FISH AND SHRIMP MIGRATIONS IN THE NORTHERN GULF OF MEXICO ANALYZED USING STABLE C, N, AND S ISOTOPE RATIOS[1]

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ABSTRACT

Natural stable isotope tags were used in the northern Gulf of Mexico to interpret migrations of five commercial fish and shrimp species: *Leiostomus xanthurus*, *Micropogonias undulatus*, *Penaeus aztecus*, *P. duorarum*, and *P. setiferus*. Along the south Texas and Florida coasts, isotopic analyses showed that seagrass meadows and possibly other shallow estuarine habitats are important feeding grounds for shrimp that are later caught in offshore fisheries. Thus stable carbon, nitrogen, and sulfur values of juvenile shrimp in grassflats coincided with isotopic values of small shrimp collected offshore. These values were −11 to −14‰ for $\delta^{13}C$, and +6 to +8‰ for both $\delta^{15}N$ and $\delta^{34}S$. In contrast to these south Texas and Florida results, $\delta^{13}C$, $\delta^{15}N$, and $\delta^{34}S$ values showed a second pattern off the Louisiana and north Texas coasts. This difference was most pronounced in the $\delta^{13}C$ values which ranged from −17 to −24‰ instead of −11 to −14‰. Because isotopic values were similar in *Spartina* marshes and open bays along this northern coast, no conclusions could be reached about the relative importance of *Spartina* marshes as inshore feeding grounds.

During feeding and growth offshore, eventual convergence about offshore isotopic values should result for the migratory species studied. However, striking differences in convergence patterns were evident for the five species, ranging from close convergence at small, subadult sizes (*P. aztecus* and *P. duorarum*) to nonconvergence among adults (*L. xanthurus*). These differences point to contrasts in the basic life history patterns of migration (especially the juvenile vs. adult size at which offshore migration occurs), and, for one species, showed that isotopic methods can trace yearly variations in these patterns.

Migrating animals constitute one form of export from estuaries to offshore waters. Most of the commercial species in the offshore Gulf of Mexico are estuarine dependent, migrating offshore after a juvenile growth phase in coastal bays (Lindall and Saloman 1977). Through their sheer numbers, estuarine dependent animals constitute an important part of benthic communities in the Gulf of Mexico (Hildebrand 1954; Moore et al. 1970). They also constitute an energy subsidy to the many offshore animals that consume them.

In this paper, I examine stable C, N, and S isotope distributions in five estuarine dependent species from the northern Gulf of Mexico. These species are brown shrimp, *Penaeus aztecus*; pink shrimp, *P. duorarum*; white shrimp, *P. setiferus*; spot, *Leiostomus xanthurus*; and Atlantic croaker, *Micropogonias undulatus*. Previous work on fish (Fry and Parker 1979) and shrimp (Fry 1981a) has shown that offshore animals have very constant isotopic values within an approximate 0.6-2.0‰ range. Against this rather uniform isotopic background, recent migrants from estuaries are often identifiable via their deviant isotopic values. These deviant values arise from consumption of foods that are isotopically more diverse in estuaries than offshore (e.g., McConnaughey and McRoy 1979a, b).

For animals migrating from estuaries, offshore feeding should lead to eventual convergence upon offshore isotopic values. Laboratory experiments and model calculations show that this convergence should be essentially complete to within ±1‰ following a fourfold increase in weight for rapidly growing animals (Fry and Arnold 1982). While this rapid convergence is primarily due to simple growth, metabolic turnover should also lead to eventual convergence upon offshore values for adult migrants that are not actively gaining weight. These considerations have two consequences for an offshore sampling program directed at studying patterns of recruitment from estuaries: 1) Animals recruiting as adults will retain isotopic traces of their estuarine past for relatively long times; and 2) recruiting juveniles, in contrast, rapidly lose their estuarine isotopic values and hence must be sampled soon after offshore migration.

This study of estuarine dependent species had two objectives. The first was to use offshore catches to infer important estuarine feeding grounds utilized prior to offshore migration. Collections were made during several seasons and years in three different

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regions of the northern Gulf of Mexico to find consistent isotopic patterns among animals recruiting to offshore areas. These patterns ultimately distinguish estuarine habitats in which animals feed prior to offshore migration. Secondly, isotopic data were used to study the importance of estuarine foods to the five species during their adult lives. By examining the rapidity of isotopic convergence upon offshore values it was possible to distinguish species that utilize estuarine foods well into adulthood.

Methods

Animals were collected with a 10.2 m otter trawl during October 1978, 1979, and 1980, along 10 offshore transects in the northern Gulf of Mexico (Fig. 1A). Additional May collections were made off the Texas coast along transects 1 and 2 (Fig. 1A) in 1980. Trawling stations were located at various depths along these transects. Station depths ranged from 5 m near the beach to 150 m on the continental shelf; the majority of trawl tows were taken at depths of 5-50 m. A bar seine was used to collect juvenile shrimp from marshes and shallow bays of the Barataria Bay region of Louisiana (Fig. 2).

In all offshore collections, animals were frozen and white muscle tissue dissected from abdomens (shrimp) or areas above the lateral line (fish). For some Barataria Bay collections, whole shrimp were used as samples rather than muscle tissue. Whole shrimp and stomach content samples were acid-treated to remove carbonates prior to isotopic analysis.

