

## Climate-index response profiling indicates larval transport is driving population fluctuations in nudibranch gastropods from the northeast Pacific Ocean

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### *Abstract*

We illustrate a novel method, climate-index response profiling, for testing mechanistic hypotheses for abundance fluctuations in long-term marine data sets. (1) Autoregressive models were fitted to time-series data for multiple species using climate indices as external regressors. The resulting regression coefficients for each species we term a climate-index response profile (CIRP). (2) Mechanistic hypotheses were rejected based on the summary response profile across species obtained by meta-analysis. (3) Monte-Carlo simulations of the CIRPs for all species at all sites were performed to generate null expectations to test the significance of nonrejected hypotheses. We applied this method to historical data of 56 nudibranch species from three intertidal sites studied independently in central California during nonoverlapping time periods between 1969 and 1995, combined with recent resurveys from these same sites. Adult populations are strongly correlated with the multivariate El Niño–Southern Oscillation index and sea-surface height, increasing during El Niño and decreasing during La Niña events. Our data are consistent with recruitment limitation via larval advection as the primary driver of adult abundance variation. El Niño conditions increase recruitment by cross-shelf onshore advection of larvae from both southern and northern populations, and alongshore larval advection from southern source populations. We hypothesize that recent declines of California nudibranchs are temporary, and populations will recover as El Niño conditions return to the California current.

Within the tightly coupled dynamic system of ocean and atmosphere, variation in climate has caused periodic restructuring of entire marine ecosystems at the scale of the ocean basin, from phytoplankton to top predators (Alheit and Bakun 2010). Understanding the biological causes of these changes is necessary for the protection of marine abundance and biodiversity, for the forecasting and management of fluctuating marine resources, and for an understanding of population regulation, especially in species with a larval phase vulnerable to large-scale ocean conditions (Roughgarden et al. 1991).

Shallow-water nudibranch mollusks are colorful, conspicuous, nonharvested, and easily censused model indicator species that have undergone sharp declines recently in central California (Figs. 1 and 2). Causes of these declines are unknown, but climatic variation has been hypothesized to limit population density in at least three direct ways: (1) changes in sea-surface temperature (SST) may interfere with physiology and behavior more rapidly than populations can adapt (temperature limitation hypothesis); (2) changes in strength or frequency of nutrient-laden currents may alter productivity and trophic dependencies, causing periodic loss of multiple age classes (trophic limitation hypothesis); and (3) changes in velocity of advective currents (cross-shelf or alongshore) may greatly alter rates

of larval recruitment into suitable habitat (larval advection hypothesis).

These hypotheses are difficult to test experimentally because properly controlled, in situ manipulations are not feasible. However, the temporal course of decline of any species is expected to be different under different mechanisms, because the strength of each mechanism has a distinct temporal course of variation. This temporal course can be inferred from known monthly changes in the ocean climate. These changes are expressed in local records of SST, sea-surface height (SSH), atmospheric pressure at sea level (SLP), upwelling strength, and in published climate indices that summarize conditions over the entire ocean basin. For the 70% of nearshore benthic invertebrates that produce planktonic eggs or larvae potentially advected to tens or hundreds of kilometers from their source population, basin-scale or ‘synoptic’ indices might be more informative than local conditions about processes limiting local adult population density.

The dominant modes of climatic variation proposed for the North Pacific basin are based on principal-component analyses of anomalies in either SST or SSH, which are highly positively correlated. The Pacific Decadal Oscillation (PDO) is the first principal component of monthly SST anomalies in the Pacific north of 20° N latitude (Mantua and Hare 2002). The ‘Victoria’ mode is the second principal component of SST anomalies over the same region (Bond et al. 2003). The North Pacific Gyre Oscillation (NPGO) is

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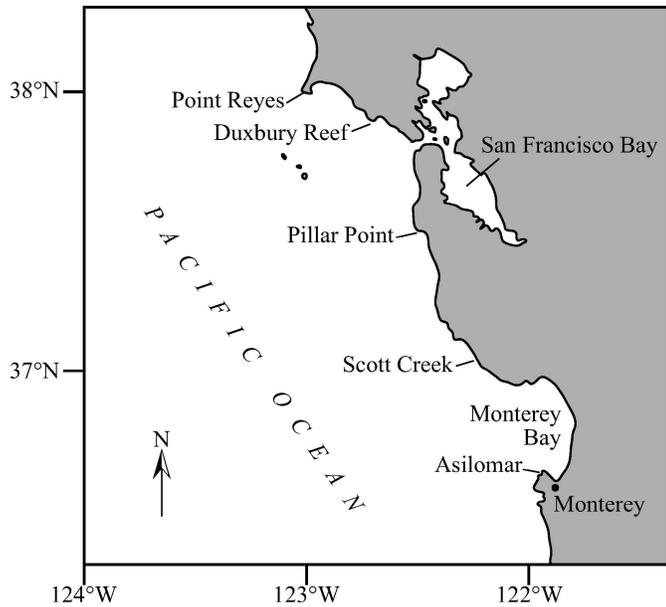


Fig. 1. Map of study sites at Pillar Point, Scott Creek, and Asilomar, California.

the second principal component of the monthly SSH anomalies from 25° to 62° N latitude, and is highly positively correlated with the Victoria mode (Di Lorenzo et al. 2008). The El Niño–Southern Oscillation (ENSO) is the dominant mode of combined atmospheric and oceanic variation over the entire Pacific Ocean, and can be defined as the first principal component of the combined anomalies of SLP, SST, zonal and meridional wind components, air temperature, and total cloudiness in the tropical Pacific (30° S to 30° N latitude), otherwise known as the multivariate ENSO index (MEI; Wolter and Timlin 1993).

Although these climate modes are in part intercorrelated, each possesses a unique ecological profile that can be used to differentiate hypotheses about the causes of biological variation (Table 1). Hydrodynamically, positive PDO is associated with a strong subarctic gyre within which gyre upwelling and coastal downwelling are dominant, and with a weak subtropical gyre within which upwelling is weak. Positive NPGO is associated with greater strength of both subarctic and subtropical gyres and their consequent gyre and coastal upwelling, respectively. El Niño events transiently reverse the normal summer flow of the California Current system from southward and offshore to northward and onshore, and with typical wind anomalies disrupt coastal upwelling cells or convert the system to persistent downwelling (Lluch-Belda et al. 2005). Averaged over the north Pacific basin, SST is uncorrelated with the NPGO but highly positively correlated with PDO, especially along the coast to several hundred miles offshore (Di Lorenzo et al. 2008). Nutrients, sea-surface salinity, and chlorophyll-*a* are all strongly intercorrelated and positively correlated with NPGO but uncorrelated with PDO. Coastal upwelling and biological productivity south of 38° N latitude (Point Reyes, California) are strongly positively correlated with NPGO, and north of 38° N latitude are strongly negatively correlated with PDO

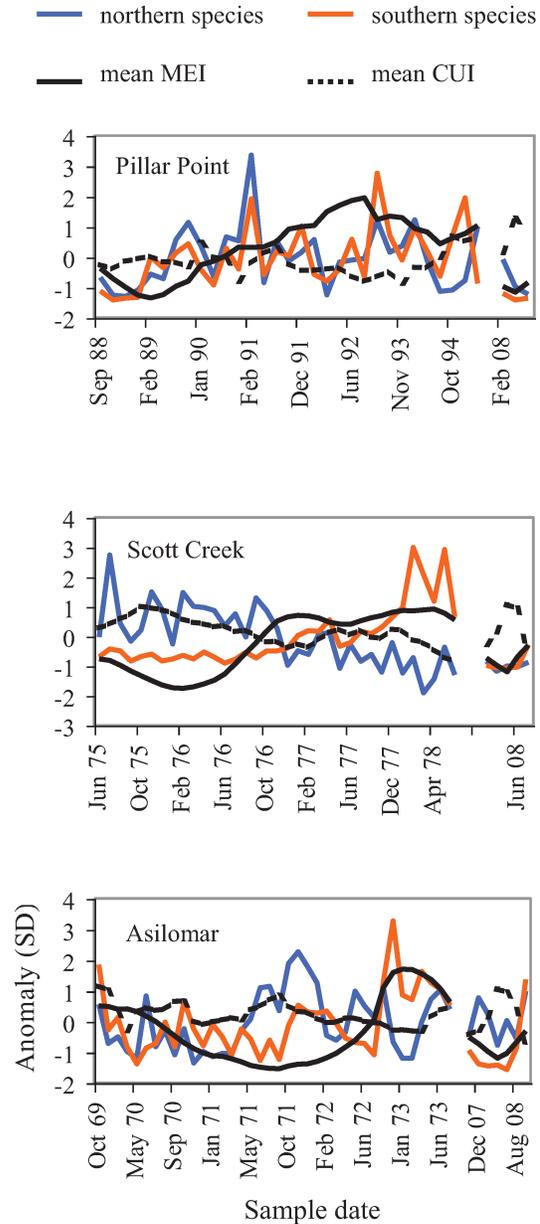


Fig. 2. Monthly abundance trajectories of southern and northern nudibranch species at each study site and 6-month moving average (1-month lag) of the multivariate ENSO index (MEI) and coastal upwelling index (CUI), all data plotted as anomalies (deviation from mean over the periods of the original studies in units of standard deviation).

