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Modeling Physical-Biological Responses to Climate Change in the California Current System

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ABSTRACT. Understanding the effects of climate change on planktonic ecosystems requires the synthesis of large, diverse data sets of variables that often interact in nonlinear ways. One fruitful approach to this synthesis is the use of numerical models. Here, we describe how models have been used to gain understanding of the physical-biological couplings leading to decadal changes in the southern California Current ecosystem. Moving from basin scales to local scales, we show how atmospheric, physical oceanographic, and biological dynamics interact to create long-term fluctuations in the dynamics of the California Current ecosystem.

INTRODUCTION

The sardine population crash in the California Current System (CCS) in 1945 led to the development of the California Cooperative Oceanic Fisheries Investigation (CalCOFI) program, whose first cruise was in 1949, with fairly regular and extensive cruises since. The spatially and temporally resolved CalCOFI sampling program has documented decadal changes in marine populations in a way that is unprecedented in the ocean. Though the fluctuations in chemical and biological properties were clear in the data, the dynamics underlying these variations were often not apparent. These long-term fluctuations are often a result of complex interactions among atmospheric forcing, the ocean's physical response, and the integrative effects of biological dynamics. It is difficult to move beyond simple correlations in analyzing these diverse data sets in the absence of a dynamical framework.

Coupled physical-chemical-biological models are excellent platforms for both synthesizing diverse data sets and gaining understanding of the interactions among complex, nonlinear processes. Advances in computing power have enabled us to perform global-scale simulations with high regional-scale resolution. Combining such models with the long-term data sets offered by programs such as CalCOFI and California Current Ecosystem Long Term Ecological Research (CCE LTER) gives us the opportunity to gain a deeper understanding of the atmospheric and oceanic forcings that result in the observed biological fluctuations. Here, we describe some of the novel insights we have gained by using models to explore the physical-biological couplings underlying the interannual and decadal fluctuations observed in the CCS. We begin by describing the oceanic response to atmospheric forcing at basin scales using two dominant modes of atmosphere-ocean coupling: the Pacific Decadal Oscillation (PDO) and the North Pacific Gyre Oscillation (NPGO). Because the NPGO drives much of the low-frequency variability of nutrients in the CCS, we then explore the influence of the NPGO on planktonic ecosystems in the CCS at regional scales, and show how physical-biological interactions determine planktonic community structure. Finally, we link these long-term changes in physical forcing to the intense biological dynamics found at frontal systems in the CCS.

BASIN SCALES

Significant advances in our understanding of decadal fluctuations of oceanic properties in the CCS and their coupling to atmospheric forcing have been obtained using the Regional Ocean Modeling System (ROMS; Shchepetkin and McWilliams, 2005; Haidvogel et al., 2008), a primitive-equation, generalized, terrain-following-coordinate, free-surface model. The computational grid of the model covers the central and eastern North Pacific region 180°W–110°W and 25°N–62°N. Di Lorenzo et al. (2008, 2009) used an ensemble of six eddy-permitting ocean modeling hindcasts over the period 1950 to 2008 to identify and quantify the fraction of oceanic response that was deterministically forced by atmospheric variability. The model ensemble mean solution showed that the physical-biological models reproduced much of the observed low-frequency fluctuation of temperature, salinity, nutrients, and chlorophyll *a* in the 60-year-long CalCOFI (California Current) and Line-P (Gulf of Alaska) data sets (Figure 1). Interestingly and importantly, the physical controls of temperature variability are different from those driving low-frequency changes in salinity and nutrients. This finding led to further diagnostic analysis of the low-frequency variability of the ocean models that has expanded our understanding of the forcing dynamics of the Northeast Pacific (Chhak et al., 2009).

A budget analysis of Northeast Pacific ROMS model hindcasts reveals that interannual and decadal fluctuations in the CCS are captured by two dominant patterns of large-scale ocean climate: the PDO and NPGO (Di Lorenzo et al., 2008). Both modes are forced responses to two dominant patterns of North Pacific sea level pressure atmospheric variability: the Aleutian Low and the

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North Pacific Oscillation (NPO; Chhak et al., 2009; Figure 2).

The PDO is defined as the first mode of sea surface temperature (SST) anomaly variability of the North Pacific north of 20°N. A deeper and southward-displaced Aleutian low-pressure system (the Aleutian Low) causes a positive PDO, with strong coastal downwelling conditions, a weakening of the CCS poleward of ~ 38°N, and strengthening of the Alaskan Gyre (Figure 2b, red arrows; Chhak and Di Lorenzo, 2007).

