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Review

The problem of isotopic baseline: Reconstructing the diet and trophic position of fossil animals

Michelle M. Casey [a,*], David M. Post [b]

[a] Yale University, Department of Geology and Geophysics, P.O. Box 208109, New Haven, CT, 06520–8109, USA
[b] Yale University, Department of Ecology and Evolutionary Biology, Osborn Memorial Laboratory, New Haven, CT, 06520–8106, USA

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ABSTRACT

Stable isotope methods are powerful, frequently used tools which allow diet and trophic position reconstruction of organisms and the tracking of energy sources through ecosystems. The majority of ecosystems have multiple food sources which have distinct carbon and nitrogen isotopic signatures despite occupying a single trophic level. This difference in the starting isotopic composition of primary producers sets up an isotopic baseline that needs to be accounted for when calculating diet or trophic position using stable isotopic methods. This is particularly important when comparing animals from different regions or different times. Failure to do so can cause erroneous estimations of diet or trophic level, especially for organisms with mixed diets. The isotopic baseline is known to vary seasonally and in concert with a host of physical and chemical variables such as mean annual rainfall, soil maturity, and soil pH in terrestrial settings and lake size, depth, and distance from shore in aquatic settings. In the fossil record, the presence of shallowing upward suites of rock, or parasequences, will have a considerable impact on the isotopic baseline as basin size, depth and distance from shore change simultaneously with stratigraphic depth. For this reason, each stratigraphic level is likely to need an independent estimation of baseline even within a single outcrop. Very little is known about the scope of millennial or decadal variation in isotopic baseline. Without multi-year data on the nature of isotopic baseline variation, the impacts of time averaging on our ability to resolve trophic relationships in the fossil record will remain unclear. The use of a time averaged baseline will increase the amount of error surrounding diet and trophic position reconstructions. Where signal to noise ratios are low, due to low end member disparity (e.g., aquatic systems), or where the observed isotopic shift is small ($\leq$1‰) the error introduced by time averaging may severely inhibit the scope of one's interpretations and limit the types of questions one can reliably answer. In situations with strong signal strength, resulting from high amounts of end member disparity (e.g., terrestrial settings), this additional error maybe surmountable. Baseline variation that is adequately characterized can be dealt with by applying multiple end-member mixing models.

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* Corresponding author. Tel.: +1 763 229 3126; fax: +1 203 432 3134.
E-mail address: michelle.casey@yale.edu (M.M. Casey).

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1. Introduction

Stable isotopes are powerful tools for investigating the flow of energy or material through biological systems such as food webs, because isotopic compositions record information about both source and processing of that material (Peterson and Fry, 1987). Variation in the distribution of isotopic signatures of organic and inorganic materials sets up an isotopic baseline, which can be used to trace the dietary sources of organisms. The process of biological fractionation modifies this isotopic baseline, during which organisms differentially use naturally occurring stable isotopes to build organic tissues. The relatively small biological fractionation of carbon (<1‰) after photosynthesis makes $\delta^{13}C$ useful for tracing the identity and relative contribution of different diet sources (Deniro and Epstein, 1978; Post, 2002b; McCutchan et al., 2003). The biological fractionation of nitrogen is relatively large (~3.4‰) making $\delta^{15}N$ useful for calculating the trophic position of consumers (Deniro and Epstein, 1981; Vander Zanden and Rasmussen, 2001; Post, 2002b; McCutchan et al., 2003; Caut et al., 2009). In modern systems, stable isotopic signatures are used extensively to reconstruct organismal diets and trophic positions, calculate food-chain length, determine the path of material through food webs, and examine niche partitioning between species (Peterson and Fry, 1987; Post et al., 2000; Post, 2002a; Bearhop et al., 2004; Takimoto et al., 2008; Walters and Post, 2008). Because stable isotopic signatures of organisms are integrated among dietary sources consumed at different times of the day or seasons, these methods complement direct observations like gut content analysis which records only short time periods preceding capture and are available only for common, easily captured taxa (Peterson and Fry, 1987; Post, 2002b; McCutchan et al., 2003; Layman and Post, 2008). Another advantage of stable isotopic methods is their ability to capture the natural complexity of trophic interactions, such as trophic omnivory, often missing in simple food chain models (Post, 2002b). For this reason, stable isotopic trophic methods are now widely applied to both fossil and living organisms in terrestrial, lacustrine, and marine settings.

