

NATURAL STABLE CARBON ISOTOPE TAG TRACES TEXAS SHRIMP MIGRATIONS¹

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ABSTRACT

A 1978 spring and early summer survey of Texas brown shrimp, *Penaeus aztecus*, showed that stable carbon isotope (¹³C/¹²C or δ¹³C) analysis is useful for tracing shrimp movements. At least four isotopically distinct shrimp feeding grounds (three estuarine and one offshore) exist along the Texas coast. Mean δ¹³C values for brown shrimp in these feeding grounds during the spring and early summer were -12.8 to -15.4 (sea grass meadows), -16.2 to -16.8 (offshore), -17.9 to -19.6 (open bays, group 1), and -20.1 to -21.7 (open bays, group 2). Longer term seasonal studies offshore and at two sea grass stations showed that shrimp δ¹³C values become less negative by 1.2 to 2.4‰ in the fall versus spring/early summer. Many small subadult brown shrimp collected offshore and during outgoing tides in a channel leading to the offshore Gulf of Mexico had δ¹³C values typical of individuals in sea grass meadows. These and possibly other shallow-water habitats appear to supply more shrimp to south Texas offshore fisheries than do deeper estuarine bays.

Migratory movements of many commercial marine species are difficult to follow. Traditional methods include mark-recapture techniques to follow individual growth and movement while sequential trawling studies follow mass migrations. Newer techniques based on underwater acoustics or genetic differences among stocks have expanded our ability to follow marine migrations, but many movement patterns remain unresolved.

Recently, the study of stable carbon isotope ratios, ¹³C/¹²C or δ¹³C, has shown that animals acquire a natural isotopic label or tag from their diet. The carbon in animals is generally isotopically similar within a range of ±2‰ to the carbon in the diet (DeNiro and Epstein 1978; Fry et al. 1978; Teeri and Scholler 1979). Photosynthesis introduces δ¹³C variations among different plant species (Park and Epstein 1960; Smith and Epstein 1971), and the δ¹³C values of animals may be interpreted in terms of the relative carbon contributions from plants at the base of food chains. In the Gulf of Mexico, marine sea grass species have the least negative δ¹³C values (-3 to -15‰) while phytoplankton and particulate organic carbon are usually more negative (-18 to -25) and other species of marine algae are intermediate (-12 to -20) (Craig 1953; Parker 1964; Smith and Epstein

1971; Eadie and Jeffrey 1973; Fry and Parker 1979). Animals in sea grass meadows are usually less negative than animals found offshore, reflecting the general δ¹³C difference between sea grass plants and phytoplankton (Parker and Calder 1970; Thayer et al. 1978; Fry and Parker 1979; McConnaughey and McRoy 1979).

This study assesses the potential of using δ¹³C variations to trace shrimp movements. Since food availability differs between habitats such as sea grass meadows and phytoplankton-dominated open bays, the δ¹³C label acquired during feeding will differ between such habitats. Measuring the δ¹³C values of migrating shrimp should provide an indication of which habitats they came from and a basis for evaluating which habitats are relatively important numerical contributors to commercial shrimp fisheries.

During 1978, I analyzed the δ¹³C values of the migratory brown shrimp, *Penaeus aztecus*, and to a lesser extent, of the pink shrimp, *P. duorarum*. These shrimp share a similar life history pattern of offshore spawning, juvenile growth in estuaries, subsequent offshore migration of subadults, and final maturation to adults that spawn offshore (Cook and Lindner 1970). Several nonmigratory shrimp and one offshore stomatopod species were also collected to facilitate interpretation of δ¹³C patterns as due to local conditions vs. migration. Seasonal studies assessed the rate at which local food variations cause a change in shrimp δ¹³C.

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METHODS

Shrimp samples were collected at 22 bay and 3 offshore stations along the Texas coast (Figure 1). Most bay sampling was done by the Texas Parks and Wildlife Department, Coastal Fisheries Division, as part of their 1978 spring shrimp survey. Depths at bay stations were 1-2 m; offshore trawling areas were located in 27-29 m depths. Open bay stations had unvegetated mud bottoms and were not within 0.25 km of a major swamp, sea grass meadow, or marsh. Sea grass stations were all in or on the edge of large sea grass meadows measuring at least 5 ha.

Four open bay stations deserve individual mention. Clear Lake (station 100) and the old Arroyo Colorado (station 13) receive substantial amounts of domestic sewage. Station 94, at the mouth of the Tres Palacios River, had the lowest salinities of any station. Station 92 in Turtle Bay was in the

open bay, but well-developed *Spartina* sp. marshes were present on the shore.

