

## Examination of coupling between primary and secondary production in a river-dominated estuary: Apalachicola Bay, Florida, U.S.A.

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### Abstract

To examine the influence of river-borne organic material on estuarine communities, we conducted a dual stable isotope study in an estuary heavily influenced by alluvial runoff. Despite significant alluvial influence, secondary production in Apalachicola Bay depends more upon estuarine primary production than upon a detrital food web supported by floodplain primary production. Two simple mixing models, floodplain–marine and floodplain–estuarine, indicated that the upper limits for the contribution of terrestrial organic matter to estuarine consumer diets averaged 37, 25, and 27% and 20, 19, and 25% for East Bay, Cat Point, and Dry Bar, respectively. Systematic  $\delta^{13}\text{C}$  variation of consumer organisms was found for differing locations and attributed to increasing influence of terrestrial organic matter and  $^{13}\text{C}$ -depleted dissolved inorganic carbon (DIC) closer to the river mouth. The  $\delta^{34}\text{S}$  data exhibited significant variation with river flow that was attributed to an admixture of terrestrial floodplain detritus with estuarine and marine organic matter. Both  $\delta^{13}\text{C}$  and  $\delta^{34}\text{S}$  isotope data demonstrated clear distinctions between benthic and water column feeding types. Our results suggest that the estuary is dependent on riverine inflows to provide floodplain detritus during the high-flow period and dissolved nutrients for estuarine primary productivity during the low-flow season. Any alteration of river hydrology may adversely affect estuarine secondary production, especially during the low-flow period when the estuary is dependent on input of dissolved nutrients to maintain a high level of primary productivity.

Seminal works by Darnell (1958, 1961) and Odum and Heald (1972) focused on the role of detritus in the diets of a variety of fishes and macroinvertebrates. Yet, despite these and numerous other more recent feeding studies, the importance of organic detritus in providing nutritional support for estuarine food webs remains unclear. With the advent of stable isotope techniques, our understanding of the origins and flows of organic matter in estuarine, salt marsh, and near-shore environments has been greatly improved (Haines and Montague 1979; Fry 1983, 1988; Peterson et al. 1985, 1986; Peterson and Howarth 1987; Deegan et al. 1990; Newell et al. 1995; Deegan and Garritt 1997; Kwak and Zedler 1997; Moncreiff and Sullivan 2001). Initially the technique was employed, using carbon alone, to question the idea that detritus from *Spartina alterniflora* marshes was driving productivity in a Georgia estuary (Haines 1977). With the use

of multiple stable isotope tracers, it has been shown that *Spartina* detritus, estuarine phytoplankton, and benthic microalgae are all important primary producers supporting marsh and estuarine secondary production (Peterson and Howarth 1987; Sullivan and Moncreiff 1990; Currin et al. 1995; Deegan and Garritt 1997; Kwak and Zedler 1997; Stribling and Cornwell 1997).

Studies of food web relationships in seagrass meadows have also questioned the long-standing idea that detritus is a dominant source of organic matter for many estuarine animals (Thayer et al. 1978; Fry 1984; Kitting et al. 1984; Fry et al. 1987). In a multiple stable isotope study of trophic dynamics in seagrass beds in Mississippi Sound, Moncreiff and Sullivan (2001) determined that the importance of detritus of the seagrass *Halodule wrightii* was minimal and that the food web was supported primarily by seagrass epiphytes, benthic microalgae, and phytoplankton. Stable isotope results were supported by direct measurements of epiphytic primary production (Moncreiff et al. 1992). All studies, however, have not shown such clear dominance of seagrass epiphytes over seagrass blades in supporting the consumer populations of meadows (e.g. Fry and Parker 1979; Zieman et al. 1984; Fry et al. 1987).

The picture of trophic organization that is emerging is one that deemphasizes the role of detritus whether it is from terrestrial POM, marsh macrophytes, or seagrass. There appears to be a greater role for phytoplankton, benthic microalgae, and seagrass epiphytes. The importance of terrestrial inputs, however, has not been fully examined. Peterson and Howarth (1987) were unable to detect organic matter inputs from terrestrial sources as contributors to the food

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chain of Georgia estuaries. However, they suggested that work be carried out “nearer the mouth of several major rivers” to further explore and define the influence of river-borne organic material on estuarine communities. Deegan and Garritt (1997) found little evidence of terrestrially derived organic matter in the Plum Island Sound system in Massachusetts, U.S.A.; however, the discharge of the Plum River is minor, averaging only  $1 \text{ m}^3 \text{ s}^{-1}$ .

The objective of this research was to test the hypothesis that terrestrial organic matter derived from alluvial transport fuels secondary production in Apalachicola Bay, an estuary with major freshwater input. The alternative hypothesis is that terrestrial organic matter is not an important food source in the estuary and that secondary production is driven by in situ estuarine productivity. Both hypotheses leave the estuary dependent upon river input, but in different ways, which has significant implications for water management decisions.

We also hypothesized that the importance of terrestrial detritus to consumer organisms would wax and wane with river flow. We thought that organisms collected at the end of the high-water flow period would appear more terrestrial (i.e., like floodplain organisms, with depleted  $^{13}\text{C}$  and  $^{34}\text{S}$  relative to marine organisms) than organisms collected following periods of low river flow. Our investigation is timely due to proposed reallocation of upstream waters from the Chattahoochee and Flint Rivers for municipal, industrial, and agricultural users. Potential reallocation has raised concerns regarding the effects of reduced freshwater inflows on the secondary productivity of the downstream estuary. To test our hypotheses we employed stable isotope analysis (examining  $\delta^{13}\text{C}$  and  $\delta^{34}\text{S}$ ) of producers, consumers, and sedimentary organic matter in the riverine floodplain, delta marshes, estuary, and nearshore waters of the Gulf of Mexico.

## Methods

**Study site**—Apalachicola Bay (Fig. 1) is a shallow coastal plain estuary located in the panhandle of Florida at the terminus of the Apalachicola-Chattahoochee-Flint (ACF) River system. The Apalachicola River is the 21st largest river in the coterminous USA, the largest river in Florida, and the major source of fresh water to Apalachicola Bay. The average annual flow rate of the river during the period of this study was  $926 \text{ m}^3 \text{ s}^{-1}$  (Mortazavi et al. 2000a). Flow rate has ranged from 110 to  $8,235 \text{ m}^3 \text{ s}^{-1}$  (mean daily flow) over the period of record (1929 to present). Maximum river flows occur during late winter–early spring months and are highly correlated with Georgia rainfall (Meeter et al. 1979); low flows occur during the late summer and early fall. River DIN and DON concentrations vary from 200–500 and 50–200  $\text{mg N m}^{-3}$ , respectively, resulting in an annual N flux to the bay of  $170 \text{ mg N m}^{-2} \text{ d}^{-1}$  (Mortazavi et al. 2000a). The river is bordered by an extensive floodplain of bottomland hardwood and tupelo-cypress forests (*Nyssa aquatica*, *N. ogeche*, and *Taxodium distichum*, Leitman et al. 1983). Forest vegetation contributes  $800 \text{ g m}^{-2} \text{ yr}^{-1}$ , on average, of litter to the forest floor, resulting in an annual deposition of  $3.6 \times 10^5$  metric tons of organic material in the floodplain (Elder

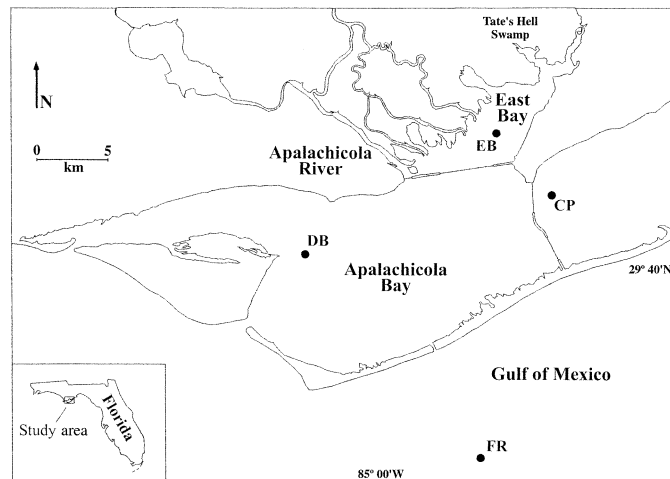


Fig. 1. Location of study sites. East Bay (EB) is the nursery area, Dry Bar (DB) and Cat Point (CP) are the midbay stations, and Franklin Reef (FR) is the marine station. River samples were collected 104, 92, 60, and 15 miles above the river's mouth at the estuary.

and Cairns 1982). Much of this material is carried from the floodplain downstream to the estuary when the river inundates its banks (Livingston 1981). Over half of the annual detrital input to the estuary occurs during spring floods (Matraw and Elder 1984).

The bay encompasses about  $620 \text{ km}^2$  of open water with an average depth of 1.9 m at mean low tide. Approximately 80% of the open water zone is composed of soft muddy unvegetated sediments with the remainder divided between oyster reefs and submerged aquatic vegetation (SAV). SAV is scattered throughout the narrow, shallow-water zone (depths  $<1 \text{ m}$ ) in varying densities, with the largest concentrations located in bayous connected to East Bay and in the eastern portions of St. George Sound (outside the study area). SAV is restricted in its distribution in the bay primarily as a result of the highly turbid nature of the water. East Bay vegetation is composed of fresh and brackish species (e.g., *Vallisneria americana*, *Ruppia maritima*), while outer bay beds are dominated by sparse *Halodule wrightii* (Livingston 1984). A freshwater marsh surrounds the river delta and is composed predominantly of sawgrass (*Cladium* spp.), bulrush (*Scirpus* spp.), cattail (*Typha* sp.), and black needlerush (*Juncus roemerianus*) (Livingston 1984). Apalachicola Bay is a highly productive estuarine system supporting a diverse and sizeable recreational and commercial fishery. The bay accounts for about 90% of Florida's oysters (8–10% of the national crop), and had the third highest catch of shrimp statewide (Livingston 1984).

