

# Sedimentation, carbon export and food web structure in the Mississippi River plume described by inverse analysis

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**ABSTRACT:** The Mississippi River stimulates the coastal marine ecosystem directly with dissolved organic matter and indirectly with inorganic nutrients that enhance primary production. To understand the river's effect, we need to track the fate of both sources of organic matter. Using readily available data, we investigated the planktonic ecosystem of the buoyant Mississippi River plume using an inverse analysis technique to describe the carbon flow for the complete planktonic system. For each season we divided the marine waters receiving Mississippi River discharge into 4 dilution regions connected by movement of river water. Our results show that during 3 seasons (spring, summer, and fall) mid-salinity waters (15 to 29 psu) exported organic matter (strongly net autotrophic), whereas the other regions imported it (net heterotrophic). More than 20% of total plume primary productivity was exported from the entire modeled region, as continued water movement carried organic carbon into surrounding waters. In contrast, the winter plume was net-heterotrophic everywhere, as high bacterial respiration overwhelmed relatively low primary production, and riverine dissolved organic carbon (DOC) and organic carbon from resuspended sediments were required to balance a carbon deficit. From the spring through fall, sedimentation of organic carbon was linked to primary production, with strongest sedimentation in mid-salinity regions. Sedimentation was enhanced beneath less productive, higher-salinity regions, by import of organic carbon moving out of mid-salinity regions. In contrast, winter organic carbon sedimentation rates were calculated to be zero in all model regions. The analysis showed a dynamic relationship between primary production and sedimentation and provides a good starting point for future development of mechanistic models that directly address the relationships between nutrient input, primary production, sedimentation and hypoxia on the Louisiana Shelf.

**KEY WORDS:** Inverse analysis · River plume · Mississippi River · Louisiana Shelf · Food web · Trophodynamics · Hypoxia

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## INTRODUCTION

The Mississippi River is the largest river in North America, with a watershed covering more than 40% of the contiguous United States. The river discharges an average of 380 km<sup>3</sup> of freshwater into the northern Gulf of Mexico each year (Meade 1995), an amount representing more than half of the total annual freshwater input to the Gulf of Mexico (Deegan et al. 1986). Its watershed encompasses some of the most inten-

sively farmed and fertilized regions in the world, and the Mississippi carries high concentrations of nitrate (>100 µM) and other nutrients to the northern Gulf of Mexico (Howarth et al. 1996, Rabalais et al. 1999). During the past 100 yr, nutrient concentrations in the Mississippi have tripled with increasing rates of agricultural fertilization, resulting in eutrophication and seasonal bottom-water hypoxia over much of the Louisiana Shelf that receives its discharge (Rabalais et al. 1994, 1999, Goolsby et al. 1999).

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It was recognized as early as 1937 that Mississippi River discharge enhances primary production on the Louisiana Shelf (Riley 1937). River-enhanced primary productivity, in turn, has been observed to increase sedimentation there, but establishing a clear and direct relationship between primary production and sedimentation has proven difficult (Eadie et al. 1994, Trefry et al. 1994). Concurrent measurements of primary productivity and sedimentation made in 1990 and 1991 did not appear related; highly productive summer months had the lowest sedimentation rates, while weakly productive winter months had the highest (Redalje et al. 1994). Redalje et al. (1994) speculated that these processes might be uncoupled over the Louisiana Shelf because carbon pathways in plume and shelf ecosystems might not distribute particulate organic material predictably in time or space. Variable but intense grazing in the water column by both micro- and mesozooplankton, as well as enhanced bacterial activity in areas of higher primary productivity were suggested as mechanisms for remineralizing organic carbon before it could sink to the benthos. The result would be variable export production, masking any relationship to primary production (Redalje et al. 1994). The numerous ecological possibilities for controlling export are difficult and costly to test, requiring synchronous measurement of a large number of ecosystem processes over the shelf and in the plume. In this situation, ecosystem modeling has great potential to explain the processes that control export production.

Although a relationship between hypoxic water formation and river nutrient input has been established, many ecosystem processes affecting the intensity of hypoxia are poorly understood (Rabalais et al. 1994, 1996, 1999). Some ecosystem processes, however, have been well characterized, particularly in the wake of oceanographic programs in the late 1980s and early 1990s that were initiated specifically to address Louisiana Shelf hypoxia. The LaSER (Louisiana Search for Excellence in Research) and NECOP (Nutrient Enhanced Coastal Ocean Productivity) programs were especially important in this respect. Resulting data have led to conceptual syntheses as well as some mathematical modeling results (Bierman et al. 1994, Justić et al. 1997, 2002, Rowe 2001). In the light of its impact on the Gulf of Mexico, however, the Mississippi River plume ecosystem has been the subject of only modest modeling efforts. For the present study, we used a technique from applied mathematics known as inverse modeling to do so.

Vézina & Platt (1988) adapted an inverse approach to describe a marine food web, analyzing food-web dynamics along the British coast. Their approach has been used to describe carbon and nitrogen flow in a wide range of marine and limnetic environments since

then, including the North Pacific (Vézina & Savenkoff 1999), an atoll lagoon (Niquil et al. 1998, 1999), both planktonic (Jackson & Eldridge 1992) and benthic (Eldridge & Jackson 1993) communities in Southern California, the Baltic Sea (Donali et al. 1999) and a Michigan lake (Vézina & Pace 1994).

We start with a conceptual compartmental ecosystem model for the Mississippi River plume which incorporates all possible carbon flows between living and nonliving organic carbon pools within the planktonic food web. Our analysis then calculates the carbon flow through the system taking the 'shortest' path consistent with a set of physical and biological realities (i.e. field measurements of ecosystem processes, known physiological constraints and mass balance). The result is a food-web network wherein all carbon flows have specific numeric values, providing a more integrated picture of the ecosystem in the buoyant Mississippi River plume.

## METHODS AND MODEL APPROACH

**Model domain.** As it mixes with ocean water, Mississippi River discharge evolves from a turbid light-limited system to a clear nutrient-limited system (Dagg & Breed 2003). To describe the spatial and temporal evolution of the discharge, we divided the plume into 4 regions, and modeled only the buoyant surface layer. Each region was considered to be both vertically and laterally well-mixed, gaining water from its upstream neighbor and the underlying water and losing water to its downstream neighbor (Figs. 1 & 2).

Because surface salinity provides a good measure of dilution, it was used to define the centers and borders of model regions (Redalje et al. 1994, Dortch 1998, Lohrenz et al. 1999, Rabalais et al. 1999). Plume Region 1 ( $P_1$ ) is nearest the river mouth and defined to have a mean salinity of 10 psu. This region tends to be light-limited with low primary productivity. Plume Regions 2 ( $P_2$ ) and 3 ( $P_3$ ) have mid-salinity values of 23 and 29 psu. Region 4 ( $P_4$ ) has the highest average salinity, 33 psu. The breakpoints between regions were decided somewhat arbitrarily, and are:  $P_1$  to  $P_2$  = 18 psu;  $P_2$  to  $P_3$  = 27 psu;  $P_3$  to  $P_4$  = 32 psu;  $P_4$  to outside study area  $\approx$  34.5 psu.

The planktonic ecosystem of each region was divided into 8 compartments, representing 6 living groups of plankton and 2 non-living components (Fig. 2). Phytoplankton were divided into large (phL,  $>8 \mu\text{m}$ ) and small (phS,  $<8 \mu\text{m}$ ) groups (Redalje et al. 1994). There were compartments for bacteria (bac) and grazers of 3 size classes: mesozooplankton (mes,  $>200 \mu\text{m}$ ), microzooplankton (mic, 63 to 200  $\mu\text{m}$ ), and protozoans (pro,  $<63 \mu\text{m}$ ). Each grazer class had a set of grazing rules for-

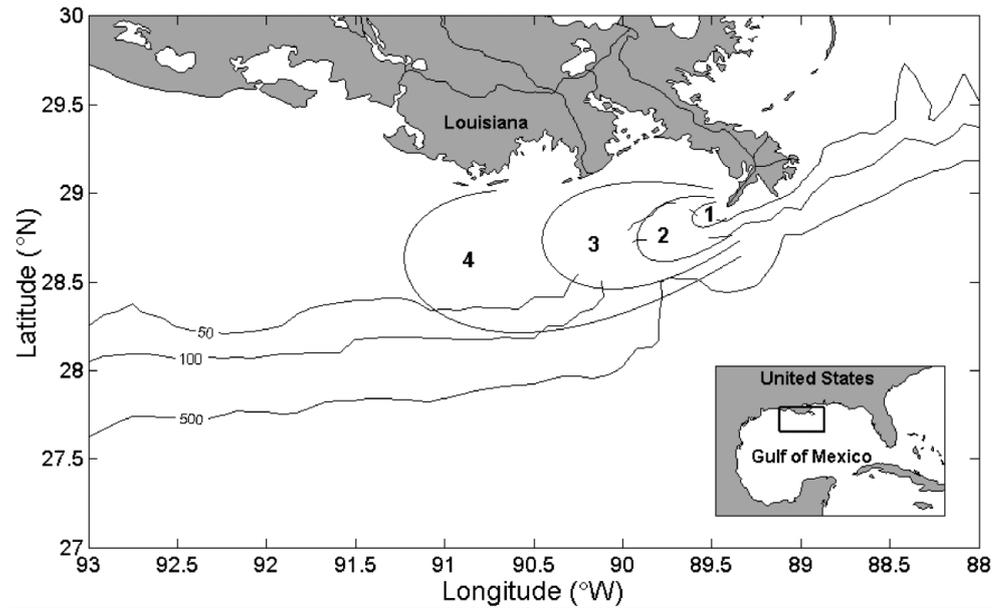


Fig. 1. Study region and regions. Model food web was divided into 4 regions to account for varying physical, biological, and chemical conditions along salinity gradient. Boundaries between regions were not geographically fixed and were defined by salinity