(Chhak and Di Lorenzo 2007). ENSO is negatively correlated with nutrients and productivity within the California Current, and positively correlated with SST, SSH, depth of thermocline and nutricline, and strength of the California undercurrent and Davidson currents, especially south of 48° N latitude (Lluch-Cota et al. 2001; Peterson et al. 2002).

These ecological profiles can be compared to long-term time-series of population abundance to test hypotheses about the major drivers of abundance variation. This method, which we call ‘climate-index response profiling’

Table 1. Ocean climate-index acronyms, names, scale, and use as proxies for testing mechanistic hypotheses. See Table 2 for criteria for hypothesis rejection.

| Abbreviation | Name                           | Scale    | Proxy for   |
|--------------|--------------------------------|----------|---|
| MEI          | Multivariate ENSO Index        | Synoptic | Alongshore current (northward)<br>Cross-shelf surface current (onshore)<br>Sea-surface temperature (positive)<br>Upwelling (negative)<br>Biological productivity (negative) |
| PDO          | Pacific Decadal Oscillation    | Synoptic | Sea-surface temperature (positive)  |
| SSH          | Sea-surface height             | Local    | Cross-shelf surface current (onshore)   |
| CUI          | Coastal Upwelling Index        | Local    | Cross-shelf surface current (offshore)<br>Upwelling (positive)<br>Biological productivity (positive)  |
| SST          | Sea-surface temperature        | Local    | Sea-surface temperature (positive)  |
| NPGO         | North Pacific Gyre Oscillation | Synoptic | Alongshore surface current (southward)<br>Upwelling south of 38° N latitude (positive)<br>Biological productivity (positive)  |

has three assumptions: (1) population abundance is correlated, at the appropriate time lag, with proxies for the mechanisms that drive its fluctuations; (2) advection of larvae to suitable settlement sites alongshore is directional, with the primary source populations for a given species at a study site in the direction toward the center of the species' geographic distribution; and (3) temperature limitation follows a north–south gradient, such that, on average, positive temperature anomalies favor southern more than northern species, and vice-versa. The method provides strong hypothesis testing: it rejects candidate hypotheses for the driving mechanisms if population densities are negatively correlated with proxies that are positively correlated with those mechanisms. Although other workers have reported relationships between biological variables and multiple climate indices (Tolimieri and Levin 2005; Menge et al. 2009), the present method in addition applies an explicit mechanistic hypothesis-testing framework to the response profile that takes into account intercorrelations among the environmental indices.

At our study sites in central California, the primary synoptic proxies of trophic conditions are MEI (negative) and NPGO (positive), and the local proxy is the local coastal upwelling index ([CUI] positive; Table 1). Synoptic temperature proxies are the PDO and MEI (both positive), and the local SST. Populations may be limited by larval advection either cross-shelf or alongshore. The proxies for alongshore advective currents are the MEI (pole-ward and primarily subtropical) and NPGO (equator-ward and primarily temperate). The primary synoptic proxy for onshore surface currents is the MEI (positive), and the local proxies are CUI (negative) and SSH (positive).

Here we present the method of climate-index response profiling and demonstrate its use in testing the hypotheses of trophic limitation, temperature stress, and larval advection as the major drivers of nudibranch population variation at our study locations in the central California rocky intertidal. Using the above presumptive relationships, we show that long-term population time series are inconsistent with either trophic limitation or temperature stress as primary mechanisms driving population fluctua-

tions, leaving larval advection as the mechanism most consistent with our recorded fluctuations in abundance.

## Methods

*Study sites and sampling*—Time series of population abundance for 56 species of nudibranchs (Web Appendix, Table A1, <[www.aslo.org/lo/toc/vol\\_56/issue\\_2/0749a.html](http://www.aslo.org/lo/toc/vol_56/issue_2/0749a.html)>) were constructed from surveys originally conducted independently during separate time periods between late 1969 and 1996 at three rocky, low intertidal sites in central California (Fig. 1): Pillar Point (37°29'38"N, 122°30'00"W), Scott Creek (37°02'45"N, 122°14'17"W), and Asilomar (36°37'38"N, 121°56'27"W). Pillar Point was sampled on a largely monthly basis by W. E. Pence and D. E. Mason (unpubl.) from September 1988 to November 1996, with temporal gaps of irregular length (see Web Appendix, Table A2). The study area consisted of 10 major pools and adjacent rock walls and overhanging ledges located below 0-m tide level on a large shale bench. Scott Creek was sampled monthly by J. H. R. Goddard (unpubl.) from June 1975 to June 1978, plus during an additional 10 months dispersed between October 1978 and June 2006 (see Web Appendix, Table A2). This site consisted of all pools and low overhangs within a total area of about 400 m<sup>2</sup> located between the 0.30-m and –0.15-m tide levels on a gently sloping bench composed of Santa Cruz mudstone. Loose rock was rare here and at the Pillar Point site and present only at the bottom of deeper pools. Asilomar was sampled monthly and described by Nybakken (1974, 1978) and consisted of all low-lying area and tide pools below –0.5-m tide level in an area ~ 50 × 50 m “on a dissected granite rocky shore characteristic of most of the Monterey Peninsula. The topography of the intertidal is irregular, containing loose rock, massive rocks ridges rising vertically to 2 m and tide pools of varying sizes” (Nybakken 1978: p. 131). Pillar Point and Asilomar are 110 km apart. Owing to irregular topography, gently sloping bottom profiles, or the presence of offshore rocks, all three sites can be classified as protected outer coast, and each has abundant wave-protected microhabitats supporting luxuriant

growths of sponges, cnidarians, bryozoans, and ascidians preyed on by nudibranchs.

Beginning in late 2007 we have been repeating bimonthly to quarterly the sampling originally conducted on a generally monthly basis at the above sites. Sampling consists of timed counts, by one or two observers, of all nudibranchs found in the study areas at Pillar Point and Scott Creek, and following Nybakken (1978), counts over a 1-h period by three observers, each sampling a different subarea, at Asilomar. We avoided sampling during conditions that could impede the counts, particularly high wave surge. For all analyses, we standardized nudibranch counts to number of individuals  $\text{h}^{-1}$  observer $^{-1}$ . We excluded two sampling dates at Asilomar for which conditions were noted as adverse (Nov 1972 and Mar 1973), and 1 month at Asilomar (Aug 1972) in which J. Nybakken's absence significantly depressed the count of *Triopha maculata*, a common species. We also excluded untimed counts in the original study at Pillar Point. Monthly counts of each of the larger species from the original study at Asilomar were shared with us by J. Nybakken, and the monthly total abundances for all species pooled at this site were reconstructed for a subset of the original study using the monthly totals for the smaller species reported by Nybakken (1974; Fig. 1). Species recorded in timed counts from the original studies and the more recent surveys are listed in Web Appendix, Table A1, and the standardized monthly counts of each species at each site are listed in Web Appendix, Table A2. We used information on geographic ranges from the primary literature and Behrens and Hermosillo (2005), supplemented by our personal observations, to define southern species as those with northern range limits typically in northern California or southern Oregon and northern species as those with southern limits in southern California or northern Baja California. We defined widespread species as those extending both north of the southern species and south of the northern species.

