

A Coastal Ocean Extreme Bloom Incubator

John P. Ryan,¹ James F. R. Gower,² Stephanie A. King,² W. Paul Bissett,³ Andrew M. Fischer,¹ Raphael M. Kudela,⁴ Zbigniew Kolber,¹ Fernanda Mazzillo,⁴ Erich V. Rienecker,¹ and Francisco P. Chavez¹

¹*Monterey Bay Aquarium Research Institute, Moss Landing, California, USA.*

²*Institute of Ocean Sciences, Sidney, B.C., Canada.*

³*Florida Environmental Research Institute, Tampa, Florida, USA.*

⁴*University of California, Santa Cruz, California, USA.*

Abstract

Novel remote sensing methods and in situ observations reveal that intense phytoplankton blooms occur frequently in Monterey Bay. These events can contain surface chlorophyll concentrations exceeding 500 $\mu\text{g l}^{-1}$ and occupy ~ 5 to 80 km^2 . They occur primarily during August - November and can persist for > 1 month. Maximum bloom frequency and mean intensity are in shallow (< 25 m) water of the northeastern bay, in coincidence with the warmest surface water, low wind stress, and retention of shallow waters. These conditions favor dinoflagellates, which can vertically migrate to acquire nutrients in the thermocline and aggregate as “red tide” near the surface. High-resolution mapping and sampling in the bloom area indicate that concentration of dinoflagellate blooms can occur in frontal zones. This bloom area receives nutrients from natural oceanographic processes and agricultural land drainage. Such coastal bloom incubation areas may disproportionately influence regional bloom ecology.

1 **Introduction**

2 Dense accumulations of phytoplankton that imbue the surface ocean with reddish
3 color, commonly called “red tide”, are one type of extreme bloom that can negatively
4 affect ecosystems and human health [Anderson, 1995; Glibert *et al.*, 2005; Kudela *et al.*,
5 2005]. Increasing global occurrence of harmful algal blooms (HABs) motivates
6 improved understanding of natural and human influences on bloom location, frequency
7 and severity [Hallegraeff, 2003]. Approximately 50% of all red tide forming species and
8 75% of all HAB species are dinoflagellates [Sournia, 1995; Smayda, 1997]. Where
9 phytoplankton growth is limited by low surface nutrient concentrations, and stratification
10 impedes renewal of surface nutrients by turbulent vertical mixing, dinoflagellate motility
11 provides a competitive advantage because their populations can migrate downward at
12 night to acquire nutrients [Cullen and Horrigan, 1981; Heaney and Eppley, 1981;
13 Donaghay *et al.*, 2006]. When these populations migrate up to the surface for
14 photosynthesis during the day, their dense aggregations produce strong bio-optical
15 signals that are detectable by satellite and airborne remote sensing.

16 Studies have documented intense dinoflagellate red tide blooms in Monterey Bay,
17 including species known to cause harm [Ryan *et al.* 2005; Donaghay *et al.* 2006; Kudela
18 *et al.* 2008; Curtiss *et al.* 2008; Ryan *et al.*, 2008a]. Here we apply unprecedented time
19 series of remote sensing and in situ data to identify and describe an “extreme bloom
20 incubator” in an area of Monterey Bay, and to examine conditions and processes
21 underlying this phenomenon.

22

23

Data and Methods of Analysis

Quantifying extreme bloom intensity and distributions using remote sensing requires measurement of the near-infrared (NIR) peak in upwelling radiance caused by such blooms [Gower *et al.*, 2005; Dierssen *et al.*, 2006; Schalles, 2006]. Only one multi-spectral satellite sensor, MERIS (Medium Resolution Imaging Spectrometer), has been designed to permit computation of an extreme bloom index, termed the Maximum Chlorophyll Index (MCI), using the NIR signal [Gower *et al.*, 2005; Gower and King, 2007]. We apply MCI images to illustrate synoptic bloom patterns and to compute long-term bloom statistics. The MCI image archive was screened to eliminate images having questionable signal in Monterey Bay near cloud edges or at steep satellite viewing angles, resulting in 75 good images in the August – November periods of 2002 - 2007. Of these images, 31 were full resolution (300 m), and 44 were reduced resolution (1200 m).

