigma(m)^2)$ of its m sized population at location x , where $\mathcal{N}(x; x_i, \sigma(m)^2)$ is the normal distribution, meaning that the spatial distribution of a species is $N_i(m, x) = N_i(m) \mathcal{N}(x; x_i, \sigma(m)^2)$. An alternative interpretation is that $\mathcal{N}(x; x_i, \sigma(m)^2)$ is the percentage of time an individual of the populations spends at location x .

A predator has the spatial density distribution $N_i(m, x)$ and its prey has the distribution $N_j(m_p, x)$. An m sized predator encounter prey of size m_p , and the total amount of encountered food is:

$$\begin{aligned} \varepsilon_i(m) &= v(m) \int \mathcal{N}(x; x_i, \sigma(m)^2) \int s_i(m, m_p) N_j(m_p) \mathcal{N}(x; x_j, \sigma(m_p)^2) m_p dm_p dx \\ &= v(m) \int s_i(m, m_p) \Omega(x_i - x_j, m, m_p) N_j(m_p) m_p dm_p, \end{aligned}$$

where $\Omega(x_i - x_j, m, m_p) = \int \mathcal{N}(x; x_j, \sigma(m_p)^2) \mathcal{N}(x; x_i, \sigma(m)^2) dx = \mathcal{N}(0; x_i - x_j, \sigma(m_p)^2 + \sigma(m)^2)$ is the spatial interaction kernel. Explicitly the spatial interaction kernel between two individuals is given as:

$$\Omega(x_i - x_j, m, m_p) = \frac{\exp \left(\frac{-(x_i - x_j)^2}{2[\sigma_x(m)^2 + \sigma_x(m_p)^2]} \right)}{\sqrt{2\pi[\sigma_x(m)^2 + \sigma_x(m_p)^2]}}. \quad (3)$$

Growth, reproduction, and death

The search volume, feeding kernel, and the spatial interaction kernel is used to calculate the mass density of encountered suitable food (M6).

An individual has a maximal food intake rate of hm^n , and the degree to which this maximum is achieved is described with a feeding level which varies between 0 and 1 (M7). Consumption is determined by a type II functional response $f(m)hm^n$. Food is assimilated with efficiency α and metabolic costs km^p are covered with highest priority, such that the net available energy is (M8). Juvenile individuals use all available energy for somatic growth, and as individuals grow in size and mature a size-dependent fraction of the energy is routed to reproduction (M9-10). Energy routed to reproduction is converted with efficiency ϵ into a flux of m_0 sized offspring through the boundary condition $g_i(m_0)N_i(m_0) = R_i$ in (1), and multiplied with 1/2 since only half the population is assumed to be females (M11). The maximum size an individual can obtain is the asymptotic size $M = m_*/\eta_*$, which is obtained when all surplus energy is used for reproduction ($\psi(M, m_*) = 1$). Growth may stop

at a smaller size if the metabolic costs exceed the assimilated food intake (stunted growth).

The described feeding process causes predation mortality on smaller individuals (M12). Additional mortality arise from starvation (M13) and a constant background mortality (M14), which is assumed inversely proportional to generation time. Starvation mortality occurs when the energy intake is smaller than the metabolic costs, and is assumed proportional to the energy deficit and inversely proportional to reserve size.

The spatial resource landscape

Resource dynamics are described with semi-chemostatic growth (M15). The total resource carrying capacity of the system is $\int km^{-\lambda}dx = \Delta x km^{-\lambda}$, where $\Delta x = x_{max} - x_{min}$ is the spatial size of the ecosystem. The resource carrying capacity experienced by a single species is $\int km^{-\lambda}\Omega(x_i - x, m)dx = km^{-\lambda}$, meaning that the resource level experienced by each species is invariant of ecosystem size. To avoid boundary effects at the edges of the ecosystem periodic boundary conditions are used (meaning that space is folded such that location x_{min} and x_{max} are equivalent). When periodic boundary conditions are used the size of the system has to be strictly larger than the home range of the largest individuals ($\Delta x \gg \sigma_x(m_{max})$).

Individual growth			
f_0	0.7	-	Initial feeding level
α	0.6	-	Assimilation efficiency
h	85	g^{1-n}/yr	Max. food intake
n	0.75	-	Exponent for max. food intake
k	10	g^{1-p}/yr	Std. metabolism and activity
p	0.75	-	Exponent of std. metabolism
σ	1	-	Width of feeding kernel
q	0.8	-	Exponent for search volume
$\sigma_{x,0}$	$\sqrt{1/2}$	-	Offspring spatial distr. width
Reproduction			
m_0	0.5	mg	Offspring mass
η_*	0.25	-	m_* rel. to asymptotic mass M
ϵ	0.1	-	Efficiency of offspring production
u	10	-	Width of maturation transition
Mortality			
ξ	0.1	-	Fraction of energy reserves
μ_0	0.84	g^{1-n}/yr	Background mortality
Resource spectrum			
κ	$5 \cdot 10^{-3}$	$g^{\lambda-1}/m^3$	Magnitude of resource spectrum
r_0	4	g^{1-p}/yr	Regeneration rate of resources
m_{cut}	0.5	g	Upper limit of resource spectrum
Δx	50	-	Spatial size of ecosystem
Derived parameters			
$\gamma(f_0)$	$\frac{f_0 h \beta^{2-\lambda}}{(1-f_0)\sqrt{2\pi\kappa\sigma}}$		Search volume ($m^3 g^{-q}/yr$)
λ	$\lambda = 2 - n + q = 2.05$		Slope of resource spectrum

Table 2: Parameter values for a temperature of 10°C (Hartvig et al., 2011). Time is expressed in units of years (yr).

Methods

Implementation

The model is parameterised for fish communities, as these constitute a widespread example of strongly size-structured systems, but it may be reparameterised for other less strongly size-structured taxa as well (Hartvig et al., 2011). A species independent parameter set is obtained through scaling with body mass m and maturation size m_* (Table 2). The parameters determining maximum consumption h , search volume γ , and resource carrying capacity κ determine the *initial feeding level* f_0 small individuals experience when feeding on a resource spectrum at carrying capacity. Since it is difficult to assess γ , initial feeding level f_0 is used as a parameter to calculate $\gamma(f_0)$ (Hartvig et al., 2011).

The model given by (1) and its linked components in table 1 is solved numerically with a first order semi-implicit upwind finite-difference scheme (Press et al., 1992; Hartvig et al., 2011). The species mass grid [$m_0, 85$ kg] is discretised to 200 logarithmically even sized mass groups, the x grid is represented by the interval $[-25; 25]$ which is linearly discretised using $dx = 0.2$, and the time step used for integration is 0.02 years (\sim one week). It was checked that the results do not depend on the chosen discretisation.

Assembly algorithm

Communities are assembled by sequentially allowing new species to invade from a small population biomass of $B_{inv} = 10^{-10}$ g/vol (Post and Pimm, 1983; Drake, 1990; Law, 1999). An infinite species pool is used, and species which are characterised by (m_*, β_i, x_i) are drawn randomly from continuous distributions. If invasion fitness is positive the system is simulated till it reaches steady state. Fitness is defined as $w = d \log(B)/dt$ (number of logarithmic decades the biomass changes per unit time), and a species is assumed to be in steady state if its absolute fitness is smaller than $w_{SS} = 1/1000 \text{ yr}^{-1}$. During simulation species are removed if they are heading to extinctions, defined as 1) the biomass drops below the extinction threshold $B_{ext} = 10^{-20}$ g/vol, 2) fitness is smaller than $-1/250 \text{ yr}^{-1}$ while the biomass is below 10^{-5} g/vol, or 3) fitness is smaller than $-w_{SS}$ while the biomass is below B_{inv} . When the new system has equilibrated, or if the invader had negative invasion fitness, the assembly process proceeds to a new invader.

Maturation size is drawn from a logarithmically uniform distribution ($m_* \in [1 \text{ mg}, 20 \text{ kg}]$), preferred predator-prey mass ratio is selected from $\beta = 10^d$ where d is drawn from a truncated normal distribution (mean 2, SD 0.5, $d \in [1; 3]$), and x_i is drawn from a uniform distribution.

Data analysis

Communities resulting from successful species invasions are used for analysis. Biomass, abundance, and diversity distributions are analysed by pooling species into 20 logarithmic evenly spaced m_* groups.

Obtaining food web statistics is non-trivial, as the set of prey varies through the different life-stages. The food web matrix will thus vary depending on which

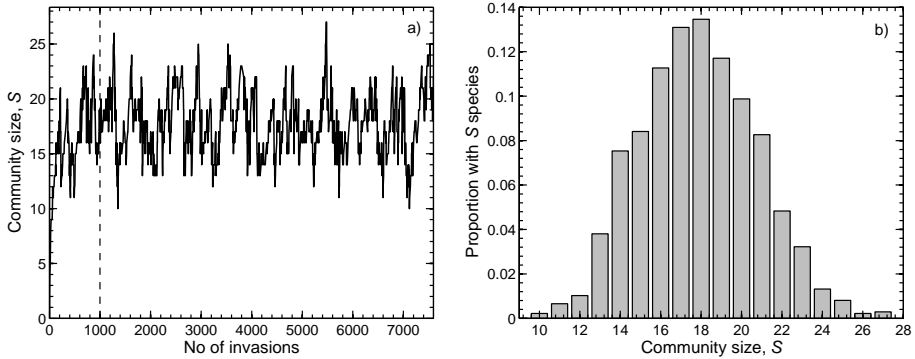


Figure 2: a) Number of species in the community as it builds up through species invasions. Communities following successful invasions after invasion attempt 1000 (dashed line) are used for analysis (1367 communities). b) Distribution of community sizes. In average the analysed communities contained 17.9 species.

parts of the populations that are included in the analyses. To overcome this the populations are sampled using four approaches: 1) individuals of all body sizes are sampled, 2) individuals from two orders below maturation size are sampled (2DEC, $m \geq 10^{-2}m_*$), 3) $m \geq 10^{-1}m_*$ individuals are sampled (1DEC), and 4) only adults are sampled ($m \geq m_*$). A link to a given prey is included in the binary food web matrix if the prey constitutes at least 5% of the total diet of the sampled individual. The effect of link threshold is examined in Appendix B. The 2DEC sampling method is the default sampling process used for all figures, as this sampling process seems close to what is done in empirical studies (different gear is typically used for species of different sizes). To enable comparison with natural food webs the model webs are standardised: 1) webs containing disconnected sub-webs are discarded, 2) the resource spectrum is lumped into a single resource species (Rossberg et al., 2006), and 3) trophically equivalent species are lumped into single trophic species (Martinez, 1991) where (m_*, β_i, x_i) is the mean trait values of the equivalent species. 0.5 to 2 species were typically removed in step 3) depending on sampling method and community size.

The following food web properties are calculated for the standardised food webs: (S) number of species, (C) directed connectance (Martinez, 1991), (Top) proportion of top predator species, (Can) proportion of cannibalistic species, ($Ddiet$) diet discontinuity which is a measure of intervality (Cattin et al., 2004), ($Clust$) the clustering coefficient representing the degree of node clustering (Dorogovtsev and Mendes, 2002), ($maxSim$) maximum similarity being the web average of all species maximum trophic similarity index (Williams and Martinez, 2000), and ($genSD$, $vulSD$) relative SD of number of resources (generality) or predators (vulnerability) per species (Williams and Martinez, 2000).

Results

Community analysis

Starting from a community comprised only by resources invaders are introduced sequentially leading to augmentation or extinction(s) of resident species in successful invasion attempts (Fig. 2.a). After the initial transient the chosen ecosystem size Δx leads to succession of communities with $S = 10..27$ (mean 17.9) species (Fig. 2.b).

As the preferred predator-prey ratio β_i is drawn randomly long term dynamics involving system-level evolution towards larger or smaller values of β is theoretically possible, but not present (Appendix, Fig. S1). It is however noted that the realised communities have a mean β , which is higher than the mean of 100 used in the species pool (Fig. S1). It could also be suspected that the maximum trophic level gradually builds up in the succession of communities (Fig. 2.a), which however is not the case as the maximum trophic level do not vary systematically with community size S , but is determined by the actual values of m_* in the community (Appendix, Fig. S5). This allows the communities after the initial transient of the community build-up to be used for analysis.

Large species span a larger fraction of space in their adult life compared to smaller species resulting. Consequently there is room for fewer large than small species in the assembled communities (Fig. 3.a). The species diversity distribution can be described with an allometric exponent of -0.26 – a void of species around 0.1 g is noted. Population biomass distribution across species is close to constant and almost invariant of sampling method (Fig. 3.b). Biomass accumulates more intensively in the largest m_* group as these species experience very little predation mortality in their adult life. The increased biomass triggers a trophic cascades downwards in the biomass distributions (Andersen et al., 2009). Compared to previous work the magnitude of the cascade is less strong as species have different β_i values in the current model (Hartvig et al., 2011). The depletion in biomass around 0.1 indicates that the lower density of species in the same size range is caused by the top-down cascade.

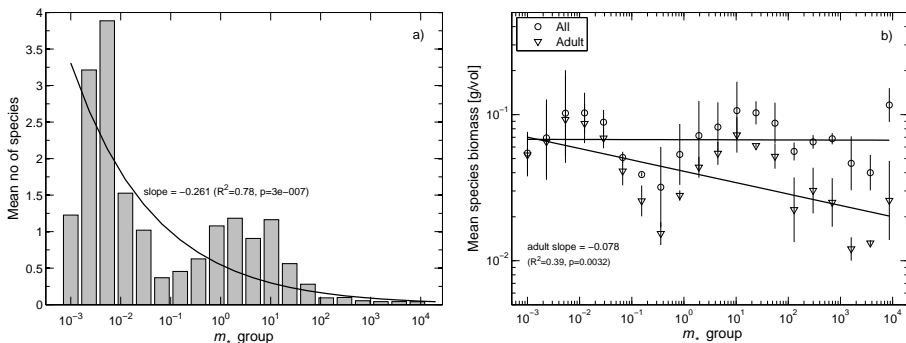


Figure 3: a) Mean no. of species in a community as a function of m_* . b) Distribution of biomass per species in m_* groups. Solid lines show the result of linear regression on $(\log(m_*), \log(y \text{ mean data}))$.

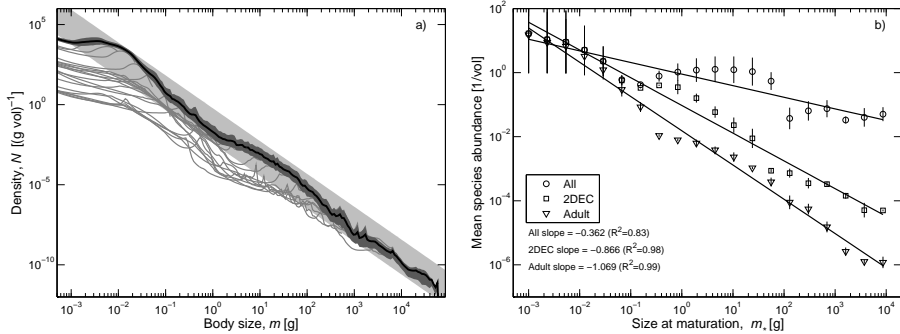


Figure 4: a) Mean community abundance spectrum (black, SD dark grey). The slope of they light grey box follows the expected $\kappa_c m^\lambda$ scaling form equilibrium theory (Andersen and Beyer, 2006). Mean species population structures are shown with grey lines. b) Number of individuals in a m_* species. Regression line from mean values.

The community spectrum follows – or might be a little steeper – the $m^{-2.05}$ scaling expected from equilibrium theory (Andersen and Beyer, 2006) meaning that the biomass ($= \int N_c m dm$) distribution along m (irrespective of species identify) is close to constant (Fig. 4.a). Individual species spectra are packed such that larger m_* species have lower offspring abundance.

Number of individuals within a species decreases as a function of m_* as equal amounts of biomass (Fig. 3.b) has to be shared by progressively larger individuals (Fig. 4.b). The slope of the decline depends strongly on sampling method, as the sampling leaves out the smallest individuals in the population, which at the same time are the most abundant.

Food web analysis

The availability of prey items is given by the spatial overlap between populations, and the prey items an individual species member consumes depends on the relative abundance and body size of potential prey items. This results in changes of diet compositions as individuals grow in body size (ontogenetic niche shifts). Fig. 5 shows the time average of the diet composition of individuals of all sizes across species in a community. When sampling a food web ecological information is lost as the food web matrix only considers species-specific interactions (Fig. 6). When comparing the two representations the diet map allows identifying species 1, 2, 3, 7, and 10 as potential keystone prey species, while the binary food web only identifies species 1 and 3. Potential keystone predators can be identified by constructing a map, similar to the diet map, that shows the relative importance of different predators. The food web matrix shows that larger species generally consumes smaller species. Links to larger species do however also exist as offspring and juveniles of large species can be significant food sources for smaller species. Additionally it is seen that the diet range of a predator is not contiguous as it does not have spatial access to all prey species.

Trophic position in a binary food web can be calculated in a variety of ways, where the short-weighted method produces the best result (Williams and Martinez,

2004a). Short-weighted trophic level is the average of a species' shortest path to the resources and the prey-averaged trophic level (Levine, 1980). The trophic level of a species increases with its maturation size, as large members of larger m_* species consume larger prey items (Fig. 7). Regression analysis (not included) shows that (m_*/β_i) is a better predictor of trophic position compared to m_* , as having a large β_i involves eating smaller lower trophic level species. Species density clusters at low trophic levels, as such species only have few links that needs averaging before the resources are reached.

Topological measures of the assembled and standardised food webs are listed in table 3 for different sampling methods along with values from natural food webs. Number of species S in the model webs are smaller than in natural webs, as a small spatial system size Δx was selected for computational reasons. When sampling adults only, or from decade below m_* (1DEC), all properties of the model food webs are within one SD of the natural webs. When sampling all individuals, or using 2DEC sampling, the properties Ddiet, Clust, and vulSD are above the range expected from natural webs: Diet discontinuity here becomes less contiguous as the

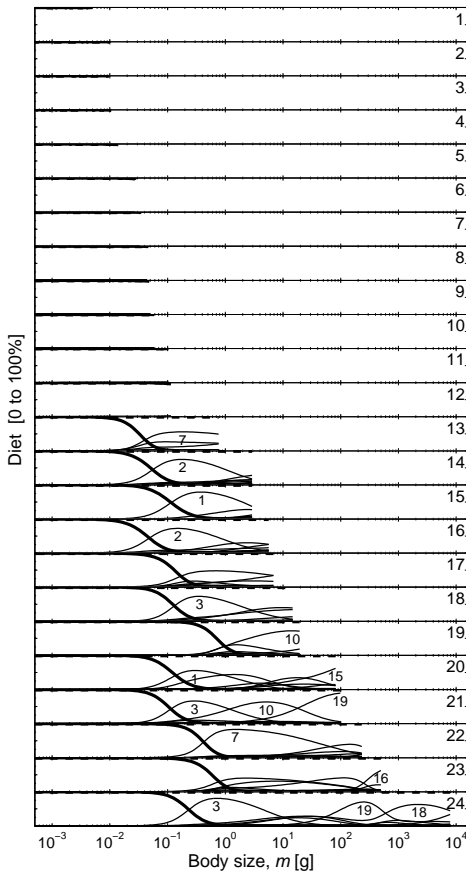


Figure 5: Diet composition as a function of body mass m for each species in a 24 species community. Species are ordered from small to large m_* vertically. The smallest species only consume food from the resources (thick lines). Thin lines indicate diet form other species, and diets exceeding 50% are marked with the species number of the prey.

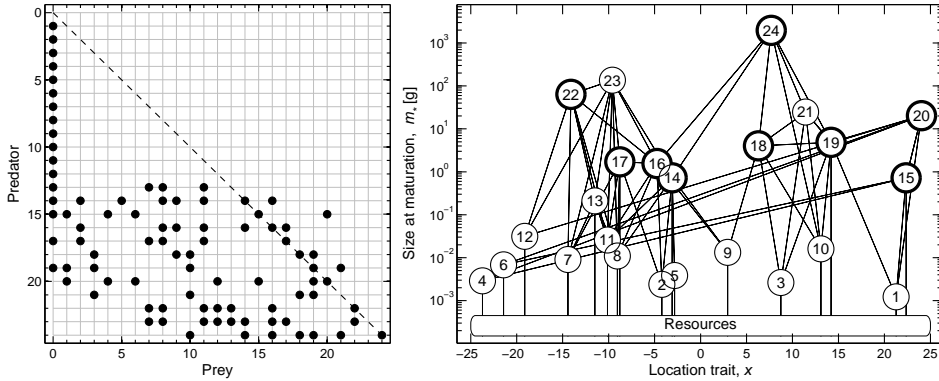


Figure 6: Food web matrix (sorted by m_*) and network of the community in Fig. 5. Species marked with thicker line widths are cannibalistic. The food web is obtained by sampling stomachs in individuals larger than $10^{-2}m_*$. A link to a prey is included if the prey constitutes more than 5% (link threshold) of the total diet in a sampled predator stomach.

small individuals, which have a different diet than the adults, from large m_* species will be included in the construction of the food web matrix. Clustering becomes more pronounced, and vulSD increases, as all species increase their number of links.

How the food web properties vary with community size, connectance, and link threshold can be found in the appendix (Figs. S2-S4). The link threshold directly determines the connectance of, and the degree of cannibalism in, the system, as it sets level for which links to include. Additionally the fraction of top species (Top), D_{diet} , and vulSD are strong functions of the link threshold.

The scaling b of number of links $L \propto S^b$ (Fig. 3) depends strongly on link threshold when the threshold is above 1% (Fig. S4). As empirical studies probably rarely employ a threshold larger than 5% the exponent $b \approx 1.55$ (Table 3) should be interpreted as the lower bound predicted by the model. For thresholds 1 to 0.01% the model predicts the link scaling to $b \approx 1.8..1.9$.

