LONG-TERM AND SEASONAL TRENDS IN PHYTOPLANKTON PRODUCTION AND BIOMASS IN TAMPA BAY, FLORIDA.

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ABSTRACT

Phytoplankton production is a basic process in aquatic ecosystems that converts inorganic carbon into organic matter and provides an important indicator of trophic state. The City of Tampa Bay Study Group maintains a 32 year long monthly record of phytoplankton production rates and biomass (chlorophyll-a) in Hillsborough Bay (HB) and Middle Tampa Bay (MTB), and a recent record during the last nine years for Old Tampa Bay (OTB). Production is measured using the classic *in situ* ^{14}C method with samples incubated vertically in the water column. Annual production rates during the most recent decade are about $410gCm^{-2}$ for HB, $350gCm^{-2}$ for MTB, and $390gCm^{-2}$ for OTB. The current rates for the two former bay segments are near half the rates measured during 1980-1985. Reductions in biomass have been greater; current HB and MTB concentrations are near 70% lower than those measured during 1980-1985. Water column averaged chlorophyll-a concentrations during the most recent decade are about $10mgm^{-3}$ for HB, $5.8mgm^{-3}$ for MTB, and $6.3mgm^{-3}$ for OTB. The decreases in production and biomass, and also reductions in phytoplankton abundance, are reflected in a large reduction in anthropogenic nitrogen loading to the bay that primarily occurred during the late 1970s and early 1980s. This is strong evidence the long-term trend in Tampa Bay phytoplankton production and biomass has been regulated by the supply of nitrogen from external sources. However, similar to other productive estuarine and coastal systems, in-bay recycling provides a substantial fraction of the nitrogen needed to sustain the observed daily production rates. The vertical distribution of phytoplankton production in HB and MTB has shifted during the study period, most noticeable during the wet summer seasons, from a large proportion of total water column production occurring in the upper meters to a more even distribution with depth. Further, seasonal water column production generally reaches maximum during the summer months and follows variations in water temperature. Finally, a comparison of current phytoplankton and seagrass carbon production in the bay segments studied indicates that pelagic phytoplankton dominates production and will most likely continue to do so in the future.

INTRODUCTION

The phytoplankton community is the major producer of organic matter to most of the world’s estuaries, including Tampa Bay, and is thus an important contributor to the estuarine food web in those systems. This organic matter sustains diverse estuarine ecosystems by providing energy to secondary producers and higher trophic levels.

The autotrophic conversion process of inorganic substances into organic matter by the phytoplankton is measured as carbon production rates. These measurements provide information on the trophic state of water bodies which can not directly be derived from instantaneous phytoplankton biomass determinations. Further, the measured production rates can provide information about the physiological state of the phytoplankton population that can be related to estuarine conditions and processes, including water column light availability and nutrient uptake and recycling.

Tampa Bay is one of the largest river dominated estuaries in the south-eastern United States with an open water surface area of about 1000km^2 and with a water volume of nearly four billion m^3. The current average daily standing crop of the phytoplankton contained within this large water body is, when expressed as carbon weight, close to 2000 metric tons. A fundamental understanding of phytoplankton carbon production rates is required to, at least at a basic level, comprehend the complex estuarine processes involved with the maintenance and utilization of this biomass.

The purpose of this report is to build on the early Tampa Bay phytoplankton community information that was presented at the first Tampa Bay Area Scientific Information Symposium (BASIS) near 30 years ago (Johansson et al. 1985); and also to update more recent information presented at BASIS 4 in 2003 (Johansson 2005).

METHODS

The City of Tampa Bay Study Group (BSG) maintains a 32 year long monthly record of phytoplankton production rates in Hillsborough Bay (HB) and Middle Tampa Bay (MTB), and a recent record during the last decade for Old Tampa Bay (OTB). Two locations have been sampled in HB (COT4; depth 3.8m and COT12; depth 5.4m) since 1978, one location in MTB (COT13; depth 6.4m) since 1979 and one location in OTB (COT40; depth 4.8m) since 2000 (Figure 1). For this report, measurements from the two HB stations have been combined to reflect the overall conditions in HB.

Production measurements were conducted using the classic *in situ* ^{14}C method developed by Steemann Nielsen (1952) and modified by Strickland and Parsons (1968). Water collected at 1m intervals from surface to near bottom is screened through a 202µm mesh to remove larger grazers. The water is then dispensed into glass bottles, which are inoculated with a measured amount of sodium [^{14}C] bicarbonate solution. Triplicate bottles from each depth level are suspended in the water column at the depth of collection for a 3hr to 5hr day-light period. After the incubation period, the samples are brought to the laboratory and the phytoplankton community is captured on 0.45µm pore size membrane filters. The radioactivity of the filters is determined in a liquid scintillation counter. The hourly carbon production rate during the incubation period is calculated and then corrected to daily production rates using daily solar radiation data for Tampa.

Also, un-screened aliquots are taken from the water samples at each depth level for phytoplankton biomass (chlorophyll-a) estimates, and from the surface samples only, for microscopic determinations of phytoplankton abundance and composition. Additional measurements include: standard multi-probe physical parameters (temperature, salinity, dissolved oxygen and pH), PAR light attenuation, beam attenuation at 660nm, Secchi disk depth, turbidity; and concentrations of colored dissolved organic matter (CDOM), total suspended solids (COT 4 only), total carbonate and dissolved ammonia.

RESULTS

Long-Term Trends in Phytoplankton Production and Biomass:

Trends in annual phytoplankton production and biomass, expressed on an areal basis, for the period of record and for the three bay segments studied are shown in Figure 2. It is clear that large reductions in both production and biomass have occurred in HB and MTB since the late 1970s and early 1980s. A long-term record for production rates is not available for OTB, however, the recent OTB record tracks HB and MTB closely. Further, based on the long-term Hillsborough County Environmental Protection Commission’s (HCEPC) chlorophyll-a record for OTB (Boler 2002), it is known that large phytoplankton biomass reductions have also occurred in this bay segment (Table 1). It is reasonable to assume that phytoplankton production also has decreased in OTB in a similar manner as seen in HB and MTB.

A comparison of production rates and biomass concentrations in the bay segments studied (Table 1) show that total water column production in HB and MTB during the current decade is near half of that measured during the 1980-1985 period. In contrast, water column biomass concentrations have decreased almost three-fold. Similar changes have also occurred in surface production and biomass for the two bay segments between the two time periods. However, estimated biomass in OTB has apparently only been reduced by a third between the early and current period.

Long-Term Trends in HB Phytoplankton Parameters and External DIN Loading:

Hillsborough Bay is the only Tampa Bay segment with a long-term record of dissolved inorganic nitrogen (DIN) loading from external sources; the form of nitrogen most readily available for phytoplankton growth (Johansson 2005). A comparison of HB records for DIN loading and phytoplankton production and biomass (Figure 3) indicates that major reductions, in both production rates and biomass concentrations have followed the substantial DIN loading reductions during the late 1970s and early 1980s. However, biomass concentrations apparently responded faster than production rates to the DIN reductions.

Biomass was substantially reduced in 1984, about 5 years following the initiation of the large DIN loading reduction. At that time, the amount of a seasonally occurring large filamentous planktonic blue-green alga (*Schizothrix* sp.) was greatly reduced in HB and other bay segments (Johansson and Lewis 1992; Dixon et al. 2009). Phytoplankton production, in contrast, was maintained at high levels throughout the DIN loading transition period and was not substantially reduced until 1988.

The reduction in biomass was clearly linked to the decline in blue-green biomass and abundance; however, it is less certain why production remained elevated for four years following the substantial decline in biomass. An examination of seasonal production patterns for HB during the four year period shows that summer production rates were very high. These high rates may have been maintained by temperature-regulated internal nitrogen recycling from the high organic sediments present in HB (see Johansson and Squires 1989).