To compute bloom statistics from MCI images, we define blooms as $MCI > 0.3$, which corresponds to chlorophyll concentrations exceeding $\sim 30 \mu\text{g l}^{-1}$ [Gower *et al.*, 2005]. We computed indices of bloom probability (detection frequency) and mean intensity. Maps of bloom statistics were constrained to pixels that were well sampled through the time series (at least 80% of the maximum possible sample count). Illustration of average bloom intensity was constrained to pixels for which a representative mean could be calculated, defined as pixels having a bloom frequency of at least 25% of the maximum frequency.

To examine MCI statistics relative to oceanographic and meteorological conditions, we computed mean sea surface temperature (SST) and surface wind stress. SST images were from the MODIS (Moderate Resolution Imaging Spectroradiometer)

1 satellite sensor for August – November of 2002 - 2007; details of MODIS image
2 processing are in *Ryan et al.* [2008a]. Surface wind stress was from the COAMPS
3 (Coupled Ocean / Atmosphere Mesoscale Prediction System) high-resolution (3-km, 12-
4 hour) model of central California for August – November 2006.

5 Hyperspectral imaging spectrometers effectively measure the NIR reflectance
6 peak of extreme blooms. We present NIR-G-B composite images from the AVIRIS
7 (Airborne Visible-Infrared Imaging Spectroradiometer) and PHILLS (Portable
8 Hyperspectral Imager for Low Light Spectroscopy) sensors flown on aircraft over
9 Monterey Bay during the extreme bloom season. Details of these sensors and data
10 processing for coastal ocean studies are found in *Davis et al.* [2002] and *Ryan et al.*
11 [2005]. NIR, green and blue channel center wavelengths were {711, 549, 462} nm for
12 AVIRIS and {708, 540, 458} nm for PHILLS.

13 To describe water column structure in the bloom environment, we analyzed a
14 time-series of vertical sections mapped by an autonomous underwater vehicle (AUV)
15 between the inner shelf region of extreme bloom development and outer Monterey Bay.
16 From 24 surveys during August through November of 2003 - 2007, we computed mean
17 hydrographic sections. Details of AUV sensors and sampling are in *Ryan et al.* [2008b].
18 Valid means were constrained to well-sampled grid points (at least 80% of maximum
19 possible sample count).

20 During September 2007 the bloom environment was studied using multi-platform
21 observations, including drifter deployments, surface property mapping from a small boat,
22 and phytoplankton sampling. To track the movement of shallow waters in which red tide
23 dinoflagellates aggregate, satellite-tracked drifters were drogued between 1 and 2 m

1 depth. The flow-through mapping system drew water from 2 m depth and measured
2 temperature and salinity (SeaBird 45 thermosalinograph), chlorophyll fluorescence and
3 the maximum quantum yield [Kolber *et al.*, 1998]. Surface phytoplankton samples were
4 immediately preserved with 1% glutaraldehyde and kept in the dark at 4°C. Samples were
5 filtered through 5µm polycarbonate black filters and DAPI stained. Filters were mounted
6 on slides with immersion oil, and cell counts were performed using epifluorescence
7 microscopy.

9 **Results**

10 Shown in Figure 1 are remote sensing images of extreme blooms in Monterey
11 Bay. The MCI images (Figure 1a-f) show bloom scales from ~ 5 km² (Figure 1c) up to ~
12 80 km² (Figure 1f). Extracted surface chlorophyll concentrations measured during
13 blooms in 2006 (Figure 1e) and 2007 (Figure 1f) exceeded 500 µg l⁻¹. The large 2007
14 bloom (Figure 1f) persisted for more than a month, from early October to mid-November.
15 These examples, as well as the full image series, exhibit a preponderance of extreme
16 blooms in the northeastern bay. Images from all months show that extreme blooms are
17 limited primarily to the annual period of August – November. Airborne imaging
18 spectrometry provides less frequent coverage, but its high spatial resolution emphasizes
19 the patchiness of such extreme blooms (Figure 1g-i), as well as small-scale physical
20 processes influencing bloom distributions (e.g. eddy in Figure 1i).