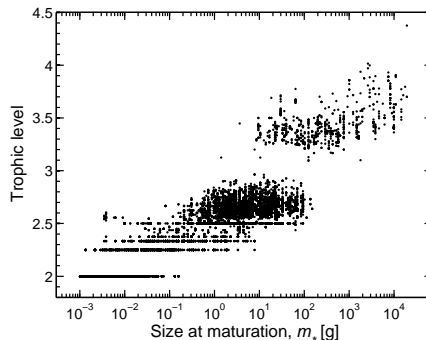


Figure 7: Trophic level (short-weighted) of species against their size at maturation.

Table 3: Topological properties of food webs (mean \pm SD, or R^2 in parenthesis). Properties are shown for different sampling methods (cf. *Methods*) in the model data, and for 17 natural food webs.

		Model				Empirical webs*
		All	2DEC	IDEC	Adults	
Webs analysed	n_{webs}	1367	1367	1367	1367	17
Number of species	S	17 ± 3.5	17 ± 3.6	17 ± 3.6	17 ± 3.6	54 ± 35
Connectance	C	0.16 ± 0.03	0.16 ± 0.02	0.15 ± 0.02	0.14 ± 0.02	0.16 ± 0.10
Link scaling	b	$1.58 (0.91)$	$1.57 (0.92)$	$1.55 (0.93)$	$1.54 (0.93)$	$1 \text{ to } 2^\dagger$
Fraction top species	Top	0.20 ± 0.08	0.20 ± 0.08	0.20 ± 0.08	0.21 ± 0.08	0.18 ± 0.19
Fraction cannibals	Can	0.30 ± 0.08	0.30 ± 0.08	0.30 ± 0.08	0.30 ± 0.08	0.16 ± 0.19
Diet discontinuity	Ddiet	$0.58 \pm 0.18^\ddagger$	$0.51 \pm 0.18^\ddagger$	0.23 ± 0.16	0.06 ± 0.07	0.22 ± 0.15
Clustering coefficient	Clust	$0.75 \pm 0.05^\ddagger$	$0.72 \pm 0.06^\ddagger$	0.56 ± 0.10	0.38 ± 0.10	0.50 ± 0.15
Maximum similarity	maxSim	0.56 ± 0.04	0.56 ± 0.04	0.54 ± 0.04	0.51 ± 0.05	0.60 ± 0.10
Rel. SD of generality	genSD	0.85 ± 0.06	0.84 ± 0.06	0.81 ± 0.06	0.76 ± 0.07	1.13 ± 0.44
Rel. SD of vulnerability	vulSD	$1.32 \pm 0.16^\ddagger$	$1.29 \pm 0.17^\ddagger$	1.16 ± 0.21	1.02 ± 0.21	0.98 ± 0.18

*Rossberg et al. (2008). † Dunne (2009). ‡ Property not within one SD of empirical data.

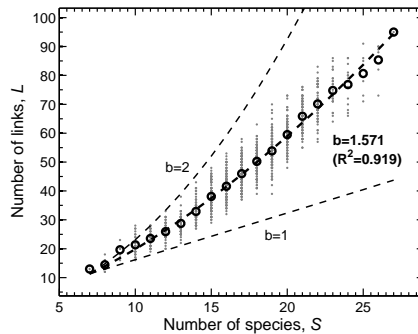


Figure 8: Number of links vs. number of species in the food web. The result from linear regression of $L = aS^b$ is shown (thick dashed line) along with the expected scaling range (thin dashed), and the mean link number for each food web size (circles). Scaling value b from other sampling methods are found in table 3.

Discussion

Species in the model are characterised by three traits: size at maturation m_* , location x_i , and preferred predator-prey mass ratio β_i . The entire life-history of individuals are resolved by a continuous body size representation of the species' population compositions. Size at maturation sets the life-history strategy: small species have large mass-specific allocation to reproduction, whereas large species have the possibility of growing to large body sizes by paying the price of a lower mass-specific allocation to reproduction. Species populations are spatially distributed such that their abundances peak at x_i and decreases when moving away from this point. Larger individuals of the population span a larger fraction of space as they have a larger home range. The spatial overlap between populations and the relative size difference between individuals determines the possibility of predator-prey interactions. Preferred β_i determines the size of prey a predator is most successful at capturing. If species have equal $\beta_i = \beta$ higher trophic levels of communities are only rarely occupied (results not included). Diversity in β_i strategies enables a heterogeneity of energy 'channels' that transfer biomass from low to high trophic levels, where

channels comprised of large β_i 's transfers biomass faster. The presence of fast and slow channels have been shown to promote stability (Rooney et al., 2006), whereas the current work demonstrates that the heterogeneity even promotes diversity.

Model interpretation

The conceptual representation of space is inspired by the ideas of Holt (1996), and the actual implementation with a spatial interaction kernel is similar to the approach by Zhang et al. (2011). The spatial size of a community is given by Δx , and increasing the size leads to the possibility of more species as expected from species area relationships (Connor and McCoy, 1979; Rosenzweig, 1995).

Space is characterised by a single dimension. Increasing dimensionality is desirable, but computationally demanding. Augmenting dimensionality to a 2D landscape will probably not change the qualitative behaviour. As the model is parameterised for fish communities a 3rd dimension, capturing the differences and couplings between the benthic and pelagic zones is interesting, but belongs to a more specialised study. That the one-dimensional caricature reproduces empirical data (cf. below) justifies the use of the reduced dimensionality.

The x dimension may alternatively be interpreted as a niche dimension, where the resource landscapes represents different kinds of resources (MacArthur and Levins, 1967). In this interpretation the spatial interaction kernel should be interpreted as the degree to which the species is specialised to x type organisms, and where the degree of generality (the width of the kernel) increases with body size. It seems like a probable scenario that larger predators do not care whether its prey consumes resource type 1 or 2, whereas the consumers may be bad at feeding on the resources to which they are not specialists.

Model inferences & validation

Species diversity as a function of body size is bell shaped in macroecological studies, where the tail towards larger body sizes can be described with a power law (Blackburn and Gaston, 1994; Loder et al., 1997). Whether the bell shape is an artifact of low resolution of small-sized organism remains to be seen (e.g. May, 1990; Brown et al., 2004). There is some evidence for diversity to be allometric functions of body size for animals (Marquet et al., 2005) and plants (Niklas et al., 2003). The allometric exponent for macroecological species diversity has been hypothesised to be $-2/3$ and $-3/4$ (Hutchinson and MacArthur, 1959; Marquet et al., 2005). Reuman et al. (2008) analysed biomass and species distributions within a huge ensemble of natural food webs. From table S2 in Reuman et al. (2008) the mean allometric exponent of species diversity within food webs can be calculated to -0.23 ± 0.07 SD (range: -0.33 to $+0.12$). The model food webs in the current study has a species distribution with exponent -0.26 , which is within the empirical range.

Biomass distribution in the model is roughly a constant function of both body mass and m_* . Empirically a constant community biomass as a function of body mass, irrespective of taxa, is known as the Sheldon hypothesis (Sheldon et al., 1972), which has been validated empirically (e.g. Boudreau and Dickie, 1992), with the complication that heavily harvested systems have a decline in biomass for increasing body

size (Shin et al., 2005). Constant biomass as a function of m_* has been termed the ‘Extended Sheldon hypothesis’ (Hartvig et al., 2011). Analysis of data in table S2 in Reuman et al. (2008) yields an m_* biomass exponent of -0.53 ± 0.14 SD (range: -1.13 to -0.08). Data from Reuman et al. (2008) is mostly from communities less strongly size-structured compared to aquatic communities. Data from the North Sea indicate that the m_* biomass distribution for aquatic systems is slightly declining or close to constant (Jennings et al., 2007). When model data are sampled with a method that can be compared to trawling the model exhibits a slight decline (exponent -0.08) in the m_* biomass distribution, signalling that model data is comparable to the data from the North Sea. As the North Sea is heavily fished and displays a decreasing Sheldon biomass spectrum it is interesting that the m_* distribution of biomass is close to constant, as it indicates that the m_* distribution might be invariant of fishing pressure. The difference between data from Reuman et al. (2008) and Jennings et al. (2007) call for a more thorough analysis and comparison of biomass distributions across system types. The data on m_* distribution of biomass in size-structured systems are weak, but along with the Sheldon distribution it may be concluded that the model complies with contemporary data on biomass distribution within and across species identities.

Abundance distribution in the community (scaling of abundance as a function of body mass irrespective of taxa) as a whole complies with the Sheldon scaling. Data for validating the scaling of individual spectra has not been found. The abundance of individuals as a function of m_* depends strongly on sampling method meaning that when comparing to data the data should be corrected for sampling bias. That abundance distributions are more sensitive to sampling than biomass distributions is not surprising, as a size-structured population has the highest abundance density at small body sizes, which often is not caught when sampling adults or larger juveniles. The Sheldon scaling is not notably affected by sampling as large species have a much lower abundance of offspring compared to smaller species.

The Eltonian Pyramid is present for both biomass and abundances when species identity is considered. In the case of biomass the model predicts population biomass to be invariant of m_* , but as small species are more numerous the total community biomass of m_* species is a decreasing function of m_* . However, if taxonomic identity is ignored there is no pyramid of biomass as a function of body mass, as the Sheldon biomass spectrum is constant.

Food web structure is often produced from statistical algorithms, that from a set of parameters generate food webs matrices with properties similar to natural webs. The most widely used method is the niche model (Williams and Martinez, 2000) belonging to a class of purely statistical phenomenological models that at least take desired number of species S and connectance C as input parameters (Cohen and Newman, 1985; Williams and Martinez, 2000; Cattin et al., 2004; Allesina et al., 2008). Recently more process driven approaches involving phylogenetic correlations (Rossberg et al., 2006) or foraging theory (Petchey et al., 2008) have been introduced; both approaches have C (and Rossberg et al. (2006) additionally S) as an emergent property, while several input parameters are tuned using optimisation to provide a best fit to natural webs. In the current model food web structure emerges from

the rules that 1) prey needs to have a suitable size, and 2) prey and predator must co-occur in space. Thus all food web properties in the model (including S and C) are emergent properties of population and community dynamics, and it should be stressed that no optimisation or parameter tuning is employed. The emergent structures have been compared to natural webs, and when sampling only adults or from one logarithmic decade below m_* all food web properties are within one SD of empirical data.

Diet discontinuity, D_{diet} , describes the degree of non-intervality of a food web, and the departure from intervality has been ascribed to phylogenetic constraints on a species' diet (Cattin et al., 2004). Current results show that non-intervality can result from the spatial distributions of species as well, as morphologically possible links are not realised if the species populations do not have a spatial overlap. Results additionally show that non-intervality results from ontogenetic niche shifts causing small and large individuals within a species to have different diets: a higher D_{diet} is measured when all contrary to only larger individuals are sampled. The ladder obstacle of diet discontinuity in strongly size-structured food webs was also recently found in aquatic food web studies by Woodward et al. (2010).

The scaling b of number of links, $L \propto S^b$, is of fundamental interest to understand the scaling in food webs. Early food web studies showed that number of links per species, L/S , was constant (i.e. $b = 1$, Cohen and Briand, 1984). Schoener (1989) challenged this scale-invariance, and more detailed food webs documented that link density increases with species richness (i.e. $b > 1$, Polis, 1991; Martinez, 1991). This led to the constant connectance, L/S^2 , hypothesis ($b = 2$, Martinez, 1992), which was supported by new food web data (Warren, 1989; Martinez, 1993). Montoya and Solé (2003) rejected both the constant links per species and the constant connectance hypothesis, and found $b \approx 1.5$ from analysis of newer and larger data sets. A recent analysis of the largest contemporary compilation of high resolution food webs yielded $b = 1.57$ (Riede et al., 2010). Depending on sampling method the analyses of the assembled communities in the current study yield b in the range 1.54-1.58 demonstrating that sampling method is not a serious issue when determining b . It is however found that b is sensitive to link threshold, and lowering the link threshold below 1% gives a b of 1.8-1.9. The scatter of empirical data (Riede et al., 2010, 65 webs) and the scatter from deterministic model runs (1367 webs, Fig. 8), along with the sensitivity to link threshold, indicate that obtaining a precise value of b is problematic. From the current study it may be concluded that $b = 1.55$ should be expected to be the lower value of link scaling in natural food webs, and that depending on employed link threshold the expected range of b is 1.55-1.9. To address the issues of link threshold the link strength distribution within individual food webs should be analysed, and subsequently b should be estimated from comparisons across food webs. Previous process driven attempts tried estimating b with foraging theory and underestimated b to the range 1.2-1.3 (Beckerman et al., 2006).

Cannibalism is more widespread in model webs compared to natural webs irrespective of sampling method and link threshold. Historically the presence of cannibalism has been underestimated, but presently it is recognised that cannibalism is a very widespread and common interaction type across taxa (Fox, 1975; Polis, 1981;

Smith and Reay, 1991; Elgar and Crespi, 1992). Whether contemporary webs underestimate cannibalism is not known, but this could be the case as $\sim 35\%$ of the webs in the current food web collection (Riede et al., 2010) were published prior to the recommendations of paying attention to cannibalism when collecting food web data (Cohen et al., 1993), and as data collection takes years the actual number of studies that potentially underreport cannibalism might be substantially higher. Current data show that cannibalism in marine webs, which the current model is parameterised for, have a higher degree of cannibalism compared to other system types (Riede et al., 2010), meaning that the model is expected to have a higher degree of cannibalism. As individuals of a species naturally has a full spatial overlap with its own population one could speculate that cannibalism would be common for all species in the current model. However, inspecting diet compositions (Fig. 5) shows that cannibalism at least never dominate a species diet. It should be noted, that when individuals grow in body size their home range increases yielding a spatial coupling strength to m_p sized individuals of its own species that decreases as $1/\sqrt{2\pi(\sigma_x(m)^2 + \sigma_x(m_p)^2)}$. Small individuals do not need cannibalism as plenty of alternative resources are available at high density from the resource spectrum, and large m_* species have low abundance density in earlier life stages compared to smaller species, meaning that the largest scope for cannibalism is present for larger individuals in intermediate sized m_* species.

The food web abstraction

Food web properties are calculated on binary food webs, whereas natural food webs mostly have weak links that are important for e.g. food web stability (Berlow et al., 2004; Wootton and Emmerson, 2005). Additionally topological properties depends on the link threshold employed to determine whether or not to include a link in the binary food web matrix (Winemiller, 1990; Martinez et al., 1999). When collapsing flow based food webs, that resolve relative prey diet contributions, to binary webs some species may become trophically unique (having identical sets of predator and prey). To resolve this problem equivalent species are lumped into a single trophic species before calculating topological properties (Martinez, 1991), a procedure which however also has several complications (Yodzis and Winemiller, 1999). The ideal solution to circumvent these problems is to base topological properties on a flow based rather than a binary food web representation.

Food webs describe trophic interactions at the species level, whereas trophic interactions occur at the individual level. Ideally the food web matrix should be four-dimensional, as predator-prey sizes as well as their identities are important (Emmerson and Raffaelli, 2004). As the two body size dimensions are continuous they are actually infinite dimensional – a problem that in practice should be resolved by representing the size dimensions with discrete size classes. The current food web approach captures the $2 \times$ infinite-dimensional nature of trophic interactions, and I demonstrate that collapsing the individual-level trophic interactions to a species revolved food web matrix naturally excludes useful ecological insight. It is also demonstrated that topological properties in addition to link threshold depend on sampling method (i.e. which size range of the population is sampled). Advancing

empirical food web matrices to include four dimensions may not be feasible in all situations – when not feasible an alternative approach would be to measure size-dependent feeding kernels along with a two-dimensional food web of potential prey (i.e. as the current model is constructed).

Conclusion

Large and complex communities have been assembled, and the emergent food web structure has been validated with empirical data on food web topology as well as empirical data on diversity and biomass distributions. Contrary to previous approaches (Loeuille and Loreau, 2005; Rossberg et al., 2008), that rely on model fitting and parameter-tuning, the realism of the current approach is solely due to ecological processes at the individual level, which drives the size-structured population dynamics. In short: including individual-level ecological processes in population dynamics lead to complex and realistic food webs.

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Appendix A. Spatial interactions within the resource spectrum

As resources are uniformly and continuously distributed along the x -axis the encountered food by a predator is invariant of the shape of the probability distribution that determines the spatial spread of resources at location x . This means that $\sigma_x(m_p) = \sigma_{x,0}$ can be used without changing the qualitative behaviour of the model. What can change to a minor extent is the distance $x_i - x_j$ required for two species with equal m_* and β to coexist.

The resource spectrum is discretised along x and m ($X \times M_R$ grid points). Each m grid point (M grid points) for each species (S number of species) requires a $X \times M_R$ matrix for $\Omega(\cdot)$. This means that the required memory scale as $S \cdot M \cdot X \cdot M_R \sim SM^3$ (>1GB for a 20 species food web). To make computations feasible we employ $\sigma_x(m_p) = \sigma_{x,0}$ where the required memory scales as SM_g^2 (~ 6 MB for 20 species).

Appendix B. Additional figures

Community buildup: β distribution

A truncated normal distribution (with mean 100) is used to assign invaders a preferred predator-prey mass ratio β_i . The realised β distribution of the assembled communities are shifted towards larger β (Fig. S1.a), meaning that species with large β_i generally has a higher fitness. This could have the consequence that the system tries evolving towards increasing the mean β of all species in the community, which however is not the case (Fig. S1.b).

Food web structure

Fig. S2 shows how the food web properties varies as a function of food web size and connectance, and Fig. S3 shows how connectance scale with food web size.

The link threshold is the minimum percentage a prey has to constitute in the predators diet before it is counted as a link. As number of links changes the food web properties also changes when the threshold is varied (Fig. S4).

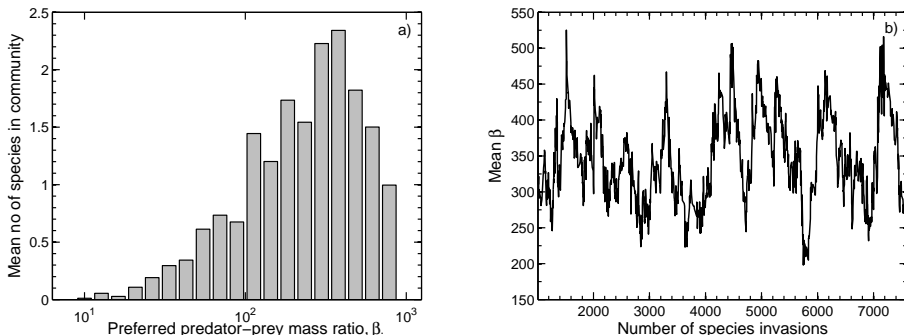


Figure S1: a) Average β distribution in analysed communities, and b) time-evolution of the mean β of the assembled communities.

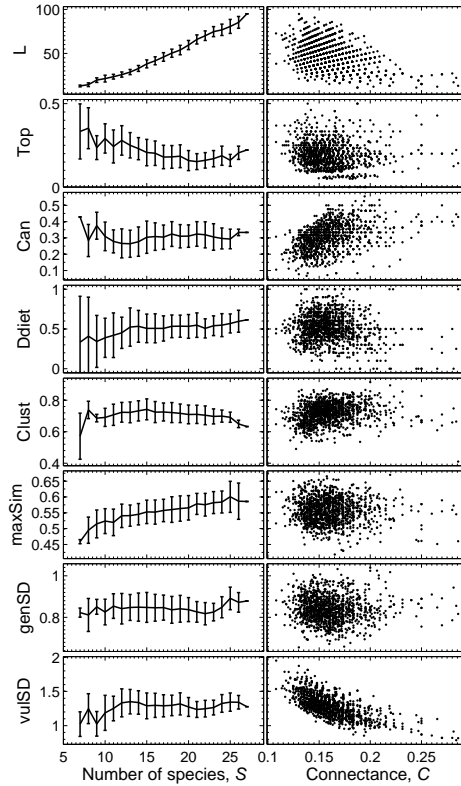


Figure S2: Food web properties against food web size (left column) and connectance (right column). See *Methods* description of food web properties.

Trophic level

A species' trophic level is correlated with the size at maturation m_* , as larger species consume larger prey (Fig. 7). The maximum trophic level obtained by any species in the community falls into two distinct ranges: a lower range between 2.5 and 3, and an larger range between 3 and 4 (Fig. S5.a). Whether a realised system falls into the lower or upper range is determined by the size of the largest m_* species, where however intermediate sizes may fall into either category (Fig. S5.b). Actually a third range might be feasible, but only one of the 1367 webs had a maximum trophic level of ~ 4.5 .

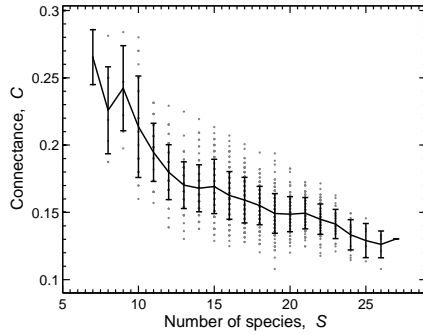


Figure S3: Connectance against food web size.

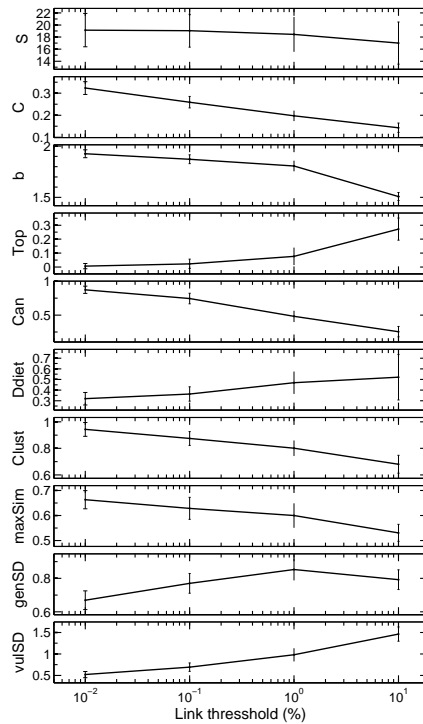


Figure S4: Food web properties and their dependence on link threshold. Link threshold is the minimum percentage a prey has to constitute in the predators diet before it is counted as a link.