Long-Term and Seasonal Vertical Distribution in Phytoplankton Production and Biomass:

The collection of water samples at one meter intervals from near surface throughout most of the water column allows for long-term and seasonal evaluations of trends in the vertical distribution of both phytoplankton production and biomass.

Long-Term Trends:

The vertical distribution patterns of phytoplankton production and biomass have changed very differently during the long-term in both HB and MTB (Figures 4 and 5). Phytoplankton biomass shows a near uniform vertical distribution for the two bay segments during the period of study. This distribution pattern indicates that the water column was well mixed and has lacked density stratification on most sampling occasions and that the large historical reductions in biomass generally occurred throughout the water column. Vertical chlorophyll-a patterns in Tampa Bay have also been discussed by Johansson (2006).

In contrast to the vertical patterns seen in phytoplankton biomass, the long-term distribution pattern for production rates shows large vertical differences, with higher rates, as expected, near the surface and lower rates deeper in the water column. It is evident that the major reductions in phytoplankton production rates during the period of record have mainly occurred in the upper portion of the water column. The vertical pattern seen for production indicates that water column light attenuation is controlling production with depth. Further, it appears that reduction in light penetration caused by the phytoplankton community itself (i.e. self-shading) plays an important roll in the vertical distribution of production rates. Of course, other factors also affect water column light attenuation including turbidity, CDOM concentrations and the water itself (Kirk 1994). Light reductions caused by these constituents would also be reflected in the seasonal distribution patterns of production rates.

It is also apparent, and expected, that a greater fraction of the water column production currently occurs at deeper depths in HB and MTB than during the early period of higher production and biomass. This is likely because of increased water clarity associated with reductions in algal biomass.

Seasonal Trends:

The average monthly vertical distribution patterns of phytoplankton production rates and biomass concentrations for the three bay segments during the last decade are shown in Figures 6, 7 and 8. It is evident that a strong seasonal signal is present in all three bay segments for both parameters and that, as expected, high rates and concentrations generally occur during summer and early fall. Similar to the long-term vertical distribution patterns, the seasonal distribution of biomass has relatively small differences with depth while production has large vertical differences, specifically during the warm period. Further, the vertical production pattern indicates that water column light attenuation is also controlling the seasonal production with depth.

The seasonal patterns for biomass are similar between the three bay segments with maximum concentrations generally found from August through October. The seasonal patterns of phytoplankton production in the upper portion of the water column are, on the other hand, quite dissimilar between OTB and the other two bay segments. Both HB and MTB generally have maximum surface rates between July and October, while OTB has a prolonged season of elevated rates from late spring to fall. Further, there appears to be a distinct depression of near surface production rates in OTB in August. Reasons for the prolonged elevated production season in OTB and the August depression are not clear at this time.

Seasonal Variation in Production Rates and Abiotic Parameters:

The seasonal variation in HB water column phytoplankton production rates and several abiotic parameters are shown in Figure 9 as monthly means for the recent 10 year period. Total water column production peaks during a prolonged period in the summer and follows the seasonal variation in water temperature most closely; also, as expected, there is a general agreement between seasonal production and solar radiation (see Day et al. 1989). The seasonal pattern in production does not appear to be strongly associated with the seasonal variations in external DIN loading to HB.

DISCUSSION

Long-Term Trends in Tampa Bay Phytoplankton Production and Biomass:

Tampa Bay phytoplankton production sustains the phytoplankton biomass present in the bay and, therefore, it could be expected that temporal changes noted in production rates would be relatively equivalent to changes in biomass. However, the current biomass concentrations in HB and MTB have decreased almost three-fold when compared to the early period of the record, while current production rates are near half of the early rates (Table 1). There are several explanations for the disproportional changes in phytoplankton production and biomass.

First, a major change in phytoplankton composition occurred in the upper bay segments in the mid 1980s when the abundance of the seasonally occurring planktonic blue-green alga (*Schizothrix* sp.) was greatly reduced (Johansson and Lewis 1992; Dixon et al. 2009). Subsequent to the blue-green losses, the phytoplankton community has most often been dominated by diatoms and small flagellates and biomass has been substantially reduced. The efficiency of the phytoplankton community to produce carbon per unit biomass may have changed with the change in communities. If the current diatom and flagellate community is capable of a higher carbon production per unit biomass than the blue-green dominated community, then a disproportional increase in phytoplankton production relative to biomass would have resulted during the period of study. A comparison of ratios between production rates and biomass concentrations from samples collected near the surface in HB and MTB during the period of record show a general trend of increasing values, in support of this scenario. However, specific information of carbon production per unit biomass for the two major phytoplankton communities is lacking for Tampa Bay.

A second, and more easily substantiated scenario, is related to the documented improving trend of water column light penetration in the upper portions of Tampa Bay (Boler 2002; Johansson 2002; Greening and Janicki 2006). The improving light penetration, which to a great degree has been caused by a reduction in phytoplankton biomass, has deepened the photic zone. The deeper photic zone has allowed for a proportionally greater amount of production to now occur deeper than during the early period (Figures 4 through 8). Phytoplankton biomass, on the-other-hand, has been relatively homogenous with depth and the reduction in biomass has occurred throughout the water column. Therefore, as a consequence of these changes, a proportionally smaller reduction has occurred during the period of record in water column production relative to biomass.

Nutrient Limitation by the Tampa Bay Phytoplankton Community:

The finding of a strong positive association between the long-term HB trends of external DIN loading rates, and phytoplankton production rates and biomass concentrations (Figure 3) was anticipated based on earlier studies of phytoplankton biomass and nitrogen relationships in Tampa Bay (Johansson 1991; Janicki and Wade 1996) and for other estuaries as well.

The strong nitrogen control of the Tampa Bay phytoplankton community is also evident from ongoing nutrient addition experiments that the BSG has conducted since 1993 on the natural community found in the four major bay segments (Figure 1). The bioassay method used is modified from Fisher et al. (1992). Of 152 bioassay tests conducted to date, 149 have shown that nitrogen was the most limiting nutrient to phytoplankton growth (Figure 10). None of the tests have indicated that phosphorous was the most limiting nutrient; only three tests in OTB have shown a lack of response in growth to either nitrogen or phosphorous additions.

One of the three OTB tests which resulted in a no response to nitrogen and phosphorous additions was conducted in late August 2009 during an extensive dinoflagellate (*Pyrodinium bahamense*) bloom in this bay segment. *P. bahamense* dominated the test community; and it is possible that the dinoflagellate was dependant on organic nitrogen for growth and less so by the inorganic nitrogen that was added to the bioassay vessels. It is well known that dinoflagellate species, as well as phytoplankton species from other groups, have the ability to assimilate organic forms of nitrogen (e.g Glibert et al. 2006).

Finally, the finding that nitrogen is the most limiting nutrient to phytoplankton growth in the four major Tampa Bay segments has also been concluded from other bioassay studies. Results from a bay-wide study conducted in 1993 and 1994 by Vargo et al. (1994), using the green alga *Dunaliella tertiolecta* as assay organism, also showed that nitrogen was the most limiting nutrient and that additions of phosphorous did not enhance biomass.

