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Climate-driven trends and ecological implications of event-scale upwelling in the California Current System

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Abstract

Eastern boundary current systems are among the most productive and lucrative ecosystems on Earth because they benefit from upwelling currents. Upwelling currents subsidize the base of the coastal food web by bringing deep, cold and nutrient-rich water to the surface. As upwelling is driven by large-scale atmospheric patterns, global climate change has the potential to affect a wide range of significant ecological processes through changes in water chemistry, water temperature, and the transport processes that influence species dispersal and recruitment. We examined long-term trends in the frequency, duration, and strength of continuous upwelling events for the Oregon and California regions of the California Current System in the eastern Pacific Ocean. We then associated event-scale upwelling with up to 21 years of barnacle and mussel recruitment, and water temperature data measured at rocky intertidal field sites along the Oregon coast. Our analyses suggest that upwelling events are changing in ways that are consistent with climate change predictions: upwelling events are becoming less frequent, stronger, and longer in duration. In addition, upwelling events have a quasi-instantaneous and cumulative effect on rocky intertidal water temperatures, with longer events leading to colder temperatures. Longer, more persistent upwelling events were negatively associated with barnacle recruitment but positively associated with mussel recruitment. However, since barnacles facilitate mussel recruitment by providing attachment sites, increased upwelling persistence could have indirect negative impacts on mussel populations. Overall, our results indicate that changes in coastal upwelling that are consistent with climate change predictions are altering the tempo and the mode of environmental forcing in near-shore ecosystems, with potentially severe and discontinuous ramifications for ecosystem structure and functioning.

Keywords: California Current System, climate change, coastal ecosystem, environmental forcing, recruitment, rocky intertidal, upwelling

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Introduction

Eastern boundary current systems, such as the California Current System (CCS) in the eastern Pacific Ocean, are among the most productive ecosystems on Earth. Although such regions account for <1% of the ocean surface, they support 20% of global commercial fishery yields (Pauly & Christensen, 1995). The high productivity of these systems is largely dependent upon coastal upwelling, a wind-driven process that promotes the growth of phytoplankton, the base of the coastal food web, by bringing large pulses of deep, nutrient-rich water to the sunlit surface. As the upwelling process is driven by large-scale atmospheric patterns, it is expected to respond to global climate change. In 1990, Andrew Bakun hypothesized that increased concentrations of greenhouse gases would drive stronger and more persistent upwelling (Bakun, 1990), a prediction recently confirmed along the coast of California (Garcia-Reyes & Largier, 2010). Coastal ecosystems – and the services they provide – will likely demonstrate a diverse range of significant, complex, and potentially discontinuous responses to changes in the upwelling process (Harley *et al.*, 2006). Our understanding of these responses is critical for successful ecosystem-based management of these important systems.

Coastal upwelling occurs when equatorward wind stress along the coast drives surface waters offshore, a phenomenon known as Ekman transport. Surface waters are replaced by subsurface waters that are drawn up from depth along the coast (Huyer, 1983). Periodic reversals of upwelling-favorable winds, termed ‘wind relaxations’, break the upwelling process into a series of upwelling events (Huyer, 1983; Papastephanou *et al.*, 2006; Melton *et al.*, 2009). Upwelling events are particularly characteristic off upwelling along the coast of Oregon, with periods of days to

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weeks, whereas upwelling further south tends to be more persistent with fewer wind relaxations (Huyer, 1983). However, there is increasing evidence to suggest that climate change is causing stronger and more persistent upwelling in Eastern boundary current systems around the world (Bakun, 1990; Mendelssohn & Schwing, 2002; McGregor *et al.*, 2007; Garcia-Reyes & Largier, 2010). Increased greenhouse gas concentrations cause continents to warm faster than oceans, and thus lead to a more intense pressure gradient in coastal regions as hot air rises over land and cooler air sinks over water (Bakun, 1990; Snyder *et al.*, 2003). In eastern boundary systems, this increased pressure gradient would favor fewer, longer upwelling events over the course of the upwelling season.

Most prior studies of the long-term effects of global climate change on upwelling systems have focused on the atmospheric and oceanographic conditions that change with the coastal upwelling process, typically at an annual or seasonal temporal scale, such as changes in the seasonal onset of upwelling (Garcia-Reyes & Largier, 2010). The scale and focus of this study is on the changing frequency and duration of upwelling events in the CCS and the potential ecological ramifications for a model ecosystem, the rocky intertidal. The Oregon rocky intertidal has long been a hotbed of experimental ecology, which makes it an ideal model system to begin to understand the ecological ramifications of long-term changes to the upwelling regime. Much is understood about how environmental forcing drives community structure in the rocky intertidal, particularly through the recruitment dynamics of two major space occupiers, mussels and barnacles (e.g., Menge *et al.*, 1997a,b, 2003, 2009).

Increases in the strength and persistence of upwelling events due to climate change have the potential to affect a wide range of significant ecological processes through changes in water chemistry, water temperature, and the transport processes that influence species dispersal and recruitment. The most important and widely recognized ecological consequence of upwelling is the delivery of nutrient-rich waters to the surface, causing blooms of phytoplankton that drive the high productivity of these coastal ecosystems. However, upwelled waters are also low in dissolved oxygen and any phytoplankton production that enters the detrital pool can further deplete oxygen concentrations at depth, due to bacterial respiration of sinking detritus (Bakun *et al.*, 2010). Additional phytoplankton production resulting from more persistent upwelling would likely exacerbate the current hypoxic, and sometimes anoxic, summertime conditions at depth on the continental shelf (Grantham *et al.*, 2004; Chan *et al.*, 2008).

Changes in the frequency and duration of upwelling events would also have consequences for how local oceanographic circulation patterns affect larval dispersal and recruitment. For the majority of intertidal and subtidal invertebrates and fishes, reproductive success depends on the dispersal of tiny pelagic larvae and their return to shore (Scheltema, 1986). Larvae have been observed to recruit to the adult, rocky intertidal habitat in episodic pulses linked to the periodic relaxation of upwelling-favorable winds and the subsequent onshore flow of surface waters (Farrell *et al.*, 1991; Roughgarden *et al.*, 1991; Dudas *et al.*, 2009). Not all species exhibit this response, however, due to behavioral differences in their position in the water column (Shanks & Brink, 2005; Broitman *et al.*, 2008; Rilov *et al.*, 2008; Shanks & Shearman, 2009). Changes in the upwelling regime may also result in species range expansion/contraction. For example, Lima *et al.* (2006) documented the northern expansion of the limpet *Patella rustica* that coincided with a period of weak upwelling, strong inshore poleward circulation, and warmer sea surface temperatures.

The relationship between larval recruitment and wind relaxations also depends on the strength of offshore advection and the effects of coastline and bathymetry on circulation patterns. For example, during upwelling conditions in northern Oregon (north of ~44.5°N), the upwelling current flows roughly parallel and relatively close (<30 km) to the coastline, causing classic Ekman circulation nearshore and setting up a barrier to extreme offshore transport (Castelao & Barth, 2005). In central Oregon, from ~44.5 to 43°N, the large shallow submarine Heceta Bank extends >100 km out to sea, causing the upwelling current to flow around its margin. Between the current and the coastline is a large retentive area of re-circulating upwelled water (Barth *et al.*, 2005; Kirincich *et al.*, 2005). Here, advection is low and plankton biomass is considerably higher than in other areas along the coast (Keister *et al.*, 2009). Farther south at 42.8°N, the current encounters Cape Blanco, where the angle of the coastline deviates and the upwelling current separates from the coast and flows strongly offshore. This results in large advective losses far offshore for the plankton community, but the flow is generally weak and not strongly directional in areas close to shore, where surface waters still flow shoreward during wind relaxations (Keister *et al.*, 2009). Upwelling in southern Oregon is generally much stronger than further north, with offshore Ekman transport about 3–4 times larger (Samelson *et al.*, 2002), making successful larval recruitment potentially more reliant on wind relaxations.