The NPGO is defined as the second mode of sea surface height anomaly (SSHa) variability in the Northeast Pacific (Di Lorenzo et al., 2008). A positive NPGO is forced by a north-south dipole pattern in atmospheric sea level pressure anomaly (SLPa) associated with the NPO pattern (Figure 2d). The large-scale Ekman pumping forced by the NPO drives upwelling conditions in the center of the Alaskan Gyre (negative SSHa) and downwelling conditions in the subtropical gyre (positive SSHa; Figure 2e). The resulting gradient in the SSHa strengthens the North Pacific Current, the CCS, and the Alaskan Gyre (Figure 2e, blue arrows). Fluctuations in the alongshore components of NPO winds (Figure 2d) drive variability of coastal upwelling in the central and southern CCS (south of ~ 38°N) where the signature of the Aleutian Low alongshore winds is weaker (Figure 2a; Di Lorenzo et al., 2008). The NPGO index thus indicates changes in the strength of the gyre-scale circulation and of coastal upwelling in the California Current. NPGO dynamics drive a large share of the decadal fluctuations of nutrients, salinity, and chlorophyll *a* in both the Gulf of Alaska and the central/southern CCS (Di Lorenzo et al., 2009; Figure 1).

The El Niño-Southern Oscillation (ENSO), which can cause warming of the upper waters off the California coast, also drives interannual variability in the CCS. This warming occurs through a deepening of the nearshore thermocline, decreased coastal upwelling, and a weaker CCS. The ENSO signature reaches the CCS through both atmospheric teleconnections and poleward-propagating coastally trapped waves. Different balances of atmospheric and oceanic teleconnections lead to two different types of ENSO: the canonical El Niño and a central tropical Pacific warming El Niño (Ashok and Yamagata, 2009; Kug et al., 2009). Positive winter SST and SSH anomalies in the eastern tropical Pacific lead to a canonical El Niño; when these anomalies occur in the central tropical Pacific, a central tropical Pacific warming El Niño develops. The canonical El Niño is coupled to the PDO by the propagation of SSH anomalies into the CCS and the excitation of atmospheric Rossby waves by SST anomalies that influence the Aleutian Low. Indeed, most of the PDO interannual power is derived from El Niño. In contrast, the central tropical Pacific warming El Niño drives variability of the NPGO (Di Lorenzo et al., 2010). During a central tropical Pacific warming El Niño, the SST and SSH anomalies
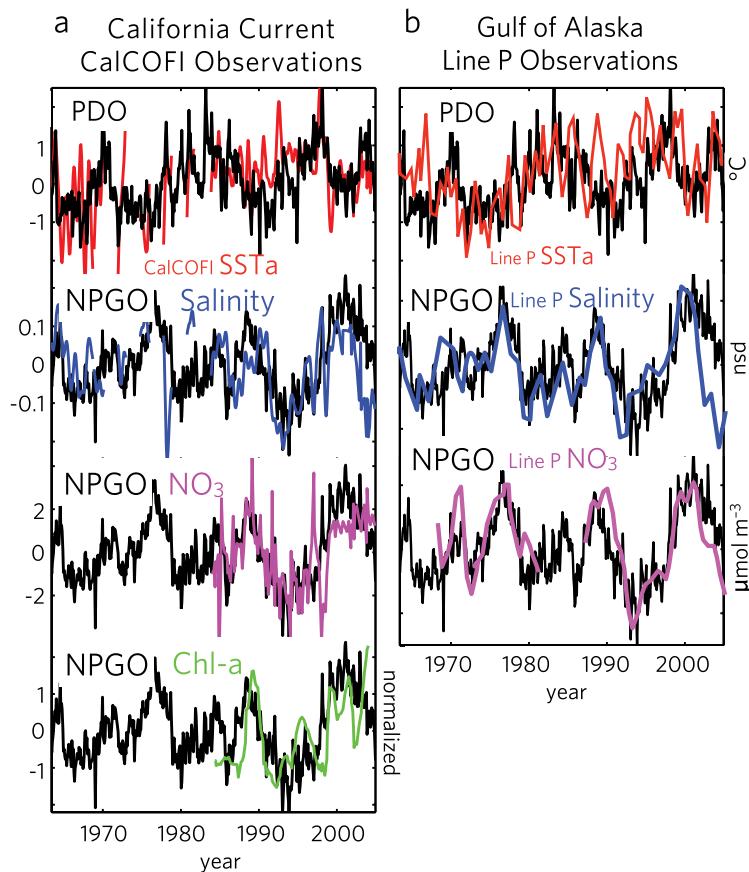
Figure 1. Comparison of fluctuations in the Pacific Decadal Oscillation (PDO; top panels, black line) and North Pacific Gyre Oscillation (NPGO; all other panels, black line) to decadal variations in sea surface temperature anomaly (SSTa, red), salinity (blue), nitrate (magenta), and chlorophyll *a* (green) measured in (a) the California Cooperative Oceanic Fisheries Investigation (CalCOFI) region and (b) Gulf of Alaska line P. *After Di Lorenzo et al. (2008, 2009)*

are far removed from the coast, so the coastally trapped wave signal to the CCS is weak. However, the atmospheric tropical circulation anomalies of the central tropical Pacific warming strongly influence the southern pole of the NPO, forcing fluctuations in the NPGO.

