

Abstract—Brown shrimp (*Farfantepenaeus aztecus*) are abundant along the Louisiana coast, a coastline that is heavily influenced by one of the world's largest rivers, the Mississippi River. Stable carbon, nitrogen, and sulfur (CNS) isotopes of shrimp and their proventriculus (stomach) contents were assayed to trace riverine support of estuarine-dependent brown shrimp. Extensive inshore and offshore collections were made in the Louisiana coastal zone during 1999–2006 to document shrimp movement patterns across the bay and shelf region. Results showed an unexpectedly strong role for nursery areas in the river delta in supporting the offshore fishery, with about 46% of immigrants to offshore regions arriving from riverine marshes. Strong river influences also were evident offshore, where cluster analysis of combined CNS isotope data showed three regional station groups related to river inputs. Two nearer-river mid-shelf station groups showed isotope values indicating river fertilization and productivity responses in the benthic shrimp food web, and a deeper offshore station group to the south and west showed much less river influence. At several mid-shelf stations where hypoxia is common, shrimp were anomalously ^{15}N depleted versus their diets, and this $\delta^{15}\text{N}$ difference or mismatch may be useful in monitoring shrimp movement responses to hypoxia.

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Mississippi River sustenance of brown shrimp (*Farfantepenaeus aztecus*) in Louisiana coastal waters

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Brown shrimp (*Farfantepenaeus aztecus*) have an estuarine-dependent life history that is well known (Gaidry and White¹). Adults spawn offshore, and postlarvae enter bays to settle as benthic juveniles. The juveniles typically reside in bays for 1–3 months until they reach about 70–100 mm total length, then leave for offshore shelf areas where they may double in length before completing a largely annual life cycle. Both estuarine and offshore phases of this life cycle have been studied in detail; recent shrimp studies in estuaries have focused on loss of marsh nursery habitats (Peterson and Turner, 1994; Haas et al., 2004), and offshore studies have focused on bottom water hypoxia that can impede shrimp migrations and decrease overall habitat area for brown shrimp (Craig et al., 2005).

The brown shrimp fishery of Louisiana is one of the largest fisheries in the United States and occurs downstream of Mississippi River inflows that fertilize the Louisiana coastal zone (Moore et al., 1970). Nutrient loading from the Mississippi River has increased at least 2–4 times in recent decades in contrast to historical background levels (Turner and Rabalais, 1991; Turner et al., 2007), and this increase in fertilization of the coastal zone may be affecting offshore shrimp dynamics. In this study,

stable isotopes were used to trace how the river currently supports brown shrimp populations because isotopes are increasingly used to trace linkages between riverine nutrients and coastal fisheries (Schlacher et al., 2005; Leaky et al., 2008).

The Mississippi River is one of the world's largest rivers in terms of catchment size, total discharge, and sediment load (Deegan et al., 1986; Rabalais et al., 1996). Most of the river flows into northern Gulf of Mexico in the Bird's Foot Delta south of New Orleans, and also into Fourleague Bay west of New Orleans where the Atchafalaya River carries 30% of the river flow into the Gulf of Mexico. During spring and early summer months when brown shrimp are found in coastal bays, most flow of the river is to the west along the coast and has typically high productivity and high chlorophyll levels in the shallow offshore waters within 5–10 km of the barrier islands (Walker and Rabalais, 2006). Eddies force some river water into bays where phytoplankton use nitrates from the river. Tides subsequently export productive phytoplankton to the Gulf of Mexico (Das et al., 2009). The high nutrients and strong water column mixing create conditions for high shrimp productivity that are similar to those observed in shrimp aquaculture ponds, but the coasts and bays are more open and allow extensive brown shrimp migrations at 10–100 km scales. In these open systems, it can be difficult to trace the connections between life history stages and populations that are important for managing fisheries.

¹ Gaidry, W. J., III, and C. J. White. 1973. Investigations of commercially important penaeid shrimp in Louisiana estuaries. LA Wildl. Fish. Comm. Tech. Bull. #8, 154 p. LA Wildl. Fish. Comm., New Orleans, LA.

Previous studies of stable isotopes for offshore brown shrimp were conducted mostly along the south Texas shelf, showing that isotope “tags” allow some estimates about those estuarine habitats that are most important in supporting offshore populations (Fry, 1981, 1983). In particular, seagrass meadows produced shrimp with high $\delta^{13}\text{C}$ values and small shrimp entering the offshore fishery often had these distinctive isotope tags, indicating a strong linkage between inshore seagrass meadows and offshore populations (Fry, 1981). Offshore shrimp populations in Texas waters and the deeper Gulf of Mexico had very uniform carbon isotope values within a 2‰ range, consistent with relatively uniform average isotopic compositions of phytoplankton and phytodetritus that support offshore benthic food webs (Fry, 1983; Fry et al., 1984). Estuarine shrimp had a much greater ($>5\times$) diversity of isotope values, reflecting the much more diverse set of food types supporting benthic food webs in estuaries (Fry, 1981), but shrimp arriving offshore as immigrants gradually lost these divergent estuarine labels and their isotope values converged to relatively uniform offshore values. Experiments showed that this change in isotope label was due to shrimp replacing their old estuarine biomass during normal metabolism, while also acquiring new biomass from offshore foods (Fry and Arnold, 1982). Calculations indicated that a 2–4 \times increase in mass was generally sufficient to lose the estuarine isotope tags for rapidly growing shrimp that had switched to a new diet (Fry and Arnold, 1982; Fry, 2006). This tag loss could occur in 1–3 weeks for smaller-size (<125 mm) shrimp that grow at rates near 1 mm/day and occurs over a longer (3–8 week) period for any larger immigrant animals that grow more slowly offshore, but all immigrants gradually become residents as they acquire the distinctive offshore isotope tags. Experimental and field results thus both indicated that this type of food-related “disappearing” isotope tag had a relatively short life for rapidly growing brown shrimp, but work with the isotope tags was nonetheless interesting because shrimp acquire the isotope tags naturally without handling or stress, all shrimp are tagged instead of just a few, and the isotope tags provide information about origins that is very difficult to obtain otherwise (Fry 1981; 1983; 2008). These initial studies and much subsequent research has shown that isotopes can be used as tracers, tags, or labels for studying animal diets, origins, and movements (Hobson and Wassenaar, 2008; West et al., 2010).

Given that previous studies of shelf areas off Texas and deeper waters of the Gulf of Mexico show uniform carbon isotope values in areas that lack strong river inputs, a comparative examination of isotopes in Louisiana waters was undertaken in the present study to identify river impacts on brown shrimp origins and diets. A first goal was to test origins of shrimp along the Louisiana coast. Seagrass meadows that are hot spots of shrimp abundance in Texas waters are largely lacking along the Louisiana coastline owing to turbid waters, but Louisiana brown shrimp are nonetheless common in open bays and areas near salt marshes.

Brown shrimp are especially abundant in Barataria and Terrebonne bays along the central Louisiana coast and these bays are sampled regularly by personnel of the Louisiana Department of Wildlife and Fisheries (LADWF) to help set various opening and closing dates for shrimp fishing seasons. These bays have relatively little input from the Mississippi River but are often considered the major estuarine source regions for Louisiana shrimp production (Gaidry and White¹). However, during the course of this study brown shrimp were found to be also abundant in delta marshes in the Bird’s Foot Delta around the mouth of the Mississippi River, just to the east of the central coast and Barataria and Terrebonne bays. To test whether bays of the central coast or riverine marshes were more important shrimp source areas for the offshore fishery, small shrimp were collected as they arrived as immigrants to the offshore system and tested for their isotope tags. A second goal of this study was to test for a distinctive riverprint or isotope landscape (“isoscape”; West et al., 2010) by mapping offshore shrimp isotopes to trace river subsidies to benthic food webs. The Mississippi River supplies most ($>90\%$) of the freshwater in the Gulf of Mexico so that any river-related signals could be expected to be stronger in areas closer to the river.

Combinations of C, N, and S stable isotope measurements were investigated as possible tracers of river influences. Carbon isotopes were used to investigate bay origins and linkages to offshore productivity, with low $\delta^{13}\text{C}$ values ($<-18\%$) generally indicating estuarine origins, and highest offshore values (near -15%) indicating higher phytoplankton productivity at the base of the food web (Fry, 1981; Fry and Wainright, 1991). For nitrogen isotopes, studies of nitrates in the Mississippi River show a relatively high average value near 8‰ (Fry and Allen, 2003), so that estuarine food webs incorporating nitrates became enriched in ^{15}N , a bottom-up labeling of whole food webs also observed in other human-impacted systems (Schlacher et al., 2005). Higher $\delta^{15}\text{N}$ was expected for shrimp from river-influenced delta marshes than for shrimp from Barataria and Terrebonne bays that have much smaller river inputs. Sulfur isotopes also can provide an interesting label when high productivity in the water column leads to more organic matter settling to the seafloor and more sulfate reduction in benthic sediments (Peterson and Howarth, 1987). Pelagic plants and animals have high $\delta^{34}\text{S}$ values near the $+21\%$ value of marine sulfate (Rees et al., 1978; Peterson et al., 1985), but sulfides that are produced in sediments from sulfate reduction have low $\delta^{34}\text{S}$ values and enter benthic food webs, resulting in lower $\delta^{34}\text{S}$ values of 5–15‰ for animals such as estuarine brown shrimp (Fry, 2008). Geochemical studies in the northern Gulf of Mexico indicate that most sedimentary sulfides are bound with iron (Lin and Morse, 1991), but it is still possible that some of these sulfides are used by benthic bacteria and enter the organic food web, so that lowest shrimp $\delta^{34}\text{S}$ values might be expected for eutrophic river-influenced areas.

