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CAN STABLE ISOTOPE RATIOS PROVIDE FOR COMMUNITY-WIDE MEASURES OF TROPHIC STRUCTURE? COMMENT

David J. Hoeinghaus^{1,3} and Steven C. Zeug^{2,4}

Over the last few decades, the use of stable isotope ratios in ecological studies has increased greatly, most notably in the area of trophic ecology and food webs (Peterson and Fry 1987, Fry 2006). However, applications of stable isotopes in food web studies have been mostly qualitative to date, prompting the recent development of quantitative approaches to investigate different aspects of trophic ecology and food web structure using stable isotope data (e.g., Bearhop et al. 2004, Newsome et al. 2007, Schmidt et al. 2007). One such contribution (Layman et al. 2007a) proposed a series of six metrics that provide community-wide measures of trophic structure using a dual-isotope framework. However, the metrics as proposed by Layman et al. (2007a) will not accurately represent aspects of trophic structure for most ecological systems. Herein we summarize the framework and metrics proposed by Layman et al. (2007a), identify key limitations that prevent their widespread application, and discuss other directions that may facilitate the development of quantitative food web approaches using stable isotope data.

Summary of the proposed community-wide metrics

The six metrics proposed by Layman et al. (2007a) are derived from commonly applied methods in studies of ecomorphology and community assembly. The first four are measures of the extent of species means in $\delta^{13}\text{C}$ – $\delta^{15}\text{N}$ bi-plot space, and are suggested to summarize different aspects of trophic diversity. The remaining two measures describe the relative spacing of species means in the isotope bi-plot, and are suggested to index trophic redundancy. All of the proposed metrics are calculated using mean carbon and nitrogen isotope ratios of consumer taxa only.

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¹Division of Biology, Kansas State University, 104 Ackert Hall, Manhattan, Kansas 66506 USA

²Section of Ecology, Evolutionary Biology and Systematics, Department of Wildlife and Fisheries Sciences, Texas A&M University, 2258 TAMU, College Station, Texas 77843-2258 USA

³E-mail: djhoeing@ksu.edu

⁴Present address: Department of Ecology, Evolution, and Marine Biology, University of California, Santa Barbara, California 93106 USA.

1) $\delta^{15}\text{N}$ range (NR) is the distance between the two species with the most enriched and most depleted $\delta^{15}\text{N}$ values (i.e., maximum $\delta^{15}\text{N}$ – minimum $\delta^{15}\text{N}$). NR is proposed to represent vertical food web structure.

2) $\delta^{13}\text{C}$ range (CR) is the distance between the two species with the most enriched and most depleted $\delta^{13}\text{C}$ values (i.e., maximum $\delta^{13}\text{C}$ – minimum $\delta^{13}\text{C}$). CR is suggested to represent niche diversification at the base of the food web.

3) Total area (TA) is the convex hull area encompassed by all species in $\delta^{13}\text{C}$ – $\delta^{15}\text{N}$ bi-plot space. TA is a measure of the total area of space occupied, and is suggested to represent the total extent of trophic diversity.

4) Mean distance to centroid (CD) is the average Euclidean distance of each species to the $\delta^{13}\text{C}$ – $\delta^{15}\text{N}$ centroid, which is calculated as the mean $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ value for all species in the food web. This metric is proposed to measure the average degree of trophic diversity.

5) Mean nearest neighbor distance (NND) is the mean of the Euclidean distances to each species' nearest neighbor in $\delta^{13}\text{C}$ – $\delta^{15}\text{N}$ bi-plot space. NND is suggested to represent the overall density of species packing and trophic redundancy.

6) Standard deviation of nearest neighbor distance (SDNND) is the standard deviation of the Euclidean distances to each species' nearest neighbor in $\delta^{13}\text{C}$ – $\delta^{15}\text{N}$ bi-plot space. SDNND is proposed as a measure of the evenness of species packing and trophic redundancy.

