

# Measurement of body size and abundance in tests of macroecological and food web theory

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## Summary

1. Mean body mass ( $W$ ) and mean numerical ( $N$ ) or biomass ( $B$ ) abundance are frequently used as variables to describe populations and species in macroecological and food web studies.
2. We investigate how the use of mean  $W$  and mean  $N$  or  $B$ , rather than other measures of  $W$  and/or accounting for the properties of all individuals, can affect the outcome of tests of macroecological and food web theory.
3. Theoretical and empirical analyses demonstrate that mean  $W$ ,  $W$  at maximum biomass ( $W_{mb}$ ),  $W$  when energy requirements are greatest ( $W_{me}$ ) and the  $W$  when a species uses the greatest proportion of the energy available to all species in a  $W$  class ( $W_{mpe}$ ) are not consistently related.
4. For a population at equilibrium, relationships between mean  $W$  and  $W_{me}$  depend on the slope  $b$  of the relationship between trophic level and  $W$ . For marine fishes, data show that  $b$  varies widely among species and thus mean  $W$  is an unreliable indicator of the role of a species in the food web.
5. Two different approaches, ‘cross-species’ and ‘all individuals’ have been used to estimate slopes of abundance–body mass relationships and to test the energetic equivalence hypothesis and related theory. The approaches, based on relationships between (1)  $\log_{10}$  mean  $W$  and  $\log_{10}$  mean  $N$  or  $B$ , and (2)  $\log_{10} W$  and  $\log_{10} N$  or  $B$  of all individuals binned into  $\log_{10} W$  classes (size spectra), give different slopes and confidence intervals with the same data.
6. Our results show that the ‘all individuals’ approach has the potential to provide more powerful tests of the energetic equivalence hypothesis and role of energy availability in determining slopes, but new theory and empirical analysis are needed to explain distributions of species relative abundance at  $W$ .
7. Biases introduced when working with mean  $W$  in macroecological and food web studies are greatest when species have indeterminate growth, when relationships between  $W$  and trophic level are strong and when the range of species’  $W$  is narrow.

**Key-words:** abundance–body mass relationships, energetic equivalence, food webs, metabolic scaling theory, predator–prey interactions, size spectra, stable isotope analysis.

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## Introduction

Rates of metabolism are related to body mass ( $W$ ) and ultimately determine the life histories of animals and their role in food webs (Brown *et al.* 2004). Consequently, mean  $W$  is often used as a variable in macroecological and food web analyses (Gaston & Blackburn 2000;

Cohen, Jonsson & Carpenter 2003; Brown *et al.* 2004; Emmerson & Raffaelli 2004; Reuman & Cohen 2005; Woodward *et al.* 2005). When using mean  $W$  as a variable, two sets of issues need to be considered. First, whether estimated mean  $W$  reflects actual mean  $W$  during the sampling or study period and whether mean  $W$ -values in compilations of data collected in different areas and/or on different time-scales and/or for species with different body compositions are comparable. Second, whether estimated mean  $W$  usefully and consistently conveys information about the life history of a population or species and its role in the food web.

In this paper we focus on the latter set of issues and ask what information  $W$  conveys about the trophic level and energetics of populations when testing macroecological and food web theory.

In addition to the widely used mean  $W$ , many other possible measures of  $W$  could be used to describe body size. These include  $W_{mb}$ , the weight at which the biomass in the population is greatest or  $W_{me}$ , the weight at which the energy demand is greatest. Mean  $W$  is probably so widely used because it is easy to measure and report, but interpretation of analyses based on mean  $W$  would be improved if the biases it introduces were known. For example, trophic level is often reported at a mean or 'typical'  $W$ , as if it were a fixed parameter rather than a function of evolution, feeding opportunities and feeding behaviour. Such reports of trophic level at mean  $W$  can be misleading, particularly for aquatic species that often grow through six orders of magnitude in  $W$  and three trophic levels in the course of their life history; thus playing significant roles in many parts of the food web (Cushing 1975).

Abundance–body mass relationships are typically described as the slopes of relationships between  $\log_{10}$  numerical ( $N$ ) or biomass abundance ( $B$ ) and  $\log_{10} W$ . Although the same energetic explanations have sometimes been advanced to account for observed slopes (Damuth 1981; Cyr 2000; Brown & Gillooly 2003), slopes have been estimated in two different ways. First, from 'cross-species' relationships between  $\log_{10}$  mean  $N$  or  $B$  and  $\log_{10}$  mean  $W$ , often for taxonomically or functionally defined groups of species, such as plants, birds or mammals (Blackburn & Gaston 1997). Second, for 'all individuals' in a food web or specified size range, from relationships between  $\log_{10} N$  or  $B$  in a body mass class and  $\log_{10} W$  at the lower bound or midpoint of the class (Dickie, Kerr & Boudreau 1987). The former approach has principally been explored for terrestrial communities and the latter for aquatic communities, where abundance– $W$  relationships are usually dubbed size-spectra (Sheldon & Parsons 1967).

Damuth (1981) conducted a 'cross-species' study of abundance– $W$  relationships in mammalian populations and demonstrated that  $N$  scaled as  $W^{-0.70}$ , which was not significantly different from  $W^{-0.75}$ . As metabolic rate was known to scale as  $W^{0.75}$ , Damuth proposed that energy use was independent of  $W$ , and that body size did not provide any population with an energetic advantage. There have been many attempts to test whether Damuth's hypothesis, subsequently termed the 'energetic equivalence hypothesis', applied to other groups. Blackburn & Gaston (1997), for example, reviewed many of the published studies and calculated that the mean scaling of  $N$  and  $W$  was  $W^{-0.51}$  rather than  $W^{-0.75}$ . Conversely, Belgrano *et al.* (2002) and Li (2002) demonstrated that energetic equivalence correctly predicted scaling of numerical abundance and  $W$  in phytoplankton and plant communities. There have also been tests of the extent to which modifications of this hypothesis, such as those that account for the

reduced energy availability at  $W$  in a size-structured food web (Cyr 2000; Brown *et al.* 2004), can predict abundance– $W$  scaling (Jennings & Mackinson 2003).

Notwithstanding that some tests of  $N \propto W^{-0.75}$  and  $B \propto W^{0.25}$ , as predicted by the energetic equivalence hypothesis, have been applied to subsets of food webs that feed at different trophic levels (and therefore do not share the same source of energy; Cyr 2000; Maxwell & Jennings 2006) and/or that a range of methods that yield different results have been used for slope estimation (Cohen & Carpenter 2005), other issues arise when testing whether energy availability can predict the scaling of abundance and  $W$ . Foremost, is the use of both the 'all individuals' and 'cross-species' methods to describe abundance– $W$  relationships, despite little understanding of the relationships between them. If these methods yield different slopes and/or confidence intervals for slopes with the same data, then it is necessary to clarify when the different methods are appropriate.

