



Developing a high taxonomic resolution food web model to assess the functional role of forage fish in the California Current ecosystem



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ABSTRACT

Understanding the role of forage fish in marine food webs is an important part of ecosystem-based fisheries management. Food web models are a common tool used to account for important characteristics of forage fish and their trophodynamics. One primary limitation of many existing food web models is that the taxonomic resolution of forage fish and their predators is overly simplified. Here, we developed a food web model with high taxonomic resolution of forage fish and their predators in the California Current to more comprehensively describe trophic linkages involving forage fish and examine the ecological role of forage fish in this system. We parameterized a mass-balanced food web model (Ecopath) with 92 living functional groups, and used this to quantify diet dependency on forage fish, determine the main predators of forage fish, identify the topological position of forage fish in the food web, and calculate an index that identifies forage species or species aggregations that have key ecological roles (Supportive Role to Fishery ecosystem, SURF). Throughout, we characterized parameter uncertainty using a Monte Carlo approach. Though diets revealed some predators had high diet dependencies on individual forage fish species, most predators consumed multiple forage fish and also had notable diet overlap with forage fish. Consequently, no single forage fish appeared to act as a vital nexus species that is characteristic of “wasp-waisted” food webs in other upwelling regions. Additionally, no single forage fish was identified as “key” by the SURF index, but if predators and fisheries view certain pairs of forage fish as functionally equivalent, some plausible pairs would be identified as key assemblages. Specifically, sardine & anchovy (*Sardinops sagax* & *Engraulis mordax*) and herring & anchovy (*Clupea pallasii* & *E. mordax*) are key when predator populations depend on the aggregate availability of these species. This food web model can be used to support generalized equilibrium trade-off analysis or dynamic modeling to identify specific predators that would be of conservation concern under conditions of future forage fish depletion.

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1. Introduction

Recently there has been movement in fisheries management away from a single-species management focus towards a more holistic, ecosystem management focus, known as ecosystem-based fisheries management. However, the empirical information needed

to assess direct and indirect effects of fishing in an ecosystem context are lacking for many marine systems (Frid et al., 2006; Mace, 2001). Therefore, models are commonly used as strategic, scientific tools for ecosystem-based fisheries management (Plagányi, 2007). In this capacity, ecosystem models are frequently used to evaluate harvest strategies (Fulton et al., 2014), to identify ecological risk and biological limits at which risk is amplified (Smith et al., 2011), or to determine key data gaps or needs (Walters, 1986).

One key ecosystem-based management issue in fisheries is the sustainability of forage fish fisheries; particularly in regards to impacts these fisheries may have on predators. Fisheries on forage fish comprise around 25–30% of global fish landings (FAO, 2015; data from 2011 to 2013). At the same time forage fish (small, pelagic

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schooling species) are a primary food source for a range of predators (Fréon et al., 2005; Furness, 2007; Brodeur et al., 2014), including many that are also targeted by fisheries (Pikitch et al., 2014). Therefore, forage fish fisheries introduce potential trade-offs between the revenue generated by harvesting these species directly versus leaving them in the ocean and harvesting their predators. The shapes of these trade-off relationships can be difficult to anticipate and are commonly evaluated using food web models (Hannesson et al., 2009; Kaplan et al., 2013; May et al., 1979; Shin et al., 2004; Smith et al., 2011). However, Essington and Plagányi (2014) found that many available food web models did not incorporate several relevant characteristics of forage fish or their predators, largely because the models used to evaluate impacts of forage fish fisheries were not specifically designed for that purpose. Thus, advances in ecological models are needed to better describe the relationships between forage fish and other species in food webs and ultimately to evaluate the species and fisheries most at risk from forage-fish depletion.

A common limitation of many food web models is poor taxonomic resolution of forage fish species and their predators. Aggregating many predators into a single group makes it difficult to identify individual predator sensitivities to forage fish depletion (Essington and Plagányi, 2014). The appropriate degree of aggregation of forage fish species in a model depends on the ecosystem context and question addressed. For example, if a predator is a generalist and can readily switch feeding among forage fish species based on availability, then model predictions that represent forage fish as a single functional group might be robust to this aggregation (Fulton et al., 2003 and references therein). Alternatively, if some fisheries and predators are specialists on individual forage species, models that aggregate forage fish into a single functional group might not detect risk to predators that are dependent on individual species. Given that one rarely knows if any of these conditions are true *a priori*, there are likely benefits from starting model development at a high taxonomic resolution around species of interest, and evaluating the consequences of aggregation as needed.