**Sample collection and preparation**—Our sampling design included a range of environmental conditions, grading spatially and temporally from full riverine to full marine influence. We collected samples over a 3-yr period from the river floodplain, the delta marsh, three estuarine sites (East Bay, Dry Bar, and Cat Point), and an offshore marine site (Franklin Reef) (Fig. 1). Bay sites were sampled seasonally and varied from marine dominated during periods of low river

flow (summer–fall) to river dominated during periods of high river flow (late winter–spring). A series of floodplain samples were taken at river miles (rm) 102–106, 92, 60, 15, and 4 (river miles refer to distance from the river mouth at the estuary, which is 0).

Materials collected for isotopic analysis included seston (plankton), sediments, the major primary producers, and a variety of consumer organisms including the dominant benthic and water column feeders. Samples of nonplankton primary producers were collected in fall 1992 and spring 1994 and included floodplain vegetation, marsh vegetation, SAV, and macroalgae. Tree litter was collected from the forest floor and separated into leaves from the individual dominant species. Marsh emergent macrophytes and SAV were clipped just above the marsh/sediment surface; attached macroalgae were collected by hand.

Seston/plankton and fauna were sampled from bay sites during and at the end of periods of low river flow, when the estuary was under marine influence (September–October 1992, 1993, 1994), and following periods of sustained high river flow, when the estuary was river dominated (April–May 1993, 1994, 1995). Offshore sites were sampled in July 1993 and April 1994. Seston/plankton collection techniques were described by Chanton and Lewis (1999). Samples of consumer organisms were collected by trawling for 10–30-min intervals at bay stations and by spear or by hand at the marine site. Oysters were collected with tongs. In the floodplain, consumer organisms were collected by electric shock (Rick Long, Florida Fish and Wildlife Conservation Commission) and by dip nets. Sediments were collected with an Ekman grab; only the flocculent surface layer (1 cm) was taken for analysis. A baywide sediment collection was conducted in late April to early May 1994. At the three estuarine stations sediment samples were collected seasonally: once in summer, twice in fall, and three times in spring. Estuarine polychaete and amphipod samples were taken from separate grabs other than those used for sediment analysis.

Upon returning from the field, all consumer organisms except oysters were immediately frozen. Oysters were stored on ice overnight and opened the following day. Oyster tissue was removed from the shell; muscle and gut tissue were carefully divided and frozen separately. Prior to processing, all other consumer samples were thawed and muscle tissue was removed from bone, head, and internal organs. All cleaned tissue was freeze-dried, ground, and stored frozen. The samples were then divided into two subsamples. One subsample (for  $\delta^{13}\text{C}$  analysis) was treated with 10% hydrochloric acid and rinsed with deionized water to remove any remaining carbonate that might interfere with organic carbon isotopic analysis. A second subsample was rinsed three times in deionized water to remove seawater sulfate and set aside for  $\delta^{34}\text{S}$  isotopic analysis. Comparison of  $\delta^{13}\text{C}$  results on acid versus water-washed bone-free tissue showed no consistent difference between the two techniques (Chanton and Lewis 1999). All water column samples were acid treated for consistency. Sediment and submersed vegetation samples were acid treated in a similar fashion to remove carbonates. Sulfur analysis was not run on sediments. Emergent vegetation was not acid washed.

*Analytical procedures*—In consumer collections, both individual and pooled groups of organisms were analyzed to investigate within-species variations in isotopic composition. Some concern has been expressed over the effects of pooling of samples, in particular, that variability of individual organisms is lost when samples are pooled. This variation can be due to motility, carbon turnover time in the body, and temporal and spatial distribution of food (Montague et al. 1981). While certain species must be pooled in order to obtain enough tissue for sulfur isotope analysis, pooling larger individuals may result in values typical of a larger population (Deegan and Garritt 1997).

Primary producers are imprinted with distinctive stable isotopic ratios due to isotopic fractionation caused by different enzymatic pathways by which elements (e.g., carbon) are processed or different pools from which specific elements are taken up. These characteristic ratios may be used as tracers (Fry and Sherr 1984), allowing distinctions to be drawn as to the origin of the material in question. The ratios of light to heavy isotopes are expressed in  $\delta$  notation, indicating a depletion (negative) or enrichment (positive) of the heavy isotope relative to the light isotope compared to a known standard. The notation is defined as

$$\delta X\text{‰} = \{(R_{\text{sample}}/R_{\text{standard}}) - 1\} \times 1000$$

where  $X$  is either  $^{13}\text{C}$  or  $^{34}\text{S}$  and  $R$  is the corresponding ratio of  $^{13}\text{C}:^{12}\text{C}$  or  $^{34}\text{S}:^{32}\text{S}$ . Standards were Peedee Belemnite for carbon and Canyon Diablo troilite for sulfur.

All samples were analyzed for  $\delta^{13}\text{C}$  and  $\delta^{34}\text{S}$  by Coastal Science Laboratories (Austin, Texas). This lab was also used by Kwak and Zedler (1997) and Moncreiff and Sullivan (2001). Here, the samples were combusted to form  $\text{CO}_2$  and  $\text{SO}_2$ , purified cryogenically, and run on a dual inlet, isotope ratio mass spectrometer. Precision for these analyses was 0.2‰ for  $^{13}\text{C}$  and 0.3‰ for  $^{34}\text{S}$ .

Analysis of variance (ANOVA) was conducted with the Tukey test using Sigma Stat statistical software, version 2.0 (SPSS). Three-way ANOVA analyses with factors of location (East Bay, Cat Point, or Dry Bar), river flow (high or low), and feeding type (benthic or water column) were conducted on grouped consumer data for fauna that were collected at all locations, and during both high and low flow. These fauna included oyster, anchovy (water column feeders), shrimp, blue crab, spot, croaker, silver perch, catfish, and flounder (benthic feeders). Two-way ANOVA analyses were conducted on the individual organisms listed above, testing location and river flow.

## Results

*Primary producers*—Isotopic values for primary producers are reported in Table 1 and depicted graphically in dual isotope plots of carbon and sulfur (Fig. 2). Boxes are drawn in the figures around each group of primary producers approximating the range of isotopic values. For ease in comparisons, these boxes are included on all later figures for consumer organisms.

Isotopic values of floodplain tree litter averaged  $-28\text{‰}$  (range,  $-30$  to  $-26\text{‰}$ ) for carbon and  $1\text{‰}$  ( $-1$  to  $4\text{‰}$ ) for sulfur (Table 1, Fig. 2). River seston values were similar

Table 1. Isotopic composition of primary producers collected from various habitats within the Apalachicola system. Salinity regime during collection is given as F = freshwater, O = oligohaline, M = mesohaline, H = high salinity. SAV = submerged aquatic vegetation. Each entry represents one sample. Seston/plankton values are reported in Chanton and Lewis (1999).

Habitat	Salinity	Sample type	$\delta^{13}\text{C}\text{‰}$	$\delta^{34}\text{S}\text{‰}$
Floodplain	F	<i>Nyssa</i> spp. (Tupelo)	-28.5	1.4
	F	<i>Fraxinus</i> spp. (ash)	-29.9	-1.4
	F	<i>Ulmus americana</i> (elm)	-27.5	0.2
	F	<i>Quercus</i> spp. (oak)	-29.0	2.3
	F	<i>Taxodium distichum</i> (baldcypress)	-26.3	1.3
	F	<i>Liquidambar styraciflua</i> (sweetgum)	-27.4	3.7
	F	Tree root	-27.3	nd*
	F	Floodplain soil	-26.7	2.7
Marsh	F	<i>Typha</i> sp. (cattail)	-27.0	16.7
	F	<i>Juncus roemerianus</i> (black needlerush)	-27.1	-2.8
	F	<i>J. roemerianus</i> (different sample location)	-27.2	6.0
	F	<i>J. roemerianus</i> : dead	-26.6	5.3
	F	<i>Cladium jamaicense</i> (sawgrass)	-26.1	9.7
	F	<i>C. jamaicense</i> (different sample location)	-26.0	10.6
	F	<i>C. jamaicense</i> : dead	-24.7	9.3
	F	<i>Phragmites australis</i> (giant reed)	-26.0	9.8
	F	<i>P. australis</i> : dead	-26.2	12.2
	F	<i>Eichhornia crassipes</i> (hyacinth)	-26.9	15
	F	<i>E. crassipes</i> : leaves	-27.8	4.2
	F	<i>E. crassipes</i> : roots	-26.6	4.7
	F	<i>Scirpus</i> sp. (bulrush)	-25.8	9.0
	F	<i>Scirpus</i> sp.: dead	-26.4	10.8
	F	<i>Spartina cynosuroides</i>	-14.2	12.5
	F	<i>S. cynosuroides</i> : dead	-13.4	9.0
	O	<i>Spartina alterniflora</i> (low flow)	-13.2	7.7
	O	<i>S. alterniflora</i> (high flow)	-14.0	-9.5
	O	<i>S. alterniflora</i> : dead (high flow)	-13.4	3.1
	O	<i>S. alterniflora</i> epiphytes	-29.1	16.3
H	<i>S. alterniflora</i>	nd*	-3.6	
H	<i>S. alterniflora</i>	nd*	-3.5	
H	<i>S. alterniflora</i> : dead	nd*	-1.5	
H	<i>S. alterniflora</i> : dead	nd*	3.0	
SAV	F	<i>Vallisneria americana</i> (tapegrass)	-26.6	11.1
	F	<i>Ruppia maritima</i> (widgeon grass)	-26.7	11.1
	O	<i>Vallisneria americana</i> (low flow)	-22.3	17.0
	O	<i>V. americana</i> (high flow)	-28.6	7.4
	O	<i>Ruppia maritima</i>	-23.9	15.5
	O	<i>R. maritima</i> : dead	-26.0	-1.7
	M	<i>Gracilaria</i> sp. (red alga)	-20.7	11.5
	M	<i>Gracilaria</i> sp. (different sample location)	-19.9	14.5
	M	<i>Wrangelia</i> sp. (red alga)	-21.6	16.2
	M	<i>Ulva lactuca</i> (sea lettuce)	-21.5	nd*
	M	<i>U. lactuca</i> (different sample location)	-18.9	17.9
	M	<i>U. lactuca</i> (different sample location)	-20.2	16.5
	H	<i>Halodule wrightii</i> (shoal grass)	-14.4	2.2
	H	<i>H. wrightii</i>	-14.5	7.5

\* nd, not done.