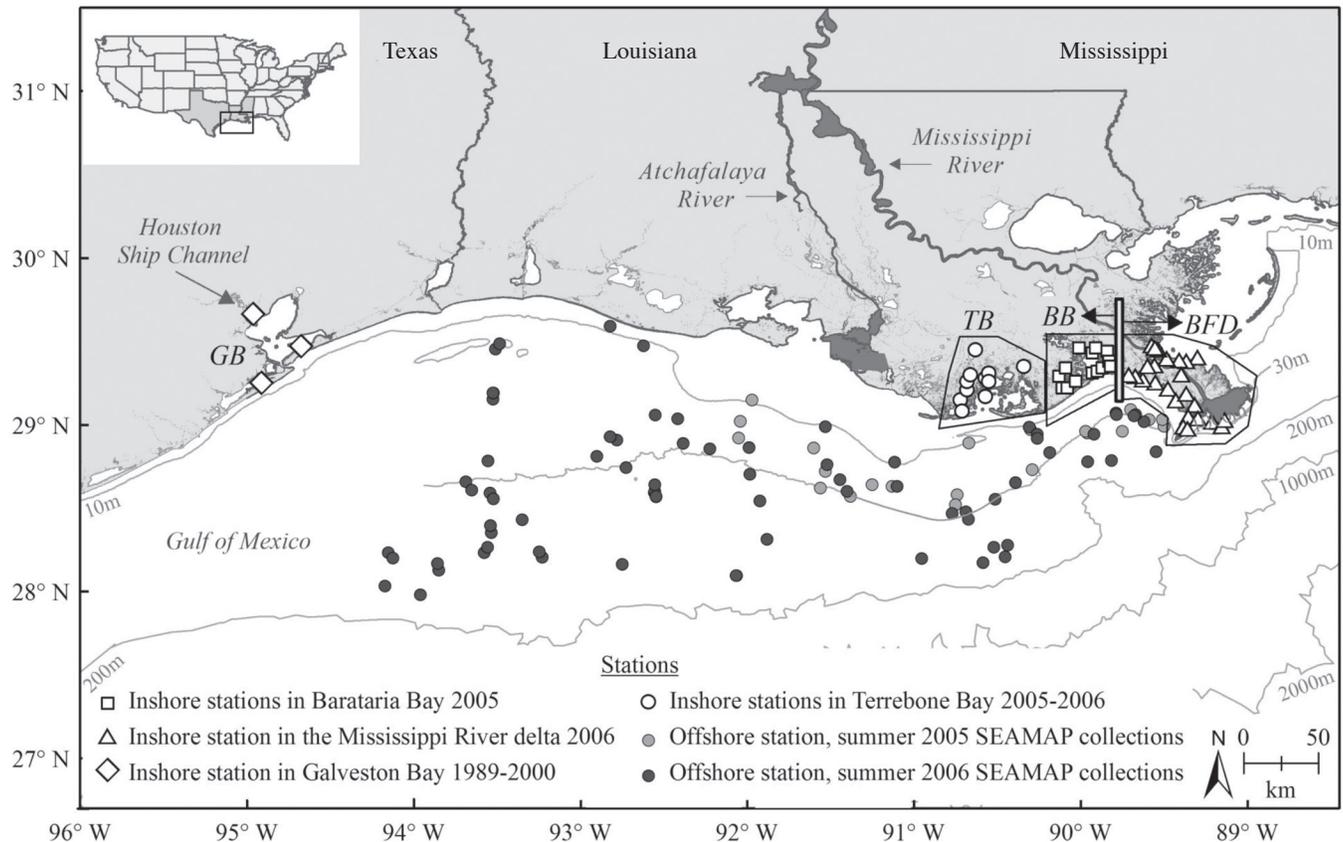


Figure 1

Study area along the Louisiana-Texas coast, northern Gulf of Mexico. River inflows important in this study are the Mississippi River at the Bird's Foot Delta, the Atchafalaya River along the central coast, and the Houston Ship Channel that flows into upper Galveston Bay. GB=Galveston Bay, TB=Terrebonne Bay, BB=Barataria Bay, BFD=Bird's Foot Delta. The north-south dividing line between BB and BFD marks the zero-km reference used in Figure 3. SEAMAP=Southeast Area Monitoring and Assessment Program.

Isotope studies are complementary to taxonomy-based studies of diets and generally show contributions from plants and bacteria in supporting food webs rather than details of predator-prey interactions (Fry, 2006). Taxonomic work was not part of this study but isotope data were collected for the proventriculus (stomach) contents of brown shrimp to help map river support of the benthic food web. The CNS isotope studies reported add to an extensive literature about shrimp isotopic variation in food webs of the Gulf of Mexico (Fry 1981, 1983, 2008; Fry et al., 1984, 2008) and also complement recent studies of stable isotope studies of fish in the northwestern Gulf of Mexico (Roelke and Cifuentes, 1997; Senn et al., 2010).

Materials and methods

Samples were collected from several locations in the northern Gulf of Mexico, from Galveston Bay in the west to the Bird's Foot Delta in the east (Fig. 1). Most samples from Louisiana bays were collected during spring (April and May) brown shrimp trawl surveys

conducted by LADWF in 1999 and 2005 in Barataria and Terrebonne bays. Additional shrimp were collected with seines during June 2006 in Terrebonne Bay and in the Bird's Foot Delta. Offshore animals were collected during the National Marine Fisheries Service June–July summer SEAMAP (Southeast Area Monitoring and Assessment Program) surveys in 2005 and 2006. Offshore station depths declined gradually from 10 m inshore near barrier islands to the 200-m isobath at about 28°N (Fig. 1) and included intermediate mid-shelf areas regularly affected by summer hypoxia (Rabalais et al., 2002). Offshore isobaths run approximately parallel to the coast through most of the study region.

Shrimp were placed on ice and frozen soon after collection for 6–24 months until further processing. A few Galveston Bay samples were analyzed that were collected in previous studies in the 1990s and preserved in formalin (Rozas and Zimmerman, 2000). Preservation in formalin has been shown to influence C and N isotope composition, but not S isotope values (Edwards et al., 2002). Accordingly, isotope values reported here for the Galveston Bay samples have been adjusted by

+1.1‰ for $\delta^{13}\text{C}$ and $-0.5‰$ for $\delta^{15}\text{N}$ to account for the effects of formalin (Edwards et al., 2002).

In the laboratory, shrimp were thawed, total length and blotted wet mass were measured, and white muscle tissue was dissected from the tail area. Muscle tissue was cleaned by rinsing it under running tap water, then soaking the tissue in deionized water in glass vials for 15–60 minutes to remove saltwater. The water used for soaking was discarded, tissues were dried at 60°C, and then pulverized with a Wig-L-Bug automated grinder (Dentsply International, York, PA). Proventriculus contents were obtained by dissection, acidified with 10% HCl, centrifuged, and the stomach contents pellet was kept, and the acid was discarded. To further rinse and remove acid and traces of seawater, the pellet was resuspended with 20 mL of deionized water and then centrifuged again. This rinsing process was repeated three times before final drying of the pellet at 60°C. Shrimp were analyzed as individuals, but proventricu-

lus contents were pooled by station to obtain enough material for analysis. Samples were analyzed according to established procedures for stable C, N, and S isotopic determinations (Fry, 2007, 2008). These procedures involve combustion of samples to CO_2 , N_2 , and SO_2 gases in an elemental analyzer, followed by chromatographic separation and measurement of these gases with an isotope ratio mass spectrometer. Results are reported in δ notation as a ‰ difference from standards according to the formula

$$\delta \text{ (in ‰)} = (R_{\text{SAMPLE}}/R_{\text{STANDARD}} - 1) * 1000,$$

where standards are PDB (PeeDee Belemnite) limestone for $\delta^{13}\text{C}$, nitrogen gas in air for $\delta^{15}\text{N}$, and CDT (Canyon Diablo troilite) for $\delta^{34}\text{S}$, and corresponding R values are $^{13}\text{C}/^{12}\text{C}$, $^{15}\text{N}/^{14}\text{N}$, or $^{34}\text{S}/^{32}\text{S}$ (Fry, 2007).

Possible continued digestion during long-term storage in freezers and repeated washing of acidified proventriculus samples undoubtedly removed some labile organic matter from the proventriculus samples, but samples were treated similarly and used for between-sample and between-station comparisons. Shrimp tissues had low C/N ratios of 3.3–3.7 that were consistent with a mostly protein composition with little lipid content, and consequently no corrections were made to the carbon isotope data for lipid contributions (Fry and Allen, 2003; Post et al., 2007).