Sustainable management and trade-offs of forage fish fisheries is particularly relevant in the California Current ecosystem, an eastern boundary upwelling ecosystem that supports many forage fish species and a diversity of predators that feed upon them (Block et al., 2011). Forage fish in the California Current are an important prey source for multiple predators (Ruzicka et al., 2012; Szoboszlai et al., 2015) including protected, threatened, and endangered seabirds (marbled murrelets, *Brachyramphus marmoratus*) and mammals (humpback whales, *Megaptera novaeangliae*). Forage fish fisheries in the California Current are economically valuable as well. Pacific sardine (*Sardinops sagax*) catch on the U.S. West coast from 2004 to 2013 averaged over 82 000 mt yr⁻¹ with an average ex-vessel revenue of \$13.7 million USD, while northern anchovy (*Engraulis mordax*) catch was just over 7000 mt yr⁻¹ with an average revenue of \$1 million (Pacific Fishery Management Council, 2014a). Additionally, forage fish are a main conservation issue in this region, exemplified by the recent initiative to prohibit the formation of fisheries on unmanaged forage species (Pacific Fishery Management Council, 2014b). Finally, multiple food web models already exist for the California Current ecosystem (see Field, 2004; Ruzicka et al., 2007; Kaplan et al., 2013), however these models possess many of the limitations discussed above with respect to aggregation (either forage fish aggregation, predator aggregation, or both) because they were not constructed specifically to address questions surrounding forage fish and their fisheries.

Here, we constructed a food web model of the California Current with high taxonomic resolution of forage fish and their predators to better describe the role of forage fish in this system. Our specific objectives were to (1) collate all available food web data at a fine taxonomic scale and use these to develop a mass-balanced food web model; (2) describe the trophic linkages of individual for-

age fish species in this system; and (3) calculate food web metrics that are designed to identify “key” forage fish species in terms of ecological function. Throughout we consider the consequences of taxonomic resolution on model predictions, and explicitly consider consequences of parameter uncertainty. In addition to the increase in taxonomic resolution of forage fish and forage fish predators, this is to our knowledge, the first food web model for the entire California Current region (from British Columbia, Canada to Baja California, Mexico), capturing the full ranges of many forage fish and predators.

2. Methods

2.1. Food web model

We constructed a food web model of the California Current ecosystem that focuses on forage fish and their predators. For the food web model, we used the Ecopath framework (Christensen and Walters, 2004) because it is widely accepted, information required to populate the model is readily available, and the properties of the model are well understood. An Ecopath model is a mass-balanced, instantaneous snapshot of an ecosystem at a given period of time (usually a year), representing trophic interactions between ecological guilds and accounting for flows of biomass among food web compartments. Mass-balanced refers to all biomass production in the system equaling all biomass loss (through predation, fishing, etc.). Species or species groups are represented as functional groups, or biomass pools, that are internally homogeneous. We assumed steady state conditions, and did not include migration. Under these assumptions, all energy entering a species compartment equals all outbound energy (including respiration and excretion), such that production of each biomass pool equals the biomass losses:

$$B_i \times PB_i \times EE_i = C_i + \sum_{j=1}^n B_j \times QB_j \times DC_{ji} \quad (1)$$

where B_i and B_j are the biomass of group i or their consumer(s) j , respectively, PB_i is the production to biomass ratio, C_i is the fisheries catch of species i (including bycatch and discards), QB_j is the consumption to biomass ratio, and DC_{ji} is the proportion of prey i in the diet of predator j . EE_i is the ecotrophic efficiency, which is the proportion of total production that is explicitly depleted by predator-prey interactions and fisheries in the model. Based on these parameters, the model has n linear equations for n functional groups. The model requires that three of the four parameters (B_i , PB_i , EE_i , QB_i) be explicitly defined for each group (Table 1) and requires a diet matrix (DC_{ji}) (Appendix A in Supplementary material). The model then solves the system of equations to calculate the missing input parameter value for each functional group. Although we did not explicitly model migration, we accounted for feeding outside of our model domain by adjusting diet fractions in the “input consumption” category (see diet matrix and Appendix A in Supplementary material for more specifics). The model and all subsequent models and analyses were run in R Studio (version 0.98.501) and R version 3.1.2 (2014-10-31) (R Development Core Team, 2014).

We focused our modeling efforts on forage fish, specifically small, pelagic, schooling species, and their predators and intended to represent the most recent state of the ecosystem, averaged over 2000–2014. Many forage fish species were represented as species-specific biomass pools including: Pacific sardine, northern anchovy, Pacific herring (*Clupea pallasii*), Pacific sand lance (*Ammodytes hexapterus*), and whitebait smelt (*Allosmerus elongatus*). We used an aggregate group for other smelt (*Osmeridae* spp.), which included night smelt, *Spirinchus starksi*; surf smelt, *Hypome-*

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