

## Estimating the assimilation of mangrove detritus by fiddler crabs in Laguna Joyuda, Puerto Rico, using dual stable isotopes

ROBERT FRANCE

*Harvard University, Graduate School of Design, 48 Quincy St., Cambridge, MA 02138, USA*

*(Accepted 22nd January 1998)*

---

**ABSTRACT.** Dual stable isotope analyses ( $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$ ) of fiddler crabs from a forest-fringed, land-locked lagoon in Puerto Rico indicated the differential assimilation of material from ingested sediments. Fiddler crabs preferentially selected for nitrogen-fixing benthic microalgae (cyanobacteria) over vascular plant detritus. These results question the assumption that mangrove detritus is always the principal source of energy to estuarine consumers. Previous research from this lagoon as well as from Amazonia suggests that the magnitude of land-water ecotonal coupling may be low for these particular tropical systems where benthic algal productivity is presumably high.

**KEY WORDS:** benthic microalgae, differential assimilation, fiddler crabs, mangroves, stable carbon and nitrogen isotopes

### INTRODUCTION

Mangrove forests in coastal estuaries provide an invaluable habitat resource for numerous organisms including those supporting important sustainable fisheries (e.g. Lugo & Snedaker 1974). Conventional wisdom has suggested that mangroves provide the primary carbon source fueling detrital-based foodwebs, and as such, represent the major route of energy flow in such systems (e.g. Austin & Austin 1971, Flores-Verdugo *et al.* 1987, Odum & Heald 1975, Qasim & Sankaranarayana 1972, Wells 1984). Mangroves, once a prevalent feature of Puerto Rican coastlines and estuaries (e.g. Gleason & Cook 1927), are now seriously threatened: loss of 86% of original surface area cover (Lugo & Cintron 1975). Research on mangroves in Puerto Rico has centred more on understanding basic biological attributes (e.g. Cintron *et al.* 1978, Golley *et al.* 1962, Levine 1981, Pool *et al.* 1977, Wadsworth 1959) than on predicting the effects of deforestation. Quantifying the incorporation of terrestrial forest

detritus into estuarine foodwebs would provide insight into the magnitude of ecotonal coupling and might be used in the managerial design of protective buffer strips around sensitive areas (France 1996a).

Although there is a long tradition heralding the importance of vascular plant detritus as a direct food source for estuarine consumers (e.g. Darnell 1961, Marples 1966), such assumptions have been criticized by others (e.g. Walker 1973). Odum & Heald (1975), however, presented evidence from an estuarine mangrove system in Florida which they believed 'refutes these [critical] arguments'. Because they found that more than 20% of material contained in the digestive tracts of all herbivores and omnivores contained mangrove detritus, Odum & Heald (1975) considered that 'the principal flow of energy is along the route: mangrove leaf detritus → bacteria and fungi → detritus consumers → lower carnivores → higher carnivores'. However, simple ingestion of detritus does not necessarily imply any direct assimilation of that material. Therein lies the advantage in using stable isotope analysis over traditional gut content analysis in determining real pathways of energy flow in mangrove ecosystems (Marguillier *et al.* 1997, Newell *et al.* 1995, Stoner & Zimmerman 1988, Zieman *et al.* 1984). For example, Rodelli *et al.* (1984) recorded mangrove detritus in the guts of offshore animals in Malaysia for which there was no isotopic evidence for any mangrove assimilation.

Because consumer  $\delta^{13}\text{C}$  values became less negative with distance from mangrove swamps to offshore waters, Rodelli *et al.* (1984) interpreted this effect as being due to the progressive reduction in assimilation of mangrove detritus. By focusing on only fiddler crabs, and extending the analysis to include more recent global data, a similar trend can be seen whereby  $\delta^{13}\text{C}$  values are more negative in forested estuaries than in open marine-influenced areas (Figure 1).

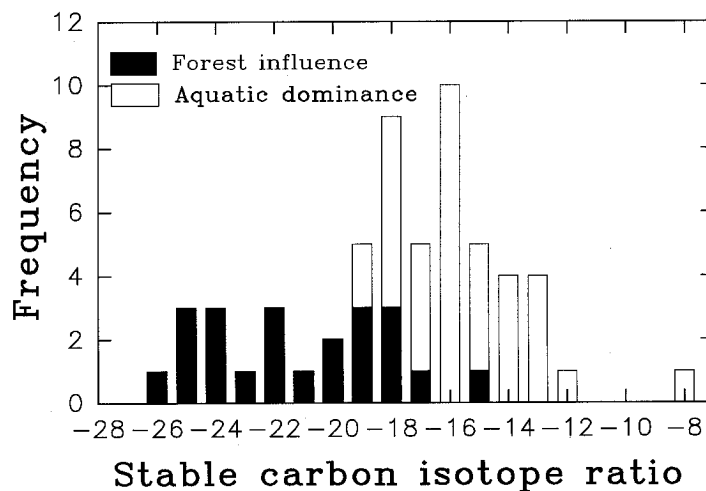


Figure 1. Frequency distributions of stable carbon isotope ratios ( $\delta^{13}\text{C}\text{‰}$ ) from the literature for various species of fiddler crabs collected from regions of either aquatic dominance (e.g. seagrasses, saltmarshes,  $n = 22$ ) or riparian forest influence ( $n = 36$ ). Data sources available upon request.

Interpreting such findings as unequivocal evidence for the direct assimilation of mangrove detritus may be incorrect. This occurs because the seaward enrichment in  $^{13}\text{C}$  could also result from the diminishing outwelling of respiratory  $\text{CO}_2$  that is produced by heterotrophic activity associated with decomposing mangrove detritus; i.e. all organisms, regardless whether they are autotrophs or consumers, with or without any likelihood of ingesting mangroves directly, are  $^{13}\text{C}$ -depleted in mangrove swamps (Fleming *et al.* 1990, France & Holmquist 1997, Hemminga *et al.* 1994, Lin *et al.* 1991, Marguillier *et al.* 1997, Zieman *et al.* 1984), just as they are in other areas when exposed to high rates of decomposition, microbial activity and respiration (e.g. del Giorgio & France 1996, France 1996b, France *et al.* 1997). The purpose of the present study is to use a dual isotope approach ( $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  analyses) in an attempt to determine whether mangrove detritus is actually incorporated into a population of fiddler crabs.

