WHAT CAN STABLE ISOTOPE RATIOS REVEAL ABOUT MANGROVES AS FISH HABITAT?

Craig A. Layman

ABSTRACT

Stable isotope ratios are applied in many ways to explore the relationship between mangroves and fishes. Here I summarize information pertinent to three central questions regarding the mangrove-fishes link: Can stable isotope ratios be used to (1) identify basal resource pools that support fishes associated with mangrove habitat?, (2) reveal aspects of consumer trophic structure in mangrove fish communities?, and (3) describe fish movement patterns with respect to mangroves? I review recent research developments that pertain to each question, including a discussion of the limitations of stable isotope ratios in understanding the mangrove-fishes link. I emphasize promising avenues for future research, including labeled isotope tracer experiments, probabilistic and spatial analyses of potential basal resource pools, novel community-wide and intraspecific metrics, and utilization of differential tissue turnover rates within and among organisms. Stable isotope ratios alone provide numerous insights into the role of mangroves as fish habitat, but the most thorough understanding of the mangrove-fisheries link is likely to stem from integrative approaches that combine stable isotope ratio analyses and other methodologies into a broad research framework.

Analysis of stable isotope ratios is a common tool employed in many sub-disciplines of biological and ecological research, and applications to deduce potential links between mangrove habitat and fishes are no exception. Through examination of natural variation in stable isotopes ratios of three elements (carbon, nitrogen, and sulfur), and the underlying reasons that drive this variation, many aspects of the mangrove-fishes link have been inferred. For nitrogen, the ratio of ^{15}N to ^{14}N (expressed as $\delta^{15}N$) exhibits stepwise enrichment with trophic transfers, and is a powerful tool to estimate trophic position of organisms (Minagawa and Wada, 1984; Peterson and Fry, 1987; Post, 2002b). The ratio of carbon isotopes ($\delta^{13}C$) varies substantially among primary producers with different photosynthetic pathways (e.g., C3 vs C4 plants), but changes little with trophic transfers (DeNiro and Epstein, 1981; Peterson and Fry, 1987; Post, 2002b). Therefore, $\delta^{13}C$ can be used to determine ultimate sources of dietary carbon. Similarly, the ratio of sulfur isotopes ($\delta^{34}S$) changes relatively little with progression through a food web, and thus can be used to identify important resource pools (Peterson et al., 1986; Connolly et al., 2004).

Because stable isotope applications have become commonplace, it is germane to this symposium volume to review the question: what can stable isotopes reveal about the role of mangroves as fish habitat? Numerous reviews have addressed aspects of stable isotope application to mangrove/estuarine research (e.g., Lee, 1995; Fry and Ewel, 2003; Sheridan and Hays, 2003; Herzka, 2005), and I do not endeavor to review all of that information here. Further, I do not delve into the myriad issues regarding preparation of marine plant and animal samples for stable isotope analysis (i.e., acidification, isolation of appropriate basal resource pools, etc.). Instead, my purpose is to summarize emergent themes regarding the role of mangroves as fish habitat as suggested through field-based inquiry using stable isotope ratios. Specifically, I address three questions:

(I) Can stable isotope ratios be used to identify *basal resource pools* that support fishes associated with mangrove habitat?,

(II) Can stable isotope ratios reveal particular aspects of consumer *trophic structure* (i.e., food web structure) in mangrove habitats?, and

(III) Can stable isotope ratios be used to describe fish *movement patterns* in relation to mangrove habitat?

I place specific emphasis on future directions within each of these thematic areas, and highlight applications of stable isotopes that have been under-utilized to address longstanding questions in the field ("Future Directions" sections). Throughout the text, I use the phrase "mangrove community" to refer to fish assemblages (and the food webs in which they are embedded) associated with a coastal water body that contains a significant amount of mangrove vegetation. I attempt to identify broad themes that span substantial variation in the structure and function of ecosystems in which mangroves are a conspicuous component (Ewel et al., 1998; Lovelock et al., 2005), and hope to provide a foundation from which to develop future scientific inquires in the field.

