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Modeling food web effects of low sardine and anchovy abundance in the California Current

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ABSTRACT

Populations of sardine, anchovy, and other forage species can fluctuate to low levels due to climate variability and fishing, leading to indirect effects on marine food webs. In the context of recent declines of sardine (*Sardinops sagax)* and anchovy (*Engraulis mordax)* in the California Current, we apply an end-to-end Atlantis ecosystem model that is spatially explicit, includes trophic interactions, and allows high and low recruitment regimes (production of juveniles). Our simulations suggest that depleted sardine populations, whether caused by fishing or natural cycles, may lead to declines in predator groups such as dolphins and large piscivorous flatfish (e.g. California halibut *Paralichthys californicus*). Birds exhibited more moderate declines, and California sea lions (*Zalophus californianus*) exhibited relatively weak declines. The Atlantis ecosystem model also predicted indirect positive effects of sardine depletion, primarily for prey species such as zooplankton. Overall our model predicted moderate declines in most predators during simulated severe declines in sardine and anchovy, illustrating the important buffering role provided by forage species other than sardine and anchovy. This 'buffered response' is weaker than what would be suggested by another ecosystem model (Ecosim), as predicted by diet information and a global synthesis of Ecosim models (the PREP equation). One limitation of the Atlantis model is that it did not include processes that might give rise to localized depletion of sardine at scales relevant to central place foragers, such as birds and pinnipeds. This analysis will contribute to a collaborative multi-model approach that evaluates the role of sardine in the California Current.

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1. Introduction

Sardine, anchovy, and other forage species support economically valuable fisheries and are a main prey source for many valuable predator species (Pikitch et al., 2014); therefore fluctuations in abundance can have large implications for both fisheries and food webs (Smith et al., 2011). For instance, in the California Current off the West Coast of the USA, revenue from the Pacific sardine (*Sardinops sagax*) fishery recently peaked at over $21 million in 2012 (Pacific Fishery Management Council, 2014). Pacific sardine and northern anchovy (*Engraulis mordax*) are also main prey sources for economically valuable predators such as salmon (*Oncorhynchus* spp.) and albacore tuna (*Thunnus alalunga*) and threatened and endangered species such as humpback whales (*Megaptera novaeangliae*) (Szoboszlai et al., 2015).

Populations of sardine, anchovy, and other forage species can fluctuate to low levels due to climate variability and fishing (Lindegren et al., 2013; Essington et al., 2015). For instance, sardine in the California Current have recently drastically declined to 9% of peak 2007 abundance (Hill et al., 2015), and anchovy in Southern California had declined to ~1% of peak abundance by 2011 (MacCall et al., 2016). This has raised concerns about the implications for dependent predators and fisheries in this region. Of particular concern is that anchovy and sardine are simultaneously at low abundance. Concurrent periods of low abundance are atypical but problematic: Lindegren et al. (2016) analyzed the 60 year time series from CalCOFI surveys and associated data and suggested that it is the asynchrony between anchovy, sardines, and other small pelagic fish that leads to community-level stability. Functional complementarity of these small fish species in the

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diets of generalist predators may typically support resilience in this ecosystem, as long as some of these forage species remain abundant. Recently, synchronous declines in forage fish species have been linked to reduced pup weights of California sea lion (*Zalophus californianus*) (McClatchie et al., 2016) and breeding failure of brown pelican (*Pelecanus occidentalis*) in the Southern California Bight (Henry, 2015).

The consequences of depleted forage fish functional groups in the California Current have been tested previously using two ecosystem models (Kaplan et al., 2013). Both the Atlantis model (Horne et al., 2010) and an Ecosim model (Field, 2004) were consistent in predicting that forage fish depletion would lead to declines in large flatfish and increases in euphausiids, cephalopods, myctophids, and mackerel. The Ecosim model also suggested tradeoffs between forage fish harvest and seabird abundance, with compensatory increases in some planktonic prey of forage fish, not seen in Atlantis. This difference suggested higher responsiveness of the Ecosim model to changes in forage fish biomass. Each of the models was limited in different capacities; Ecosim lacks spatial resolution (i.e. no potential for local depletion via fishing) and this application of Ecosim assumed extremely low sardine abundance, and the Atlantis model contained poor taxonomic resolution for forage fish groups and some predator groups. While this earlier analysis was able to identify some consistent results between models, discrepancies and the overall higher responsiveness of Ecosim versus Atlantis were unresolved in the analysis.

