

How does abundance scale with body size in coupled size-structured food webs?

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Summary

1. Widely observed macro-ecological patterns in log abundance vs. log body mass of organisms can be explained by simple scaling theory based on food (energy) availability across a spectrum of body sizes. The theory predicts that when food availability falls with body size (as in most aquatic food webs where larger predators eat smaller prey), the scaling between log N vs. log m is steeper than when organisms of different sizes compete for a shared unstructured resource (e.g. autotrophs, herbivores and detritivores; hereafter dubbed 'detritivores').

2. In real communities, the mix of feeding characteristics gives rise to complex food webs. Such complexities make empirical tests of scaling predictions prone to error if: (i) the data are not disaggregated in accordance with the assumptions of the theory being tested, or (ii) the theory does not account for all of the trophic interactions within and across the communities sampled.

3. We disaggregated whole community data collected in the North Sea into predator and detritivore components and report slopes of log abundance vs. log body mass relationships. Observed slopes for fish and epifaunal predator communities (–1.2 to –2.25) were significantly steeper than those for infaunal detritivore communities (–0.56 to –0.87).

4. We present a model describing the dynamics of coupled size spectra, to explain how coupling of predator and detritivore communities affects the scaling of log N vs. log m . The model captures the trophic interactions and recycling of material that occur in many aquatic ecosystems.

5. Our simulations demonstrate that the biological processes underlying growth and mortality in the two distinct size spectra lead to patterns consistent with data. Slopes of log N vs. log m were steeper and growth rates faster for predators compared to detritivores. Size spectra were truncated when primary production was too low for predators and when detritivores experienced predation pressure.

6. The approach also allows us to assess the effects of external sources of mortality (e.g. harvesting). Removal of large predators resulted in steeper predator spectra and increases in their prey (small fish and detritivores). The model predictions are remarkably consistent with observed patterns of exploited ecosystems.

Key-words: allometric scaling, benthic–pelagic coupling, community ecology, ecosystem effects of fishing, macroecology, North Sea, size spectrum

Introduction

Empirical studies have shown that the trophic positions of aquatic animals can depend more on body size than taxonomic identity (Jennings *et al.* 2001). This is consistent with the

observation that most of the primary producers in aquatic food webs are phytoplankton (Duarte & Cebrián 1996), that aquatic animals can grow over several orders of magnitude in body mass during the course of their lives (Cushing 1975), and that larger predators eat smaller prey (Cohen *et al.* 1993).

Given the importance of body size, the structures and dynamics of aquatic food webs have sometimes been conceptualized as a continuous size gradient of particles, within which particles grow as a result of eating smaller particles and die, in part, as

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a result of being eaten by larger particles (Kerr & Dickie 2001). The empirical distribution of log particle size vs. log numerical abundance (referred to as a size spectrum) which emerges from this is a widespread macro-ecological phenomenon that exhibits remarkable regularity over a size range from bacteria to the largest predators and in systems differing greatly in primary production, temperature and depth (Boudreau & Dickie 1992). The slope of the size spectrum (based on log numbers of animals binned into log body mass classes) is in the region of -1 in most aquatic communities which have been investigated (Kerr & Dickie 2001; Jennings & Mackinson 2003), consistent with simple energetic considerations about the efficiency of transfer of resources from one trophic level to another, and the average ratio of predator to prey body size (Borgmann 1987; Brown & Gillooly 2003).

However, the aggregation of particles of all types into a single size spectrum can oversimplify the structure of the food web if different components of the ecosystem have different feeding characteristics. For instance, a slope of about -0.75 , rather than around -1 , has been suggested for organisms of different sizes which share a resource rather than eating one another, and slopes shallower than -0.75 have been reported in the unusual case when larger animals feed at lower trophic levels (Maxwell & Jennings 2006). Clearly, the slope obtained after aggregating such different spectra would be hard to interpret.

The need for disaggregation is especially evident in shelf seas where predators in the pelagic zone feed primarily according to body size and yet many benthic animals share common resources such as detritus or phytoplankton irrespective of their body size. Benthic animals can account for a significant proportion of total secondary production (e.g. Warwick 1980; Thompson & Schaffner 2001). For example, Greenstreet *et al.* (1997) estimated that the production of deposit and filter feeding invertebrates in the North Sea was 85.2% of total macrobenthic production and 3.8 times fish production. Macrobenthic carnivores, which would be considered part of the predation-based food web, accounted for 14.8% of total macrobenthic production.

Here we describe the relationships between two trophic pathways in size-structured communities: one comprised of predators feeding on each other according to body size (dominated by mobile fish and predatory invertebrates, mostly in the water column) and the other comprised of animals sharing food (dominated by filter-feeding and deposit-feeding macrobenthic invertebrates). For simplicity, we call the latter group detritivores since in most benthic invertebrate communities, detritus forms the bulk of their food (but it can also be supplemented by living phytoplankton). First, we show that the slopes of empirical detritivore size spectra are shallower than those of predator size spectra. Then we develop a dynamical model for coupled predator and detritivore spectra, to see if some simple assumptions about the feeding mechanisms of these groups are sufficient to account for differences between the spectra. Finally, we use the model to predict how the effects of fishing may alter the size structure of a coupled community.

Methods

DATA

Few studies of size spectra have considered the functionality of component individuals, and therefore allowed the comparison of detritivore, predator and whole spectrum slopes for a single community. This reflects the difficulty of reliably sampling all groups that contribute to biomass in a size class. However, for a subset of size classes, Jennings, Warr & Mackinson (2002) sampled the whole community in the central North Sea in \log_2 body mass bins. We disaggregate their data into detritivore and predator components to compare slopes with those for the whole community, by allocating infauna to the detritivore spectrum and fish and epifaunal invertebrates to the predator spectrum. \log_2 body mass was converted to \log_{10} body mass before comparison.

Since only three size classes in the above data were represented by detritivores, additional published size spectra data for detritivores were used for further comparison. We report data for infaunal invertebrates sampled at three sites in the North Sea during 2003 and 2004. These data were also used to cross-validate the coupled size spectrum model. Sample collection, processing and analysis were described in Maxwell & Jennings (2006).

For predators, the first part of our analyses were limited to those parts of the predator size spectrum where direct biomass reductions due to fishing have not been observed, in this case animals < 256 g (Jennings *et al.* 2002). We later use data for the predator size spectrum that includes the larger sizes sampled (256 g–4 kg) along with reported slopes of fish size spectra as calculated for six regions by Bianchi *et al.* (2000) to cross-validate our model that directly incorporates fishing effects on the predator spectrum.

