

# Predator–prey body size, interaction strength and the stability of a real food web

MARK C. EMMERSON\*† and DAVE RAFFAELLI‡

\*Department of Biology, University of York, PO Box 373, York, YO10 5YW, UK; †Department of Zoology, Ecology and Plant Science, University College Cork, Lee Maltings, Prospect Row, Cork, Ireland; and ‡Environment Department, University of York, York, YO10 5 DD, UK

## Summary

1. We examined the empirical relationship between predator–prey body size ratio and interaction strength in the Ythan Estuary food web.
2. We have refined a previously published version of the food web and explored how size-based predatory effects might affect food web dynamics. To do so, we used four predatory species *Crangon crangon* (Linnaeus), *Carcinus maenas* (Linnaeus), *Pomatoschistus microps* (Krøyer) and *Platichthys flesus* (Linnaeus) and one common prey species *Corophium volutator* (Pallas) from the food web.
3. All predators and prey were sorted into small, medium and large size classes and placed into mesocosms in all possible pairwise combinations of size and species identity to determine per capita effects of predators on prey ( $a_{ij}$ ).
4. Using Lotka–Volterra dynamics the empirical body size relationships obtained from these experiments and other relationships already available for the Ythan Estuary, we parameterized a food web model for this system. The local stability properties of the resulting food web models were then determined.
5. We found that by choosing interaction strengths using an empirically defined scaling law, the resulting food web models are always dynamically stable, despite the residual uncertainties in the modelling approach. This contrasts with the statistical expectation that random webs with random parameters have a vanishingly improbable chance of stability.
6. The patterning of predator and prey body sizes in real ecosystems affects the arrangement of interaction strengths, which in turn determines food web stability.

*Key-words:* allometric, community, ecosystem, functioning, power law.

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## Introduction

Empirically measured interaction strengths are highly variable (Paine 1992; Fagan & Hurd 1994; deRuiter, Neutel & Moore 1995; Raffaelli & Hall 1996; Wootton 1997; Sala & Graham 2002) and their distributions are commonly skewed towards weaker interactions (Paine 1992; Fagan & Hurd 1994; Raffaelli & Hall 1996; Wootton 1997); however, other patterns have been documented (deRuiter *et al.* 1995; Sala & Graham 2002). Several studies indicate that the patterning of interaction strengths has consequences for food web (and hence community and ecosystem) stability (Yodzis 1981;

deRuiter *et al.* 1995; McCann, Hastings & Huxel 1998; Haydon 2000; Neutel, Heesterbeek & deRuiter 2002). While the patterning of species interactions in real biological communities (Paine 1992; Fagan & Hurd 1994; deRuiter *et al.* 1995; Raffaelli & Hall 1996; Wootton 1997) affects both their stability (Yodzis 1981; McCann *et al.* 1998; Neutel *et al.* 2002) and ecosystem functioning (Hulot *et al.* 2000; Duffy 2002; Paine 2002), the biological mechanisms producing these patterns of interaction strength have remained elusive.

Documenting the distribution of interaction strengths for all links in complex food webs is probably not realistically achievable. If more tractable metrics can be used as surrogate-correlates of interaction strength, then community ecologists would be better able to evaluate the effects on the stability and ecosystem functioning of systems following biodiversity loss (McCann 2000; Loreau *et al.* 2001). One such surrogate may be body

Correspondence: Mark Emmerson, Department of Zoology, Ecology and Plant Science, University College Cork, Lee Maltings, Prospect Row, Cork, Ireland. Tel. + 353 (0) 21 4904355; Fax: + 44 (0) 21 4270562; E-mail: m.emmerson@ucc.i.e.

size. Empirical allometric body size relationships in plant and animal communities are well documented (Peters 1983; Calder 1996; Enquist, Brown & West 1998), and the structuring effects of body size in food webs has been acknowledged for some time (Cohen 1978; Warren & Lawton 1987; Cohen, Briand & Newman 1990; Cohen *et al.* 1993; Warren 1996; Williams & Martinez 2000). The relationship between body size, metabolism and ingestion rate has been used previously to explore food web and community dynamics (Peters 1983; Yodzis & Innes 1992; McCann & Hastings 1997), and assumptions regarding the body sizes of predators and their prey have been used to constrain species interaction strengths dynamically (Law & Morton 1996; Jonsson & Ebenman 1998). Despite the history in ecology of dynamic constraints structuring food chains (Pimm 1982), some authors (Leaper & Huxham 2002) have argued that it is too early to use body size as a determinant of interaction strength in dynamic models. Real food webs contain many taxa whose feeding habits do not conform to the hierarchical pattern predicted by static food web models (Cohen *et al.* 1990), e.g. parasites often feed on prey much larger than themselves. Such arguments are only of concern for food web dynamics if interaction strengths are considered to be functions of larger predators consuming smaller prey. Small predators do consume larger prey and use of the predator–prey body size ratio to predict interaction strength would overcome such issues. To our knowledge empirical exploration of the relationship between predator–prey body size ratio and the patterning of interaction strengths has remained wholly unexplored.

The aim of the present paper is to explore the relationships between predator and prey body sizes and interaction strength and to assess whether such relationships could explain food web patterns and dynamics in real systems. To this end we conducted two empirical studies of the effects of body size on the strength of species interactions (per capita effects) for an assemblage of predators and prey from the Ythan Estuary, north-east Scotland. We then used the results of these empirical investigations to inform a theoretical exploration of body size effects in the much larger Ythan food web. The Ythan food web has been studied extensively (Milne & Dunnet 1972; Baird & Milne 1981; Hall & Raffaelli 1991; Raffaelli & Hall 1992; Huxham & Raffaelli 1995; Huxham, Beaney & Raffaelli 1996; Leaper & Raffaelli 1999) and presently represents one of a few systems for which the abundance and body size of many constituent species are known (deRuiter *et al.* 1995; Woodward & Hildrew 2001; Neutel *et al.* 2002; Cohen, Jonsson & Carpenter 2003). The Ythan Estuary system therefore represents a useful ‘model’ system in which to explore size based predator–prey effects. The distribution of empirically measured interaction strengths, for a subset of the feeding links in Ythan Estuary food web has been documented previously (Raffaelli & Hall 1996) and the biology and ecology of many species is well known.

## Materials, models and methods

We investigated the effects of predator–prey body size ratios on the magnitude of per capita interaction strength in a laboratory-based mesocosm study. The measurement and reporting of interaction strengths in the literature has caused much confusion in the past, mainly because empirical and theoretical ecologists have quantified interaction strengths in a variety of ways. Berlow *et al.* (1999, 2003) review and clarify these differing terms. Here we have used the well-established log–ratio measure of interaction strength (Berlow *et al.* 2000), which expresses the effects of a predator on a prey species population in relation to the abundance of the prey in the absence of the predator. Specifically, the per capita interaction strength of species  $j$  on species  $i$ , so that;  $\alpha_{ij} = \ln(P/C)/Xt$ , where  $P$  is the abundance of prey in the treatment where predators are present and  $C$  is the abundance of prey where the predators are absent.  $X$  is the abundance of the predator and  $t$  is the time period over which the experiment is carried out. This measure is theoretically equivalent to  $\alpha_{ij}$  in the discrete-time version of Lotka–Volterra equations, used traditionally in stability analyses of communities (Pimm 1982). Although the dynamics implied by this measure of interaction strength are simplistic, i.e. a linear type I functional response, its use here is motivated by the need for empirical measures of species interactions, which can be used by the existing suite of models available for such analyses. We have not attempted to quantify empirically the effects of prey on predators  $\alpha_{ji}$ .