Shrimp were collected either with bar seines or trawls and then frozen in seawater for later identification and $\delta^{13}\text{C}$ analysis. Surface temperature and salinity were measured at the time of collection. Spring samples were mostly collected during a 6-wk period from mid-April to 1 June 1978. Offshore samples were collected 26 July 1978.

White muscle tissue was dissected from shrimp abdomens for $\delta^{13}\text{C}$ analysis. Both composite and individual samples were prepared. Composite samples contained equal-weight tissues from individual shrimp. Preliminary analysis of the number of pooled brown shrimp required for an accurate estimate of mean shrimp $\delta^{13}\text{C}$ showed that combining five or six individuals is generally sufficient (Figure 2); accordingly, composite sample sizes were ≥ 10 for all shrimp, and averaged 34 individuals/sample. For individual shrimp, mus-

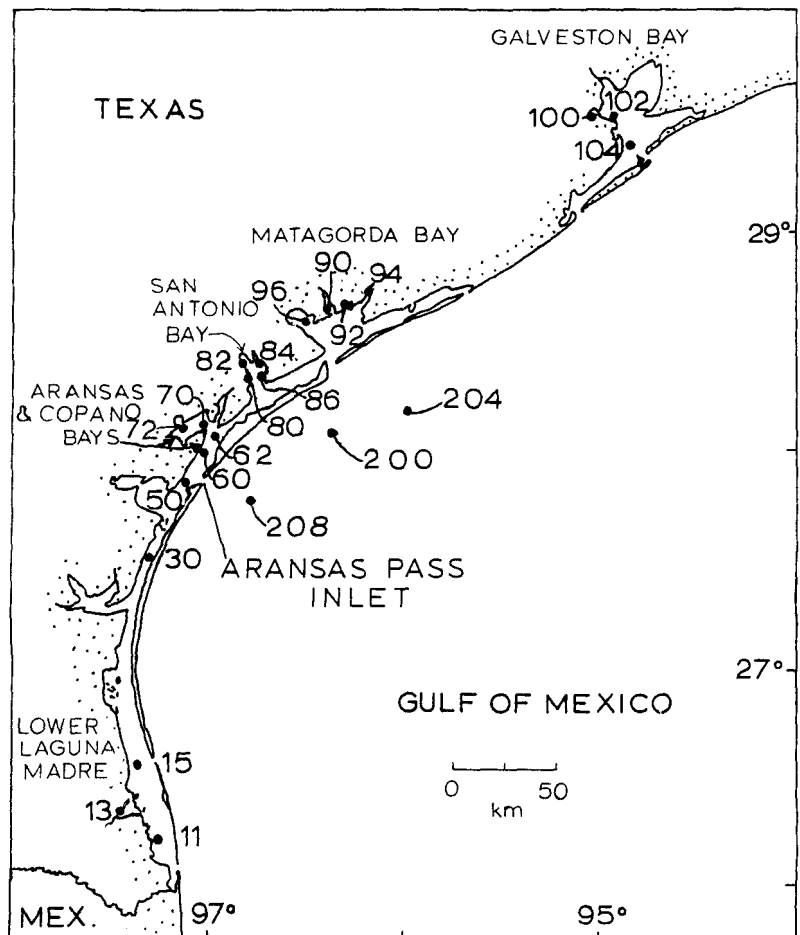


FIGURE 1.—Shrimp collection stations in the northwestern Gulf of Mexico.

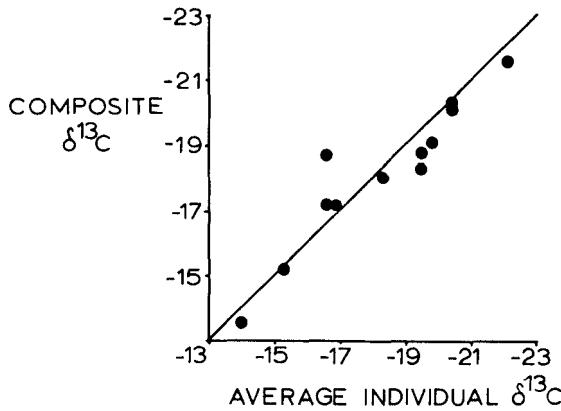


FIGURE 2.—Agreement between two methods of estimating mean shrimp $\delta^{13}\text{C}$ at 12 bay stations. The mean $\delta^{13}\text{C}$ value of five or six individuals is plotted as the x coordinate; the $\delta^{13}\text{C}$ value of the composite sample from which the individuals were subsampled is plotted as the y coordinate. The 45° reference line indicates complete agreement between the two methods.

cle tissue taken from the same shrimp showed a maximum $\delta^{13}\text{C}$ range of 0.3‰ (three shrimp, each sampled thrice), and subsampling one piece of tissue per shrimp was therefore considered adequate.

