Title

Long-term Faunal Changes in California Nudibranchs: Climate Change and Local Ocean Health

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Long-term Faunal Changes in California Nudibranchs:
Climate Change and Local Ocean Health

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Project Hypothesis
(1) The abundance, species richness, and community composition of nudibranchs in central California has changed significantly in the past 30 to 70 years.

(2) The observed changes are consistent with those predicted by climate variability on interannual and decadal time scales. Specifically, during warm phases: (a) the proportional abundance and species richness of southern species should increase, as northern species decline, and (b) geographic ranges should shift poleward. The reverse of these should occur during periods of cooling. Further, these changes should be apparent at multiple, widespread sites (otherwise, more localized environmental factors, and not broad scale climate factors, would be implicated as the cause).

(3) Long-term, anthropogenic climate warming is superimposed on natural climate variation, and its biological signal (similar to that described above for natural periods of warming) should be apparent by comparing the abundance, species richness, and community composition across (1) full cycles of natural decadal variation, preferably at multiple sites, and (2) across entire single phases of decadal variation.

(4) While climate change may be the ultimate factor behind community changes we document, especially those related to shifts in geographic ranges, climatic impacts on ecologically important species could result in a cascade of indirect effects on other species. In 1977, the large aeolid nudibranch, *Phidiana hiltoni*, began spreading northward from Monterey, California. By 1992 it had reached Duxbury Reef, 100 km to the north, where other nudibranchs subsequently appeared to decline. We will also test the hypothesis that *P. hiltoni* attacks and consumes other species of nudibranchs and has caused these apparent declines.

Project Goals and Objectives
Our main objectives were to determine (1) if long-term changes have occurred in the abundance and community composition of rocky intertidal nudibranch gastropods in central California, and (2) if the observed changes can be explained by broad-scale climate variability and change, or more localized environmental factors. We were motivated by apparent, recent declines in the abundance of nudibranchs on the Monterey Peninsula and at Duxbury Reef, a State Marine Conservation Area just

north of San Francisco. We also planned to incorporate our results on these colorful and popular organisms in exhibits at the California Academy of Sciences in San Francisco to (1) highlight the importance of historical ecology and long-term monitoring studies for detecting significant ecological changes, and (2) illustrate the contributions that students can make to Marine Science. The latter stemmed from the fact that many of the historical data utilized in this project were originally collected by two of us (JG and TG), when we were students ourselves.

Briefly describe project methodology

Our overall approach for distinguishing between the effects on nudibranch communities of regional vs. local scale factors was to compare the abundance fluctuations of species across multiple sites. Concordant fluctuations would be consistent with the influence of large-scale factors, while significant differences between sites would implicate more local scale factors, either natural, such as local differences in bathymetry and oceanography, or anthropogenic, such as degraded water quality. With both interannual and decadal climate variation in mind, we used historical data sets, along with recent sampling, to extend the time scale of our study from years to decades.

From fall 2007 to fall 2010 we conducted, approximately quarterly, timed counts of all nudibranchs in fixed areas at four rocky intertidal sites originally studied independently during non-overlapping time periods between 1969 and 1995: Duxbury Reef in Marin County, Pillar Point in San Mateo County, Scott Creek in Santa Cruz County, and Asilomar in Monterey County. With climate-related geographic range shifts in mind, we grouped the 56 total species recorded from these sites into three geographic range categories: northern, southern, and widespread, and constructed time series of population abundance for each one, using number of individuals/hour/observer. Already knowing that southern species had increased in abundance at Scott Creek during the 1976-77 climate regime shift, as northern species declined, we originally planned on comparing abundance and community composition by phase of the Pacific Decadal Oscillation (PDO). However, we expanded the analysis to incorporate six indices of ocean climate, all of which bear on the ecology of nearshore organisms in the California Current System: (1) Multivariate ENSO Index (MEI), (2) PDO, (3) Sea surface height (SSH) at San Francisco, (4) Sea surface temperature (SST) off Monterey, (5) North Pacific Gyre Oscillation (NPGO), and (6) Coastal upwelling index (CUI), also near Monterey.