21 Indices of extreme bloom probability (Figure 2a) and mean intensity (Figure
22 2b) show the prevalence of intense blooms in the NE bay, in waters shallower than 25 m.
23 The entire bay except a thin border along the coast was well sampled, so most of the bay

1 is accurately described by low to zero probability of extreme bloom detection. The NE
2 bay, where bloom probability and mean intensity are highest, exhibits the warmest mean
3 SST during the extreme bloom season (Figure 2c). These warm waters are adjacent to
4 the swath of coldest average SST, which is due to filaments of recently upwelled water
5 that enter the bay from the north [Rosenfeld *et al.*, 1994]. Surface wind stress is also
6 lowest over the inner bay, and the warm waters of the NE bay are in a region of minimum
7 average wind stress.

8 In the area where mean bloom MCI is highest (Figure 2b), drifter studies
9 demonstrated retention of a red tide bloom. On September 25, 2007 remote sensing and
10 in situ observation showed the presence of an intense surface bloom in the NE bay
11 (Figure 2d; note the reddish color in the MODIS image). Drifters released within the
12 bloom waters were retained in the same area for three days, despite the nearby influence
13 of an eddy that entrained waters from other areas of the bay (Figure 2d). MODIS
14 chlorophyll fluorescence line height for 9/25/2007 (not presented) indicates eddy
15 entrainment from nearshore waters of the northern bay, south of where the drifters
16 showed retention. This retention pattern contrasts with other drifter studies, which show
17 that surface waters in the NE bay can be rapidly transported ~50 km in three days out of
18 the bay and northward along the coast [Ryan, unpubl. data].

19 The in situ climatology from the AUV survey line (Figure 2a) shows that the
20 increases in bloom probability and mean intensity toward the coast (Figure 3a)
21 correspond with thermal stratification of a shallow warm lens (Figure 3b). Further,
22 relatively high salinity waters shoal toward the coast and extend into the thermocline

1 below the warm lens (Figure 3b), presumably indicating relatively high nutrient
2 availability in the thermocline on average.

3 In situ surface observations showed patterns consistent with the description from
4 remote sensing. A very dense red tide patch was observed in the NE bay (Figure 4a), in
5 the region where mean bloom MCI is highest (Figure 2b). The patch exhibited not only
6 high chlorophyll and strong reddish discoloration, but also high maximum quantum yield
7 (Fv/Fm; Figure 4b), indicating a healthy bloom population. The intense red tide patch
8 was within a frontal zone, defined by relatively strong gradients in temperature and
9 salinity (Figure 4c,d). The highest dinoflagellate abundance of 2.8×10^5 cells l⁻¹ was
10 found in the sample nearest the peak in chlorophyll (Figure 4a). Dinoflagellate species
11 sampled in this bloom area included *Akashiwo sanguinea*, *Alexandrium catenella*,
12 *Ceratium divaricatum*, *Ceratium furca*, *Cochlodinium fulvescens*, *Preperidinium* sp., and
13 *Protoperidinium* sp.

14 15 **Discussion**

16 Monterey Bay is the largest open embayment along the U.S. west coast, and an
17 area of the bay is the site of frequent extreme blooms, especially in the fall between
18 August and November. New remote sensing techniques permitted this discovery and
19 provided the impetus for closer study of this ecologically significant area. The strong
20 bio-optical signal of these blooms is due to dense surface aggregations of phytoplankton
21 containing exceptionally high chlorophyll concentrations. Dinoflagellates that aggregate
22 near the surface during the day have been observed with remote and in situ sensing
23 during these extreme blooms in NE Monterey Bay [Ryan *et al.*, 2005; 2008a; Kudela *et*

1 *al.*, 2008; *Rienecker et al.*, 2008], and this specific type of bloom presumably underlies
2 the characterizations from remote sensing.

3 Observed natural conditions that would favor dinoflagellates include relatively
4 strong thermal stratification, low wind stress (promoting maintenance of stratification),
5 and high nutrient availability in the thermocline. Dinoflagellates would be favored
6 because they can migrate into the thermocline to acquire nutrients, an ecological
7 phenomenon illustrated by studies in Monterey Bay [*Donaghay et al.*, 2006]. Frequent
8 observation of dense surface aggregations also implies relatively weak dispersal. Low
9 wind stress in the NE bay would minimize dispersal by wind-driven turbulent vertical
10 mixing. Drifter studies showed reduced dispersal by lateral advection (i.e. enhanced
11 retention) of a red tide bloom in the NE bay. The example of bloom retention we
12 observed in the area of highest average bloom intensity is distinct from the recirculation
13 pattern described for the entire northern bay during periods of upwelling [*Graham and*
14 *Largier*, 1997]. This emphasizes the need for studying very near-shore circulation
15 patterns in understanding bloom dynamics.