Mean values are given with standard errors of the mean (SE), unless otherwise stated. Statistical comparisons among multiple means were made by using Fisher's least significant difference method with significant differences indicated when $P < 0.05$. Cluster analysis was done with the program Statgraphics Plus vers. 5.1 (Statpoint Technologies, Warrenton, VA).

Results

Analysis of CNS isotope values for 969 offshore brown shrimp showed that isotope values of larger animals generally converged to a narrow range that was considered representative of offshore resident animals (Fig. 2). The number of samples was not equal for large and small shrimp (Fig. 2) because of the irregular availability of samples, but the pattern of convergence to much narrower isotope ranges for large animals was the expected pattern and the same as that observed in previous extensive studies of shrimp and fish in the northern Gulf of Mexico (Fry, 1981, 1983). In many cases, smaller shrimp had these same convergent isotope values likely due to early migration from estuaries and rapid growth on offshore diets (Fry, 1981). Divergent isotope values were more interesting, especially for $\delta^{15}\text{N}$, where small animals had values both above and below the values for larger shrimp

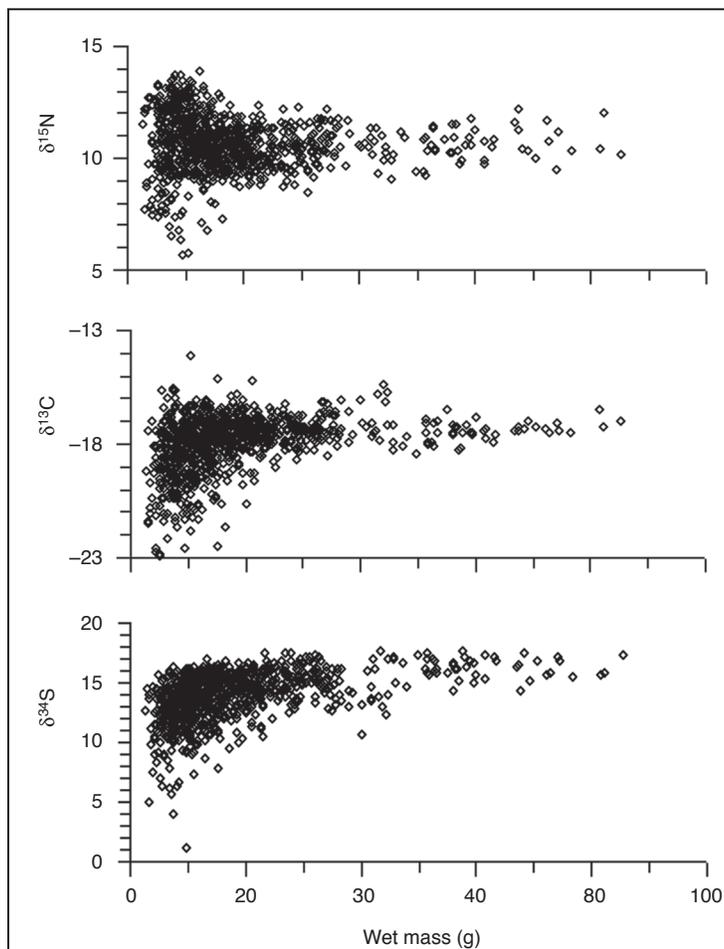


Figure 2

Stable isotope carbon, nitrogen, and sulfur (CNS) compositions ($\delta^{13}\text{C}$, $\delta^{15}\text{N}$, $\delta^{34}\text{S}$; in units of ‰) of brown shrimp (*Farfantepenaeus aztecus*) collected offshore in the Gulf of Mexico in summers of 2005 and 2006.

(Fig. 2). The spread in $\delta^{15}\text{N}$ values for small shrimp was an indication that different estuarine source regions might be involved, source regions with higher and lower $\delta^{15}\text{N}$ values than the offshore values. In contrast, smaller immigrant shrimp with $\delta^{13}\text{C}$ and $\delta^{34}\text{S}$ values divergent from those of the largest offshore animals had values mostly lower than the offshore values, so that estuarine source regions seemed likely to be similar in $\delta^{13}\text{C}$ and $\delta^{34}\text{S}$ values.

Shrimp were collected over several years to test these ideas about possible isotopic differences among estuarine source regions. Surveys of inshore Louisiana bays showed that shrimp from the Bird's Foot Delta had a combination of relatively high $\delta^{15}\text{N}$ values and low $\delta^{13}\text{C}$ values in contrast to shrimp from Terrebonne and Barataria bays (Fig. 3). Highest $\delta^{15}\text{N}$ values were reached in the central delta and extended along the eastern side of the delta. Stations along the northwest side of the delta at the margin of Barataria Bay showed the beginnings of an increase in $\delta^{15}\text{N}$, but the coordinated pattern of higher $\delta^{15}\text{N}$ and lower $\delta^{13}\text{C}$ developed about 20 km farther east of this margin (Fig. 3, Table 1). This same dual isotope pattern of high $\delta^{15}\text{N}$ and low $\delta^{13}\text{C}$ values was also found in another river-influenced bay system, at a station sampled in upper Galveston Bay near inflows from the Houston Ship Channel (Table 1, station Upper Galveston Bay vs. other Galveston Bay stations).

Both shrimp size and isotope information were used to estimate immigrant origins in offshore populations. First, shrimp were selected that were relatively small (125 mm or less, 13 g wet mass or less). These shrimp were closest in size to shrimp collected in inshore bays, where the inshore shrimp averaged 85 mm and 4.7 g wet mass, whereas the <125 mm shrimp collected offshore averaged 109 mm and 9 g wet mass. It was the <125 mm offshore shrimp that were expected to have arrived most recently offshore and therefore best reflect prior feeding in inshore bays (Fry, 1981; Fry and Arnold, 1982), and it was these smaller animals that accounted for most of the variation in the offshore isotope values (Fig. 2). Secondly, the C and N isotope information for large offshore shrimp was used to set bounds or cut-off values expected for resident shrimp that had grown for longer periods of time offshore and had time to equilibrate with the offshore diets. As with approaches used earlier (Fry, 1981, 1983), data for largest shrimp were used as a second criterion to define isotope ranges characteristic for offshore residents, and shrimp >175 mm (>35 g wet mass) ranged from -15.3‰ to -18.4‰ for $\delta^{13}\text{C}$ and from 9.1‰ to 12.2‰ for $\delta^{15}\text{N}$. Overall, offshore residents were defined as >125 mm shrimp with isotope values between -15.3‰ to -18.4‰ for $\delta^{13}\text{C}$ and between 9.1‰ to 12.2‰ for $\delta^{15}\text{N}$. Isotope values for residents fell within the boxes in Figures 4 and 5.

Inshore studies showed that riverine shrimp from the Bird's Foot Delta generally had higher $\delta^{15}\text{N}$ and lower

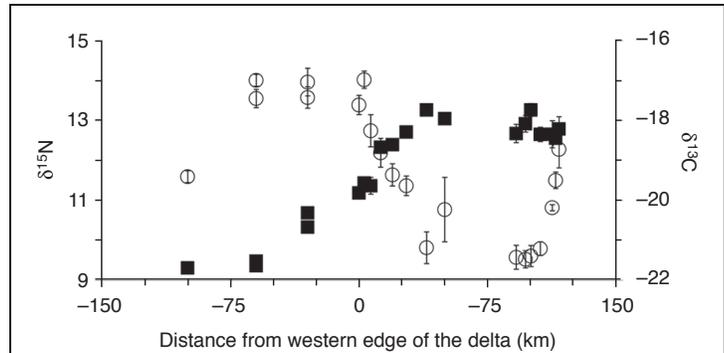


Figure 3

Average $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values (in units of ‰) for inshore brown shrimp (*Farfantepenaeus aztecus*) collected in Terrebonne Bay (-100 km), three regions of Barataria Bay (west bay at -60 km, central bay at -30 km, and east bay at 0 km), and in the Bird's Foot Delta region (5 – 110 km). The north-south dividing line between Barataria Bay and Bird's Foot Delta shown in Figure 1 marks the zero-km reference used here. Values are means \pm standard error from Table 1. Squares represent $\delta^{15}\text{N}$, circles $\delta^{13}\text{C}$.

$\delta^{13}\text{C}$ than resident offshore animals (Fig. 4). Inshore shrimp from Barataria and Terrebonne bays had more diverse isotope values, but always had $\delta^{15}\text{N}$ values less than 11.6‰ (Fig. 4). Based on these isotope distributions, two types of immigrant shrimp to offshore systems were identified: riverine immigrants with high $\delta^{15}\text{N}$ and low $\delta^{13}\text{C}$ ($>11.6\text{‰}$ and $<-18.4\text{‰}$, respectively; solid squares in Fig. 5) and bay immigrants with lower $\delta^{15}\text{N}$ plus $\delta^{13}\text{C}$ values that were outside the range of offshore resident values that were outside the range of offshore resident values (triangles in Fig. 5). A last group of shrimp was considered likely to be resident (open diamonds in Fig. 5, see *Discussion* section).

