

# Individual-Based Food Webs: Species Identity, Body Size and Sampling Effects

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## SUMMARY

The study of food webs has been a central theme within ecology for decades, and their structure and dynamics have been used to assess a range of key properties of communities (e.g. complexity–stability relationships) and ecosystems (e.g. fluxes of energy and nutrients). However, many food web parameters are sensitive to sampling effort, which is rarely considered, and further, most studies have used either species- or size-averaged data for both nodes and links, rather than individual-based data, which is the level of organisation at which trophic interactions occur. This practice of aggregating data hides a considerable amount of biologically meaningful variation and could, together with potential sampling effects, create methodological artefacts. New individual-based approaches could improve our understanding of, and ability to predict, food web structure and dynamics, particularly if they are derived from simple metabolic and foraging constraints. We explored the effect of species-averaging in four highly-resolved individual-based aquatic food webs (Broadstone Stream, the Afon Hirnant, Tadnoll Brook and the Celtic Sea) and found that it obscured structural regularities resulting from intraspecific size variation. The individual-based approach provided clearer insights into seasonal and ontogenetic shifts, highlighting the importance of the temporal component of size-structuring in ecological networks. An extension of the Allometric Diet Breadth Model predicted the structure of the empirical food webs almost twice as accurately as the equivalent species-based webs, with the best-fitting model predicting 83% of the links correctly in the Broadstone Stream size-based web, and the few mismatches between the model and data were explained largely by sampling effects. Our results highlight the need for theoretical explanations to correspond closely with methods of data collection and aggregation, which is the exception rather than the rule at present. We suggest how this situation can be improved by including individual-level data and more explicit information on sampling effort when constructing food webs in future studies.

## I. INTRODUCTION

### A. Recent Advances in Food Web Data and Theory

Trophic interactions are key determinants of population abundance and dynamics, the structure and persistence of communities, and the rate and sustainability of ecosystem processes (Ings *et al.*, 2009; McCann, 2000; Neutel *et al.*, 2002; Otto *et al.*, 2007; Olesen *et al.*, 2010; Petchey *et al.*, 2004; Reiss *et al.*, 2009; Woodward *et al.*, 2010). As such, the study of food webs, which

can include tens to hundreds of species and thousands of feeding links, has long been a key theme in ecology, especially in recent decades, as highlighted by the exponential increase in publications in this field since the 1970s (Ings *et al.*, 2009). A mainstay of this research has been the collection, compilation, and analysis of food webs from natural ecosystems, although the quality and resolution of these data have not always been appropriate for the tasks to which they have been put (Bersier and Sugihara, 1999; Cohen *et al.*, 1993; Hall and Raffaelli, 1993; Ings *et al.*, 2009; Paine, 1988, 1992; Polis, 1998).

Early food web research highlighted the importance of taxonomic resolution, with seemingly marked changes in network structure being observed depending on whether species, genera, families, or even coarser taxonomic entities were used as the interacting entities (Goldwasser and Roughgarden, 1997; Martinez, 1991). Serious concerns were also raised about systematic biases in taxonomic resolution being confounded with trophic position: large top predators were typically described to species, whereas smaller organisms at the lower trophic levels were often either aggregated far more coarsely (e.g. 'algae') or simply ignored altogether, as pointed out by Cohen *et al.* (1993), Hall and Raffaelli, 1993, and Schmid-Araya *et al.* (2002a,b). In addition to this patchy information on the identity of the nodes and links, the amount of sampling effort used to detect them was, and in many cases still is, highly variable both within and among webs. Some food webs have been constructed from inferential data on interactions from the literature, expert knowledge, or theoretical predictions (e.g. Dunne *et al.*, 2008; Martinez, 1991) and a few have been based solely on direct observation (e.g. Figueroa, 2007; Schmid-Araya *et al.*, 2002a,b; Woodward *et al.*, 2005a), whilst probably most have used some combination of the two (e.g. Layer *et al.*, 2010a,b; Woodward *et al.*, 2008). The former case can risk including links that are not necessarily realised in a particular local food web (although they may be present in other systems), whereas the exclusive reliance on directly observed data can be problematic if no information is provided on the sampling effort used to detect nodes or links, as this can have a huge impact on many web parameters (Martinez *et al.*, 1999).

The recognition of the shortcomings of the early datasets helped to trigger the construction of a new generation of food webs that are more completely sampled and based on more uniform taxonomic data than was the case for many of their precursors (e.g. Banašek-Richter *et al.*, 2009; Benke and Wallace, 1997; Closs and Lake, 1994; Cohen *et al.*, 2003, 2005; de Ruiter *et al.*, 1995; Lafferty *et al.*, 2006; Layer *et al.*, 2010a,b; Martinez, 1992; O'Gorman and Emmerson, 2009; Riede *et al.*, 2010; Schmid-Araya *et al.*, 2002a,b; Tylanakis *et al.*, 2007; van Veen *et al.*, 2008; Warren, 1989; Woodward *et al.*, 2005a,b). These new webs have provided clearer pictures of the structure of trophic networks and have largely superseded the earlier datasets used in the pioneering work carried out in the 1970s and 1980s (e.g. Cohen, 1978; Pimm, 1982).

Many of the data that emerged from about the early 1990s onwards revealed that networks were far more complex than had been previously thought, challenging the theoretical suggestion (May, 1972, 1973; Pimm, 1980, 1982) that complexity was destabilising and should, therefore, be rare. In parallel with the improvements to the empirical data over the last two decades, a range of new dynamical models began to unearth some of the posited 'devious strategies' (May, 1972) by which complex food webs might be stabilised. These included the prevalence of weak versus strong links (McCann, 2000; McCann, *et al.*, 1998), the role of feeding loops (Neutel *et al.*, 2002; Neutel *et al.*, 2007), and the damping of potentially destabilising 'fast' food chains with 'slower' pathways (Rooney *et al.*, 2006). Many of these dynamical models have stressed the importance of body mass as a determinant of interaction strength, and hence stability (e.g. Berlow *et al.*, 2009; Emmerson *et al.*, 2005; Yodzis and Innes, 1992). In addition, a new suite of structural models, building on the initial work of Cohen and colleagues (e.g. Cohen and Newman, 1985; Cohen *et al.*, 1990) have revealed how complex networks might be based on simple rules related to morphological, metabolic, or foraging constraints, many of which are closely correlated with body size (e.g. Beckerman *et al.*, 2006; Cattin *et al.*, 2004; Petchey *et al.*, 2008; Warren, 1996; Williams and Martinez, 2000).

From these multiple lines of evidence, it has become increasingly clear that the body size of species often exerts a powerful influence on ingestion rates and the dynamical and structural attributes of many food webs (Ings *et al.*, 2009; Montoya *et al.*, 2006, 2009; Perkins *et al.*, 2010; Reiss *et al.*, 2010; Reuman *et al.*, 2009a,b; Woodward and Hildrew, 2002a; Woodward *et al.*, 2005a). A key, but largely overlooked, point of relevance here is that trophic interactions occur between individual organisms, not species *per se* (Stouffer, 2010; Woodward and Warren, 2007). The functional constraints on feeding imposed by size operate at the individual level, and many of the sampling biases in webs are related to the likelihood of observations being made of feeding events. However, the conventional approach to documenting food webs, which has focused primarily on taxonomic entities (species, etc.), may conceal much of this information on size structure, particularly where intraspecific size variation may equal or even exceed that between species averages, and this point has also been largely ignored in both structural and dynamical models (Woodward, 2009; Woodward and Warren, 2007). Although body size is now measured routinely in many food web studies (e.g. Cohen *et al.*, 2003), individual-level variation or the yield–effort data needed to assess potential sampling effects are still rarely considered (but see Goldwasser and Roughgarden, 1997; Ings *et al.*, 2009; Martinez *et al.*, 1999; Woodward and Hildrew, 2001).

We sought to address whether, given that individuals are the relevant interacting entities, constructing networks from this level of organisation could improve upon the traditional process of aggregating via species or size classes

and whether considering both size- and species-based perspectives together provide deeper insights than provided by either alone. We addressed these questions using a set of four unusually highly resolved food webs that include information on sampling effort and directly observed data on species identity and the body sizes of the individuals involved in actual feeding interactions.

## **B. Species Identity and Body Size as Determinants of Food Web Structure**

Body size has often been invoked, either implicitly or explicitly, as a potentially key driver behind a range of both dynamical and static food web models. The latter include a group of structural models based on morphological, metabolic, or foraging constraints, and include the cascade (Cohen and Newman, 1985), niche-based (Warren, 1996; Williams and Martinez, 2000), hierarchical (Cattin *et al.*, 2004), and allometric diet breadth models (ADBM) (Petchey *et al.*, 2008). All the species-based approaches described above effectively deal with ball-and-stick representations of food webs as networks of taxonomic entities (nodes) connected to one another by their trophic interactions (links), following in the footsteps of the first such diagram drawn 130 years ago by Camerano (1880).

Much of the research effort devoted to improving taxonomic resolution and completeness of food webs reflects the field's historical roots in population and community ecology (e.g. *sensu* Elton, 1927; Hutchinson, 1959; MacArthur, 1955), where species identity is often seen as being key (Ings *et al.*, 2009; Raffaelli, 2007). Growing recognition of the role of size in food webs has given rise to more concerted attempts to enrich binary networks of nodes and links by including body size information, whilst retaining the traditional species-based classification. This enrichment has typically involved assigning an average body size to each of the taxonomic entities in a food web; thus allometries describe variation among taxonomic entities. Such taxonomically constructed relationships are the most common types of allometries encountered within the context of community ecology (e.g. Brown *et al.*, 2004; Damuth, 1987; Peters, 1983).

Increasingly, traditional food web networks have been enriched by including data on species' average sizes and their abundance, to produce so-called trivariate food webs (*sensu* Cohen *et al.*, 2003). Here, mean abundance ( $N$ ) and body mass ( $M$ ) of each species population are plotted on a log-log scatterplot, with feeding links overlain between the interacting nodes (e.g. Cohen *et al.*, 2003; Jonsson *et al.*, 2005; Layer *et al.*, 2010a,b; McLaughlin *et al.*, 2010; O'Gorman and Emmerson, 2010; Woodward *et al.*, 2005a,b). The allometric  $MN$  scaling relationship across the food web as a whole can be remarkably consistent both over time and among systems (e.g. Layer *et al.*, 2010b;

Woodward *et al.*, 2005b), despite considerable species turnover, leading some to suggest that this might point to fundamental ecological constraints that are manifested at this whole-system level of organisation (O’Gorman and Emmerson, 2010). Within trivariate webs, the angles and distances between pairs of connected nodes can also be used to make inferences about the flux of energy and the strength of interactions between species populations, which can have important implications for the functioning and stability of the system as a whole (e.g. Cohen *et al.*, 2003; Emmerson *et al.*, 2005; Layer *et al.*, 2010a; Reuman and Cohen, 2005) and even if abundance data are missing, species-averaged predator–prey mass ratios may be used to infer *per capita* interaction strengths (e.g. Berlow *et al.*, 2009; Emmerson and Raffaelli, 2004). However, these structural and dynamical models effectively ignore the potentially critical variation that occurs within both nodes and links.

A very different approach to documenting trophic networks, body sizes, and abundances has developed in parallel with the species-based approaches described above. Instead of taxonomic entities (such as species), individuals are grouped into size classes (also known as size bins) irrespective of their taxonomy (Petchey and Belgrano, 2010): as such, these size-based approaches are free from the so-called ‘*curse of the Latin binomial*’ (Raffaelli, 2007). The resulting relationships between abundance and size (of a size class) have been termed as size spectra and individual-size distributions. Since they refer to scaling of abundance with body size, one could refer to these relationships as allometries, but care must be taken not to confuse these with ‘taxonomically constructed’ allometries (Reuman *et al.*, 2008; Yvon-Durocher *et al.*, 2008, 2010).

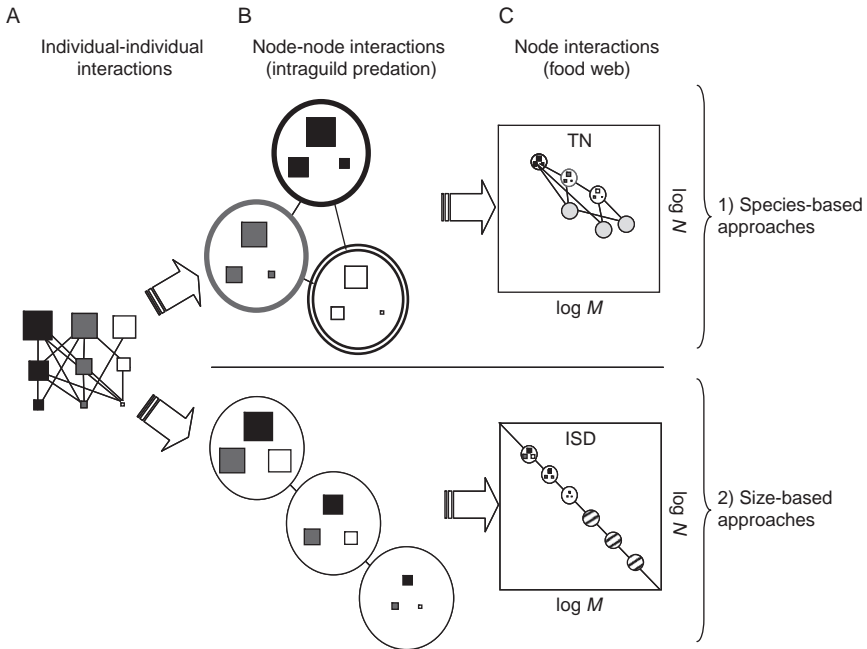
Size spectra have been used to characterise broad macroecological patterns in energy flux and biomass production for entire ecosystems, with some of the most ambitious studies including ‘particles’ that range in size from phytoplankton to whales (Kerr and Dickie, 2001). This approach offers a potentially powerful means of simplifying otherwise complex food webs into far more tractable, and hence predictable, forms. Because the slope of a size spectrum describes how quickly abundance declines with size, it can be used, for instance, to gauge the impact of size-selective harvesting of fish assemblages (Pope *et al.*, 1994) and to model the impacts of commercial exploitation on marine ecosystems (e.g. Jennings and Brander, 2010). Size spectra have been most widely used to characterise pelagic marine ecosystems in which gape-limited feeding and indeterminate growth over many orders of magnitude of body mass occur (e.g. for fishes). For instance, as an individual fish grows from a small larva into a large predator weighing tens of kilos (e.g. Atlantic cod), there may be such marked intraspecific ontogenetic shifts in its trophic ecology that the concept of treating each species as a single discrete node often makes little sense (e.g. Hardy, 1924). Consequently, size-based approaches can provide a comparatively straightforward and logistically

efficient alternative means of capturing many of the major biologically relevant characteristics within a food web, even in the absence of any information about the taxonomic identity of individuals.

### C. Identifying the Relevant Entities and Suitable Measures of Body Size

A critical question that has clouded studies of the size structure of food webs is: ‘the size of what?’ (Yvon-Durocher *et al.*, 2010). It is essential to define and measure the interacting entities at appropriate levels of organisation and it is important to bear in mind that the individuals that are interacting within a feeding link might be of very different sizes than the averages for their respective species populations. Although species-based approaches have provided invaluable insights into the size structure and dynamics of food webs (e.g. Cohen *et al.*, 2003; Reuman *et al.*, 2005) and macroecological patterns among systems (e.g. Woodward *et al.*, 2005b), they inevitably obscure potentially important individual-level information. Similarly, if the identities of the interacting species are unknown, potentially valuable information is also lost when employing solely size-based approaches. Consequently, individual-level data should not only provide a possible means of better characterising trophic interactions, but could also be used to examine food webs from both species-based and size-based perspectives simultaneously (Figure 1).

