



ELSEVIER

Contents lists available at [SciVerse ScienceDirect](http://www.sciencedirect.com)

Continental Shelf Research

journal homepage: www.elsevier.com/locate/csr

Research papers

Natural intrusions of hypoxic, low pH water into nearshore marine environments on the California coast

J. Ashley T. Booth^{a,*}, Erika E. McPhee-Shaw^b, Paul Chua^c, Eric Kingsley^d, Mark Denny^a, Roger Phillips^d, Steven J. Bograd^e, Louis D. Zeidberg^f, William F. Gilly^a^a Hopkins Marine Station, Stanford University, 120 Oceanview Boulevard, Pacific Grove, CA 93950, USA^b Moss Landing Marine Laboratories, California State Universities, 8272 Moss Landing Road, Moss Landing, CA 95039, USA^c Scripps Institution of Oceanography, University of California, San Diego, La Jolla, CA 92093, USA^d Monterey Bay Aquarium, 886 Cannery Row, Monterey, CA 93940, USA^e Environmental Research Division, Southwest Fisheries Science Center, NOAA, 1352 Lighthouse Avenue, Pacific Grove, CA 93950, USA^f Department of Ecology & Evolutionary Biology, University of California, Los Angeles, 100 Stein Plaza, Los Angeles, CA 90094, USA

ARTICLE INFO

Article history:

Received 21 January 2012

Received in revised form

14 June 2012

Accepted 21 June 2012

Available online 29 June 2012

Keywords:

Hypoxia

Oxygen

pH

Internal tides

Coastal ecosystems

Upwelling

ABSTRACT

A decade-long time series recorded in Central California demonstrates that a shallow, near-shore environment (17 m depth) is regularly inundated with pulses of cold, hypoxic and low-pH water. During these episodes, oxygen can drop to physiologically stressful levels, and pH can reach values that potentially result in dissolution of calcium carbonate. Pulses of the greatest intensity arose at the onset of the spring upwelling season, and fluctuations were strongly semidiurnal and diurnal. Arrival of cold, hypoxic water on the inner shelf appears to be driven by tidal-frequency internal waves pushing deep, upwelled water into nearshore habitats. We found no relationship between the timing of low-oxygen events and the diel solar cycle. These observations are consistent with the interpretation that hypoxic water is advected shoreward from the deep, offshore environment where water masses experience a general decline of temperature, oxygen and pH with depth. Analysis of the durations of exposure to low oxygen concentrations establishes a framework for assessing the ecological relevance of these events, but physiological tolerance limits to such hypoxic events are not well documented for most near-shore organisms expected to be impacted.

© 2012 Elsevier Ltd. All rights reserved.

1. Introduction

Continental shelves off the west coast of North America do not experience the eutrophication and severe hypoxia from terrestrial-nutrient-driven algal production experienced by regions such as the Gulf of Mexico (Rabalais and Turner, 2002). However, observations of dissolved oxygen (DO) over the past decade demonstrate the prevalence of seasonal hypoxic conditions on the shelves of Washington, Oregon, and California (Diaz and Rosenberg, 2008; Whitney et al., 2007; Chan et al., 2008). Seasonal upwelling and its shoreward transport of previously deep, low-DO water, is a known contributor to these events, and this factor, along with interannual variations in the oxygen concentrations of source water plays a strong role in determining the oxygen climate over mid- and outer shelves in this system (Grantham et al., 2004). However, upwelling draws from depths shallower than the 600- to 1300-m depth of the oxygen

minimum zone (OMZ), and onshore advection of deep water cannot alone explain hypoxic events.

Studies over Washington and Oregon shelves demonstrate the importance of upwelling of low-oxygen water, but also show that benthic and water-column biogeochemical processes are additional factors necessary to explain reduced oxygen concentrations in these regions (Connolly et al., 2010). Low DO has been found on Oregon shelves both over mid- and shallow-shelf depths, and some of the shallower observations were documented during an extreme hypoxia/anoxia event that were biologically driven (Grantham et al., 2004). Less is known about variability and short-term advection of low oxygen over shallow and mid-depth shelves. Surface mixing and atmospheric equilibration maintain high DO concentrations in near-surface waters, but below the thermocline DO decreases with depth, and fluctuations in thermocline depth, surface mixed-layer thickness, and onshore/offshore advection can all affect oxygen concentrations on the inner shelf. Oxygen at depths of < 40 m on the Oregon and Washington shelves shows variability at shorter time scales than does oxygen on the middle and outer shelf depths (Connolly et al., 2010; Grantham et al., 2004). However, little is known about how onshore transport of deep waters affects oxygen concentrations in the shallow,

* Corresponding author. Tel/fax.: +1 650 283 2364.

E-mail address: abooth@atmos.ucla.edu (J.A.T. Booth).

inner shelf (depth < 20 m, roughly within 1-km of the coast). We also know less about oxygen on shelves of Central California than we do about shelves in the northern part of the California Current System off Oregon.

Here we take advantage of a decade-long data set to examine oxygen variability on the inner shelf off of Central California. The Monterey Bay Aquarium in Monterey, California, has been monitoring oxygen concentrations in the seawater pumped into their facility in order to ensure proper oxygenation for aquarium fauna. Records of oxygen, along with temperature and sometimes pH, were collected regularly at a site close to shore (~340 m) with a water depth of ~19 m. These data provide an extremely valuable glimpse of coastal oxygen variability in an area of great ecological importance. Our objectives were to document the range and temporal variability of oxygen concentrations in near-bottom inner-shelf waters in order to better understand oxygen stress on the subtidal communities of this productive rocky environment. We found intense temporal variation in near-coast oxygen and pH, and surprisingly low oxygen concentrations for such shallow waters. Variability occurred on both short (semidiurnal and diurnal) and much longer (seasonal) time-scales, with the seasonal pattern being dominated by variation in wind-driven in offshore areas. A tight relationship between temperature, DO and pH, combined with a lack of evidence for daily-scale local consumption of oxygen, suggest that most variability at the monitoring site was due to advection onshore of previously deeper, low-DO water, by seasonal upwelling modulated by semidiurnal baroclinic motions.