Estimates of Nitrogen Loading Required to Sustain Phytoplankton Production:

The amount of nutrients that are needed to sustain an observed production rate can be estimated by assuming that the phytoplankton assimilate nutrients during the photosynthetic process in proportion to Redfield ratios (e.g. Boynton et al. 1995). Results from the calculations (Table 2) indicate that estimated historic (worst case) external total nitrogen (TN) loading to HB potentially could provide about 50% of the nitrogen needed to sustain the observed production rates during the early period of the record. The current external TN loading to HB can potentially provide about one third of the nitrogen required. The corresponding estimates for MTB and OTB (current only) were much lower, indicating that the external TN loading to these bay segments may supply less than one tenth of the nitrogen required.

Although recognized as uncertain, the estimates generally agree with studies from other productive estuaries (e.g. Boynton et al. 2008; Nixon et al. 2009). They are also in general agreement with water quality model derived estimates for Tampa Bay (Morrison et al. 1999; Wang et al.1999). The model studies concluded that the external TN loads to Tampa Bay could support less than 20% of the observed Tampa Bay phytoplankton production and resulting biomass. The finding that the current external TN load to Tampa Bay only appears to supply a fraction of the observed daily production suggests that internal nitrogen recycling, occurring in both the sediments and the water column, may be a substantial nitrogen source. This conclusion appears supported by the finding that the elevated summer production in HB does not appear to be strongly associated with inputs of external DIN loading, but is better associated with water temperature and solar radiation (Figure 9). Temperature-regulated internal nitrogen cycling (e.g. Kemp and Boynton 1984) may therefore have contributed to the high summer production noted in HB.

Field studies of nitrogen releases from the sediments in HB, which were conducted in the mid 1980s by the BSG, also support the potential importance of internal nitrogen recycling in Tampa Bay (Johansson and Squires 1989). Those studies showed that nitrogen releases from sediments at that time had the potential to supply a substantial fraction (34%) of the observed phytoplankton production nitrogen demand. However, it is not certain that the fraction of nitrogen supplied by the sediments in HB has remained constant since those studies were conducted (see Nixon 2009). It could be expected that the nitrogen fraction supplied by the sediments would decrease during time as a result of the long-term reductions in external nitrogen loading to HB and a continuous depletion of the reactive sediment nitrogen supply (Johansson 1991; Wang et al.1999).

The nitrogen supply estimates reported above suggest that a large fraction of the nitrogen needed to maintain the observed Tampa Bay daily production rates can be supplied by internal loading. Nevertheless, both direct measurements and model estimates have shown that the long-term trends in both phytoplankton biomass and production have been controlled by the external supply of nitrogen (Johansson 1991; Janicki and Wade 1996; Wang et al. 1999). Other potentially important sources of nitrogen to Tampa Bay have also been recognized, including in-bay nitrogen fixation and nitrogen transport from the Gulf of Mexico, however, these sources have received little study to date.

Phytoplankton Production in Tampa Bay and Other Estuaries:

A comprehensive review and comparison of phytoplankton production rates for estuaries world-wide was published by Boynton et al. in 1982. A section of the comparison, addressing river dominated estuaries, has been modified here to include the mean daily rates during the recent decade for the three Tampa Bay segments studied (Figure 11).

It is evident that the current production rates for the three Tampa Bay segments fall within the high range of the listed estuaries. The annual mean rates are 210gCm^{-2} for all listed estuaries excluding Tampa Bay, and 385gCm^{-2} for the three Tampa Bay segments. Further, the rates measured in Tampa Bay are similar to those measured in Mid-Chesapeake Bay and Apalachicola Bay.

The annual range of production varies greatly between estuaries, but the seasons of minimum and maximum rates are generally similar for most of the listed estuaries, including Tampa Bay. Maximum production rates usually occur during summer and minimum rates during winter. The association of maximum production during summer is a pattern common to most well-mixed estuaries. It has been suggested that the high summer phytoplankton production rates are supported by the increased availability of recycled nutrients, from both the sediments and the water column, that occur during the warm season (e.g. Boynton et al. 1982).

Estimated Current Annual Carbon Production of Phytoplankton and Seagrass:

The contribution of carbon production by different plant groups to the Tampa Bay system has been discussed previously (Pomeroy 1960; Johansson et al.1985; Jensen and Gibson 1986; Lewis and Estevez 1988; Johansson 2005). These comparisons have emphasized the importance of the pelagic phytoplankton community to supply organic matter to the bay ecosystem. The Tampa Bay seagrass community (with epiphytes) and other plant communities, including macro-algae and benthic micro-algae, appear to be of secondary importance in these comparisons.

An updated comparison of carbon production by the phytoplankton and seagrass communities for the three bay segments studied is provided in Table 3. Only phytoplankton and seagrass carbon production are considered in the comparison. The contributions by macro- and micro-algae are clearly important in the shallow portions of the bay, however, their contribution to the total Tampa Bay system appears low (Pomeroy 1960; Johansson et al.1985). Further, the comparison of phytoplankton and seagrass is of specific interest because of Tampa Bay ecosystem management goals. These goals emphasize the maintenance of phytoplankton biomass at levels appropriate for restoring seagrass areal coverage to historical levels (Johansson and Greening 2000; Greening and Janicki 2006).

The results from the comparison indicate, similar to the earlier estimates, that phytoplankton carbon production dominates system production of organic matter in the three bay segments studied. Further, based on the relatively steady but slow rate of current seagrass expansion in Tampa Bay (Greening and Janicki 2006; Avery et al. 2010) it can be expected that the pelagic bay habitat will continue to dominate system carbon production in the foreseeable future.

CONCLUSION

Annual Tampa Bay phytoplankton production rates during the most recent decade are about 410gCm^{-2} for HB, 350gCm^{-2} for MTB, and 390gCm^{-2} for OTB. These rates are near half of the rates measured during the 1980-1985 period, though, a comparison of production rates between numerous estuaries world-wide indicate that the current Tampa Bay rates fall in the high range. Reductions in biomass have been greater; current HB and MTB concentrations are near 70% lower than those measured during 1980-1985. Water column averaged chlorophyll-a concentrations during the most recent decade are about 10mgm^{-3} for HB, 5.8mgm^{-3} for MTB, and 6.3mgm^{-3} for OTB. The decreases in production and biomass, and also reductions in phytoplankton abundance, followed a large reduction in external DIN loading to Tampa Bay 30 years ago.

The depth distribution of production in HB and MTB during the period of record has shifted from a large proportion of total water column production occurring near the surface to a more even distribution with depth. The shift is most likely a result of improvements in Tampa Bay light penetration and a deepening of the photic zone. Further, self-shading by the phytoplankton population appears to be important in determining the depth distribution of production.

Total water column production in HB peaks during a prolonged period in the summer and follows the seasonal variation in water temperature most closely. As expected, there is also a general agreement between seasonal production and solar radiation. The seasonal production pattern does not appear to be strongly associated with the pattern in external DIN loading. Temperature-regulated internal nutrient cycling in HB may be an important contributor to the high summer production.

Estimates of the amount of nitrogen needed to sustain the observed daily Tampa Bay production rates indicate that internal nitrogen recycling processes may be an important supply source. However, direct measurements and model estimates have indicated that long-term trends in phytoplankton production and biomass have been controlled by the external supply of nitrogen. Other potentially important sources of nitrogen to Tampa Bay have also been recognized, including in-bay nitrogen fixation and nitrogen transport from the Gulf of Mexico, however, these sources have received little study to date.

The strong dependence on nitrogen by the Tampa Bay phytoplankton community is evident from long-term nutrient addition experiments. Of 152 bioassay tests conducted to date, 149 have shown that nitrogen was the most limiting nutrient to phytoplankton growth. None of the tests have indicated that phosphorous was the most limiting nutrient.

Finally, a comparison of current Tampa Bay phytoplankton and seagrass production indicates that the pelagic phytoplankton community dominates the production of organic matter. Based on the relatively steady but slow rate of current seagrass expansion in Tampa Bay it can be expected that the pelagic bay habitat will continue to dominate system carbon production in the foreseeable future.

