“Internal tide pools” prolong kelp forest hypoxic events

Paul R. Leary 1,*, C. Brock Woodson,2 Michael E. Squibb 3, Mark W. Denny,4 Stephen G. Monismith,5 Fiorenza Micheli4

1Department of Physics, Naval Postgraduate School, Monterey, California
2College of Engineering, University of Georgia, Athens, Georgia
3Center for Ocean Solutions, Stanford University, Stanford, California
4Hopkins Marine Station, Stanford University, Pacific Grove, California
5Department of Civil and Environmental Engineering, Stanford University, Stanford, California

Abstract

This study uses field observations within a single kelp bed in southern Monterey Bay, California, to evaluate the retention of cold, hypoxic water within depressions in the rocky reef following relaxation of internal wave events. Just as tide pools in the rocky intertidal zone persist in depressions following the relaxation of surface waves and tides, “internal tide pools” persist in depressions in the subtidal reef following the relaxation of internal waves. When internal waves contain low dissolved oxygen (DO) water, the duration of hypoxic events can be extended for organisms within the pooling zone. Additionally, we suggest that internal wave run-up can cause the early arrival of cold hypoxic water in these same areas, thereby extending hypoxic events further. Together, internal tide pools and wave run-up extend event durations by 20% on average. However, some events are extended up to 160% of the regional-scale event length, which may be more ecologically relevant than the mean extension. When internal waves contain other environmental covariates (e.g., low pH, nutrients), internal tide pools are expected to create a similar time extension and patchy landscape in these quantities. We attribute the slowing of the relaxation of sub-thermocline water within pooling zones to retention within the reef itself rather than a drag effect of the kelp bed. Following hypoxic internal bores, internal tide pools cause a period of extreme spatial variability in the DO and temperature field which is likely to impact the distribution and behavior of local organisms.

Expansion of oxygen minimum zones linked to global climate change has led to an increase in hypoxic events along the inner-to-mid continental shelf of the northeastern Pacific, with severe consequences for marine ecosystems (Grantham et al. 2004; Bograd et al. 2008; Chan et al. 2008; Stramma et al. 2010; Booth et al. 2014). In contrast to the historic understanding of hypoxic events that develop from eutrophication in sheltered waters such as estuaries and lakes (Breitburg 1992, 2002; Rabalais et al. 2002; Breitburg et al. 2009; Rabalais 2009), hypoxic events in this eastern boundary current system are strongly connected to the advection of deep, offshore-sourced low-oxygen waters onto the shelf via upwelling (Chan et al. 2008). As such, oxygen (and the concomitant pH) fluctuations are often strongly coherent with temperature and salinity fluctuations (Booth et al. 2012; Walter et al. 2014).

Low oxygen events have been documented within nearshore kelp forests of 10–20 m depth or less (Booth et al. 2012; Frieder et al. 2012; Micheli et al. 2012). While kelp forest events low enough to fall under the traditional definition of hypoxia (< 2.0 mg L−1 dissolved oxygen [DO]) are uncommon (Booth et al. 2012), events low enough to significantly impact local biodiversity (< 4.6 mg L−1) are regular occurrences, and we take this as our operative definition of hypoxia (Vaquer-Sunyer and Duarte 2008). Such hypoxic events in upwelling zones are characterized by strong semi-diurnal and diurnal DO and pH fluctuations due to the advection of deep, offshore low-oxygen waters (Booth et al. 2012). During and after low oxygen and low pH events, strong spatial gradients occur between sites (Kapsenberg and Hofmann 2016), as well as along cross-shore and vertical axes within a site (Frieder et al. 2012). Spatial gradients in DO have been attributed to different drivers in different
settings (Booth et al. 2012; Frieder et al. 2012; Micheli et al. 2012), but direct mechanistic relationships between these regional-scale drivers and the local-scale DO dynamics within kelp forests and associated rocky reefs are not well understood. It is critical to build an understanding of these relationships if we hope to predict temporal and spatial DO variability in novel future settings.

Within Monterey Bay, a known upwelling zone and the location of this study, the regional-scale transport processes responsible for delivering low DO water into kelp forests (nearshore internal bores) are well studied, allowing us to parse in detail the mechanisms of event development and relaxation. However, little is known of how these processes occur within a single kelp forest, or across a complex rocky reef. Water-column temperature (T), DO structure, and currents in southern Monterey Bay are dominated by semi-diurnal internal tides (Storlazzi et al. 2003; Walter et al. 2012). Here, strong regional upwelling winds draw the offshore thermocline (and oxycline) onto the shallow shelf, where local surging internal waves then deliver this cold and hypoxic water into the shallow nearshore in distinct pulses (Booth et al. 2012; Walter et al. 2012, 2014). Internal waves in southern Monterey Bay, and other areas, have been shown to play an important role in many other processes as well (McPhee-Shaw et al. 2007; Cheriton et al. 2014; Rosenberger et al. 2016). The internal wave field of southern Monterey Bay is not strongly influenced by surface swell and is thus only weakly correlated with the free surface (Storlazzi et al. 2003; Woodson 2013). By contrast, the amplitude and frequency of nearshore internal wave events appear to be modulated by offshore upwelling winds via the offshore thermocline height, where a shallower thermocline yields smaller, higher frequency waves, with the reverse for a deeper thermocline (Walter et al. 2014). Internal wave events in this region are also different from the traditional, shallow-slope nonlinear internal bore model, in which an internal wave shoals and breaks on a gentle slope forming a bolus with a turbulent trailing edge (Leichter et al. 1996). Instead, the waves do not shoal and break classically, but behave more like a surging wave with a highly stratified cold front and significant vertical mixing during the relaxation due to high shear (Walter et al. 2012). These features would be most properly referred to as surging nonlinear internal waves, however for simplicity’s sake, we will refer to them hereafter as bores, consistent with other recent literature from the area. Regardless, it is very unlikely that this distinction would significantly affect the small scale processes discussed in this article.

While regional-scale internal bore processes are well studied for this location, our understanding of their fate within the geometrically complex kelp forest and reef is limited. It is possible that internal bores which penetrate the kelp forest remain stratified throughout the arrival and relaxation cycle due to the kelp’s stabilizing effect on the water-column through reduction of shear. Within the kelp forest, currents are reduced and high frequency velocity fluctuations are damped considerably compared to outside the forest (Jackson 1984, 1997). These effects are depth related, with the highest reductions occurring at the surface and decreasing with depth (Rosman et al. 2007). The damping of velocity fluctuations is also frequency dependent, such that high frequency internal waves and turbulent fluctuations are damped, whereas tidal frequencies are not (Rosman et al. 2007). Thus, the overall effect of the kelp bed may be an evening of the vertical flow profile, reducing shear such that vertical mixing within the kelp bed itself is suppressed (Rosman et al. 2007).

