

**Provided for non-commercial research and educational use only.
Not for reproduction, distribution or commercial use.**

This chapter was originally published in the book *Advances in Ecological Research*, Vol. 45 published by Elsevier, and the attached copy is provided by Elsevier for the author's benefit and for the benefit of the author's institution, for non-commercial research and educational use including without limitation use in instruction at your institution, sending it to specific colleagues who know you, and providing a copy to your institution's administrator.



All other uses, reproduction and distribution, including without limitation commercial reprints, selling or licensing copies or access, or posting on open internet sites, your personal or institution's website or repository, are prohibited. For exceptions, permission may be sought for such use through Elsevier's permissions site at: <http://www.elsevier.com/locate/permissionusematerial>

From: Takefumi Nakazawa, Masayuki Ushio and Michio Kondoh, Scale Dependence of Predator–Prey Mass Ratio: Determinants and Applications.

In Andrea Belgrano and Julia Reiss, editors:
Advances in Ecological Research, Vol. 45,
Amsterdam, The Netherlands, 2011, pp. 269-302.
ISBN: 978-0-12-386475-8
© Copyright 2011 Elsevier Ltd.
Academic press.

Scale Dependence of Predator–Prey Mass Ratio: Determinants and Applications

TAKEFUMI NAKAZAWA,^{1,†} MASAYUKI USHIO^{1,†} AND
MICHIO KONDOH^{2,3,*}

¹*Center for Ecological Research, Kyoto University, Hirano, Otsu, Japan*

²*Faculty of Science and Technology, Ryukoku University, Yokoya, Otsu, Japan*

³*PRESTO, Japanese Science and Technology Agency, Honcho, Kawaguchi, Japan*

Abstract	270
I. Introduction	270
A. Size Matters to Food Webs	270
B. Predator–Prey Mass Ratio: Its Use and Problems	271
C. Goal of the Present Study	276
II. Data	276
III. Scale Dependence of Predator–Prey Mass Ratio	278
A. Methods and Results	278
B. Mechanisms	279
C. Application	283
IV. Determinants of Predator–Prey Mass Ratio	283
A. Statistical Analysis	283
B. Results	284
C. Application	288
V. Perspectives	290
A. Other Determinants of Predator–Prey Mass Ratio	290
B. Functional Response	293
C. Food-Web Modelling	296
VI. Conclusion	298
References	299

[†] These authors contributed equally to this work.

*Corresponding author. E-mail: mkondoh@rins.ryukoku.ac.jp

ABSTRACT

Body size exerts a critical influence on predator–prey interactions and is therefore crucial for understanding the structure and dynamics of food webs. Currently, predator–prey mass ratio (PPMR) is regarded as the most promising modelling parameter for capturing the complex patterns of feeding links among species and individuals in a simplified way. While PPMR has been widely used in food-web modelling, its empirical estimation is more difficult, with the methodology remaining controversial. This is because PPMR (i) may be defined at different biological scales, such as from individuals to communities, and (ii) may also vary with biological factors, such as species identity and body mass, both of which conflict with the conventional model assumptions. In this chapter, we analyse recently compiled gut content data of marine food webs to address the two fundamental issues of scale-dependence and determinants of PPMR. We consider four definitions of PPMR: (i) species-averaged PPMR, (ii) link-averaged PPMR, (iii) individual-predator PPMR, and (iv) individual-link PPMR. First, we show that PPMR values have a complicated scale-dependence characterised by data elements, such as body mass and sample counts of predators and prey, due to averaging and sampling effects. We subsequently used AIC to systematically evaluate how the four types of PPMR are related to predator species identity and body mass. The results indicate that the model providing the best explanation for individual-predator and individual-link PPMRs incorporates both species identity and body mass. Meanwhile, the best model for species-averaged and link-averaged PPMRs was unclear, with different models being selected across sampling sites. These results imply that the size-based community-spectrum models describing individual-level interactions should include taxonomic dissimilarities. Based on the present study, we suggest that future research regarding PPMR must account for scale dependence and associated determinants to improve its utility as a widely applicable tool.

I. INTRODUCTION

A. Size Matters to Food Webs

Body size is regarded as a key parameter towards understanding ecological systems at multiple biological levels (Hildrew *et al.*, 2007; Woodward *et al.*, 2010; Yvon-Durocher *et al.*, 2011b). Body size characterises individual fitness and behaviour, and thus should be directly linked with the processes and patterns occurring at the individual level. Body size exerts a critical influence on various feeding-related behaviours of individuals, such as predation and

predation avoidance, as well as constraining metabolic rate and affecting the rate at which interactions occurs between predators and prey (Cohen *et al.*, 1993; Peters, 1983). By scaling the individual-level effects of body size up to higher biological levels, such as population and community, our understanding of patterns and processes at these organisation levels may be improved (e.g. Jacob *et al.*, 2011). Indeed, recent development in food-web research has largely benefitted from the body-size-based approach. The assumption that the body-size effect at an individual level may be scaled up to the species level has provided new insights about how the food-web structure and dynamics are constrained and associated to predator and prey body sizes (Woodward *et al.*, 2005).

However, scaling up from individual to higher organisation levels may not be valid when there is intraspecific variation in body size. Such variation adds considerable complexity to the body-size-based view with respect to higher levels of organisation. For example, intraspecific variability may arise through individual growth. The majority of animal species undergo a substantial increase in body size during individual growth, and hence body size varies considerably within species (Ebenman and Persson, 1988). For example, fish species grow by several orders of magnitude in size between hatching and death, generally outweighing interspecific variations (Hildrew *et al.*, 2007). Ontogenetic growth is often accompanied with dietary shifts in life history parameters. This process is known as ontogenetic niche shift (Werner and Gilliam, 1984; Wilbur, 1980) and creates within-species variability in resource use and the strength of trophic interactions. As a consequence, the food web has a complex size structure, whereby different species have different size structures, in which different individuals are characterised by different body sizes. Understanding and ultimately predicting the dynamics of such complex systems is a central goal of ecological research.

B. Predator–Prey Mass Ratio: Its Use and Problems

Despite variations in body size existing within a species, there is an expectation to identify a body-size-related pattern and its ecological consequences in nature. This expectation has stimulated empirical research on body-size differences of interacting predators and prey (Barnes *et al.*, 2008, 2010; Brose *et al.*, 2006a; Gilljam *et al.*, 2011; Woodward and Warren, 2007), as well as the development of food-web models that assume specific predator–prey body-size relationships (Brose *et al.*, 2006b; Castle *et al.*, 2011; Jennings, 2005; Maury *et al.*, 2007; Petchey *et al.*, 2008; Silvert and Platt, 1980; Thierry *et al.*, 2011). Currently, the empirical and theoretical study of the predator–prey body-size relationship is being developed to utilise the useful concept of predator–prey mass ratio (PPMR). PPMR is considered to be the most

promising parameter for studying size-structured food webs and has been used to model food-web structure and dynamics (Brose *et al.*, 2006b; Jennings, 2005; Maury *et al.*, 2007; Petchey *et al.*, 2008; Silvert and Platt, 1980; Thierry *et al.*, 2011). PPMR represents the number of magnitude by which predator individuals are larger than their prey individuals and is ideally measured by direct gut content observations. A number of studies and reports have provided such data for a wide range of animal species. The compilation of these studies has recently revealed that, in general, the body mass of predators is about 100 times larger than that of their prey, although marked variations have also been found (Barnes *et al.*, 2010; Brose *et al.*, 2006a; Woodward and Warren, 2007).

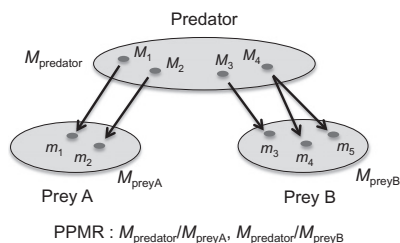
In theoretical studies, two main classes of size-structured food-web models have been developed, specifically species-based and size-based models. While both modelling approaches utilise PPMR as a key parameter, there are differences in the basic assumptions. The species-based approach assumes that body size is a characteristic of species (not individuals) and that feeding relationships between species are systematically determined based on a PPMR value (Brose *et al.*, 2006b; Petchey *et al.*, 2008; Thierry *et al.*, 2011). This modelling approach inevitably omits intraspecific variations in body size and resource use. Meanwhile, the size-based approach describes the size spectrum of a community, in which it is assumed that a single PPMR value regulates the frequency that prey–predator interactions occur between individuals (not species) to govern the dynamics of the community size spectrum (Jennings, 2005; Maury *et al.*, 2007; Silvert and Platt, 1980). This modelling approach incorporates intraspecific variation in body size, but often excludes species identity. Although species-based and size-based models are distinct in basic model structure, they share a common assumption that all individuals have an identical value of PPMR, irrespective of species identity and body mass. In other words, PPMR is regarded as a community-specific parameter representing some trophic characteristics of food webs.

While PPMR has been widely used in size-structured food-web modelling, the empirical estimation of PPMR is not straightforward and still remains controversial. There are two critical issues that may influence PPMR estimations, specifically scale dependence and variability.

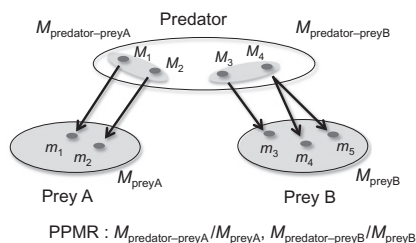
1. Scale Dependence of Predator–Prey Mass Ratio

PPMR may be defined at various biological scales, depending on the way in which predator and prey body mass is defined. As a result, several analytical procedures may be implemented for the empirical evaluation of PPMR. Woodward and Warren (2007) presented four definitions of PPMR ranging from low to high resolution, which we term (i) species-averaged PPMR,

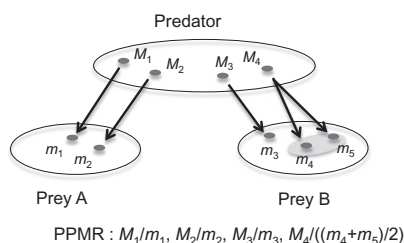
A Species-averaged PPMR



B Link-averaged PPMR



C Individual-predator PPMR



D Individual-link PPMR

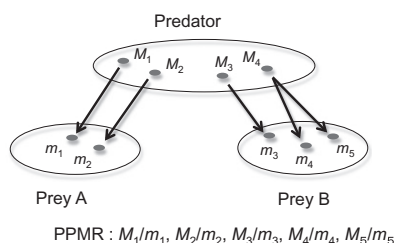


Figure 1 The four definitions of PPMR. Here, we use an example where four individuals of one predator species consume five individuals of two prey species (A and B, respectively). Dots and circles indicate individual and species identity, respectively. Arrows represent individual feeding links. M_i and m_i denote the body masses of predator and prey individuals, respectively. (A) Species-averaged PPMR is calculated as $M_{\text{predator}}/M_{\text{preyA}}$ and $M_{\text{predator}}/M_{\text{preyB}}$, where M_{predator} and M_{preyA} (or M_{preyB}) denote the mean body masses of the predator and prey species, respectively. (B) Link-averaged PPMR is calculated as $M_{\text{predator-preyA}}/M_{\text{preyA}}$ and $M_{\text{predator-preyB}}/M_{\text{preyB}}$, where $M_{\text{predator-preyA}}$ (or $M_{\text{predator-preyB}}$) denotes the mean body mass of predator individuals that consume prey species A (or B). (C) Individual-predator PPMR is calculated by using individual-predator mass M_i and the average prey mass (e.g. $(m_4$ and $m_5)/2$ for a predator). (D) Individual-link PPMR is calculated for each predation event. Grey regions indicate different analytical scales from individual to link to species resolution.

