Estuaries and Coasts (2011) 34:745–757
DOI 10.1007/s12237-010-9312-3

Non-linear Responses of a Coastal Aquatic Ecosystem to Large Decreases in Nutrient and Organic Loadings

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Received: 10 March 2010 / Revised: 3 April 2010 / Accepted: 29 May 2010 / Published online: 16 June 2010

Abstract Between 1991 and 2000, Boston Harbor, a bay–estuary in the northeast USA, experienced a decrease in loadings of total nitrogen (TN), total phosphorus (TP), and particulate organic carbon (PC) of between ~80% and ~90%. The average concentrations of TN and TP in the harbor water column were decreased in linear proportion to the loadings. The changes to the chlorophyll-*a* (chl-*a*), PC, and bottom water DO concentrations were curvilinear relative to the loadings, with larger changes at low than high loadings. For TN and TP, the starts of the decreases in concentrations coincided with the starts of the decreases in loadings. For the three variables that showed curvilinear responses, the starts of the changes lagged by 2 to 3 years the starts of the decreases in TN loadings. Total suspended solid concentrations and water clarity in the harbor were unchanged. The study shows that for systems such as Boston Harbor, decreases in nutrient loadings will have quite different effects depending on the base loadings to the system.

Keywords Nutrient loadings · Wastewater · Eutrophication · Nitrogen · Phosphorus · Boston Harbor

Introduction

A number of coastal aquatic ecosystems in the USA and elsewhere have experienced decreases in the loadings of the materials (nutrients and organic matter) that cause eutrophication (Smith et al. 1981; Mallin et al. 2005; Carstensen et al. 2006; Jaworski et al. 2007; Testa et al. 2008). The responses of coastal ecosystems subjected to decreases in nutrient loadings can follow different trajectories, and the responses can be non-linear relative to the loadings (Duarte et al. 2009). Little is known of the trajectories or of the non-linear responses.

Between 1991 and 2000, Boston Harbor, a highly enriched, well-flushed bay–estuary, experienced decreases in loadings of total nitrogen (TN), total phosphorus (TP), and particulate organic carbon (PC) of between 80% and 90% (Taylor 2010). A large wastewater project, the Boston Harbor Project (BHP), was responsible for the decreases. The BHP upgraded the treatment of the wastewater discharges to the harbor and then diverted the discharges offshore. Before the BHP, the TN loadings to the harbor were among the highest reported for bays or estuaries in the USA (Kelly 1997; Dettmann 2001).

The harbor showed symptoms of eutrophication typical of a highly enriched, but well-flushed bay–estuary (Taylor 2006). Concentrations of TN, TP, and chlorophyll-*a* (chl-*a*) in its water column were elevated (Oviatt et al. 2007). Dissolved oxygen (DO) concentrations were lowered in the bottom waters of the deeper more estuarine portions of the harbor (Fig. 1; Taylor 2006). The benthic invertebrate communities of the harbor were typical of a moderately degraded bay–estuary (Gallagher and Keay 1998; Maciolek et al. 2009; Diaz et al. 2008), and its once extensive seagrass beds had almost completely disappeared.

This paper documents the changes in eutrophication-related conditions in the water column of the harbor relative to the changes in loadings brought about by the BHP. The paper focuses on the harbor water column. Taylor (2010) has provided details of the changes in

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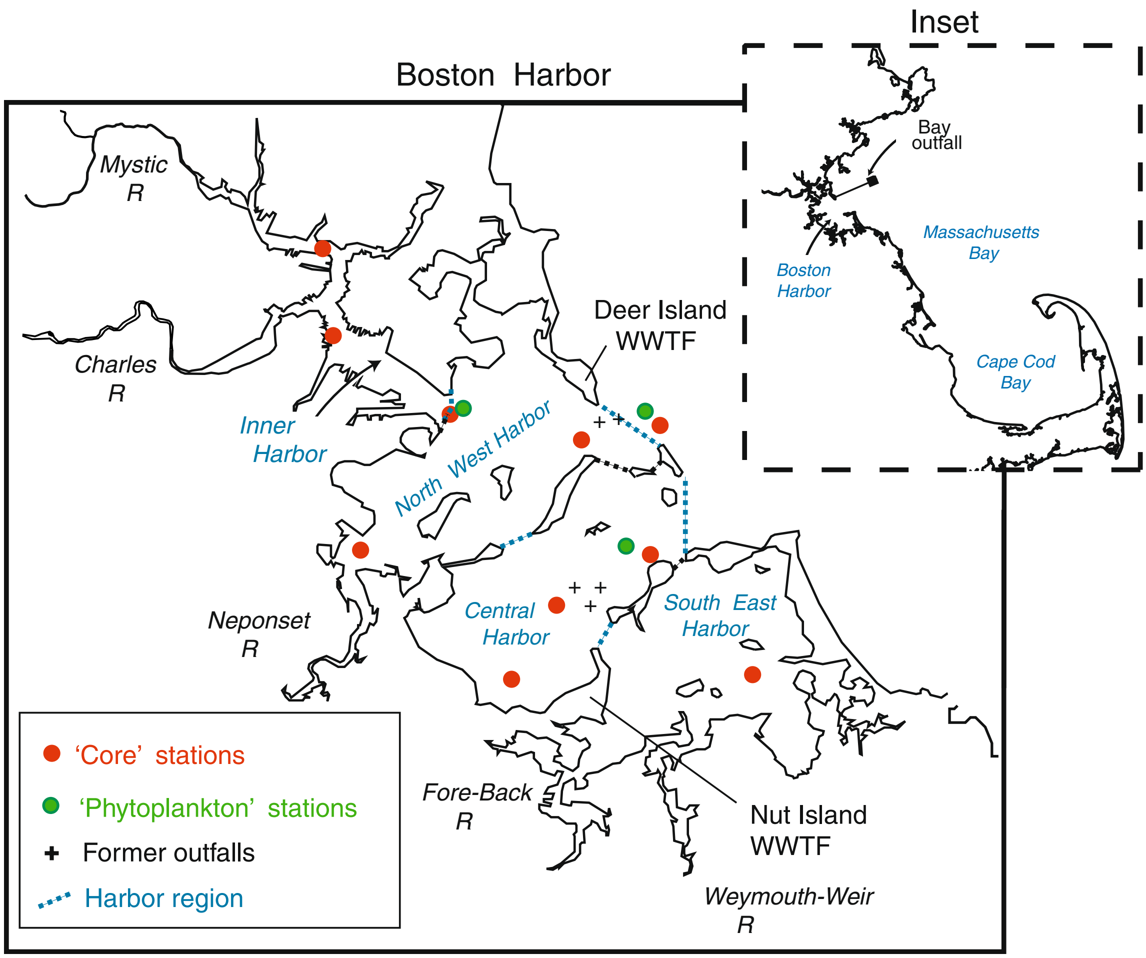

Fig. 1 Boston Harbor showing the locations of the former WWTF outfalls, the four regions of the harbor, and the two sets of monitoring stations. The *insert* shows the locations of the harbor and bay outfall in Massachusetts Bay

loadings to the harbor. Others have described the changes to the benthic invertebrate communities (Maciolek et al. 2009; Diaz et al. 2008) and to the benthic metabolism and sediment–water nutrient fluxes of the harbor (Tucker et al. 2009; Giblin et al. 1997).