Very few food web studies have recorded data about interacting *individuals*, but those that have suggested individual- and species-averaged analyses of size structure can indeed provide very different insights (Ings *et al.*, 2009; Woodward and Warren, 2007). One exception is a recent study carried out in Broadstone Stream, in which several thousands of individuals were identified to species and measured in the environment and in the guts of predators (Woodward and Warren, 2007). When the standard approach of using species-averaged data was used to construct the food web, some predators appeared to feed on prey nearly 100 times larger than themselves (Woodward *et al.*, 2005a), but when exactly the same data were used to construct the food web from an individual-level perspective, predators did not consume prey larger than themselves (Woodward and Warren, 2007). This apparent paradox arose because large individuals of ‘small’ species fed on small individuals of ‘large’ species, particularly when generations overlapped. Clearly, the effects of aggregating up to the species level can have large and potentially misleading effects on our perception of the size structure of communities. The current shortage of information about the sizes of interacting individuals within food webs is undoubtedly related to the considerable time and effort required to collect such data, but in recent years several datasets based on



**Figure 1** Schematic of (1) species-based and (2) size-based approaches to the construction of food webs, highlighting how both are underpinned by interactions between individuals (depicted as squares, with the three colours each representing a different species). The use of such data therefore enables both perspectives to be viewed simultaneously, across multiple levels of organisation from (A) individual–individual interactions to (B) food web modules (e.g. intraguild predation) to (C) to the entire community as a trophic network (TN), size spectrum or individual-size distribution (ISD).

individual-level interactions have started to emerge (e.g. Barnes *et al.*, 2008; Woodward and Warren, 2007) and the current study is, to the best of our knowledge, the first formal analysis of such data from a range of systems.

#### D. Coupling Size- and Species-Based Approaches with Individual-Level Data

One of the principal objectives of our study was to assess how switching between taxonomic and size-based views alters the perceived structure of a food web. As well as calculating standard measures of food web structure, we estimated how well a theoretical model could predict the structure of species- versus size-averaged food webs constructed from individual-level data. The structural models we used to compare the two approaches were



developed from the ADBM of [Petchey \*et al.\* \(2008\)](#), which predicts the positioning of links within the feeding matrix using a set of rules based on foraging constraints. The ADBM was used as a relatively simple model of size effects on diet due to the authors' familiarity with it: comparing different types of size-based models of food webs was not the aim of the research presented in this chapter. Although the original incarnation of the ADBM successfully captured much of the variation in network structure from a range of species-averaged food webs, there was considerable variation in its predictive ability and only about 40% of links were predicted correctly for the Broadstone Stream web ([Petchey \*et al.\*, 2008](#), based on the data of [Woodward \*et al.\*, 2005a](#)). Some of this variability in explanatory power among food webs could be ascribed to variation in the types of trophic interactions (e.g. predatory and herbivorous interactions were predicted more accurately than pathogenic, host–parasitoid, or parasitic ones). It is also possible that mismatches might have arisen from sampling effects and/or species-averaging. In the former case, links that were predicted by the model but 'missing' from the empirical webs might simply reflect incomplete characterisation of consumer's diets, the extent of which can be assessed via yield–effort curves (e.g. [Woodward and Hildrew, 2001](#)). In the second case, species-averaging might create 'mirages' due to the crude treatment of body size as a single value for each species. For instance, the relatively poor match between the Broadstone Stream data and the ADBM seemed somewhat surprising, given the strong size-structuring of the web described elsewhere (e.g. [Woodward and Hildrew, 2002a](#); [Woodward \*et al.\*, 2005](#)), but in the [Petchey \*et al.\* \(2008\)](#) study no information was included on the variation in individual size within either the nodes or links.

We constructed and modelled food webs of predator–prey interactions, using both species-based and size-based approaches derived from individual-level data for four systems: the Broadstone Stream food web (e.g. [Hildrew, 2009](#); [Olesen \*et al.\*, 2010](#)), the Celtic Sea ([Blanchard \*et al.\*, 2005](#)), and two previously undescribed food webs: the Afon Hirnant stream in Wales and the Tadnoll Brook in southern England. For each food web, we collated information on the abundance of species and size classes in the environment and the diets of individuals using directly observed gut contents data, in which the individual body sizes of both consumers and resources were recorded.

We also explored potential sampling effects and how these might influence the attributes of the empirical food webs and the fit of the models to the data: e.g. were predicted links between rare predators and rare prey (as either species or size classes) most likely to be missing from the empirical webs due to undersampling? Finally, we focused on the Broadstone Stream food web as a detailed case study, by using the individual-level data to explore some of the supposed anomalies that are commonly observed in species-averaged food webs (e.g. cannibalistic and mutual predation loops) but which should,

according to theory, be rare, due to their perceived destabilising effects (e.g. May, 1973; Pimm, 1982; Tanabe and Namba, 2005; Vandermeer, 2006). This system was selected for more detailed study because predator–prey interactions within its species-averaged food web have been studied intensively for four decades (e.g. Hildrew, 2009; Hildrew and Townsend, 1982; Olesen *et al.*, 2010; Petchey *et al.*, 2008; Schmid-Araya *et al.*, 2002a,b; Townsend and Hildrew, 1977, 1979; Woodward and Warren, 2007; Woodward *et al.*, 2005a), and because it had the most extensive dataset for examining seasonal and ontogenetic effects among our four systems.

## II. METHODS AND STUDY SITES

Each of the four study systems and their respective food webs are described in turn below. Only predatory interactions were considered and non-animal basal resources were excluded from all the food webs. Although some of the detailed methods of sample collection differ to some extent between systems, the temporal and spatial scales over which the data were collected, and the extent of sampling effort used, individual level and directly observed data on nodes and links were used to construct the trophic network of each. Within the stream food webs, to standardise taxonomic resolution, and to minimise possible biases arising from the different mesh apertures used for sampling, the very small permanent meiofauna (body length < 500  $\mu\text{m}$ ) were excluded. We fitted the ADBM to the data in the same way for each food web, such that the number of entities (i.e. nodes) in the species-based taxonomic web was the same as for its size-based equivalent.

### A. Study Sites and Empirical Data Collection

#### 1. *The Celtic Sea Food Web*

The Celtic Sea is an area of continental shelf bordered by Ireland, the U.K. and the Bay of Biscay. The abundance data by size classes and species were extracted from the annual Cefas Celtic Sea groundfish surveys (after Warnes and Jones, 1995). The data were standardised to account for differences in trawl durations and therefore are indices of relative abundance (numbers of individuals per hour). Only locations consistently sampled through the 1987–2001 time series with the Portuguese high-headline trawl were used (Blanchard *et al.*, 2005). Ideally, abundance data would be derived from exactly the same locations and times as the stomach contents data. However, precise sampling locations and dates were not given in the Barnes *et al.* (2008) dataset, from where the data used in this chapter were extracted.

Consequently, we pooled data over the whole time-period and locations to capture general patterns in the abundance of species and size classes. Due to the size selectivity of fishing gear used in these research surveys, the smaller size classes of fish are not adequately sampled. Species-specific size distributions were extrapolated to smaller classes using linear regression of log abundance versus log body mass class (Jennings *et al.*, 2002).

The feeding links of fishes in the Celtic Sea have been described in a published global dataset of individual predator and prey body sizes and taxonomy (Barnes *et al.*, 2008): in total, 2091 feeding events from 29 predator species were included in the food web presented here. The original stomach contents data were collected from dissections carried out onboard the research vessels Cirolana, Scotia, and Clione during the annual surveys carried out by Cefas (Pinnegar *et al.*, 2003): of all the predators that were dissected, 491 individuals contained  $\geq 1$  identifiable prey item. Predator and prey length were recorded and converted to body mass by Barnes *et al.* (2008) using established weight to length relationships from regression analysis. Only vertebrate prey were identified and measured, and a vast majority were identified to species (see Appendix 1.1 for the species list).

## 2. The Tadnoll Brook Food Web

The Tadnoll Brook is a nutrient-rich (mean soluble reactive phosphorus and total oxidisable nitrogen  $122.9 \mu\text{g L}^{-1}$  and  $7.0 \text{ mg L}^{-1}$ , respectively), circum-neutral, tributary (mean annual discharge  $0.35 \text{ m}^3 \text{ s}^{-1}$ ) of the River Frome in southern England (Edwards *et al.*, 2009a,b).

Between February and December 2005, a 240-m reach was sampled ( $50^\circ 41' \text{N}$ ,  $2^\circ 19' \text{W}$ , 30 m a.s.l.) to construct the summary food web. The numerical abundance (numbers  $\text{m}^{-2}$ ) and biomass (mg dry mass  $\text{m}^{-2}$ ) of fish populations were measured every 2 months, using two-pass depletion electrofishing (Seber and LeCren, 1967) or using 30 large-bore Hess samples ( $0.12 \text{ m}^2$ ) for *Cottus gobio* L. (after Woodward *et al.*, 2008). Invertebrate abundance was quantified bimonthly using a benthic Surber sampler ( $0.06 \text{ m}^2$  quadrat; mesh aperture  $300 \mu\text{m}$ ), with 20 sample-units taken on each date. Invertebrates were identified to the lowest possible taxonomic level (usually species). Linear dimensions of each individual were measured to the nearest 0.1 mm and used to estimate dry body mass from published length-mass regressions (Benke *et al.*, 1999; Burgherr and Meyer, 1997; Edwards *et al.*, 2008; Edwards *et al.*, 2009a,b; Meyer, 1989; Smock, 1980).

Fishes were anaesthetised using 2-phenoxyethanol, measured and weighed. The guts of brown trout (*Salmo trutta* L.)  $> 70 \text{ mm}$  fork length were then flushed and the contents immediately preserved in 4% formalin. For smaller trout and other fish species, samples of specimens were killed and

frozen for subsequent dissection. Gut content analysis was carried out for the fish assemblage on each sampling occasion, whereas invertebrate diets were characterised only in May and October. Individuals of the most common invertebrate taxa in the benthos were taken from the Surber samples, and dissected for determination of gut contents. The contents of the foregut were examined for animal prey, which were identified at 400 $\times$  magnification to species wherever possible and linear body dimensions measured. Dry mass of individual prey items was calculated via the use of published regression equations (Benke *et al.*, 1999; Burgherr and Meyer, 1997; Edwards *et al.*, 2009a,b; Ganihar, 1997; Gonzalez *et al.*, 2002; Meyer, 1989; Sabo *et al.*, 2002). Of all the predators that were dissected, 688 individuals contained  $\geq 1$  identifiable prey item. All trout captured were fitted with a peritoneal passive integrated transponder (PIT) tag (Prentice *et al.*, 1990) and scanned for subsequent reidentification during each subsequent sampling occasion: this enabled growth rates and diets to be characterised repeatedly for individuals that were recaptured and the use of in-river PIT tag readers enabled us to follow life history of the tagged trout (Edwards *et al.*, 2008).

### 3. *The Afon Hirnant Food Web*

The Afon Hirnant is a tributary of the Welsh Dee in North Wales, U.K. (52° 52'N 03° 34'). The study was conducted at three sites (mean annual discharge of 7.26 m<sup>3</sup> s<sup>-1</sup>, 4.93 m<sup>3</sup> s<sup>-1</sup>, and 2.08 m<sup>3</sup> s<sup>-1</sup>, respectively) that were sampled on four dates between 2004 and 2005 (Figuerola, 2007). Within each site, pH ranged from about 5.5 to 7 over the course of the year.

Invertebrates were collected using a benthic Hess sampler (sampling area: 0.028 m<sup>2</sup>; mesh aperture 80  $\mu$ m). Fifteen randomly placed samples were taken at each site on each date, giving a total of 180 samples for the whole sampling period, which were preserved immediately in 100% ethanol and subsequently sorted in the laboratory. All individuals within the benthic samples were counted and identified to the lowest possible taxonomic level (usually species). The foreguts of invertebrates were removed by dissection and examined at 400 $\times$  magnification. Prey items were identified from a combination of taxonomic keys and reference slides of previously identified species, after Schmid-Araya *et al.* (2002a,b).

The body length of each individual in the benthos (and for prey items in consumers' guts) was measured and used as the dimension of body size in the study (as opposed to mass, as in the other systems). If prey items were too highly digested for body lengths to be measured reliably, previously established regressions based on head capsule width were used as an alternative linear dimension. Of all the predators that were dissected, 253 individuals contained  $\geq 1$  identifiable prey item.

#### 4. The Broadstone Stream Food Web

Broadstone Stream (51° 05' N 0° 03' E; 120 m above sea-level) is a second-order tributary of the River Medway in south-east England (see [Hildrew, 2009](#) for a detailed site description). The acidity of the stream (pH 4.7–6.6) excludes fish, resulting in an invertebrate-dominated food web (Woodward and Hildrew, 2001). There are about 25 common invertebrate species ([Woodward \*et al.\*, 2005a](#)). Among the common predators, there are three large species (*Cordulegaster boltonii* Donovan, *Sialis fuliginosa* Pict. and *Plectrocnemia conspersa* [Curtis]) and three small species (the larvae of the tanypod midges *Macropelepis nebulosa* [Meigen], *Trissopelopia longimana* [Staeger], and *Zavrelimyia barbatipes* [Kieffer]), which we focus on in detail here when investigating size-structuring within the intraguild subweb. Detritivorous stoneflies and chironomids dominate the prey assemblage in winter and summer, respectively ([Woodward \*et al.\*, 2005a](#)). Trophic interactions have been studied intensively over four decades, culminating in one of the most completely described food webs for any system (e.g. [Hildrew \*et al.\*, 2004](#); [Hildrew, 2009](#); [Layer \*et al.\*, 2010b](#); [Schmid-Araya \*et al.\*, 2002a,b](#); [Woodward \*et al.\*, 2005a](#)).

Thirty randomly dispersed benthic Surber sample-units (25 cm × 25 cm quadrat; mesh aperture 330 µm) were taken every 2 months between June 1996 and April 1997 and preserved immediately in 5% formalin. All invertebrate taxa were described to species wherever possible, and the few that could not be distinguished with certainty were grouped to the next taxonomic level (usually genus). Very rare taxa (i.e. <0.01% of mean annual standing stock) were excluded from the webs. Most species were univoltine and present only as larvae, so populations were not continually reproducing and recruitment was largely restricted to the summer. Linear body dimensions of all individuals collected from the benthos (or identified in gut contents) were measured and converted to dry mass using published regression equations (listed in [Woodward and Hildrew, 2002b](#)).

The foreguts of the predators collected in the Surber samples were dissected and examined at 400× magnification. Gut contents were identified from reference slides: because prey were generally consumed whole, or in large fragments, they could usually be identified to species relatively easily, and their individual body masses were calculated using the same methods as for the benthic samples ([Woodward \*et al.\*, 2005a](#)).

We constructed a summary food web that included all links and species (or size classes) recorded over the six 1996–1997 sampling occasions. In total, 1016 of the dissected predators contained at least one identifiable prey item within their gut, amounting to a total of 1818 prey individuals. Each predator and prey individual involved in a feeding link was measured and transformed into their respective body masses, which resulted in 2909 unique measurements. Sampling effort (the number of predator guts containing at least

one recognisable prey items) and predator size were fitted as independent variables in an OLS multiple regression model used to predict total diet width (i.e. the asymptotic number of prey species eaten) for each predator species. This regression model was used to gauge the joint effects of body size and sampling effort on diet characterisation.

## B. Construction of the Food Webs

All individuals were grouped into their respective species to create a taxonomic food web from the feeding interaction data. A trophic link assigned between two species if an individual of one was ever found in the gut of at least one individual of the other species. To create a size-based food web, the size range of all individuals in the web was divided into equal logarithmic size classes, with as many size classes as there were species in the same web (for comparability), and individuals were allocated to those size classes irrespective of their taxonomy. Logarithm size classes were used so that the distribution of individuals per size classes was more even than would have been the case if arithmetic sizes were used. A trophic link was assigned between two size classes if any individual from one size class was ever found in the gut of any individual from another size class. Estimates of abundance of individuals within species, and of individuals within size classes were compiled from samples not associated with the interaction data. Suctorial predators were omitted from the food webs, because their feeding links could not be described (after [Closs and Lake, 1994](#)).

