8

Food Web Dynamics in Stable Isotope Ecology: Time Integration of Different Trophic Levels

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CONTENTS

8.1 Introduction

Stable isotopes are becoming a standard analytical tool in food web ecology. Differences in carbon and nitrogen isotope ratios between consumers and their diet provide information on energy flows, nutrient sources, and trophic relationships. Typically, carbon provides information on the primary energy source (e.g., benthic vs. pelagic photosynthesis), while nitrogen allows discrimination among trophic levels. Relative enrichment with increasing trophic level often allows a better interpretation of dietary relationships than gut content analysis alone because stable isotopic ratios record material that is actually assimilated (Michener and Schell, 1994). A recent survey has shown an average enrichment of 0.05‰ ± 0.63 $\delta^{13}C$ and 3.49‰ ± 0.23 $\delta^{15}N$ in field studies (Vander Zanden and Rasmussen, 2001), and these values are similar to the frequently used average trophic fractionation values of 1‰ $\delta^{13}C$ and 3.4‰ $\delta^{15}N$ (Minagawa and Wada, 1984; Michener and Schell, 1994). The ease of stable isotope analyses makes them an appealing tool in ecology, but both sampling design and interpretation of the results should be undertaken carefully (Gannes et al., 1997; O'Reilly et al., 2002). An isotopic ratio of an organism represents its diet, but it should be remembered that this isotopic value is also time specific and is an average ratio related to tissue turnover rate and the life of the organism.

The pelagic food web in Lake Tanganyika, East Africa, provided an excellent example of how stable isotopic analyses of food web structure is not always straightforward. Lake Tanganyika is a deep (mean 570 m; max 1470 m), large (mean width 50 km; length 650 km) lake located a few degrees south of the equator (Figure 8.1). The lake is permanently stratified and is anoxic below 100 to 150 m. The pelagic food web is relatively simple, and trophic relationships have been previously established from

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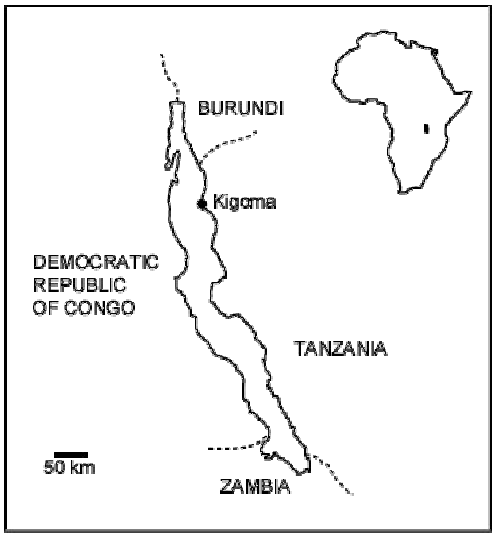

FIGURE 8.1 Location of Lake Tanganyika in East Africa. This study took place off shore from Kigoma, Tanzania.

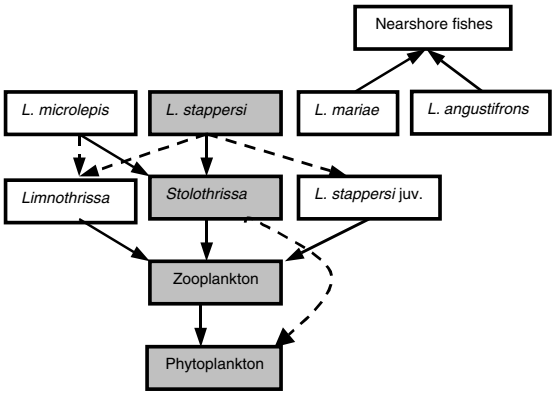

FIGURE 8.2 The pelagic food web of Lake Tanganyika. The heavy lines indicate major food preferences; the dashed lines indicate other prey relationships. Each of the *Lates* species includes *Stolothrissa tanganicae* and *Limnothrissa miodon* among their prey. The shaded boxes represent the dominant species of the pelagic zone and illustrate the linear food chain relationship. (Modified from Coulter, 1991.)

