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Drivers of phytoplankton dynamics in old Tampa Bay, FL (USA), a subestuary lagging in ecosystem recovery

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A B S T R A C T

In the past four decades, consistent and coordinated management actions led to the recovery of Tampa Bay, FL (USA) – an estuary that was declared dead in the 1970s. An exception to this success story is Old Tampa Bay, the northernmost subestuary of the system. Compared to the other bay segments, Old Tampa Bay is characterized by poorer water quality and spring and summer blooms of cyanobacteria, picoplankton, diatoms, and the saxitoxin-producing dinoflagellate *Pyrodinium bahamense*. Together, these blooms contribute to light attenuation and lagging recovery of seagrass beds. Yet, studies of phytoplankton dynamics within Old Tampa Bay have been limited – both in number and in their spatiotemporal resolution. In this study, we used field sampling and continuous monitoring to (1) characterize temporal and spatial variability in phytoplankton biomass and community composition and (2) identify key drivers of the different phytoplankton blooms in Old Tampa Bay. Overall, temporal variability in phytoplankton biomass (using chlorophyll *a* as a proxy) and community composition surpassed spatial variability of these parameters. We found a base community of small diatoms and flagellates, as well as certain dinoflagellates, that persisted year round in the system. Seasonally, freshwater runoff stimulated phytoplankton growth, specifically that of chlorophytes, cyanobacteria and other dinoflagellates – consistent with predictions based on ecological theory. On shorter time scales, salinity, visibility, and freshwater inflows were important predictors of phytoplankton biomass. With respect to *P. bahamense*, environmental drivers including salinity, temperature and dissolved nutrient concentrations explained ~24% of the variability in cell abundance, indicating missing explanatory parameters in our study for this taxon, such as cyst density and location of cyst beds. Spatially, we found differences in community trajectories across north–south and west–east gradients, with the northernmost sampling station being the most unique in the region. This work contributes to the knowledge of phytoplankton biomass and community composition in Tampa Bay by generating spatially and temporally rich phytoplankton community and environmental data for the Old Tampa Bay subestuary. Moreover, it enhances our understanding of bloom drivers and provides recommendations for ecosystem management. Specifically, our findings support continued nutrient reduction measures as a way to mitigate seasonal blooms of diatoms, cyanobacteria and chlorophytes, but not necessarily blooms of *P. bahamense*. Prediction and mitigation of *P. bahamnese* blooms should incorporate first order drivers such as cyst location and abundance.

1. Introduction

Increased nutrient loading to aquatic systems, a pervasive phenomenon resulting from human activities, has triggered or exacerbated phytoplankton blooms globally, leading to cascading negative effects such as hypoxia or anoxia, habitat loss, and changes in the structure and function of food webs (Cloern, 2001; Nixon, 1995). Although reversing the effects of eutrophication requires actions beyond reducing nutrient loading (Duarte et al., 2009), implementing coordinated management strategies has led to at least partial recovery in some systems (Borja et al., 2010; Jones and Schmitz, 2009).

The restoration of Tampa Bay provides a notable success story of the reversal of eutrophication (Greening and Janicki, 2006; Greening et al., 2014; Lewis et al., 1998). Tampa Bay, the largest

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(1036 km^2) open-water estuary in Florida, is a shallow (4 m average depth), wide (8–16 km), vertically well mixed, Y-shaped system with a watershed greater than 5500 km^2 in area (Yates and Greening, 2011). Four major rivers and more than 100 tributaries flow into Tampa Bay, which is typically partitioned into four segments: Old Tampa Bay, Hillsborough Bay, Middle Tampa Bay, and Lower Tampa Bay (Fig. 1A, Lewis and Whitman, 1985). As a designated estuary of national significance, the bay provides economic and ecosystem services including moderation of climate, nursery grounds, shipping, and recreation, with a total economic benefit estimated at 55 billion USD annually (Yates and Greening, 2011). In the late 1970s, Tampa Bay was characterized by excessive dissolved nutrient concentrations and phytoplankton biomass, as well as nuisance blooms of macroalgae including *Ulva* spp. and the filamentous cyanobacterium *Schizothrix calcicola* (Johansson and Lewis, 1992; Morrison and Greening, 2011). During the following four decades, consistent regulatory and voluntary reductions in point-source nutrient loading effectively curtailed eutrophication in Tampa Bay. In 2008, primary production by phytoplankton was approximately half of that recorded between 1980 and 1985 (Johansson, 2010). Compared to 1982, seagrass coverage increased ~38%, and in recent years the estuary has generally met the chlorophyll targets set by local management agencies (Greening et al., 2014; Sherwood, 2014).

