

Co-occurring and opposing freshwater inflow effects on phytoplankton biomass, productivity and community composition of Galveston Bay, USA

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ABSTRACT: Freshwater inflow effects on phytoplankton have long interested aquatic ecologists. More recently, timing and magnitude of inflow events have been a focus as they can be strong drivers of phytoplankton diversity and productivity. In the present research, we empirically and theoretically explored the effects of inflow events on phytoplankton of Galveston Bay, Texas, a bay system whose freshwater inflow arises primarily from 2 rivers, the San Jacinto and Trinity. We found that conditions in the upper regions of Galveston Bay adjacent to these rivers had opposing influences on phytoplankton. In the region near the San Jacinto River, inflows mostly stimulated biomass and productivity, while in the region near the Trinity River, inflows had the opposite effect. This suggested that the phytoplankton reproductive growth rate was at times nutrient limited near the San Jacinto River and that population growth responded rapidly to nutrient loadings. This also suggested that population growth was controlled at times by other processes near the Trinity River, thereby negating the effects of nutrient loadings. Decreased phytoplankton biomass occurred in this region due, in part, to hydraulic displacement. These co-occurring and opposing inflow effects extended into the mid- and lower bay regions, but the extension varied in time and location with no seasonal trend. Such observations underscore the challenges of predicting system responses to altered inflows. Phytoplankton composition was also affected by inflows, and some taxonomic trends were regionally specific. Attributes of phytoplankton relating to use of alternative sources of nutrition, differential growth rates and immigration of euryhaline species from rivers likely influenced the spatiotemporal distribution of taxa.

KEY WORDS: Freshwater inflows · Phytoplankton biomass · Primary productivity · Inorganic nutrients

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INTRODUCTION

Ecosystem form and functioning is affected by inflows, a relationship that has long been an interest of aquatic ecologists (Ketchum 1951, 1954, Brook & Woodward 1956). More recently, special sessions at Society of Environmental Toxicology and Chemistry (SETAC) and Association for the Sciences of Limno-

logy and Oceanography (ASLO) conferences focused on this topic, with dedicated issues in *Journal of Plankton Research* (volume 33, 2011) and *Canadian Journal of Fisheries and Aquatic Sciences* (volume 69, 2012) following these meetings. The extent and composition of seagrass beds, diversity of periphyton communities and timing of algal blooms are examples of ecosystem forms that are influenced by inflows

(Grover et al. 2011, Santos & Lirman 2012, Stanish et al. 2012). Ecosystem functions affected by inflows include primary productivity, microbially driven remineralization and various geochemical processes affecting nutrient availability (Seitzinger et al. 1991, Hitchcock et al. 2010, Westhorpe et al. 2010). Inflow effects occur over varied time scales. Eutrophication and salinification issues are typically associated with cumulative inflow effects (Jassby et al. 1995, Sklar & Browder 1998), whereas shifts in community composition are commonly associated with effects of inflow events (Spatharis et al. 2007, Mitrovic et al. 2011, Roelke et al. 2011).

In regard to the effects of inflow events, phytoplankton responses are a common focus. Phytoplankton growth rates and species interactions occur over periods of hours to days, while the effects of these interactions can be observed over periods of days to weeks. In theory, inflow events can profoundly enhance phytoplankton productivity, biodiversity and energy transfer to higher trophic levels while preventing blooms (Roelke et al. 1999, Roelke 2000). These notions were confirmed in laboratory microcosm experiments (Buyukates & Roelke 2005, Miller et al. 2008) and in field mesocosm experiments (Hayden et al. 2012). Characteristics of inflow events, such as timing and magnitude, are sensitive to changes in water use that arise from human population increase and altered water cycles that result from climate change (Johns et al. 2004, Richter & Thomas 2007). So, discerning the relationship between inflow events and ecosystem form and functioning is necessary to better predict ecosystem responses to future scenarios of altered hydrology.

The relationship between inflow events and ecosystem form and functioning is challenging to characterize in bays and estuaries. Here, inflows refer to river discharges. There are many other processes that influence bays and estuaries. These include tidal exchange, light limitation and foodweb structure. These processes have the capacity to buffer and mask inflow effects (Cloern 2001). For example, tidal exchange can be large relative to inflows, diluting the effects of hydraulic displacement and nutrient and sediment loadings originating from river discharges (Bricker et al. 2008, Swaney et al. 2008, Duarte & Vieira 2009a,b). In addition, phytoplankton can be strongly light-limited (Bouman et al. 2010, Xu et al. 2010) or top-down controlled (Kemp et al. 2005, Newell et al. 2005, 2007), both of which can regulate accumulation of phytoplankton biomass and assemblage composition to the point where freshwater inflows have little effect. Furthermore, the roles of

these processes change seasonally and are system specific.

Galveston Bay (GB), Texas, is the second largest bay system in the western Gulf of Mexico. It is of economic, ecological and recreational value to the region. Like many bays and estuaries, it is facing a future of uncertain freshwater inflows. Watershed planning for GB strongly considers the effects of cumulative inflows, especially as they relate to salinification. Planning does not consider as much the effect of inflow events as these effects are not as well characterized. In the present research, we focus on the effects of inflows over shorter periods. Our monitoring spanned 2 yr and captured a period of dynamic inflow, salinity and nutrients, thereby enabling a thorough analysis of relationships between phytoplankton and inflows.

MATERIALS AND METHODS

Site description

The GB system (Fig. 1) is the largest estuary along the Texas coast (USA), covering 1554 km² in area with a mid-tidal volume of 2.5×10^9 m³ (Lowery 1998). Water depth averages ~2.1 m. Two rivers comprise the majority of freshwater inflow into GB. The San Jacinto River enters GB from the northwest side and is a part of the Houston Ship Channel. Historically, it

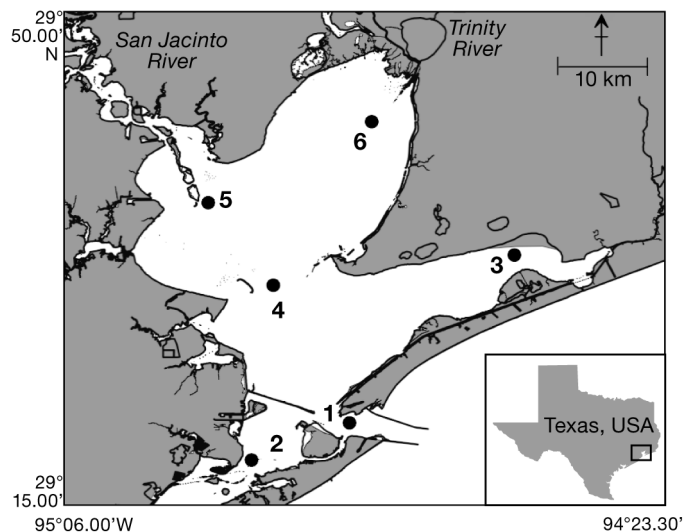


Fig. 1. Galveston Bay, Texas, is a large, shallow bay system located in the western Gulf of Mexico characteristic of restricted ocean water exchange. The dominant freshwater sources for this bay system are inflows from the San Jacinto and Trinity Rivers. Circles show the locations of sampling stations

provides ~28% of total freshwater inflow to the system (for the period from 1941 to 1990; Villalon et al. 1998). The Trinity River enters GB from the northeast and historically accounts for ~54% of the total freshwater inflow (Villalon et al. 1998). Tidal exchange between GB and the Gulf of Mexico mainly occurs through a narrow pass across a barrier island, with tidal ranges of ~0.15 to ~0.5 m. Much of the land surrounding GB is urban (residential, commercial and industrial), and the watershed contains Houston and the Dallas-Fort Worth metroplex, two of the most populated areas in the USA.

Sampling

Monthly samplings were carried out over a period of 22 mo at 6 fixed stations within GB from February 2005 to November 2006 (Fig. 1), where a suite of physical, chemical and biological parameters were sampled from surface (0.5 m) and bottom (between 2 and 4 m depending on the station) waters. Seldom did we detect differences between surface and bottom waters in this shallow and vertically well-mixed bay system. Therefore, the present study made use of just the parameters measured in surface waters. To complement these data, daily freshwater inflow from the San Jacinto River was estimated from discharges from Lake Houston, and daily discharge from the Trinity River was compiled from gauged data (US Geological Survey, Romayer Stn #08066500). For the Trinity River, inorganic nutrients (nitrate and soluble reactive phosphorus [SRP]) were collected daily using a refrigerated auto-sampler set up near Liberty, Texas, ~48 km upriver from the bay. The sampler was set up after January 2006. Due to the high riverbank and dynamic range of Trinity River stage at this location, the sampler could only collect water during periods of stage greater than ~2 m.

