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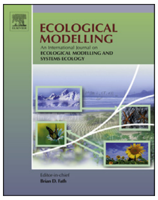

Developing a high taxonomic resolution food web model to assess the functional role of forage fish in the California Current ecosystem

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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.

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 forage 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:

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

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-*

Table 1

Parameters – biomass (*B*), production to biomass ratio (*PB*), consumption to biomass ratio (*QB*), ecotrophic efficiency (*EE*, proportion of mortality included in the model), and catch (*C*) – for each functional group in the model. Parameters marked with "–" are solved for by the model. Also included are the specified coefficients of variation (CV) values for each parameter based on data quality ranking in Table 2.

Groups	*B*	B CV	PB	PB CV	QB	QB CV	EE	*C*	C CV
Phytoplankton	–	0	120	0.1	0	0	0.40093	0	0
Infauna	–	0	2.5	0.2	12	0.2	0.84010	0	0
Amphipods	–	0	3.5	0.2	22	0.2	0.8	0	0
Epibenthic	–	0	2	0.2	10	0.2	0.8	0	0
Microzooplankton	–	0	100	0.2	300	0.2	0.8	0	0
Copepods	–	0	14	0.1	70	0.2	0.8	0	0
Euphausiids	–	0	8	0.2	40	0.2	0.8	0	0
Carnivorous zoop.	–	0	2	0.2	10	0.2	0.8	0	0
Small jellies	–	0	9	0.15	30	0.15	0.8	0	0
Large jellies	–	0	3	0.15	12	0.15	0.8	0	0
Pandalid shrimp	–	0	2	0.1	10	0.2	0.8	0.10558	0.1
Benthic shrimp	–	0	2.5	0.2	12	0.2	0.8	0.00010	0.1
Dungeness crab	–	0	0.75	0.1	3.8	0.15	0.64168	0.09198	0.1
Tanner crab	–	0	0.3	0.15	1.5	0.15	0.8	0	0
Mesopelagics	9.93377	0.25	0.6	0.1	3	0.1	–	0	0
Benthic fish	–	0	0.5	0.15	2.5	0.15	0.8	0	0
Surf perch	–	0	1.3	0.1	6	0.15	0.8	0	0
Other cephalopod	–	0	2	0.2	6	0.2	0.8	0	0
Market squid	–	0	2.75	0.2	10	0.2	0.8	0.26699	0.1
Sardine	3.24050	0.15	0.515	0.05	5	0.2	–	0.48748	0.1
Anchovy	1.50173	0.25	1.09	0.1	6	0.2	–	0.03866	0.1
Herring	0.66225	0.35	1.6	0.15	7.489	0.15	–	0.00646	0.1
Pacific Mackerel	0.49184	0.15	0.514	0.05	6	0.15	–	0.02689	0.1
Sand lance	–	0	1	0.15	3.65	0.2	0.8	0	0
Whitebait smelt	0.08027	0.25	1.6	0.2	6	0.2	–	0	0
Other smelt	–	0	1.5	0.2	6	0.2	0.8	0	0
Saury	1.14967	0.35	1.6	0.15	3.65	0.15	–	0	0
Juvenile rockfish	–	0	1.5	0.2	6	0.2	0.8	0	0
Juvenile hake	–	0	1.75022	0.28051	6.10087	0.08225	0.8	0	0
Juvenile flatfish	–	0	1	0.2	4	0.2	0.8	0	0
Juvenile roundfish	–	0	1.5	0.2	5.12501	0.2	0.8	0	0
Juvenile thornyhead	–	0	0.5	0.2	2.5	0.2	0.8	0	0
Yellowtail Rockfish	0.54516	0.2	0.146	0.1	1.7	0.05	–	0.01377	0.1
Black rockfish	0.12420	0.04357	0.129	0.1	2.01	0.05	–	0.00315	0.1
Nearshore rockfish	0.08012	0.02422	0.158	0.1	2.01	0.15	–	0.00169	0.1
Yelloweye rockfish	0.00898	0.2	0.0505	0.05	2.2	0.15	–	0.00004	0.1
Greenstriped rock.	0.09782	0.25	0.125	0.15	2.2	0.15	–	0.00013	0.1
Shelf rockfish	0.43997	0.2	0.159	0.15	2.2	0.15	–	0.00153	0.1
Shortbelly rockfish	0.36026	0.2	0.26	0.05	2.2	0.15	–	2.48E-08	0.1
Petrale sole	0.07856	0.2	0.32	0.1	1.7	0.05	–	0.00535	0.1
Halibut	0.18513	0.2	0.47	0.1	2.12	0.15	–	0.00319	0.1
Hake	8.04387	0.15	0.41	0.05	1.95652	0.1	–	0.94690	0.1
Lingcod	0.31246	0.15	0.295	0.1	2.4	0.05	–	0.00364	0.1
Arrowtooth	0.34408	0.2	0.264	0.1	2.12	0.15	–	0.03420	0.1
Sablefish	0.89623	0.15	0.0984	0.1	2	0.05	–	0.02502	0.1
Albacore	0.09562	0.2	0.36	0.15	7.3	0.15	–	0.00364	0.1
Salmon	0.12464	0.25	1.76	0.1	5.3	0.15	–	0.02537	0.1
Grenadiers	0.36436	0.25	0.2	0.15	1	0.05	–	0.00036	0.1
Dogfish	0.85909	0.2	0.0694	0.05	2.5	0.1	–	0.00474	0.1
Canary Rockfish	0.07756	0.2	0.113	0.1	1.66	0.05	–	0.00218	0.1
Pacific Ocean Perch	0.10093	0.25	0.0689	0.24646	2.07	0.05	–	0.00228	0.1
Widow Rockfish	0.25945	0.2	0.1287	0.05	2.2	0.05	–	0.00509	0.1
Splitnose Rockfish	0.33672	0.2	0.07478	0.1	1.91	0.15	–	0.00121	0.1
Slope rockfish	0.23033	0.2	0.06465	0.1	1.91	0.15	–	0.00304	0.1
Shortspine thorny.	1.09813	0.2	0.0545	0.05	0.47	0.15	–	0.00350	0.1
Longspine thorny.	0.30880	0.2	0.1213	0.05	0.35	0.15	–	0.00308	0.1
Flatfish	3.56936	0.2	0.35	0.15	2	0.2	–	0.04902	0.1
Skates	0.40242	0.25	0.2216	0.2	2	0.2	–	0.00394	0.1
Sharks	–	0	0.18	0.15	2.8	0.15	0.75	0.00268	0.1
Common Murre	0.00327	0.1	0.08409	0.29063	169.5	0.05	–	0	0
Cassin's auklet	0.00123	0.2	0.23388	0.04091	266.9	0.05	–	0	0
Rhinoceros auklet	0.00028	0.2	0.11898	0.10223	202.2	0.05	–	0	0
Tufted Puffin	0.00018	0.2	0.06500	0.20688	181.1	0.05	–	0	0
California gull	0.00065	0.15	0.13529	0.29342	193.9	0.05	–	0	0
Western Gull	0.00096	0.2	0.13216	0.16087	168.65	0.05	–	0	0
Kittiwake	0.00013	0.2	0.09289	0.16396	216.2	0.05	–	0	0
Albatross	0.00075	0.1	0.04042	0.69947	124.25	0.05	–	0	0
Northern Fulmar	0.00024	0.15	0.04338	0.21067	199.7	0.05	–	0	0
Shearwater	0.00364	0.1	0.07	0.25	182.75	0.05	–	0	0
Leach's storm petrel	0.00060	0.2	0.12404	0.37046	407.9	0.05	–	0	0
Brandt's cormorant	0.00073	0.1	0.235	0.14498	138.1	0.05	–	0	0
Double-crest corm.	0.00036	0.05	0.15	0.05	147	0.05	–	0	0