The mesocosms consisted of polyethylene tanks (4 L), which were filled with 1.5 L of azoic sediment (frozen at  $-20\text{ }^{\circ}\text{C}$  for 5 days, thawed and then sieved through a 500- $\mu\text{m}$  mesh) and 2.5 L of prefiltered (UV sterilized) natural seawater. Each feeding arena had its own air supply.

### EXPERIMENT 1

In our first experiment we manipulated the size of four predatory species and one prey species. We varied predator and prey size simultaneously, so that all possible pairwise combinations of predator identity, predator size and prey size were investigated for a total of 117 treatments, including nine reference controls (minus predators). The four predators – *Carcinus maenas* (common shore or green crab), *Platichthys flesus* (flounder), *Crangon crangon* (brown shrimp) and *Pomatoschistus microps* (common goby) – were collected from the Ythan Estuary and sorted into three broad size categories, small, medium and large. These predatory species were chosen because they are dominant intermediate predators in the system, because they represent both vertebrate and invertebrate taxa and because they could be collected in sufficient numbers and sorted into distinct size categories for use in this study. The mud shrimp *Corophium volutator* is the most important prey to all four species. *C. volutator* was collected from the Ythan

and then sorted into three size classes using sieves – small, medium and large.

Fifty *C. volutator* were added to each arena and allowed to construct burrows, settling into the tanks over a period of 48 h. One individual predator was added to the respective feeding arena after 48 h and the experiment ran for a further 64 h, after which predators were removed from the arenas killed and fixed in 70% alcohol for later measurement. The remaining *C. volutator* were then sieved from sediments and fixed in 70% alcohol for enumeration and measurement.

## EXPERIMENT 2

In the second experiment, we collected three additional prey species *Hydrobia ulvae* (Pennant; mud snail), *Macoma balthica* (Linnaeus; baltic clam) and *Nereis diversicolor* (Müller; ragworm) from the Ythan to manipulate prey species identity. The aim of this second experiment was to determine the effects of predator size when presented with multiple prey species. Size was kept constant for each prey species (although size differences existed between prey species), 50 large *C. volutator*, 50 *H. ulvae*, 10 *Mbalthica* and 10 *Ndiversicolor* were placed into each tank and allowed to settle for 48 h. These densities reflect the natural abundance of each prey species in the field. The four predatory species were sorted into large and small size classes. Each of the predator × size combinations and controls (minus predators) were replicated three times for a total of 27 tanks. The experiment ran for 64 h and the predators and prey were enumerated as for experiment 1. After completion of both experiments, the size (length mm) of all predators was measured using callipers and prey from control tanks were measured individually using image analysis and direct measurement with callipers as appropriate. Body lengths were converted to dry weight biomass (g) using empirical length–weight relationships derived from a personal database for the Ythan.

Both experiments 1 and 2 were analysed using analysis of variance. We also described the relationship between predator–prey size ratio and interaction strength using a power formula. Such an approach is commonly used for describing allometric relationships (Peters 1983; Calder 1996), where  $y = \phi W^\theta$ , here  $\phi$  and  $\theta$  are empirically derived constants, while  $W$  is the predator–prey size ratio. The basal metabolic rate of an organism can be approximated using a power function with an exponent of 0.75 (or ingestion 0.66; Farlow 1976), where respiration represents the rate at which an individual animal uses its resources to meet the demands placed on it by the environment (Peters 1983). In this context we might expect that interaction strength will reflect an individual organism's demands on its trophic resources.

## MODELLING THE YTHAN WEB

We have revised and updated a previously published binary version of the Ythan Estuary food web (Hall &

Raffaelli 1991). In the present study we aim to determine the effects of body size on interaction strength and hence on food web dynamics. In the previously published version of the Ythan system a number of attributes of the published web make an exploration of food web dynamics difficult. For instance, certain species such as *Acarina* (Buxton 1975), *Alderia modesta* (Lovén), *Hesionodae*, *Parathemisto* sp. (Summers 1974) and *Nototropis* sp. (Healey 1969) have only ever been recorded rarely from the stomach contents of predators in the Ythan Estuary. They have never been found in the field and their own prey is therefore undetermined. In the absence of such dietary information these species would have to be treated as basal resources with positive per capita birth rates rather than negative death rates, as for other consumer species in the system. For this reason it was sensible to exclude them from the present analysis. In contrast to the previously published version of the web featuring the three basal resources detritus, phytoplankton and macroalgae, we have defined four basal resources, particulate organic matter (POM), brown algae, diatoms and *Enteromorpha* sp. Further, we have added the red fox, *Vulpes vulpes* (Linnaeus), which predated the eider, *Somateria mollissima* (Linnaeus) during the summer nesting season and we have added a link between greater black backed gulls, *Larus marinus* (Linnaeus) and eider juveniles. As in previous studies (Leaper & Raffaelli 1999; Leaper & Huxham 2002), using direct measurements, published information and unpublished undergraduate and graduate theses we calculated the body sizes of the 88 species in the food web (see Appendix I for details of those species included).

We explored the behaviour of the revised Ythan Estuary food web using standard predator–prey Lotka–Volterra dynamics of the form:

$$\frac{dX_i}{dt} = X_i \left( r_i + \sum_{j=1}^n a_{ij} X_j \right) \quad i = 1, \dots, n. \quad \text{eqn 1}$$

where  $n$  is the number of species,  $X_i$  is the density of species  $i$ , and  $a_{ij}$  represents the effects of predators on prey (if  $i \neq j$ ) and intraspecific competition (if  $i = j$ ). The effects of prey on predators ( $a_{ji}$ s) were related to  $a_{ij}$ s by an ecological efficiency  $e$ , which was set equal to 0.1 (where  $a_{ji} = e.a_{ij}$ ). Ecological efficiencies show no size dependence but are related rather to physiological characteristics, e.g. ectotherm, endotherm, carnivore or herbivore (Peters 1983). In common with similar studies (Christianou & Ebenman, unpublished data), we assumed further that intraspecific competition ( $a_{ii}$ ) would be stronger for primary producers (basal species,  $a_{ii} = -1$ ) than for consumers (nonbasal species,  $a_{ii} = -0.01$ ). It should be noted that  $r_i$  has different meanings for different species within the food web. For basal species  $r_i$  is positive and is the per capita birth rate. For non-basal species, consumer species  $r_i$  represents the per capita death rate and is negative. To assess the dynamical behaviour of food webs such as the Ythan Estuary we used the empirical

relationships obtained from our experiments manipulating predator and prey body size to estimate the interaction coefficients ( $a_{ij}$ ) of eqn 1. The equilibrium population densities ( $X_i^*$ ) of each species were estimated using empirical body size–density relationships for those species present in the Ythan Estuary ecosystem. Using the interaction coefficients and equilibrium population densities, we calculated the Jacobian matrix,  $C$ . The elements of  $C$ ,  $c_{ij}$ , are the partial derivatives of species  $i$ 's growth equations with respect to the equilibrium population density of species  $j$  ( $c_{ij} = \partial f_i / \partial X_j$ , where  $f_i = dX_i/dt$  and  $c_{ij} = a_{ij}X_i^*$ ). The local stability of the system can then be determined by examination of the eigenvalues ( $\lambda$ ) of the Jacobian matrix. The food web is locally stable if the real parts of all eigenvalues are negative. As a final check on the feasibility of the resulting food webs we solved for the intrinsic birth and death rates ( $r_i$ ) of each species so that  $r = -AX$ , where  $r$  is a vector of intrinsic rates,  $A$  is the matrix of interaction coefficients and  $X$  a vector of population densities. Our check was made to determine whether each species had an appropriately signed intrinsic rate, i.e. positive for basal producers and negative for non-basal consumer species.