Limitations of the proposed community-wide metrics

These proposed metrics accurately describe the spatial extent and spacing of continuous, standardized bivariate data. However, what these metrics are proposed to represent (trophic diversity and redundancy) likely cannot be inferred with confidence within a bivariate isotope framework due to several limitations that affect the vertical or horizontal distribution of points in $\delta^{13}\text{C}$ – $\delta^{15}\text{N}$ bi-plot space, the relative spacing of those points, and interpretations based on the proposed metrics. The limitations we will discuss can be summarized by two primary issues: failure to account for sources in metric calculations, and scaling of axes and standardization.

Isotopic values of basal sources are not incorporated in the metrics.—Layman et al. (2007a) argued that stable isotope ratios are one representation of a consumer's trophic niche because its isotope ratios are the integration of all trophic pathways leading to that consumer. This representation of the consumer's trophic niche is dependent on the isotopic signatures of sources at the base of the food web, and therefore cannot be interpreted independently from them (see Matthews and Mazumder 2004, Newsome et al. 2007). Other recently proposed quantitative approaches (e.g., Schmidt et al. 2007) also recognize the importance of

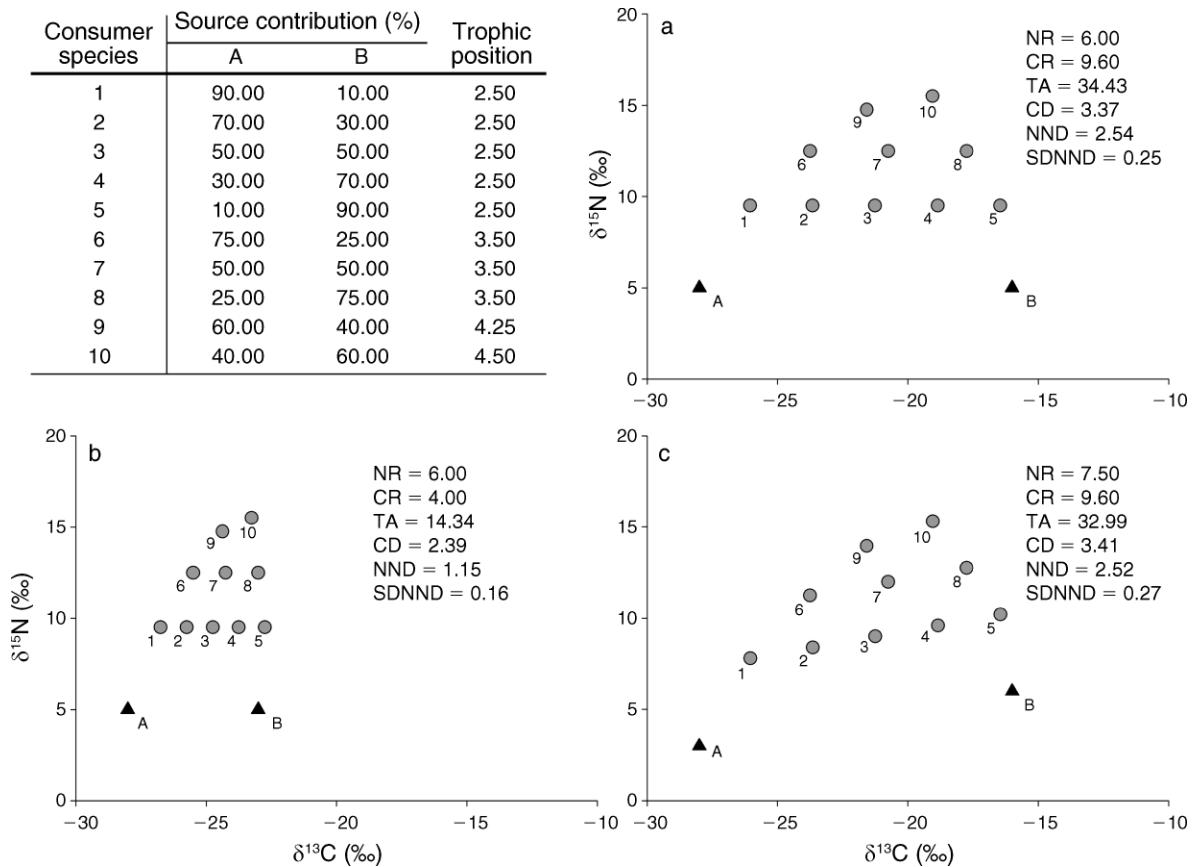


FIG. 1. Examples of how different metric values can be obtained for simple two-source food webs with identical trophic structure (estimated consumer trophic position and relative importance of carbon sources; top left panel) due to the relative spacing of basal carbon sources. Metric values calculated following Layman et al. (2007a) are provided in the top right corner of each bi-plot in panels (a)–(c): NR, $\delta^{15}\text{N}$ range; CR, $\delta^{13}\text{C}$ range; TA, total area; CD, mean distance to centroid; NND, mean nearest neighbor distance; SDNND, standard deviation of nearest neighbor distance. Trophic structure estimates were calculated using conservative trophic fractionations of 0.5‰ and 3.0‰ for carbon and nitrogen, respectively. Basal carbon sources are shown as black triangles; consumers are shown as gray circles. Source and consumer labels in bi-plots correspond to those in the top left panel.