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Table 1. Average annual water column (A) and surface (B) phytoplankton production rates and chlorophyll-a concentrations measured in HB, MTB and OTB over two time periods.

A

Water Column Phytoplankton Production ($gCm^{-2}\ yr^{-1}$)

Bay Segment	Period		Reduction %
	1980-1985	1999-2008	
HB	750	410	45
MTB	630	350	44
OTB		390[1]	

Water Column Chlorophyll-a (mgm^{-2})

Bay Segment	Period		Reduction %
	1980-1985	1999-2008	
HB	170	47	72
MTB	110	37	65
OTB		30[1]	

[1] 2000-2008

B

Surface Phytoplankton Production ($gCm^{-3}\ yr^{-1}$)

Bay Segment	Period		Reduction %
	1980-1985	1999-2008	
HB	520	260	50
MTB	220	110	47
OTB		190[1]	

Surface Chlorophyll-a (mgm^{-3})

Bay Segment	Period		Reduction %
	1980-1985	1999-2008	
HB	35	10	72
MTB	15	5.5	64
OTB	13[2]	8.6[1,2]	31

[1] 2000-2008

[2] HCEPC Station 40 (mid depth samples) located close to COT 40 (Figure 1).

Table 2. Estimated amount of total nitrogen (TN) required to sustain phytoplankton production rates in HB, MTB and OTB on an annual basis for the periods listed. Also shown is the fraction of phytoplankton production rates that potentially could be sustained by estimated TN loading supplied from external sources.

Bay Segment	Phytoplankton Production ($gCm^{-2}yr^{-1}$)	TN Load Required to Sustain Production ($mtTNyr^{-1}$)	External TN Load ($mtTNyr^{-1}$)	Percent of Production that can be Sustained by External TN Load
HB Worst Case[1]	750	10700	5010	47
HB Current[2]	410	5900	1780	30
MTB Worst Case[1]	630	24700	1480	6
MTB Current[2]	350	16000	640	4
OTB Current[3]	390	9300	560	6

[1] Phytoplankton production 1980-85; external TN loading 1976 (Zarbock et al. 1994).
[2] Phytoplanton production 1999-08; external TN loading 2003-07 (TBNMC 2009).
[3] Phytoplanton production 2000-08; external TN loading 2003-07 (TBNMC 2009).

Table 3. Estimated current annual phytoplankton and seagrass carbon production rates in HB, MTB and OTB.

Bay Segment	Phytoplankton[1]	Seagrass+Epiphytes	Relative Production by Phytoplankton (%)
	mtCyr^{-1}	mtCyr^{-1}	
HB	33000	54[2]	99.8
MTB	83200	6700[3]	92
OTB	58800	5900[3]	90

[1] Areas deeper than 2m.

[2] Based on 2006-2008 seagrass coverage (BSG estimate); shoal grass, annual production rate $90\mathrm{gCm}^{-2}$ (adapted from Neely 2000).

[3] Based on 2008 seagrass coverage (Kaufman pers. comm.): mixed species, estimated annual production rate $250\mathrm{gCm}^{-2}$.

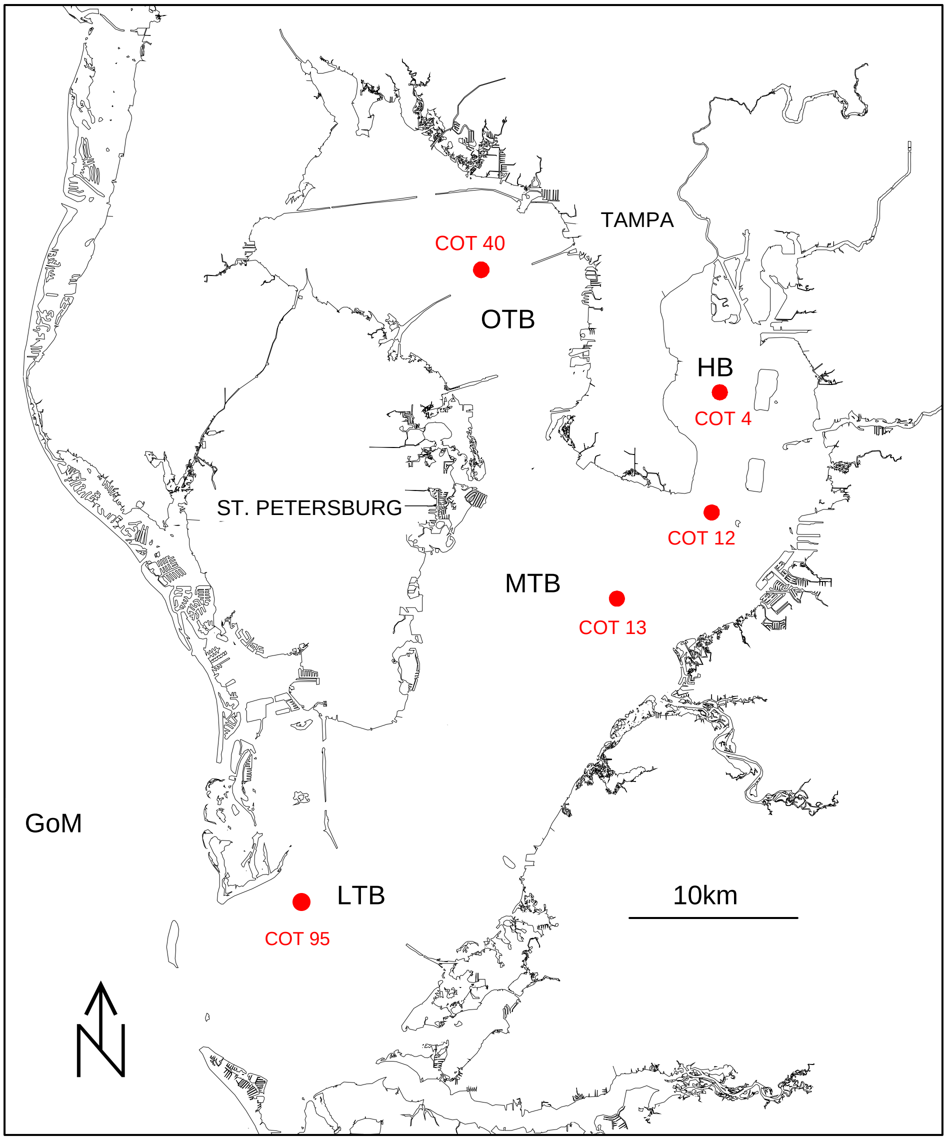

Figure 1. Phytoplankton monitoring locations in Tampa Bay maintained by the City of Tampa Bay Study Group. Phytoplankton production is measured at COT 4 (depth 3.8m), 12 (depth 5.4m), 13 (depth 6.4m) and 40 (depth 4.8m). Phytoplankton bioassay experiments are conducted on water collected at COT 4, 13, 40 and 95 (depth 8.6m).

Figure 2. Long-term trends in water column phytoplankton production rates (A) and chlorophyll-a concentrations (B) in HB, MTB and OTB.