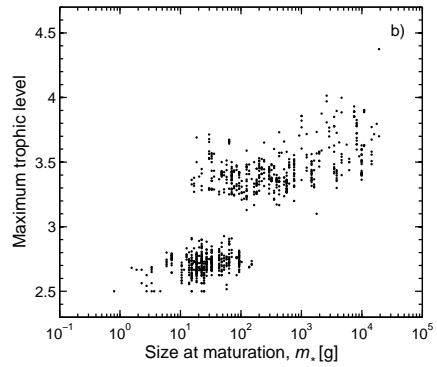
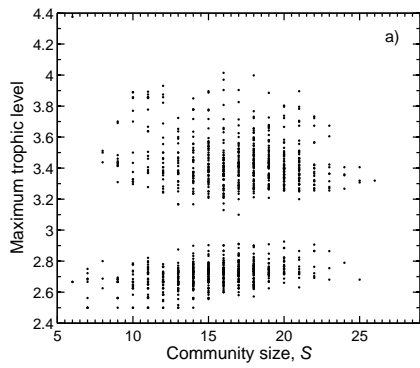


Figure S5: a) Maximum trophic level (short-weighted) in a food web against its number of species (a), and maximum m_* species (b).

Life-history constraints on the
success of the many small eggs
reproductive strategy

Paper III

Appeared in:

Andersen, K.H., Beyer, J.E., Pedersen, M., Andersen, N.G., and Gislason, H. 2008.
Life-history constraints on the success of the many small eggs reproductive strategy.
Theoretical Population Biology, 73(4):490–497.

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Life-history constraints on the success of the many small eggs reproductive strategy

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Received 16 August 2007

Available online 16 February 2008

Abstract

The reproductive strategy of most fishes is to produce a large number of tiny eggs, leading to a huge difference between egg size and asymptotic body size. The viability of this strategy is examined by calculating the life-time reproductive success R_0 as a function of the asymptotic body size. A simple criterion for the optimality of producing small eggs is found, depending on the rate of predation relative to the specific rate of consumption. Secondly it is shown that the success of the reproductive strategy is increasing with asymptotic body size. Finally the existence of both upper and lower limits on the allowed asymptotic sizes is demonstrated. A metabolic upper limit to asymptotic body size for all higher animals is derived.

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Keywords: Size spectrum; Life history; Asymptotic size; Marine ecology

1. Introduction

The majority of bony fish (osteichthyes) in aquatic ecosystems share a particular life-history strategy with respect to reproduction: they spawn a huge number of tiny eggs (e.g. Duarte and Alcaraz (1989) and Winemiller and Rose (1993)). A fraction of fish species are viviparous (spawn live offspring), but even then the larvae are small (Fig. 1). This reproductive strategy is also found in a number of invertebrate phyla, like marine invertebrates (Christiansen and Fenchel, 1979) and nematodes (Herreras et al., 2007), but in the animal kingdom the most extreme ratios between eggs size and adult size occur among the bony fish. As an example, an adult female cod of 10 kg spawns around 5 million eggs every year, each hatching to a larva weighing around 0.5 mg. This larval cod has to grow 6 orders of magnitude in body mass, facing a tremendous risk of being eaten, before reaching

the elusive goal of maturation. It has been demonstrated that the strategy of many small eggs indeed is optimal in patchy environments (Winemiller and Rose, 1993) or related to physiology (Ware, 1975; Thygesen et al., 2005), but still it is remarkable that it is successful for creatures with an asymptotic body mass M ranging from few grams to the largest teleosts with M of hundreds of kilograms. There are essentially five different trade-offs associated with different aspects of this reproduction strategy: (1) the total fecundity (no. of eggs per female) increases with size, pointing towards higher success of fishes with large asymptotic size; (2) however the individual specific fecundity (no. eggs per kg of body mass) decreases with asymptotic size (Gunderson, 1997), and (3) the time to reach maturation is increasing with size at maturation, leading to a higher risk of dying before maturation. The trade-offs associated with egg size are: (4) the total fecundity increases with decreasing egg size, (5) however just as in point (3) above, smaller eggs mean increased time to maturation and therefore larger cumulated mortality. These five factors are combined in a quantitative exploration of the question: what is the relative success of the many small eggs reproductive strategy for fishes with different asymptotic size? It will be shown that there exists

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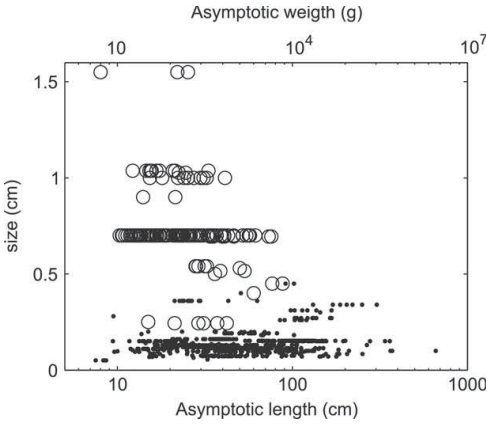


Fig. 1. Diameter of eggs of oviparous fishes (points) and length of larvae of viviparous fishes (circles) as a function of the asymptotic length or weight of the species. Weight is calculated from lengths by the relation $\text{weight} = al^3$, with $a = 0.01 \text{ g cm}^{-3}$. Data comprises 2029 stocks from 172 marine and 38 freshwater species, with 1797 stocks being of oviparous species and 232 of viviparous species (Froese and Pauly, 2000).

not only an upper limit to the asymptotic size for which this strategy is successful, but also a lower one.

The argumentation is developed around a calculation of the reproductive success, or fitness, of a species with a given asymptotic size. The derivation is based on two generally accepted assumptions: individual growth is modeled by a von Bertalanffy-like growth curve and mortality is a decreasing function of size. This is first used to give an approximate derivation of the reproductive success. A more elaborate mathematical analysis is then performed using equilibrium size spectrum theory (Andersen and Beyer, 2006). This theory is part of a larger effort to develop physiologically structured models of marine ecosystems, consisting of species defined by their most important trait, namely the asymptotic size M . The framework is based only on processes described on the individual level, in particular a von Bertalanffy-like mass budget. A simple rule of big-fish-eat-smaller-fish leads to a predation mortality declining with size. This predation mortality represents the effect of the ecosystem on an individual which is used to derive the size distribution of the whole population. The reproductive success of a population with a life history defined by its asymptotic size is then derived by combining the size distribution with a specification of individual allocation to reproduction.

2. Life-history model

The bioenergetic budget describing the fate of food consumed by an individual of mass m is described by a von Bertalanffy-like equation:

$$\dot{m}m^n = g(m) + km, \tag{1}$$

where $\dot{m}m^n$ is the rate of assimilated mass left after standard metabolism and $g(m)$ is the somatic growth rate. The term km is available energy (in terms of mass), which is used for

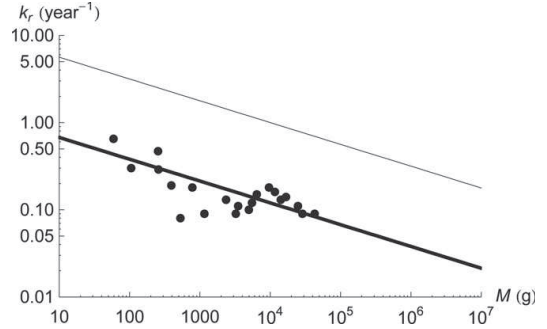


Fig. 2. Mass-specific available energy $k = \dot{h}M^{n-1}$ (upper line) and allocation to reproduction $k_r(M)$ (thick line). Data points represent the total reproductive output over a whole year divided by body mass for oviparous fish (Gunderson, 1997).

reproduction and activity. For $n = 2/3$, Eq. (1) corresponds to the common form of the von Bertalanffy growth curve (von Bertalanffy, 1957), and for $n = 3/4$ to the recent proposal by West et al. (2001). When the individual reaches its asymptotic size, M , no energy is used for growth, $g(M) = 0$, meaning that the prefactor for available energy can be written as $k = \dot{h}M^{n-1}$.

2.1. Reproductive investment

To find an expression for the reproductive output we will return to the available energy km in (1). The prefactor $k = \dot{h}M^{n-1}$ is a decreasing function of asymptotic size M and represents the amount of energy that is used for reproduction and activity. Thus smaller fishes can invest more energy in reproduction and activity relative to their body size than large ones. Strictly speaking, reproduction only takes a part of the available energy $k_r m$ after maturation. Owing to this ontogenetic change at maturation, the growth equation will therefore not follow (1) exactly. However, as available energy is a small part of the total intake before maturation, the growth curves generated by Eq. (1) and an equation with a step function at maturation are in practice indistinguishable (West et al., 2001; Andersen et al., 2007). Assuming that some fraction of the available energy:

$$k_r = \varepsilon_r \dot{h}M^{n-1} \tag{2}$$

is used for reproduction produces a good fit with data (Fig. 2). This corresponds to a total allocation of energy to reproduction per time of $\propto M^n$, in agreement with theoretical life-history predictions for other taxa (Charnov et al., 2001).

2.2. Reproductive success

Usually the calculation of life-time expected reproductive output, R_0 , is achieved using the expected adult reproductive output multiplied by the probability of reaching maturation (e.g. Charnov (1993)). For this a description of the mortality rate is needed. The mortality stemming from predation can be derived by a formalization of the rule “big-fish-eat-small-fish”

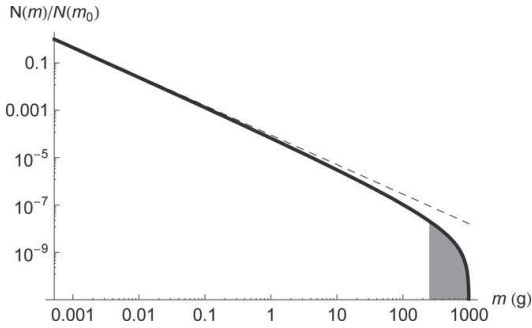


Fig. 3. The size spectrum of a species with $M = 1$ kg (thick line). The dashed line is the asymptotic scaling m^{-n-a} and the hatched area indicate the reproductively active individuals. For values of the parameters, see Table 1.

leading to a predation mortality $\mu_p = \alpha_p m^{n-1}$, where α_p is a constant setting the level of predation, and the exponent n is the one appearing in the mass balance (1) (Andersen and Beyer, 2006). Assuming now for simplicity that fish mature at their asymptotic size, the total lifetime after maturation is $1/\mu(M) \propto M^{1-n}$ and the expected number of offspring produced by an adult is therefore $\sim M^{1-n} k_r M/m_0 \propto M/m_0$, i.e. proportional to the adult size. The probability of reaching maturation is $P = \exp[-\int_{m_0}^M \mu/g dm]$, where g is the growth given by (1). Ignoring the allocation to reproduction km in the growth equation leads to $P = (M/m_0)^{-a}$, where $a = \alpha_p/\bar{h}$ is the ratio between predation mortality and specific intake; in the following called the physiological level of predation (Beyer, 1989). Multiplied with the expected number of offspring, this gives a rough estimation of the expected adult reproductive output, $R_0 \propto (M/m_0)^{1-a}$. Circumventing the approximations used in the above line of reasoning requires a more in-depth analysis, which will be performed in the following.

R_0 will now be calculated as the ratio between the total reproductive effort and the effort required to keep the population in steady state. The total reproductive investment of a population is the investment of an individual with mass m , $k_r(M)m$ multiplied by the population density of individuals $N(m)$ and integrated over the mature population. The steady-state size distribution of a population $N(m)$ can be derived as a solution to the McKendrick–von Foerster equation (McKendrick, 1926; von Foerster, 1959):

$$\frac{\partial}{\partial m} [g(m)N(m)] = -\mu(m)N(m), \tag{3}$$

where growth $g(m)$ is specified by Eq. (1). The mortality $\mu(m)$ contains a predation part $\mu_p(m)$ and a constant background mortality μ_0 , so $\mu(m) = \mu_p(m) + \mu_0$. With that, the solution to (3) is (Appendix):

$$N(m) = \kappa m^{-n-a} \left[1 - \left(\frac{m}{M} \right)^{1-n} \right]^{\frac{a+a_0}{1-n}-1}, \quad \text{for } m < M, \tag{4}$$

where κ is an integration constant (see Appendix for its value). Here again the physiological level of predation appear in the exponents. Analogous we have defined the physiological

Table 1
Parameters used in the life-history model

Parameter		Value
n	Scaling of intake and standard metabolism	3/4
\bar{h}	Prefactor for effective assimilated mass	$10 \text{ g}^{1/4} \text{ year}^{-1}$
μ_0	Background mortality	0.1 year^{-1}
η	Fraction of asymptotic size to mature at	0.25
m_0	Mass of larva	0.5 mg
ε_r	Fractioning between gonads and activity	0.12

Theoretical (Jensen, 1996) and empirical (Froese and Binohlan, 2000; He and Stewart, 2001) studies show that size at maturation is roughly 0.63 times the asymptotic length, leading to $\eta \approx 0.25$. The mass of a newly hatched larvae is calculated from an egg diameter of 1 mm (Chambers, 1997). The value of ε_r was chosen to achieve a fit with measurements of yearly gonado-somatic index (Fig. 2) (Gunderson, 1997). The value of the background mortality of 0.1 year^{-1} is typically used in fisheries assessments as an order-of-magnitude estimate of mortality due to other processes than predation and fisheries. The prefactor for the effective rate of intake \bar{h} is estimated from a relation between the von Bertalanffy growth rate and asymptotic size based on data from 57 fish species (Kooijman, 2000). The estimate was corrected to a temperature of 10°C using a Q_{10} of 1.83 (Clarke and Johnston, 1999) and an average shape factor of 0.225.

background mortality as $a_0 = \mu_0 M^{1-n}/\bar{h}$. While the physiological predation is independent of asymptotic size, the physiological background mortality is an increasing function of asymptotic size, because larger asymptotic size means longer time to maturation, and therefore a larger cumulative effect of the background mortality. The solution for the size spectrum consists of a scaling part with exponent $-n-a$ multiplied by the term in the square brackets, which makes the population density decline to zero when the size approaches the asymptotic size M (Fig. 3). As the physiological predation essentially determines the exponent of the size spectrum of the population, it is a crucial parameter in what follows.

Individuals mature when they reach a certain fraction η of their asymptotic size (Table 1). The total reproductive effort of the population measured in number of offspring per time is then $\frac{1}{2} k_r(M) \int_{\eta M}^M m N dm / m_0$, where the factor $\frac{1}{2}$ is because only females produce gonads. For the population to be in steady state the reproductive flux has to balance the flux needed at the size of offspring, m_0 , in the lower end of the size spectrum. This flux is the term inside the square brackets in the von Foerster equation (3), $g(m_0)N(m_0)$. Evaluating the ratio of the reproductive effort over the required effort requires the evaluation of the integral over the population structure, yielding:

$$R_0 = \frac{1}{2} \varepsilon_r \left(\frac{M}{m_0} \right)^{1-a} \left[1 - \left(\frac{m_0}{M} \right)^{1-n} \right]^{-\frac{a+a_0}{1-n}} f(n; a, a_0), \tag{5}$$

where the function $f(n; a, a_0)$ can be evaluated in terms of Beta functions (Appendix). When the asymptotic size is much larger than the egg size ($M \gg m_0$) and $n < 1$, the term in the angular brackets is close to one. This corresponds to the approximation that almost all of the assimilation intake is used for growth for

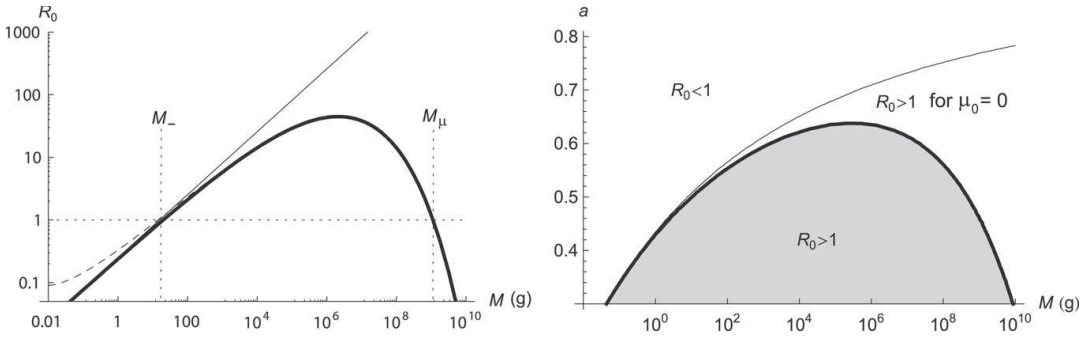


Fig. 4. (a) The reproductive success R_0 as a function of asymptotic size for a predation pressure $a = 0.5$, based on the approximation (6) (thick line), based on the full solution from the appendix with background mortality $\mu_0 = 0.1 \text{ year}^{-1}$ (dashed line) and without background mortality $\mu_0 = 0$ (thin line). The horizontal line is drawn at $R_0 = 1$. (b) The limits to reproductive success defined by $R_0 = 1$ as a function of asymptotic size and predation pressure using $\mu = 0.1 \text{ year}^{-1}$ (thick line) and $\mu = 0$ (thin line). The gray area shows the life histories with $R_0 > 1$.

small individuals, i.e. $\ll hm_0^n$. In this case:

$$R_0 = \frac{1}{2} \varepsilon_r \left(\frac{M}{m_0} \right)^{1-a} f(n; a, a_0), \quad \text{for } M \gg m_0. \quad (6)$$

The quantity R_0 is the “expected number of offspring per lifetime” or number of offspring per offspring, which is a fitness measure of a population in equilibrium where the density dependence takes place before maturation, which is probably the case for most fish populations (Mylius and Diekmann, 1995). Whether it is indeed the correct fitness measure which is maximized is not crucial to what follows as we are not optimizing this function, but are mainly concerned with the points where $R_0 = 1$. The validity of the approximation $M \gg m_0$ is demonstrated by the fact that over the relevant range of asymptotic sizes, results from Eq. (6) are indistinguishable from the full solution from Eq. (5) (Fig. 4(a)).

2.3. Limits to asymptotic size

The expression for reproductive success R_0 (6) highlights four important points: (i) The reproductive success is a power-law function of the egg size proportional to m_0^{a-1} . This means that if $a < 1$, the most successful strategy is to produce as small offspring as possible. (ii) For small values of asymptotic size where the background mortality is much smaller than the predation mortality, the reproductive success is $R_0 \propto M^{1-a}$. As $a < 1$, the exponent is positive, making R_0 a growing function of asymptotic size. In other words: the reproductive strategy of many small eggs becomes increasingly successful the larger the asymptotic size. (iii) This means that there exists a lower asymptotic size M_- where $R_0 = 1$, below which the reproductive strategy can no longer sustain the population (Fig. 4(a)). (iv) When M becomes very large, the reproductive success diverges towards zero, as $f(n; a, a_0) \rightarrow 0$ when $M \rightarrow M_\mu$ as a_0 is an increasing function of M . This break-down at the asymptotic size M_μ is associated with the existence of the constant background mortality μ_0 , which has a cumulated impact over the whole life, increasing with asymptotic size. The points where $R_0 = 1$ therefore defines both upper and

lower limits to the asymptotic size. The limits are governed by the value of the physiological predation parameter a , which is predicted from equilibrium size spectrum theory to be $a \simeq \beta^{2n-1.8}/\alpha$, where β is the predator-prey mass ratio, and α the assimilation efficiency (Andersen and Beyer, 2006). Using $\beta = 100$ and $\alpha \approx 0.5$ gives $a \approx 0.5$.

The expression (6) can be used to calculate the region where $R_0 > 1$ as a function of the asymptotic size and the predation parameter a (Fig. 4(b)). This has been done both without background mortality and with a constant background mortality of $\mu_0 = 0.1 \text{ year}^{-1}$. The region below the curve $R_0 = 1$ delineates the viable life-history strategies in terms of asymptotic size and the physiological predation a .

2.4. Consequences of exponents of intake and standard metabolism

In the development of the growth equation (1) it was implicitly assumed that the scaling of intake and standard metabolism with mass had the same exponents. This is strictly speaking not the case, as the scaling of intake has an exponent related to the uptake of food through a surface area, $n \approx 2/3$, while the standard metabolism for fish $k_s m^p$ has a higher exponent, of $p \approx 0.8$ (Winberg, 1956). With an explicit representation of standard metabolism the mass balance becomes:

$$\alpha hm^n = g(m) + km + k_s m^p, \quad (7)$$

where the assimilated mass αhm^n is diverted to somatic growth $g(m)$, available energy km and standard metabolism $k_s m^p$. An absolute upper limit to asymptotic size M_+ can be derived as the point where the requirement for standard metabolism $k_s m^p$ equals the assimilated food intake αhm^n (Fig. 5):

$$M_+ = \left(\frac{\alpha h}{k_s} \right)^{\frac{1}{p-n}}, \quad \text{for } p > n. \quad (8)$$

This result is extremely sensitive to the values of the exponents n and p . Using the procedure in Table 1 with an exponent $n = 2/3$ we get the assimilated intake

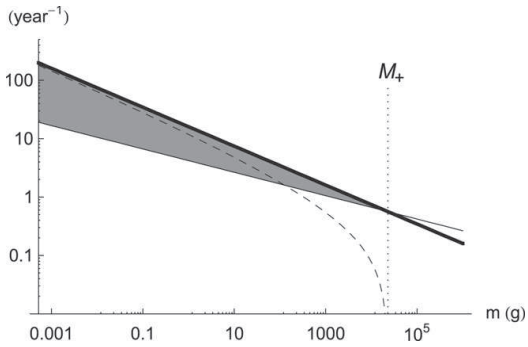


Fig. 5. The difference between the individual specific assimilated intake αhm^{n-1} (thick) and the specific standard metabolism (thin) limits the specific available energy k (gray area and dashed line). The point where the standard metabolism is equal to the assimilated intake defines the metabolic upper limit to asymptotic size M_+ .