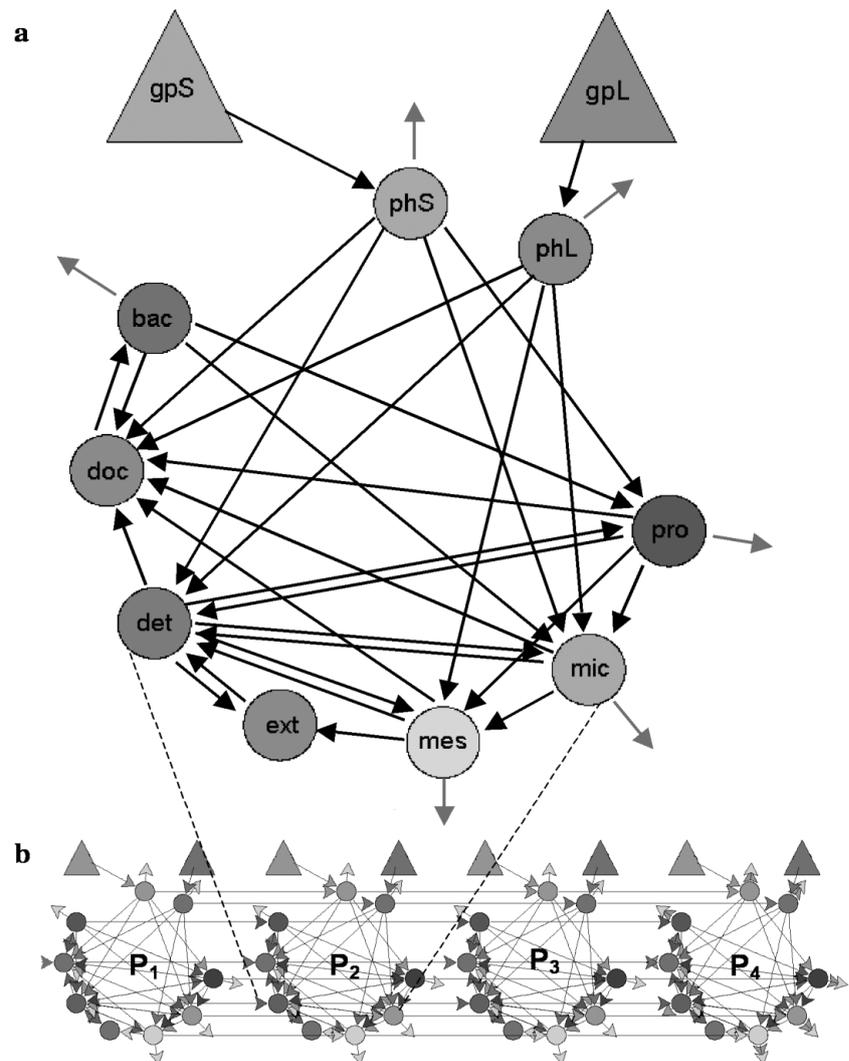


Fig. 2. Food-web model structure. (a) Trophic network representing each model region; circles represent compartments of carbon, either a taxonomic group (phS, phL, mes, mic, pro, or bac) or non-living carbon pool (det or doc); triangles indicate gross primary production of large (gpL) and small (gpS) phytoplankton; arrows pointing away from center of food webs indicate respiration; ext: flows into and out of ecosystem. (b) Food-web connections between regions represent advection of carbon; river input enters at left, flowing into region P<sub>1</sub> and moving westward (left to right) through P<sub>2</sub>, P<sub>3</sub>, and P<sub>4</sub>. Other abbreviations as in Table 1

mulated for its size (Sherr & Sherr 1984). We also included 2 non-living compartments: dissolved organic carbon (doc), which supplied bacterial growth, and detritus (det). All compartments were used in all analyses, regardless of the data available, so that all inferred food webs are comparable. Within each region, there were flows in and out of the system (ext) to accommodate sedimentation, sediment resuspension, and export to unresolved higher trophic levels (Fig. 2). There were also flows between equivalent compartments in different regions consistent with water movements.

Each compartment label has a numeric suffix between 1 and 4 appended to the compartment name to designate its region. Flows between compartments are designated  $F_{i,j}$ , where  $i$  is the compartment from which a flow originates and  $j$  is the destination compartment (e.g.  $F_{\text{phL2, mes2}}$ ). Flows between regions are designated 'I' for import or 'E' for export and a single compartment subscript (e.g.  $I_{\text{phL3}}$ ).

Table 1. Biomass concentration values ( $C_{i,j}$ ) for compartments and background ( $C_{j,0}$ ) values used to approximate advection and dilution rates. Most values represent data or estimates derived from data, but detritus concentration values used in summer models are essentially conservative guesses to produce realistic constraints because no data were available to make estimates. All values are  $\text{mgC m}^{-3}$ . Where biomass values are not given, export flows were unconstrained. Sources from which parameters were estimated: Gardner et al. (1994), Redalje et al. (1994), Trefry et al. (1994), Dagg 1995, Strom & Strom (1996), Opsahl & Benner (1998), Goolsby et al. (1999), Lohrenz et al. (1999), Benner & Opsahl (2001). P1 to P4: plume regions investigated; phS, phL: small, large phytoplankton, respectively; mes: mesozooplankton; mic: microzooplankton; pro: protozoans; bac: bacteria; det: detritus, doc: dissolved organic carbon

Area	phS	phL	mes	mic	pro	bac	det	doc
Winter								
P1	25	15	–	–	–	13.3	–	100.62
P2	100	100	39	2.2	1.3	42	69	95
P3	48	72	14	0.42	0.22	38	160	161
P4	50	1	–	–	–	18	200	88
$C_{j,0}$	20	20	10	0.5	0.1	10	20	30
Spring								
P1	20	20	–	–	–	18	–	78.23
P2	125	125	33	13.3	6.8	20	79.6	178
P3	397	214	13.4	5.2	2.7	50	163.8	294
P4	75	0	–	–	–	30	–	61
$C_{j,0}$	40	40	10	5	5	20	50	25
Summer								
P1	24.6	13.2	–	–	–	50	50	138.2
P2	211.5	113.8	57	33.86	17.4	38	50	175.5
P3	151.8	178.2	77	14.75	7.58	36	50	433.9
P4	50	0	–	–	–	8	–	103
$C_{j,0}$	27	27	15	10	10	20	50	100
Fall								
P1	48	32	–	–	–	20	42.5	87.48
P2	105	70	99.9	11.9	6.11	50	69.3	138
P3	189	21	32.7	12.1	6.2	50	160	216
P4	150	0	–	–	–	20	200	96
$C_{j,0}$	75	75	20	12	6	20	35	50

**Advection and dilution.** Flows between regions are unidirectional, moving organic carbon westward with the advection and dilution of river water (Fig. 2b). Estimates of inter-region flows were calculated using the current velocities, biomass concentrations, and salinity changes. Flow velocities between regions were estimated using drifter data (Lohrenz et al. 1994, Dagg 1995, M. J. Dagg et al. unpubl.).

Each region was treated as if it were well-mixed, with any gain or loss of water determined by the constant  $R_i$ , where the hydraulic residence time is  $R_i^{-1}$ . Its value was estimated using the inverse of the transit time between the centers of adjacent regions

$$R_i = \frac{\text{plume velocity}}{\text{distance between subregion centers}} \quad (1)$$

The rate at which material is exported from  $P_j$  is  $E_{i,j} = C_{i,j} R_i$ , where  $C_{i,j}$  is the concentration of material in Compartment  $i$  of Region  $j$ . Uncertainties in the values of  $C_{i,j}$  made it impossible to impose export-flow values. Instead, the values of  $E_{i,j}$  were constrained to be nearly this value:

$$0.5(C_{i,j} \times R_i) \leq E_{i,j} \leq 2(C_{i,j} \times R_i) \quad (2)$$

Values of flows leaving a compartment in one region and entering the next differed because of dilution. Dilution was assumed to occur by vertical mixing with underlying waters having a salinity of 35 psu (Wright & Coleman 1971) and biomass concentrations typical of those in deep water  $C_{i,0}$  (Table 1). The dilution  $D_{j+1}$  between  $P_j$  and  $P_{j+1}$  was calculated as

$$D_{j+1} = \frac{S_{j+1} - 35}{S_j - 35} \quad (3)$$

where  $S_j$  and  $S_{j+1}$  were the average salinities of  $P_j$  and  $P_{j+1}$ , and  $D_{j+1}$  was the fraction of water in a volume of  $P_{j+1}$  that originated in  $P_j$ . Since biomass concentration was assumed to be similarly diluted, the import rate was given by

$$I_{i,j+1} = E_{j,i} \times \left[ D_{j+1} + (1 - D_{j+1}) \frac{C_{i,0}}{C_{i,j}} \right] \quad (4)$$

where  $I_{i,j+1}$  is the import flow to Compartment  $i$  of  $P_{j+1}$ .