(Chanton and Lewis 1999). Organic matter collected in these river samples contained 80 to 99% unidentifiable detrital material. Offshore seston/plankton  $\delta^{13}\text{C}$  and  $\delta^{34}\text{S}$  values were enriched relative to most estuarine samples (Fig. 2). With the exception of macroalgae, *Spartina*, and *Halodule*,  $\delta^{13}\text{C}$  values for most estuarine primary producers (marsh, SAV, and seston/plankton, Table 1, Fig. 2) fell between that of the floodplain litter and offshore marine seston/plankton end members. Sulfur values were consistently  $^{34}\text{S}$  enriched in estuarine primary producers relative to floodplain or riverine

samples (Table 1, Fig. 2). Estuarine seston/plankton isotopic composition varied from -29‰ to -22‰ for  $\delta^{13}\text{C}$ , and from 7‰ to 20‰ for  $^{34}\text{S}$  (Chanton and Lewis 1999, Fig. 2). Mean  $\delta^{13}\text{C}$  in East Bay plankton was significantly  $^{13}\text{C}$  depleted ( $p < 0.001$ ) relative to midbay sites (Cat Point and Dry Bar), which were similar. The  $\delta^{34}\text{S}$  values did not differ among the three sites (*see below*).

Isotopic values for brackish/freshwater marsh C-3 emergent macrophytes (e.g., *Juncus*, *Cladium*, *Typha*) varied from -28‰ to -25‰ ( $\delta^{13}\text{C}$ ), and from -3‰ to 17‰ ( $\delta^{34}\text{S}$ ).

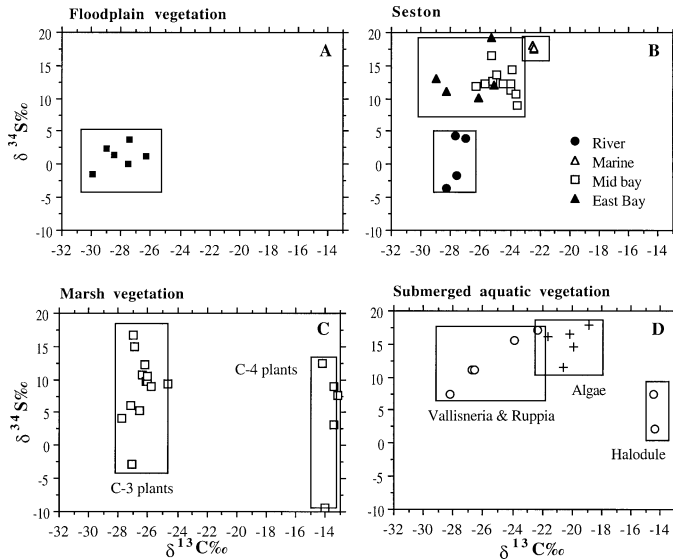


Fig. 2. Dual isotope plots of  $\delta^{13}\text{C}$  (‰) and  $\delta^{34}\text{S}$  (‰) from primary producers in the Apalachicola system. Plots include (A) floodplain vegetation, (B) seston/plankton, (C) marsh vegetation, and (D) submerged aquatic vegetation. Boxes are drawn outlining the range of isotope values. Each symbol represents a single sample.

C-4 plants (e.g., *Spartina alterniflora* and *S. cynosuroides*) were considerably more  $^{13}\text{C}$  enriched than C-3 plants, ranging from  $-14$  to  $-13$ ‰. The dominant freshwater/brackish submersed aquatic vegetation (SAV), *Vallisneria americana* and *Ruppia maritima*, was generally  $^{13}\text{C}$  depleted ( $-29$  to  $-22$ ‰) relative to the marine seagrass, *Halodule wrightii*, which had a signature of  $-14$ ‰. Macroalgae collected within the estuary (e.g., *Gracilaria* sp., *Wrangelia* sp., *Ulva lactuca*) were generally  $^{13}\text{C}$  and  $^{34}\text{S}$  enriched relative to other primary producers and thus had an apparent marine signal (Table 1, Fig. 2).

**Sedimentary organic carbon**—Sediment  $\delta^{13}\text{C}$  values varied from  $-27$ ‰ within the river to  $-21$ ‰ toward the estuary's inlets to the Gulf of Mexico (Fig. 3). The baywide survey data were collected in spring, following the period of high river flow, and thus will tend to produce upper limit values of the percentage terrestrial contribution. At the three estuarine stations, seasonal sampling produced mean values of  $-24.7 \pm 0.9$ ‰,  $-23 \pm 0.4$ ‰, and  $-23.6 \pm 0.6$ ‰ for East Bay, Cat Point, and Dry Bar. The number of data was insufficient for a statistical analysis, but seasonal variations were not apparent.

**Consumer organisms**—Stable isotopic analysis indicated clear distinctions between consumers collected within the two-end member environments (Table 2, Fig. 4). Marine

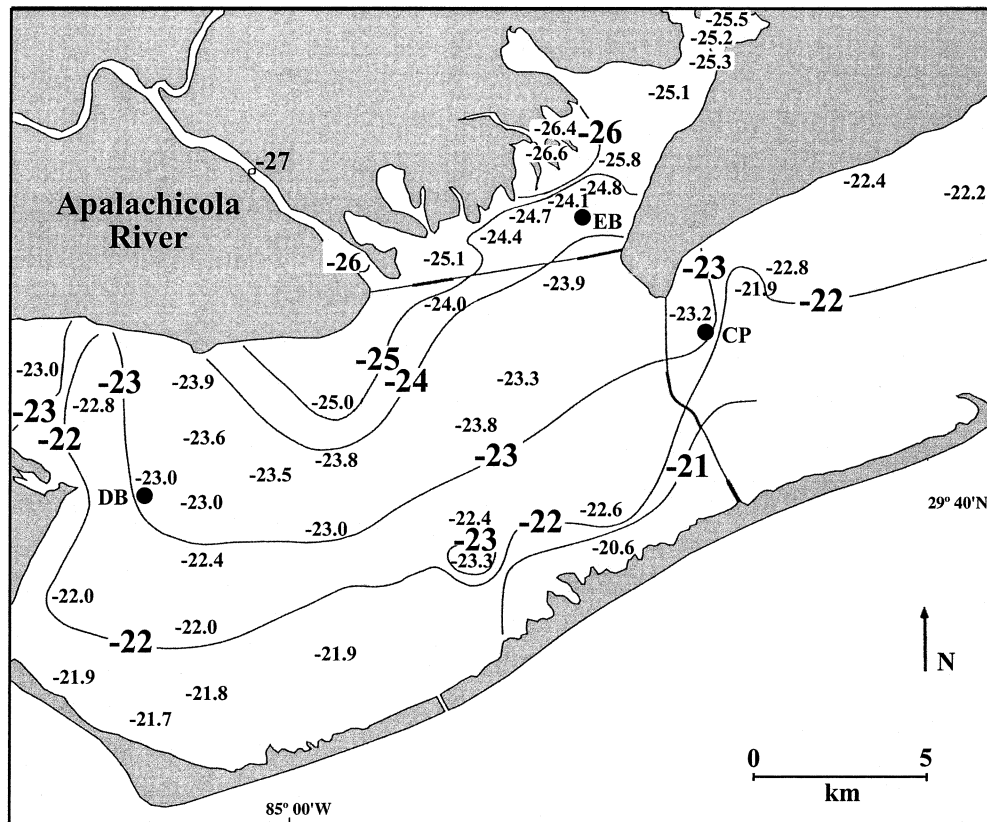


Fig. 3. The  $\delta^{13}\text{C}$  (‰) values of Apalachicola Bay sediments. Numbers indicate locations and values (‰) at each station. Each number indicates a single sample. Contours are drawn around these values.

Table 2. Average  $\delta^{13}\text{C}$  (‰) and  $\delta^{34}\text{S}$  (‰) isotopic values for grouped organisms sorted by station, flow regimes, and feeding type. Standard deviation and number of samples ( $n$ ) are shown in parentheses. Water column and benthic feeders are separated only for East Bay, Cat Point, and Dry Bar stations. These data were used in ANOVA tests summarized in Table 3.