We propose that the aforementioned processes may interact to create a retention mechanism for sub-thermocline, low DO water within the kelp bed’s rocky reef topography following internal bore relaxation, which we call the “internal tide pool” hypothesis. It is possible that during internal bore relaxation, cold water residing within the reef topography during the relaxation process may not mix vertically (Bell and Thompson 1980), but instead pool or otherwise “drain” by gravity through the reef contours, impeded by the restriction and relative enclosure of reef depressions, such as those formed by low points in bedrock or sand patches between rocky outcrops. This is likely enhanced by the presence of kelp, and thus by reduction of vertical mixing, as described above. In this state, sub-thermocline water within the topography, left behind by the relaxing internal bore, would resemble an internal analog to the tide pools common in the rocky intertidal zone during low tide, which we call the “internal tide pool” (Fig. 1).

This conceptualization of retention of sub-thermocline water is not intended as an exact mechanism that applies wholly in every case. The degree (or time) that sub-thermocline water may be retained by reef topography is likely a function of local reef morphology, individual bore characteristics (e.g., propagation direction, speed, stratification), and other factors. Many of these factors are also influenced by regional characteristics, such as shelf slope and location of the continental shelf break. Therefore “pooling,” as described above, is likely not a binary process, but rather can be thought of as a continuum of relative retention spanning permanent residence of sub-thermocline water to draining at a rate identical to a smooth bottom. “Pooling” however, is distinct from a more general “trapping” of sub-thermocline water by the rocks and kelp, as pooling is concentrated within topographic lows with kelp having little retentive effect.

Besides internal pooling during the relaxation process, these same depressions may experience more rapid onset of cold and hypoxic conditions during internal wave run-up as it interacts with the reef topography. As an internal bore propagates onshore, its leading edge is accelerated and raised higher in the water-column inshore than offshore, due to the sloping bottom (Wallace and Wilkinson 1988; Jensen
et al. 2003). Therefore, the arrival of cold water will occur earlier at inshore locations for sensors mounted on or near the bottom, than for similar depths in the water-column offshore.

The objective of this study is to document observation of and, to the extent possible from measurements at one location, evaluate this novel “internal tide pool” hypothesis, and assess its potential to prolong hypoxic events within our local kelp forest and reef. We deployed an array of moored temperature and DO loggers at sites inside and outside a kelp forest to compare the retention of sub-thermocline water within the reef to outside the kelp/reef for a number of internal bore events. We use indexing techniques to delineate water delivered by bores from other water masses as well as to separate stages of an individual bore event, describe the generalized nature of bore events for each site within the forest, and compare events among sites.

Methods

Site description

Hopkins Marine Station (HMS) in Pacific Grove, California (32.62053°N, 121.904°W) is located in the southern portion of Monterey Bay, on the central coast of California, U.S.A. The Pacific Grove coastline is unusual for the California coast in that it faces generally northeast, and is thus

---

**Fig. 1.** Conceptual cartoon of the formation of “internal tide pools” in the kelp forest reef. Dashed line symbolizes the pycnocline in all panels. (a) The arrival-phase where an internal bore (gray) propagates into the otherwise well mixed water-column, gradually filling the water column from the bottom (Walter et al. 2012), and spilling into topographic depressions. (b) The internal bore has stratified the water-column and most of the water-column is cold and hypoxic (main phase). (c) The relaxation-phase where the sub-thermocline water within the unobstructed water-column propagates offshore, but sub-thermocline water within the topography is impeded by rock structure. (d) Internal tide pools are formed due to retention of sub-thermocline water within the rocky topography for a period following the general relaxation.
sheltered from the dominant swell and wind forcing (NW and W) which are characteristic of the larger region. The reef at HMS is oriented at roughly 85° in the cross-shore direction (i.e., the shoreline faces 85° offshore). The contiguous reef spans ~100 × 250 m, and is composed of high relief granite substrate (> 2 m relief for 60% of the reef), interspersed with sandy patches (70% bedrock, 30% loose rock and sand), and a dense *Macrocystis pyrifera* kelp forest (average kelp stipe density of 3.5 stipes m⁻²; [http://www.piscoweb.org/](http://www.piscoweb.org/)). The northeast corner of the reef, where this study took place, has high relief with pronounced depressions.

Currents within Monterey Bay are dominated by the M₂ tidal component (12.42 h period, up to 0.2 m s⁻¹) ([Breaker and Broenkow 1994](https://www.sciencedirect.com/science/article/pii/0967064594900315)). Internal waves in this region typically originate from the Monterey Canyon mouth ([Petruncio et al. 1998](https://doi.org/10.1080/00268929809359783); [Walter et al. 2012](https://doi.org/10.1080/00268929809359783)). These internal waves arrive on a median heading of 195.4° at roughly 0.1 m s⁻¹, and relax on a median heading of 153.8° at roughly 0.16 m s⁻¹ ([Walter et al. 2012](https://doi.org/10.1080/00268929809359783)).

Experimental setup

Four miniDOT DO and temperature sensors ([PME, Vista, California](https://www.pime.com)) were deployed within the rocky reef in the kelp forest outside HMS from 12 June 2014 to 24 August 2014 at two sites (referred to hereafter as the benthic sites), roughly centered on 36.6234°N, 121.9022°W (Fig. 2a).

The benthic sites were roughly 30 m apart in the center of the kelp bed, both on the 10 m depth contour. These sites targeted depressions within the reef. At each site, a pair of miniDOT sensors was deployed with one sensor at the concave bottom or “trough” of one of the depressions, and the other placed nearby atop the rocky “ridge” that defines the boundary of the depression (henceforth referred to as the trough and ridge sensors, respectively). This configuration was deemed sufficient to demonstrate observations of retention within chosen reef depressions, but we acknowledge that more replication, and in different locations and habitats, is required to extrapolate or generalize the phenomenon. In addition, offshore water-column temperature data were taken from a thermistor chain moored at 36.62094°N, 121.90044°W, at 15 m water depth, with thermistors placed at 1 m, 4 m, 7 m, 10 m, and 13 m above the bottom (Fig. 2b). We refer to this thermistor chain as the offshore site.

Consistency between sensors was checked using a common water bath before and after deployment, with no significant deviations between sensors and thus no corrections performed. All data from these checks, as well as the deployment, met quality control guidelines given in the associated instrument manuals.

Data processing

Thermistor-chain data were processed by interpolating between individual thermistors using piecewise cubic Hermite interpolation ([MATLAB, Mathworks, Natick, Massachusetts](https://www.mathworks.com)) to a vertical resolution of 0.05 m. “Trough-equivalent” and “ridge-equivalent” offshore temperatures for comparison to the benthic sites were taken from these interpolated values from the offshore thermistor-chain, at depths equivalent to those at both benthic sites (6 m and 8 m above the bottom, respectively). As the trough and ridge sensors at the benthic sites measure these event dynamics as they occur deep within the rocky reef (trough) and the kelp forest water-column (ridge), the trough-equivalent and ridge-equivalent measurements at the offshore site serve as a depth-equivalent comparison, absent any effects of topographic structure.