Table 1 (*Continued*)

Groups	*B*	B CV	PB	PB CV	QB	QB CV	EE	*C*	C CV
Pelagic cormorant	0.00026	0.1	0.15	0.15	142.6	0.05	–	0	0
Marbled murrelet	0.00003	0.05	0.12077	0.30341	255.1	0.05	–	0	0
Pigeon Guillemot	0.00010	0.15	0.175	0.23716	205.9	0.05	–	0	0
Caspian tern	0.00009	0.2	0.10887	0.11189	189.9	0.05	–	0	0
Brown Pelican	0.00027	0.15	0.2	0.2	120.7	0.05	–	0	0
Transient Orcas	0.00267	0.15	0.02542	0.1	14.87591	0.05	–	0	0
Resident Orcas	0.00109	0.15	0.02542	0.15	14.87591	0.05	–	0	0
Porpoises	0.02651	0.33	0.07	0.33391	36.52	0.05	–	0	0
Humpback whale	0.24993	0.15	0.0377	0.15	7.58	0.05	–	0	0
Minke whale	0.00520	0.3	0.0511	0.1	8.69	0.05	–	0	0
Fin whale	0.14008	0.18	0.0377	0.2	6.51686	0.05	–	0	0
Sperm whale	0.01829	0.31	0.021	0.2	8.812	0.05	–	0	0
Harbor seals	0.01962	0.15	0.08265	0.1	24.594	0.05	–	0	0
Sea Lions	0.09872	0.15	0.076	0.1	15.1	0.15	–	0	0
Juv. N. Ele. seals	0.03795	0.15	0.31038	0.1	14.76	0.15	–	0	0
Adult N. Ele. seals	0.07750	0.15	0.22759	0.05	14.76	0.05	–	0	0
Fur seals	0.00787	0.15	0.091	0.1	52.04	0.05	–	0	0
Blue whale	0.63938	0.24	0.05	0.2	5.5	0.05	–	0	0
Gray whale	0.97349	0.15	0.037	0.2	11.82933	0.05	–	0	0
Dolphins	0.07128	0.33	0.07563	0.48877	32.33	0.05	–	0	0
Detritus	10	0	0	0	0	0	–	0	0