Location	All feeders	Water column feeders		Benthic feeders	
		Low flow	High flow	Low flow	High flow
River (above rm 15)					
$\delta^{13}\text{C}$	-28.9 (2.0, 25)				
$\delta^{34}\text{S}$	3.7 (1.8, 20)				
East Bay					
$\delta^{13}\text{C}$	-22.4 (1.9, 65)	-23.0 (2.0, 11)	-23.2 (1.7, 7)	-22.0 (1.6, 23)	-22.3 (1.4, 24)
$\delta^{34}\text{S}$	12.0 (2.1, 62)	14.7 (1.5, 11)	13.0 (1.7, 6)	11.9 (1.0, 23)	10.6 (1.8, 22)
Cat Point					
$\delta^{13}\text{C}$	-20.7 (2.0, 60)	-22.2 (1.5, 11)	-21.4 (1.9, 13)	-19.6 (1.1, 10)	-20.0 (0.9, 26)
$\delta^{34}\text{S}$	12.6 (2.2, 57)	14.7 (0.9, 9)	14.4 (1.6, 12)	11.4 (1.5, 10)	11.2 (1.7, 26)
Dry Bar					
$\delta^{13}\text{C}$	-20.3 (1.9, 74)	-21.4 (1.4, 15)	-22.4 (2.2, 8)	-19.6 (1.4, 26)	-19.7 (2.8, 25)
$\delta^{34}\text{S}$	12.5 (2.1, 70)	14.9 (1.2, 15)	14.4 (2.1, 8)	12.4 (1.1, 24)	10.7 (2.4, 23)
Franklin Reef					
$\delta^{13}\text{C}$	-17.8 (0.7, 11)				
$\delta^{34}\text{S}$	16.2 (0.9, 10)				

consumers were  $^{13}\text{C}$  enriched ( $-17.8 \pm 0.7\text{‰}$ ,  $n = 11$ ), while floodplain consumers were  $^{13}\text{C}$  depleted ( $-28.9 \pm 2.0\text{‰}$ ,  $n = 25$ ). Marine consumers were enriched in  $^{34}\text{S}$  ( $16.2 \pm 0.9\text{‰}$ ,  $n = 10$ ) relative to floodplain consumers ( $3.7 \pm 1.8\text{‰}$ ,  $n = 20$ ). No seasonal variations were observed in the floodplain or marine consumers (Chanton 1997).

Isotopic values for estuarine consumers fell between the floodplain and marine end members with mean values ranging from  $-22.4$  to  $-20.3\text{‰}$  for  $\delta^{13}\text{C}$  and from  $12$  to  $12.6\text{‰}$  for  $\delta^{34}\text{S}$  (Table 2). Individual samples varied widely at the estuarine sites, ranging from  $-31.8$  to  $-17.0\text{‰}$  for  $\delta^{13}\text{C}$  and from  $5.3$  to  $19.4\text{‰}$  for  $\delta^{34}\text{S}$  (Fig. 4).

Significant spatial (location), temporal (high or low river flow), and feeding type differences in isotopic values were observed for estuarine consumers, depending on the isotope examined (Tables 2 and 3). Only organisms listed in Table 3 were used in the pooled three-way ANOVA since they were collected under all treatments. Carbon values were similar at the midbay stations (Cat Point and Dry Bar) and  $^{13}\text{C}$  enriched relative to samples collected from East Bay. Sulfur isotopic values did not vary significantly among estuarine sites. Both  $\delta^{13}\text{C}$  and  $\delta^{34}\text{S}$  values varied significantly for benthic versus water column feeders. Benthic feeders exhibited  $^{13}\text{C}$  enrichment and  $^{34}\text{S}$  depletion relative to water column feeders (Tables 2 and 3). Water column feeders included anchovies and oysters; all other fauna species were considered benthic feeders. River flow characteristics (i.e., low versus high flow) also influenced  $\delta^{34}\text{S}$  values for estuarine consumers while  $\delta^{13}\text{C}$  values were unaffected (three-way ANOVA, Table 3).

Two-way ANOVA for individual organisms showed that carbon clearly indicated differences in location, whereas sulfur was a weaker indicator. Significant differences in  $\delta^{13}\text{C}$  for location were found for all individual consumers except blue crabs (Table 3). Only oysters and shrimp differed sig-

nificantly in  $\delta^{34}\text{S}$  among locations. Flow effects were strongly indicated in oysters by both carbon and sulfur data and by single isotopes for flounder, croaker, and spot.

## Discussion

The main objective of this research was to test the hypothesis that terrestrial organic matter derived from alluvial transport fuels secondary production in Apalachicola Bay. Our approach toward evaluating this hypothesis will be as follows. First we will examine the isotopic composition of organic matter sources, including sedimentary organic matter, to determine the relative importance of terrestrial versus marine inputs. Next we will examine the variability and differences in the isotopic composition of consumer organisms. Last will be a comparison of estuarine consumers' isotopic composition with values obtained from marine, freshwater, and estuarine faunal end members to allow a quantitative assessment of the upper limit of floodplain primary production in fueling secondary production.

*Isotopic values of organic matter sources*—Isotopic values of the most important estuarine primary producers, seston/plankton, C-3 marsh vegetation, and *Vallisneria/Ruppia* (SAV), fell between marine seston/plankton and floodplain/river isotopic values. The C-4 marsh vegetation, *Halodule*, and macroalgae were  $^{13}\text{C}$  enriched relative to marine seston/plankton, but their  $\delta^{34}\text{S}$  values were intermediate between the floodplain and marine end members.

Generally, the  $\delta^{13}\text{C}$  of estuarine seston/plankton followed (offset by  $20\text{‰}$ ) the  $^{13}\text{C}$  of the dissolved  $\text{CO}_2$  (DIC) measured in the water in which they were collected (Chanton and Lewis 1999). As has been observed in other estuaries (Fogel and Cifuentes 1993; Coffin et al. 1994; Coffin and Cifuentes 1999), DIC  $\delta^{13}\text{C}$  values were directly related to

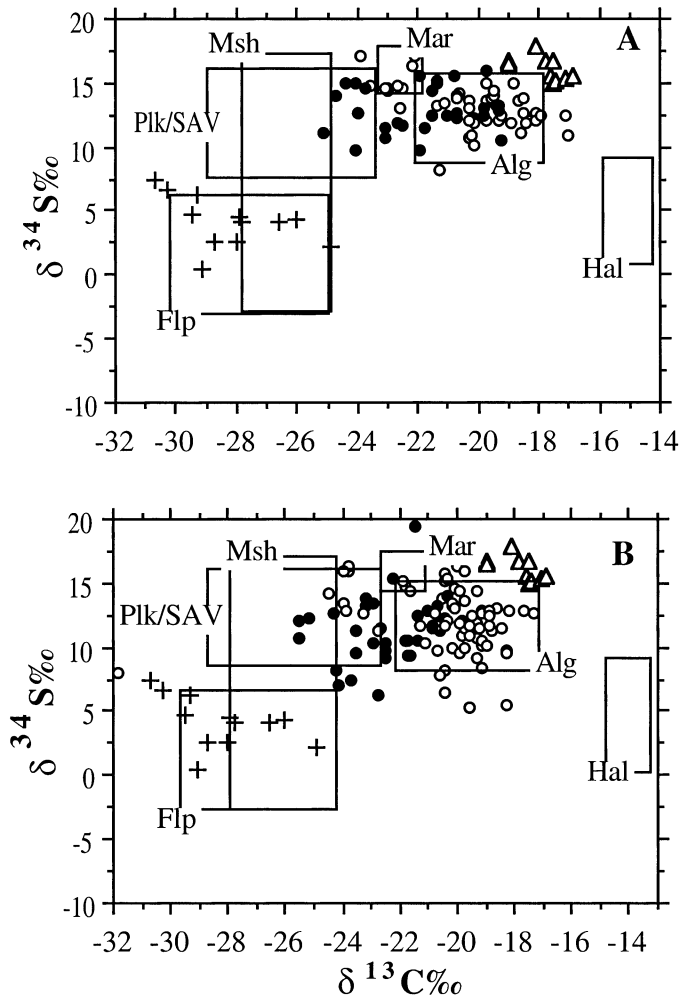


Fig. 4. Dual isotope plots of  $\delta^{13}\text{C}$  (‰) and  $\delta^{34}\text{S}$  (‰) for consumers in the Apalachicola Bay system during (A) low- and (B) high-flow seasons. Plus signs indicate floodplain fauna, open triangles marine fauna (Franklin Reef), open circles midbay sites (Cat Point and Dry Bar), and closed circles East Bay sites. Each symbol represents a single sample. Floodplain and marine fauna showed no seasonal trends, and all data are plotted in each figure. Boxes in this figure are carried over from Fig. 2 and represent the location of source isotopic values.

salinity differences and were due to mixing of riverine DIC that was  $^{13}\text{C}$  depleted ( $-11$  to  $-12$ ‰) with marine DIC that was  $^{13}\text{C}$  enriched (0‰, Chanton and Lewis 1999). Although samples were generally 100% zooplankton (particularly *Acartia tonsa* and larvae and nauplii of zooplankton and barnacles, Chanton and Lewis 1999), the good correspondence of seston/plankton  $\delta^{13}\text{C}$  values and DIC  $\delta^{13}\text{C}$  values strongly indicates that seston/plankton samples represented phytoplankton as assumed by Sullivan and Moncreiff (1990).

The  $\delta^{34}\text{S}$  of seston/plankton was depleted relative to marine sulfate. The bay is shallow, and large amounts of sediment are suspended in the water column under windy conditions. To avoid excessive sediment material, we sampled on calm days and verified sample quality by microscopic examination. However, even small quantities of sediment

within seston/plankton samples might skew isotopic results toward lower (more terrestrial) values because of the large difference in  $\delta^{34}\text{S}$  between the sediments, which are influenced by microbial sulfate reduction ( $\delta^{34}\text{S} = -24$  to  $-6.3$ ‰) and the “theoretical value” for marine plankton of  $+20$ ‰ (Peterson and Howarth 1987).