(ii) link-averaged PPMR, (iii) individual-predator PPMR, and (iv) individual-link PPMR, respectively (Figure 1).

The first definition, species-averaged PPMR, is measured by using the average body sizes of predator and prey species (Figure 1A):

$$\text{Species-averaged PPMR} = \frac{\text{Mean mass of predator individuals of a species}}{\text{Mean mass of prey individuals of a species}} \quad (1a)$$

The estimation of species-averaged PPMR only requires descriptive information about predator and prey species and independent information of representative body sizes. In contrast to the other three types of PPMR, species-averaged PPMR does not necessarily require individual-level gut content information and

individual predator and prey sizes. Hence, due to the technical ease of this method, species-averaged PPMR is the most commonly used form, as shown in the compilation of global datasets by [Brose *et al.* \(2006a\)](#). However, species-averaged PPMR may differ from the PPMRs defined at the individual level, when feeding habits vary within a species, for example, due to ontogenetic niche shifts ([Werner and Gilliam, 1984](#); [Wilbur, 1980](#)).

Link-averaged PPMR also utilises the mean body mass of multiple individuals within a species, but differs from predator-averaged PPMR by being based on the individual body masses of predators and prey that actually consume or are consumed by the interacting species ([Figure 1B](#)):

$$\text{Link-averaged PPMR} = \frac{\text{Mean mass of predator individuals consuming a prey species}}{\text{Mean mass of prey individuals consumed by a predator species}} \quad (1b)$$

Species-averaged and link-averaged PPMRs are species based, in the sense that these PPMRs use the mean body mass of multiple individuals.

The other two definitions of PPMR are individual based and are measured from the predator- and prey-centred viewpoints, respectively. Individual-predator PPMR is evaluated by viewing a predator individual as a scale at which predator body mass is defined and by averaging prey body masses found in the gut of predator individuals ([Figure 1C](#)):

$$\text{Individual-predator PPMR} = \frac{\text{Mass of an individual predator}}{\text{Mean mass of prey individuals consumed by a predator individual}} \quad (1c)$$

Individual-link PPMR focuses on each predation event of a prey individual ([Figure 1D](#)) and is defined as

$$\text{Individual-link PPMR} = \frac{\text{Mass of an individual predator}}{\text{Mass of a prey individual consumed by a predator individual}} \quad (1d)$$

PPMR may have several other definitions, depending on the selection of scale at which body mass and prey–predator pairs are defined. For example, species-averaged PPMR may be modified to fuse the prey species into a single category. Alternatively, as a modification of individual-predator PPMR, the prey individuals found in each predator gut may be divided by species.

The number of data samples that are available from the same gut content data varies among the four types of PPMR. The number of species-based PPMRs (species-averaged and link-averaged PPMRs) available from a given dataset is equal to that of predator–prey species-pair combinations. Meanwhile, the number of available individual-predator and individual-link PPMRs is equal to that of predator and prey individuals in the dataset, respectively. More importantly, it should be also noted that the estimated PPMR may vary depending on the definition (i.e. scaling from individuals to species). In a pioneering study, [Cohen *et al.* \(2005\)](#) examined the body lengths of 37 species of parasitoids and 12 species of their aphid hosts. This study showed that the relationship between host and parasitoid body size is

sensitive to the biological level at which body size is defined. Thereafter, [Woodward and Warren \(2007\)](#) performed a detailed analysis about how PPMR varies with respect to the four definitions in a freshwater invertebrate community (also see [Woodward and Hildrew, 2002](#)) and found that PPMR using averaged body sizes (in particular, species-averaged PPMR) was lower than individual-link PPMR by about one order of magnitude. As far as we know, these are the only two studies ([Cohen *et al.*, 2005](#); [Woodward and Warren, 2007](#)) that have thus far revealed the scale dependence of predator–prey (or parasitoid–host) body-size relations. Although still limited, the available evidence clearly indicates that the use of averaged body sizes to evaluate PPMR may generate a misleading interpretation of the real feeding relationships within food webs.

2. *Variability of Predator–Prey Mass Ratio*

The other critical issue regarding the empirical evaluation of PPMR is that, contrary to the assumptions made for size-structured food-web models, PPMR may not be identical among all individuals of all species in real food webs. Only a few exceptional studies have dealt with the issue of intra and/or interspecific variability of PPMR. [Cohen *et al.* \(2005\)](#) showed that primary, secondary, hyper-, and mammy parasitoids have different body-size relations with their host individuals and concluded that PPMR may vary among trophic niche positions. [Brose *et al.* \(2006a\)](#) analysed global datasets covering a wide range of animals and habitats and showed that PPMR varies across different habitats (e.g. higher in freshwater habitats than in marine or terrestrial habitats), predator types (e.g. higher for vertebrate than for invertebrate predators) and prey types (e.g. higher for invertebrate than for ectotherm vertebrate prey). Although these results clearly show that PPMR may vary among animal types or habitats, the study was only based on species-averaged PPMR, and thus the implications for individual-level predator–prey interactions remain uncertain. More recently, [Barnes *et al.* \(2008\)](#) compiled published gut content data of marine food webs, for which the body sizes of individual predators (mainly fish) and prey in their guts are available. Using this dataset, [Barnes *et al.* \(2010\)](#) illustrated that individual-predator PPMR varies among sampling sites and predator size classes. Their important finding is that PPMR increases with individual-predator mass, which implies that the relationships between the log body masses of predators and prey are non-linear, and clearly diverge from the conventional assumption that PPMR is common within species. All of the available examples indicate that PPMR may vary with various factors, such as species identity, body mass, and food webs. Logically, if all individuals of all species had a common PPMR, the different definitions of PPMR should produce an

identical value. Thus, the intraspecific or interspecific variability in PPMR is related to the issue that different PPMR values are obtained depending on the definition. However, at present we do not yet know exactly how PPMR varies with factors and which factors should be considered when using each definition of PPMR.

C. Goal of the Present Study

In brief, there is a gap between the empirical evaluation of PPMR and its application to the food-web modelling, which arises from the issues of scale dependence and variability of PPMR values. Hence, our primary goal was to address the two fundamental issues in more detail than previously, using the recently compiled gut content data of marine food webs (Barnes *et al.*, 2008). First, we show how the PPMR value varies among different definitions and suggest the potential mechanism that creates scale dependence. Second, we evaluate how the PPMRs defined at different scales are affected by predator species identity and body mass. Our analysis aims to provide insights towards improving our understanding of PPMR, facilitating future research with respect to PPMR.

II. DATA

We use the recently compiled gut content dataset of marine food webs (Barnes *et al.*, 2008). The original dataset comprised 34,931 records of prey–predator individual interactions from 27 locations, covering a wide range of environmental conditions from the tropics to the poles. The dataset includes 93 predator species (mainly fish) with size ranges of 0.1 mg to over 415 kg, and 174 prey types with size ranges of 75 pg to over 4.5 kg. Prey organisms are not always identified to the species level and are sometimes placed in an ‘unidentified’ category. Barnes *et al.* (2010) analysed the data from 21 sampling sites and examined the effects of habitat properties (e.g. productivity and water temperature) and body mass on PPMR. However, as neither the scale dependence of PPMR nor the possible effects of species identity were measured, the relative role of species identity and body mass, and its dependence on the scale at which PPMR was measured, remains unclear. We first conduct an analysis on the scale dependence of PPMR by using the existing data (Barnes *et al.*, 2010; Table 1). In addition, we examine the effects of species identity and body mass with respect to each definition of PPMR, for which we select 11 sampling sites that included more than two predator species.

Table 1 Sample sizes of predators and prey in the dataset (after [Barnes *et al.*, 2010](#))

Site	Location	Latitude	Longitude	Predator		Prey	
				Species	Individual	Category	Individual
01	East Greenland Shelf	60°00'N	40°00'W	2	23	3	49
02	Gulf of Alaska	49°00'N	123°00'W	19	414	16	606
03	Gulf of Mexico	29°40'N	85°10'W	3	73	1	115
04	Gulf of Alaska	56°50'N	156°00'W	1	16	11	43
05	NE Atlantic	44°00'N	16°00'W	1	77	30	827
06	NE US Continental Shelf	42°00'N	70°00'W	1	196	13	1909
07	Mid-Atlantic	39°50'N	73°00'W	1	113	2	113
08	NE US Continental Shelf	40°10'N	73°10'W	1	101	1	297
09	Antarctic Peninsula	63°00'S	58°00'W	2	689	27	2103
10	Antarctic Peninsula	62°00'S	55°00'W	1	90	10	105
11	Celtic-Biscay Shelf	51°52'N	04°10'W	1	14	1	1315
12	Mid-Pacific	12°00'S	144°00'W	2	233	4	4011
13	North Sea	57°00'N	08°00'W	1	21	1	21
14	West Greenland Shelf	66°20'N	56°00'W	2	163	3	163
15	Bay of Bengal	08°24'N	97°53'W	4	34	1	34
16	Celtic-Biscay Shelf	50°50'N	08°00'W	29	499	40	2091
17	NE Atlantic	45°00'N	18°00'W	2	39	12	3585
18	Mediterranean Sea	40°55'N	02°40'W	6	244	7	420
19	Kuroshio Current	37°00'N	143°00'W	2	111	23	414
20	NE US Continental Shelf	40°00'N	71°00'W	18	10,191	1	10,994
21	Mediterranean Sea	38°00'N	23°00'W	1	12	17	367

Site code corresponds to that of [Barnes *et al.* \(2010\)](#). Note that in the original dataset prey are not necessarily identified to the species level, and non-fish prey are sometimes counted by category, such as stage (e.g. egg and larvae) or common name (e.g. amphipod and squid). We analysed the data based on the original categorisation.

III. SCALE DEPENDENCE OF PREDATOR–PREY MASS RATIO

A. Methods and Results

The four types of PPMR were calculated using the data from all 21 sites to study the scale dependence of PPMR. The calculation of PPMRs requires information on predator and prey body masses, predator species identity, and prey category. The mean and median values were selected as representative values for each PPMR definition.

