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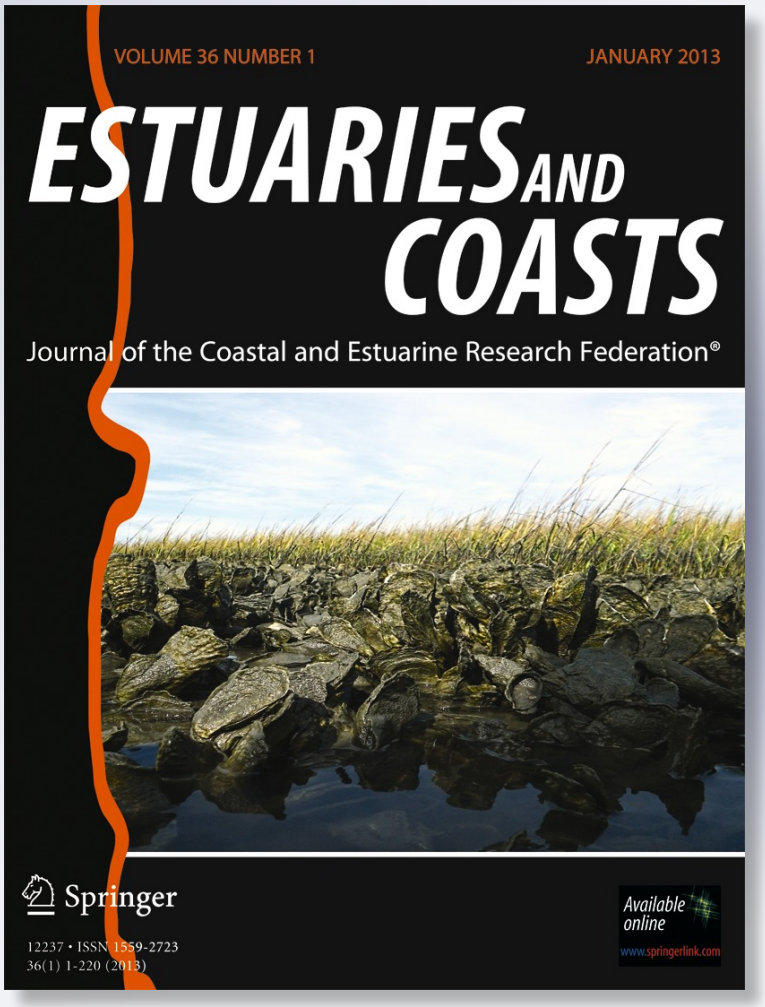

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Abstract Fish mortality and hypoxic events occur in many coastal and inland systems and may result from natural or anthropogenically mediated processes. The effects of consequent changes in water biogeochemistry have been investigated for communities of benthic invertebrates and pelagic metazoans. The responses of micro-plankton assemblages, however, have remained largely unstudied. The northern basin of King Harbor, a small embayment within Santa Monica Bay, CA, USA, suffered a massive fish kill in March 2011 as a consequence of acute hypoxia. Dissolved oxygen concentrations < 0.1 $ml l^{-1}$ were measured in the northern basin of the harbor for several days following the mortality event, and a strong spatial gradient of oxygen was observed from the northern basin to waters outside the harbor. The microplankton community within King Harbor differed significantly from a diatom-dominated community present in neighboring Santa Monica Bay. The latter region appeared unaffected by physicochemical changes, induced by the fish kill, that were observed within the harbor. A trophic shift was observed throughout King Harbor from a photoautotrophic-dominated assemblage to one of heterotrophic forms, with relative abundances of bacterivorous ciliates increasing by more than 80 % in the most impacted part of the harbor. Significant changes in community structure were observed together with dramatically reduced photosynthetic yield of the remaining phytoplankton, indicating severe physiological stress during the extreme hypoxia.

Keywords Hypoxia · Microplankton · Trophic shifts · Mortality event

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Introduction

Hypoxia (dissolved oxygen < 1.4 $ml l^{-1} \approx 2$ $mg l^{-1}$ (Diaz and Rosenberg 1995)) can occur seasonally, with tidal cycle, and aperiodically in many marine and freshwater ecosystems (Grantham et al. 2004; Marti-Cardona et al. 2008; Palsson et al. 2008). The causes of hypoxic events can be attributed to both natural and anthropogenically enhanced processes (Grantham et al. 2004; Lowe et al. 1991), and the frequencies and extent of coastal hypoxia are reported to be increasing (Diaz and Rosenberg 1995, 2008). This trend is predicted to persist with future climate change as a consequence of warming of surface waters which may decrease gas solubility, increase organismal metabolic rates, and increase surface stratification (Meehl et al. 2007). Continued eutrophication and decreased oxygen content in eastern boundary currents may also contribute to these events (Diaz and Rosenberg 2008; Poertner and Peck 2010). Hypoxia can occur in a variety of aquatic habitats including enclosed inland seas and hydrodynamically constrained estuaries,

fjords, and the continental shelf where sharply delimited "oxygen minimum zones" result from increased deposition of organic material in productive upwelling regions (Bograd et al. 2008; Diaz and Rosenberg 1995, 2008; Levin 2003; Wetz et al. 2011).

The effects of hypoxia on marine macrobiota and communities are varied and have been the subject of many studies (e.g., as reviewed in Diaz and Rosenberg (1995)). Motile species such as fish tend to be metabolically affected by decreased oxygen concentrations, often experiencing reduced growth and biomass as a result of exposure (as reviewed in Wu (2002)). Such highly mobile species may rely on physiological or behavioral strategies to adapt to or avoid regions of hypoxia (Bell and Eggleston 2005; Eby and Crowder 2002; Wu 2002) and may respond to hypoxic conditions by moving to shallower or more near-shore spatial locations. Several species of fish exposed to low dissolved oxygen have displayed behavioral abnormalities, including denser schooling and periods of inactivity during hypoxia in the Hood Canal in Puget Sound, WA, USA (Palsson et al. 2008). Decreased fish biomass, aggregations of fish at the edges of hypoxic waters, and reduced spatial overlap of fish populations with their mesozooplankton prey have also been reported from the seasonally hypoxic northern Gulf of Mexico (Zhang et al. 2009).

Slow-moving benthic and sessile organisms, while often more physiologically tolerant of hypoxic conditions than motile pelagic taxa (Gray et al. 2002), are typically unable to avoid areas of decreased oxygen (Stachowitsch et al. 2007). Infaunal benthic organisms may move from their protective sediment habitats (Diaz and Rosenberg 1995), but for many other members of the benthos, large-scale migration is not an option. Consequently, a large volume of research has been published on the physiological tolerances and metabolic and behavioral adaptations of benthic macro- and meiofaunal communities. These studies have generally reported diminished overall biomass, loss of large, long-lived species, reduced species richness and biodiversity, dominance of deposit feeders over suspension feeders, and replacement of mega- and macrofauna by meiofaunal and microbially dominated assemblages (Diaz and Rosenberg 1995; Levin 2003; Wu 2002; Yoshino et al. 2010).

Relatively few studies have investigated the effects of hypoxia on planktonic species of pelagic and coastal ecosystems. Macrozooplankton (primarily copepods) have been examined to some extent because of their important role in pelagic food webs and have been found to have remarkable tolerances to low dissolved oxygen. Significant mortality occurs under severely hypoxic concentrations (0.05 $ml l^{-1}$), but moderate survival can occur at concentrations >0.20 ml l^{-1}, probably due to a combination of anaerobic respiration and vertical migration into more oxygenated waters (Marcus 2001). Zooplankton abundance has been shown to increase in transition zones between oxygenated and hypoxic waters during spatially limited events, although reduced abundance and species richness within strongly hypoxic waters have been noted (Boullion 1985). It has been suggested that hypoxia may provide a refuge from predators for macrozooplankton (Boullion 1985; Marcus 2001). Additionally, it has been reported that microzooplankton (primarily protistan species) supersede crustacean zooplankton as the primary mediators in the trophic transfer of organic matter during hypoxic events (Marcus 2001). This inference is supported by the findings of Fenchel et al. (1990), where shifts in protozoan community composition were documented along vertical oxygen gradients in eutrophic Danish fjords. Bacterivorous scuticociliates dominated along oxyclines, while more specialized anaerobic ciliates were common in the deeper, anoxic waters.