Export from the last region,  $P_4$ , was estimated by the inverse procedure. Labile DOC input from the river to  $P_1$  was estimated from data presented in Opsahl & Benner (1998) and Benner & Opsahl (2001), while the refractory portion was assumed inert and was ignored.

**Inverse calculations.** Details of the inverse procedure for planktonic food webs can be found in Vézina & Platt (1988) & Vézina (1989). The numerical calculations were made using programs written with Matlab™ Versions 5.3 to 6.0.

Empirical data were used to set the value of trophic flows where field-measured rates of biological activity/carbon flux were known and to set biologically realistic constraints on unmeasured flows which the model calculated. The known flows in the trophic web provided mathematical equalities that needed to be satisfied. The constraints were derived from a general set of physiological knowledge and were used to set a realistic range of values for the unknown carbon flows. Most of the constraints used in this study were originally described by Vézina & Platt (1988), but have been updated with results from more recent work (Chen-Leo & Benner 1992, Vézina & Pace 1994, Straile 1997, Vézina et al. 2000) and, especially, the allometric equations of Moloney & Field (1989). In addition, due to the tendency for models to limit phytoplankton excretion to theoretical minima (1 to 2% of net primary production, NPP) when conditions were unlikely to support such low rates, the minimum excretion rate was set to 10% of NPP (Lancelot 1983, Zlotnik & Dubinsky 1989).

A total of 181 potential carbon flows were present in the complete 4-region model, for which there were only 51 to 53 equations, leaving the system mathematically under-determined. Although the constraints reduce the range of potential solutions, there still exist an infinite number. To arrive at a single solution, a principle of parsimony was employed, and the single 'best' solution was that which minimized the sum of squares of all flows.

**Data sources.** Models were prepared for 4 seasons: July–August (summer); September–October (fall); February–March (winter); and April–May (spring). Since the summer model used data from an extraordinarily productive period, and probably unusually so (see Chen et al. 2000—data from Atchafalaya plume), an alternative summer model (low summer) was prepared by halving summer data for net primary production in  $P_2$  but keeping all other data the same. Data from 3 mo seasons over multiple years were combined into single-season descriptions. Field data were assigned regions using the surface salinities of the areas where samples were collected. The resulting data for the equations are shown in Table 2 and the constraints in Table 3.

The working units of this analysis were the daily average rates of carbon flow per unit volume in the surface mixed layer, here expressed as  $\text{mgC m}^{-3} \text{d}^{-1}$ . Rates integrated over the mixed layer (e.g.  $\text{mgC m}^{-2} \text{d}^{-1}$ ) were converted by dividing by the depth of the mixed layer (DML). Rates reported for measurements

made for periods shorter than 1 d, such as bacterial growth and respiration rates, were assumed to hold for an entire day. Data reported only in units of chlorophyll were converted to carbon using C:chl ratios of 20, 25, 30, and 50 for  $P_1$ ,  $P_2$ ,  $P_3$ , and  $P_4$  respectively (Dagg 1995, Dortch 1998). Sediment-trap data were available, but were used to validate the models rather than formulate them (see 'Discussion').

**Sensitivity analysis.** The sensitivity of the results to small variations in data values was assessed by observing the effect of perturbing data inputs by  $\pm 10\%$ . Parameters varied, included primary productivity, grazing and bacterial production rates as well as biomass, temperature and mixing rates. The sensitivity of individual flows focused on  $P_2$  and  $P_3$ , while the global effects on the sum of all flows included all 4 regions.

## RESULTS

Fig. 3 shows the flow network of summer results; similar high resolution figures for all 5 models can be viewed online at the Ecosystem Modeling Group website of the Texas A&M Department of Oceanography, as can a table detailing the numeric value of every flow in each network ([www-ocean.tamu.edu/~ecomodel/publications/publications.html](http://www-ocean.tamu.edu/~ecomodel/publications/publications.html)).

### Primary production

Gross primary production rates (GPP) were highest for all seasons in  $P_2$  (100 to  $950 \text{ mgC m}^{-3} \text{d}^{-1}$ ) and lowest in  $P_4$  (5 to  $20 \text{ mgC m}^{-3} \text{d}^{-1}$ ) (Fig. 4); rates were intermediate but higher in  $P_3$  (60 to  $300 \text{ mgC m}^{-3} \text{d}^{-1}$ ) than in  $P_1$  (25 to  $150 \text{ mgC m}^{-3} \text{d}^{-1}$ ). Carbon from  $P_3$  provided a substantial portion of the carbon input to  $P_4$ . Winter GPP rates were the lowest for all regions.

The general trends of each model as the plume evolves can be seen in Fig. 4. All seasons have peak community respiration as well as peak GPP in  $P_2$  (Fig. 4). The spring, fall and both summer systems functioned similarly, with GPP generally exceeding community respiration and non-zero sedimentation in  $P_2$  to  $P_4$ . Winter results were dramatically different, with respiration exceeding production everywhere and no sedimentation. In addition, GPP in  $P_2$  was twice as high in the summer model as in the model for any other season. GPP in  $P_3$  for the spring system was only 25% of that during summer and fall, possibly lower than that expected of a typical spring.

GPP includes the NPP usually measured, as well as phytoplankton respiration and excretion. Because there was no additional information on phytoplankton respiration, the inverse procedure calculated the mini-

imum respiration allowed, here 5% of GPP. Excretion was calculated as needed to support the system; it was usually the minimum value allowed, 10% GPP, but did reach 16 to 25% of GPP during the winter. As a result of the low and constant offsets, GPP values essentially mirror the NPP data that are the basis of the calculations and that have been previously reported by Redalje et al. (1994) and Lohrenz et al. (1999).

### Grazing

Total grazing rates on phytoplankton in a region were defined as the sum of the rates for microzoo-

plankton, mesozooplankton and protozoans, and are expressed as a fraction of regional GPP. They can exceed 100% when there was a significant import of phytoplankton from upstream. Relative grazing rates were smaller in P<sub>1</sub> and P<sub>2</sub> during the non-summer months than in P<sub>3</sub> and P<sub>4</sub> (Fig. 5). These relative grazing rates during winter were not strikingly different from rates during other seasons, although the absolute rates were less because of the smaller GPP. Smaller grazers (microzooplankton and protozoans) consumed most of the GPP (Fig. 5).

In addition to phytoplankton grazing, model results indicated that consumption of detritus by grazers was important where primary production was high, and

Table 2. Model parameters. Rate and conversion data used to construct fall inverse solution. W, Sp, Su, F = winter, spring, summer, fall respectively. Except for net primary production (PP), summer a and b models used same data. Units: 1 = mg C m<sup>-3</sup> d<sup>-1</sup>; \*2 = d<sup>-1</sup>; 3 = m; 4 = d; 5 = °C; 6 = psu. Abbreviations as in Table 1

Parameter (region)	W	Sp	Su	F	Units	Source
PhL net PP (1)	15.5	10	12	48	1	Lohrenz et al. (1999)
PhS net PP (1)	10	10	28.8	72	1	Lohrenz et al. (1999)
PhL net PP (2)	42	175	285a, 143b	180.1	1	Redalje et al. (1994)
PhS net PP (2)	27	175	532a, 266b	270.1	1	Redalje et al. (1994)
PhL net PP (3)	34	32	132	24.87	1	Redalje et al. (1994)
PhS net PP (3)	11	37	113	223.8	1	Redalje et al. (1994)
PhL net PP (4)	0	0	0	0	1	Lohrenz et al. (1999)
PhS net PP (4)	3.3	6	20	13.3	1	Lohrenz et al. (1999)
Mes grazing (2)	7.7	0.05*	55.6	22.8	1,*2	Dagg (1995), M. J. Dagg et al. unpubl.
Mes grazing (3)	20.6	0.21*	55.6	39.5	1,*2	Dagg (1995), M. J. Dagg et al. unpubl.
Mic grazing (2)	–	0.42*	0.25*	93.5	1,*2	Strom & Strom (1996)
Mic grazing (3)	–	41.5	0.22*	94.9	1,*2	Strom & Strom (1996)
Mic grazing (4)	–	7.6	–	–	1	M. J. Dagg et al. unpubl.
Bac production (1)	10.9	14.8	9.8	43.2	1	Gardner et al. (1994)
Bac production (2)	22.2	57	30.2	100	1	Gardner et al. (1994)
Bac production (3)	18.1	74	7.7	60.48	1	Gardner et al. (1994)
Bac production (4)	6.9	37	10.9	14.4	1	Gardner et al. (1994)
Bac respiration (1)	40.3	–	–	–	1	Gardner et al. (1994)
Bac respiration (2)	97.9	86	213	126.4	1	Gardner et al. (1994)
Bac respiration (3)	66.2	61.6	69.1	60.9	1	Gardner et al. (1994)
Bac respiration (4)	25.9	2.9	–	–	1	Gardner et al. (1994)
DOC input from river	149	78.2	62.4	89.6	1	Benner & Opsahl (2001)
Mixed layer depth (1)	5	5	5	5	3	Murray (1998)
Mixed layer depth (2)	10	10	10	10	3	Murray (1998)
Mixed layer depth (3)	10	10	10	10	3	Murray (1998)
Mixed layer depth (4)	15	15	15	15	3	Murray (1998)
C:chl (1)	20	20	20	20	–	Dortch (1998)
C:chl (2)	25	25	25	25	–	Dortch (1998)
C:chl (3)	30	51	30	30	–	Dagg (1995), Dortch (1998)
C:chl (4)	50	50	50	50	–	Dagg (1995), Dortch (1998)
Residence time (1)	1	1	1	1	4	M. J. Dagg et al. unpubl.
Residence time (2)	1.5	1.5	1.5	1.5	4	M. J. Dagg et al. unpubl.
Residence time (3)	6	6	6	6	4	M. J. Dagg et al. unpubl.
Temperature (1)	9	21	29.5	23	5	
Temperature (2)	16	22	29.5	24	5	
Temperature (3)	17	23	29	24.5	5	
Temperature (4)	20	23	29	25	5	
Mean salinity (1)	10	10	10	10	6	
Mean salinity (2)	23	23	23	23	6	
Mean salinity (3)	29.5	29.5	29.5	29.5	6	
Mean salinity (4)	33	33	33	33	6	

