Estimation of predator-prey mass ratios using stable isotopes: sources of errors.

Eric Hertz[1,3]*, James PW Robinson[1,3], Marc Trudel[1,2], Asit Mazumder[1], Julia K Baum[1]

[1]Department of Biology, University of Victoria, PO BOX 3020, Station CSC, Victoria British Columbia, Canada, V8W 3N5

[2]Pacific Biological Station, Department of Fisheries and Oceans Canada, 3190 Hammond Bay Road, Nanaimo, British Columbia, Canada, V9T 6N7

[3] These authors contributed equally to this work.

*corresponding author:
hertzy@uvic.ca
Phone: 1 (250) 721-8099
Fax: 1 (250) 472-4766

Running page head: Predator-prey mass ratio error sources

Key words: body size, diet dependent discrimination factor, North Sea, size spectra, PPMR, food webs, size structure

This preprint is the original submission of a recently accepted article in Marine Ecology Progress Series. We will update this preprint with a final version once the revised article is published online.

PeerJ PrePrints | http://dx.doi.org/10.7287/peerj.preprints.544v1 | CC-BY 4.0 Open Access | rec: 17 Oct 2014, publ: 17 Oct 2014

Abstract:

In aquatic systems, the ratio of predator mass to prey mass (PPMR) is an important constraint on food web structure, and has been correlated with environmental stability. One common approach of estimating PPMR uses nitrogen stable isotopes ($\delta^{15}N$) as an indicator of trophic position, under the assumption that the discrimination between diet and tissue is constant with increasing diet $\delta^{15}N$ (an additive approach). However, recent studies have shown that this assumption may not be valid, and that there is a negative trend between the $\delta^{15}N$ of the diet and the discrimination value (a scaled approach). We estimated PPMR for a simulated food web using the traditional additive approach and improved scaled approach, before testing our predictions with isotope samples from a North Sea food web. Our simulations show that the additive approach gives incorrect estimates of PPMR, and these biases are reflected in North Sea PPMR estimates. The extent of the bias is dependent on the baseline $\delta^{15}N$ and trophic level sampled, with the greatest differences for samples with low baseline $\delta^{15}N$ sampled at lower trophic levels. The scaled approach allows for the comparison of PPMR across varying $\delta^{15}N$ baselines and trophic levels, and will refine estimates of PPMR.

PeerJ PrePrints | http://dx.doi.org/10.7287/peerj.preprints.544v1 | CC-BY 4.0 Open Access | rec: 17 Oct 2014, publ: 17 Oct 2014

Introduction

Body size is of critical importance in ecology, reflecting key ecological processes including metabolism and feeding interactions (Elton 1927; Peters 1983; Brown et al. 2004). Aquatic communities are size structured, with individual organisms generally feeding on prey smaller than themselves (Jennings et al. 2001; Barnes et al. 2010). The mean predator-prey mass ratio (PPMR) reflects constraints on community size structure (Trebilco et al. 2013), and is correlated with the general food web properties of food chain length and stability (Jennings & Warr 2003). Empirical sub-community estimates of PPMR vary by over an order of magnitude, from approximately 100 in the North Sea (Jennings & Mackinson 2003) to over 7000 in the Western Arabian Sea (Al-Habsi et al. 2008), though it is unclear if this variability reflects methodological biases or real food web differences.

PPMR can be estimated using direct observations of the size of prey in predator stomach contents or indirectly through stable isotope analysis (Jennings et al. 2002, Barnes et al. 2010). Although stomach contents allow identification of prey types, and direct measurement of predator and prey body masses, this approach is limited because stomach contents reflect only recent feeding events, do not represent assimilated material, and can be biased by differences in digestibility amongst prey items (Polunin & Pinnegar 2002). Given these limitations, stable isotope analysis of nitrogen ($\delta^{15}N$) has been increasingly employed to estimate PPMR (Jennings et al. 2002; Al-Habsi et al. 2008). In this approach, for a community spanning several orders of magnitude in mass, each sampled body mass class is assigned a biomass-weighted mean $\delta^{15}N$ value that is used as a proxy for trophic position (Jennings et al. 2002). Assuming a linear relationship between trophic position and body mass class, the slope (b) is then used to estimate PPMR,

$$\mathrm{PPMR} = n^{(\Delta 15\mathrm{N}/b)} \qquad \text{(Equation 1)}$$

where n reflects the log base used to bin mass values (often 2) and $\Delta^{15}N$ is the assumed change in $\delta^{15}N$ between predator and prey, known as the isotope discrimination value (Figure 1).

