



Synoptic-scale upwelling indices and predictions of phyto- and zooplankton populations



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ARTICLE INFO

Article history:

Received 13 June 2012

Received in revised form 26 August 2013

Accepted 26 August 2013

Available online 4 September 2013

ABSTRACT

Seasonal upwelling is responsible for the biologically rich and productive ecosystems of coastal eastern boundary currents. In most studies of physical – biological interactions in these systems, upwelling statistics are computed on monthly, seasonal, and annual time scales, whereas upwelling naturally occurs at high frequencies (days to weeks). This simplification of the upwelling process may misrepresent relationships between upwelling and biological populations. Based on 31 years (1982–2012) of hourly-measured winds and sea surface temperature at buoys off the central-northern California coast, we characterized upwelling and relaxation events at synoptic time scales, and used event-scale statistics to relate to local lower trophic level populations. We defined three metrics to quantify synoptic-scale upwelling: (i) *Intensity*, a measure of cumulative wind stress forcing during each upwelling event, (ii) *SST_{event}*, a measure of the oceanic response to wind forcing, and (iii) *Nutrient Upwelling Index (NUI)*, a measure of the nitrate availability at the surface during upwelling events. We compared cumulative values of *Intensity* and *NUI*, and average values of *SST_{event}* during the peak of the upwelling season (April–June in central-northern California) to proxies of phytoplankton biomass (chlorophyll-*a* concentrations) and krill abundance to assess the abilities of high frequency upwelling indices to predict biology. Wind forcing alone (*Intensity*) did not explain population variability, but *SST_{event}* and *NUI* showed excellent relationships to chlorophyll concentrations (44% and 54% of variance explained, respectively) and krill abundance (68% of variance explained). All relationships appeared to be dome-shaped, supporting the hypothesis that moderate upwelling and ocean temperature are optimal for these populations. *SST_{event}* and *NUI* performed better than the traditional Bakun upwelling index in predicting populations. We conclude that investigating upwelling characteristics on event scales can improve understanding of lower trophic level dynamics in eastern boundary current systems.

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1. Introduction

From the early days of fisheries science (Hjort, 1914), research has focused on relating environmental variation to fish recruitment, populations and their fisheries. Thus, for the past century studies of temporal, and now spatial, environmental variability have formed a cornerstone of fisheries oceanography (Cury et al., 2008). However, despite decades of research, environmental mechanisms of recruitment and population processes remain poorly understood. Part of the problem is that most population responses at the upper trophic levels are indirect, modulated by variation in habitat characteristics and food availability. Therefore, for this field to advance it is critical to derive robust predictive relationships that can be used to understand and forecast variability in the lower

trophic level organisms that are key to the trophic dynamics of fish. If such connections can be made, this could improve understanding and management of the biological environment faced by upper trophic level organisms of economic and conservation concern (Beaugrand et al., 2003; Link, 2010).

In Eastern Boundary Upwelling Ecosystems (EBUE), lower-trophic-level productivity is fueled by wind-driven coastal upwelling of deep nutrient-rich waters (Chavez and Messié, 2009). Coastal upwelling refers to the vertical flux of waters from below the thermocline into the upper euphotic zone and is strongest near the coast, where alongshore winds drive an offshore transport of surface waters (Ekman transport) that must be replaced by the upward flux. Understanding variability in upwelling-driven nutrient input to the surface is critical to understanding variability in populations and ecosystem dynamics.

Coastal upwelling is structured in space and time. Upwelling centers are typically associated with coastal promontories, such as Cape Mendocino (Largier et al., 1993) and Point Arena (Largier et al., 2006) in California and Cape Columbine (Penven et al.,

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2000) in South Africa. Equatorward winds responsible for upwelling are interrupted by synoptic-scale meteorological disturbances, thus demarcating *upwelling events* as periods of persistent along-shore wind. Upwelling events typically last 3–10 days (Largier et al., 1993) and rarely longer than 14 days (Beardsley et al., 1987). The weak-wind periods between upwelling events are known as *relaxation events* as these periods are characterized by relaxation of atmospheric structures set up during upwelling (e.g., Send et al., 1987; Largier et al., 1993; Washburn et al., 2011). Alternation of upwelling and relaxation events appears critical for the development of robust phytoplankton blooms (Lasker, 1975; Joint et al., 2002; Botsford et al., 2003, 2006; Wilkerson et al., 2006). Consistently high upwelling may diminish productivity by causing turbulence that disrupts the reproduction and feeding of zooplankton (Lasker, 1975; Cury and Roy, 1989), or by continuous offshore advection that exports plankton from shelf habitats (Botsford et al., 2003, 2006). Thus, upwelling is thought to have a non-linear functional relationship to aspects of marine ecosystem productivity – a concept known as the “optimal environmental window” (Cury and Roy, 1989).

Upwelling can be measured in many ways, but direct assessments of vertical water movements or isopycnal shoaling of the water column are quite rare and not a practical monitoring strategy. Most often, measurements of upwelling forcing (i.e., along-shore wind stress) have been used in studies of physical-biological interactions. In particular, the upwelling index derived by Bakun (1973) has been described as “the workhorse of fisheries oceanography for decades” (Bograd et al., 2009). The Bakun Upwelling Index (BUI) is an estimate of cross-shelf Ekman transport due to geostrophic wind stress calculated from large-scale atmospheric pressure gradients. Analyses of the BUI have been used for various purposes including assessments of ecosystem dynamics and fisheries health (Parrish et al., 1983) and investigations of potential bio-physical effects of anthropogenic global warming (Bakun, 1990; Bograd et al., 2009; Iles et al., 2012). Although the BUI has long-standing service to science and management, its utility in ecosystem studies is equivocal. Relationships between the BUI and biota are not easily found and when relationships are found, explanatory power may be low due to lack of oceanographic processes in this index (e.g., water transport is derived only from wind when other factors may be of interest). For example, in 13 randomly selected published papers for the California Current in which the BUI was related to fish population or life history parameters, only 15% (39 of 254 correlations) were significant, and none explained more than ~35% of the biotic variation (Sydeman and Thompson, 2013). Chlorophyll concentrations, a proxy of phytoplankton biomass, show poor correlations with BUI in California (Kahru et al., 2009; Thomas et al., 2009). Therefore, there is a need to develop upwelling indices or proxies of upwelling with greater application and significance to biology.

The availability of atmospheric data (e.g., winds and air pressure) facilitates quantifying coastal upwelling by forcing, but for the purposes of tracking ecosystem variability more useful indices may include oceanographic responses, including variability in temperature and upper-ocean nutrient content. Because temperature fluctuations are dominated by the balance between upward advection of cold water and surface warming (Beardsley et al., 1998), strong relationships are typically found between upwelling-favorable winds and ocean physical conditions (e.g., Largier et al., 1993; Wing et al., 1995). However, it is more difficult to isolate and describe relationships between upwelling forcing and plankton populations. There can be a lag in the timing of primary productivity associated with upwelling and variation in plankton concentration. If time-scales of production and persistence of plankton are longer than the upwelling-relaxation time scale, cumulative effects may occur with repeated upwelling-relaxation events. For example,

the response of plankton may depend on initial conditions (i.e., nutrient concentration, light availability, phytoplankton concentration, water column stability) and the persistence depends on conditions within and between upwelling events (including advection and near-surface mixing). To circumvent this problem, cumulative wind and BUI approaches have been used in previous research, both on event scales (Iles et al., 2012) and on annual scales (Hickey et al., 2006). Furthermore, temporal lags lead to spatial offsets in the presence of alongshore and offshore flows. Plankton are typically under-sampled in space and time and thus plankton data generally do not show a coherent relationship to upwelling on event scales (Botsford et al., 2006).