Table 3. Constraint relationships. Gro. effic.: growth efficiency; Assim. effic.: assimilation efficiency; other abbreviations as in Table 1

Process	Compartment	Bound	Relationship	Source
Respiration	bac	Lower	$0.2 \times (\text{bacterial ingestion})$	Vézina et al. (2000), Vézina & Pace (1994)
Respiration	bac	Upper	$1.7W^{-0.25} \times e^{0.0693 \times (T-20)} \times \text{biomass}$	Moloney & Field (1989)
Respiration	phs, phl	Lower	5 % of GPP	Vézina & Platt (1988)
Respiration	phs, phl	Upper	30 % of GPP	Vézina & Platt (1988)
Respiration	pro	Lower	$0.2 \times (\text{pro ingestion})$	Vézina et al. (2000), Vézina & Pace (1994)
Respiration	mic	Lower	$0.2 \times (\text{mic ingestion})$	Vézina et al. (2000), Vézina & Pace (1994)
Respiration	mes	Lower	$0.2 \times (\text{mes ingestion})$	Vézina et al. (2000), Vézina & Pace (1994)
Respiration	mes	Upper	$14W^{-0.25} \times e^{0.0693 \times (T-20)} \times \text{biomass}$	Moloney & Field (1989)
Excretion	phs, phl	Lower	$0.1 \times (\text{NPP})$	Present study
Excretion	phs, phl	Upper	$0.55 \times (\text{NPP})$	Baines & Pace (1991)
Excretion	pro	Lower	$0.1 \times (\text{pro ingestion})$	Vézina & Pace (1994)
Excretion	mic	Lower	$0.1 \times (\text{mic ingestion})$	Vézina & Pace (1994)
Excretion	mic	Upper	$1 \times (\text{mic respiration})$	Vézina & Platt (1988)
Excretion	mes	Lower	$0.1 \times (\text{mes respiration})$	Vézina & Pace (1994)
Excretion	mes	Upper	mes respiration	Vézina & Platt (1988)
Ingestion	bac	Upper	$3.6W^{-0.25} \times e^{0.0693 \times (T-20)} \times \text{biomass}$	Moloney & Field (1989)
Ingestion	mes	Upper	$63W^{-0.25} \times e^{0.0693 \times (T-20)} \times \text{biomass}$	Moloney & Field (1989)
Gro. effic.	bac	Lower	$0.05 \times \text{ingestion}$	Chen-Leo & Benner (1992)
Gro. effic.	bac	Upper	$0.5 \times \text{ingestion}$	Vézina & Platt (1988)
Gro. effic.	pro	Lower	$0.1 \times \text{ingestion}$	Straile 1997, Vézina & Platt (1988)
Gro. effic.	pro	Upper	$0.4 \times \text{ingestion}$	Straile 1997, Vézina & Platt (1988)
Gro. effic.	mic	Lower	$0.1 \times \text{ingestion}$	Straile 1997, Vézina & Platt (1988)
Gro. effic.	mic	Upper	$0.4 \times \text{ingestion}$	Straile 1997, Vézina & Platt (1988)
Gro. effic.	mes	Lower	$0.1 \times \text{ingestion}$	Straile 1997, Vézina & Platt (1988)
Gro. effic.	mes	Upper	$0.4 \times \text{ingestion}$	Straile 1997, Vézina & Platt (1988)
Assim. effic.	pro	Lower	$0.5 \times \text{ingestion}$	Straile 1997, Vézina & Platt (1988)
Assim. effic.	pro	Upper	$0.9 \times \text{ingestion}$	Straile 1997, Vézina & Platt (1988)
Assim. effic.	mic	Lower	$0.5 \times \text{ingestion}$	Straile 1997, Vézina & Platt (1988)
Assim. effic.	mic	Upper	$0.9 \times \text{ingestion}$	Straile 1997, Vézina & Platt (1988)
Assim. effic.	mes	Lower	$0.5 \times \text{ingestion}$	Straile 1997, Vézina & Platt (1988)
Assim. effic.	mes	Upper	$0.9 \times \text{ingestion}$	Straile 1997, Vézina & Platt (1988)

was especially important where measured grazing rates were also low. Rates of detritus consumption were highest in  $P_2$  during all times of the year, but remained high in  $P_3$ . Detrital consumption rates followed a spatial and seasonal pattern similar to GPP rates (data not presented). In all models, detritus consumption in  $P_2$  and  $P_3$  was correlated to the amount of phytoplankton primary production moving directly into the detritus pool ( $r^2 = 0.85$ ).

### Bacterial production and respiration

Seasonally, spring and fall had the highest bacterial production rates ( $55$  to  $100 \text{ mgC m}^{-2} \text{ d}^{-1}$ ) in  $P_2$  and  $P_3$ ; rates during summer or winter did not exceed  $35 \text{ mgC m}^{-2} \text{ d}^{-1}$ . Bacterial production was lowest in  $P_4$  ( $10$  to  $35 \text{ mgC m}^{-2} \text{ d}^{-1}$ ), and intermediate in  $P_1$  ( $15$  to  $65 \text{ mgC m}^{-2} \text{ d}^{-1}$ ). In spring, summer and fall models, bacterial respiration was highest in  $P_2$  and  $P_3$ , and the resulting bacterial production efficiency (BPE) was lowest in the mid-salinity regions  $P_2$  ( $12$  to  $40\%$ ) and  $P_3$  ( $10$  to  $54\%$ ). BPE in spring, summer and fall models was essentially inversely related to *in situ* primary production. BPE in

regions of low primary productivity ( $P_1$  and  $P_4$ ) was  $56$  to  $81\%$ , considerably higher than in the productive regions  $P_2$  and  $P_3$ . Unlike other periods, winter model BPEs were relatively uniform in all regions, ranging between  $19$  and  $28\%$ .

### Community respiration

Community respiration rates (sum of respiration by all living groups) were low in  $P_1$  ( $20$  to  $90 \text{ mgC m}^{-3} \text{ d}^{-1}$ ), highest in  $P_2$  ( $120$  to  $450 \text{ mgC m}^{-3} \text{ d}^{-1}$ ), high in  $P_3$  ( $90$  to  $220 \text{ mgC m}^{-3} \text{ d}^{-1}$ ), and low in  $P_4$  ( $30$  to  $45 \text{ mgC m}^{-3} \text{ d}^{-1}$ ) (Fig. 6). In general, regions with high primary productivity generated more carbon than they respired (i.e. were net-autotrophic), while less productive regions respired more than they produced (i.e. were net-heterotrophic). The ratio of community respiration to GPP indicated a tendency for net autotrophy in  $P_1$ ,  $P_2$  and  $P_3$  during spring, summer and fall (Fig. 7). During winter, the entire plume required external sources of organic carbon to meet respiratory demand (Fig. 7). Bacteria accounted for the largest fraction ( $30$  to  $90\%$ ) of respiration in  $P_2$  and  $P_3$ ,

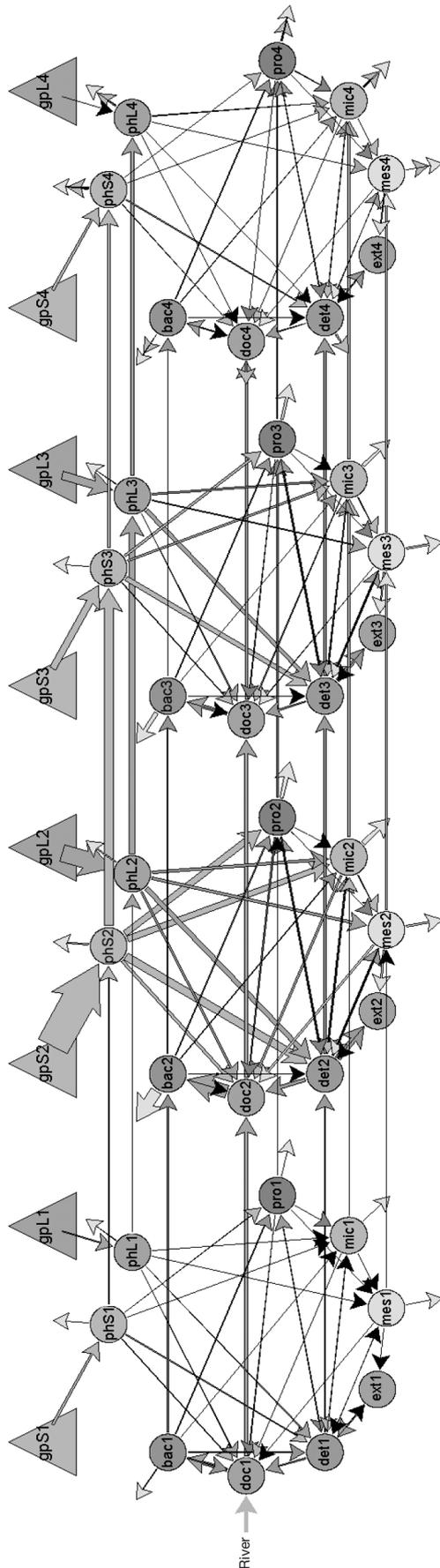


Fig. 3. Inverse solution for summer season. Widths of arrows indicate magnitude of carbon flow scaled against largest flow in the ecosystem, in this case primary productivity of small phytoplankton in region P<sub>2</sub> ( $616 \text{ mg C m}^{-3} \text{ d}^{-1}$ ). Similar flow networks available for all seasons at <http://oceanography.tamu.edu/~ecomodel/publications/publications.html>. Abbreviations as in Table 1

although non-bacterial respiration occasionally exceeded bacterial respiration (Fig. 6).