## C. Modelling and Analyses

Predation matrices are frequently used to visualise aspects of food web structure, such as size structure and diet contiguity. As well as visual inspection, we calculated a range of food web statistics for each study system, including: maximum chain length (the number of trophic elements in the longest food chain); directed connectance was calculated as  $C = L/S^2$  ([Martinez, 1992](#)), where  $L$  is the number of realised trophic links observed and  $S$  is the number of trophic elements in the web; complexity was calculated as  $SC = S(L/(S[S - 1]/2))$  (after [Polis, 1991](#)). The mean number of links per species,  $d$ , was calculated as  $L/S$ . Mean shortest path lengths and clustering coefficients were calculated using the functions `shortest.paths()` and `transitivity()` in the `igraph` R package ([Csardi and Nepusz, 2006](#)).

In addition, each food web was separately modelled using the ADBM, following [Petchey \*et al.\* \(2008\)](#). This model has two main components: First, a set of allometric relationships that relate body size to variables that

influence and represent individual foraging, namely, attack rates, handling times, energy contents, and densities. Second, and separately for each consumer, the contingency model of optimal foraging (Emlen, 1966; MacArthur and Pianka, 1966) translates these variables into predicted diets. Since available empirical data about the allometries of foraging variables was insufficient and/or unsuitable for parameterising the model [Supplementary Information in Petchey *et al.* (2008)], we selected allometries that resulted in predicted connectance equal to observed connectance and also the maximum number of links predicted correctly (Petchey *et al.*, 2008). In all the food web modelling, we assumed that individuals could be *a priori* assigned as predators or non-predators. Therefore, the models attempted only to explain the diets of consumer taxa/size classes. For comparison, we also calculated the proportion of observed links that were correctly predicted if we simply assumed that all the predatory nodes consumed all other species.

We also analysed characteristics of the species that were involved in links that were either observed but not predicted, or predicted but not observed. Specifically, we used logistic regression to assess if a false-positive prediction, whereby the model predicted a link that was not observed in the data, was related to the abundances of the prey and predator involved in the link (i.e. a potential sampling effect). Also, we used randomisations to test if false-negatives, whereby empirical data described a link that was not predicted by the model, could be explained by coincidental (rather than intentional) ingestion of prey by predators; for instance, we tested if unusually small prey were disproportionately over-represented in predator guts that contained another more typically sized prey item, and potential instances of ‘Russian dolls’ in which the gut contents of a large predator also included the gut contents of a smaller predator it has ingested.

### III. RESULTS

#### A. General Properties of Empirical Food Webs and Comparisons Between Models and Data

The food webs contained 28–59 nodes and 112–170 links in the taxonomic versions, and 190–484 links in the size-based versions. In all cases, the size-based webs were more densely connected than their taxonomic equivalents: on average, the number of links, linkage density, and connectance were about twice as high; clustering coefficients and maximum and mean trophic height were higher; and path lengths were shorter (Table 1). Predator–prey mass ratios were also higher than in the taxonomic webs. Predator diet width ( $W$ ,  $\log_{10}$  number of links) in the taxonomic webs was well predicted by both consumer body mass ( $M$ ,  $\log_{10}$  mg) and sample size ( $NG$ ,  $\log_{10}$  number of

**Table 1** Parameters for the four study systems for their respective species- and size-based food webs

	Celtic Sea		Tadnoll Brook		Afon Hirnant		Broadstone Stream	
	Species	Size	Species	Size	Species	Size	Species	Size
Number of guts dissected that contained prey	491	491	688	688	253	253	1016	1016
Nodes feedings on smaller nodes (%)	0.98	0.98	0.98	0.98	0.92	0.92	0.82	0.82
Individuals feeding on smaller individuals (%)	1	1	1	1	0.90	0.90	0.99	0.99
Number of nodes	48	48 (2)	59	59 (6)	33	33 (1)	28	28 (1)
Number of links	169	376	170	484	112	190	124	185
Linkage density	3.52	7.83 (8.17)	2.88	8.2 (9.13)	3.39	5.76 (5.94)	4.43	6.61 (6.85)
Directed connectance	0.07	0.16 (0.17)	0.05	0.14 (0.17)	0.10	0.17 (0.19)	0.16	0.24 (0.25)
Predatory nodes (%)	0.6	0.56	0.32	0.66	0.39	0.58	0.32	0.57
Top predators (%)	0.38	0.19	0.1	0.24	0.24	0.18	0	0.14
Basal species (%)	0.4	0.33	0.68	0.24	0.61	0.42	0.68	0.39
Intermediate species (%)	0.23	0.38	0.22	0.42	0.15	0.39	0.32	0.43
Cannibalistic species (%)	0.12	0	0.02	0	0.06	0.15	0.25	0.32
Mean shortest path length	2.3	1.59	2.04	1.69	1.84	1.74	1.69	1.50
Clustering coefficient	0.3	0.5	0.2	0.39	0.28	0.56	0.50	0.70
Maximum trophic height of a node	4	3.67	2.7	4.08	3.13	3.57	2.60	4.26
Mean trophic height of a node	2	1.99	1.42	2.61	1.52	1.95	1.45	2.36
Mean predator prey size ratio (by links between nodes)	1.3	2.2	1.4	3.7	1.1	1.3	1.48	3.72
Mean predator prey size ratio (individual interactions)	42.7	42.7	10715.2	10715.2	3.8	3.8	117.49	117.49
ADBM predictive success (%) (allometric abundances)	0.3	0.73	0.43	0.73	0.42	0.5	0.63	0.83
ADBM predictive success (%) (actual abundances)	0.3	0.74	0.45	0.74	0.43	0.53	0.62	0.83



guts that contained prey) in three of the webs (Celtic Sea:  $W = -0.254 + 0.116M + 0.627NG$ ;  $r^2_{(\text{adj})} = 0.92$ ;  $F_{2,27} = 158.33$ ;  $p < 0.001$ ; Tadnoll Brook:  $W = 0.218 + 0.053M + 0.531NG$ ;  $r^2_{(\text{adj})} = 0.87$ ;  $F_{2,18} = 58.31$ ;  $p < 0.001$ ; Broadstone Stream:  $W = 0.216 + 0.156M + 0.389NG$ ;  $r^2_{(\text{adj})} = 0.96$ ;  $F_{2,8} = 88.94$ ;  $p < 0.001$ ), and by sample size alone in the Afon Hirnant ( $W = 0.133 + 0.584NG$ ;  $r^2 = 0.92$ ;  $F_{1,12} = 117.69$ ;  $p < 0.001$ ). In terms of predicting the positioning of the links within the feeding matrix, in each case the ADBM showed a marked improvement in the fit between the model and the data in the size-based webs (30–61% correctly predicted) relative to their species-based (50–84% correctly predicted) equivalents. The Broadstone Stream food web provided the best fit between the models and data in both cases (62% and 83% in the species- and size-based webs, respectively), with the most marked improvement between the species-based (30%) and size-based (74%) web being evident in the Celtic Sea web (Table 1).

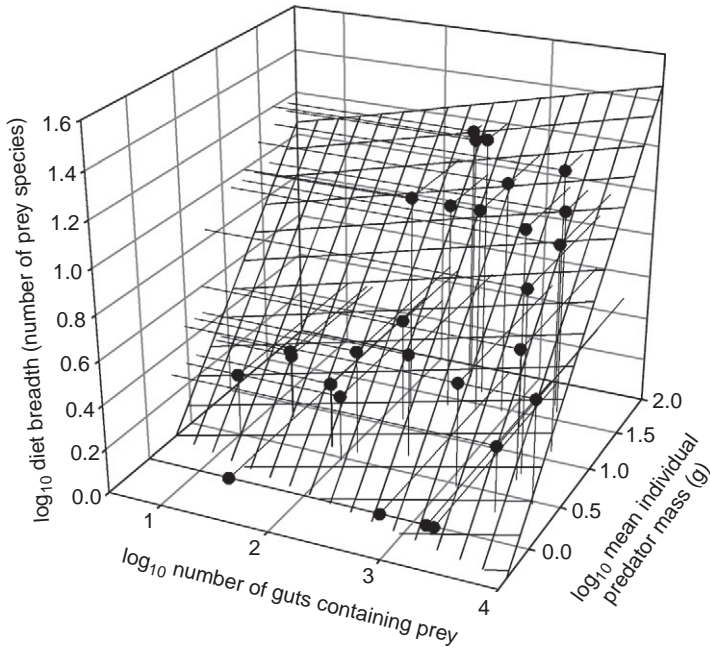
## B. Specific Properties of Each Empirical Food Web and Comparisons Between Models and Data

### 1. Celtic Sea Food Web

a. Properties of the Species- and Size-Based Webs. The diet breadth of the predators within the food web was well described by their mean individual mass and the number of guts examined that contained prey (Figure 2). The species-based food web contained 48 taxa and 169 links (Figure 3). Nineteen of these consumed no other taxa; the 29 other taxa were both predators and prey, and six of these were cannibals (Figure 3A). This food web contained the highest proportion of top predators (0.38) among all eight networks across the four systems, and the longest single food chain (4) (Table 1).

The size-based food web contained 376 links (Figure 3B). Thirty-two size classes were consumers, of which nine, of the predominantly larger classes, were not themselves consumed. There were 16 (predominantly smaller) ‘basal’ size classes that did not consume any other, but were themselves consumed. Eighteen were intermediate, and none were cannibals. Five size classes (mostly smaller ones) were neither consumers nor prey and were therefore unconnected because no individuals occurred in these size classes. Up to 21 size classes were present in the diets of the predatory size classes. The individuals in each size class represented up to 18 taxa, and the number of species displayed a hump-shaped relationship with size (Figure 3B) as did the number of prey species and predator species in each size class.

In both versions of the food web 98% of nodes fed on smaller prey: on average, predators were 1.3 and 2.2 times larger than their prey in the species and size-based webs, respectively, and across all individuals predators were



**Figure 2** *Celtic Sea food web*. Diet breadth of as a function of sampling effort and mean individual predator body mass ( $\log_{10}$  number of links =  $-0.254 + 0.116$  (mean individual predator mass,  $\log_{10}$  mg) +  $0.627(\log_{10}$  number of guts);  $r^2_{(\text{adj})} = 0.92$ ;  $F_{2,27} = 158.33$ ;  $p < 0.001$ ).

43 times larger than their prey (Table 1). The size-based web was more reticulate than the species-based version, with higher connectance, linkage density, and clustering coefficients and lower mean shortest path length (Table 1)

b. Explaining the Arrangement of Feeding Interactions. A simple 'model' that assumed that the 29 predator species could consume all 48 species (including themselves) predicted  $29 \times 48$  links (1392), of which 169 are correctly assigned ( $169/1392 = 12\%$ ). The apparent vulnerability of prey (the number of species the prey is consumed by) was significantly positively associated with their abundance (generalised linear model, Poisson errors,  $z$  value of slope = 4.7, 27 df for error,  $p < 0.0001$ ). The apparent generality of predator taxa (the number of taxa they consumed) was not associated with their abundance (generalised linear model, Poisson errors,  $z$  value of slope = 0.1, 27 df for error,  $p = 0.89$ ).

The ADBM correctly predicted 30% of the links in the taxonomic food web; consequently the patterning of predicted links was clearly different from the observed links (Figure 3A): the diets were predicted to include a much smaller range of prey taxa, and much more diet contiguity, than was observed. When given the identity of the predatory size classes, however, the ADBM predicted 74% of the links correctly (Figure 3B; Table 1). Most of the deviations occurred due to the lack of predicted links from consumers to relatively small size classes. The chance of the ADBM predicting a link incorrectly was higher when the prey taxa or either prey or predator size class involved in link was rare (binomial generalised linear models,  $p < 0.05$  for the relevant model terms) (Figure 4).

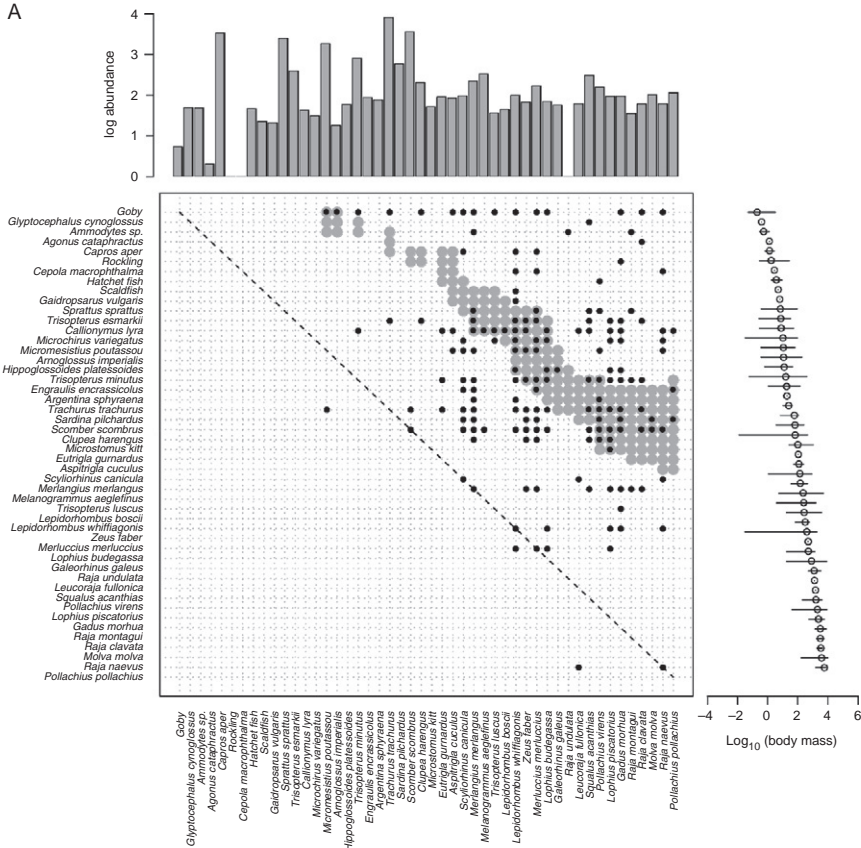
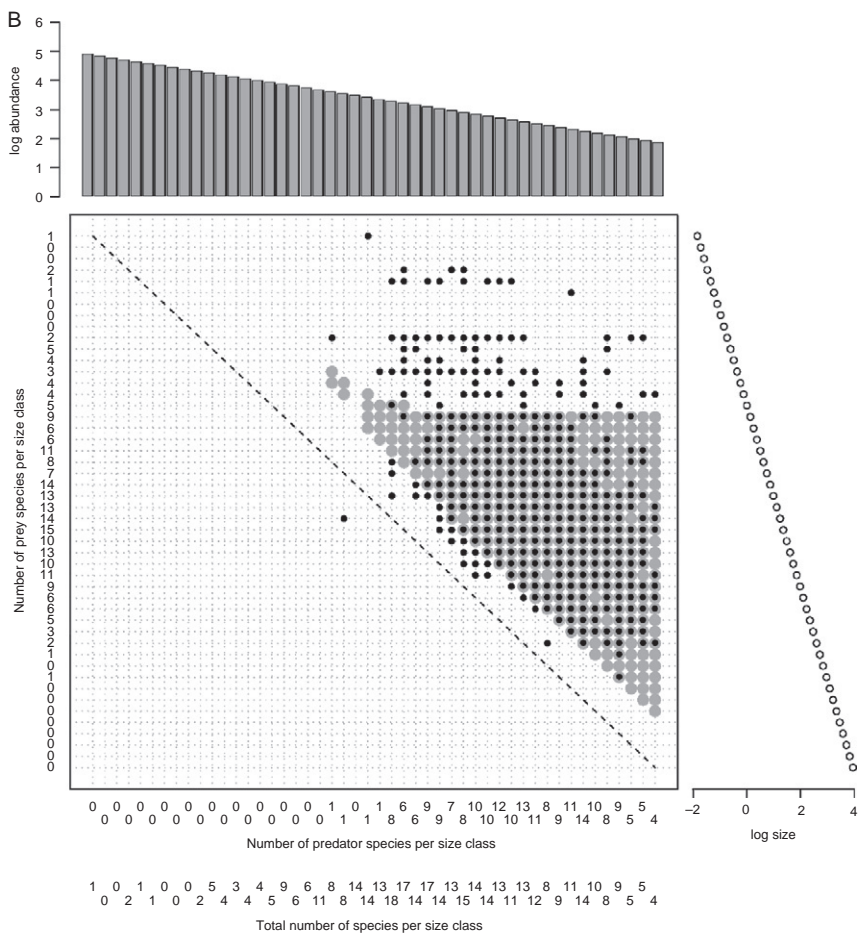
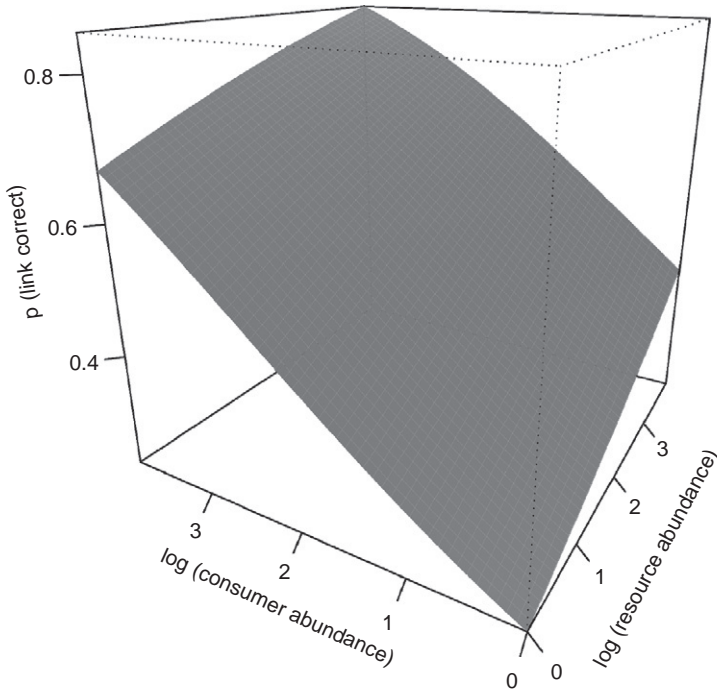


