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### A physically coupled end-to-end model platform for coastal ecosystems: Simulating the effects of climate change and changing upwelling characteristics on the Northern California Current ecosystem

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#### ABSTRACT

We describe a spatially explicit, intermediate complexity end-to-end model platform that integrates physical, trophic, and nutrient cycling processes. A two-dimensional advection and mixing model drives nitrate input into the model continental shelf domain, the transport of nutrients and plankton between sub-regions, and the export of nutrients and plankton from the model domain. Trophic relationships are defined by classical mass-balanced food web model techniques (e.g., ECOPATH). Inclusion of nitrate and ammonium nutrient pools and bacterial recycling of detritus allows consideration of alternate "new" vs. "recycled" production regimes. The model platform was applied to the Northern California Current (NCC) shelf ecosystem. Seasonal upwelling of nutrients along the coast is the primary driver of NCC productivity, however the characteristics of upwelling vary considerably between years and are expected to change into the future as a result of global climate change. The model was run under alternate physical driver scenarios to examine the effects of changing upwelling characteristics on the production and spatial distribution of functional groups across all trophic levels. Productivity on the shelf had a dome-shaped relationship with upwelling strength. As the intensity of individual upwelling events increased, productivity increased throughout the food web. However, strong upwelling had a detrimental effect when the physical export of plankton exceeded the capacity of phytoplankton to exploit higher nutrient supply rates and the capacity of zooplankton to exploit higher phytoplankton production. As the duration of individual upwelling events increased (an implication of some climate change scenarios) model simulations predicted an overall reduction of productivity at all trophic levels and a shift in the size composition of the phytoplankton community, especially within the nearshore region.

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#### 1. Introduction

Ocean ecosystems are as much defined by their physical characteristics as they are by their species composition and community interactions. A central issue in understanding ecosystem dynamics is the role of the physical context in determining community structure, productivity, and response to natural and anthropogenic perturbations. Model-based comparisons of the dynamics of different ocean ecosystems (e.g., Gaichas et al., 2009; Ainsworth et al., 2011; Ruzicka et al., 2013) focus on the role of food web structure

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http://dx.doi.org/10.1016/j.ecolmodel.2016.01.018 0304-3800/© 2016 Elsevier B.V. All rights reserved. - the network of trophic relationships and energy flow pathways through pelagic and benthic communities. With the development of food web modelling platforms like ECOPATH with ECOSIM (Pauly et al., 2000; Christensen and Walters, 2004), analyses and simulations of variable trophic interactions, resource management actions, and effects of changing community composition have been standardized. The addition of physical processes to trophic models increases the level of complexity. For example, ATLANTIS models (Fulton et al., 2004; Link et al., 2010) link 3-dimensional physical ocean models, NPZD plankton production models of the lower food web, and non-linear prey-predator relationships among higher trophic levels to build complete end-to-end model systems – describing both the physical transport of nutrients and biomass as well as the production and transfer of biomass throughout the food

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Fig. 1. The cumulative upwelling index anomalies off the central Oregon coast between 1998 and 2013. (A) Daily cumulative anomaly, (B) Cumulative summer anomaly (July–Sept.).

web, from the input of nutrients, to fisheries production, and finally to detritus and nutrient recycling. Currently, these highly complex end-to-end model systems are used more for exploration of individual ecosystems than as frameworks for comparative systems analysis.

We present the theoretical framework for a spatially explicit, intermediate complexity end-to-end ecosystem model platform that integrates physical and biological processes. The ultimate goal of this model framework is to define physical and biological components with sufficient generality to allow standardized comparisons among diverse ecosystem types (e.g., upwelling, downwelling, shallow bank, or semi-enclosed sea) but still encompass the essential physics and trophic structure of each ecosystem. As a test of model behaviour, we apply this framework to the Northern California Current (NCC), an eastern boundary current upwelling ecosystem.

The defining chemical, biological and physical features of coastal upwelling systems are the wind-driven input of nutrient-rich sub-surface waters into the euphotic zone along the coastline, seasonally high rates of primary and secondary productivity, and the lateral transport of plankton production across the shelf (Huyer, 1983; Strub et al., 1987). The characteristics of NCC upwelling – the seasonality, intensity, and duration of upwelling and relaxation events - have varied greatly between years (Bograd et al., 2009; Fig. 1) and are expected to further deviate from current conditions with the progress of global climate change (Bakun, 1990). Changing seasonal and event-scale upwelling characteristics drive variability in the productivity, taxonomic composition, and spatial distribution of the phytoplankton community (Wilkerson et al., 2006; Du et al., 2015) with consequences to the greater consumer food web it supports (e.g., Fisher and Pearcy, 1988). Here, we use the integrated physical-biological model platform to simulate NCC ecosystem response, across all trophic levels, to changing physical conditions. In particular, we investigate the effects of alternate upwelling intensities and event durations.

#### 2. Methods

In the following sections, we first describe the theoretical framework for the construction of an intermediate complexity, physically coupled end-to-end (E2E) model built upon traditional ECOPATH food web models. We then describe an application of this model platform to the Northern California Current upwelling ecosystem and use the model to simulate ecosystem response to changing upwelling conditions: upwelling strength and upwelling event duration.

#### 2.1. Theoretical framework – generic model structure

#### 2.1.1. Overview

A physically coupled end-to-end (E2E) model describing energy or biomass transfer through an ecosystem has four essential components: (1) a description of the network of trophic interactions between all living functional groups, (2) defined primary production rates, (3) a description of recycling processes and rates, and (4) a description of the physical environment defining the transport of material within and across ecosystem boundaries and conditions controlling physiological rates. Although taxonomic resolution, demographic resolution, and spatial-temporal resolution vary greatly among models and applications, all E2E models incorporate these essential components. The E2E framework presented here is applicable to shelf ecosystems, where the dominant physical fluxes between explicitly defined subregions (Fig. 2) may be described in 2-dimensions: cross-shelf advection, horizontal and vertical mixing, and particle sinking. Because the underlying food web model is built by averaging trophic interactions over large alongshore distances, we make the simplifying assumption that the system is reasonably 2-dimensional over these alongshore scales (e.g., Lentz, 1987).

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