Ocypodid (fiddler) crabs are ideal subject organisms in which to measure the relative importance of allochthonous and autochthonous dietary contributions. Fiddler crabs are conspicuous residents of the land-water ecotone in many mangrove swamps (Macintosh 1982, Montague 1980, Warner 1969), being behaviourally terrestrial but physiologically aquatic. Fiddler crabs feed by scooping sediment into their buccal cavities where water from the branchial chamber is used to suspend organic material (Miller 1961). This material adheres to the maxillipeds bordering the mouthparts as water is withdrawn, and is then transferred to the mouth via the maxillae. Heavier inorganic particles settle to the floor of the buccal cavity and are formed into a pellet for removal. Therefore, by having small chelipeds adapted to filtering small particulate matter such as algae, bacteria and detritus from the surface of the substratum, fiddler crabs may be true generalists, facultatively capable of preferentially assimilating either benthic algae or vascular plant detritus under different situations (Crane 1975) as superficially implied by Figure 1.

#### STUDY AREA

Laguna Joyuda is a tropical lagoon situated on the west coast of Puerto Rico ( $18^\circ 07' \text{N}$  latitude,  $67^\circ 07' \text{W}$  longitude) 8 km south of the city of Mayaguez (see maps in Stoner 1986, 1988) within a Subtropical Moist Forest that receives up to 200 cm of annual rainfall (Levine 1981). Surface area of the lagoon is  $1.21 \text{ km}^2$  (122 ha) within a total drainage area of  $5.95 \text{ km}^2$ . Average lagoon depth is 1.5 m with two deeper regions of 2.5 m (Armstrong 1978). The lagoon is thought to have been formed about 500 y ago through the accretion of two sandbanks which enclosed the small embayment (Comer 1969). Today, a single small channel (3 m mean width;  $<0.5 \text{ m}$  mean depth) connects the lagoon with the ocean at Passage de la Mona located 0.5 km away. The lagoon is therefore almost completely landlocked and can be referred to as being 'choked' (*sensu* Kjerfve 1986). Tidal ranges are less than 15 cm (Stoner 1988) with volumes of

$3.5 \times 10^3 \text{ m}^3$  over 12 h, a very small amount compared with the total lagoon volume of  $1.8 \times 10^6 \text{ m}^3$  (Armstrong 1978). The lagoon is brackish with long-term salinities ranging from between 4 to 44‰ (Stoner & Lopez 1985) and averaging between 20 to 30‰ (Armstrong 1979, Pagan & Austin 1970). Water temperature ranges from 24 to 32°C annually. Due to strong winds, the lagoon is fairly homogeneous both longitudinally and vertically with regard to temperature, salinity and dissolved oxygen.

Laguna Joyuda is nearly completely fringed by red mangroves (*Rhizophora mangle*) ranging in riparian width from 5 to 40 m. Individual trees are often over 22 m in height, and thus among the tallest specimens of this species found in Puerto Rico. Annual litterfall approaches  $2000 \text{ g dw m}^{-2}$ , of which half ( $2.6 \text{ g dw m}^{-2} \text{ d}^{-1}$ ) is from mangroves (Levine 1981). These values are greater than those of many other mangrove systems, and were considered by Levine (1981) to be the highest leaf fall rates ever recorded for any forest ecosystem. All litterfall is decomposed within a year's submersion (Levine 1981) and contributes substantially to the high organic content of the sediments (Comer 1969). Seagrasses (*Thalassia testudinum*) cover only a small portion of the lagoon bottom, possibly as a result of secchi depths being consistently below 0.6 m.

Over 40 species of fishes, 12% of which are year-round residents (Stoner 1986), and up to 10 species of large crustaceans (Stoner & Zimmerman 1988), including four penaeid shrimps (Stoner 1988), inhabit the lagoon. Some of these species support a local fishery for nearby restaurants. Severe drought or heavy rainfall events can cause sudden changes in salinity and temperature and consequent periodic kills of fish and both pelagic and benthic invertebrates (Pagan & Austin 1970). Stoner & Zimmerman (1988) conducted a preliminary  $\delta^{13}\text{C}$  survey of selected invertebrates of the lagoon.

#### METHODS

##### *Sampling and analysis*

During September 1994, 80 fiddler crabs (*Uca vocator*) of a wide size range (5.5–22.6 cm carapace width) were hand-collected from underneath the intertidal forest along the southern shoreline of Laguna Joyuda. Such a high sampling effort was adopted to account for the possibility, disregarded in most studies (France 1996d) due to specimen pooling (e.g. Haines 1976), of ontogenetic diet shifts (France 1996c), as suggested by previous observations of intraspecific variability exceeding 4‰ in  $\delta^{13}\text{C}$  for fiddler crabs (Rodelli *et al.* 1984). Twenty samples of red mangrove leaf litter of two types (freshly senescent, still green; and yellow with a copious microbial biofilm) were sampled from water depths of several cm. Twenty samples of intertidal sediment composed of both small particles of organic detritus and inorganic grains were collected from the water's edge.

All samples were frozen (after allowing time for gut clearance for the crabs), dried, pulverized, acid-washed in dilute hydrochloric acid to remove inorganic

carbonates, redried, weighed and packed in tin capsules. Samples were measured for stable isotopes and C/N ratios on a Europa tracer-mass spectrometer interfaced with a Roboprep-CN analyzer. An average SD of  $\pm 0.3\text{‰}$  was obtained for replicate sub-samples after correction for weight-related bias. Samples were run in 12 sequences of five per tray, each sequence being separated by paired standards (i.e. a blank to clear the combustion tube followed by an identical standard), with duplicates never occurring in the same run sequence. If there were differences of  $>1\text{‰}$  between the values of paired duplicates, these samples were disregarded (this occurred for 12 crabs, three mangrove samples and four sediment samples).