At each station within GB, we measured physical and chemical variables. Physical variables included surface temperature, salinity and light transparency. Temperature and salinity, along with pH, were recorded using a Hydrolab Quanta multiprobe. Light transparency was estimated with a Secchi disk. Chemical variables included inorganic nutrients, total nitrogen (TN) and total phosphorus (TP). Inorganic nutrient samples were filtered in the field using Whatman GF/F filters, and unfiltered samples for TN and TP were also obtained, then nutrient samples were frozen for transport to the laboratory. An OI Analytical 'Flow Solutions IV' auto-analyzer was employed to analyze inorganic nutrients that included

nitrate + nitrite (NO_x), ammonium (NH_4^+) and SRP using the methods of Armstrong et al. (1967) and Harwood & Kühn (1970). TN and TP were transformed to inorganic form by digesting with equal volume of 160 mM alkaline persulfate at 121°C for 45 min (Solórzano & Sharp 1980, Patton & Kryskalla 2003) before using the auto-analyzer method.

Biotic variables measured at each station included phytoplankton biomass and assemblage composition. For an estimate of phytoplankton biomass, chlorophyll *a* (chl *a*) was determined using the fluorometric method of Strickland & Parsons (1968). Triplicate samples (50 ml) were collected and filtered through GF/F filters in the field and immediately frozen for transport to the laboratory. For an approximation of phytoplankton assemblage composition, taxa biomass was determined using measurements of phytopigment concentrations (Pinckney et al. 1998) and CHEMTAX, a matrix factorization program (Mackey et al. 1996, Wright et al. 1996). For the CHEMTAX model initiation, cyanobacteria, euglenophytes, chlorophytes, haptophytes, cryptophytes, diatoms and dinoflagellates were selected because of their historical prevalence in GB (Örnolfsdottir et al. 2004).

Another biotic variable was primary productivity, calculated from measurements of net productivity and community respiration. These values were measured at stations by incubating surface water consistently between 10:00 h and 14:00 h using a modified light and dark bottle technique (Wetzel & Likens 1991). In addition to the traditional transparent bottles (L) used for measuring net productivity and the opaque bottle (D) used for measuring community respiration (R), we included 2 additional treatments: a 'killed' transparent bottle (LK) and a 'killed' opaque bottle (DK). It was assumed that all living organisms in these bottles were killed after the addition of 1 ml saturated mercuric chloride (HgCl_2). These additional treatments were added to the incubations to account for both photochemical reactions and peroxidase reduction in the LK treatment and for peroxidase reduction in the DK (Pamatmat 1997). Incubations (2 h) of light/dark bottles were deployed on deck in a screen-covered enclosure (~67% light reduction) with surface water circulated through to maintain ambient temperature. The initial and final dissolved oxygen (DO) concentrations were recorded using a DO meter (YSI Model 58 meter with 5905 BOD stirring probe). Using a photosynthetic quotient of 1.2 and respiratory quotient of 1.0, changes in DO enabled us to estimate net productivity (after L was corrected using LK) and community respiration (after corrections in D using DK) from surface water. Primary productivity was calculated by

summing net productivity and community respiration from surface water samples. Note that these primary productivity calculations only reflect surface water phytoplankton assemblages growing at surface water light intensities.

Statistics

To facilitate our analysis, data were divided into subsets based on the similarity between stations for each of the monthly samplings. Similarity was measured using hierarchical cluster analyses (Matlab 7.14, The MathWorks), and all station parameters mentioned in the previous section were included. There were 22 sampling trips conducted during the present study, but on 3 occasions, not all parameters were measured due to inclement weather. Those incomplete data sets were excluded from this part of the research, resulting in 19 cluster analyses being performed. Based on the results from those cluster analyses, we created 4 data subsets that comprised the upper bay near the San Jacinto River (Stn 5 only), upper bay near the Trinity River (Stn 6 only), lower bay near the pass with the Gulf of Mexico (Stns 1 and 2) and mid- and lower bay combined (Stns 1 through 4). Comparisons between the lower bay grouping and the mid- and lower bay combined grouping were limited following this approach due to the degree of shared data between these data subsets.

Multivariate analyses were then conducted on the 4 data subsets using non-metric multidimensional scaling (NMS) statistics (PC-ORD). Data used as the primary matrix in these NMS analyses incorporated all station parameters. A secondary matrix was also used that comprised the discharge data from the San Jacinto and Trinity Rivers. For each river, daily discharge was averaged over a short period (see below) prior to the day of sampling. NMS solutions for these data subsets had final stress levels of 7.39, 5.84, 7.71 and 10.1, respectively. NMS analysis for the upper bay near the San Jacinto River produced a 2-dimensional solution, while the other 3 data subsets had 3-dimensional solutions.

All statistics were repeated using daily river discharges averaged over different 'short' periods, which were 7, 15 and 30 d. These periods were selected because they span intervals over which phytoplankton assemblages are capable of responding to hydraulic disturbances. Spatiotemporal relationships between variables were consistent between the 7, 15 and 30 d analyses. Consequently, in the present manuscript, we only report on the results using the 30 d

averaged daily inflows because it better matched our sampling schedule.

Numerical modeling

To better assess the range of potential effects on phytoplankton biomass resulting from 30 d inflows, a numerical model was explored representing a simplified plankton system. In these simulations, only the mechanistic effects of hydraulic displacement and nutrient loading were considered. Through this theoretical exercise, we explored the potential relative influences of hydraulic displacement and nutrient loading during periods when phytoplankton are not growth-limited and during periods when growth rate is limited. Calibrating simulations to reproduce observed system dynamics was not the purpose here and is beyond the scope of the present research. The model followed equations of the following form:

$$\frac{d\phi}{dt} = (\mu - d)\phi \quad (1)$$

$$\frac{dS}{dt} = d(S_{in} - S) - Q_S\mu\phi \quad (2)$$

where ϕ is the phytoplankton population density, μ is the specific growth rate, d is the daily flushing rate calculated by dividing inflow by volume, S and S_{in} are the concentrations of the growth-limiting substrate ambient and in the source, respectively, and Q_S is the fixed cellular content of the substrate for phytoplankton. While d is constant in this model, μ varies and is determined using the Monod equation:

$$\mu = \mu_{max} \left(\frac{S}{S + k_S} \right) \quad (3)$$

where μ_{max} is the maximum specific growth rate for the population, and k_S is the half-saturation coefficient for substrate-limited population growth.

The model was parameterized using observations from our data and standard values from the literature. The maximum 30 d averaged daily inflow for the San Jacinto and Trinity Rivers combined (taken during a period of peak inflows, see 'Results') divided by the volume of GB was used to determine d , which was 0.035 d^{-1} . An initial value for ambient S of $2 \text{ } \mu\text{M}$ was used, which was representative of NO_x concentrations observed in many areas of GB. Values used for Q_S ($0.2 \text{ } \mu\text{M N million cells}^{-1}$), μ_{max} (1 d^{-1}) and k_S ($0.2 \text{ } \mu\text{M N}$) were typical for many common phytoplankton (Roelke et al. 2003).

An analysis of model behavior was achieved by performing multiple simulations in which the con-

centrations of river NO_x was changed (3 simulations) and the inflow was removed (Simulation 4). For the first 3 simulations, the river NO_x concentrations used were 20, 2 and 0 μM . These simulations depicted conditions representative of measured NO_x concentrations in the Trinity River and in the upper GB and of no nutrients in the river, respectively. A fourth simulation was also run in which there was no inflow. All model results showed a deflection point in the phytoplankton population dynamics where the rate of biomass accumulation changed. Early in the simulation, before the deflection point, phytoplankton growth was not limited. Later in the simulation, after the deflection point, phytoplankton growth was limited.

The potential effects of hydraulic displacement and nutrient loading were evaluated by comparing simulation results. For example, we assessed the effects of hydraulic displacement independent of nutrient loading by comparing the rate of phytoplankton biomass accumulation during the period when growth was not limited (the first ~6 d of simulations, prior to the deflection point). We assessed the potential impact of increased nutrient loading given the observed nutrient values in the Trinity River (and assuming the San Jacinto River was similar) by comparing the accumulated biomass at the end of the 30 d simulation (after ~24 d of growth limitation) between Simulations 1 and 2. Finally, we assessed the potential impact of hydraulic displacement under a condition when growth rate was zero by comparing the accumulated biomass after 30 d between Simulations 2 and 3. In a natural setting, this condition might arise with severe light limitation or when grazing losses are on par with reproduction.

The mathematical equations were solved numerically using ordinary differential equation solving routines that were a part of a commercial software package (Matlab 7.14, The MathWorks). The routines were based on fourth-order Runge-Kutta procedures and used a variable time step that was based on a local error tolerance set at 10^{-6} .