Armed with numerous species in three geographic range groups, as well as knowledge of some biophysical correlates of the different climate indices, we realized that we might be able to move beyond the usual correlative approach used in investigating climate influences on population fluctuations, and test mechanistic hypotheses about the drivers of those fluctuations. For example, during El Niños, there is increased poleward and onshore transport of surface waters off California, increased stratification, reduced upwelling, and generally lower productivity. If food limitation, in either the larval or benthic stage, were driving abundance fluctuations, we might expect the abundance of all nudibranch species to be negatively correlated with the MEI. We can generate similar predictions, some specific to particular geographic range groups, for each of the climate indices. We considered three mechanisms most likely to explain the observed fluctuations: (1) trophic, or food, limitation. (2) Temperature limitation, and (3) larval advection. With Dr. Stewart Schultz, a colleague from Oregon and the University of Zadar in Croatia, we developed a novel method, climate-index response profiling (CIRP), for formally testing these hypotheses. We think this method, which is summarized below and fully described in Schultz et al. (2011, in press, Limnology and Oceanography) will be generally applicable to long-term marine abundance datasets, including species—like mussels and barnacles—important in studies of rocky intertidal ecology, as well as fishery species.

Climate-index response profiling was performed in a three-step process. First, the relationship between population abundance 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 were used to reject specific mechanistic hypotheses, according to criteria based on biophysical correlates of the climate indices. These rejections were performed over the entire dataset, and within subsets categorized by study site and species' geographic range. 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 non-rejected hypotheses were evaluated by constructing a null model of regressions conditional on the intercorrelations among the coefficients for the climate indices. Our study sites and the historical datasets are also described in Schultz et al. (2011, in press, *Limnology and Oceanography*).

Owing to the climate-related, northward range shift starting in 1977 of the nudibranch, *Phidiana hiltoni*, from the Monterey Peninsula to Duxbury Reef, and anecdotal evidence that *P. hiltoni* preys on other nudibranchs, in this project we also examined the role of this species in the apparent decline of nudibranchs specifically at Duxbury Reef. First, we investigated its diet in the wild, and in the laboratory, its propensity to attack other nudibranchs. Based on the results of these studies, we grouped nudibranchs from Duxbury Reef according to their demonstrated or inferred vulnerability to predation by *P. hiltoni*. We then utilized historical abundance data from Duxbury Reef, Pillar Point, and Scott Creek, combined with recently obtained survey data from these sites, to compare the abundance of vulnerable and non-vulnerable species at each site before and after the arrival of *P. hiltoni*. We reasoned that if *P. hiltoni* negatively affects other species of nudibranchs, then those impacts should be greatest where it has become most abundant in its new range. The study site at Duxbury Reef and methods used in this part of the study are fully described in Goddard et al. 2011, in press, *Marine Biology* doi:10.1007/s00227-011-1633-7).

PROJECT MODIFICATIONS:

1. As described above, we expanded our planned analysis to include six, not one, indices of climate, and in collaboration with colleague Dr. Stewart Schultz, developed a novel method, climate-index response profiling (CIRP) for testing mechanistic hypotheses for abundance fluctuations in long-term marine datasets.

2. William Pence and Douglas Mason generously shared their historical data on nudibranchs at Pillar Point, allowing us to add a fourth study site to our project.

3. As described in our second year progress report, we discontinued after the first year a small part of the original project aimed at examining embryonic development of nudibranchs for evidence of site-specific, negative environmental effects on nudibranch populations.

PROJECT OUTCOMES:

1. Fluctuations in total abundance and abundance by geographic range group were concordant at our study sites, pointing to a greater influence of broad-scale, regional environmental factors compared to local factors.

2. Total abundance of nudibranchs intertidally in California is strongly correlated with the multivariate El Niño-Southern Oscillation index (MEI) and sea surface height, increasing during El Niño and decreasing during La Niña events and appears to be driven by variations in cross-shelf and alongshore advection of their larvae. Data obtained recently (and independently) from Pt Lobos suggest that our findings may be applicable subtidally as well. Overall, total abundance of nudibranchs at our study sites fluctuated by two orders of magnitude, and mean total abundance was greater by a factor of approximately two during El Niño episodes than during La Niña events.

3. The abundance of southern species at our study sites declined during the 2008 La Niña to levels comparable to those observed during La Niña events in the 1970s, 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 1976–77 climate regime shift, has persisted in abundance at its new

northern range limit at Duxbury Reef, north of San Francisco, despite the apparent end of the recent warm phase of the Pacific Decadal Oscillation in 2007. *Phidiana hiltoni* has also persisted at Pillar Point and Scott Creek, two other sites within its new range. Owing to the short lifespan of *P. hiltoni*, its persistence at these sites may therefore represent an early signal of changes in the fauna due to global warming.