Here, we develop a theoretical model to describe relationships between mean  $W$ ,  $W_{mb}$ ,  $W_{me}$  and the  $W$  at which the greatest proportion of energy available to a  $W$  class is used ( $W_{mpe}$ ). An understanding of these relationships is necessary because the use of mean  $W$  in tests of energetic equivalence theory pre-supposes that mean  $W$  and mean abundance provide information on the expected energetic demands of a population. We relate the outputs from the theoretical analyses to observations in a marine fish community over a 3-year period, where we uniquely sample and assign a trophic level, as estimated using nitrogen stable isotope analysis, to every individual. The approach does not involve full population and food web analysis, as these are impracticably data intensive for all species in the community, but it does allow us to incorporate information about food web interactions into population and community analyses that would not be conveyed by the use of mean  $W$  alone. The outputs of the analyses are used to understand how different measures of mean  $W$  can affect tests of trophic level– $W$  and abundance– $W$  relationships.

## Materials and methods

### THEORY

Theoretical analyses were conducted to explore the relationship between mean  $W$  and other measures of  $W$  that could be used to describe the energetic requirements of populations. The analyses require that we can compare mean  $W$  with the  $W$  of an individual at the time of maximum cohort biomass  $W_{mb}$  (as determined by the trade-off between the decline in numbers owing to mortality and the increase in individual  $W$  owing to growth) and the  $W$  of an individual at the time when the largest quantity of energy (measured as primary production required,  $P_r$ ) is needed to support a cohort ( $W_{me}$ ). We assume that the modelled population is at

**Table 1.** Species included in the study, parameters  $\alpha$  and  $\beta$  in the weight-length relationship  $W = \alpha L^\beta$  (Coull *et al.* 1989) and estimated asymptotic body mass  $W_\infty$  as calculated from values of  $W_\infty$  in Jennings, Greenstreet & Reynolds (1999) and CEFAS (unpub.). Species nomenclature follows the taxonomic list of Wheeler (1992)

Species	Common name	$\alpha$	$\beta$	$W_\infty$ (g)
<i>Lophius lophius</i>	Anglerfish	0.0153	3.00	18045
<i>Gadus morhua</i>	Cod	0.0065	3.10	19380
<i>Limanda limanda</i>	Dab	0.0074	3.11	211
<i>Eutrigla gurnardus</i>	Grey gurnard	0.0062	3.10	886
<i>Melannogrammus aeglefinus</i>	Haddock	0.0056	3.13	3075
<i>Clupea harengus</i>	Herring	0.0060	3.09	379
<i>Microstomus kitt</i>	Lemon sole	0.0255	2.76	551
<i>Hippoglossus platessoides</i>	Long rough dab	0.0044	3.20	133
<i>Scomber scombrus</i>	Mackerel	0.0030	3.29	965
<i>Trisopterus esmarki</i>	Norway pout	0.0052	3.12	68
<i>Pleuronectes platessa</i>	Plaice	0.0215	2.79	1466
<i>Pollachius virens</i>	Saithe	0.0100	2.96	8271
<i>Trachurus trachurus</i>	Scad	0.0034	3.29	950
<i>Raja radiata</i>	Starry ray	0.0409	2.90	2348
<i>Merlangius merlangius</i>	Whiting	0.0052	3.12	594

equilibrium, and therefore that the changes in size and abundance of any cohort over time are equal to the differences in size and abundance among size-classes in the population at any instant in time.

Holt (1958), derived a function to predict the  $W$  when a cohort attains maximum biomass  $W_{mb}$

$$W_{mb} = W_\infty [k/(k + M/3)]^3 \quad \text{eqn 1}$$

where  $W_\infty$  is the asymptotic or theoretical maximum  $W$ , as estimated by fitting the von Bertalanffy Growth Equation to weight at age data,  $k$  is the Brody growth coefficient in the von Bertalanffy Growth Equation (e.g. Quinn & Deriso 1999) and  $M$  is the instantaneous rate of natural mortality.

Holt (1958) assumed that

$$W \propto L^3 \quad \text{eqn 2}$$

where  $L$  is body length. Equation 2 is a good approximation of the relationship between  $W$  and  $L$  for most fish species (e.g. Table 1).

Dividing the numerator and denominator of the term in the square brackets in eqn 1 by  $k$  allows  $W_{mb}$  to be expressed as a function of  $M/k$  ratio, thus

$$W_{mb} = W_\infty [1/(1 + M/3k)]^3 \quad \text{eqn 3}$$

$M/k$  has been of long-standing interest to fish population biologists given the difficulties associated with estimating  $M$ . While  $M$  and  $k$  vary considerably among species, the  $M/k$  ratio is relatively constant, typically ranging from 1 to 2 (Beverton & Holt 1959). If we assume that  $M/k = 1.5$ , then

$$W_{mb} = W_\infty (2/3)^3 \text{ and } W_{mb} \approx 0.3 W_\infty \quad \text{eqn 4}$$

The alternate solutions for  $M/k = 1$  and  $M/k = 2$  would be  $W_{mb} \approx 0.4 W_\infty$  and  $W_{mb} \approx 0.2 W_\infty$  respectively. Thus

$W_{mb}$  will typically occur at a similar proportion of  $W_\infty$  in different species.

For the purposes of this example, we make the simplifying assumption that the energy ( $E$ ) required to support metabolism, growth and reproduction scales within and among species as

$$E = c W^{0.75} \quad \text{eqn 5}$$

where  $c$  is a constant. In reality, the  $W^{0.75}$  scaling may differ within and among species and  $c$  may not be a constant (e.g. Glazier 2005; van der Meer 2006), but we followed a generic approach because it was not logistically feasible to produce energy budgets for all the individuals and populations considered in our study.

Given that the primary production required ( $P_r$ ) to meet the energy requirements at a given trophic level ( $E_\lambda$ ) (e.g. Ware 2000) is

$$P_r = E_\lambda / \epsilon^{\lambda-1} \quad \text{eqn 6}$$

where  $\epsilon$  is transfer efficiency and  $\lambda$  is trophic level, eqn 5 can be substituted in to eqn 6 to express the primary production required to support the energy requirements as

$$P_r = c W_\lambda^{0.75} / \epsilon^{\lambda-1} \quad \text{eqn 7}$$

Further, since  $W_\lambda$  is defined by the relationship

$$W_\lambda = 10^{\frac{\lambda-a}{b}} \quad \text{eqn 8}$$

where  $a$  and  $b$  are fitted parameters of the linear relationship (Jennings, Warr & Mackinson 2002)

$$\lambda = a + b \log_{10} W \quad \text{eqn 9}$$

$P_r$  can be expressed in terms of  $W$  and  $\epsilon$  by substituting eqn 8 and eqn 9 into eqn 7 and simplifying

$$P_r = c W^{0.75} / \epsilon^{a+b \log_{10} W - 1} \quad \text{eqn 10}$$

For a cohort, the change in total biomass with time is a function of the change in the number of individuals owing to mortality and the change in the size of those individuals owing to growth. The number of individuals in a cohort at time  $t$  can be estimated using (e.g. Quinn & Deriso 1999)

$$N_t = N_0 e^{-Mt} \quad \text{eqn 11}$$

where  $N_0$  is the number of individuals present at  $t = 0$ . To include consideration of additional (fishing) mortality, this equation can be expressed as

$$N_t = N_0 e^{-(F+M)t} \quad \text{eqn 12}$$

where  $F$  is the instantaneous rate of fishing mortality. The von Bertalanffy Growth Equation can be used to describe  $W$  at time  $t$  as a function of  $W_\infty$  (e.g. Quinn & Deriso 1999)

$$W_t = W_\infty (1 - e^{-k(t-t_0)})^3 \quad \text{eqn 13}$$

where  $t_0$  is the time when  $W$  is theoretically zero. Thus  $P_r$  at time ( $P_{r,t}$ ) to support an entire cohort will be

$$P_{r,t} = N_t c W_t^{0.75} / \epsilon^{a+b \log_{10} W_{t-1}} \quad \text{eqn 14}$$

where  $N_t$  is the number of individuals present at time  $t$  as determined from eqn 11 or eqn 12 (with additional mortality) and  $W_t$  is determined from eqn 13.