Shrimp were sorted by species by hand, and identification checked with a dissecting microscope on 5-10 specimens per composite sample using several keys (Zamora and Trent 1968; Pérez-Farfante 1970; Wood 1974).

Composite and individual samples were dried in an oven or freeze dryer, then shredded through a #40-mesh screen with a Thomas-Wiley Mill³ or ground to a fine powder with mortar and pestle. Samples were combusted in a modified Leco radio frequency furnace (Parker et al. 1972) and analyzed for $\delta^{13}\text{C}$ values using a Nuclide 6-60 dual collector isotope ratio mass spectrometer. All results are expressed relative to the international PDB⁴ standard where:

$$\delta^{13}\text{C} = \left(\frac{^{13}\text{C}/^{12}\text{C}_{\text{sample}}}{^{13}\text{C}/^{12}\text{C}_{\text{standard}}} - 1 \right) \times 10^3.$$

Based on analysis of 53 paired replicate samples, the mean error $\pm 95\%$ confidence limits was $0.45 \pm 0.77\%$.

RESULTS

Bay Shrimp

Figure 3 shows the $\delta^{13}\text{C}$ values of brown shrimp

from all bay stations sampled during the spring and early summer. The sampling effort was unequal at these stations, primarily due to fluctuations in shrimp numbers from week to week. At most stations, three or more composite samples were collected at irregular intervals over the 2-mo period; individual subsamples of pooled composite samples were collected between 1 and 15 May.

Analysis of variance showed highly significant differences between station means computed from composite samples ($P < 0.01$). The LSD multiple range test showed that bay stations formed at least three significantly different groups on the basis of their mean $\delta^{13}\text{C}$ values (Figure 3; vertical bars at right margin). Most stations were open bay stations and had mean $\delta^{13}\text{C}$ values between -17.9 and -19.6% (stations 60-84). Mean $\delta^{13}\text{C}$ values were higher in sea grass meadows, -12.8 to -15.4% . Several open bay stations formed a third group, having more negative average values of -20.1 to -21.7% (stations 80-13).

Analysis of the open bay stations showed that the more negative shrimp $\delta^{13}\text{C}$ values tended to occur in lower salinity bays which have been historically well flushed by freshwater inflows (Table 1).

TABLE 1.—Brown shrimp $\delta^{13}\text{C}$ and salinity at open bay stations and freshwater flushing rates for five Texas bays and the Gulf of Mexico.

Bay	$\delta^{13}\text{C}$ ¹ mean \pm SD(N)	Salinity ² mean \pm SD(N)	Mean bay turnover rates (times/yr) ³	
			Historical	1951-68
Galveston	$-20.0 \pm 0.9(19)$	$20.2 \pm 2.5(24)$	3.9	3.1
San Antonio/ Espiritu Santo	$-19.2 \pm 1.1(17)$	$16.7 \pm 4.8(25)$	2.6	2.2
Matagorda	$-18.3 \pm 1.3(17)$	$20.9 \pm 5.0(25)$	1.3	1.3
Copano/Aransas	$-17.7 \pm 0.6(9)$	$22.5 \pm 2.2(30)$.2	.2
Laguna Madre*	$-17.6 \pm 0.6(2)$	$32.0 \pm 4.4(3)$.02	.02
Offshore, July	$-16.5 \pm 0.6(15)$	≈ 36	≈ 0	≈ 0

¹Based on composite samples only.

²Salinity taken at the time of shrimp collection (mid-April to mid-June 1978).

³Turnover rate is the ratio of annual freshwater inflow volume to the volume of a bay. Calculated from Table 8, Diener 1975.

⁴Station 13 in the Old Arroyo Colorado is not included in this average.

Size and Bay Brown Shrimp $\delta^{13}\text{C}$

Systematic $\delta^{13}\text{C}$ changes with size might be expected if shrimp foods available to different size classes possessed different $\delta^{13}\text{C}$ values. Shrimp sizes ranged from 20 to 110 mm total length (TL),

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

⁴Abbreviation in the isotopic literature for a fossil belemnite, *Belemnitella americana*, from the PeeDee formation in South Carolina.