For all penaeid shrimp, total length (tip of rostrum

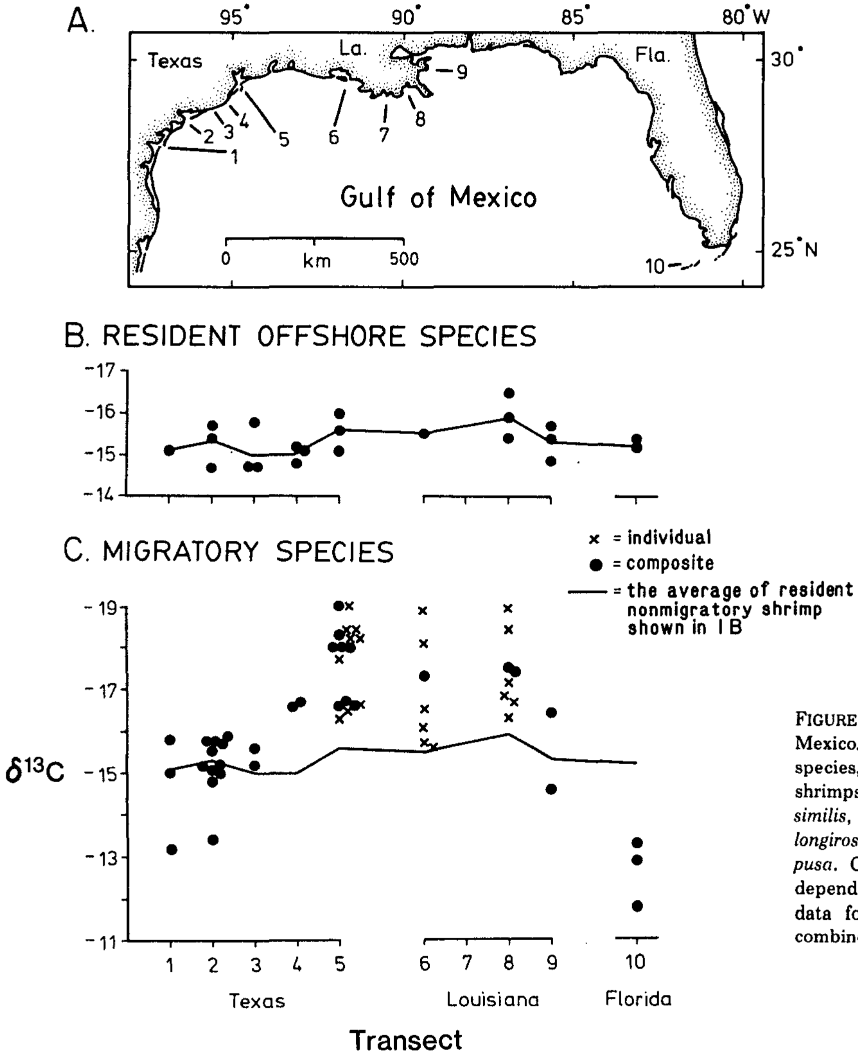

FIGURE 1.—A, Collection areas in the Gulf of Mexico. B, $\delta^{13}C$ values of offshore resident species, October 1978; species included the shrimps *Sicyonia dorsalis*, *Trachypenaeus similis*, *Solenocera vioscai*, and *Parapenaeus longirostris*, and the stomatopod *Squilla empusa*. C, $\delta^{13}C$ values of migratory, estuarine-dependent penaeid shrimp, October 1978; data for brown, pink, and white shrimp combined.

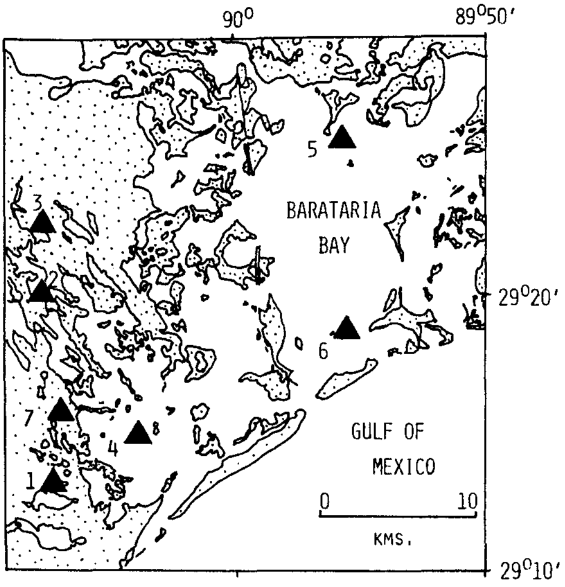

FIGURE 2.—Sampling locations in the Barataria Bay complex of Louisiana. This area is located landward of transect 8 (Fig. 1A). 1 = Airplane Lake; 2 = Bay Rambo; 3 = Round Lake; 4 = Caminada Bay; 5 = St. Mary's Point; 6 = Independence Island; 7 = Bayou Garci.

to tip of the telson) and weights (when possible) were taken. Shrimp were often pooled by size categories in which individuals typically did not differ by more than 10 mm in length. Weights were obtained in three ways: 1) Directly on a laboratory balance to the nearest 0.1 g, 2) when seas were calm, estimated to within ±15% with a pan balance, or 3) estimated from length using the length-weight regressions of Fontaine and Neal (1971) for combined sexes.

Fish were measured for total length to the nearest millimeter, and, if not weighed directly in the laboratory, their weights were estimated by using Dawson's (1965) length-weight regressions.

In the laboratory, tissue samples were rinsed in freshwater, dried, and powdered. Gas samples for mass spectrometry were prepared from powdered tissues as follows: 1) For carbon, 3-8 mg subsamples were combusted in sealed Pyrex[3] tubes at 590°C using CuO as an oxidant (Sofer 1980); 2) for nitrogen, 10-20 mg subsamples were mixed with a CuO/Cu mixture in quartz tubes and combusted at 900°C for ½ h (Macko 1981); 3) for sulfur, 0.5-1 g subsamples were combusted in a Parr bomb, the resulting sulfate precipitated with barium, and SO_2 subsequently generated by thermally decomposing $BaSO_4$ in a sealed quartz tube (Fry et al. 1982). Following combustion, all sealed tubes were broken under vacuum, and gases purified and transferred using liquid N_2 and dry ice/acetone mixtures. Gases were analyzed for their stable isotope contents using a dual inlet, isotope ratio mass spectrometer (VG-Micromass, Model 620E). Results are reported in δ notation where $\delta X = [R_{sample}/R_{standard}) - 1] \times 10^3$, $R = {}^{13}C/{}^{12}C$, ${}^{15}N/{}^{14}N$, or ${}^{34}S/{}^{32}S$, and X = ${}^{13}C$, ${}^{15}N$, or ${}^{34}S$. Values reported in this paper are given relative to PDB carbonate, air, and Canyon Diable troilite standards for C, N, and S, respectively. Mass spectrometric corrections were applied for oxygen contributions in both carbon and sulfur measurements (Craig 1957; Nakai and Jensen 1964). Replicate determinations showed that measurements were generally precise to within ±0.3‰ for $\delta^{13}C$, ±0.2‰ for $\delta^{15}N$ and ±0.5‰ for $\delta^{34}S$.