The time when a cohort has the maximum energy requirement  $t_{me}$  can then be determined by substituting eqn 11 and eqn 13 into eqn 14, differentiating with respect to  $t$  and solving for  $t_{me}$  when the first derivative is set to 0.

$$t_{me} = t_0 + \log_e \left[ 1 + \frac{9}{4} \left( \frac{k}{M} \right) - 3b(\log_e \epsilon)(\log_{10} e) \left( \frac{k}{M} \right) \right]^{1/k} \quad \text{eqn 15}$$

Equation 15 can be substituted into eqn 13 to give  $W_{me}$  and into eqn 11 to give  $N_{me}$ . Substituting into eqn 13, the equation for  $W_{me}$  reduces to

$$W_{me} = W_\infty \left[ 1 / \left( 1 + \frac{M}{3k[0.75 - b(\log_e \epsilon)(\log_{10} e)]} \right) \right]^3 \quad \text{eqn 16}$$

Thus  $W_{me}$  can be determined solely from knowledge of  $W_\infty$ ,  $b$ , the  $M/k$  ratio and  $\epsilon$ .

Our subsequent analyses use the preceding equations to examine relationships between  $E$ ,  $B$ ,  $P_r$ ,  $W$ ,  $W_{mb}$ ,  $W_{me}$  and  $b$ . For the main analyses we assume a fixed  $M/k$  ratio of 1.5,  $c = 2$  and values of  $k = 0.2$ ,  $\epsilon = 0.125$  and  $t_0 = -0.5$  (e.g. Beverton & Holt 1959; Ware 2000). We also present sensitivity analyses for ranges in parameter values where appropriate.

#### DATA COLLECTION

Fishes were caught at 21 stations in fixed locations in the northern North Sea, in an area from 57.5°N to 61.5°N and 1°W–4°E, with a Grande Overture Verticale (GOV) bottom fished otter trawl net fitted with a 20-mm cod-end liner and towed for 30 min at 4 knots. The area was sampled in late August and early September 2002, 2003 and 2004 during the North Sea English Bottom Trawl Survey. All fishes in the catch were sorted to species and weighed. All individuals in species groups or subsamples of species groups were then measured to produce raised length–frequency distributions for all species. Abundance estimates were corrected for catchability by species, using the correction factors published by Sparholt (1990). Although these factors were calculated for a Granton trawl rather than a GOV trawl, they are the best available estimates of catchability for all species caught by survey trawls in the North Sea.

For each of the 15 species shown to have the highest rank  $B$  in trawl survey data collected before 2002, up to four individuals were collected from each of 10–13 length classes spanning the total range of total body lengths caught. Length class intervals ranged from 1 cm (*Trisopterus minutus*) to 7 cm (*Gadus morhua* and *Pollachius virens*), depending on the range of total body lengths present. The total length and total  $W$  of each individual assigned to a length class was recorded to the nearest mm and g, respectively. Five cm<sup>3</sup> of white muscle tissue was dissected from the dorsal musculature of each individual and immediately frozen to –20 °C and stored frozen until processing, a procedure that has no effect on the nitrogen stable isotope composition of the tissue (Sweeting, Polunin & Jennings 2004). The tissue was subsequently freeze dried to constant mass, and ground with pestle and mortar to fine homogeneous powder. The nitrogen stable isotopic composition of the powdered samples was determined using a Europa Scientific 20–20 IRMS with a Europa Scientific Roboprep-CN preparation module at Iso-Analytical Ltd (Sandbach, UK). Two reference samples were analysed after every four to six samples of fish tissue. The reference material used during analysis of all samples was IA-R014 (an Iso-Analytical working standard powdered bovine liver, 9.98% nitrogen and 49.87% carbon with a  $\delta^{15}\text{N}$  of 7.25‰). The  $^{15}\text{N}$  composition of the tissue samples was expressed in conventional delta notation ( $\delta^{15}\text{N}$ ), relative to the abundance of  $^{15}\text{N}$  in atmospheric  $\text{N}_2$ . Experimental precision in all years was < 0.2‰ (standard deviation of  $\delta^{15}\text{N}$  for replicates of reference material).

#### DATA ANALYSIS

To calculate trophic level ( $\lambda$ ), and to achieve internal consistency when making year to year comparisons among individuals and species, all values of  $\delta^{15}\text{N}$  were rebased to a common standard. This was the predicted  $\delta^{15}\text{N}$  of an individual *Clupea harengus* (herring) of mass  $W_h$ , here taken as 200 g, and  $\lambda$  was calculated as

$$\lambda = \frac{\delta^{15}\text{N} - (a' - b' \log_{10} W_h)}{\Delta \delta^{15}\text{N}} + 4 \quad \text{eqn 17}$$

where  $\Delta \delta^{15}\text{N}$  is the assumed trophic fractionation of  $\delta^{15}\text{N}$  (3.4‰),  $a'$  and  $b'$  are the fitted slope and intercept of the relationship between  $\delta^{15}\text{N}$  and  $\log_{10} W$  and 4 is the assumed trophic level ( $\lambda$ ) of the herring. For the fish sampled for isotope analysis, the relationship between  $\lambda$  and  $W$  (eqn 9) was described for each species in each year. The fitted parameters were then used to assign  $\lambda$  to all individuals of each species in each year. The 3.4‰ value for  $\Delta \delta^{15}\text{N}$  is a mean, but there are likely to be variations in  $\Delta \delta^{15}\text{N}$  due to individual and population-specific differences (Post 2002; Sweeting, Jennings & Polunin 2005). These differences may affect the relative trophic levels of different species, but would not affect our key conclusions that there can be significant positive and negative trends in trophic level with  $W$  and that

these will influence the relationship between body size and the energy demands of a population.

The estimated primary production required ( $P_r$ ) to support all individuals in defined  $W$  classes and species was calculated with eqn 10. The proportion of primary production required ( $P_{pr}$ ) to sustain individuals in each  $W$  class was calculated for each species in the class as

$$P_{pr} = P_{r,i} / \sum_{i=1}^{15} P_{r,i} \quad \text{eqn 18}$$

where  $P_{ri}$  is the  $P_r$  by the  $i$ th species ( $i = 1, \dots, 15$ ).