$\alpha hm^n = 16 m^{0.67}$ g/year at 10 °C. The exponent of the standard metabolism is $p = 0.8$ and the prefactor is $k_s = 4.2 \text{ g}^{1-p}$ /year at 10 °C (Winberg, 1956). This gives an exponent in Eq. (8) of 7.7 leading to $M_+ \approx 28$ kg. Changing the exponent of the intake to just $n = 0.7$ increases M_+ to 600 kg!

If the complete mass balance in (7) is used as a basis for the calculation of R_0 , it would be significantly harder to arrive at analytical solutions. Still the effect can be understood qualitatively. If the metabolic limit is smaller than the limit given by the background mortality M_μ , then the effect will be to induce a sharp divergence of R_0 towards 0 as M approaches M_+ . In the opposite case R_0 will diverge before reaching the metabolic limit rendering that limit irrelevant.

3. Discussion

We have derived the reproductive success R_0 as a function of asymptotic size M for fishes employing a many-small-eggs strategy. The derivation was based on two assumptions: von Bertalanffy-like individual growth and a decreasing mortality with size. A consequence of the von Bertalanffy-like growth is that the individual specific reproductive effort (eggs per kg of body mass) has to decrease as asymptotic size increases, being in good agreement with measurements of reproductive output as a function of asymptotic size. Combining this with the decreasing mortality with size resulted in an adult life-time allocation to reproduction roughly proportional to asymptotic size. The main result in (6) provides an explanation for the success of the particular life-history strategy employed by most bony fish, and shows how life-history choices are influenced by the asymptotic size and the physiological level of mortality. The result gives a very clear criterion for the feasibility of the many-small-eggs strategy, namely that the physiological level of predation a (the ratio between predation mortality and specific assimilated intake) should be less than 1. In this case the strategy is indeed optimal (i.e. maximizing R_0), demonstrating that for most fish, a does not exceed 1. The essence of this result stems from the realization that

expected life-time adult allocation to reproduction scales with asymptotic size, which has to be discounted by the probability to reach maturation scaling as M^{-a} . This explanation is a generalization of the classical explanations in terms of an interplay between growth and a constant mortality (Ware, 1975), or prey patchiness (Winemiller and Rose, 1993). The explanation does not contain a mechanism for setting a lower limit to the egg size, it just predicts that fitness increases as egg size decreases. In reality a mechanism determining a lower limit must exist as the distribution of egg sizes of fish is rather narrow around a 1 mm diameter (Chambers, 1997) (Fig. 1). This mechanism could be the availability of suitable prey for the larvae (typically copepod nauplii) or sperm limitation, which is hypothesized to be at work in marine invertebrates (Levitán, 1993).

The theory developed here shows that not only is the many-small-eggs strategy optimal, its success also increases with asymptotic size, until a large size. Both lower and upper limits for the successful application of this strategy have been derived, depending on the value of the physiological predation a . At a maximum value of $a \approx 0.63$, only life histories with an asymptotic size around 100 kg has the possibility of reproductive success. Lowering a , either through a decrease in the predation mortality or faster growth, opens up a larger range of possible asymptotic sizes. The lower limit for asymptotic size M_- is determined by a break-down of the many-small-eggs reproductive strategy. This is tightly tied to R_0 depending on the ratio M/m_0 . As m_0 is fixed this means that the smaller the asymptotic size the fewer eggs can be produced until at asymptotic sizes $< M_-$ R_0 drops below 1. When a fish has a life history with an asymptotic size approaching M_- , it therefore has to modify its reproductive strategy to increase reproductive success. There are many examples of this for small fishes (but as far as we are aware no systematic study): sticklebacks (*Gasterosteidae*) and gobies (*Gobiidae*) guard their eggs; *Poeciliidae* and related species (e.g. guppies) do not spawn eggs but fully capable juveniles; cichlids (*Cichlidae*) have developed mouth-brooding as parental care, etc. The predicted lower limit, corresponding to a value of the physiological predation of $a \approx 0.5$, is at an asymptotic size of around 10 g. There are also examples of larger viviparous teleosts (e.g. rockfish), but these examples appear to be less frequent the larger the asymptotic size, and even in those cases the larvae are rather small (Fig. 1).

The result that small offspring size is optimal, however less so for smaller asymptotic size, was also shown qualitatively for marine invertebrates (Christiansen and Fenchel, 1979). This is not surprising as they share the marine environment with the fish. The current derivation adds the identification of the upper limits to the asymptotic size by considering the full life history and not only the larval phase.

From the detailed considerations of the mass balance, an upper limit for asymptotic body size M_+ was found at the point where all the intake was used to fuel the standard metabolism (8). We conjecture that this limit is a general limit, applicable to all higher animals obeying the general mass balance (7). This includes endotherms, and in particular mammals, as they follow a similar metabolic budget albeit with an added term to account

for heat loss (Kooijman, 2000). As this scales with surface area $m^{2/3}$ it has the same exponent as the intake, and it can therefore effectively be contained in the factor αh . Using values for fish we have determined the value of the metabolic upper limit. It is, however, not easy to estimate the exact value as it is very sensitive to small variations in the difference between the exponents of intake and standard metabolism. However the existence of the metabolic upper limit hinges on the fact that the exponent of the standard metabolism is larger than that of the intake, which is well established for fish. There is therefore no doubt about the existence of the limit, but rather on the exact value of it.

The uncertainty in the determination of M_+ is not crucial to the existence of an upper limit for M as there exists another upper limit M_μ governed by the background mortality. This limit is of the order of 100 tonnes, i.e. rather large compared with the largest extant bony fish.

The values of both lower and upper limits depend on the prefactor for the assimilated intake \bar{h} , such that an increase in \bar{h} increases both limits. An increase in \bar{h} can come about by an increase in the total metabolism, which would lead to a decrease in the physiological background mortality a_0 , leading to an increase in M_μ . An increase in \bar{h} can come about by raising the body temperature by inertial homeothermia (e.g. tuna). If the scaling of standard metabolism and intake with temperature is the same, this alone will not increase the metabolic upper limit M_+ . However it does lead to more energy being available to reproduction and activity by the same factor as the increase in \bar{h} . In this manner, increasing the body temperature makes it possible to increase the asymptotic size and push the reproductive upper limit closer towards the metabolic limit M_+ .

The derivation contains a number of parameters, but it is important to stress that the main result $R_0 \propto (M/m_0)^{1-a}$ only depends on the ratio between asymptotic size and egg size and on the life-history parameter a . The exact value of the upper and lower limits where $R_0 = 1$ are sensitive to the exact parameter values in the mass balance equation. Using estimates for the values of the parameters, we show that the values of the limits are indeed reasonable.

It is tempting to relate the presence of the upper limits in asymptotic size to the discrete change in the reproductive strategy with respect to offspring size that happens when the asymptotic size reaches a few hundred kilograms, namely the transition from bony fish producing many small eggs to elasmobranchs and marine mammals producing few, large offspring (Freedman and Noakes, 2002). There are three possible explanations for this transition: (1) that the many-small-eggs strategy breaks down due to the background mortality (M_μ), (2) that it breaks down as it reaches the metabolic upper limit M_+ or (3) that the fitness of the reproductive strategy with extensive parental care employed by the marine mammal is higher than that of the many-small-eggs strategy, even before the limits due to background mortality or the metabolism reduces R_0 . Which of the three is relevant cannot be answered definitely by the present calculation, as this would require an assessment of the utility of parental care,

which is hard to quantify. Finally, other constraints not related to the reproductive strategy, like the ability to extract sufficient oxygen from the water may limit the asymptotic size (Pauly, 1981; Freedman and Noakes, 2002).

The calculation illustrates clearly how trade-offs formed by basic energetic considerations shapes the options available for successful life histories. It underlines the importance of a proper understanding of the energy budget of the individual, e.g. how energy is allocated between growth, reproduction and activity. It also demonstrates that the exact values of the scaling exponents of intake rate and standard metabolism matters, as the existence of the metabolic limit M_+ hinges on the difference between these two exponents; if standard metabolism scales with the same exponent as the intake ($n = p$), this limit does not exist.

The calculation of the fitness measure R_0 raises two final and important questions, pointing to the limitations of equilibrium size spectrum theory: why are there any small fishes at all, as large fishes seem to have larger fitness? Which processes limit the fitness R_0 to be equal one for all life-history strategies, i.e. all values of M ? The answer to the first question can be understood within equilibrium size spectrum theory. This showed that the slope of the community size spectrum should be $n - 2.8 \approx -2$, as a less steep spectrum would not provide sufficient food for growth. A spectrum consisting only of fishes with a large asymptotic size would have a slope equal to the slope of their population spectra, $-n - a > -1.75$ Eq. (4). This spectrum would therefore not be sufficiently steep to support only large fishes. This is another way of saying that large fishes cannot survive on cannibalism or eating fish with similar life-asymptotic sizes alone. Fishes with large asymptotic size therefore need small fishes to provide food. The mechanism regulating this is not explained by equilibrium size spectrum theory, but could be incorporated by a change in the predation parameter a with asymptotic size following the curve in (Fig. 4(b)), such that large fishes have a higher physiological predation than small fishes. Note that this does not mean that the predation mortality for an adult cod of 10 kg should be higher than that for an adult herring, but rather that it should be higher for cod than for herring of the same size. This may seem strange, but there is some support for this from multi-species assessment models (Gislason et al., in press). The analysis of the energy budget as a function of asymptotic size provides a hint at how small fishes can achieve lower levels of predation mortality than large fishes. This analysis demonstrated that small fishes have higher specific available energy for activity and reproduction than large fishes of the same individual size. If some of that energy is invested in predator avoidance, e.g. schooling or defense mechanisms, this would exactly lower their mortality, effectively leading to a being an increasing function of asymptotic size. An important implication of this mechanism would be a partial invalidation of the use of the scaling relation for mortality $\mu \propto m^{-1/4}$ across species of different asymptotic size in aquatic environments. Another mechanism regulating R_0 is density-dependent regulation during the larval stage, i.e. due to competition for food, with a strong dependency on the asymptotic size

(Hall et al., 2006; Pope et al., 2006). That however raises the question of how density dependence can be orders of magnitudes stronger for large fishes than for small ones.

Acknowledgments

MP was supported by the European Marie Curie Research Training Network FishACE (Fisheries-induced Adaptive Changes in Exploited Stocks), funded through the European Community’s Sixth Framework Program (Contract MRTN-CT-2004-005578).

Appendix. Analytical solution to R_0

The full solution to the size spectrum equation (3) can be written as:

$$N(m) = N(m_0) \left(\frac{m}{m_0}\right)^{-n-a} \left[\frac{1 - \left(\frac{m}{M}\right)^{1-n}}{1 - \left(\frac{m_0}{M}\right)^{1-n}} \right]^{\frac{a+a_0}{1-n}-1}, \tag{A.1}$$

which can be verified by inserting the solution into (3). In the main text, the part that does not depend on m has been absorbed in an integration constant κ :

$$\kappa = N(m_0)m_0^{n+a} \left[1 - (m_0/M)^{1-n} \right]^{1-\frac{a+a_0}{1-n}}. \tag{A.2}$$

It is not possible to arrive at a general analytical expression for the expected life-time reproductive success R_0 in closed form. However, R_0 can be expressed in terms of Beta functions and it is possible to derive a number of useful approximations, some of which will be given here. The expression for R_0 is:

$$R_0 = \frac{k_r(M)}{2m_0g(m_0)N(m_0)} \int_{\eta M}^M mN(m)dm, \tag{A.3}$$

where $N(m)$ is the size spectrum given by (A.1), $g(m)$ is the growth expressed via (1) and k_r is the size-specific reproductive investment (2). Inserting k_r and $g(m)$ and rearranging the expression can be written as:

$$R_0 = \frac{1}{2} \varepsilon_r \left(\frac{M}{m_0}\right)^{1-a} \left[1 - \left(\frac{m_0}{M}\right)^{1-n} \right]^{\frac{a+a_0}{1-n}} f(n; a, a_0), \tag{A.4}$$

where the function f is defined as:

$$f(n; a, a_0) = \int_{\eta}^1 x^{1-n-a} \left(1 - x^{1-n} \right)^{\frac{a+a_0}{1-n}-1} dx. \tag{A.5}$$

This function can be written in terms of incomplete Beta functions:

$$f(n; a, a_0) \tag{A.6}$$

$$= \frac{1}{1-n} \left[B\left(1; \frac{2-a-n}{1-n}, \frac{1+a_0}{1-n}\right) - B\left(\eta^{1-n}; \frac{2-a-n}{1-n}, \frac{1+a_0}{1-n}\right) \right], \tag{A.7}$$

where the incomplete Beta function is defined as:

$$B(z; a, b) = \int_0^z u^{a-1} (1-u)^{b-a} du. \tag{A.8}$$

When the asymptotic size is much larger than the size of offspring $M \gg m_0$, the term in the second set of angular brackets in (A.4) is close to one.

For values of the asymptotic size larger than m_0 , but still small, such that $a_0 \ll 1$, the last argument in the Beta function is independent of M . In this case the function f can be written as $f(n, a)$, and R_0 becomes:

$$R_0 = \frac{1}{2} \varepsilon_r \left(\frac{M}{m_0}\right)^{1-a} f(n, a) \quad \text{for } m_0 \ll M \ll \left(\frac{\hbar}{\mu_0}\right)^{\frac{1}{1-n}}. \tag{A.9}$$

This expression is also relevant when the background mortality is ignored, $\mu_0 = a_0 = 0$.

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Widespread coexistence in
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Paper IV

Hartvig, M. and Andersen, K.H. 2011. Widespread coexistence in size-structured intraguild predation systems with life-history omnivory. *Submitted*.

Widespread coexistence in intraguild predation systems with life-history omnivory

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Abstract

Intraguild predation (IGP) may arise as a consequence of life-history omnivory: two species, which change body size and diet throughout ontogeny, may compete for a shared resource in early life-stages, and predate on the competitor in the adult life-stage. Empirical studies of IGP have documented coexistence at high resource levels, whereas previous theoretical investigations of IGP predict lack of coexistence. We study a model system of size-structured species populations, where IGP naturally emerges from size-dependent feeding and food-dependent growth. A trait-based model formulation enables a general analysis of the species identities and resource levels that allow coexistence of two species involved in IGP. Contrary to previous investigations, which did not include a general analysis of species identities, we find coexistence for all resource levels above a critical level required to cover metabolic costs.

Keywords: community module, species interaction, exploitative competition, body size, size-structure, trait based model

Introduction

Intraguild predation (IGP) is a form of omnivory where a predator competes for a shared resource with a consumer while also preying on the consumer (Polis et al., 1989; Diehl and Feiel, 2000; Rosenheim, 2007). Feeding relations often change during ontogeny, and IGP may emerge as a consequence of this life-history omnivory: species, which change body size and diet throughout ontogeny, may compete for a shared resource in early life-stages, and predate on the competitor in the adult life-stage (Werner and Gilliam, 1984; Polis et al., 1989; Mylius et al., 2001).

Theory predicts that coexistence in IGP modules only occur in a limited range of intermediate resource levels, as the consumer excludes the predator at low resource levels and vice versa at high levels (Holt and Polis, 1997; Mylius et al., 2001). This stands in contrast to empirical studies where coexistence is found at high resource

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levels (Amarasekare, 2008). Arim and Marquet (2004) examined the occurrence of IGP in empirical food webs, and found IGP to be a widespread interaction in nature, pointing to a fundamental discrepancy between theory and data which needs to be resolved.

To explain the persistence of intraguild prey at high resource levels theoretical models typically recourse to additional stabilising factors as e.g. additional resources (Holt and Huxel, 2007; Daugherty et al., 2007), or spatial and temporal refuges (HilleRisLambers et al., 2006; Janssen et al., 2007; Amarasekare, 2007, 2008). However, one might ask whether the resource axis is the correct dimension to examine to understand the coexistence of species involved in IGP? Examining the range of resource levels allowing IGP coexistence is interesting from a stability point of view, as it answers the question of how much the environment can be perturbed before the system loses a species. In nature species are adapted to the environment they live in, and hence there is no a priori reason to assume that a given set of coexisting species should be able to coexist for large perturbations of the resource level. Instead, we suggest to examine the dimensions spanned by the two competitors' species identities, to see if sets of species, that allow stable IGP systems, can be found for all resource levels.

We apply a recent general size- and trait-based model framework to describe the population dynamics of size-structured interacting populations (Hartvig et al., 2011). As the model resolves individual life-history, and the size distribution of each population, IGP naturally emerges as a consequence of size-dependent feeding and food-dependent growth: small individuals of each species population competes for the same small resource items, and as individuals grow in size they consume progressively larger resource items, and eventually individuals reach a size that permits feeding on smaller individuals from the other species or conspecifics. When the difference of the species' adult body size is sufficiently large the large sized species may even consume adults from the smaller species. A species is characterised solely by the trait size at maturation, and all parameters are made species-independent through scaling with the trait and individual body size. This allows a general analysis of coexistence through continuous variation of the resource level and species identities (i.e. size at maturation). The key questions we ask are: (i) How can the states of a single species persisting on resources and cannibalism be characterised? (ii) Which combinations of maturation sizes allow two species to coexist at different resource levels? (iii) How can the coexistence states be characterised? (iv) Which subset of the coexistence states corresponds to IGP states?

From the single species analysis we learn that a lower critical resource level exists, below which no species can exist due to insufficient food supply to cover metabolic costs. Further, two alternative stable population states exists; i.e. two different size distributions which allow coexistence with the resource. The two states are used to characterise the coexistence states found in the two-species case. In regards to the two-species analysis our most important finding is that IGP coexistence can be found for all resource levels above the critical resource level. This finding stands in contrast to previous theoretical investigations, which invoke extra stabilising components to explain IGP coexistence at high resource levels.

Model

We apply a physiologically structured population model (PSPM, Metz and Diekmann, 1986; de Roos and Persson, 2001) with a trait-based species description (Hartvig et al., 2011), which explicitly models the entire life-cycle from birth, through maturation, reproduction, and ultimately death. The solution of the model is the continuous population structure of each species i represented in the form of a size-spectrum $N_i(m, t)$ at time t . $N_i(m, t)$ is the number density of individuals as a function of body mass m , and $N_i(m, t)dm$ is the number of individuals in the size range $[m, m + dm]$. The dynamics of the species size-spectra is governed by the conservation equation (McKendrick, 1926; von Foerster, 1959) stating that changes in number density at size m is determined by somatic growth g_i and mortality μ_i :

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

The main assumption of the model is that a species can be characterised by a single trait: size at maturation m_* . Secondly we assume that individuals ignore prey identity and only consider relative prey size when selecting prey through an implementation of 'big individuals eat smaller individuals'. From these assumptions a conceptually simple, but ecologically realistic, model can be derived (table 1).

The biotic environment an individual experiences is given by the community spectrum $N_c(m)$, which contains food for growth and reproduction as well as enemies which may consume the individual. N_c is the sum of the species spectra and a resource spectrum (M1), which represents additional smaller food items having their dynamics described with semi-chemostatic growth (M2). Individuals search the biotic environment for food with a volumetric search rate (M3). Prey items are selected with a size-selective feeding kernel having a preferred predator-prey ratio β (M4). From these processes the encountered suitable food is calculated (M5).

An individual has a maximal food intake rate of hm^n , and the degree to which this maximum is achieved is described with a feeding level which varies between 0 and 1 (M6). Consumption is determined by a type II functional response $f(m)hm^n$. Food is assimilated with efficiency α and metabolic costs km^p are covered with highest priority, such that the net available energy is (M7). Juvenile individuals use all available energy for somatic growth, and as individuals grow in size and mature a size-dependent fraction of the energy is routed to reproduction (M8-9). Energy routed to reproduction is converted with efficiency ϵ into a flux of m_0 sized offspring through the boundary condition $g_i(m_0)N_i(m_0) = R_i$ in (1), and multiplied with 1/2 since only half the population is assumed to be females (M10). The maximum size an individual can obtain is the asymptotic size $M = m_*/\eta_*$, which is obtained when all surplus energy is used for reproduction ($\psi(M, m_*) = 1$). Growth may stop at a smaller size if the metabolic costs exceed the assimilated food intake (stunted growth).

The described feeding process causes predation mortality on smaller individuals (M11). Additional mortality arise from starvation (M12) and a constant background mortality (M13), which is assumed inversely proportional to generation time. Starvation mortality occurs when the energy intake is smaller than the metabolic costs,

Table 1: Model equations. m is individual mass, m_p mass of a prey item, and m_* is maturation size.