2. Data collection and study site

During the past decade the Monterey Bay Aquarium (MBA) has monitored seawater temperature, DO and pH from the inner shelf of southern Monterey Bay (36.621°N, 121.899°W; Fig. 1). The site is in the southeastern corner of the Bay where the coast is generally

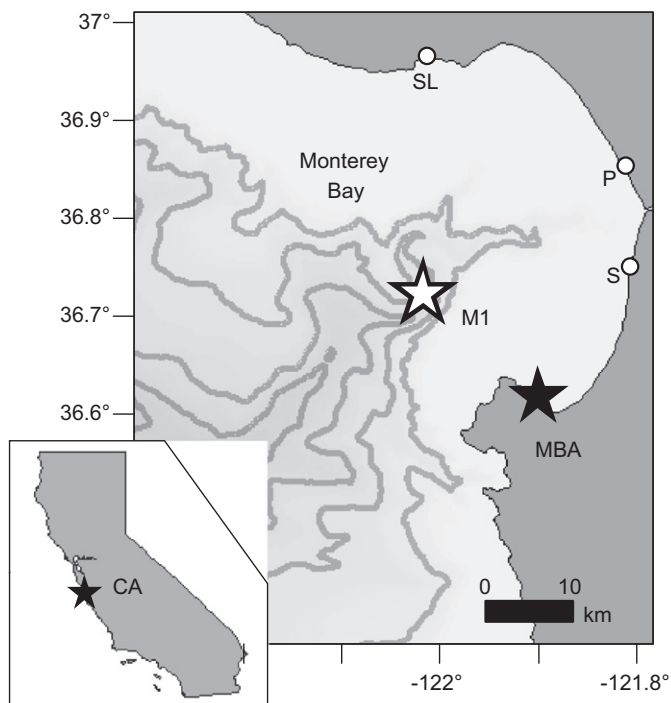


Fig. 1. Map of study area showing locations of MBA and shallow cast (black star) and deep-water cast (white star). Bathymetric contours are at 500 m intervals. Locations of river mouths are also noted—Salinas (S), Pajarro (P) and San Lorenzo (SL).

protected from surface swell and strong surf. Seawater is sampled from intake pipes that draw in water from 17-m depth, 2 m above the bottom, and routinely monitored as part of the animal husbandry division's water quality program. Measurements are made every 5 min and automatically logged. Recording started for temperature in June 1995 (only data after April 2000 are analyzed here), DO in April 2000 and pH in September 2009, and monitoring continues to the present. Typical flow rate was $\sim 110 \text{ L s}^{-1}$ and sensors were cleaned weekly and calibrated monthly. Oxygen was measured with a Point Four OxyGuard Type 1 Stationary Probe (OxyGuard International, Birkerød, Denmark), and temperature was measured with an AGM single element type "J" thermocouple (AGM Electronics, Tucson, AZ). On 24 September 2009 a GLI Encapsulated LCP (Liquid Crystal Polymer) differential pH sensor with internal preamplifier and glass electrode (Hach, Loveland, CO) was installed and has since been calibrated monthly using NBS-certified standards (Fisher Scientific, Pittsburgh, PA). In addition, manual 'spot checks' of pH have been taken once or twice per week since 18 June 1996 using initially a Corning then a Hach IntelliCAL liquid-filled pH electrode (results discussed in Ref. Woodson et al. (2007)). The pH probes were calibrated approximately every one to three months during this period using NBS-certified standards. Although use of NBS low-salinity standards does not achieve the accuracy possible with buffers of seawater salinity (Millero et al., 1993), any error is much smaller than the natural variations described and does not affect the conclusions of this study.

3. Consideration of errors

Raw DO measurements were taken in units of mg L^{-1} from 1 April 2000 to 15 December 2003, but the unit recorded was changed to percent saturation from 2004 to present. To achieve consistency over the record, we converted percent saturation readings to mg L^{-1} using the recorded temperature, an assumed salinity of 34 and published oxygen-solubility equations (Colt, 1984). Based on several conductivity-temperature-depth (CTD) profiles obtained with a Seabird SBE19plus profiler (Seabird Electronics, Bellevue, Washington) at the study site in March and April of 2009, salinity was found to fluctuate between 33.5 and 34.0. Such variation could lead to a maximum predicted error of 0.01% for the DO conversion, and thus would have negligible effect on our results. Between April 1, 2000 and August 15, 2001, the oxygen monitoring system was programmed to record measurements only up to 10 mg L^{-1} , but after that period the range was extended to 20 mg L^{-1} because DO concentrations often exceeded the original limit. For the entire study period, 19.6% of DO and 2.7% of temperature readings were unusable or missing, generally due to system maintenance issues.

Salinity, temperature and DO were also recorded for three short time-series from a moored CTD stationed at two locations within 150 m of the intake pipe site (36.6214°N, 121.8996°W and 36.6212°N, 121.9005°W) (1 October–17 November 2009; 16 July–3 August 2010; 17 August–30 September 2010). Instrumentation included a Seabird SBE16plus CTD equipped with an optode DO sensor (Aanderra Data Instruments, Bergen, Norway). The CTD was moored between 14–16 m depth in 17 m of water. A comparison between the moored CTD and MBA temperature and DO time series showed that MBA measurements lagged the environment by approximately 10 min and that some high-frequency variation was reduced in the MBA record, presumably by mixing in the input plumbing system. Temperatures at the three sites were significantly correlated (mean cross-covariance coefficient = 0.96, p -values < 0.001). DO measurements showed a mean cross-correlation value of 0.84 (p -values < 0.001) and MBA DO values were on average 0.86 mg L^{-1} higher in the seawater

intake system than at the moored CTD across all three deployments. Estimates of errors from records previous to 2009 were not available. A detailed description of the monitoring system and error analysis are provided elsewhere (Booth, 2011).

Four CTD casts were also conducted within 50 m of the MBA intake in April 2009 with a Seabird SBE19plus equipped with a SBE43 DO sensor to capture a snapshot of water-column under different degrees of stratification and a measure of salinity (Fig. 2). Deep-water profiles typical of the offshore region (Fig. 2) were conducted in March 2010 in the Monterey Submarine Canyon (36.726°N, 122.017°W) with the same CTD profiler and are considered representative of those waters (Silguero and Robison, 2000).