sus pretiosus; and eulachon, *Thaleichthys pacificus*, because little is known of these species individually in terms of biomass and diet. Other species in the model may be considered forage species, but we focused on the most common vertebrate species that are pelagic and schooling for the majority of their life. Upper trophic functional groups consisted mainly of forage fish predators, including 27 piscivorous fish groups, 18 seabird groups, and 15 marine mammal groups. Of these groups, 43 were species-specific biomass pools. A full list of all functional groups (including lower trophic groups not mentioned here), species included in each group, and full descriptions and references for parameters can be found in Appendix B in Supplementary material.

The model spatial domain extended from the Northern end of Vancouver Island in British Columbia, Canada to Punta Eugenia in Baja California, Mexico, including the northern and southern extents of the upwelling system (Fig. 1) in order to cover the distributions of many forage fish species and their predators in the California Current. The model is not spatially explicit, however spatial structure is often implicit in the diet linkages (e.g. a northern-ranging species will not extensively consume a southern-ranging species). For example, albacore tuna (*Thunnus alalunga*) when in the model domain are usually found offshore in the Southern portion of the California Current (Kimura et al., 1997) and therefore, of the forage fish, tuna mainly consume sardine (a offshore, southern forage fish species, Zwolinski et al., 2012) and to a lesser extent anchovy and herring (more inshore and/or northerly). Additionally, if diet studies existed for multiple regions (Canada, Washington, Oregon, California, or Baja) for a single species, these diets were combined using a weighted average based on biomass of the species in each region. Offshore, the model extended to the 2000-m isobath, capturing the majority of the region where commercially important forage fish are present and interact with predators. The model domain encompassed many important seabird breeding colonies near the northern end of Vancouver Island (specifically Triangle Island) and important pinniped breeding rookeries on the Baja Peninsula. The total model domain area was 302 000 km^2.

2.2. Parameterization and uncertainty

We provide an overview of the data sources we used, and note that more detailed documentation can be found in Appendix B in Supplementary material. Many estimates of fish biomass and catch were derived from the most recent stock assessments available from the Pacific Fishery Management Council for the portion of the model domain within United States territorial waters. Total U.S. biomass was scaled up to the ecosystem scale based on the distribution of the fish species and the ratio of area inside and outside U.S. waters. Catch data were collated for all fish species managed by the Pacific Fishery Management Council in the U.S. (part of the groundfish, salmon, highly migratory species, pacific halibut, and coastal pelagic species fisheries management plans), and for three invertebrate groups: pandalid shrimp, benthic shrimp, and state-managed dungeness crab (*Metacarcinus magister*) (see individual references in Appendix B in Supplementary material). Canadian catch data came from the Fishery Operations System (FOS) maintained by Fisheries and Oceans Canada (DFO) for 2007–2014 and Mexican catch data came from the Comisión Nacional de Acuacultura y Pesca (CONAPESCA, 2015). Biomass or density of most forage fish species (other than sardine) came from primary literature or was solved for by the model through top-down balancing. Because we assumed a steady state and forage fish biomass fluctuates widely, we used 10-year averages of biomass for forage fish species where we had biomass estimates and 10-year averages for catch. A similar 10-year average was used for Hake (*Merluccius productus*) biomass and catch and humpback whale biomass (*Megaptera novaeangliae*) because of trends in biomass (see Appendix B in Supplementary material).

