ORIGINAL PAPER

Coupled energy pathways and the resilience of size-structured food webs

Julia L. Blanchard · Richard Law · Matthew D. Castle · Simon Jennings

Abstract Size-based food-web models, which focus on body size rather than species identity, capture the generalist and transient feeding interactions in most marine ecosystems and are well-supported by data. Here, we develop a size-based model that incorporates dynamic interactions between marine benthic (detritus-based) and pelagic (primary producer based) pathways to investigate how the coupling of these pathways affects food web stability and resilience. All model configurations produced stable steady-state size spectra. Resilience was measured by the return speed obtained from local stability analysis. Return times following large perturbations away from steady-state were also measured. Resilience varied nonlinearly with both predator and detrital coupling, and high resilience came from predators (1) feeding entirely in the slow benthic zone or (2) feeding across the two energy pathways, with most food coming from the fast pelagic pathway. When most of the energy flowed through the pelagic pathway, resilience was positively related to turnover rate. When most of the energy flowed through the benthic pathway, resilience was negatively related to turnover rate. Analysis of the effects of large perturbations revealed that resilience for pelagic ecosystems depended on the nature of the perturbation and the degree of benthic–pelagic coupling. Areas with very little or no benthic–pelagic coupling (e.g. deep seas or highly stratified water columns) may return more quickly following pulses of detrital fallout or primary production but could be much less resilient to the effects of human-induced mortality (harvesting).

Keywords Benthic–pelagic links · Food web dynamics · Predator–prey · Size spectrum · Stability · Trophic interactions

J. L. Blanchard (✉) · S. Jennings
Centre for Environment, Fisheries and Aquaculture Science,
Lowestoft Laboratory,
Lowestoft NR33 0HT, UK
e-mail: j.blanchard@imperial.ac.uk

R. Law
Biology Department, University of York,
PO Box 373, York YO1 5YW, UK

M. D. Castle
Department of Plant Sciences, University of Cambridge,
Downing Street,
Cambridge CB2 3EA, UK

Present Address:
J. L. Blanchard
Division of Biology, Imperial College London,
Silwood Park Campus, Buckhurst Road,
Ascot, Berkshire SL5 7PY, UK

Introduction

Energy pathways bases on detritus and primary producers are found in many ecosystems (Odum 1969). The coupling of these energy pathways is important for understanding ecosystem dynamics because the nutrients that support production come from a common pool and predators may use energy from both pathways (Vander Zanden and Vadeboncoeur 2002; Post et al. 2000; McCann et al. 2005). Detritus pathways typically exhibit slower turnover than primary producer-based pathways (Neutel et al. 2002; McCann et al. 2005; Rooney et al. 2006). It has been suggested that stability of complex ecosystems could depend on the existence of fast (primary producer-based) and slow (detritus) energy pathways and

the presence of mobile predators to couple them (Moore et al. 2004).

The dynamics and stability of coupled energy pathways have usually been studied in food-web models with nodes that represent species or functionally equivalent groups of species, arranged from lower to higher trophic levels (McCann et al. 2005; Rooney et al. 2006). Since body size is well-known to be an important factor governing the feeding behaviour of organisms in aquatic food webs, average body sizes for the 'species' are sometimes incorporated into these theoretical food-web models to account for allometric metabolic demands and size-based predator–prey relationships (Brose et al. 2006). For aquatic ecosystems, a drawback of this view is that individual organisms often change in body size over several orders of magnitude within the course of their lives (Kerr and Dickie 2001; Belgrano et al. 2005), and trophic links are more strongly dictated by an individual's body size than species identity (Jennings et al. 2001).

An alternative approach is to consider body size at the level of the individual (rather than species), scaling directly to the community level and allowing individuals to grow by feeding on others. In such models, the community is described as a continuous distribution of density or biomass density across a wide range of body sizes (termed the size spectrum). Changes in the size spectrum over time are modelled through predation-driven growth and mortality (Silvert and Platt 1980; Benoît and Rochet 2004; Zhou and Huntley 1997; Maury et al. 2007) and produce body mass distributions consistent with observed community size-abundance data (Boudreau and Dickie 1992; Bianchi et al. 2000). These approaches have focused on the pelagic community where predation is most strongly governed by body size.

Blanchard et al. (2009) extended size spectrum dynamics beyond the pelagic community and considered a wider range of trophic interactions and recycling of material that occurs as a result of benthic–pelagic coupling in marine ecosystems. Steady-state predictions, validated with data from the North Sea, showed that food-web coupling and increased primary productivity buffered the effects of harvesting predators. Very little is known, however, about the stability properties of dynamical size spectra and their resilience to perturbations (Law et al. 2009).

Here, we examine the effects of different types of coupling on the stability and resilience of size-structured food webs for the first time. The analysis is framed in the context of a marine ecosystem with a benthic pathway (slow, detritus-based) and a pelagic pathway (fast, phytoplankton-based) coupled by predators that feed in both the pelagic and benthic zones and by detritus that flows into the benthic zone. Since the potential coupling of pathways will vary widely in marine ecosystems, owing to differences in depth, stratification, nutrient supply and seabed characteristics, knowledge on how stability and resilience may vary systematically across systems is required for an improved understanding of the vulnerability of ecosystems to human-induced impacts.

Methods

Model structure

A coupled dynamic size spectrum model was used to test the effects of predator and detritus coupling on community dynamics. In this model, the state of the pelagic–benthic ecosystem at time t has the following four components. (1) N_{pp} (m, t) is the density of pelagic planktonic primary producers of body mass m occupying the smallest size range $[m_{min}, m_{P,min})$ in the model. We refer to this as the primary producer spectrum because it is dominated by phytoplankton and is the ultimate source of energy in the ecosystem, although, in reality, this size range also includes bacteria and nano- and micro-planktonic secondary producers. (2) N_p (m, t) is the density of pelagic predators, consisting of meso- and macrozooplankton, fish and cephalopods and is distributed across larger sizes $[m_{P,min}, m_{max}]$ in the pelagic zone. Pelagic predators feed on smaller pelagic organisms, including the primary producers, and can potentially feed in the benthic zone. (3) N_B (m, t) is the density of consumers in the benthic zone comprised of macrobenthic filter feeders and deposit feeders (dubbed the detritivores) sharing a non-size-structured food pool and spanning a size range $[m_{Bmin}, m_{max}]$. (4) B_D (t) is the unstructured biomass density of food comprised of sinking phyto- and zooplankton, faeces from the pelagic predator size spectrum and other dead organic matter from both communities (the detritus). Although detritus can be size-structured, the trophic level of detritivores is typically independent of size (Maxwell and Jennings 2006) and was not incorporated into the model. Also, for simplicity, we assume the phytoplankton consumed by benthic detritivores is decaying (and hence part of the detritus), but, in very well-mixed and coastal regions, the food they share may also include live phytoplankton (Blanchard et al. 2009).