Background on Boston Harbor and the BHP

Boston Harbor is an urbanized bay–estuary partially surrounded by the City of Boston (Fig. 1). At mid-tide, the harbor has a surface area of 108 km^2, a water depth of 4.9 m (Signell and Buttman 1992), and a volume of 643×10^6 m^3 (Stolzenbach and Adams 1998). It has an average tidal range of 2.7 m, an average hydraulic residence time of 5–7 days (Stolzenbach and Adams 1998), and its water column is vertically well mixed. Salinity in the harbor averages 30.4 psu. Water temperatures average 4°C in winter and 16°C in summer. The harbor is partitioned into four regions: the Inner Harbor, North West Harbor, Central Harbor, and South East Harbor.

The BHP involved five major construction milestones, four of them completed during this study (Fig. 2). At the start of the study (top panel), two wastewater water treatment facilities (WWTF) discharged primary (1°)-treated effluent to the harbor. The Deer Island (DI) WWTF, the larger of the facilities, discharged effluent to the outer North West Harbor. The Nut Island (NI) facility discharged effluent to the mid-Central Harbor. The first milestone completed during the study, the construction of a new 1°-treatment facility at the DI WWTF, was completed in July 1995.

The new 1°-treatment facility at the DI WWTF removed ~60% of solids, ~21% of total organic carbon (TC), ~10% of TP, and <5% of TN from the wastewater passing through the facility (Butler et al 1997). Primary treatment is a physical or settling treatment process. Secondary (2°) treatment, an aerobic biological treatment process, was phased in at the DI WWTF from July 1997 through March 1998 (milestone 2). With the upgrade to 2° treatment, the percent removal of total suspended solids (TSS), TC, TP, and TN at the DI WWTF was increased to ~85%, ~80%, ~40%, and ~15%, respectively (Butler et al. 1997).

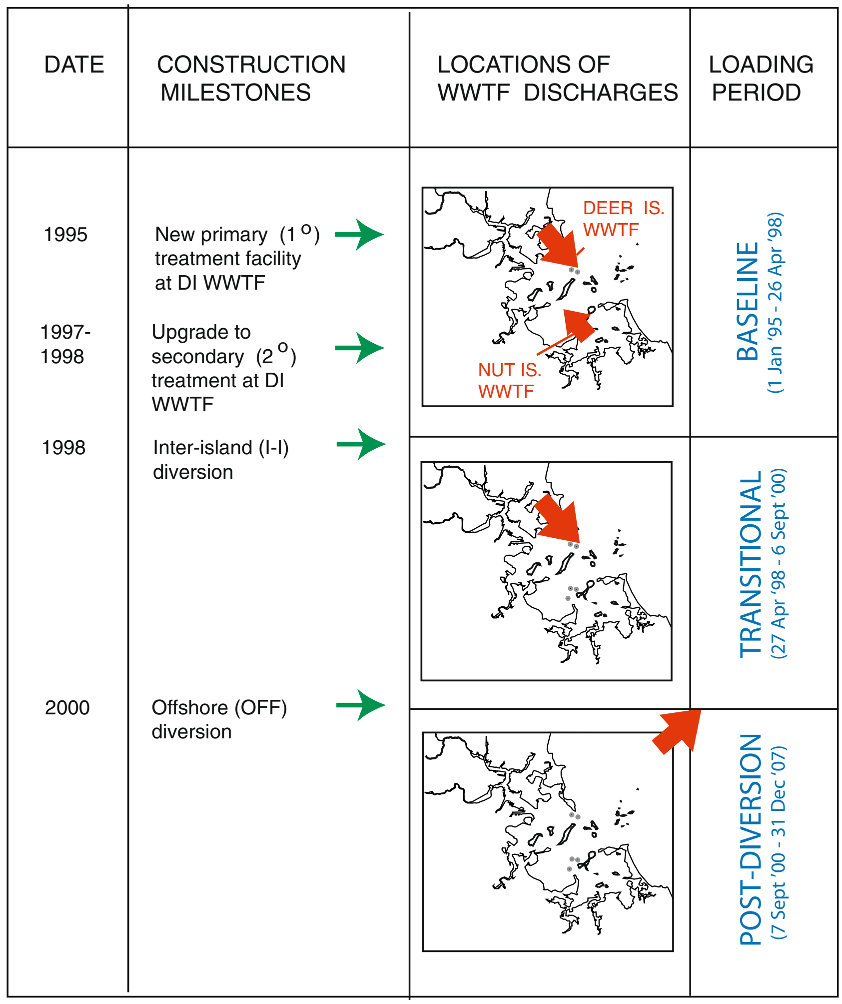

Fig. 2 Schematic of the four construction milestones of the BHP completed during the study, the changes to the locations of the WWTF discharges to the harbor, and the "baseline", "transitional", and "post-diversion" loading periods

On 26 April 1998, the effluent formerly treated at the NI WWTF was diverted through the DI WWTF (milestone 3). With this "inter-island" diversion, the wastewater from both facilities were subjected to 2° treatment at the DI WWTF and discharged to the mouth of the North West Harbor. On 6 September 2000, the now combined and 2°-treated effluent from the DI WWTF was diverted 15-km offshore for diffusion into the bottom waters of Massachusetts Bay (milestone 4). This "offshore" diversion ended over a century of direct WWTF discharges to the harbor. Less than three percent of the wastewater discharged from the bay outfall re-entered the harbor (Taylor 2010).

Based on the changes to the locations of the WWTF discharges, the study could be partitioned into three loading periods: the "baseline", "transitional", and "post-diversion" periods. These were equivalent to the loading periods II, III, and IV in Diaz et al. (2008) and Taylor (2010). During the "baseline" period, two WWTFs discharged to the harbor, one to the mouth of the North West Harbor and the other to the mid-Central Harbor. During the "transitional" period, the WWTF's discharges were focused at the mouth of the North West Harbor. During the "post-diversion" period, the harbor no longer received direct WWTF discharges.

Materials and Methods

We sampled the harbor water column at two sets of stations: ten "core" stations and three "phytoplankton" stations (Fig. 1). The ten core stations were sampled weekly from May through October and every 2 weeks from November through April from 1995 through 2003. Thereafter, the stations were sampled every 2 weeks year-round. The three phytoplankton stations were sampled six times per year, once per month during February, March, April, June, August, and October, through the study. Details of the methods employed at the core stations have been provided in Taylor (2006). Oviatt et al. (2007) and Hunt et al (2010) have provided details of the methods employed at the phytoplankton stations.