Over the two years of summer collections, 406 shrimp were collected offshore that were <125 mm, and according to the above isotope-based criteria for distinguishing immigrants and residents, 185 of these shrimp were classified as residents at the time of collection and 221 were immigrants. About 46% of these immigrants had a riverine origin and 54% had a bay origin. The fraction of riverine immigrants was very similar in the two years, 48% in 2005 and 45% in 2006. The <125 mm immigrants were present mostly as mixed populations (bay+riverine+residents) along the inner and mid-shelf, and riverine shrimp were dominant (50% or greater of the <125 mm shrimp) at stations nearest the Bird's Foot Delta and along the central coast at stations to the south and west of the Atchafalaya River (Fig. 6).

The dual isotope label present in shrimp from the Bird's Foot Delta, as high $\delta^{15}\text{N}$ and low $\delta^{13}\text{C}$, was also present in proventriculus contents, i.e., both delta shrimp tissues (Fig. 4) and shrimp diets (Fig. 7) had relatively high $\delta^{15}\text{N}$ and low $\delta^{13}\text{C}$ values. The question was whether this riverine dual label would persist in offshore foods, so that animals feeding offshore might acquire this riverine dual label offshore and thus be

Table 1

Mean isotope values \pm standard error (number of samples, n) for estuarine brown shrimp muscle tissue, 1999–2006, and isotope values for pooled, single samples of pro-ventriculus (prov) contents for brown shrimp (*Farfantepenaeus aztecus*) in the Mississippi River delta. Distance in km is from the western edge of the delta (see Fig. 1).

km	Area	Site	Latitude (°N)	Longitude (°W)	$\delta^{13}\text{C}\%$ muscle	$\delta^{15}\text{N}\%$ muscle	$\delta^{34}\text{S}\%$ muscle	$\delta^{13}\text{C}\%$ prov	$\delta^{15}\text{N}\%$ prov	$\delta^{34}\text{S}\%$ prov
-100	Terrebonne Bay	2005–06 samples			-19.4 \pm 0.1(310)	9.3 \pm 0.1(310)	9.3 \pm 0.2(310)			
-60	Barataria Bay, western stations	1999, 4 western lower bay stations			-17.4 \pm 0.2(32)	9.5 \pm 0.1(32)	9.8 \pm 0.3(32)			
-60		2005, western bay stations			-17.0 \pm 0.2(112)	9.4 \pm 0.1(112)	9.9 \pm 0.1(112)			
-30	Barataria Bay, eastern stations	1999, 4 eastern lower bay stations			-17.0 \pm 0.3(39)	10.3 \pm 0.1(39)	10.4 \pm 0.2(39)			
-30		2005, eastern bay stations			-17.4 \pm 0.3(63)	10.7 \pm 0.1(63)	11.5 \pm 0.1(63)			
0	western Delta				-19.6					
3	Lanaux Island Cut		29.30	89.71	-17.6 \pm 0.2(10)	11.2 \pm 0.1(10)	11.8 \pm 0.4(10)	-20.8	16.0	5.8
7	Shell Island		29.29	89.67	-17.0 \pm 0.2(10)	11.4 \pm 0.2(10)	12.5 \pm 0.3(10)	-20.1	13.7	2.1
13	Shell Island		29.27	89.63	-18.3 \pm 0.4(10)	11.4 \pm 0.1(10)	12.3 \pm 0.2(10)	-19.9	11.0	0.3
20	Scofield Pass Bay		29.25	89.55	-18.8 \pm 0.4(10)	12.3 \pm 0.1(10)	12.1 \pm 0.2(10)	-19.6	13.9	4.5
28	Red Pass		29.22	89.47	-19.4 \pm 0.3(10)	12.4 \pm 0.1(10)	9.7 \pm 0.4(10)	-20.8	16.2	7.5
39	Tiger Pass		29.15	89.43	-19.6 \pm 0.2(10)	12.7 \pm 0.1(10)	9.4 \pm 0.4(10)	-23.1	18.1	11.2
45	West Bay		29.05	89.35	-21.2 \pm 0.4(6)	13.3 \pm 0.3(6)	7.9 \pm 0.6(6)			
	Tiger Pass		29.19	89.36	-20.9 \pm 0.3(5)	14.5 \pm 0.3(5)	3.4 \pm 0.9(5)			
	central and eastern delta									
50	Central East Bay		29.02	89.21	-20.2 \pm 0.8(5)	13.1 \pm 0.2(5)	9.6 \pm 0.4(5)	-24.2	15.0	12.2
92	Baptiste Collette		29.40	89.30	-21.4 \pm 0.3(10)	12.7 \pm 0.2(10)	10.3 \pm 0.4(10)			
97	Grand Bay		29.38	89.37	-21.5 \pm 0.2(10)	12.9 \pm 0.2(10)	11.0 \pm 0.3(10)	-21.5	15.2	4.6
100	Battledore Reef		29.39	89.41	-21.4 \pm 0.3(10)	13.3 \pm 0.2(10)	10.0 \pm 0.4(10)	-22.8	16.3	-0.7
106	Racoon Pass		29.40	89.48	-21.2 \pm 0.2(9)	12.7 \pm 0.3(9)	10.5 \pm 0.3(9)	-23.0	15.5	-1.6
113	California Point		29.45	89.53	-20.2 \pm 0.1(10)	12.7 \pm 0.1(10)	13.4 \pm 0.3(10)	-20.5	14.3	-5.5
115	Mangrove Point		29.30	89.55	-19.5 \pm 0.2(10)	12.6 \pm 0.3(10)	11.7 \pm 0.4(10)			
117	Sunrise Point		29.48	89.57	-18.7 \pm 0.5(10)	12.8 \pm 0.2(10)	11.6 \pm 0.5(10)			
	Galveston Bay									
	Upper Galveston Bay				-19.5 \pm 0.4(18)	13.9 \pm 0.2(18)	8.1 \pm 0.6(16)			
	Sportsmans Road				-15.8 \pm 0.2(9)	8.3 \pm 0.1(9)	5.9 \pm 0.4(9)			
	Oyster Drop				-15.0 \pm 0.3(18)	8.6 \pm 0.1(18)	6.9 \pm 0.3(18)			
	Elmgrove Point				-17.0 \pm 0.2(18)	9.3 \pm 0.2(18)	7.5 \pm 0.4(18)			

misclassified as immigrants from deltaic regions. In a test of this idea, proventriculus contents from near-delta offshore areas (open squares and open triangles in Fig. 7A) were sampled but generally did not show this riverine dual isotope label, i.e., 15 of 16 near-delta samples did not have the dual isotope delta label, but were relatively enriched in ^{13}C and followed the same isotope trend as that found for other samples collected from deeper offshore areas (Fig. 7B). Only one offshore proventriculus sample collected very close to the shore west of the Atchafalaya Delta had the dual-label riverine combination of low high $\delta^{15}\text{N}$ and low $\delta^{13}\text{C}$ (see open triangles with arrows, Fig. 7, A and B).

Because the inshore bay and delta regions contained geographic isoscape distinctions that were useful in following shrimp movements, the offshore data for residents also were examined for possible geographic patterns. Cluster analysis was used to identify separate groups by using multivariate data for 48 stations sampled in 2006 where measurements included CNS isotope values for proventriculus samples and parallel CNS isotope values for muscle samples. For the cluster analysis, the muscle averages were compiled by using only larger animals (>125 mm total length) that, as above, had C and N isotope values within the range of largest (>175 mm) resident animals, and therefore were classified as offshore residents. The resulting cluster analysis identified three general regional offshore groups of shrimp: two mid-shelf groups inshore and closer to the river, and one offshore group farther away from the river to the south and west (Fig. 8). The two mid-shelf groups were mostly in or near the area identified by Rabalais et al. (2002) as regularly affected by summer hypoxia and linked to inputs from the Mississippi River (Fig. 8, polygon), whereas the offshore group was largely on the southwest side of this region, away from river inputs (Fig. 8). The offshore group was significantly different in average isotope values from the inshore group in all cases for the mid-shelf transition group and in all but one case for the mid-shelf hypoxic group (Table 2).