4. Scales of variability

The high-resolution record (5 min sampling) recorded at MBA reveals short-term (< 24 h) intense fluctuations in DO, temperature

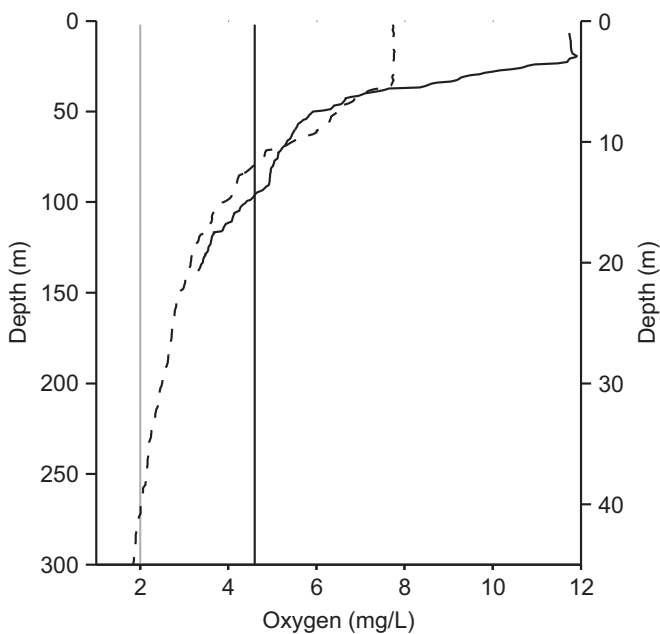


Fig. 2. Oxygen concentration from a typical deep-water CTD cast over the Monterey submarine canyon (dashed line, left vertical scale) compared to shallow cast (solid black line, right vertical scale) during an hypoxic event near the MBA intake pipe (see Section 4). The 4.6 mg L^{-1} sublethal level is given by the black vertical line, and the 2 mg L^{-1} potentially lethal threshold is shown by a grey vertical line.

and pH (Fig. 3). During such events, DO at the MBA intake often fell as low as approximately 25–50% saturation ($2\text{--}4.6 \text{ mg O}_2 \text{ L}^{-1}$), a range that is typically found at much greater depths in offshore waters (Silguero and Robison, 2000) (Fig. 2). Oxygen concentrations in this range are low enough to constitute a hypoxic physiological stress (Vaquer-Sunyer and Duarte, 2008) as discussed later in this paper.

Inner-shelf hypoxic events were most pronounced in spring and summer. A dramatic rise in the amplitude of DO fluctuations coincided with the onset of the spring upwelling season, typically in March–April (Bograd et al., 2008) (Fig. 4). This timing strongly suggests a connection between hypoxic events and wind-driven seasonal upwelling of water from a depth above the offshore OMZ. Concomitant variations in temperature and pH at the MBA intake site (Fig. 3) demonstrate that low oxygen and pH is associated with cold water, and strongly suggests that onshore advection of dense, deeper water is a dominant source of low oxygen. Ten-minute averaged DO and temperature from April 2000 to April 2011 were significantly correlated (correlation coefficient=0.52, p -value < 0.001) with no lag, similarly DO and pH from September 2009 to February 2011 were significantly correlated (correlation coefficient=0.82, p -value < 0.001). Off-shore waters overlying the OMZ are the closest source of water with this suite of properties. In the Monterey Bay region, the upper boundary of the OMZ occurs at depths of about 400 m where the oxygen concentration is 0.5 mg L^{-1} , but a concentration of 4.6 mg L^{-1} , a sublethal stress threshold (Vaquer-Sunyer and Duarte, 2008), typically occurs at a depth of 80–100 m of the water column (Silguero and Robison, 2000) (Fig. 2).

Seasonal DO variability (Fig. 4) did not intensify towards the end of the upwelling season. This would be expected if microbial respiratory processes cumulatively depleted DO on the continental shelf over the course of the spring and summer, a situation that can occur off the Oregon/Washington shelf (Grantham et al., 2004; Hales et al., 2006; Connolly et al., 2010). However, the Monterey Bay shelf is much narrower. Even in the retentive “upwelling shadow” in the northern corner of Monterey Bay, peak residence times are 8 to 17 day (Woodson et al., 2007). Depth-averaged tidal excursions are small, usually less than a few kilometers (Carter, 2010), but lower frequency wind-forced, along-coast currents are often 5 to 10 cm/s on the Monterey southern shelf at mid-shelf depths (McPhee-Shaw, unpublished data), suggesting the likelihood of shelf-scale flushing during wind reversal events common throughout all seasons. However the primary evidence arguing against accumulation of depleted DO over shelf sediments is that the temperature-dissolved oxygen relationship did not change (i.e., progressively lower oxygen concentration for the same temperature) as the season progressed.

Another potential source of hypoxia could involve remineralisation of primary production fuelled by run-off of terrestrial nutrients into Monterey Bay as occurs in many coastal areas of the US East and

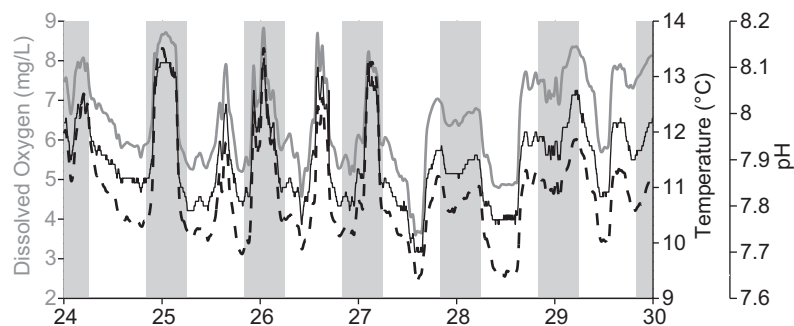


Fig. 3. Example of covariation of oxygen (grey), temperature (dashed black) and pH (black). Data are from MBA seawater intake during a series of intense hypoxic/low pH/cold episodes in April, 2010. Nighttime hours are shaded.