Can Stable Isotope Ratios Be Used to Identify Basal Resource Pools that Support Fisheries Associated with Mangrove Habitats?

In the 1970s, Bill Odum and colleagues introduced evidence that sub-tropical and tropical estuarine food webs were supported primarily by a mangrove detritus-based resource pool (Odum and Heald, 1975), and this paradigm served as the model for estuarine food web research for almost two decades. Over the last decade, however, stable isotope ratios have served as the primary tool to overturn this paradigm (Fry and Ewel, 2003). Although results vary among systems and geographic regions, the balance of evidence now suggests that other basal resource pools are the primary energy sources in sub-tropical or tropical mangrove fish communities (e.g., Lee, 1995; Newell et al., 1995; Primavera, 1996; Lonergan et al., 1997; Bouillon et al., 2002a; Hsieh et al., 2002; Kieckbusch et al., 2004; Benstead et al., 2006). Only in specific circumstances, for example, when particular species are restricted to mangrove-dominated portions of a wetland system, has mangrove detritus been suggested as a critical nutritional source (Rodelli et al., 1984; Newell et al., 1995; Sheaves and Molony, 2000; Christensen et al., 2001; Bouillon et al., 2004).

Yet if not mangrove detritus, what basal resource(s) support the productive fisheries typically associated with mangroves? Potentially important resource bases include epiphytic algae, macroalgae, microphytobenthos, particulate organic matter, phytoplankton, and seagrass. In specific cases, stable isotopes have provided valuable insights into the likely importance of one or more of these resources in supporting particular consumers of interest (e.g., Lee, 1995; Newell et al., 1995; Primavera, 1996; Lonergan et al., 1997; Bouillon et al., 2002a; Hsieh et al., 2002; Kieckbusch et al., 2004). Yet determination of the exact contribution of each of these resources to a particular consumer is usually not feasible because the number of major basal source pools (often 6 or more) exceeds the number of stable isotope ratios (typically 2 or 3). More generally, for any number (n) of isotopes employed, an exact combination for only n+1 potential sources can be determined (Phillips and Gregg, 2003). As such, in most mangrove fish communities, without a priori aggregating potential resource

pools (Phillips et al., 2005), it is impossible to quantify the exact contribution of each basal resource to a focal species, population, or individual.

Two general approaches have been proposed to deal with situations in which the number of resource pools exceeds the number of isotope ratios: the Isosource model developed by Phillips and Gregg (2003), and a spatially-based approach that relies on correlations among isotopic signatures of a consumer of interest and signatures of potential resource pools (Melville and Connolly, 2003). The Isosource model derives all feasible combinations of basal resource pools that can account for observed isotope values of a consumer. Data typically are presented in the form of frequency histograms that illustrate the complete range of possible percent contributions of each basal resource. This model has been widely applied in ecosystems in which mangroves are one of many potential resource pools (e.g., Melville and Connolly, 2003, 2005; Abed-Navandi and Dworschak, 2005; Connolly et al., 2005b; Benstead et al., 2006). Although more informative than qualitative inference based on $\delta^{13}C$, $\delta^{15}N$, and $\delta^{34}S$, the model remains a probabilistic approach that cannot reveal a unique solution as to the actual contribution of each source pool. As such, caution is advised when applying this approach, especially when the derived range of potential source contributions is wide (Phillips and Gregg, 2003), as is often the case in mangrove fish communities (e.g., Melville and Connolly, 2003, 2005; Abed-Navandi and Dworschak, 2005; Connolly et al., 2005b; Benstead et al., 2006).