gut content analysis (Figure 8.2) (Coulter, 1991). The zooplankton are dominated by the copepod *Tropodiaptomus simplex*, which is a major dietary component of the two clupeid fish species, *Stolothrissa tanganicae* and *Limnothrissa miodon*. The upper trophic level is composed of two species that rely on nearshore fishes as a food source throughout their lives, *Lates angustifrons* and *L. mariae*. One species, *L. microlepis,* spend their larval and juvenile stages near shore and recruit to the pelagic as adults. Only one species, *L. stappersi,* has a fully pelagic life cycle. Thus, the dominant species of the pelagic food web form a linear food "chain" from phytoplankton to the copepod *T. simplex* to the zooplanktivorous *Stolothrissa* to the predatory *L. stappersi*. The isotopic structure of this food web should be a distinct sequential enrichment in the carbon and nitrogen isotopes with increasing trophic level.

8.2 Methods

Our study took place near Kigoma, Tanzania, during the dry season (May to September). Food web samples were collected two consecutive years, in 1999 (FW-A) and 2000 (FW-B). FW-B was collected

by the second author over several sampling periods in August 2000. For this food web, particulate organic matter (POM) and zooplankton samples were taken at least 10 km offshore from Kigoma. POM was collected by filtering whole water samples (n = 4) on 0.45 µm quartz filters, which were then rinsed with 10% *N* HCl and distilled water. Zooplankton were collected using 100 m vertical tows (n = 6) with a 100 µm mesh and collected on 0.45 µm quartz filters. Fish specimens of *Stolothrissa* (n = 7; 71 to 85 mm), *Limnothrissa* (n = 4; 83 to 125 mm), *Lates stappersi* juveniles (n = 7; 69 to 136 mm), and *L. stappersi* (n = 4; 219 to 372 mm) were obtained from fishermen in the morning after they returned from fishing offshore from Kigoma. FW-A was collected by the first author, with all samples collected during the night of 1 August 1999, approximately 15 km offshore (4°50′ S, 29°29′ E). For FW-A, phytoplankton were collected using vertical tows with a 50 µm mesh net (n = 6). Samples were filtered through 100 µm mesh to remove zooplankton, then collected on 0.45 µm glass-fiber filters and rinsed with 10% *N* HCl and distilled water. Zooplankton were caught using 100 m vertical tows with a 100 µm mesh net (n = 4). They were placed in filtered lake water for 2 h to clear gut contents, then collected on 0.45 µm glass-fiber filters and rinsed with 0.01 *N* HCl and distilled water. Fish specimens of *Stolothrissa* (n = 6; 80 to 90 mm), *Limnothrissa* (n = 5; 107 to 120 mm), *Lates stappersi* juveniles (n = 4; 130 to 160 mm), and *L. stappersi* (n = 4; 262 to 322 mm) were obtained from local fishermen who were fishing adjacent to the site when the plankton samples were collected.

For all species except *Stolothrissa*, the stable isotopic analyses were done on a section of white muscle tissue from behind the dorsal fin. As *Stolothrissa* were too small to obtain a large muscle sample, the entire body was used after removing the head, tail, and viscera, with the spine additionally removed from the samples in FW-B. Fish samples were washed with distilled water, dried, and homogenized before analysis. All samples were dried at 50°C and stored wrapped in aluminum foil.

Samples were analyzed at the University of Waterloo Environmental Isotope Lab on an Isochrom Continuous Flow Stable Isotope Mass Spectrometer (Micromass) coupled to a Carla Erba Elemental Analyzer (CHNS-O EA1108). The isotope ratios are expressed in delta notation with respect to deviations from standard reference material (Pee Dee belemnite carbon and atmospheric nitrogen). Standard error is 0.2‰ for carbon and 0.3‰ for nitrogen. Statistical analyses were done using JMP IN (SAS Institute, Inc.).