To address the need for biologically relevant estimates of upwelling and nutrient enrichment, we developed a novel Nutrient Upwelling Index (NUI) based on water surface temperature during upwelling events and related it to phytoplankton and zooplankton populations. Our study area in north-central California is downstream of the Point Arena upwelling center. We used sea surface temperature (SST) data from a long-term weather buoy to calculate NUI. To evaluate its biological relevance, we compared the event-scale upwelling index to chlorophyll-*a* concentrations and estimates of mesozooplankton (krill) abundance in the immediate vicinity of the buoys and also downstream in the Gulf of the Farallones.

2. Material and methods

2.1. Data

Wind speed and direction and sea surface temperature (SST) were obtained from the NOAA buoy NDBC 46013 (referred to here as N13) located at 38.24°N, 123.30°W off Bodega Bay, California (Fig. 1). Data from 1982 to 2012 are available at <http://www.ndbc.noaa.gov>. Following García-Reyes and Largier (2010, 2012), high correlations with neighboring buoys allowed data gaps to be filled: correlations for alongshore wind with buoys 46014 (39.23°N, 123.97°W), 46012 (37.36°N, 122.88°W), and 46026 (N26, 37.76°N, 122.84°W) are $r = 0.90$, $r = 0.89$, and $r = 0.94$, respectively, and $r = 0.78$, $r = 0.72$, and $r = 0.77$ for SST. Filled data accounted for 14% of the time series, and the largest gap was ~11 months. Wind stress was calculated using the drag coefficient defined by Large and Pond (1981). The alongshore component of wind stress (τ_y) was calculated using the orientation of the wind principal axis since wind is highly polarized in the alongshore direction (Dorman and Winant, 1995).

Profiles of temperature and nitrate (NO_3) concentration in the vicinity of buoy N13 were obtained during the Wind Events and Shelf Transport program (WEST; see Largier et al., 2006 and Wilkerson et al., 2006 for details). Bottle samples during 650 CTD casts from January 2002, May 2001/2002, and June 2000/2001/2002 were analyzed to determine the relationship between temperature and nitrate in the water column around Bodega Bay.

Composites of surface chlorophyll-*a* (chl-*a*) concentration were obtained from 1997 to 2012. These composites were obtained by merging data from four satellite sensors (OCTS [1997], SeaWiFS [1997–2010], MODISAqua [2002–2012], MERIS [2002–2012]) using the CalFit algorithm developed and validated with over 10,000 *in situ* measurements by Kahru et al. (2012). To avoid gaps in the data, a monthly spatial averaged value was calculated for two areas (25 km in diameter) – one centered at buoy N13 off Bodega Bay, and another centered at buoy N26 in the Gulf of Farallones (Fig. 1). Each monthly value is the product of averaging between 18 and 35 daily images.

Krill are an important link between primary productivity and higher trophic levels including fish, birds and marine mammals

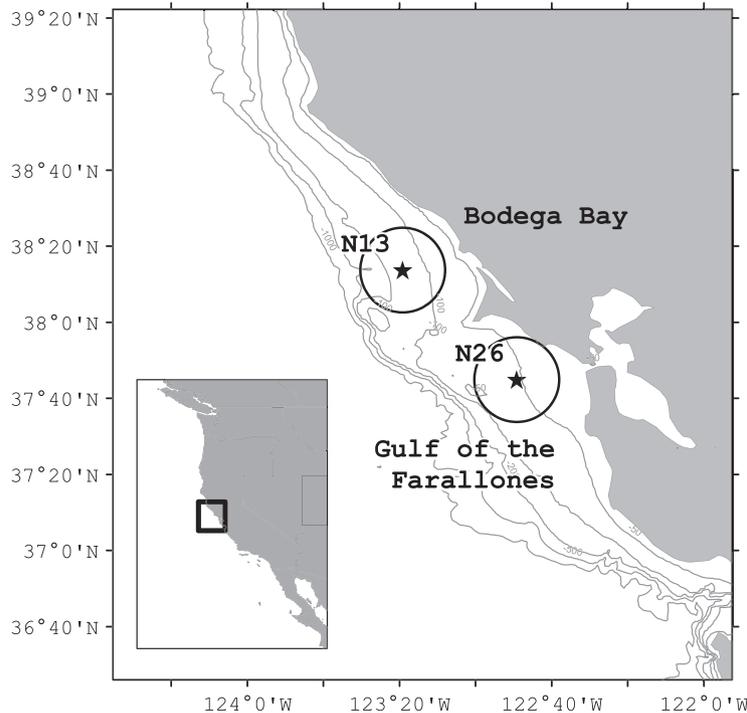


Fig. 1. Location of NDBC buoys N13 off Bodega Bay and N26 in the Gulf of Farallones. Black circles show the averaged region for chlorophyll-a concentration satellite data.

in this system (Field et al., 2006). Data on the relative abundance of krill, primarily three species, *Euphausia pacifica*, *Thysanoessa spinifera*, and *Nyctiphanes simplex*, were obtained from the National Marine Fisheries Service's (NMFS) annual survey for juvenile rockfish (*Sebastes* spp.) in the Gulf of the Farallones and adjacent marine environments. The krill data used in this report came from mid-water trawl samples obtained at 14 stations occupied annually in May–June off Bodega Bay and in the Gulf of the Farallones; the overall sampling design for the NMFS survey is described by Sakuma et al. (2006). From these stations, data from a total of 912 tows were summarized. The number of tows varied from a high of 78 in 1990 to a low of 16 in 2008, with an average of 48 tows per year across all years. Over the period 1991 through 2007, the range in tows per year varied from 36 (2002, 2005) to 56 (1991), with an overall average of 48.1 tows per year. For each tow, krill were separated from the catch of fish, volumetrically sub-sampled, and enumerated. To assess variability in krill populations in the region we calculated and used the geometric mean (i.e., average of natural log of number individuals haul⁻¹) from 1990–2008. As all trawls were conducted similarly, these values represent a standardized annual catch per unit effort (Ralston et al., 2013). Because the sample size of tows was relatively low in 2008, we excluded this year from the analysis.

2.2. Methodology

To quantify upwelling in synoptic time-scales, we developed three different indices. All indices were based on a common definition of upwelling event, but quantify different characteristics of the upwelling process. The first index quantifies only the forcing (i.e., alongshore wind stress), the second index considers the physical response to upwelling through SST, and the third index considers the chemical response through nutrients (NO_3) brought to the surface layer during upwelling events. These indices are described further below.

Following Roughan et al. (2006), Wilkerson et al. (2006), and Cury and Roy (1989), upwelling events were defined as any period

of time with alongshore winds stronger than 5 m/s in the upwelling-favorable direction (i.e., equatorward). Since the shelf off Bodega Bay is an area with strong alongshore winds (García-Reyes and Largier, 2012), half of the days during April–July had winds above this threshold. SST at buoy N13 showed a significant decrease in temperature for alongshore winds that exceed 5 m/s, indicating an upwelling response. Other authors more interested in the physics of upwelling used higher thresholds to define upwelling events (Beardsley et al., 1987; Taylor et al., 2008), however, Botsford et al. (2003) found in a model study that wind speeds of 5–6 m/s may be sufficient to account for declines in primary or secondary productivity due to offshore advection of coastal waters. As some authors suggest that strong winds need to last at least three days to be ecologically significant (Dugdale et al., 1990; Botsford et al., 2006; Wilkerson et al., 2006), we separated events into three categories: short events (≤ 3 days), medium-length events (4–10 days), and long events (> 10 days). Any day not included in an upwelling event was labeled a relaxation day, and relaxation events were also categorized according to the same lengths as upwelling events.