The different response of local currents to upwelling-favorable winds has been shown to affect community

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structure, particularly in rocky intertidal ecosystems (Menge *et al*., 1997a; Kirincich *et al*., 2005). For instance, sites within the retentive Heceta Bank region have higher phytoplankton productivity, higher recruitment and growth rates of filter feeding mussels and barnacles, and stronger rates of predation and grazing than sites further north or south (Menge *et al*., 1997b, 2011a). Hence, at sites located within the Heceta Bank region, competitively superior filter feeding mussels are abundant in the low intertidal zone, whereas outside of the Heceta Bank region, competitively inferior macrophytes dominate the low zone (Menge *et al*., 1997b).

In addition to altering recruitment patterns, upwelling can have a profound impact on coastal communities by reducing near-shore water temperatures. The effects of temperature at the organismal level (i.e., biochemical kinetics) are well known, and we are beginning to understand the effects at the population and community levels (Gillooly *et al*., 2001; Brown *et al*., 2004). For instance, cooler water temperatures suppress larval developmental rates and increase the duration of the larval period, which alters dispersal distances and survival (O'Connor, 2007). Cooler water not only decreases the growth rates of the dominant space occupier in the rocky intertidal, the mussel *Mytilus californianus* (Menge *et al*., 2008) but also decreases the feeding rate of its main predator, the sea star *Pisaster ochraceus* (Pincebourde *et al*., 2008a,b). Thus, by altering demographic rates and species interactions in sometimes countervailing ways, temperature can have complex and critical effects on the structure and dynamics of ecological communities.

To detect changes in event-scale upwelling and assess their ecological consequences, we quantified long-term temporal trends in upwelling event frequency, duration and strength over 43 years in Oregon and California. We then related event-scale upwelling to water temperature measurements and recruitment patterns of mussels and barnacles at three rocky intertidal sites over the last 10–21 years. We hypothesized that there would be long-term increasing trends in the persistence and strength of upwelling events, consistent with climate change predictions (Bakun, 1990; Bakun *et al*., 2010). We also hypothesized that increased duration of upwelling events would be related to lower water temperatures and reduced recruitment. Our analyses of long-term upwelling, water temperature, and recruitment along the CCS provide us with a unique opportunity to (1) test existing predictions about how climate change will affect the frequency, duration, and magnitude of upwelling events along Eastern boundary currents and (2) determine the likely impacts on the structure and functioning of coastal ecosystems.

Methods

Regional upwelling index dataset

We used the Pacific Fisheries Environmental Laboratory (PFEL) 43-year time series (1967–2010) of 6-hourly upwelling indices for five latitudes along the CCS: 45°N, 42°N, 39°N, 36° N, and 33°N (http://www.pfeg.noaa.gov; Fig. 1). PFEL calculates coastal upwelling indices from 1°-resolution sea level pressure fields obtained from the US Navy Fleet Numerical Meteorology and Oceanography Center. The index is based on estimates of Ekman mass transport of surface water due to wind stress and the Coriolis force (Bakun *et al*., 1974). Positive

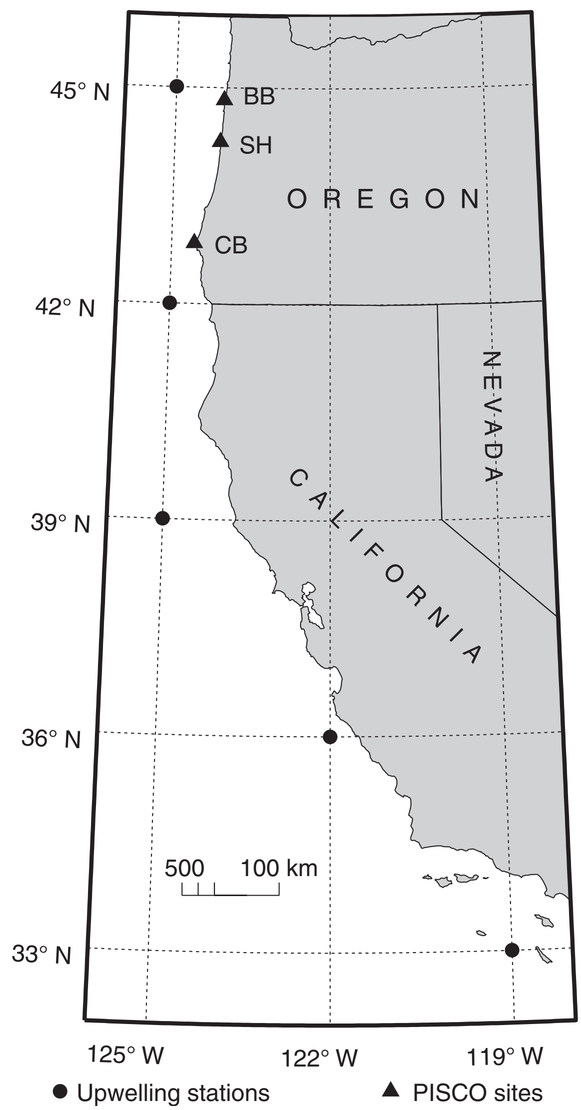

Fig. 1 Map of the study region. Shown are the locations of the five PFEL upwelling stations in the CCS off the coast of Oregon and California (circles) and the three rocky intertidal field sites along the Oregon coast (triangles): Boiler Bay (BB), Strawberry Hill (SH), and Cape Blanco (CB).

values, the result of equatorward wind stress, are an estimate of the amount of water upwelled from the base of the Ekman layer ($m^3{\cdot}s^{-1}{\cdot}100\ m^{-1}$ of coastline). Negative values imply downwelling, accompanied by the onshore advection of surface waters. We performed all analyses on the offshore component of the upwelling index and replaced missing values using linear interpolation.

Trends in the annual number, duration, and magnitude of upwelling events

We calculated annual summary statistics to characterize the frequency, duration, mean, and total magnitude of upwelling events, and then related the summary statistics to time using simple linear regression. We considered ‘upwelling events’ as periods of time when the upwelling index is positive. The end of an upwelling event is termed a ‘wind relaxation’ and marks the transition from upwelling to downwelling. For each upwelling event, we recorded the end date (the date of the wind relaxation), the event duration, and the mean and total magnitude of upwelled water over the course of the event. Because there is a lag period between when the winds build and when upwelled water actually reaches the surface, others have classified only those upwelling events that last for at least 3 days as ‘ecologically significant’ (Garcia-Reyes & Largier, 2010). We did not impose an arbitrary minimum duration for upwelling events to qualify as ‘ecologically significant’; instead we determined the robustness of the results using sensitivity analyses. Sensitivity analyses involved sequentially changing the definition of the minimum duration of an upwelling event from 0–14 days and rerunning all regressions.