REGIONAL SCALES

PDO, ENSO, and NPGO all have significant signatures at regional scales in the CCS. In particular, the NPGO, through its link to coastal wind stress, explains much of the decadal variability of salinity and fundamental oceanic biological variables in the CCS that cannot be explained by other modes (Di Lorenzo et al., 2008). Analyses of CalCOFI data in the CCS have revealed long-term shifts in

pelagic communities, from plankton to fish, that may alter global biogeochemical cycles and affect carbon sequestration by changing vertical fluxes. Although many studies have shown statistically significant relationships between large-scale climate modes and long-term variability of biological components of the CCS ecosystem, the mechanisms coupling climate modes and ecosystem responses are often unexplained.

Using ROMS to simulate the period 1965–2008, Combes et al. (2013) investigated the low-frequency dynamics of coastal upwelling and cross-shelf transport in the CCS. The relative influence of Ekman upwelling and mesoscale eddies on the advection of coastal waters was studied using an ensemble of passive

tracers. Low-frequency variability of coastal upwelling and cross-shelf transport of the upwelled water mass were strongly correlated with alongshore wind stress, and were coherent between the central and southern CCS. In contrast, when examining offshore transport of tracers released at the surface, the two regions were no longer coherent, and intrinsic mesoscale cyclonic eddies controlled the cross-shelf exchanges. Understanding the interaction between intrinsic (eddy activity) and deterministic (Ekman upwelling) dynamics in controlling the cross-shelf exchanges in the context of ecosystem processes may lead to an improved understanding of the dynamics of marine populations that rely on both the nutrient inputs
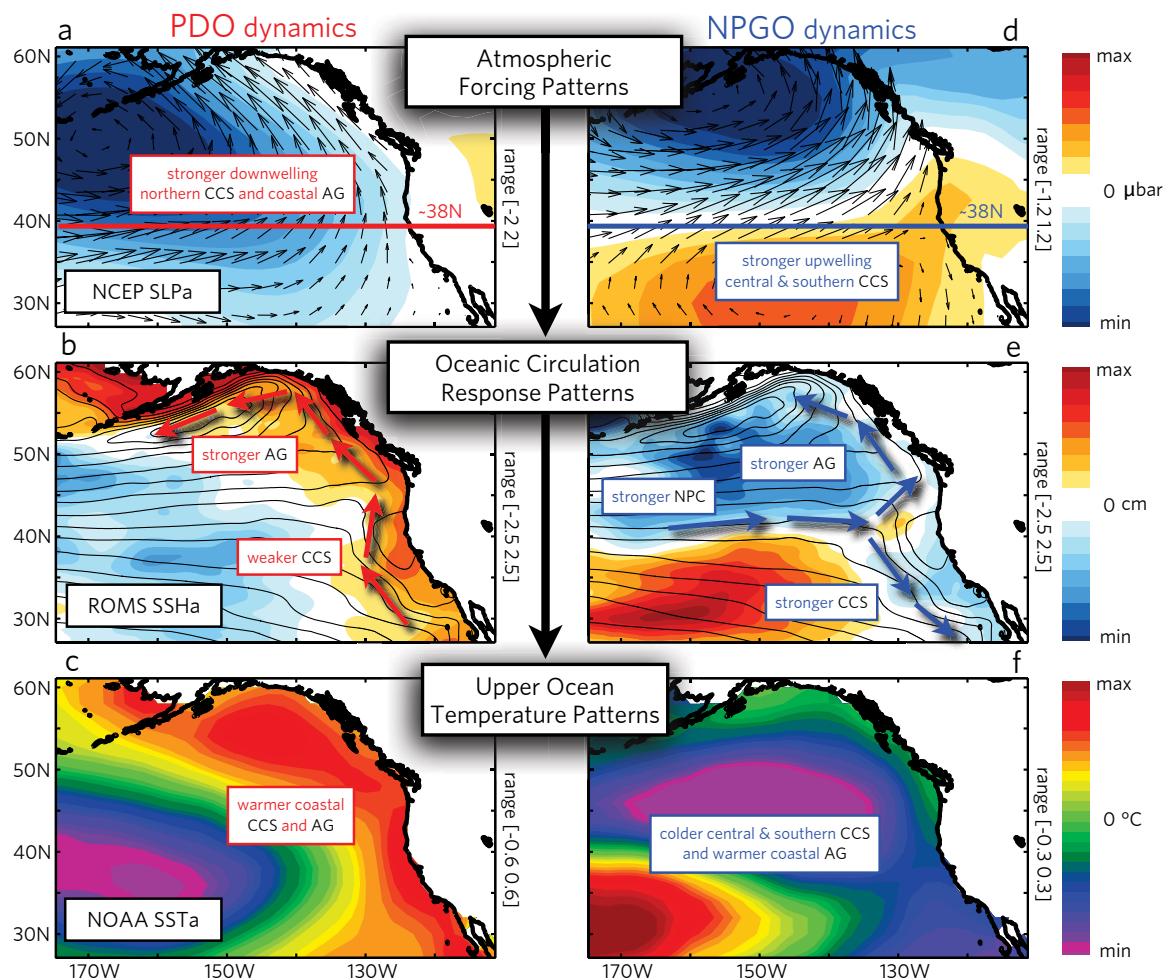
Figure 2. Spatial patterns of the PDO (left panels) and NPGO (right panels). (top row) Sea level pressure anomaly (SLPa) reflecting surface wind forcing. (middle row) Modeled sea surface height anomaly (SSHa) under positive PDO and NPGO indices. (bottom row) Sea surface temperature anomaly (SSTa) driven by positive PDO and NPGO.

and the retention dynamics associated with eddies.