Our analysis showed that different values are obtained depending on the definition of PPMR (Figure 2), in agreement with Woodward and Warren (2007). However, closer investigation showed two major differences in the pattern found in our analysis compared to this earlier study. First, individual-link PPMR was higher by about one order of magnitude than link-averaged PPMR, which is in sharp contrast with the pattern reported by Woodward

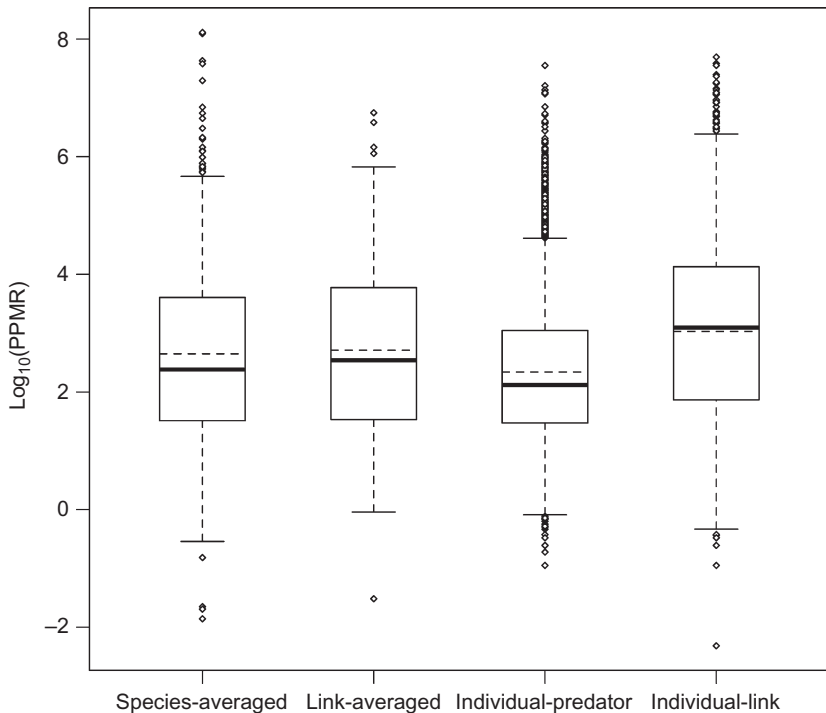


Figure 2 Scale dependence of PPMR estimation. In the boxplots, thick solid and thin dashed lines represent the median and mean values of PPMR, respectively.

and Warren (2007), whereby the value for individual-link PPMR was comparable with link-averaged PPMR. Second, the species-averaged PPMR value was similar to the link-averaged PPMR, whereas Woodward and Warren (2007) showed that the former was lower by about one order of magnitude than the latter. We observed that individual-predator PPMR was lower by about one order of magnitude than individual-link PPMR, while having a similar value to link-averaged PPMR. However, this pattern cannot be directly compared with that of Woodward and Warren (2007), because they provided individual-predator PPMR of a single predator, rather than of all predators in the community.

B. Mechanisms

What mechanism makes a PPMR value higher or lower than another PPMR? Why are the patterns that are observed different between studies? Here, we show that there are two potential major effects, specifically averaging and sampling effects. We show that these effects may generate variation among different PPMR definitions, and we suggest that the combination of the two effects may have led to the difference between the earlier study (Woodward and Warren, 2007) and ours. Woodward and Warren (2007) attributed the lower value for species-averaged PPMR to the averaging effect. Species-averaged PPMR assumes that all sizes of a predator population feed equally on prey of all sizes. However, this is unlikely when evaluating the other definitions of PPMR, because in reality, intraspecific variations exist in predator-prey interactions. In particular, smaller predator individuals are unlikely to consume larger prey individuals. The averaging effect arises from unrealistic links between smaller predator and larger prey that are inevitably incorporated in the procedure of species averaging and may lead to the underestimation of PPMR (Woodward and Warren, 2007; Yvon-Durocher *et al.*, 2011b).

Yet, their explanation of the averaging effect is based on a verbal model, and more formal arguments would be required to confirm the logic. More importantly, the averaging effect may not be the only effect making PPMR scale-dependent. In fact, the species-averaged and link-averaged PPMRs had similar values in our analysis (Figure 2), indicating that there may be a counter-effect to increasing the former PPMR and compensating for the averaging effect. As a result, it is still uncertain whether species averaging always results in lower PPMR values. Here, using simple mathematics and numerical simulations, we illustrate that species averaging may, or may not, result in lower PPMR and that the sampling effect also plays a major role.

Suppose that species-averaged and individual-predator PPMRs of the same predator species feeding on a prey species are compared. For simplicity, we assume that body-mass variation does not exist in prey that interact

with a predator individual. Assume that predator individuals of size class m_i ($m_{i-1} \leq m_i$) have the individual-predator PPMR r_i (i.e. their average prey mass is m_i/r_i) and that their proportion in the population is p_i . We also consider that each predator includes n_i prey individuals in the gut, with the biologically reasonable assumption that larger predator individuals consume more prey (i.e. $n_{i-1} \leq n_i$). Then, the average individual-predator PPMR of the predator species is given as

$$\sum p_i r_i = \bar{r}, \quad (2a)$$

where the bar represents the averaging among the predator size classes based on the proportion p_i . Meanwhile, the species-averaged PPMR is calculated by dividing the average predator body mass with the average prey body mass:

$$\sum p_i m_i / \frac{\sum p_i n_i m_i / r_i}{\sum p_i n_i} = \bar{m} / \frac{\overline{nm/r}}{\bar{n}}. \quad (2b)$$

According to the Chebyshev's sum inequality (i.e. $\overline{a\bar{b}} \leq \bar{a}\bar{b}$ if $a_{i-1} \leq a_i$ and $b_{i-1} \leq b_i$), it holds that

$$\bar{n}\bar{m} \leq \overline{nm}. \quad (3)$$

If the individual-predator PPMR is identical among all individuals (i.e. $r_{i-1} = r_i = \bar{r}$) as is conventional, it follows that

$$\frac{\bar{n}\bar{m}}{\bar{r}} \leq \overline{nm/r}. \quad (4)$$

This inequality illustrates that the individual-predator PPMR (Eq. (2a)) is higher than the species-averaged PPMR (Eq. (2b)) for any particular species. If the individual-predator PPMR varies within the predator species, and larger individuals have smaller values (i.e. $1/r_{i-1} \leq 1/r_i$), using the Chebyshev's sum inequality we obtain

$$\overline{nm} \overline{1/r} \leq \overline{nm/r} \quad (5)$$

because the arithmetic mean is always larger than the harmonic mean (i.e. $\overline{1/r} \geq 1/\bar{r}$). Together with inequalities (3) and (5), inequality (4) always holds, illustrating that the individual-predator PPMR is higher than the species-averaged PPMR. This seems consistent with the suggestion of Woodward and Warren (2007), whereby species averaging underestimates PPMR. However, this is not the case. In fact, the species-averaging effect may not lower PPMR values in the presence of small modifications that are added to the assumptions of the above equations. For example, when larger individuals have larger PPMR values (i.e. $r_{i-1} \leq r_i$; Barnes *et al.*, 2010; also see Section IV.B), or when there is no regularity in the

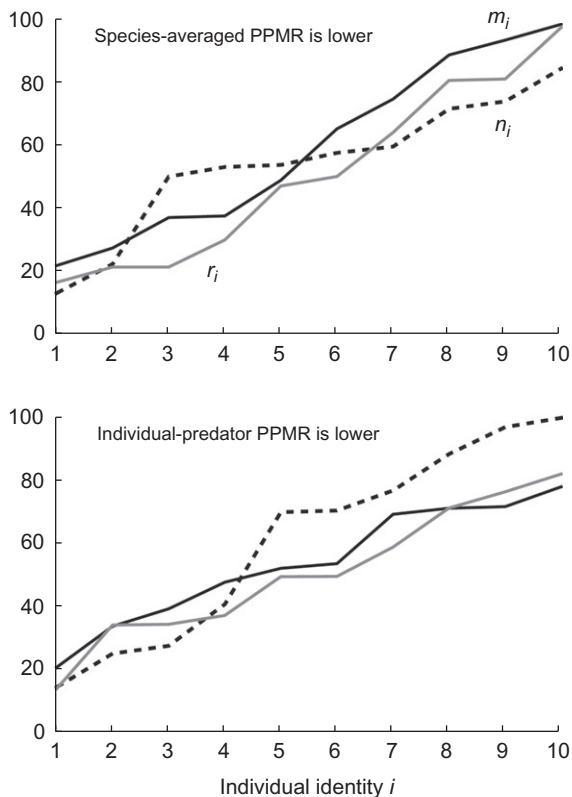


Figure 3 Example distributions of body mass m_i , prey count n_i , and PPMR r_i of predator individuals within a species when the inequality (4) is (upper) satisfied and (lower) not. Solid, dashed, and grey lines indicate m_i , n_i , and r_i , respectively. We randomly assigned values between 10 and 100 to the parameters of 10 predator individuals, with the assumptions that larger individuals have more prey in the guts and that larger values of PPMR (i.e. $m_{i-1} \leq m_i$, $n_{i-1} \leq n_i$, and $r_{i-1} \leq r_i$).

relationship between individual body mass m_i and PPMR r_i (e.g. random), individual-predator PPMR may be lower than the species-averaged PPMR. We may easily identify these counter-examples through numerical experiments (Figure 3). Next, let us consider the comparison of individual-predator and species-averaged PPMRs at the community level. Suppose that predator species j has individual-predator PPMR $\bar{r} = R_j$ and consists of N_j individuals, and that S predator species are included in the data (i.e. $j=1$ to S). The species-averaged and individual-predator PPMRs of the community are calculated, respectively, as

$$\sum R_j/S = \bar{R} \quad (6a)$$

and

$$\sum N_j R_j / \sum N_j = \overline{NR} / \bar{N}. \quad (6b)$$

Noting that parameters N_j and S are independent, it follows that, even when individual-predator PPMR is larger than species-averaged PPMR at the species level, we cannot immediately determine which is higher or lower at the community level. Meanwhile, if species with a smaller abundance (i.e. with larger average body mass) have larger PPMR (i.e. $N_{j-1} \geq N_j$ and $R_{j-1} \leq R_j$; Barnes *et al.*, 2010; also see Section IV B), using the Chebyshev's sum inequality we obtain

$$\bar{N}\bar{R} \geq \overline{NR}. \quad (7a)$$

This inequality is transformed to

$$\bar{R} \geq \overline{NR} / \bar{N}. \quad (7b)$$

This result means that species averaging overestimates PPMR compared to individual-predator PPMR at the community level. This result contrasts with the suggestion of Woodward and Warren (2007), yet supports our observations that species-averaged PPMR was larger than individual-predator PPMR (Figure 2). The overestimation of PPMR values caused by the species averaging is explained by the fusion of abundant individuals with small values of PPMR for a single data point. Therefore, the individual-predator PPMR may be lower than the species-averaged PPMR at the community level. For example, this may arise when sample counts of species with relatively lower species-averaged PPMR are much greater than the counts of species with high species-averaged PPMRs.

Our present analysis is focused towards comparing species-averaged and individual-predator PPMRs. However, a similar explanation may be extended and applied to the comparison between other scales. For example, the prey count of each predator individual should also affect whether individual-predator or individual-link PPMR of a community is greater, as well as the total predator species number and individual count of each species. By combining this information with the results of Woodward and Warren (2007), we conclude that different definitions of PPMR may lead to different values that are higher or lower based on the detail of data elements that are used, such as body mass and sample counts of prey and predator individuals and species. Therefore, the argument that the species averaging leads to a low PPMR (Woodward and Warren, 2007; also see Yvon-Durocher *et al.*, 2011b) is not a general pattern, with the number of sample counts being crucial.