16 Where favored by environmental conditions, dense dinoflagellate populations
17 would have an advantage in utilizing periodic nutrient influx. The primary natural
18 nutrient sources to this region are upwelling filaments [*Rosenfeld et al.*, 1994] and
19 internal tidal pumping from Monterey Canyon [*Shea and Broenkow*, 1982]. The northern
20 shelf is distinguished from the southern shelf by stronger influence of recently upwelled
21 waters (Figure 2c) [*Rosenfeld et al.*, 1994]. Shelf bathymetry may also influence nutrient
22 transport and coupling to benthic nutrient processes. The shallow shelf area of the
23 northern bay, where the blooms are prevalent, is much larger than that in the southern

1 bay. The roles of natural nutrient supply processes and shelf bathymetry require further
2 study to evaluate their relative importance in the sustenance of these extreme blooms.

3 Monterey Bay coastlands also host intensive agriculture, and these lands drain
4 into rivers and a tidally forced estuary that connect with the bay. MERIS images show
5 nearshore bloom patches located at riverine and estuarine outflows. The first MERIS
6 detection of the extensive 2007 bloom was over a nearshore area between riverine and
7 estuarine outflows, shortly after the first major rain of the fall season. This rain event
8 resulted in very high nutrient loading that was measured by moored sensors near the
9 estuarine outflow. Drifter studies during fall and winter show that the outflow plumes in
10 the central bay flow predominantly northward into the region where extreme blooms are
11 most frequent and intense [*Fischer*, 2008]. The potential for bloom initiation by
12 agricultural nutrient inputs exists, and the potential role of this ecosystem perturbation
13 must be examined.

14 Beyond growth, accumulation and low dispersal, active concentration of bloom
15 biomass through biological-physical interactions likely plays a significant role in the
16 intensity and patchiness of some of these extreme bloom aggregations. One interaction
17 involves concentration in convergence zones, where populations of motile species can
18 overcome downwelling by swimming toward the surface. Convergent fronts in this
19 region have been associated with particularly intense red tide aggregations [*Ryan et al.*,
20 2005]. The in situ survey presented here also showed an intense, strongly colored,
21 dinoflagellate bloom patch in a frontal zone, consistent with this mechanism of
22 concentration. Biological-physical interactions may also influence the bloom
23 environment itself. Color loading due to dense aggregations of phytoplankton and high

1 concentrations of colored dissolved organic matter intensifies shallow absorption of solar
2 insolation, thereby promoting thermal stratification [*Cahill et al.*, 2008].

3 Process studies show that dense blooms in NE Monterey Bay can seed larger
4 blooms as populations are advected [Ryan et al., 2005; 2008a; Kudela et al., 2008;
5 Rienecker et al., 2008]. By promoting frequent development of extreme blooms, this
6 area of the California coast may exert a disproportionately large influence on adjacent
7 coastal regions. Drifter studies show that when upwelling favorable winds relax, the
8 shallow waters of the NE bay are rapidly flushed out of the bay and northward along the
9 coast [*Ryan et al.*, 2008b; *Ryan*, unpubl. data]. Similar “bloom incubators” are indicated
10 by observations from other sheltered regions of coastal upwelling systems, including
11 northern San Louis Obispo Bay on the California coast [*M. Moline*, personal
12 communication] and Lisbon Bay on the Iberian coast [*Moita et al.*, 2006]. Understanding
13 the ecology of such incubator regions, where natural and human influences can both be
14 significant, is important to understanding red tide and HAB ecology of the larger marine
15 ecosystems in which they reside.