MODEL

We developed a model of coupled community size spectra where coupling consists of predation and production linkages between two size-structured communities: 'pelagic predators' and 'benthic detritivores' (Fig. 1). The pelagic community encompasses two components: (i) the size range dominated by planktonic primary producers but also occupied by nano- and microplanktonic secondary producers (the plankton), and (ii) the predation-driven consumer size range (the predators). The predators encompass the size range dominated by fish but also include some meso- and macrozooplanktonic as well as macrobenthic predators and feed on individual organisms that are smaller than themselves in both communities, including the plankton. The benthic community consists of the size range comprised of macrobenthic filter feeders and deposit feeders (the detritivores) sharing a non-size-structured food pool. The food pool is comprised of detritus produced by sinking phyto- and zooplankton, faeces from the pelagic predator size spectrum, and other dead organic matter from both communities. For simplicity, we assume the phytoplankton they consume is decaying (and hence part of the detritus) but in very well mixed and coastal regions, the food they share would also include live phytoplankton.

In both communities, we are concerned with the continuous function $N(m, t)$ ($\text{m}^{-3} \text{g}^{-1}$) which gives the density per unit mass per unit volume for organisms of mass m at time t . The abundance of organisms per unit volume N (m^{-3}) across a given size range $[m_{\min}, m_{\max}]$ at time

$$t \text{ is given by the integral } \bar{N}(t) = \int_{m_{\min}}^{m_{\max}} N(m, t) dm.$$

Since analyses of size spectra typically work with log-transformed mass and because spectra usually span many orders of magnitude in

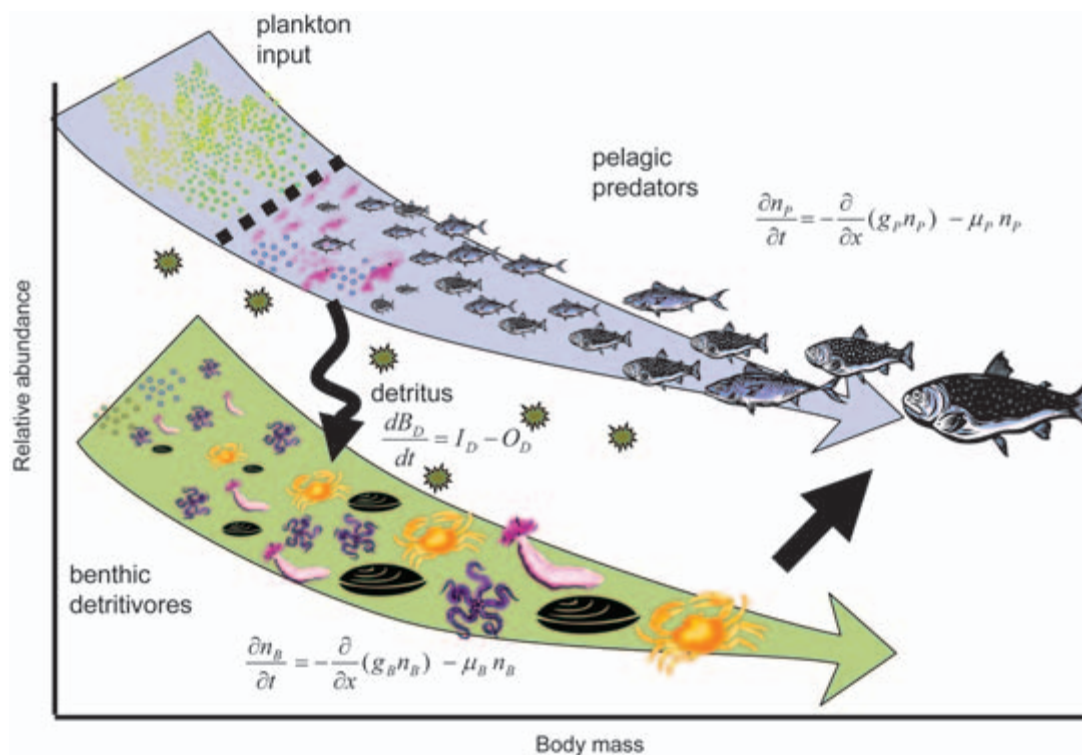


Fig. 1. Conceptual illustration of two size structured communities with trophic interactions resulting in growth and mortality. The pelagic community consists of predators feeding on increasingly larger prey, as they themselves grow larger. Animals in the benthic zone share and compete for the same food: sinking detrital particles that are comprised of phyto-detritus, faeces and dead animals. See Table 1 for equations.

mass, we make the transformations: $m = e^x$: (where m is the weight measured in g) and $N(m, t) = e^{-x}n(x, t)$, so the state variable $n(x, t)$ returns the number of individuals per unit volume at a logarithmic mass at time t and the biomass per unit volume at a logarithmic mass at time t is: $n(x, t)e^x$.

The continuous processes of growth and mortality that arise from organisms encountering and eating available and suitable food govern the temporal dynamics of each size spectrum and this leads to the partial differential equations and descriptions given in Table 1. Parameter values and sources are shown in Table 2.

Predator vs. detritivore feeding

The feeding rates of both predators and detritivores are driven primarily by food requirements and food availability, and by the rates that they encounter and subsequently consume the food. In the predator spectrum, search rates play a role in determining the number of prey encountered, with a volume searched being a function of gape and visual radius and the search rate increasing allometrically for optimally foraging fish predators (Ware 1978). The probability of a predator of size x eating an encountered prey of size x' is $\phi(x-x') = \exp[-(x-x'-\beta)^2/2\sigma^2] \cdot 1/\sigma\sqrt{2\pi}$ when $x-x' > 0$ and $\phi(x-x') = 0$ otherwise; where $x-x'$ is the logarithm of the predator:prey mass ratio, β is the preferred logarithmic predator:prey mass ratio and σ measures the diet breadth on the log scale. In addition to feeding on prey within their own size spectrum, predators also feed on prey in the benthic detritivore spectrum, leading to coupling between the two communities. The fraction of time, ω , spent by predators in each size spectrum, i , can take values between 0 and 1 under the condition that predators trade-off time spent in the two size spectra (i.e. $\omega_b + \omega_p = 1$). These combined processes lead to the

feeding rate $F_p(x, t)$ for predators (Table 1). If predators only feed on prey within their own size spectrum, the equations governing the main processes within the predator size spectrum are essentially the same as the deterministic models in Law *et al.* (2008) and Benoit & Rochet (2004), and the model shares some of the properties of the pioneering work by Silvert & Platt (1980) and more recent developments by Maury *et al.* (2007) and others.

The detrital material produced in the pelagic community is assumed to sink to the detritus pool and support the benthic detritivore size spectrum. In the benthic detritivore spectrum, the effective volume of water from which detritivores can obtain food determines their encounter rate. The effective volume of water searched or filtered per unit mass (A_b) is taken to be approximately 1/10 that of the predators volume searched and detritivore intake rates increase allometrically to the power $\alpha_b = 0.75$. Detritivores with different feeding strategies will obtain the available food in different ways but this is not considered explicitly in the model. The lower values of A and α for detritivores are consistent with the lower metabolic demands associated with a sedentary lifestyle compared to mobile foraging predators (Peters 1983). In the detritivore spectrum, all size classes compete for the same food, which is not size structured, leading to the expression for feeding rate $F_b(x, t)$ of detritivores (Table 1). Mortality in the detritivore spectrum is similar to that for the pelagic system, with nonpredation, senescence and predation mortality effects. When predators do not eat food in the benthic size spectrum (i.e. $\omega_b = 0$), detritivores do not experience predation mortality.