The impact of hypoxia on phytoplankton biomass and community structure remains largely unknown despite the fact that eutrophication-enhanced algal growth and/or harmful algal blooms are leading causes of hypoxia in oxygen-minimum zones, estuaries, and enclosed bodies of water (Backer 2009; Diaz and Rosenberg 2008; Gannon et al. 2009; Gray et al. 2002; Kemp et al. 2005; McInnes and Quigg 2010; Thronson and Quigg 2008). Borics et al. (2000) documented decreased algal biomass, species richness, and diversity in a stagnant, hypertrophic fish pond dominated by the cyanobacterium *Cylindrospermopsis raciborskii* following chemical treatment that resulted in total fish mortality (but not hypoxia). Wu (2002) noted a shift to nanoplankton and microflagellate dominance in hypoxia-exposed microplankton communities. These findings imply a strong but presently undocumented impact of hypoxia on pelagic microbial communities.

The goal of the current study was to determine the effects of physical and chemical perturbations caused by a massive fish kill, subsequent hypoxia, and a penultimate storm-mediated mixing event on the microplankton community composition and structure within and outside a man-made, semi-enclosed harbor in the Southern California Bight. Extreme hypoxia resulted in a severe reduction in the abundance of eukaryotic taxa and observed diversity, evenness, and taxonomic richness. The photoautotrophic community showed signs of severe photosynthetic stress during the period of hypoxia. Initial recovery of the system was dominated by microzooplankton, followed by mixotrophic algae. Return to pre-event conditions took place over a 3-week period.

Methods

Study Site King Harbor is a semi-enclosed, recreational harbor within Santa Monica Bay (SM Bay) in the City of

Redondo Beach located within Los Angeles County. The harbor is protected by a rubble breakwater with a channel at the southern end providing the main connectivity to SM Bay. The harbor is effectively divided into three regions: the northern and southern marina basins and the outer harbor connecting the two basins (Fig. 1). The two marina basins are hydrographically distinct and connect to the coastal ocean only through the outer harbor. The exchange of water between the harbor and adjacent bay through the rubble breakwater is not known.

Sensor Data In situ water quality sensors have been maintained since 2006 at sites within the northern and southern marina basins of King Harbor, attached from floating docks at the locations indicated in Fig. 1. Water Quality Monitors (WQM; WetLabs) have been employed for monitoring at these locations since May 2010 in the upper meter of the water column. These sensors were programmed to record temperature (°C), salinity (psu), dissolved oxygen ($ml l^{-1}$), chlorophyll *a* fluorescence (chl *a*) at 695 nm ($\mu g l^{-1}$), and turbidity at 700 nm (NTU) for 10 s at 30-min intervals. The effects of biofouling were minimized by equipping each WQM with a copper BioWiper (WetLabs) installed over the optical sensors and bleach injection system (BLIS), which injected 28 μl 10 % bleach into the dissolved oxygen sensor module on an hourly basis (Orrico et al. 2007). In addition to the WQM sensors, an active fluorometer (Phytoflash; Turner Designs) was co-deployed at the same depth of the WQM optical package in the northern basin. The submersible Phytoflash is a solid-state, short-pulse, multiple-turnover active fluorescence system. The optics consist of three low-intensity 465-nm light-emitting diodes (LEDs) measuring minimal fluorescence (F_0) and six high-intensity LEDs measuring maximal fluorescence (F_m) equipped with <500- and 680AF80-nm excitation and emission filters, respectively. Variable fluorescence is calculated as the difference in minimal and maximal fluorescence ($F_v = F_m - F_0$), and the ratio F_v/F_m (yield) indicates the functional proportion of photosystem II reaction centers (Kolber and Falkowski 1993).The fluorometer was blanked to 0.2-μm filtered seawater in lab prior to deployment and programmed to measure photosynthetic yield at 30-min intervals using a 500-ms saturating flash. The downward-looking Phytoflash was equipped with a shade cap to minimize interference of ambient light on fluorescence measurements and a battery pack for autonomous deployment. All deployed sensors were cleaned and data were downloaded at 2-week intervals.

Each WQM was factory-calibrated prior to deployment (May 2010) and again in November 2010. The two WQM systems used in this study were standardized to a third, laboratory-calibrated multi-parameter datasonde (DS5, Hach Hydrolab), which was used to vertically profile at sampling locations during the study. Data from the WQM sensors were correlated to data obtained simultaneously with the DS5, averaged over the upper 0.5 m of the water column. Good agreement between the WQM and DS5

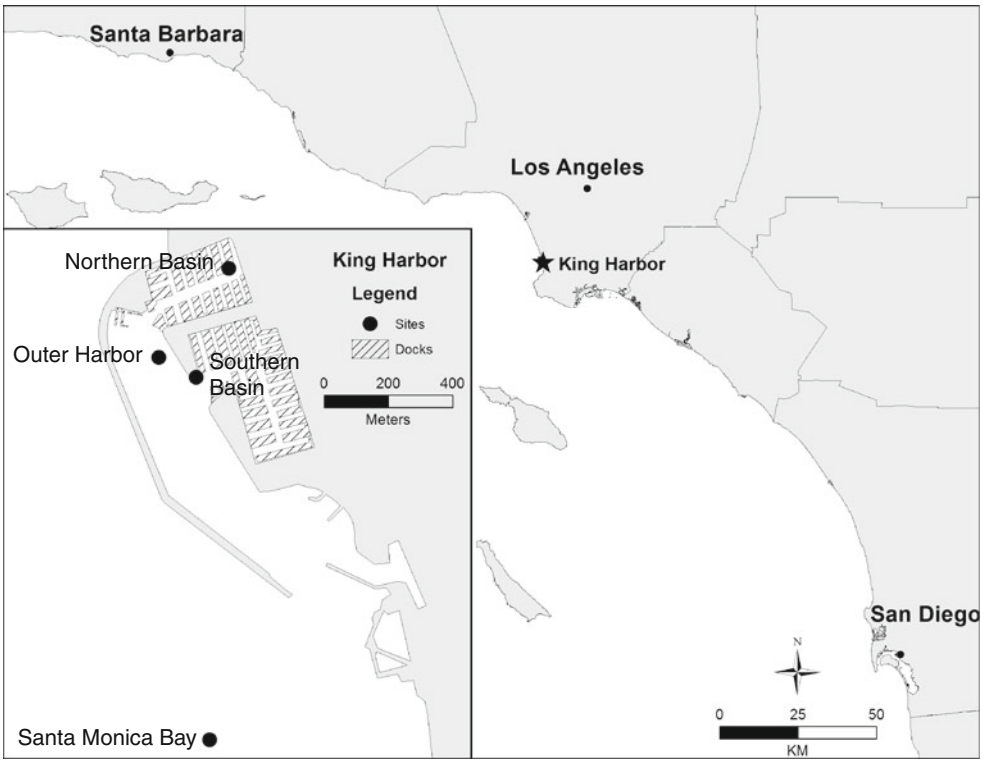

Fig. 1 Map of King Harbor (*inset*), within the Southern California Bight, showing the sampling and sensor locations

datasets was obtained (R^2>0.88). The DS5 sensor was calibrated in the lab following the study period using conductivity and turbidity standards (Hach), and the dissolved oxygen sensor (% saturation) was calibrated weekly using the manufacturer-prescribed, air-saturated water method. In vivo chl *a* fluorescence from the WQM and/or the DS5 sensors were related to each other as described earlier and further translated to units of μg chl *a* l^{-1} by comparison of sensor data to extracted chl *a* of approximately 15 samples taken from the location of each sensor deployment (see below). All sensor data are therefore presented as normalized to the DS5 sensor and calibrated to the in vitro field samples from each location.

