Ocean Dynamics

Physical-Ecological Response of the California Current System to ENSO events in ROMS-NEMURO

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Physical-Ecological Response of the California Current System to ENSO events in ROMS-NEMURO

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Abstract

We analyze the bottom-up El Niño/Southern Oscillation (ENSO) driven physical-biological response of the California Current System (CCS) in a high-resolution, "eddy-scale" ocean model with multiple classes of phytoplankton and zooplankton. The response of the SSTa over the CCS is asymmetrical, with La Niña events being more consistently cold than El Niño events are consistently warm, which is in agreement with previous studies. The biogeochemical and ecological response is represented by ENSO-composite anomalies, lag-correlations with an ENSO index, and histograms for ENSO years. The results show lower trophic level interactions during El Niño and La Niña events in which the larger components (diatoms, euphausiids, and copepods) are suppressed in the coastal upwelling zones during El Niño, while the smaller

components (flagellates and ciliates) are enhanced. In addition, standing eddies of the CCS modulate the latitudinal structure of the ecological response to ENSO. The results point towards future research to understand how bottom-up changes may lead to variability of patterns in ecological response, including fish populations and top predators.

Keywords: ***ENSO composite, CCS, mesoscale, upwelling, bottom-up biophysical interactions***

Declarations

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Conflicts of interest

Not applicable

Availability of data and material

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1 Introduction

The California Current System (CCS) is one of the major Eastern Boundary Upwelling Systems (EBUS) in the world e.g., Hickey, 1998; Checkley and Barth, 2009; Miller et al., 2015). The particular dynamics that set up the environment for this highly productive region of the U.S. West Coast are under the influence of major climate events such as El Niño Southern Oscillation (ENSO) which remotely imprints variability in coastal upwelling via changes in the main wind patterns (e.g., Schwing et al., 2005; Jacox et al., 2020). These large-scale changes can be well represented by global earth system models but these types of models tend to exhibit large biases in representing the finer-scale dynamics of the EBUS (e.g., Van Oostende et al., 2018; Cordero-Quirós et al., 2019).

In this study we examine the physical-biological response in the California Current to ENSO variability using a high-resolution, "eddy-scale" ocean model that is forced with observed winds. In previous work, we considered the ENSO-forced CCS ecological response in a coarse-resolution climate model (Cordero-Quirós et al., 2019). The high (~7km) resolution here now allows proper representation of upwelling fronts along the irregular U.S. West Coast as well as the generation of an energetic and unstable mesoscale eddy field over realistic topography (e.g., Marchesiello et al., 2003; Frischknecht et al., 2015). The ecological model here includes two size classes of phytoplankton and three size classes of zooplankton (Kishi et al., 2007; Curchitser et al., 2015), which is more sophisticated than the two size class model of phytoplankton and single size class model of zooplankton ENSO response considered by Cordero-Quirós et al. (2019). The model biogeochemistry, in contrast, is less sophisticated here in that it includes only two nutrients (nitrate and silicate) and excludes the carbonate cycle.

The basic state of the spatial distributions of phytoplankton communities, and the dependent zooplankton communities that feed on them and each other, establishes biogeographical regions across and along the CCS in the presence of complicated coastline variations and inhomogeneous eddy fields (e.g., Venrick, 2009; Goebel et al., 2013). We consider here how the local physical and ecological response of the CCS is perturbed by ENSO forcing in this context. We focus on individually analyzing the two phytoplankton groups and three zooplankton groups to provide a more fine-scaled view of the bottom-up response of the California Current Ecosystem (CCE) to ENSO compared to less sophisticated coarse-resolution models. The results reveal coherent responses for both warm and cold events, in spite of the mesoscale eddy "noise", and some interesting and surprising features in the ecology.

We first explain the basic framework of the physical and ecological models. Then we introduce our methods for statistical analyzing the system. We follow that with a presentation of results, and a summary and conclusion section.

