

# Concentration-dependent Stable Isotope Analysis of Consumers in the Upper Reaches of a Freshwater-dominated Estuary: Apalachicola Bay, FL, USA

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**Abstract** The goals of this study were to quantify organic matter source utilization by consumers in the freshwater-dominated region (East Bay) of a high river flow estuary and compare the results to consumers in marine-influenced sites of the same estuary to understand how organic matter utilization by consumers may be changing along the salinity gradient. We used the results from these evaluations to establish the baseline against which we isotopically determined trophic level for consumers in East Bay. Average isotope values for consumers sampled in East Bay ranged from  $-20.1\text{‰}$  to  $-24.8\text{‰}$  for carbon and from  $8.9\text{‰}$  to  $14.3\text{‰}$  for sulfur. These values were well-constrained by the four identified sources: plankton, benthic organic matter, macroalgae, and terrestrial detritus. Application of a concentration-corrected mixing model resulted in contributions of benthic production and detrital sources (averaged over the food web) to East Bay consumers of 41% and 33%, respectively, with the remainder made up of plankton and benthic macroalage. While benthic organic matter was an important organic matter source for consum-

ers at both sites, we found that the influence of terrestrial detritus varied significantly throughout the bay. Terrestrial detritus contributed only 18% of average total organic matter in organisms inhabiting marine-influenced sites. Although terrestrial detritus did contribute to all consumers examined, most fish species in Apalachicola Bay reflect a greater reliance on autochthonous sources. Our results suggest that, while terrestrial detritus does appear to be a major contributor to commercially important shellfish species (most notably oysters and penaeid shrimp), it is not the major source fueling the diversity of secondary production in Apalachicola Bay. Thus, production in Apalachicola Bay is highly dependent on riverine influx in two ways: (1) economically important bivalves and crustaceans are being fueled by terrestrial organic matter supplied by river flooding and (2) secondary and above consumer fish species are supported by in situ production which, in turn, is reliant on nutrients supplied by the Apalachicola River. These findings are significant in light of decisions regarding water usage and river flow restrictions in the Apalachicola-Chattahoochee-Flint drainage basin. The results of this study confirm that in situ estuarine organic matter is the dominant source supporting secondary production in this river-dominated estuary.

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## Introduction

Estuaries, by definition, experience a gradient in physico-chemical characteristics. Biota inhabiting the estuary, in turn, may reflect this gradient in their utilization of organic matter sources and in trophic organization (Deegan and Garritt 1997). In freshwater-dominated regions of the

estuary, dissolved inorganic carbon (DIC) concentrations are higher and more variable than those found in marine dominated regions (Peterson et al. 1994; Chanton and Lewis 1999). The DIC concentrations and  $\delta^{13}\text{C}$  values at low salinity sites are inversely related to river flow volume (Peterson et al. 1994) indicating that flooding, droughts, or other changes in flow regime can have a significant influence on carbon sources in estuarine systems.

Stable isotope analyses have been used successfully to track organic matter source (Peterson et al. 1994; Granek et al. 2009) and utilization (Peterson and Howarth 1987; Chanton and Lewis 2002) in estuarine food webs. Stable isotopes of sulfur and carbon are particularly useful for tracing organic matter flow because of their conservative properties once incorporated into the food web (Peterson and Fry 1987). Freshwater DIC is depleted in  $\delta^{13}\text{C}$  relative to marine waters (Wada et al. 1993; Peterson et al. 1994; Chanton and Lewis 1999; Fry 2002). Mixing of riverine and marine waters can be tracked via carbon isotopic analysis when low concentrations of  $\delta^{13}\text{C}$ -depleted DIC in riverine water mix with high concentrations of  $\delta^{13}\text{C}$ -enriched water from marine influences. Primary producers dependent on water-column carbon sources reflect the resulting gradient in DIC  $\delta^{13}\text{C}$  values. Consumers reflect the isotopic variations throughout the estuary resulting both from variations in source isotope values and from changes in source utilization (Deegan and Garritt 1997). Although comparisons across species should be regarded cautiously, numerous studies have demonstrated that estuarine consumers exhibit high site fidelity and tend to reflect the organic matter produced close to the area of the estuary they inhabit (Deegan and Garritt 1997; Guest and Connolly 2004; Litvin and Weinstein 2004). Thus, consumers within an estuary experience a gradient in both organic matter sources and the isotope composition of those sources along the salinity gradient. Differences in available primary producers can affect trophic structure while variations in isotopic values of those sources can affect our interpretation of trophic structure. It is, therefore, necessary to determine how isotopic values of potential sources vary throughout the estuary and to use that information when interpreting organic matter utilization by consumers.

Because of their propensity to fractionate within the trophic web (by ca 3.5‰ per trophic level), nitrogen isotopes are useful in estimating relative trophic positions among consumers (Minagawa and Wada 1984). Before trophic levels can be established, however, the base  $\delta^{15}\text{N}$  enrichment of the system must be established by determination of the relevant sources to secondary consumers (Post 2002). Since both available sources and their isotopic values have the potential to vary along the salinity gradient of the estuary, the first step in evaluating trophic levels is an estimation of the isotope values of relevant primary

producers (or failing that, reasonable isotopic proxies) in the system.

Apalachicola Bay is a dynamic system in which the food web is supported by multiple sources of organic matter (Chanton and Lewis 2002). Consumer source utilization varies along the salinity gradient. In the freshwater-dominated regions, terrestrial sources have been shown to have a small but significant influence on consumer diet (Chanton and Lewis 2002). This influence, however, fades traveling towards the marine-dominated regions of the bay (Chanton and Lewis 2002). In this study, we will quantify the contributions of individual organic matter sources to consumers occupying the freshwater-dominated East Bay site using a simultaneous, multi-isotope approach. We will then calculate relative trophic positions of these consumers using previously described techniques and compare these results to those observed in the middle portion of the bay (Wilson et al. 2009a) to determine whether and to what extent this gradient in organic matter utilization affects trophic structure in Apalachicola Bay.

The goals of this study were to quantify organic matter source utilization by consumers in the freshwater-dominated sites of a high river-flow estuary and compare the results to marine-influenced sites to understand how organic matter utilization by consumers may be changing along the salinity gradient. These results establish the baseline against which we isotopically determined trophic level for consumers in East Bay. Our previous study (Wilson et al. 2009a) indicated that terrestrial organic matter is a minor source for secondary production at the middle bay sites and we wish to evaluate whether dependence on terrestrial sources is related to freshwater influence. Our hypothesis was that terrestrial organic matter contributes more to consumers at the low salinity East Bay site relative to the marine-influenced middle bay sites previously examined. Historically, in estuarine systems, the focus has been on the importance of detrital pathways in driving estuarine production (Darnell 1961 and Odum and Heald 1972). More recently, many have questioned the importance of terrestrially derived detritus to secondary estuarine production (Deegan and Garritt 1997; Smith and Hollibaugh 1997; Sobczak et al. 2002). However, these studies focus on estuaries with either long water residence times (~21–100 days Smith et al. 1989; Sobczak et al. 2002) or low river flow ( $\sim 1 \text{ m}^3 \text{ s}^{-1}$ , Deegan and Garritt 1997). When water residence time is short, phytoplankton can become nitrogen limited through advective loss of nitrogen (Cloern et al. 1985), thus phytoplankton production may be favored in estuaries with long water residence times (Mortazavi et al. 2000a). Low flow rates could bias against detrital inputs because of a reduced supply of alluvially borne detritus. Here, we present results of organic matter utilization by secondary consumers in a subtropical estuary

with high river flow rates ( $926 \text{ m}^3 \text{ s}^{-1}$  during the sampling period; Mortazavi et al. 2000b) and short residence times (average  $\sim 6$  days Mortazavi et al. 2000b). Dependence on terrestrial organic matter sources provide one mechanism by which estuarine food webs may be influenced by river flow conditions.