When using $\delta^{15}N$ to determine trophic position, the isotope discrimination value ($\Delta^{15}N$) is assumed to be a constant value, typically 3.4‰ (Minagawa & Wada 1984; Vander Zanden & Rasmussen 1999; Post 2002). Recent laboratory experiments and syntheses of published data have, however, shown that this is not necessarily the case. Instead, there is a significant negative linear relationship between the $\delta^{15}N$ of an organism's diet (hereafter dietary $\delta^{15}N$), and the $\Delta^{15}N$ experienced by that organism (Caut et al. 2008; 2009; Dennis et al. 2010; Hussey et al. 2014). At low dietary $\delta^{15}N$ values (e.g. < 6‰), the $\Delta^{15}N$ experienced by an organism can be significantly higher than 3.4‰, while at high dietary $\delta^{15}N$ values (e.g. > 12‰), the $\Delta^{15}N$ can be significantly lower than 3.4‰, and may even become negative at very high

PeerJ PrePrints | http://dx.doi.org/10.7287/peerj.preprints.544v1 | CC-BY 4.0 Open Access | rec: 17 Oct 2014, publ: 17 Oct 2014

dietary $\delta^{15}N$ (Dennis et al. 2010; Hussey et al. 2014). As a consequence, estimation of PPMR from stable isotope data may be systematically biased by assuming a constant $\Delta^{15}N$ of 3.4‰.

Here, we examine to what extent estimates of PPMR would be affected by systematic differences in $\Delta^{15}N$ with increasing dietary $\delta^{15}N$. We estimate trophic position and PPMR for simulated $\delta^{15}N$ data, first using the traditional assumption of a constant discrimination of 3.4‰ and second using a correction for variable discrimination values depending on dietary $\delta^{15}N$. We then test our approach with stable isotope estimates from a North Sea food web (Jennings et al. 2002, Jennings & Warr 2003). Comparison of these two approaches reveals that the traditional approach substantially underestimates PPMR at low $\delta^{15}N$ and overestimates PPMR at high $\delta^{15}N$, and that the extent of the bias is dependent on the range of $\delta^{15}N$ sampled.

Materials and methods

PPMR estimation

To assess the extent of bias in PPMR estimation, we estimated the trophic position of an organism in two distinct ways. First, we assumed that $\Delta^{15}N$ is constant across dietary $\delta^{15}N$ at a value of 3.4‰. In this additive approach, the trophic position of an organism is calculated as

$$TP_{additive} = TP_{base} + \frac{\delta^{15}N_{fish} - \delta^{15}N_{base}}{\Delta^{15}N} \qquad \text{(Equation 2)}$$

where $\Delta^{15}N$ is 3.4‰, $\delta^{15}N_{fish}$ is the $\delta^{15}N$ value of the organism, and $\delta^{15}N_{base}$ is the $\delta^{15}N$ value of a baseline consumer (Cabana & Rasmussen 1996; Post 2002). Second, we varied $\Delta^{15}N$ systematically with the dietary $\delta^{15}N$ (i.e. scaled approach). In this scaled approach $\Delta^{15}N$ declines systematically with dietary $\delta^{15}N$, and trophic position is calculated using a $\delta^{15}N$ enrichment model, based on a formulation of the von Bertalanffy growth equation,

$$TP_{scaled} = \frac{\log(\delta^{15}N_{lim} - \delta^{15}N_{base}) - \log(\delta^{15}N_{lim} - \delta^{15}N_{fish})}{k} + TP_{base} \qquad \text{(Equation 3)}$$

where $\delta^{15}N_{lim}$ and k are parameters from Hussey et al.'s (2014) meta-analysis. In both approaches PPMR is then estimated using Equation 1. After conversion of $\delta^{15}N$ to trophic position, the equation to estimate PPMR becomes