16

17

1 **Acknowledgements**

2 The David and Lucile Packard Foundation funded MBARI field operations and MBARI
3 co-author efforts. We thank MBARI AUV and R/V Zephyr personnel, and G. Friederich
4 and M. Suro for assistance with drifters. The European Space Agency provided MERIS
5 data; MERIS data processing was funded by Fisheries and Oceans Canada and the
6 Canadian Space Agency. MODIS Level 1 data were provided by the LAADS data
7 system, and data processing was enabled by the NASA SeaDAS team and the MODIS
8 Ocean Biology Processing Group. AVIRIS airborne remote sensing was supported by
9 NASA Grant NAG5-12692. PHILLS airborne remote sensing, data processing and data
10 management were supported by NOAA Programs: CICORE (Center for Integrative
11 Coastal Observation, Research, and Education) and MERHAB (Monitoring and Event
12 Response for Harmful Algal Blooms, Grant NA05NOS4781220), and by the Office of
13 Naval Research. COAMPS atmospheric model results were provided by Fleet Numerical
14 Meteorology and Oceanography Center.

15

16

References

- Anderson, D.M. (1995), Toxic red tides and harmful algal blooms: a practical challenge in coastal oceanography, *Reviews of Geophysics*, 33(suppl.), 1189-1200.
- Cahill, B., O. Schofield, R. Chant, J. Wilkin, E. Hunter, S. Glenn, P. Bissett (2008), Dynamics of turbid buoyant plumes and the feedbacks on near-shore biogeochemistry and physics, *submitted to Geophys. Res. Let.*
- Cullen, J. J., and S. G. Horrigan (1981), Effects of Nitrate on the Diurnal Vertical Migration, Carbon to Nitrogen Ratio, and the Photosynthetic Capacity of the Dinoflagellate *Gymnodinium splendens*, *Marine Biology*, 62, 81-89.
- Curtiss, C. C., G. W. Langlois, L. B. Busse, F. Mazzillo, and M. W. Silver (2008), The emergence of *Cochlodinium* along the California Coast (USA), *Harmful Algae*, 7, 337–346.
- Davis, C. O., J. Bowles, R. A. Leathers, D. Korwan, T. V. Downes, W. A. Snyder, W. J. Rhea, W. Chen, J. Fisher, W. P. Bissett and R. A. Reisse (2002), Ocean PHILLS hyperspectral imager: design, characterization, and calibration, *Optics Express*, 10(4), 210-221.
- Dierssen, H. M., R. M. Kudela, J. P. Ryan, and R. C. Zimmerman (2006), Red and black tides: Quantitative analysis of water-leaving radiance and perceived color for phytoplankton, colored dissolved organic matter, and suspended sediments, *Limnol. Oceanogr.* 51(6), 2646-2659.
- Donaghay, P. L., J. M. Sullivan, J. E. Rines, J. Graff, A. K. Hanson, and D. V. Holliday (2006), The Importance of Swimming Behavior in Controlling the Formation, *EOS Trans. Am. Geophys. Union*, 87(36).

1 Fischer, A. M. (2008) The structure, composition, and dynamics of a central California
2 estuarine discharge plume. PhD Thesis, in prep.

3 Glibert, P. M., D. M. Anderson, P. Gentien, E. Graneli, and K. G. Sellner (2005), The
4 global complex phenomena of harmful algal blooms, *Oceanography*, 18, 137-147.

5 Gower J., S. King, G. Borstad, and L. Brown (2005), Detection of intense plankton
6 blooms using the 709 nm band of the MERIS imaging spectrometer, *Int. J. Remote*
7 *Sensing*, 26, 2005-2012.

8 Gower, J., and S. King (2007), An Antarctic ice-related “superbloom” observed with the
9 MERIS satellite imager, *Geophys. Res. Let.*, 34, L15501,
10 doi:10.1029/2007GL029638.

11 Graham W. M., and J. L. Largier (1997), Upwelling shadows as nearshore retention sites:
12 the example of northern Monterey Bay, *Cont. Shelf Res.*, 17, 509-532.

13 Hallegraeff, G. M. (2003), Harmful algal blooms: a global overview, in *Manual on*
14 *Harmful Marine Microalgae.*, edited by G.M . Hallegraeff, D. M. Anderson and A.
15 D. Cembella, pp. 25-49, UNESCO, Paris.

16 Heaney, S. I., and R. W. Eppley (1981), Light, temperature and nitrogen as interacting
17 factors affecting diel vertical migrations of dinoflagellates in culture, *J. Plankton*
18 *Res.*, 3(2), 331-344.