#### *Background data for autochthonous food sources*

Aquatic autotrophs display considerable variability in their isotopic composition in relation to such environmental factors as light, temperature, season, turbulence and water chemistry (e.g. Boon & Bunn 1994; France *et al.* 1997, Fry *et al.* 1986). Consequently, it may be difficult to speculate about the use of various food sources from the basis of individual studies in which the isotopic variability of aquatic autotrophs may often be underestimated through inadequate sampling replication (France 1995a, 1996e). In such cases, a compilation of literature values can provide some indication of the range of presumed food sources which often bracket the few study-specific measurements that were obtained (e.g. Boon & Bunn 1994, Currin *et al.* 1995). Therefore, for this reason (as well as the logistic limitation that no watercraft were available), the isotopic composition of autochthonous autotrophs in Laguna Joyuda was estimated from the literature. Whenever possible, values for mangrove estuaries were used over simple global values.

## RESULTS AND DISCUSSION

#### *Background data for autochthonous food sources*

Plankton  $\delta^{13}\text{C}$  in Laguna Joyuda (Stoner & Zimmerman 1988) averaged  $-25.8 \pm 1.1\text{‰}$ . Seagrass  $\delta^{13}\text{C}$  from mangrove swamps averaged  $-14.1 \pm 2.7\text{‰}$ , similar to the single value measured by Stoner & Zimmerman (1988) in Laguna Joyuda of  $-16.1$  for *Thalassia testudinum*. Macro- and microalgal  $\delta^{13}\text{C}$  from mangrove swamps averaged  $-19.9 \pm 3.3\text{‰}$ , similar to the two values of  $-14.2$  and  $-20.2$  determined respectively for *Spirulina* sp. and *Caulerpa sertularoides* in Laguna Joyuda by Stoner & Zimmerman (1988). As expected (France 1995b), due to differences in boundary layer diffusion resistance (Hecky & Hesslein 1995; France & Holmquist 1997),  $\delta^{13}\text{C}$  values of attached algae in Laguna Joyuda are enriched compared with those of plankton. All these  $\delta^{13}\text{C}$  values for autotrophs in mangrove estuaries are  $^{13}\text{C}$ -depleted relative to similar autotrophs (France 1995b, 1996f) sampled away from the heterotrophic activity associated with mangrove detritus decomposition (cf. Marguillier *et al.* 1997). Plankton and macroalgae were presumed to have  $\delta^{15}\text{N}$  values of about  $6.3 \pm$

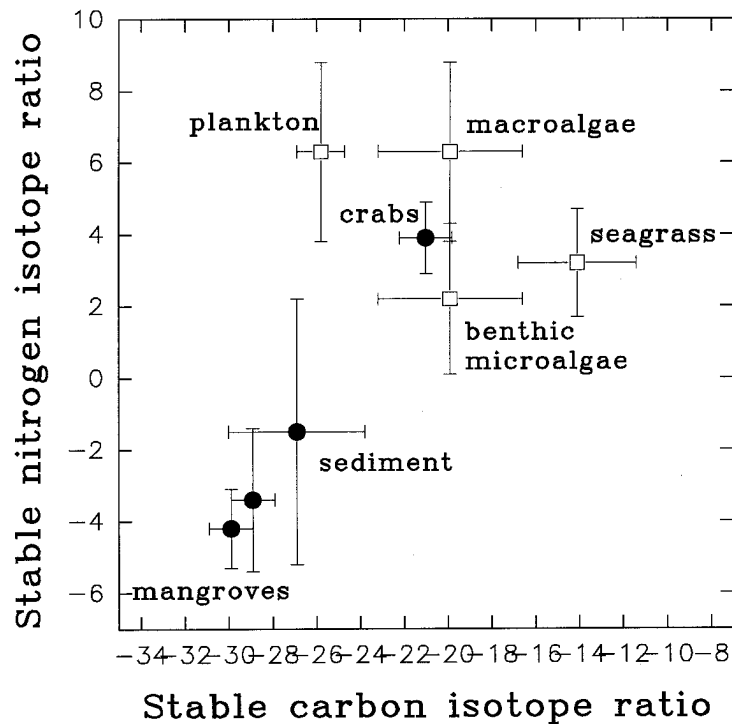


Figure 2. Stable carbon and nitrogen isotope ratios ( $\pm$  SD) of fiddler crabs, sediments and mangroves from Laguna Joyuda, and of presumed autochthonous autotrophs obtained from the literature (see text).

2.5‰ based on worldwide marine data (France 1995c, France *et al.* 1998). Average seagrass  $\delta^{15}\text{N}$  values ( $3.2 \pm 1.5$ ‰) are generally low compared to those of plankton and macroalgae as a result of nitrogen fixation (e.g. Fry *et al.* 1986). Likewise, the presence of nitrogen-fixing cyanobacteria in estuarine mudflats (Pulich & Scalan 1987) also reduces the average  $\delta^{15}\text{N}$  values of benthic microalgae ( $2.2 \pm 2.1$ ) compared to plankton and macroalgae (Currin *et al.* 1995).

#### *Mangroves and sediment*

Freshly senescent, still green, mangrove leaves had  $\delta^{13}\text{C}$  values of  $-29.9 \pm 1.0$  (SD)‰, and when covered by a thick biofilm growth after losing their green photopigments, were  $-28.9 \pm 1.0$ ‰ (Figure 2). These values are close to those recorded for various mangrove species in other studies (Marguillier *et al.* 1997, Newell *et al.* 1995, Rao *et al.* 1994, Rezende *et al.* 1990, Rodelli *et al.* 1984, Zieman *et al.* 1984), including two measurements previously determined by Stoner & Zimmerman (1988) for green ( $-29.2$ ‰) and dead ( $-27.3$ ‰) red mangrove leaves from Laguna Joyuda. Freshly senescent leaves displayed  $\delta^{15}\text{N}$  values of  $-4.2 \pm 1.1$ ‰, whereas microbially colonized leaves averaged  $-3.4 \pm 1.6$ ‰. These values are representative of those found for about a quarter of all terrestrial plants (France 1995c) as well as the few values

determined by Zieman *et al.* (1984) for decomposing red mangroves in Florida, and are only slightly lower than those determined by Marguillier *et al.* (1997) for fresh leaves from nine mangrove species in Kenya. Zieman *et al.*'s (1984)  $\delta^{15}\text{N}$  values of 6 to 8‰ for fresh mangroves are very high compared to the synthesis of worldwide data for terrestrial plants presented in France (1995c). Newell *et al.*'s (1995)  $\delta^{15}\text{N}$  values of  $5.40 \pm 0.66$  for mangroves are also higher than those found in the present study and may be a consequence of the mangroves in Laguna Joyuda deriving their inorganic nitrogen from the brackish water.