2 Model Framework

2.1 Regional Ocean Circulation Model

The physical fields used for this analysis are from a simulation using the Regional Ocean Modeling System (ROMS; Haidvogel et al., 2008; Shchepetkin and McWilliams, 2005). The study domain spans the zonal extent of the CCS, roughly 1200 km offshore, from Vancouver Island (50^{o}N) to southern Baja California (20^{o}N), over a grid with 1/15^{o} (~7 km) horizontal resolution (Van Oostende et al., 2018). The air-sea fluxes are computed using the Coordinated

Ocean-Ice Reference Experiment (CORE; Griffies et al. 2009) protocol using observed reanalysis 6-hourly fields from 1958-2007 for the atmospheric variables and model SST. Boundary and initial conditions for temperature, salinity, and velocity are monthly values from the Simple Ocean Data Assimilation (SODA) model output (version 2.1.6), and atmospheric forcing is from the Modern Era Retrospective-analysis for Research and Applications (MERRA) reanalysis products (Van Oostende et al., 2018). Vertical mixing of momentum and tracers is performed along a vertical grid of 50 terrain-following surfaces (Van Oostende et al., 2018). Daily model fields were averaged into monthly means for all model variables for the full model time period from Jan 1959 to December 2007. Climatological monthly mean averages were then formed and subtracted from the monthly means to obtain 1959-2007 monthly anomalies.

2.2 Ecosystem model

The ecological model is called NEMURO (North Pacific Ecosystem Model for Understanding Regional Oceanography; Kishi et al., 2007) and was developed by PICES CCCC (North Pacific Marine Science Organization, Climate Change and Carrying Capacity Program) as a prototype model to represent the basic trophic structure of the marine ecosystem components in the North Pacific. This lower trophic level nutrient-phytoplankton-zooplankton-detritus (NPZD) model has eleven state variables: nitrate (NO_3), ammonium (NH_4), small phytoplankton (PS), large phytoplankton (PL), small zooplankton (ZS), large zooplankton (ZL), predatory zooplankton (ZP), silicic acid ($Si(OH)_4$), and three detrital pools represented by dissolved organic nitrogen (DON), particulate organic nitrogen (PON), and particulate organic silicate (Opal). The PS and PL groups use parameters that represent flagellates and diatoms, respectively. ZP uses parameters that correspond to euphausiids (or krill) that feed on the

mesozooplankton group PL (parameters for copepods), the microzooplankton group ZS (parameters for ciliates), as well as diatoms (PL). The copepods feed on both the diatoms (PL) and the flagellates (PS) as well as the ciliates (ZS). The ciliates (ZS) feed only on the flagellates (PS). The three zooplankton groups were also preyed upon by the modeled sardine and anchovy populations (discussed next). NEMURO uses nitrogen as its primary "currency", but also includes silicon as a limiting nutrient for diatoms. All the state variables are tracked in units of mmol N m^{-3}. The full details and balance equations of NEMURO are given in Kishi et al., 2007.

3 Composite analysis method

In order to isolate the ENSO signal and remove the impact of long-term trends and decadal climate variability, monthly mean anomalies for all ROMS fields were first high-pass filtered using Lanczos method with a cut-off frequency of 10 years, following Cordero-Quirós et al. (2019). Identification of El Niño and La Niña years then follows the NOAA protocol (NCEP/NOAA,http://origin.cpc.ncep.noaa.gov/products/analysis_monitoring/ensostuff/ONI_v5.php), but only include the moderate-to-strong events and exclude the weak events. In brief, we identify El Niño years as those when Niño-3.4 3-month averaged SSTa ≥1.0 °C and La Niña years as those when SSTa ≤-1.0 °C, where the anomalies persist during both the fall (SON) and winter (DJF) seasons. The composites for each month of the ENSO cycle, from September to August over the wintertime peak of each event, were computed using the same method as Cordero-Quirós et al. (2019).

The years from the ROMS-NEMURO simulation time period included in the 12-month El Niño composite are: 1963-1964, 1965-1966, 1968-1969, 1972-1973, 1982-1983, 1986-1987,

1987-1988, 1991-1992, 1994-1995, 1997-1998, and 2002-2003. The resulting years for the La Niña composite are: 1970-1971, 1971-1972, 1973-1974, 1975-1976, 1983-1984, 1984-1985, 1988-1989, 1995-1996, 1998-1999, 1999-2000. That yields a total of 11 El Niño events, and 10 La Niña events.

All of the composite variables were tested for significance using a simple bootstrap test at a 90% significance level and the grid locations where the composite variability is above this threshold are marked with black dots in the figures. Rather than showing all the composite months in the following section, we only focus on key months of the composites and key lag relationships between variables. For this analysis, the nitrate was averaged from 25m to 100m, and the other NPZ model ecological variables were averaged from the surface to 100m.