19 Kolber, Z. S., O. Prasil, and P. G. Falkowski (1998), Measurements of variable
20 chlorophyll fluorescence using fast repetition rate techniques. I. Defining
21 methodology and experimental protocols, *Biochem. Biophys. Acta*, 1367, 88-106.

22 Kudela, R. M., G. Pitcher, T. Probyn, F. Figueiras, T. Moita, and V. Trainer (2005),
23 Harmful Algal Blooms in coastal upwelling systems, *Oceanography*, 18, 184-197.

1 Kudela, R. M., J. P. Ryan, M. D. Blakely, J. Q. Lane, and T. D. Peterson (2008), Linking
2 the physiology and ecology of *Cochlodinium* to better understand harmful algal
3 bloom events: a comparative approach, *Harmful Algae*, 7, 278-292.

4 Moita, M.T., S. Palma, P. B. Oliviera, T. Vidal, A. Silva, and M. G. Vilarinho (2006),
5 The return of *Gymnodinium catenatum* after 10 years: bloom initiation and transport
6 of the Portuguese coast. Proceedings of 12th International Congress on Harmful
7 Algae, PO.06-14, September 2006, Copenhagen.

8 Rienecker, E. R., J. P. Ryan, R. Marin III, M. Blum, C. Dietz, and F. P. Chavez (2008),
9 Synoptic mapping of the phytoplankton size distribution, with applications to the
10 ecology of red tides and harmful algal blooms, *Limnol. Oceanogr. Methods*, in press.

11 Rosenfeld, L. K., F. B. Schwing, N. Garfield, and D. E. Tracy (1994), Bifurcated flow
12 from an upwelling center: a cold water source for Monterey Bay, *Cont. Shelf Res.* 14,
13 931-964.

14 Ryan, J. P., H. M. Dierssen, R. M. Kudela, C. A. Scholin, K. S. Johnson, J. M. Sullivan,
15 A. M. Fischer, E. V. Rienecker, P. R. McEnaney, and F. P. Chavez (2005), Coastal
16 ocean physics and red tides: an example from Monterey Bay, California,
17 *Oceanography*, 18, 246-255.

18 Ryan, J. P., A. M. Fischer, R. M. Kudela, J. F. R. Gower, S. A. King, R. Marin III, and F.
19 P. Chavez (2008a), Remote sensing of red tide bloom advection, fertilization, and
20 retention in Monterey Bay, California, *Submitted to Cont. Shelf Res.*

21 Ryan, J. P., M. A. McManus, J. D. Paduan, and F. P. Chavez (2008b), Phytoplankton thin
22 layers within coastal upwelling system fronts. *Mar. Ecol. Prog. Ser.*, 354, 21-34.

1 Schalles, J. F., 2006, Optical remote sensing techniques to estimate phytoplankton
2 chlorophyll a concentration in coastal waters with varying suspended matter and
3 CDOM concentrations, in *Remote Sensing of Aquatic Coastal Ecosystem Processes:
4 Science and Management Application*, edited by L. L. Richardson, and E. F.
5 LeDrew, Springer, Berkeley, pp. 27-75.

6 Shea, R. E., and W. W. Broenkow (1982), The role of internal tides in the nutrient
7 enrichment of Monterey Bay, California, *Estuarine, Coastal and Shelf Science*, 15,
8 57-66.

9 Smayda, T. J (1997), Harmful algal blooms: their ecophysiology and general relevance to
10 phytoplankton blooms in the sea, *Limnol. Oceanogr.*, 42:1137-1153.

11 Sournia, A. (1995), Red-tide and toxic marine phytoplankton of the world ocean: an
12 inquiry into biodiversity, in *Harmful Marine Algal Blooms*, edited by P. Lassus, G.
13 Arzul, E. Erard-Le Denn, P. Gentien, and C. Marcaillou-LeBaut, Lavoisier, Paris, pp.
14 103-112.