Event selection

The thirty clearest examples of “typical” internal bores, i.e., those that most clearly fit the bore characterization of previous studies in this location ([Walter et al. 2012](https://doi.org/10.1080/00268929809359783)), were selected from the offshore water-column-temperature time series. Automated selection of these events yielded similar results, however, manual selection was more straightforward and intuitive and is therefore reported here. The nearshore arrival, residence, and relaxation periods of a single nonlinear internal wave (i.e., a bore) have been defined in the literature using different terminology in different contexts. Here, we refer to the “arrival-phase” as the period when the bore is...
propagating inshore, and bottom temperature and oxygen within the kelp forest is declining. The period in which the bore has maximally filled the water-column, and bottom temperature or oxygen is at or near its lowest and does not appreciably change through time, is referred to as the “main phase.” Finally, the “relaxation-phase” is defined as the period when the bore is propagating offshore and bottom temperature and oxygen are increasing (Fig. 3). In many reported results, the time axis includes the first or last 60 min of the main phase, so as to capture the transition between the phases. We refer to the “transition” as the period when a bore front is passing a given sensor, and the temperature and oxygen are changing most rapidly. Only bores with clearly defined arrival and relaxation-phases, and a distinct stable low temperature main phase with little temporal variability during this time were used in analyses. During these bores, cold water masses caused a temperature decrease of at least 3.5°C, with the thermocline rising to more than 8 m above the bottom (i.e., shallow enough to reach all sensors), and durations ranging from 1 h to 8 h. Examples of water masses that were not used included multiple or interacting bores, bores with significant high-frequency variability, anomalous cold water masses (cold water masses that behaved nothing like an internal wave, such as directly-upwelled water), and bores driving very short events, all of which are likely the product of, or at least complicated by, other regional scale transport processes (Fig. 4). Added complexity from these conditions makes comparisons between events extremely difficult.

Once individual bores were identified, the starting and ending times for the main phase were defined by selecting the beginning and end of the flat portion of the offshore “trough-equivalent” (6 m above bottom) temperature time series, that is, between the decreasing $T$ portion during bore arrival, and increasing $T$ portion during bore relaxation (Fig. 3). These offshore temporal bounds encompassed the event at the regional scale, providing a baseline for comparison between sites, and were thus kept constant between sites for each event. All other indexing (detailed below) was done using automated methods, referenced from these time points (i.e., in further analyses, the chosen start and end points of the main phase define $t=0$ for that specific arrival or relaxation).

**Analysis**

A primary indication of “internal tide pooling” is the early (leading) appearance of cold water during arrivals and delayed (lagged) departure of cold water during relaxation at the benthic sites, especially near the trough sensors. We quantified this time of increased exposure to low cold hypoxic water at the benthic sites, during both arrivals and relaxations, with what we refer to as “added exposure time” defined as the time that is added to this regional-scale total event time within the benthic sites, and quantified as follows. A temperature range was quantified as the total temperature range across all sensors of equivalent depth (e.g., trough and trough-equivalent sensors) for a 6-h window following the end of the main phase (e.g., $T_{\text{range}} = T_{\text{max}}$, all trough sensors, 6-h window) $- T_{\text{min}}$, (all trough sensors, 6-h window)). For a given sensor following a given main phase, the “exposure time” is defined as the time before the beginning (arrivals) or after the end (relaxations) of the main phase when $T_{\text{sensor}} = T_{\text{min}} + 0.4 \ T_{\text{range}}$. All of these calculations used a smoothed temperature time series (30 min moving-window averaging).

The factor of 0.4 was chosen because all sensors reached a temperature above this threshold during each event. By contrast, in some events, all sensors did not necessarily reach a higher threshold (e.g., 0.5). The arrival-phase start was defined similarly relative to a 6-h window preceding the start of the main phase. The “added exposure time” during arrival, for each benthic sensor, was defined as the difference in arrival-phase start times between the offshore thermistor chain and the benthic sensor (offshore–benthic). During relaxation, added exposure time was the difference in relaxation-phase end times between the benthic and offshore (benthic-offshore) sites. In both the arrival and relaxations, the “added exposure time” defines how much longer the exposure is at the benthic site sensors, over their equivalents at the offshore site. The total exposure time for the offshore site (which defines the event length at the regional scale) was defined as the time between the start of the arrival phase and end of the relaxation at the offshore thermistor chain site. The “added exposure time” is the time that is added to the total exposure time within the benthic sites. Differences in mean added exposure times were tested with a one sample $t$-test, where the null hypothesis is no difference in time...
between the benthic and offshore sites (i.e., mean difference = 0). In addition, bore propagation delays between sites were measured by comparing the timing of noticeable high-frequency features (e.g., large but brief temperature fluctuations from high-frequency internal waves or similar), apparent at all sensors during arrival and relaxations.

To describe the generalized characteristics of the arrival and relaxation process unique to each sensor location, we constructed normalized arrival and relaxation curves. We normalized the temperature (or oxygen concentration) during each arrival or relaxation by the temperature (or oxygen concentration) range across all paired sensors for a 6-h period. That is, $T_{\text{normalized}} = (T_{\text{sensor}} - T_{\text{min}})/T_{\text{range}}$ or $\text{DO}_{\text{normalized}} = (\text{DO}_{\text{sensor}} - \text{DO}_{\text{min}})/\text{DO}_{\text{range}}$. This 6-h period overlapped the main phase by 1 h (to capture the transition), and extended 5 h in either direction from the main phase. That is, the interval used to normalize the relaxation characteristics began 1 h before the end of the main phase, and extended 5 h after the end of the main phase. For arrivals, we used an interval beginning 5 h before the start of the main phase, and extending 1 h into the main phase. With this approach, temperature (or oxygen concentration) was nondimensionalized, but time remained in dimensional units (minutes) as time intervals were the same across all

---

**Fig. 4.** Examples of manual bore event selection criteria and rationale. In each, axis (i) is the water column temperature, while axis (ii) is the corresponding ridge and trough-equivalent temperature, both from the offshore thermistor chain. (a) Example of internal bore event selected for its large temperature difference, clearly defined arrival and relaxation, large enough bore height to reach all sensors, as well as a significant “main phase” for comparative analysis. Arrival exposure time (as defined in text) highlighted in yellow, main phase in red, and relaxation exposure time in purple. (b) Example of internal bore event not selected due to its interaction with multiple bores, which complicate dynamics at all phase. (c) Example of internal bore event not selected due to its small bore height and temperature range, as well as the relatively short main phase.

---

2869
events. Means and standard errors of normalized temperature and oxygen were then calculated across all events at each time point. For normalized ridge-trough temperature or DO gradients ($D_{T\text{normal}} = (T_{\text{ridge}} - T_{\text{trough}})$ normalized; $D_{\text{Onormal}} = (\text{DO}_{\text{ridge}} - \text{DO}_{\text{trough}})$ normalized), values were subtracted directly in the raw data before calculating mean and standard error (rather than subtracting the means after the fact). Individual relaxation slopes were calculated from each normalized curve. For all normalized curves, where standard errors did not overlap between curves, a two-sample $t$-test between the curves at that particular time point yielded a $p$-value less than 0.05, and thus were determined to be significantly different. Normalized curves including DO were constructed only from events that contained hypoxic water, as events from non-hypoxic bores had a very different DO-$T$ relationship. We included all internal wave events for results not dealing directly with oxygen, as they still demonstrate the physical mechanism behind DO variability, during low DO events.