We limited our analyses to the upwelling season, which we defined using the mean daily cumulative upwelling index following Schwing *et al.* (2006). Specifically, for each latitude, the start (end) of the upwelling season is defined as the date when the climatological mean daily cumulative upwelling index first becomes positive (starts to decline). The upwelling season spanned the spring and the summer in Oregon, the spring through the fall in northern California, and extended to almost the entire year in southern California.

Because the distributions of upwelling event duration, mean magnitude, and total magnitude were heavily right-skewed, we applied log-transformations ($\log_{10} + 1$) prior to conducting simple linear regression to limit the effects of outliers and attain quasinormality. The *P*-values of the regressions were calculated by performing 1000 permutations of the data and determining the proportion of permutations that yielded a coefficient of determination that was greater than or equal to the one obtained with the original data (Legendre and Legendre, 1998).

Trends in the intra-annual distribution of upwelling event duration and magnitude

Summary statistics such as the annual mean can often conceal more complex intra-annual temporal trends. The sensitivity of the annual trends to the minimum duration defining an upwelling event indicated the need to document intra-annual trends trends. To accomplish this, we determined how the entire intra-annual distribution of upwelling event duration and magnitude has shifted over time by calculating quantiles of upwelling event duration, mean magnitude and total magnitude for each year and regressing them against time. This approach is similar to regressing the annual minimum or maximum against time but by dividing the data into many different quantiles, we were able to quantify the temporal trends across the entire distribution. Specifically, for data X consisting of N-values sorted from lowest to highest, the kth q-quantile Q_k (X) was obtained by selecting the value of X at index $N\frac{k}{q}$. For each year, we used this method to calculate 25 quantiles of the data, from very low (0.03) to very high (0.99).

Determining the temporal trends in the raw upwelling time series

To confirm the temporal trends observed in the annual summary statistics, we used wavelet analysis to document how the variability of the raw upwelling time series changed from 1967 to 2010. Wavelet analysis decomposes a time series into its component periodicities and reveals the relative contribution of the variability at each period to the total variability over time (Torrence & Compo, 1998; Cazelles *et al.*, 2008). Because wavelet analysis is well-resolved in both the time and frequency domains, it can reveal trends that would go unnoticed with simpler methods that are either unresolved or poorly resolved in time/frequency such as annual means. A complete description of wavelet analysis is provided in Appendix S1.

Intertidal water conditions in response to upwelling events

The upwelling index is generated from large-scale, sea level pressure fields extending far offshore in the CCS, yet the index is an estimate of how much cold, nutrient-rich upwelled water is being brought to the surface in the near-shore environment. To test the influence of temporal trends in upwelling event variability on intertidal water conditions, we related the index to long-term measurements of mean daily water temperatures at three intertidal sites collected by the Partnership for Interdisciplinary Studies of Coastal Oceans (PISCO). Boiler Bay (BB; 44°49′48″N, 124°3′36″W) is located at the southern edge of the region where the upwelling current runs close and parallel to shore and classic Ekman circulation dominates (Fig. 1). Strawberry Hill (SH; 44°15′N, 124°7′12″W) is located within the Heceta Bank region, where a large, sluggish, re-circulation zone retains plankton and upwelling drives high productivity (Fig. 1). Cape Blanco (CB; 42°50′24″N, 124°34′12″W) is located on Cape Blanco in southern Oregon where the upwelling current separates from the coastline and flows offshore (Fig. 1). Of the many PISCO sites, Boiler Bay and Strawberry Hill have the longest time series of daily water temperature measurements (1993–2009) and are within 1° latitude of the 45°N upwelling index. Although we only had 11 years of data for Cape Blanco (1999–2009), including this site allowed us to assess the relationship between temperature and a different upwelling time series, the index for 42°N, where upwelling tends to be 3–4 times stronger.

The temperature data are point source from temperature loggers (StowAway TidbiT Temperature Loggers, Onset Computer Corporation, TBI32-05 + 37) that were bolted to rocks inside wire cages in the low zone at each site with three replicates per site. Although temperature was recorded at 1 h intervals, we used tide tables to remove low tide air temperature measurements and averaged the remaining water temperature measurements for each day.

We computed the cross-correlation between daily temperature and upwelling index at each of the three Oregon locations during the upwelling season to determine the temporal lag between changes in regional upwelling conditions and local intertidal temperature. We also tested whether longer upwelling events resulted in colder water temperatures. Using simple linear regression, we related the duration of upwelling events to the change in water temperature, calculated as the difference between the average water temperature during an event and the water temperature on the day before the event started.

In addition, we used wavelet coherence (Torrence & Compo, 1998; Grinsted *et al.*, 2004; Cazelles *et al.*, 2008), a bivariate extension of wavelet analysis that describes patterns of correlation between pairs of time series in the time–frequency domain, to assess the temporal variability in the relationship between daily upwelling and intertidal temperature from 1999 to 2009 at all three Oregon locations (see Appendix S1 for a full description of wavelet coherence). Although we used wavelet coherence to document how the correlation in the fluctuations of upwelling and temperature varies over time at periods ranging from 2 to 1024 days, we focused on event-scale (<40 days), sub-annual (41–255 days), and annual (256–512 days) period blocks. These divisions were motivated by strong differences in the temporal patterns of variability across these period blocks, with upwelling and temperature exhibiting (1) seasonal and high variability at event-scale periods, (2) seasonal and weak variability at sub-annual periods, and (3) persistently high variability at annual periods (Appendix S2: Fig. S2–1, S2–3). The different temporal patterns of variability summarized above are presented in greater detail in Appendix S2.

Response of intertidal ecosystem productivity to upwelling

In addition to the temperature analyses, we determined if local ecosystem productivity at our field sites was also responding to upwelling conditions. We examined PISCO's long term nitrate, phosphate and chlorophyll-*a* data from Boiler Bay (1993–2010), Strawberry Hill (1993–2010), and Cape Blanco (1995–2010). Each month during the upwelling season, replicated (n = 3) samples were collected at low tide in flowing water at a depth of ~30 cm using opaque plastic (HDPE) bottles. For chlorophyll-*a*, a 100 mL subsample was filtered through a 25 mm combusted Whatman glass fiber filter (pore size 0.7 μm) and stored on ice. The filter was extracted in 90% HPLC acetone for 12 h in the dark at −20 °C, and the concentration of chlorophyll-*a* was determined using a Turner Designs Model 10 fluorometer calibrated with a pure chlorophyll-*a* standard (Sigma Chemical, St. Louis, MO, USA). Nitrate and phosphate were quantitated from 20 mL subsamples of the filtrate by standard auto-analyzer techniques (Atlas *et al.*, 1971). We used Spearman's rank correlations to analyze the association between nutrient and chlorophyll-*a* concentrations and (1) the number of wind relaxations, (2) the mean duration of upwelling events, and (3) the mean upwelling index over the days prior to each water sample. For nutrients, we examined upwelling event conditions from 1 to 10 days prior to the sample and from 5 to 50 days for chlorophyll-*a*.

Effects of upwelling events on recruitment to the intertidal

We investigated whether the number of wind relaxations that mark the end of upwelling events and upwelling event duration were associated with the recruitment of barnacles and mussels. We obtained long-term recruitment data from PISCO for the same three sites as the temperature analyses. We used 21 years of barnacle and mussel recruitment data for Boiler Bay and Strawberry Hill, 1989–2009, and 11 years of recruitment data for Cape Blanco, 1999–2009.