Plankton, detritus and renewal conditions

The plankton resource was held constant at its initial value: $n_p(x, t) = n_p(x, 0) = c \cdot e^{-x} = c \cdot m^{-1}$. The slope of the size spectrum for the plankton

Table 1. Model equations and description

Equations	Units	Description
Dynamical system:		Dynamics of pelagic predators, n_p , benthic detritivores, n_b and detritus, b_D . Rates of change of n_p, n_b are functions of x (ln of body mass in grams) and time t due to growth g and mortality μ . Rate of change of b_D is a function of t , with input rate I_D from deaths and faeces in both spectra, and output rate O_D from detritivore feeding. P , pelagic predators; B , benthic detritivores; D , detritus.
$\frac{\partial n_p}{\partial t} = -\frac{\partial}{\partial x}(g_p n_p) - \mu_p n_p$	$\text{m}^{-3} \text{ year}^{-1}$	
$\frac{\partial n_b}{\partial t} = -\frac{\partial}{\partial x}(g_b n_b) - \mu_b n_b$	$\text{m}^{-3} \text{ year}^{-1}$	
$\frac{\partial b_D}{\partial t} = I_D - O_D$	$\text{g m}^{-3} \text{ year}^{-1}$	
Flux terms from feeding:		
$F_{Pi}(x, t) = \omega_i A_p e^{\alpha_p x} \int \phi(x - x') n_i(x', t) e^{-(x-x')} dx'$	year^{-1}	F_{Pi} is the relative feeding rate of predators on size spectrum $i \in \{P, B\}$, where ω_i is the proportion of time spent in i . F_B is the feeding rate of detritivores. $A_p e^{\alpha_p x}$, $A_b e^{\alpha_b x}$ ($\text{m}^3 \text{ year}^{-1}$) are volumes searched and filtered by predators and detritivores, respectively. Probability of a predator of size x eating a prey of size x' is given by the Gaussian probability density function of the logarithm of the predator: prey mass ratio, $\phi(x - x')$; this applies in the range $0 \leq x - x' \leq x_{\max} - x_{\min}$, the limits over which $\phi(x - x')$ is integrated being 0 to $x_{\max} - x_{\min}$.
$F_B(x, t) = e^{-x} A_b e^{\alpha_b x} b_D(t)$		
give relative growth rates:		
$g_p(x, t) = K_p F_{pp}(x, t) + K_B F_{pB}(x, t)$	year^{-1}	
$g_b(x, t) = K_D F_B(x, t)$		
and relative egestion rates:		
$f_p(x, t) = E_p F_{pp}(x, t) + E_B F_{pB}(x, t)$	year^{-1}	K_p, K_B, K_D are gross growth conversion efficiencies, the fractions of each type of food converted to growth
$f_b(x, t) = E_D F_B(x, t)$		Functions f_i are relative egestion rates, where E_p, E_B, E_D are fractions of each type of food egested.
Flux terms from death:		
$\mu_{ip}(x, t) = \omega_i A_p \int \phi(x' - x) n_p(x', t) e^{\alpha_p x'} dx'$	year^{-1}	μ_{ip} is the death rate in size spectrum $i \in \{P, B\}$, due to predators of size x' feeding on prey of size x . Other mortality μ_{io} includes an intrinsic term that decreases as a function of body size (Lorenzen 1996; Brown <i>et al.</i> 2004), and senescent mortality. The latter increases sharply with body size at $x_s = \log(1 \text{ kg})$. Overall, this results in a u-shaped function for other mortality, consistent with the function and values given in Hall <i>et al.</i> (2006). Predation and other mortality combined give the overall mortality rate μ_i .
$\mu_{io}(x) = 0.2e^{-0.25x} + 0.2e^{0.3(x-x_s)}$		
give overall death rates:		
$\mu_i(x, t) = \mu_{ip}(x, t) + \mu_{io}(x)$	year^{-1}	
Flux in detritus from feeding, egestion, and death:		
$I_D(t) = S \int e^x n_p(x, t) [f_p(x, t) + \mu_p(x, t)] dx$	$\text{g m}^{-3} \text{ year}^{-1}$	Flux into the detritus pool, I_D , is the total rate at which mass is egested and dead mass is generated by nonpredation mortality; a term for dead plankton is also included. The proportion of detritus from the pelagic zone reaching the benthic zone is S . Within the benthic community, detritus is derived from dead biomass but not from egested material.
$+ S \int e^x n_{pl}(x) \mu_{pl}(x) dx$		The flux out of the detritus pool O_D , is the biomass density consumed per unit time by all detritivores.
$+ \int e^x n_b(x, t) \mu_b(x, t) dx$		
$O_D(t) = \int e^x n_b(x) F_B(x, t) dx$	$\text{g m}^{-3} \text{ year}^{-1}$	

community was in keeping with empirical evidence and theory, since the plankton community considered here represents more than one trophic level (Kerr & Dickie 2001; Zhou 2006). However, plankton experience predation mortality, intrinsic residual mortality (disease) or senescence mortality. When individuals die, they sink to the 'benthic' community to become part of the detritus resource, thus forming part of the energy available to benthic detritivores.

The dynamics for the biomass density of detritus are explicitly modelled, to keep track of the food for benthic detritivores. The dynamics are described by the ordinary differential equation for b_D shown in Table 1, where I_D is uptake comprised of the fraction of sinking (S) faeces and dead organic material from the pelagic community that are available as food near the seafloor and dead organic matter produced within the benthic community. O_D is the loss rate from consumption by benthic detritivores. The nutrients released from the fraction of detritus that is mineralized or recycled through the microbial loop in reality fuel some of the primary production that

drives the spectrum. Since we only consider constant plankton conditions, these processes are not explicitly included in the model.

Renewal of the abundance density through time in the smallest size class is held constant for both benthic detritivore and predator size spectra. This is equivalent to assuming constant reproduction (as in Benoît & Rochet 2004; Law *et al.* 2008). For the predator spectrum, the density of individuals at the smallest log body mass, $x_{P\min}$, is determined from the continuation of the background plankton size spectrum. The density of smallest size benthic detritivores is determined by the background density of plankton at the log body mass $= x_{B\min}$ multiplied by the sinking coefficient, S .