### Export

The loss of carbon via sedimentation was related to the regional primary production rate as well as the rate of upstream importation. The winter system had no sedimentation loss and needed to import carbon, possibly by sediment resuspension, in both P<sub>1</sub> and P<sub>2</sub> (Fig. 8). Sedimentation from P<sub>1</sub> ( $125 \text{ mg C m}^{-2} \text{ d}^{-1}$ ) occurred only in the fall. P<sub>2</sub> and P<sub>3</sub> had relatively modest sedimentation rates of 200 to  $400 \text{ mg C m}^{-2} \text{ d}^{-1}$  in spring and higher sedimentation rates of 600 to  $1100 \text{ mg C m}^{-2} \text{ d}^{-1}$  for summer and fall. Sedimentation rates in P<sub>4</sub> ranged from 150 to  $450 \text{ mg C m}^{-2} \text{ d}^{-1}$  in non-winter models.

For the non-winter models, P<sub>4</sub> had the highest sedimentation rates relative to GPP, equal to 35 to 55% of *in situ* GPP. Although regions with more primary productivity had larger absolute sedimentation rates, the rates relative to GPP were much less, between 8 and 25% in P<sub>2</sub> and P<sub>3</sub>. This suggests that as GPP increases, bacterial respiration and grazing increase to take advantage of greater concentrations of organic carbon, and although more carbon is exported as sediment, a larger fraction is respired in the water column.

Advective export was also important and occurred for all carbon pools, unlike detrital sedimentation. These export rates, like many of the trophic flows, were related to *in situ* GPP. The regions with highest GPP, i.e. P<sub>2</sub> and P<sub>3</sub>, exported large amounts of carbon. P<sub>1</sub> and P<sub>4</sub> tended to both import and export large amounts of organic carbon, so that carbon essentially passed through them, as much as 350% of *in situ* GPP exported from P<sub>1</sub> and 400% exported from P<sub>4</sub>. The limited primary production during the winter resulted in diminishing advective exports from all regions.

### Low-flow summer

The low-flow summer model had lowered rates of a number of key processes in P<sub>2</sub> and P<sub>3</sub> relative to the primary summer model. Lowered rates included advective carbon loss, community respiration and rates of detritus consumption by grazers. Grazing rates increased relative to primary production, total grazing rates approached 60% of GPP in P<sub>2</sub> and the grazing rate in P<sub>3</sub> was 52% of GPP in the low-flow scenario. P<sub>2</sub> and P<sub>3</sub> had relatively modest sedimentation rates of 200 to  $400 \text{ mg C m}^{-2} \text{ d}^{-1}$ .

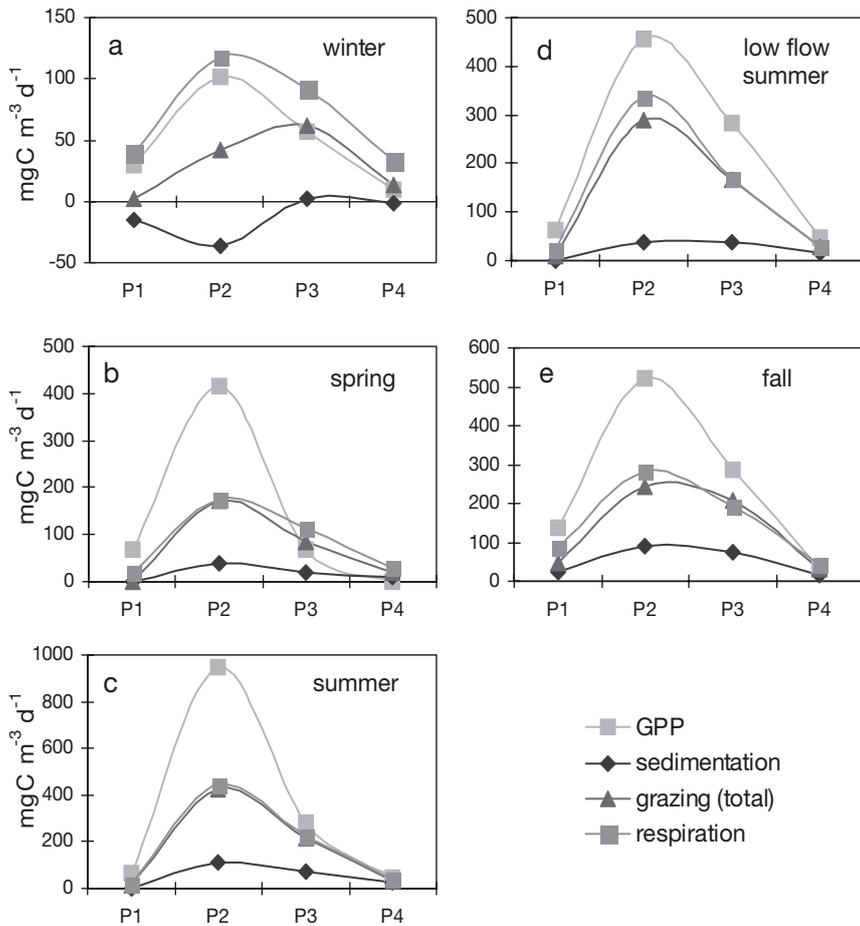


Fig. 4. General ecosystem trends across all regions. (a) Winter; (b) spring; (c) summer; (d) low-flow summer; (e) fall. Total grazing rates represent phytoplankton and detritus grazing combined. GPP: gross primary productivity

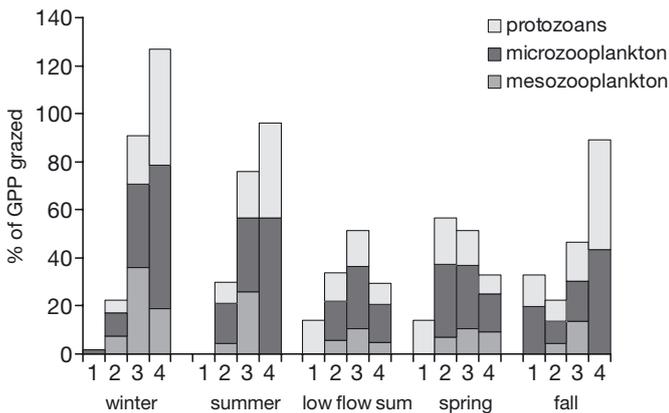


Fig. 5. Phytoplankton consumption by each grazer compartment as fraction of *in situ* gross primary productivity (GPP); y-axis is percentage of *in situ* gross primary productivity grazed, and can exceed 100% due to advective imports of phytoplankton biomass

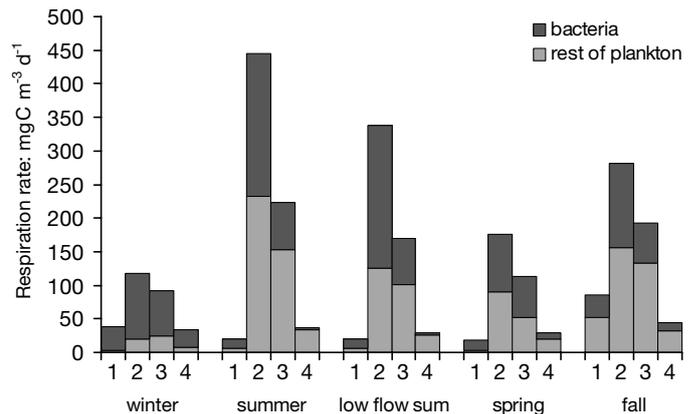


Fig. 6. Planktonic community respiration for each season and region. Respiration rate of bacteria has been separated from respiration rate of rest of the plankton

### Sensitivity analysis

The results of the sensitivity analyses are presented as sensitivity  $s = (\Delta f/f)/(\Delta p/p)$ , where  $f$  is the value of the original flow,  $\Delta f$  is change in the flow rate associated with a parameter change  $\Delta p$ , and  $p$  is the original parameter value. A negative value of  $s$  indicates that the flow change has the opposite sign as the parameter change. For example,  $s = 2$  shows that a 10% increase in  $p$  results in a 20% increase in  $f$ ;  $s = -0.5$  shows that a 10% increase in  $p$  results in a 5% decrease in  $f$ . Values of  $|s| > 1$  are considered to be sensitive to changes in the parameter.