As described elsewhere (Menge *et al.*, 2009, 2011b), recruitment of barnacles and mussels was measured using artificial substrates on which larvae readily settle when deployed in the rocky intertidal. Briefly, Safetywalk® antislip tape on PVC plate (plates) and S.O.S Tuffy® mesh pads (tuffies) were used as substrates (collectors) for barnacle and mussel recruitment respectively. Collectors were bolted to rocks in the rocky intertidal at two wave exposures (exposed and protected) and two tidal heights (mid and low zones of the intertidal), except at CB where they were deployed in the mid exposed intertidal only. Plates and tuffies were deployed for 2–4 weeks, with 5–8 replicates of each. The collectors were then brought to the laboratory where barnacle cyprids and metamorphs and whole mussels were identified and counted using dissecting microscopes. Because postsettlement mortality can increasingly influence recruitment measurements as deployment time increases (Shanks, 2009a), we did not use recruitment data for plates or tuffies deployed longer than 35 days.

For each deployment interval, we calculated the mean daily barnacle and mussel recruitment rates. Replicate measurements were averaged together before averaging over wave exposures and tidal heights. This reduced the data to one measure of mean daily recruitment for the barnacles *Balanus glandula* and *Chthamalus dalli*, and for the mussels *Mytilus* spp. for each deployment interval at each site. Because the data contain zeros and are not normally distributed, we used Spearman's rank correlations to analyze the association between recruitment and (1) the number of wind relaxations that occur during the deployment interval, (2) the mean duration of the upwelling events prior to those wind relaxations, and (3) the mean duration of the downwelling events that occur after those wind relaxations. Since both recruitment and the upwelling index exhibit annual-scale variability (both are low during winter and high during summer), and we were interested in event-scale associations, we confined the data to Oregon's upwelling season, April through September. To assess the sensitivity of the results to the minimum duration defining an upwelling event, we repeated the analysis for minimum durations from 0 to 12 days. All data processing and analyses were conducted using MATLAB 7.8 (MathWorks, R2009a, Natick, MA, USA), and R 2.11.1 (R Development Core Team 2008).

Results

Trends in the annual number, duration, and magnitude of upwelling events

At each of the five latitudes along the CCS, the number of upwelling events has declined by 23–40% from 1967 to 2010 (Table 1a). In addition, the annual mean duration of upwelling events has increased by 26% to 86% (Table 1b), and the annual mean and total magnitude of upwelling events are increasing over time (Table 1c and d). The sensitivity analyses, which sequentially redefined the minimum duration of an upwelling event, reveal that the increase in the mean annual duration of upwelling is partially due to short events (<1 day) becoming less frequent and partially due to long events (>6 days) becoming more frequent (Appendix S3 Fig. S3–1).

Trends in the intra-annual distribution of upwelling event duration and magnitude

Overall, the intra-annual distribution of event durations is shifting toward higher values over time (positive slopes) at all sites (Fig. 2). Similar trends occur in the distributions of upwelling event mean and total magnitude, indicating that events are not only becoming longer, but are also becoming stronger (Appendix S3: Fig. S3–5, S3–6). This analysis also confirms the different trends of short and long upwelling events seen in the sensitivity analysis. Indeed, the frequency of intermediate to long upwelling events durations is increasing at a faster rate than that of short upwelling events (Fig. 2). Specifically, very low quantiles (e.g., <0.2) and very high quantiles (e.g., >0.9) of upwelling event duration have smaller positive slopes than intermediate-to-high quantiles at 42°N, 36°N, and 33°N (Fig. 2c, d, g–j). At 45°N and 39°N, the relatively low quantiles are the ones showing stronger increases (largest slopes) over time (Fig. 2a, b, e, f).

The wavelet analysis of the raw upwelling time series indicates that upwelling is being increasingly dominated over time by variability at event-scale (<40 days), sub-annual (41–255 days), and super-annual (>512 days) periods instead of annual periods (256–512 days) at several latitudes (Appendix S2: Fig. S2–2). This is consistent with the observed annual trends in upwelling events: by becoming stronger and more persistent, upwelling events are accounting for a greater proportion of the variability in upwelling over time.

Table 1 Temporal trends in upwelling events. Temporal trends from 1967 to 2010 in the frequency, mean duration, mean magnitude, and total magnitude of upwelling events at five latitudes across the California Current System. Only upwelling events occurring during the upwelling season of each latitude are included. Statistics represent simple linear regression models ($y = \beta_0 + \beta_1 x$) of the effect of year on the (a) frequency, (b) mean duration ($\log_{10} + 1$), (c) mean magnitude ($\log_{10} + 1$), and (d) total magnitude ($\log_{10} + 1$) of upwelling events

Latitude	*P*-value	R^2	β_0	β_1
(a) Frequency of upwelling events				
45	**0.040**	0.103	371.332	−0.172
42	**0.002**	0.253	660.587	−0.317
39	**0.010**	0.164	475.072	−0.226
36	**0.001**	0.350	965.509	−0.465
33	**0.007**	0.175	731.596	−0.344
(b) Mean duration of upwelling events				
45	0.077	0.078	−3.147	0.002
42	**0.001**	0.249	−7.947	0.004
39	0.053	0.093	−4.205	0.002
36	**0.001**	0.453	−10.520	0.006
33	**0.001**	0.253	−5.775	0.003
(c) Mean magnitude of upwelling events				
45	0.208	0.033	−1.581	0.001
42	**0.030**	0.112	−6.523	0.004
39	0.436	0.016	−1.187	0.001
36	**0.007**	0.165	−5.700	0.004
33	0.088	0.067	−1.548	0.001
(d) Total magnitude of upwelling events				
45	0.068	0.074	−7.290	0.005
42	**0.003**	0.201	−19.407	0.011
39	0.149	0.052	−7.231	0.005
36	**0.001**	0.352	−21.616	0.012
33	**0.002**	0.205	−10.341	0.006

For each analysis, we present the *P*-value (bolded when <0.05), coefficient of determination (R^2), intercept (β_0), and slope (β_1).

Intertidal water conditions in response to upwelling events

The regional upwelling index and local intertidal water temperature are negatively correlated at time lags of 0–9 days at all three Oregon sites during the upwelling season, with the cross-correlation being strongest at time lags of 2–3 days (Fig. 3a, c, e). Furthermore, at all three Oregon sites, the change in water temperature is strongly negatively associated with the