$$\mathrm{PPMR}_{TP} = n^{(1/b)} \qquad \text{(Equation 4)}$$

Simulated data

To explore how PPMR estimates differ between the additive and scaled approaches, we simulated $\delta^{15}N$ values for a theoretical community of individuals ranging in body mass from 4 – 10^6g, binned into $\log_2$ mass classes ranging from 2 to 20 (Github). We parameterised the simulations with values to reflect biologically realistic isotope values for aquatic communities. $\delta^{15}N$ increased sequentially for each mass class by a random number drawn from a normal distribution (mean = 0.34, standard deviation = 0.05), representing the generally positive increase of $\delta^{15}N$ with mass class observed in other studies (e.g Jennings et al. 2001; Al-Habsi et al. 2008). The initial $\delta^{15}N$ (at log mass class 2) spanned a range of values of primary consumers, increasing from $\delta^{15}N_{base}$ values of 4 (Chiba et al. 2012; Hussey et al. 2014) to 11 (El-Sabaawi et al. 2012) (Supplementary Material). We examined two theoretical communities. First, we performed the simulations for a low $\delta^{15}N$ community, where the initial $\delta^{15}N$ was similar to $\delta^{15}N_{base}$. Second, since the study design and sampling gears used in some previous studies sample communities beginning at a trophic level of 4 (Jennings & Warr 2003), we also ran the simulations with initial $\delta^{15}N$ at 6 above $\delta^{15}N_{base}$ to explore the effects of sampling these higher trophic level organisms (e.g. Jennings et al. 2002).

TP_{base} for all simulations was 2.5 following Jennings & Warr (2003), though our results are robust to other biologically plausible TP_{base} values, as TP_{base} is a constant in both methods of estimating trophic position (Equation 2, 3). We show that the robustness of our simulation results does not depend on the PPMR value by repeating our simulations for communities with low PPMR (e.g. Jennings et al. 2002), and high PPMR (e.g. Al-Habsi et al. 2008) (Supplementary Material). All simulations were repeated for 10000 replicates.

North Sea data

We then reanalysed the North Sea stable isotope data from Jennings et al. (2002) and Jennings & Warr (2003) to determine the extent to which the biases evidenced from our simulations affect PPMR estimates in real food webs. We compared PPMR estimates from the additive and scaled approaches, and divided sites into high and low $\delta^{15}N_{base}$ samples to determine how estimates of PPMR varied with $\delta^{15}N_{base}$.

Results and discussion

Our analyses show that the assumption of a constant $\Delta^{15}N$ of 3.4‰ can result in vastly different estimates of PPMR than when one employs a more realistic scaled approach. The extent of this bias depends on two factors: the $\delta^{15}N_{base}$ value, and the trophic level of the sampled community. For a low $\delta^{15}N$ community, the additive approach overestimated PPMR by over 1000 at low $\delta^{15}N_{base}$ values ($\delta^{15}N_{base}$ = 4 – 8‰), but underestimated PPMR by approximately 500 at high $\delta^{15}N_{base}$ values ($\delta^{15}N_{base}$ = 8 – 11‰) (Fig. 2a). In the scaled approach, initial $\Delta^{15}N$ is much larger than 3.4‰ at low $\delta^{15}N_{base}$ values, producing lower trophic level estimates, a correspondingly lower *b*, and higher PPMR estimates (Fig. 1). As $\delta^{15}N_{base}$ increases to 8‰, $\Delta^{15}N$ approaches 3.4‰ such that PPMR estimates converge, while at $\delta^{15}N_{base}$ greater than 8‰, $\Delta^{15}N$ decreases below 3.4‰, trophic level estimates increase, and PPMR decreases (Fig. 2a).

For a high $\delta^{15}N$ community, additive PPMR estimates are overestimated by approximately 400 when $\delta^{15}N_{base}$ is 4‰, and by 1000 when $\delta^{15}N_{base} > 7$‰ (Fig. 2b). When higher trophic level organisms are sampled (corresponding with higher $\delta^{15}N$), the scaled approach estimates of PPMR decrease with increasing $\delta^{15}N_{base}$ (Fig. 2b). Since the largest difference between the scaled $\Delta^{15}N$ and the additive $\Delta^{15}N$ occurs where the dietary $\delta^{15}N$ is lowest, by sampling at high $\delta^{15}N$ the differences are muted (Fig. 2b). Results are qualitatively similar for a range of PPMR estimates under the additive approach (Supplementary Material) and show that because of the inverse relationship between $\Delta^{15}N$ and dietary $\delta^{15}N$, the estimate of PPMR depends strongly on the $\delta^{15}N_{base}$ value.