The following sets of measurements were conducted at both sets of stations: concentrations of N, P, chl-*a*, pheophytin, TSS and PC, vertical attenuation coefficients (k), secchi depth, concentrations of DO, DO % saturation, and water temperature and salinity. At the three phytoplankton stations, samples were also collected for quantitative phytoplankton identification. Rates of ^{14}C potential primary production were measured at the one phytoplankton station at the mouth of the North West Harbor.

For all parameters excluding phytoplankton counts and primary production, harbor-wide averages were computed as volume-weighted averages, using data from all 13 stations, thus: $\text{Volume} - \text{weighted average} = (a \times 0.119) + (b \times 0.418) + (c \times 0.342) + (d \times 0.12)$ where a, b, c, and d were the average concentration for all stations in the Inner Harbor, North West Harbor, Central Harbor, and South East Harbor, respectively. The constants, 0.119, 0.418, 0.342 and 0.12, were the relative volumes of the respective regions. Harbor-wide average phytoplankton counts were computed as arithmetic means of the values from the three phytoplankton stations.

The loadings to the harbor were monitored from three sets of sources: the DI and NI WWTF's, the four largest tributary rivers (the Charles, Mystic, Neponset, and Weymouth-Weir Rivers), and the non-point sources that discharged directly to the harbor (Fig. 1). The methods employed to measure the loadings have been described in detail in Taylor (2010). The loadings from the WWTFs and rivers were measured directly. The loadings from combined sewer overflows (CSOs) were computed using the EPA SWMM model 4.4. Loadings from the non-CSO non-point sources were derived from historic estimates of flows from the sources (from Alber and Chan 1994).

Results

Changes to the Loadings to the Harbor

With each improvement to the wastewater discharges, the annual average loadings of TN, TP, TSS, and PC to the harbor were decreased (Fig. 3). The average TN and TP loadings remained elevated from 1995 through 1997 (for TP) or 1998 (for TN) and then declined through 2000, the year the wastewater discharges to the harbor were diverted offshore. The start of the decrease in the TP loadings coincided with the upgrade to 2° treatment at the DI WWTF in 1997. The start of the decrease in the TN loadings coincided with the diversion of the NI WWTF discharges through the DI WWTF in 1998.

The average TSS and PC loadings showed a gradual decrease from 1995 to 2000 and thereafter remained low. For both materials, the starts of the decreases coincided with the completion of the new 1°-treatment facility at the DI WWTF in 1995. Loadings then increased again in 1996

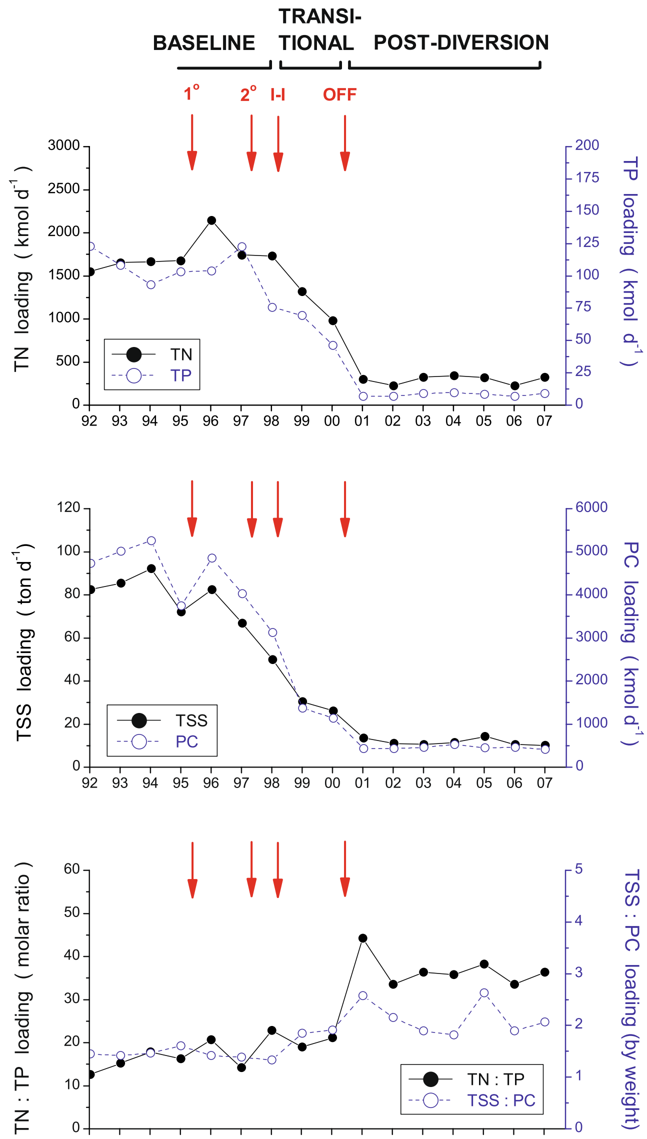

Fig. 3 Annual average loadings of TN, TP, TSS, PC, TN/TP, and TSS/PC to Boston Harbor, 1992 to 2007. *Vertical arrows* show the dates of completion of the four milestones. *1°* new primary treatment facility at the DI WWTF, *2°* upgrade to secondary treatment at the DI WWTF, *I-I* inter-island diversion, *OFF* offshore diversion

(a wet year), before declining through the 2°-treatment upgrade at the DI facility and the two diversions of the WWTF discharges. Unlike for the loadings of TN, TP, TSS, and PC, the annual average TN/TP (molar) and TSS/PC (by weight) ratios of the loadings were increased.

Changes to the Harbor Water Column

The decreases in the nutrient loadings caused the average concentrations of TN and TP in the harbor water column to decrease (Fig. 4). The average TN concentrations remained

