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Abiotic controls of potentially harmful algal blooms in Santa Monica Bay, California

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A B S T R A C T

Despite the increasing occurrence of harmful phytoplankton blooms along the North American west coast, records of phytoplankton populations and related environmental conditions are uncommon. In this study, twice monthly measurements in the upper 50 m are used to assess physico-chemical conditions contributing to the growth of potentially harmful bloom taxa over two annual cycles (2004–2005) in the Santa Monica Bay, California. Results were compared to the predictions of the Intaglio model [Smayda, T.J., Reynolds, C.S., 2001. Community assembly in marine phytoplankton: application of recent models to harmful dinoflagellate blooms. Journal of Plankton Research 23, 447–461.] of phytoplankton community assembly. Potentially harmful taxa were present in every surface sample and were numerically dominant during the largest observed blooms, contributing up to 92% of the total phytoplankton abundance $>5\,\mu m$. Large interannual variation was observed in the dominant taxa and bloom seasonality; *Pseudo-nitzschia sp.* dominated blooms in early 2004 (February and April), whereas *Prorocentrum micans* and *Lingulodinium polyedrum* blooms occurred in May and September of 2005, respectively. The *Pseudo-nitzschia sp.* blooms were associated with elevated nitrate, dissolved silicon and phosphate concentrations throughout the euphotic zone; the first bloom followed a strong upwelling and the second occurred during the onset of seasonal stratification. In contrast, the blooms of *P. micans* were associated with highly stratified, low nutrient waters. Multivariate analysis supports the roles of temperature, mixed-layer depth and nutrient concentrations as primary controls of bloom growth, following the conceptual Intaglio model. The strong presence of potentially harmful bloom species in the Santa Monica Bay during this study appears unusual in comparison to limited studies over the last several decades.

1. Introduction

In recent decades, the occurrence of harmful algal blooms (HABs) has increased in global coastal waters (Glibert et al., 2005) as well as along the North American west coast (Horner et al., 1997). These events can cause harm to marine life (e.g. Work et al., 1993; Scholin et al., 2000) and to human health, with associated detrimental economic impacts (Anderson et al., 1993). Common bloom-forming taxa in CA coastal waters include toxigenic diatoms of the genus *Pseudo-nitzschia* and the red tide forming armored dinoflagellates, *Lingulodinium polyedrum* (formerly known as *Gonyaulax polyedra*) and *Prorocentrum micans* (Allen, 1941, review by Horner et al., 1997). Accumulations of cells of these taxa can be extensive; for example, a bloom of *Pseudo-nitzschia* extended from southern California to Washington in fall 1991 (Villac et al., 1993) and a *L. polyedrum* bloom in 1995 extended from the Baja peninsula to the Monterey Bay (Kudela and Cochlan, 2000). Although the mechanisms of bloom formation are important to understand from the perspectives of ecology and water quality management, blooms in the Southern California Bight basins have generally been sampled opportunistically. Therefore, relationships between harmful blooms and annual cycles of oceanographic conditions are poorly understood.

An ecological theory relating coastal marine phytoplankton species assemblages to abiotic conditions was first developed by Margalef (1978), Margalef et al. (1979) and has been refined by Smayda and Reynolds (2001) in the Intaglio model. According to this conceptual model, nutrient accessibility and energy (a combination of mixing depth and irradiance) are the principal abiotic factors that structure assemblages. Diatom dominance is expected under "temperate" conditions, which are characterized by deep mixing and high nutrient concentrations. Nine different

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harmful dinoflagellate types occupy the remaining matrix of nutrients and energy. According to this model, *P. micans* is classified as "Type II" and is a summer bloom taxa, expected to occur under somewhat elevated nutrient conditions. *L. polyedrum* is classified as "type V" and is expected to bloom under lower nutrient concentrations, in more shallow mixed layers. Although the Intaglio model makes predictions of broad taxonomic groups based on qualitative nutrient and energy conditions, it is a useful construct for evaluation of mechanisms controlling community structure, particularly those giving rise to HAB.

In this study, we present a record of harmful bloom taxa and test these predictions of the Intaglio model by relating their abundances to environmental conditions using time-series measurements in the Santa Monica Bay (SMB), CA over two annual cycles. The SMB is a partially enclosed inshore basin located adjacent to the Los Angeles metropolitan area and circulation patterns and seasonal and interannual hydrographic variability are well described (Hickey, 1992; Hickey et al., 2003; Nezlin et al., 2004). Strong local upwelling events associated with temperature minima occur in the winter and spring (Reid et al., 1958; Hickey, 1992; Gruber et al., in prep.), whereas stratification develops over the summer and autumn. The results of upwelling events, particularly those that occur to the west, can be advected horizontally into the SMB. Although phytoplankton dynamics are likely regulated by a combination of local forcing and larger scale circulation and transport, we focus here on macronutrient concentrations and local hydrographic conditions, which have been shown to control biological production in this region (Eppley and Renger, 1988; Nezlin and Li, 2003). Results are evaluated in the context of the Intaglio model, which also suggests that nutrient and energy conditions control the phytoplankton assemblage at the level of broad taxonomic groups. Further, for harmful bloom-forming taxa, the Intaglio model explicitly predicts that there will be increases in both nutrient concentrations and mixing that support *L. polyedrum, P. micans and, Pseudo-nitzschia spp.*, respectively (Smayda and Reynolds, 2001, 2003).