Community size-spectrum	$N_c(m) = N_R(m) + \sum_i N_i(m)$	(M1)
Resource dynamics	$\frac{\partial N_R(m)}{\partial t} = r_0 m^{p-1} [\kappa m^{-\lambda} - N_R(m)] - \mu_p(m) N_R(m)$	(M2)
Volumetric search rate	$v(m) = \gamma m^q$	(M3)
Feeding kernel	$s(m, m_p) = \exp[-\ln^2(\beta m_p/m)/(2\sigma^2)]$	(M4)
Encountered food	$\varepsilon(m) = v(m) \int s(m, m_p) N_c(m_p) m_p dm_p$	(M5)
Feeding level	$f(m) = \varepsilon(m)/[\varepsilon(m) + h m^n]$	(M6)
Available energy	$E(m) = \alpha f(m) h m^n - k m^p$	(M7)
Allocation to reproduction	$\psi(m, m_*) = \left[1 + \left(\frac{m}{m_*}\right)^{-u}\right]^{-1} \left(\frac{\eta_* m}{m_*}\right)^{1-n}$ for $n = p$ †	(M8)
Somatic growth	$g(m, m_*) = \begin{cases} [1 - \psi(m, m_*)]E(m) & E(m) > 0 \\ 0 & \text{otherwise} \end{cases}$	(M9)
Reproduction	$R_i = \frac{\epsilon}{2m_0} \int N_i(m) \psi(m, m_*) E(m) dm$	(M10)
Predation mortality	$\mu_p(m_p) = \int s(m, m_p) [1 - f(m)] v(m) N_c(m) dm$	(M11)
Starvation mortality	$\mu_s(m) = \begin{cases} 0 & E(m) > 0 \\ -E(m)/[\xi m] & \text{otherwise} \end{cases}$	(M12)
Background mortality	$\mu_b(m_*) = \mu_0 m_*^{n-1}$	(M13)

†see (Hartvig et al., 2011) for the equation governing the general case of $n \neq p$.

and is assumed proportional to the energy deficit and inversely proportional to reserve size.

The model is parameterised for fish communities as these exhibit an important case of size-structured communities, but it may be reparameterised for other less strongly size-structured systems as well (Hartvig et al., 2011). A species independent parameter set is obtained by scaling with body mass m and maturation size m_* (table 2).

The model is solved numerically using a first order semi-implicit upwind finite-difference scheme (Press et al., 1992; Hartvig et al., 2011). The species mass grid [$m_0, 85 \text{ kg}$] is discretised to 200 logarithmically even sized mass groups, and the time step used for integration is 0.02 years. It was checked that the results do not depend on the chosen discretisation.

Methods

The parameters prescribing maximum consumption h , search volume γ , and resource carrying capacity κ determine the *initial feeding level* f_0 that small individuals experience when feeding on a resource spectrum at carrying capacity. We use f_0 as a physiological measure of resource level. The relevant range of f_0 is from the critical feeding level, $f_c = k/(\alpha h) m^{p-n} = k/(\alpha h) \approx 0.2$ (Hartvig et al., 2011), where the resource can just cover the metabolic requirements, to $f_0 \rightarrow 1$ where individuals are satiated.

The ecologically relevant parameter space to examine is spanned by m_* and f_0 , which characterise species identity and resource level. Using numerical bifurcation

analysis we exhaustively perform a parameter space analysis of the possible single- and two-species states. Stability in terms of coexistence is verified by direct simulation.

Results

The analysis of a system with just one species demonstrates six main points (Fig. 1): 1) There is an upper boundary to the size m_* of a single species that can invade from small numbers (thick solid line). This maximum size is determined by the resource level, described by the initial feeding level f_0 . 2) Beyond the invasion boundary species may persist, but they cannot invade from small abundances. 3) This Allee effect, which exists outside the invasion boundary, extends into the area where a species can invade, leading to the appearance of bistability (hatching types overlap), i.e., two states with non-zero biomass termed 'resource driven' and 'cannibalistic' (explained below). 4) The area with bistability is most prominent at intermediate resource levels. 5) At high resource levels it is possible to invade from small numbers into the cannibalistic state. 6) A continuous transition between the two states exists at high resource levels and intermediate sizes at maturation.

The two types of states in the bistable regime are characterised by different growth trajectories due to differences in realised feeding levels, which leads to different size-spectra (Fig. 2). In the state, which can always be reached by invasion

Table 2: Parameter values for a temperature of 10°C (Hartvig et al., 2011). Time is expressed in units of years (yr).

Individual growth			
f_0	varied	-	Initial feeding level
α	0.6	-	Assimilation efficiency
h	85	g^{1-n}/yr	Max. food intake
n	0.75	-	Exponent for max. food intake
k	10	g^{1-p}/yr	Std. metabolism and activity
p	0.75	-	Exponent of std. metabolism
β	100	-	Preferred pred.-prey mass ratio
σ	1	-	Width of feeding kernel
q	0.8	-	Exponent for search volume
Reproduction			
m_0	0.5	mg	Offspring mass
η_*	0.25	-	m_* rel. to asymptotic mass M
ϵ	0.1	-	Efficiency of offspring production
u	10	-	Width of maturation transition
Mortality			
ξ	0.1	-	Fraction of energy reserves
μ_0	0.84	g^{1-n}/yr	Background mortality
Resource spectrum			
κ	$5 \cdot 10^{-3}$	$g^{\lambda-1}/m^3$	Magnitude of resource spectrum
r_0	4	g^{1-p}/yr	Regeneration rate of resources
m_{cut}	0.5	g	Upper limit of resource spectrum
Derived parameters			
$\gamma(f_0) = \frac{f_0 h \beta^{2-\lambda}}{(1-f_0)\sqrt{2\pi\kappa\sigma}}$			Search volume ($m^3 g^{-q}/yr$)
$\lambda = 2 - n + q = 2.05$			Slope of resource spectrum

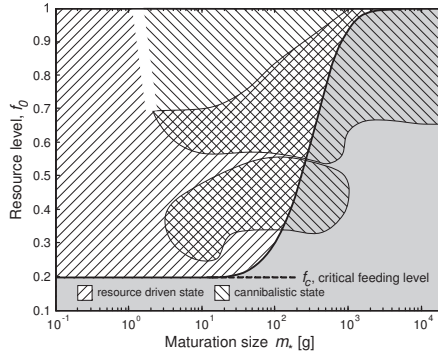


Figure 1: Invasion from small numbers is possible if the resource level is above the critical level and if the species' maturation size is small enough to allow survival on resources only (white area). Hatching type indicate if the species has a resource-driven or a cannibalistic state (cf. legend). A transition between the two state types is present in the top left quadrant. Alternative stable states, only reachable from introduction in large numbers, occur when hatching types overlap or when cannibalistic states are possible in the grey area.

in small numbers, individuals feed mainly on the resource. This leads to a depletion of the resource and a bottleneck in the feeding level around the size of maturation, where the feeding level drops below the critical feeding level. This bottleneck results in a stunted size-spectrum with a dominance of small adults. This state is referred to as the *resource-driven* state. The state which cannot necessarily be reached by invasion, but always by introducing it in large numbers, has a higher abundance of small and medium sized individuals that allows small adults to avoid the energetic bottleneck by cannibalising on these conspecifics. The higher abundance of juveniles causes a stronger depletion of smaller resources, which results in a bottleneck

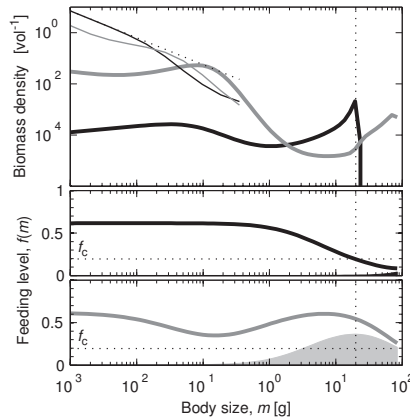


Figure 2: The two alternative single-species states: resource-driven (black) and cannibalistic (grey) for $f_0 = 0.6$ and $m_* = 20$ g. Upper panel: Biomass spectrum of species (thick lines) and resources (thin lines) along with carrying capacity of resources (dotted). Lower panels: Feeding level (thick line), feeding level resulting from cannibalism (shaded), and critical feeding level (horizontal dots). Vertical dotted line indicates size at maturation.

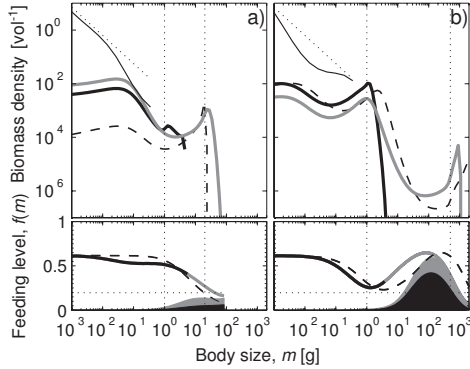


Figure 3: Illustration of the two types of coexistence states (solid lines) and their relation to the single-species states (dashed). Competitive coexistence for $f_0 = 0.6$, $m_{*1} = 1$ g, and $m_{*2} = 20$ g (a). Trophic ladder coexistence for $f_0 = 0.6$, $m_{*1} = 1$ g, and $m_{*2} = 500$ g (b). Upper panels: Biomass spectrum of species (thick lines) and resources (thin line) along with carrying capacity of resources (dotted). Lower panels: Feeding level (thick lines), critical feeding level (horizontal dots), feeding level resulting from diet on the small (black shading), and large species (grey shading). Vertical dotted lines indicate size at maturation.

in the feeding level for small juveniles. At this size growth slows down, but individuals which become sufficiently large grow faster due to cannibalism, and reach their asymptotic size as no bottlenecks are encountered in later life-stages. Cannibalism results in increased mortality and therefore a steeper size-spectrum. This state is referred to as the *cannibalistic* state, and has a higher impact on the resource as well as a larger total biomass than the resource-driven state. At high resource levels the elevated food abundance allows individuals to invade in small numbers and reach the cannibalistic state – meaning that bistability is less widespread at high resource levels (Fig. 1).

The analysis of the two-species system is more complex, but can be explained with reference to the single-species states. Coexistence states may be categorised based on whether the bottleneck in feeding level occur *at* or *before* size at maturation of the largest species as either *competitive coexistence*, corresponding to the resource-driven single species state (bottleneck at m_*), or *trophic ladder* coexistence, resembling the cannibalistic single species state (bottleneck in earlier life-stage). The two types of coexistence states are illustrated by two examples (Fig. 3). In competitive coexistence states 1) an energetic bottleneck is encountered at size of maturation, 2) the two species have similar m_* , and 3) each of them can invade a pristine system comprised only of the resources (Fig. 1). Trophic ladder coexistence are characterised by 1) an energetic bottleneck in intermediate life-stages of the large species, 2) larger differences in m_* , and 3) in these states the smaller species is often needed to allow the larger species to grow to size at maturation and hence sustain its population – i.e. the large species uses the small species as a ladder to obtain a higher trophic position. In the competitive coexistence state most energy is retrieved from the resource spectrum. In contrast predation on the smaller species, and to a smaller extent cannibalism, is driving the growth of larger individuals in the trophic

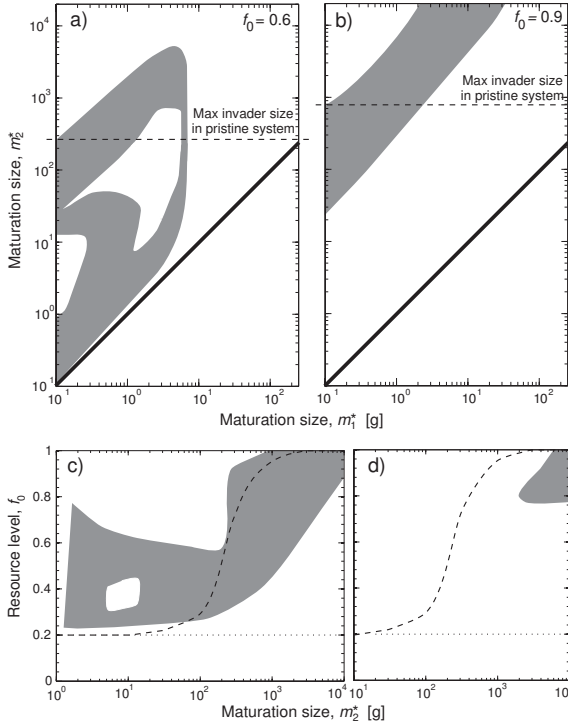


Figure 4: Coexistence (grey) of two species as a function of size at maturation for $f_0 = 0.6$ (a) and $f_0 = 0.9$ (b), and as a function of resource level f_0 for $m_1^* = 1$ g (c) and $m_1^* = 10$ g (d). For the given resource level dashed lines indicate the largest m_* species that, in small numbers, can invade into a system comprised solely by the resource spectrum. Dotted lines show the critical feeding level.

ladder states.

The most important findings in the coexistence analysis are (Fig. 4): 1) Coexistence states above the dashed line (a, b), and to the right of the curved line (c, d), are all trophic ladder states, where the largest species cannot invade from small numbers without the presence of the smaller species. 2) Below the dashed line trophic ladder states are found when the differences in m_* among the two species is large, and competitive states are mainly found when the species have similar m_* (a, b). The designation of the two types of states is largely descriptive, and a continuous transition between the states occur in parameter space (a, c). 3) When resource level is increased the maximum allowed size for the largest species increases (a-c), and 4) species need to have more different m_* to coexist (b, c), meaning that trophic ladder states dominates at high resource levels. 5) For all resource levels a little above the critical feeding level coexistence is possible provided that the smallest species is small enough (c vs d), and 6) trophic ladder states can be found for all resources level above ≈ 0.26 (c). When 7) the smallest species is small enough both competitive and trophic ladder states exist (c), whereas 8) only trophic ladder states are found when the size of the smallest species is increased (d). 9) When performing the

coexistence analysis we did not encounter any alternative states where both species are present, i.e. no alternative coexistence states.

Discussion

We have performed a systematic and general analysis of the coexistence of two size-structured species populations. Individuals of the same size across species compete on an equal basis, but may have different growth potential depending on maturation status as less energy is available for growth when reproductive investments are made. Large m_* species have a smaller mass-specific allocation to reproduction compared to smaller species, which results in a trade-off between different life-history strategies: escape predation mortality by growing to large body sizes through paying the price of a lower mass-specific reproduction, or aim for high mass-specific reproduction and tolerate the increased mortality occurring at smaller body sizes. Regardless of species identity individuals exclusively select prey from a feeding kernel with a preferred predator-prey mass ratio. This means that small individuals feed exclusively on resources, and as they grow in size they consume larger and larger prey, and eventually they start feeding on the other species and cannibalise on smaller conspecifics. This is a generalisation of the resource competition and predator-prey interactions occurring between two species populations based on life-history theory and explicit individual-level ecological processes. In systems with ontogenetic growth IGP emerges as a consequence of size-dependent feeding and food-dependent growth.

Single species states

Alternative stable states where single populations can exist with different size compositions, have been demonstrated in the PSPM framework (Claessen and de Roos, 2003; van Kooten et al., 2005; Guill, 2009). As the model we employ is physiologically structured we naturally also find that a single population can be in two states, and that continuous and abrupt shifts between the state types are possible. Through invasion in small numbers a *resource-driven* state can be reached, which is primarily driven by food from the resource spectrum. Invasion in large numbers, or invasion in small numbers in resource-rich environments, allows a species to enter a *cannibalistic* state, where the extra food from conspecifics helps individuals through an energetic bottleneck, which is experienced when individuals become too large to efficiently feed on the resources. The cannibalistic induced alternative stable state was described by Claessen and de Roos (2003), who also found that due to the population structure individuals in the resource-state have their largest cannibalistic intake early in life, whereas individuals in the cannibalistic state have their main energy intake later in life; an effect they termed the ‘Hansel and Gretel’ effect as it is most profitable to let conspecifics become large and fat before they are consumed. In the current study we do not have any notable cannibalistic intake in the resource-state. Our main contribution to the description of cannibalistic states by Claessen and de Roos (2003) is that we have performed a more complete mapping of parameter space and find i) that for increasing levels of resources the resource-driven

and cannibalistic states melt together, and ii) that bistability is present in the form of an Allee effect for large maturation sizes: if introduced in high numbers a species population may exist in a cannibalistic state, but if the population is depressed below a certain threshold, or if the population tries to invade in small numbers, it is doomed for extinction.

Two species states

When adding a second species to the system we found two types of coexistence: 1) *Competitive coexistence*, where both species can invade without the presence of the other, and have population structures similar to the resource-driven states. 2) *Trophic ladder* coexistence states, where the smaller species often is needed to allow the larger species to invade, and where population structures are similar to cannibalistic states, as predation on the competitor, and to a smaller extent on conspecifics, is pronounced. In competitive coexistence states the species have similar maturation sizes, whereas there is a larger difference in maturation sizes in trophic ladder states.

Competitive exclusion (Armstrong and McGehee, 1980) and limiting similarity (Hutchinson, 1959; MacArthur and Levins, 1967; Szab and Meszna, 2006) theory state that only one species can exist per resource in purely competitive systems. In the applied model we do not have one explicit resource, but a continuous range of resources of different sizes, which however effectively is similar to a single resource, as each species utilises different parts of the resource spectrum in different life-stages. In the competitive coexistence states the two species coexist while mainly feeding on the resources – we have tried adding more resource driven species to the system, but did not succeed in increasing the number of coexisting species. In the trophic ladder states the two species coexist in a resource competition setting while also being engaged in a predator-prey relationship. The limiting similarity term is useful in trait-based systems even when predator-prey interactions are added: the limiting similarity of two species (i.e. how different m_* are needed for coexistence) increases as the system is being enriched, and consequently trophic ladder states dominate at high resource levels.

Intraquild predation

In the model IGP emerges as a consequence of size-dependent feeding and food-dependent growth of two competing size-structured species populations. When the species have similar small maturation sizes m_* their mutual predation is negligible, and the two species are thus involved in exploitative competition. When the difference in m_* among the species increases the interaction type gradually shifts to IGP, and as the difference increases further the interaction resembles a trophic chain more and more without ever becoming a true chain, as small individuals of the larger species feeds on the resource. The types of ecological interactions thus naturally emerges from the species identities present in the system, and competitive coexistence states resemble exploitative competition situations, whereas trophic ladder states resemble IGP situations. We find trophic ladder states, and hence coexisting species pairs involved in IGP, for all resource levels a little above a critical value needed to cover metabolic requirements. The resource level needs to exceed

the critical value as the feeding level may drop below the critical level in some body size ranges due to resource depression. If food availability was constant the required resource level would exactly equal the critical level.

It has previously been demonstrated that cannibalism can increase the scope for coexistence in IGP systems (Rudolf, 2007; Amarasekare, 2008). In the applied model interaction strengths emerge from the size composition of the interacting populations, and is hence not fixed as in unstructured models. Individuals select their prey solely on the basis of predator-prey mass ratios compared to selecting on a species identity basis, and as they grow in size they undergo ontogenetic niche shifts from resource feeding to predation on other species and cannibalism. The presence of cannibalism can indeed play a role in mediating coexistence in our study. However, it should be noted that less food is retrieved from cannibalism than from predation on the intraguild prey (Fig. 3), and that cannibalism is not an unusual or exotic interaction, but a very outspread and common interaction type across taxa (Fox, 1975; Polis, 1981; Smith and Reay, 1991; Elgar and Crespi, 1992).

Van de Wolfshaar et al. (2006) also considered a physiologically structured model of IGP, which they parameterised for roach and perch. They found coexistence not to be possible for the two species, a finding confirmed by whole-lake experiments (Persson et al., 2007b). Additionally they found that size-dependent food intake and food-dependent growth demotes the possibility of IGP coexistence. The model we apply contains the same elements, but we demonstrate that coexistence indeed is possible provided that the ecological differentiation is large enough. The model by van de Wolfshaar et al. (2006) employs, as the unstructured counterparts, several (15) parameters to characterise each species. This demonstrates that a general analysis of IGP cannot be performed without turning to a trait-based description, as a $15 \times 15 = 225$ -dimensional parameter space cannot be searched exhaustively. According to our findings coexistence is expected in the model by van de Wolfshaar et al. (2006) if ecological differentiation is increased. If their parameter set is reduced to our trait, then the smallest species should be smaller or the largest larger. We conjecture that they would have found IGP coexistence if they had parameterised their model for roach and pikeperch or perch and pike.

HilleRisLambers and Dieckmann (2003) found that an intermediately strong trade-off between exploitative resource competition and predation on the competitor maximises the scope for IGP coexistence. This means that two-species systems, where one species has a tendency of specialising on resource feeding and the other on predation (strong trade off), are more likely to be stable than systems where species are equally good at resource and predatory feeding (neutral trade-off). In the applied model individuals compete for food on an equal basis, and whether a resource item or an individual from the competing species is attacked depends on the predator-prey mass ratio and the relative abundances of the suitable food items. Thus, at the individual level we have a neutral trade-off between resource competition and predation. However, whether the species as a whole spends most time feeding on resources or predating on competitors is an emergent property of the population size-structure. Our results are consistent with the results of HilleRisLambers and Dieckmann (2003), as two species persisting in an IGP relationship always consist

of one smaller species feeding mainly on resources, and a larger species that mainly predate on the competitor in late life-stages.

In unstructured models of IGP the existence of alternative stable states along the resource axis has received a lot of attention (e.g. Mylius et al., 2001; Takimoto et al., 2007; Verdy and Amarasekare, 2010), and these states, where either only the predator or both the consumer and the predator can persist, are also possible in PSPM models (Pedersen, 2006, page 82). Existence of alternative stable states is e.g. important for fisheries management as the presence of alternative states can play a crucial role in determining whether an exploited fish stock can recover or not (Persson et al., 2007a; van Leeuwen et al., 2008). It is an open question whether alternative states become more widespread, or if they disappear, when more species interact with each other. In the single-species studies we encountered alternative stable states in large parts of parameter space, whereas we did not encounter any alternative stable coexistence states where both species can be present with different size compositions. This does not mean that alternative stable coexistence states does not exist, but we conclude that they are not common.