The temporal dynamics of pelagic predators and benthic detritivores are governed by the continuous processes of growth G and mortality D that arise from organisms encountering and eating available and suitable food, leading to a partial differential equation for each size spectrum i:

$$\frac{\partial N_i}{\partial t} = -\frac{\partial}{\partial m}(G_i N_i) - D_i N_i \qquad (1)$$

The primary producer spectrum forms part of the food supply for the pelagic predator spectrum and is a source of

dead particles for the detritus pool. We do not explicitly model the dynamics of the primary producer spectrum, but treat it as constant through time: $N_{pp}(m)=cm^{-1}$. Similar boundary conditions are used in other dynamic size spectrum models that are governed by predation-driven growth and mortality (see Benoît and Rochet 2004; Maury et al. 2007; Law et al. 2009; Blanchard et al. 2009). Although many different approaches have been developed to describe the dynamics of size-structured phytoplankton communities (Moloney and Field 1991; Armstrong 1999; Baird and Suthers 2007; Stock et al. 2008), they do not use continuous-time-size equations, often including many more discrete functional groups than considered here. The prefactor c of the primary producer spectrum was derived from annually averaged estimates of plankton biomass density obtained from a validated and detailed hydro-biogeochemical model of the North Sea (see Blanchard et al. 2009).

The feeding rate $F_{Pi}(m,t)$ of a given size pelagic predator is a function of the preference for prey ω_i in spectrum i, the volume of water searched per unit time $A_P m^{\alpha_P}$ (m^{-3} year^{-1}), and the amount of suitably sized food available in spectrum i, $\int \varphi(m/m') N_i(m',t)m'dm'$ (Table S1). The probability of a predator of size m eating an encountered prey of size m' is given by the lognormal probability density function:

$$\varphi(m,m') = \exp\left[\frac{-(\ln(m/m')-\beta)^2}{2\sigma^2}\right] \cdot 1 \Big/ \left(\sigma\sqrt{2\pi}\right) \qquad (2)$$

when $m>m'$ and $\varphi(m,m')=0$ otherwise, where β is the logarithm of the preferred predator: prey mass ratio and σ the width.

Benthic consumers compete for an unstructured shared pool of food. For simplicity, we refer to benthic consumers as 'detritivores' since detritus forms the bulk of the food for most benthic invertebrate communities (although the food of filter-feeding detritivores could be supplemented by substantial quantities of living phytoplankton in a mixed water column). Detritus (B_D) is produced by sinking phyto- and zooplankton, faeces from the pelagic predator size spectrum and other dead organic matter from both communities. The feeding rate of a given size detritivore $F_B(m,t)$ depends on the volume of water either searched or filtered per unit time $A_B m^{\alpha_B}$ (m^{-3} year^{-1}) and the available biomass density of detritus $B_D(t)$ (g m^{-3}). Because detritus is unstructured, its dynamics were modelled as an ordinary differential equation with fluxes into and out of the detritus pool. Of the food consumed, only a fraction is assimilated. Assimilated food is allocated to growth G and reproduction r after accounting for losses associated with meeting metabolic requirements and activity.

The overall mortality rate D_i in each size spectrum $i\in\{P, B\}$ arises from feeding by predators (as described above) and other sources of mortality (disease, senescence). Other mortality D_{iO} includes an intrinsic term that decreases as a function of body size and senescent mortality that increases with body size at the size m_s.

Reproduction

We incorporate temporally dynamic reproduction into the coupled pelagic–benthic ecosystem model as a consequence of the food quality and the simple energy budget of individual organisms within the size spectra (c.f. Blanchard et al. 2009 assumed constant reproduction). A fraction (R_i) of the assimilated food consumed is allocated to reproduction after accounting for the fraction required for growth and losses associated with meeting metabolic requirements and activity. We assume that lower food quality is associated with lower assimilation efficiency and higher metabolic costs (hence, lower conversion efficiencies to growth and reproduction). The recruitment (renewal) of individuals in each size spectrum i (P or B) at the smallest size, $m_{i,min}$, as a function of time, t, is then determined by the reproductive rates, $r_i(m, t)$, of all individuals in the size spectrum larger than eggs, minus growth to larger sizes and deaths (see equation S.2 in supplementary text) and is similar to the approach adopted by Maury et al. (2007). The smallest sizes (egg mass) in the pelagic–predator and benthic–detritivore communities were taken to be 10^{-3} g and $10^{-3.5}$ g, respectively (Boudreau and Dickie 1992; Duplisea 1998). The reproductive investment per unit mass of an individual declines with body mass in each community and is consistent with cross-species patterns in reproductive investment reported for marine teleost fishes and bivalves (Gunderson 1997; van der Veer et al. 2006). Further details on model structure, equations, parameters and initial conditions are given the Electronic supplementary material (supplementary methods text, Tables S1 and S2).

Coupling the size spectra

We tested the effects of altering the strength of two types of pelagic–benthic coupling through: (1) detritus and (2) pelagic predators. Detritus coupling was determined by the fraction (S) of pelagic-derived detritus available for benthic detritivores. When $S=1$, all of the pelagic-derived detrital material reaches the benthic community. As S decreases, due to mineralization of detritus as it sinks to greater depths in deeper seas, the pelagic component of detritus becomes smaller. In the absence of any other benthic source of energy, the benthic community would die out when $S=0$.

Coupling of the energy pathways by pelagic predators depends on their preference for pelagic and benthic prey,

ω_P, ω_B, respectively. We assumed that ω_P and ω_B are directly related, such that the preferences of both prey types sum to one (i.e. $\omega_P+\omega_B=1$). To test the effects of predator coupling, the preference for benthic prey ω_B was varied from 0 to 1. We also contrast model results for two forms of predator functional response: linear and hyperbolic (type II, see Electronic supplementary material, equations S2 and S8).

Energy throughput

Several ecosystem-level measures of energy throughput were made at steady-state (see below for calculation of steady-state) to determine the strength of the energy pathways (see Electronic supplementary material for equations). Total system throughput was calculated as the total biomass consumption (or input) rate (g m^{-3} year^{-1}) by pelagic predators, benthic detritivores and detritus taken together. Total biomass density (g m^{-3}) and production/biomass (P/B) ratio were calculated for plankton, pelagic predators, detritus and benthic detritivores to investigate how the energy pathways were altered with increased benthic coupling by predators. P/B ratio was assumed to be equivalent to total mortality rate (per year) in keeping with Allen (1971). Utilising differences in the energy flow through the benthic and pelagic communities, we could test whether coupling of the slow and fast energy pathways by predators would make the overall pelagic–benthic system more stable.

Stability and resilience

Response of the system to small perturbations was investigated by local stability analysis of the steady state of the entire system of equations in three steps. First, numerical integration of the two partial differential equations and, in the case of detritus, one ordinary differential equation (ODE), was carried out for a period of 50 years (discretised with a daily time-step and 0.1 log10-g size intervals), to obtain an initial condition for evaluating the steady state. Second, the steady state was determined using the Newton–Raphson multidimensional root-finding method (Press et al. 1992: 380). In doing so, the dynamics describing the predator and detritivores were replaced by an ODE for each 0.1 log size class, and the system of equations (including the ODE for the detritus) were linearised. Third, the steady state obtained with the Newton–Raphson algorithm was used to evaluate the $n \times n$ Jacobian matrix and its eigenvalues, where n equals the number of size classes of predators plus the number of size classes of detritivores plus one (the detritus pool). The steady state is locally stable if the eigenvalue with largest real part, λ_{max}, is less than zero, indicating a return to the

original state following the perturbation. In cases where the steady state is locally stable, $-\lambda_{max}$ has been used as a measure of resilience, where larger resilience corresponds to faster decays to equilibrium and where the inverse of resilience is return time (Pimm and Lawton 1977; DeAngelis 1980; Carpenter et al. 1992).