C. Application

PPMR is scale dependent and may vary depending on the method of estimation. This fact has an important implication on how size-structured food-web models should be constructed and parameterised (also see Gilljam *et al.*, 2011). Size-structured food-web models implicitly or explicitly assume particular definitions of PPMR, in accordance with the model structure. Therefore, we suggest that these models should be parameterised based on the particular PPMR that reflects the assumption. For example, species-based allometric food-web models (Brose *et al.*, 2006b; Petchey *et al.*, 2008; Thierry *et al.*, 2011) exclude intraspecific variations by adopting the species averaging procedure and thus should be based on species-based PPMR, such as species-averaged and link-averaged PPMRs. On the other hand, size-based community-spectrum models (Jennings, 2005; Maury *et al.*, 2007; Silvert and Platt, 1980) assume that prey–predator interactions occur between individuals (not species) and thus should rely on individual-based PPMR, such as individual-predator and individual-link PPMRs.

Given this, conventional parameterisation of current modelling approaches could be improved. In particular, the size-based approach has conventionally employed $PPMR = 10^2$ (e.g. Andersen and Beyer, 2006; Blanchard *et al.*, 2009; Hartvig *et al.*, 2011) to quantitatively describe marine food webs. However, our analysis of marine food-web data revealed that individual-link PPMR would be greater by about one order of magnitude, while individual-predator PPMR is still close to 10^2 (Figure 2). The same results were obtained in a freshwater invertebrate community, where individual-predator PPMR is estimated to be close to 10^3 rather than 10^2 (Woodward and Warren, 2007). We therefore argue that there should be a greater focus on the scale dependence of PPMR and that size-structured food-web models should be more carefully parameterised using an appropriate definition of PPMR.

IV. DETERMINANTS OF PREDATOR–PREY MASS RATIO

A. Statistical Analysis

The scale dependence of PPMR (Figure 2; also see Woodward and Warren, 2007) implies that PPMR may not be identical among individuals of the same species and/or among species within the same food web. This casts a question as to what determines each type of PPMR. Such studies remain limited, despite previous analyses showing how PPMR is related to various factors, such as predator body size, species identity or animal type, and habitat

property (Barnes *et al.*, 2010; Brose *et al.*, 2006a). Further, analyses to systematically investigate and compare the determinants of PPMR among different definitions have never been conducted.

Here, we analyse the two major effects of predator species identity and body mass on PPMR to estimate possible determinants of PPMRs. Through the selection of 11 sampling sites containing multiple predator species from the dataset (i.e. sites 01, 02, 03, 09, 12, 14, 15, 16, 18, 19, and 20), we developed and tested the following four statistical models for each PPMR definition and each sampling site: (i) a null model assuming that PPMR is common among all individuals of all species (i.e. $\log_{10}(\text{PPMR}) = \alpha$), (ii) a taxonomic model accounting for species-specificity of PPMR (i.e. $\log_{10}(\text{PPMR}) = \alpha + \beta \times (\text{predator species identity})$), (iii) an allometric model accounting for size dependence of PPMR (i.e. $\log_{10}(\text{PPMR}) = \alpha + \beta \times \log_{10}(\text{predator body mass})$), and (iv) a combined model, including both the effects of species identity and body mass (i.e. $\log_{10}(\text{PPMR}) = \alpha + \beta_1 \times (\text{predator species identity}) + \beta_2 \times \log_{10}(\text{predator body mass}) + \beta_3 \times (\text{predator species identity}) \times \log_{10}(\text{predator body mass})$). PPMR and predator body mass are log transformed to improve normality in the statistical analysis. Note that body mass represents the averaged measurements for species-averaged and link-averaged PPMRs, while individual mass is used for individual-predator and individual-link PPMRs. We do not consider prey species identity as an explanatory factor. Yet, this decision is not because prey species identity is not expected to explain PPMR. Rather, this is simply because the information about prey species identity is often absent from the datasets. Following Barnes *et al.* (2010), we use linear mixed models for individual-predator PPMR by including individual identity as a random factor. Therefore, it should be noted that individual-predator PPMR in this study is slightly different to that shown in Figure 1C, but the basic concept is still same, since we regard a predator individual as a basic unit. On the other hand, linear models are applied for the other three definitions of PPMR. By comparing the Akaike information criteria (AIC), we determine the best statistical model. All analyses are performed in the statistical environment R (R Development Core Team, 2010). Mixed model analyses are conducted by using 'nlme' package of R (Pinheiro *et al.*, 2009).

B. Results

For species-averaged and link-averaged PPMRs, different models were selected among the sampling sites and the best model was not clear (Table 2). This may be partly due to the limitation of sample number (i.e. species number). Taxonomic and combined models performed optimally for the datasets, where multiple prey species were pooled into a single category

Table 2 AIC values of the four statistical models for the four definitions of PPMR

Site	Null	Taxonomic	Allometric	Combined	Null	Taxonomic	Allometric	Combined
	Species-averaged PPMR				Link-averaged PPMR			
01	15.8	14.8	14.8	14.8	14.3	15.2	15.5	18.5
02	212.5	220.1	199.4	220.1	180.2	191.9	179.6	201.6
03	-0.5	-∞	-∞	-∞	-2.0	-∞	-0.1	-∞
09	91.5	92.5	92.5	92.5	73.6	75.6	73.1	72.8
12	-0.6	-4.0	-4.0	-4.0	15.5	4.5	10.7	6.1
14	21.0	22.9	22.9	22.9	20.1	22.1	19.9	17.5
15	7.7	-∞	-276.5	-∞	4.5	-∞	1.7	-∞
16	440.1	406.4	387.0	406.4	418.4	340.3	403.7	350.8
18	64.1	69.8	62.2	69.8	56.4	56.4	57.6	59.6
19	68.0	69.2	69.2	69.2	65.3	67.3	67.3	70.4
20	28.9	-∞	-1194.4	-∞	24.1	-∞	24.2	-∞
	Individual-predator PPMR				Individual-link PPMR			
01	119.1	96.5	110.6	99.1	114.5	89.6	104.0	90.2
02	1415.0	1322.4	1327.1	1287.4	1410.3	1291.2	1314.8	1260.4
03	58.9	63.8	43.5	48.8	96.1	96.1	62.9	66.8
09	2652.3	2631.9	2506.1	2513.3	3613.4	3505	3191.9	3165.8
12	8916.6	8782.1	8848.4	8771.2	10,370	9478.1	9955.6	9372.6
14	372.3	375.7	361.3	355.0	366.4	367.6	354.3	347.2
15	35.0	19.9	14.6	17.0	29.3	5.0	5.2	-3.4
16	3439.8	3103.4	3413.9	3075	4159.8	3224.7	4098	3093
18	961.6	954.2	966.1	952.5	1006.2	973.4	1007.7	959.5
19	798.7	799.0	803.3	798.6	804.9	800.9	806.9	794
20	28,781	26,491	28,176	26,146	29,377	26,802	28,725	26,363

Background shading indicate the best model with the lowest AIC for each site and each PPMR definition.

(i.e. sites 03, 15, and 20), for which the AIC obtained negative infinite values. For the species-averaged PPMR, three of the models (with the exception of the null model) exhibited the same performance at sites 01, 09, 12, 14, and 19. This may be attributed to the fact that these sites include just two predator species. Interestingly, at other sites (i.e. sites 02, 16, and 18), an allometric model was commonly selected for species-averaged PPMR, although this was not always the case for link-averaged PPMR. If more predator species are sampled, a pattern showing that body mass is crucial for species-averaged and link-averaged PPMR may emerge.

Individual-predator and individual-link PPMRs were generally best explained by the combined model that included both species identity and body mass (7/11 sites for individual-predator PPMR and 9/11 sites for individual-link PPMR; Table 2). A null model was not selected in any of the sites. This result has two implications. First, interactions between predator and prey individuals are critically affected by both species identity and body mass. This develops the previous argument by Barnes *et al.* (2010), who only emphasised the effect of body mass on PPMR. Second, the determinants of PPMR may become clearer with increasing resolution of data analysis, as indicated by the result that a particular model was selected for individual-predator and individual-link PPMRs, while the best model was unclear for species-averaged and link-averaged PPMRs.

We evaluated in more detail how PPMR is determined by species identity and body mass by highlighting two of the models that explain individual-predator PPMR of each species. These comprised the model with species identity alone and the combined model with both species identity and body mass (see Barnes *et al.*, 2010 for the effect of body mass alone). The model with species identity alone is based on the assumption that PPMR is common within species. The analysis showed that there were significant interspecific differences in PPMR (i.e. the 95% confident interval of at least one of the species did not overlap with that of any other species) in 8 of 11 sites (i.e. sites 01, 02, 09, 12, 15, 16, 18, and 20; Figure 4). The most distinct differences were found at site 20, which contained almost one-third of all interaction records for the 21 sites ($n=10,994$; Table 1). At site 20 (NE US Continental Shelf), *Merluccius bilinearis* (commonly named silver hake) and *Mustelus canis* (smooth dogfish) had the lowest and highest PPMRs of $10^{1.25 \pm 0.05}$ and $10^{2.94 \pm 0.09}$, respectively, indicating a difference of about a 50-fold. No significant interspecific differences in PPMR were observed for sites 03, 14, and 19, probably due to small sample sizes ($n=115, 163, \text{ and } 414$, respectively).

We evaluated the interaction effect of species identity and body mass by comparing the regression slope of the relationship between $\log_{10}(\text{PPMR})$ and $\log_{10}(\text{individual body mass})$ of each predator species, as in the methodology of Barnes *et al.* (2010) at the community level. If the slope is positive (or negative), then it indicates that the relationship between