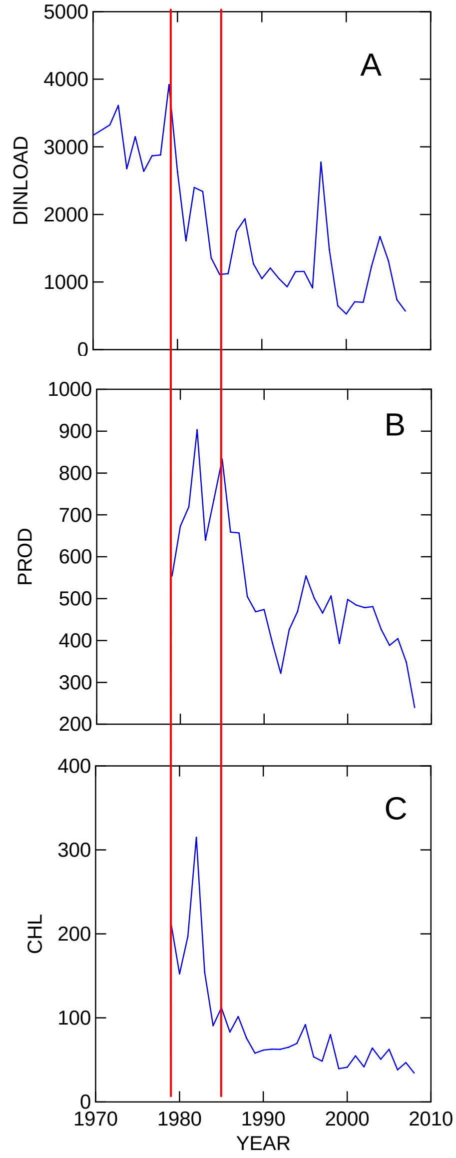

Figure 3. Long-term trends in (A) dissolved inorganic nitrogen loading (DIN) from external sources to HB (kgNday^{-1}), (B) HB phytoplankton production rates (gCm^{-2}yr^{-1}) and (C) HB chlorophyll-a concentrations (mgm^{-2}). The red lines denotes the period of major reductions in DIN loading.

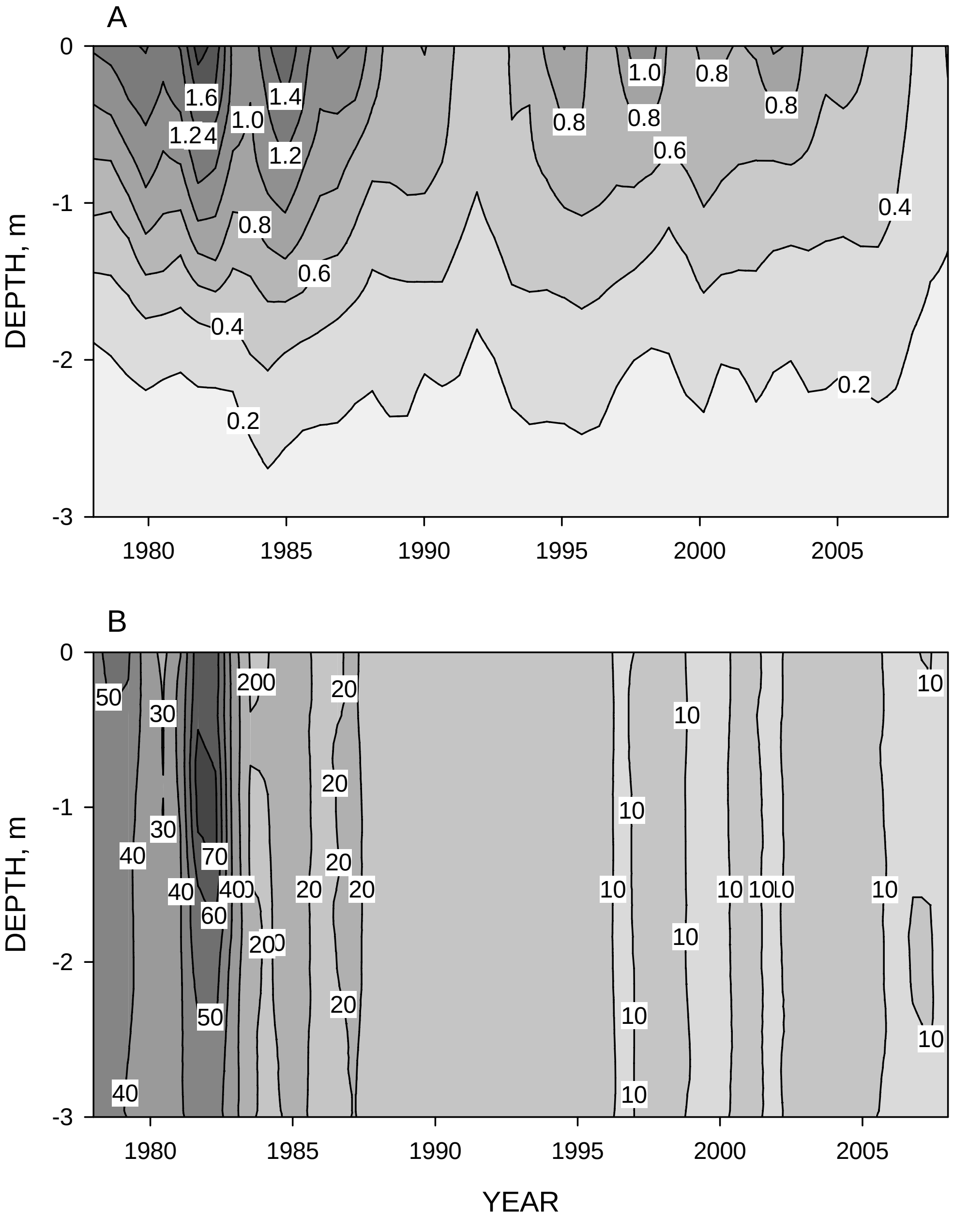

Figure 4. Long-term vertical distribution in (A) phytoplankton production rates ($gCm^{-3}day^{-1}$) and (B) chlorophyll-a concentrations (mgm^{-3}) in HB.