controlling for and including the isotopic signatures of basal sources. Figs. 1 and 2 illustrate how ignoring important variation at the base of the food web can lead to erroneous results and interpretations using the metrics proposed by Layman et al. (see also Newsome et al. 2007; Fig. 5). Identical food web structure can be represented by different metric values (Fig. 1), and very different food webs can result in identical metric values (Fig. 2). Even when changes in metric values are observed and appear to be related to other factors (e.g., Layman et al. 2007b), the results are unsubstantiated unless the isotopic ratios of basal sources fit the criteria outlined below, and are presented in conjunction with metric values so as to validate interpretations.

For example, the relative spacing of source groups along the carbon axis (or other element used to trace sources) will affect all of the metrics proposed by Layman et al. (2007a) except for NR (Fig. 1a, b). Although isotopic ratios are continuous measures, the

source groups they are used to represent do not scale in the same manner. In most cases, the difference in $\delta^{13}\text{C}$ between two basal source groups is not the same as the difference between two other source groups. In aquatic systems, for example, $\delta^{13}\text{C}$ values of C_3 plants often differ comparatively little from phytoplankton, but C_4 plants typically differ substantially from both C_3 plants and phytoplankton (e.g., Peterson and Fry 1987). In addition, $\delta^{13}\text{C}$ values of the same source (e.g., algae) frequently differ among food webs or temporal periods, and may vary spatially within the same ecosystem or in relation to local or larger-scale environmental conditions (e.g., Finlay 2001). Furthermore, different source groups may have the same carbon isotope ratios (e.g., riparian vegetation and aquatic macrophytes [Hoeinghaus et al. 2007]), which would suggest no niche differentiation based on the metrics of Layman et al. (2007a). Even if comparing simple two-source food webs, differences in $\delta^{13}\text{C}$ between the two basal source