*Sources and treatment of climate and oceanographic indices*—We used the following sources for the indicated synoptic and local indices: (1) MEI: <<http://www.cdc.noaa.gov/people/klaus.wolter/MEI/table.html>>; (2) PDO: <<http://jisao.washington.edu/pdo/PDO.latest>>; (3) SSH at 37°48.4' N, 122°27.9' W: <<ftp://ilikai.soest.hawaii.edu/woce/m551.dat>>. This was converted to the detrended monthly anomaly based on monthly mean and SD from January 1901 to December 2008; (4) SST at 36° N, 122° W: <<http://hadobs.metoffice.com/hadisst/data/download.html>>. This was converted to the detrended monthly anomaly based on monthly mean and SD from January 1870 to December 2008; (5) CUI at 36° N, 122° W: <<ftp://orpheus.pfeg.noaa.gov/outgoing/upwell/monthly/upindex.mon>>. This was converted to the detrended monthly anomaly based on monthly mean and SD from January 1946 to December 2008; (6) NPGO: <<http://www.o3d.org/npgo/data/NPGO.txt>>.

*Statistical analysis*—Climate-index response profiling was performed in a three-step process. First, the relation-

Table 2. Sufficient conditions for contradiction of the indicated mechanistic hypotheses.  $b_1$ : the regression coefficient for climate index I in the fitted autoregression model. Rejection of the hypothesis requires, in addition, rejection of the null hypothesis within the relevant geographic range group.

| Criterion   | Hypothesis             |
|---|------------------------|
| $b_{\text{MEI}} > 0$ or $b_{\text{CUI}} < 0$ or $b_{\text{NPGO}} < 0$ | Trophic limitation     |
| Northern range and $b_{\text{NPGO}} < 0$                              | Alongshore advection   |
| Northern range and $b_{\text{MEI}} > 0$                               | Alongshore advection   |
| Southern range and $b_{\text{NPGO}} > 0$                              | Alongshore advection   |
| Southern range and $b_{\text{MEI}} < 0$                               | Alongshore advection   |
| $b_{\text{MEI}} < 0$ or $b_{\text{CUI}} > 0$ or $b_{\text{SSH}} < 0$  | Cross-shelf advection  |
| Northern range and $b_{\text{MEI}} > 0$                               | Temperature limitation |
| Northern range and $b_{\text{PDO}} > 0$                               | Temperature limitation |
| Northern range and $b_{\text{SST}} > 0$                               | Temperature limitation |
| Southern range and $b_{\text{MEI}} < 0$                               | Temperature limitation |
| Southern range and $b_{\text{PDO}} < 0$                               | Temperature limitation |
| Southern range and $b_{\text{SST}} < 0$                               | Temperature limitation |

ship between population abundance (see Web Appendix, Table A2) and each climate index was investigated for each species. This was done with autoregressive, integrated, moving average (ARIMA) models. These models tested the null hypothesis that nudibranch rank-transformed abundances were not influenced by ocean climate. A separate model was fitted for each of the six indices. The resulting six regression coefficients we term the climate-index response profile (CIRP). This profile was calculated separately for each species at each study site. Second, the resulting regression coefficients for each index and each species (see Web Appendix, Table A3) were used to reject specific mechanistic hypotheses, according to the criteria in Table 2. These rejections were performed over the entire data set, and within subsets categorized by study site and species' geographic range (north, south, widespread). In both cases summary values of climate effects and their associated rejection probabilities were obtained by standard meta-analysis of the regression coefficients. Third, the nonrejected hypotheses were evaluated by constructing a null model of regressions conditional on the intercorrelations among the coefficients for the climate indices.

We consider this method to be a formalization of assumptions that are implicit in arguments frequently made in studies of ecological effects of climate change. For example, the recent conclusion of Menge et al. (2009) that synoptic trophic conditions in the north Pacific are the primary driver of mussel abundance fluctuations on the Oregon coast, based on higher simple positive correlations with NPGO than either PDO or MEI, assumes that NPGO is a trophic proxy, which then implies that the trophic limitation hypothesis would be rejected if these correlations were negative.

*ARIMA regression*: Autoregressive models were used to test the effect of the external regressors in the presence of serial autocorrelation in the time series of population abundance. In this method, a Markovian state-space model was used to represent the autoregressive process for each species (Gardner et al. 1980; Jones 1980; Durbin and Koopman 2001). The model parameters were optimized in

a maximum-likelihood procedure in which the exact likelihood was computed by Kalman filtering (Gardner et al. 1980). This method allows for any number of successive missing values: as the recursion proceeds through a missing region, the information contained in the state vector gradually approaches zero, and the method becomes equivalent to starting the recursion at the end of that region (Jones 1980: 393). No imputations of missing values are performed; rather, missing values are simply unavailable in the model-fitting procedure. For most species the fitted model contained terms only for the first- or second-order monthly autoregression and for the first-order seasonal autoregression (i.e., seasonal ARIMAs of the form  $[1, 0, 0][1, 0, 0]$  or  $[2, 0, 0][1, 0, 0]$ ). Because these lacked the moving average term, these were strictly seasonal autoregressive (AR) models.

The external regressor used for each species was the mean of 3, 4, or 6 months previous to the month that the species' abundance was measured, depending on the estimated life cycle of the species, and for the summed abundances of large species and all species the mean of 6 months previous to the month of sampling. We choose these means to integrate climate and ocean conditions over the period when most individuals in a population at any given time would have been in their planktonic larval stage. Most species of nudibranchs in California have subannual to annual life cycles with prolonged or aseasonal reproductive periods, and at any given time populations of many species are composed of individuals of widely varying size and age (Nybakken 1978; Beeman and Williams 1980; Strathmann 1987). In addition, all the species sampled in this study produce planktonic larvae, and all but two have feeding larvae with minimum planktonic periods of  $\sim 1$  month (Goddard 2004). Simple rather than partial correlations were evaluated as in Menge et al. (2009) because the goal was to reject separate mechanistic hypotheses rather than fit an overall predictive model (Tolimieri and Levin 2005).

Rejection of mechanistic hypotheses: The AR regression coefficients for each ocean condition index and its standard error were subjected to a standard meta-analysis using species and site as random factors (Petitti 1994). This analysis was performed within each site and species range group, and across all species and sites as an overall random-effects summary, weighted by species abundance. In the latter overall summary, each species was first summarized across all sites of occurrence, and then all species were summarized to give a single final effect and associated standard error for each ocean condition index. Hypotheses for the major oceanographic drivers of population abundance were then rejected only under two conditions: 1) the summary effect of the proxy for the mechanistic hypothesis in the meta-analysis was significant, and, 2) the effect was in the direction opposite that predicted by the hypothesis (i.e., it contradicted the hypothesis [Table 2]).

These conditions are based on the assumption that if a mechanism is a primary driver, then abundance must, at the least, not be significantly negatively correlated with any of its proxies. Note that this assumption leaves open the

possibility that proxies of a rejected mechanism might have positive or zero correlation with many nudibranch vital rates, such as larval survival or development rate, because this still does not prevent a negative correlation with abundance. Further, in theory it is possible that a rejected mechanism's proxy has a zero or positive partial correlation but negative simple correlation with abundance, because the primary mechanism is sufficiently strong to overwhelm any effects of the rejected mechanism in nature.

Evaluation of nonrejected hypotheses: While hypothesis rejections are valid regardless of the presence or absence of correlations among the climate-index regression coefficients, hypotheses that were not rejected may represent causally important processes, or they may simply be correlated with those processes. To determine whether the number of nonrejections was higher than expected by chance, confirmatory tests were performed using the summed number of species contradicting the hypothesis as the test statistic. A contradiction was defined as condition 2) above met for a given species. These tests were constructed by creating a null expectation of the number of contradictions of each hypothesis that is conditional on the intercorrelations among the climate-index coefficients. If the observed number of contradictions was still significantly lower than the null expectation, then we conclude that the mechanism has an independent effect on nudibranch abundance.

For these tests, we generated the null expectation in a Monte-Carlo simulation of CIRPs for all species at all study sites. Each coefficient was drawn from a normal distribution with parametric variance equal to its sample variance, creating a matrix of uncorrelated simulated coefficients. We converted this to a matrix of correlated coefficients by postmultiplication by the Cholesky decomposition of the sample correlation matrix of the coefficients (Lurie and Goldberg 1998). The resulting matrix of simulated, correlated coefficients, the list of 'null CIRPs,' was generated 10,000 times. For each simulation, we tallied the number of null CIRPs that contradicted any of the three mechanistic hypotheses (trophic limitation, temperature limitation, and larval advection alongshore or cross-shelf), according to the conditions in Table 2. This number of contradictions ( $C_0$ ) provided the null expectation for our test statistic. We generated the null distribution by constructing its empirical cumulative probability density function for each hypothesis from the 10,000 replicates. We then compared our observed number of contradictions ( $C$ ) with the density function for  $C_0$  to obtain its probability under the null hypothesis. We conducted this confirmatory test in two ways: under the complete null assumption that the parametric mean is zero for all the climate-index regression coefficients; and under the conditional null assumption that the parametric mean of at least one of the climate-index regression coefficients is equal to its sample mean.