In a general study of IGP systems employing type II functional responses and adaptive, but imperfect, diet choices Abrams and Fung (2010) argue that the “*persistence of (...) intraguild prey at higher productivity should not be regarded as puzzling because observations are consistent with a range of theoretical models that reflect commonly observed mechanisms.*”. We second that the persistence of intraguild prey is not puzzling, but simultaneously stress that theoretical models, including the ecological realism leading to IGP, allow coexistence even without additional stabilising factors as e.g. additional resources, adaptive foraging, or spatial and temporal refuges. Previous theoretical models did not find coexistence at high resource levels as they did not allow for examination of the ecologically relevant parameter space, which is spanned by the species identities over different resource levels. In the applied model ecological differentiation between species is caused by a single trait, and increasing the number of traits will increase the domain for differentiation further, meaning that increasing the numbers of traits should increase the scope for IGP coexistence. In conclusion: our theoretical analysis shows that IGP coexistence is possible for all resource levels above a critical level required to cover metabolic costs, meaning that IGP indeed can be expected to be a widespread interaction type in correspondence with empirical findings (Arim and Marquet, 2004; Amarasekare, 2008).

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Damped trophic cascades driven by fishing in model marine ecosystems

Paper V

Appeared in:

Andersen, K.H., and Pedersen, M. 2010. Damped trophic cascades driven by fishing in model marine ecosystems. *Proc. R. Soc. B*, 277(1682):795–802.

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Damped trophic cascades driven by fishing in model marine ecosystems

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The largest perturbation on upper trophic levels of many marine ecosystems stems from fishing. The reaction of the ecosystem goes beyond the trophic levels directly targeted by the fishery. This reaction has been described either as a change in slope of the overall size spectrum or as a trophic cascade triggered by the removal of top predators. Here we use a novel size- and trait-based model to explore how marine ecosystems might react to perturbations from different types of fishing pressure. The model explicitly resolves the whole life history of fish, from larvae to adults. The results show that fishing does not change the overall slope of the size spectrum, but depletes the largest individuals and induces trophic cascades. A trophic cascade can propagate both up and down in trophic levels driven by a combination of changes in predation mortality and food limitation. The cascade is damped as it comes further away from the perturbed trophic level. Fishing on several trophic levels leads to a disappearance of the signature of the trophic cascade. Differences in fishing patterns among ecosystems might influence whether a trophic cascade is observed.

Keywords: size spectrum; community model; ecosystem approach to fisheries management

Trophic cascades are the signature of indirect effects of changes in the abundance of individuals in one trophic level on other trophic levels (Pace *et al.* 1999). Trophic cascades can occur when the abundance of a top predator is decreased, releasing the trophic level below from predation. The released trophic level reacts by an increase in abundance, which imposes an increased predation pressure on the next lower trophic level, etc. In the case of marine systems the outside perturbation typically stems from fishing, which can easily exceed the 'natural' predation mortality. Trophic cascades had not been thought to occur in marine systems (Steele 1998), but recently trophic cascades have been demonstrated in several large marine systems: the Black Sea (Daskalov *et al.* 2007), the Baltic Sea (Casini *et al.* 2008; Möllmann *et al.* 2008) and parts of the Northwest Atlantic (Frank *et al.* 2005, 2006; Myers *et al.* 2007). These trophic cascades cover up to four trophic levels and reach all the way down to primary production. Despite the evidence for trophic cascades in some systems, trophic cascades appear to be absent in other systems, even though they are heavily perturbed by fishing—in particular, the North Sea (Reid *et al.* 2000). The presence or absence of trophic cascades can be attributed to high temperature (which leads to faster growth rates and therefore less sensitivity to fishing) or to a large diversity that stabilizes the system (Frank *et al.* 2007).

Trophic cascades emanating from perturbations on top predators have been described using simple box-type models, with each box representing a species at a given trophic level (May *et al.* 1979; Daskalov 2002). Box-type models do not account for the special life history of fish,

where an individual can cover several trophic levels from the larval stage at around 1 mg to maturation at 10 g to 50 kg depending on the species (Werner & Gilliam 1984). This ontogenetic development can be resolved either using stage-structured models (de Roos *et al.* 2008a) or size-structured models of each species (Hall *et al.* 2006; Pope *et al.* 2006). Here we apply a novel size- and trait-based model that is able to account for the change in trophic level during ontogeny and is readily applicable to study the effects of a size-based fishing mortality.

The model is an extension of general size- and trait-based models of marine ecosystems (Andersen & Beyer 2006; Pope *et al.* 2006). The model is mathematically complex, but based on simple ecological assumptions. The governing principle is that large fish eat smaller fish (Ursin 1973; Cohen *et al.* 1993; Jennings *et al.* 2002). This rule combined with a standard bioenergetic budget determines both the growth of individuals and the corresponding predation mortality on the smaller prey. Prey can be either fish in the community or zooplankton, which is modelled as an external resource. Model parameterization is based on general size-based scalings of search rate, ingestion, standard metabolism and mortality. The model does not resolve specific species, but represents life-history diversity through the distribution of individuals with a given individual and asymptotic (maximum) size. The model is used to investigate the effect of fishing on individuals within a given size range or within a range of asymptotic sizes.

Three fishing scenarios are simulated: (i) a consumer fishery targeting individuals larger than 1 kg; (ii) an industrial fishery targeting smaller forage fish species; and (iii) a fully developed fishery targeting fish of all sizes.

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Table 1. Model equations. m is individual weight, and M is asymptotic (maximum) size.

community size spectrum	$N_c(m) = \sum_i N_i$	(M1)
size selection of food items	$\varphi(m_{\text{prey}}/m) = \exp\left[-(\ln(\beta m_{\text{prey}}/m))^2/(2\sigma^2)\right]$	(M2)
volumetric search rate	$V(m) = \gamma m^a$	(M3)
encountered food	$E(m) = V(m) \int m_{\text{prey}} N_c(m_{\text{prey}}) \varphi(m_{\text{prey}}/m) dm_{\text{prey}}$	(M4)
feeding level	$f(m) = E(m)/(E(m) + C_{\text{max}})$	(M5)
maximum consumption	$C_{\text{max}} = hm^a$	(M6)
allocation to reproduction	$\psi(m, M) = \left[1 + \left(\frac{m}{qM}\right)^{-10}\right]^{-1} \left(\frac{m}{M}\right)^{1-n}$	(M7)
somatic growth	$g(m) = (1 - \psi(m))(\alpha f(m)C_{\text{max}} - k_s m^p)$	(M8)
predation mortality	$\mu_p(m_{\text{prey}}) = \int (1 - f(m))V(m)N_c(m)\varphi(m_{\text{prey}}/m) dm$	(M9)
background mortality	$\mu_b(M) = \mu_0 M^{n-1}$	(M10)
resource spectrum	$\frac{\partial N_i}{\partial t} = r_0 m^{n-1}(\kappa_r - N_r) - \mu_p N_r$	(M11)
resource carrying capacity	$\kappa_r(m) = \kappa m^{-2-q+n}$	(M12)

1. MODEL FORMULATION

The model is a dynamical version of the ‘charmingly simple model’ by Pope *et al.* (2006), based on the principles of classical multi-species fishery models (Andersen & Ursin 1977) and community size spectrum models (Benoît & Rochet 2004). The model is extended to include food-dependent growth and a theoretical justification for the stock recruitment relation. The model is formulated using processes at the individual level that make it possible to estimate most parameters using the physiology of individual fish and scaling relations with individual size m or asymptotic (maximum) size M . The equations in the model are given in table 1.

The two central assumptions of the model are (i) that food is selected on the basis of the size difference between individuals and is therefore not dependent upon species identity, and (ii) that the most important trait of a fish species is its asymptotic size M . The model is therefore not a traditional food-web model where species are represented explicitly, but rather a trait-based model (Norberg *et al.* 2001) with the trait being asymptotic size. The trait dimension is split into discrete asymptotic size classes. The result of the model is the size distribution of each asymptotic size class $N_i(m)$ measured in units of number per volume per mass. The number of individuals in the size range $[m, m + dm]$ and asymptotic size range $[M_i, M_{i+1}]$ is therefore $N_i(m) dm$. The dynamics of the spectrum of asymptotic size class i is governed by the conservation equation (McKendrick 1926; von Foerster 1959):

$$\frac{\partial N_i}{\partial t} + \frac{\partial g_i(m)N_i}{\partial m} = -\mu_i(m)N_i, \tag{1.1}$$

where $g_i(m)$ and $\mu_i(m)$ are the somatic growth and the total mortality of an individual of size m , respectively. The central processes of growth and mortality are prescribed at the level of individuals, and integrated up to the population level using equation (1.1). In this manner the need for explicit individual-based simulations is bypassed.

Encounter of food (M4) is modelled by a classical formulation where food is selected from the community spectrum (M1) by a log-normal size preference function (M2) with a fixed preferred predator–prey mass ratio β (Ursin 1973; Andersen & Ursin 1977). Consumption is determined by a Holling type-II functional response (M5).

Somatic growth is modelled by a standard bioenergetic model. Consumed food is assimilated with an efficiency α

and used for standard metabolism $k_s w^p$. The remaining energy is split between somatic growth and reproduction by a function $\psi(m)$ that switches from 0 to 1 around the size of maturation (M7–8; Pedersen *et al.* submitted). This formulation leads to von Bertalanffy-like growth curves when food conditions are constant and independent of size, and a constant mass-specific allocation to gonads once the individual is mature.

Mortality comes from predation (M9) and a background mortality accounting for mortality not arising from predation or fishing (M10).

The resource spectrum is modelled dynamically using a semi-chemostat growth equation with allometric scaling of the regeneration rate (M11) and a carrying capacity given by the theoretical equilibrium spectrum (M12; Andersen & Beyer 2006).

Recruitment is ‘hockey-stick’ such that the number density at the size of recruitment m_0 is determined by the egg production of the i th asymptotic size class, limited by an upper level $N_{0,i}$. The upper level is calculated using equilibrium size spectrum theory for an unexploited system (Andersen & Beyer 2006; appendix A).

The conservation equation (1.1) is discretized by a standard first order in time and semi-implicit upwind finite differences scheme (Press *et al.* 1992). The individual size axis is discretized with 100 size groups. Asymptotic size is discretized with 20 asymptotic size classes in the range 10 g to 100 kg. The time step is 0.02 years. It has been checked that the results do not depend on the discretization of mass, time or the number of asymptotic size classes used. After around 50 years of integration the solutions converge to a dynamical steady state regardless of initial conditions.

2. MODEL ANALYSIS

The use of scaling based on individual and asymptotic size make the number of governing parameters in the model relatively small. Most are determined from basic physiological scaling relations or cross-species analyses of fish communities (table 2). Three related parameters are the coefficients of maximum consumption h , search rate γ and carrying capacity of the resource spectrum κ_r . Taken together these parameters determine the feeding level (M6; functional response) of small individuals who only feed from the resource spectrum. Assuming that the resource spectrum is at the carrying capacity,

Table 2. Parameters in the model. Time is expressed in years, weight in grams, and biomass density in grams per unit volume.

<i>individual physiology</i>		
α	0.6	assimilation efficiency ^a
n	$\frac{2}{3}$	exponent of max. intake ^b
h	30	factor for max. intake ^c
p	$\frac{3}{4}$	exponent of standard metabolism ^d
k_s	4	factor for standard metabolism ^e
μ_0	0.6	background mortality factor ^f
η	0.25	size at maturation rel. to M^g
<i>individual foraging</i>		
β	100	preferred predator-prey weight ratio ^h
σ	1.3	width of selection function ⁱ
γ	526	factor for search volume ^j
q	0.9	exponent of search volume ^k
<i>primary production</i>		
κ_r	0.005	resource spectrum carrying capacity
r_0	4	growth rate of resource spectrum ^l

^aKitchell *et al.* (1977).
^bJobling (1994) states that $\frac{2}{3} < n < \frac{3}{2}$. We have used $n = \frac{2}{3}$ to be consistent with von Bertalanffy growth curves.
^cAdjusted such that emergent growth rates are in the range of those observed in the North Sea (figure 1).
^dWest *et al.* (1997).
^eThe data of Winberg (1956) indicate a standard (resting) metabolism factor for fish of about $4 \text{ g}^{0.25} \text{ yr}^{-1}$ at 10°C .
^fThis has been adjusted to lead to a background mortality of the same order as the predation mortality, but still lower than the predation mortality.
^gBeverton (1992).
^hUrsin (1973) and Jennings *et al.* (2001).
ⁱUrsin (1973) finds $\sigma = 1$ for a single species. To account for species diversity within an asymptotic size class, this has been increased to $\sigma = 1.3$.
^jSee equation (2.1).
^kConsiderations on the bioenergetic budget of swimming predict a value of q between $\frac{2}{3}$ and 1 (Andersen & Beyer 2006).
^lSavage *et al.* (2004; temperature: 10°C).

the value of γ can be determined from h and κ_r as

$$\gamma = h \frac{f_0}{\alpha_c \kappa_r (1 - f_0)}, \tag{2.1}$$

where $\alpha_c = \sqrt{2\pi} \sigma \beta^{\lambda-2} e^{-(\lambda-2)^2 \sigma^2 / 2}$ (Andersen & Beyer 2006) and $f_0 \approx 0.5$ is the expected average feeding level. In this manner the effective fundamental parameters are reduced to the prey selection parameters β and σ together with h and κ_r . The latter two parameters effectively work as scaling parameters, scaling time and abundances. They are therefore not important for the qualitative dynamics of the model, only for making the dynamics occur in the right time scale and ensuring the abundances are in the correct order of magnitude. Getting the timescale reasonably correct is important to compare levels of fishing mortality used in the model with realistic levels, and getting the abundances right matters for getting yield estimates in the correct order of magnitude. Runs of the model lead to growth curves roughly equal to expected von Bertalanffy growth curves, confirming that the time scale is in the right range (figure 1).

3. RESULTS

The starting point is an unexploited system represented by asymptotic size classes with asymptotic sizes from 4 g to 100 g (figure 2). Each of these spectra represents

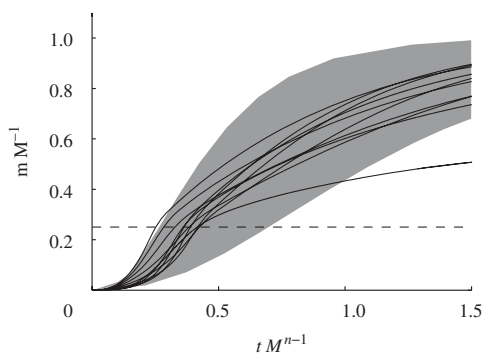


Figure 1. Growth curves of 10 asymptotic size classes with varying asymptotic sizes (thin lines) together with expected range of von Bertalanffy growth curves in the North Sea (grey patch). The thin dashed line is the size at maturation. Weight is normalized by the asymptotic size M and age t is normalized by the expected life time $\propto M^{1-n}$. The data from the North Sea are calculated using growth curves with von Bertalanffy growth rates KL_∞ within ± 1 s.d. of the mean growth of the species listed in Gislason *et al.* (2008).

the abundance of all species with asymptotic size within the corresponding asymptotic size class. The community spectrum is the sum of all asymptotic size classes. The community spectrum oscillates around the theoretically expected spectrum, which is a straight line on a log-log scale (Andersen & Beyer 2006). The oscillation is induced by the largest individuals that are not affected by predation and that therefore have a larger abundance than expected in a theoretical, infinitely large, spectrum. This oscillation is not crucial for the general reaction of the system to fishing.

Fishing on large fish is the natural starting point for exploitation of a marine system, as the largest fish typically return the highest price per kilo (figure 3a). The fishing pressure lowers the abundance of the large fish, but the abundance in the lower part of the fished range actually increases. Due to the reduction in predation mortality (figure 3b), the abundance of individuals in the size range below the fished range increases substantially. That increase in abundance leads to an increase in the predation pressure further down in the size range among the smallest fishes and the juveniles of the larger fishes. The increase in abundance of fish in some ranges is not only due to a release from predation pressure, but is also due to changes in food availability and thus growth of individuals (figure 3c). As the increased population exerts a larger predation pressure on its prey population, the prey population diminishes, leading to food limitation on the predators. Lower growth rates mean that the individuals are growing more slowly out of their size range, and individuals therefore ‘pile up’ within the size range with slower-than-average growth, thus further exacerbating the increase in abundance and the predation pressure on their prey. The lowering of growth rates is also the effect partly responsible for the increase in abundance in the lower end of the fished range. The opposite effect occurs among individuals in size ranges with decreased abundance. As the abundance of their prey is increased these individuals experience increased growth

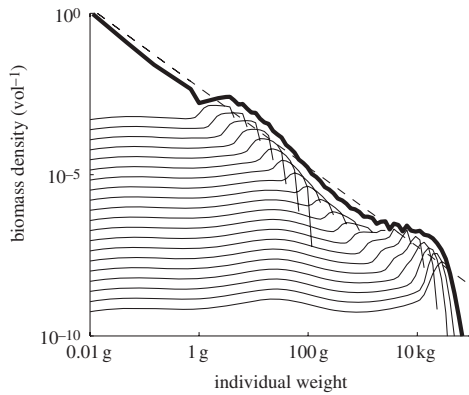


Figure 2. Biomass spectra of 20 asymptotic size classes in an unexploited ecosystem (thin lines) and community spectrum including the resource (thick line). The theoretically expected total spectrum from equilibrium size spectrum theory is the carrying capacity for the resource spectrum (dashed line).

rates and are thus growing more quickly out of their size ranges. The oscillations in the cascade are therefore created by a combination of the changes in predation pressure and food limitation. The end result is a trophic cascade that extends all the way into the resource spectrum representing zooplankton, where it is finally dissipated. As the oscillations are diminishing in magnitude the further they are away from the fished range, the cascade is a damped trophic cascade.

If the largest fish have been removed from the system by fishing, the fishery targets the intermediate size range. The fishery on the intermediately sized species might also have become more profitable due to the increase in abundance brought about by the release from predation by the larger species. This 'fishing down the food web' goes on until fish of all asymptotic sizes are being exploited (Pauly *et al.* 1998). We have used the description of an ecosystem-wide fishing mortality by Pope *et al.* (2006), inspired by the fishing pattern in the North Sea. This fishing pattern targets individuals larger than a fraction of their asymptotic size with a fishing mortality that is slightly larger for small than for large species. The result of the ecosystem-wide fishing is that the trophic cascades almost disappear and the spectrum looks like the unexploited case, except that the largest fish are now completely removed, a state that reflects that of the North Sea today (figure 4b).

Industrial fishing targets the small zooplanktivorous species that are typically used for fishmeal production. This fishing pattern is represented in the model by a fishing mortality that acts only on asymptotic size classes with small asymptotic size (figure 4a). Industrial fishing naturally lowers the abundance of small fish, but not to the same degree that large fish were lowered by the same amount of fishing mortality. This is because predation mortality on small fish is already high, so the relative effect of fishing is smaller. The depletion of smaller fishes affects the availability of food for their predators, which, as a consequence, experience lowered growth rates, which again leads to an increase in the abundance

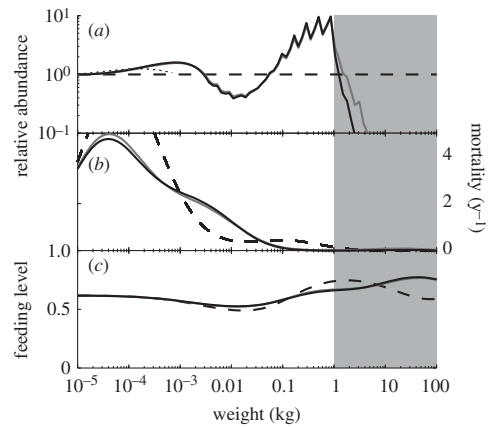


Figure 3. The unexploited system from figure 2 (dashed lines) compared to systems with fishing mortality on fish larger than 1 kg (grey patches). Fishing mortality is 0.5 yr^{-1} (grey line) and 1 yr^{-1} (black line). (a) Abundance in the fished spectrum relative to abundance in the unexploited spectrum $N_c(F)/N_c(F=0)$ for fish (solid lines) and resource (dotted lines), (b) predation mortality and (c) feeding level.

of intermediate to large-sized fish. In this example, fishing again triggered a trophic cascade, but now in both directions. The cascade upwards is driven by the lack of food for the predators leading to smaller realized maximum sizes. The mechanism for the cascade downwards is similar to that from fishing on large fish, namely through the combination of predation mortality and food limitation.

The length (in mass space) and the damping of the cascade depends on the parameters describing the prey preference selection: preferred predator-prey mass ratio β and width σ (figure 5). Qualitatively β determines the relation between trophic level and size, while σ controls the degree of smoothing of differences between trophic levels. The distance from the point of exploitation (10 kg) to the next trough indeed scales roughly with β , but the distance from the trough to the peak is apparently independent of β . Increasing σ weakens the cascade, but does not change the wavelength.

4. DISCUSSION

The model simulations demonstrate how fishing has the potential to trigger damped trophic cascades both up and down in trophic levels. The downward cascades are driven by changes in predation mortality and enhanced by food limitation. The fluctuations in abundance diminish with distance from the fished size range. This means that even if the impact of fishing on the largest fish can be seen in the plankton spectrum, the disturbance is expected to be small. Trophic cascades can also propagate upwards from industrial fishing in the middle of the size spectrum. This increase in abundance of the smallest fish species is expected to lead to an increase in abundance of intermediate-sized predators, but a decrease in productivity of the largest fish. A fully developed fishery with fishing on all trophic levels removes

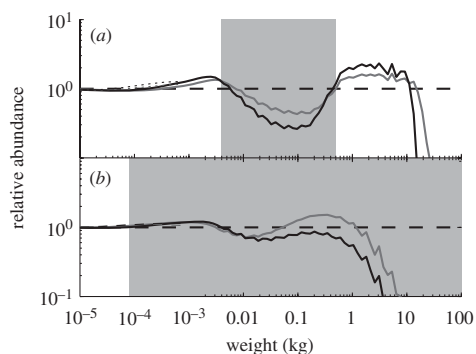


Figure 4. Comparison between the unexploited system from figure 2 (dashed lines) and one with industrial fishing on life histories with (a) an asymptotic size smaller than 0.5 kg, or (b) ecosystem-wide fishing. Solid lines: normalized size spectra: $N_c(F)/N_c(F=0)$; dotted lines: resource. Fishing mortality is 0.35 yr^{-1} (grey lines) and 0.70 yr^{-1} (black lines).

the oscillation that is a signature of the trophic cascade. The dependence of the signature of the cascade on fishing pattern may play a role in why trophic cascades are observed in some systems but not in others (Frank *et al.* 2005, 2007); for example, cascades have not been found in the North Sea (Reid *et al.* 2000), which has a well-developed industrial fishery, but have been observed in the northwest Atlantic, where fishery for fishmeal is not allowed. The differences in growth rates between unexploited and fished systems was remarkably small (figure 3c), lending support to the use of community models with fixed growth (Lewy & Vinther 2004; Hall *et al.* 2006; Pope *et al.* 2006).