RESULTS

Inflows and system salinity

The GB system experienced episodic inflows for the entire period of monitoring. During the 2005 winter (January to March) daily inflows from the San Jacinto and Trinity Rivers were as high as $2200 \text{ m}^3 \text{ s}^{-1}$. This is equivalent to a 0.08 d^{-1} whole-system flushing rate. These inflows were larger in magni-

tude and longer in duration compared to the 2006 winter (Fig. 2a), and they were in the 75th percentile of historical inflows (Villalon et al. 1998). Spring (April to June) and summer (July to September) months were similar between years, with the bulk of inflow events coming from the San Jacinto River. These inflows were in the range of the 10th to 25th percentiles of historical inflow. A brief and abnormally high inflow event reaching $1500 \text{ m}^3 \text{ s}^{-1}$ (equivalent to a 0.05 d^{-1} whole-system flushing rate) occurred during September of 2005, coinciding with Hurricane Rita. The fall months (October to December) of 2005 were characteristic of low inflow and were in the 25th percentile of historical inflows, while in 2006, fall inflow events were near the median of historical inflows. Peak 2006 fall inflows occurred in October and November that exceeded $2000 \text{ m}^3 \text{ s}^{-1}$ (equivalent to whole-system flushing rates of 0.07 d^{-1}).

GB system-averaged salinity quickly increased after the periods of high river discharge had stopped (Fig. 2b). During the 2005 winter, the total inflow was $60.8 \times 10^3 \text{ m}^3$ (summed daily inflows for the 3 mo period), and the average salinity was ~10. But following the 2005 spring and summer periods, when the total inflow was 12.0×10^3 and $12.6 \times 10^3 \text{ m}^3$, respectively, salinity increased to ~25. Hurricane Rita only slowed the salinification of GB. Following the 2005 fall, when total inflow was $6.3 \times 10^3 \text{ m}^3$, average salinity was ~30. System-averaged salinity decreased during the 2006 winter, spring and summer periods, times when the total inflow was 14.0×10^3 , 11.9×10^3 and $7.4 \times 10^3 \text{ m}^3$, respectively. The large inflow events during the 2006 fall reduced salinity to ~10 during a period when total inflow was $23.0 \times 10^3 \text{ m}^3$.

Reductions in salinity following river discharges were more pronounced in the upper regions of the bay, with the 30 d averaged daily inflow accounting for 59% of the variability in salinity (Fig. 2c). During the 2005 winter, salinities were in the range of 0 to 2 at Stns 5 and 6. Following Hurricane Rita in 2005, salinity depressions occurred in the range of 16 to 18. Following the river discharge events during 2006 winter and 2006 summer, salinity depressions occurred in the ranges of 5 to 12 and 1 to 3. Salinity peaks in these upper bay stations during periods of low inflow ranged between 5 and 27. Stations located lower in GB (Stns 1 to 4) showed a weak relationship between 30 d averaged daily inflow and salinity, with inflows accounting for only 30% of the variability in salinity. In that area of the bay, salinity ranged from 2 to 39, but most salinity observations were in the 29 to 32 range.

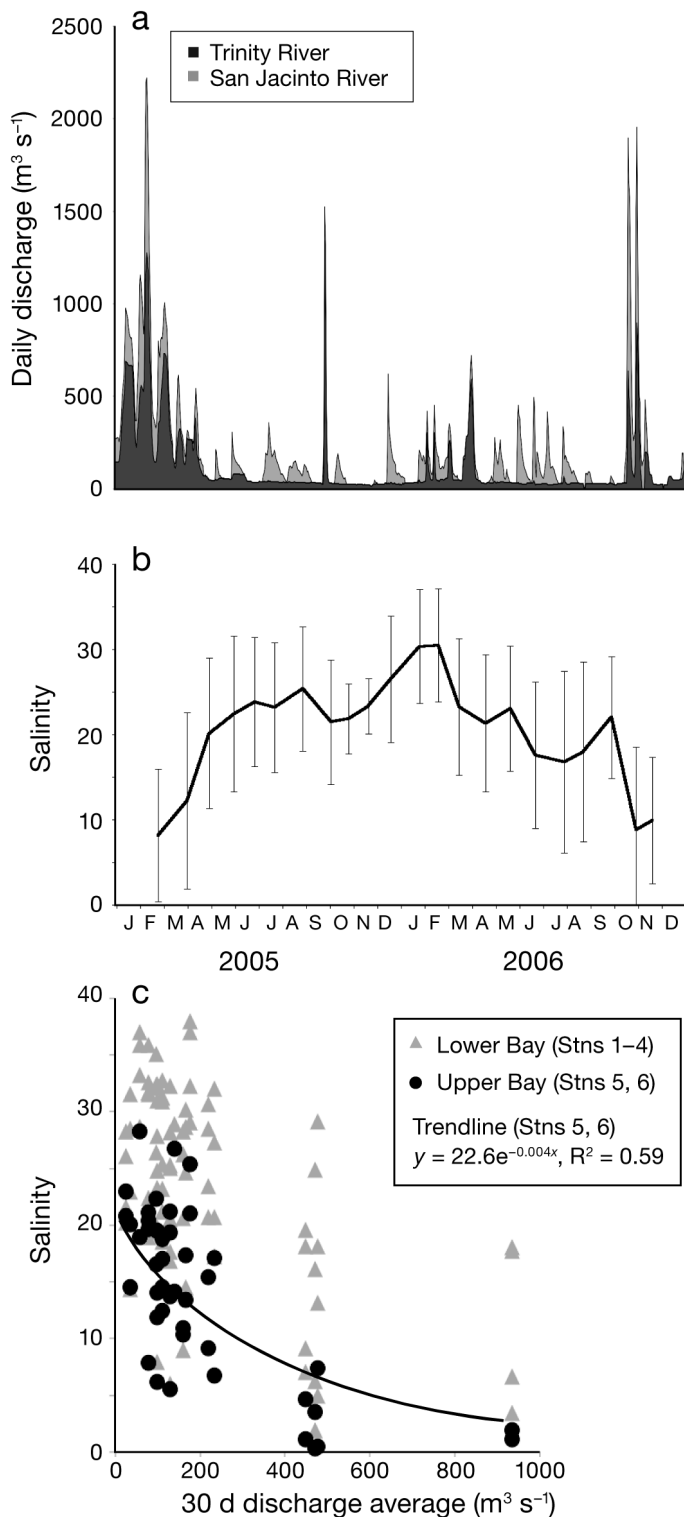


Fig. 2. (a) Freshwater inflow from the San Jacinto and Trinity Rivers, (b) monthly averaged salinity in Galveston Bay (Stns 1 to 6), with error bars representing 1 SD of the site averaged data, and (c) a scatter plot of combined 30 d inflows from the San Jacinto and Trinity Rivers with salinity, showing that the strongest relationship was observed in the upper bay, where inflows explained 59% of the variability in salinity

Trinity River nutrients

In the Trinity River during March and April 2006, NO_x was $\sim 20 \mu\text{M}$, with peak concentrations reaching $50 \mu\text{M}$. During this time, SRP was $\sim 0.5 \mu\text{M}$, with peak concentrations reaching $2 \mu\text{M}$. During August through December 2006, NO_x was $\sim 10 \mu\text{M}$ in the Trinity River, with peak concentrations reaching $20 \mu\text{M}$. During this same period, SRP was $\sim 2.5 \mu\text{M}$, with peak concentrations reaching $5 \mu\text{M}$. The river stage was too low for sampling during the January–February and May–July 2006 periods.

Station similarity

Our cluster analyses provided strong justification for our station groupings in the data subsets. For example, Stns 5 and 6, the regions of the bay closest to the San Jacinto and Trinity River discharges, respectively, seldom grouped with the other stations, and they were only similar to each other in 3 of the 19 analyses (Fig. 3). For these reasons, 1 of the 4 data subsets used in the NMS analyses comprised data from Stn 5 only (upper bay near San Jacinto River), and another data subset comprised data from Stn 6 only (upper bay near Trinity River).