Littoral sediment in Laguna Joyuda averaged  $-26.9 \pm 3.1$ ‰  $\delta^{13}\text{C}$  and  $-1.5 \pm 3.7$ ‰  $\delta^{15}\text{N}$  (Figure 2). These values are enriched for both isotopes compared with those for the major source material of mangroves, as Rao *et al.* (1994) also found for  $\delta^{13}\text{C}$  in an African coastal lagoon. This is to be expected, as Haines (1976) similarly observed, since all sources of autochthonous organic matter are substantially enriched relative to those of terrestrial plants (Figure 2). The rarity of seagrasses in Laguna Joyuda is indicated by the differences in  $\delta^{13}\text{C}$  values for these sediments compared with those found in other lagoons characterized by luxurious seagrass growth (e.g. Fry *et al.* 1977). Littoral sediment in small water bodies such as Laguna Joyuda often assume  $\delta^{13}\text{C}$  values representative of fringing riparian trees (e.g. LaZerte 1983). Stoner & Zimmerman's (1988)  $\delta^{13}\text{C}$  values of '-22.9 to -25.0' for 'detritus particles from the sediment' (no further details provided) are slightly higher than those recorded here for the complete organic sediment complex.

#### *Fiddler crabs*

Fiddler crabs from Laguna Joyuda averaged  $-21.0 \pm 1.2$ ‰  $\delta^{13}\text{C}$  (Figure 2), a value consistent with the single previous measurement by Stoner & Zimmerman (1988) of -23.0‰ as well as for the global average for various species collected from other areas of forest influence (Figure 1). What is most interesting from these findings is the large disparity of 6‰ between  $\delta^{13}\text{C}$  for crabs and that for the sediment upon which they feed. Obviously, a considerable selective assimilation of specific particles is taking place following ingestion of the bulk sedimentary organic matter. Other studies have also observed consistent differences of about  $4.4 \pm 1.4$ ‰ between substrate  $\delta^{13}\text{C}$  values and those of fiddler crabs in saltmarshes (Haines 1976, Haines & Montague 1979). Isotopically, fiddler crabs appear to be an exception to the adage that 'you are what you eat'.

Fiddler crabs from Laguna Joyuda averaged  $3.9 \pm 1.0$ ‰  $\delta^{15}\text{N}$  (Figure 2), substantially below the global mean of 9‰ for marine zoobenthos (France 1994), thereby raising the possibility of localized influences of nitrogen fixation. Stable nitrogen isotopic data for fiddler crabs are few and limited to saltmarshes. In one such system with no evidence of nitrogen fixation, a single  $\delta^{15}\text{N}$  value for a fiddler crab was 7.2‰ (Sullivan & Moncreiff 1990), whereas in two other systems with extensive microbial activity in the sediments, fiddler crabs were

found to average  $4.6 \pm 1.2\text{‰}$  (Peterson & Howarth 1987) and  $3.6 \pm 0.5\text{‰}$  (Currin *et al.* 1995)  $\delta^{15}\text{N}$ , similar to values from Laguna Joyuda.

#### *Food source provenance*

Opinions differ as to the relative importance of either predominantly benthic algal (Shanholtzer *in* Crane 1975, Schwartz & Safer 1915) or mangrove-bacterial detrital (Crane 1975, Macintosh 1982, Montague 1980, Odum & Heald 1975, Teal 1958, Whiting & Moshiri 1974) energy sustenance for fiddler crabs. As Currin *et al.* (1995) also found for a North Carolina saltmarsh, the low  $\delta^{15}\text{N}$  values of fiddler crabs in Laguna Joyuda (Figure 2) virtually rule out any substantial dietary contribution from either plankton or benthic macroalgae given the expected (Cabana & Rasmussen 1994) 3 to 4‰ enrichment in  $^{15}\text{N}$  per trophic fractionation. Dissimilarities in  $\delta^{13}\text{C}$  between benthic animals such as fiddler crabs and those of plankton are not surprising considering the widespread virtual uncoupling that often exists between benthic and pelagic foodwebs in many aquatic systems (France 1996g). Likewise, differences in  $\delta^{13}\text{C}$  between fiddler crabs and seagrasses in Laguna Joyuda (Figure 2) are to be expected as such plants rarely contribute substantially and unilaterally toward the diets of benthic animals (France 1996f). Fiddler crabs in Laguna Joyuda, therefore, can most closely be associated with a presumed benthic microalgal food source (Figure 2).

The bottom substrate in Laguna Joyuda is covered by a thick algal mat comprised predominantly of the blue-green *Spirulina* sp. which was implicated by Stoner & Zimmerman (1988) as being the major food source for various species of polychaetes (average  $\delta^{13}\text{C}$  value of  $-21.7\text{‰}$ ), molluscs ( $-19.7\text{‰}$ ) and other crustaceans ( $-16.5\text{‰}$ ). Similarly, nitrogen-fixing blue-greens were believed to be the major food source for fiddler crabs in a North Carolina saltmarsh (Currin *et al.* 1995) as well as for various arthropods in a Mexican tidal mudflat (Pulich & Scalan 1987).