8.3 Results and Discussion

8.3.1 Isotopic Structure of the Food Webs

The two isotopic studies produced radically different views of the pelagic food web. For one food web, the isotopic structure appeared as expected, with a gradual isotopic enrichment through the food chain from phytoplankton to the top predator (Figure 8.3 FW-B). For the other food web, the isotopic structure was not that of a linear food chain (Figure 8.3 FW-A). Although there was a general trend of carbon

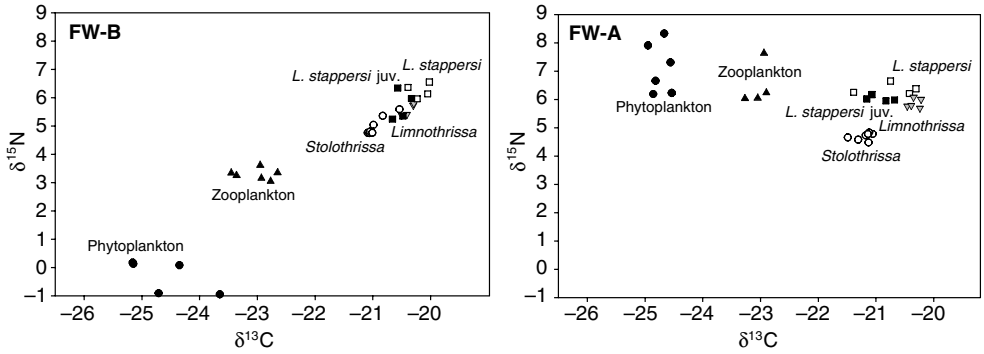

FIGURE 8.3 Isotopic structure of the food webs. FW-B shows the expected isotopic enrichment with trophic level increase. In contrast, FW-A shows a very different isotopic structure, with phytoplankton and zooplankton more enriched than would be expected.

enrichment in FW-A, there was a depletion of nitrogen with trophic level increase. Between the two years the fish species had similar values, and the differences between the two food webs appeared in the lower trophic levels — the phytoplankton and zooplankton.

The isotopic analyses for the upper food web fish species were consistent with the known dietary preferences of these fish species. Both FW-A and FW-B had similar values. The primary prey item for adult *L. stappersi* is *Stolothrissa*, and this relationship was clearly seen in the isotope data, where *L. stappersi* was approximately 1‰ enriched in ^{13}C and 2‰ enriched in $\delta^{15}N$ relative to *Stolothrissa*. Juvenile *L. stappersi* were depleted in $\delta^{15}N$ compared to the adults, which reflects the fact that their diet includes relatively more copepods (Mannini et al., 1999). The other clupeid species, *Limnothrissa,* includes smaller *Stolothrissa* in its diet, which is likely the reason for its isotopic enrichment relative to *Stolothrissa*.

Given the $\delta^{15}N$ values of the upper food web and the likely importance of atmospheric N fixation in Lake Tanganyika (Hecky, 1991), phytoplankton were expected to have a $\delta^{15}N$ value around 0‰, and zooplankton should be approximately 1‰ enriched in $\delta^{13}C$ and 3.4‰ enriched in $\delta^{15}N$ relative to phytoplankton. The results from FW-B were consistent with these expectations. In contrast, FW-A had vastly different isotopic values for the lower food web that were also inconsistent with the ratios for its upper trophic levels. FW-A phytoplankton had a $\delta^{15}N$ of between 6 and 8‰, and there was no trophic level enrichment between phytoplankton and zooplankton. In addition, the lower food web had $\delta^{15}N$ values similar to or slightly enriched compared to the upper consumer levels in that food web. Why were zooplankton and phytoplankton in FW-A so enriched?