The spatially-based analysis proposed by Melville and Connolly (2003) takes advantage of the large-scale (e.g., among estuary) variation in isotopic signatures *within* a basal resource pool. For example, it is well-documented that anthropogenic inputs to estuarine ecosystems can affect isotopic signatures of primary producers (McClelland et al., 1997; McClelland and Valiela, 1998; Fry, 1999; deBruyn and Rasmussen, 2002; Tewfik et al., 2005), and natural sources of variation in primary producer signatures also can be substantial (Marguillier et al., 1997; Bouillon et al., 2000; Fry and Smith, 2002). Melville and Connolly (2003) propose that the degree of correlation between a basal resource pool and a consumer of interest among spatially distinct areas provides an indication of the importance of that basal resource pool to the consumer. For example, Connolly et al. (2005b) used this model to demonstrate the importance of seagrass in supporting commercially valuable yellowfin whiting (*Sillago schomburgkii* Peters, 1864) in temperate Australian waters. This contribution would have been unclear from standard interpretation of the natural variation in isotope ratios or with an Isosource analysis.

Future Directions.—Future applications of stable isotope techniques in mangrove fish communities should avoid a narrow focus on assessing potential contributions of mangrove detritus to fisheries production (Fry and Ewel, 2003), and instead should work toward a broader understanding of the energy flow through food webs associated with mangroves. When seeking to determine important basal resource pools contributing to mangrove fish communities, sulfur isotope ratios are likely to reveal important insights not possible with use of $\delta^{13}C$ and $\delta^{15}N$ alone (Connolly et al., 2004). Multivariate statistical analysis derived from $\delta^{13}C$, $\delta^{15}N$, and $\delta^{34}S$ values, such as the analysis conducted by Litvin and Weinstein (2004), is one powerful way to identify critical basal resource pools. The Isosource model (Phillips and Gregg, 2003) and spatial-correlation model (Melville and Connolly, 2003) warrant further application and testing. Also, there remain interesting avenues for future research

regarding potential indirect contributions of mangroves to fishery production, such as the role of mangroves in nutrient cycling (Fry and Ewel, 2003).

Ultimately, however, documentation of critical basal resource pools in mangrove fish communities may require use of labeled isotopic tracers to directly track the flow of energy through food webs. In such experiments, a compound enriched in the heavy isotope of an element (typically ^{15}N or ^{13}C) is added to an aquatic system over a defined period of time, and extensive collections of basal resources and consumers are carried out frequently during and after the addition. Energy flow can then be tracked from basal resources to consumers, including quantification of the most important pathways, without significantly altering nutrient availability or rates of biological production. Labeled isotope tracer experiments are common in freshwater streams (e.g., Peterson et al., 1997; Hall et al., 1998; Mulholland et al., 2000; Tank et al., 2000; Hamilton et al., 2001), and also have been utilized in temperate estuaries (Holmes et al., 2000; Hughes et al., 2000; Deegan et al., 2002; Tobias et al., 2003). As an example of the latter, in the oligohaline reach of a Massachusetts estuary, Hughes et al. (2000) were able to use the labeled isotope approach to clearly show that centric diatoms dominated nitrogen uptake and served as the primary vector of nitrogen to upper trophic levels.

One central reason there have been no whole-system isotope tracer additions in mangrove ecosystems is the high connectivity between mangroves and other marine and coastal areas, i.e., these systems are relatively "open" (especially fringing mangroves along coastlines or in large estuaries) and characterized by a high degree of material and/or organism movement. However, relatively small, mangrove-lined tidal creeks (e.g., Layman et al., 2004; Valentine et al., 2007) may serve as ideal systems to conduct "whole-ecosystem" stable isotope tracer experiments. Such tidal creeks are more "well-bounded" (sensu Post et al., 2006) than other mangrove fish communities, yet often contain many of the diverse suite of habitat types and organisms that characterize back-reef ecosystems (Dahlgren and Marr, 2004; Adams et al., 2006). Such an approach was applied to track uptake and cycling of nitrogen in a relatively small salt marsh tidal creek (Gribsholt et al., 2005). Alternatively, localized additions of labeled isotopes may help resolve ambiguities among importance of selected basal resources to particular consumers of interest (Mutchler et al., 2004). Although logistically challenging and costly, these labeled isotope additions have the potential to substantially advance our knowledge of the most critical basal resource pools that support mangrove fishes and the food webs of which they are a part.