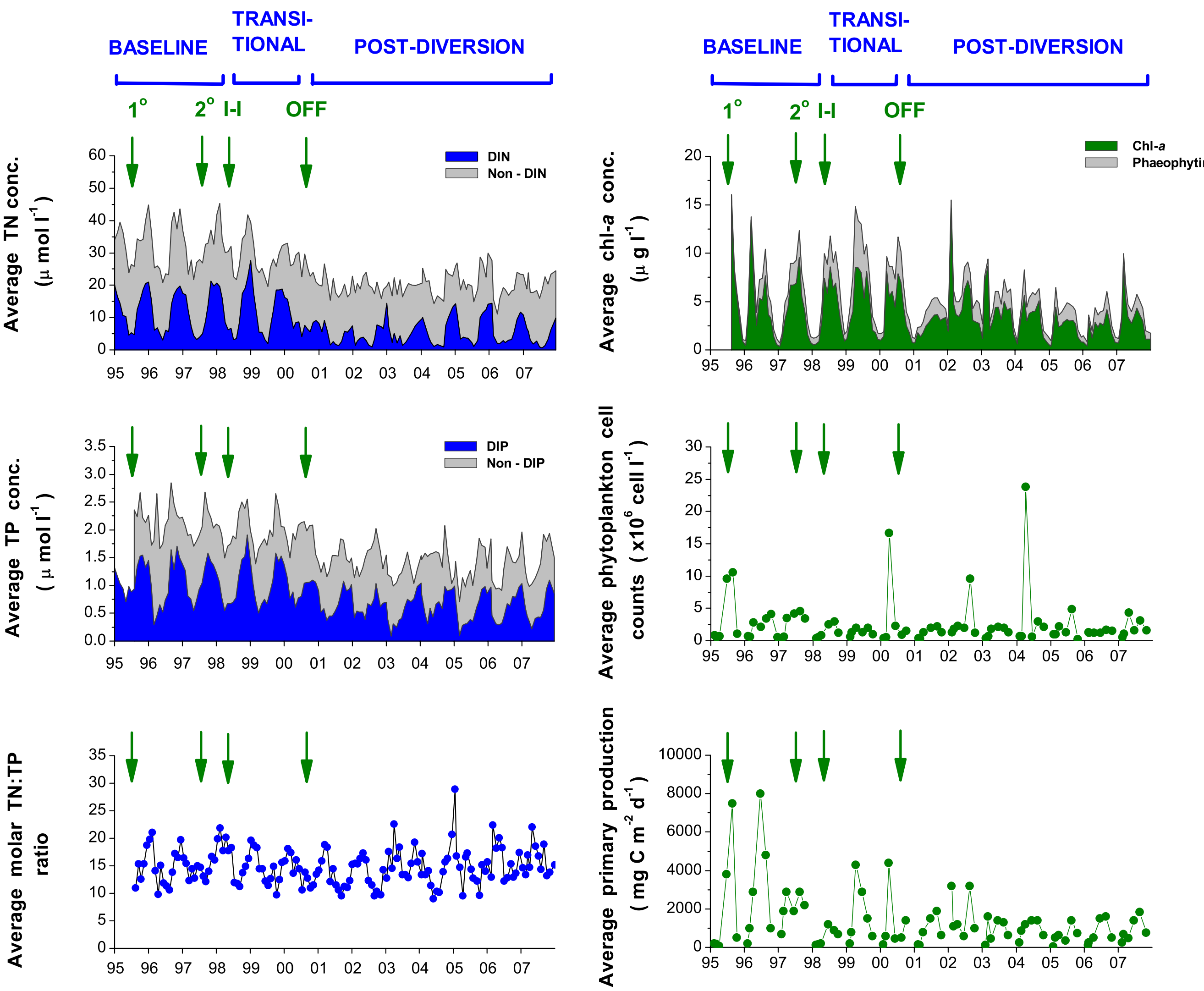

Fig. 4 Time-series plots of the monthly average concentrations of N and P, molar ratios of N/P, concentrations of chl-*a*, phytoplankton cell counts, and rates of potential primary production in the harbor, 1995–2007

elevated from 1995 to 1998 and then declined between 1998 and 2001 to ~25 µmol l^{-1}. The average concentrations of TP declined between 1997 and 2001 to ~1.8 µmol l^{-1}. For both nutrients, the starts of the decreases in the concentrations coincided with the starts of the decreases in the loadings. The annual average molar TN/TP (and DIN/DIP) ratios in the harbor were unchanged (Fig. 4).

Between the baseline and post-diversion periods, the average TN and TP concentrations declined by 11.4 µmol l^{-1} (or 35%) and 0.66 µmol l^{-1} (or 32%), respectively (Table 1). The dissolved inorganic fractions (DIN and DIP) were largely responsible for the decreases. The decrease in DIN contributed 6.8 µmol l^{-1} (or 60%) of the decrease in TN; particulate N (PN) contributed an additional 18%. DIP contributed 0.42 µmol l^{-1} (or 64%) of the TP decrease; particulate P (PP) contributed 21%. NH_4 contributed 75% of the decrease in DIN; NO_{3+2} contributed the remaining 25%.

The average concentrations of chl-*a* in the harbor were decreased (Fig. 4). The chl-*a* concentrations remained elevated from 1995 to 2000 and then declined between 2000 and 2001 to between ~3 and ~7 µg l^{-1}. The decline in the concentrations lagged by 2 to 3 years the starts of the decreases in the TN and TP loadings. Between the baseline and the post-diversion periods, the average chl-*a* concentrations declined by 1.3 µg l^{-1} (or 29%). The decreases were larger during the summers, and 2.7 µg l^{-1} (or 41%).

The total phytoplankton cell counts in the harbor were unchanged (Fig. 4). The total cell counts showed four peaks: two during the years the harbor received the wastewater discharges and two after the discharges were ended. During the post-diversion period, the average diatom and micro-

Table 1 Comparison of average values in the harbor water column during the “baseline” and the “post-diversion” periods

Parameter	Average±1×SD Baseline	Average±1×SD Post-diversion	Difference (% of baseline)
TN	32.3±6.8	20.9±3.6	−11.4 (−35%)*
DIN	12.3±6.2	5.5±3.8	−6.8 (−56%)*
DON	14.0±4.3	11.5±2.0	−2.5 (−18%)
NH_4	6.3±3.0	1.2±0.9	−5.1 (−81%)*
NO_{3+2}	6.0±4.1	4.3±3.4	−1.7 (−28%)*
PN	6.0±2.4	3.9±1.4	−2.1 (−35%)*
TP	2.05±0.32	1.39±0.38	−0.66 (−32%)*
DIP	1.06±0.37	0.64±0.27	−0.42 (−40%)*
DOP	0.58±0.16	0.42±0.12	−0.16 (−28%)
PP	0.41±0.16	0.33±0.12	−0.08 (−20%)*
TN/TP (molar)	15.8±3.2	15.0±3.1	−0.8 (−5%)
DIN/DIP (molar)	11.4±5.2	8.1±5.1	−3.3 (−29%)
Chl-*a*	4.5±3.0	3.2±2.1	−1.3 (−29%)*
Chl-*a* (summer)[a]	6.6±1.5	3.9±1.2	−2.7 (−41%)*
Total phytoplankton	2.55±3.36	2.26±3.70	−0.29 (−11%)
Microflagellates	0.91±1.10	0.72±0.36	−0.20 (−21%)
Diatoms	0.78±1.10	0.54±1.28	−0.24 (−31%)*
Phaeocystis sp.	0.26±1.35	0.39±1.8	+0.13 (+50%)*
Primary production	1962±2322	973±719	−990 (−50%)*
PC	43.5±16.0	29.6±10.2	−13.9 (−32%)*
TSS	3.0±0.8	3.6±1.1	+0.6 (+20%)
Reciprocal *k*	0.51±0.12	0.52±0.11	+0.01 (2%)
DO concentration	9.3±1.5	8.8±1.3	−0.5 (−5%)
Mid-summer DO[b]	7.1±0.8	7.4±0.6	+0.3 (+4%)*
Minimum DO	6.2±0.09	6.9±0.26	+0.7 (+12%)*