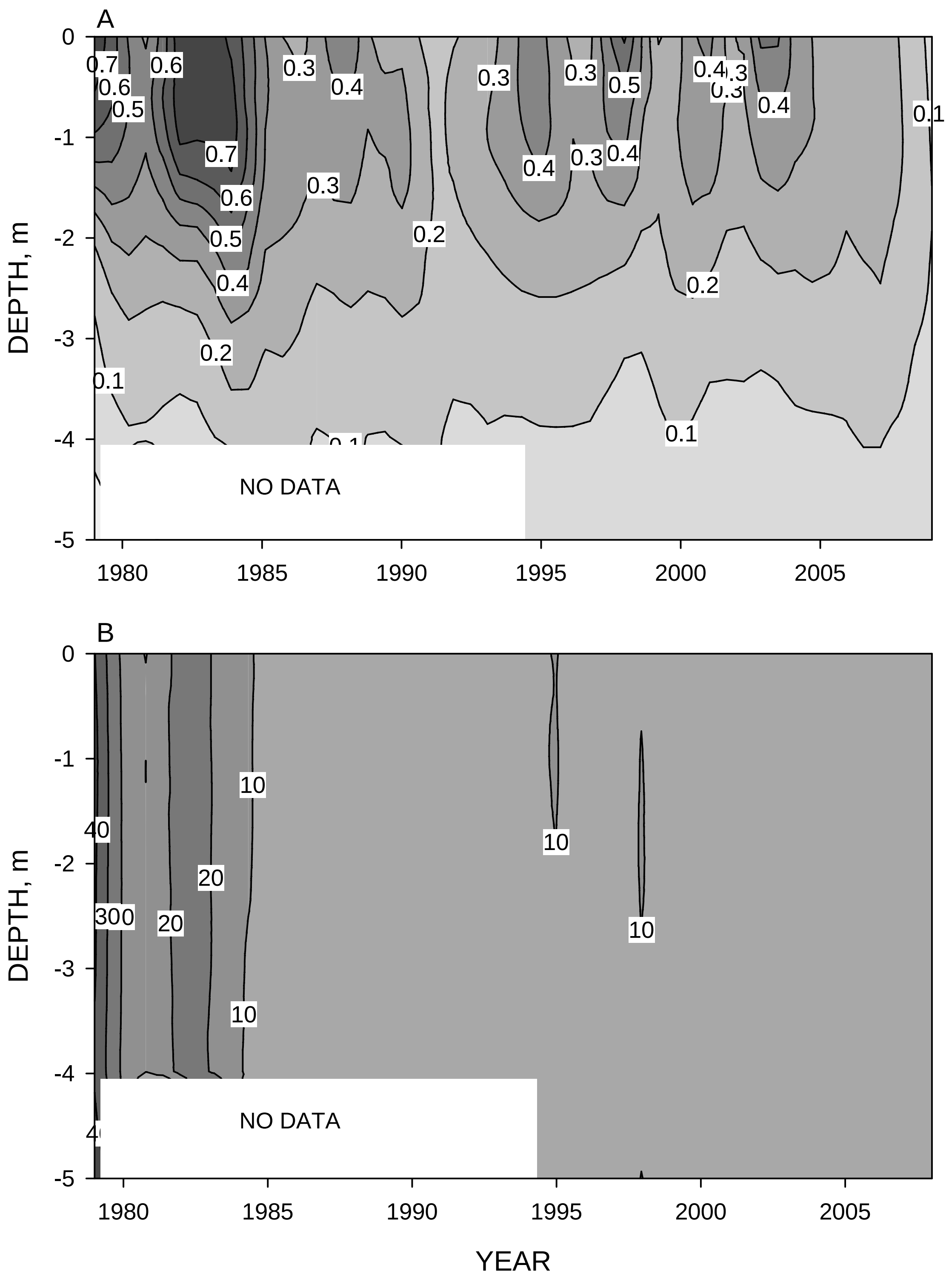

Figure 5. Long-term vertical distribution in (A) phytoplankton production rates (gCm^{-3}day^{-1}) and (B) chlorophyll-a concentrations (mgm^{-3}) in MTB.

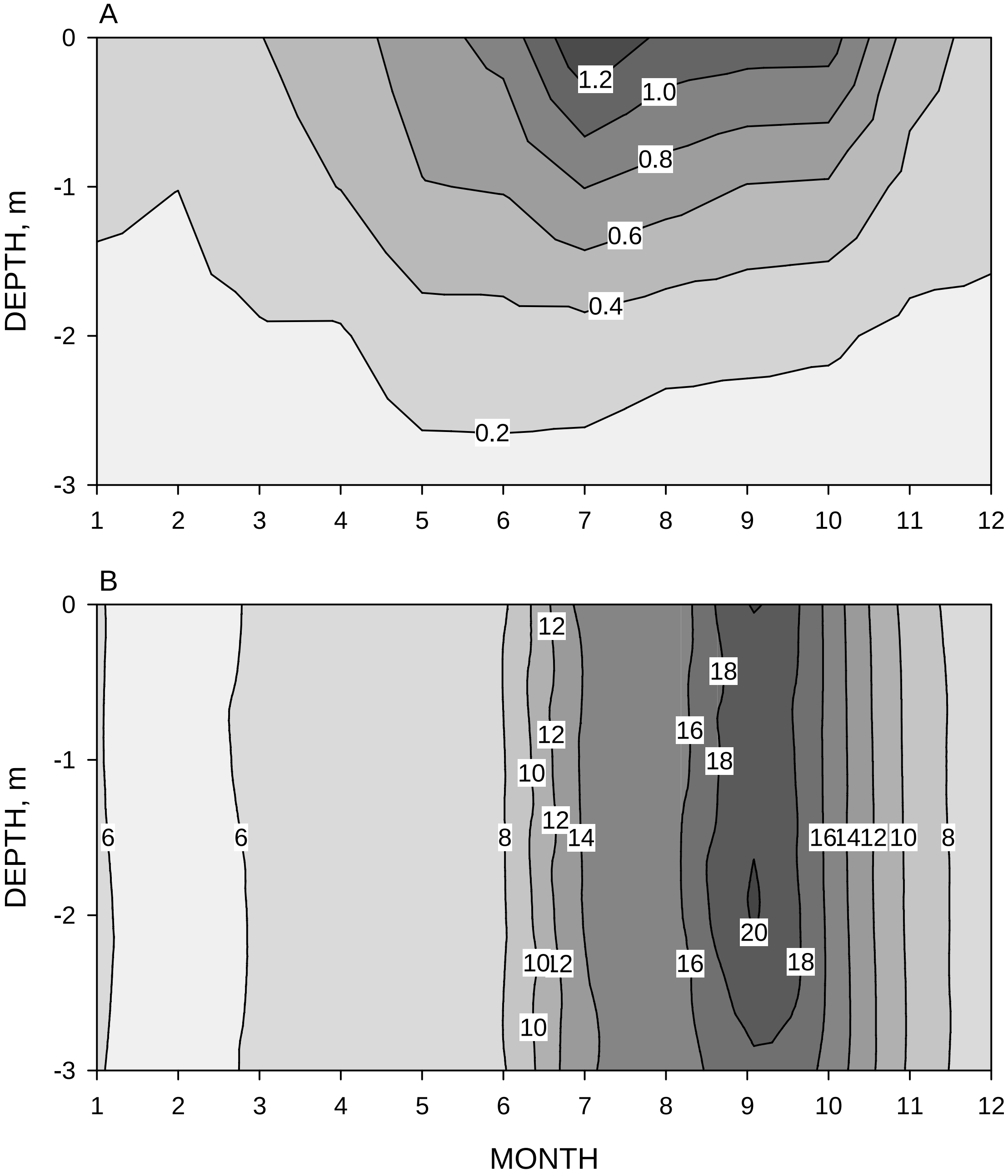

Figure 6. Seasonal vertical distribution for the period 1999-2008 in (A) phytoplankton production rates (gCm^{-3}day^{-1}) and (B) chlorophyll-a concentrations (mgm^{-3}) in HB.