Marsh vegetation yielded a wide range of values, particularly for sulfur (Table 1). As observed by Currin et al. (1995),  $\delta^{34}\text{S}$  values in standing dead *Spartina* were more  $^{34}\text{S}$  enriched than values from live *Spartina*, possibly due to fungal colonization after death. Additionally, in our system there appeared to be a wide range in values for live *Spartina* due to seasonal variations, likely associated with salinity variations within the estuary. Live *S. alterniflora* had a  $\delta^{34}\text{S}$  value of  $-9.5$ ‰ in January (when under the influence of fresh water) and  $+7.7$ ‰ in July (when the area was more saline). Standing dead *S. alterniflora* had a value of  $3.1$ ‰ in January but was not present in July. It is possible that the dead *S. alterniflora* had grown under saltier conditions. Large and systematic differences in  $\delta^{34}\text{S}$  between living and standing dead macrophyte tissue were not observed in fresh and brackish water species.

Both *Vallisneria* and *Ruppia* were depleted in  $^{13}\text{C}$  relative to marine seagrasses (e.g., *Thalassia testudinum*, *Halodule wrightii*, and *Syringodium filiforme*), which typically have signatures of  $-14$  to  $-8$ ‰ (Fry et al. 1987; Moncreiff and Sullivan 2001). The plants we sampled grew in relatively fresh water that had more  $^{13}\text{C}$ -depleted DIC than marine water. Alternatively, their growth may be more light limited than carbon limited (Durako and Hall 1992). Sulfur isotopic values for *Vallisneria* and *Ruppia* ranged from 7 to 17‰. *Halodule wrightii* collected on the bay side of St. George Island had a  $\delta^{13}\text{C}$  value of  $-14.5$ ‰ and  $\delta^{34}\text{S}$  values ranging from 2 to 7‰. For comparison, we obtained isotopic values for the seagrasses *Halodule*, *Thalassia*, and *Syringodium* from St. Joe Bay, a high salinity estuary west of Apalachicola Bay.  $\delta^{13}\text{C}$  ranged from  $-9.5$  to  $-12.2$ ‰ for these samples;  $\delta^{34}\text{S}$  values varied between 9 and 11‰.

To examine the contribution of terrestrial organic matter to the sediment composition, we assumed a mixing model between a terrestrial end member at  $-28$ ‰ (mean of floodplain vegetation) and a marine/estuarine end member at  $-20$ ‰ (the nearest integer more positive than the most  $^{13}\text{C}$ -enriched value observed, Fig. 3). The fractional contribution of organic matter due to terrestrial input ( $f$ ) can be calculated as

$$(f)(-28\text{‰}) + (1 - f)(-20\text{‰}) \\ = \text{observed sediment } \delta^{13}\text{C value} \quad (1)$$

where  $f$  represents the fraction of organic matter that is of terrestrial origin and  $(1 - f)$  is the fraction of material that is of estuarine or marine origin (Cifuentes 1991). Simple mixing appears justified; S. Opsahl (pers. comm. 1996) noted a linear relationship ( $r = 0.78$ ,  $n = 5$ ) between  $\delta^{13}\text{C}$  and lignin in a transect across Apalachicola Bay. This indicates that the observed isotopic variation must be due to the admixture of terrestrial or freshwater marsh derived organic material, as lignin is a component of such vegetation.

Applying Eq. 1 to the mean sedimentary carbon values of  $-24.7 \pm 0.9$ ‰,  $-23.4 \pm 0.4$ ‰, and  $-23.4 \pm 0.6$ ‰ at East

Table 3. Summary of ANOVA results testing differences in carbon (C) and sulfur (S) isotopic values between location, river flow, and feeding type. A three-way ANOVA was performed on grouped data on the fauna listed below examining differences in location, flow, and feeding type; two-way ANOVAs were used on individual species data examining only location and flow variables. Locations: East Bay, Cat Point, and Dry Bar. Flows: low and high. Feeding types: water column and benthic. *P* values given for significant differences. Anchovy and oyster are considered water column feeders, all others are considered benthic. Interaction terms were only significant for oyster C (flow  $\times$  location).

	Location		River flow		Feeding type	
	C	S	C	S	C	S
Three-way ANOVA						
Grouped fauna	<0.001	ns	ns	<0.001	<0.001	<0.001
Two-way ANOVA						
Primary producers						
Seston/plankton	<0.001	ns	<0.001	ns		
Sediment	0.014		ns			
Consumers						
Oyster ( <i>Crassostrea virginica</i> )	0.001	0.01	<0.001	0.007		
Shrimp ( <i>Penaeus setiferus</i> )	0.002	0.05	ns	ns		
Blue crab ( <i>Callinectes sapidus</i> )	ns	ns	ns	ns		
Spot ( <i>Leiostomus xanthurus</i> )	<0.001	ns	0.043	ns		
Croaker ( <i>Micropogonias undulatus</i> )	<0.001	ns	ns	0.016		
Anchovy ( <i>Anchoa mitchilli</i> )	0.002	ns	ns	ns		
Silver perch ( <i>Bairdiella chrysoura</i> )	0.013	ns	ns	ns		
Catfish ( <i>Arius felis</i> )	0.005	ns	ns	ns		
Flounder ( <i>Etropus crossotus</i> )	0.005	ns	0.012	ns		

Bay, Cat Point, and Dry Bar results in an estimated contribution of terrestrial organic matter to the sediments of 58%, 40%, and 40%. Similarly, the  $-25$ ,  $-24$ ,  $-23$ ,  $-22$ , and  $-21$ ‰ contour lines in Fig. 3 represent percentage terrestrial contributions of 62, 50, 37, 25, and 12%. The greatest fractions of floodplain organic matter were found near the river mouth and its distributaries in East Bay.

These values represent upper limits for the contribution of terrestrial organic matter because in situ estuarine production was not included in the calculation. It is possible to explain the  $\delta^{13}\text{C}$  of sedimentary organic carbon from in situ production alone. The  $^{13}\text{C}$  distribution in Apalachicola Bay is quite similar to that of the Mississippi Sound (Sackett and Thompson 1963), which does not have a major river. This similarity immediately suggests that alluvial-borne detritus may be of secondary importance to the estuary relative to in situ production.

Seston/plankton collected at the estuarine stations had seasonally averaged  $\delta^{13}\text{C}$  values of  $-26.8 \pm 2.3$ ‰ in East Bay,  $-24.3 \pm 2.1$ ‰ at Cat Point, and  $-24.5 \pm 1.7$ ‰ at Dry Bar (Chanton and Lewis 1999). Isotopic values for seston/plankton and sediment were similar at the two outer bay stations (Cat Point and Dry Bar), but differed at the East Bay site ( $p = 0.045$ ), where the seston/plankton appeared more terrestrial ( $^{13}\text{C}$  depleted) than the sediment! An important factor to consider is temporal variation in plankton production. If most of the plankton is produced in summer, then a weighted average (as opposed to the simple average calculated above) would be shifted toward more  $^{13}\text{C}$ -enriched values.

Estuarine sediments may be the recipients of organic matter from sources other than terrestrial leaf litter or plankton, such as *Vallisneria*, *Ruppia*, or drifting red and green macroalgae. Outer bay sediments may receive inputs from the scattered

*Halodule* beds. However, as cutin was found in only trace amounts in sediments it would appear that *Halodule* inputs were relatively minor (S. Opsahl 1996 pers. comm.).

*Isotopic values of consumers*—In ANOVA analysis of data from consumers we observed a strong spatial signal of  $\delta^{13}\text{C}$  variation associated with proximity to riverine inputs (Table 2 and 3). This variation may be attributed to two effects: the increasing influence of terrestrial organic matter as one nears the river mouth and its distributaries and the increasing influence of  $^{13}\text{C}$ -depleted dissolved inorganic carbon (DIC) in waters with decreasing salinity. Carbon data alone cannot differentiate between the two effects. These two trends reinforce each other so that clear distinctions between East Bay and the midbay stations were observed. These two effects should also work together to influence the response of organisms to river flow, so it is somewhat surprising that a stronger response in  $^{13}\text{C}$  data to flow was not observed. The  $^{34}\text{S}$  data did not show a location effect. This discrepancy between carbon and sulfur data with regard to location suggests that the location differences in  $\delta^{13}\text{C}$  are likely due to consumers feeding on estuarine primary production that is shifted to more negative  $\delta^{13}\text{C}$  values by DIC associated with the lower salinity waters found in East Bay (Chanton and Lewis 1999). Increased reliance on terrestrial organic matter would have imparted a lighter  $^{34}\text{S}$  signal to the East Bay organisms. But estuarine production would not be expected to exhibit a location effect because marine sulfate is the primary source of assimilatory sulfate during estuarine production (Chanton and Lewis 1999). In this brackish water body, the contribution of marine sulfate still overwhelms the signal of riverine sulfur, even at a salinity of 1‰.

The isotopic differences between the consumers in East Bay and the midbay sites indicate that they may not inhabit wide ranges of territory. Fry et al. (1987) illustrated similar findings in two adjacent bays, Rookery and Johnson, on the west coast of Florida. Deegan and Garritt (1997) found significant differences in isotopic composition in consumer organisms between stations along an estuarine gradient. Their study indicated that organisms were not highly mobile and that they consumed local food sources. Newell et al. (1995) also demonstrated that local availability of food determined use.