All marine mammal abundance estimates for United States waters were derived from the Marine Mammal Stock Assessment (Carretta et al., 2013), while estimates for Canada and Mexico came from various research studies. These abundance values were converted to biomass by scaling by individual body size, using values from Hunt et al. (2000). Most seabird abundance estimates came from sources that provided information for smaller regions (Canada, Washington, Oregon, California, Mexico) within the larger model domain, and were extrapolated to biomass based on individual-mass data from Hunt et al. (2000). Biomass values for lower trophic levels were solved for by the model through top-down balancing.

Many estimates of production to biomass (*PB*) and consumption to biomass (*QB*) (Eq. (1)) came from the Field (2004) Ecopath model for the Northern California Current, particularly for lower trophic levels. Production to biomass ratios are equal to total mortality for a group in mass-balanced models (Allen, 1971), therefore *PB* values were updated as needed for fish species based on natural and fishing mortality estimates from stock assessments. Most seabird mortality rates came from studies compiled by Schreiber

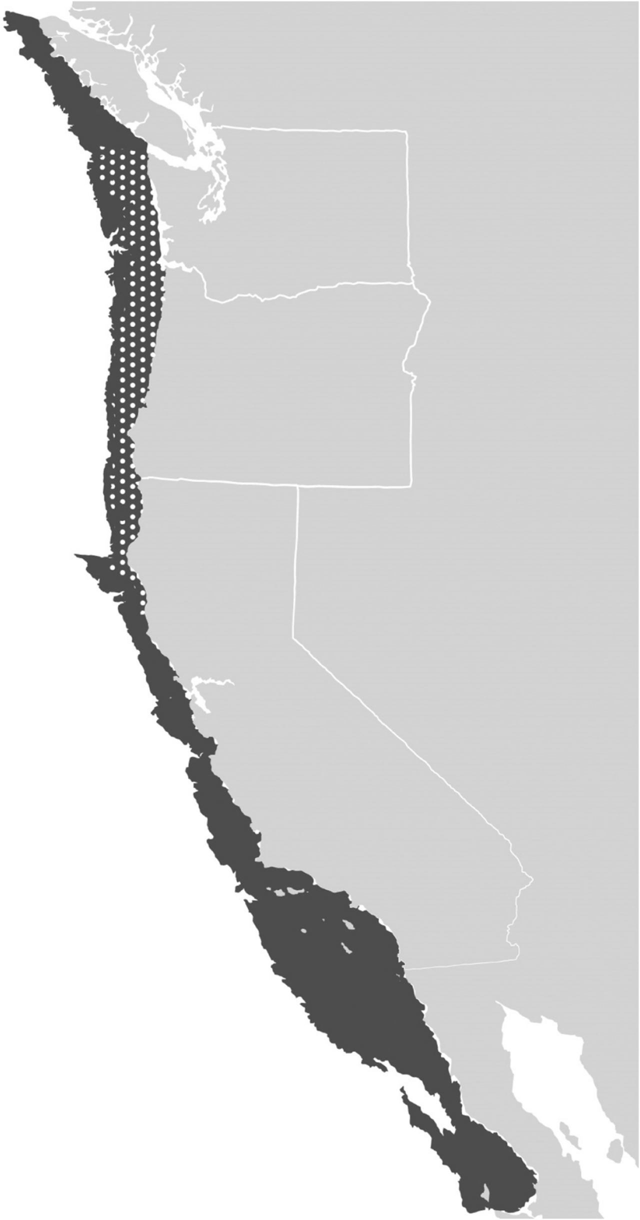

Fig. 1. Map of the total area of the California Current that was used as the domain for the food web model, extending from Vancouver Island, B.C. to Punta Eugenia, Mexico (dark grey). The white dotted region overlaid is two previous California Current Ecopath model domains (Field, 2004; Ruzicka et al., 2007) where the later stopped at 41.8° North (Southern Oregon border).

and Burger (2001). Marine mammal *PB* values were mainly taken from previous Ecopath models including Field (2004) and Aydin et al. (2007). For seabirds and marine mammals, *QB* values were calculated from daily energy consumption values and prey energy density values from Hunt et al. (2000), following equations specified in Harvey et al. (2010). For most other functional groups (fish and invertebrates), *QB* values were taken from other Ecopath models, mainly Field (2004) or other models for similar systems (largely Puget Sound, Hecate Strait, and Gulf of Alaska).

Data for the majority of diets came from studies compiled in the California Current Predator Diet Database (Szoboszlai et al., 2015), which mainly incorporated data from primary literature. We also examined diets from government documents and theses to supplement information for functional groups for which primary literature was lacking, out-of-date, or non-existent. Forage fish diet mainly came from Brodeur et al. (1987), Emmett et al. (2005), and Miller (2006). Diet information for lower trophic levels was taken from the Field (2004) Ecopath model.