Phidiana hiltoni attacked most of the dendronotid and aeolid nudibranchs presented to it in the laboratory. The pooled abundance of nudibranchs vulnerable to attack by *P. hiltoni* declined an average of two-thirds at Duxbury Reef since its arrival, compared to (1) no change in the non-vulnerable species, and (2) no change in either group at two other sites where *P. hiltoni* was one to two orders of magnitude less abundant. *Phidiana hiltoni* therefore appears to have caused this decline, likely through a combination of direct predation and competition for prey.

In contrast to the El Niños of 1973, 1977 and 1992-93, southern species at our study sites did not increase in abundance during the 2010 El Niño. This appears to be related to the influence of North Pacific Gyre Oscillation, which in contrast to the earlier periods was in a positive phase throughout virtually all of our recent sampling, indicating stronger equatorward flows in the California Current and strong regional upwelling, both of which may have impeded poleward advection of the larvae of southern species.

4. Nudibranchs, especially the larger, more conspicuous species are good indicators of ocean climate and would be appropriate for monitoring in fixed areas by biologists and citizen scientists, especially in marine protected areas.

5. During intertidal sampling related to our project, we found a two new species of nudibranchs. One found by JG in Carpinteria in 2008 and described in 2010 by TG as *Flabellina goddardi*; the other, also a Flabellina appeared in 2010 as far north as Point Reyes National Seashore and appears to be an El Niño migrant from the Pacific coast of Baja California and closely related to *F. trilineata*, which is common in the NE Pacific Ocean.

IMPACTS OF PROJECT:

1. We think that climate-index response profiling (CIRP), our novel model for elucidating climate drivers of population change, may have an impact in the fields of marine ecology and fisheries biology. Other researchers have reported relationships between biological variables and multiple climate indices, but our method in addition applies an explicit mechanistic hypothesis-testing framework to the climate response profile that takes into account intercorrelations among the environmental indices. We think this will advance our understanding of marine population dynamics, and ultimately assist in the ability to forecast population changes. Accordingly, we have already sent to colleagues and other researchers, including marine ecologists, biological oceanographers, and some fishery biologists, preprints of our paper in press in *Limnology and Oceanography*, and will send others reprints when we obtain them.

2. Nudibranchs are short-lived and their populations dynamic. Low intertidal abundance, therefore, does not necessarily reflect degraded environmental conditions, a consideration that may be of use to reserve managers and interested members of the public when they wonder—as we had at the outset of this project—where all the nudibranchs have gone. We have shown that nudibranchs are good indicators of nearshore ocean climate, and the more conspicuous species would be appropriate for monitoring in fixed areas by reserve personnel and citizen scientists.

3. Our results on *Phidiana hiltoni* at Duxbury Reef constitute one of few documented examples of the ecological impacts of a climate-related range shift by a marine species. Ours is also the first study to systematically investigate predation by a facelinid nudibranch on other nudibranchs. The impacts of *P. hiltoni* appear to be confined to retentive sites with upwelling shadows and may therefore have implications for the siting of marine protected areas aiming to protect and highlight the biodiversity of

nudibranchs and their invertebrate prey. Accordingly, we have begun sending out copies of our paper in press in *Marine Biology* to marine ecologists and personnel at marine protected areas in California.

BENEFITS, COMMERCIALIZATION, AND APPLICATION OF PROJECT RESULTS:
As mentioned above, we think our results in general, and CIRP in particular, will be of interest to marine ecologists and fishery biologists, and may benefit especially the latter in understanding and forecasting population fluctuations, including of economically important species. Owing to the popularity of nudibranchs with the general public, our results should also benefit reserve managers and educators interested in explaining to visitors some of the observed fluctuations in abundance and species present.

ECONOMIC BENEFITS generated by discovery
See previous section.

Issue-based forecast capabilities
Our results can be used in forecasting community shifts in nudibranchs. For example, (1) they are more abundant intertidally in California during El Niño events, and southern species increase in relative abundance when these events correspond to warm phases of the Pacific Decadal Oscillation and a weakened North Pacific Gyre Oscillation, and (2) if *Phidiana hiltoni* spreads further north, its ecological impacts on other nudibranchs will likely be geographically confined to sites with upwelling shadows.

Given the dominant role of ENSO in population dynamics shown by our study, and the likelihood that global warming will increase the frequency and perhaps intensity of El Niño events, 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 climate warming, results from application of the CIRP method can inform the siting process for marine protected areas and assist in the conservation of shore biodiversity.

We also expect that CIRP, with some of the parameters modified appropriately for the species under consideration, will be useful in forecasting population dynamics of other marine species, including perhaps important fishery species, as well as shifts in the ecological guilds including those species.