Values are harbor-wide averages. Units are micromoles per liter for N, P, and PC, micrograms per liter for chl-*a*, $\times 10^6$ cell l^{-1} for phytoplankton cell counts, milligrams of C per square meter per day for potential primary production, milligrams per liter for TSS and DO, and per meter for *k*. Unless indicated, the values are averages computed from year-round data

*$p \leq 0.05$, Mann–Whitney *U* test

[a] Summer = June, July, August, and September

[b] Mid-summer = August + September

flagellate counts were 0.24×10^6 cell l^{-1} (or 31%) and 0.20×10^6 cell l^{-1} (or 21%) lower than baseline (Table 1). The average counts of the prymnesiophyte, *Phaeocystis* sp., were 0.13×10^6 cell l^{-1} (or 50%) greater than baseline. Regional *Phaeocystis* blooms in Massachusetts Bay (Hunt et al. 2010) were likely responsible for the increase in *Phaeocystis* in the harbor.

As for total cell counts, the average rates of ^{14}C potential primary production measured at the mouth of the harbor showed no change (Fig. 4). The average rates were 990 mg C m^{-2} d^{-1} (or 50%) lower during the post-diversion period than baseline, but the difference was driven by unusually elevated rates during 1995 and 1996. The difference between the two periods was not significant if the 1992 through 1994 data were included in the analysis (Oviatt et al. 2007). The average rates of chl-*a*-specific primary production were also unchanged (data not shown).

The harbor showed no change in average concentrations of TSS but did show a decrease in average concentrations of PC (Fig. 5). The decrease in the average PC concentrations occurred from 1998 to 2000, lagging by 2 to 3 years the start of the decrease in PC loadings in 1995. Between the baseline and post-diversion periods, the average PC concentrations were decreased by 13.9 μmol l^{-1} or 32%. As for TSS, but not necessarily because of the TSS, the average attenuation coefficients (*k*) in the harbor were unchanged (plots not shown).

The harbor showed a small increase in its bottom water DO concentrations (Fig. 5). The increase occurred between 2000 and 2001 and lagged by 5 years the start of the

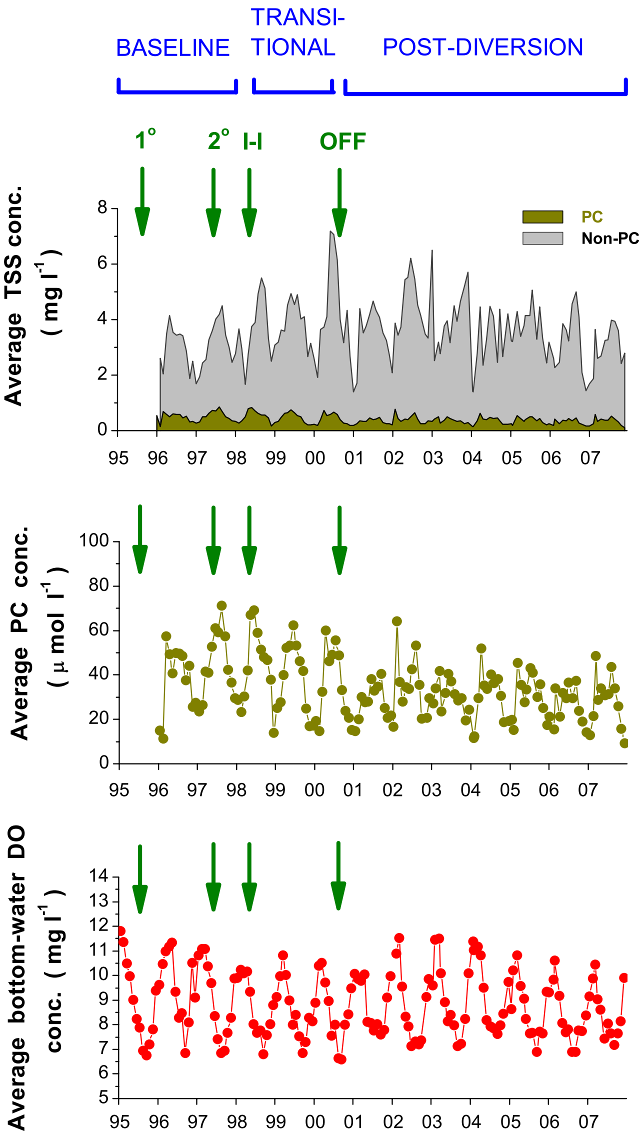

Fig. 5 Monthly average TSS, PC, and bottom water DO concentrations in Boston Harbor, 1995–2007

decrease in PC loadings, and 2 to 3 years the start of the decrease in TN loadings. During mid-summers, the average DO concentrations in the bottom waters were increased by 0.3 mg l^{-1} (or 4%) between the two periods. The minimum DO concentrations observed each summer were increased by 0.7 mg l^{-1} (or 12%). The increases in bottom water DO were observed during all seven of the post-diversion years.

Changes Relative to Loadings

The annual average concentrations of TN and TP in the harbor declined in linear proportion to the annual average loadings of TN and TP, respectively (Fig. 6). The linear relationships applied over the full range of loadings. The slopes of the relationships were the same for the two nutrients (and 0.008) and similar to the 5–7-day average hydraulic residence time of the harbor (as reported by Stolzenbach and Adams 1998). No correlations existed between the annual average TN/TP concentrations and the annual average TN/TP loadings to the harbor.

Relative to the loadings, the changes to the chl-*a*, PC, and bottom water DO concentrations were curvilinear (Fig. 6). At the high loadings at the start of the study, the decreases in the loadings had little impact on the average chl-*a*, PC, and DO concentrations. As the loadings were decreased, so the effects of the decreases in loadings on the concentrations of the three variables increased. The annual average TSS concentrations and reciprocal *k* values showed no correlation with the annual average TN, TP, TSS, or PC loadings (plots not shown).

Changes and Seasons

The effects of the decreases in loadings were different during different times of the year. The monthly average concentrations of TN were decreased year-round, with the decreases being the largest, and between 12.5 and 16.4 μmol l^{-1}, from September through February (or March; Fig. 7). The average TP concentrations were also decreased year-round, but their decreases were the largest from September through December. The average molar ratios of the TN/TP concentrations were increased from September through February.

The decreases in the average chl-*a* concentrations were confined to 6 months of the year, from April through August (Fig. 7). The average PC concentrations were decreased during nine of the 12 months, from April through December. Average bottom water DO concentrations were increased during August and September. During none of the 12 months was the monthly average TSS concentrations or the monthly average reciprocal *k* values during the post-diversion period different from baseline.