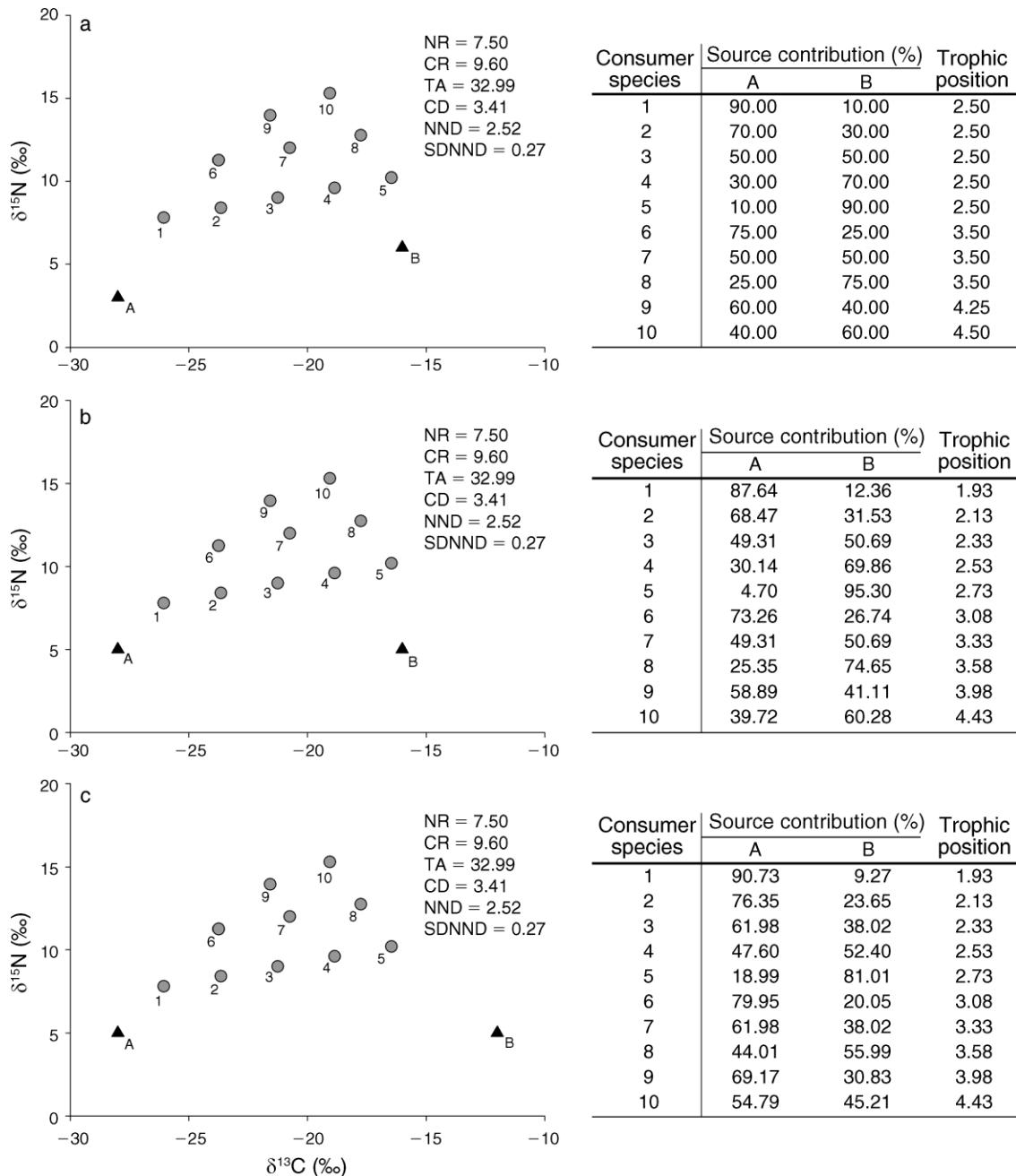


FIG. 2. Examples of how simple two-source food webs with different structures can result in identical metric values. Metric values calculated following Layman et al. (2007a) are provided in the top right corner of each bi-plot, and actual trophic structure (estimated consumer trophic position and relative importance of carbon sources) is summarized in the table adjacent to each bi-plot. Trophic structure estimates were calculated using conservative trophic fractionations of 0.5‰ and 3.0‰ for carbon and nitrogen, respectively. Basal carbon sources are shown as black triangles; consumers are shown as gray circles. Source and consumer labels in bi-plots correspond to those in the adjacent table.

groups in each food web would result in different metric values regardless of (and indistinguishable from) any real differences in trophic diversity or redundancy in those webs (Figs. 1 and 2; see also Matthews and Mazumder 2004).