The recovery of Old Tampa Bay (OTB), the northwestern segment of the estuary, has notably lagged behind that of other Tampa Bay segments. Compared with the other segments, OTB is characterized by poorer water quality (i.e., low transmittance and high turbidity, chlorophyll, and CDOM concentrations, Greening et al., 2011), a more heavily urbanized watershed (Xian and Crane, 2005), and longer water residence times (Weisberg and Zheng, 2006), in part due to three causeways that bisect it, restricting exchange with the rest of the bay (Meyers et al., 2014). Spring and summer blooms of cyanobacteria, picoplankton, diatoms, and the saxitoxin-producing dinoflagellate *Pyrodinium bahamense* commonly occur in OTB (Badylak et al., 2007). Blooms of *P. bahamense* can result in chlorophyll concentrations of ~100 μg L^{-1}, an order of magnitude greater than the target chlorophyll concentration of 8.5 μg L^{-1} established by the Florida Department of Environmental Protection. *Pyrodinium bahamense* is an armored, bioluminescent dinoflagellate that produces resting cysts (Steidinger et al., 1980; Usup et al., 2012; Wall and Dale, 1969). The deposition of cysts during bloom maintenance and termination generates cyst beds in surficial sediments that can seed future blooms. In OTB, *P. bahamense* blooms initiate in areas with high cyst abundance (Karlen and Campbell, 2012; Karlen and Miller, 2011; Lopez et al., in press). Although *P. bahamense* blooms were recorded in OTB as early as 1975, they have occurred annually only since 2000 (Karlen and Campbell, 2012). Such annual blooms are common in other systems, including Florida's Indian River Lagoon (Phlips et al., 2011) and bays in Malaysia and the Philippines (Usup et al., 2012).

Despite the central role of phytoplankton in affecting overall water quality in OTB, there have been few published studies on phytoplankton communities in the system. Moreover, the existing studies have been limited in spatial scope and temporal resolution, restricting their utility. In this study, we use a field-based approach to (1) characterize temporal and spatial variability in phytoplankton biomass and community composition in OTB and (2) identify primary bloom drivers.

2. Materials and methods

2.1. Approach

To characterize the spatial and temporal variability in phytoplankton dynamics and related environmental factors in OTB, we combined discrete sampling at nine fixed stations with continuous monitoring at a single station (Fig. 1). We used discrete sampling to characterize seasonal variability in phytoplankton dynamics and continuous sampling to characterize daily to weekly variability. From January 2012 through October 2014, we collected surface seawater twice-monthly at the discrete sampling locations for the analysis of chlorophyll *a* concentrations, *P. bahamense* abundance, biogenic silicon (Si), total nitrogen (TN), total dissolved phosphorus (TDP), and dissolved silica. From May through September 2013, the

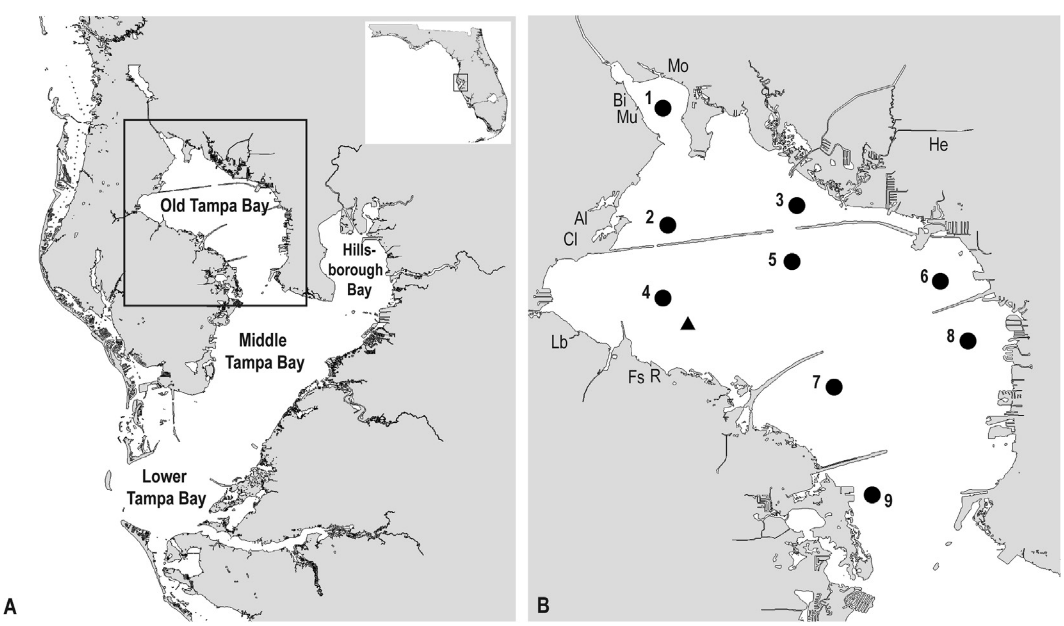

Fig. 1. The location of (A) Old Tampa Bay and (B) the discrete (circles) and continuous (triangle) sampling locations. In A, the inset shows the location of Tampa Bay along the Gulf Coast of Florida. The abbreviations in B indicate the locations of freshwater inflows or resources as follows: Al, Alligator Creek; Bi, Bishop Creek; Cl, Clearwater Treatment Plant; Fs, Feather Sound; He, Henry Creek; Lb, Long Branch Creek; Mo, Moccasin Creek; Mu, Mullet Creek; and R, Roosevelt Canal.