The scaled approach diverges markedly from the additive one when $\delta^{15}N_{base}$, and thus the corresponding dietary $\delta^{15}N$, is especially large or small. When dietary $\delta^{15}N$ is between approximately 5-13‰, however, bias in PPMR estimates between the scaled and additive approach is negligible (e.g. Figure 2, Hussey et al. 2014). The subsequent deviation in PPMR estimates is generally smaller if the body mass - $\delta^{15}N$ relationship is entirely contained in this range. However, if the dietary $\delta^{15}N$ falls at the boundaries of this range, the difference between methods is more apparent, with the scaled approach predicting $\Delta^{15}N$ values double of the additive approach at low $\delta^{15}N$, and less than half at high $\delta^{15}N$ (Caut et al. 2009; Hussey et al. 2014).

Jennings & Warr (2003) analysed isotope data of North Sea food webs with the additive approach and reported a mean community PPMR of 424:1. We reanalysed these data using the scaled approach and found mean North Sea PPMR equal to 430:1 (Fig. 3a), despite our simulations predicting a bias at similar $\delta^{15}N_{base}$ (North Sea data: 4.5-10.7‰, mean = 6.3‰) and $\delta^{15}N$ (North Sea data: 8-18‰, mean = 12.8‰) values (Fig. 2b). To explore these disparate results, we disaggregated the North Sea into low and high $\delta^{15}N_{base}$ sites and then found strong support for the model prediction (Fig. 3b, 3c). At sites with $\delta^{15}N_{base} < 7$‰, additive PPMR was 331:1 and scaled PPMR was 187:1. At sites with $\delta^{15}N_{base} > 7$‰, additive PPMR was 3915:1 and scaled PPMR was 255:1. As predicted by the high $\delta^{15}N$ model (Fig. 2b), scaled PPMR is consistently lower than additive PPMR, and the difference increases with $\delta^{15}N_{base}$.

The similar scaled and additive estimates for the full North Sea community were driven by the inclusion of the largest mass class (13.5), which was sampled only at four low $\delta^{15}N_{base}$ sites ($\delta^{15}N_{base}$ = 4.5, 4.8, 5.2, 5.5). For a single mass class sample, at low $\delta^{15}N_{base}$ the level of discrimination is greater than at high $\delta^{15}N_{base}$ and the corresponding scaled trophic position is lower. In the full community analysis, the trophic position estimate at mass 13.5 was necessarily lower relative to other mass classes (where each other $\delta^{15}N$ estimate reflected the full range of $\delta^{15}N_{base}$), contributing to a lower slope and thus greater scaled PPMR estimate. When sample sizes are equivalent across $\delta^{15}N_{base}$ values and mass classes (Fig 2b, 2c), scaled PPMR is lower than additive PPMR, thus reflecting our predictions. Note that in splitting sites by their $\delta^{15}N_{base}$ value, our approach is not indicative of the overall North Sea community PPMR but instead allows us to explore variation in PPMR across a range of $\delta^{15}N_{base.}$

Though the underlying mechanism is not understood, the inverse relationship between $\Delta^{15}N$ and dietary $\delta^{15}N$ has been demonstrated by a number of controlled laboratory experiments (Caut et al. 2008; Dennis et al. 2010) and meta-analyses of published data from across an array of aquatic organisms (Caut et al. 2009; Hussey et al. 2014). Many factors can affect $\Delta^{15}N$, including diet quality (Robbins et al. 2010), temperature (Power et al. 2003), and type of nitrogen excretion (Vanderklift & Ponsard, 2003). These other factors do not, however, vary consistently with body size and thus would not cause a systematic change in $\Delta^{15}N$. The systematic change in $\Delta^{15}N$ with dietary $\delta^{15}N$, and thus body size, demands further investigation.

Previous PPMR estimates have been calculated across the range of $\delta^{15}N$ values where we expect substantial differences between the scaled and additive approaches. According to our simulations, the additive PPMR estimates of both Jennings et al. (2008a) (PPMR = 109:1, for $\delta^{15}N$ of 7.5-14‰) and Al-Habsi et al. (2008) (PPMR=7792:1, for $\delta^{15}N$ of 14.1-19‰) may be substantially biased toward overestimating the true community PPMR value. Such biases have important implications for food web studies. As PPMR are used to build fisheries size spectra (Andersen and Beyer 2006, Blanchard et al. 2009), to describe food web structures (Cohen et al. 2003, Bascompte et al. 2005), and to discern general community properties (Riede et al. 2011, Trebilco et al. 2013), the interpretations we draw from such studies depend on the accuracy of PPMR estimates. In the aquatic size spectrum - a relationship between body size and abundance of individuals in a community - the slope is strongly constrained by PPMR and by the efficiency of energy transfer across trophic levels (Jennings and Mackinson 2003). If PPMR is overestimated, the spectrum slope will be underestimated, affecting, for example, the reliability of size spectra as indicators of ecosystem health (Petchey et al. 2010).