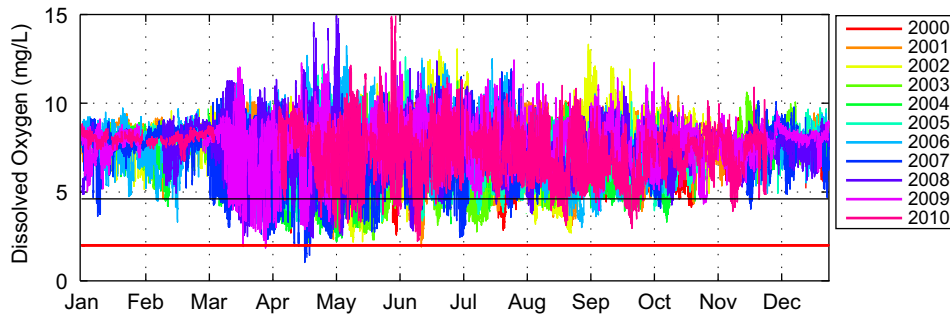


Fig. 4. Seasonal variation of dissolved oxygen with years overlaid (April 2000–December 2010) measured by MBA at the intake site. The 4.6 mg L^{-1} (sublethal) and 2 mg L^{-1} (potentially lethal) threshold concentrations are shown by black and red horizontal bars, respectively. Intense variation begins in March, at the onset of the upwelling season.

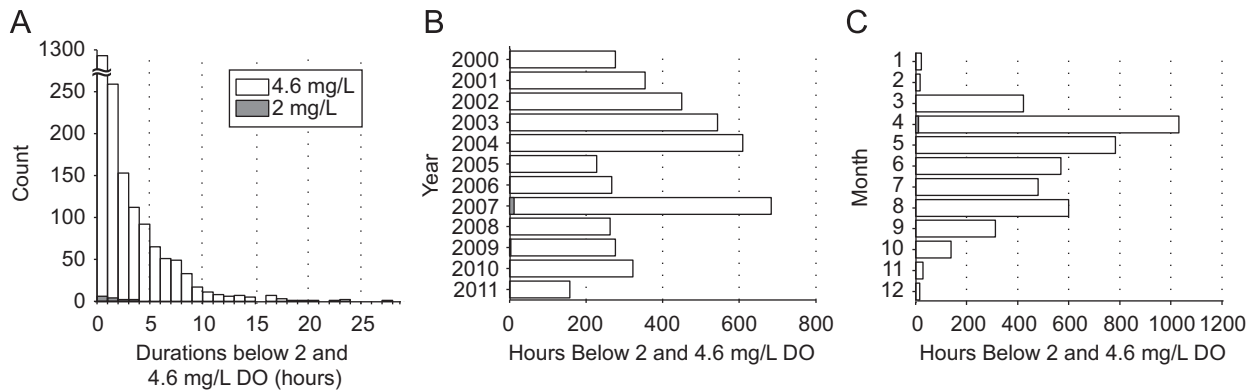


Fig. 5. (A) and (B) hours of time recorded below oxygen concentrations of ≤ 2 (grey) and ≤ 4.6 (white) mg L^{-1} for each year and month, April 2000 to April 2011, (C) distribution of durations for hypoxic-events.

Gulf of Mexico coasts (Diaz and Rosenberg, 2008). Precipitation and elevated runoff from local rivers (Salinas, Pajaro and San Lorenzo, Fig. 1) are typically limited in this area to the period between November and April (Western Regional Climate Center, 2011) and are thus out of phase with the season for hypoxic events (Figs. 4 and 5C). Moreover, terrestrial nutrient sources have been shown to play a minor role off the central California coast compared to the mass of nutrients delivered to the coast by upwelling (McPhee-Shaw et al., 2007; Carroll, 2008). It is therefore highly unlikely that injection of terrestrial nutrients and associated primary production are important in inducing hypoxia in Monterey Bay.

Spectral analysis of the entire time-series using a window length of 32,768 points (~ 114 day) with 50% overlap reveals strong semidiurnal (12 to 12.4 h= M_2) and diurnal (24 h= K_1) periodicities for the dominant variance (Fig. 6). This demonstrates a decade-long statistical persistence in the timing of individual hypoxic events such as those depicted in Fig. 3. Hourly-averaged DO and temperature from MBA showed only a weak correlation with sea level (from NOAA's Monterey tide gauge), even over short periods (monthly correlation coefficients and lags varied widely, -0.6 to 0.6 and -23 to 16 h lag).

Short-term (diel) DO fluctuations near the ocean surface have been found to be associated with plankton respiration (Johnson, 2010); however, this appears to be an unlikely forcing mechanism for the observed low-DO events for several reasons. First, respiration causes a daily maximum in subsurface DO near sunset (Johnson, 2010). In contrast, the MBA record showed no clear correlation with photoperiod (Fig. 3) and DO correlated poorly with photosynthetically available radiation (PAR) recorded at the Moss Landing Marine Laboratories (36.803°N , -121.792°W) (data

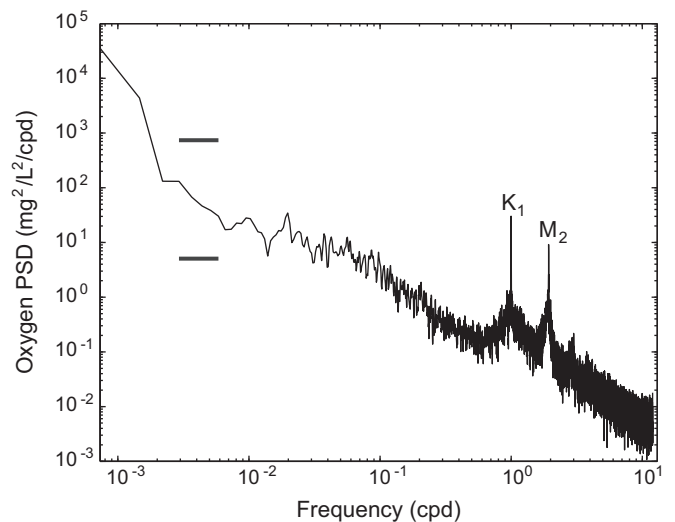


Fig. 6. Power spectral-density (PSD) plot of dissolved oxygen in $(\text{mg L}^{-1})^2 \text{ cpd}^{-1}$. X-axis is frequency in cycles per day (cpd). The dominant diurnal (K_1) and semidiurnal (M_2) tidal constituents are labeled. Black horizontal bars indicate the 95% confidence interval.

not illustrated). Second, respiration-driven DO perturbations are of small amplitude $\sim 1 \text{ mg L}^{-1}$ (Johnson, 2010), whereas the fluctuations we observed at times exceeded 4 mg L^{-1} . Finally, any respiration-driven oxygen depletion would be expected to show a measurable lag between the appearance of cold, nutrient-rich water and significant oxygen depletion (or CO_2 elevation),

but we found no detectable lag between these parameters during hypoxic events. Instead, low oxygen was tightly coupled to cold temperatures, with a cross-covariance correlation coefficient of 0.88 for the series of events depicted in Fig. 3, and 0.52 for the entire time-series averaged over 10 min.