## Materials and Methods

### Study Site

Apalachicola Bay is a river-dominated estuary located along the northwest gulf coast of Florida at the confluence of the Apalachicola River and the Gulf of Mexico (Fig. 1). The mouth of the Apalachicola River forms a delta system and several distributaries which drain to East Bay, a site in the upper estuarine reaches of Apalachicola Bay. Because of the large input of freshwater ( $\sim 900 \text{ m}^3 \text{ s}^{-1}$  during the sampling period; Mortazavi et al. 2000b) and the shallow water depths in this portion of the estuary ( $\sim 2$  m; Livingston et al. 1997), the flow of the Apalachicola River and its distributaries control salinity in East Bay. Salinities in the bay range from freshwater dominated near the river mouth (0 psu) to marine dominated at the lower estuarine sites (35 psu; Chanton and Lewis 1999).

### Sample Collection

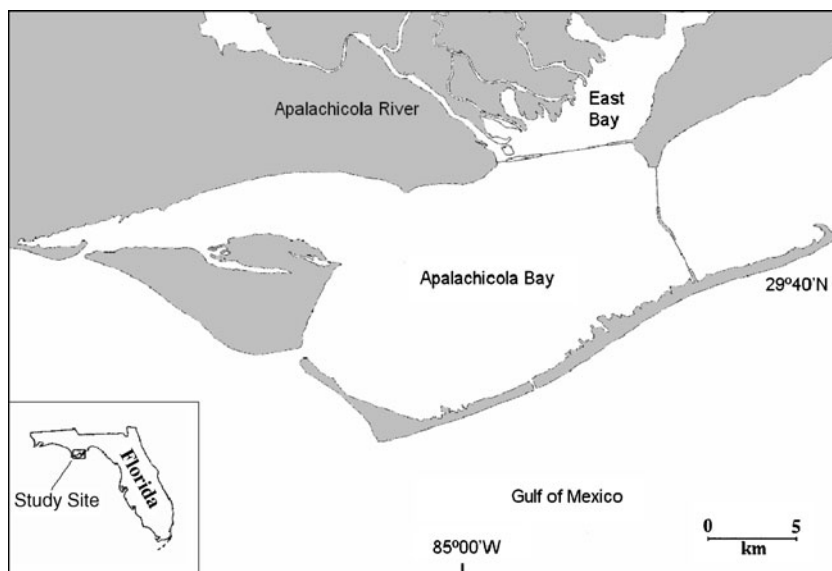
Fish and macroinvertebrate (Table 1) specimens were collected seasonally by otter trawl. Trawls were conducted from the fall of 1992 through spring of 1995 (Chanton and Lewis 2002) in East Bay. During the sampling period,

salinities in East Bay (6 psu) tended to be lower than those experienced in the middle bay (15 psu) and marine portions of the estuary (Chanton and Lewis 1999). DIC concentrations and isotopic values also indicate that freshwater influence is highest in East Bay (Chanton and Lewis 1999).

Fish species collected included the four most abundant fish species in Apalachicola Bay (in order of decreasing numerical abundance), bay anchovy (*Anchoa mitchilli*), Atlantic croaker (*Micropogonias undulatus*), sand seatrout (*Cynoscion arenarius*), and spot (*Leiostomus xanthurus*; Livingston 1984) in addition to other teleost species, crabs, mussels, oysters, and shrimp (Table 1). Muscle tissue was separated from bone, head, and internal organs, and then freeze dried and ground to a fine powder (see Chanton and Lewis 2002 for detailed sample preparation). Smaller organisms were grouped by size and pooled to obtain sufficient sample for analysis.

Plankton samples were collected by 10-min 64 and 150  $\mu\text{m}$  tows in East Bay during September 1992, April through October 1993, and in the Fall (September and October) of 1994 (Chanton and Lewis 1999). Plankton were concentrated on a 10  $\mu\text{m}$  screen and frozen. Subsamples were identified by examination under a microscope after preservation in Lugol's solution. Zooplankton (*Acartia tonsa*) dominated the plankton samples (Chanton and Lewis 1999). To reduce complications from differential isotope fractionation among plankton species (Chanton and Lewis 1999) and contamination from other particulate materials, only samples containing  $>80\%$  zooplankton were used in this study. Although phytoplankton are known to be important contributors to this system, the lack of phytoplankton in tow samples compelled us to use zooplankton as a proxy. Previous findings showing that the

**Fig. 1** Map of the study site. Sample sites include East Bay (freshwater-dominated site), and Cat Point and Dry Bar, which represent middle-bay sites



**Table 1** Isotopic values of consumers sampled in the freshwater-dominated East Bay site in Apalachicola Bay, FL, USA

Consumer	Common name	Organisms type	<i>n</i>	$\delta^{13}\text{C}$ (‰)	$\delta^{15}\text{N}$ (‰)	$\delta^{34}\text{S}$ (‰)
<i>Anchoa mitchilli</i>	Bay anchovy	Teleost fish	15	-21.7±1.5	14.3±0.5	14.1±2.0
<i>Arius felis</i>	Catfish	Teleost fish	7	-21.1±1.0	14.9±0.4	12.1±0.3
<i>Micropogonias undulatus</i>	Atlantic croaker	Teleost fish	13	-23.0±1.0	13.9±0.8	9.9±1.7
<i>Paralichthys lethostigma</i>	Flounder	Teleost fish	3	-21.8±1.5	14.3±0.6	12.2±0.8
<i>Cynoscion arenarius</i>	Seatrout	Teleost fish	4	-20.1±0.9	15.9±0.4	13.2±0.9
<i>Bairdiella chrysoura</i>	Silver perch	Teleost fish	7	-21.2±0.4	15.9±1.0	12.6±1.0
<i>Leiostomus xanthurus</i>	Spot	Teleost fish	7	-21.4±1.7	14.5±0.6	11.5±1.3
<i>Callinectes sapidus</i>	Blue crab	Crustacean	7	-21.6±1.7	12.2±0.9	12.8±3.2
<i>Ischadium recurvum</i>	Mussel	Mollusk	3	-24.8±0.6	9.3±0.1	14.0±1.7
<i>Crassostrea virginica</i>	Oyster	Mollusk	10	-24.6±0.8	10.3±0.6	14.3±1.6
Benthic worms	Worms	Polychaete	1	-21.8	8.4	8.9
<i>Farfantepenaeus</i> spp. and <i>Litopenaeus setiferus</i>	Shrimp	Crustacean	4	-23.5±1.1	12.5±0.6	11.8±1.2

Values represent averages±one standard deviation for each consumer

$\delta^{13}\text{C}$  of zooplankton samples tracked the  $\delta^{13}\text{C}$  of DIC within the bay (Chanton and Lewis 1999) justified our use of zooplankton as an isotopic proxy for pelagic production in this system. Elemental concentrations for carbon and nitrogen of zooplankton (Table 2) were well within one standard deviation of the average of two >80% *Rhizosolenia* spp. tows reported from Apalachicola Bay (Chanton 1997) indicating that the use of zooplankton in the concentration-dependent model (see below) should not unduly bias against or in favor of plankton production.