Stable isotope analyses have vastly advanced our understanding of the importance of size in food webs (Jennings et al. 2002, Jennings et al. 2008b). Here, we demonstrate that isotope-based PPMR estimates are sensitive to systematic differences in the discrimination factor. Adopting the scaled approach to studies of trophic position and PPMR in real food webs will ensure improved comparisons of food web properties across habitats with varying nitrogen baselines, and across a full range of trophic positions.

Acknowledgements:

We gratefully thank Simon Jennings for providing the North Sea community stable isotope data, and for providing comments on an earlier draft of the manuscript. We acknowledge support from The Leverhulme Trust (to JPWR) and NSERC (to MT, AM, and JKB).

Figure 1: Conceptual figure of the relationship between trophic position and log body mass (M) in a size-structured food web. The slope (*b*) of a linear regression between trophic position and body mass is used to calculate the ratio of body sizes at successive trophic positions (e.g. M2:M3), thus giving an estimate of community predator prey mass ratio (PPMR). Equation 1 accounts for the difference between trophic positions ($\Delta^{15}N$) and transforms the logged mass values (*n*).

Figure 2: Predator prey mass ratio (PPMR) estimates calculated from additive (grey) and scaled (red) estimates of trophic level across a range of $\delta^{15}N_{base}$ (4-11‰). (a) PPMR estimates for a low $\delta^{15}N$ community (initial $\delta^{15}N$ similar to $\delta^{15}N_{base}$), inset with $\delta^{15}N_{base}$ 8-11‰ at smaller PPMR scale to highlight differences between estimates. (b) PPMR estimates for a high $\delta^{15}N$ community (initial $\delta^{15}N$ 6 above $\delta^{15}N_{base}$). Note the different scales on the y-axes. In both sample types, PPMR is approximately 1000 under the additive approach.

Figure 3: Trophic level estimates from additive (grey) and scaled (red) approaches for North Sea fish data from Jennings and Warr (2003). Estimated trophic position presented for: (a) the full community, (b) sites where $\delta^{15}N_{base} < 7‰$, (c) sites where $\delta^{15}N_{base} > 7‰$.

PeerJ PrePrints | http://dx.doi.org/10.7287/peerj.preprints.544v1 | CC-BY 4.0 Open Access | rec: 17 Oct 2014, publ: 17 Oct 2014

Figure 1:

