

USING STABLE ISOTOPES IN MANGROVE FISHERIES RESEARCH – A REVIEW AND OUTLOOK

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(Received 29 April 2002; In final form 4 November 2002)

Mangrove forests are important coastal wetlands in most of the tropics, but their importance to fisheries is poorly understood. Rationales for conserving these ecosystems are partly based on ideas that mangroves are important to food webs that support fisheries. Here we review use of stable isotopes to test the strength of the mangrove forest-fish connection, suggesting that a dual focus on both food web ecology and habitat use may be most profitable in future studies of this type.

Keywords: Carbon isotopes; Detritus; Fisheries; Food webs; Mangroves; Natural variations

Mangrove deforestation is widespread across the tropical regions where coastal mangrove forests are the historically dominant landscape type in the intertidal zone. It is estimated that humans have removed more than half of the world's mangroves, with a continuing annual deforestation rate conservatively estimated at 1% [1]. Ecologists and managers alike are challenged to better understand and conserve essential features of remaining mangrove forests, and here we review stable isotope studies bearing on these issues.

Rationales for conserving mangrove forests have often relied on studies that indicated a strong food web linkage between mangrove forests and coastal fisheries, with food webs based on decaying mangrove leaves [2, 3]. Those early studies were based on gut content analyses alone, but isotopic studies soon showed that ingested mangrove material was not always assimilated. For example, although mangrove detritus from local estuaries in Malaysia was ingested by offshore shrimp, carbon isotope ($\delta^{13}\text{C}$) values of these shrimp showed no evidence for assimilation of this material [4], apparently because the detritus was too refractory. Studies in a small mangrove-lined lagoon in Puerto Rico yielded similar results, where shrimp collected from the lagoon had -16% carbon isotopic values similar to -14% benthic algae in the lagoon, with little evidence for assimilation of mangrove detritus that typically averages near -27% [5]. Production of benthic algae at the Puerto Rico site was estimated to equal mangrove production, helping to account for the observed importance of benthic algae and lack of mangrove importance in local food webs [6]. In isotopic studies of salt marshes, temperate intertidal systems that are analogous to tropical mangrove systems

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in many ways, a dominant food web role for benthic algae rather than for macrophyte detritus has also been documented [7, 8]. Overall, most mangrove studies have found a limited role for mangrove detritus in estuarine food webs, demonstrating that it is usually only animals collected inside mangrove swamps or in interior mangrove waterways that have low (-20 to -27‰) carbon isotopic values similar to -27‰ mangrove leaves [9–28]. These findings are consistent with conceptual models that show rapid dilution of mangrove materials at most estuarine locations outside the mangrove forests [29], and they indicate only low-to-moderate importance of fisheries-forest connections in mangrove systems.

One criticism of these isotopic studies is that none has directly tested isotopic fidelity in food web links between consumers and mangrove detritus. Early studies [30] showed that the “you are what you eat” carbon isotopic rule applies for salt marsh *Spartina* detritus, but similar studies have not been performed with mangrove detritus. There is little carbon isotopic change during decomposition of mangrove leaves [10, 28, 31], but isotopic changes in further assimilation steps in food webs have not been tested. Possible fractionation in assimilation steps needs to be checked in controlled laboratory experiments, for example by using small invertebrates that are capable of surviving and growing on detrital mangrove diets [32–35]. Fungi can be intermediates in detrital food webs [3] and several studies indicate that the “you are what you eat” isotopic rule may not strictly apply where fungi are important, since ^{13}C food web enrichments of up to 6‰ have been documented for fungi growing on laboratory and natural substrates [36–38]. Studies of terrestrial earthworms have shown also that detritivores can be substantially enriched in ^{13}C by $3\text{--}4\text{‰}$ vs. their diets [39–42]. If such fractionations occur routinely, then measured consumer carbon isotopic values of -21 to -24‰ rather than -27‰ may indicate 100% nutritional reliance on mangroves, with the result that previous isotopic studies generally may have underestimated the importance of mangrove foods for coastal food webs. With this in mind, careful feeding studies are needed to establish the “assimilation-adjusted” mangrove carbon isotopic value used in interpreting mangrove support of coastal food webs.