Recent and historical profiles of water column properties offshore of the Monterey Bay shelf break find 2–4.6 mg O₂ L⁻¹ concentrations at depths of about 300–80 m, respectively (Fig. 2). Given the intense semidiurnal and diurnal fluctuations in all three variables (DO, pH, temperature), we infer that semidiurnal and diurnal baroclinic motions, or internal waves likely provide an additional shoreward push of upwelled water. For this paper we will call such motions “internal tides,” and acknowledge that we are using this term to encompass some dynamics that are not true internal tides; e.g., it includes freely propagating internal tides caused by the surface tides interacting with sea floor topography, isopycnal heaving forced by barotropic tides, and baroclinic motions forced by diurnal winds, all of which are common features of central and southern California continental margins and inner shelves (Storlazzi et al., 2003; McPhee-Shaw et al., 2007; Woodson et al., 2007).

5. Offshore source water

Properties of the hypoxic, low-pH events in the inner-shelf are consistent with an advection-dominated system, instead of being forced by biogeochemical processes. Following this line of

interpretation, we can turn to deep water time series from the same region to determine at which depth water properties similar to those at the MBA intake-site exist offshore of the continental shelf. We compared the MBA temperature time series to that recorded at a mooring that is maintained by the Monterey Bay Aquarium Research Institution (MBARI) at 1000-m depth in the submarine canyon in the center of Monterey Bay (36.75°N, -122.03°W, M₁ in Fig. 1). Temperature data collected at 1, 10, 20, 40, 60, 80, 100, 150, 200, 250 and 300 m depths from October 2004 through April 2011 were used. Spectral analysis of these data showed peaks at tidal frequencies (M_2) at depths down to 300 m. Hourly-averaged temperatures at MBA were matched up with temperatures recorded at the MBARI mooring to within 0.5 °C and the corresponding depth at the mooring was noted. Throughout the year, low temperature extremes recorded at MBA were typically found at depths of 100 m at the mooring, and occasionally down to 200 m (Fig. 7B).

6. Discussion and conclusions

This decade-long record shows that even at water depths as shallow as 17 m, the inner shelf offshore of Monterey, California, commonly experiences hypoxic conditions, and temperature, DO and pH are characterized by intense, short-term variability. The strong correlations between these parameters during hypoxic events, which occur in the upwelling season and display tidal periodicities, suggest that upwelling sets the dominant seasonal-scale stage for low DO on

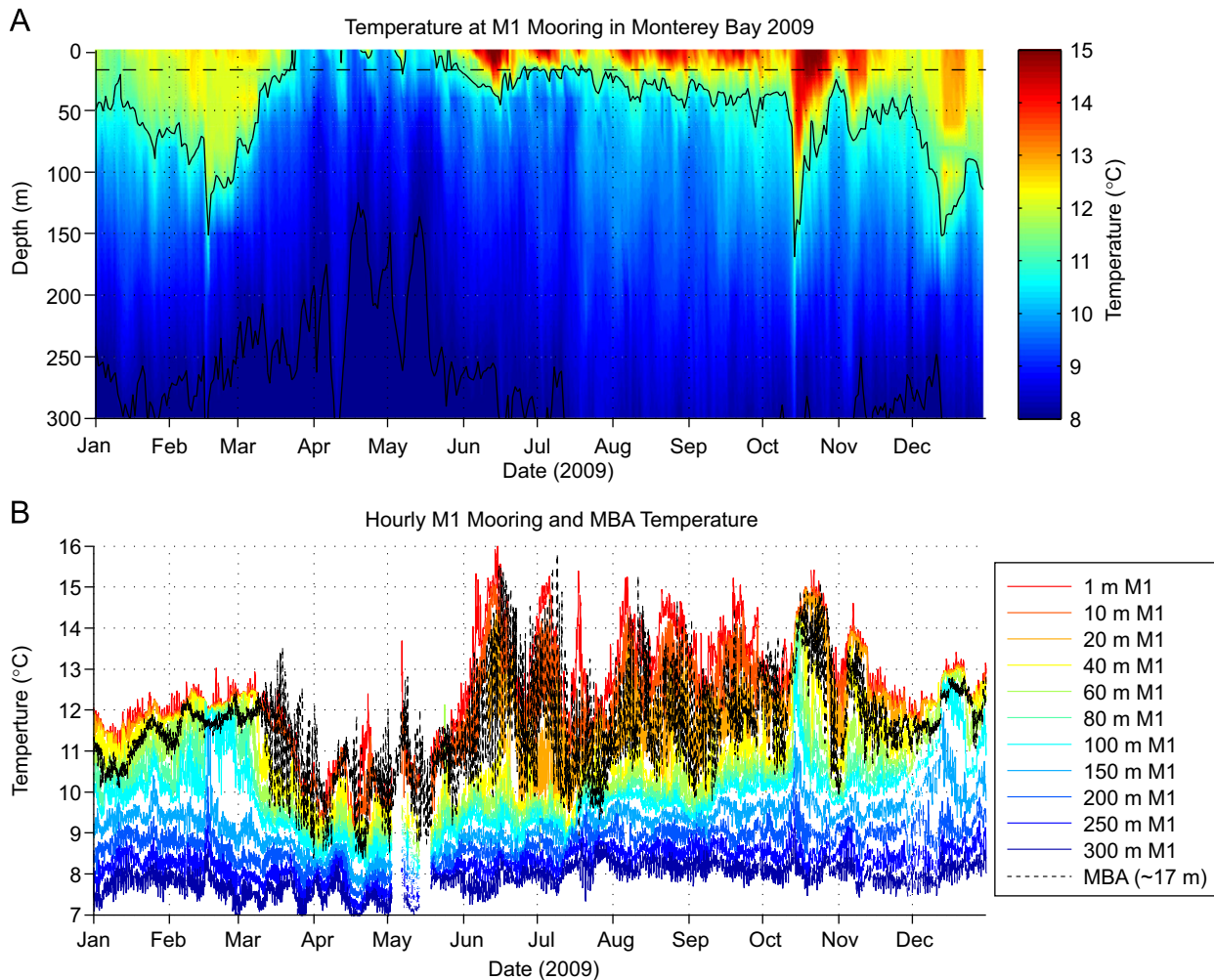


Fig. 7. (A) Daily temperature contour plot at MBARI's M₁ mooring during 2009. Dashed line indicates depth of aquarium intake pipe (17 m) and solid black contours indicate 11 and 8 °C. (B) Hourly temperature recorded by all depths of M₁ mooring (colored lines) and Monterey Bay Aquarium (MBA) (black dashed line) during 2009.