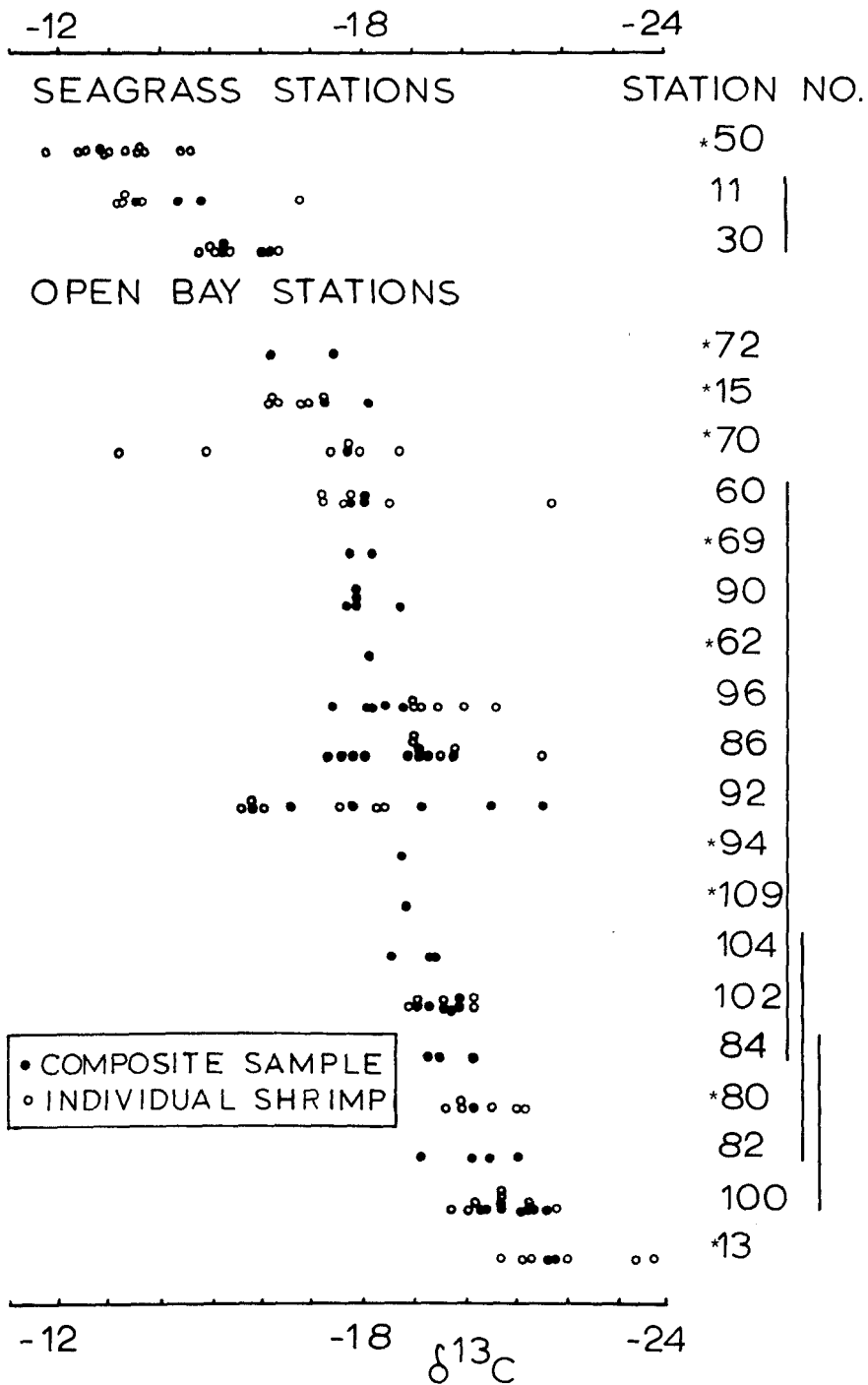


FIGURE 3.— Bay brown shrimp $\delta^{13}C$ by station, mid-April through mid-June 1978. Vertical lines (right margin) connect stations that, on the basis of their composite samples, were not significantly different ($P < 0.01$, LSD multiple range test). Stations denoted by an asterisk had one or two composite samples and were not subjected to this analysis, although they are included for completeness. Stations 69 and 109 are composites of several stations in Aransas and Galveston Bay, respectively.

generally progressing throughout the spring sampling period. Both individual and composite bay brown shrimp samples were examined by station and station group (Figure 3) using graphic, linear, and multinomial regression analysis for correlations of shrimp length, weight, or date of collection with shrimp $\delta^{13}\text{C}$. These analyses were significant only rarely, <1 case in 10, so that no consistent $\delta^{13}\text{C}$ relationships with size or date were evident.