WQM sensor data were binned to 30-min intervals using an average of ten 1-s readings taken at each time-point. Questionable data points were defined as any that exceeded three times the standard deviation for that parameter and were removed (Wilcox 2003). Missing points were not interpolated. Vertical profiles were initiated with a one-min equilibration period just below the surface of the water. The equilibration data were removed during analysis. Two gaps exist in the sensor dataset, most notably salinity data for 15 March and 4 April at the southern basin location. To facilitate analysis, standardized WQM data from the northern and southern basin locations and DS5 vertical profile data from the outer harbor and SM Bay locations were discretized by averaging around sampling time-points (± 1 h) and for the upper 0.5 m of the water column.

Discrete Water Samples Whole water samples from the surface (< 0.5 m) were collected at the two marina basin sites weekly from 15 February through 12 April 2011. Additional surface samples were collected at four sampling sites (Fig. 1) for 3 weeks after 8 March, the first day of the fish kill (Table 1). Acid-washed (5 % HCl) polycarbonate bottles were rinsed with sample water, filled with surface water, and kept cool and out of direct sunlight until subsampling took place within 3–4 h. Subsamples for dissolved inorganic nutrient analyses were filtered on-site through 0.2-μm syringe filters pre-rinsed with approximately 10 ml sample water, collected in acid-washed HDPE bottles, and frozen at −20 °C. Concentrations of nitrate (inclusive of nitrite; $NO_3^- + NO_2^{2-}$ [detection range, 0.2–300 μM]), phosphate (PO_4^{3-} [0.1–200 μM)]), and silicate ($Si(OH)_4$ [1.0–600 μM]) were measured with ±5 % precision on a QuikChem 8000 flow injection analyzer (Lachat Instruments) by the Analytical Lab (Marine Sciences Institute, University of California, Santa Barbara, CA, USA). Samples were kept frozen at −20 °C until analysis within 2 months of collection.

Duplicate subsamples were filtered onto 25-mm glass fiber filters (Whatman) for in vitro chl *a* analysis, extracted in 100 % acetone at −20 °C for 24 h, and run on a calibrated laboratory fluorometer (TD-700, Turner Designs) prior to and following acidification with 5 % HCl (Strickland and Parsons 1972). Phaeopigment concentrations were calculated from the pre- and post-acidification fluorescence measurements (Arar and Collins 1997). Subsamples were preserved with 1 % formalin for community composition analysis by microscopy using Utermöhl settling chambers (Utermohl 1931, 1958). Up to 50 ml of each sample was settled for 24–48 h; smaller volumes (10–30 ml) were settled when needed to allow for effective viewing and enumeration. The settled samples were examined, and autotrophic and heterotrophic protistan taxa within the size range of 10–200 μm were identified and enumerated to the genus and class levels, respectively. Epifluoresence with blue excitation was utilized to differentiate between unidentified auto- and heterotrophs when necessary. Samples were counted on an inverted compound microscope (Leica DMIRBE) at×400 total magnification with a minimum of 200 cells enumerated for each sample, allowing a theoretical counting error of 15 % (Hötzel and Croome 1999). A minimum of 20 fields of view were counted.

Community Structure and Diversity Relative abundances of mainly genus-level groupings were binned into functional- and class-level assemblies of heterotrophs, dinoflagellates, diatoms, euglenids, and other phytoplankton in order to assess spatial and temporal changes in the contribution of specific groups of microplankton. Raphidophytes, chlorophytes, coccolithophores, and silicoflagellates were the main contributors to the "other phytoplankton" grouping.

Community structure and diversity (observed species richness and evenness) among microplankton assemblages from all sampling locations and throughout the sampling period were compared in conjunction with physicochemical information obtained from the sensors. These analyses indicated strong shifts in environmental gradients linked to the hypoxia caused by the fish kill and a subsequent meteorological storm event that led to mixing of the water column (see "Results"). Time periods that encompassed these distinct events were defined as: pre-event (before 8 March), hypoxia (8–18 March), mixing (22–29 March), and post-

Table 1 Sampling locations, date of first sampling for each location, and notable events

Location	Coordinates	Date of first sampling
Northern Basin	33.850 N 118.398 W	15 February 2011
Southern Basin	33.847 N 118.399 W	15 February 2011
Outer Harbor	33.848 N 118.400 W	8 March 2011[a]
SM Bay	33.837 N 118.398 W	11 March 2011[b]

[a] Date of first reported fish mortalities

[b] Date of tsunami generated by the Tōhoku earthquake in Japan

event (1 – 12 April). To test the appropriateness of these time period definitions, principal components analysis (PCA) of log-transformed and normalized abiotic environmental parameters temperature, salinity, and dissolved oxygen were conducted using a maximum of five components (Clarke and Warwick 2001).

Similarities among protistan communities were examined using the Bray–Curtis coefficient within the statistical software package PRIMER v.6 (Clarke and Warwick 2001). Abundances were square root-transformed to reduce the influence of highly represented genera/classes, reducing the tendency for a few well-represented genera to drive the similarity analyses (Bray and Curtis 1957; Clarke and Warwick 2001). The Bray–Curtis coefficient is not affected by joint absences of species between samples (Clarke and Warwick 2001). The transformed results for the Bray–Curtis test were further used in cluster analysis with similarity profile permutation tests (SIMPROF) to examine if dissimilarities among the assemblages were significant (Clarke and Warwick 2001). Species diversity within microplankton assemblages was described using observed taxonomic richness (S_{obs}) and the inverse Simpson diversity index (D_s^{-1}) which takes into account the number of taxa present and their relative abundances (Simpson 1949). Confidence intervals (95 %) were calculated for observed taxonomic richness (Colwell 2009).

Results

Hypoxic Event Approximately 170 tons of fish (William Workman, City Manager, City of Redondo Beach; personal communication), mainly Pacific sardine (*Sardinops sagax*), were found dead primarily in the northern basin of King Harbor on the morning of 8 March 2011 (Barboza and Weiss 2011). Analysis of available data indicated that the mortality event was the result of extreme hypoxia brought about by the respiratory activities of an exceptionally high density of fish that entered and remained confined in the harbor (Stauffer et al. 2012). Dissolved oxygen concentrations within the harbor varied spatially during the 2 weeks following the fish kill, with levels ranging from mild hypoxia to near-anoxia. Low dissolved oxygen persisted in the harbor until a storm-mediated mixing event on 20–21 March.

Oceanographic Conditions Surface temperature within King Harbor was approximately 16 °C prior to the fish kill on 8 March. An overall decrease was observed from 15 February to 10 March in both northern and southern marina basins (Fig. 2a). Temperatures at all four sampling locations increased slightly from 11 to 18 March, until the passage of a low-pressure system on 20–21 March precipitated a drop in surface temperature to 13.0 °C in SM Bay and 13.2–13.7 °C at stations within King Harbor (Fig. 2a). Passage of the storm system was also apparent from a decrease in surface salinity from 33.3 to < 32.7 at the harbor locations (Fig. 2b).

Dissolved oxygen concentrations of 3–4 $ml l^{-1}$ were observed in the northern and southern basins for at least a month prior to the fish kill (Fig. 2c), values that are less than half of the SM Bay values. Significant decreases in dissolved oxygen were apparent in the northern basin by 24 February and in the southern basin by 2 March, a week prior to the fish kill, and additional decreases in oxygen took place in both basins on 8 March (Fig. 2c). Dissolved oxygen in the northern basin had dropped to 0.56 $ml l^{-1}$ by 8 March and continued to decrease to near-anoxic conditions (< 0.1 $ml l^{-1}$) from 10 through 18 March. Dissolved oxygen in the northern basin recovered slightly by 22 March to 0.29 $ml l^{-1}$ and continued to rise, exhibiting fluctuations from 1.03 to 2.79 $ml l^{-1}$ for the remainder of the study period (Fig. 2c). In contrast, dissolved oxygen in the nearby southern basin fell to 1.08 $ml l^{-1}$ by 8 March but returned to values generally greater than 2 $ml l^{-1}$ until 18 March when concentrations as low as 1.22 $ml l^{-1}$ were again observed (Fig. 2c).