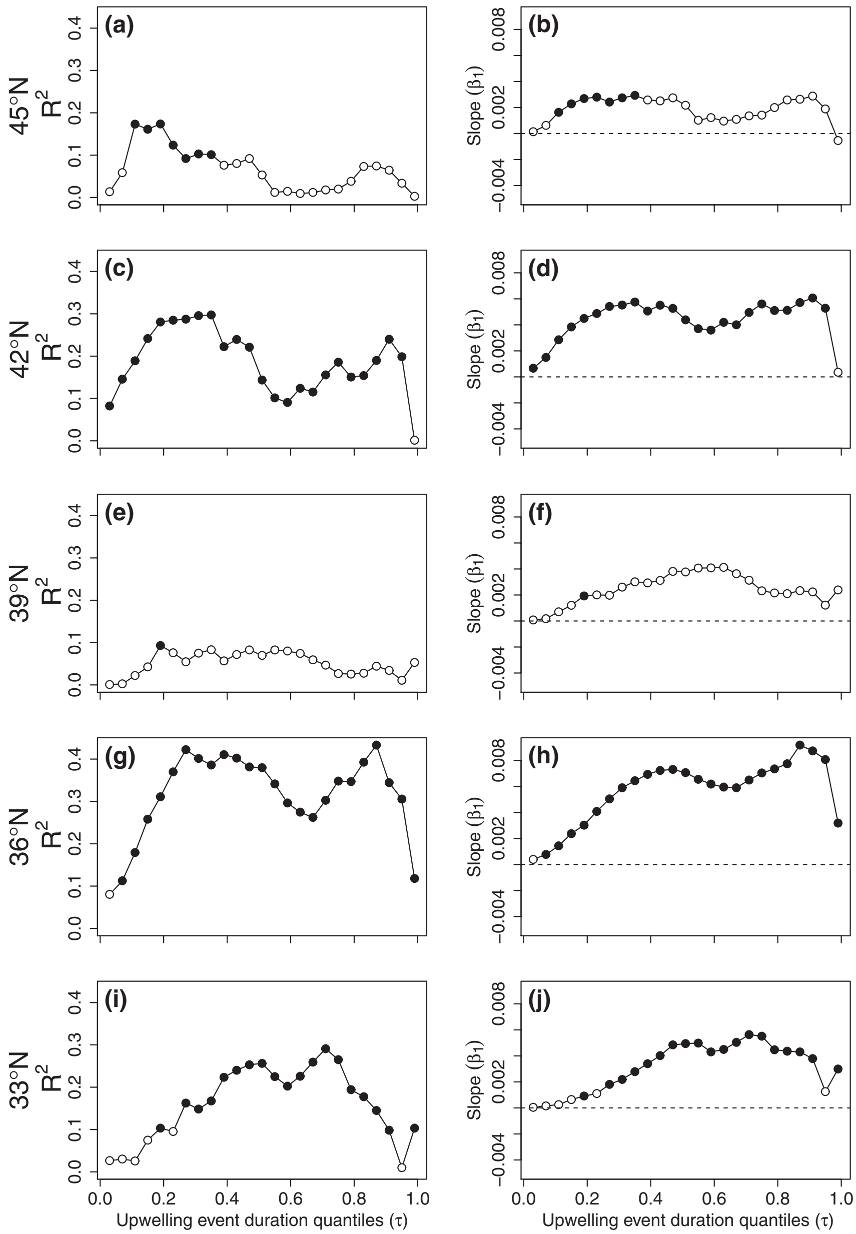

Fig. 2 Temporal trends in the intra-annual distribution of $\log_{10}$ upwelling event durations from 1967 to 2010. Within each year for each of the five latitudes, we identified the different quantiles of $\log_{10}$ upwelling event duration. The quantiles were related to year via simple linear regression models ($y = \beta_0 + \beta_1 x$), yielding a coefficient of determination (R^2, left column) and a slope (β_1, right column). Closed (open) circles indicate regressions with P-values <0.05 (>0.05). The P-values were assessed by performing 1000 permutations of the data and determining the proportion of permutations that yielded a coefficient of determination that was greater than or equal to the one obtained with the original data.

duration of upwelling events ($P < 0.0001$; Fig. 3b, d, f). Thus, upwelling events at the regional scale lead to a systematic decrease in local intertidal temperature after a lag period of 0–3 days, with longer upwelling events generating colder intertidal temperatures. Overall, these results indicate that changes in daily upwelling have both a quasi-instantaneous and a cumulative effect on local intertidal water temperature.

To determine how the relationship between fluctuations in daily upwelling and temperature at different periodicities varied over time, we conducted wavelet coherence analyses at all three Oregon sites from 1999 to 2010. Upwelling and temperature show coherent fluctuations (coherence >0.8) at event-scale (<40 days) and sub-annual periods (41–255 days) at all three sites during the summer months, with a phase difference

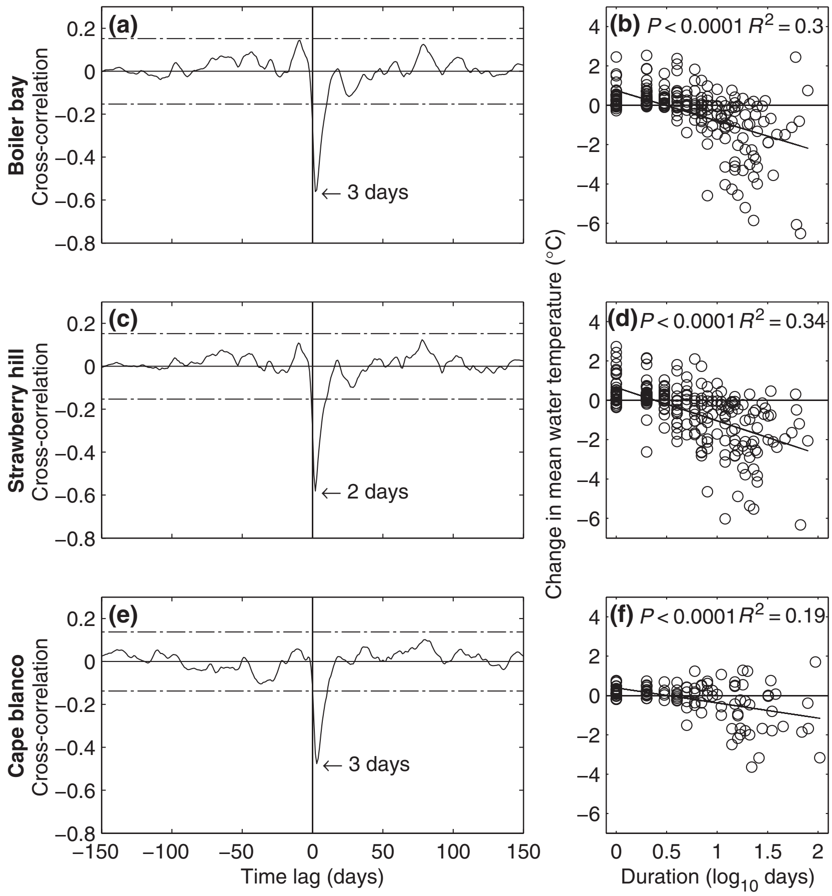

Fig. 3 The effect of daily upwelling conditions on daily rocky intertidal water temperatures from 1999 to 2010. Subplots represent cross-correlations of mean daily water temperature and mean daily upwelling index at (a) Boiler Bay, (c) Strawberry Hill, and (e) Cape Blanco. The dashed lines indicate the 95% confidence interval of cross-correlation values predicted for two uncorrelated time series. Cross-correlations outside of the confidence interval are thus significant at the $\alpha = 0.05$ level. The lag time at which water temperature was most highly correlated to the upwelling index is indicated with an arrow for each plot. Side plots represent simple linear regressions of the effect of upwelling event duration on the change in water temperature at (b) Boiler Bay, (d) Strawberry Hill, and (f) Cape Blanco. The change in water temperature is the difference between the water temperature the day before an upwelling event starts and the mean water temperature over the course of the event. The regression statistics are indicated on each plot.

between the cycles of upwelling and temperature of $-\pi/2$ (Fig. 4). This phase difference means that there is a time lag between changes in upwelling conditions and water temperature, with peaks in upwelling trailing peaks in temperature by a quarter of the amount of time a complete cycle takes. This means that through time, temperature drops follow peaks in upwelling. This pattern is consistent with a causal relationship between upwelling and temperature fluctuations at event-scale and sub-annual periods.