As noted by many others, in reality, perturbations are large and are often followed by transient dynamics (DeAngelis 1980; DeAngelis et al. 1989; Cottingham and Carpenter 1994). To evaluate resilience away from steady-state, the response of the system following simulated large perturbations was investigated by calculating: (1) the subsequent trajectories of total biomass density relative to steady-state values and (2) return time T_R, measured by integrating the magnitude of change in total biomass density, $TB(t)$ relative to the steady-state value, TB_0, over the entire history of the system following the perturbation (Neubert and Caswell 1997):

$$T_R = \frac{1}{|TB_0|^2} \int_{t=0}^{t\max} |TB(t)|^2 dt \qquad (3)$$

Perturbations were chosen to investigate whether top-down and bottom-up effects led to different responses of the communities under a range of coupling scenarios. Top-down perturbations entailed adding extra mortality on pelagic predators (50% decreases in density for those >10 g). Bottom-up perturbations comprised separate pulses of primary producers and detritus (50% density increase). Each perturbation took place from steady-state starting conditions and persisted for 30 days after which the initial speeds and return times of the biomass trajectories were evaluated.

Results

Structure of coupled ecosystems at steady-state

Different steady-states of pelagic–benthic ecosystems are possible given our model configurations. If the sea is deep, only a small fraction of detritus reaches the sea floor. Consequently, the density of benthic detritivores is low and mainly supported by the energy recycled within the benthic community (Fig. 1a: $S=0.05$, $\omega_B=0$). Alternatively, if the sea is shallow (as in a shelf sea), a large fraction of detritus reaches the benthic community (Fig. 1b–d), and predators may feed on prey in the pelagic community (Fig. 1b: $S=0.5$, $\omega_P=0$), both communities (Fig. 1c: $S=0.5$, $\omega_P=0.5$) or the benthic community only (Fig. 1d: $S=0.5$, $\omega_P=1.0$). The steady-state size spectra for both communities are considerably altered when predators exclusively prefer benthic prey. Here, at $\omega_B=1$, the benthic size spectrum is truncated with a very steep decline in abundance with body mass due

Fig. 1 Examples of steady-state spectra for pelagic (*black lines*) and benthic (*grey lines*) communities that emerge from different model configurations; a fixed plankton spectrum is shown as a *dashed line*. *Bdet* is the steady-state biomass density of detritus. **a** Deep sea and pelagic feeding: a small fraction of detritus reaches the seafloor ($S=0.05$) and predators do not feed on prey at these depths. **b** Shelf-sea and pelagic feeding: a larger fraction of detritus reaches the benthic community ($S=0.5$) and predators feed only on prey in the pelagic community $\omega_B=0$. **c** Shelf-sea and pelagic–benthic feeding: same as in **b** except predators feed on prey in both benthic and pelagic communities $\omega_B=0.5$. Predators feed only on prey in the pelagic community. **d** Shelf-sea and benthic feeding: same as in **b** except predators feed only on prey in the benthic community $\omega_B=1$. When ω_B is very high ~1.0 (**d**) size spectra become truncated
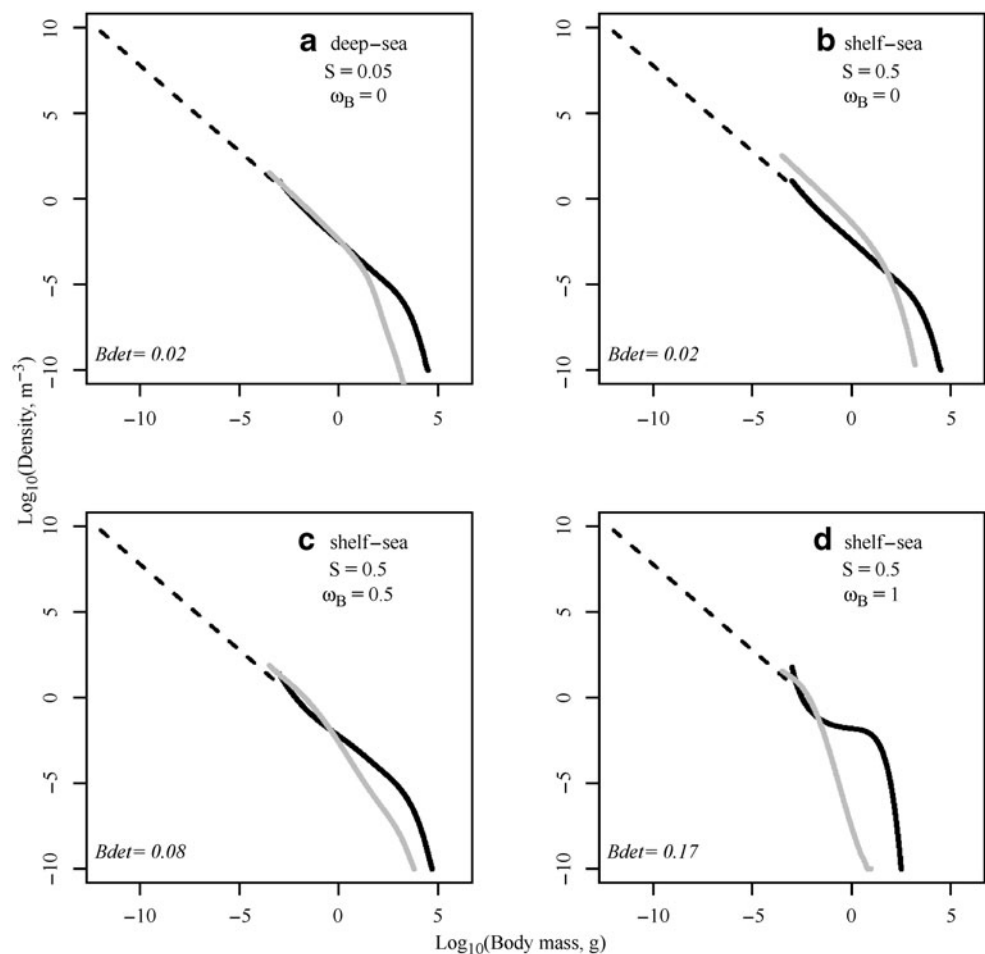
to heavy predation. With low food availability for large predators, the predator size spectrum, in turn, becomes more strongly nonlinear and truncated as well.

The model configurations investigated, based on realistic parameter values, always settled to steady-state in the numerical integrations. The results describing biomass and energy throughput use these steady-state values.

Biomass and energy throughput in benthic and pelagic pathways

Biomass in the benthic and pelagic spectra at steady-state was largely contingent on the feeding behaviour of pelagic predators (Fig. 2). If predators fed predominantly in the pelagic zone (i.e. ω_B small), the combined pelagic–benthic system was dominated by biomass of benthic detritivores, as they had no predators (Fig. 2a). If predators fed mostly in the benthic zone (i.e ω_B large), the combined system was dominated by detritus (Fig. 2a) because the predators kept the biomass of detritivores low. The biomass of predators was actually greater when ω_B was large because there was less self-predation in the predator spectrum.