To test the hypotheses that a species' CIRP was unaffected by site, geographic range, size, or their interactions, the AR regression coefficients for each species and ocean condition index (i.e., its CIRP) were subjected to permutational multivariate, factorial analysis of variance

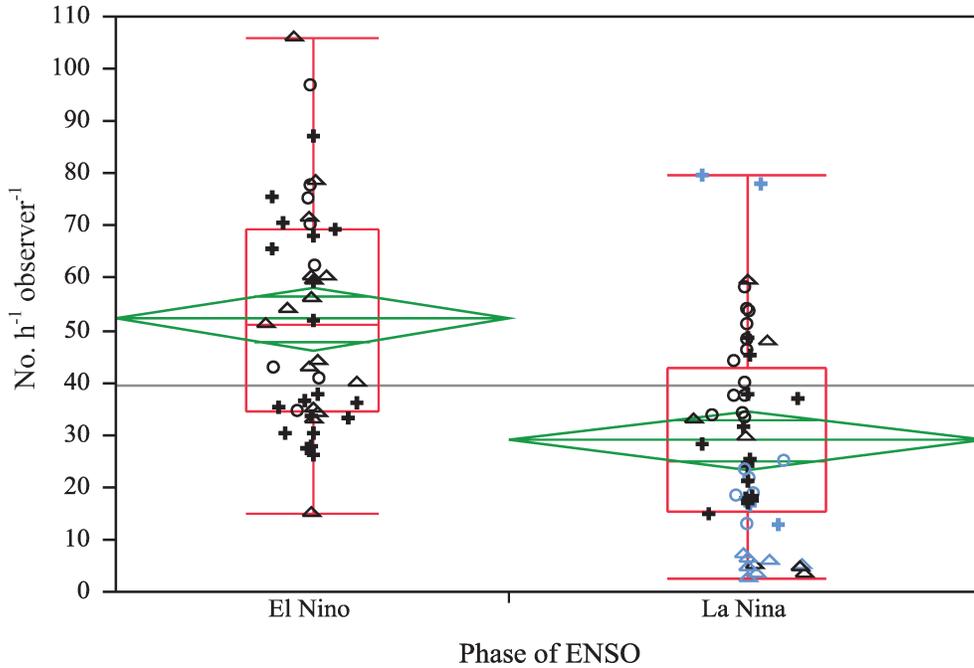


Fig. 3. Box plots of the abundance of all species of nudibranchs pooled at each site by phase of ENSO as measured by the mean of the Multivariate ENSO Index (MEI) for the 6 months prior to each sample date. O = Asilomar, + = Scott Creek, Δ = Pillar Point; blue points indicate data collected November 2007–November 2008. Here, we defined La Niña as the mean MEI  $\leq -0.5$  and El Niño as mean MEI  $\geq 0.5$ . Green diamonds depict means and 95% confidence intervals, horizontal lines in the boxes depict medians.

with site and range as predictors (Anderson 2001). To uncover the CIRP covariance structure across species and sites, we performed a principal components analysis of the AR regression coefficients' covariance matrix, and illustrated the result with a standard biplot.

Results

*Nudibranch abundance variation*—Total abundance of nudibranchs at all three study sites fluctuated by two orders of magnitude, and the abundance of southern species especially fell during the 2007–2008 La Niña to levels observed in the original studies mainly during previous strong La Niña conditions (anomalies in the mean MEI  $< -1$ ; Fig. 2). Overall, mean total abundance within each study site was greater by a factor of approximately two during El Niño episodes than during La Niña events (Fig. 3).

During the original study at Scott Creek the abundance of northern species decreased, while that of southern species increased, coincident with a change from negative to positive anomalies in the mean MEI and in concert with the 1976–1977 climate regime shift in the North Pacific Ocean (Fig. 2). Seasonal fluctuations aside, a similar relationship between the abundance of the two range groups and the mean MEI is apparent at Asilomar, but not at Pillar Point, except in 1994, when the abundance of northern species was depressed and southern species increased (Fig. 2).

*AR regression results*—The multivariate ENSO index had the strongest influence among the climate indices on nudibranch abundance, and its mean effect over all sites and species was positive (Tables 3 and 4; Figs. 4, 5). The most common CIRP showed a positive correlation of abundance with MEI, PDO, SSH, and SST, and a negative correlation with CUI and NPGO (Table 5; we call this ‘CIRP1’); the second most common CIRP showed the exact reverse correlations with every sea condition index (‘CIRP2’; Table 5). A species’ CIRP was significantly affected by its geographic range and site of occurrence, and the effect of range differed marginally in the different study sites (Tables 5 and 6; Fig. 6). Southern species showed CIRP1 with few exceptions; northern species showed CIRP1 or CIRP2 depending on their location

Table 3. Random-effects meta-analysis summaries over all sites and species for each ocean condition index. Shown are the index name, summary effect, and its associated standard error, *t*-value, probability, and hypothesis rejected (Troph: trophic limitation).

| Index | Effect | SE   | <i>t</i> | <i>p</i> | Reject |
|-------|--------|------|----------|----------|--------|
| MEI   | 3.02   | 0.67 | 4.48     | 0.00002  | Troph  |
| PDO   | 1.37   | 0.76 | 1.79     | 0.076    | —      |
| SSH   | 3.00   | 0.71 | 4.23     | 0.00005  | —      |
| SST   | 2.90   | 0.86 | 3.37     | 0.0011   | —      |
| CUI   | -2.61  | 0.92 | 2.83     | 0.0056   | Troph  |
| NPGO  | -1.23  | 1.07 | 1.14     | 0.26     | —      |

Table 4. Results of meta-analysis of AR climate-index coefficients and hypothesis rejection within species subsets defined by site and geographic range. Columns are climate index, study site, geographic range of the group summarized, the summary effect coefficient (Coef.), its standard error, *t*-value, and associated probability, and the hypothesis rejected (Troph: trophic limitation, Temp: temperature limitation, AdvC: cross-shelf larval advection, and AdvA: alongshore larval advection).