## Results

Inspection of the interaction strength data showed that there was a prevalent skew towards weaker interactions. Because per capita effects of predators on prey (interaction strengths) are negative, we  $\log_{10}$ -transformed the absolute value of the observed interactions to increase homogeneity of the variance. For the first experiment examining all possible pairwise combinations of predator–prey body size, Levene's test demonstrated that the variance across groups was homogeneous ( $P = 0.76$ ); consequently the data were analysed using an unbalanced fully factorial ANOVA (a total of 21 replicates were excluded from the analysis because either predators died during the experiment or because very small positive per capita effects were recorded due to mortality among just one or two prey individuals in control tanks). Predator body size, prey body size and species identity were treated as fixed effects.

Live animals are difficult to size accurately a priori. Predators and prey were therefore grouped broadly into small-, medium- and large-size categories; this meant that there was some variability in predator sizes within these groupings. Despite this, our analysis demonstrated significant effects of predator species identity ( $P < 0.001$ ), predator size ( $P < 0.001$ ) and prey size ( $P = 0.042$ ) on interaction strength (ANOVA, Table 1). Significant two-way interaction terms demonstrate that the effects of predator and prey size vary with predator species identity (Table 1,  $P = 0.002$  and  $P < 0.001$ , respectively). Notably the interaction between predator body size and prey body size is non-significant, indicating that size effects are species-specific and dependent on predator species identity. The three-way interaction (Table 1,  $P = 0.068$ ) is marginally non-significant but indicates that the effects of species identity may vary according to both predator and prey body size.

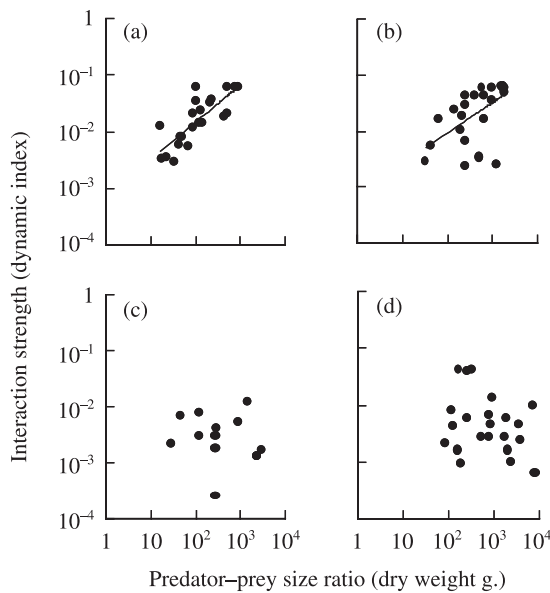
The significant predator identity–predator size interaction (Table 1) indicates species-specific size effects and we therefore explored the relationship between predator–prey body size ratio and interaction strength for each predator species individually (Fig. 1a–d). Predator–prey body size ratio is positively correlated with per capita interaction strength for the two crustacean predators *Crangon crangon* and *Carcinus maenas* (Fig. 1a,b, respectively,  $r^2 = 0.62$ ,  $P < 0.001$  and  $r^2 = 0.29$ ,  $P = 0.004$ ). The slopes of the regression lines are  $b = 0.66$  and  $b = 0.54$  (Fig. 1a,b, respectively) possibly reflecting the scaling of ingestion rate to body size  $W^{0.66}$  (Farlow 1976). The slopes of these regression lines do not differ significantly from an exponent of 0.75 (Fig. 1a,b;  $t$ -test: *C. crangon*  $t = 0.91$ , d.f. = 19; *C. maenas*  $t = 1.23$ , d.f. = 21). There is no apparent relationship for the two fish predators *Pomatoschistus microps* (Fig. 1c,  $P = 0.658$ ), and *Platichthys flesus* (Fig. 1d,  $P = 0.212$ ), the significance of which is discussed below. We have been unable to identify alternative independent covariates that might account for the variability evident in Fig. 1a–d.

In the second study, we manipulated predator size for a mixed assemblage of prey species to investigate the generality of size effects. We manipulated the size of the four predatory species (small and large predators),

**Table 1.** Analysis of variance, experiment 1. Effects of predator identity, predator body size and prey body size on interaction strength

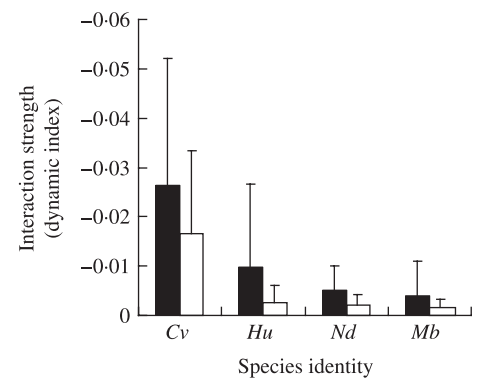
Source of variation	Per capita interaction strength*				
	SS	d.f.	MS	<i>F</i>	<i>P</i>
Predator identity (PI)	11.92	3	3.97	35.76	0.001
Predator size	1.95	2	0.97	8.76	0.001
Prey size	0.74	2	0.37	3.35	0.042
Predator size $\times$ prey size	0.69	4	0.17	1.55	0.201
PI $\times$ predator size	2.629	6	0.438	3.94	0.002
PI $\times$ prey size	3.341	6	0.557	5.01	0.001
PI $\times$ predator size $\times$ prey size	1.599	7	0.228	2.05	0.064
Error	6.223	56	0.111		
Total	30.552	86			

\*Data [absolute values (no zero values present)] were  $\log_{10}$ -transformed to conform to the assumption of normality.



**Fig. 1.** Relationship between predator-prey body size ratio and interaction strength. Regressions for the four predatory species studied, regressions are power regressions: (a) *C. crangon*:  $y = 0.0007W^{0.66 \pm 0.11(1SE, n=21)}$ ,  $r^2 = 0.62$ ,  $P < 0.001$ , (b) *C. maenas*:  $y = 0.0007W^{0.54 \pm 0.17(1SE, n=23)}$ ,  $r^2 = 0.29$ ,  $P = 0.004$ , (c) *P. microps*: not significant,  $r^2 = 0.065$ ,  $P = 0.65$ , (d) *P. flesus*: not significant,  $r^2 = 0.03$ ,  $P = 0.21$ .

and provided these predators with a range of prey species whose size was maintained within each prey type. Data were analysed using a balanced fully factorial ANOVA. Here, predator body size, predator identity and prey identity were treated as fixed factors; no mortality occurred among the predators and all per capita effects were either zero or negative. Levene's test again confirmed that the variance was homogeneous across groups after  $\log_{10}$ -transformation ( $P = 0.66$ ). The effects of predator body size were highly consistent (Fig. 2). The average interaction strength for large predators was significantly greater than for smaller predators ( $P = 0.003$ ); there were significant effects of predator identity ( $P = 0.001$ ) and significant effects of prey identity ( $P = 0.001$ ) (Table 2, ANOVA). The interaction between predator



**Fig. 2.** Predatory size effects on multiple prey species. The mean per capita effect (here untransformed) of one predator individual on different prey species (see below) is consistently greater for large predators (■) than for small predators (□). Here predator species identity is ignored. See Table 2 for details of ANOVA on the  $\log_{10}$ -transformed absolute values of per capita effects. Prey species are: Cv, *Corophium volutator*, Hu, *Hydrobia ulvae*, Nd, *Nereis diversicolor*, Mb, *Macoma balthica*.