Every seasonal model had flows sensitive to input parameter values (e.g. Fig. 9). Results were generally sensitive to changes in primary productivity data, but fewer than 5 of 99 flows were highly sensitive ( $|s| > 3$ ) to the values used for  $\text{pH}_S$  and  $\text{pH}_L$  in  $P_2$  and  $P_3$  for any season. The spring system was essentially insensitive to changes in primary productivity, with the largest  $|s| < 1.5$ . The summer system was only slightly more sensitive, only 1 flow  $|s| > 2$ ,  $F_{\text{pHL2, mic2}}$ . The fall system was relatively insensitive, but the grazing flow  $F_{\text{pHS2, mic2}}$  had values of  $s$  as great as 10. In the winter system the flows  $F_{\text{pHS2, pro2}}$ ,  $F_{\text{det3, ext3}}$ , and  $F_{\text{pro3, mic3}}$  were sensitive, with  $|s|$  between 3 and 10 when primary production was perturbed,  $F_{\text{det2, mic2}}$  being the most sensitive. Perturbations to biological rates other than primary production tended not to elicit sensitivity.

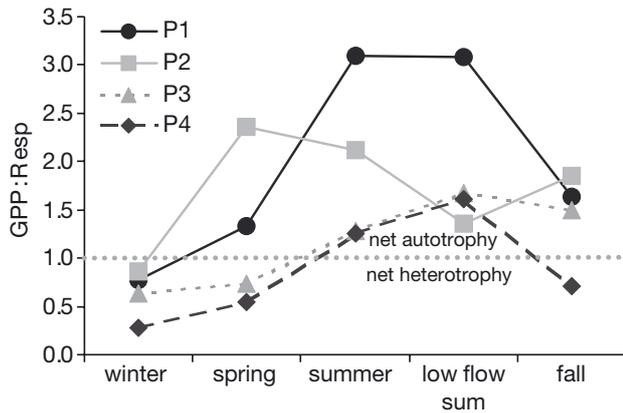


Fig. 7. Ratio of total community respiration to GPP for each region by season. When production exceeds respiration ( $>1$ , dotted line), system is net-autotrophic and needs no carbon import to meet respiratory demand

Various flows were also sensitive to parameters defining mixed layer depth (DML) and import/export between regions, because these physical parameters usually changed many biological rates calculated from them. Both summer models were relatively insensitive to mixed-layer and advection parameters, although a number of flows had values of  $lsl = 3$  to 4, including  $F_{phL2, mic2}$ ,  $F_{bac3, mic3}$ ,  $F_{pro2, doc2}$ ,  $F_{pro2, mes2}$ . The winter system was similarly sensitive to mixing and advection parameters. The spring model was the most sensitive, and perturbations to DML and advective parameters

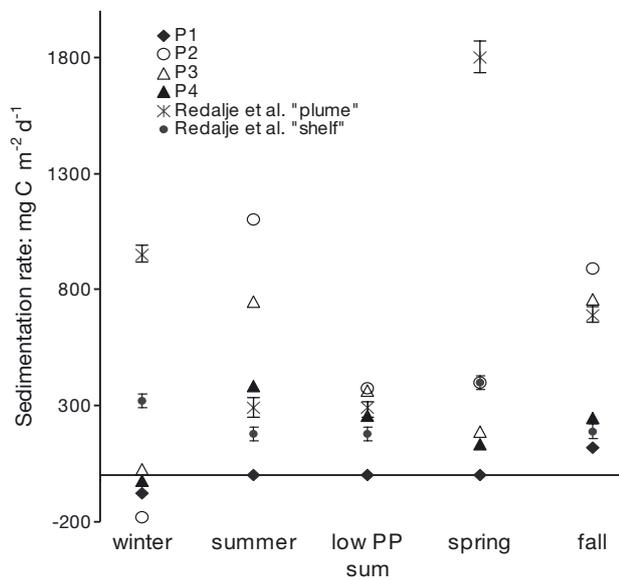


Fig. 8. Sedimentation rate of labile organic carbon by season and region. Negative values indicate sediment resuspension and import into mixed-layer ecosystem. Sediment trap data collected by Redalje et al. (1994) is plotted for comparison; error bars are  $\pm SE$

resulted in  $lsl > 2$  in a wide range of flows. Advective flows, as well as  $F_{pro3, mic3}$ , were most strongly affected. The fall model followed the same pattern of sensitivity to DML and mixing parameters as winter, but values of  $lsl$  were smaller. Only a few flows had values of  $lsl > 2$ , and these were small in original model solutions.

Sensitivity of individual flows indicates that parameters and assumptions used to formulate dilution and mixing (region salinity, residence time and DML) were more likely to perturb the food web than other parameters. However, when high sensitivity was encountered, it was generally in trophic flows that were small ( $<2\%$  of *in situ* GPP) in original model results. Changes to individual flows exceeded 2-fold the original value only 10 times out of a possible 8500 flow  $\times$  season  $\times$  sensitivity parameter combinations, and exceeded 3-fold only twice.

Although the sensitivity of individual flows could be quite high, the sensitivity of the sum of flows was much less, with  $lsl$  always  $<1$ . The sum was most sensitive to changes in the depth of the mixed layer in  $P_2$ , with  $s = 0.3$  to 0.6. The summer model was most sensitive to changes in individual primary productivity of the small phytoplankton in  $P_2$ , with  $lsl = 0.38$  for the sum of flows and lesser sensitivity to other parameters. The fall, spring and both summer models responded similarly to parameter perturbations. The strongest responses occurred when primary production was perturbed. The winter model was much less sensitive to adjustments in primary production, but reacted strongly to adjustments in bacterial respiration as well as some mixing parameters. Overall, the sums of network flows were mostly insensitive to perturbations in input parameters. Although some physical parameters had a small but pronounced effect, and a number of individual flows were clearly sensitive, the networks produced by the inverse analysis were largely robust.

## DISCUSSION

### Net autotrophy and net heterotrophy

During spring, summer and fall, the plume was highly productive in mid-salinity regions and exported at least half of the primary production downstream and below the mixed layer. Small, intensely productive areas along the mixing gradient supplied large regions of the shelf with organic carbon. Organic carbon was exported by sedimentation even in higher-salinity waters, but relied on imports from upstream to do so. In contrast, the winter ecosystem exported little organic matter and required inputs of allochthonous carbon to sustain high respiration rates.