Spatial Patterns of Changes

The areas of the harbor that showed significant changes were different for the different variables (Fig. 8). The average TN, TP, and PC concentrations were decreased at all ten core stations (map not shown for PC). Note, only data from the core stations were included in this analysis of the spatial patterns of changes. Year-round average chl-*a* concentrations were decreased at two stations, both in the west Central Harbor. During summers, the decreases in the chl-*a* concentrations were significant at all ten stations.

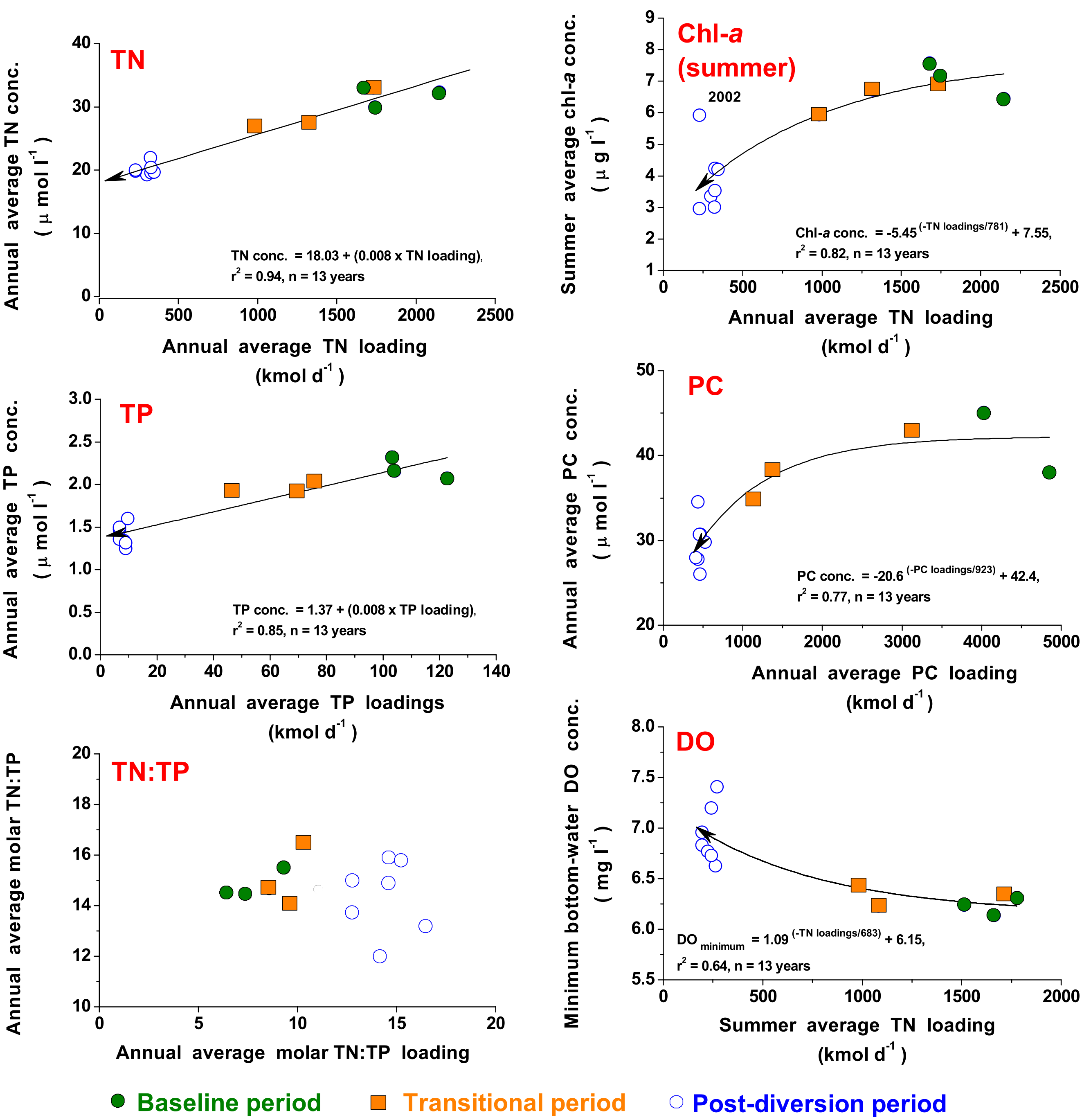

Fig. 6 Relationships between the average TN, TP, TN/TP, chl-*a*, PC, and bottom water DO concentrations in the harbor and the average loadings to the harbor, 1995–2007

Changes in average reciprocal *k* and secchi depth values were observed at two widely separate stations: an increase in clarity at one station in the upper Inner Harbor and a decrease in clarity at one station in the outer Central Harbor. Year-round average bottom water DO concentrations were unchanged at all ten stations. Mid-summer average bottom water DO concentrations were increased at six stations: four in the Inner Harbor and the North West Harbor, and two in the Central Harbor.

Discussion

Comparison of the Changes in Boston Harbor and Other Systems

When compared to seven other coastal ecosystems that have experienced decreases in nutrient loadings, the harbor had the highest base loadings of both TN and TP and also

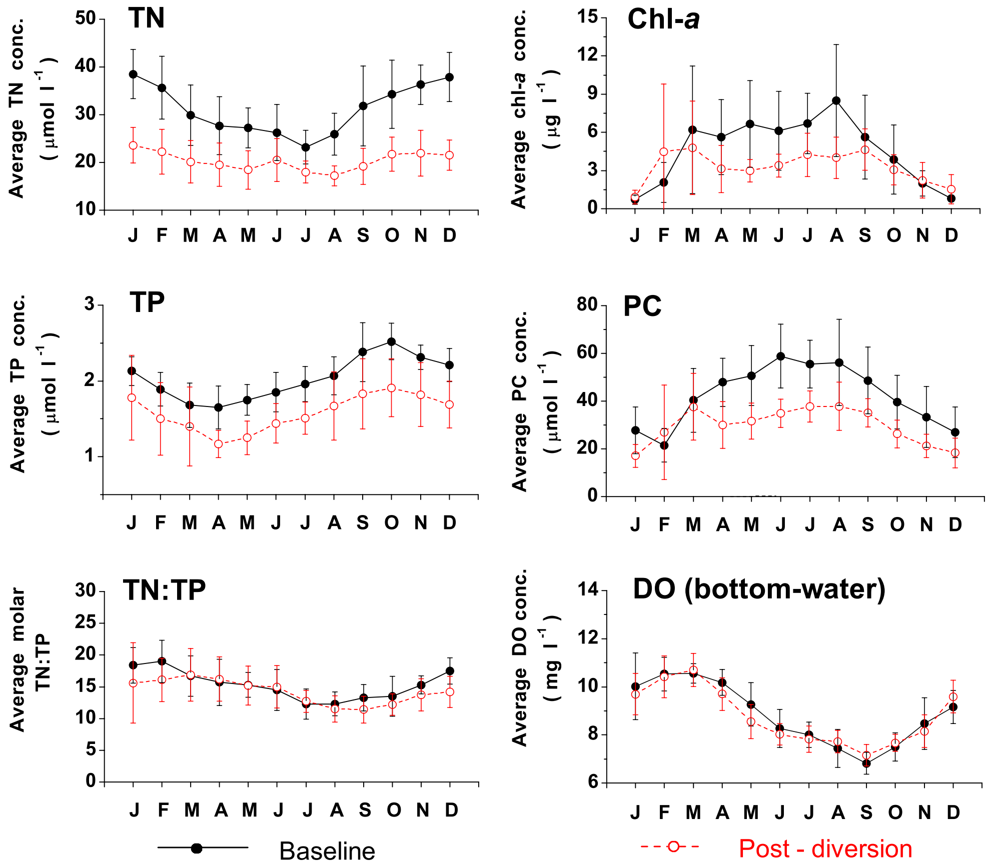

Fig. 7 Changes in monthly average conditions in the harbor by month of the year. *Error bars*=±1×SD