We hypothesized that consumers collected at the end of the high-water flow period would appear more terrestrial (like floodplain organisms, with depleted  $^{13}\text{C}$  and  $^{34}\text{S}$  relative to marine organisms) than those collected following periods of low river flow. Consumers collected after low-flow conditions were hypothesized to appear more marine-like. Our hypothesis was supported by the  $^{34}\text{S}$  results, which yielded less positive values under high flow than under low flow (Table 3). Variation in  $\delta^{34}\text{S}$  with river flow can only be attributed to a single effect—the admixture of terrestrial floodplain detritus with estuarine and marine organic matter. The grouped data indicated a clear effect with river flow, as did results from oysters and croakers. In addition, benthic feeders collected during high river flow conditions were depleted in  $^{34}\text{S}$  relative to those collected during low flow and to water column feeders collected under all flow conditions (Table 2). The sulfur results clearly demonstrated that terrestrial floodplain detritus influenced food web structure in the estuary to some degree.

Like Thomas and Cahoon (1993) and Deegan and Garritt (1997), we observed  $^{13}\text{C}$  enrichment and  $^{34}\text{S}$  depletion in benthic feeders relative to pelagic feeders. These results suggest the importance of an estuarine food source such as benthic microalgae. Such a source would exhibit  $^{34}\text{S}$  depletion and  $^{13}\text{C}$  enrichment relative to water column phytoplankton (Thomas and Cahoon 1993; France 1995a,b; Deegan and Garritt 1997). Currin et al. (1995) compiled literature values and reported means for  $\delta^{13}\text{C}$  and  $\delta^{34}\text{S}$  of  $-21\text{‰}$  and  $18\text{‰}$  and  $-15\text{‰}$  and  $10\text{‰}$  for water column phytoplankton and benthic microalgae, respectively. The  $^{34}\text{S}$  value of benthic microalgae is likely sensitive to how reducing the sediments are, with algae living over highly sulfidic muds being  $^{34}\text{S}$  depleted relative to algae living within sandy oxic sediments. Analysis of a sand dollar (used as a proxy for benthic microalgae by Moncrieff and Sullivan 2001) collected in sandy shelf sediments 10 km offshore of Apalachicola yielded values of  $-18.2\text{‰}$  and  $+17.9\text{‰}$  for  $\delta^{13}\text{C}$  and  $\delta^{34}\text{S}$ , respectively (Chanton and Lewis unpubl. data). This value is  $^{34}\text{S}$  enriched relative to the estuarine/marsh/lagoonal literature values described above. In muddy Apalachicola Bay, we suspect that benthic microalgae would have a  $^{34}\text{S}$  value on the less positive side. However, no benthic algal mats are visible overlying the unconsolidated sediments. Surficial sediments are frequently suspended by wind, possibly preventing mat development. No estimates of benthic microalgal photosynthesis are available (Mortazavi et al. 2000b).

*Comparisons of consumer organisms using dual isotope plots*—Carbon and sulfur isotopic ratios for consumer or-

ganisms are plotted for low-flow and high-flow sampling conditions (Fig. 4). Boxes representing the range of values for each group of primary producers are also shown for comparison. Floodplain consumers generally fell within the floodplain primary producer box, which indicates that the food web here was supported from organic material derived from riverine seston and/or terrestrial floodplain vegetation. Floodplain consumers included a variety of small bivalve and gastropod mollusks, insect larvae, crustaceans, and numerous fish species. Organisms sampled spanned the range of trophic positions from planktivores and detritivores to secondary consumers. Several consumers (e.g., insect larvae and gastropods) had  $\delta^{13}\text{C}$  values less than  $-30\text{‰}$  and were likely feeding on an unsampled source depleted in  $^{13}\text{C}$  relative to the group of primary producers examined.

Marine consumer  $\delta^{34}\text{S}$  values were similar to marine seston/plankton (Fig. 4), but their carbon isotopic values were  $^{13}\text{C}$  enriched by about  $4\text{‰}$ . This effect may be due to trophic position, which has been observed to increase about  $1\text{‰}$  per trophic level in some cases (McConnaughey and McRoy 1979; Rau et al. 1983; Fry 1984; Monteiro et al. 1991). The majority of marine consumers examined represented higher trophic positions, either secondary or tertiary consumers; only three samples of lower trophic groups were obtained (e.g., two bivalves and a sea star). Alternatively, these marine consumers could have been feeding on a  $^{13}\text{C}$ -enriched food source such as benthic microalgae as discussed above.

Estuarine consumer isotopic ratios varied widely, yet generally fell within the ranges of estuarine primary producers (Fig. 4). Sulfur values were noticeably  $^{34}\text{S}$  depleted during high river flows, consistent with ANOVA results (Table 3). East Bay consumers were  $^{13}\text{C}$  depleted relative to midbay consumers; midbay consumers were more similar to marine organisms than they were to floodplain organisms (Fig. 4). Midbay consumer organisms were  $^{13}\text{C}$  enriched relative to SAV (*Vallisneria* and *Ruppia*), estuarine seston/plankton, and marsh vegetation but appeared similar to benthic macroalgal  $\delta^{13}\text{C}$ . An estuarine consumer diet consistent with the observed isotopic signatures might contain a mixture of estuarine seston/plankton, SAV, benthic macroalgae, and C-3 marsh vegetation. Benthic microalgae values from the literature (discussed above) overlap the benthic macroalgae field considerably and may also have been important. The addition of small quantities of *Spartina* and *Halodule*, while possible, is unlikely given their limited areal extent in the estuary.

*Estimating the importance of terrestrial organic matter using mixing models*—To examine the relative contribution of floodplain vegetation to estuarine secondary production, we used a two-source mixing model (after Fry and Sherr 1984; Forsberg et al. 1993; Kwak and Zedler 1997). This method compares isotopic ratios from consumer organisms where the dietary sources are known with those whose dietary sources are unknown (Newell et al. 1995). We assumed that the diet of an estuarine organism is a mixture of two end members—terrestrial floodplain vegetation, as estimated by the isotopic ratios of floodplain consumers, and marine primary production, as estimated by the ratios of marine consumers. For these calculations we used an equation similar

Table 4. The average  $\delta^{13}\text{C}$  and  $\delta^{34}\text{S}$  values and estimated percentage contribution (upper limit) of terrestrial organic matter to the diet of selected estuarine consumers based on the terrestrial-marine end member model (columns 4 and 7). The terrestrial end member was estimated from the mean of pooled floodplain consumer samples; the marine end member was based on the mean of pooled Franklin Reef samples. The percentage dietary contribution was estimated separately using  $\delta^{13}\text{C}$  and  $\delta^{34}\text{S}$  values and collectively using the average of the two individual estimates (column 8). The far right column of the table is a terrestrial-estuarine model, based only on S data. End member values were 3.7 for terrestrial consumers and the oyster  $^{34}\text{S}$  value at each station.

Organism	$\delta^{13}\text{C}$			$\delta^{34}\text{S}$			Mean value	Estuarine model
	‰	<i>n</i>	% terrestrial	‰	<i>n</i>	% terrestrial	% terrestrial	% terrestrial
End members								
Floodplain	-28.9		100	3.7		100	100.0	3.7
Marine	-17.8		0	16.2		0	0.0	oyster value
East Bay								
Polychaetes	-25.7	2	71	11.0	1	41	56	30
<i>Crassostrea virginica</i> (oyster)	-24.5	9	60	14.1	9	16	38	0
<i>Brachiodontes exustus</i> (mussel)	-25.0	2	65	13.5	2	21	43	6
<i>Melongena corona</i> (crown conch)	-20.3	1	22	10.5	1	45	34	35
<i>Neritina reclivata</i> (snail)	-22.8	1	45	6.3	1	79	62	75
<i>Lolliguncula brevis</i> (brief squid)	-19.7	1	17	16.0	1	1	9	-18
Amphipods	-24.0	4	56	8.2	2	64	60	57
<i>Penaeus setiferus</i> (white shrimp)	-23.5	4	51	11.8	4	35	43	22
<i>Callinectes sapidus</i> (blue crab)	-21.6	8	34	13.1	8	24	29	10
<i>Leiostomus xanthurus</i> (spot)	-21.4	7	32	11.5	7	37	35	25
<i>Micropogonias undulatus</i> (croaker)	-23.2	15	49	9.9	14	50	49	40
<i>Anchoa mitchilli</i> (bay anchovy)	-21.7	9	35	14.1	8	16	26	0
<i>Cynoscion arenarius</i> (sand seatrout)	-20.1	4	21	13.2	4	24	22	9
<i>Bairdiella chrysoura</i> (silver perch)	-21.2	6	31	11.9	7	34	32	21
<i>Arius felis</i> (catfish)	-21.0	4	29	12.1	4	33	31	19
<i>Paralichthys</i> spp. (flounder)	-21.8	3	36	12.2	3	32	34	18
<i>Brevoortia patronus</i> (gulf menhaden)	-21.0	2	29	13.2	2	24	26	9
<i>Etropus crossotus</i> (fringed flounder)	-23.2	1	49	13.2	1	24	36	9
Mean	-22.3		40.7	12.0		33.4	37.0	20.3
Cat Point								
<i>Crassostrea virginica</i> (oyster)	-23.3	15	50	14.9	13	10	30	0
<i>Brachiodontes exustus</i> (mussel)	-23.9	1	55	16.0	1	1	28	-10
<i>Mercenaria mercenaria</i> (quahog)	-21.5	1	33	14.5	1	13	23	4
<i>Lolliguncula brevis</i> (brief squid)	-19.7	3	17	14.0	3	17	17	8
<i>Penaeus setiferus</i> (white shrimp)	-20.0	4	20	10.8	4	43	31	37
<i>Callinectes sapidus</i> (blue crab)	-21.3	2	31	13.6	2	20	26	12
<i>Leiostomus xanthurus</i> (spot)	-19.6	11	16	10.8	11	43	30	37
<i>Micropogonias undulatus</i> (croaker)	-20.7	4	26	11.5	4	37	32	30
<i>Anchoa mitchilli</i> (bay anchovy)	-20.1	12	21	14.3	12	15	18	5
<i>Cynoscion arenarius</i> (sand seatrout)	-20.3	1	22	13.7	1	20	21	11
<i>Bairdiella chrysoura</i> (silver perch)	-20.1	5	21	12.0	5	33	27	26
<i>Arius felis</i> (catfish)	-19.9	4	19	12.1	4	33	26	25
<i>Paralichthys</i> spp. (flounder)	-19.7	3	17	11.5	3	37	27	30
<i>Etropus crossotus</i> (fringed flounder)	-19.1	1	12	12.7	1	28	20	20
<i>Lagodon rhomboides</i> (pinfish)	-18.3	1	4	9.8	1	51	28	46
Mean	-20.5		24.3	12.8		26.8	25.5	18.6
Dry Bar								
Polychaetes	-22.4	3	41	12.3	2	31	36	28
<i>Crassostrea virginica</i> (oyster)	-23.4	13	50	15.5	13	5	28	0
<i>Brachiodontes exustus</i> (mussel)	-24.2	2	58	13.2	2	24	41	19
<i>Melongena corona</i> (crown conch)	-21.8	1	36	14.8	1	11	23	6
<i>Lolliguncula brevis</i> (brief squid)	-19.6	4	16	14.5	4	13	15	8
Amphipods	-22.2	1	40	10.1	1	49	44	46
<i>Penaeus setiferus</i> (white shrimp)	-20.0	15	20	10.8	13	43	31	40
<i>Callinectes sapidus</i> (blue crab)	-22.1	6	39	12.2	6	32	35	28
<i>Leiostomus xanthurus</i> (spot)	-18.3	5	4	12.1	4	33	18	29
<i>Micropogonias undulatus</i> (croaker)	-19.3	12	13	9.5	11	53	33	51