Offshore Samples

In addition to migratory brown shrimp, three other shrimp and stomatopod species were collected offshore at stations 200, 204, and 208. These species, *Trachypenaeus similis*, *Sicyonia dorsalis*, and *Squilla empusa*, are normally resident offshore and only occasionally enter estuaries (Hoese et al. 1968). Composite samples of these species fell within a narrow $\delta^{13}\text{C}$ range of -16.2 to -16.9% (Table 2). Forty-three individual rock shrimp, *Sicyonia dorsalis*, also collected at these stations showed a slightly larger $\delta^{13}\text{C}$ range of 1.9% , -15.5 to -17.4 (Table 2). Mean $\delta^{13}\text{C}$ values of migratory brown shrimp were very similar to values of the resident species, although some $\delta^{13}\text{C}$ values of smaller brown shrimp differed significantly from mean values of the offshore species (Figure 4A, B). Several other samples of small brown shrimp collected offshore or during outgoing tides 24 May and 21 June 1978 at Aransas Pass Inlet also showed $\delta^{13}\text{C}$ values significantly different from the July offshore species (Figure 4A, B). These individual and composite analyses showed that small brown shrimp may enter the offshore regions with widely differing $\delta^{13}\text{C}$ values (-12.5 to -19.1% , Figure 4). But as brown shrimp

TABLE 2.— $\delta^{13}\text{C}$ values of shrimp species caught at three offshore stations, July 1978. The standard deviation and the number of samples (*N*) are given after the means that contain more than one sample.

Item	Station		
	200	204	208
Composite samples:			
Offshore stomatopod			
<i>Squilla empusa</i>	-16.4	-16.2	-16.4
Offshore shrimp			
<i>Trachypenaeus similis</i>	-16.4	-16.6	-16.2
<i>Sicyonia dorsalis</i>	-16.4	-16.6	-16.9
Migratory brown shrimp	-16.6	-16.8	-16.2
	$\pm .6(4)$	$\pm .2(4)$	$\pm .5(7)$
Individual shrimp:			
Offshore <i>S. dorsalis</i>	-16.5	-16.2	-16.7
	$\pm .4(12)$	$\pm .5(13)$	$\pm .4(16)$
Migratory brown shrimp	-16.0	-16.2	-15.9
	$\pm .7(12)$	$\pm 1.0(12)$	$\pm 1.2(16)$