Energy flow, measured by the P/B ratio, was two to six times higher for primary producers than for the detritus (Fig. 2b), revealing that energy moves faster through the pelagic pathway than through the benthic pathway. How much faster the energy moved through the pelagic pathway depended on the feeding strategy of the predators (ω_B). When predators fed more in the benthic zone, there was more detritus accumulation, and thus a lower rate of energy flow through the detritus. When predators fed more in the pelagic zone, their P/B ratios increased and the P/B ratios of detritivores decreased. Total biomass flowed faster through the coupled system as a whole when predators fed mostly in the pelagic zone (Fig. 3a–c). Overall, these results show that the pelagic zone is a relatively fast energy pathway, and the benthic zone is a relatively slow energy pathway.

Response to small perturbations

Although the steady-state was always stable to small perturbations, coupling of the benthic and pelagic zones by predation ω_B, and detrital input S affected the rate of return to steady state, as given by $-\lambda_{max}$ (Fig. 3d). Consider first the shelf-sea scenario where $S=0.5$ (this corresponds to
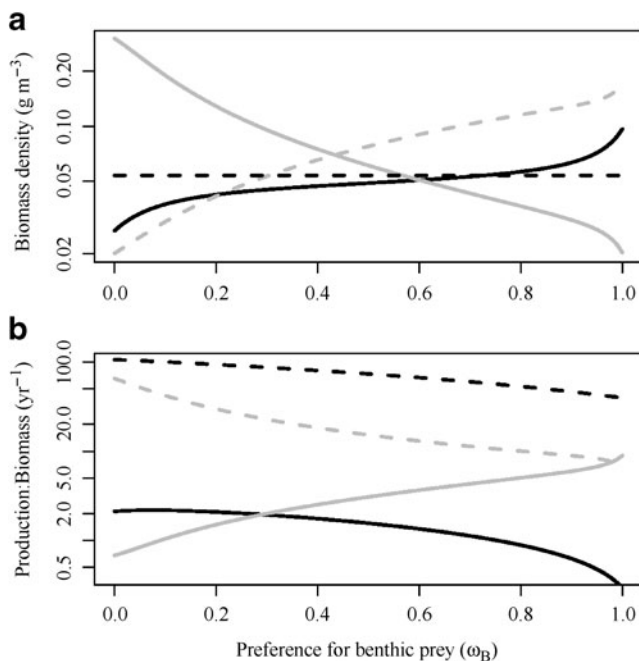
Fig. 2 Biomass and production/biomass of a coupled benthic–pelagic system in a shelf-sea ($S=0.5$). Predators can have a range of preference towards benthic prey, from $\omega_B=0$ (feeding only in pelagic zone) to $\omega_B=1$ (feeding only in benthic zone). **a** Total biomass densities (g m^{-3}) at steady-state for each component of the model: plankton (*black dashed*), detritus (*grey dashed*), pelagic predators (*black solid*) and benthic detritivores (*grey solid*). **b** Corresponding P/B ratios (per year) of each component

the solid lines in Fig. 3). Firstly, when predators fed solely within the pelagic zone, on primary producers and on smaller predators ($\omega_B=0$), the return to steady state was slowest. Secondly, as ω_B increased from zero, pelagic predators fed increasingly on prey in the benthic size spectrum, the turnover rate increased, and the rate of return to steady-state became faster ($-\lambda_{max}$ more positive), reaching a maximum at $\omega_B\sim0.15$. Beyond $\omega_B\sim0.15$, at intermediate values, the rate of return to steady-state gradually decreased, coinciding with the declining total throughput of biomass and turnover rate of the community. Thirdly, at high levels of benthic coupling, $\omega_B>0.8$, where predators fed much more on prey in the benthic spectrum than their own spectrum, the return to steady-state became fast again, while the total throughput of biomass (Fig. 3b) and turnover rate (Fig. 3c) of the community both continued to decline.

The degree of detrital coupling also affected resilience as measured by $-\lambda_{max}$ (comparison of upper and lower dashed lines relative to the solid lines in Fig. 3). Across the range of predator coupling from $\omega_B=0$ to 0.7, lowering the fraction of sinking detritus to $S=0.25$ (black dashed lines) resulted in slower return speeds following small perturbations and increasing the level of sinking detritus to $S=1$ corresponded to higher resilience, higher energy throughput but lower turnover rates (Fig. 3). When predators coupled

the benthic community more strongly than $\omega_B=0.7$, the pattern reversed and lower levels of S resulted in higher turnover rates and higher resilience. At the other extreme, when predators fed only on pelagic prey ($\omega_B=0$) most of the energy was in the pelagic pathway and altering S had no effect on return rate even though total throughputs, and turnover rates were affected.

The sensitivity of the local stability results to realistic changes in other parameters was also investigated. Increasing the intercept of the primary producer spectrum resulted in a similar pattern as that described for detrital input (Fig. S1). Changing the mean and standard deviation of the preferred predator–prey mass ratio function had large effects on resilience in spite of having very little effect on total turnover rate (Fig. S2). Wider prey size-selection resulted in faster returns to equilibrium as did smaller mean preferred predator–prey mass ratios (i.e. preference for relatively larger prey). Assuming a type II functional response resulted in only marginally different results and did not affect the above findings (see Electronic supplementary material text).

Response to large perturbations

The effects of large bottom-up and top-down perturbations were tested in systems in which predator coupling between the pelagic and benthic zones (ω_B) could be varied, using the scenario of a shelf-sea ($S=0.5$). As with the small perturbations tested above, these large perturbations were always followed by a return to steady-state.

Following the bottom-up primary producer perturbation (30-day primary producer pulse), the total biomass density of predators, detritivores and detritus sharply decreased towards steady-state (Fig. 4a). Resilience as measured by $1/T_R$ was highest when predators had weak to intermediate preference towards benthic prey ($\omega_B=0.2$–0.3; Fig. 4b). When the bottom-up pulse was propagated in the detritus, resilience was highest when predators did not feed in the benthic zone at all ($\omega_B=0$, Fig. 4c, d). Following the top-down pulse caused by 'harvesting' the density of pelagic predators, total biomass increased towards steady-state for all levels of predator coupling up to $\omega_B=0.9$. For $\omega_B=0.9$ and $\omega_B=1.0$, the biomass trajectories continued to decline after the pulse; but the declines ceased and then reversed direction after a time lag (Fig. 4e, f). The overall return rate was fastest when predators fed exclusively on benthic prey. Following large top-down perturbations, the nonlinear pattern between predator preference for benthic prey and return rate mirrored the pattern of $-\lambda_{max}$ obtained from local stability analysis (comparison of Fig. 4f with Fig. 3d). All size spectra returned to their respective equilibrium states by ~55 years and were therefore resilient to top-down perturbations in the long-term.