In addition to (and compounding the effects of) variation in carbon isotope ratios of basal sources, nitrogen isotope ratios of basal sources often differ within and among food webs. For example, in a variety of different aquatic ecosystems, from tundra ponds to

subtropical estuaries to tropical and subtropical rivers, $\delta^{15}\text{N}$ may vary by more than 6‰ among sources within and among food webs (e.g., Hoeninghaus and Davis 2007, Hoeninghaus et al. 2007, Kang et al. 2007, Rautio and Vincent 2007, Zeug and Winemiller 2008), and temporal variation in $\delta^{15}\text{N}$ of a single source in the same food web may be just as great (e.g., Syväranta et al. 2006). Considering trophic fractionation of nitrogen to be between 2.5‰ and 3.4‰ (Post 2002, Vanderklift and Ponsard 2003), this variation represents approximately two full trophic levels. For this reason, it is well recognized that nitrogen baselines need to be controlled for in food web studies (Cabana and Rasmussen 1996, Post 2002). If $\delta^{15}\text{N}$ of sources differ, even by a small amount, consumers that assimilate different fractions of those basal sources would have different $\delta^{15}\text{N}$ values even though they may feed at the same trophic position, and the range and distribution of nitrogen values observed in the consumer assemblage may vary even though trophic structure is identical in the food webs being compared. Even relatively small differences in source $\delta^{15}\text{N}$ values (Fig. 1a, c) influence all of the metrics proposed by Layman et al. (2007a) except for CR.

In the common case in which more than two potential sources could support secondary consumers, the influence of variation in carbon and nitrogen isotope ratios of basal sources on values and interpretations of the metrics proposed by Layman et al. (2007a) may be even more substantial. Source contributions supporting consumers can only be determined unambiguously when the number of sources is less than or equal to the number of isotopes plus 1. As discussed above, source $\delta^{15}\text{N}$ values must be equal (or consumers adjusted to an appropriate baseline) to make valid comparisons using the proposed metrics, which leaves only carbon isotope ratios to distinguish among sources. Therefore, the metrics proposed by Layman et al. (2007a) reflect a unique trophic “niche” only when the community is supported by two isotopically distinct basal source groups. When three or more sources are present, the “niches” represented by consumer isotope ratios are undefined because identical consumer isotope ratios may be obtained by multiple possible combinations of relative source contributions that are all equally likely (see Phillips and Gregg 2003). The end result is that Layman et al.’s (2007a) metrics are only valid in a two-source system. More importantly, metric values are only comparable among food webs or temporal periods when nitrogen isotope ratios of sources are equal or standardized, and the difference in carbon isotope ratios between the two sources is of the same magnitude for all of the webs (or temporal periods) being compared.

Aside from variation in isotope ratios of basal sources, *isotope bi-plots are not appropriately scaled for the calculation of metrics as proposed*. Isotopic ratios of nitrogen and carbon are used in the metrics of Layman

et al. (2007a) to represent two different aspects of trophic structure (trophic position and the relative importance of basal source groups, respectively), and ideally should have equal weighting when combined in metrics describing the overall trophic structure of a food web. However, when NR and CR are different (or their variances are different), the metrics based on Euclidean distances (i.e. CD, NND, and SDNND) will be more strongly affected by one of the two isotopes. This results in an artificial weighting of one aspect of trophic structure over the other. For this same reason, Z scores or other standardization techniques are commonly used in ecomorphology studies when analyzing differences among species or communities based on traits with different variances or units (e.g., Moreno et al. 2006). Cornwell et al. (2006), in their description of applications of convex hulls in ecological studies (e.g., Layman et al.’s TA metric), explicitly state that data should be standardized before calculating volumes. This issue may be compounded in comparisons among food webs or time periods if NR and CR differ not only within webs, but also among webs. In addition to artificial weighting within the food web, if the relative magnitude of NR and CR (or their variances) is reversed in food webs being compared (e.g., Fig. 1a, b), values of CD, NND, and SDNND will be more strongly affected by $\delta^{13}\text{C}$ (the relative importance of basal sources) in one food web and by $\delta^{15}\text{N}$ (vertical trophic structure) in the other. In this sense, the first two metrics of Layman et al. (2007a) directly conflict with the latter three metrics based on Euclidean distances, in that for CD, NND, and SDNND to be equally weighted for both aspects of trophic structure, NR and CR and variances on both isotope axes must be equal within and among food webs, and therefore would be uninformative. This greatly limits the application of these metrics to assess the subtle differences in trophic ecology suggested by Layman et al. (2007a) to be beneficial in an experimental context.