There are several possible reasons for a shift in isotopic ratios. In this case, the mechanism behind the enrichment in $\delta^{15}N$ must explain a shift of ~6‰ that occurred only in the lower trophic levels and is not apparent in the upper food web. A discrepancy of this magnitude cannot be explained easily by either a change in phytoplankton productivity rates or species composition and thus implies a change in nitrogen source.

8.3.2 Temporal Fluctuations in the Nutrient Source

Although the primary sources of new nitrogen are atmospheric deposition and biological nitrogen fixation, internal loading of deep-water nutrients is also an important nutrient source for the pelagic zone (Hecky, 1991). Lake Tanganyika is permanently stratified, but strong winds during the dry season cause seiche activity with a 28 to 36 day period, leading to episodic vertical metalimnion entrainment (Plisnier et al., 1999). Wind speeds vary diurnally, but daily mean speeds were significantly higher in the week preceding sampling (1.48 ± 0.09m s^{-1}) than in the week following sampling (0.81 ± 0.08 m s^{-1}), with four consecutive days where speeds were higher than the long-term seasonal mean (Johannes et al., 1999). Concurrently, nitrate concentration profiles showed upwelling of nitrate from 100 m deep around 28 July (Figure 8.4) (Johannes et al., 1999). These data provide strong evidence that an upwelling event occurred 4 to 6 days prior to sampling the food web.

This deep-water nitrogen is likely enriched in ^{15}N (François et al., 1996). The metalimnion of Lake Tanganyika has low oxygen levels and elevated nitrate concentrations (Hecky et al., 1991). As denitrification occurs in the suboxic section of the water column, the lighter isotope is selectively removed, and the remaining nitrate becomes increasingly enriched in ^{15}N. Field studies in temperate lakes have shown that fractionation during nitrogen assimilation by phytoplankton can be –4 to –5‰ if nitrogen is in excess (Fogel and Cifuentes, 1993), which implies that the nitrogen source for these phytoplankton would require a $\delta^{15}N$ of at least 10 to 14‰. Denitrification has fractionations in the range of 10 to 30‰ (Wada and Hattori, 1991), which would lead to an enriched nitrate pool in the suboxic metalimnion of Lake Tanganyika. For other lakes, investigators have measured deep-water nitrate values of 15.1‰ (Yoshioka et al., 1988) or have calculated values between 10 and 30‰ (Teranes and Bernasconi, 2000).

A short-term, episodic nutrient input from deeper water to the epilimnion would alter phytoplankton isotopic signals, eventually causing them to have $\delta^{15}N$ signatures in the range observed in this study. With high nitrate concentrations, discrimination against the heavier nitrogen isotope occurs and initially phytoplankton are depleted relative to dissolved nitrogen (Altabet and François, 1994). Following Rayleigh fractionation kinetics, the remaining nitrate becomes relatively enriched. As the algal bloom continues, however, demand for nitrogen remains high and discrimination against the heavier isotope

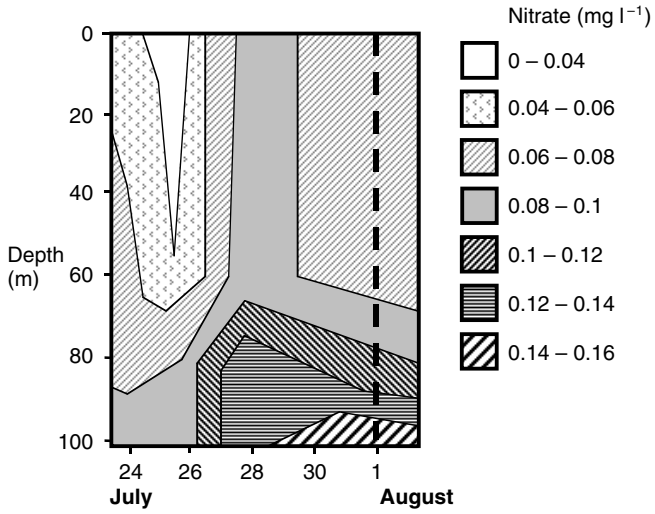

FIGURE 8.4 Nitrate concentration profiles. Nitrate concentrations from surface waters to the upper metalimnion off Kigoma Bay throughout the week prior to sampling. The dashed line indicates the sampling date. Upwelling of water from 100 m deep is indicated by the increase in nitrate concentrations around 28 July. (Data from Johannes et al., 1999.)