**Results**

**General characteristics of events within the kelp forest**

The arrival and relaxation of a bore were characterized by distinct patterns in the oxygen and temperature variability (Fig. 5). Clear examples of pooling within the reef appear when, during bore arrival, temperature readings at the trough sensors dropped several degrees below the reading at the equivalent thermistor chain depth and persisted for the duration of the arrival, before converging on the minimum (e.g., Fig. 5, time $= 10:00$–$14:00$ h). During the event itself, DO and temperature readings at ridge and trough sensors, and benthic and offshore sites, were nearly identical (e.g., Fig. 5, time $= 14:00$–$16:45$ h). Notably, upon the start of bore relaxation, ridge sensor readings in the benthic sites jumped by several degrees (or mg L$^{-1}$ DO) within minutes, while the trough sensor readings climbed gradually over a period of several hours, not converging with the reading at the ridge sensor until that time had elapsed (e.g., Fig. 5, time $= 16:45$–$21:00$ h). This effect was more pronounced at the benthic sites (Fig. 5c,d) than at the offshore mooring (Fig. 5b).

**Added exposure time in the kelp forest**

Mean added exposure times during the arrival-phase at benthic sites 1 and 2 (Fig. 6a) were significantly greater than 0 min, 32.3 min ($p < 0.001$), and 40.4 min ($p < 0.001$), respectively, at the trough sensors, and 8.0 min ($p > 0.05$, not significant) and 38.2 min ($p < 0.001$), respectively, at the ridge sensors. Mean added exposure times during the relaxation-phase (Fig. 6b) at both benthic sites were 23.3

---

![Fig. 5. Example of a single hypoxic internal wave event across all sites from 28 June 2014. Time axis is the same for all plots. Note the drop to minimum temperature and DO levels much earlier in the arrival process as well as the delayed onset of relaxation in the benthic trough sites over the equivalent offshore. Ridge sensors are more similar across all sites. (a) Color-coded water-column temperature from the offshore thermistor chain, with very apparent cold water mass arriving beginning at roughly 10:00 h, and relaxation beginning 16:00 h. Solid yellow line indicates depth of trough sensors, and dashed yellow line indicates ridge sensors, at all sites. Mab, meters above the bottom. (b) Offshore temperature at both the trough-equivalent (solid) and ridge-equivalent (dashed) locations. (c) Trough (solid) and ridge (dashed) temperature (green) and DO (blue) at benthic site 1. (d) Trough (solid) and ridge (dashed) temperature (green) and DO (blue) at benthic site 2.](image-url)
min ($p < 0.001$ at both sites) at the trough sensors, while neither sites' added exposure times were significantly different from 0 at the ridge sensors. The trough sensors followed a pattern of added exposure consistent with extension of an event due to increased filling rate of topographic depressions upon bore arrival.

The added exposure times within the benthic sites during the relaxation-phase followed a pattern where the ridge sensors exhibited insignificant added exposure times, but the trough sensors exhibited significant added exposure time (Fig. 6b). The overall events as they occur at the regional scale, taken from the start of the arrival to the end of the relaxation at the offshore site, lasted on average 384 min and ranged from 126 min to 530 min (Fig. 6c). These are the durations that benthic site added exposure extends upon.

When directly paired with their regional event duration, the added exposure times are on average 20–26% percent of the regional event lengths with positively skewed distributions (Fig. 7). We found weak or no correlation between the total event length at the regional scale and the added

---

**Fig. 6.** Histogram of the number of events at each time bin across all events in our time series. Vertical lines represent the mean of each distribution (for each sensor, see legend). (a) Distributions of added exposure times (minutes) at benthic sites 1 and 2, ridge (i) and trough (ii) sensors during arrival, all events. (b) Distributions of added exposure times (minutes) at benthic sites 1 and 2, ridge (i) and trough (ii) sensors during relaxations, all events. (c) Distributions of the total event times at the ridge-equivalent (i) and trough-equivalent (ii) sensors from the offshore thermistor chain.

---

**Fig. 7.** Added exposure times (arrival and relaxation together) at the trough sensors, expressed as a percentage of the length of their corresponding event at the regional scale, for benthic site 1 (a) and benthic site 2 (b).
exposure time in the benthic sites (Fig. 8). That is, the longest (or shortest) added exposure times did not correspond with the longest (or shortest) regional scale events, therefore, there are some instances in which long added exposure times in the benthic sites correspond to short events at the regional scale. In some instances, the exposure time in the benthic sites increases by more than 100% of the regional scale event length. For instance, we have examples of 130-min, 150-min, and 250-min regional scale events (offshore site, trough-equivalent) which are each extended an additional 150 min at the benthic sites’ trough sensors (extensions of 125%, 100%, and 60%, respectively).

**Normalized arrivals and relaxations**

During arrivals (Fig. 9a), trough sensors at the benthic sites maintained ~ 10% lower temperature, on average, for the initial half of the arrival period compared to the temperature at the equivalent depth offshore. While the normalized arrival temperature is lower at the benthic sites than offshore, this difference is significant only for a fraction of the arrival process. These patterns are consistent with the hypothesis that arriving internal waves and resulting wave run-up within the kelp forest fill depressions in the rocky reef during arrival, causing an earlier drop in trough temperature than that expected due purely to the arrival of the regional-scale event. As the arrival-phase did not demonstrate clear pooling patterns, only the relaxation-phase will be further detailed here (for the equivalent results during the arrival-phase, see Supporting Information).

During relaxation (Fig. 9b), the pattern of delayed temperature recovery at the trough sensors was quite apparent, with significant reductions in benthic site trough temperature compared to the equivalent depth offshore, starting at ~ 30 min and continuing until ~ 240 min into the relaxation process. The ridge sensors were not significantly different from the equivalent sensors offshore during any part of the relaxation-phase and the offshore trough-equivalent followed very similar patterns as the ridge sensors.

**Normalized relaxation rates**

During the relaxation transition (i.e., the transition between main phase and post-event temperature; ~60 min to 60 min), the rate of temperature change of the normalized relaxations at the offshore trough-equivalent and all ridge sensors were significantly higher than in the benthic sites, peaking at twice the benthic site rate (Fig. 10). While the offshore and benthic sites begin the relaxation at roughly the same temperature, the offshore trough-equivalent temperature maintains its faster relaxation rate throughout the entire relaxation process, over the benthic site trough temperature (Figs. 9b, 10). In contrast, all ridge sensors (benthic and offshore equivalent) relax at similar rates to each other as well as to the offshore trough-equivalent (Figs. 9, 10). Following the relaxation transition, all sensors converge on similar slopes.