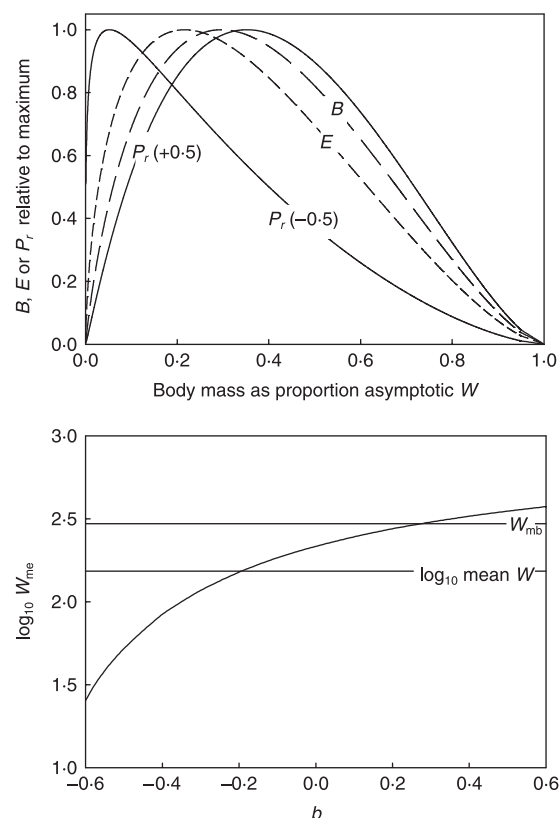
Mean predator–prey body mass ratios ( $\mu$ ) were calculated from the slope ( $b$ ) of the linear relationship between  $\lambda$  and  $\log_{10} W$  (eqn 9) where  $\lambda = 10^{1/b}$  (Jennings *et al.* 2002a). Calculations were based on the biomass-weighted mean  $\lambda$  of all individuals by  $W$  class.

Slopes of abundance– $W$  relationships were estimated in two ways. First, the individual  $W$  of each fish was estimated from length– $W$  relationships (Table 1) and fish were assigned to  $W$  classes defined by a  $\log_2$  integer scale. Cumulative biomass within each  $W$  class was calculated. This is the approach that is typically used to produce ‘size spectra’ (e.g. Dickie *et al.* 1987). A  $\log_2$  scale was used to increase the number of bins and hence the degrees of freedom in the analyses, but class midpoints were expressed as  $\log_{10} W$  in the analyses. Abundance– $W$  relationships were calculated for all individuals of all species > 64 g and for the 15 species > 64 g for which  $\delta^{15}\text{N}$  was measured. Species < 64 g were excluded from the calculation of slopes because invertebrates account for a significant proportion of total biomass at < 64 g (e.g. Jennings & Dulvy 2005). Second, slopes of abundance– $W$  relationships were calculated as cross-species relationships between  $\log_{10}$  mean  $B$  and  $\log_{10}$  mean  $W$ . This is the approach that is typically used to calculate abundance–body mass relationships in terrestrial ecology (e.g. Damuth 1981). Note that if  $B \propto W^x$  then  $N \propto W^{x-1}$  (since  $B = NW$ ), so slopes based on  $B$  can readily be interpreted in terms of  $N$ .

## Results

Relationships between  $W_{mb}$  and  $W_{me}$  depend on the slope ( $b$ ) of the relationship between trophic level ( $\lambda$ ) and  $W$  (Fig. 1). Changing  $M$  and  $k$  so that the  $M/k$  ratio remains constant changes the times at which  $W_{mb}$  and  $W_{me}$  are attained in a growing cohort, but not the values of  $W_{mb}$  and  $W_{me}$ . Thus, for a population at equilibrium,  $W_{mb}$  and  $W_{me}$  (for a given value of  $b$  in the case of  $W_{me}$ ) are fixed in relation to  $W_{\infty}$ . The relationship between  $\log_{10} W_{me}$  and  $\log_{10}$  mean  $W$  depends on  $b$  (Fig. 1). When  $b < 0$ ,  $W_{me}$  more closely approximates mean  $W$  and when  $b > 0$ ,  $W_{me}$  more closely approximates  $W_{mb}$  (Fig. 1b).

$W_{me}$ , expressed here in relation to  $W_{\infty}$ , is more sensitive to a conservative range (Table 2) of values for  $b$  (–0.5–0.5), than to expected ‘real world’ variation (Beverton & Holt 1959) in the  $M/k$  ratio (Fig. 2a). The same range of values for  $b$  has a relatively larger effect on  $W_{me}/W_{\infty}$ ,

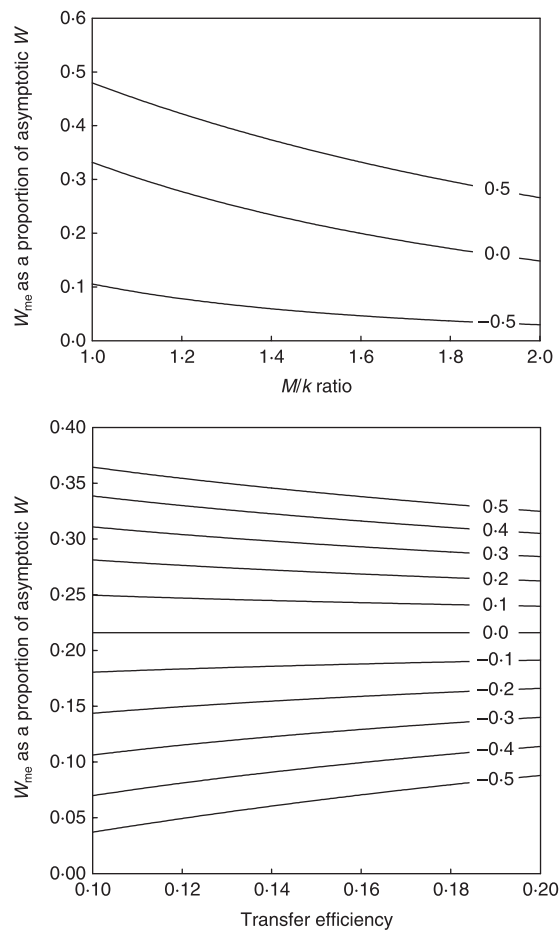


**Fig. 1.** Theoretical relationships between the energy use of a cohort ( $E$ ; broken line short dash), the primary production required to support the cohort ( $P_r$ ; solid lines, for values of 0.5 and –0.5 of  $b$ , the slopes of a linear relationship between trophic level and body mass in a population; eqn 9) or the biomass ( $B$ ) of the cohort, and body mass ( $W$ ) (upper panel), and (lower panel) the theoretical relationship between  $W$  when energy requirements are greatest ( $W_{me}$ ) and slope  $b$ . Horizontal lines indicate the weight at maximum cohort biomass ( $W_{mb}$ ) and  $\log_{10}$  mean  $W$ , respectively.

than expected variations in transfer efficiency (Ware 2000) (Fig. 2b).

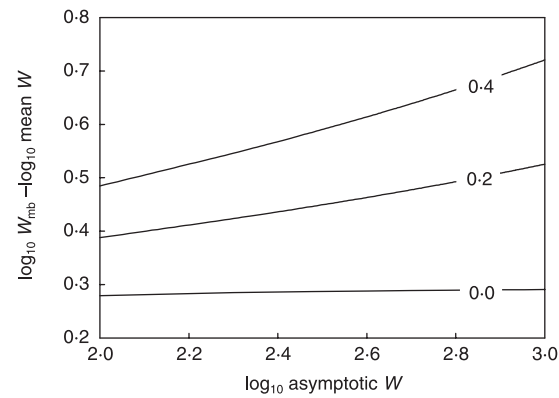
If  $L_{\infty}$  and  $k$  are related as  $L_{\infty} \propto 1/k$  (Beverton & Holt 1959) and  $W \propto L^3$ , then  $k \propto 1/e^{\ln W_{\infty}/3}$ . Setting  $k \propto 1/e^{\ln W_{\infty}/3}$ , but maintaining a constant  $M/k$  ratio for all values of  $W_{\infty}$ , it is clear that  $\log_{10}$  mean  $W$  will be a constant proportion of  $\log_{10} W_{\infty}$ . It therefore follows that  $\log_{10}$  mean  $W$  will be a constant proportion of  $\log_{10} W_{mb}$  (eqn 3) and  $\log_{10} W_{me}$  (eqn 16; when the slope  $b$  of the relationship between  $W$  and  $\lambda = 0$ ). Not surprisingly, when we simulate the effects of additional external mortality (in this case fishing mortality  $F$ , eqn 12), absolute values of mean  $W$  and  $\log_{10} W_{mb}$  fall, but mean  $W$  also decreases relative to  $W_{mb}$  as  $F$  and  $W_{\infty}$  rise (Fig. 3).