NUMERICAL SIMULATIONS

Since the model is too intricate to solve analytically, we were restricted to numerical solutions. The numerical technique used to

Table 2. Symbol definitions, parameter values and units for the dynamic coupled spectrum model. Note that in the model equations we use log transformed body mass, where $x = \log(m)$. C = with coupling, NC = without coupling

Symbol	Definition	Value	Unit	Source
1. $[m_{\min}, m_{\text{Pmin}}]$	Body mass ranges for: 1. plankton	1. $10^{-12}, 10^{-3}$	g	1, 2
2. $[m_{\text{Pmin}}, m_{\text{max}}]$	2. pelagic predators	2. $10^{-3}, 10^6$		
3. $[m_{\text{Bmin}}, m_{\text{max}}]$	3. benthic detritivores	3. $10^{-3.5}, 10^6$		
ω_B	Fraction of time spent by predators feeding in the benthic zone (or feeding in the pelagic zone: $\omega_P = 1 - \omega_B$).	$\omega_B = 0.5$ (C) $\omega_B = 0$ (NC)		3
β	Log of modal predator-prey mass ratio (PPMR)	Log (100)		4, 5
σ	Measure of the width of the log (PPMR) distribution	1.0		6, 7, 8
A	Volume of water searched by predators and filtered by detritivores per unit mass α	$A_P = 640$ $A_B = 64$	$\text{m}^3 \text{year}^{-1} \text{g}^{-\alpha}$	9, 10
α	Exponent of mass in volume of water searched by predators and filtered by detritivores	$\alpha_P = 0.82$ $\alpha_B = 0.75$		9, 10
K	Gross growth conversion efficiency. A higher value was used for predators feeding on pelagic prey. Lower value for benthic prey and detritus.	$K_P = 0.2$ $K_B = 0.1$ $K_D = 0.1$		11, 12
E	Fraction of food egested	$E_P = 0.3$ $E_B = 0.4$ $E_D = 0.4$		10

Sources: 1. Boudreau & Dickie (1992), 2. Duplisea (1998), 3. Estimated from the percent of macrobenthos in fish diets from demersal versus pelagic food chains from Greenstreet *et al.* (1997), 4. Cohen *et al.* (1993), 5. Kerr & Dickie (2001), 6. Andersen & Ursin (1977), 7. Andersen & Beyer (2006), 8. Pope *et al.* (2006), 9. Ware 1978, 10. Peters 1983, 11. Paloheimo & Dickie, (1966), 12. Cauffopé & Heymans (2005).

solve these equations was implicit time upwind finite differencing (Press *et al.* 1986). For ease of interpretation, we present results using base 10 logarithm transformations rather than the natural logarithmic notation used for mathematical convenience in Table 1. All simulations were run for a period of 50 years (with a daily time-step and $0.1 \log_{10}$ gram size intervals). Model runs without coupling were achieved by turning off the predator–detritivore feeding links in the predator spectrum (setting $\omega_B = 0$). Simulations were first carried out in the absence of fishing mortality to determine the emergent size spectra in an unexploited system.

To parameterize the dynamic size spectra models for the North Sea, values were required for (i) the numerical density of the plankton spectrum, n_{pl} , and (ii) the initial detritus biomass density, $b_D(t_0)$. Total biomass densities of planktonic primary and secondary producers across the $2 \mu\text{m}$ to $200 \mu\text{m}$ size range and labile detritus were estimated from a simulation using the coupled hydrodynamic-ecosystem model GETM–BFM (General Estuarine Transport Model–Biogeochemical Flux Model; see <http://www.bolding-burchard.com/> and <http://www.bo.ingv.it/bfm/>). The model simulates the physical and biogeochemical cycling of the main nutrients through the benthic and planktonic pelagic ecosystem. The model domain covers the English Channel and North Sea from $48^\circ 30' \text{N}$ – 60°N with a horizontal resolution of approximately 10 km and with 25 vertical levels. To capture the range of typical values, annual time series from representative locations for the well-mixed southern North Sea and the upper mixed layer of the stratified northern North Sea were considered. Estimated values for the annual mean, minimum, and maximum biomass densities were 0.41, 0.065 and $2.72 \text{ g wet weight m}^{-3}$ for plankton and 0.6, 0.05, and $1.75 \text{ g wet weight m}^{-3}$ for initial detritus values. Total biomass estimates were spread across the corresponding range of body mass for the plankton (10^{-12} to $10^{-6} \text{ g wet weight}$) to satisfy a numerical density scaling with body mass of $n_{\text{pl}} = c \cdot e^{-x}$ where $c = 0.006, 0.001$ and 0.04 for mean, minimum and maximum estimates of the number of particles per unit volume per unit mass of plankton.

The fraction of detritus that sinks to the sea floor was assumed to be $S = 0.50$ based on estimates for the southern North Sea at approximate average depths of 50 m (S) (van Beusekom & Diel-Christiansen 2007). Additional parameter values were derived from the literature and given in Table 2.

Our community size spectrum model should reflect growth rates of an average individual of a given size, being the average of growth rates of individuals with many different asymptotic sizes (Andersen & Beyer 2006). To test whether the model produced realistic average growth rates for the community, we compared the growth rates (g year^{-1}) from the model as a function of body mass (at different levels of food availability) with empirically estimated growth rates of fish predators and benthic detritivores from published estimates of the von Bertalanffy growth parameters k (year^{-1}) and L_∞ (cm) or W_∞ (g wet weight). We converted L_∞ to W_∞ from established weight–length relationships where necessary. We then evaluated growth rates using the derivative of the von Bertalanffy weight equation at sizes much smaller than their asymptotic size to avoid discrepancies between the two models, namely: the lack of a catabolic term in our growth model which is assumed in the von Bertalanffy growth equation.

A numerical experiment with fishing pressure was carried out to test the effect of removing predators on the overall scaling of abundance with body mass. Fishing mortality, expressed as an instantaneous rate, was added to the mortality part of the model equation (applied to the predator community only). Annual estimates for fishing mortality at body size for several species were obtained from multispecies virtual population analysis (ICES 2005) and were averaged over the 1990–2003 period. A linear relationship of the form $\text{mortality} = a \cdot \log_{10}(\text{mass}) + b$ was used to describe the relationship between fishing mortality and body mass for predators greater than 10 g, where fitted values of a and b were $0.09 \text{ yr}^{-1} \cdot \log(\text{g}^{-1})$ and 0.04 yr^{-1} respectively. These parameters were close to the values reported in Benoît & Rochet (2004) who used average fishing mortality estimates for the North Sea and Bay of Biscay in their simulations. Simulations with the mortality rate multiplied by 0.5, 2,

Table 3. Estimated slopes (b), 95% confidence intervals and sample sizes (number of logarithmic size classes) from regressions of \log_{10} numerical density versus \log_{10} body mass for predator and detritivore size spectra in the North Sea. The range of slopes for fish community size spectra reported by Bianchi *et al.* (2000) from a wide range of marine ecosystems is also shown. Study sites and data sources: A. North Sea, site 1) the Hills, site 2) the Middle Rough and site 3) the Indefatigable Banks (Maxwell & Jennings 2006). B. Central North Sea (Jennings *et al.* 2002). C. Range of slopes established from fish communities sampled off of East Africa, Northern South America, Angola, East Central Pacific, Northern Benguela and Western Arabian Sea (Bianchi *et al.* 2000)