Differences in how the system responds to each type of perturbation can be explained by examining the response of

Fig. 3 System-level properties as a function of predator preference for benthic prey ω_B (X-axis) and at different levels of detrital coupling S: *black dashed*=0.25 (low), *solid line*= 0.5 (medium), *grey dashed lines*=1 (high). **a** Total biomass density (g m^{-3}) **b** Total biomass throughput (g m^{-3} year^{-1}). **d** Local resilience of the steady-state measured as $-\lambda_{max}$
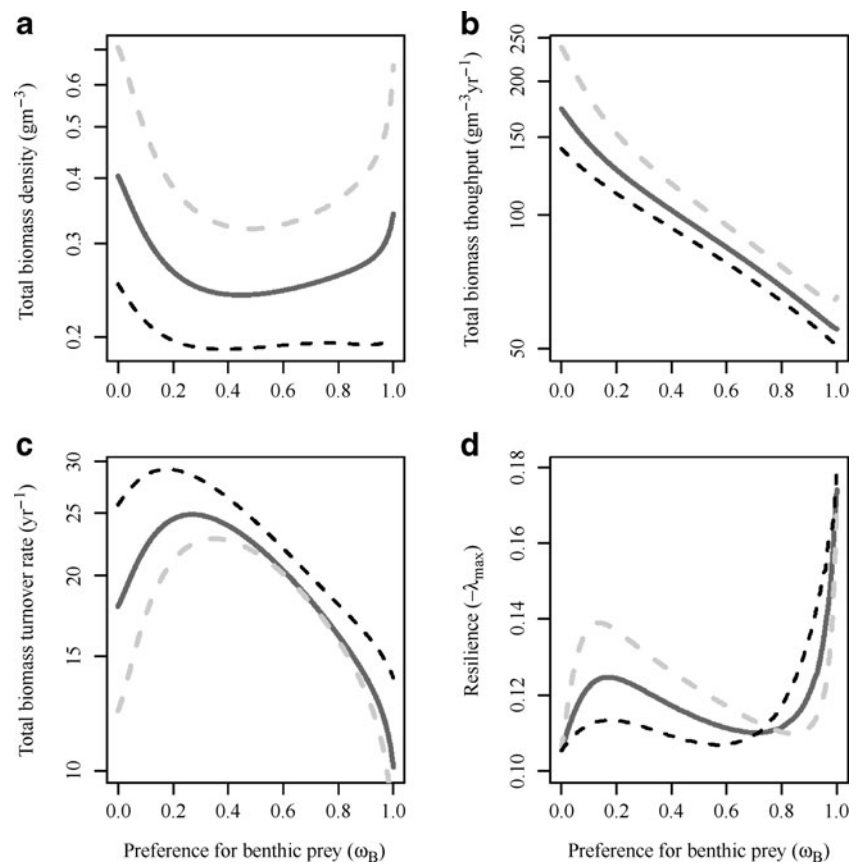

each component to the perturbations (Figs. S3, S4, and S5). For the primary producer perturbation (Fig. S3), return rate increased with increasing preference for benthic prey ω_B for predators and benthic detritivores but decreased with increasing preference for benthic prey ω_B for detritus. The combination of these two patterns leads to the overall hump-shaped response in Fig. 4b. With the predator harvesting pulse (Fig. S4) and detritus pulse (S5), return rate decreased with increasing preference for benthic prey for predators and detritus, but increased for benthic detritivores. The overall nonlinearity of the relationship between $1/T_R$ and predator coupling appear to be caused by the combined responses of each component of the ecosystem to the different types of perturbations.

Discussion

A striking feature of our pelagic–benthic ecosystems was that they always returned to steady-state when small or large perturbations were imposed. This stands in contrast to traditional, unstructured, food-web models in which local or global stability is often hard to achieve (May 1972) and in which the special properties needed to achieve stability have become the subject of much research. Non-random trophic interactions such as weak links, heterogeneous

energy pathways and realistic predator–prey mass ratios have been shown to promote stability in complex food webs (de Ruiter et al. 1995; McCann et al. 1998; Rooney et al. 2006; Brose et al. 2006). The size spectrum approach inherently allows for many weak links because predators may select prey over a wide range of sizes (O'Gorman and Emmerson 2009). The assumption of a fixed plankton spectrum will also tend to promote stability but does not ensure a steady-state attractor because a non-equilibrium, unstable, travelling-wave is known to be a possible attractor when a single pelagic size spectrum is supported by a fixed plankton spectrum (Law et al. 2009). Although coupling distinct energy pathways altered the relative stability of our pelagic–benthic ecosystems, the ability of individuals to change trophic positions throughout their lifetimes and feed across an increasingly wider range of prey sizes throughout their lifetimes may be an important mechanism governing the overall stability of food webs (Takimoto et al. 2003; Armstrong 1999).

The degree of pelagic–benthic coupling affected the resilience of the modelled ecosystems to small and large perturbations. Our local stability analyses suggest that resilience ($-\lambda_{max}$) varied nonlinearly with the degree of both predator and detrital coupling. The food-web configurations that returned fastest to steady-state came from predators (1) feeding entirely in the slow benthic zone or
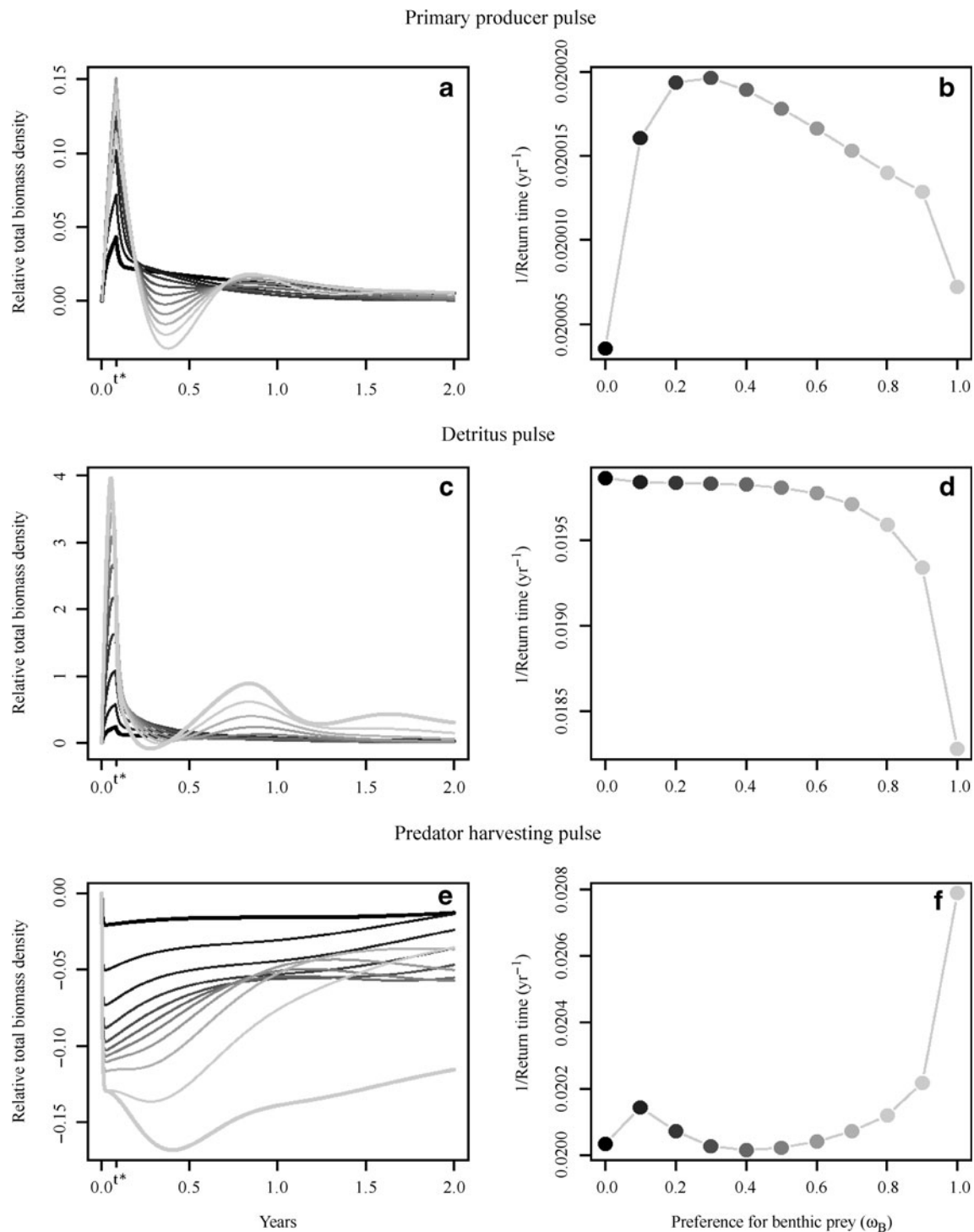
Fig. 4 Large perturbations: **a**, **b** Primary producer pulse, **c**, **d** Detritus pulse and **e**, **f** predator harvesting pulse. Each row from *left* to *right* shows: total biomass trajectories over time and corresponding resilience as measured by the reciprocal of return time $1/T_R$ for each level of predator preference for benthic prey ω_B. In all plots, the *black* *line* corresponds to predators feeding only within the pelagic community (no coupling, $\omega_B=0$). The *grey lines* show varying the strengths of coupling towards the benthic pathway (the *lightest line* corresponds to predators only feeding on benthic prey, $\omega_B=1$)