Empirical values of  $b$  for the species sampled in 2002, 2003 and 2004 (Table 2) slightly exceeded the range considered in the theoretical analysis (Fig. 1). Thus, for many populations, estimates of mean  $W$ , would not be expected to reflect the  $W$  at which the energetic requirements of the population were greatest ( $W_{me}$ ). This was confirmed by data as  $W_{me}$  and mean  $W$  were broadly correlated but, for individual species, the values of  $W_{me}$  and mean  $W$  could differ by an order of magnitude or



**Fig. 2.** Sensitivity of the ratio  $W_{me}/W_{\infty}$  (ratio of the weight at which energy requirements are greatest and asymptotic weight) to the  $M/k$  ratio for three values of  $b$  in eqn 9 (upper panel) and sensitivity of the ratio  $W_{me}/W_{\infty}$  to variation in transfer efficiency ( $\epsilon$ ) for 11 values of  $b$  (lower panel).

more (Fig. 4). If the  $W$  when a species uses the greatest proportion of the energy available to all species in a  $W$  class ( $W_{mpe}$ ) is taken as a measure of  $W$  at which the relative energetic demands of a species are greatest in a



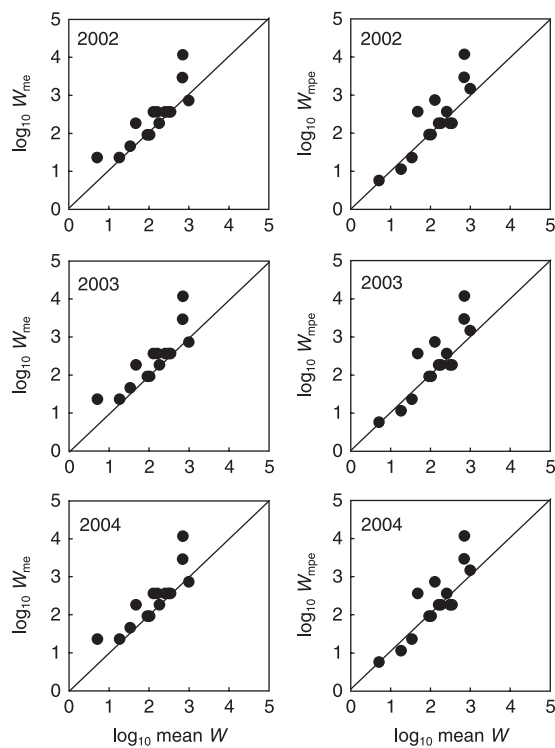
**Fig. 3.** Theoretical relationships between  $\log_{10} W_{mb}$  minus  $\log_{10} \text{mean } W$  and  $\log_{10} W_{\infty}$  for a population subject to natural mortality ( $F=0$ ) and additional external (fishing) mortality ( $F=0.2$  and  $0.4$ ).

food web, then mean  $W$  also has variable value in predicting  $W_{mpe}$  (Fig. 4).

Species exhibited a variety of relationships between  $\lambda$  and  $W$  (Table 2, Fig. 5). Slopes of relationships, among species and within years, ranged from  $b = -1.04-0.89$  (2002),  $b = -1.26-0.63$  (2003) and  $b = -1.55-0.80$  (2004). Of the relationships reported for the 15 species in each year, 8, 8 and 10 were significantly different from  $b = 0$  ( $P = 0.05$ ) in 2002, 2003 and 2004, respectively (Table 2). The cross-species relationships between mean  $\lambda$  and  $\log_{10} \text{mean } W$  (Fig. 5, Table 3) were not always significant and confidence intervals were wide (Table 3). When slopes were significant, the confidence intervals included the slopes predicted from the relationship between biomass weighted mean  $\lambda$  and  $\log_{10} \text{mean } W$  (Table 4). However, the mean slopes of the relationships between biomass weighted mean  $\lambda$  and  $W$  were consistent from year to year, always highly significant, and the confidence intervals were narrow (Table 4; Fig. 5). Thus, when  $b$  is used to estimate  $\mu$ , the estimates are relatively consistent from year to year (Table 4).

**Table 2.** Slopes ( $b$ ) and significance of relationships between trophic level and  $\log_{10} W$  for 15 species of fishes sampled in the northern North Sea from 2002 to 2004

Species	2002			2003			2004		
	$b$	$F_{df}$	$P$	$b$	$F_{df}$	$P$	$b$	$F_{df}$	$P$
<i>Lophius lophius</i>	0.57	19.1 <sub>1,16</sub>	< 0.001	0.56	17.4 <sub>1,25</sub>	< 0.001	0.33	11.4 <sub>1,24</sub>	0.003
<i>Gadus morhua</i>	0.16	5.6 <sub>1,33</sub>	0.025	0.25	15.4 <sub>1,30</sub>	< 0.001	0.14	11.0 <sub>1,30</sub>	0.002
<i>Limanda limanda</i>	0.71	73.4 <sub>1,32</sub>	< 0.001	0.55	35.6 <sub>1,29</sub>	< 0.001	0.52	10.6 <sub>1,27</sub>	0.003
<i>Eutrigla gurnardus</i>	-0.34	3.1 <sub>1,30</sub>	0.087	-0.28	3.4 <sub>1,29</sub>	0.074	-0.22	3.0 <sub>1,28</sub>	0.095
<i>Melannogrammus aeglefinus</i>	0.13	2.0 <sub>1,33</sub>	0.172	0.25	13.6 <sub>1,33</sub>	< 0.001	0.08	0.9 <sub>1,30</sub>	0.346
<i>Clupea harengus</i>	-1.04	67.2 <sub>1,29</sub>	< 0.001	-1.26	15.4 <sub>1,23</sub>	< 0.001	-1.55	26.1 <sub>1,18</sub>	< 0.001
<i>Microstomus kitt</i>	0.63	2.2 <sub>1,12</sub>	0.167	-0.07	0.3 <sub>1,22</sub>	0.580	-0.21	3.0 <sub>1,19</sub>	0.101
<i>Hippoglossus platessoides</i>	0.89	15.0 <sub>1,28</sub>	< 0.001	0.63	11.8 <sub>1,23</sub>	0.002	0.80	19.6 <sub>1,23</sub>	< 0.001
<i>Scomber scombrus</i>	0.35	3.6 <sub>1,28</sub>	0.069	0.27	2.8 <sub>1,26</sub>	0.109	0.75	30.7 <sub>1,22</sub>	< 0.001
<i>Trisopterus esmarki</i>	-0.18	0.2 <sub>1,22</sub>	0.664	-0.80	2.5 <sub>1,16</sub>	0.130	-0.64	4.8 <sub>1,16</sub>	0.044
<i>Pleuronectes platessa</i>	-0.16	1.5 <sub>1,33</sub>	0.235	0.02	0.1 <sub>1,34</sub>	0.811	-0.39	2.4 <sub>1,33</sub>	0.130
<i>Pollachius virens</i>	0.06	0.0 <sub>1,11</sub>	0.889	0.21	0.4 <sub>1,11</sub>	0.549	-0.02	0.0 <sub>1,12</sub>	0.949
<i>Trachurus trachurus</i>	0.38	24.8 <sub>1,36</sub>	< 0.001	0.24	4.3 <sub>1,21</sub>	0.051	0.56	30.1 <sub>1,22</sub>	< 0.001
<i>Raja radiata</i>	0.31	15.4 <sub>1,31</sub>	< 0.001	0.27	12.5 <sub>1,37</sub>	0.001	0.39	17.4 <sub>1,26</sub>	< 0.001
<i>Merlangius merlangius</i>	0.44	52.7 <sub>1,41</sub>	< 0.001	0.35	31.8 <sub>1,33</sub>	< 0.001	0.41	84.5 <sub>1,39</sub>	< 0.001