Figure 3 (Continued)



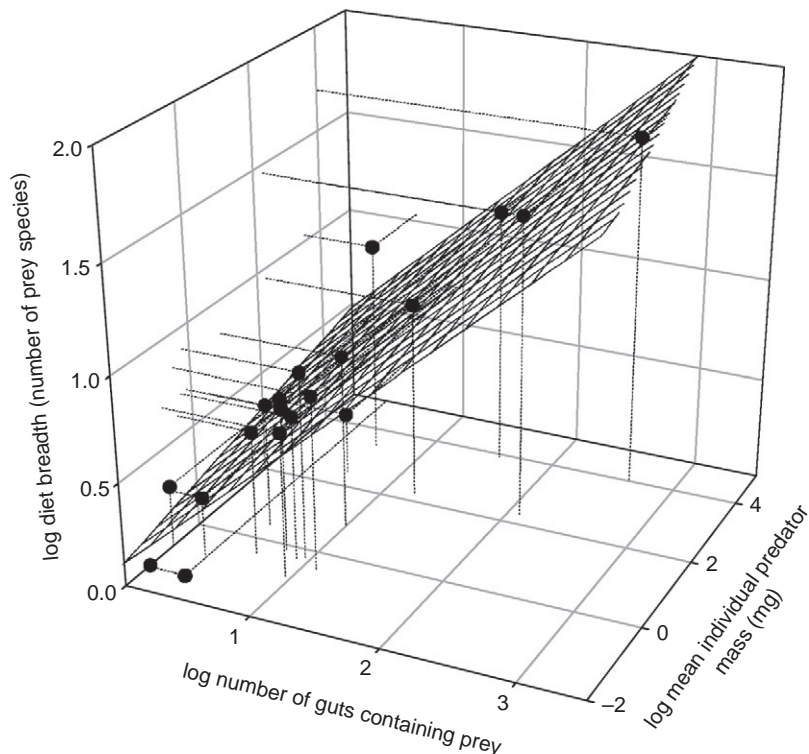
**Figure 3** *The Celtic Sea food web, abundance, and body size information.* The central predation matrix indicates an observed feeding interaction between a consumer (column) and resource (row) with a black dot. Thus, columns can be viewed as the diet composition of consumer. The larger grey dots indicate the feeding interactions predicted by the ADBM. Consumer columns and resource rows are ordered by body size, with the smallest in the top left corner and largest in the bottom right. Thus feeding interactions in which a predator is larger than its prey occur in the triangle above the diagonal dashed line. The upper bar chart shows the abundances in the environment of the species in the predation matrix. The plot on the right shows the mean and range of body sizes of individuals in each of the species in the predation matrix. (A) A version of the Celtic Sea food web in which individuals are grouped according to taxonomy. (B) A version of the Celtic Sea food web in which individuals are grouped according to size. In (B) a number of species represented in each size class are displayed to the left and below the predation matrix. All information is as in [Figures 6, 9, and 12](#), except that the abundances in (B) are allometric estimates (see Methods, in [Section III](#)), since estimates of actual abundance were constrained by sampling methods and gear, so could not be used.



**Figure 4** In the Celtic Sea food web, the relationship between the probability that the link predicted by the ADBM is present in the observed food web and the abundance of the resource and consumer involved in that link.

## 2. Tadnoll Brook Food Web

a. Properties of the Species- and Size-Based Webs. The diet breadth of the predators was well described by their mean individual mass in the benthos and the number of guts examined that contained prey (Figure 5). The taxonomic food web contained 59 taxa and 170 links (Figure 6A; Table 1). Forty of these consumed no other taxa; 13 other taxa were both predators and prey, six were predators only, and one of these was cannibalistic (Figure 6A). The predatory taxa consumed up to 50 other species. The size-based food web contained 484 links (Figure 6B). Fourteen of the mainly smaller size classes did not consume any other size classes, but were themselves consumed. Thirty-nine were consumers, of which the 14 largest were consumers but were not themselves consumed. Twenty-five were both consumed and consumers, and none of these were cannibals. Six size classes were



**Figure 5** *Tadnoll Brook food web.* Diet breadth of as a function of sampling effort and mean individual predator body mass.

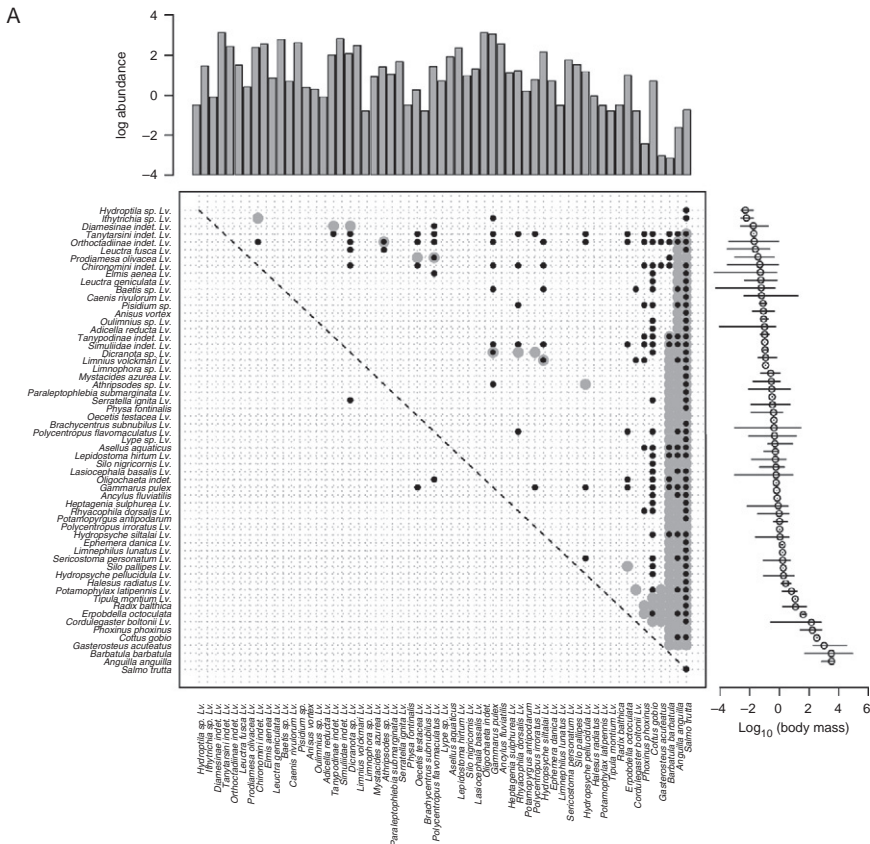
unconnected in the matrix because they contained no individuals. From 8 to 18 size classes were present in the diets of the predatory size classes. The individuals in each size class represented up to 25 taxa, and the number of species displayed a hump-shaped relationship with size (Figure 6B), as did the number of prey species and predator species in each size class (Figure 6B).

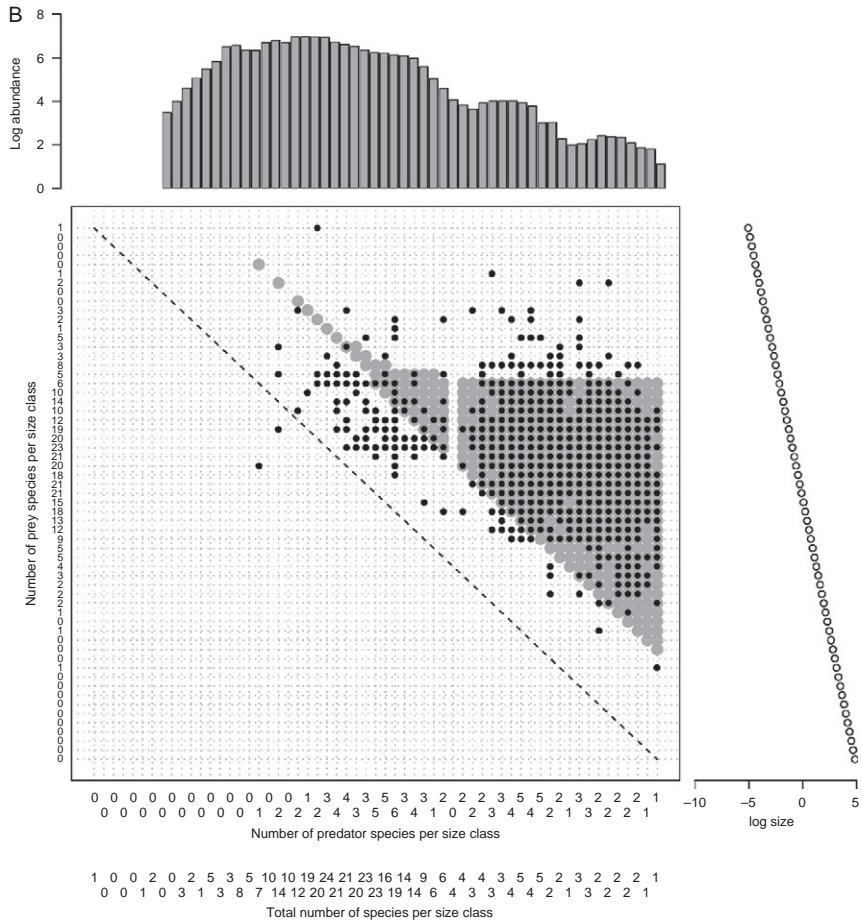
In both versions of the food web, 98% of nodes fed on prey that were smaller than themselves. On average, predators were 1.4 and 3.7 times larger than their prey in the species and size-based webs, respectively, but across all individual predators were 10,715 times larger than their prey (Table 1). As in the other webs, the size-based web had higher connectance, linkage density, and clustering coefficients and reduced mean shortest path length relative to its species-based equivalent (Table 1).



b. Explaining the Arrangement of Feeding Interactions. A simple 'model' which assumed that the 19 predator species could consume all 59 species (including themselves) predicted  $19 \times 59$  links (1121), of which 170 were correctly assigned ( $170/1121 = 15\%$ ). The vulnerability of species was significantly positively associated with their abundance (generalised linear model, Poisson errors,  $z$  value of slope = 4.7, 27 df for error,  $p < 0.0001$ ), but this was not the case for their apparent generality (generalised linear model, Poisson errors,  $z$  value of slope = 0.8, 7 df for error,  $p = 0.43$ ).

The ADBM predicted 45% of the links in the taxonomic food web correctly, with some consumers predicted to have very narrow diets, when in reality they preyed on many species. When given the identity of the predatory





**Figure 6** Tadnoll Brook food web, abundance, and body size information. See [Figure 3](#) legend for details. The upper bar chart shows the abundances in the environment of the species in the predation matrix. The plot on the right shows the mean and range of body sizes of individuals in each of the species in the predation matrix. (A) A version in which individuals are grouped according to taxonomy. (B) A version in which individuals are grouped according to size. In (B) a number of species represented in each size class are displayed to the left and below the predation matrix.

size classes, the ADBM predicted 74% of the links correctly in the size-based web (Figure 6B). The chance of the ADBM predicting a link incorrectly was higher when the prey or predator species were common, but was highest when the size class involved in link was rare (binomial generalised linear models,  $p < 0.03$  for all main effects and interaction term) (Figure 7): it is



possible that this reversal of patterns between the taxonomic and size-based webs is due to the more exhaustive sampling of the diets of the larger fish in this community.

c. Ontogenetic Dietary Shifts Within Individual Predators. The most frequently recaptured individual of the top predator species, brown trout, *S. trutta* L., was caught on eight occasions, over which period it more than doubled its body mass (from 5.2 to 13.2 g) and exhibited marked shifts in its diet, from feeding primarily within the invertebrate-dominated portion of the size spectrum to becoming markedly more piscivorous as it moved upwards through the food web (Figure 8). This shift from invertivory to piscivory was manifested when the fish exceeded 10 g, and was reflected by a sudden increase in mean ingested prey mass of about two orders of magnitude and, ultimately, a marked reduction in the size range of prey being taken.