| Index | Site         | Range | Coef. | SE   | <i>t</i> | <i>p</i> | Reject      |
|-------|--------------|-------|-------|------|----------|----------|-------------|
| MEI   | Asilomar     | N     | -2.08 | 1.43 | -1.45    | 0.15     | —           |
|       |              | S     | 4.13  | 2.11 | 1.95     | 0.054    | —           |
|       |              | W     | 3.24  | 1.80 | 1.80     | 0.074    | —           |
|       | Pillar Point | N     | 1.96  | 1.19 | 1.65     | 0.10     | —           |
|       |              | S     | 4.04  | 2.47 | 1.63     | 0.11     | —           |
|       |              | W     | 3.14  | 1.34 | 2.33     | 0.022    | Troph       |
|       | Scott Creek  | N     | 0.27  | 1.65 | 0.17     | 0.87     | —           |
|       |              | S     | 5.10  | 1.71 | 2.98     | 0.0036   | Troph       |
|       |              | W     | 3.77  | 2.02 | 1.86     | 0.065    | —           |
| PDO   | Asilomar     | N     | -4.04 | 1.86 | -2.17    | 0.032    | —           |
|       |              | S     | 1.38  | 2.45 | 0.56     | 0.57     | —           |
|       |              | W     | -1.14 | 2.01 | -0.57    | 0.57     | —           |
|       | Pillar Point | N     | 0.41  | 0.89 | 0.46     | 0.65     | —           |
|       |              | S     | 3.37  | 3.88 | 0.87     | 0.39     | —           |
|       |              | W     | 1.43  | 1.33 | 1.08     | 0.28     | —           |
|       | Scott Creek  | N     | -0.09 | 1.32 | -0.07    | 0.95     | —           |
|       |              | S     | 4.26  | 1.53 | 2.79     | 0.0064   | —           |
|       |              | W     | 2.83  | 1.74 | 1.63     | 0.11     | —           |
| SSH   | Asilomar     | N     | -3.62 | 1.73 | -2.09    | 0.039    | AdvC        |
|       |              | S     | 6.54  | 2.14 | 3.05     | 0.0029   | —           |
|       |              | W     | 3.33  | 2.16 | 1.54     | 0.13     | —           |
|       | Pillar Point | N     | 2.34  | 1.38 | 1.69     | 0.093    | —           |
|       |              | S     | 4.15  | 1.39 | 3.00     | 0.0035   | —           |
|       |              | W     | 3.62  | 1.55 | 2.34     | 0.021    | —           |
|       | Scott Creek  | N     | 0.02  | 1.49 | 0.01     | 0.99     | —           |
|       |              | S     | 2.11  | 1.56 | 1.35     | 0.18     | —           |
|       |              | W     | 3.13  | 2.08 | 1.50     | 0.14     | —           |
| SST   | Asilomar     | N     | -1.95 | 2.18 | -0.89    | 0.37     | —           |
|       |              | S     | 3.75  | 2.47 | 1.52     | 0.13     | —           |
|       |              | W     | 2.62  | 2.08 | 1.26     | 0.21     | —           |
|       | Pillar Point | N     | 2.54  | 1.01 | 2.52     | 0.013    | Temp        |
|       |              | S     | 3.32  | 1.70 | 1.95     | 0.054    | —           |
|       |              | W     | 2.96  | 1.39 | 2.13     | 0.036    | —           |
|       | Scott Creek  | N     | -0.97 | 1.51 | -0.64    | 0.52     | —           |
|       |              | S     | 7.60  | 1.49 | 5.12     | 0.0000   | —           |
|       |              | W     | 2.15  | 1.89 | 1.14     | 0.26     | —           |
| CUI   | Asilomar     | N     | 3.17  | 2.30 | 1.38     | 0.17     | —           |
|       |              | S     | -5.96 | 2.50 | -2.38    | 0.019    | Troph       |
|       |              | W     | -1.34 | 2.72 | -0.49    | 0.62     | —           |
|       | Pillar Point | N     | -2.69 | 1.70 | -1.58    | 0.12     | —           |
|       |              | S     | -4.01 | 2.02 | -1.98    | 0.050    | Troph       |
|       |              | W     | -1.05 | 1.69 | -0.62    | 0.53     | —           |
|       | Scott Creek  | N     | -0.19 | 1.89 | -0.10    | 0.92     | —           |
|       |              | S     | -2.13 | 1.96 | -1.09    | 0.28     | —           |
|       |              | W     | -3.88 | 2.43 | -1.59    | 0.11     | —           |
| NPGO  | Asilomar     | N     | 4.63  | 2.88 | 1.60     | 0.11     | —           |
|       |              | S     | -2.12 | 3.36 | -0.63    | 0.53     | —           |
|       |              | W     | -7.40 | 2.64 | -2.81    | 0.0060   | Troph       |
|       | Pillar Point | N     | -1.36 | 0.68 | -2.00    | 0.049    | Troph, AdvA |
|       |              | S     | -3.59 | 1.24 | -2.89    | 0.0047   | Troph       |
|       |              | W     | -2.37 | 0.94 | -2.52    | 0.013    | Troph       |
|       | Scott Creek  | N     | 2.22  | 1.20 | 1.85     | 0.068    | —           |
|       |              | S     | -2.84 | 1.52 | -1.87    | 0.065    | —           |
|       |              | W     | -2.30 | 1.60 | -1.43    | 0.16     | —           |

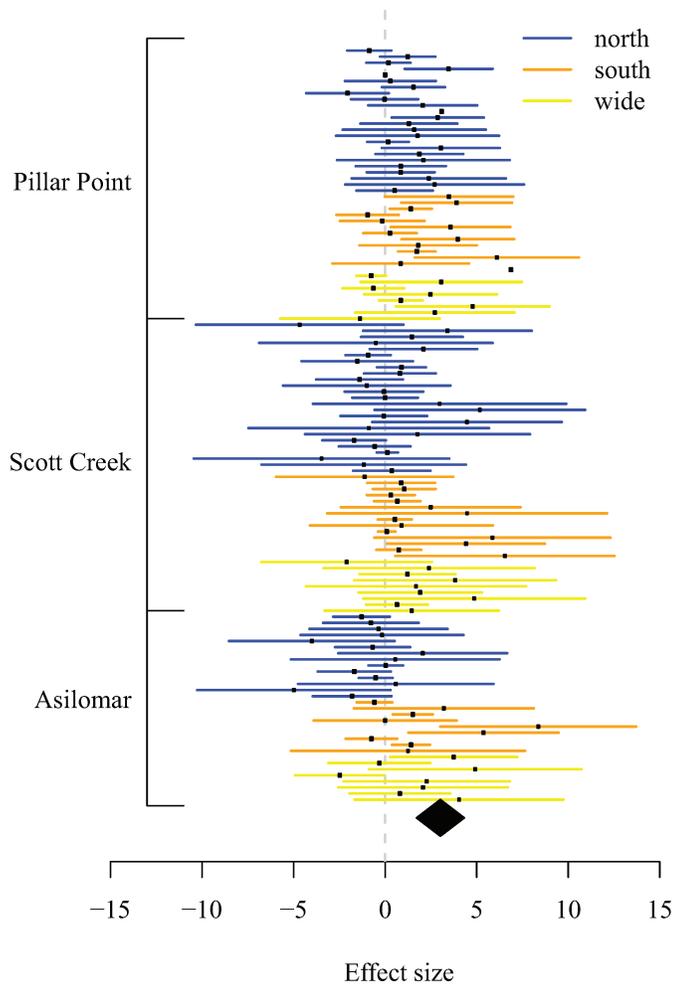


Fig. 4. Random effects meta-analysis of regression coefficients of MEI on ranked nudibranch abundance (Petitti 1994). Shown as horizontal lines are the confidence intervals corresponding to the regression coefficient for MEI for each species at each site coded as northern, southern, and widely distributed species, and the summary weighted mean effect over all species (solid diamond), whose 95% confidence interval is (1.71, 4.33).

(CIRP1 being more common at Pillar Point and CIRP2 at Asilomar [Table 5; Fig. 5]). Range and site explained 11% and 4%, respectively, of the among-species variation in CIRP (Table 6).

Principal components analysis revealed that 69% of the CIRP variation was explained by the CIRP1 to CIRP2 axis, and the second axis, defined by positive correlations with NPGO and SSH and negative with PDO and CUI, and vice-versa, explained only 13% of the overall variance (for the biplot see Fig. 6). Moreover, the abundances of species away from the origin on the first axis generally showed significant correlations with the climate indices, while those on the second axis showed few significant correlations. The species positively correlated with both NPGO and SSH were generally found across all three geographic ranges, but were generally significantly correlated (positively) only with SSH, as exemplified by *Eubranchus rustyus*, a widespread species at both Pillar