**Fig. 4.** Relationships between mean body mass ( $W$ ) and  $W_{me}$  or  $W_{mpe}$  (body mass when the maximum proportion of  $P_r$  is needed to sustain production) for northern North Sea fishes in the years 2002–04.

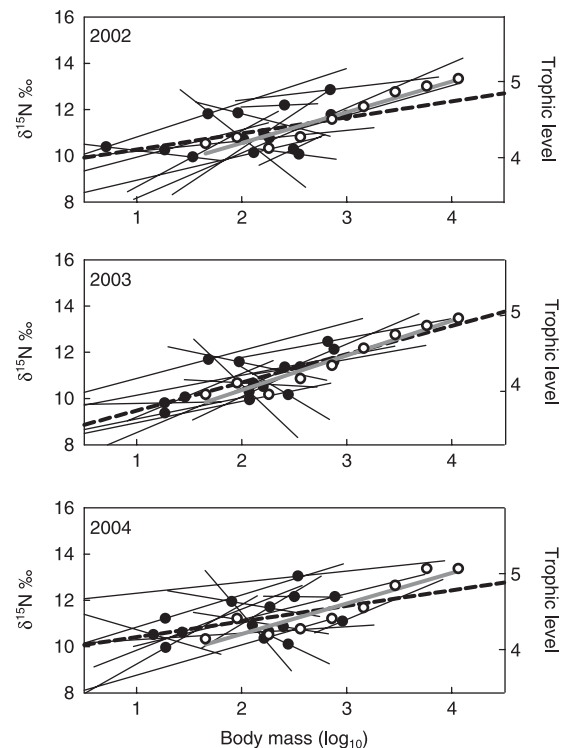
**Table 3.** Slopes ( $b$ ) and significance of ‘cross-species’ relationships between biomass weighted mean trophic level and  $\log_{10}$  mean  $W$  for all  $\delta^{15}\text{N}$  species and for those  $\delta^{15}\text{N}$  species  $> 64$  g

				95% CL ( <i>b</i> )	
	<i>F</i> <sub>df</sub>	<i>P</i>	<i>b</i>	Lower	Upper
All <sup>15</sup> N species					
2002	8·6 <sub>1,13</sub>	0·012	0·33	0·09	0·57
2003	15·9 <sub>1,13</sub>	0·002	0·43	0·20	0·67
2004	5·4 <sub>1,13</sub>	0·037	0·29	0·02	0·57
Species > 64 g mean size					
2002	3·9 <sub>1,10</sub>	0·077	0·42	−0·06	0·90
2003	5·5 <sub>1,10</sub>	0·041	0·49	0·02	0·96
2004	1·0 <sub>1,10</sub>	0·339	0·24	−0·29	0·77

**Table 4.** Slopes ( $b$ ) and significance of relationships between biomass weighted mean trophic level and body size by weight class for all  $\delta^{15}\text{N}$  species  $> 64$  g. Values of the predator-prey mass ratio ( $\mu$ ) are calculated from  $b$

Year	$F_{df}$	$P$	$b$	$\mu$	95% CL ( $b$ )	
					Lower	Upper
2002	79.5 <sub>1,6</sub>	$< 0.0001$	0.44	193	0.32	0.56
2003	93.9 <sub>1,6</sub>	$< 0.0001$	0.48	126	0.36	0.60
2004	28.7 <sub>1,6</sub>	0.0017	0.41	264	0.22	0.60

The 15 species for which relationships between  $\delta^{15}\text{N}$  and  $W$  were determined (Table 1) accounted for 83.2%, 98.4% and 97.3% of the total biomass of all species recorded in 2002, 2003 and 2004, respectively. Slopes of

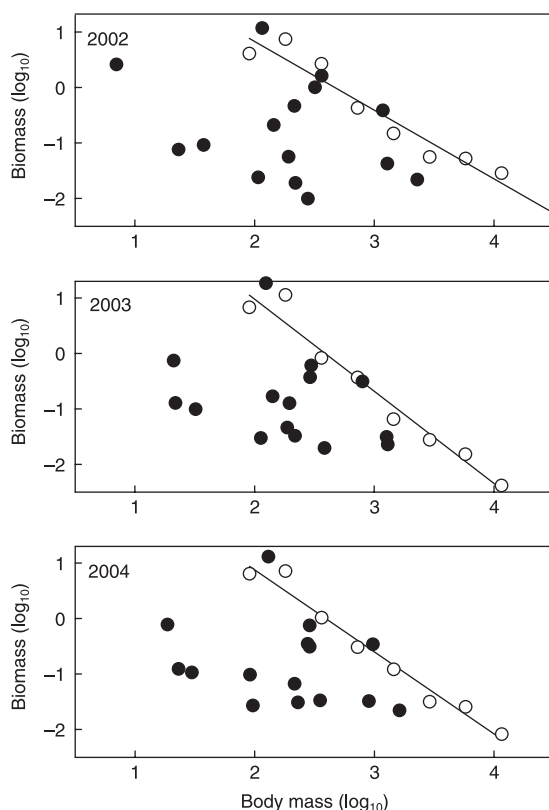


**Fig. 5.** Relationships between  $\delta^{15}\text{N}$  or trophic level ( $\lambda$ ) and body mass ( $W$ ) for northern North Sea fishes in the years 2002–04. Fine continuous lines indicate the fitted relationships between  $\delta^{15}\text{N}$  or trophic level and  $W$  (eqn 9) for the 15 species sampled in each year (Table 1) where the start and end-points of the line indicate the minimum and maximum recorded  $W$ . Fill circles on each line show the mean trophic level and mean  $W$  for each species. Open circles indicate biomass weighted mean trophic level at  $W$  when individuals were pooled by  $W$  class independent of species identity. The broken line is the fitted cross-species relationship between mean trophic level and mean  $W$  while the continuous grey line is the fitted relationship between biomass weighted mean trophic level and  $W$ . Relationships between  $\delta^{15}\text{N}$  and trophic level on the  $y$  axes differ slightly among years because trophic level was rebased year on year.