Can Stable Isotope Ratios Reveal Aspects of Consumer Trophic Structure (i.e., Food Web Structure) in Mangrove Habitats?

Since the earliest applications of stable isotope ratios to study trophic structure, a common approach has been to present bi-plots with species (or individuals, populations, etc.) depicted based on $\delta^{13}C$-$\delta^{15}N$ (or $\delta^{34}S$) values. Relative position of species in these plots typically is used to make qualitative inferences about the general structure of the food web, for example, inferring likely dietary sources of focal consumers. Recent studies in freshwater ecosystems, however, have emphasized *quantification* of particular aspects of tropic structure, such as the trophic position of consumers, food chain length, or ontogenetic diet shifts (e.g., Vander Zanden et al., 1999 ; Post, 2002a, 2003; Layman et al., 2005). For example, (Post, 2002a) proposed a detailed

framework for estimating food chain length, a methodology which has allowed for rigorous tests of long-standing questions in ecology (Post et al., 2000). In contrast, isotope studies of trophic structure in mangrove fish communities remain rather qualitative in nature (Marguillier et al., 1997; Bouillon et al., 2002b; Cocheret de la Morinière et al., 2003; Nagelkerken and van der Velde, 2004; Nagelkerken et al., 2006). In this section, I discuss the underlying reasons why even ostensibly straight-forward questions regarding food web structure (e.g., trophic position of organisms) can be especially problematic to answer in mangrove fish communities.

Many of the difficulties in quantifying aspects of food web structure in these communities arise from the difficulty in establishing a standard *isotopic baseline*. There can be substantial variation in isotope ratios of resources among habitats or ecosystems, and an isotopic baseline is required to standardize values to a common level to allow for appropriate comparisons (Post, 2002b). In freshwater ecosystems, basal resources are relatively easily isolated at a coarse level (e.g., seston and periphyton/detritus in northern U.S. lakes, Post, 2002b), or can be aggregated into distinct, ecologically meaningful, categories (e.g., autochthonous vs allochthonous pools in rivers, Layman et al., 2005). If a primary consumer taxa (e.g., snails and mussels in northern U.S. lakes) provides a spatially- and temporally-integrated measure of isotope ratios of the respective basal resource pools, it then can serve as an appropriate baseline taxa (Post, 2002b). Subsequently, such baseline taxa can be used for calculation of specific aspects of food web structure, such as food chain length, and across-system comparisons are possible (Vander Zanden et al., 1999; Post et al., 2000).

In mangrove fish communities, and more generally in estuarine ecosystems, establishing an isotopic baseline is extremely problematic. First, it is still unclear in many mangrove fish communities which of the many potential basal resource pools are most important (see Section I above). Second, these systems typically are inhabited by a very diverse suite of primary consumer taxa, many of which have highly plastic feeding behaviors and may utilize multiple basal resource pools. Even if diet of assumed primary consumers can be well-characterized (based on stomach contents or observations of feeding behavior), it may not reflect what is actually *assimilated* into tissue. All of these factors, as well as the degree of isotopic discrimination (i.e., processes which lead to different isotope ratios in the tissue of an organism from its diet), affects the realized isotopic signatures of the consumers. In a small tidal creek on Abaco Island, Bahamas, 18 macro-invertebrates in the resident food web (Layman et al., 2007) could be classified as primary consumers. Mean $\delta^{15}N$ values of these taxa range from −3.5‰ to 3.0‰. Since calculation of trophic position is derived directly from a specific primary consumer taxa and the assumed discrimination factor (Post, 2002b), estimated trophic positions of other taxa in the web could vary substantially depending on the initial choice of "the" baseline primary consumer. Assuming a mean $\delta^{15}N$ fractionation of 2.54‰ with trophic transfers (Vanderklift and Ponsard, 2003), a $\delta^{15}N$ range of 6.5‰ would span more than two entire trophic levels. As such, trophic position calculations can be especially sensitive to the isotopic baseline and variation at the base of a food web in $\delta^{15}N$ values—as is the case in most mangrove communities—rendering precise estimates of trophic positions of species extremely difficult to obtain.