Careful reading shows that previous isotopic studies also generally emphasize that mangroves are not the *dominant* food resource that supports secondary consumer production in estuarine systems, but these studies do not rule out low-level use of mangroves in estuarine food webs. For example, these studies have not tested whether mangrove detritus could supply 30–50% of the diet of consumers when other foods are scarce. More detailed experimental studies, perhaps using isotope-labeled foods, are needed to address this possible low-level assimilation of mangroves in estuarine food webs. Also, even if most mangrove carbon (C) is ultimately lost to the microbial loop, mass balance studies and isotopic tracer studies show that remineralization of mangrove N and P nutrients sometimes plays a locally important role in estuarine nutrient budgets [43–48]. An untested idea is that decomposing mangroves supply N and P nutrients to edible benthic bacteria and algae of the forest floor, with this mangrove nutrient subsidy helping to support estuarine food webs.

To date, however, results from the stable isotopic tests of fates of mangrove detritus do not make a strong case for mangrove conservation based solely on food web considerations. Instead, the main reason given around the world, in developing and developed countries, for protection of mangrove forests is their function in providing nursery habitat for commercially important fish and invertebrates [49]. Habitat is cited as the primary reason for protecting mangroves in such diverse places as Florida, where the “mangrove story” began, and in Queensland, adjacent to the Great Barrier Reef World Heritage Area. Conservation of mangrove forests because of the biodiversity of fish they support, on the other hand, seems to be of concern primarily to developed countries or in areas where diving is a popular tourist sport.

Protection of coastlines from storm surges is generally the second benefit listed, in spite of the lack of published evidence [50]. It is interesting that a widely-cited recent study

[51] found that “waste treatment” (followed by “disturbance regulation” and with “food production” and “habitat/refugia” in fourth and sixth place, respectively) is the most important ecosystem service provided by tidal marshes and mangroves. In fact, frequent flooding of mangrove forests and subsequent dispersal of waste products limits the degree of waste treatment that mangroves can provide, although careful engineering might increase their value [50].

The possibility that refuge rather than food may be the most important contribution for mangrove systems is supported by similar relationships in other shallow coastal habitats. Young juveniles of many fish species use shallow estuarine waters for nursery habitat, and lower predation in these shallow areas may be critical for good year-class strength [52–55]. Modeling shows that estuarine populations are typically much more sensitive to changes in mortality rates than to changes in growth rates (K. A. Rose and H. Haas, personal communication), so that there is a good theoretical justification for considering issues of mortality and refuge when investigating the value of mangrove systems.

Using stable isotopes to test the refuge value of mangrove systems is quite possible. The crux of this research approach is testing if animals are resident, with high residency associated with high habitat value. This approach can be illustrated with data from northern Australia mangrove systems adjacent to seagrass systems (Ref. 56; Fig. 1). *Metapenaeus* sp. shrimp collected in two seagrass meadows had fairly uniform carbon isotopic values of -9 to -13‰ , but values in two nearby mangrove systems were much more scattered, with most shrimp in one mangrove system (M1, Fig. 1) having -9 to -13‰ values consistent with a seagrass-origin. Most shrimp in the M2 mangrove system had low values typical of mangrove systems and outside the range of values seen in seagrass systems (Fig. 1). Residency of *Metapenaeus* sp. in the M1 mangrove system, and hence the value of the M1 mangrove system, could be assessed as much less than for the M2 system. Generally, it would be prudent to consider several species and not just one species when judging overall residence and system performance of a particular mangrove site.