Based on this definition of upwelling events, we calculated indices of upwelling that recognize synoptic variability as follows:

Intensity – There are two important characteristics of upwelling forcing: the length of the event and the strength of wind. To include both, the *Intensity* of the event was defined as the cumulative alongshore wind stress during the event, with units of $\text{N m}^{-2} \text{ day}$.

SST_{event} – To quantify the physical response of the ocean to wind forcing (i.e., water brought to the surface), we calculated the average SST during all days an upwelling event lasted (units °C). *SST_{event}* was defined as an average instead of cumulative owing to the magnitude of SST values compared to their variability – a cumulative SST parameter would index the length of the event rather than the temperatures during the event.

Nutrient Upwelling Index (NUI) – To quantify the chemical response of the ocean to wind forcing, we calculated an index of nutrient availability. *In situ* nutrient data are rarely available for long periods but water temperature, both at surface and depth, has been repeatedly used as a proxy to estimate it (e.g., Lada,

2003; Silió-Calzada et al., 2008; Kimbro et al., 2009; Palacios et al., 2013). In particular, water temperature has a tight relationship with NO_3 concentration (N), which controls primary productivity in upwelling regions (Dugdale et al., 1990, 2006) and it can be used to estimate biological productivity (see Kamykowski and Zentara, 1986; Kudela and Dugdale, 1996). The relationship of N with temperature (T) varies from place to place, precluding the use of a single relationship in all upwelling systems (Palacios et al., 2013). However, data acquired during the WEST program off Bodega Bay (Largier et al., 2006; Dever et al., 2006) from 2000 to 2002 allow us to calculate the relationship for this region and then use it to calculate a 3-decade surface nitrate concentration time series from SST data that have been measured at local buoys. Fig. 2 shows T and N data from three 4-week cruises in upwelling months (May–June) in 2000–2002 and one additional 2-week winter cruise in 2002. We found that N and T were highly correlated ($r = 0.94$); the relationship was well approximated by a cubic polynomial. However, a bi-linear relationship is simpler and fits the data comparably well ($r = 0.92$):

$$N = 86.2 (\mu\text{M}) - 6.6(\mu\text{M } ^\circ\text{C}^{-1})T; \text{ for } T < 13.1 ^\circ\text{C}$$

$$N = 0\mu\text{M}; \text{ for } T > 13.1 ^\circ\text{C}$$

The difference in T at which $N = 0$ between the bi-linear and cubic relationships is $0.6 ^\circ\text{C}$, but for other values of T differences between N approximations are minimal. Winter and summer relations are similar, and while the summer data are more scattered for higher temperatures, r values are similar (0.93 for summer and 0.92 for winter). While this relationship is extracted from T at different depths, during upwelling events surface water is constantly renewed by water from depth, allowing us to use this expression. Furthermore, the range of surface temperatures observed during upwelling events, in particular during winter and the upwelling season, is similar to the range of temperatures in the CTD casts from which the T – N relationship is calculated. Therefore, we have confidence in the N values calculated from SST for the Bodega Bay region. This method of estimation has been used in other upwelling regions in the world (e.g., Ladah, 2003; Silió-Calzada et al., 2008; Kimbro et al., 2009), and it provides us with a means to estimate N values on interannual to decadal scales. From this local N time series, we then derived NUI as the cumulative values of N during upwelling events (units of $\mu\text{M day}$). This is an

estimate of the total nutrient availability during an event, and thus an index of potential primary production, but not an index of actual biological productivity as nutrient uptake depends also on initial phytoplankton population and light intensity in surface waters.

SST_{event} and NUI are both based on temperature data, but beyond the averaged vs. cumulative calculation, they differ in the way they handle warm ($>13 ^\circ\text{C}$) temperatures. For SST_{event} , days of warm temperatures are considered in the calculation, but for NUI these days are excluded as $N = 0$ under these conditions. This accounts for days when no deep water is upwelled, either due to weak winds or to strong stratification of the water column (Lentz and Chapman, 2004; Jacox and Edwards, 2011). In principle, NUI should resolve the biological impact of wind and ocean conditions during upwelling events better than SST_{event} .

These three indices were calculated for each upwelling event identified in the 31-year record. Monthly time-series were developed by summing the cumulative indices (*Intensity*; NUI) and averaging SST_{event} over all events in each month. Events that start in one month and end in another were classified into the month in which the majority of days belong. An annual “upwelling season” value was obtained in a similar way by aggregating values over the period with most intense winds (April–July) for each year, and served as basis for describing interannual variability. These monthly time series were the basis for describing seasonality. To test how the synoptic-scale upwelling indices defined here compared to traditional indices of upwelling we used monthly values of the 3° Bakun Upwelling Index (BUI) at 39°N , provided by PFEL/NOAA at <http://las.pfeg.noaa.gov>, and monthly averaged values of alongshore wind stress (τ_y) and SST from buoy N13.

Bimonthly values of environmental indices were calculated for January–February, February–March, March–April, April–May, and May–June for each year to correlate against 2-month aggregates of chl-*a* (March–April and May–June) and krill abundance data (May–June). Spatially, the chl-*a* and krill data represent mesoscale averages in abundance (10s to 100s of km^2), while the upwelling data are from the N13 buoy. Despite the buoy being at a single location, data on winds and SST strongly co-vary with measured wind and SST from other buoys and shore stations from Point Arena through the Gulf of the Farallones (Dorman and Winant, 1995; García-Reyes and Largier, 2012). Therefore, we consider the indices *Intensity*, SST_{event} , and NUI to represent a similar spatial scale to that used for the chlorophyll-*a* and krill data (Dorman et al., 2006). We

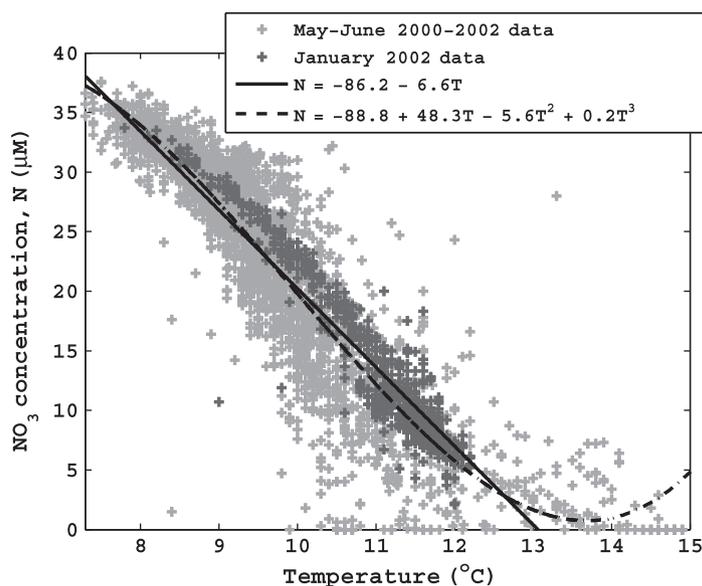


Fig. 2. Temperature vs. NO_3 concentration for water samples of the WEST program (Largier et al., 2006). Lines show a linear and a cubic polynomial fitting of the data.

used regression analyses to test for associations between upwelling indices (including the BUI) and chl-a concentration and krill abundance. Because the relationship between upwelling and productivity is thought to be non-linear (Cury and Roy, 1989), we test linear, logarithmic, and quadratic models of upwelling to fit the chl-a and krill data. We used the coefficient of determination (R^2) and Akaike's Information Criteria (AIC; Akaike, 1974) to select the best models.