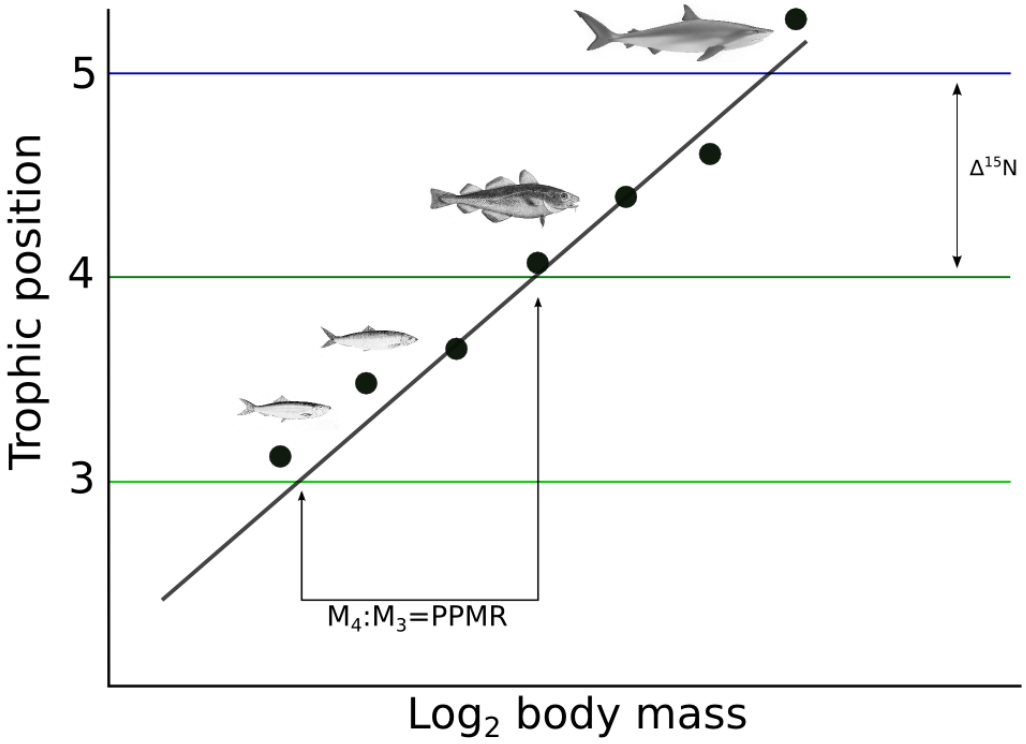


Figure 2:

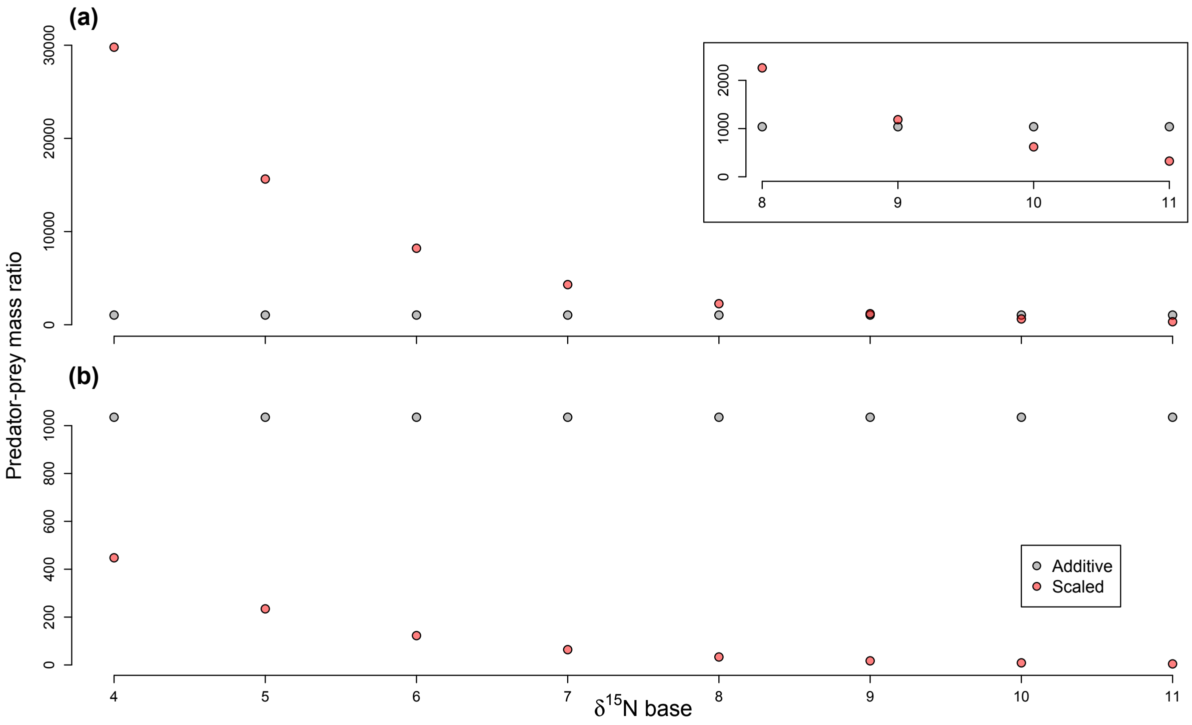
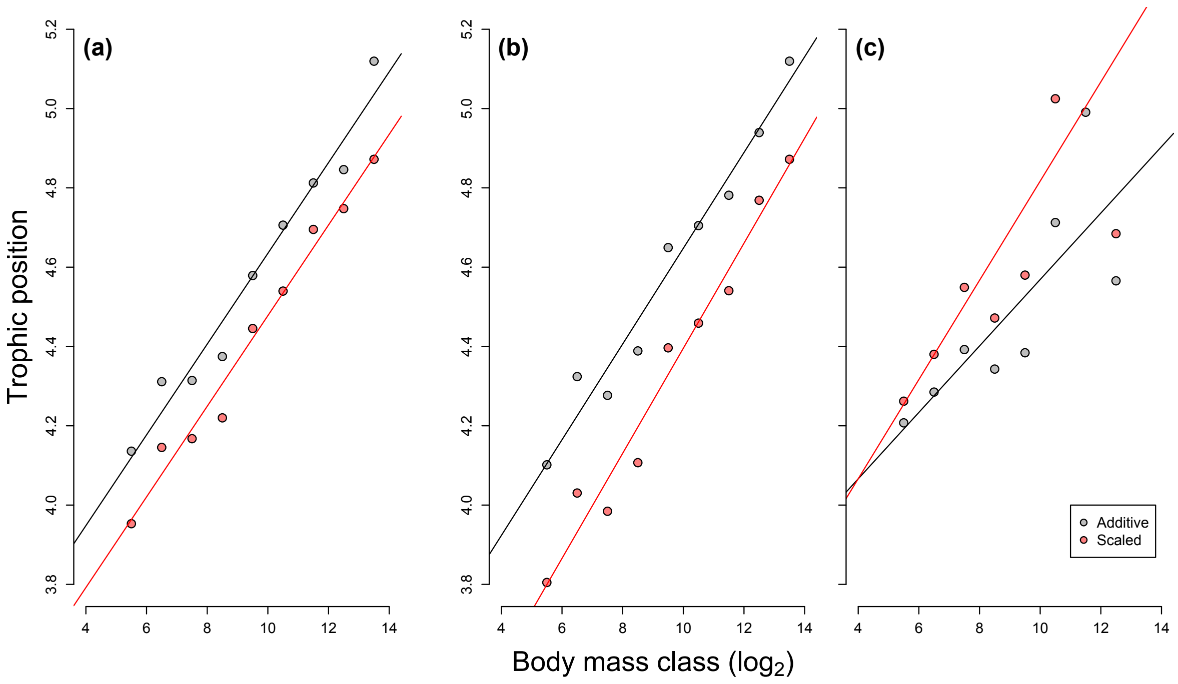