Because the inputs needed to parameterize the food web model are not known with complete precision, we used a Monte Carlo approach to generate plausible alternative parameterizations of the food web model that are consistent with the data available (similar to “Ecosense” methods in Aydin et al., 2007). We assigned a coefficient of variation (CV) to each input parameter (*B*, *QB*, *PB*, and *C*) (Eq. (1)) using values provided or an assigned level of uncertainty based on data quality (see Table 1 for CV values). Wherever possible we used the CV reported by our data sources, but this was rare. In most cases, we ranked data according to degree of confidence and assigned precision levels accordingly (Table 2). We arbitrarily selected CVs for each level of data quality ranking that produced Monte Carlo output that reflected our degree of certainty. Fish biomass values were given higher CVs than other biomass estimates (though the same data quality ranking was used) because

Table 2
Data quality ranking used to assign coefficient of variation values (CVs) for biomass (for fish, seabirds, and marine mammals separately), production to biomass (*PB*) values, and consumption to biomass (*QB*) values.

	Data quality ranking criteria
Fish biomass CV	
0.15	Recent (2000–2014) stock assessment for the whole model domain (Canada, U.S., and Mexico)
0.2	Recent (2000–2014) assessment for the U.S., used conversion factor for Canada and/or Mexico
0.25	Survey not assessment or assessment but incomplete info (spawning biomass only) or multiple sources for the U.S.
0.3	Any stock assessment before 2000
0.35	Information from before 2000 and not a stock assessment
0.4	Value taken from another ecosystem model
Seabird biomass CV	
0.05	Estimates for the entire domain (Canada, U.S., and Mexico) are from 2000 or later
0.1	Majority (>75% and <100%) of estimates are from 2000 or later
0.15	Estimates are from 2000 or later for 50% of the domain OR estimates are from 2000 or later but had to adjust (use a conversion factor to scale to a larger domain)
0.2	Some abundances from 2000 but majority are older (>75%)
0.25	All estimates from before 2000
Mammal biomass CV	
0.05	Estimates for the entire domain (Canada, U.S., and Mexico) are from 2000 or later
0.1	Majority (>75% and <100%) of estimates are from 2000 or later
0.15	Most estimates from 2000 or later but adjusted amount for biomass outside of the 2000 m isobath or scaled for regions without estimates
0.2	All estimates from 1990–2000
0.25	Estimates from before 1990
PB CV	
0.05	Data used is from a recent source (recent stock assessment or research study) or is a well established estimate (natural mortality used in stock assessment is old but has been used for multiple years/assessments)
0.1	Data from before 1990 OR estimated/calculated by Field (2004) with older information (past stock assessments) OR mortality is an average for different ages/sexes OR calculated using Siler life history model
0.15	Wrong region, but correct species OR similar species, correct region
0.2	Generalization/assumption for large/multi-species functional group
QB CV	
0.05	Uses recent data and uses established methods to calculate *QB*—a.k.a. uses numbers at age data and Essington et al. (2001) to calculate *QB*, OR uses data from Hunt et al. (2000) to calculate
0.1	Calculated based on older data (before 1990) OR certain information was estimated but based on real data
0.15	Wrong region, but correct species OR similar species, correct region OR wrong life history stage
0.2	Generalization/assumption for large/multi-species functional group OR assumed growth efficiency

these estimates are based on model fitting while other biomass estimates were derived from direct observations. Therefore, the range of possible CVs was 0.05–0.25 for *QB*, *PB*, and seabird/marine mammal biomass, but ranged from 0.15 to 0.4 for fish biomass. Fish catch values (*C*) were assigned a CV of only 0.1 because these are extensively monitored. For any biomass, *QB*, or *PB* values where literature cited a range of possible values (instead of a single value), we used that range and an assumed probability density function to specify the CV, such that the upper and lower bounds of the range correspond to the fifth and 95th percentiles of the distribution. Lognormal distributions with specified CVs were used to represent each parameter (*B*, *PB*, *QB*, and *C*) and propagate uncertainty by setting the mean of the distribution equal to the nominal parameter value.

For ecotrophic efficiency (*EE*) (Eq. (1)), we characterized uncertainty using a uniform distribution. For consumers, we used ranges of 0.5–0.9, and for producers we used ranges of 0.25–0.75. The higher values of *EE* for consumers were used because species with considerable predation and fisheries pressure typically have higher *EE* values due to models accounting for this mortality. On the other hand, much of producer (phytoplankton) mortality comes from sources other than predation (die-offs in blooms) not represented in Ecopath-type models, leading to typically lower *EE* values in models.