3. Results

3.1. Seasonality

3.1.1. Intensity and length of upwelling events

We observed a marked seasonality in the *Intensity* index, with largest values from March to August, and a maximum in June (Fig. 3a). *Intensity* increased rapidly in March, when long (>10 days) events begin, and declined sharply in July. The number of upwelling days also showed a sharp increase in March (not shown), but did not decrease in July as did *Intensity*, indicating only a change in wind strength. Short (≤ 3 days) and medium-length (4–10 days) events occurred year-round (Fig. 3d), however, short events were less frequent from May to July when long events were more frequent. Medium-length events were less frequent in December–February, and short events were more frequent in October–January. Long events, however, only occurred regularly in March–August, with rare occurrences in other months (no long events in January–February and only one in November and December in 31 years). From May to July, long events accounted for about half the *Intensity*.

3.1.2. SST during upwelling events

On average, the lowest SST_{event} occurred in April–June (Figs. 3c and S1), slightly preceding maximum *Intensity*, while the highest SST_{event} occurred in September. Some differences were seen for different event lengths. For the peak upwelling months (roughly April–July), long events showed the coldest SST_{event} with short

events SST_{event} showing much warmer values (Fig. S1). Note that long-event SST_{event} values in winter vary largely, given that mostly only one event has been observed in the record period. Although SST and wind stress are commonly thought of as similar indices of upwelling, a scatter plot of *Intensity* vs. SST_{event} for all events (not shown) shows that SST does not depend simply on *Intensity*. SST_{event} varied more consistently with season (Figs. 3c and S1) than with event length or *Intensity*.

To investigate what drives SST during upwelling events we calculated the change of SST during events, defined as $\Delta SST = SST_{event} - SST_i$ (where SST_i is the SST on the day prior to the event). Fig. 4a shows ΔSST vs. *Intensity* with SST_i in color. Generally, SST decreases with *Intensity*, but the rate at which SST decreases depends on SST_i . Therefore, linear regressions were calculated separately for SST_i in bins of 1 °C. The ΔSST response (slope in Fig. 4a) to *Intensity* increased with increasing SST_i , and can be approximated by a cubic function (Fig. 4b). However, this change in ΔSST with *Intensity* is small for coldest and warmest SST_i – for $SST_i \sim 10.5$ °C or colder, changes in ΔSST are similar and small for any *Intensity* (water cannot get much colder), and similarly for $SST_i \sim 13.5$ °C or warmer, changes in ΔSST are small (the rate of change for SST is limited by solar radiation in the area and ocean mixing). Both regressions can be combined as:

$$\Delta SST = aI + b$$

with $a = 0.02SST_i^3 - 0.66SST_i^2 + 7.70SST_i - 29.47$
and $b = -0.15^\circ C$

where I is the *Intensity* of the event with units $N\ m^{-2}\ day$, and thus has units $^\circ C\ N^{-1}\ m^2\ day^{-1}$. Since $SST_{event} = SST_i + \Delta SST$, one can see that SST_{event} depends not only on *Intensity* (through ΔSST) but also on SST_i , the temperature prior to the upwelling event.

It is worth noting that for all events, independent of their *Intensity* and SST_i , ΔSST has a maximum of ~ 4 °C (and usually < 3 °C). This means that events with high SST_i cannot yield high values of N , irrespective of *Intensity*. Clearly, SST_i is an important factor determining the quantity of nutrients entrained to the euphotic zone during an upwelling event.

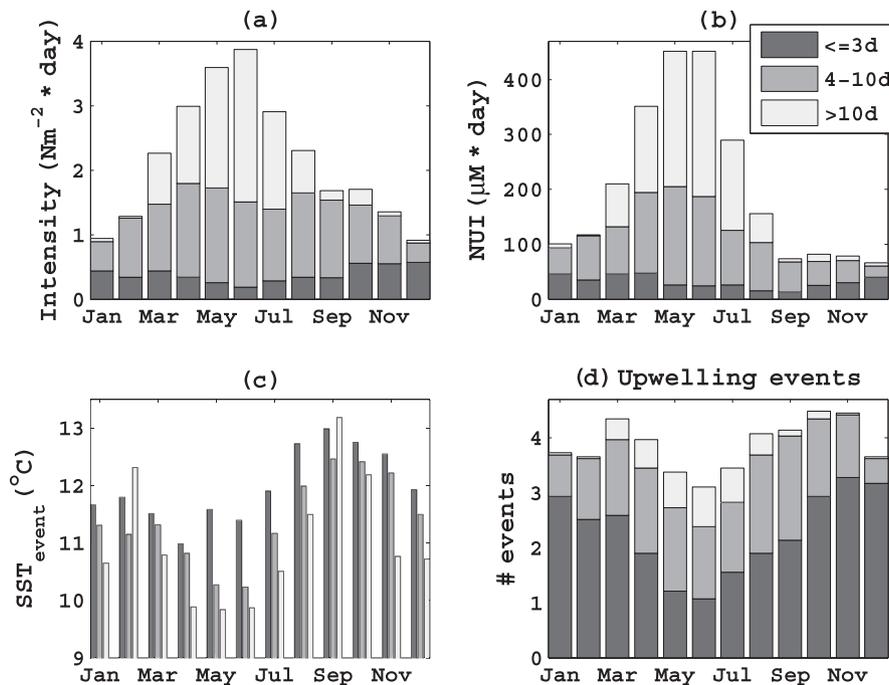


Fig. 3. Seasonality of (a) *Intensity*, (b) Nutrient Upwelling Index (*NUI*), (c) SST_{event} , and (d) upwelling events for each category of upwelling events: ≤ 3 days (dark gray), 4–10 days (medium gray), and > 10 days (light gray).