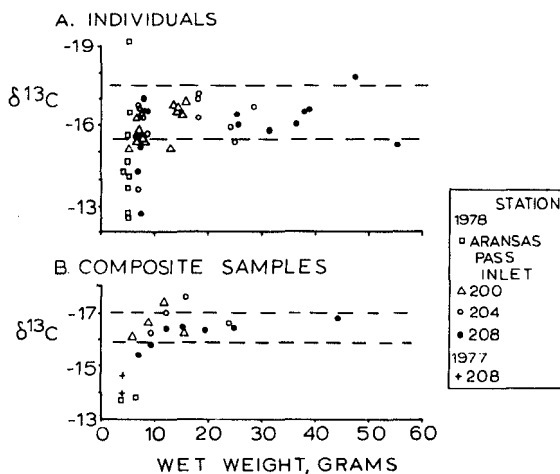


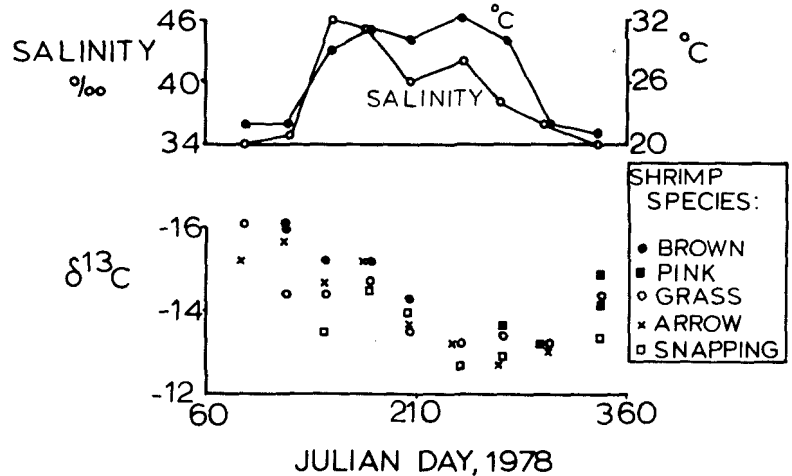
FIGURE 4.—Size dependence of brown shrimp $\delta^{13}\text{C}$ values at three offshore stations and from an outgoing tide at a major migratory pass opposite these stations. Dashed lines indicate 95% confidence limits beyond which single brown shrimp samples differ significantly from the -16.5% mean of resident offshore shrimp species listed in Table 2 (Sokal and Rohlf 1969).

feed and grow offshore, their $\delta^{13}\text{C}$ values rapidly converge on the -16 to -17% $\delta^{13}\text{C}$ values characteristic of offshore, nonmigratory species.

Seasonality

To supplement the late spring bay collections, a longer term seasonal study was undertaken at sea grass station 30. In addition to the migratory pink and brown shrimp, three small, 20-50 mm TL, nonmigratory shrimp species were also collected: grass shrimp, *Palaeomontes* sp.; arrow shrimp, *Tozouma carolinense*; and snapping shrimp, *Alpheus heterochaelis*. Mean values of these two migratory and three nonmigratory species showed a sigmoidal variation from -15.6 in late April to -13.0 to -13.2 in late August through late October to -14.2 in early December (Figure 5). Regression analysis showed that mean $\delta^{13}\text{C}$ did not correlate significantly with either temperature or salinity. Collections offshore and at sea grass station 50 showed a similar pattern in shrimp $\delta^{13}\text{C}$ variation between early summer and late fall, although collections at these stations were not made regularly as at station 30. Late October offshore composite samples averaged 1.2% less negative than late July samples ($N = 18$ and 23 , respectively); at sea grass station 50, late September composite samples averaged 2.2% less negative than late June samples ($N = 4$ and 2 , respec-

FIGURE 5.—Seasonal trends in shrimp $\delta^{13}\text{C}$ at bay sea grass station 30. All samples are composite samples; temperatures were taken between 0900 and 1200 h on each collection date.



tively). These seasonal differences between means were significant offshore ($P < 0.01$, t -test) but not at sea grass station 50 ($P > 0.05$, t -test).

DISCUSSION

To use $\delta^{13}\text{C}$ data to monitor shrimp migrations, isotopically distinct feeding grounds must be identified in which shrimp acquire significantly different, unique isotopic tags during feeding and growth. When the relationship between shrimp foods and shrimp tissue $\delta^{13}\text{C}$ is more precisely known, it should be possible to predict shrimp tissue $\delta^{13}\text{C}$ at any locality from the $\delta^{13}\text{C}$ value of locally available shrimp foods (Fry in prep.). This study relied on a more indirect method of identifying these isotopically distinct feeding grounds, i.e., monitoring the tissues of the mobile shrimp. In most cases, mean shrimp $\delta^{13}\text{C}$ values are probably a reliable index of local feeding conditions, as evidenced by the close $\delta^{13}\text{C}$ similarity of migratory brown shrimp and resident nonmigratory shrimp both offshore (Table 2) and in sea grass meadows (Figure 5).

Tests for significant differences among stations showed that sea grass stations were distinct from open bay stations which were in turn divided into two groups (Figure 3). The $\delta^{13}\text{C}$ distinction between sea grass and the more positive group of bay stations has been previously observed (Parker and Calder 1970; Fry et al. 1977; Fry and Parker 1979). These open bay stations occurred throughout the Texas bay system (Figure 3). The more negative open bay stations were found in areas which are more heavily influenced by terrestrial inputs such

as sewage (stations 100 and 13) or river-borne debris (stations in Galveston and San Antonio Bays). Numerous sediment studies have documented that river-borne detritus derived from terrestrial sources averages -25 to -30 ‰ (e.g., Hunt 1970; Shultz and Calder 1976). Brown shrimp consumption of this detritus should result in the observed more negative shrimp $\delta^{13}\text{C}$ values.