Real Community	b	95% C.I. (lower, upper)	Sample size (\log_{10} body mass range)	Study
Detritivore (infauna)	-0.74	-0.93, -0.56	7 (-1.5, -0.3)	A (site 1)
Detritivore (infauna)	-0.51	-0.65, -0.36	11 (-1.5, 1.5)	A (site 2)
Detritivore (infauna)	-0.48	-0.67, -0.28	9 (-1.5, 0.9)	A (site 3)
Detritivore (infauna)	-0.77	-2.26, -0.72	3 (0.6, 1.2)	B
Predator (fish and epifauna) unexploited	-1.2	-1.40, -1.07	7 (0.6, 2.4)	B
Predator (fish and epifauna) exploited	-1.9	-2.34, -1.4	6 (1.7, 3.2)	B
Predator (fish) includes heavily exploited regions	-2.25 to -1.25		(1.9, 3.5)	C

3 were also carried out to test the effect of different levels of fishing mortality on the size spectrum in both communities.

We also compared the slopes derived from the models with predicted slopes of $\log_{10}N$ vs. $\log_{10}m$ from simple theory on how energy available, E , scales with body mass m differently in predator and detritivore size spectra. This comes from the relationship: $N \propto E \times m^{-0.75}$ given in Brown & Gillooly (2003) and Jennings & Mackinson (2003). For detritivores sharing a common resource, $E \propto m^0$, and leads to a predicted slope for $\log_{10}N$ vs. $\log_{10}m$ of -0.75. For predator spectra, $E \propto m^{\log_{10}TE/\log_{10}PPMR}$ and assuming a transfer efficiency of 12.5% and a logarithmic predator : prey mass ratio (PPMR) of 106:1 for the North Sea fish community leads to the slope of $\log_{10}N$ vs. $\log_{10}m$ of -1.2 (see Jennings & Mackinson 2003).

Results

DATA

Slopes of the detritivore size spectra were shallower than slopes of the predator size spectra when data for the two communities were disaggregated (Fig. 2). For detritivorous infauna sampled at three sites in the North Sea during 2003 and 2004, the slopes of the numerical density size spectra were -0.74, -0.51 and -0.48 respectively. In the central North Sea during 2002, the slope of the size spectrum for infaunal detritivores was -0.77. The 95% confidence intervals for each of these estimates overlapped, suggesting that the slopes from each study are not significantly different (Table 3). However, there is a very wide 95% confidence interval for the central North Sea detritivore data, which reflects the fact that the number of data points used to fit the regression was very small (Table 3). The slope of the predator number spectrum was -1.2 and the corresponding 95% confidence intervals did not overlap with those estimated for the three infaunal study sites sampled in 2003 and 2004 (Table 3).

Bianchi *et al.* (2000) reported slopes of number spectra of -3.75 to -6.75 based on log length size classes across the range 20–70 cm using data from six exploited ecosystems. This is equivalent to slopes of -1.25 to -2.25 for number spectra based on log weight classes for fish spanning body mass range

of ~80 g to 3.4 kg (assuming $b_m = (b_l/3)$ where b_m is the slope of the weight spectrum and b_l the slope of the length spectrum; Shin *et al.* 2005). Incorporating the exploited part of the predatory fish community sampled in the central North Sea resulted in a slope of -1.9 across a roughly comparable size range (~50 g–1.5 kg) (Table 3).

MODEL

Size structure of unexploited coupled communities

The dynamics and slopes in both the uncoupled and coupled communities converged to stable values after 50 years (Fig. 3). The modelled predator and detritivore communities both persisted in the absence of coupling and without exploitation. In the uncoupled predator spectrum, all predators and prey are in the same community (as in Benoît & Rochet 2004). In the uncoupled detritivore community there is no predation mortality.

In contrast to the simple linear scaling relationships, all modelled size spectra were nonlinear (Fig. 3). The balance between growth and mortality causes this. For example, high rates of senescence mortality cause abundance to decline quickly at large sizes and steep declines in abundance can also occur at smaller sizes if the amount of food available does not enable enough growth to occur under a given level of mortality.

The different values of intercepts for the plankton spectrum (derived from mean, minimum and maximum biomass density estimates) reflect different levels of energy available at the base of the food chain in the coupled and uncoupled communities. When more energy is available to predators, there are higher densities at larger body sizes. At minimum levels of primary production, there was not enough energy to support a full range of sizes and size spectra in the predator communities were truncated with very steep slopes (Fig. 3a,b).

The density of plankton also affected the structure of the detritivore community. This is obvious without coupling,