**Normalized Atemperature and relaxations**

The differences between the ridge and trough temperatures ($\Delta T$) were significantly greater at the benthic sites for the latter ~ 70% of the relaxation, with a maximum difference in the benthic sites of more than twice the $\Delta T$ over the equivalent depth offshore (Fig. 11). That is, the reef topography helps maintain a larger ridge-trough temperature difference for longer than the equivalent depths outside. During the relaxation process, the ridge sensors all follow similar patterns, and the difference between the benthic sites and offshore $\Delta T$ is from differences in the relaxation dynamics at the trough sensors exclusively.
Relationship with DO

The normalized temperature and DO differences (\(\Delta T\) and \(\Delta DO\) between the ridge and trough sensors) follow nearly identical patterns at the benthic sites, when considering only bores that contained low DO water (i.e., all events below 4.6 mg L\(^{-1}\), minimum DO observed was 2.6 mg L\(^{-1}\)) (Fig. 12). The slight differences in pattern between the sites indicate small differences in relaxation dynamics, although the similarity of the \(\Delta T\) profiles with those in Fig. 11 indicates that most of the variability is driven by a similar process. Note that only benthic sites are reported for the relationship with DO, as no oxygen measurements exist for the offshore water-column. However, the similarity with Fig. 11 for these sites suggests that the offshore DO would...
follow a similar pattern, where the difference in DO between the ridge and trough sensors would be smaller than that seen in the benthic sites.

**Discussion**

In this study, we found that the complex rocky reef topography within a kelp forest actively increases the residence time of cold, low DO water during internal wave arrival, and relaxation. We propose that this added exposure time results from earlier arrival of bores, increased filling rate of topographic depressions during the arrival process as a result of wave run-up, delayed relaxation, and restricted draining during the relaxation process. We propose that, because these retentions within the reef are the result of an internal process analogous to retention of water in tide pools in the rocky intertidal zone, they may be thought of as “internal tide pools” (Fig. 1). Use of this model in future studies will allow us to effectively compare topographical, advective, spatially-variable properties that lead to the formation and dissipation of these pools and, ultimately, to predict their effect on benthic organisms. To our knowledge, this is the first time such a process has been described. Where these pools contain low DO water, it is likely that they create spatial heterogeneity in the exposure of benthic organisms to low oxygen conditions.

We should clarify that the differences between sites are not the result of simple bore propagation delays. We found that on average, propagation delays account for less than 3 min during arrival, and less than 5 min during relaxation. Thus, the leads and lags attributed to internal pooling (lasting hours) are substantially greater than those from simple propagation differences. The large differences between our pooling observations and our propagation delay estimates, as well as the fact that our signal is concentrated below the upper elevations of the topography (whereas a propagation delay would be visible at both ridge and trough sensors), support our internal tide pool hypothesis.

We acknowledge that the conclusions in this study are based on a small number of sites within a single kelp forest/rocky reef, although these results are based on a large number of events for this location. Therefore, while we take our conclusions as a repeatable depiction of events as they occur at our study site, our intention is not to provide a description for direct extrapolation to other locations. However, as this set of features, which create internal tide pools in our site, are common in many other locations (e.g., low-oxygen internal waves, large rocky topographies), we contend that it is likely that a process similar to this occurs elsewhere, and is worth further measurement in other locations to determine the generality of our findings.

**Direct measurements of leads and lags in the kelp forest**

In this study, we observed clear extensions to the duration of internal bore events in the kelp forest’s rocky reef topography, both during the arrival and relaxation processes. We tentatively attribute the earlier arrival (longer added exposure) at site 2 compared to site 1 to the water movement pathways between the topography as the internal wave run-up snakes upslope through different channels. We acknowledge that, absent a fine scale topographic map of the reef, as well as detailed measurements of flow patterns between the two sites, this explanation for the difference between the ridge sites during the arrival is speculative. However in a follow up on this study, these types of differences between sites are observed frequently, often having little relationship with cross-shore, or other major axes. We
also point out that, in spite of the complicated differences between sites at the ridge sensors, extensions to internal bore events are robust across a large number of events, within the topography itself. We propose that the relaxation extension to be the result of an impeded draining, or a restricted gravity current flowing through and around the reef topography.

Besides the average exposure time increases, we show that there are important, but less frequent, extreme extensions to the duration of exposure to low oxygen water from internal tide pooling. While we observed significant, positive mean added exposure times in the benthic sites during both the arrival and relaxation processes, many of the added exposure distributions are positively skewed. So, while on average these events create moderate increases in exposure time within troughs, there also exist a small number of events where these increases are extremely long. In ecology, many communities are not structured or limited by the means of their environmental conditions, but rather by the extremes (i.e., the outliers) (e.g., Wolcott 1973; Miller et al. 2009; Denny et al. 2011; Kelly et al. 2011). It could be that occasional extreme exposure events, rather than frequent minor events, push organisms over an exposure limit, with a response resembling more of a threshold effect rather than a graded response (Portner and Knust 2007; Portner 2010). Parsing the individual bore attributes (e.g., directionality, offshore conditions) which contribute to more or less added exposure time will require further study with detailed regional measurements.

**Normalized pooling dynamics**

In the normalized example of arrival dynamics, we found a small but significant difference between the offshore and benthic sites’ temperatures at the trough (and trough-equivalent) sensors during the first third of the arrival, with the trough temperature being significantly lower early in the arrival but not during most of the latter portion of the arrival (Fig. 9a). The pooling pattern during the relaxation, however, is much more significant. During this period, a strong ridge–trough temperature gradient (∆T) exists within the topography in the kelp forest for a longer period of time than the equivalent offshore sensors (Fig. 11). This appears to be the result of a delayed start to the relaxation process at the trough sensors (Fig. 9b) as well as a reduced relaxation rate at these sensors once relaxation has begun (Fig. 10). We attribute this to the impedance of the reef itself, slowing and delaying the relaxation within the kelp forest rocky reef topography. Also, the concentration of this signal at the trough sensors in the benthic sites exclusively distinguishes this pattern from a drag effect of the whole kelp forest, which would manifest as a delay and slowing of both ridge and trough sensors. Thus, we consider this to be clear evidence of retention of internal bore water within depressions in the reef topography during the relaxation process, consistent with our internal tide pool hypothesis.

While we posit that this is clear evidence of retention within the reef, which we have referred to as “pooling,” we note that this pooling could take the form of a few subtly different mechanisms, ranging from pools fully detached from the sub-thermocline water mass, to slowed draining of sub-thermocline water. Our observations are distinct from water “trapping” however, in that the retention signal is concentrated within the topography.