Relative to this offshore group, the mid-shelf groups both showed significant enrichment in proventriculus ^{15}N and ^{13}C , and depletion in ^{34}S (Fig. 9,

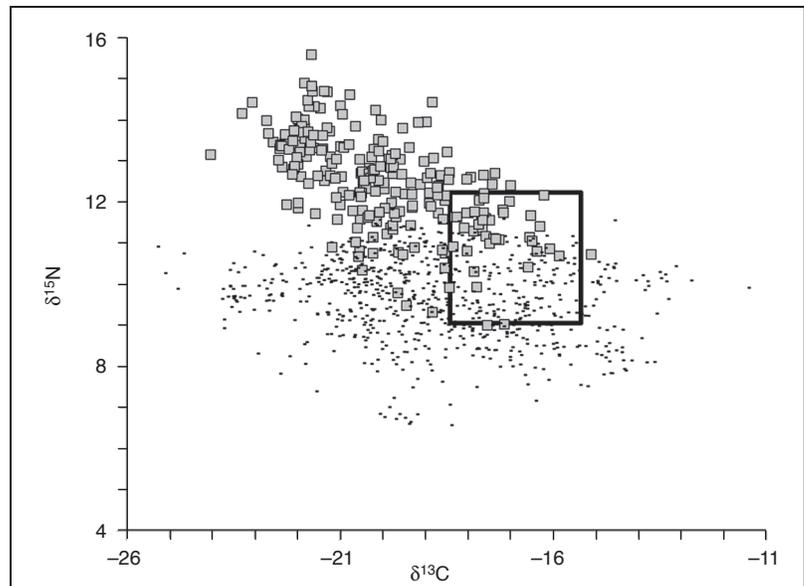


Figure 4

$\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values (in units of ‰) for inshore-collected brown shrimp (*Farfantepenaeus aztecus*). Shrimp collected in the delta (gray squares) had higher $\delta^{15}\text{N}$ than shrimp collected from Barataria and Terrebonne bays (small bars). Box indicates range of values observed in the largest (>175 mm) offshore resident shrimp.

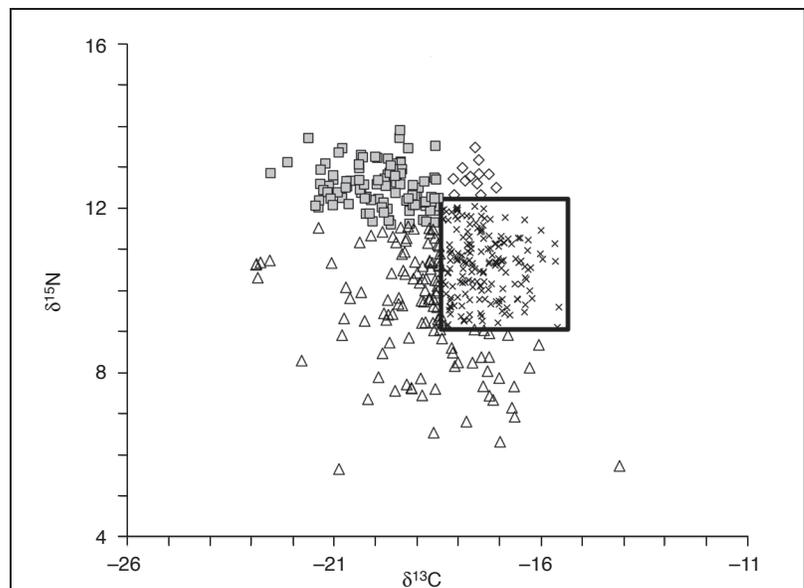


Figure 5

$\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values (in units of ‰) for smaller brown shrimp (*Farfantepenaeus aztecus*) (<125 mm total length) collected offshore and that had recently arrived from inshore estuaries. Shrimp were classified into three groups by considering the combined $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ data: riverine shrimp (gray squares), bay shrimp (triangles), residents (x's and diamonds, with diamonds indicating likely residents of the hypoxic zone, see Discussion section). The boxed values indicate the range of values observed in largest (>175 mm) offshore resident shrimp.

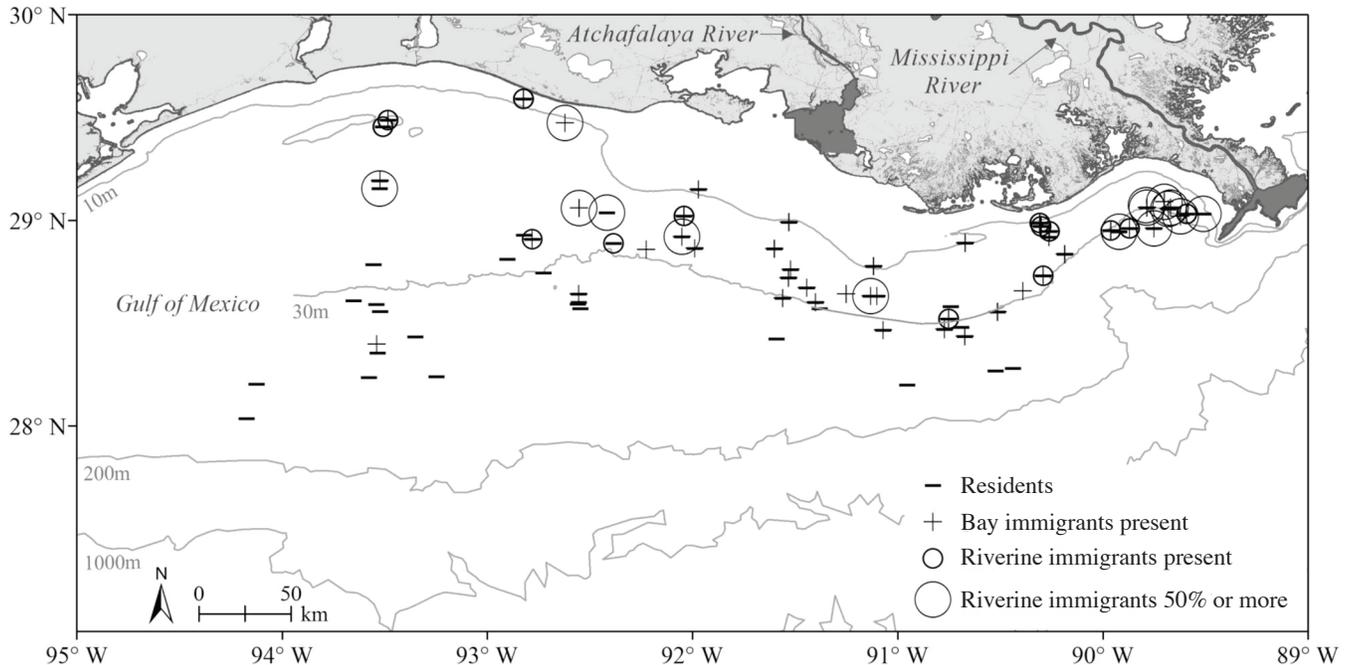


Figure 6

Offshore locations in the Gulf of Mexico where smaller (<125 mm) brown shrimp (*Farfantepenaeus aztecus*) were captured as immigrants from estuaries. Symbols indicate inferred origins of these shrimp.

Table 2), a triple isotope label associated with higher primary productivity (see *Discussion* section). These proventriculus isotope labels were strongest in the more inshore of the two groups (Fig. 9), namely the mid-shelf hypoxic group, and $\delta^{15}\text{N}$ values in the proventriculus contents were significantly higher in this group than in the offshore and mid-shelf transition group (Table 2). When all proventriculus samples were considered together, C and S isotopes were significantly ($P < 0.01$) and linearly correlated with N isotopes (Fig. 10), consistent with mixing between two food sources across the shelf. The correlation of S and C isotopes for these samples also was significant ($P < 0.01$, data not shown).

The mid-shelf and offshore station groups (Fig. 8) differed in their patterns of trophic enrichment factors (TEFs) (the difference between isotopes measured in consumers and their diets, i.e., $\text{TEF} = \text{muscle } \delta - \text{proventriculus } \delta$). Average TEFs for the most offshore group were close to expected (Peterson and Fry, 1987) at 2.8‰ and 0.2‰, respectively, for $\delta^{15}\text{N}$ and $\delta^{34}\text{S}$, but relatively high at 5.2‰ for $\delta^{13}\text{C}$ (Table 2). Inshore groups differed significantly from these offshore TEF values, notably with significantly lower nitrogen isotope TEF values for the mid-shelf groups (Table 2). For the more inshore of the two mid-shelf groups, average nitrogen isotope TEF values were unexpectedly negative (-2.2‰) because many proventriculus $\delta^{15}\text{N}$ values were >10.7‰ and therefore were higher than the average values for offshore resident shrimp (Table 2, Fig. 8, circled points).