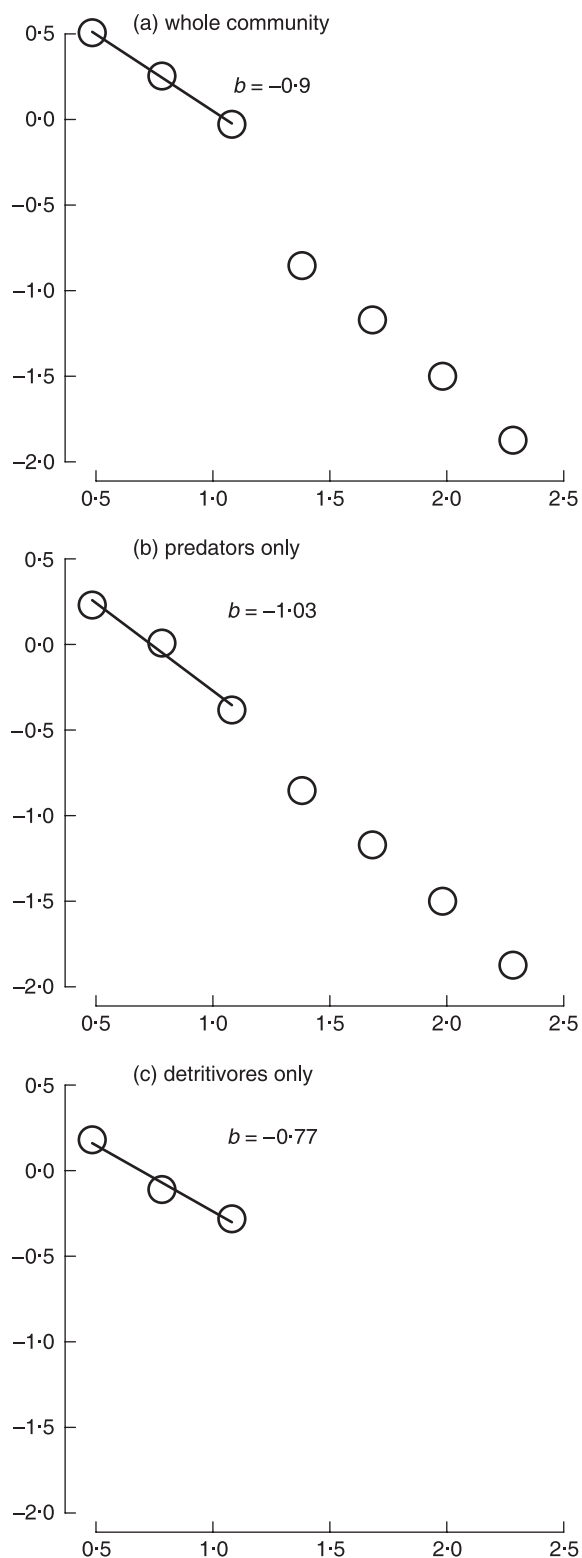


Fig. 2. Observed $\log_{10}(\text{numbers m}^{-2})$ vs. $\log_{10}(\text{body mass g})$ spectra for the (a) whole community, (b) predators only and (c) detritivores only for the North Sea. Linear regression fit fits (solid black line) to the data across the size range where both predator and detritivores overlapped show that before disaggregation, observed slopes are intermediate between the predator and detritivore communities.

when higher levels of plankton and predators increased food supply (detritus) and supported a larger detritivore community (Fig. 3c). However, the addition of predation mortality on detritivores caused a steep decline in abundance at sizes heavily impacted by predators. Here the potential benefit of increased food supply was overridden by predation pressure and reduced their size structure further (Fig. 3d).

Under mean annual plankton conditions without coupling, the slope (95% CI) of the detritivore size spectrum was shallower than the predator size spectrum, -0.60 ($-0.63, -0.58$) vs. -1.07 ($-1.08, -1.06$), up to approximately 100 g where the detritivore abundance declined sharply due to senescence (Fig. 3a,c). With coupling, the slope of the detritivore spectrum was shallower than the predator spectrum, -0.60 ($-0.63, -0.57$) vs. -1.01 ($-1.03, -0.99$), but only up to 1 g where a steep decline in abundance was caused by predators > 100 g that corresponded with a region of inflated predator abundance (Fig. 3b,d).

Comparison of data and unexploited model size spectra

Slopes were calculated from linear regression fits of \log_{10} number density vs. \log_{10} body mass across the part of the size spectrum that corresponded to the range of data (from $10^{0.5}$ g to $10^{2.5}$ g for predators and $10^{1.5}$ g to $10^{1.5}$ g for detritivores). Without coupling and under mean annual levels of primary productivity, the slopes (95% CI) of the predator spectrum at the end of the simulation period were -1.03 ($-1.04, -1.02$) and -0.63 ($-0.66, -0.61$) for the detritivore spectrum. In these cases, the size range considered was well approximated by straight-line fits and the slopes fell within the range of the data.

Coupling the two models, such that predators had access to food in both communities, resulted in predator slopes that are shallower than those in the uncoupled model -0.71 ($-0.74, -0.69$). The slopes of the detritivore spectrum were considerably steeper -1.29 ($-1.37, -1.18$) with coupling due to the effects of predation (Fig. 3). In these cases, however, the size range of the data did not correspond to part of the modelled size spectra that are well approximated by straight-line fits.

Model growth rates (g year^{-1}) as a function of body mass that emerged from different levels of plankton productivity were plotted on a log-log scale to enable comparison with a wide range of species growth rates at mass = $0.2 \cdot W_{\infty}$ (Fig. 4). Empirical growth rates fell within the range of the coupled model predictions for both communities for different levels of productivity. The empirical growth rates would be expected to be higher than the model growth rates because they reflect growth rates of immature animals not allocating energy to reproduction while the model growth rates approximate the growth of an average individual across the whole community irrespective of life-history stage (but not explicitly for those allocating energy towards to reproduction either). Although this was not a comprehensive assessment of how accurately our modelled growth rates represent the true average growth rates, they clearly fell within the range of the realistic values shown (Fig. 4). Higher densities of food at the base of the food web (plankton) resulted in faster growth rates. Predators

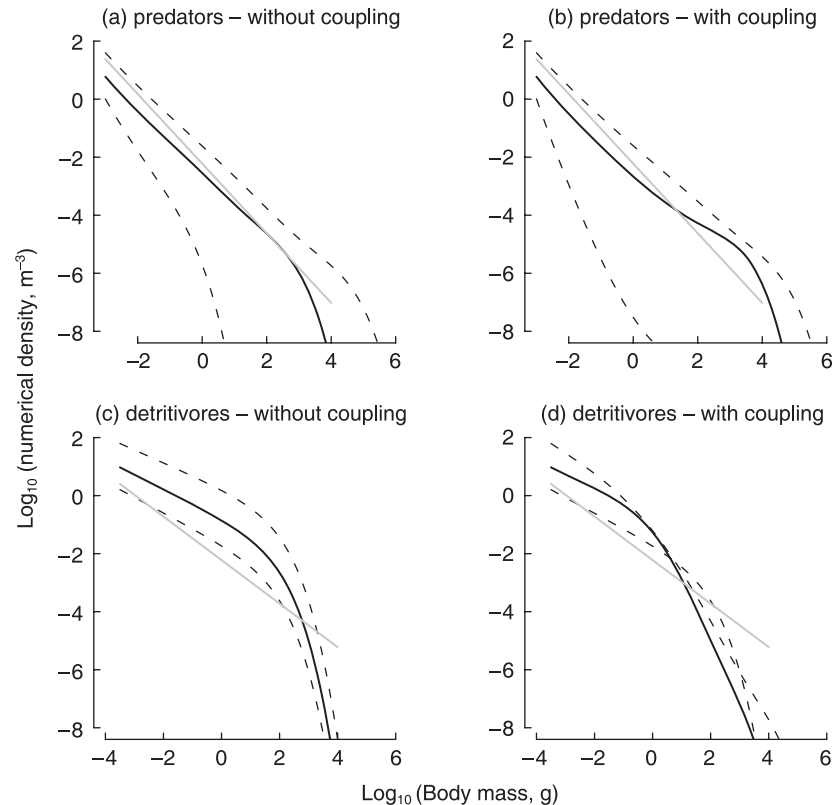


Fig. 3. Modelled \log_{10} numerical density (numbers m^{-3}) vs. \log_{10} body mass spectra after 50 years for the (a) predator community without and (b) with coupling and the (c) detritivore community without and (d) with coupling. Dark solid lines are simulation results based on mean plankton biomass density (bounded by dashed lines for minimum and maximum plankton biomass density scenarios below and above). Predicted scaling of $\log_{10}N$ vs. $\log_{10}m$ from simple scaling theory (Brown & Gillooly 2003; Jennings & Mackinson 2003) is shown in grey.

also grew faster when the communities were coupled (at a given level of plankton density), because additional resources were available to them from the detritivore community.