Stns 1 and 2, the locations in the bay closest to the marine end member, were very similar in 18 of the 19 analyses. Furthermore, in 14 of the 19 analyses, Stns 1 and 2 were the only members of the group containing these stations (Fig. 3a). Sometimes, Stns 1 and 2 were similar to another station, but only in 5 of the 19 analyses (Fig. 3b). For these reasons, the third of the 4 data subsets used in the NMS analyses was a com-

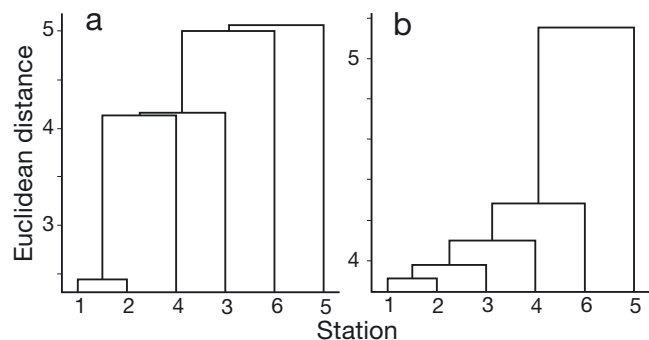


Fig. 3. Representative hierarchical cluster analyses showing that Stns 5 and 6, the regions of the bay closest to the San Jacinto and Trinity River discharges, respectively, seldom grouped with the other stations or each other, that Stns 1 and 2 commonly grouped together and that groupings involving Stns 3 and 4 were variable. Monthly sampling used here to illustrate from (a) March 2005 and (b) May 2005

bination of Stns 1 and 2 (lower bay, nearest to the marine end member).

Finally, Stns 3 and 4, located in the east bay and middle bay, were more similar to Stns 1 and 2 than they were to Stns 5 or 6 (Fig. 3a). As noted above, sometimes they grouped with Stns 1 and 2 (Fig. 3b). However, Stns 3 and 4 only grouped together separate from the other stations in 1 of 19 analyses. So it did not make sense to create a group involving only Stns 3 and 4. Because these stations sometimes grouped with Stns 1 and 2, our final data subset used in the NMS analyses combined data from Stns 1 through 4. We analyzed this last data subset with the

knowledge that sometimes attributes of the plankton environment from these stations were dissimilar.

Upper Galveston Bay, near San Jacinto River (Stn 5)

Seasonal dynamics in phytoplankton biomass were similar during 2005 and 2006 near the San Jacinto River. Peaks in phytoplankton biomass occurred during the winter, spring and summer periods and were larger during 2005 compared to 2006 (Fig. 4a). For 2005, the peaks were $\sim 45 \mu\text{g chl a l}^{-1}$ during winter, $\sim 10 \mu\text{g chl a l}^{-1}$ during spring and $\sim 30 \mu\text{g chl a l}^{-1}$ dur-

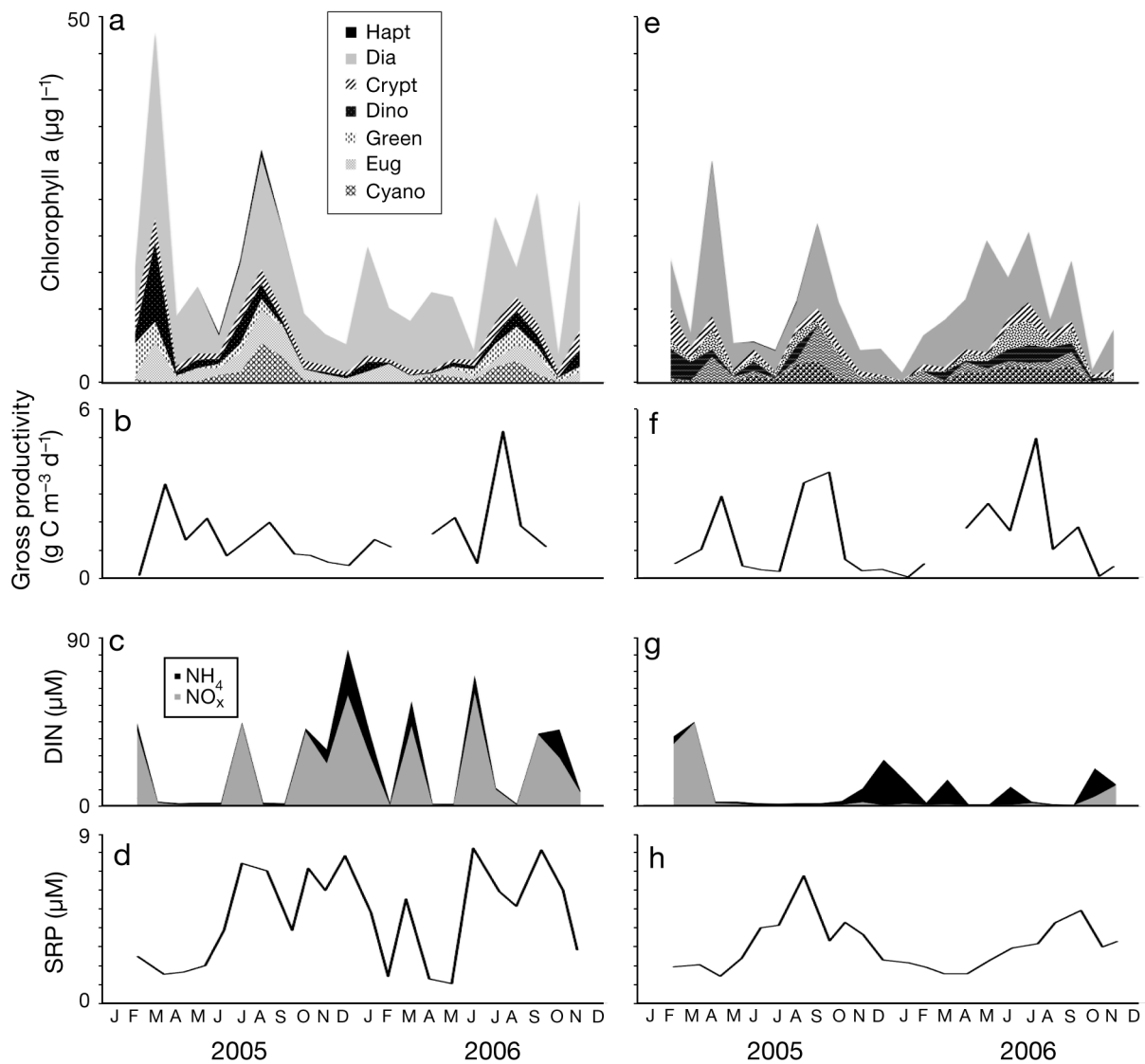


Fig. 4. (a) Phytoplankton biomass, (b) primary productivity, (c) dissolved inorganic nitrogen as nitrate + nitrite (NO_x) and ammonium (NH_4^+) and (d) dissolved phosphorus as soluble reactive phosphorus (SRP) for the upper bay region near the San Jacinto River discharge (Stn 5). The same parameters (e–h) are shown for the upper bay region near the Trinity River discharge (Stn 6). Phytoplankton were characterized into taxonomic groups that included haptophytes (Hapt), diatoms (Dia), cryptophytes (Crypt), dinoflagellates (Dino), chlorophytes (Green), euglenophytes (Eug) and cyanobacteria (Cyano)

ing summer. For 2006, phytoplankton peaks were ~ 20 , ~ 10 and $\sim 25 \mu\text{g chl } a \text{ l}^{-1}$ for the winter, spring and summer, respectively. However, no similar seasonal trend was observed for primary productivity (Fig. 4b). During 2005, primary productivity was highest during the winter at $\sim 4 \text{ g C m}^{-3} \text{ d}^{-1}$, then decreased as the season progressed. During 2006, primary productivity increased with season until its maximum during the summer of $\sim 6 \text{ g C m}^{-3} \text{ d}^{-1}$, then it decreased with the remainder of the season. Phytoplankton biomass and primary productivity weighted strongly on the second NMS axis (85% of the total variability; Fig. 5a), which correlated with 30 d inflows from the San Jacinto and Trinity Rivers. In addition, phytoplankton biomass weighted strongly on the first NMS axis (11% of the total variability), which correlated with 30 d inflows from the San Jacinto River.

Concentrations of NO_x and NH_4^+ fluctuated between minima in the range of 1 to 4 μM to maxima in the range of 70 to 80 μM (Fig. 4c). TN showed similar dynamics, with minima in the range of 30 to 40 μM to maxima in the range of 85 to 185 μM . SRP concentration showed a large dynamic range as well but seemed more seasonal than NO_x , NH_4^+ or TN, with winter and spring depressions $\sim 2 \mu\text{M}$ and summer and fall peaks $\sim 8 \mu\text{M}$ (Fig. 4d). TP followed a similar pattern, with depressions $\sim 3 \mu\text{M}$ and peaks $\sim 10 \mu\text{M}$. Nutrient concentrations, especially NO_x and NH_4^+ , weighted on Axis 2 (85% of variability, Fig. 5a) in our NMS for this region, which inversely correlated with inflows from the San Jacinto and Trinity Rivers, opposite to what was observed for phytoplankton biomass and productivity.