Discussion

There are many reasons to expect strong river support of brown shrimp production, ranging from the riverine construction of inshore habitats by natural long-term delta-building processes to more recent river and nutrient-enhanced primary productivity of the offshore ecosystem (Deegan et al., 1986; Bierman et al., 1994; Green et al., 2008). Summer surface salinities are 20–33 psu across most of the study area owing to the enormous freshwater inputs from the Mississippi River, so that Louisiana brown shrimp exist in a river-influenced marine ecosystem. The river water affects the isotope biogeochemistry of receiving waters, adding nitrates with high $\delta^{15}\text{N}$ and dissolved inorganic carbon with low $\delta^{13}\text{C}$ (Fry and Allen, 2003). Primary productivity and the wider shrimp food webs seemed to respond to these basal isotope changes in a straightforward way, with shrimp having high $\delta^{15}\text{N}$ and low $\delta^{13}\text{C}$ in the Bird's Foot Delta region that was most influenced by the river. This same pattern of a riverine dual isotope label may be fairly general in human-influenced estuaries and was observed, for example, in shrimp from Galveston Bay at a low salinity station in the upper bay (Table 1) influenced by freshwater inflows from the urban Houston Ship Channel. The more negative average $\delta^{13}\text{C}$ values of -18.5‰ or less that characterize these systems seem to develop for brown shrimp in planktonic bays of the Gulf of Mexico when salinities are <20 psu (Fry, 1981, 1983). There is less local information for the Gulf of Mexico about the determinants of spatial $\delta^{15}\text{N}$

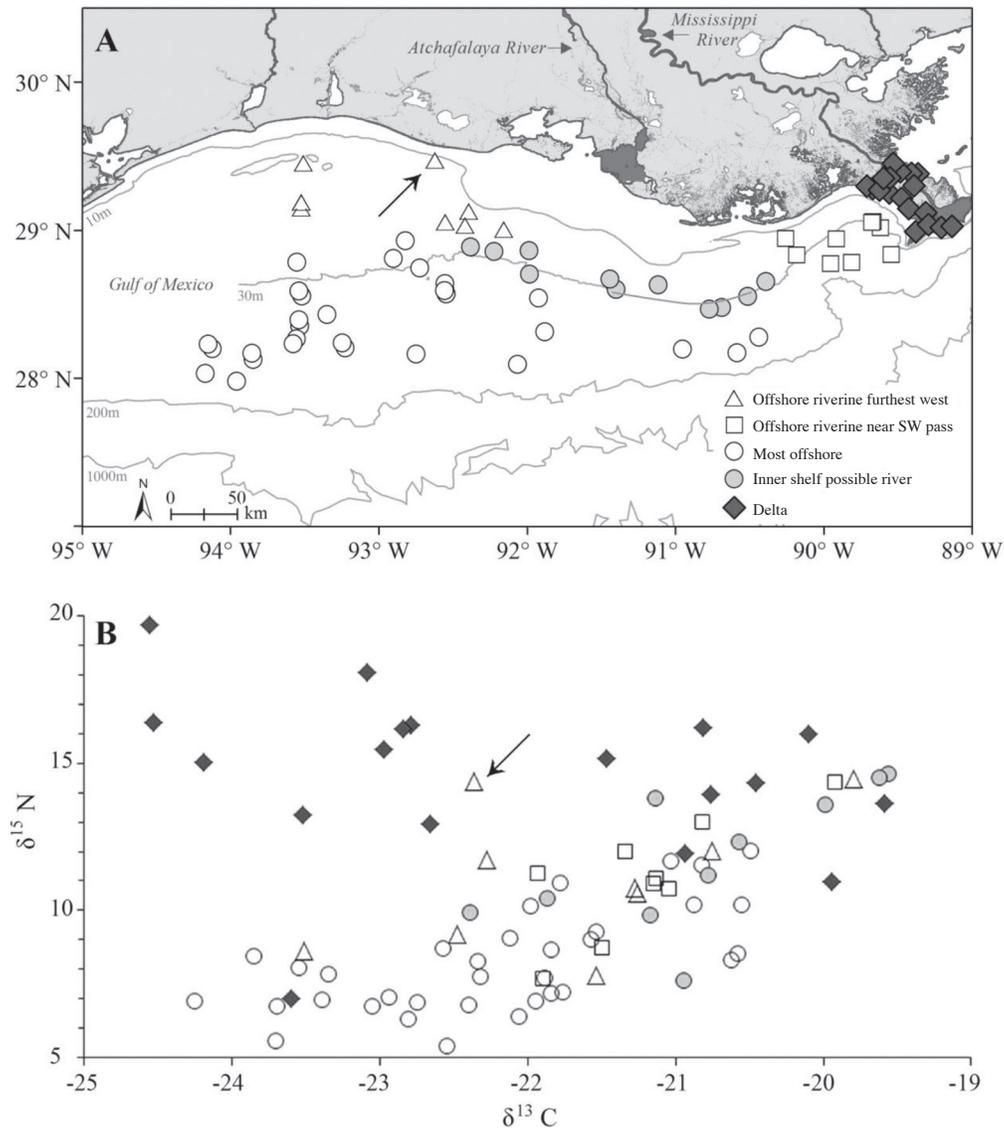


Figure 7

$\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values (in units of ‰) of proventriculus (gut content) samples collected in 2006. (A) Locations of sample collections. (B) Isotope values of samples. Arrows indicate the location (A) and isotope value (B) of the single offshore proventriculus sample that had isotope values similar to those of riverine samples (black diamonds) in the Bird's Foot Delta, as presented in the *Results* section.

patterns, but it is noteworthy that in the Bird's Foot Delta region, the high $\delta^{15}\text{N}$ values for brown shrimp extended over a greater distance than did the low $\delta^{13}\text{C}$ values (Fig. 3). Stated another way, C isotope values returned to marine values more quickly than did N isotope values at both ends of the delta (Fig. 3). This difference between the N and C isotope patterns is expected because river N nutrient concentrations are very high and dominate freshwater-marine mixing dynamics (Fry, 2002). In contrast, river and marine sources have fairly similar inorganic carbon concentrations, so that riverine signals are diluted much more quickly for C than for N.

Riverine shrimp with the unique CN isotope tags of high $\delta^{15}\text{N}$ and low $\delta^{13}\text{C}$ accounted for about half of the recent immigrants arriving offshore. There is little independent tagging information that could validate this isotope estimate. LADWF does not sample low-salinity habitats in the Bird's Foot Delta and instead focuses on routine sampling of Barataria and Terrebonne bays of the central Louisiana coast to help set the periods for shrimp season openings and closings. River-influenced areas along the Bird's Foot Delta are not given a special focus by LADWF, but the isotope estimates from the present study may indicate that they deserve more focus in future work. This may be

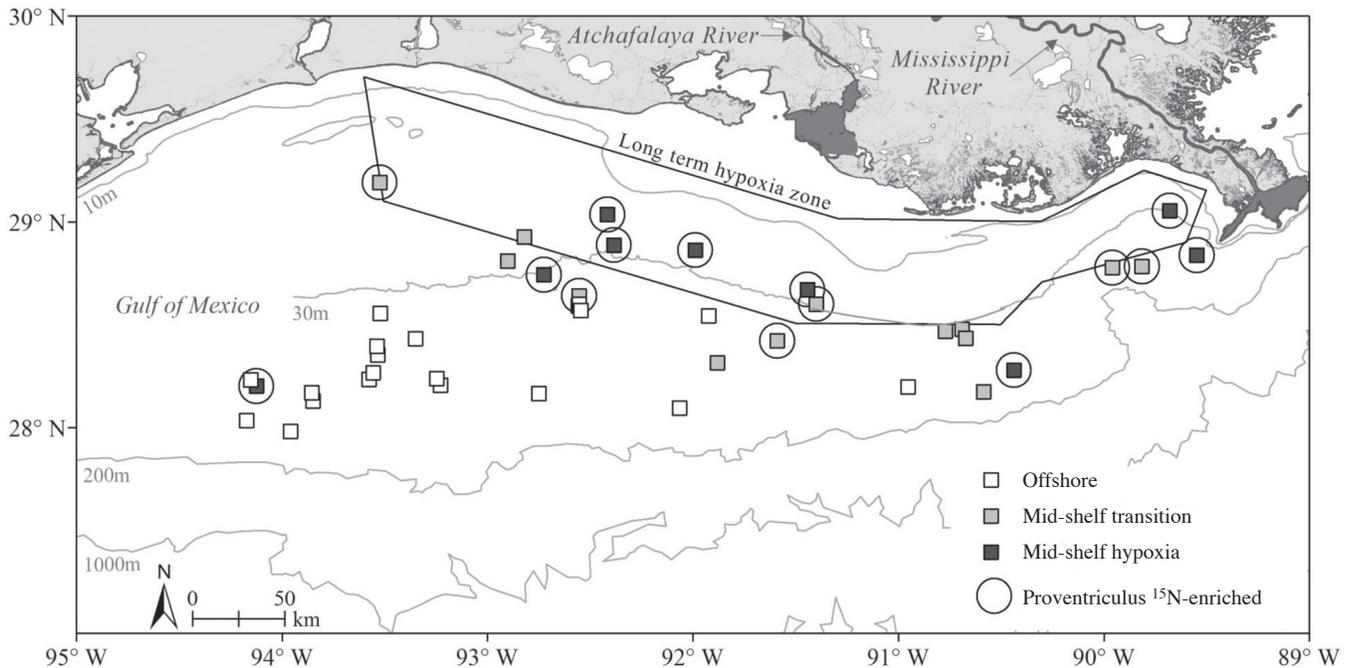


Figure 8

Station groupings from cluster analysis of samples from 2006. Circled points had ^{15}N -enriched proventriculus $\delta^{15}\text{N} > 10.7\text{‰}$, greater than average values for offshore resident brown shrimp (*Farfantepenaeus aztecus*). The polygon indicates the area of the long-term hypoxic zone documented by Rabalais et al. (2002), where hypoxia is present in $>25\%$ of summer surveys. Symbols indicate station groupings identified by cluster analysis.

especially true because of loss of inshore habitat in the Bird's Foot Delta (Britsch and Dunbar, 1993). Estimates for riverine shrimp contributions to offshore fisheries were very similar for 2005 and 2006, with 2005 having average river discharge and 2006 having about 60% average discharge (<http://www.mvn.usace>.