Fiddler crabs in Laguna Joyuda varied in  $\delta^{13}\text{C}$  from  $-24.3$  to  $-18.7\text{‰}$  and in  $\delta^{15}\text{N}$  from 1.4 to  $5.8\text{‰}$ . There were no relationships between the isotopic composition of individual crabs and their C/N ratios (Table 1), indicating that differences in presumed lipid contents cannot be invoked to explain the isotopic variability. This is similar to the situation found for benthic consumers in north-temperate lakes (France 1996h). There was no ontogenetic shift in  $\delta^{13}\text{C}$

Table 1. Correlation matrix between size, inferred lipid content as C/N ratios, and stable carbon and nitrogen isotopic composition for 68 fiddler crabs from Laguna Joyuda, Puerto Rico. P values are all  $>0.05$  except for  $\delta^{15}\text{N}$  vs.  $\delta^{13}\text{C}$  which was  $<0.01$ .

	C/N	$\delta^{13}\text{C}$	$\delta^{15}\text{N}$
Size	0.23	0.14	0.28
C/N		0.08	0.10
$\delta^{13}\text{C}$			0.81



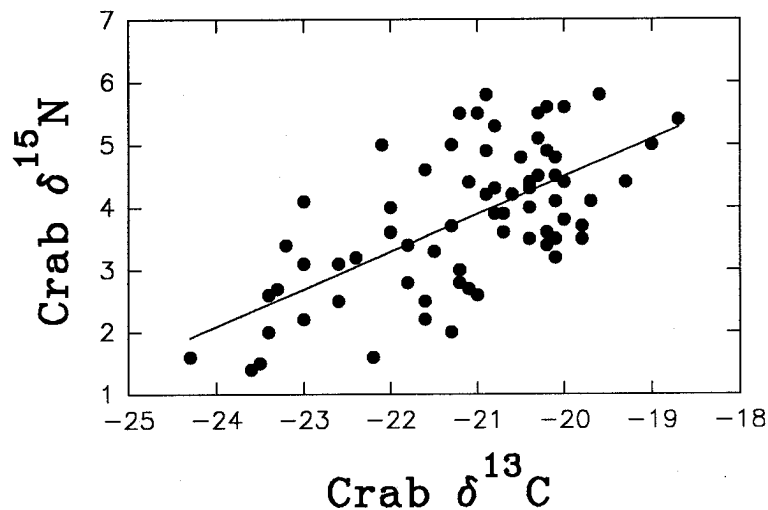


Figure 3. Relationship between carbon and nitrogen stable isotope ratios for fiddler crabs from Laguna Joyuda, Puerto Rico ( $r = 0.81$ ,  $P < 0.01$ ,  $n = 68$ ).

with fiddler crab body size (Table 1) as was the case for crayfish in north-temperate lakes (France 1996c). Measurements of  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  among individual crabs were, however, significantly correlated (Table 1; Figure 3), implying the variable assimilation of algal and mangrove food.

Fiddler crabs with  $\delta^{13}\text{C}$  values above  $-20\text{‰}$  also display higher  $\delta^{15}\text{N}$  (Figure 3) values suggesting the predominant assimilation of benthic microalgae. Individuals with lower  $\delta^{13}\text{C}$  values closer to those of mangroves also exhibit lower  $\delta^{15}\text{N}$  values as would be expected given the proportionally greater assimilation of mangrove detritus. The present results therefore support the contention that for species residing in ecotones, as for example between freshwater and marine environments (Peterson *et al.* in France 1994; Hesslein *et al.* in France 1995d), between freshwater and terrestrial environments (France 1996i) or between terrestrial and marine environments (Peters *et al.* 1978; this study),  $\delta^{15}\text{N}$  values are clearly not inviolate markers of foodweb position alone but rather reflect some combination of both trophic and food source fractionations (France 1995c). For example, crabs from a Japanese estuary (Wada *et al.* 1993) and martens from coastal Alaska (Ben-David *et al.* 1997) also demonstrated correlations between both stable isotopes, presumably reflecting variable marine-freshwater/terrestrial feeding.

There are a few other examples of consumers that indiscriminately ingest detrital matter yet display  $\delta^{13}\text{C}$  values distinct from those of the bulk mixture, thereby indicating the preferential assimilation of a particular food source from among the many available within the total organic matter pool (amphipods avoiding mangrove or macrophyte litter – Schlacher & Wooldridge 1996, Ziemann *et al.* 1984; oysters selecting for benthic diatoms despite the small

proportion of the latter in the total pool of organic matter – Riera & Richard 1996; zooplankton avoiding terrestrial detritus for phytoplankton in oligotrophic systems dominated by high allochthonous inputs – del Giorgio & France 1996; and polychaetes selectively utilizing algal components of sediments – Kikuchi & Wada 1996).

Several previous researchers, using gut content analysis, have contended that fiddler crabs rely upon a mixture of both benthic algae and mangrove detritus (Crane 1975, Teal 1962) but that ‘no definite statement, however, has been made concerning the relative use of each of these foods’ (Montague 1980). The present results (Figure 2) for *Uca vocator* from Laguna Joyuda, Puerto Rico, indicate a proportionally greater contribution of benthic algae to diets than mangrove detritus. This is counter to Odum & Heald’s (1975) belief that animals in mangrove estuaries ‘derive their nourishment primarily from a diet of vascular plant detritus and small quantities of fresh algae’. Other isotope studies from seagrass meadows and saltmarshes also indicate that, given the choice, most consumers will rely more substantially upon algae than vascular plants (e.g. Currin *et al.* 1995, Fry 1984, Kitting *et al.* 1984, Schlacher & Wooldridge 1996, Sullivan & Moncrieff 1990). The present results support other isotopic work which has suggested that aquatic consumers in or near tropical forests assimilate a proportionally greater contribution of benthic algae than they do forest detritus when the former display a high productivity (Arujo-Lima *et al.* 1986, Forsberg *et al.* 1993, Hamilton *et al.* 1992, Newell *et al.* 1995, Stoner & Zimmerman 1988).