**Implications**

Internal tide pooling has critical implications for nearshore ecology. Given that, during certain times of the year, internal bores in the area can be very low in oxygen (Booth et al. 2012; Walter et al. 2014), it follows that this pooling process has the potential to substantially prolong hypoxic events for benthic communities in the pooling areas. Except under rare circumstances, the presence of hypoxic internal tide pools is unlikely to cause direct mortality, evidenced by the fact that kelp forest and other nearshore upwelling system communities have long experienced this type of variability (Booth et al. 2012) yet still have thriving benthic communities. However, recent expansion of oxygen minimum zones (OMZs; Bograd et al. 2008; Stramma et al. 2010), and increases in coastal OMZ delivery processes (Bakun 1990), may shift these events into a regime to which these communities are not adapted. The cumulative indirect impacts of sub-lethal events have been shown to have effects equal to those of direct mortality (Breitburg et al. 2009). In many settings, variability in the physical environment at surprisingly small spatial scales can exceed variability at larger scales (Denny et al. 2004, 2011). Our finding that, through the presence of internal tide pools, the fluid environment may have important variability on similarly small scales identifies a new layer to this habitat complexity.

Many potential effects of habitat complexity do not require that internal tide pools persist for long periods. As an example, in other systems, the presence of hypoxia reduces the quality of habitat through the avoidance of hypoxic water by a variety of taxa (Eby and Crowder 2002; Eby et al. 2005). Avoidance of hypoxia can have a major influence on predation efficiency, food availability, and other density-dependent factors (Vanderloep et al. 2009), as avoidance en masse tends to concentrate organisms into tolerable habitat (Pihl et al. 1991; Eby and Crowder 2002; Tyler and Targett 2007). Such density related impacts often take place on short time scales, especially in the case of predators feeding on a concentrated prey species (Johnson 2006a,b). Moreover, where groups vary in their oxygen tolerance, avoidance is often dictated by trade-offs between oxygen stress and other factors (e.g., predation risk, food availability, etc.). These trade-offs lead to a situation known as “aggregation on the edge,” where groups of organisms aggregate in their lowest tolerable DO to maximize their refuge from less tolerant
predators or proximity to more tolerant prey (Craig 2012). Where species do not avoid these hypoxic areas, but rather employ physiological and behavioral coping mechanisms, sub-lethal hypoxic stress has been shown to reduce growth and reproductive capacity (McNatt and Rice 2004; Cheek 2011). These effects are just beginning to be studied for California Current kelp forest systems, and the internal tide pool concept, with its associated influence on oxygen spatial and temporal variability, is likely to be an essential component to understanding the role of nearshore oxygen dynamics.

Internal tide pooling likely has effects beyond exacerbating hypoxia. These cold and hypoxic waters also have a low pH (Booth et al. 2012; Frieder et al. 2012; Kapsenberg and Holfmann 2016). The same biological processes that deplete DO also increase the concentration of dissolved carbon dioxide, potentially affecting benthic organisms in internal pooling zones through impacts on calcification and other physiological processes (Fabry et al. 2008; Byrne 2011; Kroeker et al. 2013), as well as through subterranean processes such as alteration of sensory abilities in fish (Dixson et al. 2010; Simpson et al. 2011). Also, it is possible that not all impacts of internal tide pooling are negative. For instance, internal bores are often high in nutrients, and thus pooling may enhance nutrient uptake by the benthos (Shea and Broenkow 1982; Zimmerman and Kremer 1984; McPhee-Shaw et al. 2007). Also, internal bores can be important in the delivery of food and larvae to nearshore systems, so pooling could enhance food availability and aid in settlement processes (Shanks 1983; Pineda 1991, 1994; Witman et al. 1993). Furthermore, while it will require further investigation, it is likely that an internal tide pool process occurs in many systems where internal waves and complex topographies co-occur (e.g., coral reefs). The impact in these areas is yet to be determined, but is potentially important and likely situation-specific.

Hypoxic exposure experiments that do not take into account real environmental variability are likely to be limited in their ability to predict what in situ effects will arise. While this study did not seek to provide answers to the ultimate impacts of hypoxia on coastal ecosystems, we hope to have illuminated some important nuances in how local communities experience this environment. As global oxygen minima expand into shallower water and further inshore (Bograd et al. 2008; Stramma et al. 2010; Booth et al. 2014), and as coastal transport processes that drive these events increase in strength (Bakun 1990), it is likely that coastal hypoxic events will increase in frequency and severity. Therefore, understanding the environmental process at scales directly relevant to the organisms is crucial in order to understand and mitigate the potential consequences.

References

Bakun, A. 1990. Global climate change and intensification of coastal ocean upwelling. Science 247: 198–201. doi: 10.1126/science.247.4939.198

Bell, R. C., and R.O.R.Y. Thompson. 1980. Valley ventilation by cross winds. J. Fluid Mech. 96: 757. doi:10.1017/S0022112080002340

Bograd, S. J., C. G. Castro, E. Di Lorenzo, D. M. Palacios, H. Bailey, W. Gilly, and F. P. Chavez. 2008. Oxygen declines and the shoaling of the hypoxic boundary in the California Current. Geophys. Res. Lett. 35: 6. doi:10.1029/2008GL034185

Booth, J. A., and others. 2012. Natural intrusions of hypoxic, low pH water into nearshore marine environments on the California coast. Cont. Shelf Res. 45: 108–115. doi: 10.1016/j.csr.2012.06.009

Booth, J. A., and others. 2014. Patterns and potential drivers of declining oxygen content along the southern California coast. Limnol. Oceanogr. 59: 1127–1138. doi: 10.4319/lo.2014.59.4.1127

Breacher, L. C., and W. W. Broenkow. 1994. The circulation of Monterey Bay and related processes. Oceanogr. Mar. Biol. Annu. Rev. 32: 1–64.

Breitburg, D. L. 1992. Episodic hypoxia in chesapeake bay: Interacting effects of recruitment, behavior, and physical disturbance. Ecol. Monogr. 62: 525–546. doi:10.2307/2937315

Breitburg, D. L. 2002. Effects of hypoxia, and the balance between hypoxia and enrichment, on coastal fishes and fisheries. Estuaries 25: 767–781. doi:10.1007/BF02804904

Breitburg, D. L., D. W. Hondorp, L. A. Davías, and R. J. Diaz. 2009. Hypoxia, nitrogen, and fisheries: Integrating effects across local and global landscapes. Ann. Rev. Mar. Sci. 1: 329–349. doi:10.1146/annurev.marine.010908.163754

Byrne, M. 2011. Impact of ocean warming and ocean acidification on marine invertebrate life history stages: Vulnerabilities and potential for persistence in a changing ocean. Oceanogr. Mar. Biol. Annu. Rev. 49: 1–42. doi:10.1016/j.marenvres.2011.10.00

Chan, F., J. Barth, J. Lubchenco, A. Kirincich, H. Weeks, W. Peterson, and B. Menge. 2008. Emergence of anoxia in the California current large marine ecosystem. Science 319: 920. doi:10.1126/science.1149016

Cheek, A. O. 2011. Diel hypoxia alters fitness in growth-limited estuarine fish (Fundulus grandis). J. Exp. Mar. Biol. Ecol. 409: 13–20. doi:10.1016/j.jembe.2011.07.006