NPGO fluctuations strongly affect wintertime winds off California, leading to changes in the onset of the central California upwelling (Chenillat et al., 2012). The early/late upwellings of 2005/2007, for instance, match the positive/negative NPGO phase during which extreme changes of the CCS ecosystem were recorded. Following Combes et al. (2013), the influence of intrinsic and deterministic physical forcing on ecosystem response was investigated by Chenillat et al. (2013) using the ROMS-UCLA physical configuration (Capet et al., 2008) coupled to the North Pacific Ecosystem Model for Understanding Regional Oceanography (NEMURO; Kishi et al., 2007) parameterized for the CCS (Li et al., 2010, 2011).

The NEMURO biological model contains, among other state variables, three nutrients (nitrate, ammonium, and silicate), two phytoplankton classes (diatoms and nondiatoms), and three zooplankton classes (microzooplankton, macrozooplankton, predatory zooplankton). Typically, models are parameterized by comparing their outputs to measured concentrations of the modeled variables. The problem with this approach is that the concentration is necessarily the net result of competing rates. A chlorophyll concentration, for example, depends on the rate of production of chlorophyll (e.g., phytoplankton growth) and the destruction of chlorophyll (e.g., grazing). Without measurements of these underlying rates, the dynamics leading to a given concentration cannot be determined (e.g., Franks, 2009).

The CCE LTER process cruises (Landry et al., 2009) have generated an unusually powerful data set for parameterizing ecosystem models. In particular, the Lagrangian experiments have generated a vertically and horizontally resolved data set of phytoplankton growth and micro- and macrozooplankton grazing rates. Li et al. (2010, 2011) used these data to perform a statistically robust parameterization of NEMURO for subsequent investigations of planktonic ecosystem dynamics in the CCE (e.g., Chenillat et al., 2012, 2013; Li et al., 2012).

Using the ROMS–UCLA physical model and the CCE-parameterized NEMURO biological model, Chenillat et al. (2013) showed that variability in the onset of upwelling due to different winter alongshore winds affected both the coastal ecosystem during the upwelling season and the offshore ecosystem year-round. This strong offshore response (a factor of two larger than the coast in relative amplitude) to the phenology of upwelling was driven by changes in the intrinsic cross-shore transport and biological recycling, and was dominated by the highest modeled trophic level. Thus, higher trophic levels may be disproportionately affected, depending on their cross-shore habitat. This work gives new insights into the links between large-scale wind variability (NPGO) and local ecosystem response to upwelling. The role played by the cross-shore propagation of the timing of the initiation of upwelling is in agreement with Botsford et al. (2006). However, Chenillat et al. (2013) revealed that the bottom-up propagation of this signal through the ecosystem has profound consequences for the structure of the offshore ecosystem. Significant responses of the ecosystem (mainly zooplankton) to the phenology of upwelling have been observed in the CCE, for example, the late upwelling of 2005 (Mackas et al., 2006). It should be noted that mesoscale and submesoscale dynamics were underestimated in Chenillat et al. (2013); these dynamics contribute to cross-shore transport of biological tracers and may reduce new production in upwelling regions (Gruber et al., 2011). Future work should focus on gaining a better understanding of the role of eddies in the ecosystem response to coastal perturbations, such as the timing of the initiation of upwelling.

The NEMURO model represents almost the minimal model structure capable of resolving biological diversity within trophic levels (large and small phytoplankton, large and small zooplankton). Clearly, a better tool is needed to explore questions of physical-biological coupling in regulating community diversity and biogeographic distributions in the CCS. One approach is to create virtual species by randomly selecting parameters for processes such as photosynthesis and nutrient uptake from statistical distributions consistent with available measurements of living cultures (e.g., Follows et al., 2007). These organisms are then allowed to compete for available resources within a physical circulation model. Organisms best adapted (parameterized) for a particular environment thrive, and those less adapted fail.

Goebel et al. (2010) used such an ecosystem modeling approach, including in the model ammonium, nitrite, nitrate, silicate, and phosphorous, as well as four functional phytoplankton groups. Large photoautotrophs are divided into silicate-requiring diatoms and non-diatoms. Small autotrophs consist of *Prochlorococcus*-like organisms, which can use ammonium and nitrite but not nitrate, and a second category that can use all three forms of inorganic nitrogen. The different phytoplankton groups have

different light sensitivities, representing the different types and concentrations of chlorophyll pigments within different phytoplankton cells. Each phytoplankton functional group is further subdivided into about 20 modeled phytoplankton types leading to a total of about 80 virtual primary producers whose physiological rates are uniquely determined through a random sampling of appropriate normal or uniform distributions. The model also includes two zooplankton groups, loosely representing mesozooplankton (e.g., copepods) and microzooplankton (e.g., ciliates) that graze differentially on the phytoplankton groups.