Other well-acknowledged caveats associated with application of stable isotope ratios also pertain to the study of trophic structure in mangrove fish communities. Isotopic discrimination is dependent on many factors, and can be quite variable both

among tissues within a species and among species. Because a single value typically is assumed in a given study, significant error addition can be introduced into trophic position calculations (DeNiro and Epstein, 1981; Macko et al., 1982; Hobson and Clark, 1992; Post, 2002b; Vanderklift and Ponsard, 2003). This may be especially problematic in mangrove communities because organisms vary substantially in taxonomy, body size, metabolic rates, elemental concentrations, and diet—all of which may affect discrimination. The degree to which such sources of error influence characterizations of trophic structure depend on the specificity of the question being asked. If detailed diet information or movement patterns of a particular organism are being sought, extensive laboratory and field studies to quantify isotopic discrimination, tissue turnover, etc. are a necessity (e.g., Fry et al., 2003).

Future Directions.—Although characteristics of targeted species (e.g., trophic position) are often difficult to quantify in mangrove ecosystems, stable isotopes may be applied at a different level to reflect characteristics of the food webs in which these species are imbedded. For example, $\delta^{13}C$ and $\delta^{15}N$ (or $\delta^{34}S$) values provide a representation of the trophic niche of a particular species, as they are the result of all the trophic pathways that have culminated in that individual. As such, position of a species in $\delta^{13}C$-$\delta^{15}N$ bi-plot space (or 3-dimensional space with inclusion of $\delta^{34}S$) is one representation of the trophic niche of that species. When all species are plotted into this "niche space", their dispersion (spacing relative to one another) can be used to examine properties of the entire food web. The total extent of niche space occupied can be quantified as a measure of the overall degree of trophic diversity within the web. Bias at the species level due to the caveats discussed above (e.g., variable discrimination rates) have critical effects on calculations of species-level characteristics, but these effects are less critical on metrics derived across *all* species in a web—especially when comparing across gradients that have significant effects on food web structure. This may be viewed as one of the promising aspects of the community-wide approach, i.e., by looking for *overall* patterns in food web structure, intricacies of determining every factor affecting a single species' isotope ratios are not essential to elucidate.