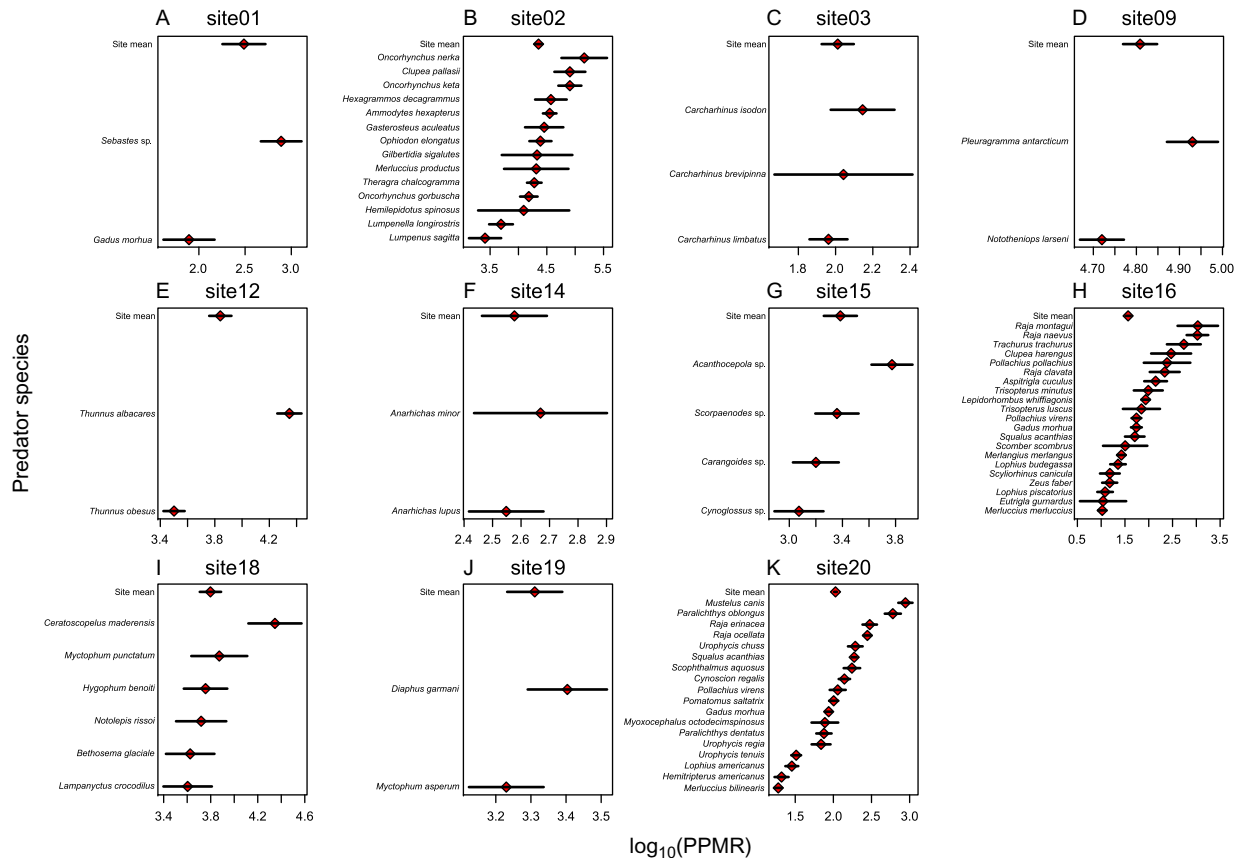


Figure 4 Species specificity of individual-predator PPMR at each sampling site. Diamonds indicate the mean values and bars represent 95% confident intervals. The site mean value is shown at the top of each panel.

$\log_{10}(\text{predator mass})$ and $\log_{10}(\text{PPMR})$ is positive (or negative) and that the predator species feeds on relatively larger (or smaller) prey as it grows. A zero slope means no change in relative prey size during individual growth, suggesting no intraspecific variation in PPMR. The analysis revealed that there were significant interspecific differences in the regression slope at sites 16, 18, and 20 (Figure 5). The most distinct differences were again found at site 20, including the largest sample size (Table 1). The species specificity of the slope may become clearer if sufficient data were available for the other sites.

C. Application

We have argued (see Section III.C) that the species-based allometric and size-based spectrum models should employ species-based (species-averaged or link-averaged PPMR) and individual-based (individual-predator or individual-link) PPMRS, respectively. The present analysis evaluates how these PPMRs could be improved by including the effects of species identity and body size. First, it is necessary to incorporate the body-mass effects on PPMR, irrespective of the type of model being used. Given that prey–predator interactions occur at an individual level, the fact that individual-based PPMRs are improved by incorporating the body-size effect might indicate that PPMRs affect trophic interaction-related behaviour in a non-linear way. Further, the incorporation of species-averaged body mass improves the explanation of species-based PPMRs (Table 2). This means that PPMR should be size dependent in species-based allometric food-web models that omit intraspecific variation. We also showed both body mass and species identity are crucial, especially for individual-predator and individual-link PPMRs (Table 2), from which it may be inferred that size-based community-spectrum models should incorporate both species-identity and body-mass effects.

Our argument, in part, counters the initial motivation of constructing size-based community-spectrum models, which aimed to reduce the complexity of size-structured food webs by overlooking interspecific variability. However, we recommend that the incorporation of both species identity and body-mass effects would provide the most useful inferences from which future research could better understand and predict food-web dynamics. Indeed, this line of argument has also been presented in the recent study of functional response (e.g. Brose *et al.*, 2008b; Rall *et al.*, 2011; Vucic-Pestic *et al.*, 2010) and food-web modelling (e.g. Andersen and Beyer, 2006; Blanchard *et al.*, 2009; Hartvig *et al.*, 2011). An important question to be addressed in future studies is which approach is better, species-based allometric modelling or size-based spectrum modelling. We cannot yet answer

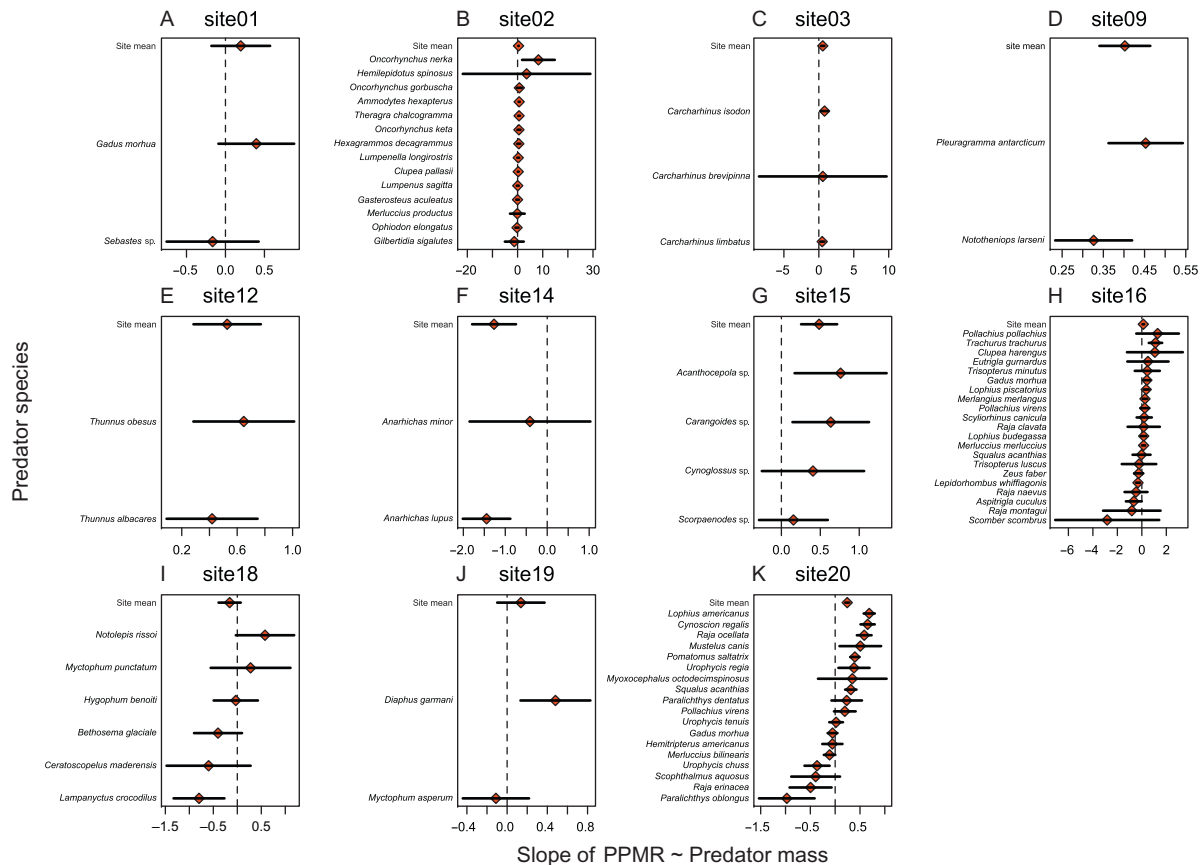


Figure 5 Species specificity of regression slopes between individual-predator PPMR and individual body mass at each sampling site. The statistical model is described as $\log_{10}(\text{PPMR}) = \text{slope} \times \log_{10}(\text{individual-predator mass}) + \text{intercept}$. Diamonds indicate species-specific slopes and bars indicate 95% confident intervals. Dashed lines indicate the regression slopes of zero, which implies constant relative prey size during individual growth.

this question conclusively, but speculate that the development of the latter model would be most productive (see Section V.C).

V. PERSPECTIVES

A. Other Determinants of Predator–Prey Mass Ratio

In the present analysis, we have shown that the body-size relationship between predator and prey varies with predator species identity and absolute body mass. Although data are still limited, it is expected that other factors also influence these patterns, which will be important issues in future studies. In this section, we briefly discuss other possible determinants of PPMR using our preliminary results.

1. Habitat Property

Environmental factors, such as water temperature and oxygen concentration, may critically affect behavioural performance, especially in aquatic animals, and the effects are expected to be size dependent (Brill, 1987; Cuenco *et al.*, 1985). The metabolic theory of ecology places particular emphasis on the importance of temperature in various biological processes and patterns (Brown *et al.*, 2004). For example, a recent study showed that increasing water temperature shifts the size spectrum of freshwater plankton communities towards smaller individuals with rapid turnover rates (Yvon-Durocher *et al.*, 2011a). It is therefore expected that environmental factors affect PPMR through changes in feeding performance and community structure, such as species composition and size distributions. Barnes *et al.* (2010) tested this hypothesis by investigating how the nonlinearity of PPMR is related to environmental conditions (e.g. water temperature, latitude, depth, and primary productivity) at 21 sampling sites, but found no significant relationship. We conducted a new analysis, which extends their analysis to include predator species and individuals as random effects, in which individuals were nested by species. Our analysis showed that mean individual-predator PPMR varies greatly with site (see Figure 4 for sites with multiple predator species). The relationships with environmental conditions were not significant in simple regression analyses (not shown). In addition, the highest and lowest values were found at the most closely neighbouring locations, specifically sites 09 (63°00'S, 58°00'W) and 10 (62°00'S, 55°00'W), where $\text{PPMR} = 10^{4.81 \pm 0.04}$ and $10^{0.65 \pm 0.14}$, respectively. These results do not contradict the previous suggestion that environmental factors do not affect PPMR (Barnes *et al.*, 2010).

2. Prey Species Identity

It is reasonable to expect that PPMR is critically affected by prey species identity (see [Henri and vanVeen, 2011](#) for host–parasitoid interactions). In general, predation avoidance is more important for prey than predation success is for predators, which is known as the life-dinner principle ([Dawkins and Krebs, 1979](#)). The evolution of defence by prey may, therefore, more effectively influence feeding relationships compared with the evolution of offence tactics by predators. To evaluate the possible effect of prey species identity on PPMR, we analysed the data from 13 sampling sites, where multiple prey species were identified to at least the genus level (i.e. sites 01, 02, 04, 05, 06, 09, 10, 14, 16, 17, 18, 19, and 21). In the analysis, we used prey species identity as an independent variable and included predator individual identity as a random effect. Unidentified prey categories were excluded from the analysis. The analysis showed that PPMR is highly variable among prey species, with significant interspecific differences being found at 12 sites, except for site 01 ([Figure 6](#)). It should be noted here that we detected predator species specificity of PPMR in just 8 of the 11 sites ([Figure 4](#)). Therefore, prey species identity may be more crucial for PPMR. Further study is required to determine the predator–prey species-pair specificity of PPMR, by focusing on prey species identity in the gut contents of predators (see Section [V.B](#)).