Effects of exploitation on coupled community size structure

Reductions of large size predators and the higher abundance of detritivores sampled in the North Sea were reproduced by the coupled model predictions of size spectra when realistic levels of fishing mortality were incorporated (Fig. 5). Predator size spectra appeared steeper with higher rates of fishing mortality. The response of the detritivores to the indirect effects of fishing was manifested as increases in the numerical densities of larger size classes (Fig. 5). The increase was linearly related to the decrease in density experienced by the exploited fish predators, reflecting the 'release' of detritivores from predation.

Fishing had a greater effect on the predator community when the two systems were not coupled, with greater reductions in the numerical density of large fish predators at the end of the 50-year simulation period. Simulation of the effects of size-based fishing mortality rates from the most recent multispecies virtual population analysis estimates for the North Sea (ICES 2005), resulted in 96% (4.0 to 16 kg) and 99% (16 to 66 kg) reductions in the biomass density of large fish when the communities were coupled and a 100% reduction in both 4.0 to 16 kg and 16 to 66 kg classes when communities were not coupled under annual mean estimates of plankton biomass density. This is because the reduced growth

rates in the uncoupled model result in slower replacement rates of larger size classes. The coupled model also predicted indirect effects that resulted in 30% and 400% increases in the biomass of small fish and detritivores 10 to 100 g.

Because of the nonlinear patterns in the directly or indirectly impacted size spectra, fitting slopes across different size ranges leads to different predictions of how the slope changes with fishing mortality and should therefore be interpreted with caution. Nevertheless, under mean annual plankton densities, we tested the effect of multiplying the current fishing scenario by 1, 2, and 3 and calculated slopes of size spectra across the size ranges of the data for exploited predators ($10^{1.7}$ to $10^{3.2}$ g) and detritivores ($10^{-1.5}$ to $10^{1.5}$ g). Slopes of the predator spectrum with coupling became steeper with fishing (-1.3 , -1.6 , -2.0) and fell within the range of observations given in Bianchi *et al.* (2000) but were much steeper without coupling (-3.3 , -4.8 , -5.8). Slopes from the detritivore spectrum became shallower with fishing in the coupled model (-1.13 , -0.82 , -0.71) and remained unaffected by fishing without coupling (-0.63).

Discussion

The dynamic size spectrum model allowed us to evaluate whether the biological processes underlying growth and mortality of two distinct size spectra could lead to the observed patterns of abundance vs. body mass. Simulation studies of size spectra have been broadly consistent with empirical observations for fish, plankton and benthic communities

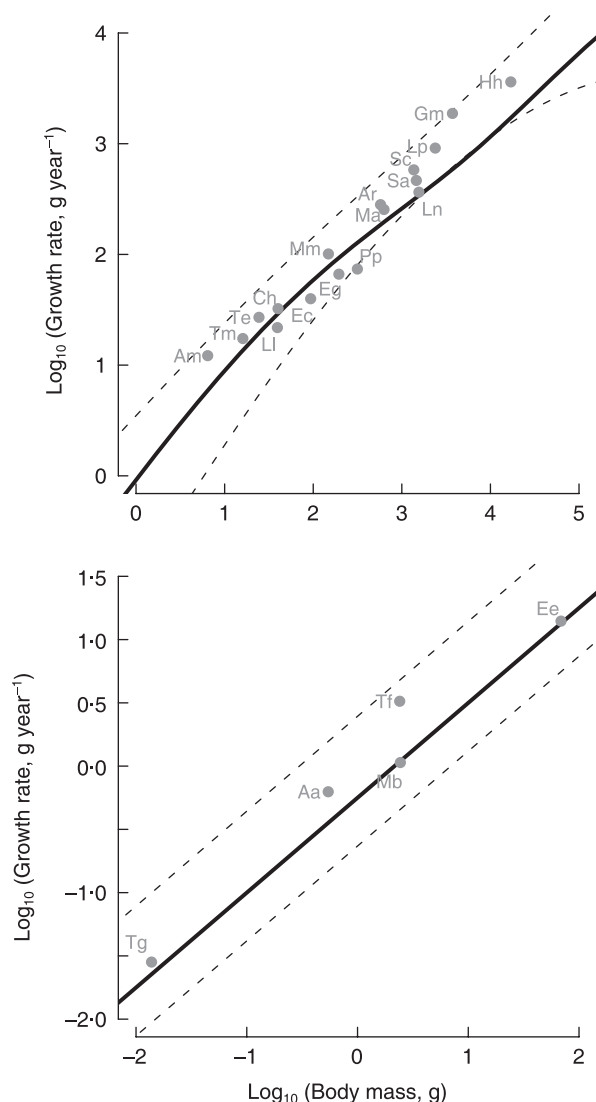


Fig. 4. Model and observed growth rates (g yr^{-1}) as a function of body mass (g) shown on a log-log scale. (a) Predator community and (b) detritivore community. Thick black lines are modelled growth rates under mean plankton conditions bounded lower and upper levels of productivity shown by dashed lines. Grey symbols in (a) show empirically derived von Bertalanffy growth rates calculated at body mass = $W_{\infty} \cdot 0.2$ for North Sea fish predator species: Gm, *Gadus morhua* L. (cod); Hh, *Hippoglossus hippoglossus* (L.) (halibut); Lp, *Lophius piscatorius* L. (anglerfish); Sc, *Scyliorhinus canicula* (L.) (lesser spotted dogfish); Ar, *Amblyraja radiata* (Donovan) (starry ray); Sa, *Squalus acanthias* L. (spurdog); Mm, *Merlangius merlangus* (L.) (whiting); Ma, *Melanogrammus aeglefinus* (L.) (haddock); Ln, *Leucoraja naevus* (Müller & Henle) (cuckoo ray); Ch, *Clupea harengus** L. (herring); Te, *Trisopterus esmarki* (Nilsson) (Norway pout); Eg, *Eutrigla gurnardus* L. (grey gurnard); Tm, *Trisopterus minutus* (L.) (poor cod); Ll, *Limanda limanda* (L.) (dab); Ec, *Enchelyopus cimbrius* (L.) (four-beard rockling); Pp, *Pleuronectes platessa* L. (plaice); and Am, *Ammodytes marinus** L. (sandeel). Source of parameters: Jennings, Greenstreet & Reynolds, 1999 except for * from Pauly, 1980. Grey symbols in the bottom panel show empirically derived von Bertalanffy growth rates calculated at body mass = $W_{\infty} \cdot 0.2$ for examples of benthic detritivore species: Tg, *Thyasira gouldi* (Philippi); Ee, *Echinus elegans* Dübén & Koren; Aa, *Abra alba* (Wood); Mb, *Macoma balthica* (L.); Tf, *Tellina fabula* Gmelin (parameters obtained from Thomas Brey, Alfred Wegner Institute, Germany).