Detrital organic matter is represented in this system by terrestrial vegetation values and terrestrial detritus (leaves) collected in East Bay. Decomposition experiments on fresh terrestrial vegetation exhibited no shifts in isotopic composition over a period of six to twelve months (Chanton 1997). Macroalgae values were taken from Wilson et al. (2009a) and averaged with a sample of *Ulva lactuca* obtained from East Bay. Although many potential sources in the system were collected, we were unable to sample all of the production endmembers in this system as evidenced by the range of isotopic values observed in consumers. The carbon enriched, sulfur-depleted values of many consumers sampled has led to the hypothesis that benthic microalgal production is an important organic matter source in the

system given the expected isotopic range for benthic production (Chanton and Lewis 2002). Unfortunately, no benthic microalgae were obtained during the period of sampling. We therefore, chose to use isotopic values measured for *Halodule wrightii* (Shoal grass) collected within the bay to represent benthic production values. *H. wrightii* isotope values were chosen as proxies for benthic microalgal isotope values based on the caveat that the limited extent of *H. wrightii* in Apalachicola Bay makes it unlikely to be a major source itself to secondary production. However, the isotopic values and elemental concentrations of *H. wrightii* are within the range of values reported for benthic microalgae from other sites (Table 3).

A hydrochloric acid (10%) wash was used to remove carbonates from samples likely to be tainted with seawater carbonate. Samples were then washed, freeze-dried, and ground for analysis. Samples destined for sulfur analysis were not acid washed, instead they were washed with distilled water to remove seawater sulfates before freeze drying and grinding.

#### Isotopic Analysis

Isotope samples were sent to Coastal Sciences Laboratory (Austin, TX, USA) for  $^{13}\text{C}$ ,  $^{34}\text{S}$ , and  $^{15}\text{N}$  stable isotope

**Table 2** Isotopic values and elemental concentration of the four organic matter sources sampled in this study

Source	$\delta^{13}\text{C}$ (‰)	$\delta^{15}\text{N}$ (‰)	$\delta^{34}\text{S}$ (‰)	[C] (%)	[N] (%)	[S] (%)
Plankton	-27.8 to -25.3	9.1 to 11.3	10.1 to 19.3	31.8	4.3	0.7
Benthic	-14.5 to -14.4	4.7 to 8.0	2.2 to 7.5	33.1	1.0	0.3
Macroalgae	-21.6 to -18.9	5.4 to 10.0	11.5 to 17.9	26.7	0.6	1.8
Detritus	-29.4 to -24.7	4.0 to 9.0	-6.2 to 10.3	45.2	1.5	0.2

Isotopic values are expressed as ranges observed for each source. Elemental concentrations ([C], [S], and [N]) are expressed as the average% measured for all samples of a given source

**Table 3** Isotopic and elemental composition of *Halodule wrightii* compared to previously published reports of benthic microphytobenthos

Type	Study	$\delta^{13}\text{C}$	$\delta^{15}\text{N}$	$\delta^{34}\text{S}$	%C	%N	%S	
Edaphic algae	Sullivan and Moncreiff (1990)	-20.6	6.1	14.3				
Benthic microalgae	Sullivan ( <i>pers comm.</i> )	-17.8						
Epiphytic microalgae	Currin et al. (1995)	-13.9	0.5	1.9				
Benthic diatoms	Stribling and Cornwell (1997)	-14.9		5.4				
Benthic microalgae	Weinstein et al. (2000)	-17.5		6.5				
Benthic microalgae	Wainright et al. (2000)	-16.4	8.8	8.5				
Microphytobenthos	Kang et al. (2003, 2006)	-14.0	10.6					
Benthic microalgae	Doi et al. (2006, 2009)	-23.0	6.7		9.7	1.7	0.3 <sup>a</sup>	
Microphytobenthos	Riera et al. (1996)	-16.0	5.7					
Benthic microalgae	Machas et al. (2003)	-14.3	5.4					
Diatoms	Sicko-Goad et al. (1984)				19.2	2.6	0.6	
<i>Asterionella</i> sp.	Krivtsov et al. (2000) <sup>b</sup>				6.0	0.8	0.2	
	Knoechel & Kalff (1978)				13.2 <sup>c</sup>	1.8 <sup>a</sup>	0.4 <sup>a</sup>	
<i>Stephanodiscus</i> sp.	Lynn et al. (2000)				34.0	4.6 <sup>a</sup>	1.0 <sup>a</sup>	
Diatom mat	Abed-Navandi & Dworschak (2005)	-12.8	-0.8		4.7	0.5	0.1 <sup>a</sup>	
Average		-16.5	5.4	7.3	14.5	2.0	0.4	
s.d.		3.1	3.8	4.6	10.9	1.5	0.3	
<i>Halodule wrightii</i>	<i>this study</i>	Average	-14.5	6.3	4.9	33.1	1.0	0.3
		s.d. <sup>d</sup>	0.1	2.3	3.7	2.4	0.0	

Values for elemental concentrations (%C, %N, and %S) are given as percentages of dry weight to match reported values for other sources

<sup>a</sup> %S, %N calculated from %C reported multiplied by the average relative C:S or C:N for diatoms based on data in Ho et al. (2003)

<sup>b</sup> The estimated %C and %N are arrived at by multiplying the %S value reported by the relative C:S and N:S derived from Ho et al. (2003)

<sup>c</sup> Dry weight values are derived from wet weight values based on the assumption that dry weight=0.25×wet weight as per Sicko-Goad et al. (1984).

<sup>d</sup> s.d. denotes standard deviation

analysis. All isotope values were reported in standard notation:  $\delta X\text{‰} = (R_{\text{sample}}/R_{\text{standard}} - 1) \times 1000$ ; where  $R$  is the ratio of the heavy to light isotope of the element of interest. Analysis was conducted on an isotope ratio mass spectrometer after combustion to  $\text{CO}_2$ ,  $\text{SO}_2$ , or  $\text{N}_2$  (respectively). Isotope ratios were measured relative to Peedee Belemnite for  $^{13}\text{C}$ , Canyon Diablo troilite for  $^{34}\text{S}$ , and atmospheric  $\text{N}_2$  for  $^{15}\text{N}$ . Precisions of 0.2‰ for  $^{13}\text{C}$ , 0.3‰ for  $^{15}\text{N}$ , and 0.5‰ for  $^{34}\text{S}$  were determined as the standard deviation of multiple measurements of a homogeneous laboratory standard. These values represent the minimum error in these samples, since inhomogeneous biological samples are likely much more variable than homogeneous laboratory standards (Jardine and Cunjak 2005).