Empirical studies have pointed to two aspects of marine ecosystems that may influence the potential cascading effects of fishing, namely species diversity and temperature (Frank *et al.* 2007). Systems with large species diversity are expected to have a high degree of redundancy of ecological function between species. Therefore if some species are depleted, either by fishing or by increased predation pressure, other species will be able to occupy their niche and consequently avoid or dampen a trophic cascade. As the present size spectrum model is trait- and not species-based, it is not able to deal explicitly with the effects of diversity. In this respect the model therefore represents a species-poor system (like the Baltic Sea or the Barents Sea) or a species-rich system where all species of a given trophic level are exploited (like the North Sea). An examination of the influence of diversity may be done by including a specific food web in the model and performing a community viability analysis (Ebenman *et al.* 2004). Describing the effects of diversity therefore requires knowledge of the interaction matrix for the specific system, or at least the statistical properties of interaction matrices in marine systems. An alternative to the explicit food web is to introduce a higher dimensional trait space (Savage *et al.* 2007).

Temperature affects the system either through a correlation between temperature and diversity (higher diversity in warm than in cold systems) or through the direct

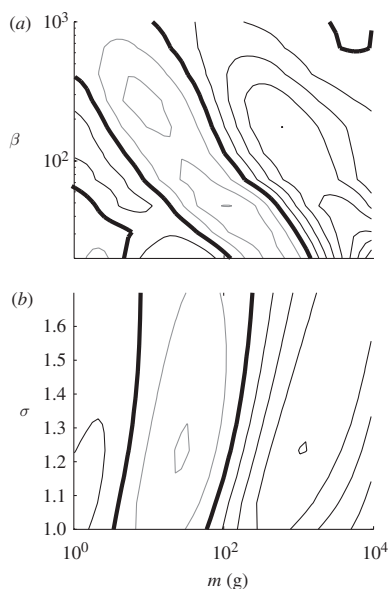


Figure 5. The influence of (a) β and (b) σ on the cascades initiated by a fishing pressure on individuals larger than 10 kg. The contour lines depict the log of $N_c(\text{fished})/N_c(\text{unfished})$, with the thick line being the zero contour line (no impact of fishing), and black and grey contour lines being positive and negative impact respectively. The distance between the contour lines is 0.1.

influence of temperature on physiological rates. The latter can be implemented in the model by a scaling of the physiological rates with temperature by a Q10 of about 1.8 (Clarke & Johnston 1999). The most important physiological parameter in the model is the factor for maximum consumption rate h . Scaling h with temperature effectively leads to a relation between the timescale of the dynamics and temperature. Thus, in the model, an increase of 10°C leads to roughly twice as large growth rates and productivity, and consequently the ability to tolerate twice as high fishing mortality. Temperature in itself is therefore expected to make warm systems more resilient to a given fishing mortality than cold systems, but the qualitative effects (e.g. cascades) remain the same.

The results of the size spectrum model suggest that marine ecosystems possess a mechanism for damping trophic cascades independently of the buffering effects of species diversity. This 'trophic damping' is an inherent feature of the trophic transfer of energy through predation and food-dependent growth of individuals. The damping was quantified as the change in the deviation of abundance induced by fishing between two trophic levels. The trophic damping was found to be about 50 per cent per trophic level. Measuring the damping of a trophic cascade from empirical data is difficult, as results of absolute densities have to be compared between different gears with different catchabilities. Existing empirical data gives different indications about the trophic damping. In the northwest Atlantic a halving of cod biomass resulted in a modest increase in large zooplankton, indicating a strong damping (Frank *et al.* 2005).

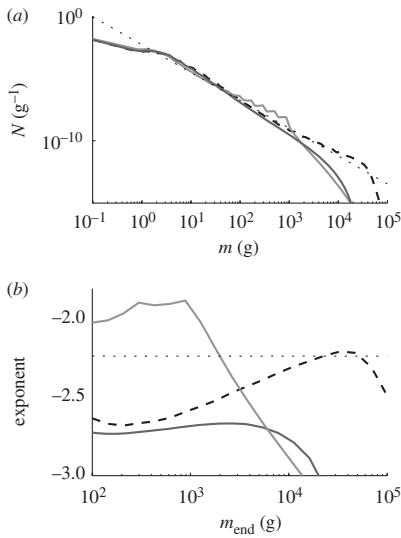


Figure 6. Illustration of the influence of the upper size limit m_{end} of data used for fitting a power law exponent to abundance size spectra. (a) The size spectra of the fish community for unexploited (dashed), large-fish fishing (light grey; figure 3) and ecosystem-wide fishing systems (dark grey; figure 4b). (b) Fitted exponent to abundances in the range from 10 g (approx. 10 cm) to m_{end} . The dotted line is the theoretically expected exponent.

On the other hand, analysis of data from the Baltic indicates almost no damping of the trophic cascade (Casini *et al.* 2008).

The degree of trophic damping depends on the parameters of the prey size selection function, in particular on the width of the size selection function σ . Systems dominated by species with a large trophic breadth in their diet are expected to have strongly damped trophic cascades. A systematic variation of the trophic diet breadth with size may also influence how far a trophic cascade can propagate down the size spectrum. To our knowledge, analysis of the trophic breadth of individuals only exists for fish larvae in particular systems (Munk 1997; Østergaard *et al.* 2005), but a more systematic analysis may be carried out using larger data compilations (Barnes *et al.* 2008).

Environmental stochasticity influencing recruitment can be added to the stock–recruitment relationship (appendix A). It was found that noise did not influence the model appreciably, and, more importantly, that noise is not able to induce different stable states, as shown in, for example, the Baltic (Casini *et al.* 2009). The lack of different stable states is due to the use of a stock–recruitment relationship to stabilize the model. If recruitment is determined only by egg production, the model system would allow for different stable states (de Roos *et al.* 2008b; van Leeuwen *et al.* 2008), but would have difficulties with co-existence of species (van de Wolfshaar *et al.* 2006).

A commonly used indicator for the severity of ecosystem-wide fishing is the slope of the community

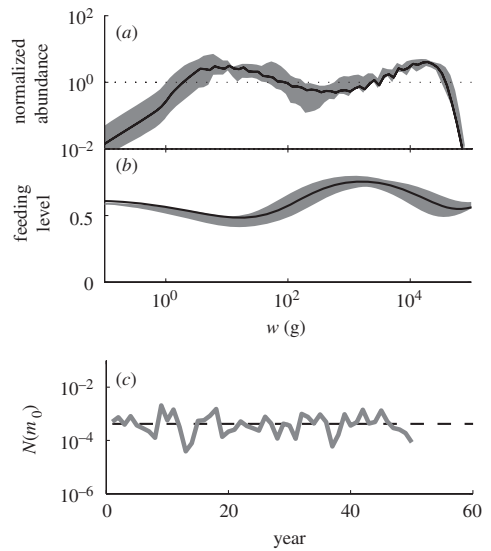


Figure 7. Comparisons of results from the unexploited system without noise (black line, solid in (a,b) and dashed in (c)) and with stochastic recruitment, $\sigma_\epsilon = 1$ (grey area). (a) Community spectra normalized with the theoretically expected spectrum $N_c(m)w^{-2-q+n}$, (b) feeding level and (c) $N(m_0)$ for the asymptotic size class with $M = 500$ g as a function of time.

size spectrum. Historical analyses of the size spectrum of the North Sea fish community demonstrate an increase in the slope (Rice & Gislason 1996; Daan *et al.* 2005), which has been linked to the disappearance of the largest fish, which in turn leads to an increase in the abundance of the smallest fish. A change in slope of the community size spectrum appears to be at odds with the prediction from the present model, where ecosystem-wide fishing does not change the overall slope of the size spectrum appreciably, but leads to the disappearance of large fish (figure 4b). The reason for the change in slope of the community spectrum found by data analysis may be the relatively small size range that is accessible by trawl surveys (10–100 cm). The surveys may therefore only reveal one oscillation in a trophic cascade, which appears as a change in the overall slope of the spectrum. If the line that is being fitted includes points among the disappearing large fish, or if the length of the oscillation is shorter than the fitted range, the fitting of a straight line to the size spectrum depends on details of how the fit is done (figure 6). The power law scaling of abundance with size in an ecosystem is a concept that is only borne out by observations if a size range larger than the oscillations around the ideal scaling is fitted (i.e. a size range several times larger than β). The solution employed in the analysis of the results from the model has been to focus on relative changes in the size composition. This method can be robustly employed in empirical analysis as well (Daan *et al.* 2005). An alternative to fitting a power law to determine a slope is to compare the abundance or biomass between two fixed size ranges (ICES 2007).

APPENDIX A. CALCULATION OF RECRUITMENT

Here the details of the calculation of the recruitment of the i th asymptotic size class $N_i(m_0)$ is given. The recruitment is calculated using a hockey-stick function:

$$N_i(m_0) = \xi(t) \min \left\{ N_{i,0}, \frac{R_i}{g_i(m_0)} \right\}, \quad (\text{A1})$$

where R_i is the egg production, $N_{i,0}$ is the level of the flat part of the hockey-stick curve, $g_i(m_0)$ is the somatic growth of larvae and $\xi(t)$ is a stochastic component.

The egg production of an individual is found from the growth equation (M8) as $g_{i,r}(m) = \psi(m)(\alpha f(m)C_{\max} - k_s m^p)$. Integrating over the whole population gives the total egg production and multiplying by a combined efficiency and egg survival factor $\epsilon = 0.01$ gives $R_i = \epsilon \int g_r N_i(m) dm/2$.

The upper limit to recruitment is found using equilibrium size spectrum theory under the assumption that the feeding level is a constant f_0 (Andersen & Beyer 2006). From this the abundance at recruitment is given as $N_i(m_0) = \kappa_0 M_i^{2n - q - 2 + a/dM_p}$, where $a = (f_0 h)/(a f_0 h - k_s) \beta^{2n - q - 1} e^{(2n(q-1) - q^2 + 1)\sigma^2/2}$, $dM_i \propto M_i$ is the width of the asymptotic size class, and κ_0 is a measure of the abundance of the resource. The value of κ_0 is adjusted such that the community spectrum formed by the spectra of the fish populations roughly forms a continuation of the resource spectrum (figure 2).

The stochastic term $\xi(t)$ is log-normal distributed with a spread σ_ξ , independently for each asymptotic size class, and the value is renewed each year. In the simulations presented in the main text of the article there is no noise (i.e. $\xi = 1$). This was because adding noise was found only to induce variation of abundances and feeding levels around the mean value of the system without noise (figure 7).

KHA acknowledges financial support from the EU programmes IMAGE and MEECE, and the ICES PWG for discussions. M.P. is supported by the Marie Curie Research Training Network FishACE through the European Community's 6th Framework Program (Contract MRTN-CT-2004-005578). We also acknowledge the helpful review of three anonymous reviewers.

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How community ecology links natural mortality, growth, and production of fish populations

Paper VI

Appeared in:

Andersen, K.H., Farnsworth, K. D., Pedersen, M., Gislason, H., and Beyer, J.E. 2009. How community ecology links natural mortality, growth, and production of fish populations. *ICES Journal of Marine Science*, 66(9):1978–1984.

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How community ecology links natural mortality, growth, and production of fish populations

K. H. Andersen, K. D. Farnsworth, M. Pedersen, H. Gislason, and J. E. Beyer

Andersen, K. H., Farnsworth, K. D., Pedersen, M., Gislason, H., and Beyer, J. E. 2009. How community ecology links natural mortality, growth, and production of fish populations. – *ICES Journal of Marine Science*, 66: 1978–1984.

Size-spectrum theory is used to show that (i) predation mortality is a decreasing function of individual size and proportional to the consumption rate of predators; (ii) adult natural mortality M is proportional to the von Bertalanffy growth constant K ; and (iii) productivity rate P/B is proportional to the asymptotic weight $W_\infty^{-1/3}$. The constants of proportionality are specified using individual level parameters related to physiology or prey encounter. The derivations demonstrate how traditional fisheries theory can be connected to community ecology. Implications for the use of models for ecosystem-based fisheries management are discussed.

Keywords: life-history invariants, size spectrum.

Received 2 October 2008; accepted 28 April 2009; advance access publication 23 June 2009.

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Introduction

A central problem in fisheries science is to determine the adult natural mortality, M , for a specific population, or at least to establish a rule of how M relates to other easily measurable quantities. Beverton and Holt (1959) demonstrated empirically that M and the von Bertalanffy growth constant K are proportional. Pauly (1980) did a comprehensive data analysis and found a similar relation with a small correction attributable to the asymptotic (maximum) weight W_∞ and temperature. Given the widespread use of empirical relations between M and K , a theoretical explanation of how mortality can be related directly to an intrinsically physiological parameter such as K is called for.

Although mortality of adults M is assumed to be constant in the classical relations, mortality varies with individual body size (Dickie, 1976). In general, the classical theory of fisheries science has omitted explicit dependence between mortality and growth rate (see, e.g., Pitcher, 1990), despite a substantial literature on allometric patterns of this type (e.g. Peters, 1983). For example, using constant natural mortality has led to the classical relation that productivity rate P/B is equal to M (Allen, 1971). However, it is not clear that this relation is still valid if mortality varies with size or age, because analytical calculations using a size- or age-varying mortality have not previously been feasible.

Here, we show how physiological and life-history variables relate to mortality and test whether the mentioned classical relations hold when mortality is allowed to vary with individual size. In marine fish communities, trophic level strongly correlates with body size (Jennings *et al.*, 2001), allowing the community to be represented as a size spectrum (Sheldon and Parsons, 1967), from which size-dependent growth, mortality, and abundance can be derived (Benoit and Rochet, 2004; Andersen and Beyer,

2006). Specifically, we use this approach to (i) explain theoretically why predation mortality is a decreasing function of individual body size; (ii) derive a relation between K and adult predation (natural) mortality M ; (iii) derive the productivity rate P/B with non-constant mortality; (iv) show that the constants in both M/K and P/B relations involve only individual-level terms; and finally, (v) evaluate these constants assuming mass balance in the community. Our goal is to extend the roots of fisheries theory into community ecology, making use of inter-trophic flows of energy and individual physiological scaling rules. By doing so, we demonstrate an explicit link between the community as a whole and classical empirical and semi-empirical relations used at the population level.

Methods

The equilibrium size-spectrum theory that we use is founded on two primary concepts (Andersen and Beyer, 2006): first, a generalization of the rule that big fish eat smaller fish, and second, that no biomass is wasted—all that is produced is eaten by predators and used to fuel growth leading to an explicit mass balance in the system. We therefore assume that sick or weak individuals will end up being eaten by animals larger than themselves and that fish will not die of other causes of natural mortality than predation.

The theory utilizes the community size spectrum $N_c(w)$ describing the number of individuals in the weight range $[w; w + dw]$, irrespective of their species identity as $N_c(w)dw$. It is assumed that the community spectrum is a power law in weight, $N_c(w) \propto w^{-\lambda}$, and that the consumption rate of an individual predator is also a power law in body weight, hw^n , where h is a constant independent of asymptotic body weight and n the metabolic scaling exponent. The assumption of the community size

spectrum provides a specification of the ratio between the abundance of prey and predators. Combining the community spectrum with the consumption rate of an individual predator is used to derive the mortality on prey of a given weight $\mu(w_p)$. The individual level descriptions of growth and mortality can be scaled up to the population level, where populations are characterized by the asymptotic body weight of individuals in the population. This will be used in the following to provide approximations of M and the P/B rate of a given population described by the asymptotic body weight of individuals in the population.

Mortality

The derivation of the mortality of an individual can be performed by considering the community divided into discrete trophic levels (simple food chain), each containing N_i individuals with weights in the range $[w_i; w_{i+1}]$. The mortality in trophic level i is the ratio between the total consumption (weight per time) by predators in trophic level $i + 1$ and the total biomass of trophic level i :

$$\mu_i = \frac{N_{i+1} h w_{i+1}^n}{N_i w_i} \tag{1}$$

The number of individuals in trophic level i is $N_i = \int_{w_i}^{w_{i+1}} N_c(w) dw \propto w_i^{1-\lambda}$, where it has been assumed that the ratio between the weights of individuals in two consecutive trophic levels, w_{i+1}/w_i , is constant. Defining that constant as $w_{i+1}/w_i = \beta_T$ and inserting in Equation (1) together with the result for N_i gives $\mu_i = h\beta_T^{1+n-\lambda} w_i^{n-1}$, where n is the exponent of the consumption rate. A more concise derivation where the individuals are not confined to discrete trophic levels is performed in Appendix A, leading to a similar result:

$$\mu(w) = h\Phi w^{n-1}, \tag{2}$$

where Φ is a constant that depends on the shape of the prey-size selection function. For the standard lognormal prey-size selection function (Ursin, 1973), $\Phi \approx 1.05\beta^{1+n-\lambda} \approx 0.12$, where β is the preferred predator-prey weight ratio. Equation (2) shows that if $n < 1$, predation mortality is a decreasing function of body size and proportional to the consumption rate constant h .

Relation (2) describes the mortality of an individual only as a function of its size. What is mostly used in practice is the size-independent mortality of adults in a given population, M . The population is here characterized by the asymptotic weight W_∞ of individuals in the population. As the metabolic scaling exponent n is in the range $[\frac{2}{3}, \dots, \frac{3}{4}]$ (Jobling, 1994), the exponent in Equation (2) is small, and mortality only varies slowly with weight. Maturation generally is at a fixed fraction of the asymptotic weight, ηW_∞ , with $\eta \approx 0.25$ (Beverton, 1992). The variation in mortality between maturation and the asymptotic weight W_∞ of individuals in the population is therefore only a factor of $\eta^{n-1} \approx 1.6$. As there are many more individuals that have just matured than close to the asymptotic weight, it is reasonable to approximate mean adult mortality M by the predation mortality at the size of maturation, leading to

$$M = \mu(\eta W_\infty) = h\Phi(\eta W_\infty)^{n-1}. \tag{3}$$

Growth

Equation (3) relates M to the asymptotic weight of individuals in a population. We can show how this is related to individual growth rate using the von Bertalanffy growth equation. This is commonly written in terms of length l of fish as $\partial l/\partial t = K(L_\infty - l)$, where K is the von Bertalanffy growth constant and L_∞ the asymptotic length. For the present application, it is convenient to use the original formulation as a bioenergetic balance equation stating that growth of an individual is the difference between assimilated consumption (anabolism) and the energy used for activity and reproduction (catabolism): $g = \alpha h w^n - kw$, where α is the efficiency of assimilation (including standard metabolism) and kw the energy used for activity and reproduction. Solving for the asymptotic weight W_∞ , where growth is zero, leads to a growth function for individuals described in terms of the asymptotic weight W_∞ :

$$g = \alpha h(w^n - W_\infty^{n-1}w), \tag{4}$$

which is the "standard" von Bertalanffy growth equation when $n = 2/3$ and $w \propto l^3$. Transforming weight into length and bringing Equation (4) into the same form as the length-based von Bertalanffy equation leads to a relation between the length- and weight-based parameters:

$$K = \frac{\alpha h W_\infty^{-1/3}}{3}. \tag{5}$$

Using Equation (5) to express W_∞ as a function of K and inserting it in the relation for the natural mortality [Equation (3)], leads to a relation between M and the von Bertalanffy growth constant:

$$M = 3 \frac{\Phi}{\alpha} \eta^{-1/3} K. \tag{6}$$

Taking parameter values from Table 1, the proportionality constant relating M to K evaluates to 0.97 (range [0.05, ..., 11.0]). The most influential parameters on its value are the preferred predator-prey weight ratio β , and the slope of the size spectrum λ , both via Φ . The predicted relation between K and M fits well with previous empirical relationships (Figure 1).

Population P/B

Having established the relation between M and K , we now turn to the relation between the productivity of a population P/B in relation to M . The production P is the rate of biomass accumulation through individual somatic growth. In steady state, this production must exactly balance losses from predation (Economio *et al.*, 2005), so a whole population's production can be calculated from the size spectrum of that population, $N_p(w)$, and predation mortality, $\mu(w)$, as $P = \int_{w_0}^{W_\infty} \mu(w) w N_p(w) dw$. The integration over sizes from larvae w_0 to asymptotic weight W_∞ accumulates total biomass loss. Evaluating the specific production rate P/B requires specification of the total biomass of the population, $B = \int_{w_0}^{W_\infty} w N_p(w) dw$.

The size spectrum of a population with asymptotic weight W_∞ can be derived as the solution of the steady-state equation for conservation of mass (McKendrick, 1926; von Foerster, 1959):

$$\frac{\partial g(w) N_p(w)}{\partial w} = -\mu(w) N_p(w). \tag{7}$$

Table 1. Variables and parameters and their values, with ranges given in parentheses.