Dissolved oxygen concentrations in the outer harbor were approximately 2 $ml l^{-1}$ on 8 and 9 March, but concentrations at this location decreased to and remained below 1 $ml l^{-1}$ until 22 March and subsequently increased to 2–5.5 $ml l^{-1}$ for the remainder of the study period. Comparatively high concentrations of dissolved oxygen were observed in SM Bay throughout the study period, with a range between 6.5 and 8 $ml l^{-1}$ (Fig. 2c). Concentrations on 12 March, 18–25 March, and 5 and 13 April were approximately 1–1.5 $ml l^{-1}$ lower than on other sampling dates.

Environmental Shifts PCA of normalized sensor data utilized the environmental variables temperature, salinity, and dissolved oxygen, which together combined as the first (60.4 %) and second (27.7 %) principal components (PCs). They accounted for 88.1 % of the total environmental variability within King Harbor (Table 2). PC1 was strongly correlated with salinity and temperature, while PC2 was strongly correlated with dissolved oxygen and temperature and negatively associated with salinity (Table 2).

The King Harbor environment prior to the fish kill (before 8 March) was best described by temperature and salinity along a range of dissolved oxygen concentrations (Fig. 3). The environment during hypoxia (8–18 March) was largely defined by decreasing dissolved oxygen. The storm event environment (22–29 March) was highly defined by decreasing temperature and salinity and, with the exception of the northern basin, increased dissolved oxygen. Finally, the post-storm environment (1–12 April) within King Harbor was once again largely defined by temperature and salinity, along a range of dissolved oxygen concentrations generally in excess of pre-event concentrations (Fig. 3). SM Bay was well removed from the immediate

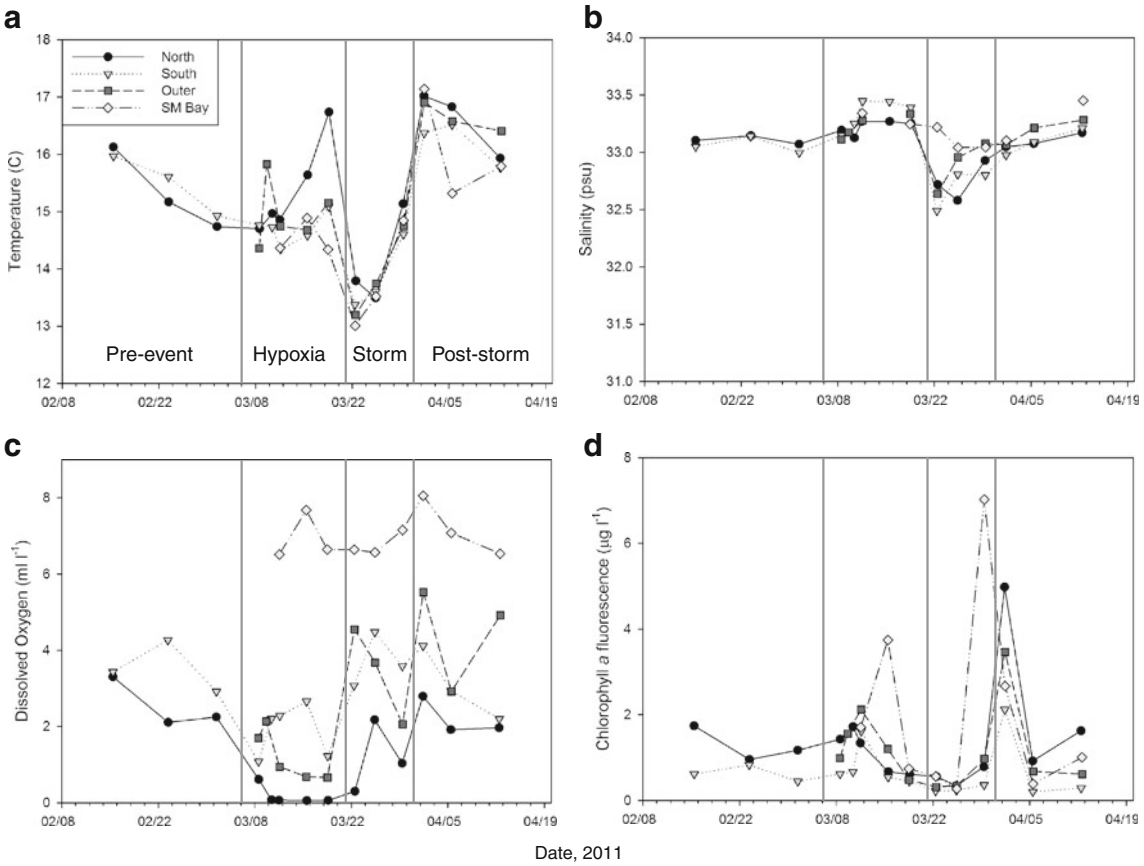

Fig. 2 Surface (< 0.5 m) environmental conditions at King Harbor and Santa Monica Bay sites from 15 Feb to 12 April. Temperature (**a**), salinity (**b**), dissolved oxygen (**c**), and chlorophyll fluorescence (**d**) have been standardized to the Hydrolab DS5 sensor used in vertical profiles at each site. *Solid vertical gray lines* indicate demarcations of pre-event (before 8 March 2011), hypoxia (8–18 March), storm (22–29 March), and post-storm (1–12 April) time periods as described by the oceanographic conditions and supported by principal components analysis of temperature, salinity, and dissolved oxygen. *X-axis ticks* are spaced at 2-day intervals for all plots

effects of the fish kill within King Harbor (Fig. 1) and did not experience dissolved oxygen concentrations < 6 $ml l^{-1}$. As a result, the environmental trends in SM Bay are principally explained by temperature and salinity changes alone as a consequence of the 20–21 March storm event (data not shown).

Table 2 PCA statistics for the normalized abiotic environmental variables temperature, salinity, and dissolved oxygen at the harbor locations. Contributions of each PC to the dataset variation, both individually and cumulatively, are given as percent variation. Linear combinations of variables making up each PC are given as eigenvectors. Negative values indicate an inverse relationship between the variable and PC

	PC1	PC2	PC3
% variation	60.4	27.7	11.9
Cumulative % variation	60.4	88.1	100
Temperature	0.634	0.666	−0.394
Salinity	0.764	−0.458	0.455
Dissolved oxygen	−0.123	0.590	0.798

Inorganic Nutrients Dissolved phosphate concentrations within the harbor were generally ≤ 5 uM prior to and 2 weeks after the fish kill but rose to local maxima of 53 and 18 μM in surface waters of the northern basin and outer harbor, respectively, on 11 March (Fig. 4a). Phosphate concentrations in the surface waters of Santa Monica Bay remained below 1.5 μM for the study period.

In contrast, lower concentrations of dissolved nitrate and nitrite were measured in waters affected by the hypoxia event (Fig. 4b). These constituents ranged from 5 to 20 μM in the southern and northern basins of King Harbor prior to the fish kill event. Values decreased dramatically in the northern basin for 2 weeks following the event, falling below detection (0.2 μM) during the period of acute hypoxia in that basin, but remained relatively high (approximately 10 μM) in the outer harbor (10 to 22 March; Fig. 4b). Combined nitrate and nitrite concentrations were variable in SM Bay throughout the study, ranging from < 0.02 μM (the limit of detection) to 8.6 μM on 11 March.