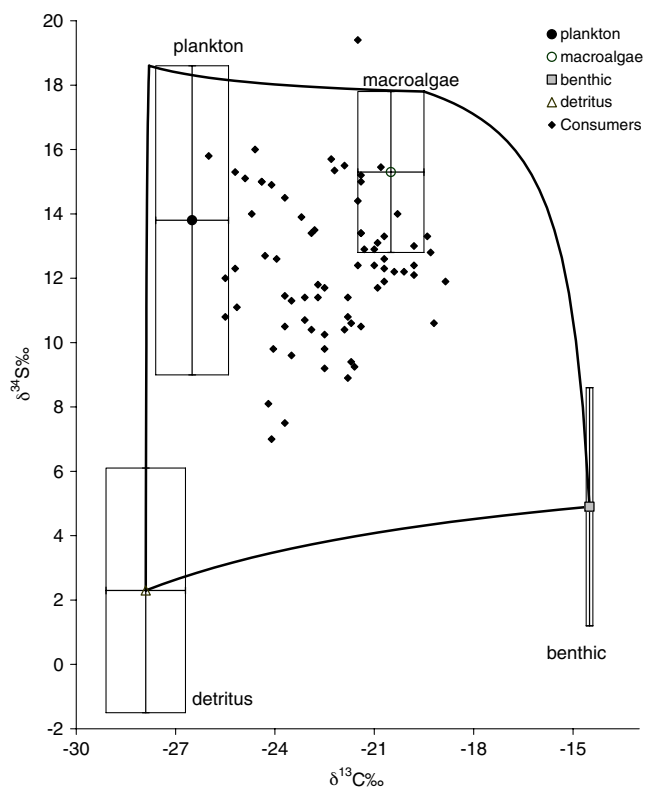
#### Organic Matter Source

Organic matter source utilization was calculated for each consumer based on carbon and sulfur isotopic values. We used a dual-isotope, multi-source, concentration-dependent

mixing model to evaluate the relative importance of sources to consumers at the East Bay site as we have previously done at the middle bay sites (Wilson et al. 2009a). The model used is described in detail in Wilson et al. (2009a). Briefly, potential organic matter contributors were evaluated by a dual-isotope comparison.  $\delta^{13}\text{C}$  and  $\delta^{34}\text{S}$  values (Fig. 2) of organic matter and consumers were plotted. Because of the (semi) conservative properties of carbon and sulfur in food webs,  $\delta^{13}\text{C}$  and  $\delta^{34}\text{S}$  values of consumers reflect the mixture of organic matter sources from which their diets are ultimately derived (Peterson and Fry 1987). Concentration-correction has been demonstrated to be an important factor to consider in food web mixing models (Phillips and Koch 2002; Wilson et al. 2009a) because significant differences in elemental concentrations among sources can result in non-linear mixing which can have significant influences on our interpretation of important sources to consumer diets.

Once potential sources were identified, a dual isotope mixing model was used to quantify source contributions to each consumer. Since four potential sources (plankton,





**Fig. 2** Dual-isotope ( $\delta^{13}\text{C}$ ,  $\delta^{34}\text{S}$ ) biplot comparison of organic matter sources and East Bay consumers. Values for sources are given as averages with whiskers representing one standard deviation in each axis. Symbols for consumers represent isotopic values of individual samples. The four sources examined (algae, plankton, terrestrial detritus, and benthic production) bound the range of isotopic values observed in consumers indicating that these four sources are likely contributing organic matter to the diets of the examined consumers. Solid lines represent mixing lines and are non-linear due to incorporation of the concentration-dependence term

benthic, algae, and detritus) were identified and we had only two isotopic values ( $\delta^{13}\text{C}$  and  $\delta^{34}\text{S}$ ) for source determinations, our model resulted in an underdetermined system (3 equations and 4 unknowns):

$$(\delta^{34}S_W - \delta^{34}S_M)[S]_W F_{W,B} + (\delta^{34}S_X - \delta^{34}S_M)[S]_X F_{X,B} + I(\delta^{34}S_Y - \delta^{34}S_M)[S]_Y F_{Y,B} + (\delta^{34}S_Z - \delta^{34}S_M)[S]_Z F_{Z,B} = 0 \tag{5}$$

$$(\delta^{13}C_W - \delta^{13}C_M)[C]_W F_{W,B} + (\delta^{13}C_X - \delta^{13}C_M)[C]_X F_{X,B} + (\delta^{13}C_Y - \delta^{13}C_M)[C]_Y F_{Y,B} + (\delta^{13}C_Z - \delta^{13}C_M)[C]_Z F_{Z,B} = 0 \tag{6}$$

$$F_{W,B} + F_{X,B} + F_{Y,B} + F_{Z,B} = 1 \tag{7}$$

Where,  $F_{i,B}$  represents the fractional contribution of source  $i$  to the consumer's overall diet,  $[S]_i$  and  $[C]_i$  represent the

elemental concentration of sulfur and carbon (respectively) in source  $i$ ,  $\delta^{13}C_i$  and  $\delta^{34}S_i$  represent the isotopic values of source  $i$ , and  $\delta^{13}C_M$  and  $\delta^{34}S_M$  represent the isotopic values of the consumer of interest. While this system cannot be solved explicitly, methods have been devised to estimate the range of possible solutions for this situation (Phillips and Gregg 2003). We have previously described one such method of incorporating concentration-dependence into dual-isotope, multi-source mixing models (Wilson et al. 2009a). Briefly, we set one of the fractional source contributions to a constant equal to 0.00 to 1.00 varied by increments of 0.01. This reduces the system to three equations and three unknowns (as the fourth unknown becomes a constant varied between 0.00 and 1.00 by 0.01 increments) which is then solved for each of the 101 possible cases. We repeat this procedure setting each of the fractional source contributions to constant values and allowing the remaining source contributions to vary continuously. The impossible solutions (fractional source contributions  $<0.0$  or  $>1.0$ ) are discarded and the remaining solutions are summarized.

### Trophic Level Calculations

While the 3.4‰ per trophic level enrichment of nitrogen isotopes in trophic webs (Minagawa and Wada 1984) complicates their use in determining organic matter sources, it does provide a metric by which to calculate relative trophic positions. Because consumers may be utilizing different combinations of sources we cannot directly compare nitrogen values of consumers to determine trophic level (Post 2002). Using  $\delta^{15}\text{N}$  to calculate the trophic level of a consumer requires reference to a “base”  $\delta^{15}\text{N}$  value (Post 2002). This base may be defined by primary consumers in a system (Post 2002), however, in dynamic estuarine environments, such as Apalachicola Bay, primary consumers can be hard to identify. We were unable to find a sufficient range of primary consumers in our system to account for the full range of (carbon and sulfur) isotopic values observed in secondary (and above) consumers. We were, therefore, compelled to calculate trophic levels by reference to a mixture of primary sources and zooplankton. We determine the  $\delta^{15}\text{N}$  value of the combination of organic matter sources being utilized by the consumer and calculate trophic level as the  $\delta^{15}\text{N}$  difference between the consumer and their respective “base” (Post 2002).

The determinations of organic matter source contributions allowed us to set a “base”  $\delta^{15}\text{N}$  for each consumer. We then calculated trophic positions as the  $\delta^{15}\text{N}$  difference between the consumer and its respective “base” divided by the 3.4‰ enrichment factor for nitrogen. This method for calculating trophic position is based on Post’s (2002) method of evaluating trophic level relative to the base

$\delta^{15}\text{N}$  in the system; however, it was expanded to incorporate concentration-dependent effects as described in Wilson et al. (2009a). Analysis of variance (ANOVA) followed by Tukey's Honestly Significant Differences post hoc evaluation was used to compare trophic levels among consumers occupying East Bay. Results from the ANOVA were used to assign trophic tiers based on  $\delta^{15}\text{N}$  values.