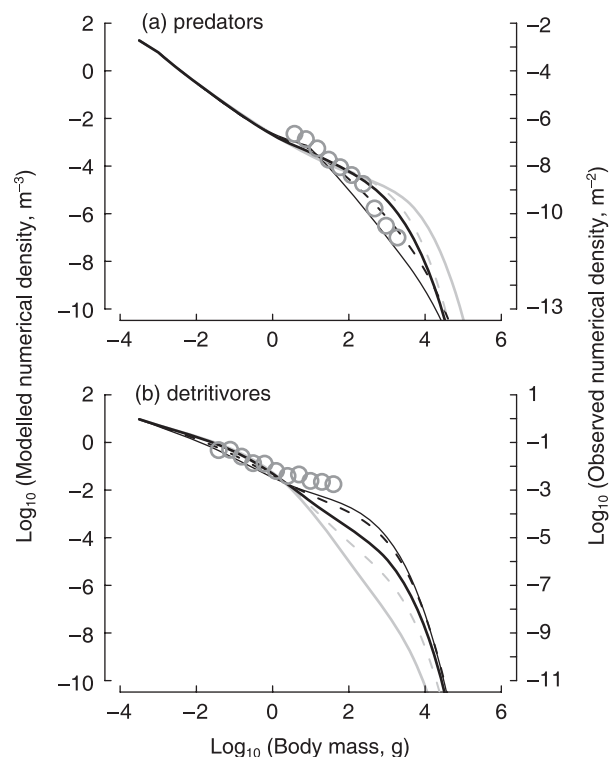


Fig. 5. The effects of fishing on size spectra: model and data. Simulation results at final time step for \log_{10} numerical density vs. \log_{10} body mass spectra at mean levels of plankton biomass density and at different levels of fishing intensity (F multipliers (top to bottom) = 0 (grey line), 0.5 (dashed grey line), 1 (thick solid black line), 2 (dashed black line) and 3 (thin black line)). (a) Predator spectra coupled and (b) detritivore spectra coupled. Note that thick solid black lines are results based on the current exploitation pattern in the North Sea. Superimposed in (a) the predator size spectrum data collected from the central North Sea (original data from Jennings *et al.* 2002) and in (b) the \log_{10} (mean numerical abundance) vs. \log_{10} (body mass) for the infaunal detritivore communities sampled from sites 1–3 in the southern North Sea (original data from Maxwell & Jennings 2006).

when considered in isolation (Zhou & Huntley 1997; Duplisea *et al.* 2002; Benoît & Rochet 2004; Maury *et al.* 2007; Law *et al.* 2008). This study incorporates coupling across different size-based communities, attempting to capture more realistically the different types of trophic interactions and recycling of material that occurs in many aquatic ecosystems while simultaneously retaining the general structure of a purely size-based approach. In the absence of any exploitation and coupling, slopes of the modelled detritivore spectrum were shallower than the predator spectrum. The inclusion of coupling did not appreciably change the slope of the predator size spectrum across the full size range, but did have a considerable effect on the detritivore spectrum resulting in truncated size spectra and steeper declines in abundance with body mass. A direct comparison with the observed size spectra collected in the North Sea revealed fewer larger fish predators and considerably higher relative densities of larger detritivores in the data compared to our coupled model predictions without fishing. Interestingly, inclusion of the

recent fishing mortality rates of the North Sea fish community removed this discrepancy making the coupled size spectra with fishing effects closer to the data. Benthic–pelagic food web coupling is an important part of the flow of energy through the North Sea ecosystem (Greenstreet *et al.* 1997) and changes over the past three decades in the North Sea have been attributed to a mixture of ‘bottom-up’ control of the pelagic planktivorous fish species and ‘top-down’ control of the benthos production and depletion of large demersal fish species by fishing (Heath 2005). The combination of steeper slopes in the predator community and shallower slopes in the benthic detritivore communities (in both the observed and model results) can arise either through the top-down effects of fishing and predation or a mixture of top-down and bottom-up processes (reduced energy available to support larger sizes).

Coupling affects community size structure and its response to harvesting. To evaluate the effects of harvesting under current climatic and environmental conditions, any baseline for the unexploited community must be standardized to the current state of the environment (Jennings & Blanchard 2004). Our model allowed us to predict: (i) a baseline for current conditions in the North Sea, and (ii) the resultant size spectra under different levels of exploitation, with and without the effects of coupling. The predicted 96% and 99% reductions in large fish (4–16 kg and 16–66 kg, respectively) under the current exploitation pattern are consistent with the findings reported in Jennings & Blanchard (2004) for the North Sea fish community.

We only considered the impacts of size-selective fishing on the size structure of the predator community and how the detritivore community would respond. Other harvesting scenarios (i.e. non-size selective) produce similar results and show a differential response of large animals to external mortality. In reality, the physical impacts of bottom fishing gears also lead to changes in the size structure and abundance of the detritivore community (Duplisea *et al.* 2002; Hiddink *et al.* 2006), and would reduce the degree to which the benthos buffers the removal of large fish.

The removal of large fish from ecosystems reduces the reproductive output of the populations that comprise the community. To investigate the steady state patterns in the size structure of the communities, we only considered scenarios where reproduction was held constant. This depended on the density of plankton and could lead to different levels of abundance at body mass when varied. Incorporation of dynamic reproductive processes (see Maury *et al.* 2007) would allow for the effects of this feedback to be evaluated and would yield improved understanding of the effects of coupling on the overall dynamics of the ecosystem and its resilience to exploitation.

When the plankton input to the size spectrum was high, the relative effects of fishing mortality on the coupled size spectra were reduced. This is, in part, because growth rates, and hence replenishment into size classes override the rates of mortality. One aspect of our model formulation is that there is no maximum feeding rate, so it is possible for individuals to grow unrealistically fast. The absence of a maximum intake rate is

equivalent to assuming a linear functional response (Lotka–Volterra), which is reasonable if the range of food density is not high enough to cause animals to be satiated (type II) or not low enough to result in disproportional lower feeding rates (type III). This assumption could lead to over-estimates of the degree to which additional resources can buffer the effects of fishing if food density is very high. Our simulations under realistic levels of productivity encompassed the range of empirically based von Bertalanffy growth rates for North Sea species, so they do not appear to be substantially overestimated. However, whether the observed growth rates are maximal and whether the incorporating satiation or other functional response terms alters our findings would require further investigation.

Several general conclusions can be drawn from this study. First, differences in spectrum slopes were apparent in empirical analyses and the slopes for predator communities are steeper than those for detritivore communities that share energy. Second, a range of slopes could arise in the model depending on (i) the extent of food web coupling, (ii) different levels of productivity at the base of the food web (usually mediated by the environment), and (iii) fishing. Lower levels of productivity should result in truncated size spectra that are less linear and, in areas where predator coupling is stronger, the slope of the detritivore spectrum should be steeper. These findings suggest several testable hypotheses for future work and highlight the need for an ecosystem approach to understanding the effects of exploitation.

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