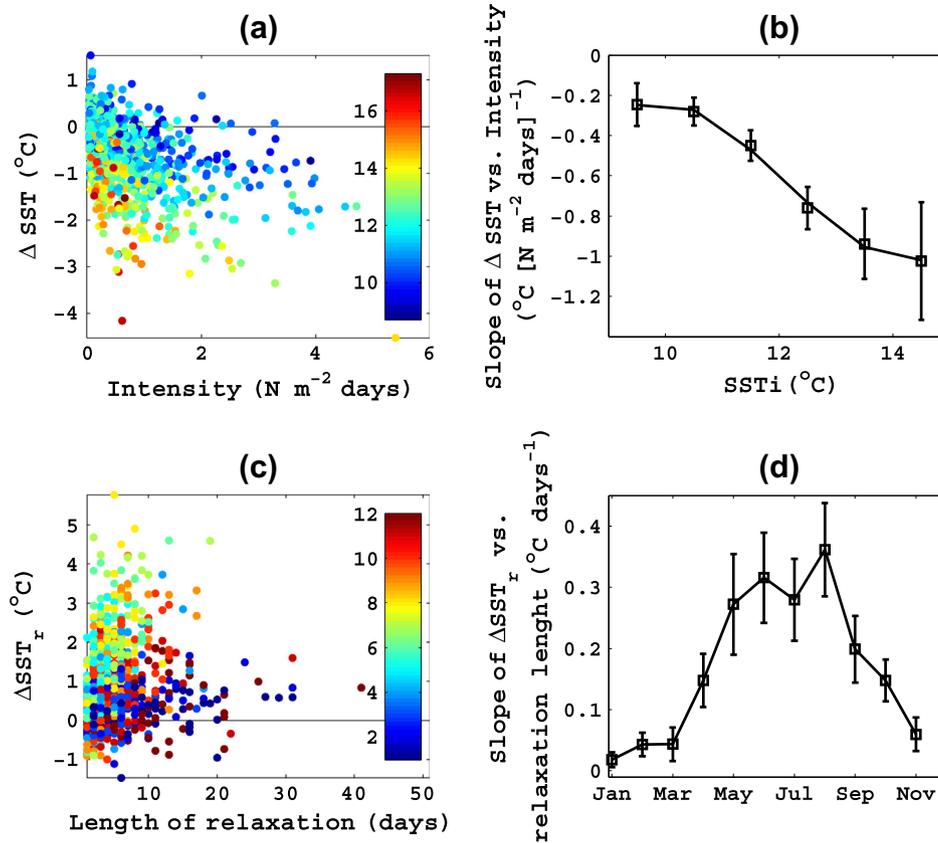


Fig. 4. (a) Change in SST (ΔSST) vs. *Intensity* for all upwelling events. Color indicates the initial SST (SST_i). (b) Relationship between SST_i and the slope of the linear regression between ΔSST and intensity in (a). Error bars indicate a significance level of $p < 0.05$ for the slope. (c) Change in SST during relaxation events (ΔSST_r) vs. length of relaxation events. Color indicates the month when the event occurred. (d) Slope of a linear relationship between ΔSST_r and length of relaxation event for each month. Error bars indicate the $p < 0.05$ significance level. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

In contrast, during relaxation periods, SST did not show a clear relationship with wind (not shown). During these periods, SST increases mostly due to local surface heating and alongshore advection (Wing et al., 1995; Beardsley et al., 1998; Washburn et al., 2011), so that stratification develops irrespective of wind. Wind forcing only plays a role during occasional downwelling events (Dorman and Winant, 1995; Dever and Lentz, 1994). However, the change in SST during a relaxation event (ΔSST_r) was linearly related to event length (Fig. 4c), with the rate of warming varying seasonally (Fig. 4d). Strongest warming occurred during summer months (May–August), when pre-relaxation SST is low and/or days are long with high surface heat flux. Weakest warming is observed during winter months (November–March), in spite of downwelling events. In fact, SST may decrease in winter during “relaxation” events (Fig. 4c) due to surface cooling associated with cold fronts.

3.1.3. Nutrient upwelling index

NUI were highest in April–July (Figs. 3b and S1), with long events accounting for the highest values due to their length and low SST. Similar to *Intensity*, *NUI* showed a sharp increase in March and a sharp decrease in July, with *NUI* changes more marked than those of *Intensity*. After July, many events exhibited temperatures close or above $13.1^\circ C$ (Fig. 3c), at which *N* is expected to be low or zero (Fig. 2 and Eq. (1)). Although many upwelling events still occur during late summer and fall (Fig. 3d, S1), weaker winds and longer relaxation periods prior to upwelling events resulted in the higher SST_i and SST_{event} , and therefore, lower *NUI* was observed. From September to February *NUI* was low but significant (about $1/4$ of upwelling season maximum values). Since *NUI* is based on SST, it is clear that *NUI* depends on both *Intensity* (wind forcing

during the upwelling events) and SST_i (pre-event ocean conditions), as does SST_{event} .

3.2. Interannual variability of conditions during the upwelling season

We chose the most intense upwelling months, April to July (Fig. 3), to calculate annual values of the synoptic indices (*Intensity*, SST_{event} , and *NUI*) for the upwelling season. *Intensity* varied by a factor of two between years (Fig. 5a) with most intense upwelling observed in 2001 and 2008 (high values also in 1999 and 2002), mainly due to medium-length and long events, given the cumulative nature of the index. The least intense upwelling was observed in 1985 and 1992 (low values also occurred in 1986 and 1998). High *Intensity* values were more frequent during the last decade, resulting in a positive although weak trend ($1.2 N m^{-2} day$ per decade, $p < 0.05$; cf. García-Reyes and Largier (2010) and Iles et al. (2012)).

Upwelling season SST_{event} also showed large interannual variability (Fig. 5b). The lowest values were observed in 1999, 2001, 2002, 2008, and 2012, years with intense upwelling, and the highest SST_{event} were observed in 1992, 1993, 1997, and 1998, years characterized by El Niño conditions. Upwelling-season *Intensity* and SST_{event} show good correlation ($r = -0.56$, $p < 0.01$), however one year, 1985, stands as an outlier, with low *Intensity* but cold SST_{event} . Discarding this year, the rank correlation became $r = -0.66$. Two other years deviated from the linear relationship (2001 and 2008), showing intense upwelling and warmer temperatures than years with weaker upwelling (1999 or 2012). Since SST_i plays an important role in determining SST_{event} (and hence *NUI*) we also averaged SST_i during the upwelling season. Seasonal

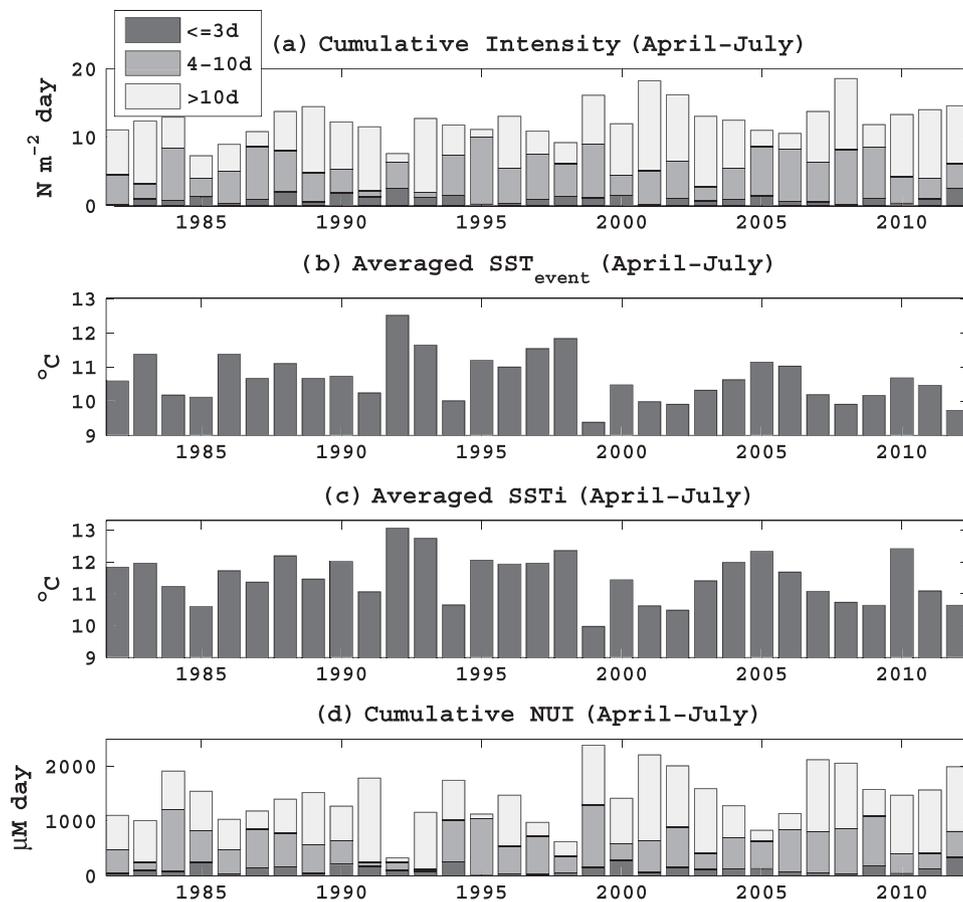


Fig. 5. Interannual variability of synoptic indices during the upwelling season (April–July): (a) cumulative *Intensity*, (b) averaged SST_{event} , (c) averaged SST_i , and (d) cumulative Nutrient Upwelling Index (*NUI*). *Intensity* and *NUI* show events categories: ≤ 3 day events (dark gray), 4–10 days (medium gray), and >10 days (light gray).