Characterizing diet uncertainty required a different approach because diet compositions are proportions that must sum to one, and therefore are better represented as a Dirichlet distribution. This distribution is a multivariate probability distribution (corresponding to individual diet fractions for a predator), so one CV alone cannot express the degree of confidence in the overall diet composition. Instead, we used a scaling factor from 0 to 1 for the entire diet composition for a species to represent the most and least certain estimates, respectively (Table 3). To generate draws from the Dirichlet distribution, we specified a parameter a_i for each prey type i in a predator's diet, which was equal to the product of the baseline diet composition and a multiplier related to the scaling factor (Table 3). The Dirichlet distribution is then defined by the vector of a_i's. For each vector (each group's diet) a new vector is pulled using the rdirichlet function in the R package 'MCMCpack' (Martin et al., 2011). This procedure generated random diet proportions that adequately conveyed our degree of confidence in the input data and summed to one. For each functional group, data quality rankings and multipliers are listed in the last two rows of the diet matrix in Appendix A in Supplementary material.

Using these specified uncertainties and distributions for each functional group and each parameter, we drew all parameters simultaneously, and then determined if the resulting parameterization returned a model that was energetically balanced. Unbalanced models (where one or more functional groups had greater removal than production) were discarded. We repeated this procedure until 500 balanced models were produced.

2.3. Food web model analysis

To assess the importance of forage fish in the food web, we calculated the proportions of predator diets consisting of forage fish and the fraction of total mortality exerted by different predator groups on forage fish, for each model generated by the Monte Carlo procedure. We did this for two distinct classifications of forage fish: "managed" forage fish (sardine, anchovy and herring) that

Table 3
Data quality ranking criteria and relevant ranking scores for diet data for each functional group and the multiplier (related to the ranking score) needed to scale baseline diet compositions when using the Dirichlet distribution to produce relevant variability in diet distributions. To reach higher than 0.6 in ranking, data must be of high quality in terms of taxonomic information and life stage information.

Diet quality ranking	Data quality ranking criteria	Dirichlet multiplier
0 (worst)	Generalization/assumption	150
0.2	From a similar system (outside domain) or for a similar species not in the functional group	300
0.4	All studies have sample sizes <25	500
0.6	Majority (>50%) of data is older (1920s–1980s)	1000
0.8	Recent data (1990s/2000s) but only for one region or one year	1500
1 (best)	Recent data (1990s/2000s) for multiple regions and majority have good sample sizes	2000

have established management plans, either by the Pacific Fishery Management Council or by state agencies, and “unmanaged” forage fish (sand lance, whitebait smelt, and other smelt species) that lack these plans. For each managed and unmanaged forage fish species or functional group, we determined the proportion of each forage fish in predator diets for each model (any diet fractions greater than zero). Additionally, for each forage fish, we calculated the fraction of that species’ or group’s total mortality caused by each predator (predation mortality fractions). Diets of predators provide a view of potential bottom-up effects of forage fish on predators, while mortality fractions show potential top-down effects by predators on forage fish.

We used two graphical methods, one with all functional groups separate and another with aggregated broad groups, to better explore the position of sardine, anchovy, and herring in the California Current food web, using the initial food web model (not including Monte Carlo draws). We first created topological graphs depicting the linkages between groups in the model based on diet fractions and the fraction of total mortality exerted by one group on another. We considered groups to be linked if either the predator’s diet fraction of a prey or the prey’s mortality fraction caused by a predator, exceeded 5%. We explored the structure of linkages through network graphs, using the igraph package in R (Csárdi and Nepuzs, 2006) and the Fruchterman Reingold layout algorithm. These graphics are useful for understanding the position of each forage fish in the food web (e.g. a “wasp–waist” position would consist of forage fish as a central node in the graph with many prey connected below and many predators above and very few connections between predators/prey and other groups), but do not permit quantification of the strength of linkages. We therefore also generated graphics that depicted the flow of energy – expressed as diet fraction for predators and mortality fraction for prey – for each forage species and aggregated groups of forage fish prey and predators, in order to summarize complex trophic dynamics of the model (Essington and Munch, 2014). This method first identifies predators or prey of forage fish based on a 5% threshold of prey diet fraction or fractions of total mortality from predation (similar to criteria for the topological graphs). Then we aggregated all species that are predators of forage fish into a single biomass compartment (following Gaichas et al., 2009), aggregated all forage fish prey species into a single prey compartment, and calculated diet fractions and fractions of mortality for the aggregated groups. Once these three main groups (forage fish, forage fish predator, and forage fish prey) were defined, we calculated the aggregate diet fraction and fraction of total mortality due to predation for each possible linkage in this condensed food web module. Linkages include: forage fish predator to forage fish predator; forage fish predator to forage fish; forage fish to forage fish prey; forage fish predator to forage fish prey; forage fish prey to forage fish prey. Both the topological graphs and energy flow graphs are meant to summarize energy flow and topological structure for the main ecological interactions between forage fish and predators or prey. Thus, the 5% thresholds removes linkages that likely represent ecologically insignificant or anomalous interactions (e.g. the prey is not a frequent, consistent occurrence in the diet of a predator).