4. Results

4.1 SST

The SSTa warming of the CCS associated with El Niño events during winter (DJF 3-month composite average), when the ENSO teleconnections peak, is shown in Figure 1 for the ROMS simulation and HadISST observations (Rayner et al., 2003). Composite winter model and observations both show that the warming of the CCS in response to El Niño tends to be significant only along a narrow band along the shore, and the warming signal weakens and becomes cool far offshore. Both the model and observations show the most intense warming off the coast of south Baja California and in the northern portion of the CCS. The near-coastal signature suggests that the response to El Niño is tightly linked to the coastal dynamics controlled by the weakening of the upwelling winds during El Niño that lead to muted upwelling and consequent warming of the SSTa.

Fig. 1 Composite DJF-average of SSTa for El Niño years (*a*,*b*) and La Niña years (*c*-*d*) for both ROMS and HadISST observations as indicated on the top right. Significant locations are marked with black dots.

Figure 1 also shows the composite DJF SSTa response of the CCS during cold events associated with La Niña. In contrast with El Niño, La Niña is associated with statistically significant cooling over nearly the entire domain of the CCS. The coldest anomalies tend to be at the southern and northern portions of the CCS, comparable to the patterns shown by El Niño-related SSTa, but they extend further offshore where they are consistently cool. This key difference in the consistency of the offshore response to El Niño and La Niña that is captured by both coarse and fine resolution is not affected by the introduction of mesoscale activity, indicating that its origin lies in the large-scale dynamical response to atmospheric forcing.

Fig. 2 Histograms of modeled (*a*,*c*,*e*) and observed (*b*,*d*,*f*) SSTa during a 12-month period from September through August over the CCS for neutral, El Niño, and La Niña years.

The asymmetry between warm and cold events that was seen in the coarse resolution model analysis of Cordero-Quirós et al. (2019) also occurs in this high-resolution simulation. Figure 2 shows the histograms of monthly mean SSTa averaged over the model domain as captured by the ROMS and observations during a 12-month period from September through August for warm, cold, and neutral ENSO conditions. The histograms show that in the model (Fig. 2, left) the SSTa during neutral and El Niño years tend to be relatively symmetric around the origin, so that cold anomalies also frequently occur during El Niño (only 57% of the SSTa are positive during warm events). In contrast, the histogram of model SSTa during La Niña shows a more consistent cooling of the CCS during those years, with much less frequent occurrences of warm months (67% of SSTa are cold). Observations are generally consistent with

the asymmetry of the model histograms, with 55% of El Niño event anomalies being warm and 64% of the La Niña anomalies being cool. But observations also exhibit stronger anomalies in the histograms. For example, observed neutral years appear to be strongly 'tailed' towards warm events, a feature that is not captured by the model. These differences may suggest possible model biases, be due to the mismatch of air-sea coupling on the eddy scale due to the forcing protocol (e.g., Seo et al., 2016), or be associated with the random mesoscale activity that occurs differently in the model and observations. Overall, these results further confirm the asymmetrical response of the CCS in which La Niña events are associated with a more consistent cooling than El Niño events are associated with consistent warming (cf., Fiedler and Mantua, 2017), even though El Niño is associated with the most extreme warm SSTa events (e.g., McGowan et al., 1998).

4.2 Lower trophic level response

We next explored the relationship of the nutrients, phytoplankton and zooplankton fields to the changes in ENSO conditions. Nitrate and small phytoplankton show a coherent response in winter but all of the ecological fields showed their largest and most significant ENSO response in the spring season when their seasonal bloom occurs. This is in contrast to the physical response that peaks significantly in late winter after the atmospheric teleconnection forcing has generated its largest oceanic signal. Rather than showing the composite maps of all the ecological variability, for brevity we first show the map for JFM 3-month composite average anomalies of nitrate (which is also representative of the spring), and then present the lagged correlation between the wintertime ENSO index (ONI) and the springtime ecological response.

The structures seen in these correlation maps are very similar to those seen in the various composite maps, which are remarkably persistent from month to month in the spring.

Fig. 3 Composite JFM-averaged anomalies of vertically averaged (25m to 100m) NO_3 for El Niño (left) and La Niña (right) years. Locations where composite response is significant are marked every 5 grid points (black dots).