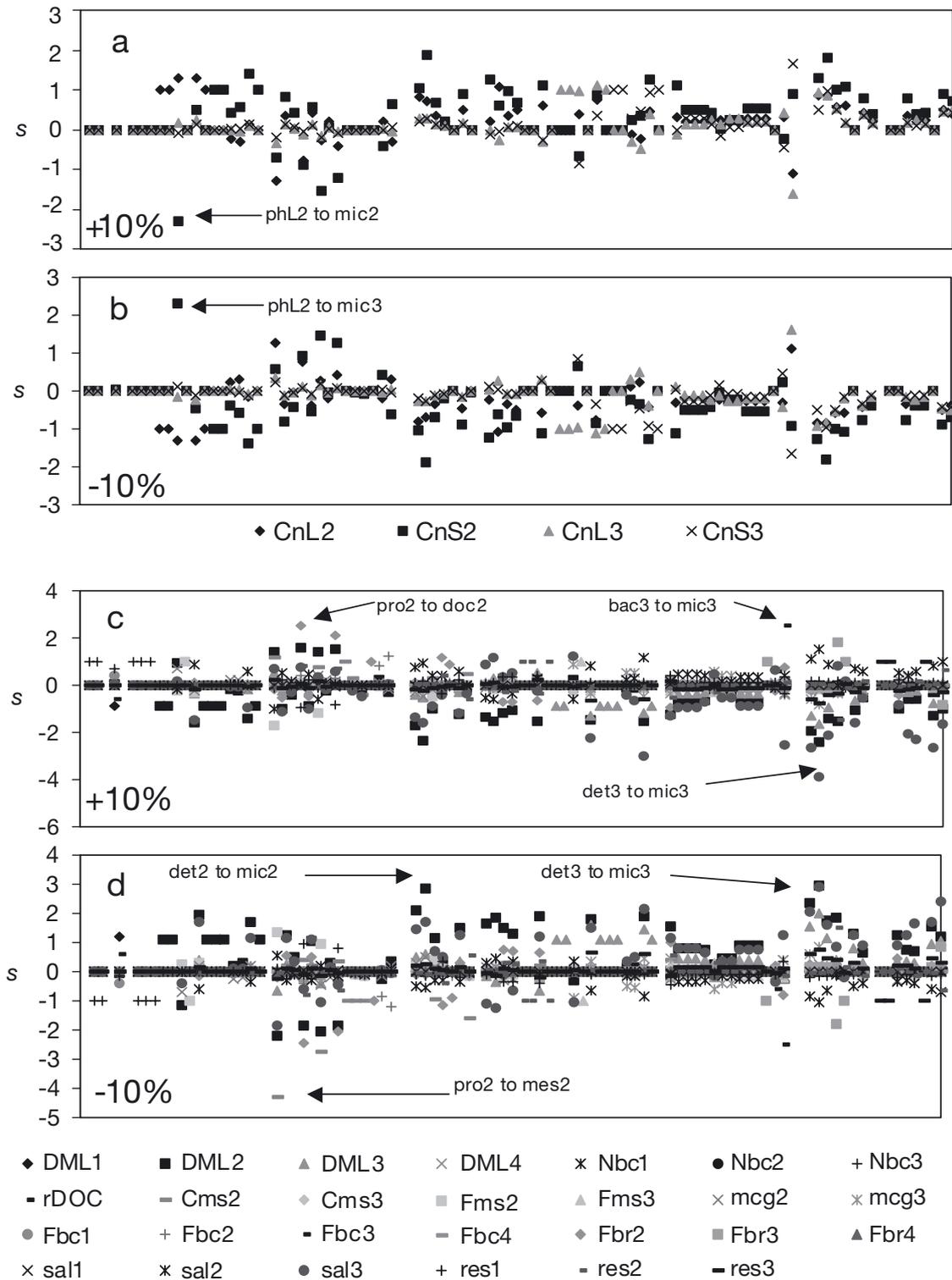


Fig. 9. Summer-model sensitivity analysis. (a) (b) Sensitivity ( $s$ ) to positive and negative perturbations in primary production respectively (CnL, CnS: net primary production of large and small phytoplankton respectively; numeric suffixes indicate region of data perturbation); (c) (d) sensitivity to positive and negative perturbations in other parameters respectively (DML: depth of mixed layer; Nbc: no. bacteria  $\text{ml}^{-1}$ ; rDOC: DOC concentration in river water; Cms: mesozooplankton biomass; Fms: mesozooplankton grazing rate; mcg: microzooplankton grazing rate; Fbc: bacterial production; Fbr: bacterial respiration; sal: salinity; res: residence time). Other abbreviations as in Table 1

Physical factors such as day length, temperature, stratification, shelf currents and river flow vary seasonally under the influence of the Mississippi River (Rabalais et al. 1996, 1999). Flow is typically highest during the spring freshet and lowest during late-summer river flow, but pulses of freshwater can occur anytime and alter the flow (Chen et al. 1997, Hitchcock et al. 1997). During the winter, along-shelf currents tend to flow downcoast (to the west), while the associated onshore Ekman transport keeps the buoyant plume close to shore (Li et al. 1997, Chen et al. 2000). During the summer, plume water usually moves westward, but strong downcoast flow is less frequent and the plume frequently pools, moves offshore, or even flows eastward. Spring is the only season of predictable intense production, but highly productive periods can occur at any time of year.

Seasonal variations in irradiance and temperature also affect primary production in the plume. Unseasonable freshets and current patterns, however, can supply the coastal system with larger than normal amounts of riverine nitrate and can shift current patterns, resulting in highly productive periods at any time of the year (Biggs 1992, Lohrenz et al. 1999, Rabalais et al. 1999). Winter-model results may be typical of any period of low primary production. Such conditions might also occur during late summer; although temperature and irradiance favor high productivity, river flow and nitrogen loading are usually at their minima. Primary production rates used to formulate the winter model may themselves be unusually low, in which case winter may normally be at least periodically net autotrophic (Chen et al. 2000). Results from other models represent the more usual intermediate and higher river flow and longer daylengths favorable to high primary productivity.

The overall effect of external forcing is a shift between 2 states of the plume ecosystem. When strong primary production is favorable, the plume is net-autotrophic, sedimentation rate increases and large amounts of organic carbon produced in the plume move downshore to the west or offshore to the south. When high rates of primary production are not favored, however, the system switches to net-heterotrophy. Imports of carbon from the river and resuspended sediment become important sources of energy. Net heterotrophy may not occur often or persist for long periods, but it punctuates cycles of productivity in the Mississippi River plume and appears more likely to occur during mid-winter and late summer.

### Sedimentation and export

Bottom-water anoxia is a critical problem for the Louisiana shelf (Turner & Rabalais 1991, Eadie et al.

1994, Rabalais et al. 1996, 1999, Justić et al. 2002). Sedimentation provides the linkage from the surface ecosystem, which is described by our model, and the hypoxia layer, which is not. Redalje et al. (1994) measured sedimentation rates in conjunction with primary productivity. During the winter, Redalje et al. (1994) found that sedimentation exceeded primary production, and stable isotope data suggested sedimenting material was marine in origin, and not from the river (Eadie et al. 1994). They suggested spatial separation between production and sedimentation might explain the discrepancy. Our inverse model is a series of regions that describe spatial separation but were still unable to incorporate both sedimentation and primary production measurements collected by Redalje et al. (1994). This was particularly true during winter when mass balance between measured primary production (PP) and sedimentation was negative, but also during spring and fall when demands upon the PP from grazer and bacterial respiration did not leave enough carbon to account for measured rates of sedimentation. Our calculated rates of sedimentation (200 to 1000 mgC m<sup>-2</sup> d<sup>-1</sup> for spring, summer and fall; Fig. 8), were consistent in size with those of Redalje et al. (1994) for the mid-salinity regions of the Mississippi River plume (290 to 1800 mgC m<sup>-2</sup> d<sup>-1</sup>), but not in seasonal timing.

It is not clear why ecosystem data, especially sediment-trap data, are inconsistent with each other to the point of prohibiting mass balance; relating observations of sedimentation to other ecosystem properties in the Mississippi River plume remains a problem. It is possible, if not likely, that a spatio-temporal segregation between the site of primary production and the site of sedimentation exists which this form of modeling and the NECOP sampling regime were unable to reconcile. Inverse models driven with sediment-trap data which infer rates of primary production in the Mississippi River plume are under development and will be explored in a future paper.

### Role of riverine organic carbon

During some periods, organic carbon supplied by the river is at least as important as the nutrients fueling primary production, while in others its role is minimal. During periods of net heterotrophy, such as winter, organic carbon from the river supplied most of, but not the entire, deficit between high respiration rates and low primary productivity. Total daily primary production over all regions during winter was approximately  $3.5 \times 10^9$  gC d<sup>-1</sup>, about one-fifth of total primary production during the fall (Table 4). Total winter riverine DOC inputs equaled almost 10 times primary production. The labile fraction equaled a much smaller but

still significant fraction of the primary production (29%). The high DOC input supported high measured rates of bacterial production and respiration. In fact, small amounts of additional organic carbon were also needed to balance the system and were supplied through the 'ext' compartment. This additional carbon may represent resuspended sediment, additional DOC assumed to be refractory, or may simply be the result of imperfect data used to construct the models.

During the remainder of the year, net-autotrophy prevailed and DOC from the river played only a minor role in supporting the bacterial community. For example, total and labile riverine DOC input during fall were only 30% and 1 to 2% of total primary production respectively (Table 4) (Opsahl & Benner 1998, Benner & Opsahl 2001). The riverine DOC affected  $P_1$  strongly, but riverine DOC was diluted to insignificance in other regions. This is consistent with sediment core data from the shelf. Sediment  $\delta^{13}\text{C}$  measurements indicate that sediments over most of the Louisiana Shelf are predominantly marine in origin, with terrestrial organic carbon restricted to very near the mouth of the river and areas directly adjacent to shore (Turner & Rabalais 1991, Eadie et al. 1994, Rabalais et al. 1999). Turner & Allen (1982) calculated the amount of labile organic carbon required to deplete bottom-water oxygen, and concluded that not

enough organic carbon was delivered by the river to produce hypoxia. Other model studies have reached similar conclusions (Justić et al. 1997, 2002). Our results are restricted to labile DOC but are consistent with the dominance of marine DOC on the shelf.

Less than 10% of the DOC pool is labile, although this fraction is larger during the winter (Opsahl & Benner 1998, Benner & Opsahl 2001). Although winter labile riverine DOC concentration was greater, the total labile DOC delivered by the river was roughly the same in winter and spring because of high spring river-flow. A significant fraction of refractory DOC from the Mississippi River becomes labile when exposed to light for periods of a week or longer (Opsahl & Benner 1998). Even so, the winter carbon input from the 'ext' compartment that we inferred to be sediment resuspension might actually be refractory riverine DOC made labile by photo-oxidation.

The plume-wide organic carbon budget for the fall model (Table 4) can also be used to estimate a nitrogen budget for the fall using typical C:N ratios to convert network flows from C to N for organic nitrogen flows (Vézina 1989) (Table 4). Inorganic flows were assumed to be the difference between inorganic inputs and organic export. The results show that two-thirds of the riverine dissolved inorganic nitrogen input (DIN) is lost

Table 4. Post-hoc carbon and nitrogen budget calculated from fall solution, Mississippi River flow, river nitrate concentration, and river DOC concentration integrated over entire modeled region. Estimate of each model region area ( $P_1$  to  $P_4$ ) was used to calculate total area  $\times$  depth-integrated carbon and nitrogen budgets for each region from volumetric model results. Unless otherwise indicated, values are expressed as  $\text{g C d}^{-1}$ . Sources: Rabalais et al. (1999), Benner & Opsahl (2001), NECOP data management website