(2) feeding across the two energy pathways, with most food coming from the fast pathway. The latter is consistent with previous findings that weak (Rooney et al. 2006) to intermediate (Post et al. 2000) levels of predator coupling can be stabilising, although for much simpler and less structured food webs than considered here. In our analysis, the pelagic plankton-based pathway was inherently the faster pathway, also in keeping with Rooney et al. (2006).

However, we found a still faster return to equilibrium when pelagic predators fed predominantly in the slow detritus pathway, even though this feeding strategy truncated the size structure of both communities (Fig. 1d). Increased detrital coupling, characteristic of shallower and mixed waters, also led to higher local resilience following small perturbations across most of the range of predator coupling. However, this pattern reversed when predators fed exclusively on benthic prey and lower detrital input corresponded with higher resilience. Evaluation of the return to steady-state following large perturbations also revealed nonlinear relationships between the degree of predator coupling and resilience (where resilience is taken to be the inverse of return time T_R measured over the lifetime of the perturbation). The precise relationship depended on the type of perturbation and the component of the ecosystem most affected.

Resilience has long been hypothesised to be positively related to the turnover rate of a limiting nutrient (DeAngelis 1980) and negatively related to food chain length (Pimm and Lawton 1977, but see Sterner et al. 1997; Walters and Post 2008). The distribution of the interaction strengths or presence of many weak links (McCann et al. 1998) and presence of shorter feedback loops have also been put forth as alternative explanations for stability and food-web resilience (Neutel et al. 2002, 2007). However, the underlying structure of the food web and presence of smaller stabilising modules may contribute the most by providing a 'stability backbone' with other factors 'fine-tuning' how quickly food webs recover from perturbations (Allesina and Pascual 2008).

It would seem that the combination of several factors gives rise to the nonlinear patterns in resilience reported here. First, the extreme values of predator preference for benthic prey ($\omega_B=0$ and $\omega_B=1$) and the intermediate values in between give rise to three substantially different food-web structures (Fig. 5). When there is no or little benthic feeding, resilience was positively related to turnover rate. At intermediate values of ω_B between 0.2–0.6 (which are the most realistic values for shelf-seas) resilience declined with declining total system throughput and turnover rate. At extreme levels of benthivory ($\omega_B>0.7$), resilience increased despite declining turnover rate and throughput. In addition, the size spectra became truncated. Since trophic level is directly related to predator body size in our model, truncated size-structure indicates shorter maximum food length, which could also support stability. Our results suggest there is more to achieving stability of size-structured food webs than coupling strong and weak energy pathways (McCann et al. 1998; Rooney et al. 2006). Much depends on details of the feedbacks operating within the energy pathways, on the behaviour of organisms in the ecosystem and on external constraints imposed on the ecosystem by the physical environment (i.e. depth, mixing etc.) which may affect the structure of the food web.
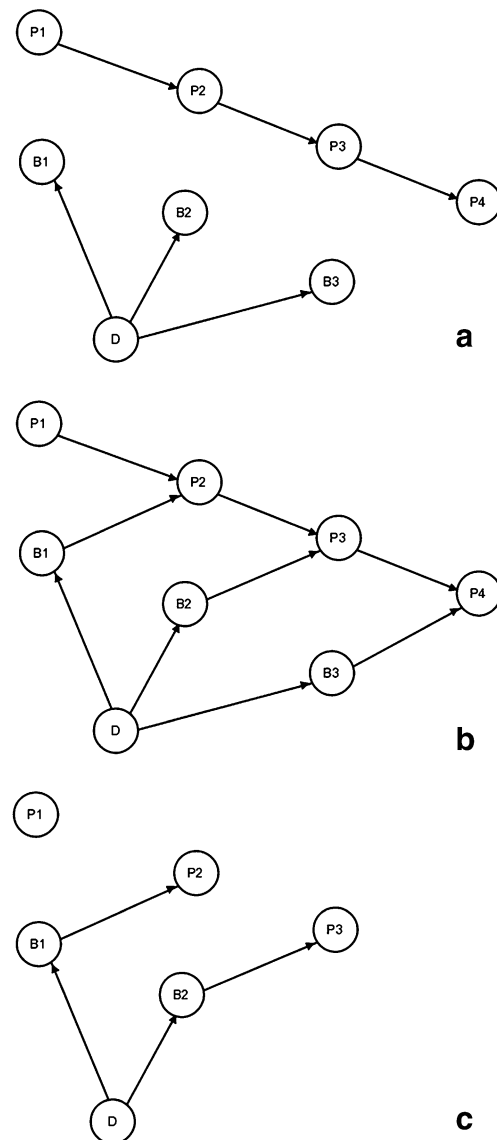
Fig. 5 A simplified caricature of the main differences in the types of interactions that may occur in parts of a size-based food web for: **a** pelagic feeding only, **b** feeding on both benthic and pelagic prey, **c** feeding only on benthic prey. *Arrows* indicate a feeding link. *D* represents detritus and *P1* the primary producers. *P2*, *P3*, and *P4* are successively larger size classes of predators and *B1*, *B2*, *B3*, and *B4* are successively larger size classes of benthic detritivores, both arranged in order of declining abundance. In **c**, the maximum sizes are *P3* and *B3* resulting in a shorter food chain

The fast return to steady-state that is associated with exclusive links to the benthic pathway ($\omega_B=1$) may be an unlikely response in most aquatic communities, with the exception of very shallow or coastal areas. In marine ecosystems, most fish are opportunistic predators that feed on any suitable prey available to them, typically 100–1,000 times smaller by mass (Barnes et al. 2008). Larger predators can feed in a range of habitats and diets of many predatory fish are also known to consist of fish and invertebrates from both pelagic and benthic habitats (Pinnegar et al. 2003).