[army.mil/cgi-bin/watercontrol](http://www.army.mil/cgi-bin/watercontrol), accessed July 2010). The similar riverine contributions in the two different years may mean that it is the long-term structure of the deltaic marsh-bay platform rather than the annual river inputs that is more important for the shrimp supply to the offshore fishery.

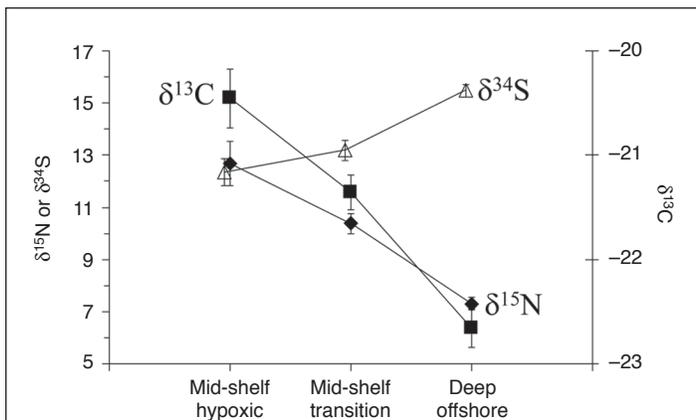
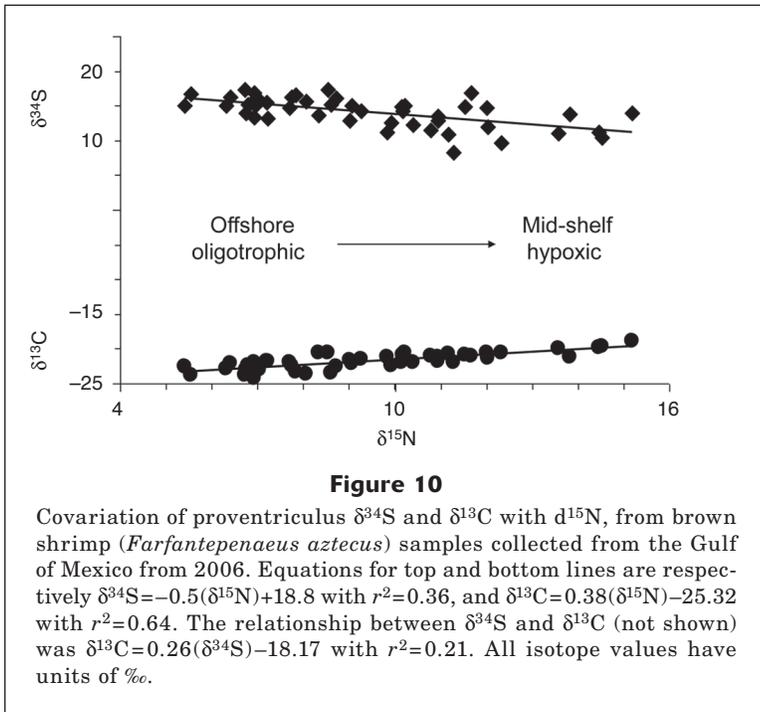


Figure 9

Trends in relation to depth for stable isotope averages (± 1 standard error) in proventriculus contents of brown shrimp (*Farfantepenaeus aztecus*) collected from the Gulf of Mexico in 2006 (see also Table 2).

There are various reasons why the isotope estimates presented here could be overestimates for the contributions of riverine shrimp to offshore populations. For example, inshore sampling showed that both riverine and bay shrimp populations produce some shrimp that have the same isotope values as resident offshore shrimp (Fig. 4). The isotope accounting done here thus underestimates the contributions of the inshore populations, and if this underestimate is more severe for bay than riverine shrimp, this would lead to the apparent strong contribution of riverine shrimp. In the extreme, if all of the <125 mm offshore shrimp with isotope values inside the resident box of Figure 5 were actually misclassified and instead were all bay shrimp, the contribution of riverine shrimp would decline from 46% to 25%. Further research should include samples nearer the mouths of bays to check whether most animals leaving bays already have isotope values classified here as resident offshore shrimp, but in the end, even a 25% contribution of riverine shrimp is probably noteworthy for management purposes.



Offshore phytoplankton productivity studies in Mississippi River plumes generally show ^{13}C -enriched values for particulate organic matter formed in inshore and mid-shelf regions (Fry and Wainright, 1991; Fry unpubl. data), so that the dual isotope tag of low $\delta^{13}\text{C}$ and high $\delta^{15}\text{N}$ used to source riverine shrimp seemed largely confined to estuaries and was only rarely present offshore (Fig. 7).

It is also possible that bays in adjacent Texas and other northern Gulf states supply some shrimp to the offshore Louisiana system. But those shrimp would likely have been offshore for extended periods of time and therefore would have been counted as residents in this study. Thus possible contributions from other states should have little effect on the estimates given above for bay and riverine contributions to Louisiana shrimp stocks.

It also was evident that estuarine conditions prevail offshore in this river-influenced shelf ecosystem that is often considered an offshore estuary. Isotopic compositions of shrimp and proventriculus contents followed the same triple isotope gradients involving high $\delta^{13}\text{C}$, high $\delta^{15}\text{N}$, and low $\delta^{34}\text{S}$ nearest the river, vs. low $\delta^{13}\text{C}$, low $\delta^{15}\text{N}$, and high $\delta^{34}\text{S}$ offshore. These gradients were largely aligned with other offshore features associated with the river, notably finfish biomass (Moore et al., 1970) and hypoxia (Rabalais et al., 2002). It is possible that some of these isotope gradients reflect normal depth-related onshore-offshore productivity gradients not associated with rivers, and this idea should be addressed in future comparative work involving continental shelf systems with little river influence. Initial data for the Texas shelf have shown some cases of onshore-

Table 2

Mean isotope values (‰ ± standard error of the mean) for brown shrimp (*Farfantepenaeus aztecus*) muscle tissue, proventriculus contents, and trophic enrichment factor at three offshore station groups in 2006. Muscle averages are for resident animals >125 mm and whose isotope values are within the isotope ranges set by animals >175 mm, as discussed in the text. Different superscript letters for mean values in a column indicate that values are significantly different ($P < 0.05$). n = number of samples.

	Muscle tissue			Proventriculus contents			Trophic enrichment factor		
	$\delta^{13}\text{C}$	$\delta^{15}\text{N}$	$\delta^{34}\text{S}$	$\delta^{13}\text{C}$	$\delta^{15}\text{N}$	$\delta^{34}\text{S}$	$\delta^{13}\text{C}$	$\delta^{15}\text{N}$	$\delta^{34}\text{S}$
Offshore ($n=22$)	-17.43 ± 0.04 ^A	10.15 ± 0.06 ^A	15.7 ± 0.2 ^A	-22.7 ± 0.2 ^A	7.3 ± 0.2 ^A	15.5 ± 0.2 ^A	5.2 ± 0.2 ^A	2.8 ± 0.2 ^A	0.2 ± 0.2 ^A
Mid-shelf transition ($n=14$)	-17.18 ± 0.07 ^B	10.61 ± 0.11 ^B	14.5 ± 0.2 ^B	-21.4 ± 0.2 ^B	10.4 ± 0.4 ^B	13.2 ± 0.4 ^B	4.2 ± 0.1 ^B	0.2 ± 0.4 ^B	1.3 ± 0.4 ^B
Mid-shelf hypoxic ($n=10$)	-17.30 ± 0.06 ^{AB}	10.53 ± 0.13 ^B	14.0 ± 0.5 ^B	-20.5 ± 0.3 ^C	12.7 ± 0.5 ^C	12.3 ± 0.9 ^B	3.2 ± 0.3 ^C	-2.2 ± 0.5 ^C	1.7 ± 0.7 ^B

offshore and seasonal C isotope changes in shrimp (Fry et al., 1984), but N and S isotope changes have not yet been systematically investigated. Comparative work might also focus on other river-influenced shelf systems and one recent study of the Thames River estuary (Leakey et al., 2008) has shown the same triple isotope riverine-offshore gradients observed in this study for the Mississippi River. Because of these similar results for the Thames River, and because the pattern of isotope signals is consistent with a riverine source with high $\delta^{15}\text{N}$, it seems likely that the Mississippi River is forcing many of the isotope signals observed on the Louisiana shelf.

The three regional shelf groups shown in Figures 8 and 9 were identified by cluster analysis by using three proventriculus isotope variables and three muscle isotope variables. These six variables were used in concert for two reasons. First, the separated proventriculus and muscle results each gave strong mid-shelf vs. offshore patterns (see significant differences among averages in Table 2), and therefore results could be legitimately combined for a stronger overall assessment. Second, the proventriculus and muscle samples show somewhat different aspects of shrimp biology and available diets, with proventriculus samples providing stronger local information and muscle samples providing stronger time-integrated samples. On the negative side, the proventriculus samples are often the leftovers after digestion and can include inorganic sediment grains with pyritic sulfides (Howarth, 1979, 1984), whereas muscle samples are taken from shrimp that are mobile and may reflect diets from another place. Because there were both positive and negative aspects to using the separated proventriculus and muscle isotope data, the combined data (Table 2) were used to reach a balanced overall assessment in the cluster analysis.