Parameter	$P_1$	$P_2$	$P_3$	$P_4$	Total
Area ( $\text{m}^2$ )	$1.40 \times 10^9$	$1.40 \times 10^9$	$2.80 \times 10^9$	$4.05 \times 10^9$	$9.65 \times 10^9$
Depth (m)	5	10	10	15	
Gross primary production	$9.80 \times 10^9$	$7.29 \times 10^9$	$7.98 \times 10^9$	$1.88 \times 10^9$	$1.81 \times 10^{10}$
Labile river DOC input	$6.21 \times 10^8$				$6.21 \times 10^8$
Refractory DOC input	$2.18 \times 10^{10}$				$2.18 \times 10^{10}$
Total inputs					$4.05 \times 10^{10}$
Total labile C inputs					$1.87 \times 10^{10}$
Total respiration	$5.84 \times 10^8$	$3.36 \times 10^9$	$4.55 \times 10^9$	$2.00 \times 10^9$	$1.04 \times 10^{10}$
Sedimentation	$1.57 \times 10^8$	$6.75 \times 10^8$	$1.48 \times 10^9$	$6.99 \times 10^8$	$3.00 \times 10^9$
Advection out				$3.67 \times 10^9$	$3.67 \times 10^9$
To higher trophic levels	0	$3.33 \times 10^8$	$8.29 \times 10^8$	$2.52 \times 10^8$	$1.40 \times 10^9$
Total C losses					$1.87 \times 10^{10}$
River nitrogen input					
Total water flow ( $\text{m}^3 \text{d}^{-1}$ )	$1.21 \times 10^9$				$1.21 \times 10^9$
DIN concentration ( $\text{g m}^{-3}$ )	1.8				
Total DIN flux	$2.18 \times 10^9$				$2.18 \times 10^9$
Labile DON flux					$1.18 \times 10^7$
DIN+DON flux	$2.19 \times 10^9$				$2.19 \times 10^9$
Nitrogen losses					
Export to higher trophic levels					$3.21 \times 10^8$
Sedimentation of N					$4.91 \times 10^8$
Advective export of N					$6.21 \times 10^8$
Total N losses					$1.43 \times 10^9$
Surplus nitrogen					$7.56 \times 10^8$

as organic nitrogen losses (sedimentation, advection or export to higher trophic levels) and one-third as inorganic N. Such a loss rate is consistent with an average DIN concentration of 0.5  $\mu\text{M}$  in waters leaving the region (Lohrenz et al. 1999).

### Grazing

Poor spatial and temporal coverage for grazing measurements made the use of these data difficult (Dagg 1995, Strom & Strom 1996), although a number of papers have recently been published which are filling the gaps (Jochem 2003, Liu & Dagg 2003). Grazing rates of zooplankton from the high-turbidity, low-salinity regions of the plume are especially lacking because of the difficulty of filtering water for dilution experiments. In addition there are seasonal data gaps, with little grazing data for microzooplankton available in summer and no grazing data in winter. In such situations, grazing rates from other seasons were substituted (spring rates were used for the summer models in  $P_2$  and  $P_3$ ), or otherwise left to be calculated by the inverse procedure.

We investigated the effect of omitting grazing data from our formulations of the summer and fall models. The resulting model inferred that grazing rates were 50 to 100% higher than the measured values for  $P_2$  and  $P_3$  and sedimentation rates were 40 to 60% lower, but most network flows were unaffected. This result suggests that grazing competes with sedimentation for carbon. However, except for these differences, model results using measured grazing rates were not drastically different from those omitting them. This suggests that the unavailability of grazing data in winter was not responsible for the calculated net-heterotrophy. The lowered sedimentation rates in models with undefined grazing rates might suggest that the lack of sediment in the winter model was due to lack of grazing data. However, high bacterial respiration and paucity of organic carbon due to low GPP were more likely to have been responsible.

Detrital consumption by grazers were also important flows in these results. The detritus compartment was included in the *a priori* model because it is a realistic feature of many marine food-webs. However, as an unconstrained compartment, it allows a great deal of carbon to flow directly from both large and small phytoplankton to the detritus, which is subsequently ingested by all size classes of grazers. This breaks barriers in prey size class of each grazer compartment. In our results, a large fraction of phytoplankton production did in fact move first to detritus before being grazed. When the unconstrained detritus compartment was not included, discrepancies in data between graz-

ing rates of large and small grazers often prevented the network from achieving mass balance due to constraints elsewhere in the flow network. Given that detritus grazing is a common feature in marine food webs (e.g., Roman 1984), that it is to be expected in the Mississippi River plume, and the inability to achieve mass balance without it, we chose to include 'det' as an unconstrained compartment.

### Analysis limitations

A number of potential problems exist with our approach. One is common to all attempts to synthesize data from a complex system; measurements are not all made at the same locations and times. While we tried to use data to describe a season from either 1 or 2 sequential cruises, we needed to augment these with measurements taken during other years. Although the general patterns of productivity tend to recur every year, the actual rates and spatial distributions of production and other processes do vary annually. This variability can be particularly great at a given spatial location, as winds and currents move the plume even during a single cruise (Lohrenz et al. 1999, Rabalais et al. 1999, Justić et al. 2002).

Each model, however, may not characterize the 'normal' conditions of the season it represents. Most data used to describe a season were collected during a short period of a single year. Additionally, the most comprehensive data sets were collected during a few years in the early 1990s: the summers of 1990 and 1993 were unusually wet and the spring of 1992 was drier than normal (Rabalais et al. 1999). Net primary productivity measurements in mid-salinity regions were between 3 and 6  $\text{g C m}^{-2} \text{d}^{-1}$  during the spring of 1988, about 2  $\text{g C m}^{-2} \text{d}^{-1}$  in spring 1992, and 1  $\text{g C m}^{-2} \text{d}^{-1}$  or less in the spring of 1993 (Lohrenz et al. 1999, M. J. Dagg et al. unpubl.). Similarly, net primary production rates were less than 1.1  $\text{g C m}^{-2} \text{d}^{-1}$  in September 1991, but were 4.5  $\text{g C m}^{-2} \text{d}^{-1}$  in fall 1992, when data used in our fall model were collected (Lohrenz et al. 1999, M. J. Dagg et al. unpubl.). Although comprehensive primary productivity data were available from only 1 summer in the Mississippi River plume, summertime primary productivity was similarly variable in the neighboring Atchafalaya River plume (Chen et al. 2000).

The resulting data inconsistency could potentially affect our results, but sensitivity analyses on the solutions indicated that the food webs were relatively insensitive to small changes in the data used to describe the system. Even with larger perturbations, such as those achieved by changing the mixed-layer depth, the overall effect on the system was small. The size of changes in ecosystem flows was relatively less

than that of the parameter perturbations. Admittedly, variation in the Mississippi River plume is much larger than perturbations in our sensitivity analysis, but it does demonstrate some measure of confidence and generality in our results. Large parameter perturbations are difficult because they often result in mass balance violations, even in otherwise insensitive models.

Flows that were sensitive tended to be small in original networks and usually involved grazers, possibly because of the limited number of constraints and incomplete grazing data available.

A second potential problem involves the dilution scheme. Mixing of plume water with ocean waters occurs mostly by vertical eddy diffusion (Wright & Coleman 1971), although turbulent eddies forming along the plume front can accelerate lateral mixing to rates comparable with vertical mixing. The distinction between the two is in the concentration of organic matter that mixing introduces. We diluted the river plume with water containing compartment concentrations typical of deep water ( $C_{i,0}$  values) that had concentrations of phytoplankton, microzooplankton, mesozooplankton and protozoans smaller than at the surface, but concentrations of DOC, detritus, and bacteria closer to, but still less than, in the mixed layer (Lohrenz et al. 1990, Justić et al. 2002). Although rates of both sedimentation and advective export were reduced when biomass was not present in dilution water, sedimentation dropped no more than 30% of the original, and surface export of carbon out of the ecosystem was affected even less (Table 1). When we quadrupled the  $C_{i,0}$  values to values approximately equal to mixed-layer concentrations, sedimentation nearly doubled, but other export rates increased only slightly. Overall, effects of biomass import from deep water on export were limited.

### Steady state and region homogeneity

These solutions are for a river plume system that is at steady state, although individual parcels of river water evolve as they move from region to region. As a result, the model can capture ecosystem dynamics, including a spike in primary production in  $P_2$ , and a decline as water moves west into  $P_3$  and  $P_4$ . The steady-state assumption, however, does not allow the models to capture variation occurring on the longer temporal scales of weeks or months or the shorter temporal scales of hours within a region. The development of seasonal models allowed us to describe changes over annual timescales.

For these models, each region is spatially uniform, with exchange between regions occurring in discrete steps. This is equivalent to a finite difference model with very coarse resolution. Giving up fine-scale resolution allows the use of measurements from slightly

different conditions to describe the same region. The models have captured the gross scale dynamics of the plume ecosystem in a way that allowed comparisons between different seasons and different regions. When the dynamics of the system are better understood, a coupled physical–biological model might offer an enhanced understanding of the system, but might be no better at synthesizing the diverse measurements that have been made. The results presented herein have captured enough detail to incorporate a large, disparate collection of data and to advance ideas and hypotheses concerning the Mississippi River plume and Louisiana Shelf ecosystems. However, the localized nature of the data makes their use to describe other river plumes, such as of the Atchafalaya or Amazon Rivers, problematic.

A better understanding of ecosystem processes that affect export production and hypoxic water formation is important, especially since hypoxic events have become more intense and frequent on the Louisiana Shelf during the past 20 yr. These events have been correlated with nitrate loading by the Mississippi River, and nitrate concentrations in river water are now 2 to 3 times historical values (Turner & Rabalais 1991, Eadie et al. 1994, Goolsby et al. 1999, Rabalais et al. 1999). Any mitigation of future hypoxia events will require a better understanding of the interaction of the Mississippi River discharge with coastal waters. These results demonstrate that sedimentation is probably not a simple linear relationship with N-loading as others have assumed, and ecosystem dynamics and variation on both spatial and temporal timescales must be considered in management decisions.

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