Silicate was relatively high (≥ 5.0 to ≥ 30 μM) at all sampling locations for 3–4 days following the fish kill

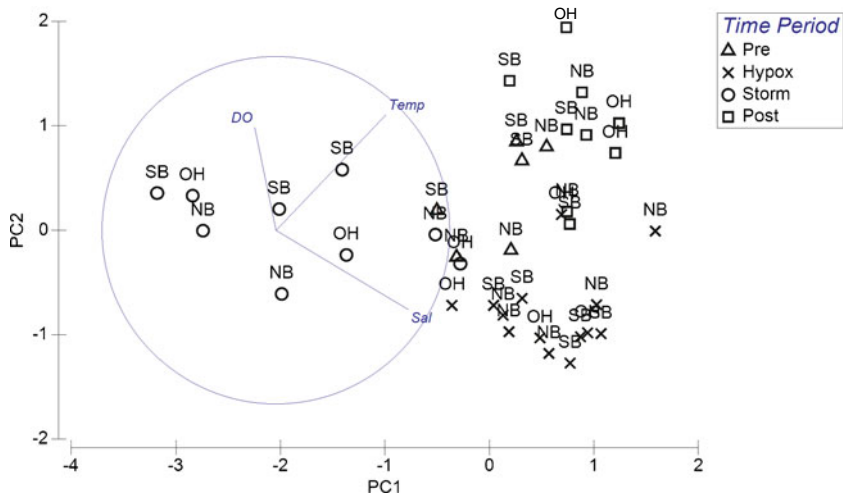

Fig. 3 PCA of normalized abiotic environmental variables (temperature [*Temp*], salinity [*Sal*], and dissolved oxygen [*DO*]) from southern basin (*SB*), northern basin (*NB*), and outer harbor (*OH*) locations. Environmental variables were averaged for each site for the following time periods as defined by oceanographic conditions: pre-event (before 8 March), harbor hypoxia (8–18 March), storm (22–29 March), and post-storm (1–12 April). Together PCs 1 and 2 account for 88.1 % of variation in the dataset

event, followed by generally lower and more variable concentrations through 15 March (Fig. 4c). The northern basin yielded the highest values of silicate (33 μM), with the exception of mid-April when all samples yielded equivalent concentrations.

Algal Biomass and Physiology Absolute values and temporal patterns for in vivo chlorophyll fluorescence (Fig. 2d) were generally in agreement (Pearson's r=0.98, 0.67, 0.52, and 0.81 for the northern and southern basins, outer harbor, and SM Bay locations, respectively) with chlorophyll concentrations obtained from extracted samples (Fig. 5a). Chlorophyll concentrations were < 2 $\mu g l^{-1}$ in both basins during the month prior to and at the time of the fish kill (Fig. 2d). A modest increase (to 3.7 $\mu g l^{-1}$) was observed in SM Bay on 15 March; however, fluorescence at the other sites remained comparatively low until 29 March and 1 April when higher values were observed at all sampling locations (peaks of 4.98 and 7 $\mu g l^{-1}$ in the northern basin and SM Bay, respectively; Fig. 2d). Low algal biomass prior to the fish kill was confirmed by in vitro (extracted) chlorophyll measuring < 2.3 $\mu g l^{-1}$ in the northern and southern basins (Fig. 5a). A slight peak in in vitro chlorophyll was observed in SM Bay and the southern basin on 11 and 15 March, respectively, but levels elsewhere remained low until 29 March and 1 April when up to 10 $\mu g l^{-1}$ was measured in the northern basin and SM Bay.

Concentrations of phaeopigments were < 2 $\mu g l^{-1}$ in the northern and southern basins prior to the mortality event (Fig. 5b). Phaeopigment concentration increased on 29 March and 1 April in the outer harbor and northern basin, respectively, coincident with increased chlorophyll *a* values. Increased phaeopigments were also observed on 11 March in the southern basin and outer harbor.

Photosynthetic yield (F_v/F_m), an indicator of physiological status of photosystem II, decreased dramatically in the northern basin during the hypoxia event (Fig. 6). Prior to the fish kill, F_v/F_m was high relative to a theoretical maximum of approximately 0.65 (Kolber and Falkowski 1993), with a 2-day average of 0.47 through 9 March (Fig. 6). By midnight on 9 March, however, F_v/F_m values dropped to < 0.3 and reached a minimum of 0.003 by late afternoon 13 March, much lower than the lowest values observed over diurnal cycles of the previous several weeks. Values of F_v/F_m did not consistently recover to pre-event levels until 23 March, following the storm event and initial re-oxygenation of the water column in King Harbor.

Community Composition Four taxonomic groupings (in order from most the dominant: *Chaetoceros* spp., a *Uronema*-like scuticociliate, *Prorocentrum* spp., and Euglenids) comprised approximately 68 % of the microplankton community across all sites and sampling periods (Table 3). Ten other groups of microplankton contributed to the total 91 % of the community, including diatoms of the genera *Pseudo-nitzschia*, *Cylindrotheca*, *Cyclotella*, *Navicula*, and *Thalassiosira*, four members of the Dinophyceae, including small gymnodinoid dinoflagellates, *Akashiwo sanguinea*, *Scrippsiella* spp., and cysts. Oligotrichous ciliates were also present at significant abundances.

Dominance of diatoms, photosynthetic dinoflagellates, euglenids, and heterotrophic protists showed marked changes spatially and through time (Fig. 7). Euglenids were dominant in early February at the two basin locations (data not shown). By mid-February, photosynthetic dinoflagellates (mainly *Prorocentrum* spp.) were dominant, but their relative abundances consistently decreased from 15 February to 1 and 8 March in the northern and southern basins, respectively, at which time community composition was more evenly distributed among groups. The outer harbor and SM Bay were both heavily dominated by diatoms on 8 and 11 March, respectively. The relative contribution of

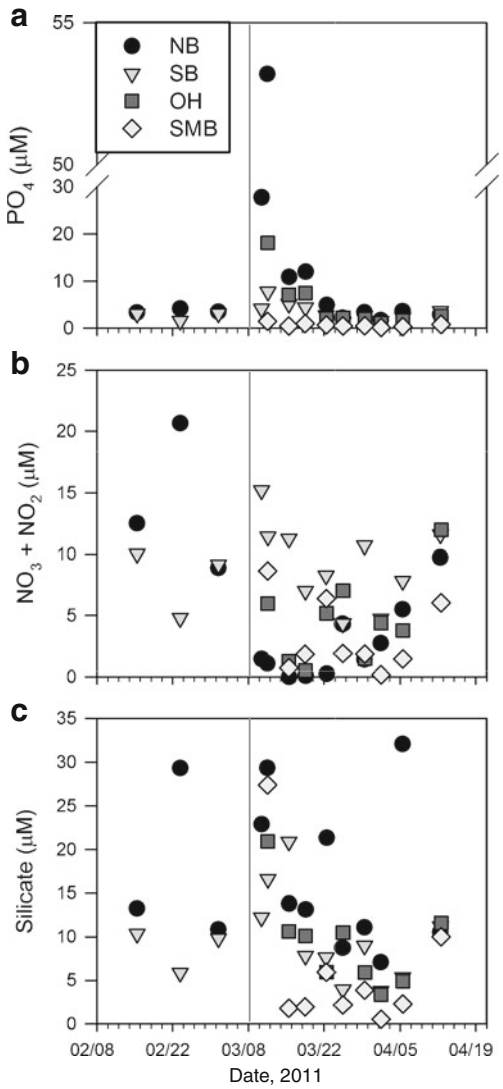

Fig. 4 Surface dissolved inorganic nutrients in King Harbor and SM Bay. Concentrations of PO_4 (**a**), NO_3+NO_2 (**b**), and silicate (**c**) in the northern (*circles*) and southern (*triangles*) basins, outer harbor (*square*), and SM Bay (*diamond*) were measured following filtration through 0.2-µm syringe filters. *Solid vertical gray line* indicates 8 March, the first reported day of the fish kill and beginning of the hypoxia time period. *X-axis ticks* are spaced at 2-day intervals