In this manner, quantitative metrics based on species dispersion in niche space can provide a robust means with which to compare food webs across environmental gradients of interest or to evaluate responses of food webs to specific perturbations (Layman et al., 2007). In Figure 1, I provide two (obviously over-simplified) hypothetical food webs where each circle represents a single species in $\delta^{13}C$-$\delta^{15}N$ niche space. In each plot, both filled and open circles represent species in the food web before a specific perturbation, and only open circles represent those species that remain following a perturbation. Three metrics could be used to describe trophic structure in these webs: total area of the convex hull encompassing all species (*TA*), the $\delta^{15}N$ range (*NR*), and $\delta^{13}C$ range (*CR*) (for more detailed description of these and additional metrics, see Layman et al., 2007). In both food web A and B, *TA* is 4 (the larger triangle in each plot), but *NR* in A is twice that in B, reflecting real underlying differences in food web structure. Since $\delta^{15}N$ typically increases with trophic transfers, a larger *NR* will likely reflect additional trophic levels within a food web (Minagawa and Wada, 1984; Peterson and Fry, 1987; Post, 2002b). As such, larger *NR* in A could signify presence of top predators that are not found in B. Alternatively, larger *CR* in B suggests a more diversified set of basal resources that can support a more diverse set of primary consumers. Post-perturbation (shaded triangles) *TA* values are 2 in both
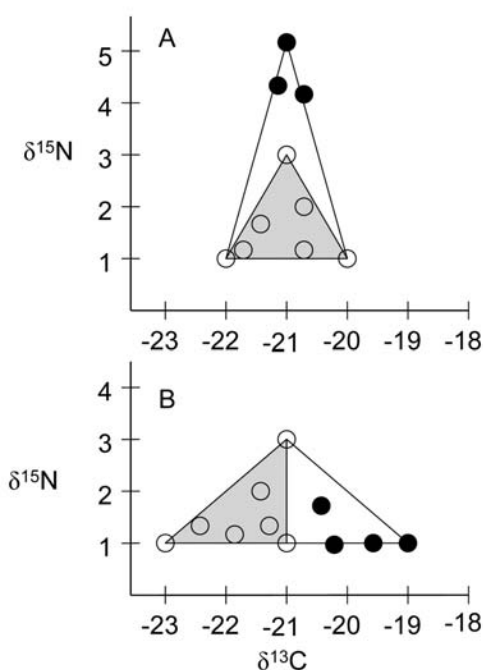
Figure 1. Two hypothetical food webs as represented by positions of species in δ^{13}C-δ^{15}N bi-plot space. Each circle represents a different species. Filled and open circles are species in an initial food web, with open circles the only species remaining in a food web following a perturbation. The larger triangle indicates the total area (*TA*) occupied by species in bi-plot space before the perturbation, and the shaded triangle is *TA* after the perturbation. The shape of the triangles represent underlying differences in food web structure, and how perturbations can affect food webs in different fashions.

webs, but each provides a different conceptual scenario illustrating how the metrics may indicate very specific shifts in food web structure. In A, smaller *NR* drives the reduction in *TA*. This example could simulate a change in food web structure following over-exploitation of top predators, i.e., "fishing down" food webs (Pauly et al., 1998). In B, the perturbation has primarily affected the diversity of primary consumers, i.e., loss of species that were at the base of the triangle.

This quantitative approach also can be used to examine feeding ecology at the population level, as variation in individuals' δ^{13}C-δ^{15}N signatures in a population provides information as to the degree of intraspecific niche variation (Bearhop et al., 2004). For example, the *TA* metric provides a direct measure of the amount of overall niche space occupied by a group of individuals, and thus can be used as one representation of the population's niche width (Layman et al., 2007). In an example from mangrove-lined tidal creeks in the Bahamas (sites described by Valentine et al., 2007), niche width of gray snapper *Lutjanus griseus* (Linnaeus, 1758) as measured by *TA* appears to contract in the two creek systems in which tidal connectivity is restricted (fragmentation categories based on Layman et al., 2004) (Fig. 2). This is likely driven by a decrease in prey diversity in fragmented tidal creeks, and an associated decrease in the between-individual variation in resource usage (Van Valen, 1965; Bolnick et al., 2003). Building from extensive applications of stable isotope ratios in mangrove communities, these community-wide and population-level isotope
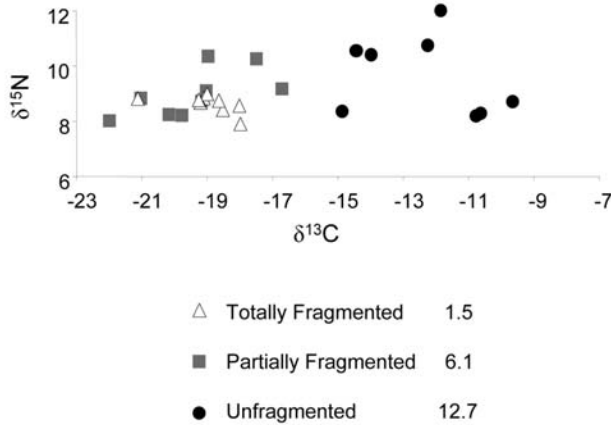
Figure 2. Plot representing $\delta^{13}C$ and $\delta^{15}N$ values of nine gray snapper (*Lutjanus griseus*) individuals from each of three mangrove-lined tidal creeks on Andros Island, Bahamas. One creek was classified as fragmented, one partially fragmented, and one unfragmented, following the categories from Layman et al. (2004). Values given below the plot are the total areas of the convex hull encompassing the nine individuals from each creek. This population-level "total area" metric (*TA*) provides for a quantitative measure of niche width of each population.