With the exception of cyanobacteria and haptophytes, phytoplankton taxonomic groups co-occurred

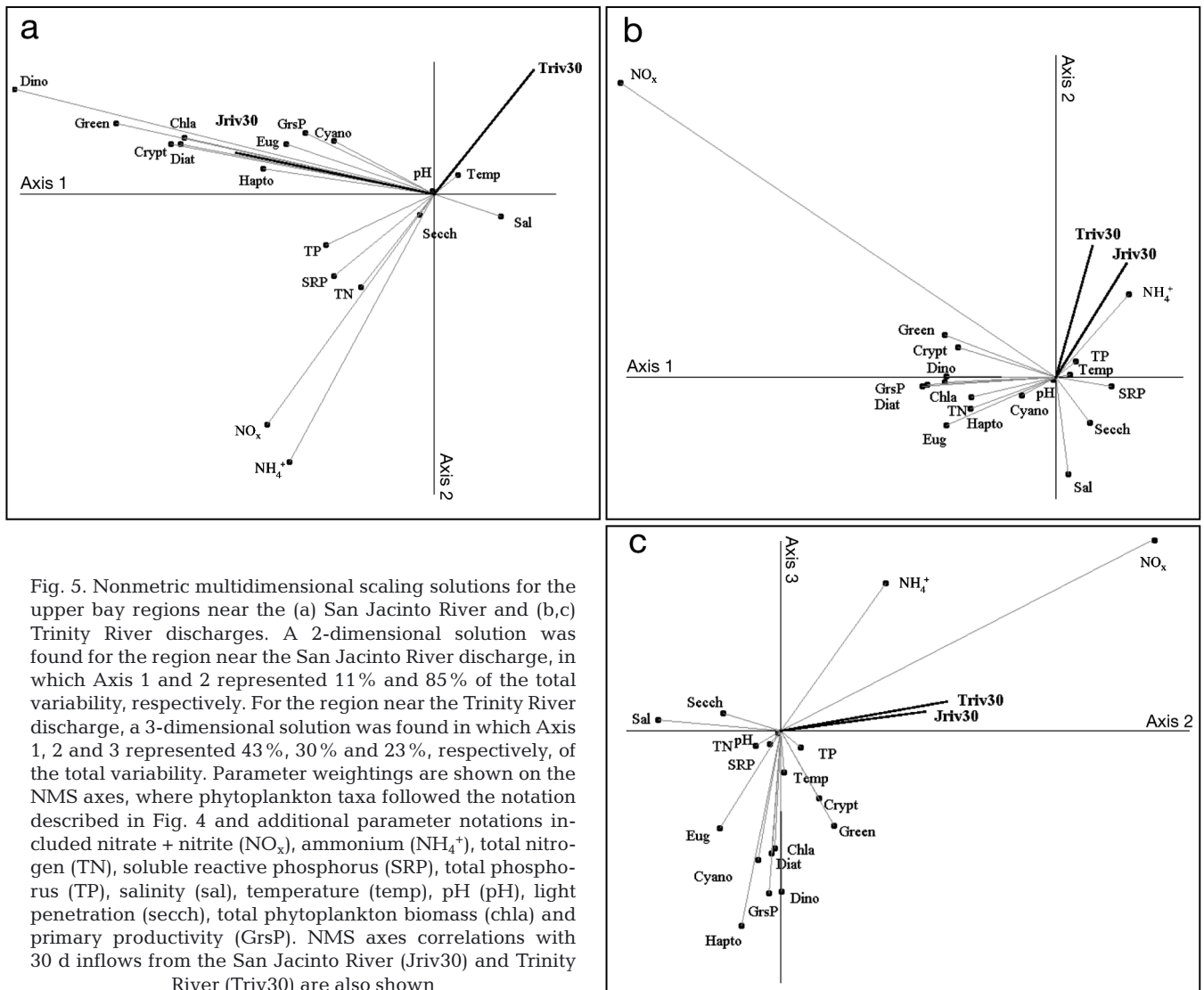


Fig. 5. Nonmetric multidimensional scaling solutions for the upper bay regions near the (a) San Jacinto River and (b,c) Trinity River discharges. A 2-dimensional solution was found for the region near the San Jacinto River discharge, in which Axis 1 and 2 represented 11% and 85% of the total variability, respectively. For the region near the Trinity River discharge, a 3-dimensional solution was found in which Axis 1, 2 and 3 represented 43%, 30% and 23%, respectively, of the total variability. Parameter weightings are shown on the NMS axes, where phytoplankton taxa followed the notation described in Fig. 4 and additional parameter notations included nitrate + nitrite (NO_x), ammonium (NH_4^+), total nitrogen (TN), soluble reactive phosphorus (SRP), total phosphorus (TP), salinity (sal), temperature (temp), pH (pH), light penetration (secch), total phytoplankton biomass (chl) and primary productivity (GrsP). NMS axes correlations with 30 d inflows from the San Jacinto River (Jriv30) and Trinity River (Triv30) are also shown

during the periods of high phytoplankton biomass (Fig. 4a). These mixed assemblages showed more evenness of biomass between taxonomic groups during 2005 compared to 2006. The winter and spring blooms during 2006 were diatom dominated. With the exception of euglena, the relationships between these co-occurring taxonomic groups were strongly associated with 30 d inflows from the San Jacinto River (Fig. 5a).

Temperature, pH and Secchi depth did not weigh notably on either axes of this NMS.

Upper Galveston Bay, near Trinity River (Stn 6)

Opposite to what was observed near the San Jacinto River, seasonal dynamics in phytoplankton biomass did not show a similar trend in 2005 and 2006 in the upper bay adjacent to the Trinity River (Stn 6; Fig. 4e). No consistent seasonal trend was observed for primary productivity either (Fig. 4f). Phytoplankton biomass and primary productivity showed a relationship with 30 d inflow from the rivers, but opposite (decreasing trend) to the pattern observed near the San Jacinto River. Distinct peaks in phytoplankton biomass of ~ 30 and $\sim 25 \mu\text{g chl } a \text{ l}^{-1}$ occurred during the early spring and late summer periods, respectively, during 2005. These were accompanied by primary productivity peaks of $\sim 3 \text{ g C m}^{-3} \text{ d}^{-1}$ and $\sim 4 \text{ g C m}^{-3} \text{ d}^{-1}$. During 2006, accumulation of phytoplankton biomass was slower, with less distinct maxima of $\sim 2 \mu\text{g chl } a \text{ l}^{-1}$ occurring in the late spring and early summer. These peaks were accompanied by primary productivity maxima of 3 and $5 \text{ g C m}^{-3} \text{ d}^{-1}$. Phytoplankton biomass and primary productivity weighted on Axes 1 and 3 of our NMS for this region (43% and 23% of the total variability, respectively; Fig. 5b,c), which inversely correlated with 30 d inflows from both rivers.

Only a few nutrient parameters were associated with inflows from the San Jacinto and Trinity Rivers. Here, NO_x and NH_4^+ were closely related to 30 d inflows, while TN, SRP and TP were not. The trend is seen on NMS Axes 2 and 3 for NO_x and on all NMS axes for NH_4^+ (Fig. 5b,c). As at Stn 5, the relationship between inflows and NO_x and NH_4^+ was opposite to the relationship between inflows and phytoplankton biomass and productivity. Regarding nitrogen availability, NO_x and NH_4^+ concentrations were in the range of 20 to 25 μM during the 2005 winter. They were quickly depleted by the 2005 fall, at which time NH_4^+ was the dominant dissolved inorganic nitrogen form. During 2006, NO_x and NH_4^+ peaks occurred during the winter, spring and fall. They were in the

range of 10 to 15 μM , with all peaks dominated by NH_4^+ (Fig. 4g). TN showed similar dynamics. During 2005, a winter peak of $\sim 49 \mu\text{M}$ and a fall maximum of $\sim 6 \mu\text{M}$ occurred. During 2006, peaks of ~ 11 , ~ 2 and $\sim 14 \mu\text{M}$ occurred in the winter, spring and fall, respectively. Regarding availability of phosphorus, SRP concentrations showed a large, dynamic range. It was also more seasonal than NO_x , NH_4^+ and TN. In 2005 and 2006, SRP increased with season until it peaked at $\sim 7 \mu\text{M}$ and $\sim 5 \mu\text{M}$ during these summers (Fig. 4h). TP followed a similar pattern with summer peaks of $\sim 8 \mu\text{M}$ and $\sim 6 \mu\text{M}$.

With the exception of green algae and cryptophytes, all phytoplankton groups showed an inverse correlation with inflows on all 3 axes of the NMS solution for this region (Fig. 5b,c). The exception was on Axis 2 (30% of the variability), where green algae and cryptophytes showed a positive correlation with inflows. Diatoms and dinoflagellates most strongly related to phytoplankton biomass and productivity maxima.

Unlike the region of the upper bay near the San Jacinto River (Stn 5), the region of the upper bay near the Trinity River (Stn 6) showed similar relationships between in-water parameters and both rivers on all NMS axes. But similar to the region of the upper bay near the San Jacinto River, temperature, pH and Secchi depth did not weigh notably on any of the axes of this NMS.