15

16

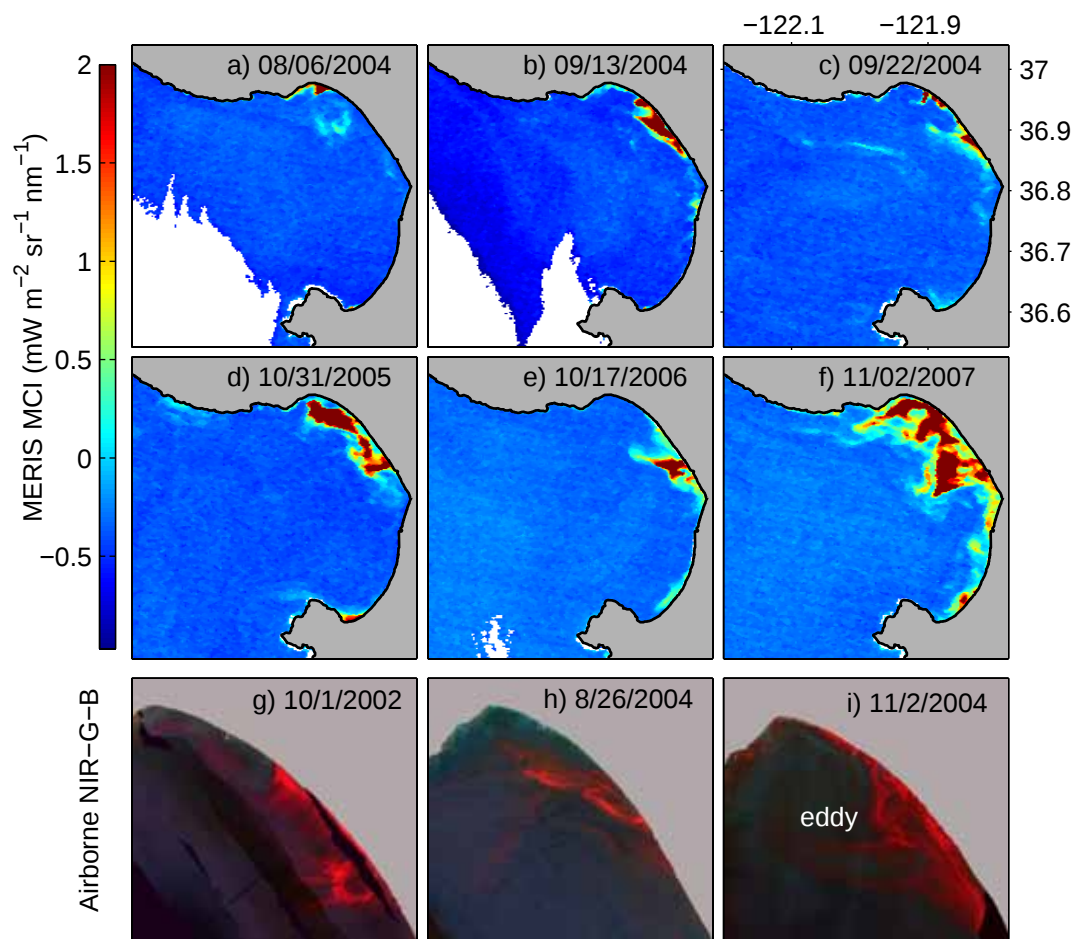
Figure Captions

Figure 1. Remote sensing images of extreme blooms in Monterey Bay, California. In all images, red indicates extreme “red tide” bloom patches. (a-f) Full-resolution (300 m) images of the Maximum Chlorophyll Index (MCI) from the MERIS satellite sensor. (g-i) NIR-G-B composite images from hyperspectral airborne remote sensing of the NE bay; (g) and (i) are from PHILLS (2 m resolution); (h) is from AVIRIS (17 m resolution).

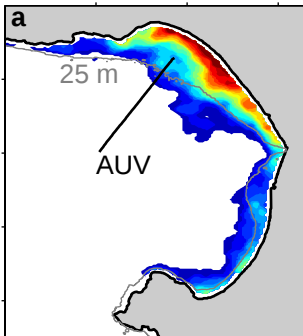
Figure 2. Bloom statistics and relevant oceanic and atmospheric conditions. (a) bloom probability (detection frequency); (b) mean bloom intensity; (c) sea surface temperature (SST) and wind stress; (d) retention of red tide shown with 9/25/2007 MODIS true color image and 9/25/2007 to 9/28/2007 drifter tracks (white dots).