metrics may provide new perspectives from which to assess the role of fishes in these food webs.

Can Stable Isotope Ratios be Used to Describe Fish Movement Patterns in Relation to Mangrove Habitat?

Natural variation in stable isotope ratios can be used to infer movement patterns because organisms acquire the signature of their diet which is often habitat-specific (Fry et al., 2003). Thus, if a fish is collected in habitat A but has an isotopic signature reflective of habitat B (which is distinct from A), movement between habitats could be inferred. An obvious requirement for this approach is that habitat types (and prey items in these habitats) differ significantly in at least one stable isotope ratio. Carbon ratios are useful to distinguish movements between habitat types dominated by basal resources pools with different photosynthetic pathways, such as between seagrass and mangroves. Nutrient enrichment can lead to elevated $\delta^{15}N$ values (McClelland et al., 1997; McClelland and Valiela, 1998; Fry, 1999; deBruyn and Rasmussen, 2002; Tewfik et al., 2005), and difference in the resulting isotopic baseline may allow for identification of movements between areas with high and low anthropogenic nitrogen inputs (Hansson et al., 1997). Sulfur isotopes are especially useful to distinguish pathways of benthic and pelagic production (Peterson et al., 1986; MacAvoy et al., 1998), and thus can be used to identify movements between shallow and open water areas of an ecosystem. In any movement study based on stable isotope ratios, it is critical that organisms have remained resident in a habitat long enough (or feed consistently in a given area) to become equilibrated to the local food sources, and that additional sources of variability (e.g., variation in the isotopic contents of prey) do not exceed the differences among focal habitat types. Any such study will rely directly on detailed knowledge of tissue turnover times, and thus the rate at which a

signature from one site will be lost following a feeding shift in the new habitat (Dalerum and Angerbjörn, 2005; Herzka, 2005).

Ontogenetic and seasonal habitat shifts are the movement patterns that are most likely to be detected with stable isotope ratios. For example, using multivariate analyses based on $\delta^{13}C$, $\delta^{15}N$, and $\delta^{34}S$, Litvin and Weinsetin (2004) were able to provide convincing evidence of ontogenetic movements of juvenile weakfish *Cynoscion regalis* (Bloch and Schneider, 1801) from the Upper Delaware Bay and adjacent marsh areas to open waters near the mouth of the Bay. Fry and colleagues demonstrated that shrimp caught in offshore waters had spent a portion of their life cycle in estuarine habitats (Fry, 1983), and distinguished among individuals that inhabited seagrass beds and mangrove areas (Fry et al., 1999). Such studies provide important insight into aspects of connectivity among coastal habitat types, without the need to individually mark and re-capture numerous individuals of the focal population (Rubenstein and Hobson, 2004).