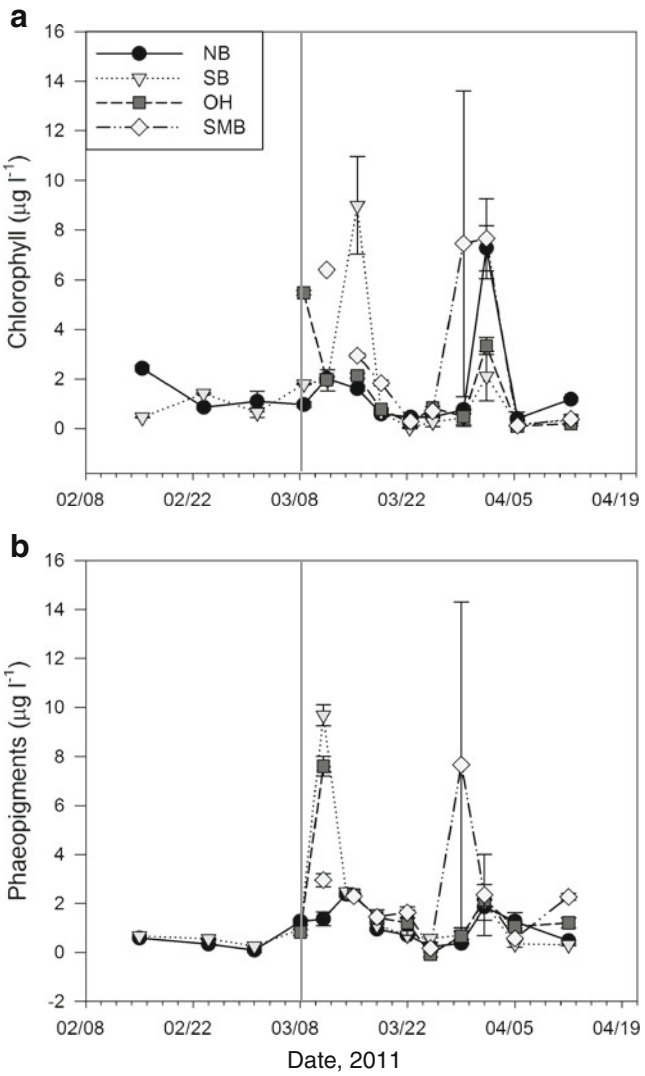

Fig. 5 Surface (< 0.5 m) chlorophyll *a* (**a**) and phaeopigment (**b**) concentrations for northern (*circles*) and southern basin (*triangles*), outer harbor (*squares*), and SM Bay (*diamonds*) locations. Samples were run in duplicate; as such, *vertical bars* indicate range around mean pigment concentrations. *Solid vertical gray line* indicates 8 March, the first reported day of the fish kill and beginning of the hypoxia time period. *X-axis tick* labels are at 2-day intervals

diatoms at all sites decreased following the fish kill, but these diatom species reestablished dominance by 29 March in SM Bay (Fig. 7d) and 1 April in the outer harbor and marina basins (Fig. 7a–c).

Heterotrophic microplankton assemblages were dominated by a *Uronema*-like scuticociliate that increased in relative abundance and became dominant in the outer harbor and marina basins between 11 and 29 March (Fig. 7a–c). This trophic shift took place in the southern basin and outer harbor as early as 14 and 18 March, respectively, but lagged behind by nearly a week in the northern basin, becoming highly abundant (> 80 %) by 22 March at that site. Relative abundances of heterotrophic protists never exceeded 20 % in SM Bay (Fig. 7d). Relative abundances of heterotrophs decreased across all sites during the storm event period (22–29 March), with diatoms and photosynthetic dinoflagellates becoming once again dominant by 1 April (Fig. 7).

Community Structure, Diversity, and Taxonomic Richness

Changes in community structure were investigated using cluster analysis based on Bray–Curtis similarity coefficients (Clarke and Warwick 2001). Assemblages that differed significantly ($p < 0.05$) in their composition were found under different hypoxic conditions and/or locations within or outside of King Harbor (data not shown). Non-metric multidimensional scaling (MDS) analyses described three distinct

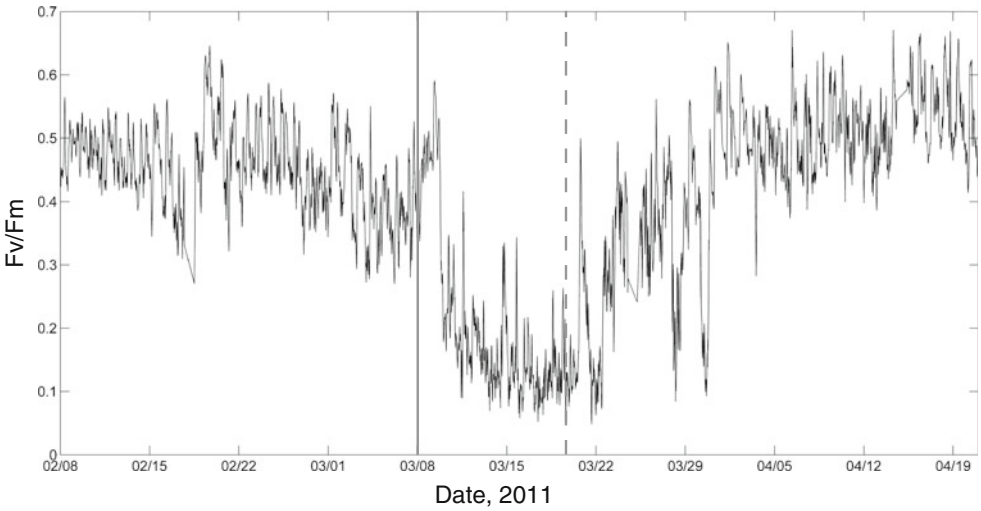

Fig. 6 Photosynthetic yield (F_v/F_m) of surface (0.5 m) community at the Northern basin location. Data are averaged to 1-h intervals. *Vertical gray line* represents first reporting of fish mortality on 8 March. *Vertical dashed gray line* indicates initiation of the storm event on 20–21 March. *X-axis tick* labels are at 2-day intervals

microplankton assemblages in the northern basin (similarities > 45 % within each group; significantly different at the 95 % level) that were detected during the pre-event and hypoxic time period (group 1), during the storm event and associated water column mixing (group 2), and during restabilization of the water column following the storm event (group 3; Fig. 8). Similar clustering among assemblages was observed for the southern basin (data not shown). In contrast, no significant groupings were found for outer harbor assemblages (data not shown), with each assemblage seemingly distinct from others at this site. Some similarities were observed for assemblages from the SM Bay; however, assemblages largely clustered according to successive dates different from those observed for sites inside the harbor (on the approximate time scale of 1 week) and largely removed from the hypoxic event within King Harbor.

Taxonomic richness (S_{obs}) and Simpson diversity (D_s^{-1}) were lowest (10 and 1.7, respectively) at all sites during the period of the storm event (22–29 March) and increased (to 21 and 6.0, respectively) for the subsequent post-storm communities (Table 4). In general, the northern basin community revealed low richness of the microplankton assemblage presumably as a consequence of the hypoxic event. Richness estimates were low in the northern basin during the hypoxia and storm event time periods but increased significantly ($p < 0.05$) to a site-specific maximum of 21 taxa during the post-storm period (Table 4). Alternatively, the lower species richness may have also resulted from an inability to account for rare taxa in the presence of highly dominant groups. Simpson indices for the assemblages were generally variable among sites and sampling periods. These indices represent conservative estimates of species richness and diversity, as morphologically nondescript, small (< 15 μm), and rare (on average < 1–2 cells ml^{-1}) species were not effectively identified and/or enumerated by the microscopical methods used in this study.

Table 3 Dominant microplankton taxonomic units. Total abundance was computed as a sum across all sites and sampling dates, and relative abundance was computed as percent contribution to the total sum across all taxa, sites, and sampling dates

Taxonomic grouping	Class/subclass	Relative abundance (%)
Chaetoceros spp.	Bacillariophyceae	38.2
Uronema-like scuticociliate	Oligohymenophorea	13.8
Prorocentrum spp.	Dinophyceae	9.09
Eutreptiella spp.	Euglenoidea	7.01
Pseudonitzschia spp.	Bacillariophyceae	5.14
Small gymnodinoid spp.	Dinophyceae	4.41
Cyclotella spp.	Bacillariophyceae	2.73
Cylindrotheca spp.	Bacillariophyceae	2.55
Oligotrichous ciliates	Spirotrichea	2.55
Dinoflagellate cysts	Dinophyceae	1.61
Scrippsiella spp.	Dinophyceae	1.56
Navicula spp.	Bacillariophyceae	1.37
Thalassiosira spp.	Bacillariophyceae	1.23
Akashiwo sanguinea	Dinophyceae	0.99