In the field of archeology, stable isotope methods have been applied to the problem of determining human diet in the past. Archeologists have used the difference in $\delta^{13}C$ between C_3 plants and maize, a C_4 plant, to identify the onset of agriculture in human civilizations (Van der Merwe and Vogel, 1978). This technique was further developed to examine dietary differences between social classes (Schurr, 1992), test for links between agricultural intensification and economic or cultural complexity (Schurr and Schoeninger, 1995), and track population migration (Ambrose and Deniro, 1986; Sealy and Van der Merwe, 1986; Pate, 1995). Subsequent archeological analyses have used the difference in the isotopic baseline of carbon and nitrogen between terrestrial and marine systems to track marine supplementation in the diets of ancient humans (Tauber, 1981; Schoeninger et al., 1983) or changes in nitrogen isotopic signature to determine the age of weaning (Schurr, 1998). Archeologists and paleontologists have applied this technique to vertebrate organisms to investigate the relative contribution of C_3 and C_4 plants to diet (Wang et al., 1994; Macfadden and Cerling, 1996), niche separation (MacFadden et al., 2004; Feranec and MacFadden, 2006; Fricke and Pearson, 2008), age of weaning (Rountrey et al., 2007), and trophic structure (Ostrom et al., 1993) in organisms ranging from dinosaurs to mammals.

Modern ecologists have successfully employed stable isotopic methods to tackle long-standing questions within ecology. One particularly lucrative application of stable isotopes is the use of $\delta^{15}N$ signature to calculate food-chain length in a variety of settings. Food-chain length, or the number of trophic levels between primary producers and top predators within an ecosystem, is of immense importance to a number of issues within trophic ecology including the productivity of fisheries, the effects of trophic cascades on ecosystems, and the bioaccumulation of toxins (Vander Zanden et al., 1999; Post, 2002a; Vander Zanden and Fetzer, 2007; Takimoto et al., 2008; Walters and Post, 2008). $\delta^{15}N$ derived estimates of food-chain length provide a robust method for testing competing hypotheses for variation in food-chain length, including resource availability, ecosystem size, and disturbance (Post, 2002a; Vander Zanden and Fetzer, 2007; Takimoto et al., 2008; McHugh et al., 2010). Application of this method to fossil record could provide valuable information on the nature of food-chain length in ecosystems before anthropogenic disturbance, or the response of food-chain length to large scale disturbances such as rapid climate changes or extinction events which are difficult to recreate experimentally in modern settings.

Another successful application of stable isotopes to a long standing ecological question was the use of multiple stable isotope tracers to examine the fate of salt marsh primary productivity in marine food webs. The extremely productive salt marsh plant *Spartina alterniflora* does not appear to support upper trophic levels directly through grazing, but indirectly as the dominant source of the detritus. The presence of multiple potential food sources (e.g., phytoplankton, salt marsh detritus, benthic algae, and upland organic matter) made it impossible to determine the ultimate source of detrital material using the isotopic signature of carbon alone. Peterson et al. (1985) were able to use a combination of carbon, nitrogen, and sulfur stable isotopes to demonstrate that a large proportion of the diet of ribbed mussels was, in fact, derived from *Spartina* detritus. The simultaneous application of multiple isotopic tracers detailed above has allowed researchers to map the flow of energy through ecosystems in a quantitative manner that was previously impossible. Utilization of this method in the fossil record could further resolve issues of energy flow through different types of ecosystems (Mae et al., 2007) or changes in energy flow resulting from natural or anthropogenic ecosystem alterations.

While not an exhaustive list, the above examples demonstrate the breadth of questions that can be addressed by stable isotopic methods, some of which, like the ratio of C_3 to C_4 plants comprising diet, have been widely and readily applied to fossil taxa while others, such as food-chain length, have not. All of the above examples could not be satisfactorily addressed without the use of stable isotopic techniques and none of these applications could be performed without an accurate estimation of isotopic baseline or end members for mixing models. In particular, the salt marsh example highlights the utility of multiple stable isotope tracers to examine food webs that contain multiple potential sources of dietary carbon. Both aquatic and terrestrial ecosystems commonly contain at least two distinct carbon sources (e.g., littoral and pelagic producers in aquatic systems; C_3 and C_4 plants in terrestrial systems) each with distinct $\delta^{13}C$ and $\delta^{15}N$ signatures. Therefore, to accurately estimate the trophic position of an