4.3 Composite variability of NO_3

The biogeochemical response of the CCS during warm and cold events is succinctly represented by composite anomalies of nitrate (NO_3) concentrations in the water column (averaged from 25 to 100 m) during JFM. Similar results hold for the silicate field. Figure 3 shows that the composite vertically averaged anomalies of NO_3 in the model captures the nutrient depleted conditions along the coast due to muted coastal upwelling during El Niño, and nutrient enhancement due to stronger upwelling during La Niña. The spatial distribution of ENSO-related composite NO_3 anomalies is confined to a roughly 500km region along the coast, with more patchy structure offshore during both warm and cold events. Unlike composite SSTa, the composite anomalies of NO_3 are quite symmetric over the CCS in both their spatial pattern and significance, except for slight differences off Southern California Bight and Baja California. The upwelling-driven response of the NO_3 in the water column may be further amplified by changes in the biogeochemistry of the source waters (Rykaczewski and Dunne, 2010; Bograd et al., 2015) but further research is necessary to address this issue.

4.4 Lagged correlation of lower trophic levels with the ONI

Figure 4 shows the 3-month lagged correlation between January ONI values and April anomalies of the ecological fields in NEMURO. Positive values (red) indicate that biomass

anomalies during April over the CCS are in phase with the SSTa in January over the tropical Pacific. During El Niño conditions over the CCS when upwelling favorable winds tend to be weaker, the nutrient supply to the photic zone decreases, as shown by the negative lagged-correlations of vertically averaged NO_3 (which is similar to the silicate fields) along the coastal region. As a consequence of the nutrient-depleted waters, large phytoplankton (diatoms, Fig. 4-c) biomass decreases along the coastal band and in patchy areas offshore. The response of the predatory zooplankton (krill, Fig. 4-f) and mesozooplankton (copepods, Fig. 4-e) that each graze partly on diatoms resembles this diatom field. The predatory zooplankton has a stronger correlative response to ONI than mesozooplankton since it preys upon the now-reduced field of mesozooplankton. Thus, the larger components of the food web respond as expected with reductions in biomass for El Niño conditions and enhancements for La Niña conditions.

Fig. 4 Lagged correlation of ecological fields during April with January of the Oceanic Niño Index (ONI). Locations where correlations are >95% confidence level are marked with black dots.

In contrast, along the coastal region Figure 4 shows that positive anomalies of small phytoplankton (flagellates, Fig. 4-b) biomass occur during warm event conditions (positive ONI). This is consistent with smaller phytoplankton cells having lower nutrient requirements and more effective uptake, which gives them competitive advantage over larger cells (diatoms) under low nutrient conditions (Van Oostende et al., 2018; Edwards et al., 2012). Small zooplankton (ciliates, Fig. 4-d) also increases in these near-coastal areas, both due to the enhancement of its only food source (the flagellates) and to the reductions in both of its predators (euphausiids and copepods). Figure 4 clearly shows that NEMURO captures this kind of ecosystem dynamics where the smaller phytoplankton groups thrive under lower nutrient conditions nearshore due to muted upwelling during El Niño. This type of response to El Niño, where there are winners in

the smaller components of the food web near the coast, is an unexpected result of our analysis and shows the efficacy of adding more complexity to the food web compared to more simplistic ecological models.

Another interesting feature of the ecological correlation maps (and seen consistently in the month-to-month composite response as well, as in Figure 3) is the occurrence of ecological anomalies locked spatially around standing eddies (also called permanent meanders or stationary waves) in the simulated California Current. These have been previously discussed for the physical fields of currents and sea level (Marchesiello et al., 2003; Centurioni et al., 2008), but we have not noticed this type of response being linked so clearly to the ecology, especially in the context of modulation of the ecological fields by ENSO. Figure 5 shows the mean sea-level height field over the entire period of our simulation. Its meandering structure is consistent with what was previously found by Centurioni et al., (2008) for a shorter-term mean of the SSH field from ROMS. The large-scale standing eddies (roughly four-to-five of them, undulating north-south along the CCS) are climatologically locked to major capes and bathymetric features and can also be associated with local enhancements of the mesoscale eddy field.

Fig. 5 Long term mean of sea surface height (SSH) from the ROMS monthly fields from 1959 to 2007.