Benthic–pelagic coupling is also an important feature of freshwater lake communities where field studies have shown that steeper benthic size spectrum slopes arise from higher levels of fish predation, consistent with the results shown here (Blumenshine et al. 2000). It is difficult, however, to envisage an entire pelagic fish community feeding exclusively on non-pelagic prey, and even fish species that spend a great deal of the lives feeding in the benthic zone do not feed entirely on benthic detritivores (Pinnegar et al. 2003; Greenstreet et al. 1997). Although our globally set preference parameter (ω_B) was a simplistic and crude representation of reality, it allowed us to investigate a wide range of predator coupling scenarios. This could be improved by considering how preference is constrained by the relative availability of the different prey resources, either globally (e.g. Pitchford and Brindley 1999; Edwards et al. 2007) or perhaps more mechanistically by combining the model presented here with an optimal preference model that takes into account prey profitability and size (e.g. Petchey et al. 2008).

To establish the qualitative states of size spectra that exist under a range of scenarios, we considered some simple cases of detritus coupling where the sinking dead and faecal particulate matter produced in the pelagic community enters the benthic detritus pool entirely or fractionally, and the levels of this input affected how quickly the system responded to perturbations. These forms of coupling conceptually correspond to a range of shallow or well-mixed areas and the very deep sea. In reality, detritus coupling in most systems would fall somewhere in between the extreme values and vary in space and time. The model predicts steeper slopes of benthic size spectra when the flux of detrital food is lower. These findings are supported by observations of benthic size spectra slopes becoming steeper with increasing depth in Antarctic waters (Saiz-Salinas and Ramos 1999). In many marine systems, the flux of pelagic material that reaches deeper areas has been estimated from sediment traps and relates strongly with depth (Martin et al. 1987). The size distribution of plankton, mass of faecal pellets, association of biominerals or 'ballast' with sinking material and levels of vertical and horizontal mixing and water column circulation can also affect sinking rates (Buesseler et al. 2007). For example, when Buesseler et al. (2007) compared the fluxes of particulate organic matter (POC) at two oceanic sites with similar depths but different biophysical characteristics they found that only 20% of the POC flux reached 500 m in a warm, low macronutrient oligotrophic subtropical gyre compared with the 46–55% in a highly productive subarctic gyre. This implies that the resilience of marine food webs can vary significantly in different regions and ecosystems, thus influencing the relative response to biomass removal and environmental variation and change.

Our quantitative analyses focussed on the shelf-sea scenario where predator coupling is likely to be strongest.

We also tested the effects of deeper and shallower sea scenarios where 25% and 100% of the detritus fallout reaches the sea floor (Fig. 3). Return to steady-state was slowest following small perturbations in the deeper scenario. This suggests that, all else being equal, systems characterised by low detritus fallout (and therefore most deep water communities) are likely to be less stable. Since we did not model plankton dynamics, our approach did not account for the remineralisation of sinking material (via the microbial loop and evolution of detritus), which is an important feedback to primary producers in real systems. Inclusion of primary producer dynamics and remineralisation will most likely have an effect on the way the system responds to perturbations, and we do not know how this will affect our present results. Future work on linking physical processes, nutrient and plankton dynamics to the dynamics of fish and macrobenthic size-structured communities may help to elucidate whether or not such processes are compensatory and improve understanding of ecosystem resilience. A size spectrum framework linking these processes may provide a powerful yet simple approach to understanding ecosystem dynamics across a wide range of aquatic environments and for explicit evaluation of human impacts.

In conclusion, the strength of benthic–pelagic coupling (via predation and detrital input) affects the resilience of size-structured food webs to perturbations. We suggest that communities with very little benthic–pelagic coupling, such as those found in ocean gyres, are potentially more vulnerable to human impacts than strongly coupled systems. Overall, it is too simplistic to conclude that the presence of weak (asymmetric) links is solely responsible for stabilising the ecosystem. The real effects of coupling are much more intricate and point to the need for more knowledge of the feedback mechanisms between the pelagic and benthic communities. Managers should be aware that human impacts leading to reduced benthic–pelagic coupling (e.g. benthic oxygen minima) could affect the vulnerability of ecosystems and their component populations to additional impacts. Significant further work would be needed to establish precautionary management measures that take this into account.

References

Allen KR (1971) Relation between production and biomass. J Fish Res Board Can 28:1573–1581

Allesina S, Pascual M (2008) Network structure, predator-prey motifs, and stability in large food webs. Theor Ecol 1(1):55–64

Armstrong RA (1999) Stable model structures for representing biogeochemical diversity and size spectra in plankton communities. J Plankton Res 21(3):445–464

Baird ME, Suthers IM (2007) A size-resolved pelagic ecosystem model. Ecol Model 203(3):185–203

Barnes C, Bethea DM, Brodeur RD, Spitz J, Ridoux V, Pusineri C, Chase BC, Hunsicker ME, Juanes F, Kellermann A, Lancaster JE, Menard F, Bard FX, Munk P, Pinnegar JK, Scharf FS, Rountree RA, Stergiou KI, Sassa S, Sabates A, Jennings S (2008) Predator and prey body sizes in marine food webs. Ecology 89:881

Belgrano A, Scharler UM, Dunne J, Ulanowicz RE (2005) Aquatic food webs: an ecosystem approach. Oxford University Press, Oxford

Benoît E, Rochet M-J (2004) A continuous model of biomass size spectra governed by predation and the effects of fishing on them. J Theor Biol 226:9–21

Bianchi G, Gislason H, Graham K, Hill L, Jin X, Koranteng K, Manickchand-Heileman S, Paya I, Sainsbury K, Sanchez F, Zwanenburg K (2000) Impact of fishing on size composition and diversity of demersal fish communities. ICES J Mar Sci 57:558–571

Blanchard JL, Jennings S, Law R, Castle MD, McCloghrie P, Rochet M-J, Benoit E (2009) How does abundance scale with body size in coupled size-structured food webs? J Anim Ecol 78:270–280

Blumenshine SC, Lodge DM, Hodgson JR (2000) Gradient of fish predation alters body size distributions of lake benthos. Ecology 81:374–386

Boudreau PR, Dickie LM (1992) Biomass spectra of aquatic ecosystems in relation to fisheries yield. Can J Fish Aquat Sci 49:1528–1538

Brose U, Williams RJ, Martinez ND (2006) Allometric scaling enhances stability in complex food webs. Ecol Lett 9:1228–1236