Lower Galveston Bay, nearest to the marine end-member (Stns 1 and 2)

As mentioned previously, the relationship between inflows and salinity was weaker in the lower bay (see Fig. 2c), and this was reflected in the NMS for this region. Salinity only weighted on Axis 3, which accounted for 29% of the total variability (Fig. 6a,b). Despite this region's distance from either river and its close proximity to the Gulf of Mexico, relationships between in-water parameters and inflows were still observed in the NMS results.

While not as strongly weighted as with the upper bay regions, phytoplankton biomass and productivity were still related to inflows from both rivers but with opposite trends. For example, phytoplankton biomass and productivity weighted on Axes 2 and 3 (37% and 29% of variability, respectively; Fig. 6b), which were more strongly (and positively) correlated with inflows from the San Jacinto River. Based on the NMS observation weightings (not shown), this positive relationship was most pronounced during March and September 2005 and June–July and September–November

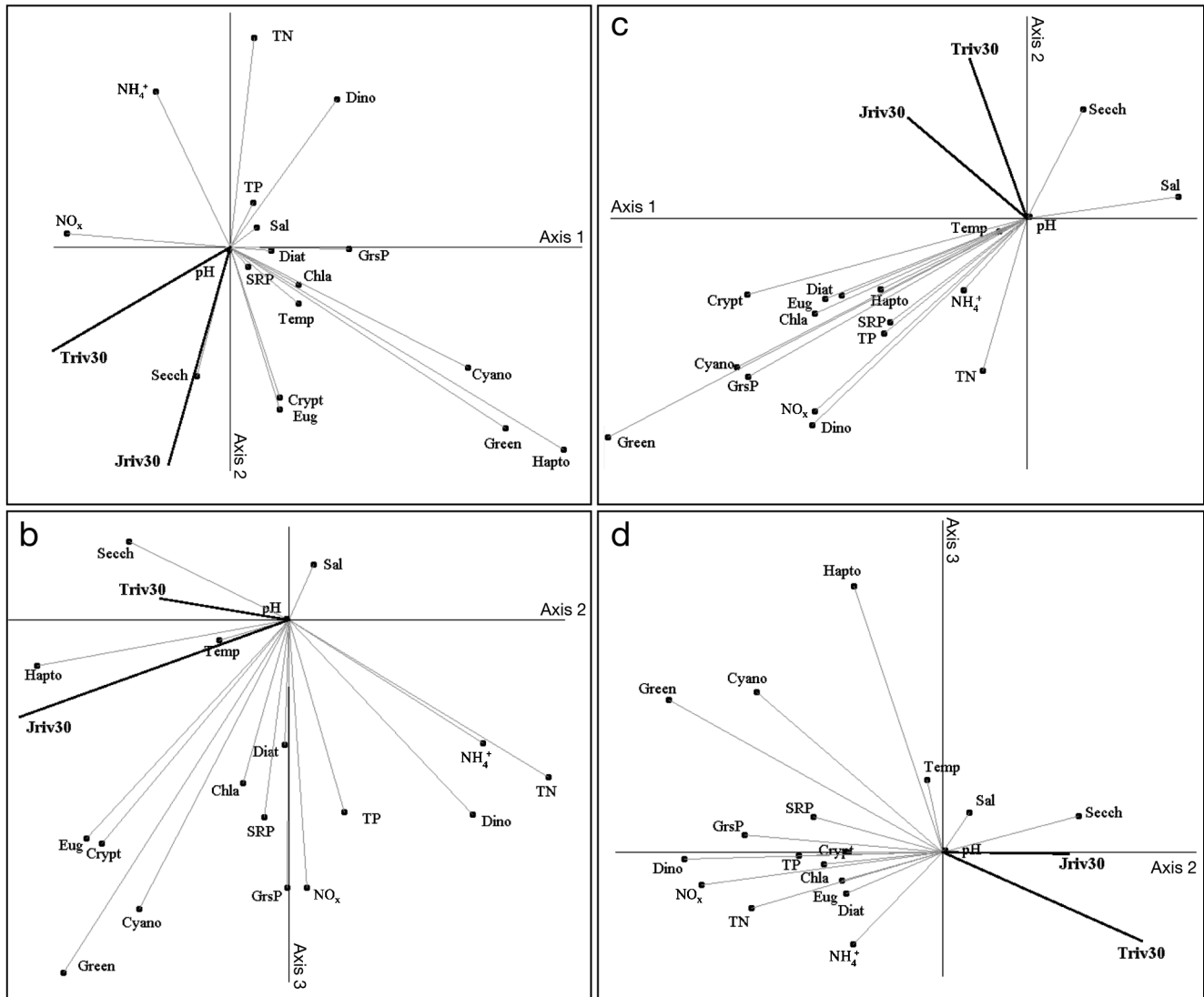


Fig. 6. Nonmetric multidimensional scaling solutions for (a,b) the lower bay region and (c,d) the mid- and lower bay regions combined. For both NMS statistics, 3-dimensional solutions were found. For the lower bay, Axis 1, 2 and 3 represented 31%, 37% and 29%, respectively, of the total variability. For the mid- and lower bay combined, Axis 1, 2 and 3 represented 44%, 38% and 12%, respectively, of the total variability. Parameter weightings are shown on the NMS axes, where notation followed the notation described in Fig. 5. NMS axes correlations with 30 d inflows from the San Jacinto River (Jriv30) and Trinity River (Triv30) are also shown

2006 (Stn 1 only during November 2006). Phytoplankton biomass and productivity also weighted on Axis 1 (31% of variability; Fig. 6a), which was more strongly (but now inversely) correlated to inflows from the Trinity River. Based on the NMS observation weightings (not shown), this negative relationship was most pronounced during November 2005 and 2006 (Stn 2 only during November 2006).

It should be noted here that the relationships between inflows and in-water parameters in this region are in regards to parameter values of lower magnitude and dynamic range. For example, phytoplankton biomass ranged from ~ 5 to $\sim 15 \mu\text{g l}^{-1}$, with max-

ima occurring during summers (Fig. 7a), and primary productivity ranged from 0.25 to $\sim 3 \text{ g C m}^{-3} \text{ d}^{-1}$ with a maximum only occurring during the summer 2006.

Nutrients also showed opposing relationships with inflows, especially in regard to NO_x and NH_4^+ (Figs. 6a,b). These nutrients weighted on NMS Axis 2 (37% of variability), which was more strongly correlated to inflows from the San Jacinto River as mentioned above, but now the relationship was inverse, with lower nutrients occurring when inflows were higher. NO_x and NH_4^+ also weighted on Axis 1 (31% of variability), which was more strongly correlated with inflows from the Trinity River. Here, the relation-