[3]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

RESULTS

Regional Patterns

Throughout the northern Gulf of Mexico, benthic shrimp and stomatopod species that reside offshore have $\delta^{13}C$ values that usually range between −14.5 and −17.5‰ (Fry 1981a, b). Figure 1B shows this broad geographic similarity for one set of collections obtained in October 1978; isotopic values among 21 composite samples showed only a 1.8‰ range, from −14.7 to −16.5‰. In contrast to this relatively uniform distribution of $\delta^{13}C$ values, isotopic values for migratory, estuarine dependent shrimp showed regional patterns (Fig. 1C). The $\delta^{13}C$ values for migratory shrimp averaged less negative than offshore values along the south Texas and south Florida coasts; along the Louisiana and north Texas coasts, in contrast, isotopic values were more negative than the offshore values (Fig. 1C). The transition between the south vs. north Texas regions occurred at transect 4, approximately opposite Freeport, Tex. (Fig. 1C).

Further sampling showed that these less vs. more negative regional divisions were consistently present over the 3 yr of study (Figs. 3-5). The regional patterns held true not only for shrimp but also for two estuarine dependent fish species, spot and croaker (Figs. 3F, 5E, 5F).

While striking regional patterns among estuarine dependent animals were discernable in the carbon isotope results, this was not true of the nitrogen and sulfur results. Figure 6 shows that for both N and S, isotopic values of estuarine dependent shrimp

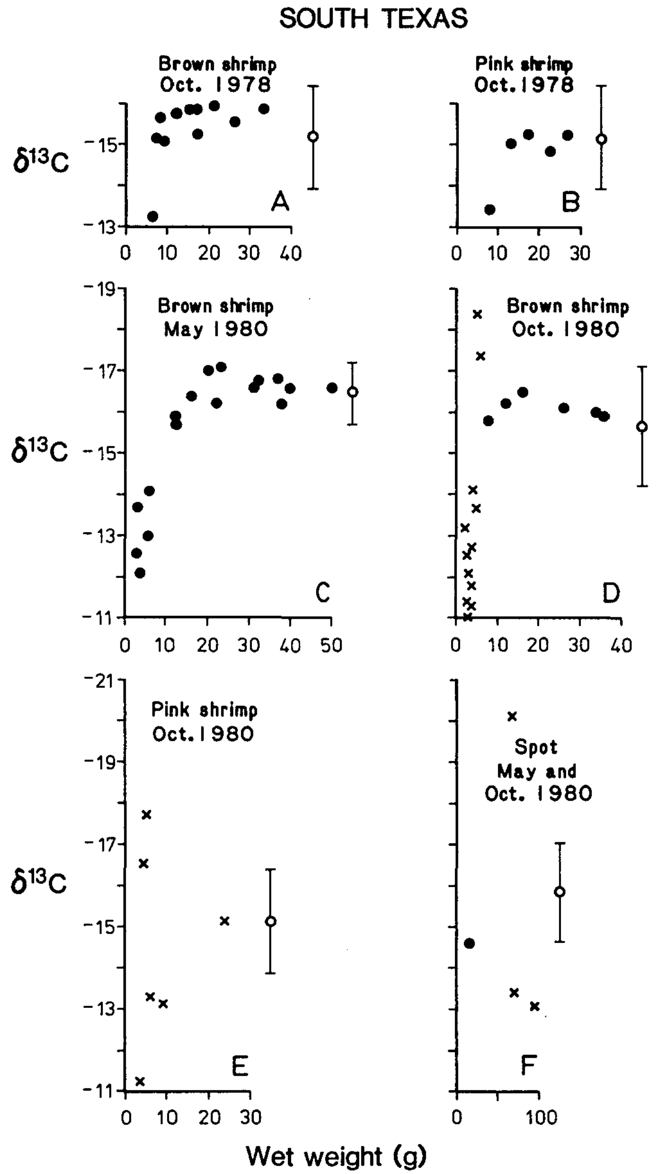

FIGURE 3.—$\delta^{13}C$ variation with size for collections made along the south Texas coast (transects 1-4, Fig. 1A). Symbol to the right of each figure indicates 1) mean (○) of 5-15 composite samples of benthic shrimps and stomatopods that reside offshore, and 2) confidence limits (vertical bar) beyond which single samples differ from the offshore mean at the 95% confidence level (Sokal and Rohlf 1981). x = individual; ● = composite sample.

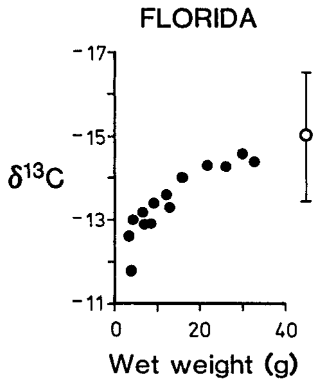

FIGURE 4.—$\delta^{13}C$ variation of pink shrimp with size for the October 1978, 1979, and 1980 collections in the Tortugas fishing area, Florida (transect 10, Fig. 1A). Symbols as in Figure 3.