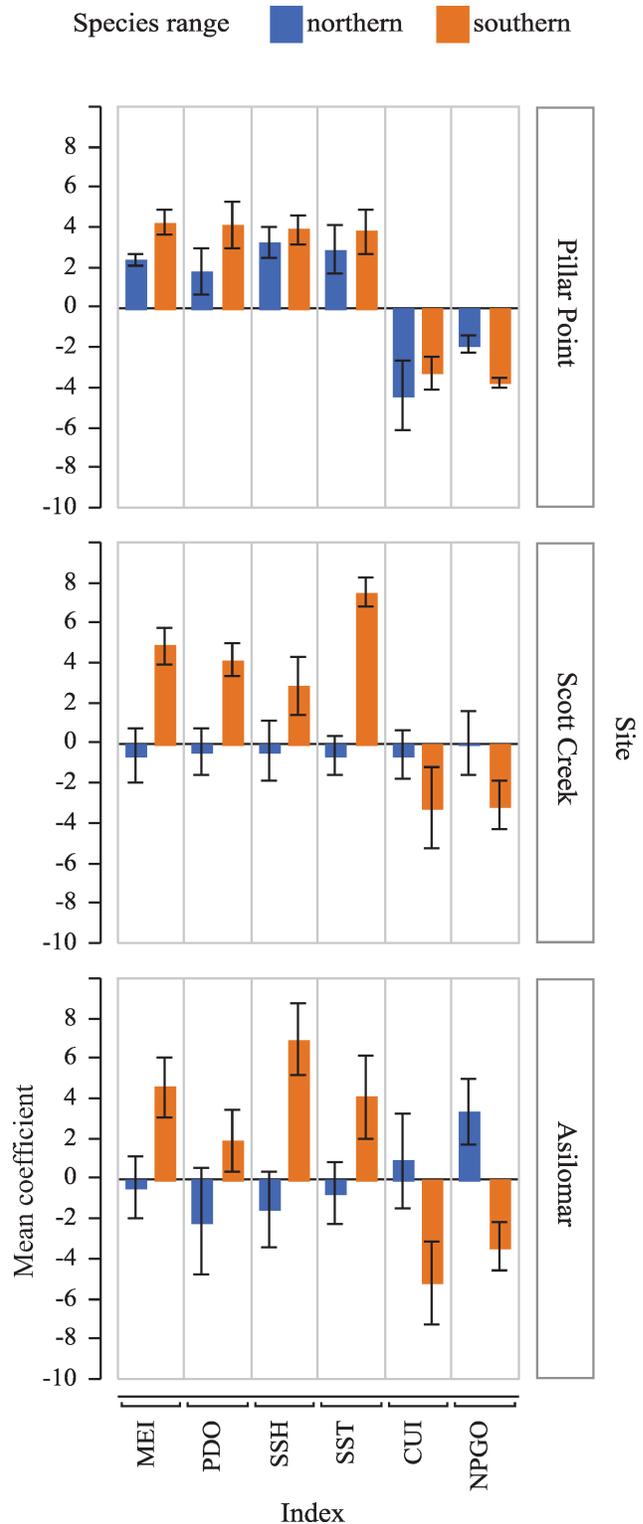


Fig. 5. Climate-index response profiles of nudibranch species at each study site. Shown are the unweighted mean and standard error of the mean coefficient relating animal abundance to the indicated climate index, taken over northern or southern species at the study sites, within the autoregression model relating the abundance time series to the climate index, for models showing normally distributed residuals. Widely distributed species showed mean response profiles similar to southern species.

Table 5. Number of species with indicated binary CIRP and range. Order of indices in the CIRP: MEI, PDO, SSH, SST, CUI, and NPGO. +: positive coefficient; -: negative coefficient. Talled are only species with at least one significant coefficient.

| CIRP                | N | S | W |
|---------------------|---|---|---|
| <b>Pillar Point</b> |   |   |   |
| - - - - + +         | 1 | 1 | 1 |
| - - - + + -         | 1 | 0 | 0 |
| - - + + - +         | 0 | 0 | 1 |
| + - + - - -         | 2 | 1 | 0 |
| + - + - + -         | 1 | 0 | 0 |
| + - + + - -         | 3 | 0 | 1 |
| + - + + - +         | 1 | 0 | 0 |
| + + + - - -         | 0 | 1 | 0 |
| + + + + - -         | 6 | 8 | 1 |
| + + + + - +         | 0 | 0 | 1 |
| + + + + + -         | 0 | 0 | 1 |
| <b>Scott Creek</b>  |   |   |   |
| - - - - - +         | 1 | 0 | 1 |
| - - - - + +         | 7 | 0 | 0 |
| + - + + - -         | 0 | 0 | 1 |
| + - + + - +         | 1 | 0 | 0 |
| + + - + + +         | 1 | 0 | 0 |
| + + + + - -         | 4 | 5 | 2 |
| + + + + - +         | 1 | 2 | 1 |
| + + + + + -         | 0 | 1 | 0 |
| <b>Asilomar</b>     |   |   |   |
| - - - - - +         | 1 | 0 | 0 |
| - - - - + +         | 4 | 0 | 1 |
| + - - - - -         | 1 | 0 | 0 |
| + - - + + -         | 0 | 0 | 1 |
| + - + + - -         | 0 | 0 | 2 |
| + + + + - -         | 0 | 4 | 1 |
| + + + + + -         | 0 | 1 | 0 |

Point and Scott Creek. The species negatively correlated with these two indices were primarily northern species, and the only significant correlation was shown by a single northern species at Pillar Point, *Cuthona divae*, which was negatively correlated with local SSH. Conversely, the species positively correlated with both PDO and CUI were also primarily northern species, whose correlations with CUI were not significant. The only significant correlations in this group were with PDO, and were shown by a single southern species, *Okenia rosacea* at Asilomar and Scott Creek. Thus with few exceptions the strongest species response to the climate indices was along the first principal component axis, as summarized above, and as illustrated by the CIRPs of the mean coefficients in Fig. 5, and shown

by the summary meta-analysis over the entire data set (Table 3).

*Rejection of mechanistic hypotheses*—Over the entire data set, the trophic limitation hypothesis was strongly rejected due to highly significant summary correlations across all species and sites with the trophic proxies MEI (positive) and CUI (negative; Tables 2 and 3). Within sites and geographic range groups, the trophic-limitation hypothesis was rejected by all species groups at Pillar Point, by southern and widespread species at Asilomar, and by southern species at Scott Creek (Table 4). Except for northern species at Asilomar, all species groups at all sites were negatively correlated with local trophic proxy CUI, and all but the northern species at Asilomar and Scott Creek were negatively correlated with the synoptic trophic proxy NPGO.

Although the trophic-limitation hypothesis can be tested across all range groups, the directional hypotheses (temperature and longshore advection) can be evaluated only within the northern and southern species. The temperature-limitation hypothesis was rejected by northern species at Pillar Point, whose abundance was significantly positively correlated with local SST, and among the synoptic temperature proxies, more positively correlated with MEI than PDO (Table 4). The temperature-limitation hypothesis was also contradicted by observations that several species (e.g., *Acanthodoris nanaimoensis* and *Dendronotus albus*) were significantly positively correlated with local SST at one site and negatively at another (result not shown).

The cross-shelf surface advection hypothesis was rejected by northern species at Asilomar, which were significantly negatively correlated with local SSH, and somewhat less negatively correlated with synoptic shoreward flow proxy MEI (Table 4). The alongshore advection hypothesis was rejected by northern species at Pillar Point, which were negatively correlated with NPGO (Table 4).

The site with the strongest correlations with the climate indices, Pillar Point, showed rejections of the trophic limitation, temperature limitation, and the alongshore advection hypotheses, leaving only cross-shelf advection in surface waters as the driving force consistent with all geographic range groups (Table 4).

*Evaluation of nonrejected hypotheses*—Although the Monte-Carlo analysis also rejected the trophic limitation hypothesis over our entire data set, it showed fewer contradictions of the cross-shelf advection hypothesis than

Table 6. Permutational multivariate analysis of variance table, CIRP as response, and range, site, and interactions as predictors. Columns are degrees of freedom (df), sums of squares (SS), mean squares (MS), the *F*-ratio, the coefficient of determination (*R*<sup>2</sup>), and *p*-value.

|            | df  | SS     | MS    | <i>F</i> | <i>R</i> <sup>2</sup> | <i>p</i> |
|------------|-----|--------|-------|----------|-----------------------|----------|
| Range      | 2   | 620.9  | 310.5 | 8.2      | 0.11                  | 0.0001   |
| Site       | 2   | 243.4  | 121.7 | 3.2      | 0.04                  | 0.0155   |
| Range×site | 4   | 279.8  | 70.0  | 1.9      | 0.05                  | 0.0672   |
| Residuals  | 115 | 4337.8 | 37.7  | —        | 0.79                  | —        |
| Total      | 123 | 5482.0 | —     | —        | 1.00                  | —        |