2. Methods

Time-series measurements of potentially harmful phytoplankton taxa and environmental conditions were conducted at the Santa Monica Bay Observatory (SMBO) interdisciplinary mooring site: 33°55.900 N, 118°42.937 W. This station is part of the Southern California Coastal Ocean Observing System (SCCOOS, http://www.sccoos.org/) and forthcoming publications will address diurnal studies of atmospheric and oceanic dissolved inorganic carbon and longer term phytoplankton dynamics. We report here data from 54 sampling dates between January 2004 and December 2005 (Tables 1 and 2). Cruises were generally conducted on a twice monthly basis, with an additional cruise during a large phytoplankton bloom in February 2004. Sampling of the upper water column aboard the R/V *Sea World UCLA* began at the mooring site at approximately 9:30 a.m. local time. Temperature, pressure and conductivity were measured during the downcast of a Seabird SBE9/11+conductivity temperature depth (CTD) profiler. During routine maintenance of the Seabird profiler, between May 24, 2005 and October 25, 2005, an Applied Microsystems MicroCTD unit was used. Mixed-layer depth was defined as the depth at which potential density changed by $\geqslant 0.01\,\mathrm{kg\,m^{-3}}$ over 3 m (Brainerd and Gregg, 1995). On some dates, heavy precipitation resulted in a large density gradient over the first 2–3 m. Near-surface temperatures were also measured at 1 h intervals using a SeaBird SBE9 attached to the moored buoy, beginning in April 2005. Niskin bottle samples were collected at 6

Table 1
Cruise number, sampling date in 2004, mixed-layer depth (m), total cell abundance (cells $\mathrm{l^{-1}}$) and percent contribution of *Pseudonitzschia spp., Lingulodinium polyedrum* and *Prorocentrum micans* to total phytoplankton abundance in surface waters (1 m)

	Date	mld (m)	Cell abundance	% *Pseudo. spp.*	% *L. polyedrum*	% *P. micans*
1	20 Jan	29	10,400	3	1	0
2	5 Feb	21	5000	30	16	0
3	13 Feb	35	214,000	63	1	<1
4	17 Feb	–	73,000	33	1	0
5	2 Mar	38	19,500	16	1	3
6	16 Mar	11	7160	37	15	1
7	30 Mar	9	169,000	71	1	6
8	14 Apr	10	141,000	27	1	1
9	27 Apr	12	181,000	56	<1	<1
10	11 May	9	39,600	5	19	2
11	25 May	20	32,400	1	50	0
12	8 Jun	11	24,000	19	38	0
13	22 Jun	15	37,400	3	38	0
14	6 Jul	9	2040	8	48	0
15	20 Jul	–	3970	1	1	0
16	10 Aug	8	3820	3	15	8
17	24 Aug	5	750	0	3	6
18	7 Sept	6	2190	0	14	1
19	21 Sept	17	14,000	13	1	0
20	5 Oct	15	17,000	<1	23	0
21	19 Oct	17	360	0	15	0
22	2 Nov	24	1250	0	18	9
23	16 Nov	9	1078	2	7	0
24	30 Nov	22	3740	1	31	6
25	14 Dec	34	210	0	<1	0

A percentage of "<1" indicates that cells were present, whereas "0" indicates that no cells of this taxa were observed. "–" indicates parameters that were not measured.

Table 2
As in Table 1 but for 2005

	Date	mld	Cell abundance	% *Pseudo. spp.*	% *L. polyedrum*	% *P. micans*
26	4 Jan	68	570	2	15	0
27	19 Jan	36	50,500	12	0	<1
28	25 Jan	12	4360	5	1	1
29	1 Feb	32	3650	5	1	0
30	15 Feb	31	11,800	<1	1	1
31	1 Mar	–	–	–	–	–
32	15 Mar	9	12,400	0	2	49
33	22 Mar	12	–	–	–	–
34	12 Apr	13	–	–	–	–
35	15 Apr	–	–	–	–	–
36	21 Apr	12	6510	5	1	7
37	26 Apr	13	760	0	0	37
38	10 May	5	50,400	<1	2	86
39	24 May	8	81,300	0	3	91
40	7 Jun	10	2980	5	2	3
41	21 Jun	9	4950	<1	3	27
42	6 Jul	–	6460	4	<1	1
43	21 Jul	5	23,200	<1	0	3
44	2 Aug	5	34,900	0	52	8
45	16 Aug	6	9680	0	7	1
46	30 Aug	8	9540	<1	32	2
47	13 Sept	9	3,59,900	0	90	2
48	27 Sept	11	43,300	<1	54	1
49	11 Oct	10	10,810	0	57	2
50	25 Oct	13	13,900	0	19	1
51	8 Nov	9	8010	0	36	0
52	22 Nov	18	23,900	<1	47	1
53	6 Dec	23	6020	2	6	1
54	20 Dec	–	–	–	–	–