Publications
<u>Conference Papers, Proceedings, Symposia</u>
Goddard JHR, Gosliner TM, and Pearse JS. Decline in nudibranch gastropods following a climate-related range shift of a large predatory aeolid in the NE Pacific Ocean. Western Society of Naturalists, San Diego, CA. 12 November 2010

Goddard JHR, Gosliner TM, and Pearse JS. Decline in nudibranch gastropods following a climate-related range shift of a large predatory aeolid in the northeast Pacific Ocean Society for Integrative and Comparative Biology Annual Meeting, Salt Lake City, UT. 7 January, 2011

Schultz ST, Goddard JHR, Gosliner TM, Mason DE, Pence WE, McDonald GR, Pearse VB, and Pearse JS. Going with the flow: nudibranch gastropods track large-scale fluctuations in climate. 2010 Ocean Sciences Meeting, Portland, OR. 23 February 2010.

Schultz ST, Goddard JHR, Gosliner TM, Mason DE, Pence WE, McDonald GR, Pearse VB, and Pearse JS. Going with the flow: nudibranch gastropods track large-scale fluctuations in climate. California and the World Ocean, San Francisco, CA. 7 September, 2010.

<u>Peer-reviewed journal articles or book chapters</u>

Goddard JHR, Gosliner TM, and Pearse JS. 2011 (in press) Impacts associated with the recent range shift of the aeolid nudibranch *Phidiana hiltoni* (Mollusca: Opisthobranchia) in California. *Marine Biology*. doi:10.1007/s00227-011-1633-7

Schultz ST, Goddard JHR, Gosliner TM, Mason DE, Pence WE, McDonald GR, Pearse VB, and Pearse JS. 2011 (in press) Climate-index response profiling indicates larval transport is driving population fluctuations in nudibranch gastropods from the northeast Pacific Ocean. *Limnology and Oceanography*.

DISSEMINATION OF RESULTS:

- We presented our results at five scientific meetings in three states, and in one seminar at the University of Oregon. We have in press two papers in peer-reviewed scientific journals (*Limnology and Oceanography*, *Marine Biology*), with plans for two more. Links to our dataset are in the paper in *Limnology and Oceanography*. We have sent out preprints of these papers to numerous colleagues, including marine ecologists and biological oceanographers, and will send reprints to more when the papers are published online. We will also send reprints to scientists and research coordinators at the Monterey Bay and Gulf of the Farallones National Marine Sanctuaries, Asilomar State Park, Fitzgerald Marine Reserve, and the Monterey Bay Aquarium Research Institute.
- The California Academy of Sciences in San Francisco produced for their Science in Action website, a video based on the results of our work at Duxbury Reef, titled "Killer nudibranch" http://www.calacademy.org/sciencetoday/killer-nudibranch/.
- *National Geographic Daily News*—among others—picked up a September 2010 press release by UCSB on *Flabellina goddardi*, the new species JG found and TG described during this project, and put together a photo essay on the new species: http://news.nationalgeographic.com/news/2010/09/photogalleries/100923-new-species-sea-slug-nudibranch-science-egg-doily-pictures/.
- The new species was also featured in a lively interview with Dr. Pat Krug on the Madeline Brand Show on Southern California Public Radio: http://www.scpr.org/programs/madeleine-brand/2010/09/28/new-species-of-slugs-moves-into-santa-barbara/.
- Last, but not least, much of our methods and results have been conveyed to the 17 people who volunteered, out of sheer interest in nudibranchs, much time in the field to assist in our counts, and many of them are excited to continue what they learned.

WORKSHOPS AND PRESENTATIONS:

Presentation:
Oregon Institute of Marine Biology, Summer Seminar Series, Charleston, OR, 28 July 2010
Title: Going with the flow: nudibranch gastropods track large-scale fluctuations in climate
Presenters: Jeff Goddard and Stewart Schultz

Presentation:
Anacapa School, Breakfast Club, Santa Barbara, CA, 12 October 2010
Title: Nudibranch sea slugs: not your garden variety
Presenter: Jeff Goddard

COOPERATING ORGANIZATIONS:

<u>State</u>
California State Parks, specifically Asilomar State Beach
California Department of Fish and Game (scientific collecting permit)

<u>Nongovernment</u>
California Academy of Sciences, San Francisco, CA

<u>Academic</u>
University of California, Santa Barbara

INTERNATIONAL IMPLICATIONS:
Climate-index response profiling, our novel method for elucidating climate drivers of population change, should have widespread geographic applicability, including for fishery species. This would mainly require selecting a set of climate indices appropriate for a given region and developing criteria for rejecting hypotheses based on the species under consideration and the indices used.

Volunteer Count: 5