the inner shelf, while tidal-frequency advection occasionally causes pulses of very low DO. Alternative hypotheses involving acute effects of algal or microbial respiration are not consistent with observed properties of the events. We conclude that the source-water for these periodic intrusions originates in the offshore, midwater environment above the local OMZ, generally between 50–100 m but occasionally deeper.

In general, one would expect waters of < 20 m deep on the Pacific coast to be fairly well mixed and thus well oxygenated by contact with the atmosphere, with little high-frequency fluctuations of mixed-layer thickness. This study demonstrates that coastal stratification and subsurface advective motion can effectively decouple the water column from the surface, even at shallow nearshore depths less than 20 m (Fig. 2). Available evidence suggests that the nearshore is inundated year-round by deep water advected by internal tidal motions, and that during the upwelling season bottom water comes from greater depths (characterized by lower DO, pH and temperature), and advection of this more hypoxic water causes nearshore hypoxic events.

Deep, cold water lifted by semidiurnal tidal surging was previously found to deliver cold, low DO water to shallow shelf depths near the head of Monterey Canyon in the center of Monterey Bay (Shea and Broenkow, 1982) approximately 20 km from the MBA site. The current study shows that a similar (at least superficially) phenomenon also occurs a significant distance from the canyon. We note, however, that lacking measurements of currents or a larger array of instruments, we cannot identify many details of the internal tidal motions (baroclinic motions at diurnal and semidiurnal frequencies) observed at this site. We cannot determine the direction of propagation nor the details of the horizontal and vertical DO and temperature gradients being advected. Other studies have shown that internal tides over the nearby Monterey Bay southern shelf can demonstrate both onshore and offshore propagation (Carter, 2010), and at times look like low-mode, “seiche-like” fluctuations while at other times demonstrate nonlinear behavior including onshore propagation of soliton-like features along the thermocline (Cazenave, 2008). Highly nonlinear internal waves documented at a 12-m inner shelf station a few kilometers east of our study site (Stanton and Ostrovsky, 1998; Tjoa, 1998) may play a role in rectification of transport of scalars such as DO. However with a 5-minute sampling interval the MBA time series cannot resolve the steep wave faces and rapid vertical oscillations associated with such features. Diurnal wind-driven, along-coast advection of horizontal

temperature gradients explains important diurnal temperature fluctuations over the inner shelf of the northern Monterey Bay, but the effect of such motions on DO fluctuations remains unstudied.

In short, there is much we do not yet understand about the dynamics of the semidiurnal and diurnal internal tidal motions that dominate the DO signal in the inner shelf environment offshore of the Monterey Bay Aquarium. However, this study documents the amplitude and time-course of DO fluctuations associated with these motions (Fig. 8). This is an important result since intensity and duration of these fluctuations likely have important effects on ecosystems of the Central California coast. This schematic illustrates that organisms near the study site at 17 m depth have experienced hypoxic events lasting up to 25 h below 4.6 mg L^{-1} , and 3 h below 2 mg L^{-1} (Fig. 5C). These concentrations were identified by Vaquer-Sunyer and Duarte (2008) as critical biological thresholds. High frequency monitoring of pH since September 2009 reveals fluctuations from pH 8.1 to 7.7 (NBS scale), a 2.5-fold increase in hydrogen ion concentration, over 13 h (Fig. 3). Weekly ‘spot-check’ data since March 1996 have revealed 43 values below pH 7.75 ($\text{min}=7.44$, $n=811$), a level associated with the dissolution of calcium carbonate (Feely et al., 2008; Booth, 2011). Although limitations in the accuracy of our measurements (see Section 3) makes precise quantification of exposure times difficult, the conclusion is unaltered that both DO and pH regularly fall to concentrations that are considered to be stressful. Additionally, dual exposure to hypoxia and low pH may have synergistic physiological and ecological consequences that are difficult to predict (Fabry et al., 2008; Pane and Barry, 2007; Vaquer-Sunyer and Duarte, 2008). Low pH not only alters calcification rates, but also can directly influence biochemical reaction rates and binding of substrates. For example, oxygen binding by hemocyanin, the respiratory protein in squid (and many marine invertebrates) is highly pH-sensitive over the pH range characteristic of the fluctuations observed in the MBA data, particularly at low DO concentrations (Pörtner et al., 1990; Zielinski et al., 2001). Thus, pulses of hypoxic, low pH water could potentially stress respiration and activity of squid and other sensitive invertebrates (Rosa and Seibel, 2008).

Central California and other upwelling regions with narrow shelves and close proximity to deep water may be particularly susceptible to hypoxic, low-pH events like those described here, but it is important to remember that these physical characteristics describe much of the Eastern Pacific Coast (Helly and Levin, 2004)

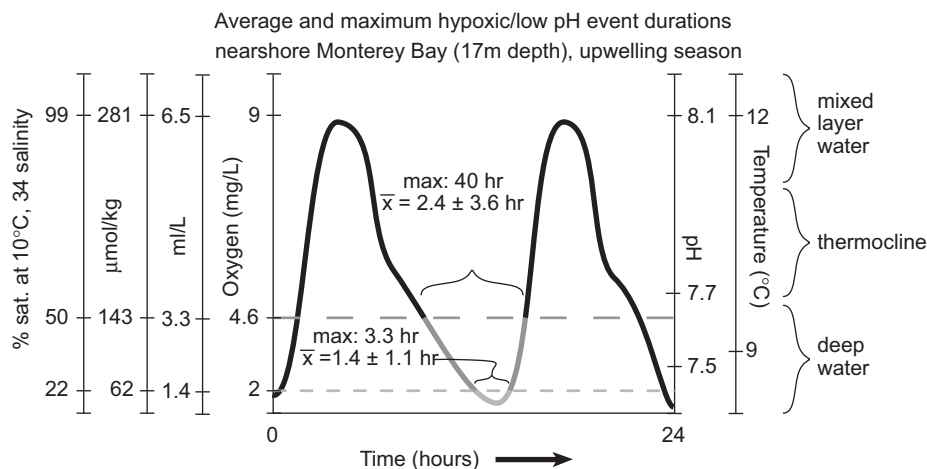


Fig. 8. Schematic of average low DO/low pH event in the nearshore of southern Monterey Bay (Monterey Bay Aquarium) over a 24 h period at ~17 m depth. Center plot shows the DO/pH/temperature signal fluctuating with the semidiurnal internal tide. Additional axes indicated different oxygen units and the associated pH and temperature ranges. Far right labels show origin of the water sampled.