Cheriton, O. M., E. E. McPhee-Shaw, W. J. Shaw, T. P. Stanton, J. G. Bellingham, and C. D. Storlazzi. 2014. Suspended particulate layers and internal waves over the southern Monterey Bay continental shelf: An important control on shelf mud belts? J. Geophys. Res. Oceans 119: 428–444. doi:10.1002/2013JC009360

Craig, J. K. 2012. Aggregation on the edge: Effects of hypoxia avoidance on the spatial distribution of brown shrimp and demersal fishes in the Northern Gulf of Mexico. Mar. Ecol. Prog. Ser. 445: 75–95. doi:10.3354/meps09437

Denny, M. W., B. Helmuth, G. H. Leonard, C. D. G. Harley, L. J. H. Hunt, and E. K. Nelson. 2004. Quantifying scale
in ecology: Lessons from a wave-swept shore. Ecol. Monogr. **74**: 513–532. doi:10.1890/03-4043

Denny, M. W., W. W. Dowd, L. Bilir, and K. J. Mach. 2011. Spreading the risk: Small-scale body temperature variation among intertidal organisms and its implications for species persistence. J. Exp. Mar. Biol. Ecol. **400**: 175–190. doi:10.1016/j.jembe.2011.02.006

Dixon, D. L., P. L. Munday, and G. P. Jones. 2010. Ocean acidification disrupts the innate ability of fish to detect predator olfactory cues. Ecol. Lett. **13**: 68–75. doi:10.1111/j.1461-0248.2009.01400.x

Eby, L. A., and L. B. Crowder. 2002. Hypoxia-based habitat compression in the Neuse River Estuary: Context-dependent shifts in behavioral avoidance thresholds. Can. J. Fish. Aquat. Sci. **59**: 952–965. doi:10.1139/f02-067

Eby, L. A., L. B. Crowder, C. M. Mcclellan, C. H. Peterson, and M. J. Powers. 2005. Habitat degradation from intermittent hypoxia: Impacts on demersal fishes. Mar. Ecol. Prog. Ser. **291**: 249–261. doi:10.3354/meps291249

Fabry, V., B. Seibel, R. Feely, and J. Orr. 2008. Impacts of ocean acidification on marine fauna and ecosystem processes. ICES J. Mar. Sci. **65**: 414–432. doi:10.1093/icesjms/fsm048

Frieder, C. A., S. H. Nam, T. R. Martz, and L. A. Levin. 2012. High temporal and spatial variability of dissolved oxygen and pH in a nearshore California kelp forest. Biogeosciences **9**: 3917–3930. doi:10.5194/bg-9-3917-2012

Grantham, B. A., F. Chan, K. J. Nielsen, D. S. Fox, J. A. Barth, A. Huyer, J. Lubchenco, and B. A. Menge. 2004. Upwelling-driven nearshore hypoxia signals ecosystem and oceanographic changes in the northeast Pacific. Nature **429**: 749–754. doi:10.1038/nature02605

Jackson, G. A. 1984. Internal wave attenuation by coastal kelp stands. J. Phys. Oceanogr. **14**: 1300–1306. doi:10.1175/1520-0485(1984)014<1300:IWABKC>2.0.CO;2

Jackson, G. A. 1997. Currents in the high drag environment of a coastal kelp stand off California. Cont. Shelf Res. **17**: 1913–1928. doi:10.1016/S0278-4343(97)00054-X

Jensen, A., G. K. Pedersen, and D. J. Wood. 2003. An experimental study of wave run-up at a steep beach. J. Fluid Mech. **486**: 161–188. doi:10.1017/S0022112003004543

Johnson, D. W. 2006a. Density dependence in marine fish populations revealed at small and large spatial scales. Ecology **87**: 319–325. doi:10.1890/04-1665

Johnson, D. W. 2006b. Predation, habitat complexity, and variation in density-dependent mortality of temperate reef fishes. Ecology **87**: 1179–1188. doi:10.1890/0012-9658(2006)87[1179:PHCACI]2.0.CO;2

Kapsenberg, L., and G. E. Hofmann. 2016. Ocean pH time-series and drivers of variability along the northern Channel Islands, California, USA. Limnol. Oceanogr. **61**: 953–968. doi:10.1002/lno.10264

Kelly, M. W., E. Sanford, and R. K. Grosberg. 2011. Limited potential for adaptation to climate change in a broadly distributed marine crustacean. Proc. R. Soc. B **279**: 349–356. doi:10.1098/rsbp.2011.0542

Kroeker, K. J., R. L. Kordas, R. Crim, I. E. Hendriks, L. Ramajo, G. S. Singh, C. M. Duarte, and J. P. Gattuso. 2013. Impacts of ocean acidification on marine organisms: Quantifying sensitivities and interaction with warming. Glob. Chang. Biol. **19**: 1884–1896. doi:10.1111/gcb.12179

Leichter, J. J., S. R. Wing, S. L. Miller, M. W. Denny, R. Wing, and L. Miller. 1996. Pulsed delivery of subthermocline water to Conch Reef (Florida Keys) by internal tidal bores. Limnol. Oceanogr. **41**: 1490–1501. doi:10.4319/lo.1996.41.7.1490

McNatt, R. A., and J. A. Rice. 2004. Hypoxia-induced growth rate reduction in two juvenile estuary-dependent fishes. J. Exp. Mar. Biol. Ecol. **311**: 147–156. doi:10.1016/j.jembe.2004.05.006

McPhee-Shaw, E. E., D. A. Siegel, L. Washburn, M. A. Brzezinski, J. L. Jones, A. Leydecker, and J. Melack. 2007. Mechanisms for nutrient delivery to the inner shelf: Observations from the Santa Barbara Channel. Limnol. Oceanogr. **52**: 1748–1766. doi:10.4319/lo.2007.52.5.1748

Micheli, F., A. Saenz-Arroyo, A. Greenley, L. Vazquez, J. A. Espinoza Montes, M. Rossetto, and G. A. de Leo. 2012. Evidence that marine reserves enhance resilience to climatic impacts. PLoS One **7**: e40832. doi:10.1371/journal.pone.0040832

Miller, L. P., C. D. G. Harley, and M. W. Denny. 2009. The role of temperature and desiccation stress in limiting the local-scale distribution of the owl limpet, *Lottia gigantea*. Funct. Ecol. **23**: 756–767. doi:10.1111/j.1365-2435.2009.01567.x

Petruncio, E. T., L. K. Rosenfeld, and J. T. Paduan. 1998. Observations of the internal tide in Monterey Canyon. J. Phys. Oceanogr. **28**: 1873–1903. doi:10.1175/1520-0485(1998)028<1873:OOTITT>2.0.CO;2

Pihl, L., S. P. Baden, and R. J. Diaz. 1991. Effects of periodic hypoxia on distribution of demersal fish and crustaceans. Mar. Biol. **108**: 349–360. doi:10.1007/BF01313644

Pineda, J. 1994. Predicting upwelling and the shoreward transport of planktonic larvae by internal tidal bores. Science **253**: 548–549. doi:10.1126/science.253.5019.548

Pineda, J. 1994. Internal tidal bores in the nearshore: Warm-water fronts, seaward gravity currents and the onshore transport of neustonic larvae. J. Mar. Res. **52**: 427–458. doi:10.1357/002240943077046

Pörtner, H. O. 2010. Oxygen- and capacity-limitation of thermal tolerance: A matrix for integrating climate-related stressor effects in marine ecosystems. J. Exp. Biol. **213**: 881–893. doi:10.1242/jeb.037523

Pörtner, H. O., and R. Knust. 2007. Climate change affects marine fishes through the oxygen limitation of thermal tolerance. *Science* **315**: 95–98. doi:10.1126/science.1135471

Rabalais, N. N. 2009. Hypoxia, p. 172–180. In *J. Steele, S. Thorpe, K. Turekian [eds.], Encyclopedia of ocean sciences*, 2nd ed. Academic Press.