SST_i showed similar variability to SST_{event} only with warmer values after 2000 (Fig. 5c). SST_{event} and SST_i showed insignificant negative trends during the last three decades (-0.2 °C/decade, $p = 0.08$ and -0.2 °C/decade, $p = 0.3$, respectively).

Interannual variability in upwelling season *NUI* varied 6-fold (Fig. 5d), although *Intensity* varied only 2-fold (Fig. 5a). *NUI* was particularly high in the last decade, with highest values observed in 1999, 2001, 2007, and 2008, which were years with strong winds and low SST. In these years, long events contributed the majority of nitrate. Lowest *NUI* occurred in 1992 and 1998, years with weak winds and warm SST related to El Niño conditions. While high *Intensity* or low SST (SST_{event} and SST_i) may be observed in other years (e.g., 1985 and 2005), it is only the combination of strong winds and cold waters that yielded high nitrate levels in the euphotic zone. *NUI* showed a weak positive and significant trend (164 μM day per decade, $p = 0.05$).

3.3. Impact on biology

To explore the environmental drivers of chl-a concentration and krill abundance, initially we treat them as independent biological variables, and focus on the months of maximum chl-a and in which krill were sampled (May–June).

3.3.1. Chlorophyll-a concentration

Chl-a concentrations during the upwelling season varied 4-fold both off Bodega Bay and the Gulf of Farallones, despite differences in magnitudes (Fig. 6a and b). We fitted linear, logarithmic and quadratic relationships between bi-monthly chl-a (and krill) values and the synoptic upwelling indices defined here (*Intensity*,

SST_{event} and *NUI*), as well as more conventional monthly indices (BUI, τ_y , and SST). The Akaike information criterion (AIC) values allowed us to choose the model and environmental index that best explained interannual variability in the observed biological data. In all cases a quadratic function was the best fit; Table 1 shows AIC numbers and coefficient of determination for quadratic models only.

May–June chl-a showed the best relationships with May–June values of most physical parameters (Table 1, Fig. 6a and b). The best correlations were found between chl-a in the Gulf of Farallones and SST (monthly and SST_{event}) and *NUI*, however, lower AIC values (better fits) were found between chl-a off Bodega Bay and SST_{event} and *NUI*. No significant relationships were found with winds (monthly τ_y , synoptic *Intensity* or BUI), except for BUI with chl-a at the Gulf of Farallones. The best fit for Bodega Bay chl-a was with SST_{event} , closely followed by *NUI*. Note that all environmental indices are from the Bodega Bay area.

Years with the highest chl-a were characterized by moderate *Intensity*, SST_{event} , *NUI*, and monthly SST values. The least productive years in both regions were similar; 1992 and 1998 represented years of low *Intensity* and *NUI*, and warm SST_{event} , while 1999 represented a year of high *Intensity* and *NUI*, and cold SST_{event} , effectively bookending more typical high-productivity years found at mid-range values. The highest chl-a values occur at $SST_{event} = 10.9$ °C for Bodega Bay and $SST_{event} = 10.6$ °C for the Gulf of Farallones.

3.3.2. Krill abundance

Krill abundance varied by five orders of magnitude between years (Fig. 6c and d). Similar statistical analyses to those for chl-a

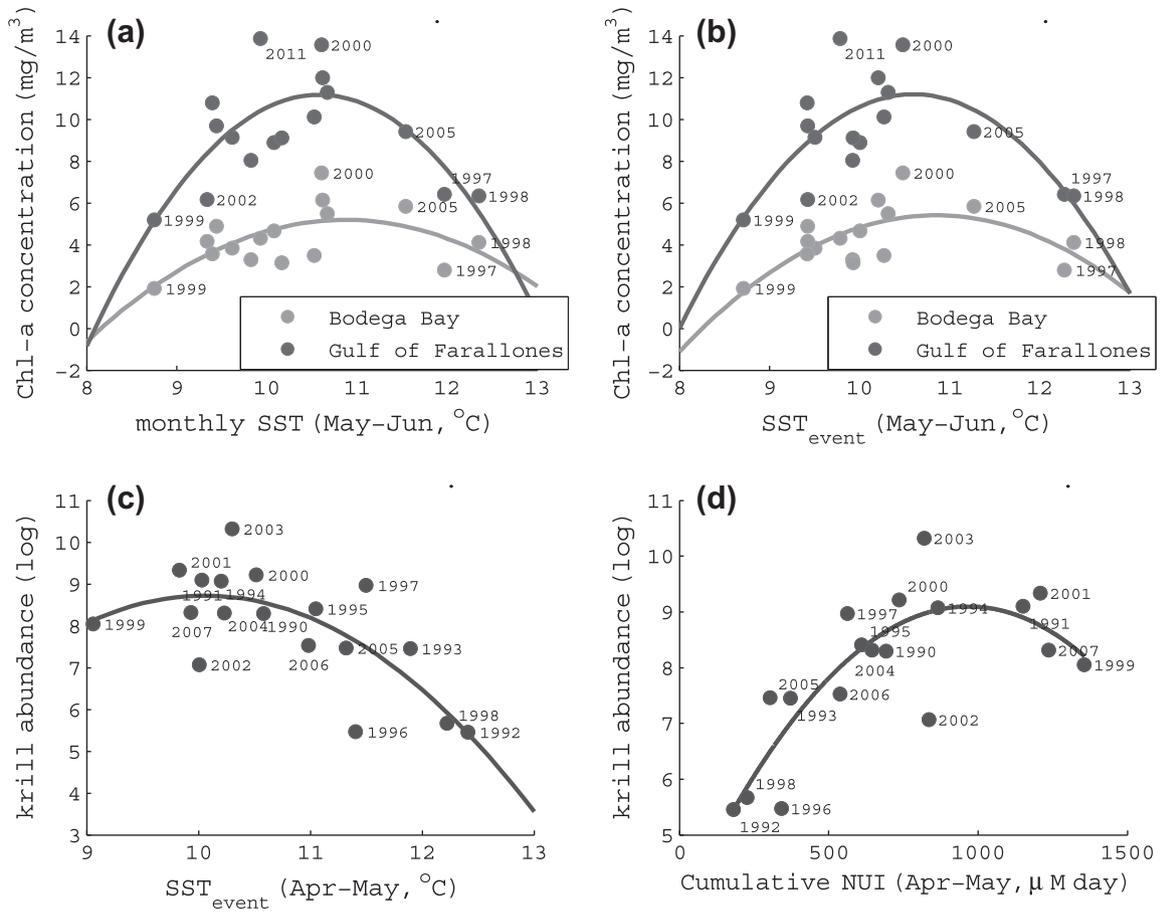


Fig. 6. Best fitted statistical model between (a) monthly SST at N13 and (b) SST_{event} at N13 with May–June chlorophyll concentrations at Bodega Bay and downstream in the Gulf of Farallones. Similar best-fit models are given for krill abundance in the area related to (c) SST_{event} and (d) NUI .

Table 1
AIC is the Akaike information criterion value and R^2 the coefficient of determination of each statistical model (quadratic) between chlorophyll concentration (May–June) and krill abundance (May–June) with monthly (BUI, τ_y , and SST) and synoptic scale indices (*Intensity*, SST_{event} , and NUI). Bold font indicates $p < 0.05$, and gray filled cells indicate the best fit (lowest AIC values and highest R^2).