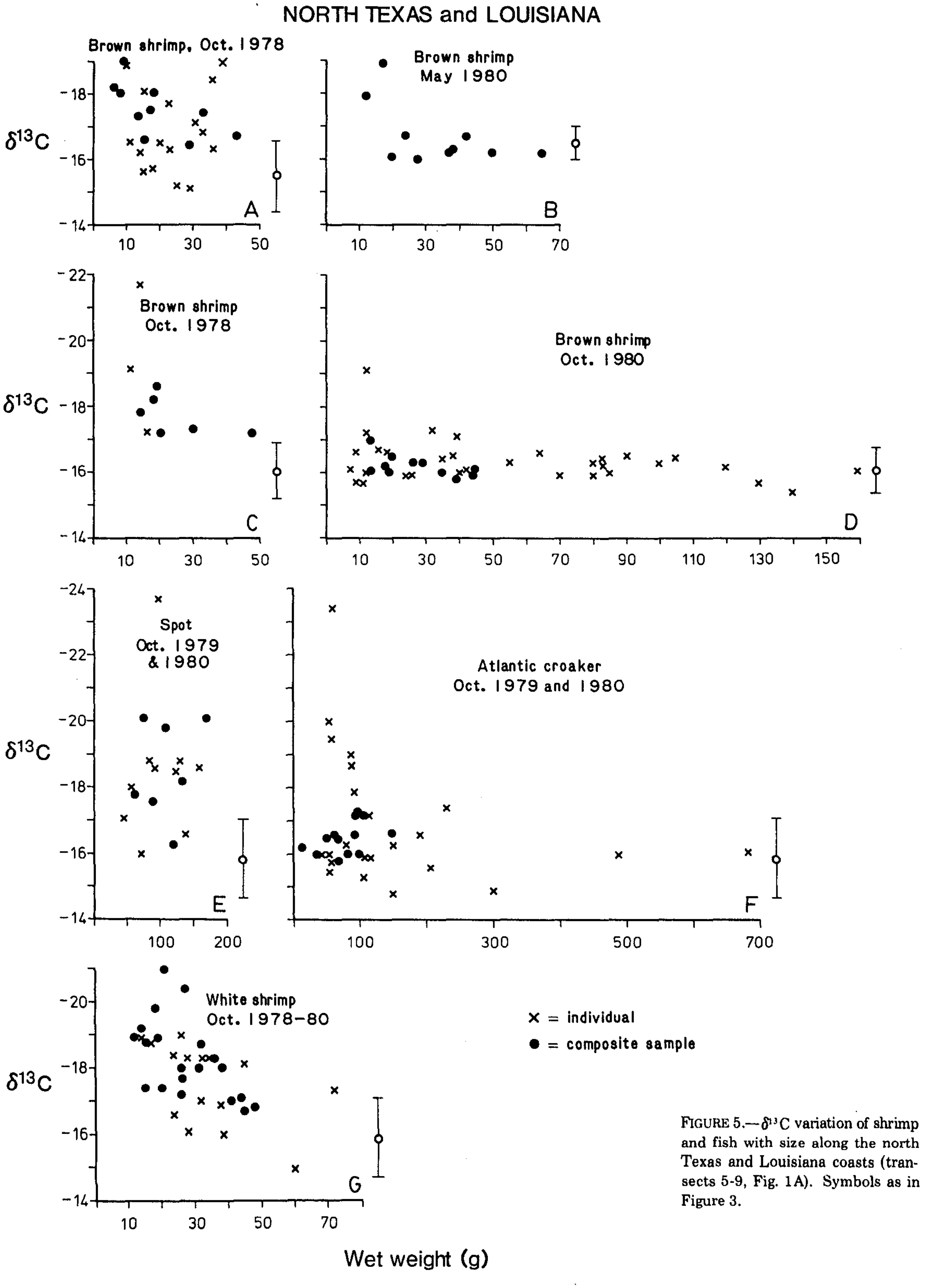

FIGURE 5.—$\delta^{13}C$ variation of shrimp and fish with size along the north Texas and Louisiana coasts (transects 5-9, Fig. 1A). Symbols as in Figure 3.

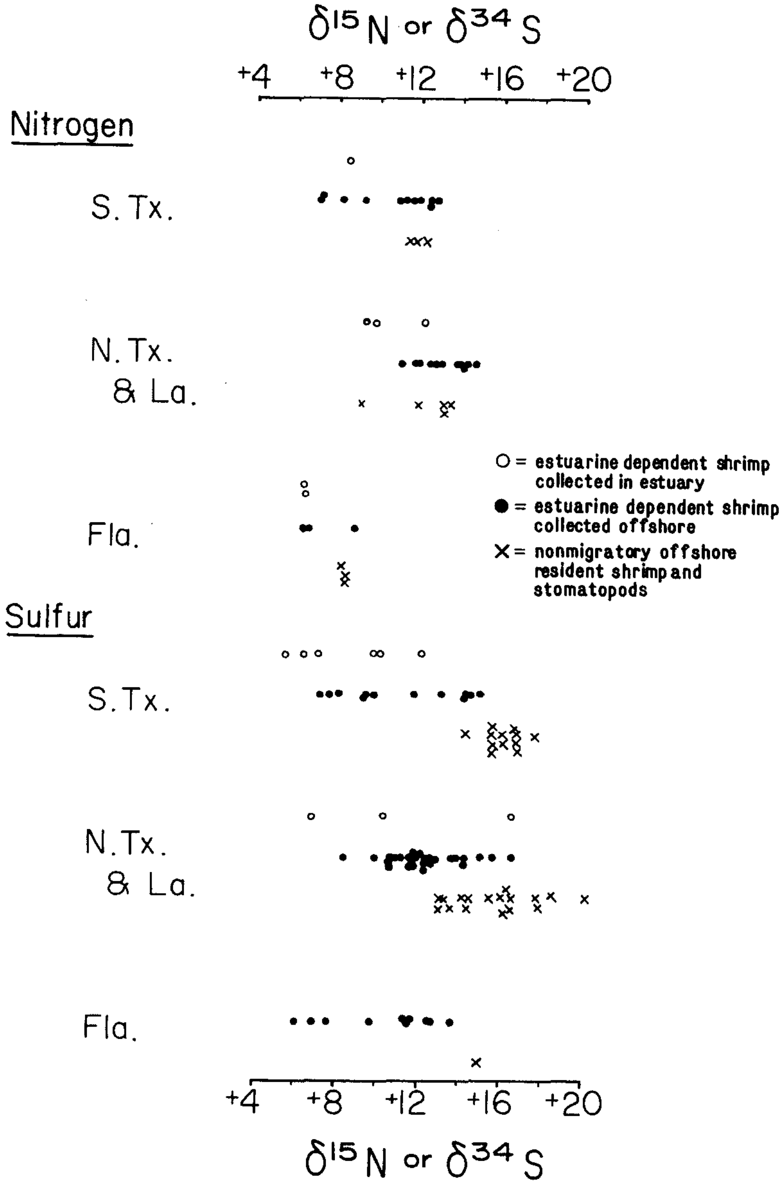

FIGURE 6.—Regional δ^{15}N and δ^{34}S values of benthic shrimp and stomatopods. Most samples are composites. Estuarine collections were made in seagrass meadows in south Texas and Florida, but in both open bays and *Spartina* marshes along the Louisiana and north Texas coasts.