decreases as nitrogen concentrations decline. The pelagic zone of Lake Tanganyika is usually nitrogen limited (Hecky et al., 1991), implying that Rayleigh fractionation continues to near completion. Thus, phytoplankton eventually attain an isotope value similar to that of their nitrogen source.

8.3.3 Temporal Integration within the Food Web

While upwelling provides a mechanism for the enriched $\delta^{15}N$ values of the phytoplankton in FW-A, time-averaging explains the lack of trophic enrichment with respect to $\delta^{15}N$ for the consumer levels. The food web has different turnover times associated with each trophic level. Phytoplankton population growth rates are 1.2 day^{-1} or higher (Hecky, 1991), and thus their stable isotope signal represents carbon and nitrogen uptake and sources over the last few days. Preliminary evidence suggests that the time to full development for copepods in Lake Tanganyika is 31 to 45 days (Hyvonen, 1997); thus their isotopic ratios represent an average of phytoplankton consumed both pre- and post-upwelling. The clupeid *Stolothrissa* integrates diet over a period of several months to 1 year, and the predatory *L. stappersi* has a life span of several years (Coulter, 1991). The effect of this greater temporal integration was seen in the upper food web in Lake Tanganyika, where the short-term fluctuation in nutrient source was not apparent.

8.4 Factors Sensitive to Time

Recognizing that temporal integration occurs in an organism is important, particularly in the development of food web models or assignment of trophic level using isotopic signatures. Isotopic signals of primary producers are subject to greater variation than other trophic levels in this system because of constantly changing nutrient sources and concentrations. It is precisely because of this variation that food web modeling using isotopes is usually based on the isotope signal of the primary consumer, whose longer-term integration is assumed to reduce the short-term variability found in primary producers (i.e., Post et al., 2000). However, this work suggests that temporal variation may be significant at the primary consumer level and could affect assessment of relative trophic level.

There are several factors that are time sensitive and may affect the isotopic structure of a food web. Because a food web consists of organisms with a range of life spans, the upper trophic levels, with larger body sizes, will generally be integrating over longer time periods than lower trophic levels. A change in isotopic signature may be caused either directly, through changes in predators and/or their prey, or

TABLE 8.1

A Compilation of Factors That Are Time-Sensitive and That Have the Potential to Affect the Isotopic Signature of an Organisms in a Way That Can Affect the Isotopic Structure of the Food Web

Directly	Change in Predator	Change in Prey
	Metabolic processes (starvation, age).	Immigration.
	Migration	
	Change in diet	
	Diet quality	
Indirectly	**Base of Food Web**	
	Change in productivity rate	
	Change in species composition	
	Change in nutrient or light availability	
	Change in nutrient source	

by indirectly affecting the nutrient base of the food web (Table 8.1). These indirect changes in the phytoplankton isotopic signature are then incorporated in the upper trophic levels at rates depending on tissue turnover.