Upwelling and temperature undergo coherent fluctuations at annual periods (256–512 days) at Cape Blanco only, with upwelling leading temperature by $\pi/2$ (i.e., a temporal lag of approximately 3 months; Fig. 4f). These coherent annual fluctuations are unlikely to be causally related but due instead to seasonality in both temperature and upwelling patterns. Upwelling peaks earlier in the year than water temperature because the sun warms the air much faster than water during the spring months, thus generating a thermal gradient between the heated land mass and the cooler coastal ocean (Bakun, 1990). The thermal gradient then generates strong alongshore winds that cause coastal upwelling to arise. This leads to a $\pi/2$ phase difference between upwelling and temperature at annual periods, with upwelling peaking in the spring and water temperature peaking in the summer (Fig. 4f, Appendix S2: Fig. S2–5f).

All water productivity indicators showed similar trends in response to upwelling at all sites. Chlorophyll-*a*, nitrate, and phosphate concentrations were negatively related to the number of wind relaxations and positively related to the mean duration of

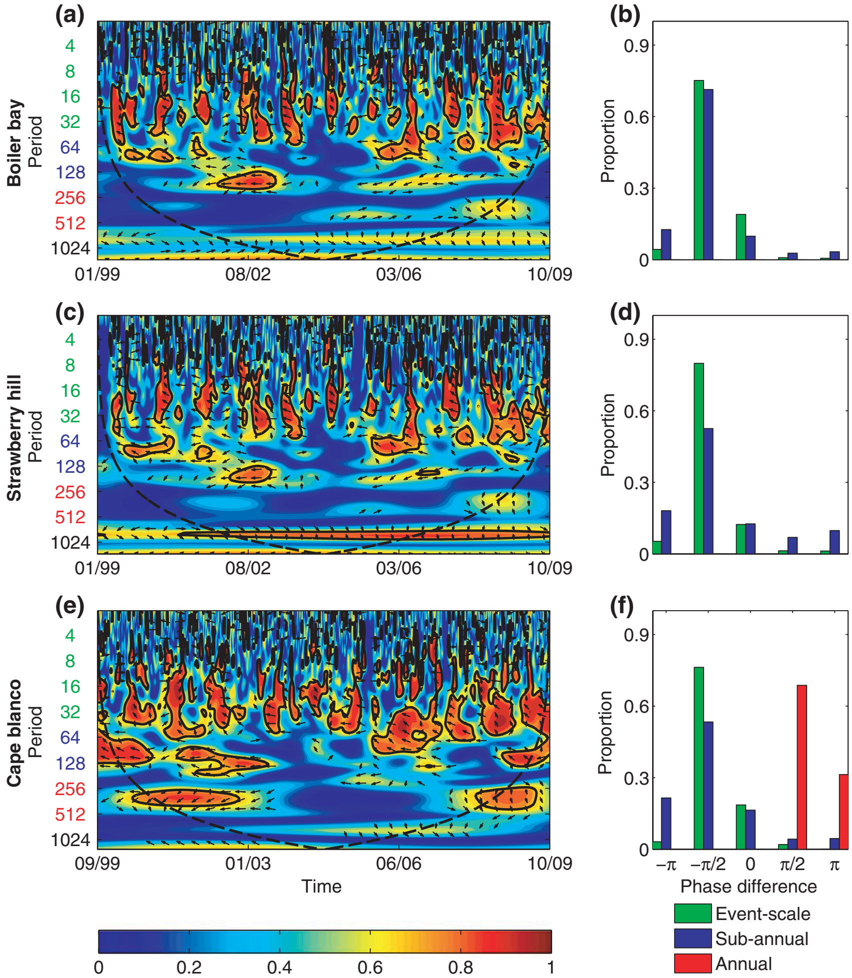

Fig. 4 Pairwise wavelet coherence analysis of daily upwelling and temperature time series from 1999 to 2010 at (a and b) Boiler Bay, (c and d) Strawberry Hill, and (e and f) Cape Blanco. The left column represents wavelet coherence analyses between (a) 45°N upwelling index and temperature at Boiler Bay, (c) 45°N upwelling index and temperature at Strawberry Hill, and (e) 42°N upwelling index and temperature at Cape Blanco. Wavelet coherence represents regions of high (low) common fluctuations between the time series in warm (cold) colors. Black arrows indicate the phase angle between the time series. When the time series move in the same direction (i.e., in phase), the arrows point to the right and when they move in opposite directions (i.e., antiphase), the arrows point to the left. Arrows pointing down indicate a $\pi/2$ phase difference between the time series, with upwelling leading temperature, and arrows pointing up indicate a $-\pi/2$ phase difference between the time series, with temperature leading upwelling. Black contours represent regions of statistically significant common variability at the $\alpha = 0.05$ level. Regions within the black dashed lines (the cone of influence) are not affected by edge effects. (b, d, f) The right column shows the distribution of phase differences between upwelling and temperature across all significant wavelet coherence regions for event-scale (<40 days; green), sub-annual (41–255 days; blue) and annual (256–512 days; red) periodicities.

upwelling events and the mean upwelling index (Appendix S4: Fig. S4–1a, b, c).

Effects of upwelling events on recruitment to the intertidal

Overall, barnacle and mussel recruitment varied with the number and mean duration of upwelling events, and these relationships depended on the minimum duration defining an upwelling event (Fig. 5). The trends observed for Boiler Bay and Strawberry Hill were stronger than for Cape Blanco. Recruitment of mussels and barnacles was positively associated with the number of wind relaxations, although this relationship often did not appear unless short upwelling events were excluded from the analysis, which indicates that larvae do not recruit in response to wind relaxations at the end of short events (Fig. 5). However, the minimum duration of upwelling events with which recruitment was most strongly associated differed between sites.