Ideally, residency would be considered along with assays of abundance and growth to form an overall picture of fisheries production in each mangrove system, but the abundance and growth assays are often difficult and time-consuming [57–59], so that the isotopic residency assays alone may provide a first index of system performance. The residency assays may be improved by considering whether animals have isotopic values in equilibrium with the locally available diet found in stomach contents. Both the long-term diet and the short-term diet can be assessed by examining isotopic values in tissues with different turnover rates [60]. Generally, isotopic values for the different types of tissues should be relatively fixed and constant when animals are not moving and are feeding consistently on local diets. Residency can also be considered in a broader way as habitat use, and isotopic indices of mangrove habitat use may be expected to increase for mobile organisms such as larger fish [61] in those mangrove systems that have particularly high system performance and value for fisheries.

In summary, ecologists interested in using isotopic tools to investigate forest-fisheries relations in mangrove systems might do well to avoid a narrow focus on whether decaying mangrove leaves provide the dominant food resource for resident and migratory consumers. A broader focus that considers habitat use and residency along with food web support may lead to a clearer overall evaluation of the value of a mangrove forest for fisheries. Many interesting natural experiments could be explored, such as how the tidal creek structure within a mangrove forest affects fish access and forest use, or whether shading of benthic algae on the forest floor by tall mangroves will increase food web reliance on mangrove detritus. Such investigations are needed in the longer term for recognizing and understanding essential features of mangrove forests that insure healthy system function [62, 63] and sustain abundant forest and fisheries yields.

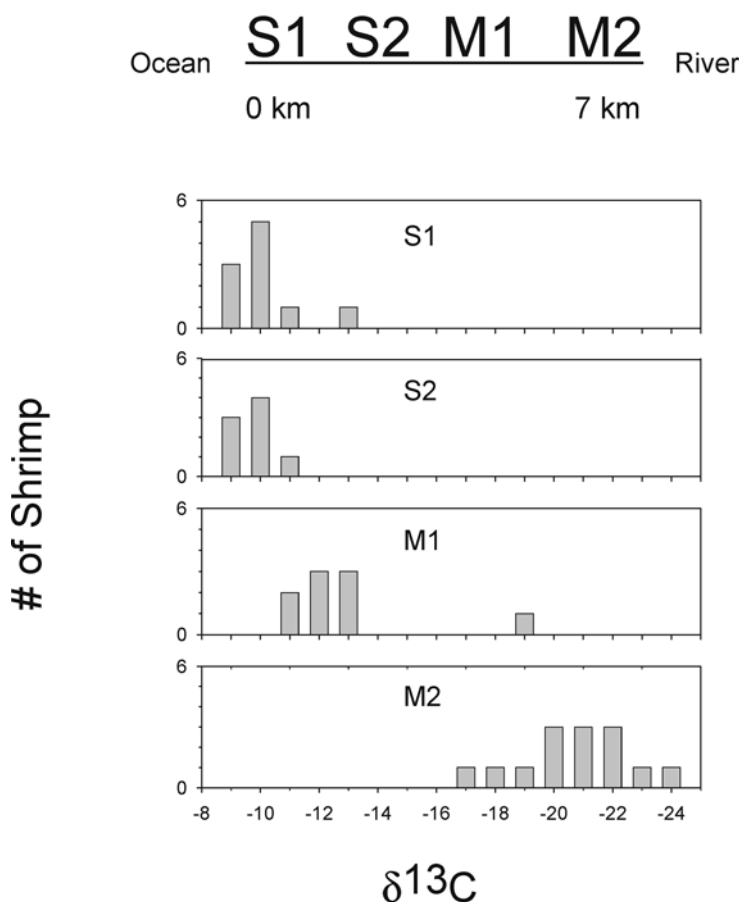


FIGURE 1 $\delta^{13}C$ values of *Metapenaeus* sp. shrimp collected in a northern Australia estuary, near the mouth of the Embley River. Shrimp were collected at 2 seaward seagrass sites (S1 and S2) and 2 mangrove sites (M1 and M2). Top schematic shows the 4 collection locations along a 7 km transect, and bottom panels show $\delta^{13}C$ histograms for individual shrimp collected at each station (data from Fig. 4d, dry season, in Ref. 56).

Acknowledgements

This work was partly supported with funds from NOAA Coastal Ocean Program grant NA06OP0526, NSF DEB-9815598, and EPA grant R-82800901.

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