Potential for community-wide measures of trophic structure derived from isotope data

There are numerous potential applications of quantitative measures of trophic structure based on stable isotope data, especially when used in conjunction with other measures such as direct observations of trophic relationships from stomach contents analyses. Such metrics could provide new ways to compare food webs across space and time in both natural and experimental settings. One can easily envision the application of such metrics to a wide range of timely issues, from examining effects of species introductions and/or extinctions, to assessing environmental impacts or restoration on food web structure and function (e.g., Schmidt et al. 2007). To move forward in this regard, it is paramount that such metrics be readily comparable among food webs in both space and time. Due to the aforementioned

limitations, the metrics as proposed by Layman et al. (2007a) are likely not suitable to this end for most food webs.

Differences in consumer isotope ratios do not necessarily equate to differences in food web structure (i.e., unstandardized bivariate isotope space does not equal niche space). It may prove more fruitful to develop quantitative approaches based on direct estimates of the trophic characteristics of interest, rather than inferring them from the relative spacing of consumers in the $\delta^{13}\text{C}$ - $\delta^{15}\text{N}$ bi-plot. Species trophic positions can be estimated using stable isotope ratios following the methodology of Post (2002), and the relative dietary importance of basal sources can be quantified by converting δ -space into p -space (dietary proportions of basal sources [Newsome et al. 2007]). When the number of potential sources is greater than one more than the number of isotopes, ranges of potential source contributions can be estimated using mixing models such as IsoSource (Phillips and Gregg 2003), and dietary data from stomach contents analyses can be incorporated as constraints in IsoSource models to increase resolution of dietary contributions. Resulting estimates of consumer trophic position and/or relative dietary contributions may be standardized and used in multivariate analyses, combined in a series of metrics in a manner similar to that proposed by Layman et al. (2007a), or used in available individual-level (e.g., Bolnick et al. 2002) or community (e.g., Cornwell et al. 2006) approaches. Such analyses would greatly benefit from measures of uncertainty associated with sample sizes of individual species, variability in isotope ratios of prey items and basal sources, and the resulting estimates for each trophic characteristic. Although there is great potential for community-wide measures of trophic structure derived from stable isotope data, the isotopic concentrations of basal food sources need to be directly incorporated and data appropriately standardized in order to make valid comparisons.

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CAN STABLE ISOTOPE RATIOS PROVIDE FOR COMMUNITY-WIDE MEASURES OF TROPHIC STRUCTURE? REPLY

Craig A. Layman^{1,3} and David M. Post²

Unraveling the complexities of food web structure and dynamics can be exceedingly difficult (Winemiller and Layman 2005). Tools used to this end include theoretical modeling, experimental manipulations, direct diet analysis and, especially in the last decade, stable isotopes. Each of these approaches has distinct strengths and weaknesses, and is intended to elucidate specific characteristics of food webs. For example, direct diet analysis offers greater taxonomic resolution than stable isotope techniques but provides only a snapshot of recent diet items. Stable isotopes, in contrast, typically suffer from poor taxonomic resolution but can provide temporally integrated information regarding what an organism has consumed and assimilated. Because of their complementary nature, multiple food web methodologies often compensate for the weaknesses of any single approach, and ultimately can provide compelling descriptions of food web structure and dynamics. For example, stable isotope data are especially informative when applied in conjunction with diet analysis (Vander Zanden and Rasmussen 1996, Post 2003, Layman et al. 2007b, Winemiller et al. 2007).