#### Comparison to Middle Bay Sites

Multivariate analyses of variance (MANOVA) were used to compare fractional source contributions to consumers between the East Bay and middle bay sites. Trophic levels of consumers were compared between East Bay and middle bay using two-sided *t* tests. A significance level of 0.05 was used for all statistical tests.

## Results

### Isotopic Analysis

Average  $\delta^{13}\text{C}$  values of consumers sampled in East Bay range from  $-20.1\text{‰}$  in seatrout to  $-24.8\text{‰}$  in mussels (Table 1). Source carbon isotopic values range from  $-14.4\text{‰}$  for benthic organic matter to  $-29.4\text{‰}$  for terrestrial detritus (Table 2). Average sulfur values of consumers range from  $8.9\text{‰}$  for worms to  $14.3\text{‰}$  in oysters (Table 1). Sulfur values of sources range from a low of  $-6.2\text{‰}$  for terrestrial detritus to a high of  $19.3\text{‰}$  for planktonic production (Table 3). Consumer isotopic values are well constrained within the values of the potential organic matter sources.

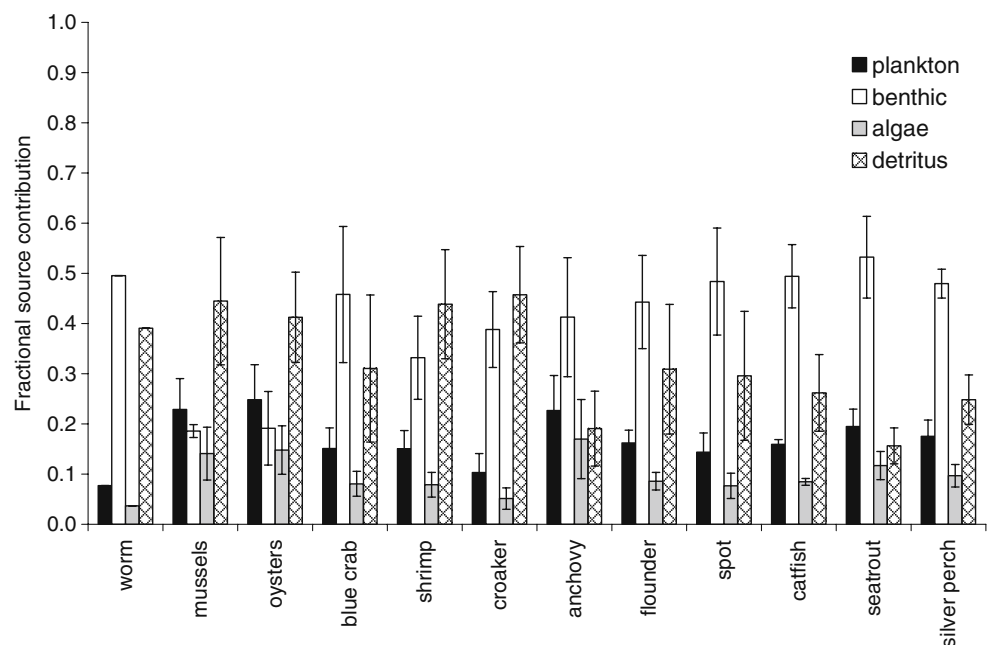
Nitrogen values of consumers in East Bay range from an average of  $8.4\text{‰}$  for worms to  $15.9\text{‰}$  for seatrout and silver perch (Table 1). This indicates that consumers sampled in East Bay range  $>7\text{‰}$ . This equates to approximately two trophic levels based strictly on nitrogen isotopic values. However, East Bay nitrogen source values range from  $4.0\text{‰}$  for terrestrial detritus to  $11.3\text{‰}$  for plankton (Table 2). Reducing zooplankton  $\delta^{15}\text{N}$  by  $3.4\text{‰}$ , to account for the trophic difference between zoo and phytoplankton, results in a range of  $4.0\text{--}7.9\text{‰}$ .

### Organic Matter Source

A biplot comparison of  $\delta^{34}\text{S}$  and  $\delta^{13}\text{C}$  values of consumers and putative organic matter sources in East Bay showed that the range of consumer isotopic values could be described by plankton, benthic production, algae, and detrital values (Fig. 2). The non-linear mixing lines (solid black curves in Fig. 2) arise from the correction introduced by incorporating a concentration-dependence term. Since elemental concentrations vary among the sources examined, isotope mixing is curvi-linear, weighted by the respective elemental concentrations. Because this is a mathematically underdetermined system, we cannot solve the system explicitly. However, we are able to solve for a range of feasible values for fractional source contributions. This approach is similar to the "brute force" approach used by the non-concentration-corrected program IsoSource (Phillips and Gregg 2003) except that fractional source contributions are allowed to vary continuously rather than held to discrete values.

In East Bay, the average contribution of plankton to consumer organic matter biomass utilization ranged from

**Fig. 3** Fractional source contributions. Bars represent average fractional contributions of each source to the consumers underlying diet. These values do not indicate, necessarily, that a consumer is directly feeding on a given source, but rather that the isotopic values of the consumer are consistent with organic matter derived (however far trophically removed) from the combination of sources shown



**Table 4** Fractional source contributions compared between middle bay and east bay sites by species

Species	Plankton		Benthic		Macroalgae		Detritus	
	East Bay	Middle Bay	East Bay	Middle Bay	East Bay	Middle Bay	East Bay	Middle Bay
Bay anchovy	23±7	20±4	41±12	43±10	17±8	24±12	19±7	13±4**
Blue crab	15±4	22±4*	46±14	46±8	8±2	15±6*	31±15	18±9
Catfish	16±1	18±4	49±6	58±5**	8±1	11±4	26±8	13±4***
Croaker	10±4	13±6	39±8	62±9***	5±2	9±6*	46±10	17±8***
Flounder	16±3	17±4	44±9	55±9	9±2	11±7	31±13	17±8
Mussels	23±6	28±5	19±1	22±7	14±5	15±10	44±13	35±9
Oysters	25±7	33±7	19±7	19±9	15±5	27±14*	41±9	21±9***
Shrimp	15±4	17±4	33±8	59±8 (°)	8±2	7±2	44±11	18±8 (°)
Seatrout	19±3	21±3	53±8	45±3	12±3	22±8*	16±4	12±2
Silver perch	18±3	19±5	48±3	54±10	10±2	12±2	25±5	15±8***
Spot	14±4	16±5	48±11	61±7**	8±3	9±4	30±13	15±7**
Worms	8	22±6	50	41±6	4	9±3	39	28±2
Averages	17	20	41	47	10	14	33	18

Values are given as average percent for a species±one standard deviation. Significant results from the MANOVA comparison are indicated by asterisks in parentheses following each source pair

Data for middle bay sites is reported in Wilson et al. (2009a)

\* $p < 0.05$  significance

\*\* $p < 0.01$  significance

\*\*\* $p < 0.001$

8% in worms to 25% in oysters (Fig. 3; Table 4). Benthic organic matter contributed 19% in mussels and oysters to 53% in seatrout. Algal sources ranged from 4% in worms to 17% in bay anchovy. Terrestrial detrital sources ranged from 16% in seatrout to 46% in croaker. Surprisingly, terrestrial detritus had a large influence on East Bay oyster and mussel diets (41% and 44%, respectively; Fig. 3; Table 4). Benthic macroalgal contributions were low averaging 10% overall to the system (Table 4) and no more than 20% of the contributions to any one individual species.