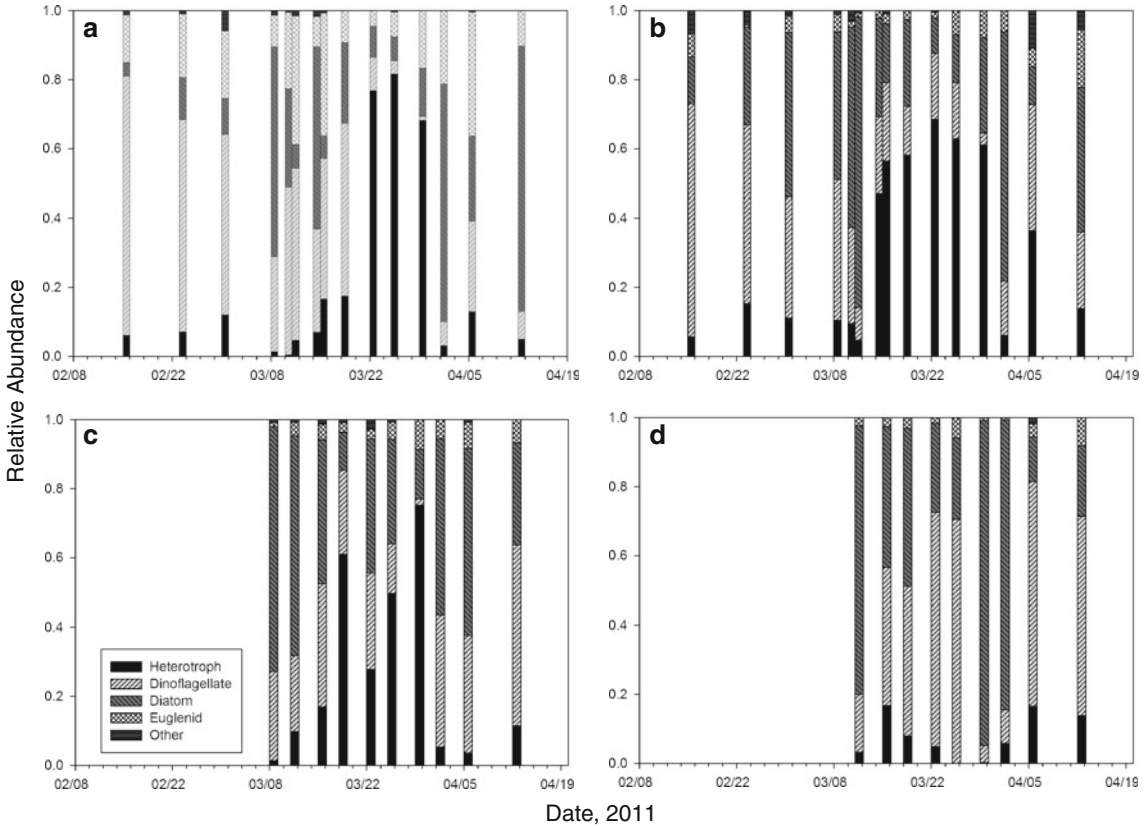

Fig. 7 Relative contributions of heterotrophs, dinoflagellates, diatoms, euglenids, and other phytoplankton to the surface microplankton community composition in northern (**a**) and southern (**b**) basins, outer harbor (**c**), and Santa Monica Bay (**d**). "Other" phytoplankton include raphidophytes, chlorophytes, coccolithophores, and silicoflagellates. *X-axis tick* labels are at 2-day intervals

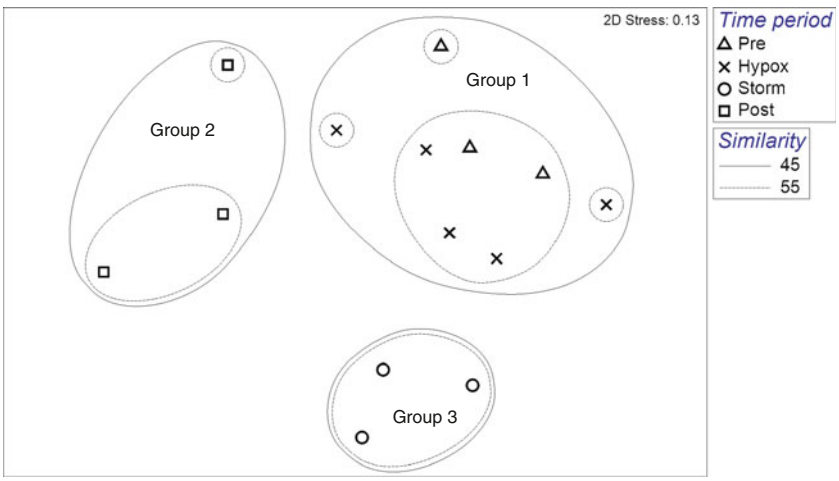

Fig. 8 MDS of northern basin microplankton communities based on the Bray–Curtis coefficient of dissimilarity. Mean abundances for each of approximately 60 genus- and class-level taxonomic units were calculated for the four time periods as physico-chemically defined in this study: pre-event (before 8 March 2011), hypoxia (8–18 March), storm event (22–29 March), and post-storm (1–12 April). All abundances were square root-transformed. *Solid* and *dashed black ellipses* indicate 45 and 55 % similarity levels, respectively, and were significant at the 95 % level by cluster analysis. Stress value=0.13

Table 4 Diversity estimates for King Harbor and Santa Monica Bay sampling sites prior to the fish kill (pre-8 March 2011), during hypoxic conditions within the harbor (8–18 March), during the storm event (22–29 March), and post-storm during water column re-stabilization (1–12 April)

Time period	S_{obs} (95 % CI)				D_s^{-1}			
	NB	SB	OH	SMB	NB	SB	OH	SMB
Pre-event	18 (11-25)	19 (13-25)	nd	nd	5.4	11.5	nd	nd
Hypoxia	12 (6-18)	23 (16-30)	27 (19-35)	28 (23-33)[a]	6.0	7.5	9.7	5.2
Storm event	10 (5-15)[a]	18 (12-24)	16 (10-22)	15 (9-21)	1.7	2.4	3.3	1.7
Post-storm	21 (16-26)	18 (12-23)	20 (14-26)	16 (11-21)	6.0	2.7	5.2	1.9

Taxonomic richness (S_{obs}) and inverse Simpson diversity index (D_s^{-1}) are given. Confidence intervals (95 %) for S_{obs} are reported within parentheses

nd no data

[a] Site-specific significant differences as determined by non-overlapping 95 % confidence intervals

Discussion

The 2011 fish kill in King Harbor, City of Redondo Beach, CA, USA, highlighted the susceptibility of semi-enclosed bodies of water to extreme oceanographic conditions and massive animal mortalities. Correlations between acute hypoxia within the harbor and increased upwelling in the region of SM Bay, and arrival of a large shoal of Pacific sardines within the harbor, appear to have combined to cause this sizable mortality event (Stauffer et al. 2012). Reduced hydrodynamic mixing and flushing within King Harbor, especially in the northern basin where most of the fish mortality was observed, contributed to the severity of the event and subsequent hypoxia within the harbor. Our findings further clarify that neither enhanced phytoplankton biomass nor significant abundances of harmful algae were present within King Harbor at the time of the fish kill and subsequent hypoxia (Stauffer et al. 2012).

The ecological effects of hypoxia on marine communities have been studied in many ecosystems, including the oxygen minimum zones of semi-enclosed seas and estuaries (Eby and Crowder 2004; Levin 2003; Palsson et al. 2008). The effects of hypoxia on marine pelagic and benthic communities have indicated fundamental changes in biomass and behavior of many marine species of fish and macrobenthic invertebrates (Diaz and Rosenberg 1995; Palsson et al. 2008; Stachowitsch et al. 2007). Shifts in community diversity and species richness for neritic and oceanic populations have also been documented as a result of hypoxia (Diaz and Rosenberg 1995; Wu 2002). The current study represents a significant investigation into the magnitude of effects of fish kill-mediated severe hypoxia on the microplankton assemblage of an enclosed embayment, revealing the relationships between physical forcing and the physiological health and structure of the biological community.