3. Evolutionary History

What determines species identity of predator and prey? One proposal is that feeding relationships may reflect the evolutionary history of food webs. [Bersier and Kehrli \(2008\)](#) supported this idea by showing that phylogeny and trophic relationships are closely linked in a size-structured food web. With the same framework, [Rohr et al. \(2010\)](#) predicted that the structure of food webs is explained by species-specific latent parameters, as well as by body size, which they suggested were size-unrelated traits determining predator foraging and prey vulnerability (i.e. species identity). Although these studies are formed on the species-based approach without intraspecific variations, it is noteworthy that the incorporation of the evolutionary perspectives of food webs ([Melián et al., 2011](#)) might enhance our understanding of prey–predator feeding relationships, and thus possibly PPMR.

We examined the phylogenetic relationships of individual-predator PPMR to identify the possible effect of phylogeny on PPMR. Following [Nelson \(2006\)](#), we assigned phylogenetic ranks, ranging from 1 to 16, to all available orders of fish predators. Note that the dataset includes one species of squid predator, which we treat as the most ancestral order, with a ranking of 1.

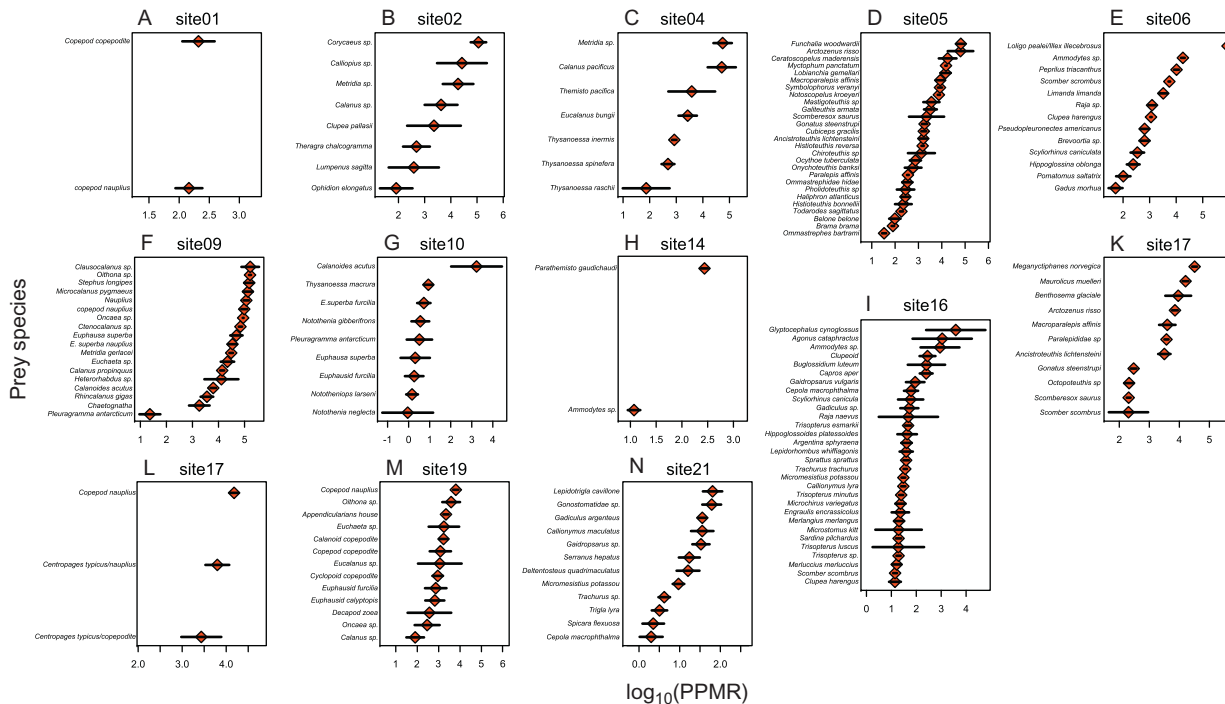


Figure 6 Prey species specificity of PPMR at each sampling site. Diamonds indicate the mean values and bars represent 95% confident intervals.

Interestingly, we found that some orders (e.g. Lophiiformes, Myctophiformes, Rajiformes, and Salmoniformes) have a relatively narrow range of PPMR despite being sampled at distant locations, while other orders (e.g. Gadiformes, Perciformes, and Scorpaeniformes) have wide variations across about four orders of magnitude (Figure 7). These results may suggest that the nature of the predator–prey body-size relationship is contingent, to some extent, on evolutionary history, although sample size was limited in the present analysis and further investigation is required. The relationship between the order mean of individual-predator PPMR and phylogenetic rank (simply assigned from 1 to 16) was significant, where $\log_{10}(\text{PPMR}) = 0.301 \times \log_{10}(\text{phylogeny rank}) + 2.078$ ($p < 0.001$), implying that more recently evolved orders may have higher values of PPMR. Recently, Romanuk *et al.* (2011) showed that descendant orders of fish have smaller body masses and lower trophic levels (i.e. smaller prey mass), while the regression slope is more strongly negative for the relationship between phylogenetic rank and body size. Their results appear to support our findings.

4. Temporal Variability

The present and most previous data of feeding relationships represent ‘snapshots’ of time-varying trophic relationships, which is a long-standing problem in the study of feeding relationships (McLaughlin *et al.*, 2010; Warren and Lawton, 1987). Through the use of stable isotope analysis, Nakazawa *et al.* (2010) showed that the relationship between body size and trophic niche position of a freshwater fish species may change over a period of more than 40 years. In other words, the PPMR of species may change through time. Although McLaughlin *et al.* (2010) showed seasonal and ontogenetic changes in PPRM, long-term evidence remains scarce, which is crucial for a better understanding of food-web dynamics. Gut content analysis from archival specimens collected over a long period may provide a means of directly addressing this issue (Nakazawa *et al.*, in preparation).

B. Functional Response

Finally, we review recent advances and future directions in the study of size-dependent trophic interactions and its use in food-web modelling by focusing on two specific topics. First, we address issues of functional response, another important concept in foraging ecology, through which we strongly emphasise the importance of both body size and species identity in predator–prey interactions. Thereafter, we describe how size-structured food-web models should be improved based on current knowledge.

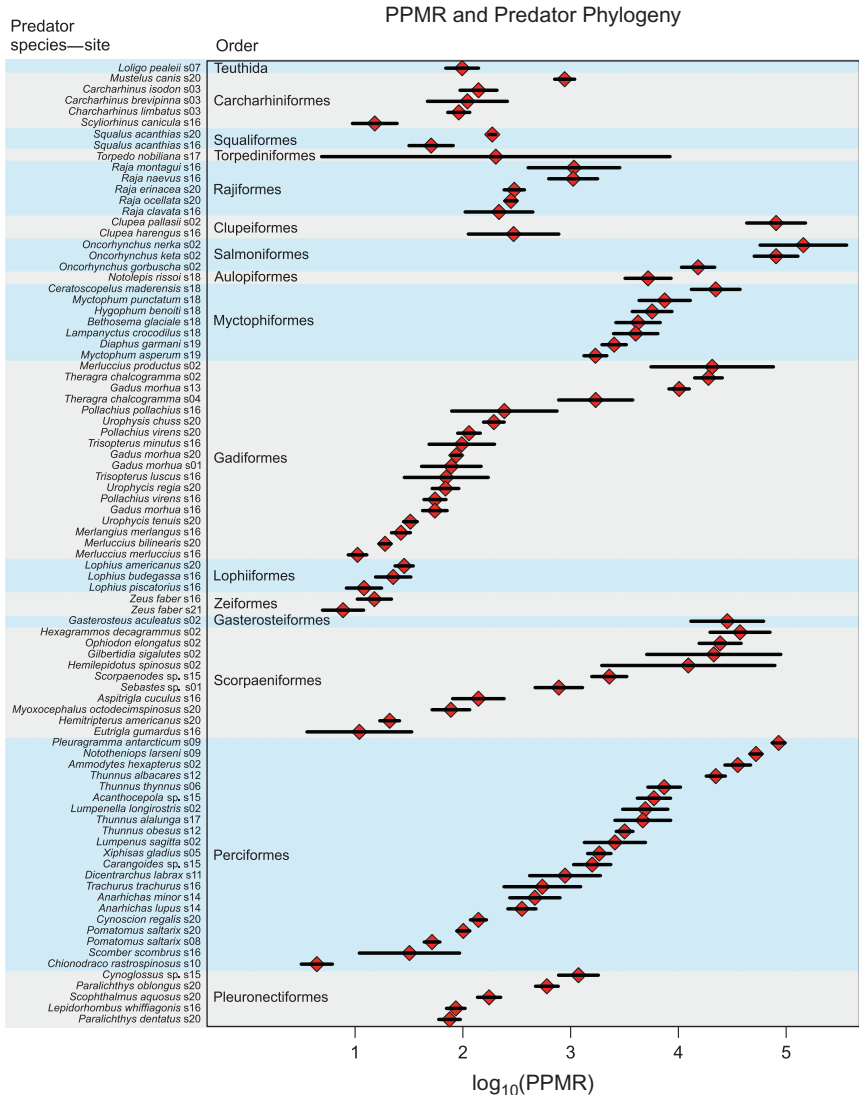


Figure 7 Phylogenetic relationships of PPMR. Following Nelson (2006), phylogenetic ranks are assigned to 15 orders of fish predator. Note that the top order Teuthida represents one species of squid that is the most ancestral. Predator species are arranged in a descending sequence of individual-predator PPMR within each order. Diamonds indicate species-specific slopes and bars indicate 95% confident intervals.

PPMR has been measured in pattern-oriented approaches based on empirical data obtained from natural ecosystems (Barnes *et al.*, 2008; Brose *et al.*, 2006a; Woodward and Warren, 2007). It is therefore difficult to understand fully the factors that mediate predator–prey size relationships. On the other hand, looking back over the history of ecology, we easily find a large amount of process-oriented work on predator–prey interactions (e.g. functional responses and strength distribution) and associated ecological consequences (e.g. system stability and species coexistence). In particular, it has recently been acknowledged that weak interactions and optimal foraging have stabilising effects on food webs (e.g. Kondoh, 2003; McCann *et al.*, 1998). These studies have either explicitly or implicitly assumed that different species would behave differently for predation and predation avoidance, which is in sharp contrast to the conventional view that PPMR is common among all species. To bridge the gap between pattern-oriented and process-oriented approaches, it is necessary to obtain a more detailed evaluation on the role of body size and species identity in predation processes. Indeed, empiricists are now becoming more interested in these issues.