Attempts also have been made to infer whether organisms undertake daily/tidal feeding migrations, or feed on local resources and thus are resident to that habitat type. Nagelkerken and van de Velde (2004) reported that $\delta^{13}C$ values of haemulids (grunts) and lutjanids (snappers) that shelter in mangroves during the day were significantly enriched compared to available food items in the mangrove habitat. They concluded that fishes must move to seagrass areas to feed, as the consumer isotope signatures fell between values of mangrove- and seagrass-associated food items. However, the extent to which this pattern can be attributed to underlying movement patterns is severely limited by the number of basal resource pools, with distinctly overlapping isotope ratio ranges, that may be supporting prey. That is, assuming mangrove and seagrass (or any other subset) of resources are the only possible endpoints creates a false dichotomy that may a priori ignore basal resource pools critical to the food web of interest. Isotope ratios also have been used to demonstrate that organisms draw the majority of their energy from local (i.e., a scale of meters) basal resources, and thus used to infer that these organisms undertake little or no among-habitat feeding movements (Weinstein and Litvin, 2000; Hsieh et al., 2002; Guest and Connolly, 2004; Guest et al., 2004, 2006). However, conclusions from all of these studies are tenuous because many basal resource pools can be readily transported at small spatial scales within mangrove ecosystems (Connolly et al., 2005a; Melville and Connolly, 2005), and there may be many other distinct sources of environmental variation that affect local resource isotope ratios (Herzka, 2005).

FUTURE DIRECTIONS.—Simultaneous use of $\delta^{13}C$, $\delta^{15}N$, and $\delta^{34}S$ will provide the most comprehensive foundation to infer fish movement patterns (Litvin and Weinstein, 2004; Herzka, 2005). Within each study system, detailed research is necessary to explicitly document species-specific tissue turnover times, and the time it takes organisms to equilibrate to local food sources. Recent research (MacAvoy et al., 2005; Perga and Gerdeaux, 2005; Sakano et al., 2005; Trueman et al., 2005; MacNeil et al., 2006) continues to highlight the importance of understanding effects of both growth rate and metabolism in determining tissue turnover rates (Fry and Arnold, 1982; Hesslein et al., 1993; Herzka, 2005). Yet more research is direly needed to provide for a general conceptual framework that can be applied broadly across study organisms and systems. Species-specific experiments are a necessity if different tissue types within an organism are to be used to infer movement patterns (Hesslein et al., 1993; Dalerum and Angerbjörn, 2005; Phillips and Eldridge, 2006). For example, Fry

et al. (2003) conducted extensive field enclosure experiments to examine differential turnover rates among brown shrimp *Farfantepenaeus aztecus* (Ives, 1891) tissue types, and then applied these rates to assess movement patterns based on the degree to which the different tissues had equilibrated to the local diet signature.

For a broader view of the relationship between fishes and mangroves, stable isotopes are most likely to provide useful insights when integrated with other tools and approaches. For example, a combination of isotopic analyses and direct tracking of fish movement patterns would be a powerful approach to detail complex intricacies of fish trophic ecology (Cunjak et al., 2005), especially with recent advances in tagging methodologies and acoustic telemetry technologies that allow for detailed descriptions of movements of individuals. Coupled with stable isotope analyses, feeding migrations of individuals can be identified at multiple temporal and spatial scales. Especially interesting would be study on the incidence of individual trophic specialists within a fish population (Bearhop et al., 2004). For example, in the Miramichi River in New Brunswick, Canada, a combination of passive integrated transponder (PIT) tags and stable isotope ratio analyses were used to distinguish three apparently distinct trophic groupings within a population of Atlantic salmon. Consistent data from PIT tag monitoring and stable isotope analysis suggested some individuals that remained in tributaries to feed, a second group that resided and fed in the main river channel, and a third group that fed in both the main stem and tributary (Cunjak et al., 2005). Such multi-faceted studies could provide valuable insight into trophic ecology of mangrove fishes, and help resolve ambiguities with respect to the specific role that mangroves fill with regard to fish habitat.

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ADDRESS: (C.A.L.) *Florida International University, Department of Biological Sciences, Marine Sciences Program, 3000 NE 151st St., North Miami, Florida 33181. E-mail: <cal1634@ yahoo.com>, Telephone: 786-390-0578.*

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