averaged less than values of offshore residents in all three regions of the Gulf. The only striking regional difference in these two smaller data sets was not among the estuarine dependent animals but in the δ^{15}N data for offshore resident species. Residents collected in offshore Florida waters averaged +8.3‰, significantly less ($P < 0.05$) than the +11.8 and +12.2‰ means of the western Gulf. While mean offshore values may thus vary by region, the regional uniformities in δ^{15}N and δ^{34}S values of estuarine dependent species did not suggest striking regional differences in the isotopic compositions of estuarine foods.

Estuarine Sampling

To clarify the regional patterns observed in the δ^{13}C data and also to establish δ^{15}N and δ^{34}S values of some estuarine animals prior to their offshore migrations, a limited number of estuarine samples was analyzed. The causes of the more negative $\delta^{13}C$ values observed among estuarine dependent animals off the Louisiana coast were investigated in estuarine collections from the Barataria Bay region (Table 1). With the exception of two brown shrimp collections from Caminada Bay ($\delta^{13}C = -13.9$ to -15.1‰), shrimp values fell between -16.6 and -22.0‰ and did not differ significantly between the *Spartina* and open bay habitats sampled (Table 1). The -16.6 to -22.0‰ estuarine range is in good accord with the -17 to -21.8‰ range observed off Louisiana among small recruiting shrimp (Fig. 5A-D, G).

For $\delta^{15}N$ and $\delta^{34}S$, a few samples were analyzed from seagrass meadows in Texas and Florida and from both *Spartina* marshes and open bays in Louisiana (Fig. 6). Low $+5.6$ to $+8.4$‰ $\delta^{15}N$ and $\delta^{34}S$ values were frequently observed among shrimp from seagrass meadows (Fig. 6); animals recruiting off south Texas and Florida initially possessed values in this range (Fig. 7A, B). Sampling in Louisiana marshes and open bays yielded scattered results for both $\delta^{15}N$ and $\delta^{34}S$ (Fig. 6) but showed that values of $+10$‰ or lower are not confined to seagrass meadows.

Isotopic Convergence

During offshore feeding and growth, the isotopic values of estuarine dependent animals should gradually converge upon average offshore values. In fact, four patterns of convergence and nonconvergence were evident, when isotopic values were plotted against animal weight. Most commonly, a close and rapid convergence toward the mean value of resident, offshore species was observed for C, N, and S (e.g., Figure 7B). Less frequently, convergence occurred, but the end-value reached by larger migratory animals was significantly different than the mean value for offshore residents (Fig. 5C; Fig. 7A, $\delta^{34}S$ data). Nonconvergence, a third pattern, was most evident in the $\delta^{13}C$ data for spot (Figs. 3F, 5E). Finally, a mixed pattern of very gradual convergence with a few deviant large individuals was indicated in two cases (Fig 5A, G).

TABLE 1.—$\delta^{13}C$ Values of estuarine shrimp from the Barataria Bay region of Louisiana, 1980. BS = brown shrimp; WS = white shrimp; GS = grass shrimp.

Location,[1] collection date, and sample size		Mean dry weight (g)	Total length (range in mm)	$\delta^{13}C$ Whole shrimp	Muscle	Stomach contents
Open bays						
Caminada Bay						
8 April	10 BS	0.04	19-24	−15.1	—	—
15 April	20 BS	0.07	23-33	−13.9	—	—
Independence Island						
29 July	6 WS	—	72-107	—	−19.5	—
29 July	1 WS	—	130	—	−19.9	—
29 July	35 seabob[2]	—	50-70	—	−16.6	—
1 October	9 BS	1.2	74-90	—	−19.5	−20.5
1 October	25 WS	0.8	70-107	—	−17.5	−20.0
St. Mary's Point						
1 April	6 WS	2.2	69-102	−19.0	—	−20.7
8 April	20 GS	0.065	22-26	−19.5	—	−21.0
Spartina marshes						
Airplane Lake						
25 March	20 BS	0.04	19-30	−17.8	—	—
25 March	5 BS	0.7	47-62	−17.6	—	—
8 April	20 BS	0.08	24-33	−19.6	—	—
8 April	6 BS	0.8	45-67	−17.8	—	−19.3
15 April	20 BS	0.14	24-42	−17.8, [3]−17.5	—	[4]−25.5
1 October	40 WS	0.4	60-70	—	−17.0	—
1 October	3 BS	0.7	63-86	—	−18.4	—
Bayou Garci						
25 March	11 BS	0.55	36-54	−18.3	—	—
Bay Rambo						
18 March	20 GS	0.045	17-21	−18.3	—	—
8 April	20 GS	0.06	21-23	−19.8	—	−21.1
18 April	20 BS	0.05	21-30	−17.2	—	—
18 April	7 BS	0.9	52-73	−18.3	—	−19.3
Round Lake						
3 March	9 BS	0.22	28-42	−22.0	—	—
1 April	15 GS	0.05	14-23	−20.4	—	—
15 April	20 BS	0.03	18-23	−20.9	—	−25.2
15 April	2 BS, 5 WS	0.9	57-75	−21.3	—	—

[1]Locations are shown in Figure 2.
[2]*Xiphopenaeus kroyeri.*
[3]Replicate samples, 20 brown shrimp each.
[4]Hindgut, rather than stomach (proventriculus) sample.