#### Trophic Level Calculations

Average trophic positions of consumers as calculated relative to their individual bases ranged from 1.6 for benthic worms to 3.8 for silver perch. Mussels and oysters formed the lowest trophic tier averaging 2.0. Blue crabs and shrimp had an average trophic level of 2.7. The remaining consumers examined formed a trophic continuum where significant differences existed between groups of consumers, but enough overlap occurred to prevent the division into smaller trophic tiers (Fig. 4). Anchovy and croaker, (average trophic level=3.3) were the lowest trophic level consumers in this group. Flounder, catfish, and spot had similar trophic levels (average=3.4). Silver perch and seatrout had the highest trophic level of any of the

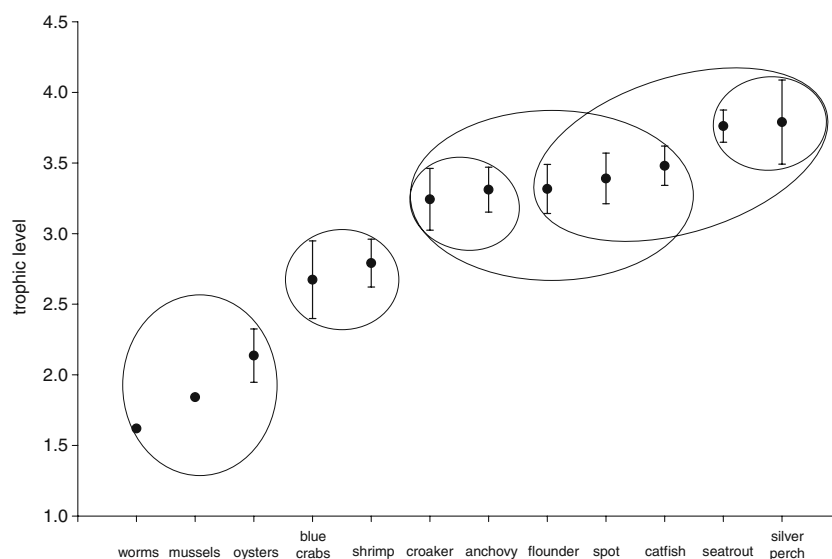
consumers examined (3.8). Worms (trophic level=1.6) were excluded from the ANOVA because there was sufficient isotopic evidence to calculate trophic level on only one sample.

#### Comparison to Middle Bay Sites

East Bay consumer isotope values were consistent with diets based on terrestrial detritus, plankton, algae, and benthic organic matter sources (Fig. 2). In the middle bay, these same four sources also contributed to consumer diets (Wilson et al. 2009a). Organic matter fractional contributions for consumers from East Bay were compared to those obtained for the same consumer species from the middle bay sites (Table 4). Bay anchovy, blue crab, catfish, croaker, spot, oysters, seatrout, silver perch, and shrimp differed in organic matter fractional contributions of at least one source between the upper and middle bay sites. Catfish, croaker, spot, and shrimp all relied on significantly less benthic organic matter in East Bay relative to the middle bay sites (Table 4). Blue crab relied on a significantly greater proportion of planktonic sources in the middle bay sites relative to East Bay (22% vs. 15%). Bay anchovy, catfish, croaker, oysters, shrimp, silver perch, and spot in East Bay were significantly more reliant on detrital sources than those same species at the marine influenced sites. When differences were significant, detrital sources were



**Fig. 4** Comparison of trophic levels among consumers occupying East Bay. Circles bound consumers with statistically similar trophic levels. Circles that touch indicate the enclosed consumers have statistically similar trophic levels, while circles that do not overlap indicate that the consumers contained within those boxes have significantly different trophic levels based on  $\delta^{15}\text{N}$  values



always more influential to the diets of consumers in East Bay than in middle bay sites. Similarly, when differences were significant, benthic organic matter sources were always greater contributors to middle bay consumers than their East Bay conspecifics. Seatrout ( $p < 0.05$ ,  $\text{mean}_{\text{middle bay}} = 3.5$ ,  $\text{mean}_{\text{East Bay}} = 3.8$ ) and silver perch ( $p < 0.01$ ;  $\text{mean}_{\text{middle bay}} = 3.3$ ,  $\text{mean}_{\text{East Bay}} = 3.8$ ) had significantly higher trophic positions at the East Bay site relative to mid-bay samples.

## Discussion

In this study, we demonstrate that dependence of secondary consumers on organic matter sources varies along the salinity gradient of a freshwater-dominated estuary. As expected, dependence on terrestrial organic matter sources is highest at the lower salinity site (East Bay). However, for all consumers, terrestrial organic matter contributions were less than the combined in situ sources. Among the most dependent on terrestrial organic matter sources are estuarine bivalves. Our results, however, indicate that secondary production in Apalachicola Bay, at all sites, is largely fueled by in situ estuarine production and not by alluvially borne detritus.

### Isotopic Analysis

Not only can the concentration of DIC vary along the salinity gradient in an estuary, DIC isotopic values ( $\delta^{13}\text{C}$ ) also appear more depleted in the freshwater reaches than in marine dominated areas (Fry 2002; Chanton and Lewis 1999). Thus, the  $\delta^{13}\text{C}$  of the food supply to producers and ultimately consumers in estuarine environments varies along the salinity gradient of the estuary. Chanton and

Lewis (1999) demonstrated that plankton isotopic values in Apalachicola Bay track DIC values. They further showed that secondary consumers in the upper estuarine site (East Bay) exhibited  $\delta^{13}\text{C}$ -depleted values relative to their cohorts in the middle (Cat Point and Dry Bar) regions of the bay (Chanton and Lewis 2002). A confounding factor in the analysis of consumer isotopic values from this estuary is the supply of alluvially borne terrestrial detritus to East Bay. This detritus is  $\delta^{13}\text{C}$  depleted relative to benthic and macroalgal sources within the bay (Fig. 2). Thus  $\delta^{13}\text{C}$ -depleted values in secondary consumers from this region could result from a greater dependence on terrestrially derived detrital sources or from planktonic sources that rely on relatively  $\delta^{13}\text{C}$ -depleted DIC supplies, or some combination of these factors (Chanton and Lewis 2002).

### Organic Matter Source

Chanton and Lewis (2002) used two-source models to compare the influence of terrestrially derived sources to that of marine and estuarine production. They found that, even in the freshwater-dominated upper reaches of East Bay, terrestrial detritus was secondary to estuarine production. This conclusion was based on the finding that the shift in  $\delta^{13}\text{C}$  values of consumers was not correlated with a shift in  $\delta^{34}\text{S}$  values. They suggested that because all plankton, even in the freshwater-dominated East Bay, rely on marine sulfate as a sulfur source, if consumers were exchanging planktonic sources for detrital organic matter in the upper estuary there should be a concomitant depletion of sulfur values in secondary consumers (Chanton and Lewis 2002).

We wish to suggest another possible case. In the middle estuarine sites, benthic production has been suggested as a

dominant source to secondary consumers of Apalachicola Bay (Wilson et al. 2009a). Benthic organic matter is similar in  $\delta^{34}\text{S}$  values to detritus, but enriched in  $\delta^{13}\text{C}$  (Fig. 2). Another contributing source in the middle bay is benthic macroalgae. Algae are similar in  $\delta^{34}\text{S}$  and slightly  $\delta^{13}\text{C}$  enriched relative to planktonic sources (Fig. 2). We suggest that a shift from a diet supported by both benthic producers and algal sources to one based on detrital sources in the upper estuarine reaches would also be consistent with the isotopic shifts observed along the spatial gradient present in Apalachicola Bay (Fig. 2).