**Table 5.** Slopes and associated 95% confidence limits of abundance–body mass relationships for all individuals of all species  $> 64$  g and for  $\delta^{15}\text{N}$  species in the northern North Sea fish community

			95% CL (Slope)	
$F_{df}$	$P$	Slope	Lower	Upper
All species				
2002	74.9 <sub>1,6</sub>	< 0.0001	−1.23	−1.59
2003	152.7 <sub>1,6</sub>	< 0.0001	−1.65	−1.99
2004	207.7 <sub>1,6</sub>	< 0.0001	−1.48	−1.73
<sup>15</sup> N species				
2002	79.2 <sub>1,6</sub>	< 0.0001	−1.24	−1.58
2003	151.0 <sub>1,6</sub>	< 0.0001	−1.64	−1.97
2004	115.37 <sub>1,6</sub>	< 0.0001	−1.35	−1.66

abundance– $W$  relationships based on all individuals of all species and on  $\delta^{15}\text{N}$  species were not significantly different in all years (Table 5; Fig. 6). The slopes ranged from −1.23 to −1.65 for all species and −1.24 to



**Fig. 6.** Abundance–body mass relationships for northern North Sea fishes 2002–04. Open circles indicate biomass ( $B$ ) by body mass ( $W$ ) class and  $W$  class midpoint when individuals were pooled by  $W$  class independent of species identity. Fill circles indicate mean  $B$  and mean  $W$  of individual species. Continuous lines are the fitted relationships between  $B$  by  $W$  class and  $W$ .

**Table 6.** Slopes and significance of slopes of abundance–body mass relationships based on ‘cross-species’ relationship between  $\log_{10}$  biomass and  $\log_{10}$  mean body mass for all species and  $\delta^{15}\text{N}$  species

					95% CL (Slope)	
Year	$F_{\text{df}}$	$P$	$r^2$	Slope	Lower	Upper
All species						
2002	0.1 <sub>1,31</sub>	0.708	0.00	+0.10	−0.45	+0.65
2003	0.0 <sub>1,32</sub>	0.921	0.00	+0.02	−0.44	+0.49
2004	0.4 <sub>1,34</sub>	0.517	0.01	+0.15	−0.30	+0.60
$\delta^{15}\text{N}$ species						
2002	1.1 <sub>1,13</sub>	0.310	0.08	−0.38	−1.17	+0.40
2003	1.3 <sub>1,13</sub>	0.276	0.09	−0.42	−1.22	+0.38
2004	0.9 <sub>1,13</sub>	0.363	0.06	−0.32	−1.08	+0.42

−1.64 for  $\delta^{15}\text{N}$  species, and were always highly significant (different from 0) (Table 5). Thus analyses based solely on the  $\delta^{15}\text{N}$  species described most of the key attributes of the overall size and trophic structure of the sampled community.

When slopes of abundance– $W$  relationships were calculated as cross-species relationships between mean  $B$  and mean  $W$  for the  $\delta^{15}\text{N}$  species (Fig. 6), they ranged from −0.32 to −0.42, less negative than the slopes

calculated for all individuals of all species and not significantly different from 0 (Table 6). When all species were used to calculate the cross-species relationships between mean  $B$  and mean  $W$ , slopes ranged from +0.02 to +0.15 and were not significantly different from 0 (Table 6). For all slopes calculated as cross-species relationships between mean  $B$  and mean  $W$ , confidence intervals were much wider than those for the slopes of abundance– $W$  relationships based on all individuals of all species. When these calculations were repeated for fishes with mean  $W > 64$  g only, the relationships between slopes were qualitatively consistent with those reported in Table 6.

## Discussion

The theoretical and empirical analyses both demonstrate that relationships between mean  $W$ ,  $W_{\text{mb}}$  and  $W_{\text{me}}$  are strongly dependent on the slope  $b$  of the relationship between trophic level and  $W$ . If species are sharing energy and the slope is zero, then  $W_{\text{mb}}$  and  $W_{\text{me}}$  are consistently related. However, for the majority of fish species studied in each year, values of  $b$  were significantly different from zero and varied widely among species. Therefore, mean  $W$  and  $W_{\text{mb}}$  were not consistently related to  $W_{\text{me}}$  or the size at which a species requires the greatest proportion of available energy ( $W_{\text{mpe}}$ ). Even when mean  $W$  can be estimated reliably by accounting for sampling effects and spatial and temporal variation in population structure, our results show that mean  $W$  will not be systematically related to the energy requirements of populations in a ‘cross-species’ analysis. We suggest that  $W_{\text{me}}$  provides more reliable information on the relative energy requirements of each species and, if the concerns relating to ‘cross-species’ methods that are identified in subsequent paragraphs did not apply, that  $W_{\text{me}}$  would be a better measure of body size than mean  $W$  when testing whether abundance– $W$  relationships are consistent with the energetic equivalence hypothesis and related theory.

Both the ‘all individuals’ and ‘cross-species’ methods have been used to estimate slopes of abundance– $W$  relationships and to test the energetic equivalence hypothesis. The reason why different slopes and confidence intervals are obtained with these methods, when using the same data, must be considered when testing theory that has been developed to predict the slopes of abundance– $W$  relationships based on energy availability. Although the development of the energetic equivalence hypothesis was based on scalings predicted from cross-species  $\log_{10} N$  and  $\log_{10}$  mean  $W$  relationships, and knowledge of the  $W^{-0.75}$  cross-species scaling of metabolism, subsequent tests of the hypothesis based on  $\log_{10} N$  and  $\log_{10}$  mean  $W$  relationships for other groups have not consistently refuted or supported the hypothesis (Blackburn & Gaston 1997). Our results, and the observation that many studies have focused on subsets of species that are not sharing energy (Maxwell & Jennings 2006), help to explain why test results are so variable.

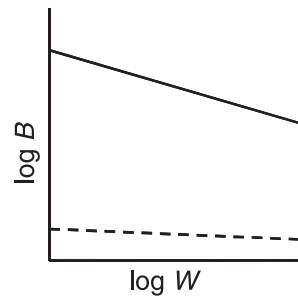


Fig. 7. Hypothetical boundaries of relationships between biomass abundance ( $B$ ) and body mass ( $W$ ). The solid line represents the upper limit of the relationship while the broken line represents the lower (uncertain) limit.

When calculating  $W_{me}$ , the ‘cross-species’ relationship between energy requirements ( $E$ ) and mean  $W$  is assumed to apply within species. Similarly, those working with the ‘all individuals’ abundance– $W$  size spectrum have assumed that the ‘cross-species’ relationship between  $E$  and mean  $W$  is equivalent to the relationship between  $E$  of all individuals by  $W$  class and  $W$  (Sheldon, Prakash & Sutcliffe 1972; Kerr & Dickie 2001). One experimental test suggests that this assumption is acceptable (Schwinghamer *et al.* 1986), even though theoretical considerations and empirical data suggest that within and among species scalings of metabolic rate and  $W$ , and hence  $E$  and  $W$ , can differ (e.g. Kooijman 2000; Glazier 2005). Given the errors associated with other aspects of tests of macroecological and food web theory, such as abundance estimates, it is unlikely that the biases introduced by assuming a common exponent in eqn 5 will affect the overall conclusions of our analyses. However, it would be desirable, although somewhat optimistic, to test this in a detailed study of the body sizes, metabolic rates and production dynamics of all individuals and species that comprise the food web.