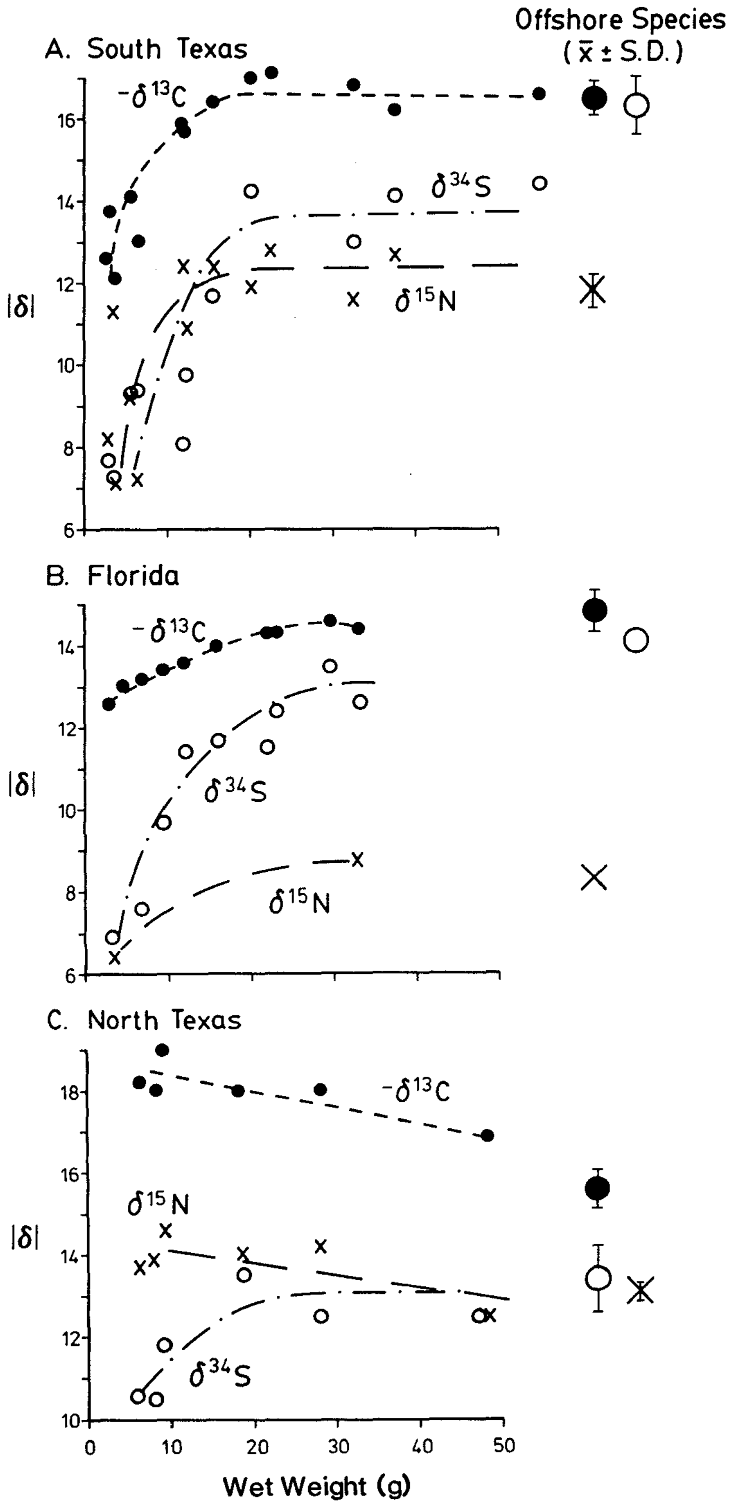

FIGURE 7.—Isotopic variations with size for migratory penaeid shrimp in three regions of northern Gulf of Mexico. All samples are composites of 5-25 individuals. Enlarged symbols at the right of each figure give the mean and standard deviation for samples of co-collected offshore resident shrimp. A, Brown shrimp, May 1980, transect 1 (Fig. 1A). B, Pink shrimp, October 1980, transect 10 (Fig. 1A). (Symbols for $\delta^{34}S$ and $\delta^{15}N$ of offshore residents lack error bars because only one species was available for analysis). C, Brown (smallest four samples) and white (largest two samples) shrimp, October 1978, transect 5 (Fig. 1A).

When these patterns are examined by species, several consistencies and contrasts are noteworthy. Rapid convergence was characteristic for pink shrimp (Figs. 3B, E, 4, 7B) and usually for brown shrimp (Figs. 3A, C, D, 5B, C, D, 7A), although one brown shrimp collection showed only a gradual convergence (Fig. 5A). With this exception, convergence was complete by subadult, 20 g sizes. In contrast to pink and brown shrimp, white shrimp exhibited only gradual convergence that was incomplete well beyond 20 g sizes (Fig 5G). The two fish species also showed contrasts in their convergence patterns. With the exception of six 50-100 g individuals collected off Barataria Bay in October 1980, Atlantic croaker in all size categories exhibited near-offshore values (Fig. 5F). Spot of all sizes, however, showed widely variable $\delta^{13}C$ values both off south Texas (Fig. 3F) and north Texas plus Louisiana (Fig. 5E).

$\delta^{13}C$, $\delta^{15}N$, and $\delta^{34}S$ Correlations

If two diets differ simultaneously in their C, N, and S isotopic compositions, and animals switch from one diet to the other, isotopic shifts occurring on the new diet should be parallel and therefore correlated for all three isotopes. In general, correlations between C, N, and S data followed this prediction and were good for the three examples examined (Fig. 7; Table 2). While C and N appeared consistently correlated (Table 2), correlations for S vs. N or C in the smaller set of north Texas samples ($N = 6$ vs. 10-12 in the other regions) were much weaker (Table 2).

TABLE 2.—Correlation coefficients (r) for $\delta^{13}C$, $\delta^{15}N$, and $\delta^{34}S$ data of Figure 7.

Region	$\delta^{13}C$ vs. $\delta^{15}N$	$\delta^{13}C$ vs. $\delta^{34}S$	$\delta^{15}N$ vs. $\delta^{34}S$
South Texas	0.90*	0.81*	0.69**
North Texas	0.93*	0.31 N.S.	0.36 N.S.
Florida	—	0.94*	—

*$P < 0.01$.
**$P < 0.05$.
N.S. = not significant.