Seasonality

The seasonal cycle observed in shrimp $\delta^{13}\text{C}$ is roughly correlated with the warmer growing season when the temperature increases and the species composition and abundance of food sources also change. These effects are difficult to separate with the present data. Marine plant species are sometimes enriched in ^{13}C when grown at higher temperatures (Sackett et al. 1965; Degens et al. 1968; Wong and Sackett 1978), although this effect does not appear to consistently apply to sea grasses (Thayer et al. 1978) nor to natural phytoplankton populations existing at temperatures typical of Texas bays (Sackett et al. 1974).

Seasonal changes in species composition and abundance occurring in sea grass meadows could also change the mean isotopic composition of shrimp foods; probably, the larger seasonal variations observed in sea grass meadows are due in part to the increasing dominance of sea grass carbon in food chains leading to shrimp. The lack of correlation between shrimp $\delta^{13}\text{C}$ values and temperature at a time when shrimp $\delta^{13}\text{C}$ values could change rapidly (mean weight increased 20 - $50 \times$ over the spring sampling period) argues against a

direct temperature effect on the carbon metabolism of shrimp.

Offshore Migrations

As brown shrimp migrate offshore from the estuaries, they encounter a new feeding ground. During subsequent offshore growth, shrimp metabolize away the estuarine carbon present in their tissues, and dilute the remainder of this old carbon with new offshore carbon. Summer $\delta^{13}\text{C}$ values of nonmigratory offshore shrimp were quite constant around -16.5% and the offshore feeding grounds appeared to be isotopically uniform over the three stations sampled (Table 2). A model that incorporates these features and predicts the change of shrimp $\delta^{13}\text{C}$ during offshore growth is shown in Figure 6. This simple model is a first approximation in that only dilution of the old estuarine carbon during offshore growth is considered, while metabolic loss of this estuarine carbon is ignored. The $\delta^{13}\text{C}$ value of shrimp at any time after emigration can be calculated from the equation:

$$\delta^{13}\text{C} = \frac{\delta^{13}\text{C}_{\text{old}}(W_e) + (W_c - W_e)(\delta^{13}\text{C}_{\text{new}})}{W_c}$$

where W_e = initial weight at emigration,

W_c = weight at time of collection offshore,

$\delta^{13}\text{C}_{\text{old}}$ = $\delta^{13}\text{C}$ at emigration,

$\delta^{13}\text{C}_{\text{new}}$ = mean offshore shrimp $\delta^{13}\text{C}$.

The weights and $\delta^{13}\text{C}$ values at the time of offshore emigration shown in Figure 6 represent two individual brown shrimp collected in May at Aransas Pass Inlet (see Figure 4A). The 5 g wet weight is typical of most brown shrimp during the annual peak spring and early summer migrations (Cope land 1965; Trent 1966; Parker 1970; King 1971; pers. obs. 1978).

The model predicts that these migrating 5 g shrimp will rapidly become isotopically indistinguishable from resident shrimp during offshore growth (Figure 6). This prediction agrees well with the results shown in Figure 4 in which shrimp weighing >15 g are generally not significantly different than the -16.5 average of nonmigratory resident shrimp. Growth from 5 to 15 g should occur in about 1.1 and 2.9 mo for female and male brown shrimp, respectively (Parrack 1979), so that the effective offshore life of the estuarine

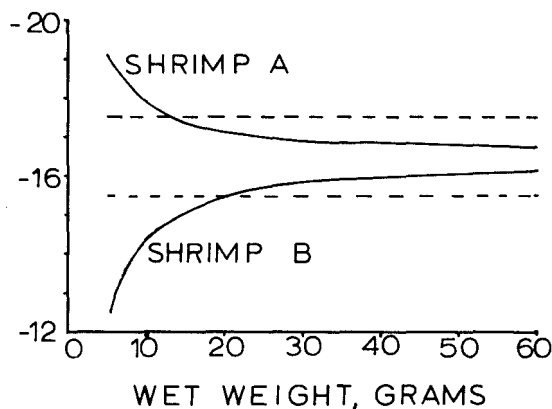


FIGURE 6.—Isotopic diet-change model for two shrimp migrating offshore from Texas estuaries. During offshore growth, these two shrimp gradually approach the characteristic $\delta^{13}\text{C}$ value of the offshore area, -16.5% , according to the equation presented in the text. Dashed lines as in Figure 4 indicate $\delta^{13}\text{C}$ values at which the estuarine $\delta^{13}\text{C}$ tag is no longer distinguishable from normal offshore values.

tag is rather brief. Larger weights at emigration and increased differences between δ_{old} and δ_{new} result in a more gradual approach to the mean offshore value, while smaller weights, decreased $\delta_{\text{old}} - \delta_{\text{new}}$ differences, or metabolic loss of estuarine carbon during offshore growth would result in a shorter detectable life for this estuarine $\delta^{13}\text{C}$ tag.