2.4. Metrics of forage fish importance

We used a two-criteria method to identify functionally important forage fish species or groups, as defined by (Plagányi and Essington, 2014). The first criterion calculated was the Supportive Role to Fishery ecosystem (SURF) index (Plagányi and Essington, 2014):

$$SURF_i = \frac{\sum_{j=1}^{S} DC_{ij}^2}{L} \tag{2}$$

where L is the total number of linkages ($DC_{ji} > 0$) in the food web. Higher SURF scores indicate a strong possibility for a dynamic model to predict indirect food web effects from fishing a forage fish species, based on the diet dependence of predators on that species and both the number and strength of linkages between predators and the forage fish. The second criterion used was the proportion of total consumer biomass (biomass of all heterotrophs; no primary producers) that each forage fish comprises (based on Smith et al., 2011). Any SURF values that exceed 0.001 or proportion of total consumer biomass values that exceed 0.05 indicate that a dynamic food web model would likely predict substantial, widespread ecological consequences (indirect and direct) if this species was depleted (Smith et al., 2011; Plagányi and Essington, 2014). Therefore, species or groups with SURF or proportion of total consumer biomass values above these thresholds are determined to be ecologically “key”. These threshold values came from Smith et al. (2011) and Plagányi and Essington (2014) by calculating either the proportion of total consumer biomass or SURF for multiple forage fish from ecosystem models and ranking the ecological impact of depleting that forage fish, where species with substantial impacts (70% or greater decline for one predator or 40–69% decline for 10% or more of secondary consumers) had criteria values above 0.05 and 0.001, respectively. We calculated SURF and the proportion of total consumer biomass for each individual forage species, and for selected pairs of forage fish (sardine & anchovy; anchovy & herring; sardine & herring). The rationale behind grouping into pairs is that some predators (or fisheries) might view these pairs as being functionally equivalent. Specifically, anchovy and sardine as well as herring and anchovy can commonly be found concurrently in predator diets (see diet matrix, Appendix A in Supplementary material) or switch-off in predator diet in different years (examples: anchovy and sardine in brown pelican (*Pelecanus occidentalis*) diet, Velarde et al., 2013; anchovy and herring in Chinook salmon (*Oncorhynchus tshawytscha*) diet, Brodeur et al., 2014). Additionally, many of the diet studies used in this model came from a period when sardine were scarce, so pairing sardine with herring or anchovy may show functional equivalency for predators in times when sardine scarcity is high.

3. Results

3.1. Characterizing food web linkages

The three managed forage fish – sardine, anchovy, and herring – generally comprised a greater fraction of predator diets than the unmanaged forage fish species (Fig. 2). Across all ($N = 58$) species that consumed the six managed and unmanaged forage fish, 22 depended on a single managed forage fish species for 10% or more of their diet (based on the median of Monte Carlo simulations). This included 12 predators on anchovy, 6 predators on herring, and 4 predators on sardine. Unmanaged forage fish (whitebait smelt, sand lance, and other smelts) constituted a smaller fraction of predator diet. Only 5 predators depended on a single unmanaged forage fish for 10% or more of their diet (based on the median of the Monte Carlo simulations), including one predator on "other smelt", four predators on sandlance, and none on whitebait smelt. The predator with the largest diet fraction for each forage fish varied across forage fish species, except brown pelican had the largest diet fraction for both anchovy and sardine (64% anchovy and 26% sardine). Generally, the ranges of diet proportions across the 500 Monte Carlo models were small, indicating that narrow ranges of diet fractions were needed to produce balanced models.

Fractions of total managed forage fish mortality caused by predators were more equally spaced out across predators than for unmanaged forage fish, with no single predator accounting for a large portion of managed forage fish mortality (no single predator with a high predation mortality fraction; Fig. 3). Only two predators each accounted for >10% of total mortality for managed forage fish, while for unmanaged forage fish, six predators each accounted for >10% of the total mortality. The proportion of mortality caused by a predator on each forage fish varied more across model parameterizations than predator diet fractions, which likely reflects the number of model inputs that contribute to calculating fractions of mortality caused by predators.