The functional response is a key concept to explain predator–prey interactions and its dynamic consequences on food webs. Traditionally, the concept has ignored the effects of body size, simply representing how the foraging efficiency of a predator individual varies with prey density, where species identity is a matter. Now, it is expected that the functional response is affected by the body sizes of interacting predators and prey. Several experiments have tested the possibility for various predator and prey taxa. For example, Elliot (2005) showed that different size classes of Trichoptera individuals have different forms of functional response for Chironomidae larvae. Further, Moss and Beauchamp (2007) used different species of salmonid fish to illustrate that size-dependent functional responses are species specific. Some researchers have examined more closely how functional response parameters, such as attack rate and handling time, are related to predator and prey body sizes and species identities (e.g. Aljetlawi *et al.*, 2004; Vucic-Pestic *et al.*, 2010). Recently, Rall *et al.* (2011) used AIC to show a combined functional response for terrestrial arthropods, showing that both body mass and taxonomic effects performed better than a species-specific functional response (which does not account for intraspecific body-size variations of predators) or an allometric functional response (which does not account for taxonomic dissimilarities). Collectively, existing studies have established that the strength of predator–prey interactions typically depend on population abundances, species identities, and the body masses of interacting predators and prey. This seems robust to taxonomic groups, including fish, being consistent with our findings of the gut content data of marine food webs.

Intriguingly, [Brose *et al.* \(2008b\)](#) illustrated that the size-related feeding properties of predatory beetles and spiders mediate, not only functional responses but also the energy flux through feeding links. Such a view has been widely applied to species-based food-web models by relating body size to population dynamics based on biologically plausible energetics and the allometric scaling of metabolism ([Arim *et al.*, 2011](#); [Brose, 2010](#); [Brose *et al.*, 2006b](#); [Emmerson and Raffaelli, 2004](#); [Weitz and Levin, 2006](#); for pioneering work, also see [Brown *et al.*, 2004](#); [Yodzis and Innes, 1992](#)). These studies have illustrated that species body size critically affects key dynamic features of food webs (e.g. variability and persistence) and, moreover, realistic food webs are likely to be stable. However, the effects of intraspecific variations have not been considered in these studies. An exceptional study is that by [Rudolf and Lafferty \(2011\)](#), which showed that ontogenetic niche shifts reduce the robustness of multispecies communities. For a better understanding of size-structured food webs, the species-based allometric model and the size-based spectrum model should be reconciled using the information provided by this study on predator–prey interactions.

C. Food-Web Modelling

The integration of species-based and size-based approaches would potentially improve our understanding of size-structured food webs. There are two possible approaches: one using the species-based model and one using the size-based community-spectrum model.

The first approach would require the incorporation of intraspecific size/stage variation into species-based allometric food-web models. Obviously, this makes the model structure more complex, the number of parameters larger, and the food-web modelling more technically difficult. However, mathematical techniques have been proposed to reduce the complexity and make this approach feasible. For example, [De Roos *et al.* \(2008\)](#) presented an analytical method to convert a physiologically structured (i.e. size-structured) population model to an easy-to-handle stage-structured biomass model. [Rossberg and Farnsworth \(2011\)](#) devised a numerical method to approximately describe the complex dynamics of stage-structured multispecies models. However, those techniques are based on specific, and often mutually contradicting, assumptions, such as constant body size (i.e. no growth) after maturation ([De Roos *et al.*, 2008](#)) and constant growth rates throughout life history ([Rossberg and Farnsworth, 2011](#)), which makes the unification of these different methodologies difficult. More sophisticated mathematical techniques are still necessary to appropriately simplify size/stage-structured food-web models. Another difficulty in adopting this approach is that the determinants of species-based PPMRs (species-averaged

or link-averaged PPMR), on which the species-based model is based, are variable among food webs (Table 2).

The second modelling approach requires the modification of size-based community-spectrum models to differentiate species. This approach has the advantage that individual-based PPMR (individual-predator or individual-link PPMR), which is the key parameter in this type of modelling, is usually directly related to species identity and body mass in most food webs (Table 2). In the original size-based spectrum model, it was assumed that primary production by small organisms is transferred directly to higher trophic levels with a constant PPMR. A way to utilise the size-based spectrum model through incorporating interspecific PPMR variation is to investigate the ecological consequence of coupling different trophic paths. Aquatic ecosystems provide a good example of such research, where pelagic food webs (i.e. phytoplankton–zooplankton–planktivores–piscivores) are usually linked to benthic food webs supported by detritus and/or periphyton (Rooney *et al.*, 2006), which is known as pelagic–benthic coupling (Schindler and Scheuerell, 2002; Vadeboncoeur *et al.*, 2002). Blanchard *et al.* (2009, 2011) presented coupling models of phytoplankton-based and detritus-based trophic pathways, which capture the PPMR-related differences between the two paths, whereby the benthic food web had less clear size-dependent feeding than the pelagic food web. Given that PPMR is expected to be larger in aquatic systems than in terrestrial systems, especially for ectothermic vertebrates (Brose *et al.*, 2006a), a similar application would be possible for aquatic-terrestrial food webs coupled through resource subsidy (Doi, 2009; Polis *et al.*, 1997, 2004) and the ontogenetic niche shift of animals, such as aquatic insects and amphibians (Nakano and Murakami, 2001; Nakazawa, 2011a,b). Given the generality and diversity of coupled food webs in nature (Bardgett and Wardle, 2010; Schindler and Scheuerell, 2002; Vadeboncoeur *et al.*, 2002), an interesting question is how individual-level PPMR differs among distinct types of ecosystems, or how the coupling of food webs with different PPMRs mediates the structure and dynamics of the whole system.

Another way to modify the size-based spectrum model is to split the community-size spectrum into species. Andersen and Beyer (2006) and Hartvig *et al.* (2011) assumed that asymptotic body size and size at maturity are species specific. The model by Hartvig *et al.* (2011) is especially notable in that different species were given different feeding efficiencies, even at the same body mass. The researchers weighted the experienced community size spectrum for each species, explaining that it would represent interspecific interaction strength, and hence species-based food-web architecture. However, their model still employs the conventional assumption that all species maximise foraging efficiency at the same PPMR, despite absolute levels being different.

VI. CONCLUSION

Although the PPMR has been widely used in size-based food-web modelling, the empirical estimation of PPMR is not simple and remains controversial. This is because PPMR may be defined in different ways, depending on the choice of biological scale from individuals to communities. Therefore, there is variation in PPMR with factors such as species identity and body mass, which contrasts with the conventional assumption of these models. Using recently compiled gut content data of marine food webs (Barnes *et al.*, 2008), we conducted a detailed study of scale dependence and determinants of PPMR. We illustrated that the scale dependence of PPMR is determined in a complex way and that the averaging and sampling effects may result in different values of PPMR, depending on data elements such as body mass and sample counts of predators and prey. The results of our study complement previous arguments that species averaging underestimates PPMR (Woodward and Warren, 2007; Yvon-Durocher *et al.*, 2011b). We also used AIC to elucidate how PPMR is explained by predator species identity and body mass for different PPMR definitions. We observed that the possible determinants of PPMR become clearer with increasing resolution of data analysis. For species-averaged and link-averaged PPMRs, different statistical models were selected among food webs, with the best model remaining unclear. For individual-predator and individual-link PPMRs, the model that combined species identity and body-mass effects gave the best explanation in most of food webs. Based on these results, we discussed the application of PPMR in food-web models. The species-based allometric food-web model relies on the species-averaged or link-averaged PPMR, the determinants of which are uncertain, and thus caution is necessary when applying the model. Meanwhile, the size-based community-spectrum model, which relies on individual-predator or individual-link PPMR, should consider taxonomic dissimilarities, although it runs counter to the initial objective to simplify the complexity of the food-web structure. We also suggest that PPMR may vary with factors other than predator species identity and body mass. To date, no theoretical models have been developed to predict the observed patterns of PPMR, such as scale dependence and interspecific or intraspecific variations. It is important to recognise that we are still at an early stage of understanding size-dependent trophic interactions and their resulting food-web dynamics. Further studies are required to accumulate high-resolution data on feeding relationships in various ecosystems and to establish a more reliable form of size-structured food-web models. Laboratory experiments are also useful for identifying the determinants of predator-prey body-size relationships. Ultimately, future research with respect to PPMR is expected to contribute to our understanding of the structure and dynamics of complex food webs.

REFERENCES

- Aljetlawi, A.A., Sparrevik, E., and Leonardsson, K. (2004). Prey–predator size-dependent functional response: Derivation and rescaling to the real world. *J. Anim. Ecol.* **73**, 239–252.
- Andersen, K.H., and Beyer, J.E. (2006). Asymptotic size determines species abundance in the marine size spectrum. *Am. Nat.* **168**, 54–61.
- Arim, M., Berazategui, M., Barreneche, J.M., Ziegler, L., Zarucki, M., and Abades, S.R. (2011). Determinants of density–body size scaling within food webs and tools for their detection. *Adv. Ecol. Res.* **45**, 1–39.
- Bardgett, R.D., and Wardle, D.A. (2010). Aboveground–Belowground Linkages: Biotic Interactions, Ecosystem Processes, and Global Change. Oxford University Press, Oxford, UK.
- Barnes, C., Bethea, D.M., Brodeur, R.D., Spitz, J., Ridoux, V., Pusineri, C., Chase, B.C., Hunsicker, M.E., Juanes, F., Kellermann, A., Lancaster, J., Menard, F., *et al.* (2008). Predator and body sizes in marine food webs. *Ecology* **89**, 881.
- Barnes, C., Maxwell, D., Reuman, D.C., and Jennings, S. (2010). Global patterns in predator–prey size relationships reveal size dependency of trophic transfer efficiency. *Ecology* **91**, 222–232.
- Bersier, L.F., and Kehrl, P. (2008). The signature of phylogenetic constraints on food-web structure. *Ecol. Complex.* **5**, 132–139.
- Blanchard, J.L., Jennings, S., Law, R., Castle, M.D., McCloghrie, P., Rochet, M.-J., and Benoît, E. (2009). How does abundance scale with body size in coupled size-structured food webs? *J. Anim. Ecol.* **78**, 270–280.
- Blanchard, J.L., Law, R., Castle, M.D., and Jennings, S. (2011). Coupled energy pathways and the resilience of size-structured food webs. *Theor. Ecol.* **4**, 289–300.
- Brill, R.W. (1987). On the standard metabolic rates of tropical tunas, including the effect of body size and acute temperature change. *Fish. Bull.* **85**, 25–35.
- Brose, U. (2010). Body-mass constraints on foraging behaviour determine population and food-web dynamics. *Funct. Ecol.* **24**, 28–34.
- Brose, U., Jonsson, T., Berlow, E.L., Warren, P., Banasek-Richter, C., Bersier, L.F., Blanchard, J.L., Brey, T., Carpenter, S.R., Blandenier, M.F.C., Cushing, L., Dawah, H.A., *et al.* (2006a). Consumer–resource body-size relationships in natural food webs. *Ecology* **87**, 2411–2417.
- Brose, U., Williams, R.J., and Martinez, N.D. (2006b). Allometric scaling enhances stability in complex food webs. *Ecol. Lett.* **9**, 1228–1236.
- Brose, U., Ehnes, R.B., Rall, B.C., Vucic-Pestic, O., Berlow, E.L., and Scheu, S. (2008). Foraging theory predicts predator–prey energy fluxes. *J. Anim. Ecol.* **77**, 1072–1078.
- Brown, J.H., Gillooly, J.F., Allen, A.P., Savage, V.M., and West, G.B. (2004). Toward a metabolic theory of ecology. *Ecology* **77**, 1771–1789.
- Castle, M.D., Blanchard, J.L., and Jennings, S. (2011). Predicted effects of behavioural movement and passive transport on individual growth and community size structure in marine ecosystems. *Adv. Ecol. Res.* **45**, 41–66.
- Cohen, J.E., Pimm, S.L., Yodzis, P., and Saldaña, J. (1993). Body sizes of animal predators and animal prey in food webs. *J. Anim. Ecol.* **62**, 67–78.
- Cohen, J.E., Jonsson, T., Müller, C.B., Godfray, H.C., and Savage, V.M. (2005). Body sizes of hosts and parasitoids in individual feeding relationships. *Proc. Natl. Acad. Sci. USA* **102**, 684–689.