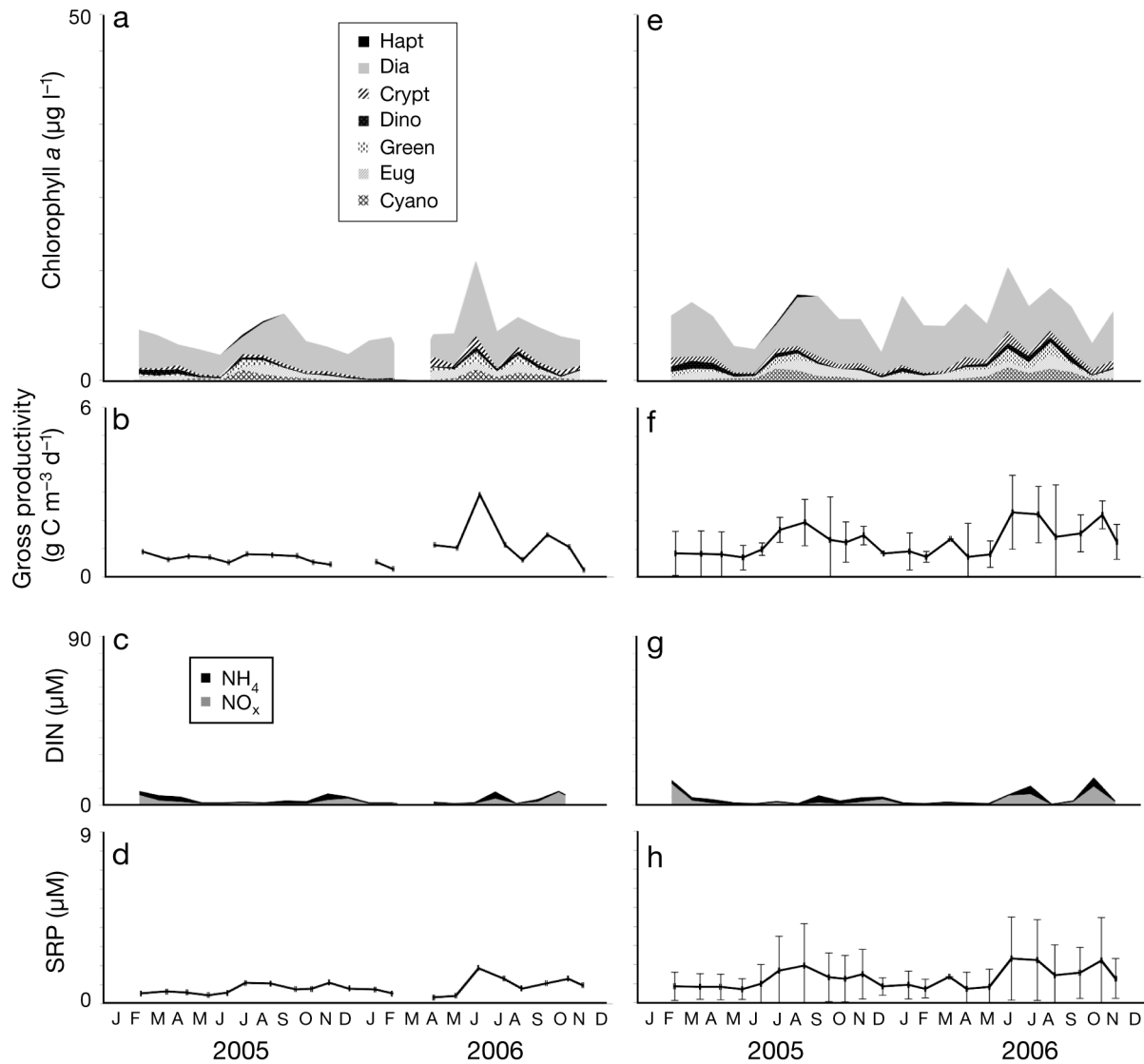


Fig. 7. (a) Phytoplankton biomass, (b) primary productivity, (c) dissolved inorganic nitrogen as nitrate + nitrite (NO_x) and ammonium (NH_4^+) and (d) dissolved phosphorus as soluble reactive phosphorus (SRP) for the lower bay region (Stns 1 and 2 combined). The same parameters (e,f,g,h) are shown for the mid- and lower bay regions (Stns 1 through 4 combined). As before, phytoplankton were characterized into taxonomic groups that included haptophytes (Hapt), diatoms (Dia), cryptophytes (Crypt), dinoflagellates (Dino), chlorophytes (Green), euglenophytes (Eug) and cyanobacteria (Cyano)

ship between inflows and NO_x and NH_4^+ was positive (Fig. 6a). But again, note that the relationships between inflows and in-water parameters in this region are in regard to parameter values of lower magnitude and dynamic range, i.e. 0.1 to 6.4 μM for NO_x , 0.5 to 3.8 μM for NH_4^+ and 0.3 to 1.9 μM for SRP (Fig. 7c,d).

Taxonomic trends with inflows in the lower bay were detected in our NMS for this region. Dinoflagellates were strongly (and inversely) correlated to inflows from both rivers on Axes 1 and 2 (which combined represented 68% of the variability; Fig. 6a). Diatoms, which comprised the bulk of phytoplankton biomass year round in this region, only weighted

higher on Axis 3 (29% of variability; Fig. 6b), which was positively correlated with inflows from the San Jacinto River. Green algae, cyanobacteria and haptophytes showed a complex relationship with inflows in this region. For example, inflows from the Trinity River more strongly correlated with decreases in the biomass of these taxa, as shown on Axes 1 and 3, while inflows from the San Jacinto River more strongly correlated with increases in biomass of these taxa, as shown on Axes 2 and 3.

Secchi depth weighted on Axes 2 and 3 for this region of GB. Temperature and pH did not weigh notably on any of the NMS axes for this region.

Composite of mid- and lower Galveston Bay (Stns 1 through 4)

Seasonal dynamics in phytoplankton biomass and productivity were not similar during 2005 and 2006 in the mid- and lower GB. Phytoplankton biomass peaks of ~ 11 and $\sim 12 \mu\text{g chl } a \text{ l}^{-1}$ occurred during the winter and summer periods, respectively, during 2005. During 2006, peak biomasses occurred during the early- and late-winter, spring, summer and fall periods, all within the range of 10 to $15 \mu\text{g chl } a \text{ l}^{-1}$ (Fig. 7e). Primary productivity in the mid- and lower bay during 2005 was maximum during the summer, $\sim 2 \text{ g C m}^{-3} \text{ d}^{-1}$, with another smaller peak occurring during the fall of $\sim 1.5 \text{ g C m}^{-3} \text{ d}^{-1}$. During 2006, a smaller peak of $\sim 1.5 \text{ g C m}^{-3} \text{ d}^{-1}$ was observed during the winter, followed by larger peaks of $\sim 2.5 \text{ g C m}^{-3} \text{ d}^{-1}$ during the early summer and fall periods (Fig. 7f).

As with the lower bay NMS analysis, phytoplankton biomass and primary productivity again showed both positive (Axis 1, which represented 44% of the variability) and negative (Axis 2, which represented 38% of the variability) relationships with inflows from both rivers (Fig. 6c). While not as prominent as observed in the upper bay regions, positive relationships in this region again correlated more strongly with inflows from the San Jacinto River. Based on the NMS observation weightings (not shown), these positive relationships were more pronounced during March and August 2005 and June–September and November 2006. Negative relationships correlated more strongly with inflows from the Trinity River, and those were more pronounced during May and September–November 2005 and February and October–November 2006. Note that both positive and negative relationships occurred at different stations in the mid- and lower region of GB within the same month of sampling.

Inflows from the San Jacinto and Trinity Rivers related to some nutrients in the mid- and lower bay. Similar to relationships with phytoplankton biomass and primary productivity, river inflows sometimes positively related to nutrients, especially NO_x (Axis 1, 44% of the variability), and sometimes negatively (Axis 2, 38% of the variability). Combined NO_x and NH_4^+ (collectively, dissolved inorganic N) fluctuated between low values of $\sim 0.5 \mu\text{M}$ and peaks of $\sim 15 \mu\text{M}$ (Fig. 7g). TN ranged from lows of $\sim 10 \mu\text{M}$ to peaks of $\sim 95 \mu\text{M}$. SRP fluctuated between lows of $\sim 0.3 \mu\text{M}$ and peaks of $\sim 2 \mu\text{M}$ (Fig. 7h), and TP ranged from ~ 0.5 to $\sim 4 \mu\text{M}$.

Diatoms dominated phytoplankton biomass in the mid- and lower bay throughout the sampling period, but not completely as most other taxonomic groups

that co-occurred (Fig. 7e). All phytoplankton taxa related to phytoplankton biomass and primary productivity on Axes 1 and 2 (which combined represented 82% of the variability; Fig. 6c). Of all the taxa, haptophytes showed the weakest relationship with phytoplankton biomass and primary productivity. More subtle relationships were revealed with Axis 3 of this NMS, which represented 12% of the variability (Figs. 6d). For example, haptophytes were inversely related with the 30 d inflows from the Trinity River and with NH_4^+ , and cyanobacteria and green algae were inversely related to inflows from both rivers.

Secchi depth weighted on Axis 2 for the mid- and lower bay region. Temperature and pH did not weigh notably on any of the NMS axes for this region.

Modeled inflows

The numerical model of the simplified phytoplankton system showed the range of potential effects of hydraulic displacement and nutrient loading (Fig. 8). During the period when phytoplankton growth was not limited and nutrient-loading effects were minimized, the influence of hydraulic displacement was small. The accumulation of biomass was only delayed by several hours, with the maximum accumulated biomass remaining the same. During the period when phytoplankton growth was limited, nutrient loading had a profound effect. With nutrient loads set

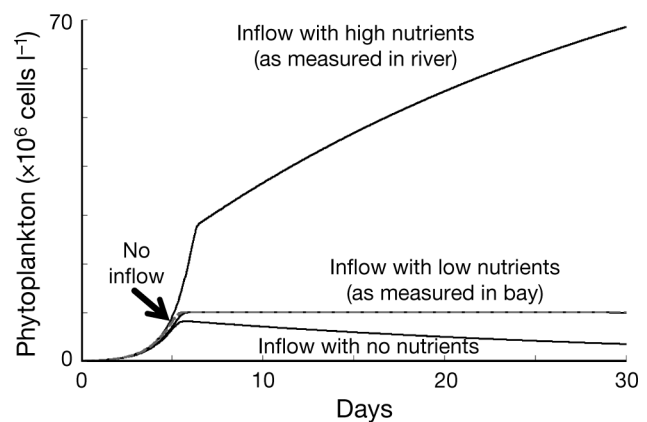


Fig. 8. Numerical solution to a simplified phytoplankton model depicting a fixed-volume, flow-through system. Solid lines represent the change in phytoplankton population when source nutrient concentrations were high (based on concentrations measured in the Trinity River), lower (based on concentrations measured in the upper bay) and zero. The dashed line, which falls mostly identical to the middle solid line (it reaches steady state hours before the second simulation), represents the change in phytoplankton population when there was no inflow

at levels representative of the Trinity River, a 7-fold increase in accumulated biomass occurred. In contrast, when nutrient loading effects were negated but hydraulic displacement of cells remained (here achieved by setting the river nutrient concentration to zero), a 70% reduction in phytoplankton biomass resulted over a period of 30 d.