#### ACKNOWLEDGEMENTS

This work was supported by a Canadian NSERC Strategic Grant to Robert Peters and Robert France to study the effects of riparian-littoral ecotonal coupling. Travel to and field expenses in Puerto Rico were provided by Circo Caribe through Debberino Soles. Grace Chung, Shapna Mazumder and Grace Cabana are thanked for analyzing the samples, as is Jeff Holmquist for providing access to library facilities at the University of Mayaguez.

#### LITERATURE CITED

- ARMSTRONG, D. P. 1978. *A study of the plankton in Laguna Joyuda, a tropical lagoon, on the west coast of Puerto Rico*. M.Sc. Thesis. University of Puerto Rico, Mayaguez. 108 pp.
- ARUJO-LIMA, C., FORSBERG, B. R., VICTORIA, R. & MARTINELLI, L. 1986. Energy sources for detritivorous fishes in the Amazon. *Science* 234:1256–1258.
- AUSTIN, H. M. & AUSTIN, S. 1971. The feeding habits of some juvenile marine fishes from the mangroves in western Puerto Rico. *Caribbean Journal of Science* 11:171–178.
- BEN-DAVID, M., FLYNN, R. W. & SCHELL, D. M. 1997. Annual and seasonal changes in diets of martens: evidence from stable isotope analysis. *Oecologia* 111: 280–291.
- BOON, P. I. & BUNN, S. E. 1994. Variations in the stable isotope composition of aquatic plants and their implications for food web analysis. *Aquatic Botany* 48:99–108.
- CABANA, G. & RASMUSSEN, J. B. 1994. Modelling food chain structure and contaminant bioaccumulation using stable N-isotopes. *Nature* 372:255–257.

- CINTRON, G. A., LUGO, A. E., POOL, D. & MORRIS, G. 1978. Mangroves of arid environments in Puerto Rico and adjacent islands. *Biotropica* 10:110–121.
- COMER, J. B. 1969. *Sedimentology and physical-chemical environment of a tropical lagoon, western Puerto Rico*. M.Sc. Thesis. University of Wisconsin. 98 pp.
- CRANE, J. 1975. *Fiddler crabs of the world (Ocypodidae; Genus Uca)*. Princeton University Press, New York. 324 pp.
- CURRIN, C. A., NEWELL, S. Y. & PAERL, H. W. 1995. The role of standing dead *Spartina alterniflora* and benthic microalgae in salt marsh food webs: considerations based on multiple stable isotope analysis. *Marine Ecology Progress Series* 121:99–116.
- DARNELL, R. M. 1961. Trophic spectrum of an estuarine community based on studies fo Lake Pontchartrain, Louisiana. *Ecology* 42:553–568.
- DEL GIORGIO, P. & FRANCE, R. 1996. Ecosystem-specific patterns in zooplankton and POM or microplankton  $\delta^{13}\text{C}$ . *Limnology and Oceanography* 41:359–365.
- FLEMING, M., LIN, G. & STERNBERG, L. 1990. Influence of mangrove detritus in an estuarine ecosystem. *Bulletin of Marine Science* 47:663–669.
- FLORES-VERDUGO, F. J., DAY, J. W. & BRISENO-DUENAS, R. 1987. Structure, litter fall, decomposition, and detritus dynamics of mangroves in a Mexican coastal lagoon with an ephemeral inlet. *Marine Ecology Progress Series* 35:83–90.
- FORSBERG, B. R., ARAUJO-LIMA, C., MARTINELLI, L. A., VICTORIA, R. L. & BONASSI, J. A. 1993. Autotrophic carbon sources for fish of the central Amazon. *Ecology* 74:643–652.
- FRANCE, R. L. 1994. Nitrogen isotopic composition of marine and freshwater invertebrates. *Marine Ecology Progress Series* 115:205–207.
- FRANCE, R. L. 1995a. Critical examination of stable isotope analysis as a means for tracing carbon pathways in stream ecosystems. *Canadian Journal of Fisheries and Aquatic Sciences* 52:651–656.
- FRANCE, R. L. 1995b. Carbon-13 enrichment in benthic compared to planktonic algae: foodweb implications. *Marine Ecology Progress Series* 124:307–312.
- FRANCE, R. L. 1995c. Source variability in  $\delta^{15}\text{N}$  of autotrophs as a potential aid measuring allochthonoy to freshwaters. *Ecography* 18:318–320.
- FRANCE, R. L. 1995d. Stable nitrogen isotopes in fish: literature synthesis on the influence of ecotonal coupling. *Estuarine and Coastal Shelf Science* 41:737–742.
- FRANCE, R. L. 1996a. Scope for use of stable carbon isotopes in discerning the incorporation of forest detritus into aquatic foodwebs. *Hydrobiologia* 235:219–222.
- FRANCE, R. L. 1996b. Carbon isotope ratios in logged and unlogged boreal forests: examination of the potential for determining wildlife habitat use. *Environmental Management* 20:249–255.
- FRANCE, R. L. 1996c. Ontogenetic shift in stable carbon isotope ratios in crayfish as a measure of ecotonal coupling. *Oecologia* 107:239–242.
- FRANCE, R. L. 1996d. Problems, practical and psychological, using stable carbon isotope ratios for discerning utilization of allochthonous detritus by stream fauna: a tale of two studies. *Land Water Management Proceedings*, Calgary, Alberta, in press.
- FRANCE, R. L. 1996e. Carbon-13 conundrums: limitations and cautions in the use of stable isotope analysis in stream ecotonal research. *Canadian Journal of Fisheries and Aquatic Science* 53:1916–1919.
- FRANCE, R. L. 1996f. Stable isotopic survey of the role of macrophytes in the carbon flow of aquatic foodwebs. *Vegetatio* 124:67–72.
- FRANCE, R. L. 1996g. Benthic-pelagic uncoupling of carbon flow. *Trends in Ecology and Evolution* 11:471.
- FRANCE, R. L. 1996h. Absence or masking of metabolic fractionations of  $^{13}\text{C}$  in oligotrophic lakes. *Freshwater Biology* 36:1–6.
- FRANCE, R. L. 1996i. Stable carbon and nitrogen isotopic evidence for ecotonal coupling between boreal forests and fishes. *Ecology of Freshwater Fishes* 6:78–83.
- FRANCE, R. L. & HOLMQUIST, J. G. 1997.  $\delta^{13}\text{C}$  variability of macroalgae: effects of water motion via baffling by seagrasses and mangroves. *Marine Ecology Progress Series* 149:305–308.
- FRANCE, R., HOLMQUIST, J., CHANDLER, M. & CATTANEO, A. 1998.  $\delta^{15}\text{N}$  evidence for nitrogen fixation associated with macroalgae from a seagrass-mangrove-coral reef system. *Marine Ecology Progress Series*, in press.
- FRANCE, R., DEL GIORGIO, P. & WESTCOTT, K. 1997. Productivity and heterotrophy influences on zooplankton  $\delta^{13}\text{C}$  in north temperate lakes. *Aquatic Microbial Ecology* 12:85–93.
- FRY, B. 1984.  $^{13}\text{C}/^{12}\text{C}$  ratios and the trophic importance of algae in Florida *Syringodium filiforme* seagrass meadows. *Marine Biology* 79:11–19.
- FRY, B., MACKO, S. A. & ZIEMAN, J. C. 1986. Review of stable isotopic investigations of food webs in seagrass meadows. *Florida Marine Research Publication* 42:189–209.
- FRY, B., SCALAN, S. & PARKER, P. L. 1977. Stable carbon isotope evidence for two sources of organic matter in coastal sediments: seagrasses and plankton. *Geochimica Cosmochimica Acta* 41:1875–1877.
- GLEASON, J. A. & COOK, M. T. 1927. Plant ecology of Puerto Rico: scientific survey of Puerto Rico and the Virgin Islands. *Proceedings of the New York Academy of Science* 7:1–96.