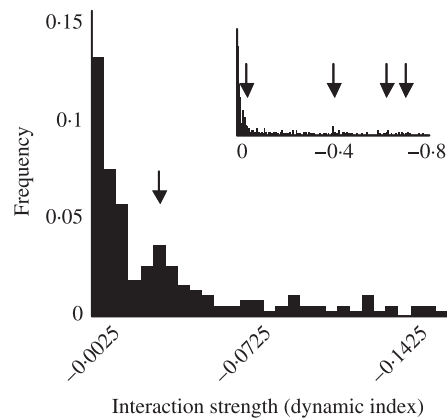
size and predator identity was also significant (Table 2,  $P = 0.001$ ), indicating that interaction strength varied with predator identity and predator body size, confirming our previous observation that size effects were specific to different predators. The non-significant predator size-prey identity interaction (Table 2,  $P = 0.392$ ) indicates that predator body size effects did not vary with prey species identity, i.e. that size effects were consistent. However, the significant predator identity-prey identity interaction term (Table 2,  $P = 0.005$ ) indicates that there were specific predator-prey effects detectable in the experiment. Examination of the regressions between predator-prey body size ratio and interaction strength for these mixed predator-prey treatments indicates no significant relationships when different prey species are combined in a single regression (cf. experiment 1) and thus confirms the result that predatory effects are species-specific.

To determine whether patterns of body size could affect the stability of food webs, we used our findings to explore the stability properties of the Ythan Estuary

**Table 2.** Analysis of variance, experiment 2. Effects of predator body size, predator identity and prey identity on interaction strength

Source of variation	Per capita interaction strength*				
	SS	d.f.	MS	F	P
Prey id.	$1.001 \times 10^{-3}$	3	$3.337 \times 10^{-4}$	23.482	0.001
Predator id.	$6.107 \times 10^{-4}$	3	$2.036 \times 10^{-4}$	14.323	0.001
Predator size	$1.389 \times 10^{-4}$	1	$1.389 \times 10^{-4}$	9.772	0.003
Prey id. $\times$ predator id.	$3.859 \times 10^{-4}$	9	$4.288 \times 10^{-5}$	3.017	0.005
Predator size $\times$ prey id.	$4.327 \times 10^{-5}$	3	$1.442 \times 10^{-5}$	1.015	0.392
Predator size $\times$ predator id.	$4.170 \times 10^{-4}$	3	$1.390 \times 10^{-4}$	9.780	0.001
Predator size $\times$ predator id. $\times$ prey id.	$2.328 \times 10^{-4}$	9	$2.587 \times 10^{-5}$	1.820	0.082
Error	$9.095 \times 10^{-4}$	64	$1.421 \times 10^{-5}$		
Total	$3.739 \times 10^{-3}$	95			

\*Data (absolute values +1) were  $\log_{10}$ -transformed to conform to the assumption of normality.



**Fig. 3.** The frequency distribution of interaction strengths ( $n = 421$ ). For the Ythan Estuary food web the frequency distribution of interaction strengths is strongly skewed towards weak interactions. Predator–prey body size ratios were determined for all links in the web and interactions were calculated using the regression equation  $y = 0.0007W^{0.66}$  (see Fig. 1a), where  $W$  is predator–prey body size ratio. The frequency distribution shown here contains 199 observations; the remaining 222 represent the tail of the frequency distribution, a section of which is illustrated in the inset. Arrows highlight possible modes in the tail of the interaction strength distribution.

food web. We assumed that the relationship between predator–prey body size ratio and interaction coefficients could be described accurately by a power regression. We used the two empirically obtained exponents of 0.66 and 0.54 for *Crangon* and *Carcinus* (Fig. 1a,b) and parameterized all predatory interactions ( $a_{ij}$ s) by calculating predator–prey size ratios for all links in the web using the average adult body sizes of all species (data on the size structure within each individual species population is not available for the Ythan Estuary). Qualitatively, these interaction strength distributions show a strong skew towards weak interactions (Fig. 3, corresponding to an exponent of 0.66). Possible modes do exist in the long tail of the interaction strength distribution (Fig. 3 inset), but inspection of the remaining tail ( $< -0.8$ ) reveals no modes with a frequency larger than 0.0071.

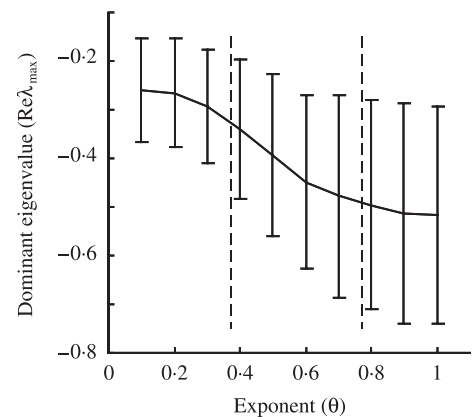
Using Lotka–Volterra dynamics the stability of any food web can be determined using a local stability analysis (Pimm 1982), which requires the use of the Jacobian matrix ( $C$ ) at equilibrium, where the elements of  $C = c_{ij} = a_{ij}X_i$ . For the Ythan Estuary food web body size–density relationships are well documented (Leaper & Raffaelli 1999) and we used such relationships to estimate equilibrium population densities. The adult body sizes of species included in the Ythan Estuary food web were reviewed from the literature and unpublished PhD and Masters' theses. Where available, abundance was scaled to the intertidal area of the estuary (1.85 km<sup>2</sup>) and plotted as a function of adult body size. The resulting relationship  $X_i = 95.92W_i^{-1.18}$  was then used to estimate the equilibrium population size of species  $i$ . We determined that it was more appropriate to work in units of biomass density  $B_i$  (biomass per unit area) rather than density

**Table 3.** Sensitivity analysis. Sensitivity of stability to the exponent  $\theta$ , where  $\theta$  is: (a) empirical exponents obtained from experiments using *Crangon crangon* and *Carcinus maenas* as predators; (b) incremented at 0.1 intervals over the range 0.1–1; (c) a random variable between 0 and 1 for each link in the food web; and (d) the interaction coefficient  $a_{ij}$  was treated as a uniformly distributed random variable between 0 and 1 and was therefore independent of the effects of body size ratio and the exponent,  $\theta$

Exponent ( $\theta$ )	Permutations			
	% Stable	$a_{ij}B_i$	$B_i$	$a_{ij}$
(a) 0.66	100	0	99.7	0
0.54	100	0	100	0.2
(b) 0.1	100	4.5	100	100
0.2	100	0.4	100	99.2
0.3	100	0	100	53.4
0.4	100	0	100	6.7
0.5	100	0	100	1
0.6	100	0	99.7	0.1
0.7	100	0	98.7	0
0.8	99	0	95.4	0
0.9	97.7	0	91.4	0
1	95.3	0	85.1	0
(c) Random	95.4	0.4	96.4	10.1
(d) Uniform	0.5	0	0	0

*per se* (abundance per unit area). This use of units reflects both ingestion, the consumption of biomass by a predator and also concepts associated with biodiversity and ecosystem functioning, so that  $B_i = 95.92W_i^{-0.18}$ . For each species in the food web we defined biomass density randomly from within the 95% confidence intervals associated with the density body size power regression, to produce 1000 vectors containing the population densities for all species. Using these equilibrium biomass density vectors we then calculated  $C$  and determined the stability of the system to small perturbations from the equilibrium (the real parts of all eigenvalues must be negative for the dynamic system to be locally stable). For the Ythan Estuary food web, we found that 100% of the resulting Jacobian matrices parameterized with either an exponent of 0.66 or 0.54 were stable (Table 3a). To determine whether this high proportion of locally stable parameterizations resulted from quasi-diagonal dominance (qdd) (Neutel *et al.* 2002), we permuted randomly all positive and negative off diagonal elements while maintaining predator–prey pairings, *sensu* Yodzis (1981). This procedure maintained both food web topology and the sign of each interaction within a predator–prey pair. The randomization changed only the position of a predator prey pairing within the food web, i.e. non-zero  $c_{ij}$  terms remained non-zero, the negative  $c_{ij}$  terms remained negative and were located in the upper triangular portion of the matrix; each corresponding positive  $c_{ji}$  term was located in the lower triangle of the matrix. The diagonal  $a_{ii}$  terms remained unpermuted. These permuted Jacobian matrices were then again checked for local stability (Table 3a). We found that none of the resulting webs were stable.