In order to determine whether benthic or planktonic source contributions were changing across the salinity gradient, we employed a four-source model that is capable of quantifying the relative contributions of these sources. An evaluation of organic matter sources showed  $\delta^{15}\text{N}$  values of primary producers that ranged  $\sim 4\text{‰}$ . This difference in  $\delta^{15}\text{N}$  values represents a trophic level among the sources based on the canonical trophic discrimination of 3.4‰ reported by Minagawa and Wada (1984). Thus, the “base” nitrogen input to the system varies considerably depending on the ultimate source of organic matter used. At the middle-bay sites, a 4‰ difference in  $\delta^{15}\text{N}$  values among sources was enough to necessitate the use of the concentration-corrected mixing model rather than the simpler linear model proposed by Phillips and Gregg (2003; Wilson et al. 2009a).

The results of our model indicate that the major source contributing to secondary production in East Bay is benthic organic matter (Table 4). Some species, most notably bivalves are largely dependent on terrestrial organic matter (Fig. 3). However, for all consumers examined, the sum of in situ sources (plankton, benthic organic matter, and algae) is greater than the contribution of terrestrial detritus (Table 4). These results are surprising given the plethora of suggestions in the literature that terrestrial organic matter is a significant source underlying riverine and estuarine production (Haines 1977; Mann 1988; Stribling and Cornwell 1997). Interestingly, bivalves are among the consumers most reliant on terrestrial organic matter sources (Fig. 3). Previous studies have similarly suggested a high reliance of bivalves on terrestrial organic matter sources in freshwater-influenced estuaries (Riera and Richard 1996; Riera and Richard 1997; Riera 1998; Kasai and Nakata 2005). This has led to speculation that bivalves provide an important link between terrestrial organic matter sources and higher trophic level consumers that lack the necessary enzymes to digest cellulose themselves (Antonio et al. 2009). Our results however, indicate that, at least in this freshwater-dominated estuary, little of the terrestrial organic matter is being thus transferred to higher trophic levels. Rather, secondary consumers, even in the low-salinity East Bay site, are more dependent on

available in situ organic matter sources than on alluvially borne detritus.

#### Trophic Level Calculations

The consumers sampled in East Bay spanned two trophic levels. This is similar to the result estimated based on absolute  $\delta^{15}\text{N}$  values. A comparison of trophic levels among consumers at East Bay found that mussels and oysters, as a group, as well as blue crabs and shrimp, as a group, were distinguishable from all other consumers (Fig. 4). The remaining consumers did not form discrete trophic levels, but rather a trophic continuum. This is expected as these consumers tend to be highly opportunistic in feeding habit, capturing a range of prey organisms (Sheridan 1978; Sheridan 1979; Stoner and Livingston 1984). In contrast however, the differing trophic levels among teleost fishes within the continuum were unexpected. For example, anchovy and croaker (average trophic level=3.3) were significantly different from seatrout and silver perch (3.8). At the middle bay site four general trophic tiers were found; teleost fishes occupied the highest tier and none were significantly different from other teleost fishes examined (Wilson et al. 2009a).

Twelve consumer species were sampled in common between the East Bay and mid-bay sites. Of those, only seatrout and silver perch had significantly different trophic levels in East Bay relative to their conspecifics sampled in the middle bay sites. The trophic level differences were small (0.3–0.5 trophic levels) and not obviously correlated with organic matter utilization.

We have previously shown that the size ranges of fish are not significantly different at the two sites (Wilson et al. 2009b) thus variations in size or age are not likely contributing to the observed variation. Whether these differences in trophic level reflect true trophic variation or are an artifact of the sampling procedure is unknown; however, these findings warrant further investigation into trophic structure at these sites and into other sites experiencing strong physicochemical gradients.

#### Comparison to Middle Bay Sites

We compared the results of organic matter utilization and trophic level for East Bay consumers to values previously reported for consumers from the middle estuarine sites (Wilson et al. 2009a). East Bay blue crabs relied less on planktonic contributions than their middle bay counterparts; however, planktonic contributions were similar between the two sites for all other species examined. With the exception of blue crabs, oysters, and seatrout, utilization of macroalgal sources was also consistent throughout the bay. In East Bay, the contributions of benthic production and

detrital sources averaged over the food web were 41% and 33% respectively (Table 2). At the middle bay sites the contributions of these two sources to the overall food web were 47% and 18%, respectively (Wilson et al. 2009a). Our data indicate that the major shift in source utilization that occurs in Apalachicola Bay is from terrestrially derived detrital sources in the freshwater-dominated regions to an increased reliance on benthic sources at the marine-dominated sites (Table 2). Previous reports of isotopic data on sediments from Apalachicola Bay have indicated that sediments in East Bay (and indeed elsewhere in the bay) are depleted in  $\delta^{13}\text{C}$  (average =  $-24.7 \pm 0.9\%$ ; Chanton and Lewis 2002). While this finding seems to negate the possibility of large amounts of benthic organic matter in this system, we present two possibilities to reconcile the apparent discrepancy between depleted sediment values and a large input of enriched benthic production. The first is the possibility that benthic organic matter producers (i.e., diatoms) are present in only a thin layer on the surface of the sediments and (since isotopic analysis was conducted on a 1-cm depth section of sediment) it is possible that the depleted sediment signal overwhelms any enriched benthic production signal. The other possibility is that we do not find isotopic evidence of benthic organic biomass in the sediment samples because benthic organic matter production rates are very close to consumption rates by predators. In this case, while benthic organic matter production is high and a large contributor to the base of the Apalachicola Bay food web, it is being consumed so quickly by herbivores that there is not a large reserve in the sediment and thus bulk sediment isotope values are not enriched.

Previously a two end-member approach was used to determine the contribution of terrestrial sources to consumers inhabiting Apalachicola Bay (Chanton and Lewis 2002). In an estimate of the upper limit of detrital input, marine production was used as the second end-member in a linear mixing model. Carbon and sulfur isotopes were each used to estimate the contribution of the two sources and the results from each isotope mixing model were averaged. Chanton and Lewis (2002) estimated an average detrital input to East Bay of 37% (33% this study) and an average detrital input to the middle bay of 26% (18% was estimated by Wilson et al. 2009a) using this approach. Because this model ignores estuarine production which can exhibit  $\delta^{13}\text{C}$  values intermediate between terrestrially derived DIC and marine carbon, it tends to overestimate detrital influences. To correct for this, Chanton and Lewis employed a second mixing model using estuarine production as the second end-member. This case, however, used only isotopes of sulfur because of the difficulty inherent in distinguishing  $\delta^{13}\text{C}$ -depleted detritus from variation in planktonic values resulting from the addition of freshwater ( $\delta^{13}\text{C}$ -depleted) DIC. One problem that they had with this approach was

that  $\delta^{34}\text{S}$ -depleted benthic sources were indistinguishable from terrestrial detritus, thus resulting in an overestimation of detrital inputs in regions where benthic organic matter may have been important. While terrestrial detritus and benthic organic matter sources in this system have similar  $\delta^{34}\text{S}$  values, they are distinguishable using  $\delta^{13}\text{C}$ . Thus, we wish to compare the results obtained by Chanton and Lewis (2002) to our results using a four-source, simultaneous isotope mixing model. In our model, we can both account for estuarine production and distinguish between terrestrial detritus and benthic organic matter sources.