We looked with more detail into this persistent mesoscale structure of the CCS in ROMS by analyzing composites of sea surface height anomalies (SSHa) during winter for El Niño and La Niña events. Fig. 6 shows that a consistent rise in sea level occurs during El Niño and a consistent lowering of sea level occurs during La Niña all along the coastal region of the CCS. This implies a large-scale weakening of the surface California Current during El Niño and a

strengthening of the surface current during La Niña. This can be caused by both thermal expansion effects and dynamically driven thermocline depth changes associated with CCS ENSO anomalies. The patterns of eddy structures seen throughout the coastal regions in Fig.6, however, are not consistently localized around the standing eddies of Fig. 5 and they do not occur with opposite signs for warm and cold conditions. This suggests that the large-scale forcing from the atmosphere modulates the mean state of the CC during ENSO events, rather than by consistently changing the local mesoscale eddy dynamics around the persistent meanders in this simulation. Additional dynamical analysis will be required in future work to confirm this interpretation.

The positive composite anomalies of vertically averaged NO_3 for JFM in Fig. 3 are consistent with the composite negative anomalies of the SSH field during January along the coast during La Niña (Fig. 6, right). Likewise, the composite response to El Niño, which is stronger than the La Niña response, is also consistent with the simulated negative anomalies of vertically averaged NO_3.

Fig. 6 Composite anomalies of the ROMS sea surface height (SSHa) for El Niño (left) and La Niña (right) events.

The north-south spatial distribution of composite NO_3 anomalies is much more similar to the mean state of SSH (Fig. 5), as it clearly follows its climatological meanders, than to any of the eddy structures seen in Fig. 6. This suggests that variability of NO_3 during El Niño and La Niña events is affected by large-scale changes in the upwelling favorable winds that modulate the

background state. The persistent meanders might be channels for filament ejection of biomass from coastal regions, whereby strong production near the coast is transported offshore by the eddies or the mean flow. This result needs to be further explored in future work to establish the dynamical drivers of the structures of the ecological response and its modulation by ENSO. Additional research is also necessary to better elucidate how potential variability of the mesoscale field derived from ENSO can be modulated by the background flow.

4.5 Probability distribution of ecological fields over the CCS

In order to address differences in the consistency of the ecological response of the CCE to cold and warm events, we computed histograms of the ecological fields in NEMURO over a coastal swath from 22° N to 48° N extending roughly 300 km offshore, which is the region of strongest response to ENSO seen in the composites. The histograms of NO_3 anomalies show a fairly consistent depletion during El Niño years with fairly consistent enhancement of NO_3 during La Niña (Figure 7). Negative anomalies represent 71% of the total distribution for El Niño years, and 77% of the anomalies are positive for La Niña years, which is much more symmetric than found for the SSTa histograms.

Fig. 7 Histograms of anomalies of vertically averaged NO_3, biomass of small phytoplankton, and diatoms, during a 12-month period from September through August over a coastal swath of ~300 off-shore from 22° N to 48° N. Anomalies are shown for neutral years (*a*,*b*,*c*), El Niño (*d*,*e*,*f*) and La Niña (*g*,*h*,*i*) and are expressed in units of mmol N m^{-3}.

Histograms for diatoms, in contrast, have more consistency during cold events, with 70% of negative anomalies during La Niña and 59% of positive anomalies during El Niño (Figure 7). The ciliates, however, are less consistently altered (Figure 7) than diatoms for both warm (49%) and cold events (57%) indicative of their narrower coastal response and higher signals in the

high latitudes (see Figure 4). The distribution for predatory zooplankton (Figure 8) is less consistent than for diatoms, with El Niño (La Niña) events having 64% (70%) of their associated anomalies on the negative (positive) side of the distribution. Similar results hold for the copepod distributions (50% vs. 69%). And the ciliates reflect the flagellate distribution (47% vs. 63%) but with a stronger consistency during La Niña events. The percentage of cold and warm anomalies associated to each event for every ecological group and SST are summarized in Table 1. In general, the histograms of the biological fields in NEMURO do not exhibit such a strong asymmetry as that associated with SSTa. This suggests more complicated dynamics that go beyond a linear response to wind variability imprinted by ENSO teleconnections.

Fig. 8 Histograms of anomalies of biomass for small zooplankton, large zooplankton, and predatory zooplankton during a 12-month period from September through August over a coastal swath of ~300 off-shore from 22^{o} N to 48^{o} N. Anomalies are shown for neutral years (*a*,*b*,*c*), El Niño (*d*,*e*,*f*) and La Niña (*g*,*h*,*i*) and are expressed in units of mmol N m^{-3}.

TABLE 1: Percentage of warm anomalies during El Niño years (second column) and of cold anomalies during La Niña years (last column) for ecological variables and SST.