By defining the Jacobian matrix in this way, body size ( $W_i$ ) effects enter into the matrix in two ways: first, through generating the assumed equilibrium biomass densities ( $B_i = \phi W_i^\theta$ ) and secondly, in the values of  $a_{ij} = \phi (W_j/W_i)^\theta$ . To determine through which route body size effects exert a greater stabilizing effect, we conducted two further permutations. First, each vector of biomass densities was permuted before calculating the Jacobian, and secondly, the specific internal patterns of interaction coefficients of  $A$  were permuted (as described above for the Jacobian) before the Jacobian was generated. This procedure showed that permuting the biomass densities ( $B_i$ ) has little effect on the stability of the food webs, but once the patterning of interaction coefficients ( $a_{ij}$ ) is altered, there is a dramatic decline in the stability of the resulting Jacobian matrices (Table 3a). We analysed further the sensitivity of stability to the value of the exponent  $\theta$  by incrementing the exponent at intervals of 0.1 over the range 0.1–1. The three forms of permutation were also carried out to determine the relative contribution of body size to food web stability as the exponent,  $\theta$ , changed (Table 3b). The sensitivity analysis shows that as  $\theta$  increases in magnitude, there is a gradual decline in the probability that an unpermuted Jacobian matrix will be stable. Body size exerts greatest influence over the probability of stability occurring by determining the pattern and arrangement of interaction coefficients when interaction coefficients alone are permuted; none of the perturbed food webs are stable when  $\theta = 0.7$  (Table 3b). The pattern of biomass densities has little effect on stability. Examination of the dominant eigenvalue ( $\lambda_{\max}$ ) reveals how stable different food web parameterizations are with respect to one another. The dominant eigenvalue describes how quickly a system will return to equilibrium following a small perturbation; the more negative the eigenvalue the more quickly it will return, i.e. its resilience increases. As the exponent,  $\theta$ , increases, so the mean  $\lambda_{\max}$  for each set of stable Jacobian matrices declines, becoming more negative (Fig. 4). At the same time as  $\theta$  increases so the variance of the mean  $\lambda_{\max}$  also increases. This means that as  $\theta$  increases the stable food webs become more resilient, that is more stable. Our empirical results suggest that body size effects are predator species specific. To investigate this we treated  $\theta$  as a random variable between 0 and 1 for each of the links in the food web and examined the stability of the resulting webs (Table 3c). This shows that even when  $\theta$  is treated as a random variable, over 95% of the resulting webs are stable. We also treated the predatory interaction coefficients  $a_{ij}$  as uniformly distributed random variables between 0 and 1, which were then independent of body size (Table 3d). Body size does still exert a stabilizing influence on the food webs through the biomass densities ( $B_i$ ). Only 0.5% of the resulting webs were stable. None of these remained stable after the permutations were carried out. This illustrates that it is the specific internal patterning of interaction coefficients in the matrix,  $A$ , that determine predominantly the stability of the dynamical system.



**Fig. 4.** The stability of the Ythan Estuary food web. The mean dominant eigenvalue for 1000 parameterizations of the Ythan Estuary food web declines (becomes more negative) as the exponent,  $\theta$ , increases. Coincidentally the variance increases (error bars represent  $\pm 1$  SD). The two dashed vertical lines represent the lower and upper confidence limits of the two empirically measured exponents (see Fig. 1a,b).

Finally, previous studies (May 1973; Pimm & Lawton 1977, 1978) have defined the feasibility of food webs as the existence of positive and finite population densities. Using this criterion all of the food webs in this study would be feasible. To provide a check on our approach we also calculated the intrinsic birth or death rate ( $r = -AX$ ) of each species, to determine whether the food webs had an appropriate sign structure, i.e. positive intrinsic rates for primary producers and negative for consumers. We found that, consistently, three consumer species had positive per capita death rates (100% of parameterizations using an empirical exponent of 0.66). These were *Vulpes vulpes* (red fox), *Eteone longa* (Fabricius) and *Retusa obtusa* (Montagu). All are predatory species consuming single prey species in the current food web. When these predatory species were removed from the food web, over 90% of parameterizations had an appropriate sign structure and 100% were stable.

## Discussion

Previous studies indicate that predator size plays an important role in structuring communities (Cohen 1978; Williams & Martinez 2000), and that the range of prey sizes a predator is capable of consuming could determine food web structure (Warren 1996). Here we have demonstrated that body size feeding relationships exist and that the per capita strength of trophic interactions can be dependent on the body size ratio among certain, but not all, predators and prey. Interaction coefficients can then be considered a function of predator and prey body size  $\phi(W_i, W_j)$ . For such body size effects the relationship between predator-prey body size ratio and interaction strength can be approximated using a power formula with an exponent  $\theta$  of between 0 and 1, so that  $a_{ij} = \phi(W_j/W_i)^\theta$ . Empirical measures

indicate that the actual exponent may lie between 0.5 and 0.7, possibly reflecting an underlying process such as the scaling of ingestion or metabolism with body size, although this requires more confirmatory experiments.

Our empirical data indicate that predatory size effects are predator species specific, and that species-to-species-specific predatory effects are present; this has important implications for arguments concerned with biodiversity and ecosystem functioning. If body size effects are dependent on species identity, and body size effects can determine food web structure (Cohen 1978; Warren 1996; Williams & Martinez 2000), then the loss of particular species from ecosystems may have important consequences for their structure and ecosystem functioning. Our simulations show that scaling interaction strength to predator–prey body size ratio using a general exponent increases the probability of finding highly stable food webs. Even when this exponent is treated as a species-specific parameter of the model (a random variable between 0 and 1 for each interaction), we find that a large proportion of the resulting food webs are stable. This advocates the use of such a general relationship and highlights the importance of body size not only for determining food web topology (Warren 1996; Williams & Martinez 2000), but also for food web dynamics (Law & Morton 1996).

Our analysis of the stability of the Ythan food web assumes explicitly that per capita effects scale with predator–prey body size ratio, with an exponent of around 0.6. Our feeding trials show that there is compelling evidence to support that assumption for the two crustacean predators, but not for the two fish predators (experiment 1). There are two competing explanations for these apparently contrasting results. First, the relationship really is different for fish and for crustaceans, or more generally is dependent on taxon. Secondly, the experimental arenas and or the condition of the predators did not allow the fish to feed properly. The first explanation seems unlikely, as larger consumers must ingest more food resources to satisfy their increased metabolic demands (Peters 1983; Calder 1996). Other studies indicate that the feeding behaviour of *P. microps* is affected under laboratory conditions (Healey 1969), and based on our experience with the experimental system this is the most parsimonious explanation for the lack of a relationship. The two crustacean predators are able to excavate actively prey such as *C. volutator* from their burrows within the sediment, whereas both the goby (*P. microps*) and flounder (*P. flesus*) are ambush predators and rely on prey moving within their sphere of influence. The arenas used may have been inappropriate to permit this behaviour. Nevertheless, the clear-cut nature of the stability analyses using a scaling exponent of approximately 0.6 points to a need to characterize the exponent for a much greater range of taxa in future work.