Figure 3. Mean water column structure underlying the extreme bloom region along the repeated AUV transect (location in Figure 2a). (a) bloom probability and mean intensity; (b) mean water column temperature (contours) and salinity > 33.5 psu (shaded).

Figure 4. In situ mapping of bloom scales, species, and relationships to hydrography. Survey was conducted on September 19, 2007. (a) Calibrated fluorometric chlorophyll and dinoflagellate cell counts at sampling stations; (b) maximum quantum yield (F_v/F_m); (c) temperature; (d) salinity.

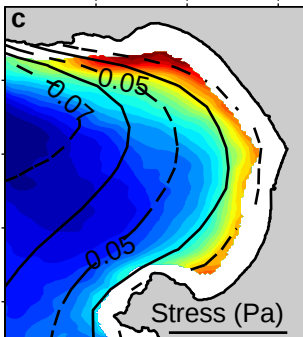
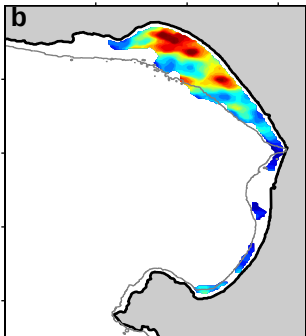
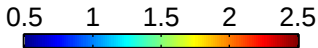


Bloom Probability (%)



Mean MCI

($\text{mW m}^{-2} \text{sr}^{-1} \text{nm}^{-1}$)

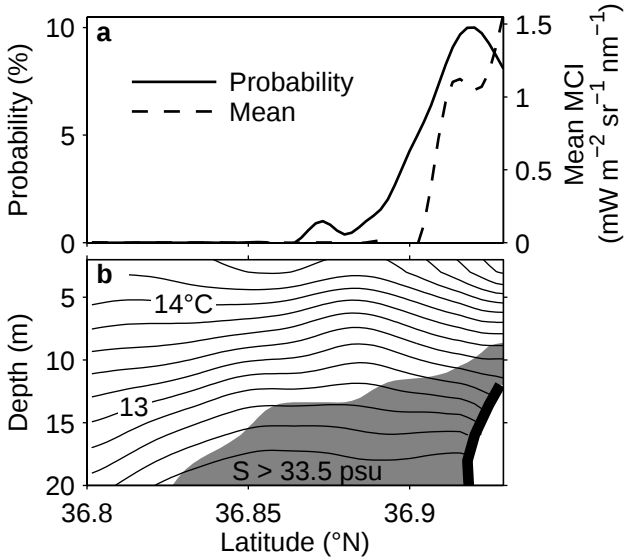


13 13.5 14 14.5

SST ($^{\circ}\text{C}$)

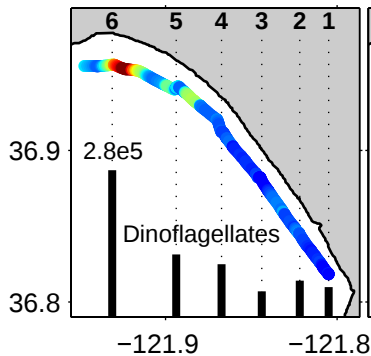
A horizontal color bar ranging from blue (13) to red (14.5), with intermediate colors for 13.5 and 14.





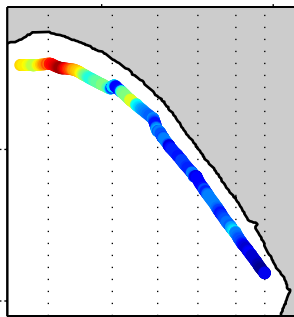
a) Chlorophyll ($\mu\text{g l}^{-1}$)

20 30 40 50

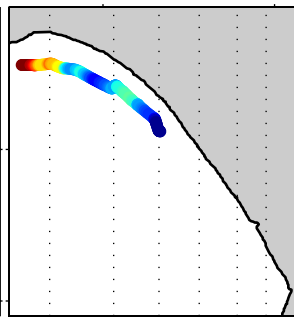


b) Fv/Fm

0.4 0.45 0.5

c) Temperature ($^{\circ}\text{C}$)

15.5 15.8 16.1 16.4



d) Salinity (psu)

33.49 33.5 33.51