		Monthly			Synoptic		
		BUI	τ_y	SST	Intensity	SST_{event}	NUI
Chl – Bodega Bay	AIC	28.4	30.3	26.9	30.4	25.9	26.5
	R^2	0.23	0.03	0.37	0.02	0.44	0.40
Chl – Gulf of Farallones	AIC	37.5	38.7	33.6	38.7	34.1	34.0
	R^2	0.30	0.18	0.56	0.18	0.54	0.54
Krill abundance	AIC	33.3	32.0	28.0	28.2	26.9	23.5
	R^2	0.11	0.18	0.48	0.46	0.53	0.68

were completed (Table 1). No significant relationships were found with BUI or monthly τ_y . The best fit was found for NUI ($R^2 = 0.68$, $p < 0.05$), which leads krill data by one month (Table 1, Fig. 6d). NUI identified low krill years due to inadequate upwelling (notably 1992 and 1998), and captured lower krill productivity when upwelling was strong (notably 1999 and 2007). The year with the most abundant krill (2003) showed moderate-high NUI , and maximum krill abundance is predicted at $NUI = 968 \mu M \text{ day}$. While NUI is based on SST, and SST_{event} shows good correlation with krill abundance as well, NUI is clearly better at explaining low-krill years (1991, 2001, and 2007). This shows the importance of accounting for periods during upwelling events when deep, cold and nutrient-rich water is not upwelled to the euphotic zone (days when $N \sim 0 \mu M$). Although representing a remarkable skill for an

environmental index (explaining 2/3 of the interannual krill variance), 2002 is a notable outlier (anomalous low krill abundance given moderate levels of NUI) and is better explained by SST_{event} (compare Figs. 6c and d). This anomaly deserves more in-depth analysis, but could be related to an anomalous intrusion of sub-arctic water detected in spring and summer (Venrick et al., 2003) which could have led to low SST_{event} and NUI values not directly related to upwelling. However, the results did not change (although R^2 improved) when 2002 values were removed.

3.3.3. Chlorophyll and krill

In the Gulf of Farallones, krill abundance in May–June was best correlated with phytoplankton in the preceding months (March–April chl-a values; $r = 0.7$, $p < 0.05$), consistent with the idea that

krill populations grow during times of high food availability. However, no significant correlation was found between krill and chl-a at Bodega Bay for any time lag.

4. Discussion

Our analysis of 31 years of winds off Bodega Bay showed that upwelling events occur year-round, but exhibit different seasonal characteristics. The ocean response to upwelling event forcing is, in turn, modulated by seasonal and interannual variability of ocean temperature. Here, we have used three indices to quantify seasonal and interannual changes in upwelling on event time scales: forcing, ocean response, and potential biological productivity. The indices were defined as: (i) *Intensity*, which quantifies wind forcing during an upwelling event, (ii) *SST_{event}*, which quantifies the response of the ocean in terms of upwelling of cold water, and (iii) *NUI*, which quantifies nutrients in the euphotic zone during an event, based on a *T-N* relationship for upwelled water.

4.1. Seasonality

Coherent seasonal variability is observed in the three synoptic-scale indices, illustrating three distinctive periods in the year (Fig. 3). First, April–July has the most intense upwelling: strong winds prevail in long events leading to the highest *Intensity*, lowest *SST_{event}*, and highest *NUI*. This season is followed by a period of weak winds and *Intensity* (August–October). As a result of longer relaxations and significant surface heating, *SST_i* (*SST* the day before upwelling begins) values are high during this period. Moreover, in the subsequent upwelling event, *SST_{event}* does not decrease to low values associated with high *N* (Fig. 4). These results are for a buoy 25 km offshore, however one may observe colder water breaking the surface nearer to the shore (e.g., Largier et al., 1993). This result suggests that one needs alongshore currents to remove warm surface waters at distances of more than the baroclinic Rossby radius from shore, so that cold high-nitrate waters can be entrained into the near-surface euphotic zone across a broader swath of shelf waters during upwelling events. Lentz and Chapman (2004) and Jaxco and Edwards (2011) demonstrated, using numerical models, that during periods of strong stratification (indicated by high *SST_i*; Murphree et al., 2003) water tends to be upwelled from the mixed layer rather than from the cold, nutrient-rich layers below the thermocline, since wind stress struggles to break the stratification. Water from the mixed layer or thermocline is warmer and low in nitrate, leading to a sharp decrease in *NUI* values for this season. Finally, during the winter season (November–February), short upwelling events occur and low *Intensity* is observed. *SST_{event}* exhibits average values, but it is weakly related to upwelling. During these months, *NUI* is low, but not zero, and similar to that in the fall (September–October), indicating year-round nutrient input. The importance of winter upwelling in preconditioning the ecosystem has been explored by Schroeder et al. (2009, 2013) and Black et al. (2010, 2011); however, the impact of upwelling events on biological productivity during the relaxation and winter seasons are out of the scope of this study.

Overall, this seasonality is similar to that found in other studies (Strub et al., 1987; Dorman and Winant, 1995; Taylor et al., 2008). However, by considering event-scale variability and the role of water temperature in the ocean response to wind forcing, we find a truncated upwelling season in terms of nutrient availability. Our definition of upwelling seasonality aims to be more relevant to biological productivity by integrating ocean temperatures and nutrient entrainment, in contrast to wind-only definitions (*BUI* and wind stress), which show weak or non-significant relationships with biological parameters (for example, Kahru et al., 2009 and Iles

et al., 2012). This shorter upwelling season was also proposed by García-Reyes and Largier (2012) based on monthly mean wind stress and variability.

4.2. Interannual variability

In general, the interannual variability of the three indices during the upwelling season showed a similar pattern: coincident high *Intensity*, cold *SST*, and high *NUI* in 1999, 2001, 2002, 2007, and 2008, and vice versa, coincident low *Intensity*, high *SST*, and low *NUI* in 1992 and 1998 (El Niño years). In contrast, 1997 and 2005 showed average *Intensity* but relatively low *NUI* values due to high *SST* conditions during both upwelling and relaxation events. The reverse case was also observed in 1985 when *Intensity* was weak, however, due to low *SST* conditions, indicating weak stratification, cold water can be easily upwelled from depth and *NUI* values were average instead of low. Notably, 1985 was a biologically productive year, whereas 1993 and particularly 2005 were generally unproductive (Bjorkstedt et al., 2010).

4.3. Long-term trend

A case of particular interest is the intensification of coastal upwelling proposed by Bakun (1990) due to increased atmospheric greenhouse gas concentration. The net effect on productivity will depend not only on the strength of the wind but also on the competing effect of increasing global ocean temperatures (Di Lorenzo et al., 2005). For the 31 years of data analyzed here, we observed an increasing trend in *Intensity* (also reported by García-Reyes and Largier (2010) and Iles et al. (2012)) and *NUI*. However, the trend in *SST_{event}*, although negative and consistent with increasing upwelling, has no statistical significance largely due to values from El Niño years. The *NUI* trend, though small, shows that at Bodega Bay stronger winds overcome increasing surface temperatures and stratification observed further offshore in the California Current (Palacios et al., 2004), allowing an increase in nutrient entrainment to the euphotic zone in the shelf waters.