and high-frequency fluctuations in DO and pH have recently been observed at several California locations (Hofmann et al., 2011; Frieder et al., 2012). We do not know the history of these hypoxic events beyond our 10-year study, but it is likely that nearshore species of the Pacific coast have either evolved in the presence of this phenomenon or have successfully adapted to this variable environment. Thus, values for hypoxia thresholds used here (2 and 4.6 mg L⁻¹) may not be appropriate, because relatively few nearshore species from coastal upwelling ecosystems were reviewed by Vaquer-Sunyer and Duarte (2008).

Nearshore Pacific coast species may be tolerant of hypoxic events, but ongoing changes in the offshore OMZ may lead to a significantly higher level of stress in the future. A general, large-scale shoaling of the OMZ in the eastern Pacific over the last several decades has recently been documented (Whitney et al., 2007; Chan et al., 2008; Bograd et al., 2008; Stramma et al., 2008), along with acidification in offshore upwelling regions (Feely et al., 2008; Hauri et al., 2009). Although the precise causes of OMZ shoaling are not yet clear, but both global warming (Keeling et al., 2010) and natural decadal whether from increasing anthropogenic effects or part of the ocean's intrinsic low-frequency variability (McClatchie et al., 2010; Deutsch et al., 2011) are likely to be important. Nevertheless, dynamic onshore movement of hypoxic, deep water in intrusions like those described here will continue to impact shallow ecosystems on the inner shelf, and long-term shoaling of the upper boundary of the OMZ (0.5 mg L⁻¹ DO) will almost certainly increase the occurrence, intensity, duration, and spatial extent of hypoxic intrusions on the Pacific coast. Biological tolerances for hypoxic and low pH water by individual nearshore Pacific species are currently not well documented (Fabry et al., 2008), making identification of the most vulnerable taxa difficult. It is therefore vital to identify tolerance levels in individual species and to consider the ecosystem perspective of at-risk communities. It will also be critical to monitor changes in both offshore OMZ and inshore habitats on a variety of time scales, to develop predictive models that warn of incipient intrusions, and to consider the potential interactions of these events with terrestrial-runoff and other drivers of coastal hypoxia in any marine spatial planning efforts in impacted regions.

Acknowledgements

We acknowledge L. Breaker, J. Stewart, K. Coale, K. Johnson, and D. Staaf, and for valuable advice and discussions. We would like to thank B. Woodson, S. Monismith and the Monterey Bay Aquarium Research Institute for the use of their water monitoring data from their moorings. This research was supported by the Marine Life Observatory program of Hopkins Marine Station, California Sea Grant, Ocean Protection Council and the US National Science Foundation.