Symbol	Parameter or variable	Value
n	Exponent of consumption rate	2/3
h	Proportionality constant for consumption rate ^a	27 g ¹⁻ⁿ year ⁻¹
α	Efficiency of assimilation and std. metabolism	0.6 (0.3, . . . 0.8)
a	Physiological predation constant = Φ/α	0.2 (0, . . . , 1)
Φ	Geometric factor from size selection function	$\approx \beta^{1+n-\lambda} \approx 0.12$
β	Preferred predator-prey mass ratio ^b	100 (10, . . . , 1000)
η	Size at maturation divided by asymptotic size ^c	0.25 (0.10, . . . , 0.5)
w_0	Mass of larvae ^d	0.001 g
λ	Slope of size spectrum in equilibrium ^e	2.8 - n
W_∞	Asymptotic size of individuals in a population	
K	von Bertalanffy growth parameter	
P	Production of a population (mass per time)	
B	Total biomass of a population	
M	Adult natural mortality	
$\mu(w)$	Mortality of an individual with weight w	

^aAt 10°C (Andersen *et al.*, 2008b).

^bUrsin (1973) and Jennings *et al.* (2002).

^cBeverton (1992).

^dThe mass of a newly hatched larvae is calculated from an egg diameter of 1 mm (Chambers, 1997).

^eAndersen and Beyer (2006).

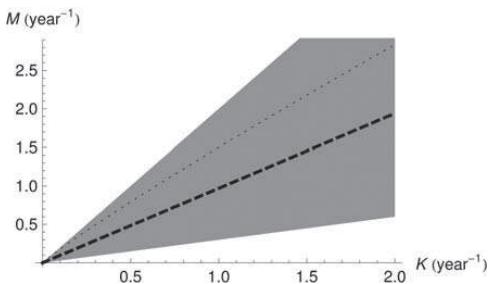


Figure 1. Relation between adult mortality M and the von Bertalanffy growth constant K from Equation (6) (thick dashed line) and from Pauly (1980) at 10°C (dotted line). The grey area represents the range of fitted values for the four groups Gadiformes, Pleuronectiformes, Clupeidae, and Sebastidae (Beverton, 1992).

Using the growth equation (4) and that for mortality (2), Equation (7) can be solved for $N_p(w)$ (Andersen and Beyer, 2006):

$$N_p(w) \propto w^{-n-a} \left[1 - \left(\frac{w}{W_\infty} \right)^{1-n} \right]^{a/(1-n)-1}, \quad \text{for } w < W_\infty. \quad (8)$$

where $a = \Phi/\alpha$. The productivity can now be calculated using the

size spectrum (8) and the mortality function (2):

$$\frac{P}{B} = \frac{\int_{w_0}^{W_\infty} \mu w N_p dw}{\int_{w_0}^{W_\infty} w N_p dw}. \quad (9)$$

Appendix B shows that an approximate solution can be derived analytically by performing the integrations from an individual weight of 0, rather than the larval weight w_0 , to yield

$$\frac{P}{B} \approx \alpha h \frac{a}{1-a} W_\infty^{n-1} = \frac{3a}{1-a} K. \quad (10)$$

Numerical integration of Equation (9) demonstrates that the approximation (10) yields an accurate estimate of P/B (Figure 2). Substituting for K from Equation (6) gives a relation between production and natural mortality:

$$\frac{P}{B} = \frac{\eta^{1/3}}{1-a} M. \quad (11)$$

The numerical value of the constant in front of M is 0.8 [0.54, . . . , 2.5], using values from Table 1. The prediction of P/B rate is compared with the observations compiled by Banse and Mosher (1980; Figure 2), comprising unexploited fish species with asymptotic weight in the range 8 g to 2 kg. The prediction lies in the range of the empirical values of P/B , though with a small underestimation.

Example: the effect of fishing

The calculation of P/B above was for an unexploited population, but most populations of interest are fished. The prediction of the relative yield of a fishery, Y/B , from a surplus production model is that it is equal to the fishing mortality F (e.g. Murray, 2003, Chapter 1.7). To evaluate this prediction, the size spectrum equation for a population (7) is solved numerically in the presence of fishing mortality. Fishing is assumed to be size-selective with a knife-edge selectivity around 1/20 of the asymptotic weight (Pope *et al.*, 2006). The results are compared with the prediction that total productivity $(P + Y)/B \approx M + F$ (Figure 3), where the natural mortality M is given by Equation (3). The calculations demonstrate that the prediction $Y/B \approx F$ is generally quite good, with some overestimation for small fish.

Discussion

Size-spectrum theory, founded on the concept of the community size spectrum, has been used to explain relations between the seemingly unrelated population-level quantities P/B , natural adult mortality M , and growth parameters K or h .

The analysis shows that a size-based approach yields relevant analytical approximations, which is not possible with an age-based approach. The derivations of P/B , together with the derivation of growth and trophic efficiency (Andersen *et al.*, 2008a), provide a complete link between energetic (or trophic) descriptions of communities (Lindeman, 1942) and size-spectrum theory (Andersen and Beyer, 2006).

More concretely, several “invariance” laws have been derived. First, a relation between the von Bertalanffy growth constant and asymptotic weight, $K \propto W_\infty^{-1/3}$ [Equation (5)], such that KL_∞ is constant as $L_\infty \propto W_\infty^{1/3}$. This follows directly from the assumption that consumption is proportional to $w^{2/3}$ and is

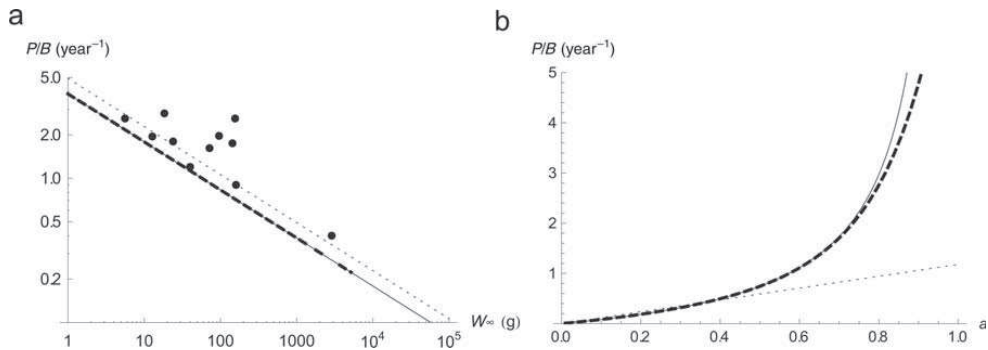


Figure 2. The production to biomass P/B rate (a) as a function of asymptotic mass, and (b) as a function of the parameter a for a species with asymptotic weight $W_\infty = 10$ kg. The figures show full numerical integration (thick dashed line), analytical approximation (10) (solid line), and P/B approximated as the mortality at maturation M from Equation (6) (dotted line). The values of the parameters are in Table 1. The points are the measured values of P/B from Banse and Mosher (1980).

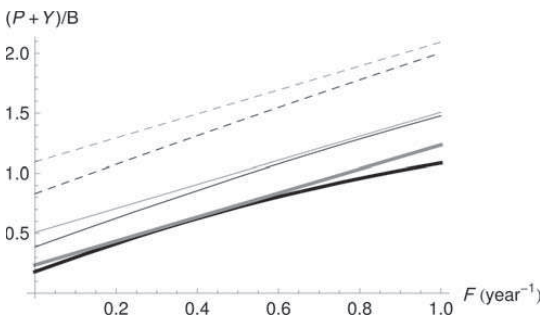


Figure 3. Total productivity of a population as a function of fishing mortality F for $W_\infty = 100$ g (dashed lines), $W_\infty = 1$ kg (solid lines), and $W_\infty = 10$ kg (thick lines). The black lines are full numerical solutions, and the grey lines are predictions based on $(P + Y)/B \approx M + F$, where the natural mortality is predicted using Equation (6).

hence a straightforward consequence of the von Bertalanffy growth formalism (Jensen, 1997). This relation was also demonstrated from basic physiological principles and empirically validated by Kooijman (2000, Chapter 8). The relation may be invalid for large fish, which have elevated metabolism because of inertial homeothermia, e.g. scombroids or white sharks. Second, we derived a relation between expected mortality and individual body weight: $\mu \propto hw^{-1/3}$ [Equation (2)], so μl is constant. This arises from the mass balance assumption that all consumption results in corresponding predation mortality at the community level. $\mu \propto h$ formalizes the intuitive insight that there is a correspondence between consumption (and hence growth) and mortality in the community: greater consumption leads to higher growth rates but also higher rates of mortality. This result has been derived previously (Dickie, 1976; Andersen and Beyer, 2006).

The results that $K \propto W_\infty^{-1/3}$ and that mortality of an individual is $\mu \propto hw^{-1/3}$ were used to derive relations between M and K and P/B for a given population. We found that M/K is a constant, in accordance with classical empirical relationships, by assuming that

M is equal to the mortality at maturation. The constant of proportionality can be written as $3a\eta^{-1/3}$, where η is the weight at maturation relative to asymptotic weight, and $a = \Phi/\alpha$ is what has been termed the physiological predation constant (Beyer, 1989). Reasonable parameter values (Table 1) predict a value of $M/K \approx 0.97$. Empirical studies have found M to be approximately proportional to K , with the constant in the range 0.2, ..., 2.5 for the four groups Gadiformes, Pleuronectiformes, Clupeidae, and Sebastidae (Beverton, 1992). Pauly (1980) examined the relation between M , K , L_∞ , and temperature T over a large number of fish stocks and found $M = CW_\infty^{0.082} K^{0.68} T^{0.46}$, with $C = \exp(-0.2107)$ (K and M are in units of year $^{-1}$). Using the relation between K and W_∞ [Equation (5)] to account for the inherent dependence of K on asymptotic weight, Pauly's relation can be rewritten as $M = C_1 K^{0.92}$ (where $C_1 \approx 2.5$ for $ah = 16 \text{ g}^{1/3} \text{ year}^{-1}$ at a temperature of 10°C). The relation therefore demonstrates an almost proportionality between M and K , which in practice is indistinguishable from $M \propto K$ (Figure 1), except for small mortalities (large fish), which have slightly elevated growth rates. A recent extended analysis of empirical estimates of natural mortality for marine and brackish water fish also took individual size into account and found M to scale with both individual length raised to a power of -1.69 , asymptotic length raised to a power of 0.93, and K suggesting that h or a may depend on asymptotic weight (Gislason *et al.*, 2008a). However, with respect to M/K , their relationship leads to $M/K \approx W_\infty^{-0.07}$, assuming a constant η , i.e. a weak dependence on asymptotic weight. The constancy of M/K found via the arguments put forward here relies on the physiological predation parameter $a = \Phi/\alpha$ being constant. Theoretical considerations of the recruitment of fish with different asymptotic size have indicated that a may be a weak function of asymptotic weight (Andersen *et al.*, 2008b; Gislason *et al.*, 2008b). This would lead to M/K being a weak function of asymptotic weight, in agreement with the above-mentioned analysis of empirical data.

The relation between M and K , or equivalently between M and age of maturation, has also been explained from optimal life-history theory (Roff, 1984; Charnov and Berrigan, 1991; Lester *et al.*, 2004). The essential result of the arguments is that if W_∞ is given and η assumed constant, then for this to be an optimal

strategy, M/K must be constant. However, the optimal life-history argument does not provide an explanation for the mechanism which would adjust η to be constant. In the present work, it is argued that a constant value of M/K is a consequence of the mass balance of the community, based on the assumption that η is constant. This allows the life-history argument to be turned around such that instead of being an argument for M/K being constant, it explains that a constant value of η across life histories is an optimal strategy. This interpretation lends a theoretical justification to the assumption that η is constant.

Finally, the community approach with size-dependent mortality led to the analytical result that productivity rate of a population P/B is approximately proportional to W_{∞}^{n-1} , in confirmation of other theoretical approximations that assume a constant mortality (Allen, 1971; Mertz and Myers, 1998; Ecomomo *et al.*, 2005). Using standard von Bertalanffy scaling ($n = 2/3$), this also fits with empirical findings (Humphreys, 1979; Banse and Mosher, 1980; Dickie *et al.*, 1987; Randall and Minns, 2000). That the scaling has the form W_{∞}^{n-1} is to be expected from simple dimensional arguments, stating that weight-specific rates should scale as weight raised to the power of $n - 1$ (West *et al.*, 1997). Another commonly employed approximation is $P/B = M$ (Mertz and Myers, 1998). Figure 2b shows that this is a fair approximation for some reasonable values of a , but underestimates P/B when a is large. We therefore recommend the use of either the relation between P/B with asymptotic size or the von Bertalanffy growth parameter instead of $P/B = M$, if possible. Numerical calculations demonstrated that in the presence of fishing, the approximation $(P + Y)/B \approx M + F$ was reasonable, though with some overestimation for small fish.

How do these results influence the tools and decisions in current and future management practice? First, the results provide a theoretical confirmation of the M/K relationship often used to estimate natural mortality in single-species assessments in data-poor situations. This is a comforting result because it reinforces current practice. More important, the demonstrated strong link between growth (K) and mortality (M) calls for a truly community-orientated approach to determining both parameters. There are currently three ways to address this:

- (i) Multispecies virtual population analysis types of model (Gislason and Helgason, 1985), stochastic multispecies models such as Gadget (Begley and Howell, 2004), SMS (Lewy and Vinther, 2004), or multispecies size-based simulation models (Hall *et al.*, 2006; Pope *et al.*, 2006). In these models, the multispecies aspect is that mortality depends on the abundance of predators. However, growth of predators (K) is fixed, and total *per capita* food intake is assumed to be independent of the amount of available food.
- (ii) This discrepancy is solved by multispecies models which incorporate strict mass balance, like the Ecopath type of network models (Pauly *et al.*, 2000). These models depend on a specification of the productivity P/B of the populations, which is usually difficult to estimate directly. Therefore, simple relations like $P/B \approx M$ or $P/B \propto K$ are often employed. The explicit derivation demonstrated that $P/B \approx M$ may provide a significant underestimation of P/B in systems with large values of a and that the constant of proportionality between P/B and K depends on a , which is expected to vary between ecosystems.
- (iii) The most recent approach is the community size-spectrum models. This type of model was first formulated by Silvert and Platt (1980), then operationalized by Benoit and Rochet (2004) and Maury *et al.* (2007). In these models, growth and mortality are explicitly linked, and they do not have a need for a specification of P/B . For these models, however, the specification of the trophic efficiency can be a tricky issue (Andersen *et al.*, 2008a), and more important they only provide information on the community level, not the species level. They can therefore not provide, for example, P/B for a specific species or a group of species.

This calls for a unity of the three approaches, namely multispecies models with explicit mass balance that do not rely on the specification of P/B and trophic efficiencies. A promising starting point would be an extension of the Silvert and Platt/Benoit and Rochet framework to a multispecies model, or an extension of size-based multispecies models to include food-dependent growth.

Acknowledgements

MP is supported by the Marie Curie Research Training Network FishACE through the European Community's 6th Framework Program (Contract MRTN-CT-2004-005578). KHA is supported by the Danish Research Council, grant no. 272-07-0485. KDF is supported by a Beaufort Marine Research Award from the Marine Institute, under the Sea Change Strategy and the Strategy for Science, Technology, and Innovation, funded under the Irish National Development Plan (2007–2013). HG is supported by a grant from the Danish Research Council to the research network Fishnet. Verena Trenkel and anonymous reviewers made useful comments on earlier drafts.

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Appendix A Derivation of predation mortality

Predation mortality was derived as a function of trophic level. Here, this derivation is repeated with explicit usage of a size-specific prey preference function. The result of the calculation is the same as in Andersen and Beyer (2006), but performed without reference to the “search volume” concept.

The predation mortality is calculated as in Equation (1), namely by finding (i) the total biomass of prey in the size range $[w_p; w_p + dw_p]$ (the denominator), and (ii) the total consumption of prey in that size range by all predators (the nominator). The first step is the easy one, the biomass of prey is simply $N_c(w_p)w_p dw_p$, where $N_c(w) = \kappa w^{-\lambda}$ is the community size-spectrum. The total consumption by predators of size w is $N_c(w)hw^n$, which should be weighted by how much of that is consumed from prey of size $[w_p; w_p + dw_p]$. The size distribution of consumed prey is determined by a prey-size selection function $\phi(w/w_p)$, assumed to be a function of the ratio between predator and prey weight (Ursin, 1973). The amount of food available from w_p sized prey is therefore $N_c(w_p)w_p \phi(w/w_p)dw_p$, and the total amount of available food is the integral of that, $\int N_c(w_p)w_p \phi(w/w_p)dw_p$. The consumption of prey of size w_p by predators of size w is therefore the ratio of the available food from size w_p divided by the total

available food multiplied by total consumption:

$$C(w_p, w) = N_c(w)hw^n \frac{w_p N_c(w_p)\phi(w/w_p) dw_p}{\int_0^\infty w_p N_c(w_p)\phi(w/w_p) dw_p}. \tag{A1}$$

The total consumption of prey of size w_p [numerator of Equation (1)] is the integral of $C(w_p, w)$ over all predator sizes, so the mortality is

$$\begin{aligned} \mu(w_p) &= \frac{\int_0^\infty C(w_p, w) dw}{N_c(w_p)w_p dw_p} = h\tilde{\phi} \int_0^\infty w^{n-2} \phi(w/w_p) dw \\ &= h\Phi w_p^{n-1}, \end{aligned} \tag{A2}$$

where Φ is a constant that depends on the specific size-selection function. For a lognormal size-selection function (Ursin, 1973),

$$\phi(w_p/w) = \exp\left[-\frac{(\ln(w/(\beta w_p)))^2}{2\sigma^2}\right], \tag{A3}$$

where β is the preferred predator-prey mass ratio and σ the width of the size-selection function, the constant becomes $\Phi = \beta^{1+n-\lambda} e^{(n+1-\lambda)(n-3+\lambda)\sigma^2/2}$. As λ is ~ 2 and $\sigma \approx 1$, the exponential term becomes $\approx e^{1/18} \approx 1$, so the most important contribution comes from the first term with the preferred predator-prey mass ratio. As the exponent of β is small, the value is not overly sensitive to the value of β . For $\sigma = 1$ and the parameter values from Table 1, the constant evaluates to $\Phi \approx 0.12$.

It is important to realize that the main result does not depend on the shape of the selection function, because this only influences the constant Φ . Using another selection function, e.g. where predators eat all prey smaller than themselves until some maximum

preferred predator-prey size ratio β , the constant factor becomes $\Phi = (\beta^{n-1} - 1)/[\ln(\beta)(1 - n)]$ for $\lambda = 2$.

Appendix B Derivation of the approximation of P/B

Here, the derivation of approximation (10) is performed. The total production and biomass are calculated as

$$P = h\Phi \int_0^W w^n N_p(w) dw, \tag{B1}$$

$$B = \int_0^W w N_p(w) dw. \tag{B2}$$

The integrals in the above expressions can be written generally as

$$\begin{aligned} \int_0^W w^k N_p(w) dw &= \kappa W_\infty^{1-n-a} \int_0^W w^{k-n-a} \\ &\quad (W_\infty^{1-n} - w^{1-n})^{a/(1-n)-1} dw, \end{aligned} \tag{B3}$$

with $k = 1$ for the biomass, and $k = n$ for the production. The latter integral can be looked up in standard tabulations of integrals, leading to

$$P = \kappa h\Phi \frac{\Gamma[a/(1-n)]\Gamma[(1-a)/(1-n)]}{(1-n)\Gamma[1/(1-n)]} W_\infty^{1-a}, \tag{B4}$$

$$B = \kappa \frac{\Gamma[a/(1-n)]\Gamma[(2-a-n)/(1-n)]}{(1-n)\Gamma[(2-n)/(1-n)]} W_\infty^{2-a-n}. \tag{B5}$$

As $\Gamma(x + 1) = x\Gamma(x)$, the ratio between P and B can be reduced to the result in Equation (10).

doi:10.1093/icesjms/fsp161

The following is a list of Doctoral theses (Lund University, Sweden) from the Department of Animal Ecology (nos. 1-78, from no. 79 and onwards denoted by (A)) and Theoretical Ecology (T). (E) refers to Doctoral theses from the Department of Chemical Ecology/Ecotoxicology during the years 1988-1995.

1. CHARLOTTE HOLMQVIST. Problem on marine-glacial relicts on account on the genus *Mysis*. 6 May 1959.
2. HANS KAURI. Die Rassenbildung bei europäischen Rana-Arten und die Gültigkeit der Klimaregeln. 9 May 1959.
3. PER DALENIUS. Studies on the Oribatei (Acari) of the Torneträsk territory in Swedish Lapland. 14 May 1963.
4. INGEMAR AHLÉN. Studies on the history of distribution, taxonomy and ecology of the Red Deer in Scandinavia. 21 May 1965.
5. STAFFAN ULFSTRAND. Bentic animal communities of river Vindelälven in Swedish Lapland. 8 May 1968.
6. SAM ERLINGE. Food habits, home range and territoriality of the otter *Lutra lutra* L. 6 May 1969.
7. GUNNAR MARKGREN. Reproduction of moose in Sweden. 17 May 1969.
8. ARNE BERGENGREN. On genetics, evolution and history of the heath-hare, a distinct population of the arctic hare, *Lepus timidus* L. 17 October 1969.
9. HÅKAN HALLANDER. Habitats and habitat selection in the wolf spiders *Pardosa chelata* (O.F. Müller) and *P. pullata* (Clerck). 20 March 1970.
10. ULF SCHELLER. The Pauropoda of Ceylon. 29 May 1970.
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14. STURE ABRAHAMSSON. Population ecology and relation to environmental factors of *Astacus astacus* Linné and *Pacifastacus leniusculus* Dana. 3 June 1971.
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35. SÖREN SVENSSON. Fågelinventeringar - metoder och tillämpningar. (Bird censuses - methods and applications.) 23 May 1979.
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