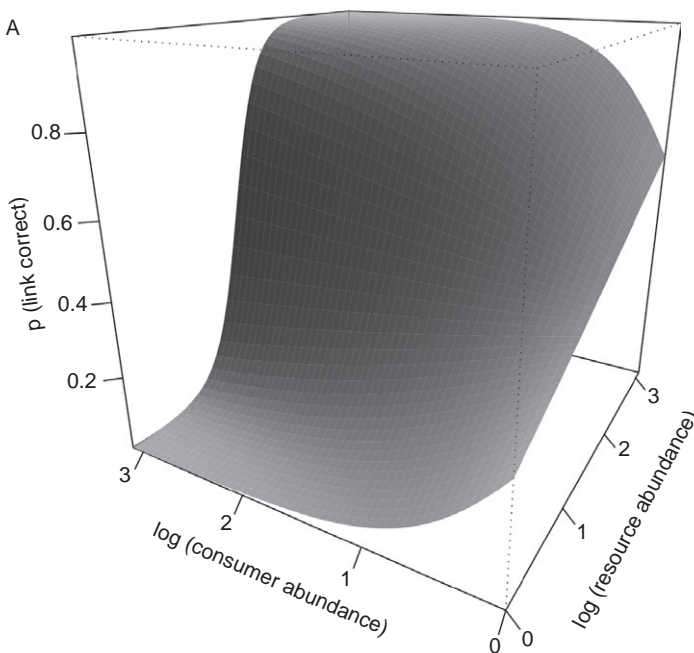
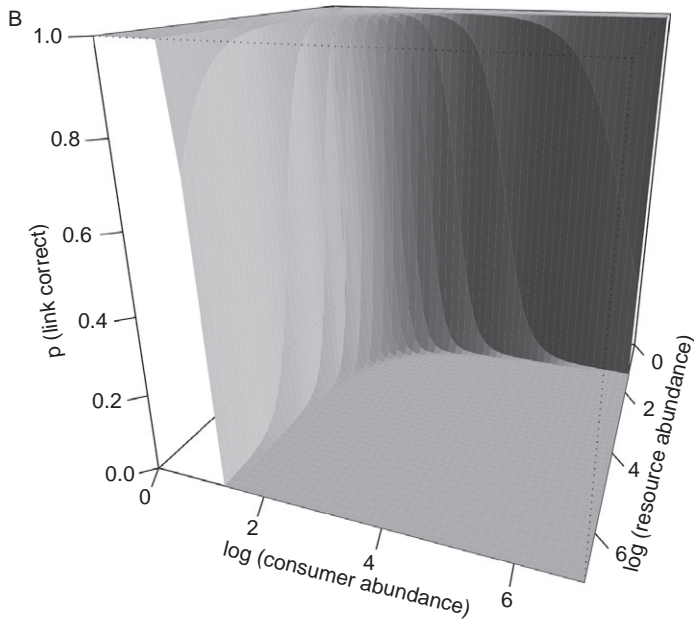


Figure 7 (Continued)

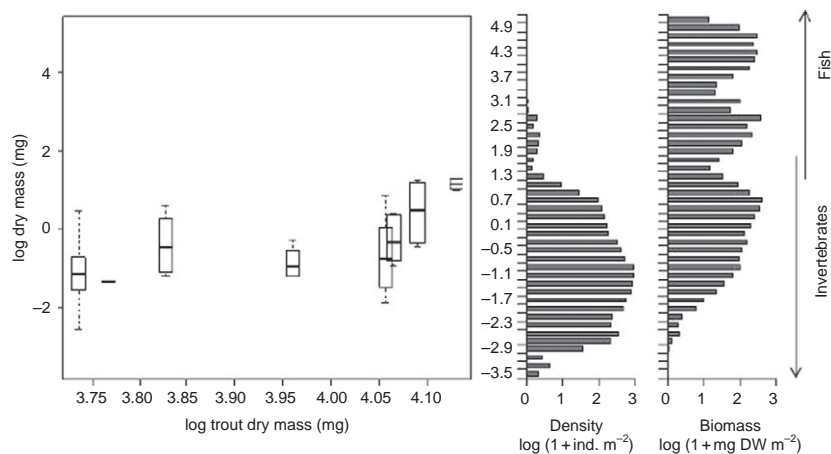


**Figure 7** In the Tadnoll Brook food web, the relationship between the probability that the link predicted by the ADBM is present in the observed food web, and the abundance of the resource and consumer involved in that link. The surface is that predicted by a binomial regression fitted to the data. (A) Model of the taxonomic version of Tadnoll Brook food web. (B) Size-based version of the Tadnoll Brook food web. In both cases, the resource and consumer abundance were both significantly associated with probability of correct prediction.

### 3. *Afon Hirnant Food Web*

a. **Properties of the Species- and Size-Based Webs.** The diet breadth of the predators was well described by the number of guts examined that contained prey (Figure 9). The taxonomic food web contained 33 taxa and 112 links (Figure 10A). Twenty of these consumed no other taxa, 13 other taxa were both predators and prey, eight were predators only, and two of these were cannibalistic (Figure 10A). The predatory taxa consumed up to 19 other species.

The size-based food web contained 190 links (Figure 10B). Fourteen size classes were ‘basal’ nodes and these were mostly located in the smaller size classes. Nineteen size classes were consumers, of which six were ‘top predators’ that were not eaten by other size classes, and 13 size classes were intermediate. Up to 23 size classes were preyed upon. The individuals in each

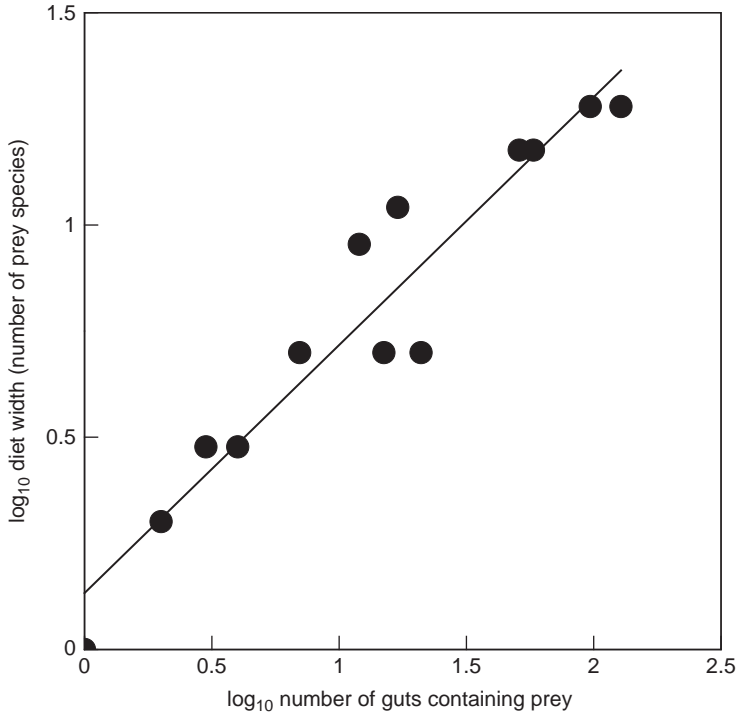


**Figure 8** Ontogenetic changes in the size range of prey in the diet of an individual trout with increasing consumer size. The trout in the Tadnoll Brook were tagged on first capture enabling us to follow changes in the diet of individuals (by repeated gut-flushing). The box plot represents data for one trout repeatedly sampled over eight occasions in its first year of growth. Box plots of the size distributions of prey items consumed by this individual trout are plotted against its mass. The two histograms in the right-hand panels represent the density and biomass of size categories of potential prey in the environment. The arrows on the far right indicate size range of invertebrates and fish.

size class represented from 1 to 15 taxa, and the total number of species per class displayed a unimodal relationship with size, as did the number of prey and predator species (Figure 10B).

In both versions of the food web, 92% of the consumer nodes fed on smaller prey: on average, predators were 1.1 and 1.3 times larger than their prey in the species and size-based webs, respectively, and across all individual predators were 3.8 times larger than their prey (Table 1). The size-based web was again more densely connected than was the case for the species-based version: connectance, linkage density, and clustering coefficients were all higher and mean shortest path length was reduced (Table 1).

b. Explaining the Arrangement of Feeding Interactions. Assuming that the 13 predator species could consume all 33 species (including themselves) predicted  $13 \times 33$  links (429), of which 112 were correctly assigned ( $112/429 = 26\%$ ). The ADBM predicted 43% of the links in the taxonomic food web correctly but when supplied with the identity of the predatory size classes this increased to 53% in the size-based webs (Figure 10B; Table 1). The chance of the ADBM predicting a link incorrectly was higher when the



**Figure 9** *Afon Hirnant food web.* Diet breadth of as a function of sampling effort and mean individual predator body mass ( $\log_{10}$  number of links =  $0.133 + 0.584(\log_{10}$  number of guts);  $r^2_{(\text{adj})} = 0.92$ ;  $F_{1,12} = 117.69$ ;  $p < 0.001$ ).

predator species or size class involved in link was rare (binomial generalised linear models,  $p < 0.01$  for all main effects; [Figure 11](#)).

#### 4. Broadstone Stream Food Web

a. Properties of the Species- and Size-Based Webs. The diet breadth of the predators in the Broadstone Stream food web was well described by mean individual predator mass in the benthos and the number of guts examined that contained at last one prey item ([Figure 12](#)). The taxonomic food web contained 28 taxa and 124 links ([Figure 13A](#)). Nineteen of these consumed no other taxa; the nine other taxa were both predators and prey, and seven these were cannibals. The predatory taxa consumed 6–25 other species, and some (e.g. *Zavrelinmyia* feeding on *Trissopelopia*) appeared to feed on species that were nearly 20 times larger than themselves ([Figure 13A](#)).

The size-based web contained many more (185) links (Figure 13B). Eleven (mostly small) size classes were ‘basal’ nodes and the four largest size classes represented ‘top predators’ that were not preyed upon. Twelve size classes were intermediate consumers and nine of these were ‘cannibals’. One size class (the second smallest) was empty and unconnected within the matrix because no individuals occurred within it. Between 8 and 19 size classes were present in the diets of the predators. There were 11 instances (i.e. < 5% of links) of predators eating prey that were larger than themselves, and 55% of these were represented by size classes adjacent to one another on the ordinal body size scale (Figure 13B). Each size class represented 0–23 species, and the total number of species per node displayed a hump-shaped relationship with size, as did both the number of prey species and predator species (Figure 13B).

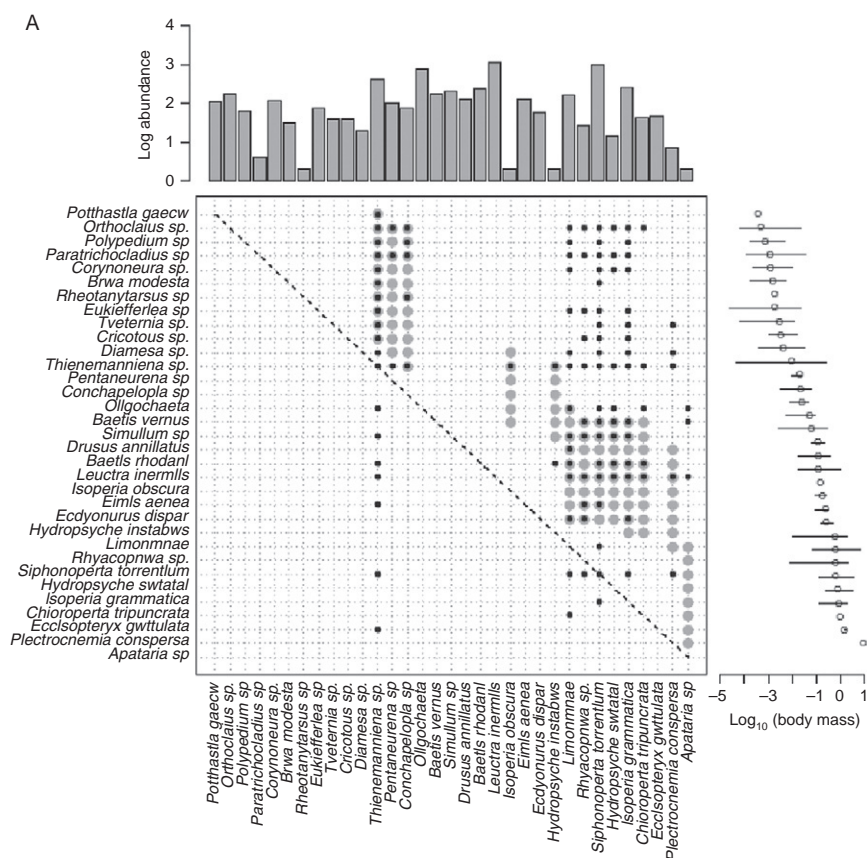
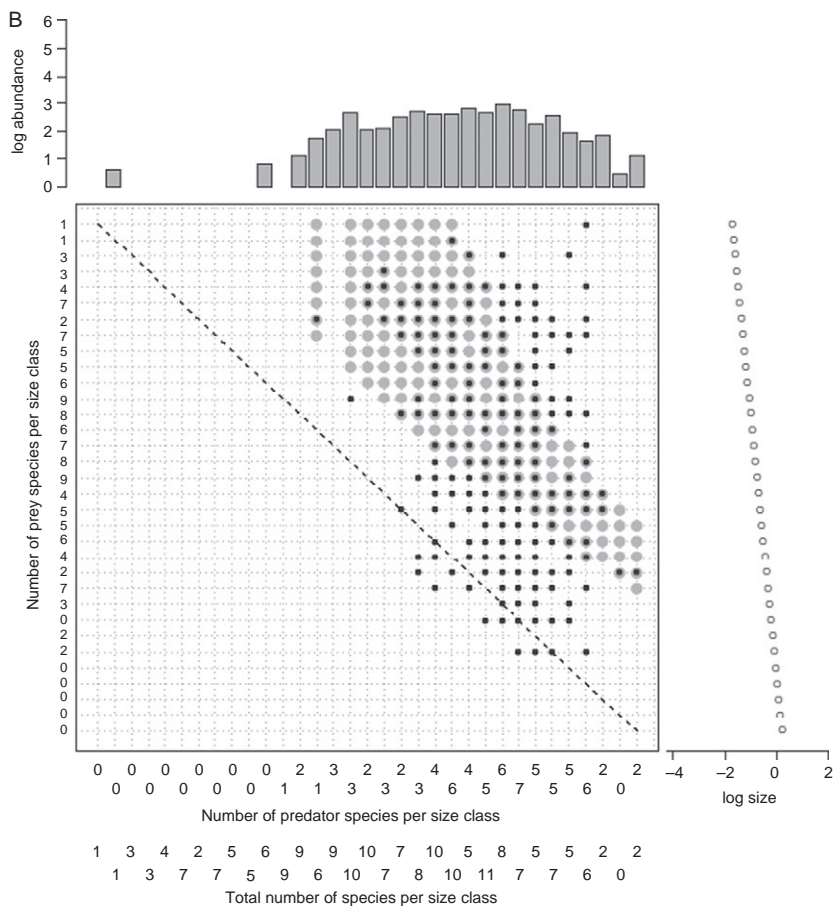
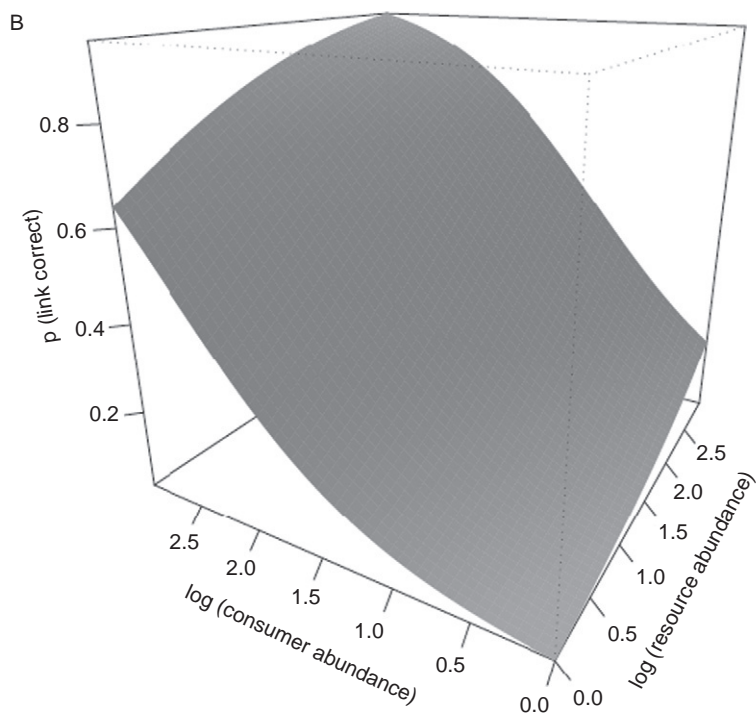
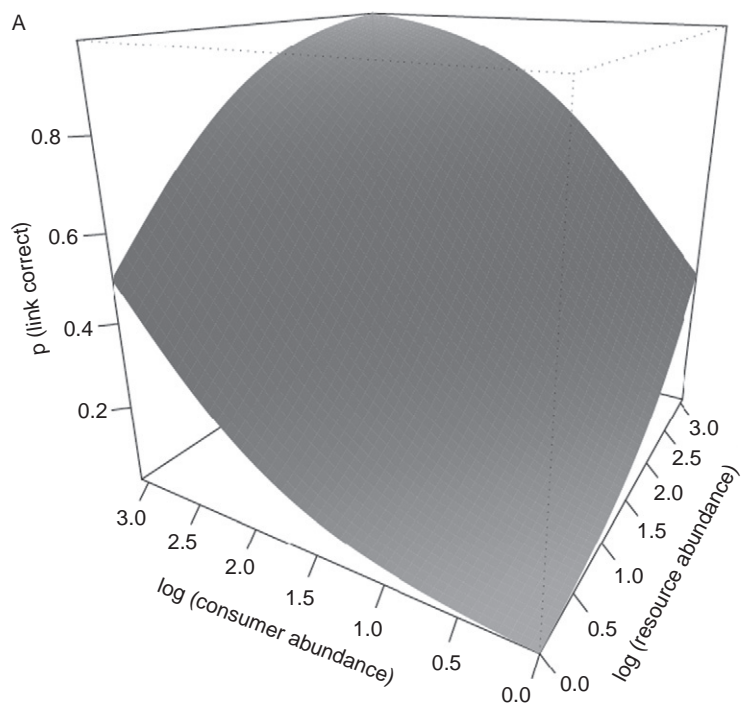