The sensitivity analysis of food web stability to the exponent  $\theta$  illustrates that when  $\theta$  is small, i.e. close to zero, irrespective of the ratio ( $W_j/W_i$ ) there is only a

weak-structuring effect of body size. To illustrate what we mean by a structuring effect of body size on the arrangement of interaction coefficients consider two predators, one large and one small, both feeding on small prey. When  $\theta$  is close to zero these predators will have approximately equivalent effects on the prey species and the structuring effect of body size will be weak. If however,  $\theta$  was large (closer to 1) then the larger predator would have a stronger per capita effect on the small prey species, and the structuring effect of body size on the pattern of interaction coefficients would be strong. Our analysis shows that the internal structure of interaction coefficients in the matrix,  $A$ , is important. For instance, as  $\theta$  increases towards 1, its effect on the ratio ( $W_j/W_i$ ) becomes more pronounced, along with the internal arrangement of interaction coefficients in the matrix  $A$ . This means that when  $\theta$  is close to zero and the internal arrangement of interactions throughout the matrix  $A$  is much less pronounced, permuting these coefficients has little effect on food web stability. There is a qualitatively similar effect of body size on the pattern of biomass density. From our data for the Ythan Estuary, the relationship between body size and density is  $X_i = 95.92W_i^{-1.18}$ . To calculate biomass density we simply multiply density by body size, so that  $B_i = 95.92W_i^{-1.18+1}$ . The exponent is now close to zero, i.e.  $-0.18$ , so that biomass density is essentially equivalent irrespective of body size. Permuting these biomass densities will have little effect on the structure of biomass, as biomass density is essentially distributed uniformly with body size. The effect of the exponent can be seen clearly in the results of the sensitivity analysis. As  $\theta$  increases, the percentage of webs that remain stable after the interaction coefficients are permuted decreases. Permuting the biomass densities  $B_i$  has little effect on food web stability as the exponent,  $\theta$ , increases (Table 3b). A large percentage of food webs remain stable. Recently, Jansen & Kokkoris (2003) have shown that as the mean and variance of interaction coefficients in a food web increase so stability declines. Over a given range of body size ratios as the exponent,  $\theta$  increases so the mean and variance of the predicted interaction coefficients also increases. Based on the observations of Jansen & Kokkoris (2003) we might predict that as the exponent increases so stability should decline. Our sensitivity analysis supports these findings and this offers a possible explanation of why the proportion of stable food webs declines as  $\theta$  increases. However, as  $\theta$  increases, on average the dominant eigenvalue of the Jacobian matrix declines (becomes more negative) and the variability increases (Fig. 4). This means that as  $\theta$  increases, the probability that a food web will be stable declines, but the resulting food webs, which are stable, are more resilient.

When the exponent,  $\theta$ , is treated as a random variable between 0 and 1, separately for each link in the food web, 95% of the resulting food webs are found to be stable. Each of the interaction strengths is therefore an independent (nonuniform) random variable between the fixed constant  $\phi$  (fixed with respect to variation of

the predator and prey body size if  $\theta = 0$ ) and the ratio of body masses of the predator and prey, multiplied by the same fixed constant,  $\phi$ , if  $\theta = 1$ . This is surprising and may indicate that stability results from food web topology. However, when the  $a_{ij}$  terms are treated as uniformly distributed random variables between 0 and 1 (independent of predator prey body size ratio and  $\theta$ ) only 0.5% of the resulting food webs were stable (Table 3d). In addition, the frequency distribution of interaction coefficients generated when  $\theta$  is a random variable between 0 and 1 is also skewed strongly towards weak interactions and has a long tail, as for Fig. 3. In combination this indicates that it is the arrangement of predator–prey body size ratios that determine food web stability.

To provide a check on our approach we have extended classic measures of feasibility, which require positive and finite population densities, to include constraints on the signs of the intrinsic rates in our parameterized food webs. Given classic measures of feasibility, all the food webs considered here would be feasible. Our extended measure of feasibility indicates that three species within the food web have consistently positive intrinsic death rates. These species are all consumers in the food web feeding on single prey species. The positive death rates occur for a number of possible reasons: The current version of the Ythan Estuary food web does not truly represent the feeding interactions of these three species; for instance, it is widely acknowledged that *Vulpes* (red fox) is an omnivorous predator of terrestrial systems feeding on a wide variety of prey. In the current version of the Ythan web it feeds only on *Somateria mollissima*; in reality *Vulpes* would obtain prey from a number of sources. The positive effects of its prey *S. mollissima* are not currently sufficient to support the population size we use here and so analytically the death rate must be positive. This may also be the cause for the positive death rates of *E. longa* and *R. obtusa*; alternatively, the positive per capita death rates might occur because our estimation of abundance in the Ythan food web is inaccurate for these predators. These positive intrinsic death rates indicate where future research might be focused, identifying alternative prey for these species in the system.

The Ythan Estuary food web that we use here contains 88 species; there are 421 links in the web and 1467 omnivorous loops. Loops here are defined after Neutel *et al.* (2002). Classic studies have argued that omnivory (where species feed at more than one trophic level) should be statistically rare in food webs, because a large proportion of randomly parameterized simple omnivorous food webs were unstable (Pimm & Lawton 1977, 1978). Given the prevalence of omnivory in the Ythan Estuary food web, we would expect that parameter choices for which the resulting dynamic system has a stable equilibrium should be statistically rare. Additionally, the parameter space for such a complex dynamical system is vast: for the Ythan Estuary as presented here there are 930 dimensions, so that the stable and feasible

subregion of this large parameter space will be small and difficult to find, akin to finding a needle in a haystack (May 1973; Pimm 1982). Lawlor (1978) argued that parameter combinations representative of realistic model ecosystems probably represent only a tiny fraction of the full parameter space. She showed that the probability of finding a stable randomly parameterized food web with 60 species was vanishingly small (1 in a googol, where a googol =  $10^{100}$ ). Given the large size of the Ythan food web (88 species) and the high degree of omnivory present we might expect that parameter choices that yield stable solutions to eqn 1 would be very rare or difficult to find, yet using body size we have been able to find such parameterizations. Using our empirical knowledge of this real ecosystem detailing the *composition* of species and the *structure* of the food web, we have been able to refine our search of parameter space using species body sizes. This is important. We now possess a tool with which we can inform theoretical approaches to the study of ecosystem functioning. We have used a simplistic approach to the dynamics (Lotka–Volterra and linear type I functional responses) to investigate the dynamic properties of the Ythan food web and alternative modelling approaches are needed to evaluate the robustness of our findings. Despite the need for validation of our results, we propose that it is the dynamic constraints on the strength of species interactions, possibly determined by body size and underlying processes such as metabolism, that determine extant and evolved food web topology. This implies that many of the static topological patterns documented for food webs may in fact be a reflection of the dynamic constraints on the strength of species interactions. Combinations of species interactions, which are either too strong or too weak and which do not result in persistent coexisting sets of species, are unlikely to be seen in the real world. Our results show that the body sizes of predators and prey can be used to predict the strength of trophic interactions, which will result in such persistent sets of species.