4.4. Biological response to upwelling

Recognizing that the juxtaposition of upwelling and relaxation events is critically important for biological productivity (Lasker, 1975; Joint et al., 2002; Botsford et al., 2003, 2006; Dugdale et al., 2006; Wilkerson et al., 2006), we have sought new indices of upwelling that are cognizant of this synoptic variability and developed the *NUI* as an index of the availability of nitrate due to upwelling (where nitrate is the nutrient that limits primary production in the euphotic zone). Nevertheless, linking event-scale environmental indices to biological indices is not simple as they differ in spatial and temporal scales (specifically where environment parameters index productivity rates and biological indicators index population states). Further, biological sampling is much more limited than sampling of water properties and wind forcing. In this work, we related bi-monthly upwelling indices to bi-monthly chl-a concentrations and krill abundance in May–June, when chl-a is maximum and when krill was sampled. The spatial footprints of the indices are comparable, and possible spatial offset due to a lagged response in the presence of advection is accounted for by also considering downstream chl-a and krill values in the Gulf of Farallones. Our results show that chl-a is best correlated with May–June *SST_{event}* and *NUI* values. Additionally, a greater proportion of variance is explained for the Gulf of Farallones, which is downstream of N13 (Largier, 2004; Kaplan et al., 2005; Halle and Largier, 2011), than for the shelf waters in the vicinity of N13. Regional krill abundance for May–June correlates best with April–May environmental parameters (environmental conditions lead

by one month), consistent with the expected lag in the response of zooplankton biomass to phytoplankton productivity (Hayward and Venrick, 1998) and environmental conditions.

It is remarkable to find these significant relationships between synoptic environment indices and both chl-a concentration and krill abundance in the upwelling season, which suggests that we have captured the essence of the physical-biological coupling for selected plankton in this coastal upwelling system. The best relationships are found as quadratic functions (Fig. 6), with the dome-shaped curve representing an 'optimal environmental window' for lower-trophic-level productivity, similar to that introduced by Cury and Roy (1989) and further described by Botsford et al. (2003, 2006). Key to this result is the recognition that surface water temperature plays an important role in modulating the response of the ocean to upwelling winds – so that wind forcing alone is not a skillful index for productivity. High temperatures lead to strong stratification and therefore poor entrainment of nutrients to the euphotic zone during subsequent upwelling events, thus decreasing biological productivity. SST, evaluated both at monthly and synoptic scales, is a good indicator of primary productivity seen at the surface (chl-a), however, the synoptic indices SST_{event} and in particular NUI are a better fit for krill, as they better track the time-scale at which the upwelling process acts. Further, NUI introduces the bi-linear relation of nitrate to temperature, so that periods of warmer water represent times when nutrient availability is near-zero and primary production is also expected to be near-zero. The dome-shape relationship between physical conditions and biological productivity reflects a trade-off between two processes, both related to upwelling: (i) nutrient supply, which is controlled by wind strength and near-surface stratification and (ii) plankton loss through offshore advection associated with upwelling (Lasker, 1975; Botsford et al., 2003, 2006). Krill, due to their motility and propensity for being at depth during daytime, are less likely to be advected by offshore Ekman transport during upwelling events and show less decrease in abundance for stronger upwelling (Fig. 6). While cold temperatures are known to slow down the metabolic rate of zooplankton (i.e., Alcaraz et al., 2013), the range in temperature change during upwelling events is not large enough to explain changes in krill concentrations. Other physical processes, such as eddies (Gruber et al., 2011) or geostrophic flow, resulting from readjusting pressure gradients (Marchesiello and Estrade, 2010) that could affect upwelling and advection (alongshore and offshore) of nutrients and biological organisms are not contemplated here.

The different relationships for phytoplankton (indexed by satellite estimates of surface chl-a) and mesozooplankton (indexed by May–June mid-water trawl samples) deserve further attention in future work. Here we note that chl-a concentrations include diatom blooms, typical of strong upwelling conditions and dominating the months of the upwelling season, as well as dinoflagellate blooms that typically occur during stratified conditions most common in the fall. Stratified conditions are favorable for the growth of motile dinoflagellates (Margalef, 1978; Kudela et al., 2005) since they can access nutrients within and below a shallow thermocline and can use recycled nutrients in the mixed layer. Simple relations for between winds or water temperature and surface chl-a concentration have proved to be difficult partly due to these seasonal differences in diatom and dinoflagellate ecology and spatial distribution, but also because phytoplankton blooms depend on a pre-existing population of phytoplankton, which typically grows during a prior upwelling event. As phytoplankton are short-lived (many blooms last only a couple of weeks or less), one can expect times when NUI conditions are high but no bloom results due to an absence of an initial phytoplankton inoculum. In contrast, krill are much longer lived and one can expect a continuous krill population through the upwelling season. If conducive conditions develop

one can expect a response in krill abundance, even if the response is slower. Furthermore, krill diet is dominated by diatoms, which require high-nitrate upwelling events that are well indexed by NUI . Together this may explain why correlations between krill and event-based indices are higher than those for chl-a, or the good krill correlations may be related to better temporal and depth coverage of krill abundance than surface chl-a measurements, which are only satellite derived.

Our $T-N$ relationship is based on winter and summer data, which for Bodega Bay both seasons yield a similar relationship. However, other seasons (Silió-Calzada et al., 2008; Palacios et al., 2013), and other regions (Palacios et al., 2013) may show different relationships. Therefore, year-long data would be useful to fully validate our NUI time series. The results presented here for chl-a concentration and krill abundance belong to a season when data are available, adding confidence to those results.

5. Conclusion

In this study we defined event-scale upwelling indices ($Intensity$, SST_{event} and NUI) over the shelf off Bodega Bay, California and studied their seasonality, interannual variability, and relationship to lower trophic level productivity in the region. We show that $Intensity$, based only on wind forcing, cannot adequately describe the variability in biological productivity. However, both SST_{event} and NUI (quantifying the entrainment of cold water and nutrients to the surface layer) showed good relationships with biological productivity since they proxy not only the upwelling forcing but also integrate the modulating effect of ocean conditions on the effect of wind forcing. The relationships between SST_{event} and NUI with chl-a concentration and krill abundance follow a dome-shape function, indicating highest productivity during moderate upwelling conditions, both in wind and SST, but decreasing during strong/weak upwelling and warm ocean temperatures.

Acknowledgments

We thank M. Kahru (Scripps Institution of Oceanography) for compiling and providing the chlorophyll-a data, J. Field, the NMFS/NOAA Juvenile Rockfish Survey, B. Marinovic (UCSC) for data on krill abundance, and R. Dugdale (San Francisco State University) for nitrate data collected during WEST. Special thanks to S.A. Thompson for reviewing this manuscript. This work was in part supported by the UC Davis/BML Fellowship on Ocean Acidification, the Central and Northern California Ocean Observing System (CeNCOOS), and National Science Foundation (NSF) awards ATM-0619139 and 1130125 (B.A. Black, W.J. Sydeman, and S.J. Bograd, co-PIs).

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		Monthly			Synoptic		
		BUI	τ_y	SST	<i>Intensity</i>	<i>SST_{event}</i>	<i>NUI</i>
Chl - Bodega Bay	AIC	28.4	30.3	26.9	30.4	25.9	26.5
	R ²	0.23	0.03	0.37	0.02	0.44	0.40
Chl - Gulf of Farallones	AIC	37.5	38.7	33.6	38.7	34.1	34.0
	R ²	0.30	0.18	0.56	0.18	0.54	0.54
Krill abundance	AIC	33.3	32.0	28.0	28.2	26.9	23.5
	R ²	0.11	0.18	0.48	0.46	0.53	0.68

Table 1. AIC is the Akaike information criterion value and R² the coefficient of determination of each statistical model (quadratic) between chlorophyll concentration (May-June) and krill abundance (May-June) with monthly (BUI, τ_y , and SST) and synoptic scale indices (*Intensity*, *SST_{event}*, and *NUI*). Bold font indicates $p < 0.05$, and gray filled cells indicate the best fit (lowest AIC values and highest R²).