High concentrations of phosphate and silicate were observed within King Harbor in the immediate aftermath of the fish kill (Fig. 4) and were likely attributable to microbially mediated decomposition of dead fish as well as the resuspension of sediment-bound nutrients during a clean-up effort by Redondo Beach officials. These high nutrient concentrations, however, did not substantially stimulate phytoplankton population growth in the weeks immediately following the fish kill, as measured by both in vivo and in vitro chlorophyll fluorescence (Figs. 2 and 5a, respectively). Increased phaeopigment concentrations at both marina basins were observed a few days following the fish kill event and onset of hypoxia (Fig. 5b). These increased concentrations were presumably a result of pigment degradation, increased grazing pressure in these environments, and/or resuspension of degraded particulate and organic material from the benthos.

A dramatic decrease in photosynthetic yield (F_v/F_m) revealed severe physiological stress of the phytoplankton assemblage during the period of extreme hypoxia in the northern basin (Fig. 6). Nutrient stress can significantly reduce photosynthetic yield (Rodriguez and Duran 2010). However, despite depleted concentrations of nitrate (inclusive of nitrite) during the period of hypoxia in the northern basin (Fig. 4c), high phosphate concentrations suggest the presence of high ammonium during the hypoxic event. Ammonium was not measured but often accompanies fish kills and hypoxic events (Gray et al. 2002). While ammonium can serve as a highly utilizable form of nitrogen for primary producers, acute ammonium toxicity has also been shown to negatively affect photosynthesis through impairments to the xanthophyll cycle in higher plants (Britto and Kronzucker 2002) and significantly reduced F_v/F_m in cyanobacteria of the *Nostoc* genus when re-hydrated in 0.5 mM NH_4Cl solution. Extreme reductions in photosynthetic yield have also been observed in mosses and symbiotic dinoflagellates exposed to hypoxic conditions (Jones and Hoegh-Guldberg 2001; Rzepka et al. 2005). Hydrogen sulfide, though not directly measured in this study, was also likely

present at high concentrations in the harbor (and indeed a distinct sulfidic odor was apparent) as the decomposition of fish biomass and near-anoxic conditions persisted for several days. Sulfide has also been shown to be highly toxic to higher marine plants (Goodman et al. 1995) as well as cyanobacteria (Cohen et al. 1986) and algae (Gasol et al. 1993), in all cases inhibiting photosynthesis through often irreversible damage to photosystem II. Thus, the decrease in yield observed in this study may be attributed to state transitions and photochemically inactive reaction centers, likely the result of an extremely reduced plastoquinone pool in photosystem II (Falkowski and Raven 2007) and/or to acute ammonium and hydrogen sulfide toxicity. Increased phytoplankton abundance was not observed within the harbor communities until 1–5 April when dissolved oxygen had returned to the system via mixing (Fig. 2c) and photosynthetic yield in the northern basin returned to pre-event levels (Fig. 6).

Environmental conditions within King Harbor shifted in response to the hypoxia, brought on by the fish kill, and the storm event 2 weeks later (Fig. 3). While storm-induced mixing affected the water column in SM Bay, significant decreases in oxygen concentration were not detected, underscoring the general confinement of the effects of hypoxia on water column structure to King Harbor. For much of the study period, the microplankton assemblage within SM Bay was dominated by diatoms (largely *Chaetoceros* spp.) typical for spring in the Southern California Bight (Corcoran and Shipe 2011; Venrick 2002). SM Bay microplankton assemblages underwent restructuring on a scale of approximately 1 week, which differs from the temporal succession of communities observed within the harbor during the same period. Conversely, microplankton assemblages within the basins of King Harbor grouped according to environmental conditions imposed by the hypoxia and the subsequent storm events. The coupling between environmental conditions and changes in community structure was strongest in the northern basin (Fig. 8), while the outer harbor assemblages were largely dissimilar to each other through time. The southern basin also showed significant groupings relative to environmental conditions, but a noteworthy exception at this site, sampled on 11 March, coincided with the arrival of the tsunami generated by the Tōhoku earthquake in Japan. This southern basin community clustered significantly ($p < 0.05$) with the post-storm and -mixing community on 1 April, suggesting a significant influence of a short-term, extreme physical disturbance on the microplankton assemblage. Microplankton assemblages in the outer harbor were not significantly similar from one sampling date to the next, indicating a temporally variable community that perhaps served as a conduit between the two marina basins and between King Harbor and SM Bay.

A fundamental shift in the microplankton community structure was also tied to changed trophic structure inside the harbor. In particular, small bacterivorous scuticociliates (e.g., *Uronema* spp.) rose to dominance in the three harbor regions that experienced significantly decreased dissolved oxygen (Fig. 5). These ciliates attained highest relative abundances in the northern basin which experienced the most extreme and prolonged near-anoxic conditions. Ciliates of the *Uronema* genus comprised >80 % of the microplankton assemblage in this basin and remained common even during the storm event (25 March). Comparatively, heterotrophic protists never contributed >20 % of the more photoautotroph-dominated microplankton assemblage at the SM Bay sampling site.

Fenchel et al. (1990) reported the dominance of scuticociliates within the genera *Cyclidium* and *Pleuronema* in the oxyclines of Danish fjords. Other studies have suggested a similar replacement of macrozooplankton by microzooplankton species that are more tolerant of hypoxia in regions subjected to these events (Marcus 2001). Trophic shifts from macro- to microzooplankton dominance may have a significant cascading effects on planktonic food web structure, directly linking the microbial loop to higher-level consumers (Ptacnik et al. 2004). The shift to dominance of the microplankton assemblage by bacterivorous ciliates in King Harbor presumably resulted from an increase in bacterial abundance resulting from decomposition of the dead fish. This trophic shift could explain, in part, high concentrations of nutrients within the euphotic zone following the fish kill (Johannes 1965). The relative dominance of scuticociliates in this and other studies suggests that these species are hypoxia-tolerant opportunists (Fenchel et al. 1977), able to take advantage of increased microbial production and decreased grazing pressure from less-tolerant macrozooplankton while the photoautotrophic population experienced severe physiological stress.

Protistan microplankton diversity within the northern basin during the period of hypoxia was generally lower than in the nearby southern basin, as measured both by taxonomic richness and the Simpson diversity index (Table 4). Assemblages within SM Bay during the same period were characterized by relatively high taxonomic richness, reflecting the highly variable nature of that location and the presence of several species of diatoms that comprised the community over time. Based on diversity analyses integrated over time periods defined by distinct environmental conditions (Table 4), minimal values of taxonomic richness and the Simpson index were observed for each site following the storm event, and these changes were similar in magnitude to changes observed during the hypoxic event both within and outside of the harbor. Diversity increased at each site following the storm event, but the changes were most pronounced in the northern basin, implying that the community was significantly restructured following the storm event. We speculate that enhanced vertical mixing

and water exchange with the outer bay, in addition to storm-induced reoxygenation of the water column, may have contributed to an increase in detected taxa due to the presence of a larger number of more equally represented taxa. However, these results must also be interpreted keeping in mind that increased relative abundances of rare (< approximately 1–2 cells ml^{-1}) and/or small (≤ 15 μm) taxa would not have been effectively detected.

As eutrophication-intensified dead zones spread along coastal margins, oxygen content within upwelling systems is further reduced, and metabolic demands increase for organisms living in a warmer ocean, the potential for significant hypoxic and mortality events will likely grow (La and Cooke 2011). The current study illustrates how such events can bring about fundamental shifts in the microplankton assemblage and its trophic structure that ultimately impact carbon and nutrient cycling. Nutrient concentrations increased dramatically during and following the mortality event, presumably due in part to microbially mediated remineralization of organic matter. Despite increased nutrient concentrations in the harbor, the conditions did not stimulate the development of an algal bloom in the aftermath of the fish kill. Sustained extreme hypoxia, toxic levels of ammonium and/or hydrogen sulfide, the lack of a physiologically healthy seed population, and/or cell degradation suffered by the population during the hypoxic event may have been factors in preventing the development of such a bloom. The stimulation of an algal bloom in the aftermath of a hypoxic event in geographically constrained ecosystems clearly poses the potential for even greater disturbance to the coastal ecosystem. Hypoxic events may therefore enact complex and far-ranging effects on environmental parameters in marine ecosystems. The overall outcomes of such events are dependent on the extent and nature of the hypoxia, hydrography of the basin, and the oceanographic processes influencing it.

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