Figure 10 (Continued)



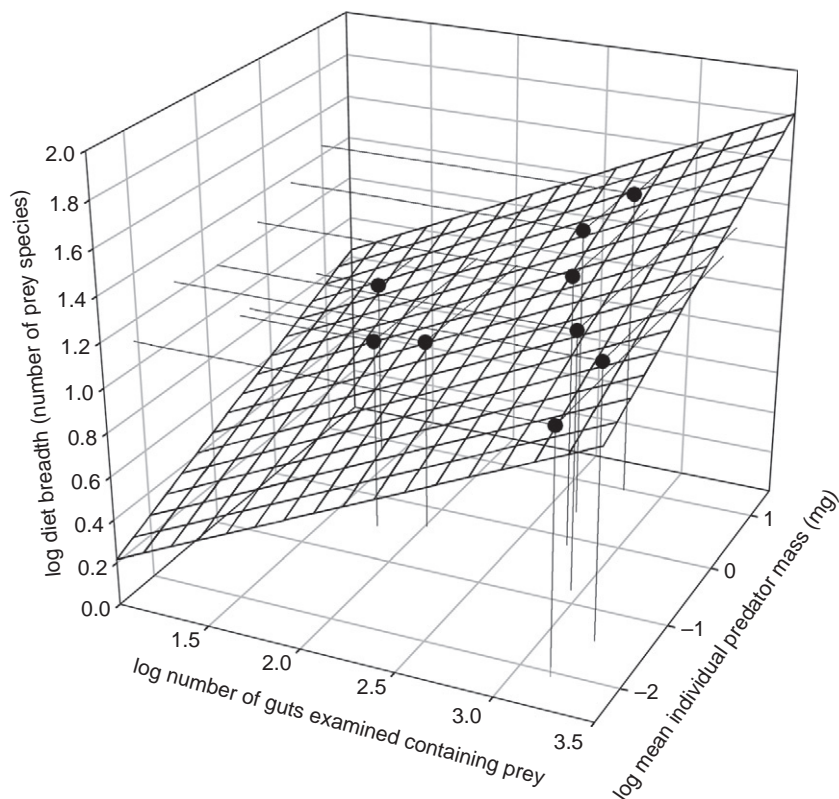
**Figure 10** *Afon Hirnant* food web, abundance, and body size information. The central predation matrix indicates an observed feeding interaction between a consumer (column) and resource (row) with a black dot. See [Figures 3 and 6](#) for details. (A) A version in which individuals are grouped according to taxonomy. (B) A version in which individuals are grouped according to size. In (B) the number of species represented in each size class are displayed to the left and below the predation matrix.

Eighty-four percent of the nodes in both versions of the food web preyed on nodes were smaller than themselves. On average, predators were 1.5 and 3.7 times larger than their prey in the species and size-based webs, respectively, and across all individuals, predators were 117 times larger than their prey ([Table 1](#)). The size-based web was again markedly more



**Figure 11** (legend on following page)





**Figure 12** Estimating diet breadth in the species-averaged Broadstone Stream food web, as a function of sampling effort (the number of predator guts examined that contained at least one prey item) and mean predator body mass ( $r^2_{(adj)}=0.96$ ;  $F_{2,8}=88.94$ ;  $p < 0.001$ ). Note all axes are  $\log_{10}$  transformed.

interconnected than the species-based version, with higher connectance, linkage density, and clustering coefficients and reduced mean shortest path length (Table 1).

**Figure 11** In the Afon Hirnant food web, the relationship between the probability that the link predicted by the ADBM is present in the observed food web, and the abundance of the resource and consumer involved in that link. The surface is that predicted by a binomial regression fitted to the data. (A) Model of the taxonomic version of Afon Hirnant food web. (B) Size-based version of Afon Hirnant food web. In both cases, the resource and consumer abundance were both significantly associated with probability of correct prediction.



b. Explaining the Arrangement of Feeding Interactions. If we assume that the nine predator species can consume all 28 species (including themselves)  $9 \times 28$  links (252) are predicted, of which 132 were correctly assigned ( $132/252 = 52\%$ ). The vulnerability of species was significantly positively associated with their abundance (generalised linear model, Poisson errors,  $z$  value of slope = 4.7, 27 df for error,  $p < 0.0001$ ), but this was not the case for their apparent generality (generalised linear model, Poisson errors,  $z$  value of slope = 0.8, 7 df for error,  $p = 0.43$ ).

The ADBM correctly predicted 62% of the links in the taxonomic food web, but the patterning of predicted links was clearly different to the observed links (Figure 13A). For example, the diets of some consumers were predicted to be nearly empty, when in reality they preyed on many of the other species. In addition, none of the taxa were predicted to feed on taxa much larger than themselves, whereas this was not the case in the empirical

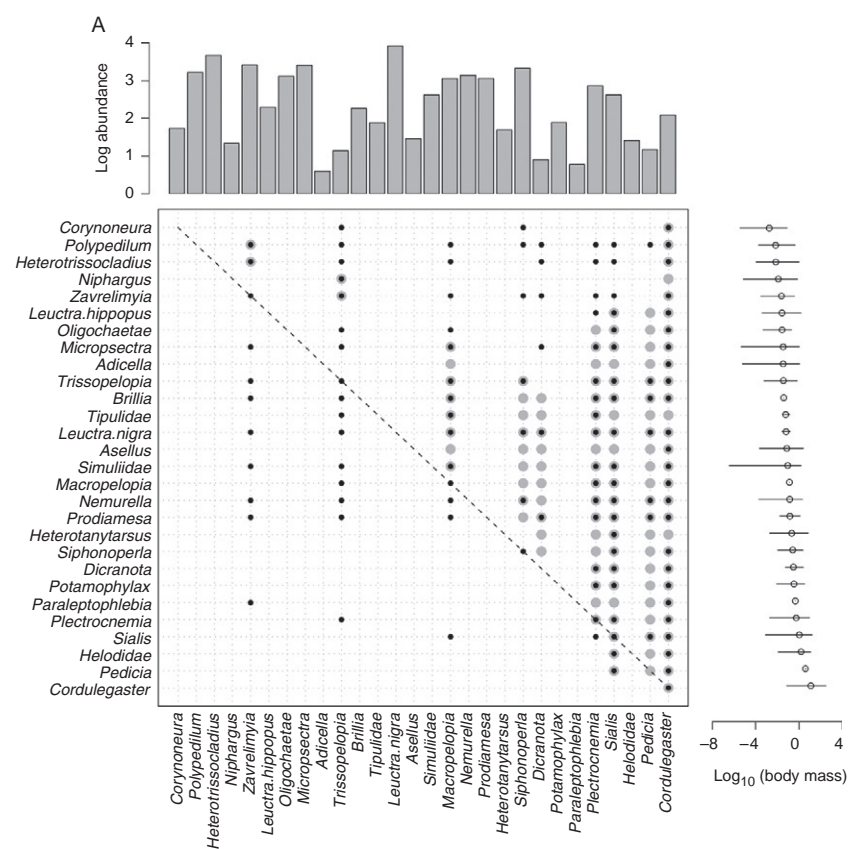
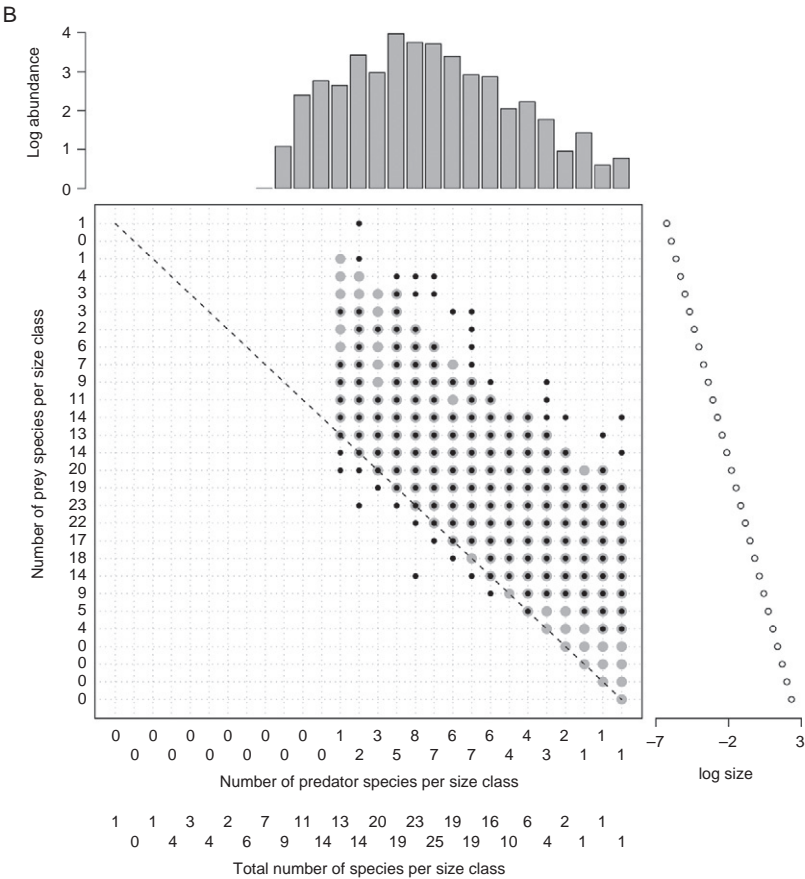


Figure 13 (Continued)



**Figure 13** *Broadstone stream food web, abundance, and body size information.* The central predation matrix indicates an observed feeding interaction between a consumer (column) and resource (row) with a black dot. See [Figures 3 and 6](#) for details. (A) A version of Broadstone stream in which individuals are grouped according to taxonomy. (B) A version of Broadstone stream in which individuals are grouped according to size. In (B) a number of species represented in each size class are displayed to the left and below the predation matrix.

data. Note that this value of 62% is different from the ~40% given in [Petchey \*et al.\* \(2008\)](#), due to differences in the empirical data: in [Petchey \*et al.\* \(2008\)](#) data were extracted from [Brose \*et al.\* \(2005\)](#), whereas the current analyses are based on the raw individual diet data. For the size-based web the ADBM predicted 83% of the observed links correctly ([Figure 13B](#)). The chance of the ADBM predicting a link incorrectly was higher when the predator species or

size class involved in link was rare (binomial generalised linear models,  $p < 0.01$  for all main effects; Figure 14). These findings tallied with the yield–effort curves, which indicated incomplete sampling of the diets of *Pedicia* (7 prey), *Dicranota* (6 prey), *Siphonoperla* (7 prey) (cf. Woodward *et al.*, 2005a), which were all at least one order of magnitude rarer than the six other predator species.

### C. Seasonal and Ontogenetic Shifts Within the Broadstone Stream Food Web

When feeding links within the trivariate species-based food web were decomposed into their associated size–frequency distributions for nodes and links, the previously hidden variation of species-averaging became more readily apparent (Figure 15). This was highlighted for one of the most frequently observed interactions in the web, that of the top predator *C. boltonii* preying upon the stonefly *N. pictetii*. The frequency distribution of individual predator–prey mass ratios within this link was log-normal, and only a subset

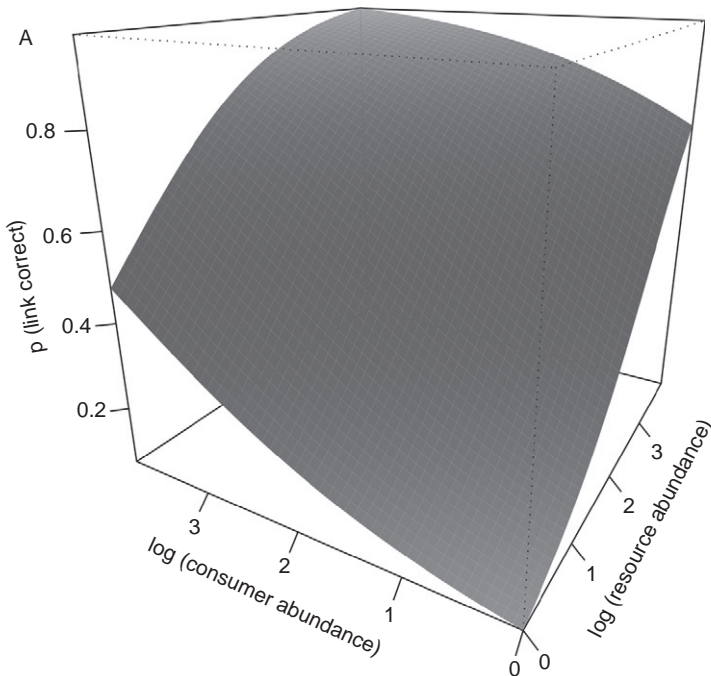
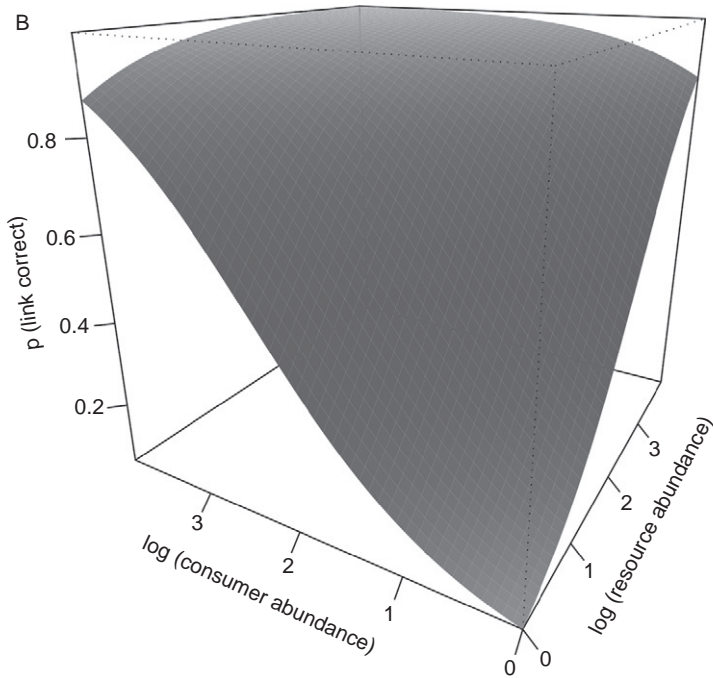
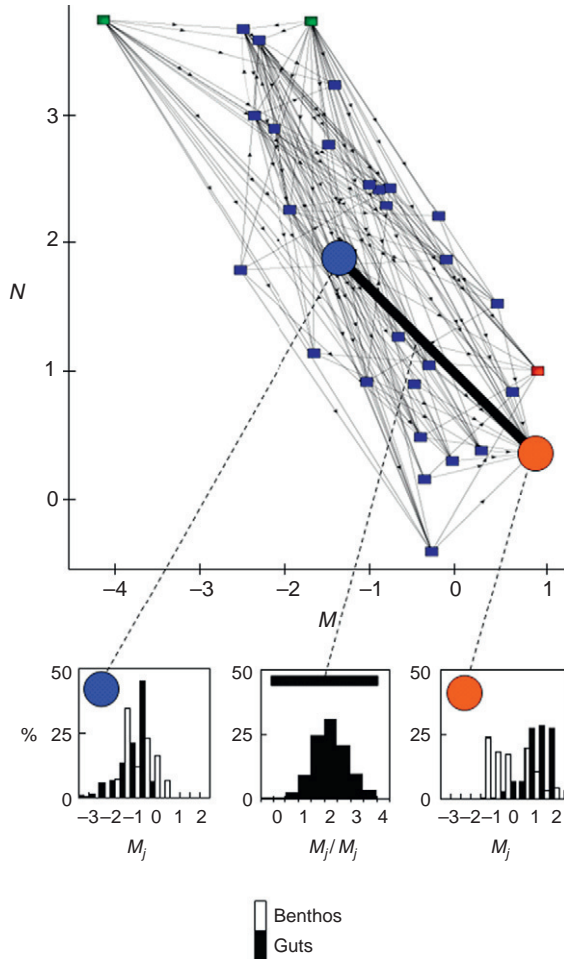


Figure 14 (Continued)



**Figure 14** In the Broadstone stream food web, the relationship between the probability that a link predicted by the ADBM is present in the observed food web, and the abundance of the resource and consumer involved in that link. The surface is that predicted by a binomial regression fitted to the data. (A) Model of the taxonomic version of Broadstone stream food web. (B) Size-based version of Broadstone stream. In both cases, the resource and consumer abundance were both significantly associated with probability of correct prediction.