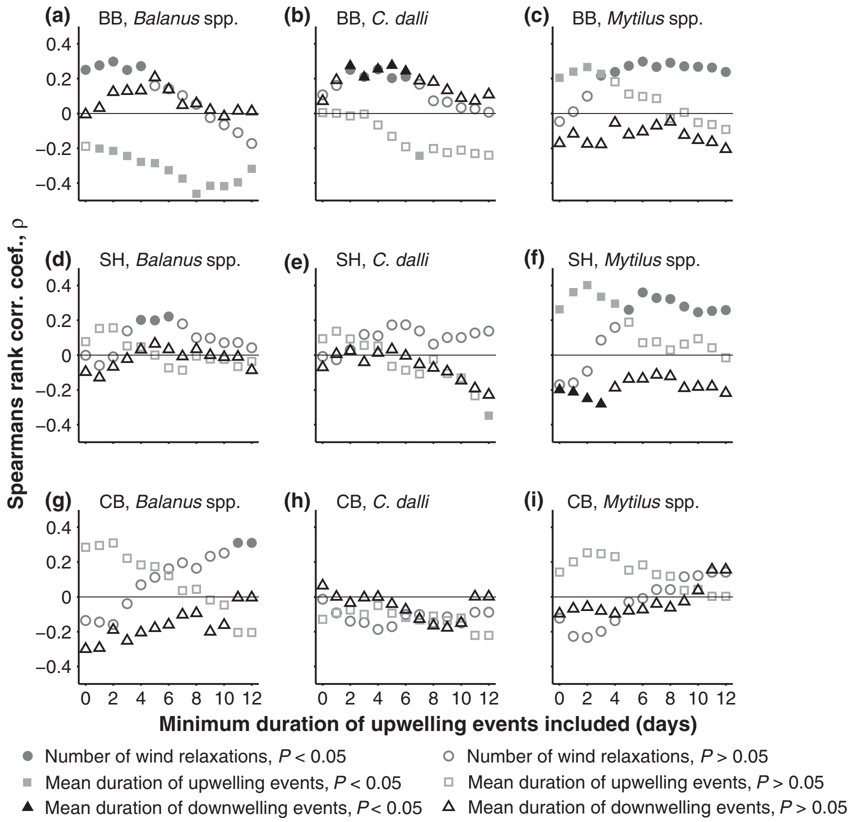

Fig. 5 Correlation analyses of barnacle and mussel recruitment with upwelling event conditions. Plotted on the y-axis are the coefficients of the Spearman's rank correlation analyses of barnacle and mussel recruitment versus (1) the number of wind relaxations (circles), (2) the mean duration of the upwelling events that occur before (squares), and (3) the mean duration of the downwelling events that occur after those wind relaxations (triangles). The x-axis is the minimum duration of upwelling events included in the analysis, from 0 to 12 days. Correlation coefficients that account for a statistically significant proportion of the variation in the data at the $\alpha = 0.05$ level are represented by closed symbols, nonsignificant coefficients have open symbols. Results are presented for the barnacles *Balanus* spp. (a, d, g), *Chthamalus dalli* (b, e, h), and for the mussels *Mytilus* spp. (c, f, i), at three rocky intertidal field sites: Boiler Bay (a–c), Strawberry Hill (d–f), and Cape Blanco (g–i).

The correlation coefficients of *Balanus* spp. recruitment peaked at a minimum duration of 2 days at Boiler Bay (Fig. 5a), 6 days at Strawberry Hill (Fig. 5d), and 12 days at Cape Blanco (Fig. 5g). The correlation of *C. dalli* recruitment also peaked at 2 days for Boiler Bay (Fig. 5b) and 6 days at Strawberry Hill (Fig. 5e), but the patterns of the correlation coefficients at Strawberry Hill and Cape Blanco for this species were nonsignificant and close to zero. *Mytilus* spp. recruitment was also positively associated with the number of wind relaxations at a minimum duration of 6 days at Boiler Bay (Fig. 5c), 6 days at Strawberry Hill (Fig. 5f), and a peak in the correlation coefficient at 12 days at Cape Blanco (Fig. 5i), although the latter was not statistically significant. Barnacle recruitment at Boiler Bay was negatively associated with upwelling event duration (Fig. 5a and b). However, for *Mytilus* spp. recruitment at all three sites (Fig. 5c, f, i) and for *Balanus* spp. recruitment at Strawberry Hill (Fig. 5d) and Cape Blanco (Fig. 5g), the association with the mean duration of upwelling event is positive when short events are included in the analysis. This relationship is only significant for mussel recruitment at Boiler Bay and Strawberry Hill and as short events are excluded, these relationships decline and become nonsignificant (Fig. 5c, f).

The positive association of mussel recruitment with the duration of short upwelling events at Strawberry Hill is complemented by negative associations with the duration of downwelling events (Fig. 5f). Similar relationships are evident for mussels at Boiler Bay (Fig. 5c) and *Balanus* spp. at Cape Blanco (Fig. 5g), but these are not significant. Similarly, the negative association of barnacle recruitment with the duration of upwelling events at Boiler Bay is reflected in positive associations with duration of downwelling events (Fig. 5a and b), although this relationship is only significant for *C. dalli* recruitment.

Discussion

Upwelling events in the CCS have become longer in duration, stronger in magnitude and fewer in number, which is consistent with Bakun's hypothesis about how climate change would impact Eastern Boundary Currents (Bakun, 1990). The increase in upwelling event duration reflects both the increased persistence of events and the loss of short events (<1 day long), especially in the southern regions of the CCS. The strong, quasi-instantaneous, and cumulative effect of upwelling events on intertidal water temperatures suggests that the increased persistence and strength of upwelling events will result in colder upwelled water shoaling over longer periods in the near-shore environment. Furthermore, our results show that larval recruitment, nutrient availability and phytoplankton concentration in coastal regions are strongly related to larger-scale upwelling events. Overall, our findings suggest that changes in the distribution, persistence and strength of event-scale upwelling are likely to have important consequences for the structure and functioning of near-shore ecosystems.

Temporal trends and climate change hypotheses

The observed increase over time in the duration and magnitude of upwelling events in Oregon is consistent with the recently documented increase in annual upwelling in California (Garcia-Reyes & Largier, 2010). The similarity in these trends over 12° of latitude (~1400 km) along the US west coast suggests that coastal climate forcing at the scale of the entire CCS is shifting. Our results are consistent with Bakun's, (1990) upwelling intensification hypothesis, which predicts that increased greenhouse gas emissions lead to a stronger thermal gradient between the warm land mass and the cooler coastal ocean, thereby driving more persistent upwelling-favorable winds in coastal upwelling systems worldwide (Bakun, 1990; Mendelssohn & Schwing, 2002; Santos *et al*., 2005; McGregor *et al*., 2007; Bakun *et al*., 2010). Thus, we predict that these trends would likely be found in similar coastal upwelling systems and that they will continue to strengthen with further global climate change (Bakun, 1990; Snyder *et al*., 2003).

Intertidal water temperature response to upwelling conditions

On a global scale, climate change is causing higher average sea surface temperatures (Scavia *et al*., 2002). However, this effect is negated or reversed in coastal upwelling regions where climate change is predicted to cause stronger and more persistent upwelling during the upwelling season. We have shown that upwelling event conditions at the regional scale are strongly associated with the quasi-instantaneous shoaling of cold water in local near-shore environments and that upwelling events have a cumulative effect on near-shore temperatures, with longer upwelling events leading to colder temperatures. Hence, our results suggest that stronger and more persistent upwelling may lead to a reduction in water temperatures in the coastal ocean despite a global trend toward higher temperatures. However, increased solar heating and reduced mixing may enhance stratification and deepen the thermocline to the point at which upwelling would only turnover water above the thermocline and no longer bring cold, nutrient-rich deep water to the surface (Harley *et al*., 2006). Although such a deepening of the thermocline can decouple upwelling events from their expected effects on the temperature and productivity of coastal waters (Roemmich & McGowan, 1995), our results indicate that upwelling remains strongly related to (1) temperature, (2) nutrients, and (3) chlorophyll-*a* despite a 26–86% increase in upwelling strength and persistence over the last 43 years.