The Ythan Estuary food web represents one of just a few food webs for which body size, abundance and biomass are known (deRuiter *et al.* 1995; Woodward & Hildrew 2001; Neutel *et al.* 2002; Cohen, Jonsson & Carpenter 2003). Even the Ythan data are not entirely comprehensive; the abundances of certain species are either known imprecisely or not currently available. Testing our approach in similarly well-resolved food webs could validate or question the generality of such body size effects on the dynamics of these food webs. Several versions of the Ythan Estuary food web have been used in the literature, including one with meta-zoan parasites (Huxham *et al.* 1996), and we have not investigated the per capita effects of parasites on their hosts. Such interactions are unlikely to conform to the types of body size effects we report here, although recent studies have argued for lower triangularity in parasite subwebs and a lack of size effects in determining static food web patterns (Leaper & Huxham 2002). It is

possible that parameterization of food webs featuring parasites may be possible using predator–prey body size ratios. Using our approach such interactions would be weak with small predators feeding on large prey. Whether this would reflect empirical per-capita effects realistically remains to be seen and is certainly worthy of further investigation.

In conclusion, ingestion scales with predator body size by two-thirds (Farlow 1976), but the biomass of prey consumed will depend on prey body size, i.e. the interaction between a predator and its prey cannot be predicted by predator body size alone. We provide a biological mechanism that explains the skewed distributions of interaction strengths in real communities, which are emergent features of food webs that reflect patterns of body size. Anthropogenically mediated shifts in body size structure are a common feature of harvested populations. Such shifts, which happen coincidentally with species loss, may occur over short time scales, at a rate that natural communities are demographically unable to track (Conover & Munch 2002). In real ecological systems the patterning of interaction strengths is correlated with ecosystem and community stability (McCann *et al.* 1998; Haydon 2000; Neutel *et al.* 2002), and we have shown that both the patterning and distribution of interaction strengths can be determined by the body size distributions of predators and prey. Human-induced shifts in body size structure of natural populations through exploitation (Jennings, Warr & Mackinson 2002; Conover & Munch 2002) could therefore have significant effects on the stability of those systems.

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### References

- Baird, D. & Milne, H. (1981) Energy flow in the Ythan estuary, Aberdeenshire, Scotland. *Estuarine and Coastal Shelf Science*, **13**, 455–472.
- Berlow, E.L., Neutel, A.-M., Cohen, J.E., De Ruiter, P.C., Ebenman, B.O., Emmerson, M., Fox, J.W., Jansen, V.A.A., Jones, J.I., Kokkoris, G.D., Logofet, D.O., McKane, A.J., Montoya, J.M. & Petchey, O.L. (2004) Interaction strengths in food webs: issues and opportunities. *Journal of Animal Ecology*, **73**, 585–598.
- Berlow, E.L., Navarrete, S.A., Briggs, C.J., Power, M.E. & Menge, B.A. (1999) Quantifying variation in the strengths of species interactions. *Ecology*, **80**, 2206–2224.
- Buxton, N.E. (1975) *The feeding behaviour and food supply of the common shelduck (Tadorna tadorna) on the Ythan Estuary, Aberdeenshire*. PhD thesis, University of Aberdeen, Aberdeen.
- Calder, W.A. (1996) *Size, Function and Life History*. Dover Publications, New York.
- Cohen, J.E. (1978) *Food Webs and Niche Space*. Princeton University Press, Princeton.
- Cohen, J.E., Briand, F. & Newman, C.M. (1990) *Community Food Webs: Data and Theory. Biomathematics*, Vol. 20. Springer, Berlin.
- Cohen, J.E., Jonsson, T. & Carpenter, S.R. (2003) Ecological community description using the food web, species abundance, and body size. *Proceedings of the National Academy of Sciences USA*, **100**, 1781–1786.
- Cohen, J.E., Pimm, S.L., Yodzis, P. & Saldana, J. (1993) Body sizes of animal predators and animal prey in food webs. *Journal of Animal Ecology*, **62**, 67–78.
- Conover, D.O. & Munch, S.B. (2002) Sustaining fisheries yields over evolutionary time scales. *Science*, **297**, 94–96.
- DeRuiter, P.C., Neutel, A.-M. & Moore, J.C. (1995) Energetics, patterns of interaction strengths, and stability in real ecosystems. *Science*, **269**, 1257–1260.
- Duffy, J.E. (2002) Biodiversity and ecosystem function: the consumer connection. *Oikos*, **99**, 201–219.
- Enquist, B.J., Brown, J.H. & West, G.B. (1998) Allometric scaling of plant energetics and population density. *Nature*, **395**, 163–166.
- Fagan, W.F. & Hurd, L.E. (1994) Hatch density variation of a generalist arthropod predator – population consequences and community impact. *Ecology*, **75**, 2022–2032.
- Farlow, J.O. (1976) A consideration of the trophic dynamics of a late Cretaceous large-dinosaur community (Oldman Formation). *Ecology*, **57**, 841–857.
- Hall, S.J. & Raffaelli, D. (1991) Food-web patterns – lessons from a species-rich web. *Journal of Animal Ecology*, **60**, 823–842.
- Haydon, D.T. (2000) Maximally stable model ecosystems can be highly connected. *Ecology*, **81**, 2631–2636.
- Healey, M.C. (1969) *The distribution and abundance of sand gobies Gobius minutus in the Ythan Estuary*. PhD thesis, University of Aberdeen, Aberdeen.
- Hulot, F.D., Lacroix, G., Lescher-Moutoué, F. & Loreau, M. (2000) Functional diversity governs ecosystem response to nutrient enrichment. *Nature*, **405**, 340–344.
- Huxham, M., Beaney, S. & Raffaelli, D. (1996) Do parasites reduce the chances of triangulation in a real food web? *Oikos*, **76**, 284–300.
- Huxham, M. & Raffaelli, D. (1995) Parasites and food-web patterns. *Journal of Animal Ecology*, **64**, 168–176.
- Jansen, V.A.A. & Kokkoris, G.D. (2003) Complexity and stability revisited. *Ecology Letters*, **6**, 498–502.
- Jennings, S., Warr, K.J. & Mackinson, S. (2002) Use of size-based production and stable isotope analyses to predict trophic transfer efficiencies and predator–prey body mass ratios in food webs. *Marine Ecology Progress Series*, **70**, 934–944.
- Jonsson, T. & Ebenman, B. (1998) Effects of predator–prey body size ratios on the stability of food chains. *Journal of Theoretical Biology*, **193**, 407–417.
- Law, R. & Morton, R.D. (1996) Permanence and the assembly of ecological communities. *Ecology*, **77**, 762–775.
- Lawlor, L.R. (1978) A comment on randomly constructed model ecosystems. *American Naturalist*, **112**, 445–447.
- Leaper, R. & Huxham, M. (2002) Size constraints in a real food web: predator, parasite and prey body–size relationships. *Oikos*, **99**, 443–456.
- Leaper, R. & Raffaelli, D.G. (1999) Defining the abundance–body size constraint space: data from a real food web. *Ecology Letters*, **2**, 191–199.
- Loreau, M. *et al.* (2001) Biodiversity and ecosystem functioning: current knowledge and future challenges. *Science*, **294**, 804–808.
- May, R.M. (1973) *Stability and Complexity in Model Ecosystems*, 2nd edn. Princeton University Press, Princeton.