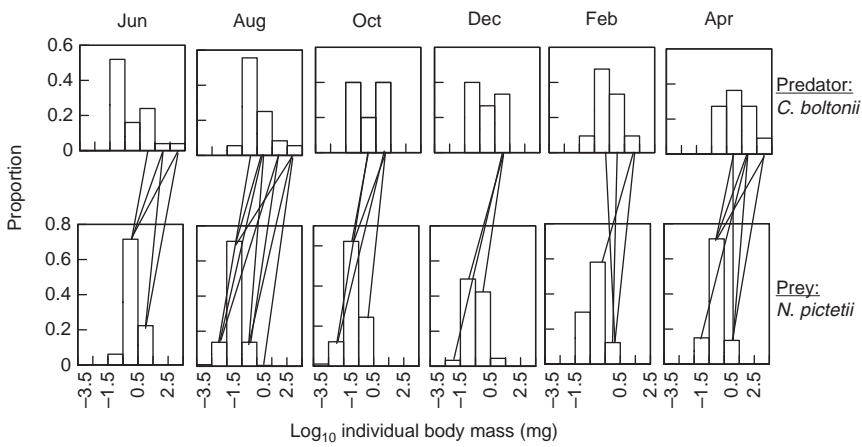
of the predator population interacted with a subset of the prey population (Figure 15). For the highlighted *C. boltonii*–*N. pictetii* feeding link, the predators were represented by the larger individuals and the prey by the smaller individuals within their respective populations: thus the individual-based ratio was about 1.7 times higher than that of the species-averaged data due to the implicit inclusion of the larger (invulnerable) prey in the calculations of the latter ratio. When resolved temporally (Figure 16), marked ontogenetic and seasonal shifts in the occurrence of this link were revealed, with apparent mismatches occurring at certain times of the year (e.g. in June) when interactions between particular size classes were not observed. These contrasted with other periods of more intense linkages when the size disparity



**Figure 15** Species-averaged  $MN$  scaling in the Broadstone Stream food web. Trivariate patterns in the Broadstone Stream food web, in which log abundance ( $N$ ) is plotted as a function of log mean individual body mass ( $M$ ) with feeding links overlain. The species-averaged graph obscures the considerable variation in body masses of individual protagonists within each predator–prey interaction, as revealed in the lower panels.

was sufficient to enable a greater proportion of the predators to exploit this common prey species more extensively (e.g. in August).

Within the guild of the six common predators, there were clear differences in the sizes of the individuals that interacted with one another as either predators or prey relative to their respective populations as a whole. This was evident from the distinct size–frequency distributions for the IGP subweb



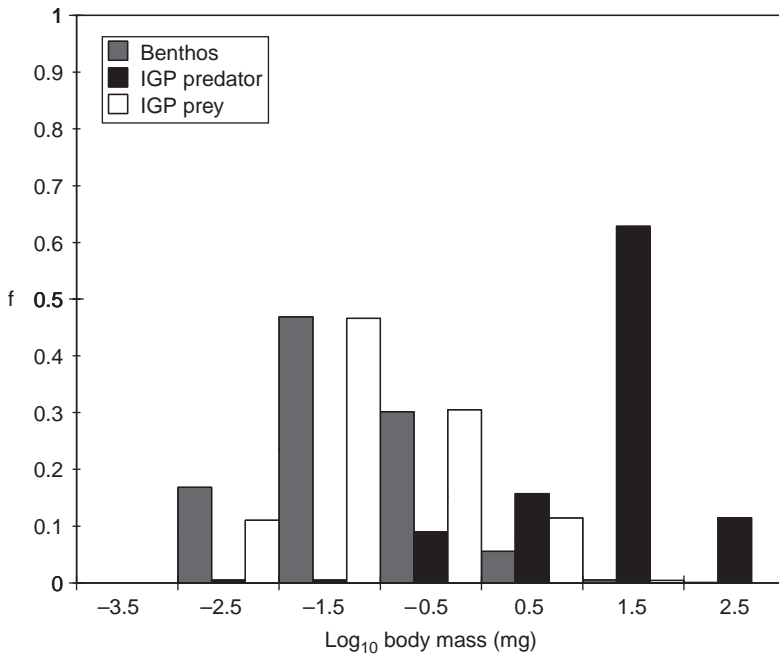
**Figure 16** Size distributions of predators and prey in the environment for the *C. boltonii*–*N. pictetii* feeding link highlighted in [Figure 15](#), showing seasonal patterns in the manifestation of the link and the size classes involved.

as a whole versus those for the individuals actually involved in trophic interactions as either ‘predators’ or ‘prey’ ([Figure 17](#)). Although mutual predation and cannibalism occurred in many permutations within the IGP subweb, when these predator species were subdivided into size classes ([Figure 18](#)), all interactions were accounted for by small predators being eaten by larger individuals, irrespective of species identity. Size refugia were also evident within the IGP subweb for both very large and very small size classes: that is, there was a ‘window of vulnerability’ at intermediate size ratios. IGP was rarely manifested by the smallest predator size classes, which tended to feed instead on smaller primary consumers. In contrast, *C. boltonii* fed on all other predator species and exploited a wider range of progressively larger ‘prey’ as it grew, until it eventually became the largest predator at the top of the food web. Consequently, feeding loops both between and within species were accounted for by life-history omnivory when individual-based predator–prey mass ratios > 1, rather than species identity *per se*.

#### IV. DISCUSSION

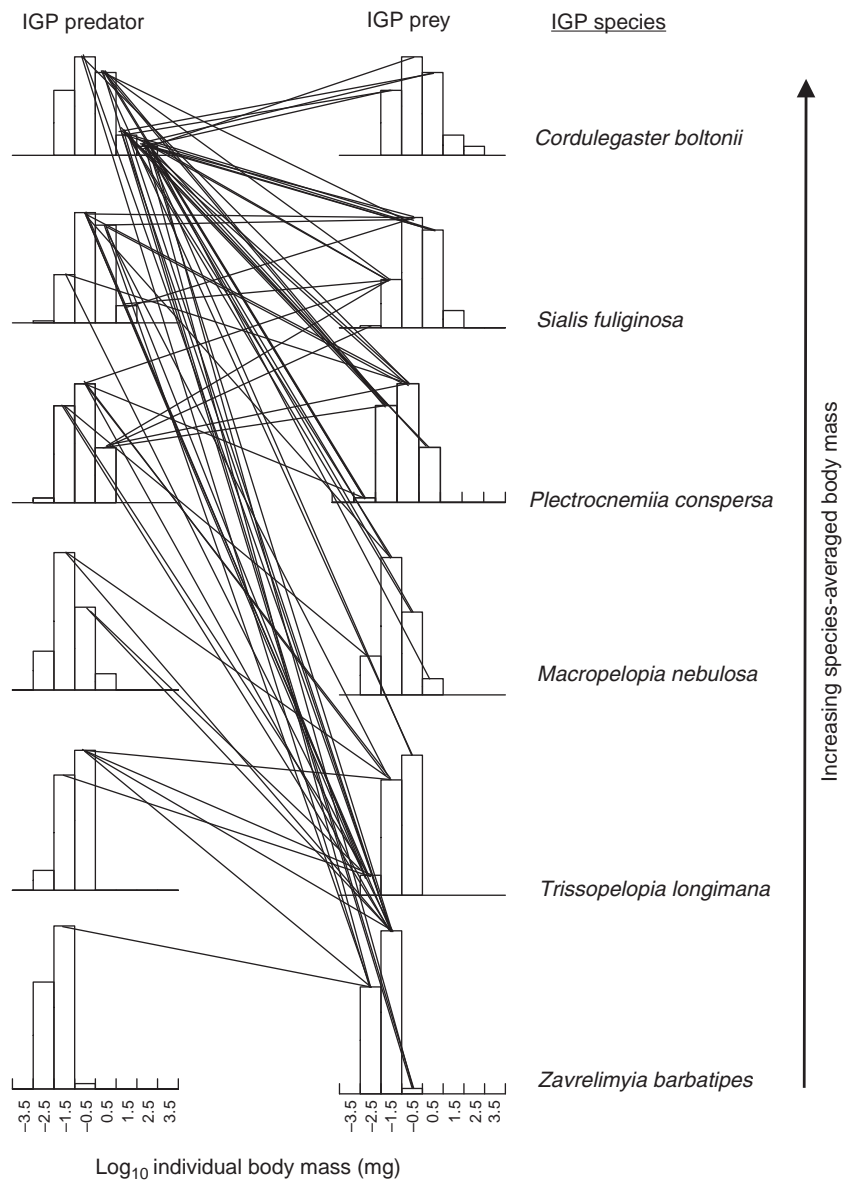
##### A. Size-Based and Species-Based Food Webs

The taxonomic and size-based food webs presented and analysed above highlight the marked differences in our perception of network structure that the two views can create. Both the structure of the predation matrices



**Figure 17** The individual-based body size distribution of nodes and links for the six dominant species within the intraguild predator assemblage of Broadstone Stream. Grey bars represent the body size distribution of predators in the environment; black bars represent the body size distribution of predators acting as consumers in IGP interactions; white bars represent the body size distribution of predators acting as prey in IGP interactions.

and the ability of a model to explain the structure were affected markedly by the choice of how to group individuals. For all four systems, the two versions of each food web differed markedly in many key attributes. The number of links, linkage density, connectance, and the match between the empirical data and the models were, on average, almost twice as high in size-based webs relative to their species-based equivalents. They also exhibited more pronounced ‘small world’ properties (e.g. [Dunne \*et al.\*, 2002](#); [Dunne, 2005](#); [Montoya \*et al.\*, 2006](#)), with higher clustering coefficients and reduced mean shortest path lengths. Taxonomic grouping of individuals has, to date, dominated food web research, raising the possibility that the dominance of this approach might be limiting our ability to understand more fully the drivers of food web structure. Both body size and sampling effort played important roles in determining the number of links recorded in each web, and also their patterning within the web, which was generally well predicted by the ADBM, especially for the size-based webs.



**Figure 18** Decomposing the species-averaged food web into size-based interactions within the predator guild in Broadstone Stream. The six common predator species are arranged vertically, with the largest (*Cordulegaster boltonii*) at the top. Each row represents one predator species, as either predators or prey (thus links within rows represent cannibalism). In no instance did an individual predator consume a larger individual, either within or between species.



We stress that neither the taxonomic nor the size-based approach is necessarily the 'correct' way to represent a food web, as both have their limitations. Taxonomic food webs are unable to capture the size structure of feeding interactions completely, whilst size-based food web cannot characterise the role of taxonomy in determining the presence and patterning of feeding interactions. For instance, unlikely or seemingly impossible predator-prey ratios (e.g. prey that were more than an order of magnitude bigger than their consumers) occurred frequently in our taxonomic webs. Similarly, in the size-based web non-predatory species occurred in size classes that contained predatory individuals. Thus, in both taxonomic and size-based webs a link between two entities in the matrix did not mean that all individuals in that group could potentially feed on all individuals in the other.

Species-averaging masked the fact that predators and prey interacted via subsets of their respective size distributions, such that prey that survived to a large size could become invulnerable to the smaller predators, whilst at the other end of the spectrum very small (and hence energetically unrewarding) prey were rarely taken by the larger predators. In extreme cases, size disparities within the predator guild could even be sufficient to reverse trophic status, as occurred when large individuals of 'small' species were able to prey upon small individuals of 'large' species (Figure 18), which occurred when generations overlapped (Woodward and Hildrew, 2002a,b). This is suggestive of foraging constraints on the ability to detect and handle prey effectively determining the presence (and strength) of feeding links, and emphasises the connection between individual behaviour and the more complex system-level properties of the food web as a whole (Woodward and Warren, 2007).

Foraging theory based on individuals' decisions about what resource types to include in their diets appeared less effective in describing the patterns observed in the taxonomic food webs (30%, 45%, 43%, 62% of links correctly predicted) than in the size-based food webs (74%, 74%, 53%, 83% of the links correctly predicted). Thus, ignoring species identities, and constructing a food web based only on the size of individuals produced an often extremely good fit between the observed data and the model, with up to 83% links being predicted correctly in the size-based Broadstone Stream web. At one level, this is perhaps not surprising: if we construct a food web in such a way as to unambiguously reflect the size relationships of consumers and their resources, then a model based on mechanisms that are also size dependent should provide a better fit to those data than the same food web expressed in taxonomic form. This is not a test of the model *per se*, but an examination of the extent to which understanding the potential role of particular mechanisms, or processes in determining food web structure, is a process of reflection between model and data, considering the processes each encapsulates. It seems likely that other models incorporating rules based on size dependent foraging would also fit better to size-based than taxonomic webs.

Nonetheless, we would observe that the improved fit of the model to the size-based webs, is consistent with the view that foraging theory coupled with body size allometries in individual foraging behaviour could provide plausible explanations of food web structure (but see [Allesina 2008](#); [Rohr \*et al.\*, 2010](#)). This raises the often neglected question of how food web models should be evaluated. The scarcity of food web data, and its limitations have tended to mean that the data are taken as a given, and models, even rather differently constructed or motivated models, are compared to each other on the strength of their performance against that one representation of the food webs. Whilst the concept of a food web is simple, their empirical representation is neither straightforward nor singular, and perhaps evaluation of increasingly sophisticated food web models will require more attention to the nature of the data representation, as well as the details of the models themselves.

## **B. Understanding the High Explanatory Power of the ADBM**

The ADBM predicted some of the important features of the size-based food webs very effectively, such as absence of predation by larger size classes on the smallest size classes (lower size-refugia). This occurs because the relationship between profitability (energetic value of a resource divided by handling time) and resource size is hump-shaped: thus intermediate sized resources should have the highest profitability, whereas more extreme size disparities reduce profitability. Large consumers could, in theory, consume the smallest resources, but this appears not to be the case as doing so would decrease the overall rate at which they gain energy.