Goebel et al. (2010) embedded this model in the ROMS physical model at 1/10th degree resolution and 42 vertically varying levels to investigate how local physical forcing and biological dynamics combined to generate regional-scale biogeographic patterns in the phytoplankton community. Accounting for specific temperature ranges allowed different phytoplankton types to achieve their optimal growth rate in different geographic areas. In the annual average,

diatom-like organisms dominated coastal waters, small *Prochlorococcus*-like organisms showed low concentrations in coastal waters but were considerably more abundant offshore during winter, and small *Synechococcus*-like organisms grew well in coastal and offshore waters during spring. Large phytoplankton that were not dependent on silicate were found mostly in coastal waters during autumn after the upwelling-fueled diatom bloom.

Each of these functional groups can be divided into subtypes whose different temperature sensitivities limit their spatial ranges. The CCS exhibits substantial temperature variation both meridionally through changes in insolation and across shore associated with upwelling. The combination of varying temperatures and nutrients at the surface creates multiple surface biomes within which different organisms thrive, forming a mosaic across the CCS (Figure 3). While productivity and biomass distributions for summed diatoms and small phytoplankton types agree qualitatively with observations and simpler models

such as NEMURO, this approach enables the new consideration of fundamental questions in ecology, specifically, how biodiversity is related to overall productivity (Goebel et al., 2012) and in turn how diversity influences overall ecosystem function (Goebel et al., in press). For example, these modeling results suggest that biodiversity enhances system-wide productivity through both complementarity of ecological niches and also by facilitation resulting from nutrient recycling. Because such questions are challenging or impossible to address with sparse observations in a fluid environment or using simple models with only a few phytoplankton, our approach is identifying new implications of phytoplankton competition and interactions within the marine ecosystem.

LOCAL SCALES

Fronts—regions of strong horizontal density gradient in the ocean—are often sites of enhanced biological processes (e.g., Franks, 1992). In the CCS, fronts are formed during wind-driven upwelling, with subsequent advection in eddies
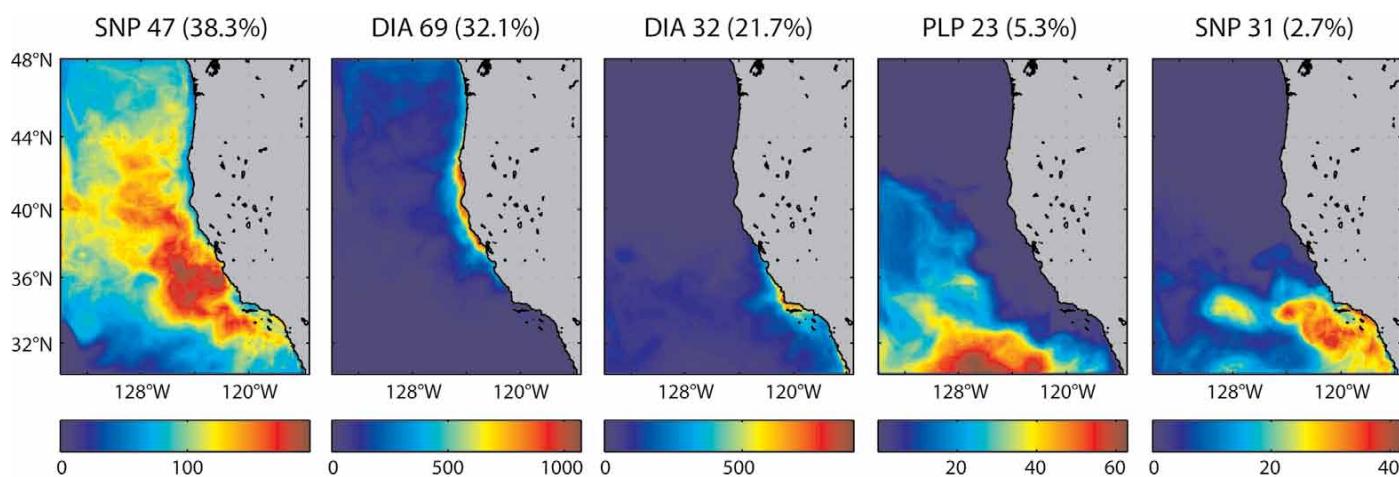

Figure 3. Regional simulation of different phytoplankton types from a self-emergent ecosystem model. Annually averaged, vertically integrated primary productivity (mg C m^{-2} d^{-1}) for five dominant phytoplankton types. The combination of varying temperature and nutrients at the surface drive multiple surface biomes within which different organisms thrive. Phytoplankton types (diatoms [DIA], small *Prochlorococcus*-like and non-*Prochlorococcus*-like phytoplankton [PLP and SNP, respectively]) are ranked from highest (left) to lowest (right) percent contribution to total primary productivity, as indicated in plot titles. Note different color bar scales.

and filaments. Kahru et al. (2012) show that in the southern end of the CCS, fronts have increased in frequency over the last decade or more, consistent with climate-driven changes in wind and stratification. The intense biological signatures found at fronts underscores the need for a better understanding of the biological responses to physical drivers at these features.