We estimated that terrestrial detritus contributes 33% of the overall organic matter to the East Bay food web, while at the middle bay sites that percentage falls to 18%. These results are approximately 4–8% lower than the (upper limit) estimates of Chanton and Lewis (2002) using a marine-terrestrial mixing model. Thus our findings agree that terrestrial input is secondary to estuarine production in this system and demonstrate that the two end-member, sequential isotope mixing model used by Chanton and Lewis (2002) was a reasonable first-order approximation of the processes occurring in Apalachicola Bay. Even at the more terrestrially influenced East Bay site, the majority of consumers are dominated by estuarine sources (Fig. 3). Terrestrial inputs are the major (single) organic matter source only in mussels, shrimp, oysters, and croaker at the East Bay site (Fig. 3; Table 2) and by the middle of the bay only mussels are still dominated by terrestrial inputs (Wilson et al. 2009a).

The Apalachicola River deposits an average annual detrital carbon input of 30,000 mt (Matraw and Elder 1984). During the sampling period, the annually averaged inputs of in situ phytoplankton production amounted to 64,000 mtC per year. This number is based on the average production over multiple sites ( $255 \text{ mgC m}^{-2}\text{d}^{-1}$ ) in Apalachicola Bay reported by Mortazavi et al. (2000b), multiplied over the combined dimensions of Apalachicola and East Bay (20,959 and 3, 981 ha, respectively; Livingston 1984). Based on these estimates, detrital carbon inputs are at most 30% of total carbon inputs in the bay. This percentage is similar to the overall average of percent contribution of detritus to consumers sampled in East Bay (Table 2). Thus organic matter sources appear to be utilized in their relative proportions of availability within the estuary. However, there are currently no estimates of benthic organic matter production for the system. Any amount of benthic primary production would increase the estimates of in situ production which would decrease the relative inputs of detrital C to the total C pool in the system. Thus detrital carbon inputs are at least as important (and likely more important) to the East Bay food web as other carbon inputs relative to their availability in the bay. If detritus in East Bay is more important relative to availability, it is possible that detrital carbon is depleted quickly by

consumers in East Bay. In this scenario, detrital inputs would not be homogenous throughout the bay, but would be highest in East Bay where it would be used up very quickly and then diminish toward the middle bay sites. This would account for the overall reduction in detrital organic matter contributions in the middle of the estuary.

Another possibility in the system is the input of marsh plant production from the extensive marsh adjacent to East Bay. Saltmarsh plants in this region include both  $C_4$  (*Spartina alterniflora* and *Spartina cynosuroides*) and  $C_3$  (including *Juncus roemerianus*, *Typha* spp., *Scirpis* spp. and *Phragmites australis*) plants, with very distinct  $\delta^{13}C$  values. *Spartina* spp. have enriched  $\delta^{13}C$  and depleted  $\delta^{34}S$  values similar to benthic organic matter sources (Chanton and Lewis 2002). The very small extent of *S. alterniflora* in the marsh, however, has led to the conclusion that it cannot be a major source of production for the estuary. However, the extent of *S. cynosuroides* is unknown in this area and cannot be ruled out as a possible contributor to this system. If it is a large contributor, it is necessarily combined as some portion of the benthic contribution since the two cannot be isotopically distinguished based on carbon and sulfur data.  $C_3$  marsh plant isotopic values are similar to those obtained for terrestrial detritus in this system (Chanton 1997). Since  $C_3$  marsh plants could not be distinguished from terrestrial inputs based on isotopic values, the designation “terrestrial detritus” in our study must necessarily include  $C_3$  marsh plant contributions as well.

In summary, we have established that plankton, benthic organic matter, terrestrial detritus, and macroalgae are important organic matter contributors to consumers throughout Apalachicola Bay. However, organisms occupying East Bay utilize different proportions of organic matter sources than their counterparts in the middle estuary. Our multi-source, multi-isotope approach supports earlier results indicating that terrestrially derived sources are less important than estuarine production to consumers in this system (Chanton and Lewis 2002). In addition to differences in organic matter dependence, trophic structure of consumers also varied along the estuarine gradient. These results highlight the difficulty in comparing trophic organization among geographic sites even within a semi-confined system.

We have shown that terrestrial sources do contribute to consumers in Apalachicola Bay, specifically in the upper, East Bay, portion of the estuary where it accounts for ca. 33% of overall average organic matter used. Utilization of terrestrial detritus decreases at the middle bay site where it accounts for only 18% of the total organic matter utilization. Changes in freshwater inflow to the estuary could potentially affect the availability of terrestrially derived organic matter in this estuary which in turn could influence consumers, particularly in East Bay. While the number of such studies have been increasing (Deegan and

Garritt 1997; Chanton and Lewis 2002; Guest and Connolly 2004), Fry (2002) has pointed out the dearth of estuarine food web studies that have been sampled specifically across salinity gradients and suggests that such studies are of interest because estuarine production and trophic patterns may be susceptible to changes in flow regime. Our sampling was conducted during a period of relatively high-flow conditions ( $926 \text{ m}^3 \text{ s}^{-1}$  Mortazavi et al. 2000a) and therefore our results represent high-flow consumer conditions in Apalachicola Bay. During low flow regimes, both terrestrial detritus and dissolved inorganic nitrogen (DIN) inputs to the bay decrease. We have shown that production in East Bay is at least partly reliant on detrital inputs and changes in DIN are known to influence in situ estuarine production, thus reductions in river flow have the potential to impact trophic structure in East Bay.

The importance of detrital organic matter to estuarine ecosystems has been estimated to be large (Darnell 1961; Haines 1977; Mann 1988) and proximity of freshwater-influenced estuaries to upland environments has been hypothesized to contribute to increased terrestrial organic matter inputs to consumers occupying such sites (Stribling and Cornwell 1997). Variations in carbon isotopic values of oysters (*Crassostrea gigas*) and bivalves (*Corbicula japonica*) along estuarine gradients has led to the suggestion that terrestrial organic inputs are an important carbon source in freshwater-influenced estuaries (Riera and Richard 1996; Kasai and Nakata 2005). Our results suggest that while terrestrial detritus does appear to be a major contributor to commercially important shellfish species (most notably oysters and penaeid shrimp) it is not the major source fueling the diversity of secondary production in Apalachicola Bay. Expanding on Chanton and Lewis's (2002) original findings, production in Apalachicola Bay is highly dependent on riverine influx in two ways: (1) economically important bivalves and crustaceans are being fueled by terrestrial organic matter supplied by river flooding and (2) secondary and above fish species (with the exception of Atlantic croaker) are supported by in situ production which, in turn, is reliant on nutrients supplied by the Apalachicola River. We suggest the possibility that such a disconnect between bivalve and fish production occurs at other sites and urge researchers to investigate whether reliance on terrestrial sources is also observed in secondary and above fishes in estuaries where bivalve dependence on terrestrial organic matter has been demonstrated. These findings highlighting the reliance of Apalachicola Bay consumers on river flow through the dependence of estuarine production on supplied nutrients and through dependence on alluvially supplied detritus are significant in light of decisions regarding water usage and river flow restrictions in the Apalachicola-Chattahoochee-Flint drainage basin.

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