DISCUSSION

The two most striking results of this study were 1) a strong regional division in the carbon isotopic composition of estuarine dependent species (Fig. 1) and 2) marked contrasts in the rate at which carbon isotopic values of these species converged on offshore values (Figs. 3, 4, and 5). The comparative C, N, and S data also allow preliminary observations on isotopic fractionations occurring in food webs of the Gulf of Mexico.

Regional Patterns in $\delta^{13}C$

The striking regional patterns found in $\delta^{13}C$ values of estuarine dependent shrimp closely parallel regional $\delta^{13}C$ patterns previously documented in nearshore sediments. These sediments have $\delta^{13}C$ values averaging less negative than deeper offshore sediments along the Florida and south Texas coasts (Plucker 1970; Calder 1971[4]; Fry et al. 1977; Behrens et al. 1980), but more negative than offshore sediments along the north-central Gulf coast (Sackett and Thompson 1963; Shultz and Calder 1976; Hedges and Parker 1976; Gearing et al. 1977). Similar less vs. more negative regional patterns were also evident in the $\delta^{13}C$ data for estuarine dependent animal species (Figs. 1, 3, 4, 5). For sediments, the regional variations have been ascribed to average $\delta^{13}C$ differences of the carbon that nearshore sediments receive from rivers and estuaries. In the former two regions, abundant ^{13}C-enriched seagrasses and macroalgae ($\delta^{13}C \cong -10$ to $-15‰$) grow or are exported offshore, while near the large rivers of the north-central Gulf coast, $-27‰$ terrestrial matter is carried offshore (Plucker 1970; Calder footnote 3; Shultz and Calder 1976). Interestingly, the isotopic transition between the north-central Gulf vs. the south Texas region occurs at about the same place for both sediments and shrimp—approximately offshore of Freeport, Tex. (Fig. 1, transect 4; Gearing et al. 1977).

While regional patterns are thus very consistent, their origin along the north-central Gulf coast is somewhat puzzling. Extensive stands of $-13‰$ *Spartina* marshes replace seagrasses as sources of ^{13}C-enriched carbon along this coast (Chabrech 1972; Diener 1975), yet this replacement is not sufficient to maintain the ^{13}C-enrichments (less negative $\delta^{13}C$ values) observed along the Florida and south Texas coasts (Fig. 1C). Sampling small juvenile shrimp within *Spartina* marshes showed that even in areas where *Spartina* influences should be strongest, shrimp $\delta^{13}C$ values were substantially more negative than *Spartina* values and ranged from -17 to $-22‰$ (Table 1). Similar discrepancies between $-13‰$ *Spartina* values and more negative values for C in animals, sediments, and water-borne particulates in marshes have also been found in previous studies (Haines 1976a, b, 1977; Spiker and Schemel 1979; Hackney and Haines 1980), and Peterson et al. (1980) have discussed one possible explanation for these discrepancies.

[4]Calder, J. A. 1971. Carbon isotope ratios of shelf sediments. Paper presented at the 1971 Annual Fall Meeting of the American Geophysical Union, San Francisco, Calif.

Regional results from Florida and south Texas more clearly show the importance of feeding on ^{13}C-enriched foods prior to offshore migration (Figs. 3, 4). Such foods are found in shallow areas such as seagrass meadows and some shoreline algal mats (Fry 1981b) rather than in deeper open bays (Fry 1981a). The isotopic data thus point to the importance of these shallower habitats as feeding grounds for spot, pink shrimp, and brown shrimp prior to their offshore migrations. The N and S isotopic results shown in Figure 7A and B are consistent with this conclusion, as the +6 to +8‰ values found among small migratory shrimp were also found in shrimp from seagrass meadows (Fig. 6). Additionally, this conclusion agrees well with previous studies that have documented high abundances of these three species in grassflats (e.g., Hutton et al. 1956; Hellier 1962; Hoese and Jones 1963; Kobylinski and Sheridan 1979; Orth and Heck 1980).

In summary, isotopic values found among small migrants in all three offshore regions closely mirrored isotopic values found in local estuaries. The sharp division in $\delta^{13}C$ values occurring opposite Freeport, Tex. (Fig. 1A, transect 4), suggests little migratory interchange between offshore regions, at least for smaller sized shrimp. Future sampling near transect 4 and in other areas where two isotopically contrasting regions interface could be useful in tracing the movements of shrimp and fish after their offshore migrations. This should be easiest for animals that migrate offshore as adults and show only a slow convergence upon offshore values.

Convergence

To understand the four patterns of isotopic convergence and nonconvergence that were observed, it is useful to consider two extreme cases. In the first, animals migrate offshore as small juveniles and remain permanently offshore during growth to adult sizes. This leads to the pattern of early isotopic convergence that was most often observed (e.g., Figure 7A). Alternately, animals may mature in estuaries, migrating offshore as large adults. When sampled offshore, animals of this kind will show very little convergence upon offshore values, for most of their tissues have been formed from estuarine foods. Results for spot most clearly conformed to this pattern (Figs. 3F, 5E).

Gradations exist between these extreme cases. For example, if some species have mixtures of small juvenile and large adult migrants, the result may be a gradual convergence such as that observed for white shrimp (Fig. 5G). Such mixed cases could also result 1) if animals do not stay permanently offshore but freely move between estuarine and offshore regions, or 2) if animals stay offshore but consume small migrants or detrital foods that come from estuaries.

The isotopic results thus lead to some predictions about the migratory life histories of these species—predictions that can be checked against previous findings of mark-recapture and trawl studies. The five species studied can be divided into two groups on the basis of migration patterns and offshore location as adults. Trawling studies of both pink and brown shrimp show that they move offshore as small juveniles and continue to move into deeper waters as they mature (Iverson et al. 1960; van Lopik et al. 1979[5]). The other three species—white shrimp, croaker, and spot—are more coastal, with the center of their offshore ranges at <10 m depths (Chittenden and McEachran 1976). For these latter three species, several reports exist documenting 1) occasional or frequent reentry into estuaries from the offshore Gulf of Mexico (Simmons and Hoese 1958; White and Chittenden 1977; van Lopik et al. footnote 4), and 2) delayed migration until adult sizes are reached in estuaries (e.g., Gunter 1950; Suttkus 1955; Hellier 1962; van Lopik et al. footnote 4).