- McCann, K.S. (2000) The diversity–stability debate. *Nature*, **405**, 228–233.
- McCann, K. & Hastings, A. (1997) Re-evaluating the omnivory–stability relationship in food webs. *Proceedings of the Royal Society Series B*, **264**, 1249–1254.
- McCann, K. & Hastings, A. & Huxel, G.R. (1998) Weak trophic interactions and the balance of nature. *Nature*, **395**, 794–798.
- Milne, H. & Dunnet, G.M. (1972) Standing crop, productivity, and trophic relations of the fauna of the Ythan estuary. *The Estuarine Environment* (eds R.S.K. Barnes & J. Green), pp. 86–106. Applied Science Publishers, UK.
- Neutel, A.-M., Heesterbeek, J.A.P. & deRuiter, P.C. (2002) Stability in real food webs: weak links in long loops. *Science*, **296**, 1120–1123.
- Paine, R.T. (1992) Food-web analysis through field measurement of per-capita interaction strength. *Nature*, **355**, 73–75.
- Paine, R.T. (2002) Trophic control of production in a rocky intertidal community. *Science*, **296**, 736–739.
- Peters, R.H. (1983) *The Ecological Implications of Body Size*. Cambridge University Press, Cambridge.
- Pimm, S.L. (1982) *Food Webs*. Chapman & Hall, London.
- Pimm, S.L. & Lawton, J.H. (1977) Number of trophic levels in ecological communities. *Nature*, **268**, 329–331.
- Pimm, S.L. & Lawton, J.H. (1978) On feeding on more than one trophic level. *Nature*, **275**, 342–344.
- Raffaelli, D. & Hall, S.J. (1992) Compartments and predation in an estuarine food web. *Journal of Animal Ecology*, **61**, 551–560.
- Raffaelli, D.G. & Hall, S.J. (1996) Assessing the relative importance of trophic links in food webs. *Food Webs: Integration of Pattern and Dynamics* (eds G. Polis & K. Winemiller), pp. 185–191. Chapman & Hall, New York.
- Sala, E. & Graham, M.H. (2002) Community-wide distribution of predator–prey interaction strength in kelp forests. *Proceedings of the National Academy of Sciences USA*, **99**, 3678–3683.
- Summers, R.W. (1974) *The feeding ecology of the Flounder Platicthys flesus (L.) in the Ythan Estuary, Aberdeenshire*. PhD thesis, University of Aberdeen, Aberdeen.
- Warren, P.H. (1996) Structural constraints on food web assembly. *Aspects of the Genesis and Maintenance of Biology Diversity* (eds M.E. Hochberg, J. Clobert & R. Barbault), pp. 142–161. Oxford University Press, Oxford.
- Warren, P.H. & Lawton, J.H. (1987) Invertebrate predator–prey body size relationships – an explanation for upper-triangular food webs and patterns in food web structure. *Oecologia*, **74**, 231–235.
- Williams, R.J. & Martinez, N.D. (2000) Simple rules yield complex food webs. *Nature*, **404**, 180–183.
- Woodward, G. & Hildrew, A.G. (2001) Invasion of a stream food web by a new top predator. *Journal of Animal Ecology*, **70**, 273–288.
- Wootton, T. (1997) Estimates and tests of per capita interaction strength: diet, abundance, and impact of intertidally foraging birds. *Ecological Monographs*, **67**, 45–64.
- Yodzis, P. (1981) The stability of real ecosystems. *Nature*, **289**, 674–676.
- Yodzis, P. & Innes, S. (1992) Body size and consumer–resource dynamics. *American Naturalist*, **139**, 1151–1175.

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## Appendix I

Taxa from the Ythan Estuary ecosystem used in the present version of the Ythan food web\*

1. <i>Lutra lutra</i>	31. <i>Anguilla anguilla</i>	61. <i>Corophium volutator</i> †
2. <i>Vulpes vulpes</i>	32. <i>Pollachius virens</i>	62. <i>Bathyporeia pilosa</i>
3. <i>Phalacrocorax carbo</i> †	33. <i>Ciliata mustella</i>	63. <i>Gammarus</i> sp.
4. <i>Ardea cinerea</i> †	34. <i>Ammodytes tobianus</i>	64. <i>Idotea emarginata</i>
5. <i>Cygnus olor</i> †	35. <i>Pholis gunnellus</i>	65. <i>Jaera albifrons</i>
6. <i>Tadorna tadorna</i> †	36. <i>Zoarces viviparus</i>	66. <i>Eurydice pulchra</i>
7. <i>Anas penelope</i> †	37. <i>Pomatoschistus minutus</i> †	67. <i>Pygospio elegans</i> †
8. <i>Somateria mollissima</i> (adult)†	38. <i>Pomatoschistus microps</i> †	68. <i>Capitella capitata</i>
9. <i>Somateria mollissima</i> (juvenile)†	39. <i>Myxocephalus scorpius</i>	69. <i>Manayunkia aestuarina</i> †
10. <i>Haematopus ostralegus</i> †	40. <i>Agonus cataphractus</i>	70. <i>Aricia</i> sp.
11. <i>Charadrius hiaticula</i> †	41. <i>Gasterosteus aculeatus</i>	71. <i>Tubificoides benedeni</i>
12. <i>Pluvialis apricaria</i> †	42. <i>Syngnathus rostellatus</i>	72. <i>Tubifex</i> sp.†
13. <i>Pluvialis squatarola</i> †	43. <i>Pleuronectes platessa</i> (juvenile)	73. <i>Hydrobia ulvae</i> †
14. <i>Vanellus vanellus</i> †	44. <i>Platicthys flesus</i> (adult)†	74. <i>Littorina littorea</i> †
15. <i>Calidris alpina</i> †	45. <i>Platicthys flesus</i> (juvenile)†	75. <i>Littorina saxatilis</i>
16. <i>Limosa lapponica</i> †	46. <i>Salmo trutta</i>	76. <i>Retusa obtusa</i> †
17. <i>Numenius arquata</i> †	47. <i>Neomysis integer</i>	77. <i>Mya arenaria</i>
18. <i>Tringa totanus</i> †	48. <i>Crangon crangon</i> †	78. <i>Macoma balthica</i> †
19. <i>Arenaria interpres</i> †	49. <i>Carcinus maenas</i> †	79. <i>Mytilus edulis</i> †
20. <i>Larus canus</i>	50. <i>Hediste diversicolor</i> †	80. <i>Cerastoderma edule</i> †
21. <i>Larus ridibundus</i>	51. <i>Nereis virens</i>	81. Nematodes†
22. <i>Larus argentatus</i>	52. <i>Phyllodoce mucosa</i> †	82. Foraminifera†
23. <i>Larus marinus</i>	53. <i>Eteone longa</i> †	83. Chironomidae
24. <i>Sterna sandvicensis</i>	54. <i>Arenicola marina</i> †	84. Dipteran larvae
25. <i>Sterna hirundo</i>	55. Ostracods	85. Brown algae
26. <i>Sterna paradisea</i>	56. <i>Calanoid copepods</i>	86. <i>Enteromorpha</i> sp.
27. <i>Corvus frugilegus</i>	57. <i>Harpacticoid copepods</i>	87. Diatoms
28. <i>Corvus corone</i>	58. <i>Semibalanus balanoides</i>	88. Particulate organic matter
29. <i>Sprattus sprattus</i>	59. <i>Hyale nilssoni</i>	
30. <i>Clupea harengus</i>	60. <i>Talitrus saltator</i>	

\*A binary version of the Ythan Estuary food web is available on request from the authors.

†Species for which population densities on the Ythan Estuary are known.