The data presented in Figure 4 allow a preliminary assessment of the probable estuarine origins of most brown shrimp recruits to the offshore fishery. A trend among smaller shrimp towards $\delta^{13}\text{C}$ values more typical of sea grass meadows, rather than those typical of open bays, was evident at both Aransas Pass Inlet in May and June and offshore during late July (Figure 4). Shrimp from two other shallow-water habitats, salt marshes (Haines and Montague 1979), and blue-green algal mats (Fry, unpubl. data) also have isotopic compositions similar to shrimp from sea grass meadows. The $\delta^{13}\text{C}$ label thus distinguishes deeper water, open bays from shallow marsh, algal mat, or sea grass habitats. These initial results suggest that the shallow-water habitats are the more important feeding grounds for shrimp that enter the south Texas offshore commercial fishery. This conclusion is in good agreement with other studies that show that shrimp are exceptionally abundant in sea grass meadows (Loesch 1965; Young 1978) and that sea grass meadows are quite extensive in south Texas estuaries (Diener 1975).

Bay Migrations

The $\delta^{13}\text{C}$ data also trace migrations between different estuarine habitats. Brown shrimp are smaller and grow more rapidly in estuaries than offshore, further abbreviating the useful life of the initial $\delta^{13}\text{C}$ tag a shrimp possesses when entering a new feeding ground. Despite this, brown shrimp $\delta^{13}\text{C}$ values were highly variable at bay stations 60, 70, 86, and 92 (Figure 3). High variability may indicate that these stations lie on migration routes where shrimp converge from several isotopically distinct feeding grounds. In support of this idea, one may note that a high $\delta^{13}\text{C}$ range, 6.7%, was observed among migrating individuals at Aransas Pass Inlet, and that offshore, small migrating brown shrimp caused a larger $\delta^{13}\text{C}$ range than that found in offshore resident species (Figure 4).

To identify which stations lie on migratory routes, one must distinguish the normal variability expected from local feeding conditions from a higher variability due to migration. Local variation is probably 2.2% or less and 3% or less for composite and individual samples, respectively. These estimates are based on the $\delta^{13}\text{C}$ ranges observed at frequently sampled bay stations, i.e., stations 90, 100, and 102 for composite samples and station 50 for individual samples (Figure 3). Further study will undoubtedly refine these estimates, or, alternatively, future studies may use large differences between shrimp tissue $\delta^{13}\text{C}$ and local food $\delta^{13}\text{C}$ as a criterion to identify locations where migratory activity occurs. These techniques should allow the delineation of underwater migratory routes whose existence has been suggested by Parker (1970).

CONCLUSION

This paper proposes to trace shrimp movements by matching the $\delta^{13}\text{C}$ values of migrating shrimp with the $\delta^{13}\text{C}$ values of shrimp living in habitats such as sea grass meadows and planktonic bays where available shrimp foods, and hence the shrimp themselves, differ substantially in their $\delta^{13}\text{C}$ values. There are several limitations to this method, as well as some advantages. The utility of the method is limited by the number of habitats that $\delta^{13}\text{C}$ analysis can differentiate. Future analyses of other stable isotopes such as hydrogen/deuterium may allow additional distinctions between habitats such as marshes and sea grass meadows. The rapid growth rate of shrimp im-

poses a second limitation. The maximum amount of information about migratory movement is gained by sampling slower growing animals soon after they begin their migrations. For shrimp, sampling males offshore or in migratory passes during the times of peak migrations will give clearest results. Seasonal changes in shrimp $\delta^{13}\text{C}$ occur, but are gradual and can be avoided by sampling during the 1-3 mo peak migration period.

This method should be equally applicable to other migratory animals, both terrestrial and aquatic. Fish movements may be easier to analyze than those of shrimp because of the age-specific $\delta^{13}\text{C}$ historical records that fish lay down in their scales. Such analyses could yield information not only about which areas an animal had fed in, but also at what stage in the life cycle and with what frequency these feeding episodes occurred. The initial data presented for the south Texas coast show that shallow water habitats such as sea grass meadows are important suppliers of shrimp to commercial fisheries. Direct extensions of these investigations should yield quantitative information on which estuarine habitats supply the bulk of shrimp and fish caught in commercial fisheries.

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