The Hoeinghaus and Zeug (2008) criticism of Layman et al. (2007a) primarily hinges on the criticism that the proposed stable isotope-based metrics may be misleading under particular sets of circumstances. We agree with this perspective, as the metrics were not intended as universal tools to be applied in all situations. Quoting from Layman et al. (2007a): “Application of a variety of research methodologies, as well as a thorough understanding of natural history of organisms and of species interactions, will lead to the most thorough understanding of food webs. Community-wide metrics based on stable isotope representations of species’ niches are one additional tool that deserves consideration.” In other studies, we detail the importance of establishing robust isotopic baselines (e.g., Post 2002, Layman 2007), and

we concur with the concerns about standardization raised by Newsome et al. (2007) and Hoeinghaus and Zeug (2008) (although the simple standardizations proposed in each of these papers are not possible in most systems because of the diversity of resource pools available to consumers). Many of the other problems raised by Hoeinghaus and Zeug (2008) can be resolved by including covariates (e.g., species richness), by standardizing across study systems (e.g., using baselines), or by employing complementary methods.

Our initial paper was intended as a conceptual introduction of a new tool for food web ecologists, and not as a methodological treatise. Hoeinghaus and Zeug (2008) go too far in their reply because they focus only on the particular circumstances when our proposed approach will *not* be especially informative, and they fail to acknowledge the advantages of stable isotope techniques when coupled with complementary methods. For example, Layman et al. (2007b) use a stable isotope-based metric to demonstrate a robust ecological pattern (niche width contraction of a top predator) across a gradient of ecosystem fragmentation. Stable isotopes were employed as part of a broad research program that included “>3500 individual isotope samples, hundreds of stomach content analyses, and extensive quantitative floral and faunal surveys.” The stable isotope metrics of niche width were not applied in isolation, but were complemented with additional information that supported the ecological mechanisms inferred from stable isotopes. But stable isotope-based metrics were the most direct way to convey the data, primarily because they provided for a standardized methodology that reflected long-term feeding patterns.

It has been pointed out repeatedly that application of stable isotopes to disentangle food web complexity becomes increasingly problematic as the number of resource pools for a particular consumer increases (Phillips and Gregg 2003, Newsome et al. 2007). For example, in estuarine ecosystems, precise estimations of trophic position and percentage contribution of resources to consumers can be very problematic because of the myriad basal resource pools (Layman 2007). Yet it does not follow that the stable isotope-based metrics are “only valid” in the restrictive circumstances that Hoeinghaus and Zeug (2008) outline. In fact, even in systems with many resource pools, the metrics may be an excellent quantitative method by which to characterize interesting patterns in food web structure (Layman et al. 2007b). These patterns could be generated by various mechanisms, some of which may stem from methodological artifacts. But stable isotope analyses still retain many potential advantages, for example, the ability to analyze many individuals (i.e., generate large sample sizes) across diverse taxonomic groups for which direct diet analysis may be difficult.

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¹ Marine Sciences Program, Department of Biological Sciences, Florida International University, North Miami, Florida 33181 USA

² Department of Ecology and Evolutionary Biology, Yale University, New Haven, Connecticut 06520-8106 USA

³ E-mail: laymanc@fiu.edu

A simple analogy best summarizes our viewpoint. A carpenter would never use a screwdriver to pound a nail, nor wield a saw to remove a screw. Hoeinghaus and Zeug (2008) seem to devote their response to explaining why a screwdriver cannot be used to do the job of a hammer. Food web ecologists must understand situations under which particular tools, including stable isotope-based metrics (Layman et al. 2007b, Schmidt et al. 2007), will prove most useful. Yet a carpenter would not throw away his hammer because it is not needed for one particular job at hand. Likewise, the stable isotope-based metrics should not be discarded because they are less effective under certain circumstances. The complexity of food webs necessitates multifaceted research programs employing a variety of methodologies, and, in many cases, stable isotope-based niche metrics may be an important addition to the food web ecologist's tool box.

Acknowledgments

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