Figure 3:


(a)
(b)
(c)
Trophic position
3.8
4.0
4.2
4.4
4.6
4.8
5.0
5.2
4
6
8
10
12
14
Body mass class ($\log_2$)
Additive
Scaled

References

Andersen KH, Beyer JE (2006) Asymptotic size determines species abundance in the marine size spectrum. Amer Nat 168:54–61

Al-Habsi SH, Sweeting CJ, Polunin NVC, Graham N (2008) δ^{15}N and δ^{13}C elucidation of size structured food webs in a Western Arabian Sea demersal trawl assemblage. Mar Ecol Prog Ser 353:55-63

Bascompte J, Melián CJ, Sala E (2005) Interaction strength combinations and the overfishing of a marine food web. Proc Natl Acad Sci U.S.A. 102(15):5443-5447

Barnes C, Maxwell D, Reuman DC, Jennings S (2010) Global patterns in predator-prey size relationships reveal size dependency of trophic transfer efficiency. Ecology 91(1):222-232

Blanchard JL, Jennings S, Law R, Castle MD, McCloghrie P, Rochet MJ, Benoît E (2009).How does abundance scale with body size in coupled size-structured food webs?. J Anim Ecol 78(1):270-280

Brown JH, Gillooly JF, Allen AP, Savage VM, West GB (2004) Toward a metabolic theory of ecology. Ecology 85(7):1771-1789

Cabana G, Rasmussen JB (1996) Comparison of aquatic food chains using nitrogen isotopes. Proc Natl Acad Sci U.S.A. 93(20):10844-10847

Caut S, Angulo E, Courchamp F (2008) Caution on isotopic model use for analyses of consumer diet. Can J Zool 86(5): 438-445

Caut S, Angulo E, Courchamp F (2009) Variation in discrimination factors (Δ^{15}N and Δ^{13}C): the effect of diet isotopic values and applications for diet reconstruction. J Appl Ecol 46(2):443-453

Chiba S, Sugisaki H, Kuwata A, Tadokoro K, Kobari T, Yamaguchi A, Mackas DL (2012) Pan-North Pacific comparison of long-term variation in *Neocalanus* copepods based on stable isotope analysis. Prog Oceanogr 97:63-75

Cohen JE, Jonsson T, Carpenter SR (2003) Ecological community description using the food web, species abundance, and body size. Proc Natl Acad Sci U.S.A. 100(4):1781-1786