Larger predators, on average, eat smaller prey (Cohen *et al.* 1993; Brose *et al.* 2005). As energy transfer from prey to predators is inefficient, the total supply of energy available to small animals is greater than that available to large ones. Small animals (summed across all species) are thus more numerous. Within ‘small’ or ‘large’, species can be rare or abundant. However, the observed range in the abundance of small species is wider than that of large species because energy availability allows the most abundant small species to be more abundant than the most abundant large species (Lawton 1989; Fig. 7). As a result, the slopes of ‘cross-species’ abundance– $W$  relationships are expected to be shallower and to have wider confidence intervals than those based on ‘all individuals’.

If mean  $B$  and mean  $W$  are calculated for species in a random sample of individuals, the slope will lie between the bounds identified in Fig. 7 rather than at the upper bound. This is because the probability of sampling small species is relatively high when there are more small species of higher mean population size (for

example, in one study in the central North Sea, species richness declined by 66% when  $\lambda$  increased by 1 and  $W$  increased by a factor of 109; Jennings *et al.* 2002b). As more species are sampled, the slope of the cross-species abundance– $W$  relationship would be expected to become even shallower, consistent with the results of this study.

Possible solutions to the biases associated with ‘cross-species’ analyses cannot be assessed without knowing the relative abundance of different species in  $W$  classes. For example, quantile regression, or regression based solely on mean  $W$  and abundance of the most abundant species in  $W$  classes, might provide an approximation of the slope based on ‘all individuals’, but this would require that the distribution of relative species’ abundances at  $W$  was not affected by  $W$ . As the distributions of species’ relative abundances at size will have a marked effect on slope, it is important to understand whether these are consistent among size classes and taxa. To achieve this, new empirical work and theoretical development will be needed to describe and predict the distributions of species’ relative abundance at size. The new work would need to account for trends in species numbers with  $W$  and for the distribution of the relative abundances of species at  $W$ . Hall *et al.* (2006) and Pope *et al.* (2006) have begun to progress this type of analysis, by modelling the dynamics of individual species (where ‘species’ are defined on the basis of their asymptotic size) within the ‘all individuals’ abundance– $W$  relationship.

The slope of the ‘cross-species’ abundance– $W$  relationship also depends on the slope of the lower bound of the region in which mean  $B$  and mean  $W$ -values lie, and this will be determined by the minimum viable population sizes of species. Lawton (1989) has argued that minimum viable population sizes tend to be higher in smaller species, leading to the lower bound shown in Fig. 7. The upper and lower bounds in Fig. 7 may converge at an endpoint where food chain length is too long to provide sufficient energy for any species to attain a minimum viable population size.

The incomplete and inconsistent inclusion of species in ‘cross-species’ analyses will lead to bias and inconsistency in empirical slope estimates. Similar issues could arise with the ‘all individuals’ approach if all the most abundant species were not sampled. However, excluding a few very rare species is unlikely to have a significant effect on the ‘all individuals’ slope, as confirmed by our comparison of slopes for  $\delta^{15}\text{N}$  and all species.

When slopes of the abundance– $W$  relationship have been estimated empirically using the ‘all individuals’ approach, the hypothesis that energy availability determines slope has not been rejected, despite relatively narrow confidence intervals for the observed slope (Jennings & Mackinson 2003). Conversely, when energetic hypotheses have been tested using ‘cross-species’ slope estimates, the results have not consistently supported or falsified these hypotheses (Blackburn & Gaston 1997). This is despite the larger confidence intervals for the

observed slopes and therefore the increased probability of type 2 statistical error (concluding that expected and observed slopes are not significantly different when they are) in 'cross-species' analyses.

Our results suggest that the 'all individuals' approach will usually support more effective tests of the role of energy availability in determining the slopes of abundance– $W$  relationships; as it takes account of all individuals using energy in a food web rather than attempting to represent them using mean  $W$  and mean  $N$  or  $B$ . This is important when juveniles of species with large  $W_{\infty}$  contribute to abundance in smaller  $W$  classes (Daan *et al.* 2005; Pope *et al.* 2006) and when mean  $W$  is not consistently related to  $W_{\text{me}}$ . However, there are two possible disadvantages associated with the 'all individuals' approach. First, the need to accept the simplifying assumption that all individuals of the same  $W$  have the same requirements for energy, when they actually have a variety of roles determined by species identity and situation. Second, the need to accept the assumption that 'all individual' abundance– $W$  relationships can be linked to cross-species relationships between energy requirements  $E$  and mean  $W$ . The first assumption is probably acceptable in strongly size-structured food webs (Jennings *et al.* 2001, 2002a), but it also needs to be tested in food webs with weaker size structuring and where component species have determinate growth. The second assumption will introduce bias, as already discussed in relation to eqn 5, but available empirical and theoretical evidence (e.g. Kooijman 2000; Glazier 2005) suggests that this bias will be small in relation to the reported errors in slope that are associated with using 'cross-species' abundance– $W$  relationships. When testing energetic equivalence and related theory, we conclude that it is generally better to work with those populations that dominate total abundance, and to try to account for all stages of their life history, than to work with mean  $W$  and mean abundance for a very comprehensive suite of species.

Cross-species relationships between mean trophic level and mean  $W$  were weak. Previous analyses have shown that adopting a phylogenetic comparative approach (Harvey & Pagel 1991), that took account of evolutionary relationships in fish and invertebrate communities, does not change this result (Jennings *et al.* 2001, 2002a) and we therefore assume that the present result is also robust. In contrast, slopes of the relationships between biomass weighted mean trophic level and  $W$  were highly significant, had narrow confidence intervals and were consistent from year to year. This supports previous observations that size rather than species identity accounts for much of the variance in trophic level in size-structured marine food webs (Jennings *et al.* 2002a). The year to year consistency in slope, and hence in calculated predator to prey mass ratios, suggests that interactions among populations may serve to stabilize trophic structure, despite variability in individual population dynamics (Duplisa & Blanchard 2005). Our results also show that assess-

ments of the relationship between trophic level and  $W$  in food webs should account for abundance, because the abundant species are responsible for more of the energy flux.

Judgements about the types of error that are acceptable/unacceptable in macroecological and food web studies depend on the objectives of study, the range of species and  $W$  included, and the capacity of the investigator to acquire population- and species-specific data. When testing theory across many orders of magnitude in  $W$ , the ways in which data are collected and treated are likely to be less critical than when working across a few orders of magnitude in  $W$ . However, in both cases,  $W$  and abundance data are usually presented and analysed without any consideration of the biases they may introduce. While macroecology is playing a vital role in linking the understanding of individuals, populations, communities and ecosystems (Brown 1995; Gaston & Blackburn 2000), and processes at the ecosystem scale can never be investigated with the criticality and control that can be applied to studies of individuals, improved awareness of biases associated with  $W$  and abundance estimation, particularly in the study of abundance– $W$  relationships, would help to explain why empirical tests of theory often yield inconsistent results. Based on our analyses, we expect that the biases introduced are greatest when species have indeterminate growth, when relationships between  $W$  and trophic level are strong and when the range of species'  $W$  is relatively narrow.

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