8.4.1 Direct Effects

Several factors affect the isotopic signature of an organism directly. As a result of preferential conversion of ^{14}N in metabolic reactions, highly metabolized molecules should be enriched in ^{15}N (Minagawa and Wada, 1984). Consequently, starvation has been associated with enriched $\delta^{13}C$ and $\delta^{15}N$ values (Overman and Parrish, 2001; Oelbermann and Scheu 2002). Although relatively few studies have been done on starvation, isotope ratios change on the order of 1. ‰ $\delta^{15}N$ and 1.5‰ $\delta^{13}C$ (Oelbermann and Sheu, 2002), which would be sufficient to confound trophic level placement. Possibly for metabolic reasons, age has been linked to increased $\delta^{15}N$ ratios for sole (Spies et al., 1989), cladocerans (Adams and Sterner, 2002), and wolf spiders (Oelbermann and Scheu, 2002) when dietary signatures were held constant. Age is also often associated with changes in dietary preferences, frequently leading to a trophic level shift from primary to higher-level consumer, which causes enrichment in both $\delta^{13}C$ and $\delta^{15}N$ (Vander Zanden et al., 1999). Migration of the predator for feeding purposes or seasonal migrations of prey might create a signature that does not reflect the predator's current environment (Hansson et al., 1997). For example, many fish species shift from benthic/littoral habitat to the pelagic at certain life stages, but may return to the littoral region for breeding purposes.

Other dietary aspects may affect an isotopic signature even though the prey items remain constant. Prey may immigrate from another locale characterized by different isotopic signatures (Hansson et al., 1997). Diet quality may also affect an organism's isotopic signature, and lower quality diets (relatively higher C:N ratios) induce nitrogen starvation, leading to enriched $\delta^{15}N$ values (Adams and Sterner, 2000; Oelbermann and Sheu, 2002). Carbon isotope ratios may also become enriched with lower diet quality (Oelbermann and Sheu, 2002).

Recognizing that different tissue types (heart, muscles, etc.) have different turnover rates is also an important consideration (Pinnegar and Polunin, 1999). For upper trophic levels, white muscles tissue is usually the preferred tissue source because of the relatively slow turnover rate compared to other body tissues like the liver, kidney, etc. Fatty tissues are depleted in $\delta^{13}C$, and thus muscle tissue with a high lipid content may need to undergo lipid extraction to ensure that the isotopic signature reflects diet.

8.4.2 Indirect Effects

More indirect perturbations affect the nutrient base of the food web, and then are gradually integrated up the food web. One of the more obvious possible mechanisms is a shift in the isotopic composition of the nutrient source for the base of the food web, as illustrated in this study. The input of a new

nitrogen source to an aquatic system is also often detectable, because nitrogen from sewage or soils has a much more enriched isotopic value than the natural variation of the system (Spies et al., 1989; Dover et al., 1992; Kendall, 1998; Tucker et al., 1999).

In addition, changes in light or relative nutrient availability or productivity rates can alter the signature of the overall phytoplankton pool (Farquhar et al., 1989; Fogel and Cifuentes, 1993; Laws et al., 1995). Nutrient availability can also have an affect on individual plankton species isotopic signatures, and lower light or nutrient availability reduces productivity rates, leading to a decrease in $\delta^{13}C$ ratios (Eek et al., 1999; Waser et al., 1999). Changes in relative nutrient availability often cause shifts in phytoplankton species composition, which can subsequently affect the isotopic signatures of the phytoplankton pool. For example, a shift toward nitrogen limitation may increase dominance by nitrogen-fixing species, whose $\delta^{15}N$ of around 0‰ may be markedly different from previously dominant plankton species that were using aqueous forms of nitrogen. These shifts are a common feature of temperate lakes during the summer, and time-averaging of this type has also been invoked in Lake Ontario, where the isotopic signature of late summer zooplankton may reflect phytoplankton consumed earlier in the summer (Leggett et al., 1999).

8.5 Conclusion

In summary, this study illustrates the importance of understanding the temporal resolution of different trophic levels and the effect of time-averaging in stable isotope ecology. In general, temporal integration increases from lower to upper trophic levels in a food web, as body size and life span increase. The interpretation of energy flow in food webs based on isotopic signatures could be incorrect without considering the possible effects of this time-averaging. The variability in time integration can also be exploited to learn more about ecosystem dynamics, through the use of either natural stable isotope abundance (Hansson et al., 1997) or tracers (Peterson, 1999).

Acknowledgments

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