In general, the isotopic patterns of convergence closely conformed to what was expected from these previous life history studies. Pink shrimp and most brown shrimp collections showed close convergence to offshore values by the 20 g size in good accord with observations that these shrimp leave estuaries at an average size <6 g (Copeland 1965; Trent 1967; Parker 1970; Ford and St. Amant 1971). The less marked convergence observed among spot, white shrimp, and, to some extent, Atlantic croaker, suggests that these species continue to rely on estuarine foods throughout their adult lives, and is consistent with their closer association with estuarine areas.

Two aspects of the isotopic data deserve special mention. First, while most of the isotopic data gathered are consistent with early migration of brown shrimp as young juveniles, this was not always true. Collections of brown shrimp made off the Louisiana and north Texas coasts in October 1978, showed only a gradual convergence (Fig. 6A) similar to that observed for white shrimp (Fig. 6G). While the causes of this one exceptional set of results are not clear, it appears that some variability can exist in migration patterns.

[5]Van Lopik, J. R., K. H. Drummond, and R. E. Condrey. 1979. Draft environmental impact statement and fishery management plan for the shrimp fishery of the Gulf of Mexico, United States waters. Gulf of Mexico Fishery Management Council.

Secondly, it is interesting to carefully contrast the isotopic data for spot and Atlantic croaker collected along the Louisiana and north Texas coasts (Fig. 5E, F). Although the migratory biology of these two species is generally held to be quite similar (e.g., Parker 1971), the isotopic results show clear differences. Of the two patterns, that of the Atlantic croaker conforms closest to findings of trawl studies which show that most animals leave estuaries as juveniles <25 g during late spring and early summer migrations (Nelson 1969; Parker 1971; Kobylinski and Sheridan 1979). The October collections of this study should thus primarily reflect summer growth offshore, and show the general isotopic convergence that was observed in the Atlantic croaker data. The six individuals with deviant $\delta^{13}C$ values that were collected off Barataria Bay in October 1980 could represent the much smaller pool of individuals that continues to reside in bays until early winter weather triggers their exodus (Gunter 1950; Suttkus 1955). It is striking that this latter class of adult migrants seems to represent a much larger fraction of the population for spot than Atlantic croaker (compare Figure 5E and F).

While further study in other seasons is required to confirm these differences between Atlantic croaker and spot, these data point out both strengths and weaknesses of this isotopic approach to studying migrations. This approach is weakest for tracing the movements of small individuals because these animals rapidly lose their estuarine isotopic tag during offshore growth. The approach is much stronger when applied to adult migrants that only gradually lose their estuarine isotopic tag during metabolic turnover offshore. Trawling methods are probably superior for studying movements of small juveniles that cannot easily avoid nets, but for larger adults that can, isotopic methods of following movements may lead to a clearer understanding of seasonal and year-to-year variations.

C, N, and S Food Web Fractionations

Table 3 summarizes C, N, and S isotopic values observed in the Gulf of Mexico and other offshore ecosystems. Relative to phytoplankton at the base of the food web, some fractionations or changes in isotopic compositions are evident at higher trophic levels for C and N isotopes. Mean δ values increase for both C and N isotopes in these food webs (Table 3). Such cumulative fractionations have been attributed to preferential respiration of $^{12}CO_2$ in the case of C isotopes (McConnaughey and McRoy 1979a) and to excretion of ^{14}N-enriched compounds in the case of nitrogen (Wada 1979).

TABLE 3.—Stable isotope values for seawater and offshore marine biota.[1]

			Marine animals			
Measurement	Seawater	Phytoplankton	Zooplankton	Fish	Benthic invertebrates	References[2]
$\delta^{13}C$	+1	−18 to −24	−19 to −22	−15 to −19	−14 to −19	1, 2, 3, 4, 11
$\delta^{15}N$	+1	−2 to 0 and 7.5 to 8.5	8 to 9.5	9.9 to 20.5	8 to 13.3	5, 6, 11
$\delta^{34}S$	+20	[3]17 to 20.3	18.1	16 to 19	12.9 to 20	7, 8, 9, 10, 11

[1]Whenever possible, values cited are those from the Gulf of Mexico or other temperate and tropical waters.
[2]References: 1 = Fry 1981b; 2 = Fry and Parker 1979; 3 = Gormly and Sackett 1977; 4 = Sackett and Moore 1966; 5 = Macko 1981; 6 = Miyake and Wada 1976; 7 = Hartmann and Nielsen 1969; 8 = Mekhtiyeva et al. 1976; 9 = Kaplan et al. 1963; 10 = Rees et al. 1978; 11 = this study.
[3]Values for macroalgae.

For S isotopes, marine algae typically show a small 0-4‰ fractionation relative to seawater sulfate and thus closely reflect its +20‰ isotopic composition (Table 3). Previous studies show that marine animals closely reflect the isotopic composition of their +17 to +20‰ algal foods and seldom have values lower than +16‰ (Kaplan et al. 1963; Mekhtiyeva et al. 1976).

In this study, the majority of resident offshore shrimp and stomatopod samples had somewhat lower +13 to +17‰ values (Fig. 6). This apparent discrepancy may reflect an undersampling of soft-bottom benthic fauna in previous studies. Recent work in estuarine marshes has shown that sulfur with low $\delta^{34}S$ values can enter rooted plants from sediments, resulting in plant tissues with $\delta^{34}S$ values lower than +5‰ (Carlson and Forrest 1982; Fry et al. 1982). Consumption of low $\delta^{34}S$ benthic bacteria or plants seems responsible for the low +6 to +8‰ values found in many estuarine and offshore samples of pink and brown shrimp (Figs. 6, 7A, B). Among offshore resident shrimp, the lowest $\delta^{34}S$ values were observed in Louisiana waters (Fig. 6), offshore of Barataria Bay (Fig. 1, transect 8). The occurrence of low $\delta^{34}S$ values in this area may have as their cause low $\delta^{34}S$ benthic bacterial foods, rather than cumulative food web fractionations. The various means by which benthic algae and bacteria take up low $\delta^{34}S$ sulfur from sediments is the subject of current investigations.

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