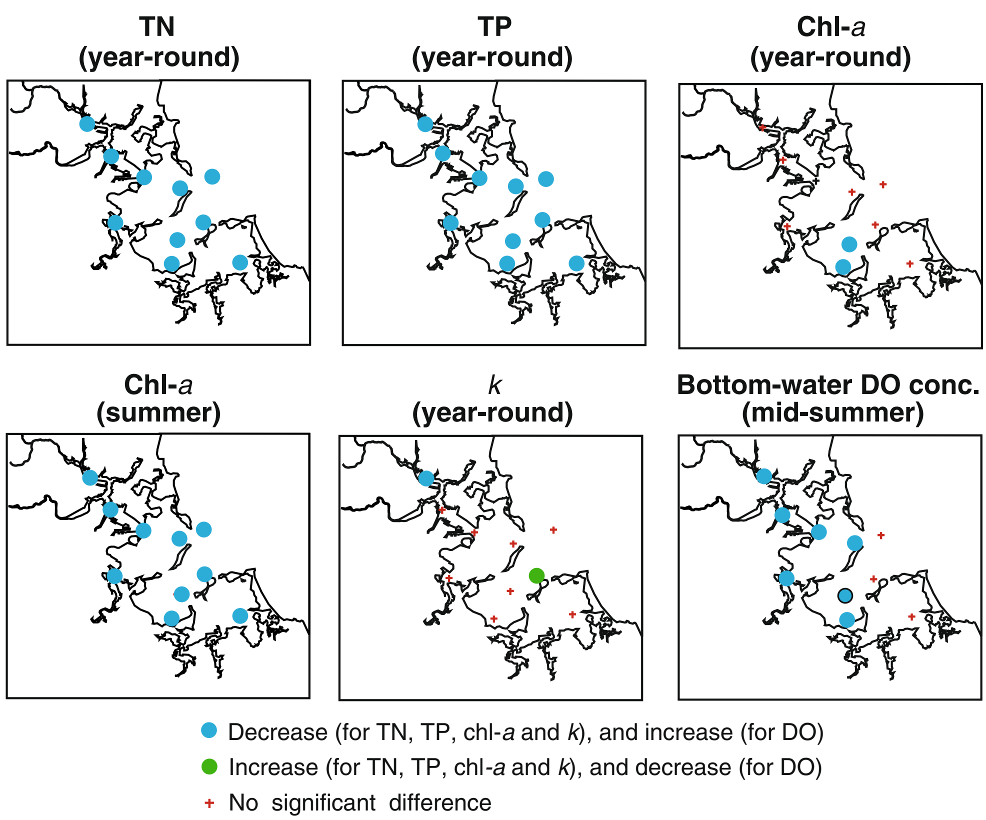

Fig. 8 Spatial patterns of changes in the harbor. *Circles* denote the stations at which the average values during the post-diversion and baseline periods were significantly different ($p \leq 0.05$, Mann–Whitney *U* test)

Table 2 Comparisons of the changes in loadings and responses of Boston Harbor and seven other coastal ecosystems that have experienced decreases in nutrient loadings

System	Type of system (hydraulic residence time)	Base loadings ($mg\ m^{-2}\ year^{-1}$)		Change in loadings ($mg\ m^{-2}\ year^{-1}$; % of base)		System responses		Reference
		TN	TP	TN	TP			
Boston Harbor (between 1995–1998 and 2001–2007)	Bay–estuary (5–7 days)	80,300	15,699	−66,065 (−82%)	−14,600 (−93%)	TN (DIN)	−35% (−56%)	Present study
						TP (DIP)	−32% (−40%)	
						chl-*a*	−29%	
						Reciprocal *k*	No change	
						Mid-summer DO	+4%	
Danish Straits (between 1989–1990 and 2000–2001)	Bay–estuary (nr)	2,433	152	−73 (−3%)	−99 (−65%)	TN (DIN)	−10% (−30%)	Carstensen et al. (2006)
						TP (DIP)	−37% (−45%)	
						chl-*a*	nr	
						Reciprocal *k*	nr	
						Minimum DO	nr	
Hillsborough Bay (mid-1970s to 1999)[a]	Estuary (nr)	42,340	nr	−17,600 (−66%)	nr	DIN	−29%	Johansson (2000)
						DIP	nr	
						chl-*a*	−80%	
						secchi	+44%	
						average DO	nr	
Kaneohe Bay (between 1976–1977 and 1978–1979)	Bay (~8 days)	6,716	1,533	−3,796 (−57%)	−1,200 (−79%)	TN (DIN)	−0% (−35%)	Smith et al. (1981)
						TP (DIP)	−48% (−66%)	
						chl-*a*	−35%	
						reciprocal *k*	−19%	
						DO	nr	
New River Estuary (between 1995–1998 and 1998–2002)[b]	Lagoon (~60 days)	2,645	93	−2,645 (?)	−93 (?)	DIN	−33%	Mallin et al. (2005)
						DIP	−21%	
						chl-*a*	−69%	
						Reciprocal *k*	−22%	
						Average DO	+3%	
Patuxent River Estuary (between 1985–1991 and 1992–2003)[c]	Estuary (30–65 days)	11,321	1,467	−6,124 (−54%)	−803 (−55%)	DIN	−35%	Testa et al. (2008)
						DIP	−33%	
						chl-*a*	+8%	
						secchi	+62%	
						DO	nr	
Potomac River Estuary (between 1965–1969 and 2000–2004)[d]	Estuary (150 days)	25,743	5,393	+11,594 (+45%)	−2,697 (−52%)	TN (DIN)	−3% (+18%)	Jaworski et al. (2007)
						TP	−43%	
						chl-*a*	−50%	
						Secchi	No change	
						Average DO	+27%	

Tampa Bay (between mid-1970s and 2000s)[e]	Estuary (150–180 days)	6,725	nr	−4,640 (−69%)	nr	DIN	−63%	Greening and Janicki (2006), Johansson (2000)
						DIP	nr	
						chl-*a*	−46%	
						Secchi	+40%	
						Average DO	nr	

nr not reported

[a] N loadings to Hillsborough Bay include only DIN loadings; the base DIN concentrations were computed for the period 1983–1987