Subsequent to the analyses of Kaplan et al. (2013), US West Coast fishery managers have called for improved ecosystem modeling tools to predict impacts of depletion of sardine and other forage fish (Pacific Fishery Management Council, 2013). Additionally, fishery managers have launched initiatives to protect forage fish species that are presently not targeted by fisheries (Pacific Fishery Management Council, 2016). Here, we address calls by fishery managers to consider the role of forage fish, improving upon earlier efforts (Kaplan et al., 2013) by developing a revised spatially-explicit Atlantis ecosystem model of the California Current (Marshall et al., 2017). In this data-rich system, the Atlantis approach allows us to mechanistically model food web impacts on predators, competitors, and prey of sardine and anchovy to ask: What are the consequences of depletion of sardine on sardine yield and spatial distribution, and on fished predators and on other species in the food web? How does this vary at high versus low regimes of sardine and anchovy productivity (Chavez et al., 2003; MacCall, 2009), including periods such as the apparent present dearth of both species? Do these results vary spatially, for instance near major sardine fishing ports?

To begin to make multi-model inference and to understand how model structure drives prediction uncertainty (Pinnegar et al., 2005; Gårdmark et al., 2013), we have conducted this work within a multi-model setting, the Ocean Modeling Forum (www.oceanmodelingforum.org). We compare our model results to those predicted using a different modeling approach, the PREP equation (Predator Response to the Exploitation of Prey). This equation generalizes results from a set of Ecosim models considered by the Lenfest Forage Fish Taskforce (Pikitch et al., 2012); the task force intended PREP as a tool in data-limited ecosystems where diet information was available but food web or ecosystem models were lacking. In a companion paper we more thoroughly compare results between model types within the Ocean Modeling Forum setting.

2. Methods

We briefly describe the Atlantis framework, and the revised implementation for the California Current. We detail the scenarios tested to understand the role of sardine and anchovy in the food web, the analyses of model output, and the comparison of Atlantis predictions to those from the PREP equation.

2.1. Atlantis framework

The Atlantis ecosystem modeling framework (Fulton, 2004; Fulton et al., 2011) is a C++ code base that simulates 'end-to-end' dynamics spanning from oceanography to ecology and the dynamics of fisheries and other human uses of the ocean. The Atlantis framework is spatially explicit in three dimensions, and within each model polygon (3D unit) it tracks abundance of primary producers, invertebrates, vertebrates, and removals due to predation mortality, fishing, and other causes. Abundance is represented in nitrogen (a proxy for biomass); for vertebrates this is calculated as the product of numbers-at-age and weight-at-age of individuals within each polygon. Model dynamics are computed utilizing forward projections of differential equations, solved via a simple adaptive difference method, typically on a 12 h time step. Vertebrate movement can be driven by foraging behavior or fixed seasonal migrations. Ocean conditions are often imported from hydrodynamics models such as a Regional Ocean Modeling Systems (Haidvogel et al., 2008), which advect plankton and nutrients and provide temperature fields that affect animal movement and metabolism.

Recent applications of Atlantis outside the California Current include those related to climate change, fisheries, pollution, and selection of ecological indicators. Griffith et al. (2011, 2012) projected the effects of climate change and ocean acidification in SE Australia, and Weijerman et al. (2015) evaluated effects of climate change, land-based pollution, and acidification on coral reefs in Guam. Consideration of ecosystem implications of fisheries policies has included testing alternative Australian fisheries management strategies (Fulton et al., 2014), the efficacy of marine reserves (Savina et al., 2013), and tradeoffs between porpoise conservation, fisheries, and other ecosystem components (Morzaria-Luna et al., 2012, 2013). Smith et al. (2015) applied a model of the Benguela Current to consider ecological indicators, and Olsen et al. (2016) recently quantified both hindcast and forecast skill of a Northeast USA Atlantis model.

2.2. California Current Atlantis model

The California Current Atlantis model simulates population dynamics and spatial distributions of five primary producer groups, 25 benthic and planktonic invertebrates, 36 fish and shark groups, 10 marine mammal groups, three bird groups, and two detritus categories (Fig. 1). Earlier versions of this California Current model have been applied to evaluate the ecological and economic implications of new management strategies and new fisheries (Kaplan et al., 2012; Kaplan and Leonard, 2012; Marshall et al., 2014), and ocean acidification (Kaplan et al., 2010), as well as depletion of forage fish (Smith et al., 2011; Kaplan et al., 2013). Additionally, results have been applied for strategic advice for management of groundfish (Pacific Fishery Management Council and National Marine Fisheries Service, 2014). This latest version of the California Current Atlantis model is fully described in Marshall et al. (2017), but we briefly summarize key features here, particularly those relevant to sardine and anchovy.

Geographic representation of the model is described in Appendix A, including spatial distributions of a subset of the species in the model: sardine, anchovy, and four predator functional groups: Pelagic feeding seabirds (including brown pelicans, *Pelecanus occidentalis*), Baleen whales (including humpback whales, *Megaptera novaeangliae*), California sea lions (*Zalophus californianus*), and Halibut (both Pacific halibut *Hippoglossus stenolepis* and California halibut (*Paralichthys californicus*). These species groups