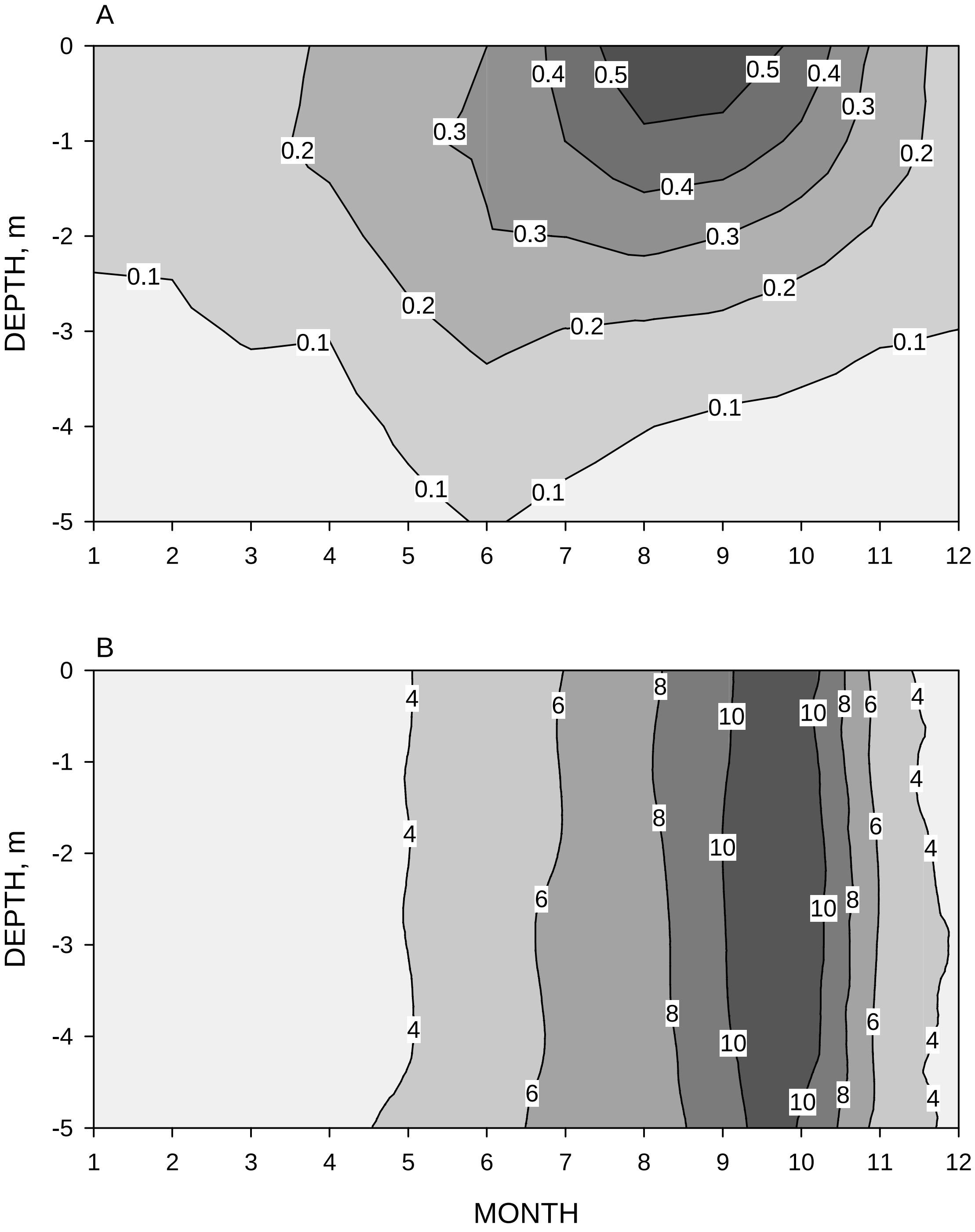

Figure 7. Seasonal vertical distribution for the period 1999-2008 in (A) phytoplankton production rates ($gCm^{-3}day^{-1}$) and (B) chlorophyll-a concentrations (mgm^{-3}) in MTB.

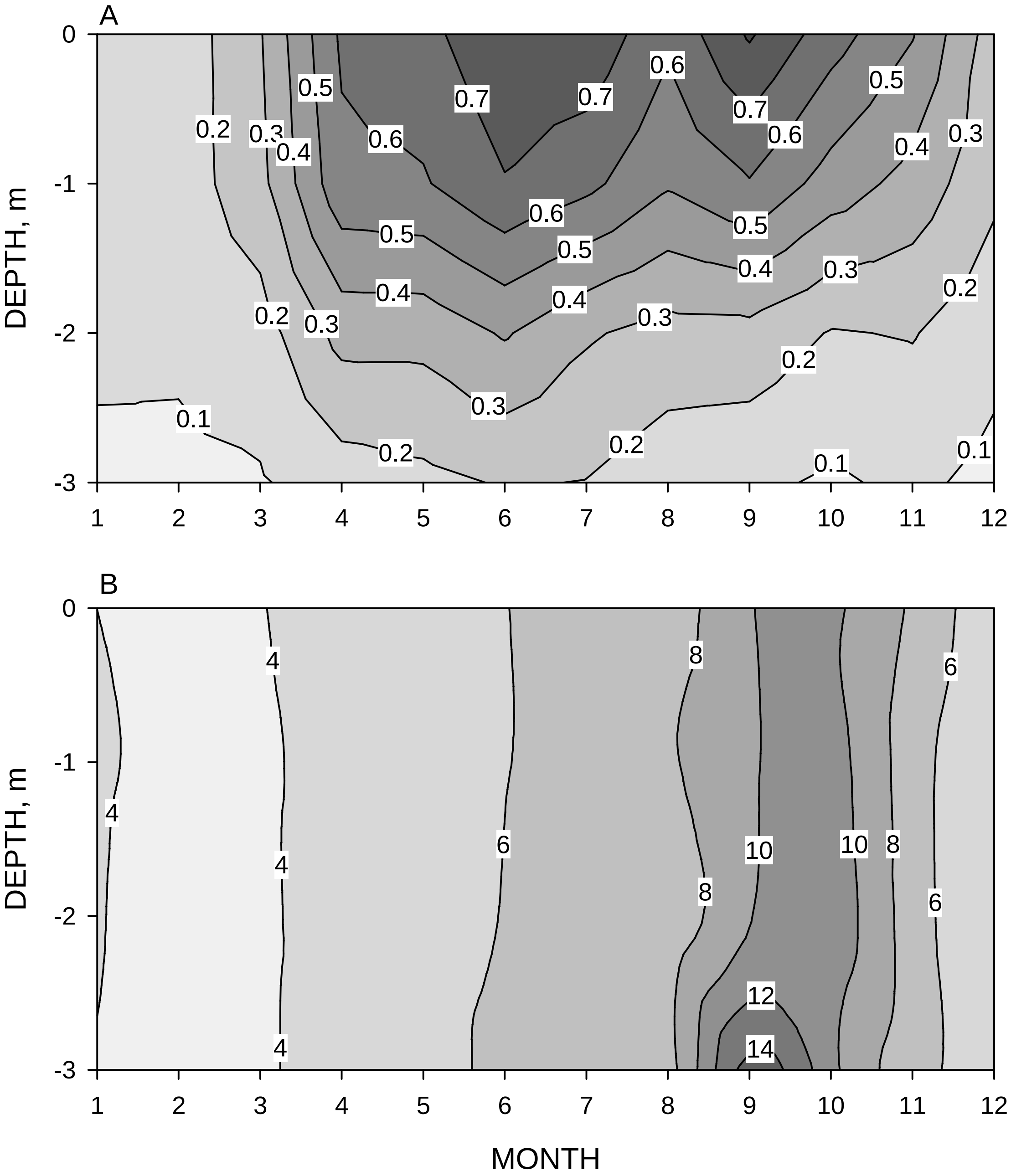

Figure 8. Seasonal vertical distribution for the period 2000-2008 in (A) phytoplankton production rates (gCm^{-3}day^{-1}) and (B) chlorophyll-a concentrations (mgm^{-3}) in OTB.