[b] Loadings data include only WWTF loadings

[c] Water-column values for the Patuxent Estuary are annual averages for the upper, middle, and lower regions of the estuary, weighted by the volumes of the surface modeled boxes of the three regions, the hydraulic residence time values are from J. Testa personal communication

[d] Water-column values for the Potomac Estuary are summer values averaged for the five station along the length of the estuary

[e] Water-column data for Tampa Bay are volume-weighted by region, the estimates of hydraulic residence time for the system are from Burwell et al. (2000), Boston Harbor loading data from Taylor (2010)

showed the largest decreases in the loadings of both nutrients, whether the decreases were expressed as absolute or percent decreases (Table 2). The average hydraulic residence time of the harbor (5–7 days) was similar to that of Kaneohe Bay (8 days) but was much shorter than the residence times of 30–180 days for the other systems. Note, only differences in loadings and system responses ≥10% in Table 2 have been considered significant.

Conley et al. (2009) and Paerl (2009) have recently argued that the loadings of both N and P need to be decreased to reverse the eutrophication of coastal estuaries. The decreases in the loadings of N and P to Boston Harbor were as for Kaneohe Bay, the New River Estuary, and the Patuxent River Estuary. They were, however, unlike for the Danish Straits, which experienced a decrease in loadings of TP alone (Carstensen et al. 2006), and the Potomac River Estuary, where the decreases in the TP loadings were accompanied by an increase in TN loadings (Jaworski et al. 2007).

The decreases in the N and P concentrations in the harbor water column were as for Kaneohe Bay, the New River Estuary, and the Patuxent River Estuary. The decreases were, however, different from the Potomac River Estuary, where the concentrations of TP were decreased, but the concentrations of N (as DIN) were increased (Jaworski et al. 2007). The 56% decrease in DIN in the harbor was similar to the 65% decrease in Tampa Bay but was greater than the 29% to 35% decreases observed for most of the other systems.

The decrease in chl-*a* in the harbor was as for five of the other systems, Hillsborough Bay, Kaneohe Bay, the New River Estuary, the Potomac River Estuary, and Tampa Bay. Unlike for DIN, the 29% decrease in chl-*a* in the harbor was smaller than the 35% to 80% decreases in the other systems. The absence of an increase in clarity in the harbor was as for the Potomac River Estuary, but unlike for Hillsborough Bay, Kaneohe Bay, the New River Estuary, the Patuxent River Estuary, and Tampa Bay. In these other systems, water clarity was increased by between 19% and 62%.

The increase in bottom water DO in the harbor was as for the Potomac River Estuary and the New River Estuary. The 4% increase in mid-summer DO in the harbor was similar to the 3% increase in year-round, bottom water DO in the New River Estuary, but was smaller than the 27% increase in summer average, bottom water DO in the Potomac River Estuary. The smaller changes in chl-*a* concentrations, water clarity, and bottom water DO in the harbor than in the other systems were likely a function of the greater rate of flushing of the harbor.

Processes Determining Ecosystem Responses to Decreases in Loadings

The decreases in the average concentrations of TN and TP in the harbor water column occurred in linear proportion to the loadings. In absolute terms, the sizes of the decreases in concentrations were the same across the full range of loadings and were apparently determined by the rate of flushing of the water column. The slopes of the loading-response relationships and hence the sizes of the decreases in concentrations relative to the loadings, will likely be greater in less-flushed systems than in the harbor.

For chl-*a*, PC, and bottom water DO concentrations, the effects of the decreases in loadings were quite different depending on the loadings. At high loadings like those observed at the start of the study, the TN and PC loadings were apparently in excess of system demand, and the decreases in the loadings had little impact on the chl-*a*, PC, and bottom water DO concentrations. As the loadings were decreased, the sensitivities of the three variables to the changes in loadings increased and in a curvilinear manner.

The excess loadings at high loadings were likely responsible for the hysteresis or time-lag that existed between the starts of the decreases in loading and the changes to the chl-*a*, PC, and bottom water DO concentrations. It also meant that the average TN and PC loadings to the harbor needed to be decreased by 40% or more, before measurable changes in the concentrations of the three variables were observed. Had the decreases in the nutrient and organic loadings been small, the N and P concentrations would have declined slightly, but the chl-*a*, PC, and DO concentrations would have been unchanged.

Curvilinear loading–response relationships are likely to be observed in other coastal ecosystems where system demand for the added nutrients and organic matter might be dampened, by rapid flushing (as was the case for Boston Harbor) or poor water clarity. The natures of the curvilinear responses will likely differ between systems, depending upon, among other factors, the rate of flushing of the systems. In systems flushed less well than the harbor, but where production is not limited by water clarity, the chl-*a*, PC, and DO responses will likely be observed at higher loadings and hence with less of a delay than in the harbor.

Changes to other Components of the Harbor Ecosystem

Over the course of the study, the numbers of benthic invertebrate species associated with the soft sediments of the harbor were increased (Maciolek et al. 2009). The numbers of species showed no change between the baseline (35 species) and transitional periods (34 species) but increased to 42 species between the transitional and post-diversion periods. The species richness of the benthic communities, measured as Fisher's log-series alpha, increased from 4.2 during baseline to 5.5 during the transitional period and then to 7.6 post-diversion (Maciolek et al.).

Diaz et al. (2008) documented a decrease in the occurrence of tube mats of the amphipod *Ampelisca* spp., on the harbor sediments. In 1995, *Ampelisca* tube mats were present in ~65% of the 61 sediment stations sampled in the harbor. By 2000, this had been reduced to ~35% and by 2006 to <5% of the sediment samples. Diaz et al. attributed the decreases to the decreases in organic loadings and primary production in the harbor. The harbor also showed an increase in the average depth of the redox potential discontinuity layer in its sediments (Diaz et al.).

The percent TC content of the sediments, averaged for four sites in the harbor, decreased from 3.5% of dry weight during baseline to 2.1% of dry weight post-diversion (Tucker et al. 2009). Between the same two periods, the average sediment oxygen demand and the net fluxes of DIN from the sediments to the water column were decreased by 31.8 mmol m^{-2} day^{-1} (or 43%) and 2.4 mmol m^{-2} day^{-1} (or 44%), respectively (Tucker et al.). The net fluxes of DIP were unchanged.

Acknowledgments Grateful thanks are extended to the two editors and the reviewers for providing comments on the article. Thanks are due to Kelly Coughlin for her assistance in almost all aspects of the work and to Laura Ducott and Ellie Baptiste-Carpenter for managing the water column monitoring at the two sets of stations. Thanks are also due to the many people who collected the water and effluent samples, analyzed the samples, and managed the data bases.

Disclaimer This paper represents the opinions and conclusions of the authors and not necessarily those of the Massachusetts Water Resources Authority.

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