DISCUSSION

Intuitively, when inflows are small relative to the size of the receiving water body, short-term effects of hydraulic displacement on phytoplankton populations should be negligible. For our study, the combined daily inflows of the San Jacinto and Trinity Rivers were small relative to the volume of GB. Even at maximum river discharges, daily whole-system flushing was only 0.08 d^{-1} , with a corresponding 30 d average of 0.035 d^{-1} . These values are low compared to potential reproductive growth rates of phytoplankton, which are typically ~ 1 to 2 d^{-1} (Reynolds 2006). Results from our simplified phytoplankton model showed that hydraulic displacement at this level would only slow the accumulation of phytoplankton biomass by several hours prior to the onset of reproductive growth limitation. This suggests that hydraulic displacement, even during times of high discharge from the San Jacinto and Trinity Rivers, would have produced little effect during periods of exponential population growth.

But in theory, rapid phytoplankton responses to inflow events could be profound, even when inflows are relatively small. For this to happen, phytoplankton growth must be nutrient limited. Our simplified phytoplankton model showed this behavior. During the period after the onset of growth limitation and when the simulated nutrient loading was based on nutrients observed in the Trinity River, a 7-fold increase in phytoplankton biomass resulted over a period of 30 d. Rapid increases in phytoplankton biomass and productivity in response to inflows are commonly observed in natural systems (Ara et al. 2011, Jutla et al. 2011, Drupp et al. 2012).

In contrast, relatively small inflows might reduce populations through hydraulic displacement. This could result if phytoplankton reproductive growth rate is not limited, but population growth is controlled by something else, such as grazing or pathogens. This effect was also demonstrated in our simplified phytoplankton model. During the period after the onset of growth limitation and when reproductive growth was absent and flushing sustained at the 0.035 d^{-1} level, a

70% decrease in phytoplankton biomass occurred over a period of 30 d. Depletion of phytoplankton following inflows due to hydraulic displacement has been observed in natural systems (Garcia et al. 2010, Roelke et al. 2010, 2011, Balch et al. 2012).

In GB, both relationships were observed to some extent. That is, phytoplankton biomass and productivity rapidly increased in response to inflow events and also decreased. These opposite responses to inflows co-occurred in GB because they happened in different regions of the bay. Recall that in the region of the bay near the San Jacinto River, 85% of the variability was explained by a positive relationship involving inflow events, phytoplankton biomass and primary productivity. This suggests that the phytoplankton reproductive growth rate was at times nutrient limited near the San Jacinto River, and population growth responded rapidly to nutrient loadings. This effect was observed previously using enrichment experiments (Örnolfsdóttir et al. 2004). In contrast, near the Trinity River, 66% of the variability was explained by an inverse relationship between inflow events and phytoplankton biomass and productivity. This suggests that population growth was controlled at times by other processes in this region, thereby negating the effects of nutrient loadings, and that decreased phytoplankton biomass occurred in this region due, in part, to hydraulic displacement. At the system level, we are unaware of previous reports showing co-occurring and opposing inflow effects such as these.

Looking at the NMS results as a whole, it is clear that inflows had a diminishing influence on phytoplankton with distance from the points of river discharge, a phenomenon described previously in nearby coastal systems (Roelke et al. 1997, Russell et al. 2006, Russell & Montagna 2007). In GB, although diminished, it appears that both positive and negative effects of inflows extended throughout the system but at different times of the year and at different locations within the mid- and lower bay. Consistent with observations from the upper bay regions, higher phytoplankton biomass and productivity were more strongly correlated to inflows from the San Jacinto River, while lower phytoplankton biomass and productivity were more strongly correlated to inflows from the Trinity River. The time of year and location when these positive and negative effects extended into the mid- and lower bay were not consistent. This characteristic of the system certainly complicates prediction of how altered inflows in the future might affect the plankton environment in GB. In addition, light penetration seems to play a more prominent role in the lower GB, with linkages to inflows.

Taxonomic groups responded differently to inflow events, and the responses varied regionally within GB. In the area of the bay near the San Jacinto River, most phytoplankton taxa were stimulated by inflows. The exceptions were cyanobacteria, haptophytes and euglena. It may be that these taxa had access to other sources of nutrition and consequently were not as sensitive to nutrient loading from the rivers. Many cyanobacteria are able to fix atmospheric nitrogen (Gruber & Sarmiento 1997), several haptophytes are mixotrophic (Granéli et al. 2012), and euglena are saprophytic (Tannreuther 1922). It may be that alternative modes of nutrition for these taxa are important in this region of upper GB.

Another possibility is that cyanobacteria, haptophytes and euglena were more vulnerable to hydraulic displacement. Many members of these taxonomic groups are characterized by low reproductive growth rates relative to other phytoplankton. This leaves them more susceptible to hydraulic displacement effects. For cyanobacteria, decreased populations following inflows have been observed worldwide (Paerl & Paul 2012, Reichwaldt & Ghadouani 2012). For haptophytes, there are not as many studies. Information from inland water bodies suggests that some populations within this taxonomic group, i.e. the cosmopolitan species *Prymnesium parvum*, are nearly obliterated due to inflows (Roelke et al. 2010, 2011). In regard to euglena, most taxa are adapted to highly eutrophic conditions and do not grow as fast when nutrients are lower (see Finni et al. 2001). So it is not surprising that cyanobacteria, haptophytes and euglena did not show a positive relationship with nutrient loading in the region of GB near the San Jacinto River, nor is it surprising that they were among the taxa diminished with inflows in the region of the upper bay near the Trinity River.

Lower in the bay, taxonomic responses to inflows also varied. Dinoflagellates were inversely related to inflows from both rivers, while diatoms, which comprised the bulk of phytoplankton biomass year round in this region, were slightly stimulated by inflows but only when the inflows originated mostly from the San Jacinto River. Other taxa showed complex relationships. For example, green algae, cyanobacteria and haptophytes showed an inverse relationship with inflows when the inflows originated mostly from the Trinity River. When inflows originated mostly from the San Jacinto River a positive relationship was observed.

Regarding haptophytes, their occurrence in GB during the summer months of 2005 followed intense fish-killing, winter-spring blooms of *Prymnesium*

parvum, a species of haptophyte, that occurred inland throughout the middle reaches of the Brazos River (Roelke et al. 2011). This species is euryhaline with an optimal salinity for growth of 22 (Baker et al. 2007, 2009), a salinity that is common in GB. This species causes devastating fish-killing blooms in coastal waters of varied salinity worldwide (Granéli et al. 2012). Along the Brazos River, *P. parvum* blooms have occurred over the past decade resulting in 10s of millions of dollars of damage to fisheries and tourism (Southard et al. 2010, Roelke et al. 2011). Water from the Brazos River finds its way into GB through various industrial practices along the coast, and toxic *P. parvum* blooms have already been observed in habitats fringing GB (Southard et al. 2010, J. Nelson pers. comm.). In addition, in laboratory settings and in-field mesocosm experiments, *P. parvum* from culture grew very well in GB waters (V. Lundgren unpubl. data). It is very likely that this organism is being introduced into GB. Other species of haptophytes are common to estuarine waters, so our observation of haptophytes in the present study does mean *P. parvum* was found in the open bay. But this combined evidence underscores a need to research the potential impact of *P. parvum* in GB given that the source of *P. parvum* immigration, i.e. the Brazos River, does not appear to be diminishing.

In summary, we showed that inflows were a dominant driver of phytoplankton variability in Galveston Bay. Effects of inflows in the upper bay regions were most important. However, the effects to phytoplankton biomass and productivity were complex, with the region of the bay near the San Jacinto River showing positive relationships with inflows and the region of the bay near the Trinity River showing negative relationships. Both positive and negative relationships extended further into the bay at different times of the year and at different locations. Over the 2 seasons sampled in the present study, the timing and location of these extended inflow effects were not consistent. Taxonomic responses to inflows were also apparent, with factors associated with access to alternative sources of nutrition, differential growth rates and immigration from rivers likely playing a role.

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