References

- Bograd, S.J., Castro, C.G., Di Lorenzo, E., Palacios, D.M., Bailey, H., Gilly, W., Chavez, F.P., 2008. Oxygen declines and the shoaling of the hypoxic boundary in the California Current. *Geophysical Research Letters* 35, L12607.
- Booth, J.A.T., 2011. Hypoxic and Low pH Water in the Nearshore Marine Environments of Monterey Bay, California: Characterizing a Decade of Oxygen and pH, and Drivers of Variability. M.S. Thesis, Moss Landing, California: Moss Landing Marine Laboratories, California State Universities.
- Carroll, D., 2008. Carmel Bay: Oceanographic Dynamics and Nutrient Transport in a Small Embayment of the Central California Coast. M.S. Thesis, Moss Landing, California: Moss Landing Marine Laboratories, California State Universities.
- Carter, G.S., 2010. Barotropic and baroclinic M_2 tides in the Monterey Bay region. *Journal of Physical Oceanography* 40, 1766–1783.
- Cazenave, F., 2008. Internal Waves over the Continental Shelf in South Monterey Bay. M.S. Thesis, Moss Landing, California: Moss Landing Marine Laboratories, California State Universities.
- Chan, F., Barth, J.A., Lubchenco, J., Kirincich, A., Weeks, H., Peterson, W.T., Menge, B.A., 2008. Emergence of anoxia in the California Current large marine ecosystem. *Science* 319, 920.
- Colt, J., 1984. Computation of Dissolved Gas Concentrations in Water as Functions of Temperature, Salinity, and Pressure. American Fisheries Society, Bethesda, MD.
- Connolly, T.P., Hickey, B.M., Geier, S.L., Cochlan, W.P., 2010. Processes influencing seasonal hypoxia in the northern California Current System. *Journal of Geophysical Research* 115, C03021.
- Diaz, R.J., Rosenberg, R., 2008. Spreading dead zones and consequences for marine ecosystems. *Science* 321, 926–929.
- Deutsch, C., Brix, H., Ito, T., Frenzel, H., Thompson, L., 2011. Climate-forced variability of ocean hypoxia. *Science* 333, 336–339.
- Fabry, V.J., Seibel, B.A., Feely, R.A., Orr, J.C., 2008. Impacts of ocean acidification on marine fauna and ecosystem processes. *ICES Journal of Marine Science* 65, 414–432.
- Feely, R.A., Sabine, C.L., Hernandez-Ayon, J.M., Ianson, D., Hales, B., 2008. Evidence for upwelling of corrosive “Acidified” water onto the continental shelf. *Science* 320, 1490–1492.
- Frieder, C.A., Nam, S.H., Martz, T.R., Levin, L.A., 2012. High temporal and spatial variability of dissolved oxygen and pH in a nearshore California kelp forest. *Biogeosciences Discuss* 9, 4099–4132.
- Grantham, B.A., Chan, F., Nielsen, K.J., Fox, D.S., Barth, J.A., Huyer, A., Lubchenco, J., Menge, B.A., 2004. Upwelling-driven nearshore hypoxia signals ecosystem and oceanographic changes in the northeast Pacific. *Nature* 429, 749–754.
- Hales, B., Karp-Boss, L., Perlin, A., Wheeler, P.A., 2006. Oxygen production and carbon sequestration in an upwelling coastal margin. *Global Biogeochem. Cycles* 20, 001, GB3.
- Hauri, C., Gruber, N., Plattner, G.-K., Alin, S., Feely, R.A., Hales, B., Wheeler, P.A., 2009. Ocean acidification in the California Current System. *Oceanography* 22, 60–71.
- Helly, J.J., Levin, L.A., 2004. Global distribution of naturally occurring marine hypoxia on continental margins. *Deep Sea Research Part A: Oceanographic Research Papers* 51, 1159–1168.
- Hofmann, G.E., Smith, J.E., Johnson, K.S., Send, U., Levin, L.A., Micheli, F., Paytan, A., Price, N.N., Peterson, B., Takeshita, Y., Matson, P.G., Crook, E.D., Kroeker, K.J., Gambi, M.C., Rivest, E.B., Frieder, C.A., Yu, P.C., Martz, T.R., 2011. High-frequency dynamics of ocean pH: a multi-ecosystem comparison. *PLoS ONE* 6, e28983.
- Johnson, K.S., 2010. Simultaneous measurements of nitrate, oxygen, and carbon dioxide on oceanographic moorings: observing the redfield ratio in real time. *Limnology and Oceanography* 55, 615–627.
- Keeling, R.F., Körtzinger, A., Gruber, N., 2010. Ocean deoxygenation in a warming world. *Annual Reviews of Marine Science* 2, 199–229.
- McClatchie, S., Goericke, R., Cosgrove, R., Auad, G., Vetter, R., 2010. Oxygen in the Southern California Bight: multidecadal trends and implications for demersal fisheries. *Geophysical Research Letters* 37, 5.
- McPhee-Shaw, E.E., Siegel, D.A., Washburn, L., Brzezinski, M.A., Jones, J.L., Leydecker, A., Melack, J., 2007. Mechanisms for nutrient delivery to the inner shelf: observations from the Santa Barbara Channel. *Limnology and Oceanography* 52, 1748–1766.
- Millero, F.J., Zhang, J.-Z., Fiol, S., Sotolongo, S., Roy, R.N., Lee, K., Mane, S., 1993. The use of buffers to measure the pH of seawater. *Marine Chemistry* 44, 143–152.
- Pane, E.F., Barry, J.P., 2007. Extracellular acid-base regulation during short-term hypercapnia is effective in a shallow-water crab, but ineffective in a deep-sea crab. *Marine Ecology Progress Series* 334, 1–9.
- Pörtner, H.O., Boutilier, R.G., Tang, Y., Toews, D.P., 1990. Determination of intracellular pH and PCO₂ after metabolic inhibition by fluoride and nitrilotriacetic acid. *Respiratory Physiology* 81, 255–273.
- Rabalais, N.N., Turner, R.E., Jr, W.J.W., 2002. Gulf of Mexico hypoxia, a.k.a. “The Dead Zone”. *Annual Reviews of Ecology Systems* 33, 235–263.
- Rosa, R., Seibel, B.A., 2008. Metabolic physiology of the Humboldt squid *Dosidicus gigas*: implications for vertical migration in a pronounced oxygen minimum zone. *Progress in Oceanography* 86, 72–80.
- Shea, R.E., Broenkow, W.W., 1982. The role of internal tides in the nutrient enrichment of Monterey Bay. *Estuarine, Coastal and Shelf Science* 15, 57–66.
- Silguero, J.M.B., Robison, B.H., 2000. Seasonal abundance and vertical distribution of mesopelagic calycophoran siphonophores in Monterey Bay, CA. *Journal of Plankton Research* 22, 1139–1153.
- Stanton, T.P., Ostrovsky, L.A., 1998. Observations of highly nonlinear internal solitons over the continental shelf. *Geophysical Research Letters* 25, 2695–2698.
- Storlazzi, C.D., McManus, M.A., Figurski, J.D., 2003. Long-term, high-frequency current and temperature measurements along central California: insights into upwelling/relaxation and internal waves on the inner shelf. *Continental Shelf Research* 23, 901–918.
- Stramma, L., Johnson, G.C., Sprintall, J., Mohrholz, V., 2008. Expanding oxygen-minimum zones in the tropical oceans. *Science* 320, 655–658.
- Tjoa, K.M., 1998. The Bottom Boundary Layer under Shoaling Inner Shelf Solitons. M.S. Thesis, Monterey, California: Naval Postgraduate School.
- Vaquer-Sunyer, R., Duarte, C.M., 2008. Thresholds of hypoxia for marine biodiversity. *Proceedings of the National Academy of Sciences of the United States of America* 105, 15452–15457.
- Western Regional Climate Center, 2011. Monterey, California—Climate Summary 1/ 7/1949 to 12/31/2005 [WWW Document]. URL <http://www.wrcc.dri.edu/cgi-bin/cliMAIN.pl?camtry+nca>.

- Whitney, F.A., Freeland, H.J., Robert, M., 2007. Persistently declining oxygen levels in the interior waters of the eastern subarctic Pacific. *Progress in Oceanography* 75, 179–199.
- Woodson, C.B., Eerkes-Medrano, D.I., Flores-Morales, A., Foley, M.M., Henkel, S.K., Hessing-Lewis, M., Jacinto, D., Needles, L., Nishizaki, M.T., O'Leary, J., Ostrander, C.E., Pespeni, M., Schwager, K.B., Tyburczy, J.A., Weersing, K.A., Kirincich, A.R., Barth, J.A., McManus, M.A., Washburn, L., 2007. Local diurnal upwelling driven by sea breezes in northern Monterey Bay. *Continental Shelf Research* 27, 2289–2302.
- Zielinski, S., Sartoris, F.J., Pörtner, H.O., 2001. Temperature effects on hemocyanin oxygen binding in an Antarctic Cephalopod. *Biology Bulletin* 200, 67–76.