Li et al. (2012) applied the Li et al. (2010, 2011) reparameterizations of NEMURO to data gathered at a specific front sampled during a CCE LTER process cruise (Landry et al., 2012). The application of the model was unusual: rather than initializing the model with observations and running it forward in time (prognostic), the model was used in a diagnostic mode. Using measurements such as dissolved nutrient concentrations, temperature, and chlorophyll *a*, the model was used to produce the underlying rates: growth rates of diatoms and nondiatoms, grazing rates of microzooplankton, primary productivity, net primary productivity, carbon:chlorophyll ratios, and others. Because the model had been carefully parameterized with rate data from the CCS, the diagnosed rates were statistically reliable. The model showed that the enhanced biomass of diatoms in the frontal zone was a consequence of enhanced vertical nitrate fluxes that stimulated growth, combined with decreased microzooplankton grazing at the front (Figure 4). Variations in phytoplankton community composition and biomass across the front led to cross-frontal gradients in subsurface irradiance with reduced growth rates on the north side of the front.

It is clear both from the modeling studies and from field data (e.g., Landry et al., 2012) that more than just the abutment of different water masses forms biological gradients at fronts. Rather, the physical forcings characteristic of fronts create distinct biological dynamics and communities at fronts. Given observations by Kahru et al. (2012) of increasing frontal frequency in the southern CCS, we might expect that the distinct and dynamic communities at fronts will play an increasing role in regional-average biologically mediated fluxes.

SUMMARY

We have shown a few examples of how we have used models to tease apart the coupling of basin-scale atmospheric forcing with ocean dynamics and its potential to affect basin-scale, regional, and local biological dynamics in the CCS. Our models have allowed us to uncover the dynamics underlying fluctuations in dominant modes of climate change—ENSO, PDO, and NPGO—and how those fluctuations affect planktonic ecosystem dynamics. We have discovered that decadal fluctuations in the NPGO are linked to changes in wind-driven upwelling, and that those changes propagate both offshore and up the planktonic food web. These atmospherically forced fluctuations explain a great deal of the variability of properties measured in long-term monitoring programs in the CCS. Furthermore, global climate change is altering the relative dominance of
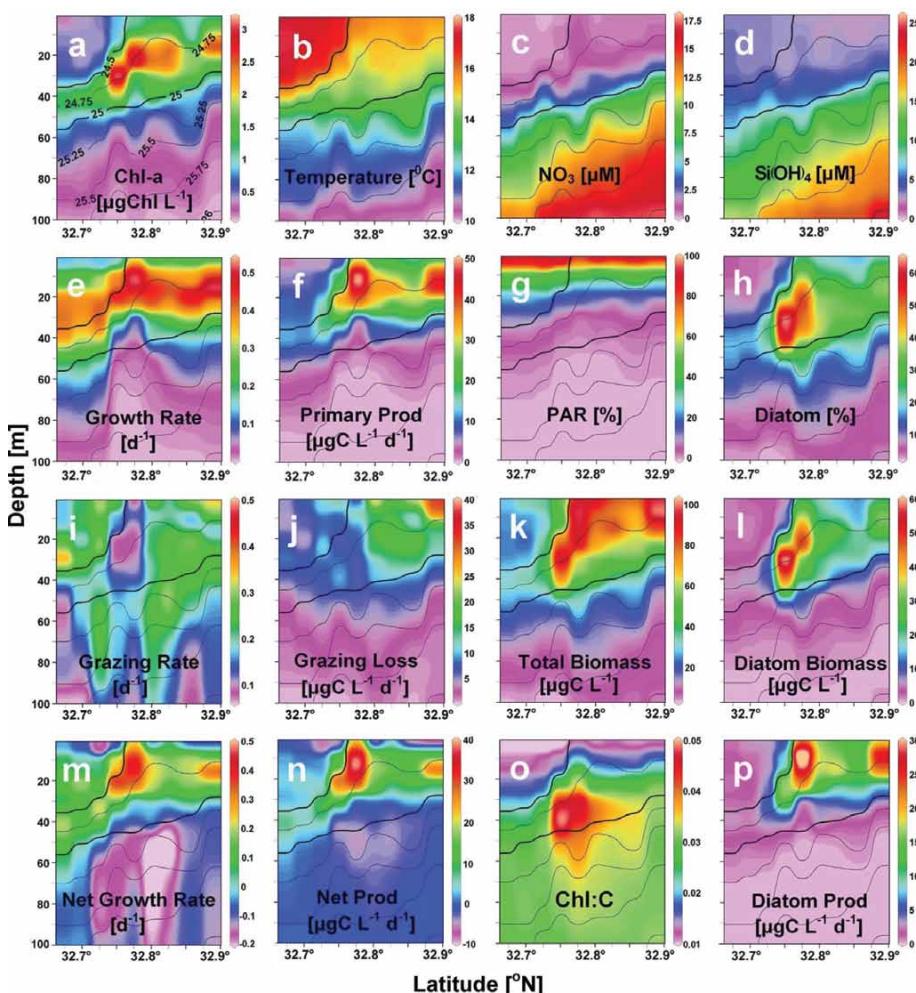