- Cuenco, M.L., Stickney, R.R., and Granta, W.E. (1985). Fish bioenergetics and growth in aquaculture ponds: II. Effects of interactions among, size, temperature, dissolved oxygen, unionized ammonia and food on growth of individual fish. *Ecol. Model.* **27**, 191–206.
- Dawkins, R., and Krebs, J.R. (1979). Arms races between and within species. *Proc. R. Soc. B* **205**, 489–511.
- De Roos, A.M., Schellekens, T., Van Kooten, T., Van De Wolfshaar, K., Claessen, D., and Persson, L. (2008). Simplifying a physiologically structured population model to a stage-structured biomass model. *Theor. Popul. Biol.* **73**, 47–62.
- Doi, H. (2009). Spatial patterns of autochthonous and allochthonous resources in aquatic food webs. *Popul. Ecol.* **51**, 57–64.
- Ebenman, B., and Persson, L. (1988). *Size-Structured Populations: Ecology and Evolution*. Springer-Verlag, Heidelberg, Germany.
- Elliot, J.M. (2005). Ontogenetic shifts in the functional response and interference interactions of *Rhyacophila dorsalis* larvae (Trichoptera). *Freshw. Biol.* **50**, 2021–2033.
- Emmerson, M.C., and Raffaelli, D. (2004). Predator-prey body size, interaction strength and the stability of a real food web. *J. Anim. Ecol.* **73**, 399–409.
- Gilljam, D., Thierry, A., Figueroa, D., Jones, I., Lauridsen, R., Petchey, O., Woodward, G., Ebenman, B., Edwards, F.K., and Ibbotson, A.T.J. (2011). Seeing double: Size-based versus taxonomic views of food web structure. *Adv. Ecol. Res.* **45**, 67–133.
- Hartvig, M., Andersen, K.H., and Beyer, J.E. (2011). Food web framework for size-structured populations. *J. Theor. Biol.* **272**, 113–122.
- Henri, D.C., and vanVeen, F.J.F. (2011). Body size, life history and the structure of host-parasitoid networks. *Adv. Ecol. Res.* **45**, 135–180.
- Hildrew, A.G., Raffaelli, D.R., and Edmonds-Brown, R. (2007). *Body Size: The Structure and Function of Aquatic Ecosystems*. Cambridge University Press, Cambridge, UK.
- Jacob, U., Thierry, A., Brose, U., Arntz, W.E., Berg, S., Brey, T., Fetzer, I., Jonsson, T., Mintenbeck, K., Mollmann, C., Petchey, O., Raymond, B., *et al.* (2011). The role of body size in complex food webs: A cold case. *Adv. Ecol. Res.* **45**, 181–223.
- Jennings, S. (2005). Size-based analyses of aquatic food webs. In: *Aquatic Food Webs: An Ecosystem Approach* (Ed. by A. Belgrano, U.M. Scharler, J. Dunne and R.E. Ulanowicz), pp. 86–97. Oxford University Press, Oxford, UK.
- Kondoh, M. (2003). Foraging adaptation and the relationship between food-web complexity and stability. *Science* **28**, 1388–1391.
- Maury, O., Faugeras, B., Shin, Y.-J., Poggiale, J.-C., Ari, T.B., and Marsa, F. (2007). Modeling environmental effects on the size-structured energy flow through marine ecosystems. Part 1: The model. *Prog. Oceanogr.* **74**, 479–499.
- McCann, K., Hastings, A., and Huxel, G.R. (1998). Weak trophic interactions and the balance of nature. *Nature* **395**, 794–798.
- McLaughlin, Ó.B., Jonsson, T., and Emmerson, M.C. (2010). Temporal variability in predator–prey relationships of a forest floor food web. *Adv. Ecol. Res.* **42**, 171–264.
- Melián, C.J., Vilas, C., Baldó, F., González-Ortegón, E., Drake, P., and Williams, R. J. (2011). Eco-evolutionary dynamics of individual-based food webs. *Adv. Ecol. Res.* **45**, 225–268.
- Moss, J.H., and Beauchamp, D.A. (2007). Functional response of juvenile pink and chum salmon: Effects of consumer size and two types of zooplankton prey. *J. Fish Biol.* **70**, 610–622.

- Nakano, S., and Murakami, M. (2001). Reciprocal subsidies: Dynamic interdependence between terrestrial and aquatic food webs. *Proc. Natl. Acad. Sci. USA* **98**, 166–170.
- Nakazawa, T. (2011a). Alternative stable states generated by ontogenetic habitat coupling in the presence of multiple resource use. *PLoS One* **6**, e14667.
- Nakazawa, T. (2011b). Ontogenetic niche shift, food-web coupling, and alternative stable states. *Theor. Ecol.* 10.1007/s12080-010-0090-0, in press.
- Nakazawa, T., Sakai, Y., Hsieh, C.H., Koitabashi, T., Tayasu, I., Yamamura, N., and Okuda, N. (2010). Is the relationship between body size and trophic niche position time-invariant in a predatory fish? First stable isotope evidence. *PLoS One* **5**, e9120.
- Nelson, J.S. (2006). *Fishes of the World*. 4th edn., John Wiley and Sons, New York, USA.
- Petchey, O.L., Beckerman, A.P., Riede, J.O., and Warren, P.H. (2008). Size, foraging, and food web structure. *Proc. Natl. Acad. Sci. USA* **105**, 4191–4196.
- Peters, R.H. (1983). *The Ecological Implications of Body Size*. Cambridge University Press, Cambridge, UK.
- Pinheiro, J., Bates, D., DebRoy, S., Sarkar, D., and Team, t.R.C. (2009). nlme: Linear and Nonlinear Mixed Effects of Models, GNU R Project.
- Polis, G.A., Anderson, W.B., and Holt, R.D. (1997). Toward an integration of landscape and food web ecology: The dynamics of spatially subsidized food webs. *Annu. Rev. Ecol. Syst.* **28**, 289–316.
- Polis, G.A., Power, M.E., and Huxel, G.R. (2004). *Food Webs at the Landscape Level*. University of Chicago Press, Chicago, USA.
- R Development Core Team (2010). *R: A Language and Environment for Statistical Computing*. R Foundation for Statistical Computing, Vienna, Austria.
- Rall, B.C., Kalinkat, G., Ott, D., Vucic-Pestic, O., and Brose, U. (2011). Taxonomic versus allometric constraints on non-linear interaction strengths. *Oikos* **120**, 483–492.
- Rohr, R.P., Scherer, H., Kehrl, P., Mazza, C., and Bersier, L.F. (2010). Modeling food webs: Exploring unexplained structure using latent traits. *Am. Nat.* **176**, 170–177.
- Romanuk, T.N., Hayward, A., and Hutchings, J.A. (2011). Trophic level scales positively with body size in fishes. *Global Ecol. Biogeogr.* **20**, 231–240.
- Rooney, N., McCann, K., Gellner, G., and Moore, J.C. (2006). Structural asymmetry and the stability of diverse food webs. *Nature* **442**, 266–269.
- Rossberg, A.G., and Farnsworth, K.D. (2011). Simplification of structured population dynamics in complex ecological communities. *Theor. Ecol.* 10.1007/s12080-010-0088-7, in press.
- Rudolf, V.H.W., and Lafferty, K.D. (2011). Stage structure alters how complexity affects stability of ecological networks. *Ecol. Lett.* **14**, 75–79.
- Schindler, D.E., and Scheuerell, M.D. (2002). Habitat coupling in lake ecosystems. *Oikos* **98**, 177–189.
- Silvert, W., and Platt, T. (1980). Dynamic energy-flow model of the particle size distribution in pelagic ecosystems. In: *Evolution and Ecology of zooplankton Communities* (Ed. by W.C. Kerfoot), pp. 754–763. University Press of New England, Hanover, USA.
- Thierry, A., Petchey, O.L., Beckerman, A.P., Warren, P.H., and Williams, R.J. (2011). The consequences of size dependent foraging for food web topology. *Oikos* **120**, 493–502.

- Vadeboncoeur, Y., Vander Zanden, M.J., and Lodge, D.M. (2002). Putting the lake back together: Reintegrating benthic pathways into lake food web models. *Bioscience* **52**, 44–54.
- Vucic-Pestic, O., Rall, B.C., Kalinkat, G., and Brose, U. (2010). Allometric functional response model: Body masses constrain interaction strengths. *J. Anim. Ecol.* **79**, 249–256.
- Warren, P.H., and 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.
- Weitz, J.S., and Levin, S.A. (2006). Size and scaling of predator–prey dynamics. *Ecol. Lett.* **9**, 548–557.
- Werner, E.E., and Gilliam, J.F. (1984). The ontogenetic niche and species interactions in size-structured populations. *Annu. Rev. Ecol. Syst.* **15**, 393–425.
- Wilbur, H.M. (1980). Complex life cycles. *Annu. Rev. Ecol. Syst.* **11**, 67–93.
- Woodward, G., and Hildrew, A.G. (2002). Body-size determinants of niche overlap and intraguild predation within a complex food web. *J. Anim. Ecol.* **71**, 1063–1074.
- Woodward, G., and Warren, P.H. (2007). Body size and predatory interaction in freshwaters: Scaling from individuals to communities. In: *Body Size: The Structure and Function of Aquatic Ecosystems* (Ed. by A.G. Hildrew, D. Raffaelli and R. Edmonds-Brown), pp. 97–117. Cambridge University Press, Cambridge, UK.
- Woodward, G., Ebenman, B., Emmerson, M., Montoya, J.M., Olesen, J.M., Valido, A., and Warren, P.H. (2005). Body size in ecological networks. *Trends Ecol. Evol.* **20**, 402–409.
- Woodward, G., Blanchard, J., Lauridsen, R.B., Edwards, F.K., Jones, I.J., Figueroa, D., Warren, P.H., and Petchey, O.L. (2010). Individual-based food webs: Species identity, body size and sampling effects. *Adv. Ecol. Res.* **43**, 211–266.
- Yodzis, P., and Innes, S. (1992). Body size and consumer-resource dynamics. *Am. Nat.* **139**, 1151–1175.
- Yvon-Durocher, G., Montoya, J.M., Trimmer, M., and Woodward, G. (2011a). Warming alters the size spectrum and shifts the distribution of biomass in freshwater ecosystems. *Glob. Change Biol.* **17**, 1681–1994.
- Yvon-Durocher, G., Ress, J., Blanchard, J., Ebenman, B., Perkins, D.M., Reuman, D.C., Thierry, A., Woodward, G., and Petchey, O.L. (2011b). Across ecosystem comparisons of size structure: Methods, approaches and prospects. *Oikos* **120**, 550–563.