The unimodal relationship between resource profitability and size results from assumptions made about how handling time scales with resource size. As resources become smaller, handling time approaches a minimum value: thus very small resource items, which necessarily have very low energetic value, take a disproportionately long time to handle. The handling time scaling function also assumes that as resource size increases and approaches a critical fraction of consumer size ( $b$ ) handling times approach infinity. That is, a consumer cannot handle a resource item larger than this fraction of its own size. Any resources above this size ratio have infinite handling time, zero profitability, and are never included in a consumer's diet. The ratio that produced the best fit of the model to the observed pattern of interactions among species was 0.78 in the Broadstone Stream analysis. In this sense, handling time as used in the model represents a measure of the mechanical (upper and lower) constraints on feeding that consumers face. In support of these arguments, there is evidence that upper- and lower-size refugia, as

assumed by the ADBM, do exist in natural food webs (Schmid-Araya *et al.*, 2002a,b; Woodward *et al.*, 2005a,b).

### C. Explaining ‘Missing’ and ‘Unlikely’ Links

The fact that the presence of ‘missing links’ were often associated with pairwise combinations of rare predators and rare prey is interesting as it suggests that the gaps could be artefacts of undersampling—that is, the model could be correctly predicting where a link is expected, but the data are not sufficiently complete to detect it. Some recently published analyses of empirical food webs concern the contiguity of diets (Allesina *et al.*, 2008; Cattin *et al.*, 2004; Stouffer *et al.*, 2006; Williams and Martinez, 2000): that is, if the available resources are ordered along a single axis, for example, body size, do consumers feed on a set of resources that occupy a contiguous set along the axis, or are there ‘gaps’? One explanation for dietary gaps relates to multiple dimensions of resource variation (i.e. body size being one dimension, and perhaps defensive structures and or chemical being a second dimension) (Allesina *et al.*, 2008; Petchey *et al.*, 2008): that is, the fact that the vulnerability of a prey to a particular consumer may be determined by a combination of traits, such as size and colouration (Allesina *et al.*, 2008; Petchey *et al.*, 2008; Warren, 1996).

It is also possible that apparent dietary gaps might be due to sampling effects, if for instance, low abundance of prey and/or predators results in incomplete characterisation of feeding links. Other anomalies related to the consumption of prey types that lie well outside the ‘core’ dietary range of a consumer, might reflect accidental ingestion or ‘Russian dolls’, whereby the gut contents of an intermediate predator are recorded in the guts of a larger predator. There are several lines of evidence that lend support to these suggestions. For instance, incomplete sampling resulted in underestimation of diet width in the empirical data and instances when the models predicted links that were missing from the empirical data were most likely for combinations of rare predators and rare prey. The individual-based size distribution was far more robust to these effects than were the species-based size distribution, as the former tended to smoothe over the effects of undersampling rare species by allocating these individuals more evenly among nodes, rather than treating them as fixed entities in the latter. The Broadstone data provide an illustrative example of these joint effects of sampling and body size, which were especially marked in the species-averaged web. Here, the three rarest predators, whose yield–effort curves for links were not saturated (see also Woodward *et al.*, 2005a,b), had observed diets that were far narrower than would be predicted on the basis of their body mass alone (Figure 12). Because they overlapped with

the six dominant predators, in terms of their body mass distributions, in the size-based web these three rare (and undersampled) species were mixed within size classes with the common species whose diet was more completely sampled. Intriguingly, in the species-averaged Broadstone Stream web these scarce predators with few observed links were also most similar in body mass to the dominant predators, with the latter being evenly spaced on a log-scale body mass gradient (cf. Figure 13 in Olesen *et al.*, 2010). This might imply that the coexistence of predators within the food web is related to the apportioning of the body mass (and hence prey availability) distribution, unless other dimensions come into play that might create contiguous dietary niches.

False-negative model predictions occurred when the empirical data described a link that was not predicted by the model. Typically, these arose where the data exceeded the 1:1 line between predator and prey body mass and also where predators ate very small prey relative to the rest of their diet. These might represent measurement errors in some cases, but they could also represent real phenomena that enable certain species to somehow bend or break the general rules of size-structuring. In many cases, these exceptions to the rule related to interactions involving the caddisfly *P. conspersa*, a species that uses a net to capture its prey and which can therefore take very small prey and also (occasionally) prey items that are larger than itself (Townsend and Hildrew, 1977, 1979). Many other instances of predators feeding on unusually small prey appeared to represent accidental ingestion or the presence of ‘Russian dolls’, whereby the prey items eaten by an intermediate predator are visible in the guts of a larger predator. For instance, of the 1087 individual predators, only 51 contained a prey individual less than four orders of magnitude smaller than themselves and 41% of these contained two or more prey individuals, a significantly higher proportion than would be expected for 51 randomly chosen predator individuals ( $p = 0.013$ ).

The overall results of the current study highlight the need for models of food web structure that can include the sampling processes that result in the observed data. Two of the key sampling processes in operation that require consideration here are the sampling of prey by predators, and the sampling of predators by researchers. Typically, both of these have been ignored in food web research, despite the powerful influences they can have on many food web properties and our ability to marry data to models in a meaningful way. An analogy may be drawn here with state space models of population dynamics (e.g. Clark and Bjornstad, 2004), which explicitly include biological and observation processes in quantitative models fit to empirical data: we are unaware of similar models of food web structure. Such models would include the potentially stochastic sampling of the environment by consumers and the stochastic

nature of sample of the consumers by ecologists, both of which couple with the biological processes to produce the observed data.

#### D. Seasonal and Ontogenetic Effects

When combined abundances were low (e.g. rare predators and rare prey) feeding links in the summary web were often missing from seasonal versions of the Broadstone Stream web, despite being within the range of feasible links based on the respective body masses of the predators and prey (e.g. [Figure 12](#) in the current study and [Figure 13](#) in [Olesen \*et al.\*, 2010](#)). The seasonal patterns in the expression of links across the six sampling occasions reported here are also reflected in shifts in the extent of dietary niche overlap within the predator guild (cf. [Woodward and Hildrew, 2002b](#)), the structure of the wider food web, and the frequency of predation (cf. [Woodward \*et al.\*, 2005a](#)). Essentially, niche overlap, network complexity and *per capita* ingestion rates peaked during the summer (i.e. when predator and prey body masses spanned the largest intraspecific range as generations overlapped during recruitment periods) and declined progressively over the winter through to spring ([Woodward \*et al.\*, 2005a](#)). Much of this seasonal variability within the food web was related to a combination of imperfect synchrony of reproductive pulses, generational overlap, and differential growth rates of predators and their prey (cf. [Woodward and Hildrew, 2002a,b](#); [Woodward \*et al.\*, 2005a](#)). Such situations, where only subsets of species populations interact intensely at certain times and at others little, or not at all, could potentially produce complex dynamics that differ considerably from those expected if all individuals are equivalent at all times ([de Roos and Persson, 2002](#)).

Mutual predation loops and omnivory often produce dynamics that are highly unstable in mathematical models and should, in theory, be rare (e.g. [May, 1973](#)). This is clearly not the case, however, in most of the well-described empirical webs, where such interactions are common (e.g. [Petchey \*et al.\*, 2008](#); [Williams and Martinez, 2000](#); [Woodward and Hildrew, 2001](#)). Our data were no exception but, unlike most previous studies, our individual-based approach enabled us to ascribe many of these apparent anomalies to ontogenetic shifts in trophic position, which would have otherwise inevitably been obscured by species-averaging. In Broadstone Stream, for instance, the predators moved progressively upwards through the food web and became more generalist as they grew, both within and among species. Thus, the biggest individuals of the dragonfly *C. boltonii* had the broadest diets within the web, and this species ultimately became an apex predator when it entered its largest size classes ([Figure 18](#); see also [Woodward and Hildrew, 2002a,b](#)). Such shifts in diet and trophic status along a continuum of body mass are likely to be prevalent in food webs that

contain predator species that overlap in body size and also display indeterminate growth, as is true for many aquatic ecosystems (e.g. Hardy, 1924).

Unfortunately, true ontogenetic shifts are often very difficult to detect in natural systems, because in most food webs the collection of gut contents involves destructive sampling. Even if this can be avoided, repeated mark-recapture of individuals over a protracted time series is often logistically unfeasible. We were unusually fortunate, therefore, to be able to obtain repeated measures of diet and body mass data for individual fish within the Tadnoll Brook food web. At this finest scale of individual-level data that we explored, body size was again a key determinant of diet and trophic position, as highlighted in the example of the dietary data from a single brown trout that was tracked and gut-flushed on eight sampling occasions as it more than doubled its body mass. When small, this individual preyed primarily on the portion of the prey assemblage that contained the most abundant size classes of invertebrates, but as it grew it began to feed higher in the food web by exploiting the larger but rarer size classes, which were predominantly fishes (Figure 8). This sudden change in diet is suggestive of a behavioural switch that occurred at a particular size threshold, and within the context of salmonid life-cycle biology, data such as these could help resolve the long-standing question as to whether there is a particular size threshold that determines whether an individual remains in freshwater as a resident brown trout or migrates to the ocean to develop into the much larger sea trout form. This exceptionally high data resolution, which is rarely available in food web studies, thus enabled us to characterise ‘true’ individual-level ontogenetic shifts in feeding directly, rather than relying on the use of proxy snapshots of a number of individuals of different size. Future studies that can embed this level of detail within empirical food webs could offer potentially much deeper insight than is currently possible: for instance, they could be used to ascertain whether the feeding niches of apparently ‘generalist species’ are comprised of a wide range of specialist individuals or a set of similarly generalist individuals.

## **E. Implications, Caveats, and Future Directions**

There are several caveats associated with both the models and data presented here that merit further consideration. For instance, the algorithm we used to create the size classes of the size-based food webs simply designated evenly log spaced size classes within the range defined by the smallest to largest individuals observed in each system. It was therefore possible for a size class to be created when in fact no organisms fell in that class, as was the case for three of the four size-based webs. We considered both the likely consequences of the creation of empty size classes, and possible alternatives. The size-based webs had a greater number of links and connectance than their

taxonomic counterparts: removing empty nodes would decrease the number of nodes (but not links), thereby increasing connectance still further and amplifying the contrasts with the taxonomic webs. Therefore, at least for differences in connectance, the presence of empty nodes has not affected the qualitative effects seen. Simply removing empty nodes would leave the size-based food webs with fewer nodes than taxonomic ones, and we were striving to keep the number of nodes (albeit potentially empty ones) equal. Another option would be to create unevenly spaced size classes, and ones that therefore could all contain individuals: this could potentially lead to additional interesting changes in the perception of size-based food web structure and could be addressed in further research.

Our study is necessarily restricted to the four highly-resolved aquatic food webs that have been described using individual-based data for both nodes and links. Since individual-level information, especially in populations of commercially exploited fish stocks, can reveal important information on the ecological effects of fishing on their dynamics (Stenseth and Rouyer, 2008), such highly-resolved data seem certain to emerge far more extensively, at least from aquatic systems, in the near future. Given the prospect of these projected increases in the number of available webs, this raises the question as to what extent this approach might be applied more generally to include other ecosystem types, including terrestrial food webs. It also highlights the need to try to standardise data collection in terms of both what measure of body size is used, how exhaustive sampling is, and how those samples are collected, since all these variables had strong effects on food web structure and the fit between theoretical predictions and empirical observations. It would also be instructive to explore how sampling effort influences the structure of both species- and sized-based webs: for instance, we assigned links based on the presence of a single feeding interaction between nodes, but other criteria (e.g. excluding very rare links and/or nodes) might alter the two types of web in different ways, with the taxonomic webs being potentially far more sensitive to sampling effects than their size-based equivalents.

There is a general perception that terrestrial and aquatic ecosystems differ fundamentally in their size structure, with the former typically being strongly size-structured and the latter seemingly less so (Ings *et al.*, 2009; Yvon-Durocher *et al.*, 2010). It is not inconceivable, however, that at least some of the perceived differences between the importance of size in aquatic and terrestrial ecosystems might be due to the respective disciplines measuring and analysing different things in different ways (Raffaelli, 2007; Yvon-Durocher *et al.*, 2010). Increasing the catalogue of available individual-based data will ultimately allow this to be tested in a more rigorous and standardised manner, and to reassess food webs that have previously been described from either species-based or size-based approaches, but not both.



Size-structuring is expected to be particularly strong where organisms are 'unitary particles' and gape-limited consumption predominates (Cyr and Curtis, 1999; Jennings and Brander, 2010; Woodward and Warren, 2007), but such conditions are not necessarily restricted to aquatic systems and they might be broadly applicable to predator–prey interactions in general (e.g. Brose *et al.*, 2006). Conversely, body size might not be expected to be a major player for different types of organism (e.g. modular species) or for other types of interaction (e.g. in mutualistic networks), where it may have a more subsidiary role to other species traits (Ings *et al.*, 2009; but see Stang *et al.*, 2006, 2009). Similarly, it might not necessarily be the case for interactions between primary consumers and basal resources: one obvious general case of a lack of size structure is the coexistence of both very small (insect) and large (mammalian) herbivores that both feed on many terrestrial plants that also vary greatly in size. This would clearly make it difficult, or even impossible, to characterise and predict the structure and dynamics of such systems based on simple size-based rules, and it is probably meaningless to attempt to do so in such cases.

There have been very few systematic and quantitative analyses of the importance of size for community structure across ecosystem types, but one exception is the extensive compilation and analysis by Brose *et al.* (2005, 2006) of resource–consumer body size information from 20 studies from marine, freshwater, and terrestrial systems. These data include four types of trophic interaction (predator, parasitoid, herbivore, and detritivore) and three consumer types (invertebrates, ectothermic vertebrates, and endothermic vertebrates), although not all possible combinations were evident within each study. Resource–consumer body size ratios differed between ecosystem types, feeding types, and consumer types, but nonetheless the vast majority of feeding interactions involved consumers that were larger than their resources (Brose *et al.*, 2006). These data and some more recent analyses (e.g. Berlow *et al.*, 2009; Yvon-Durocher *et al.*, 2010) suggest that resource–consumer interactions exhibit general size structure, but that its importance varies among systems: an individual-based approach could potentially shed further light on these apparent patterns.

The potentially universal importance of individual body size, as emphasised by its deep connections with many physiological rates (Gillooly *et al.*, 2001), provides the opportunity for it to be applied as a first principle, based on formal mathematical theory, for understanding patterns and processes in complex ecosystems (Petchey and Belgrano, 2010). Using individual size as a metric for thinking about food webs provides scope to seek commonalities and to explain unifying patterns, but it is also important for exploring deviations from these in systems where it is not the primary axis of network structure or dynamics. Despite the apparent potential for adding evermore complexity to what are already very complex systems, at any one time consumers and resources within a food web can always be ordered by body size, and underlying

size constraints on feeding can then be explored, as we have done here. Clearly, if we are to obtain more meaningful insight into food webs we need to view them as more than simply coarse-grained agglomerations of species populations or size classes, and to integrate both taxonomic and size-based approaches (Petchey and Belgrano, 2010). In reality, both taxonomy and size are likely to play important roles, as revealed by some population dynamic models (Andersen and Pedersen, 2010; Blanchard *et al.*, 2009; De Roos *et al.*, 2008; Persson *et al.*, 1998) which could potentially be extended to multispecies systems. The explicit collection of new individual-level data from natural food webs would go a long way to providing a simultaneous understanding of both the general rules (e.g. allometries) and the specific exceptions within ecology that can be related to other drivers, such as, for instance, those associated with biodiversity and biogeochemical fluxes (Belgrano *et al.*, 2002; Naeem, 2006; Reiss *et al.*, 2009).

Future research using an individual-based approach could also address a range of additional questions relating to the relative importance of intraspecific and interspecific variation in body size within food webs, and the implications of this for species coexistence: for instance, if predator diets are nested subsets based largely on body size, do predators partition resources by staggering their phenologies? This approach could therefore help to identify whether niche assembly mechanisms are driven by frequency disruptive selection or neutral processes, and it could improve our ability to develop and test a range of new mechanistic models of individual-based food webs.

## ACKNOWLEDGEMENTS

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## ELECTRONIC APPENDICES

- E1 Food web data
- E2 Yield–effort curves

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