Figure 4. Model diagnosis of rates underlying field observations across an oceanic front. (top row) Data used to force the model. (all other panels) Data products derived from the model, showing elevated primary and diatom productivity and decreased grazing at the front. *From Li et al. (2012)*

different climate modes, with the potential for significant impacts to biological dynamics on basin, regional, and local scales. But, it is only through the intimate interaction of well-resolved long-term data sets with detailed physical-chemical-biological models that we will be able to gain some predictive ability concerning changes in the CCS planktonic ecosystem in coming decades.

REFERENCES

Ashok, K., and T. Yamagata. 2009. Climate change: The El Niño with a difference. *Nature* 461:481–484, http://dx.doi.org/10.1038/461481a.

Botsford, L.W., C.A. Lawrence, E.P. Dever, A. Hastings, and J. Largier. 2006. Effects of variable winds on biological productivity on continental shelves in coastal upwelling systems. *Deep-Sea Research Part II* 53:3,116–3,140, http://dx.doi.org/10.1016/j.dsr2.2006.07.011.

Capet, X., F. Colas, J.C. McWilliams, P. Penven, and P. Marchesiello. 2008. Eddies in eastern boundary subtropical upwelling systems. Pp. 131–147 in *Ocean Modeling in an Eddying Regime*. Geophysical Monograph Series, vol. 177, M.W. Hecht and H. Hasumi, eds, American Geophysical Union, Washington, DC, http://dx.doi.org/10.1029/177GM10.

Chenillat, F., P. Rivière, X. Capet, E. Di Lorenzo, and B. Blanke. 2012. North Pacific Gyre Oscillation modulates seasonal timing and ecosystem functioning in the California Current upwelling system. *Geophysical Research Letters* 39, L01606, http://dx.doi.org/10.1029/2011GL049966.

Chenillat, F., P. Rivière, X. Capet, P.J.S. Franks, and B. Blanke. 2013. California coastal upwelling onset variability: Cross-shore and bottom-up propagation in the planktonic ecosystem. *PLoS ONE* 8:e62281, http://dx.doi.org/10.1371/journal.pone.0062281.

Chhak, K., and E. Di Lorenzo. 2007. Decadal variations in the California Current upwelling cells. *Geophysical Research Letters* 34, L14604, http://dx.doi.org/10.1029/2007GL030203.

Chhak, K.C., E. Di Lorenzo, N. Schneider, and P.F. Cummins. 2009. Forcing of low-frequency ocean variability in the Northeast Pacific. *Journal of Climate* 22:1,255–1,276, http://dx.doi.org/10.1175/2008JCLI2639.1.

Combes, V., F. Chenillat, E. Di Lorenzo, P. Rivière, M.D. Ohman, and S.J. Bograd. 2013. Cross-shore transport variability in the California Current: Ekman upwelling vs. eddy dynamics. *Progress in Oceanography* 109:78–89, http://dx.doi.org/10.1016/j.pocean.2012.10.001.

Di Lorenzo, E., K.M. Cobb, J.C. Furtado, N. Schneider, B.T. Anderson, A. Bracco, M.A. Alexander, and D.J. Vimont. 2010. Central Pacific El Niño and decadal climate change in the North Pacific Ocean. *Nature Geoscience* 3:762–765, http://dx.doi.org/10.1038/ngeo984.

Di Lorenzo, E., J. Fiechter, N. Schneider, A. Bracco, A.J. Miller, P.J.S. Franks, S.J. Bograd, A.M. Moore, A.C. Thomas, W. Crawford, and others. 2009. Nutrient and salinity decadal variations in the central and eastern North Pacific. *Geophysical Research Letters* 36, L14601, http://dx.doi.org/10.1029/2009GL038261.

Di Lorenzo, E., N. Schneider, K.M. Cobb, P.J.S. Franks, K. Chhak, A.J. Miller, J.C. McWilliams, S.J. Bograd, H. Arango, E. Curchitser, and others. 2008. North Pacific Gyre Oscillation links ocean climate and ecosystem change. *Geophysical Research Letters* 35, L08607, http://dx.doi.org/10.1029/2007GL032838.

Follows, M.J., S. Dutkiewicz, S. Grant, and S.W. Chisholm. 2007. Emergent biogeography of microbial communities in a model ocean. *Science* 315:1,843–1,846, http://dx.doi.org/10.1126/science.1138544.

Franks, P.J.S. 1992. Phytoplankton blooms at fronts: Patterns, scales and physical forcing mechanisms. *Reviews in Aquatic Sciences* 6:121–137.