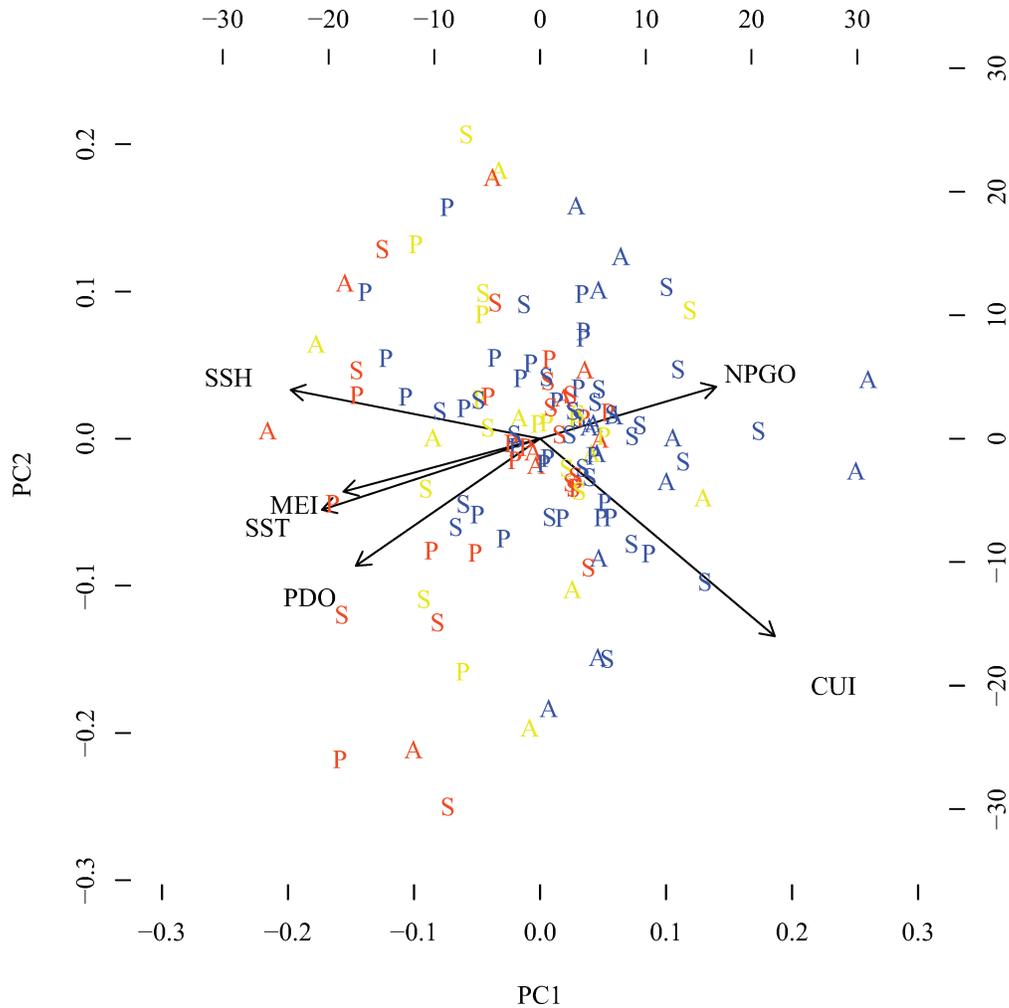


Fig. 6. Principal components biplot of ARIMA regression coefficients of the climate indices and abundance of each species coded by study site (A: Asilomar; P: Pillar Point; and S: Scott Creek) and geographic range (blue: northern; orange: southern; yellow: widespread). Variables are the regression coefficients and replicates are each species at each study site. The projection of a vector onto either principal component axis is equal to the correlation between that variable and that principal component. The cosine of the angle between any two vectors indicates the correlation between those two variables.

the null expectation, especially for southern and widely distributed species (Table 7). In southern but not northern species, contradictions of the temperature limitation hypothesis were significantly fewer than the null expecta-

tion. However, in southern species, temperature limitation was confounded with alongshore advection (e.g., pole-ward flows during El Niño events transport warmer than average water). To separate the two, the conditional hypothesis test

Table 7. Cumulative null probabilities of the observed number of rejections of the indicated mechanistic hypotheses, based on the Monte-Carlo CIRP simulations (see Methods). Simulations assumed either zero mean for regression coefficients for all indices, or that the parametric mean for  $b_{MEI}$  was equal to its sample mean. In all cases the parametric variance was assumed equal to the sample variance. Note that widely distributed species contain no information about temperature limitation or alongshore advection according to our rejection assumptions (Table 2).

| Condition                   | Range | Trophic limitation | Temperature limitation | Alongshore advection | Cross-shelf advection |
|-----------------------------|-------|--------------------|------------------------|----------------------|-----------------------|
| $b_1=0$                     | All   | 0.9921             | 0.0038                 | 0.0270               | 0.0000                |
| $b_1=0$                     | North | 0.4779             | 0.6508                 | 0.5613               | 0.0597                |
| $b_1=0$                     | South | 0.9993             | 0.0000                 | 0.0000               | 0.0000                |
| $\beta_{MEI}=\bar{b}_{MEI}$ | South | 0.7824             | 0.1913                 | 0.4277               | 0.0448                |
| $b_1=0$                     | Wide  | 0.9007             | —                      | —                    | 0.0026                |

was performed given that the parametric mean regression coefficient for MEI is equal to our observed sample mean. This tested for an additional temperature effect given a prior presence of alongshore advection during ENSO events. Under this test, the effect of temperature limitation disappeared (and alongshore advection as expected), indicating that the two processes could not be separated within southern species. However, the cross-shelf advection effect persisted (Table 7, line 4), indicating that cross-shelf and alongshore advection could be separated despite the correlations in their proxies, and cross-shelf advection had an independent effect on nudibranch abundance.

Our data set, therefore, contains no overall signal of temperature limitation in northern species, no signal of temperature limitation distinct from alongshore advection in southern species, and temperature limitation was specifically rejected in northern species at Pillar Point. Our CIRP analysis overall is consistent with cross-shelf advection in surface water as the most important driver of population variation in all species range groups, followed by alongshore advection or temperature limitation for southern species. While there is no signal of trophic effects in either direction in northern species, the trophic limitation hypothesis is strongly rejected in southern species and weakly rejected in widely distributed species (Table 7, third column).

## Discussion

*Trophic limitation*—The CIRP analyses applied to our long-term studies of monthly abundance variation of 56 nudibranch species at three California intertidal locations strongly rejects the hypothesis that populations of adults of southern species are limited by trophic conditions prevailing in the ocean, either locally or at the scale of the ocean basin (Tables 3, 4, 7). Northern and widely distributed species also contain no signal of trophic limitation. The trophic independence of adult density is consistent with the generally low biomass of adult nudibranchs relative to that of their prey (Birkeland 1974; Clark 1975), and the trophic position of adult nudibranchs as second- or third-order predators, removed by at least one trophic level from marine primary productivity (Todd 1981). This position is in contrast to suspension feeders such as the California mussel (*Mytilus californianus*), which depends directly on nearshore productivity and whose abundance is often positively correlated with the trophic proxy NPGO in central Oregon study locations (Menge et al. 2009).

Although larval growth and development appear to be frequently food-limited in many marine invertebrates (Olson and Olson 1989; Fenaux et al. 1994), and maximal growth rates of nudibranchs in laboratory culture (Avila et al. 1997) have been achieved using concentrations of phytoplankton at least an order of magnitude higher than typically observed in coastal waters (Sherr et al. 1984; Mihalatou and Moustaka-Gouni 2002), the effects of food limitation may be ameliorated in species able to take advantage of other taxa of phytoplankton, such as diatoms (Chia and Koss 1978).

*Temperature limitation*—Our CIRP analysis was inconsistent with temperature limitation, either locally or at the basin scale, as the primary driving force for nudibranch abundance at all three of our study sites. Northern species showed no temperature signal, while the temperature signal in southern species could not be separated from the alongshore advection signal. An absence of temperature limitation is consistent with the rare physiological studies indicating that heat stress in nudibranchs occurs with extremes of temperature above the levels likely to be experienced in nature (see Clark 1975).

Early developmental stages appear more sensitive than adults to temperature and other environmental fluctuations. For example, embryos of *Cadlina luteomarginata* collected subtidally from British Columbia, Canada, did not develop beyond the first few cleavage stages at 20°C (Dehnel and Kong 1979), elevated temperatures resulted in low oxygen levels inside intact egg masses of *Tritonia diomedea* at developmentally advanced stages (Moran and Woods 2007), and increased solar radiation killed embryos of intertidal *Doris montereyensis* (Biermann et al. 1992). However, the levels of the variables eliciting measurable effects in these studies appear to be above those normally encountered by the animals throughout most of their ranges.

Thus, the moderate temperature increases during El Niño or positive PDO might directly influence mortality or reproductive rates only locally at southern range limits, or at local ‘hotspots’ within the range (Helmuth et al. 2002) only for the few species commonly exposed to air at low tide, such as *Diaulula sandiegensis* and *Doris montereyensis*. Even then, transient lower demographic rates at one site may not translate reliably to population dynamics at any other locations, due to the open dynamics caused by the planktonic larval phase (Johnson 2005).