Table 4. Continued.

Organism	$\delta^{13}\text{C}$			$\delta^{34}\text{S}$			Mean value	Estuarine model
	‰	<i>n</i>	% terrestrial	‰	<i>n</i>	% terrestrial	% terrestrial	% terrestrial
<i>Anchoa mitchilli</i> (bay anchovy)	-20.2	11	22	14.2	11	16	19	11
<i>Cynoscion arenarius</i> (sand seatrout)	-20.0	5	20	14.6	5	12	16	8
<i>Bairdiella chrysoura</i> (silver perch)	-19.3	7	13	12.8	5	27	20	23
<i>Arius felis</i> (catfish)	-19.0	6	11	12.4	6	30	20	26
<i>Paralichthys</i> spp. (flounder)	-20.2	1	22	13.3	1	23	22	19
<i>Brevoortia patronus</i> (gulf menhaden)	-20.7	1	26	14.0	1	17	22	13
<i>Etropus crossotus</i> (fringed flounder)	-20.4	1	23	8.1	1	65	44	63
<i>Lagodon rhomboides</i> (pinfish)	-17.1	1	0	12.5	1	29	15	25
Mean	-20.6		25.2	12.6		28.5	26.9	24.6

to Eq. 1 and compared the seasonally averaged isotopic composition for each estuarine consumer with the mean values for terrestrial floodplain and marine organisms. This approach is overly simplistic and ignores production within the estuary, but it has heuristic value in that it yields a conservative upper limit for the importance of floodplain organic matter in the diets of estuarine consumer organisms. This model produces an upper limit value for the floodplain's contribution because estuarine-produced organic matter can have an "apparent terrestrial" signature, as it is produced from DIC with a carbon isotopic signal  $^{13}\text{C}$  depleted relative to DIC in marine waters.

Values for the marine end member represented offshore fish and macroinvertebrates collected at Franklin Reef, roughly 10 km offshore. Mean values for  $\delta^{13}\text{C}$  and  $\delta^{34}\text{S}$  were  $-17.8\text{‰}$  and  $16.2\text{‰}$  (Table 2). Freshwater consumers, the other end member, were collected above rm 15 in the river and floodplain and had mean values of  $-28.9\text{‰}$  and  $3.7$  for  $\delta^{13}\text{C}$  and for  $\delta^{34}\text{S}$ . Thus, isotopic ratios of estuarine consumers were expected to fall within a range of approximately  $11\text{‰}$  for carbon and  $12.5\text{‰}$  for sulfur. By examining the relative position of a consumer's diet (i.e.,  $\delta^{13}\text{C}$  and  $\delta^{34}\text{S}$ ) within this range, we estimated the importance of floodplain terrestrial organic matter.

Dietary percentage contribution from terrestrial sources was estimated individually for  $\delta^{13}\text{C}$  and  $\delta^{34}\text{S}$ , as well as averaged for both isotopes (Table 4). In some cases, the terrestrial fraction calculated by the two isotopes agreed well, but in other cases there were large discrepancies. Organisms showing the greatest difference included oysters, mussels, spot, croaker, and pinfish. For water column feeders like oysters and mussels, carbon values indicated a greater terrestrial contribution. However, for the benthic feeding spot, croaker, and pinfish, where differences existed, sulfur was usually the stronger terrestrial indicator. Feeding type and location within the estuary can influence the individual isotopic values. If oysters and mussels consume estuarine plankton (which we know to be the case), we would expect their carbon values to be depleted relative to marine consumers. This would likely cause an overestimation of the terrestrial contribution predicted by carbon, as was observed. Spot, croaker, and pinfish are benthic feeders and, as such, may be ingesting some  $^{34}\text{S}$ -depleted light sulfide, which could increase the estimation of their terrestrial input based on sulfur. In our opin-

ion, these results argue for using the average of the two individual isotope estimates.

Using this floodplain-marine end member model, terrestrial vegetation was estimated to provide a station-averaged upper limit ranging from 25 to 37% (Table 4) of the diet of estuarine consumers. Floodplain vegetation was more important to those organisms collected in East Bay, nearer the mouth of the river. Organisms at the base of the benthic food web (polychaete worms, snails, amphipods) also tended to be more influenced by floodplain vegetation, with diets ranging up to 56–62% terrestrial. These organisms, in turn, likely influenced such predators as spot and croaker that were estimated to be 35–49% terrestrial. Squid, anchovies, menhaden, and sand seatrout had the least terrestrial contribution of all East Bay organisms, ranging from 9 to 26%. Deegan et al. (1990) found that detritus made up 30% of the diet of menhaden in Louisiana. Squid, anchovies, and menhaden are all water column feeders, with seatrout feeding heavily on anchovies and benthic organisms like shrimp (Livingston et al. 1997). Organisms collected at midbay stations (Cat Point and Dry Bar) were less influenced by terrestrial vegetation, with water column feeders like squid and anchovies having the least influence (<20% terrestrial).

This simple two-end member approach is illustrated for each station (Fig. 5). Floodplain and marine consumers are plotted at either end of a mixing line, along with the seasonally averaged values of  $\delta^{13}\text{C}$  and  $\delta^{34}\text{S}$  for each group of estuarine organisms. Squid, anchovy, oyster, and mussels generally plotted above the mixing line (Fig. 5). Their  $\delta^{34}\text{S}$  values were more positive and their  $\delta^{13}\text{C}$  values were more negative than would be expected due to simple mixing. This trend may reflect the importance of estuarine producers in their diet. Estuarine producers also plot above the mixing line. The majority of the organisms examined from East Bay tended to fall along the terrestrial-marine mixing line. Mid-bay organisms generally fell below the mixing line, but closer to the marine end member than did East Bay organisms.

Using the above approach, we calculated an upper limit to the contribution of terrestrial inputs for estuarine consumers as a mixing of terrestrial and marine sources. However, estuarine consumers undoubtedly feed on material produced within the estuary. Estimating the terrestrial contribution based on estuarine primary production is both more realistic and problematic. Estuarine-produced organic matter can ap-