Colder water temperatures will have consequences for near-shore ecosystems through direct effects of temperature on species performance and indirectly through species interactions. The direct, physiological effect of temperature is the main factor defining the geographic distribution of marine animals (Hutchins, 1947; Helmuth *et al*., 2006). Temperature-induced changes to the distribution and population sizes of species affect other species indirectly, as mediated through the network of species interactions (Leonard *et al*., 1999; Moore *et al*., 2007). Furthermore, the strengths of species interactions are also directly dependent on temperature (Rall *et al*., 2010). Colder temperatures typically cause lower consumption rates by reducing the metabolic rates of consumers, thus weakening top-down control in ecosystems (Vasseur & McCann, 2005). Enhanced bottom-up effects from the increased provision of nutrient-rich water potentially compounds the situation. This unchecked growth of lower trophic levels could further exacerbate hypoxia and anoxia at depth on the continental shelf (Grantham *et al*., 2004; Chan *et al*., 2008).

Effects of upwelling events on recruitment

Regional scale variability in upwelling conditions within the CCS have been linked to recruitment patterns (Menge *et al*., 2011b), however, there is some debate over the physical oceanographic mechanism responsible for delivering larvae to shore. The transport hypothesis suggests that persistent upwelling limits

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recruitment in the southern CCS by preventing onshore larval transport and advecting larvae offshore, whereas frequent wind relaxations in the northern CCS cause current reversals and result in saturating recruitment pulses (Farrell *et al.*, 1991; Connolly *et al.*, 2001; Menge *et al.*, 2003; Noda, 2004; Dudas *et al.*, 2009). Our results partly support this hypothesis, as recruitment of both barnacles and mussels was positively associated with the number of wind relaxations. However, offshore larval distributions have not been found to be susceptible to offshore advection during upwelling (Shanks & Brink, 2005; Morgan *et al.*, 2009; Shanks & Shearman, 2009) and recruitment does occur in the absence of major wind relaxations. Thus, other physical oceanographic processes, such as internal waves and tidal currents, and site-specific differences in hydrodynamics may also be responsible for larval delivery (Menge *et al.*, 1997a; Shanks, 2009b; Shanks *et al.*, 2010).

The behavior of different taxa is likely to affect the recruitment response to upwelling conditions. In fact, within-site differences between mussel and barnacle recruitment are apparent in our results. At each site, barnacle recruitment tended to be more negatively (or less positively) related to the mean duration of upwelling events than mussel recruitment. Mussel recruitment consistently positively associated with event duration and only became positively associated with the number of upwelling events once short upwelling events were excluded from the analysis. One reason for this may be that mussel larvae are typically found below the thermocline and thus would not be susceptible to offshore advection during upwelling, whereas barnacles are often found in the surface Ekman layer (Shanks & Brink, 2005; Broitman *et al.*, 2008; Rilov *et al.*, 2008; Shanks & Shearman, 2009). If mussel larvae are not susceptible to offshore advection of the top water layer during upwelling, the positive effect of upwelling duration seen in the results may be due to the onshore advection of deeper water or the increased food availability associated with upwelled waters (Broitman *et al.*, 2008; Menge *et al.*, 2009). Because mussels respond positively as the duration of upwelling events increases, they will likely be positively affected by climate-driven increases in upwelling persistence.

Although barnacle recruitment is generally positively associated with the number of wind relaxations, there are large differences between sites that are likely due to how regional currents respond to upwelling events and wind relaxations. At Boiler Bay where the continental shelf is narrow and the upwelling current runs parallel and relatively close to shore (Castelao & Barth, 2005), we expect barnacle larvae to be highly dependent on wind relaxations for recruiting onshore. Conversely, we would not expect barnacle larvae to be as dependent on wind relaxations for recruitment at Strawberry Hill because of the large retentive zone which retains larvae close to shore (Keister *et al.*, 2009). Our results support this interpretation, as barnacle recruitment at Boiler Bay was positively associated with both the number of wind relaxations and the duration of the subsequent downwelling events and negatively associated with upwelling event duration whereas the relationships at Strawberry Hill were much weaker. Further south at Cape Blanco, the upwelling current separates from the coast (Springer *et al.*, 2009) causing advection of surface waters and their associated planktonic communities far offshore (Keister *et al.*, 2009). Although much less is known about near-shore currents in the shadow of the upwelling current, there is evidence to suggest that they are generally weak and not strongly directional, yet still flow shoreward during wind relaxations (Keister *et al.*, 2009). Thus, barnacle larvae at Cape Blanco may not be subject to strong advection in the upwelling current and thus not as dependent on wind relaxations for onshore recruitment. This is consistent with our weak results for Cape Blanco, although the small sample size for this site may also be a factor.

Climate-induced changes to recruitment have the potential to affect community structure and dynamics, but only if the abundance of adult populations are ultimately affected (Svensson *et al.*, 2005; Poloczanska *et al.*, 2008). This is not always the case because of post-recruitment processes. For example, the orders-of-magnitude increases in mussel recruitment observed at many sites within the last decade (Menge *et al.*, 2009) usually were not accompanied by a corresponding increase in adult mussel abundance (Menge *et al.*, 2011a). Menge *et al.* (2011a) hypothesized that the lack of response of the adult mussel populations was because recruitment of their main facilitator, barnacles, failed to increase over the same period. Barnacles facilitate mussel recruitment by providing many tiny crevices for mussel recruits to attach to the substratum (Berlow, 1997). Thus, in regions where barnacle recruitment responds even to short upwelling events, increasing persistence of upwelling will not only impact barnacle populations, but will indirectly impact mussel populations too. Such context-dependent, nonlinear responses of different species to environmental forcing are likely to be the norm.

Broader impacts

In addition to the effects of upwelling on productivity, temperature, and larval distribution, upwelled waters are also high in dissolved carbon dioxide, low in dissolved oxygen and low in pH (Grantham *et al.*, 2004; Chan *et al.*, 2008; Hauri *et al.*, 2009). In 2002, persistent upwelling caused severe inner-shelf (<70 m) hypoxia ($[O_2] \leq 0.5$ mL L^{-1}) to develop from 44.00°N to 44.65°N, which resulted in mass die-offs of fish and invertebrates (Grantham *et al*., 2004). In the summer of 2006, extremely high productivity in the same region resulted from a prolonged period of unusually intense upwelling and contributed to widespread and severe hypoxia and the first recorded instance of anoxia in the CCS (Chan *et al*., 2008). Indeed, upwelling was so persistent in 2006 at 45° N that the number of wind relaxations was the lowest of any year on record. Respiration of excess phytoplankton production also adds to dissolved CO_2 levels, which decreases pH and the carbonate saturation state (Hauri *et al*., 2009). Low pH and under-saturated waters have been observed during strong upwelling events (Feely *et al*., 2008), so longer upwelling events will likely mean higher shoaling of and longer exposure to acidic waters in the near-shore environment.

Climate-driven changes in the phenology of upwelling events have altered the tempo and the mode of environmental forcing in near-shore ecosystems of the CCS: upwelling events have become longer in duration, stronger in magnitude and fewer in number. By affecting water temperature, nutrient availability, phytoplankton productivity, larval recruitment and species interaction strength, changes in the duration, frequency and magnitude of upwelling are likely to significantly impact the structure and functioning of coastal ecosystems in Eastern boundary currents around the world.

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Appendix S1. Wavelet analysis.
Appendix S2. Wavelet analysis of temporal trends in upwelling and temperature along the California Current System.
Appendix S3. Temporal trends in the annual mean and intra-annual distribution of upwelling events along the California Current System.
Appendix S4. Chlorophyll-*a* and nutrient analysis.

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