The offshore C isotopes showed a broad pattern of river influence across the inshore and middle shelf, consistent with wide dispersal of carbon from river-influenced planktonic primary producers. The riverine influence was expressed as higher $\delta^{13}\text{C}$ values in a mid-shelf maximum standing out against a background of lower $\delta^{13}\text{C}$ values both in shallower bays and in deeper offshore waters (Tables 1 and 2, Fig. 9). Higher $\delta^{13}\text{C}$ values are found associated especially with high productivity and diatom blooms (Fry and Wainright, 1991; Fry, 1996)—conditions that regularly occur on the Louisiana shelf that is affected by Mississippi River inputs (Rabalais et al., 1996; Dagg et al., 2007; Green et al., 2008). The deeper shelf to the south and west had lower $\delta^{13}\text{C}$ consistent with lower primary productivity (Fry and Boyd, 2010).

The offshore S isotopes were perhaps the most expected results, showing a consistent onshore-offshore gradient in both proventriculus and muscle $\delta^{34}\text{S}$ values (Table 2, Fig. 9). These gradients likely originate with river-induced organic carbon gradients in primary productivity that subsequently fuel benthic sulfate reduction and sulfide production in underlying sediments.

The exact mechanism of sulfide incorporation into benthic food webs is still unknown but is likely the use of sulfides by bacteria growing in bottom sediments. Hypoxia may increase aspects of sulfide cycling, especially by decreasing the importance of oxygenic decomposition reactions while increasing the importance of anaerobic reactions such as sulfate reduction and sulfide production. Hypoxia also may decrease oxidation reactions that consume sulfide, and decreased infaunal activity and decreased bioirrigation in sediments may also occur when bottom waters become hypoxic (Eldridge and Morse, 2008). In sum, hypoxic conditions may promote more anaerobic conditions, more sulfide production and accumulation, and stronger bacterial uptake of sulfides into benthic food webs.

The N isotope results were quite surprising in the very high $\delta^{15}\text{N}$ values (up to 15.2‰) found for some proventriculus content samples in the mid-shelf hypoxic region—values that were higher than those for shrimp muscle. Ongoing studies show no large ^{15}N enrichment in particulate organic nitrogen samples collected in the water column in the offshore region, where values average 6–8‰ (Wissel et al., 2005; Fry, unpubl. data). In the absence of a planktonic origin, the source of the high $\delta^{15}\text{N}$ values likely is in the benthos. Brown shrimp are benthic carnivores that consume polychaetes and meiofauna (McTigue and Zimmerman, 1998; Fry et al., 2003), and offshore brown shrimp generally rely on a benthic food web with bacterial contributions. York et al. (2010) have speculated that nitrogen cycling in the benthos is leading to high $\delta^{15}\text{N}$ values of benthic bacteria, perhaps with some bacterial use of ^{15}N -enriched ammonium left over from nitrification or anammox reactions. Such processes are likely ubiquitous in shelf sediments, but details that are still to be elucidated could make these processes much more dominant in the low-oxygen mid-shelf hypoxic region. High $\delta^{15}\text{N}$ values were also found in inshore shrimp and proventriculus contents from the Bird's Foot Delta region (Table 2), and the common denominator leading to these high $\delta^{15}\text{N}$ values is likely eutrophic deposition of large amounts of organic phytodetritus to the benthos. $\delta^{15}\text{N}$ values >15‰ have also been observed in Mississippi River zebra mussels during summer, where high animal $\delta^{15}\text{N}$ values have been correlated with low ammonium concentrations in the river (Fry and Allen, 2003).

Whatever the mechanism underlying the high $\delta^{15}\text{N}$ values, it was evident that the proventriculus $\delta^{15}\text{N}$ values were often higher than those of offshore shrimp eating these foods (Table 2). Previous work with estuarine brown shrimp has shown that brown shrimp normally have positive trophic enrichment factors (TEFs) averaging about 2.3‰ higher than proventriculus contents $\delta^{15}\text{N}$ (Fry et al., 2003), and a similar average TEF of 2.8‰ was observed for the most offshore shrimp of the present study (Table 2). The observed opposite pattern of negative TEF values for some mid-shelf shrimp likely means that these shrimp have not spent the several weeks (that can be calculated from diet turnover dynamics) (Fry and Arnold, 1982) that they would need

in the hypoxic zone to come to equilibrium with the ^{15}N -enriched foods. This idea is reasonable given recent fisheries studies that show hypoxia is often displacing brown shrimp populations to areas of higher bottom-water oxygen (Craig and Crowder, 2005; Craig et al., 2005). In future studies, the disequilibrium or mismatch between shrimp and proventriculus $\delta^{15}\text{N}$ may help identify areas that do not continuously sustain brown shrimp populations. Areas where proventriculus $\delta^{15}\text{N}$ is higher than shrimp muscle $\delta^{15}\text{N}$ may be less suitable habitat that can be visited only briefly by brown shrimp. The isotope signals in diets of brown shrimp and their prey are built up over several weeks, so that the isotope measurements may provide longer-term information about shrimp use of hypoxic areas than do trawls that provide a more instantaneous snapshot of how brown shrimp are using an area (Craig et al., 2005).

However, occasional feeding in the hypoxic area should lead to somewhat elevated $\delta^{15}\text{N}$ values, so that higher $\delta^{15}\text{N}$ could develop in offshore resident shrimp. Several offshore shrimp were observed with high $\delta^{15}\text{N}$ that could indicate some feeding in the hypoxic zone. These animals also had high $\delta^{13}\text{C}$ values (less negative than -18‰ ; open diamonds in Fig. 5) expected for offshore residents rather than for migrants from inshore regions, and were accordingly classified as offshore residents for purposes of estimating movement and inshore contributions to offshore fisheries.

An interesting feature of this study was that offshore brown shrimp diets appeared to be linear mixtures between two sources, and variation in the source contributions accounted for most of the isotopic variation across the shelf (Fig. 10). The nature of these sources is not completely clear and may involve multiple factors. For example, high $\delta^{15}\text{N}$ values may reflect both a high value of Mississippi River nitrate at the base of coastal food webs (Fry and Allen, 2003; Wissel and Fry, 2005), and the presence of high trophic level consumers in the proventriculus contents. Conversely, low $\delta^{15}\text{N}$ may reflect relatively low values for offshore marine nitrate and prey from low trophic levels. Unfortunately, isotope values for specific prey taxa have not yet been measured for this shelf ecosystem, and therefore trophic-level effects for isotopes cannot be directly evaluated. Nonetheless, some inferences can be made from the measured isotope data for shrimp and their proventriculus contents, as follows.

The farthest offshore animals had high $\delta^{34}\text{S}$ values (Table 2) characteristic of mostly plankton-derived sulfur in the diet, with little contribution of benthic sulfides. These high $\delta^{34}\text{S}$ values are consistent with relatively oligotrophic conditions across the deeper shelf, and with lower $\delta^{34}\text{S}$ values indicating more eutrophic conditions inshore. Carbon isotope TEFs between offshore shrimp and proventriculus contents were surprisingly large at $3.2\text{--}5.2\text{‰}$ (Table 2), especially compared to the general expectation that the carbon isotope TEF is near 0‰ for animals and their diets (Peterson and Fry, 1987) and compared to a

measured carbon isotope TEF near 1‰ for estuarine Louisiana brown shrimp (Fry et al., 2003). The offshore shrimp muscle $\delta^{13}\text{C}$ values are fairly constant near -17.3‰ , so that it is the very negative proventriculus values that lead to the large observed TEFs. Nonetheless, the proventriculus $\delta^{13}\text{C}$ values are near the long-term -22‰ value associated with offshore marine primary production (Fry and Sherr, 1984), and may represent a realistic marine background value. If this is the case, then mass balance calculations would indicate that the labile foods near -17.3‰ that are being assimilated out of the -22‰ marine background are likely a small part of the proventriculus contents. A consistent picture for the C and S results is that background, low-productivity pelagic conditions determine the food availability at the offshore stations, but labile fractions that are depleted in ^{34}S and enriched in ^{13}C are increasingly found in the proventriculus contents at the more eutrophic inshore stations (Fig. 10). These ideas need further study with taxonomic analyses of prey and with further studies on isotope changes during assimilation of offshore foods (Fry et al., 1984).

In conclusion, further studies of both CNS isotopes and proventriculus contents in offshore brown shrimp could supplement annual summer water quality assessments of hypoxia and help determine hypoxia effects on living resources. Brown shrimp transit the mid-shelf hypoxic areas and isotopes in shrimp caught offshore show strong spatial signals that likely vary between years with high and low river flow. Isotope signals have been used as early warning indicators of the effects of eutrophication in coastal bays (McClelland et al., 1997), and it is possible that monitoring shrimp isotopes may help assess the effects of hypoxia on Louisiana shrimp populations. Adding benthic shrimp isoscape monitoring to ongoing water quality monitoring programs generally may be helpful for understanding changes in fisheries productivity and animal movements in this and other river-influenced marine ecosystems (Leakey et al., 2008).

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