Dennis CA, MacNeil MA, Rosati JY, Pitcher TE, Fisk AT (2010) Diet discrimination factors are inversely related to δ^{15}N and δ^{13}C values of food for fish under controlled conditions. Rapid Commun Mass Sp 24:3515–3520

El-Sabaawi R, Trudel M, Mackas DL, Dower JF, Mazumder A (2012) Interannual variability in bottom-up processes in the upstream range of the California Current system: An isotopic approach. Prog Oceanogr 106:16-27

Elton C (1927) The Animal Community. In: Animal Ecology. The MacMillan Company. New York. p 1–15

Github. (https://github.com/baumlab/ppmr-isotopes)

Hussey NE, MacNeil MA, McMeans BC, Olin JA, Dudley SF, Cliff G, Wintner SP, Fennessy ST. Fisk AT (2014) Rescaling the trophic structure of marine food webs. Ecol Lett 17(2):239-250

Jennings S, Mackinson S (2003) Abundance-body mass relationships in size-structured food webs. Ecol Lett 6(11):971–974

Jennings S, Warr KJ (2003) Smaller predator-prey body size ratios in longer food chains. P Roy Soc Lond B Bio 270(1522): 1413-1417

Jennings S, Maxwell TAD, Schratzberger M, Milligan SP (2008a) Body-size dependent temporal variations in nitrogen stable isotope ratios in food webs. Mar Ecol Prog Ser 370:199–206.

Jennings S, Barnes C, Sweeting CJ, Polunin NV (2008b) Application of nitrogen stable isotope analysis in size-based marine food web and macroecological research. Rapid Commun Mass Sp 22(11):1673-1680

Jennings S, Pinnegar JK, Polunin NV, Boon TW (2001) Weak cross-species relationships between body size and trophic level belie powerful size-based trophic structuring in fish communities. J Anim Ecol 70(6):934-944

Jennings S, Warr KJ, Mackinson S (2002) Use of size-based production and stable isotope analyses to predict trophic transfer efficiencies and predator-prey body mass ratios in food webs. Mar Ecol Prog Ser 240:11-20

PeerJ PrePrints | http://dx.doi.org/10.7287/peerj.preprints.544v1 | CC-BY 4.0 Open Access | rec: 17 Oct 2014, publ: 17 Oct 2014

Minagawa M, Wada E (1984) Stepwise enrichment of ^{15}N along food chains: Further evidence and the relation between ^{15}N and animal age. Gecochim Cosmochim Ac 48:1135-1140

Petchey OL, Belgrano A, Enquist BJ (2010). Body-size distributions and size spectra: universal indicators of ecological status? Biol Lett 22(4):434–437

Peters RH (1983) The ecological implications of body size, Cambridge University Press, Cambridge, UK.

Polunin NVC, Pinnegar JK (2002) Trophic ecology and the structure of marine food webs. In: Hart PJ, Reynolds JD (eds) Handbook of fish and fisheries. Blackwell Science, Oxford

Post DM (2002) Using stable isotopes to estimate trophic position: models, methods, and assumptions. Ecology 83(3):703-718

Power M, Guiguer KRRA, Barton DR (2003) Effects of temperature on isotopic enrichment in *Daphnia magna*: implications for aquatic food-web studies. Rapid Commun Mass Sp 17(14):1619-1625

Riede JO, Brose U, Ebenman B, Jacob U, Thompson R, Townsend CR, Jonsson T (2011) Stepping in Elton's footprints: a general scaling model for body masses and trophic levels across ecosystems. Ecol Lett 14(2):169-178

Robbins CT, Felicetti LA, Florin ST (2010) The impact of protein quality on stable nitrogen isotope ratio discrimination and assimilated diet estimation. Oecologia 162(3):571-579

Trebilco R, Baum JK, Salomon AK, Dulvy NK (2013) Ecosystem ecology: size-based constraints on the pyramids of life. Trends Ecol Evol 28(7):423-431

Vander Zanden MJ, Rasmussen JB (1999) Primary consumer δ^{13}C and δ^{15}N and the trophic position of aquatic consumers. Ecology 80(4):1395-1404

Vanderklift MA, Ponsard S (2003) Sources of variation in consumer-diet δ^{15}N enrichment: a meta-analysis. Oecologia 136(2):169-182

PeerJ PrePrints | http://dx.doi.org/10.7287/peerj.preprints.544v1 | CC-BY 4.0 Open Access | rec: 17 Oct 2014, publ: 17 Oct 2014