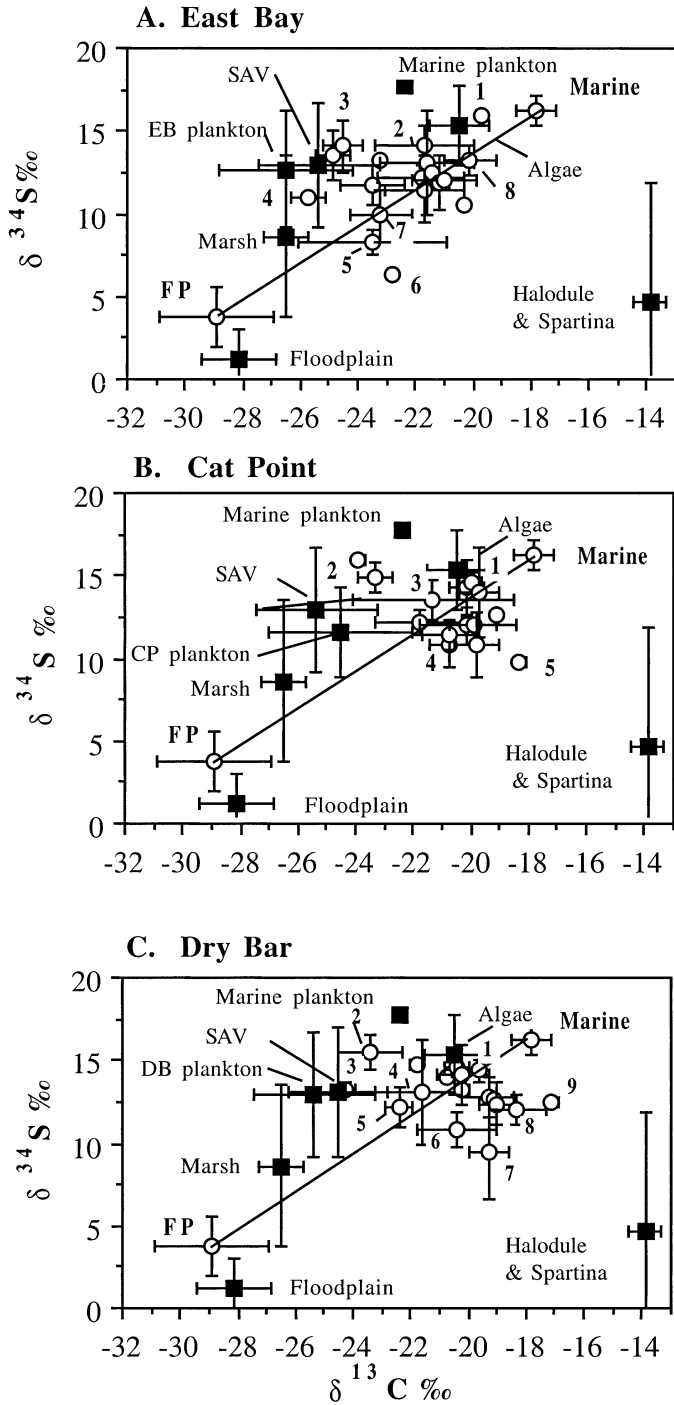


Fig. 5. Dual isotope plots of  $\delta^{13}\text{C}$  (‰) and  $\delta^{34}\text{S}$  (‰) for primary producers and consumers in the Apalachicola Bay system. Open circles are seasonally averaged values for fauna and filled squares represent seasonally averaged values for organic matter sources: algae, marine plankton, SAV (*Vallisneria* and *Ruppia*), estuarine plankton, marsh macrophytes, floodplain vegetation, and *Halodule* and *Spartina*. Error bars represent standard deviation of the mean values. A mixing line is drawn between marine and floodplain faunal end member average values (denoted Marine and FP in bold text). Numerals on each figure identify certain fauna symbols on each panel. Panel A (East Bay) 1 = squid, 2 = anchovy, 3 = oysters and mussels (two symbols close together), 4 = polychaetes, 5 = amphipods, 6 = snails, 7 = croaker, 8 = trout. Panel B (Cat

Point) 1 = squid and anchovy (2 symbols close together), 2 = oysters and mussels, 3 = crab, 4 = croaker, 5 = pinfish. Panel C (Dry Bar) 1 = anchovy and squid, 2 = oyster, 3 = mussels, 4 = crabs, 5 = polychaetes, 6 = shrimp, 7 = croaker, 8 = spot, 9 = pinfish.

pear terrestrial since it is produced from DIC with a carbon isotopic signal  $^{13}\text{C}$  depleted relative to DIC in marine waters (Chanton and Lewis 1999). However, the  $^{34}\text{S}$  signal of estuarine production should be more constant and should appear marine, since marine sulfate dominates estuarine S sources as discussed above. Thus, for a terrestrial–estuarine mixing model, it may be best to consider  $^{34}\text{S}$  data alone. Fry (pers. comm. 1997) suggested that the isotopic value of oysters could be considered as the best proxy for estuarine primary producers. Oysters are immobile and thus unlikely to have moved to their present location after sampling the cuisine elsewhere. They have a  $\delta^{34}\text{S}$  value fairly enriched relative to the other consumers, and in all cases enriched relative to the seston sampled at each station, which suggests selective assimilation. Similarly, Moncreiff and Sullivan (2001) used analysis of sand dollars as a proxy for benthic microalgae. Using the oyster  $\delta^{34}\text{S}$  value at each station as the estuarine end member (14.1, 14.9, and 15.5‰, Table 4) and the  $\delta^{34}\text{S}$  terrestrial mean value (3.7‰) as the floodplain end member yields station mean estimates of the terrestrial input ranging from 19 to 25% (far right column in Table 4). These values are lower than the estimates of 26% to 37% obtained by considering  $^{13}\text{C}$  and  $^{34}\text{S}$  in the terrestrial–marine mixing model. Problems with this approach are that we are using a water column feeder to estimate the value for the estuarine end member, which may make the more negative  $^{34}\text{S}$  values associated with benthic photosynthesis appear floodplain-like. Thus it should be considered that this approach also yields an upper limit, particularly for benthic feeders. A second problem with the approach is that it gave negative values for squid at East Bay and mussels at Cat Point because they had  $^{34}\text{S}$ -enriched tissue relative to the oysters at these stations.

In general, our results demonstrate that secondary production in Apalachicola Bay depends more upon estuarine primary production than upon a detrital food web supported by floodplain primary production. Although floodplain production is not unimportant, estuarine production is the dominant source of organic matter for the majority of secondary consumers in the bay. This finding is consistent with the finding that the  $\delta^{13}\text{C}$  of DIC was controlled by freshwater and marine mixing, not respiration of detrital organic matter (Chanton and Lewis 1999). The bay appears roughly balanced between heterotrophic and autotrophic processes. This implies that the bay's primary production is consumed within the bay, supporting secondary production.

The terrestrial–marine model, which we consider the more reliable model since it considered both isotopes, indicated that organisms in the East Bay portion of the estuary depend on terrestrial organic matter to a greater extent than those from other areas of the estuary. East Bay, located in close proximity to the river mouth and the delta marshes, is con-

←

Point) 1 = squid and anchovy (2 symbols close together), 2 = oysters and mussels, 3 = crab, 4 = croaker, 5 = pinfish. Panel C (Dry Bar) 1 = anchovy and squid, 2 = oyster, 3 = mussels, 4 = crabs, 5 = polychaetes, 6 = shrimp, 7 = croaker, 8 = spot, 9 = pinfish.

sidered as the primary nursery ground of the system (Livingston 1984). The highest juvenile densities of most species are found in this area. Thus, because of the importance of East Bay to the overall estuarine assemblage, the contribution of floodplain detritus has enhanced significance and should not be overlooked.

*Comparisons with other systems*—Recent stable isotope-derived estimates of the importance of terrestrial detritus in supporting estuarine secondary productivity have generally suggested that it is relatively inconsequential. Environments that have been examined range from salt marsh-dominated (Peterson et al. 1986; Peterson and Howarth 1987) to more open and varied systems (Deegan and Garritt 1997). Hackney and Haines (1980) reported strong influence of terrestrial inputs on fauna collected in Bay St. Louis, Mississippi, U.S.A., but examined only  $\delta^{13}\text{C}$  data. We hypothesize that the  $^{13}\text{C}$ -depleted values they observed were due to estuarine production using  $^{13}\text{C}$ -depleted DIC, which is found in fresher waters (Chanton and Lewis 1999; Coffin and Cifuentes 1999).

Our study extends three important observations of Deegan and Garritt (1997) from a system with freshwater input of  $1 \text{ m}^3 \text{ s}^{-1}$  to a system with freshwater input over 900 times greater. As observed by Deegan and Garritt, terrestrial inputs are of second order importance; organisms use local food sources; and benthic and pelagic organisms use different mixes of organic matter. The pattern emerging from isotopic studies over the last 10 years is one emphasizing the importance of algal production and deemphasizing the importance of detritus-based food webs. This study of a river-dominated estuary did not demonstrate dominance of terrestrial inputs, and we hypothesize that it is unlikely that terrestrial dominance of estuarine secondary production will ever be demonstrated, except perhaps in a deep water estuary with highly colored water that would limit light penetration and primary production.

In our opinion, work should now be focused on the causes of the differences observed in the relative importance of microalgal production (benthic and epiphytic) versus macrophyte production, both in marshes and in seagrass beds. For example, Sullivan and Moncreiff (1990) reported that benthic and planktonic algae were the dominant food sources for marsh invertebrate and fish fauna, while contributions from vascular plants were minor. Peterson et al. (1986), Peterson and Howarth (1987), Currin et al. (1995), Stribling and Cornwell (1997), and Kwak and Zedler (1997) found evidence for partial contributions from emergent macrophytes and benthic and planktonic algae. Weinstein et al. (2000) and Wainright et al. (2000) have recently reported evidence that *Phragmites australis* can contribute 73% of the inputs fueling secondary production in Delaware Bay. Within seagrass beds, Moncreiff and Sullivan (2001) have prepared an excellent discussion of the hypothesis that the importance of seagrass detritus relative to epiphytic or benthic macroalgal inputs may depend upon whether the system is eutrophic or oligotrophic. Regardless, recent studies point to the importance of in situ algal production, and our study, conducted in an end member environment, is no exception.

*Management implications*—In the Apalachicola Bay estuary, isotopic studies provide insight into the management of freshwater inflow. Estuarine primary production appears to be the main source for secondary production within the estuary, so it is necessary to maintain freshwater inflow during the period when estuarine primary production is greatest. This period generally coincides with low river flow during summer and early fall (Mortazavi et al. 2000b) when phytoplankton productivity attains maximum levels. To provide a continued coupling of primary and secondary production, it is important to maintain an uninterrupted supply of new nutrients (Iverson 1990) to the estuary. This can be accomplished by maintaining freshwater delivery, and with it nutrient load to the estuary. However, since floodplain detritus is significant, particularly in the critical East Bay nursery ground, it is also necessary to maintain peak flooding events in winter–spring that wash detritus from the forest floor into the estuary. Our results suggest that any alteration of river hydrology will affect downstream estuarine secondary production, but that the estuary will be particularly sensitive to reductions during low-flow conditions.

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