- GOLLEY, F., ODUM, H. T. & WILSON, R. F. 1962. The structure and metabolism of a Puerto Rico red mangrove forest in May. *Ecology* 43:9–19.
- HAINES, E. B. 1976. Relation between the stable carbon isotope composition of fiddler crabs, plants, and soils in a salt marsh. *Limnology and Oceanography* 21:880–883.
- HAINES, E. B. & MONTAGUE, C. L. 1979. Food sources of estuarine invertebrates analyzed using  $^{13}\text{C}/^{12}\text{C}$  ratios. *Ecology* 60:48–56.
- HAMILTON, S. K., LEWIS, W. M. & SIPPEL, S. J. 1992. Energy sources for aquatic animals in the Orinoco River floodplain: evidence from stable isotopes. *Oecologia* 89:324–330.
- HECKY, R. E. & HESSLEIN, R. H. 1995. Contributions of benthic algae to lake food webs as revealed by stable isotope analysis. *Journal of the North American Benthological Society* 14:631–653.
- HEMMINGA, M. A., SIM, F. J., KAZUNGA, J., GANSSSEN, G. M., NIEUWENSHUIZE, J. & KRUYT, N. M. 1994. Carbon outwelling from a mangrove forest with adjacent seagrass beds and coral reefs (Gazi Bay, Kenya). *Marine Ecology Progress Series* 106:291–301.
- KIKUCHI, E. & WADA, E. 1996. Carbon and nitrogen stable isotope ratios of deposit-feeding polychaetes in the Nanakita River Estuary, Japan. *Hydrobiologia* 321:69–75.
- KITTING, C. L., FRY, B. & MORGAN, M. D. 1984. Detection of inconspicuous epiphytic algae supporting food webs in seagrass meadows. *Oecologia* 62:145–149.
- KJERFVE, B. 1986. Comparative oceanography of coastal lagoons. Pp. 63–81 in Wolfe, D. A. (ed.) *Estuarine variability*. Academic Press, New York.
- LAZERTE, B. D. 1983. Stable carbon isotope ratios: implications for the source of sediment carbon and for phytoplankton carbon assimilation in Lake Memphremagog, Quebec. *Canadian Journal of Fisheries And Aquatic Sciences* 40:1658–1666.
- LEVINE, E. A. 1981. *Nutrient cycling by the red mangrove. Rhizophora mangle L., in Joyuda Lagoon on the west coast of Puerto Rico*. M.Sc. Thesis. Mayaguez, Puerto Rico. 87pp.
- LIN, G., BANKS, T. & STERNBERG, L. 1991. Variation in  $\delta^{13}\text{C}$  values for the seagrass *Thalassia testudinum* and its relations to mangrove carbon. *Aquatic Botany* 40:333–341.
- LUGO, A. E. & CINTRON, G. 1975. The mangrove forests of Puerto Rico and their management. pp. 825–846 in Walsh, G. E. & Snedaker, S. C. (eds). *Proceedings of the International Symposium Biology Management of Mangroves. Vol. II*. Gainesville, Florida.
- LUGO, A. E. & SNEDAKER, S. C. 1974. The ecology of mangroves. *Annals Review Ecology and Systematics* 5:39–64.
- MACINTOSH, D. J. 1982. Ecological comparisons of mangrove swamp and salt marsh fiddler crabs. pp. 243–257 in Gopal, B. (ed.). *Wetlands ecology and management*. National Institute for Ecology, Washington.
- MARGUILLIER, S., VAN DER VELDE, G., DEHAIRS, F., HEMMINGA, M. A. RAJAGOPAL, S. 1997. Trophic relationships in an interlinked mangrove-seagrass ecosystem as traced by  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$ . *Marine Ecology Progress Series* 151:115–121.
- MARPLES, T. G. 1966. A radionuclide tracer study of arthropod food chains in a *Spartina* salt marsh ecosystem. *Ecology* 47:270–277.
- MILLER, D. C. 1961. The feeding mechanism of fiddler crabs with ecological considerations of feeding adaptations. *Zoologica New York* 46:86–100.
- MONTAGUE, C. L. 1980. A natural history of temperate fiddler crabs (genus *Uca*) with reference to their impact on the salt marsh. *Contributions Marine Science* 23:25–55.
- NEWELL, R. I. E., MARSHALL, N., SASERUMAR, A. & CHONG, V. C. (1995) Relative importance of benthic microalgae, phytoplankton, and mangroves as sources of nutrition for penaeid prawns and other coastal invertebrates from Malaysia. *Marine Biology* 123:595–606.
- ODUM, W. E. & HEALD, E. J. 1975. The detritus-based food web of an estuarine mangrove community. Pp. 265–288 in Cronin, J. (ed.). *Estuarine research*, Vol. 1. Academic Press, New York.
- PAGAN, F. A. & AUSTIN, H. M. 1970. Report on a fish kill at Laguna Joyuda, western Puerto Rico, in the summer, 1967. *Caribbean Journal of Science* 10:203–208.
- PETERS, K. E., SWEENEY, R. E. & KAPLAN, I. R. 1978. Correlation of carbon and nitrogen stable isotope ratios in sedimentary organic matter. *Limnology and Oceanography* 23:598–604.
- PETERSON, B. J. & HOWARTH, R. W. 1987. Sulfur, carbon, and nitrogen isotopes used to trace organic matter flow in the salt-marsh estuaries of Sapelo Island, Georgia. *Limnology and Oceanography* 32:1195–1213.
- POOL, D. J., SNEDAKER, S. C. & LUGO, A. E. 1977. Structure of mangrove forests in Florida, Puerto Rico, Mexico, and Costa Rica. *Biotropica* 9:195–212.
- PULICH, W. M. & SCALAN, R. S. 1987. Organic carbon and nitrogen flow from marine cyanobacteria to semiaquatic insect food webs. *Contributions Marine Science* 50:27–37.
- QASIM, S. Z. & SANKARANARAYANA, V. N. 1972. Organic detritus of a tropical estuary. *Marine Biology* 15:193–199.
- RAO, R. G., WOITCHIK, A. F., GOEYENS, L., VAN RIET, A., KAZUNGA, J. & DEHAIRS, F. 1994.