Franks, P.J.S. 2009. Planktonic ecosystem models: Perplexing parameterizations and a failure to fail. *Journal of Plankton Research* 31:1,299–1,306, http://dx.doi.org/10.1093/plankt/fbp069.

Goebel, N., C.A. Edwards, M.J. Follows, and J.P. Zehr. In press. Modeled diversity effects on microbial ecosystem functions of primary production, nutrient uptake, and remineralization. *Ecology*, http://dx.doi.org/10.1890/13-0421.1.

Goebel, N.L., C.A. Edwards, J.P. Zehr, and M. Follows. 2010. An emergent community ecosystem model applied to the California Current System. *Journal of Marine Systems* 83:221–241, http://dx.doi.org/10.1016/j.jmarsys.2010.05.002.

Goebel, N.L., C.A. Edwards, J.P. Zehr, M.J. Follows, and S.G. Morgan. 2012. Modeled phytoplankton diversity and productivity in the California Current System. *Ecological Modelling*, http://dx.doi.org/10.1016/j.ecolmodel.2012.11.008.

Gruber, N., Z. Lachkar, H. Frenzel, P. Marchesiello, M. Münnich, J.C. McWilliams, T. Nagai, and G.-K. Plattner. 2011. Eddy-induced reduction of biological production in eastern boundary upwelling systems. *Nature Geoscience* 4:787–792, http://dx.doi.org/10.1038/ngeo1273.

Haidvogel, D.B., H. Arango, W.P. Budgell, B.D. Cornuelle, E. Curchitser, E. Di Lorenzo, K. Fennel, W.R. Geyer, A.J. Hermann, L. Lanerolle, and others. 2008. Ocean forecasting in terrain-following coordinates: Formulation and skill assessment of the Regional Ocean Modeling System. *Journal of Computational Physics* 227:3,595–3,624, http://dx.doi.org/10.1016/j.jcp.2007.06.016.

Kahru, M., E. Di Lorenzo, M. Manzano-Sarabia, and B.G. Mitchell. 2012. Spatial and temporal statistics of sea surface temperature and chlorophyll fronts in the California Current. *Journal of Plankton Research* 34:749–760, http://dx.doi.org/10.1093/plankt/fbs010.

Kishi, M.J., M. Kashiwai, D.M. Ware, B.A. Megrey, D.L. Eslinger, F.E. Werner, M. Noguchi-Aita, T. Azumay, M. Fujii, S. Hashimoto, and others. 2007. NEMURO—A lower trophic level model for the North Pacific marine ecosystem. *Ecological Modelling* 202:12–25, http://dx.doi.org/10.1016/j.ecolmodel.2006.08.021.

Kug, J.S., F.F. Jin, and S.I. An. 2009. Two types of El Niño events: Cold tongue El Niño and warm pool El Niño. *Journal of Climate* 22:1,499–1,515, http://dx.doi.org/10.1175/2008JCLI2624.1.

Landry, M.R., M.D. Ohman, R. Goericke, M.R. Stukel, K. Barbeau, R. Bundy, and M. Kahru. 2012. Pelagic community response to a deep-water front in the California Current ecosystem: Overview of the A-Front Study. *Journal of Plankton Research* 34:739–748, http://dx.doi.org/10.1093/plankt/fbs025.

Landry, M.R., M.D. Ohman, R. Goericke, M.R. Stukel, and K. Tsyrklevich. 2009. Lagrangian studies of phytoplankton growth and grazing relationships in a coastal upwelling ecosystem off Southern California. *Progress in Oceanography* 83:208–216, http://dx.doi.org/10.1016/j.pocean.2009.07.026.

Li, Q.P., P.J.S. Franks, and M.R. Landry. 2011. Microzooplankton grazing dynamics: Parameterizing grazing models with dilution experiment data from the California Current Ecosystem. *Marine Ecology Progress Series* 438:59–69, http://dx.doi.org/10.3354/meps09320.

Li, Q.P., P.J.S. Franks, M.R. Landry, R. Goericke, and A.G. Taylor. 2010. Modeling phytoplankton growth rates and chlorophyll to carbon ratios in California coastal and pelagic waters. *Journal of Geophysical Research* 115, G04003, http://dx.doi.org/10.1029/2009JG001111.

Li, Q.P., P.J.S. Franks, M.D. Ohman, and M.R. Landry. 2012. Enhanced nitrate fluxes and biological processes at a frontal zone in the Southern California Current system. *Journal of Plankton Research* 34:790–801, http://dx.doi.org/10.1093/plankt/fbs006.

Mackas, D.L., W.T. Peterson, M.D. Ohman, and B.E. Lavaniegos. 2006. Zooplankton anomalies in the California Current system before and during the warm ocean conditions of 2005. *Geophysical Research Letters* 33, L22S07, http://dx.doi.org/10.1029/2006GL027930.

Shchepetkin, A.F., and J.C. McWilliams. 2005. The regional oceanic modeling system (ROMS): A split-explicit, free-surface, topography-following-coordinate oceanic model. *Ocean Modelling* 9:347–404, http://dx.doi.org/10.1016/j.ocemod.2004.08.002.