	EN<0 (%)	**LN>0 (%)**
NO_3	71	77
PS	49	57
PL	59	70
ZS	47	63
ZL	58	69
ZP	64	70
SST ROMS	57	67
SST HadISST	55	64

5. Summary and Conclusion

We analyzed the bottom-up ENSO-driven physical-biological response of the CCS and the CCE in a high-resolution, "eddy-scale" ocean model with two classes of phytoplankton and three classes of zooplankton. The physical oceanographic responses in SSTa exhibited asymmetries similar to those in the coarse resolution model found by Cordero-Quirós et al. (2019), with La Niña events being more consistently cold than El Niño events are consistently warm (Figures 1 and 2). We used a statistical analysis strategy involving composites, lag correlations, and histograms to assess the ENSO-forced biogeochemical and ecological response (Figures 3-5). We found that the larger components (diatoms, euphausiids and copepods) are suppressed in the coastal upwelling zones during El Niño, while the smaller components (flagellates and ciliates) are enhanced.

Most observational studies of the ecological response to ENSO in this region aggregate phytoplankton and zooplankton, so it is unclear how realistic this simulation is. In general, chlorophyll is often used as a proxy for phytoplankton biomass. This approach facilitates comparison with satellite observations of chlorophyll (e.g., Thomas et al., 2012). The type of algorithms that are used for chlorophyll computation involve variables that are unique to each phytoplankton size-class, e.g., grazing and mortality rates, and saturation constants for nutrient uptakes. Thus, using chlorophyll as a proxy for phytoplankton biomass may provide a overall broad-brush view of the response of the ecosystem to ENSO, but the complexity of its calculation can obscure the interesting ecological dynamics at lower trophic levels.

The dichotomy in the details of the simulated bottom-up response of the CCE to ENSO (Fig. 4) motivates us to identify interactions between the lower trophic levels. When El Niño

drives nutrient depletion in the photic zone due to suppressed upwelling, the larger phytoplankton (diatoms) has less nutrients available for their uptake and growth, resulting in decreased biomass. It is unclear whether the decrease in diatoms biomass is dominated by mortality or by reduced size as a consequence of nutrient limitation, but future research could analyze the changes in opal detrital pool in order to address this question. Small phytoplankton is more resilient to nutrient depletion since its size allows for smaller nutrient concentrations, and at the same time they face less competition from diatoms for nutrients. During La Niña, intensified upwelling brings nutrients to the photic zones favoring phytoplankton populations, particularly the larger ones with more capacity for uptake. Once more, competition comes into play, and small phytoplankton is reduced under upwelling favorable conditions.

The results also show that vertically averaged concentrations of NO_3 in the water column increase in response to intensified upwelling during La Niña and decrease as a consequence of weaker upwelling during El Niño (Figs. 3-4). If we consider the alongshore winds stress along the CCS to be the primary driver of coastal upwelling and consequent nutrient supply, one could expect the NO_3 response to be as asymmetrical as the SSTa. However, the lack of this asymmetry suggests that other dynamics come into play when determining the ENSO related variability of NO_3. The supply of nutrients to the photic zone is also determined by subsurface ocean variability e.g., pycnocline depth and chemical properties of the source waters. Future analysis of the subsurface conditions is necessary to understand the local and advective changes that impact the supply of NO_3 into the photic zone, and how these conditions change in response to ENSO.

The high resolution of the regional circulation model accounts for the many interesting effects of mesoscale eddy features that drive variability in the EBUS like the CCS. For example, we noted a fascinating structure in the ecological response that is linked to the latitudinal structure of the standing eddies, and possibly the mesoscale eddy distribution, locked into the CCS. This response structure is clearly evident in the composites and in the correlation maps (Figs. 3 and 4, respectively), which suggests a linear modulation of the background flow fields between El Niño and La Niña events. It is still unclear how the mesoscale features of the CCS influence the variability of the biogeochemical properties of the CCE, and how this may further impact the spatial distribution of phytoplankton and zooplankton communities, both under normal conditions and during ENSO events. Further work is needed in this regard.

In conclusion, the results of this work show that a simple lower trophic level NPZD model like NEMURO is a useful tool to represent the bottom-up ENSO related response of the CCE in ROMS. Patterns of fish migration highly depend on the regions of high nutrient concentration, and fish catch is strongly related to high chlorophyll coastal regions (Stock et al., 2017). Shedding light on these dynamics will help us better address the future changes of habitat of fish populations like sardine and anchovy, as well as top predators, as a response of changes in their environmental modulators on seasonal, interannual and global-warming timescales.

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