*Larval advection*—Our CIRP analysis is consistent with larval advection, especially cross-shelf in surface waters, as the primary driver of adult nudibranch abundance variation in the intertidal zone within all subsets of our data. The significant negative correlation of northern species at Pillar Point with NPGO and positive correlation with MEI is consistent with onshore larval advection in surface waters during El Niño, and offshore advection during La Niña, as primary drivers of adult abundance. The significantly negative correlation of northern species at Asilomar with SSH and positive correlation with NPGO is consistent with alongshore advection from the north. The generally high positive correlation of southern and widespread species with MEI is consistent with larval advection either cross-shelf in surface waters, or alongshore from the south at any depth.

Transient changes in latitudinal distributions of animals (including nudibranchs and other invertebrates) are common during ENSO oscillations (Pearcy and Schoener 1987; Engle and Richards 2001; Lluch-Belda et al. 2005). The present study, however, demonstrates that total abundance of nudibranchs in the intertidal zone is high during El Niño and low during La Niña events. This indicates that poleward shifts during El Niño events are not fully compen-

sated by equator-ward shifts into our study sites during La Niña events, or despite pole-ward shifts during El Niño events, onshore larval advection of both northern and southern species results in overall increases in adult populations in the intertidal during these transient periods of pole-ward and onshore surface flow. Although these alternatives are difficult to separate at present, the latter is favored by the positive observed correlation of MEI with northern species at Pillar Point, and the overall presence of a cross-shelf advection effect in our Monte-Carlo analysis in all range groups.

The abundance of southern species declined during the 2008 La Niña, suggesting no persistent effects on the northern range limits of these species due to global warming. However, one species, the large facelinid aeolid *Phidiana hiltoni*, which spread northward from its historical geographic boundary on the Monterey Peninsula following the 1976–1977 climate regime shift, has persisted in abundance at its new northern range limit at Duxbury Reef, north of San Francisco (see Fig. 1), despite the apparent end of the recent warm phase of the PDO in 2007 (Goddard et al. in press). *Phidiana hiltoni* has also persisted at Pillar Point and Scott Creek (see Web Appendix, Table A2), and may, therefore, represent an early signal of changes in the fauna due to global warming.

The hypothesis that total intertidal abundance of adult nudibranchs is enhanced by onshore surface advection of larvae during El Niño conditions requires that larvae, regardless of geographic range, actively maintain themselves in the surface Eckman layer for a period of days to weeks, sufficient to be advected shoreward. This possibility is consistent with current knowledge of nudibranch larval development and behavior. Fifty-four of the 56 nudibranch species we studied have planktotrophic larval development (Goddard 2004), with minimum planktonic periods on the order of a month (Hadfield and Switzer-Dunlap 1984; Avila et al. 1997). In laboratory culture, most planktotrophic species have an initial upward swimming phase lasting 1–3 weeks (Todd 1981; Hadfield and Switzer-Dunlap 1984). This behavior would keep them in surface waters, and if advected onshore during this period, might result in retention in shallow benthic habitats during the remainder of the larval phase, which is characterized by downward movements, especially in response to cues associated with their prey as adults (Hadfield and Switzer-Dunlap 1984; Hadfield and Koehl 2004). The abundance of nudibranch larvae in shallow waters, at least of species specializing on fouling hydroids and bryozoans, can be inferred based on observations of (1) the speed with which adult populations can appear on fresh, isolated patches of their prey (Todd 1981; Yoshioka 1986), and of (2) sustained high recruitment rates (Lambert 1991).

Our CIRP analysis, considered with the above literature reports, thus indicates that cross-shelf advection of larvae in surface waters is likely an important process driving fluctuations of adult nudibranch populations in the intertidal zone at our study sites. This would be consistent with the ‘tattered curtain’ hypothesis of Roughgarden et al. (1991) to describe larval recruitment into intertidal populations in the California current. Under this hypoth-

esis, upwelling currents advect larvae offshore in the Eckman layer, where they accumulate at upwelling fronts. During periods of relaxation of upwelling, the surface current reverses and delivers the larvae en masse to shore. Thus, under this hypothesis, recruitment occurs primarily in pulses during upwelling relaxation, and is greater in regions where relaxation is more frequent and during climatic periods when upwelling winds are weakened or reversed (e.g., during El Niño events). Although this hypothesis appears consistent with some species, including some barnacles and urchins, whose recruitment is also positively correlated with El Niño (Connolly and Roughgarden 1999), its assumptions have been called into question recently by studies showing that larvae of intertidal and nearshore invertebrates remain close to shore, even in the presence of strong upwelling (for reviews see Morgan et al. 2009; Shanks and Shearman 2009; Morgan and Fisher 2010). Most of the nudibranchs we studied are primarily subtidal in distribution (Behrens and Hermosillo 2005), and increased cross-shelf advection during El Niño events may transport their larvae within reach of prey in intertidal habitats.

The strong dependence of adult abundance on proxies for larval advection into suitable settlement habitat implies that intertidal nudibranch populations at our study sites are limited by settlement rate, and that settlement rate is a reliable proxy for recruitment rate into adult age classes. Recruitment limitation is consistent with known aspects of nudibranch life history and biology that imply that populations are not limited by other processes, and can potentially respond rapidly to variation in recruitment. For example, most species are short-lived (Todd 1981), and many are largely protected from predation by chemical defenses and either aposematic or cryptic aspect (Gosliner 2001; Cimino and Ghiselin 2009); are rarely limited by competition for prey (Lambert 1993); do not depend directly on the lowest trophic levels as do suspension-feeders such as *Mytilus* and other bivalves (Menge et al. 2009); reside in open populations where recruitment is decoupled from local density (Knowlton and Highsmith 2000); and, therefore, show little or no density-dependence (Lambert 1991). In theory, these characteristics should allow species to fluctuate widely and rapidly in response to recruitment variation, in contrast to many larger and longer lived predators of the rocky intertidal and shallow subtidal (Forde and Doak 2004), and many suspension feeders more vulnerable to shifts in immediate pelagic trophic conditions (Menge et al. 2009). A close correspondence between settlement and recruitment has been found in other benthic invertebrates, indicating that variation in predation rates on newly settled recruits is a minor contributor to temporal population dynamics (Broitman et al. 2008).

The generally positive correlation between the abundance of northern and southern species at Pillar Point, but not at the other two sites, likely explains most of the observed range  $\times$  site interaction in the among-species variation in CIRP, and may ultimately be related to local differences in coastal topography and bathymetry and their effects on the transport of larvae. Onshore recruitment of

larvae in this region has been correlated with distance from headlands (Ebert and Russell 1988; Mace and Morgan 2006; Diehl et al. 2007). Pillar Point lies just to the south of the strong upwelling jet associated with the Point Reyes headland and may fall under the influence of the associated upwelling shadow and cyclonic retention eddy (Wing et al. 1998; Vander Woude et al. 2006).

*Some applications of the CIRP method*—Our results provide several testable predictions. Because current-forced recruitment limitation depends strongly on the vertical position of dispersing larvae in the water column (Shanks and Shearman 2009), we predict that a species' response profile will closely reflect the foraging and locomotory behavior of its larval phase, which is at present poorly known for most species. A well-supported theory linking response profile with larval dispersal mode will provide more accurate forecasting of species' individual responses to climatic variation.

If populations are limited primarily by current-forced recruitment, then response profiles will also depend on the interaction of local bathymetry with regional currents (e.g., during strong upwelling, larvae will be retained in cyclonic eddies in the lee of headlands such as Point Reyes, California [Wing et al. 1998], a location near our Pillar Point site). Intertidal monitoring should be expanded geographically to encompass key examples of local bathymetric variation, so that its influence on the shape of response profiles can be documented and used in finer scale forecasting.

Finally, a fuller understanding of the effects of anthropogenic climate change will require long-term monthly time series near the range limits of target species. Given the dominant role of ENSO in population dynamics shown by our study, and the likelihood that secular rise in global temperatures will increase the frequency and perhaps intensity of El Niño events (Tsonis et al. 2005), we predict that anthropogenic warming will cause shifts in the source-sink dynamics of nudibranch populations, and might also uncouple population dynamics of adults from those of their prey. Because comparison of climate-response profiles of predators and prey can potentially identify vulnerable predator-prey systems, and response profiles of species near their range boundaries can help to identify populations susceptible to secular change in ocean climate, results from application of the CIRP method can inform the siting process for marine protected areas and assist in the conservation of shore biodiversity.

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