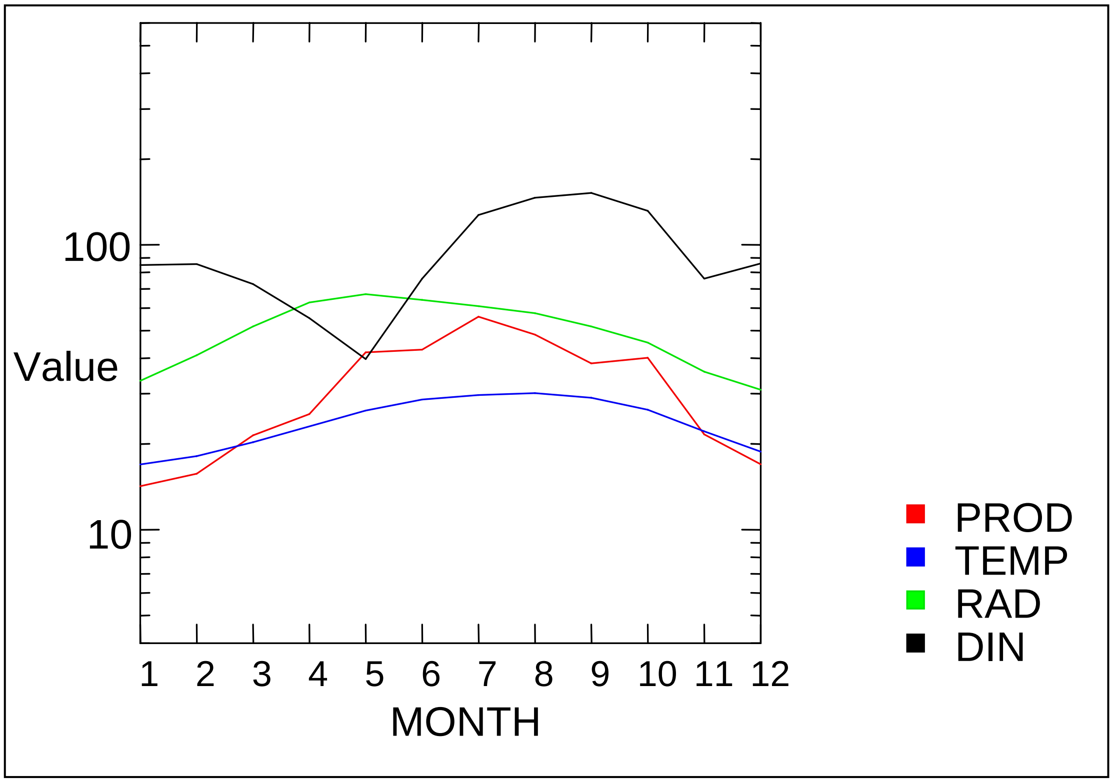

Figure 9. Seasonal averaged variations during the recent decade in HB in phytoplankton production, water temperature, solar radiation at Tampa and dissolved inorganic nitrogen loading (DIN) from external sources to HB. Values plotted are relative for illustration purposes.

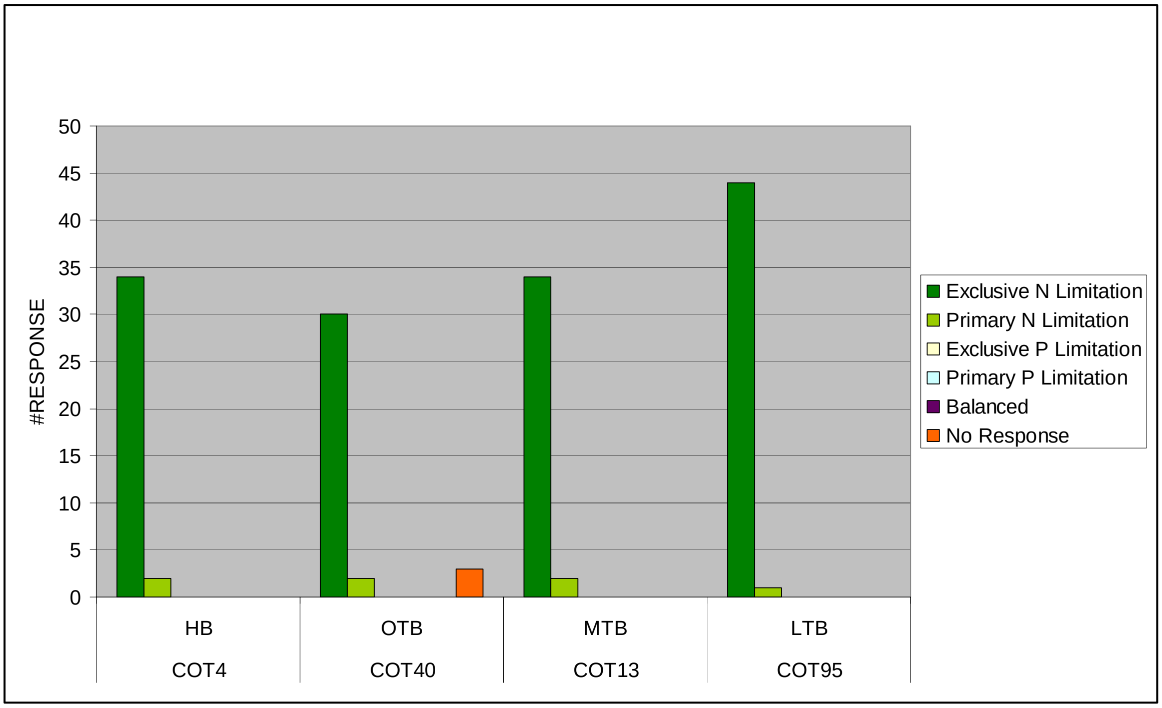

Figure 10. Results from natural phytoplankton nutrient enrichment bioassays in the four major subsections of Tampa Bay for the period 1993 – 2009 (see Figure 1 for station locations).

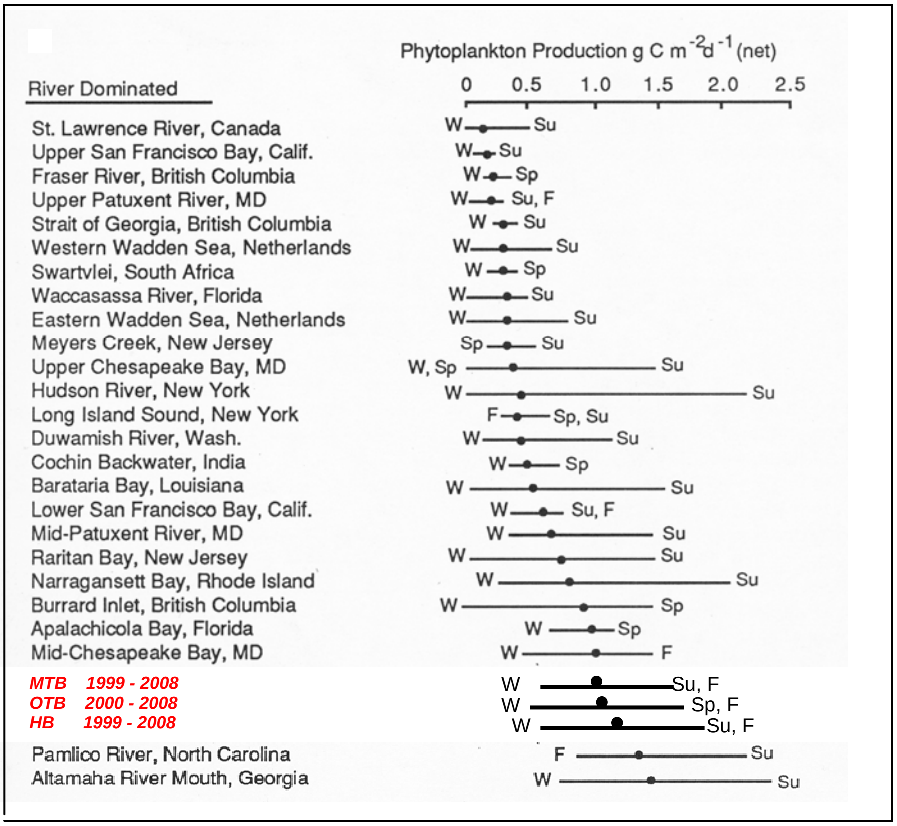

Figure 11. Average daily phytoplankton production rates (black dot) in HB, MTB, OTB and 25 other river dominated estuarine systems. The horizontal bars indicate the annual range. The seasons when maximum and minimum rates occur are also indicated (W. winter; Sp. spring; Su. summer; F. fall). Figure modified from Boynton et al. (1982).