---

Leary et al. **Internal tide pools**
Rabalais, N. N., R. E. Turner, and W. J. Wiseman. 2002. Gulf of Mexico Hypoxia, a.k.a. “the Dead Zone”. Annu. Rev. Ecol. Syst. 33: 235–263. doi:10.1146/annurev.ecolsys.33.010802.150513

Rosenberger, K. J., C. D. Storlazzi, and O. M. Cheriton. 2016. Variability of the internal tide on the southern Monterey Bay continental shelf and associated bottom boundary layer sediment transport. Cont. Shelf Res. 120: 68–81. doi:10.1016/j.csr.2016.03.016

Rosman, J. H., J. R. Koseff, S. G. Monismith, and J. Grover. 2007. A field investigation into the effects of a kelp forest (Macrocystis pyrifera) on coastal hydrodynamics and transport. J. Geophys. Res. 112: 1–16. doi:10.1029/2005JC003430

Shanks, A. 1983. Surface slicks associated with tidally forced internal waves may transport pelagic larvae of benthic invertebrates and fishes shoreward. Mar. Ecol. Prog. Ser. 13: 311–315. doi:10.3354/meps013311

Shea, R. E., and W. W. Broenkow. 1982. The role of internal tides in the nutrient enrichment of Monterey Bay, California. Estuar. Coast. Shelf Sci. 15: 57–66. doi:10.1016/0272-7714(82)90036-1

Simpson, S. D., P. L. Munday, M. L. Wittenrich, R. Manassa, D. L. Dixon, M. Gagliano, and H. Y. Yan. 2011. Ocean acidification erodes crucial auditory behaviour in a marine fish. Biol. Lett. 7: 917–920. doi:10.1098/rsbl.2011.0293

Storlazzi, C. D., M. A. McManus, and J. D. Figurski. 2003. Long-term, high-frequency current and temperature measurements along central California: Insights into upwelling/relaxation and internal waves on the inner shelf. Cont. Shelf Res. 23: 901–918. doi:10.1016/S0278-4343(03)00045-1

Stramma, L., S. Schmidtko, L. A. Levin, and G. C. Johnson. 2010. Ocean oxygen minima expansions and their biological impacts. Deep-Sea Res. Part I Oceanogr. Res. Pap. 57: 587–595. doi:10.1016/j.dsr.2010.01.005

Tyler, R., and T. Targett. 2007. Juvenile weakfish Cynoscion regalis distribution in relation to diel-cycling dissolved oxygen in an estuarine turbidity. Mar. Ecol. Prog. Ser. 152: 257–269. doi:10.3354/meps33257

Vanderploeg, H. A., and others. 2009. Hypoxia affects spatial distributions and overlap of pelagic fish, zooplankton, and phytoplankton in Lake Erie. J. Exp. Mar. Biol. Ecol. 381: 592–5107. doi:10.1016/j.jembe.2009.07.027

Vaquer-Sunyer, R., and C. M. Duarte. 2008. Thresholds of hypoxia for marine biodiversity. Proc. Natl. Acad. Sci. USA 105: 15452–15457. doi:10.1073/pnas.0803833105

Wallace, B. C., and D. L. Wilkinson. 1988. Run-up of internal waves on a gentle slope in a two-layered system. J. Fluid Mech. 191: 419–442. doi:10.1017/S0022112088001636

Walter, R. K., C. B. Woodson, R. S. Arthur, O. B. Fringer, and S. G. Monismith. 2012. Nearshore internal bores and turbulent mixing in southern Monterey Bay. J. Geophys. Res. Oceans 117: C07017. doi:10.1029/2012JC008115

Walter, R. K., C. B. Woodson, P. R. Leary, and S. G. Monismith. 2014. Connecting wind-driven upwelling and offshore stratification to nearshore internal bores and oxygen variability. J. Geophys. Res. Oceans 119: 3517–3534. doi:10.1002/2014JC009999

Witman, J. D., J. J. Leichter, S. J. Genovese, and D. A. Brooks. 1993. Pulsed phytoplankton supply to the rocky subtidal zone: Influence of internal waves. Proc. Natl. Acad. Sci. USA 90: 1686–1690. doi:10.1073/pnas.90.5.1686

Wolcott, T. G. 1973. Physiological ecology and intertidal zonation in limpets (Acmaea): A critical look at limiting factors. Biol. Bull. 145: 389–422. doi:10.2307/1540048

Woodson, C. B. 2013. Spatiotemporal variation in cross-shelf exchange across the inner shelf of Monterey Bay, California. J. Phys. Oceanogr. 43: 1648–1665. doi:10.1175/JPO-D-11-0185.1

Zimmerman, R. C., and J. N. Kremer. 1984. Episodic nutrient supply to a kelp forest ecosystem in Southern California. J. Mar. Res. 42: 1984. doi:10.1357/00222408478850631

Acknowledgments

We thank S. Litvin, J. Beers, J. Goldbogen, M. Carr, and members of the labs of M. Denny, F. Micheli, and S. Monismith for their helpful discussions and input. This work would not have been possible without the capable assistance of many scientific divers at Hopkins Marine Station. This study utilized habitat data collected by California Sea Grant R/R-MPA-1 and the Partnership for Interdisciplinary Studies of Coastal Oceans: a long-term ecological consortium funded by the David and Lucile Packard Foundation and the Gordon and Betty Moore Foundation. Bathymetry data used in this study were acquired, processed, archived, and distributed by the Seafloor Mapping Lab of California State University Monterey Bay. This work was funded by the National Science Foundation through grants Division of Environmental Biology (DEB)-1212124 (to Micheli, Monismith, Woodson), OCE-1130095 (to Denny), and Oceanography (OCE)-1235552 (to Monismith), as well as the University of Georgia College of Engineering and the Center for Ocean Solutions. This material is based upon work supported by the National Science Foundation Graduate Research Fellowship under grant number DGE-114747. Leary was supported by the National Science Foundation Graduate Research Fellowship as well as the Stanford Biology Department.

Conflict of Interest

None declared.