- Carbon, nitrogen contents and stable carbon isotope abundance in mangrove leaves from an east African coastal lagoon (Kenya). *Aquatic Botany* 47:175–183.
- REZENDE, C. & LACERDA, L. D., OVALLE, A., SILVA, C. & MARTINELLI, L. A. 1990. Nature of POC transport in a mangrove ecosystem: a carbon stable isotopic study. *Estuarine and Coastal Shelf Science* 30:641–645.
- RIERA, P. & RICHARD, P. 1996. Isotopic determination of food sources of *Crassostrea gigas* along a trophic gradient in the estuarine bay of Marennes-Oleron. *Estuarine and Coastal Shelf Science* 42:347–360.
- RODELLI, M. R., GEARING, J. N., GEARING, P. N., MARSHALL, N. & SASSKUMAR, A. 1984. Stable isotope ratio as a tracer of mangrove carbon in Malaysian ecosystems. *Oecologia* 61:326–333.
- SCHLACHER, T. A. & WOOLRIDGE, T. H. 1996. Origin and trophic importance of detritus – evidence from stable isotopes in the benthos of a small, temperate estuary. *Oecologia* 106:382–388.
- SCHWARTZ, B. & SAFER, J. R. 1915. The natural history and behavior of the fiddler crab. *Cold Spring Harbour Monographs* 8:1–24.
- STONER, A. W. 1986. Community structure of the demersal fish species of Laguna Joyuda, Puerto Rico. *Estuaries* 9:142–152.
- STONER, A. W. 1988. A nursery ground for four tropical *Penaeus* species: Laguna Joyuda, Puerto Rico. *Marine Ecology Progress Series* 42:133–141.
- STONER, A. W. & LOPEZ, J. M. 1985. Cycling and transport processes in a tropical estuarine lagoon. Pp. 1–86 in *Proceedings on Joyuda Lagoon*. Report Energy Environment Research, University Puerto Rico, Mayaguez, 189 pp.
- STONER, A. W. & ZIMMERMAN, R. J. 1988. Food pathways associated with penaeid shrimps in a mangrove-fringed estuary. *Fisheries Bulletin* 86:543–551.
- SULLIVAN, M. J. & MONTCREIFF, C. A. 1990. Edaphic algae are an important component of salt marsh food webs: evidence from multiple stable isotope analyses. *Marine Ecology Progress Series* 62:149–159.
- TEAL, J. M. 1958. Distribution of fiddler crabs in Georgia salt marshes. *Ecology* 39:185–193.
- TEAL, J. M. 1962. Energy flow in the salt marsh ecosystem of Georgia. *Ecology* 43:614–624.
- WADA, E., KABAYA, Y. & KURIHARA, Y. 1993. Stable isotopic structure of aquatic ecosystems. *Journal of Bioscience* 18:483–499.
- WADSWORTH, F. H. 1959. Growth and regeneration of white mangroves in Puerto Rico. *Caribbean Forestry* 20:59–71.
- WALKER, R. A. 1973. Wetlands preservation and management on Chesapeake Bay: the role of science in natural resource policy. *Journal of Coastal Zone Management* 1:75–101.
- WARNER, G. F. 1969. The occurrence and distribution of crabs in a Jamaican mangrove swamp. *Journal of Animal Ecology* 38:379–389.
- WELLS, F. E. 1984. Comparative distribution of macromolluscs and macrocrustaceans in a north-western Australian mangrove system. *Australian Journal of Marine Freshwater Research* 35:591–596.
- WHITING, N. H. & MOSHIRI, G. A. 1974. Certain organism-substrate relationships affecting the distribution of *Uca pugnax* (Crustacea: Decapoda). *Hydrobiologia* 44:481–493.
- ZIEMAN, J. C., S. A. MACKO & MILLS, A. L. 1984. Role of seagrasses and mangroves in estuarine food webs: temporal and spatial changes in stable isotope composition and amino acid content during decomposition. *Bulletin of Marine Science* 35:380–392.