Buesseler KO, Lamborg CH, Boyd PW, Lam PJ, Trull TW, Bidigare RR, Bishop JKB, Casciotti KL, Dehairs F, Elskens M, Honda M, Karl DM, Siegel DA, Silver MW, Steinberg DK, Valdes J, Van Mooy B, Wilson S (2007) Revisiting carbon flux through the ocean's twilight zone. Science 316:567–570

Carpenter SR, Kraft CE, Wright R, He X, Soranno PA, Hodgson JR (1992) Resilience and resistance of a lake phosphorus cycle before and after a food web manipulation. Am Nat 140:781–798

Cottingham KL, Carpenter SR (1994) Predictive indices of ecosystem resilience in models of north temperate lakes. Ecology 75:2127–2138

de Ruiter PC, Neutel AM, Moore JC (1995) Energetics, patterns of interaction strengths, and stability in real ecosystems. Science 269:1257–1260

DeAngelis DL (1980) Energy flow, nutrient cycling, and ecosystem resilience. Ecology 61:764–771

DeAngelis DL, Bartell SM, Brenkert AL (1989) Effects of nutrient recycling and food chain length on resilience. Am Nat 134:778–805

Duplisea DE (1998) Benthic organism biomass size spectra in the Baltic Sea in relation to the sediment environment. Limnol Oceanogr 45(3):558–568

Edwards HJ, Dytham C, Pitchford JW, Righton D (2007) Prey selection, vertical migrations and the impacts of harvesting upon the population dynamics of a predator–prey system. Bull Math Biol 68:1827–1846

Greenstreet SPR, Bryant AD, Broekhuizen N, Hall SJ, Heath MR (1997) Seasonal variation in the consumption of food by fish in the North Sea and implications for food web dynamics. ICES J Mar Sci 54:243–266

Gunderson DR (1997) Trade-off between reproductive effort and adult survival in oviparous and viviparous fishes. Can J Fish Aquat Sci 54(5):990–998

Jennings S, Pinnegar JK, Polunin NVC, Boon T (2001) Weak cross-species relationships between body size and trophic level belie powerful size-based trophic structuring in fish communities. J Anim Ecol 70:934–944

Kerr SR, Dickie LM (2001) The biomass spectrum: a predator–prey theory of aquatic production. Columbia University Press, New York

Law R, Plank MJ, James A, Blanchard JL (2009) Size spectra dynamics from stochastic predation and growth of individuals. Ecology 90(3):802–811

Martin JH, Knauer GA, Karl DM, Broenkow WW (1987) VERTEX: carbon cycling in the northeast Pacific. Deep-Sea Res 34:267–285

Maury O, Faugeras B, Shin Y-J, Poggiale JC, Ari TB, Marsac F (2007) Modeling environmental effects on the size-structured energy flow through marine ecosystems. Part 1: the model. Progr Oceanogr 74(4):479–499

Maxwell TAD, Jennings S (2006) Predicting abundance-body size relationships in functional and taxonomic subsets of food webs. Oecologia 150:282–290

May RM (1972) Will a large complex system be stable? Nature 238:413–414

McCann KS, Hastings AG, Huxel R (1998) Weak trophic interactions and the balance of nature. Nature 395:794–798

McCann KS, Rasmussen JB, Umbanhowar J (2005) The dynamics of spatially coupled food webs. Ecol Lett 8:513–523

Moloney CL, Field JG (1991) The size-based dynamics of plankton food webs. I. A simulation model of carbon and nitrogen flows. J Plankton Res 13:1003–1038

Moore JC, Berlow E, Coleman DC, de Ruiter PC, Dong O, Hastings A, Johnston NC, McCann KS, Melville K, Morin PJ, Nadelhoffer K, Rosemond AD, Post DM, Sabo JL, Scow KS, Vanni MJ, Wall DH (2004) Detritus, trophic dynamics and biodiversity. Ecol Lett 7:584–600

Neubert MG, Caswell H (1997) Alternatives to resilience for measuring the responses of ecological systems to perturbations. Ecology 78:653–665

Neutel A-M, Heesterbeek JAP, De Ruiter PC (2002) Stability in real food webs: weak links in long loops. Science 296:1120–1123

Neutel AM, Heesterbeek JAP, van de Koppel J, Hoenderboom G, Vos A, Kaldeway C, Berendse F, de Ruiter PC (2007) Reconciling complexity with stability in naturally assembling food webs. Nature 449:599–602

Odum EP (1969) The strategy of ecosystem development. Science 164:262–279

O'Gorman EJ, Emmerson MC (2009) Perturbations to trophic interactions and the stability of complex food webs. PNAS 106:13393–13398

Petchey O, Beckerman AP, Riede J, Warren PH (2008) Size, foraging and food web structure. PNAS 105(11):4191–4196

Pimm SL, Lawton JH (1977) Number of trophic levels in ecological communities. Nature 268:329–331

Pinnegar JK, Trenkel VM, Tidd AN, Dawson WA, Du Buit MH (2003) Does diet in Celtic Sea fishes reflect prey availability? J Fish Biol 63(Supplement A):197–212

Pitchford JW, Brindley J (1999) Iron limitation, grazing pressure and oceanic high nutrient-low chlorophyll (HNLC) regions. J Plankton Res 21(3):525–547

Post DM, Conners ME, Goldberg DS (2000) Prey preference by a top predator and the stability of linked food chains. Ecology 81:8–14

Press WH, Teukolsky SA, Vetterling WT, Flannery BP (1992) Numerical recipes—the art of scientific computing, 2nd edn. Cambridge University Press, New York

Rooney N, McCann K, Gellner G, Moore JC (2006) Structural asymmetry and the stability of diverse food webs. Nature 442:266–269

Saiz-Salinas JI, Ramos A (1999) Biomass size-spectra of macro-benthic assemblages along water depth in Antarctica. Mar Ecol Prog Ser 178:221–227

Silvert W, Platt T (1980) Dynamic energy flow model of the particle size distribution in pelagic ecosystems. In: Kerfoot W (ed) Evolution and ecology of zooplankton communities. University Press of New England, Illanover, pp 754–763

Sterner RW, Bajpai A, Adams T (1997) The enigma of food chain length: absence of theoretical evidence for dynamic constraints. Ecology 78:2258–2262

Stock CA, Powell TM, Levin SA (2008) Bottom-up and top-down forcing in a simple size-structured plankton dynamics model. J Mar Syst 74:134–152

Takimoto G (2003) Adaptive plasticity in ontogenetic niche shifts stabilizes consumer-resource dynamics. Am Nat 162:93–109

Van der Veer HW, Cardoso JFMF, Van der Meer J (2006) Estimation of DEB parameters for various North Atlantic bivalve species. J Sea Res 56:107–124

Van der Zanden MJ, Vadeboncoeur Y (2002) Fishes as integrators of benthic and pelagic food chains in lakes. Ecology 83:2152–2161

Walters AW, Post DM (2008) An experimental disturbance alters fish size structure but not food chain length in streams. Ecology 89 (12):3261–3267. doi:10.1890/08-0273.1

Zhou M, Huntley M (1997) Population dynamics theory of plankton based on biomass spectra. Mar Ecol Prog Ser 159:61–73