Balanced models indicated strongly asymmetric predator-forage fish interactions; in some cases, species with high diet fractions of forage fish account for low proportions of forage fish mortality, and some predators with small diet fractions of forage fish account for high proportions of forage fish mortality. In other words, we saw no relationship between predator diet fractions and the fraction of mortality caused by each predator for both groups of forage fish (managed and unmanaged). For each of the six forage fish groups, we compared the top five predators in terms of diet proportions with the top five predators responsible for the highest fractions of mortality. There were only 12 out of 30 instances where a predator in the top five for the highest diet proportions on a forage fish, was also among the top five predators causing the highest predation mortality for that forage fish. This asymmetry was particularly pronounced for seabirds. These predators' diets had some of the largest fractions of forage fish (18 instances in the top 5), but rarely ($N = 3$) were among the top five most important predators in terms of predation mortality fractions (Figs. 2 and 3), most likely because of the low density of seabirds.

3.2. Food web model structure

Analysis of topological graphs revealed differences in food web connections among the main managed forage fish species (Fig. 4), but no single forage fish was a clear central node in the food web. Of the three species, anchovy was the most connected in the food web, particularly in terms of numbers of predators. Of the 422 linkages that met our criteria, 29 involved anchovy, and most of these (25/30, 83%) were predators. Herring was involved in 19 total linkages (37% less than anchovy). On the other hand, sardine was only involved in 13 linkages total, less than half of the amount for anchovy. Points representing functional groups in the topological graph are located in the same location for each forage fish, showing that the three species also appear to be connected to different assemblages of predators, although there was some overlap. Of the 34 total predators linked to the managed forage fish, half (17 predators) were linked to two or more forage fish, while the remaining 17 were only linked to one forage fish. For prey, the three managed forage fish were connected to similar assemblages, with four out of six prey species linked to two or more forage fish. None of the forage fish species appeared to be a central node in this food web, which we would expect to see if this was a wasp-waist food web (Cury et al., 2000). Instead, predators on forage fish consumed multiple forage fish and also consumed many other non-forage fish prey including shared prey with forage fish. In other words in Fig. 4, though each forage fish (in red) is connected to multiple predators (dark blue) and multiple prey (gold), these predators and prey are also connected to many other functional groups (light blue), so the system is not wasp-waisted and there are multiple pathways for energy flow.

The complexity of food web structure is further emphasized via energy flow diagrams (Fig. 4), showing a substantial degree of diet overlap between forage fish and their predators. The total contribution of each forage fish to the combined predator diet ranged from 3% to 8%, while the contribution of shared prey items ranged from 14% to 51%, with the greatest diet overlap between herring and herring predators and sardine and sardine predators (both 51%). In other words, on aggregate, predators consumed roughly four times as much shared prey of forage fish than they consumed of forage fish directly. Moreover, there was substantial self-consumption and self-inflicted mortality within each guild of forage fish predators and prey. For example, predators on herring also consumed other predators on herring, so an aggregate 26% of herring predator mortality was derived from other herring predators. Mortality on anchovy predators from other anchovy predators was also high (30% of mortality). For both anchovy and sardine, forage fish prey derived nearly all of their energy from consuming other forage fish prey. This is likely because both of these forage species consume both phytoplankton and zooplankton, the latter of which feeds on phytoplankton.

3.3. Metrics of forage fish importance

No single forage fish species was classified as ecologically "key" based on the specified thresholds of the two criteria we calculated – proportion of consumer biomass and SURF – but some forage fish pairings led to criteria scores that exceeded thresholds (Fig. 5). Therefore, a dynamic food web model would likely not predict substantial ecological consequences (indirect and direct) from fishing one of the individual species, but would for fishing multiple forage fish. When sardine and anchovy and anchovy and herring were combined, the paired groups were key based on the SURF metric ($\text{SURF} = 0.0012$ and 0.0011, respectively). In contrast, when herring and sardine were aggregated as a paired group, this group was not key based on either metric ($\text{SURF} = 0.0004$, proportion of biomass = 0.03). No pairings of forage fish were found to be crucial based on the proportion of consumer biomass criterion.

4. Discussion

We constructed a food web model with high taxonomic resolution of forage fish and their predators to directly consider the ecological importance and interactions of forage fish in the California Current ecosystem. We found that many predators feed on multiple forage fish species rather than specializing on any single species, which implies that ecosystem-based management of

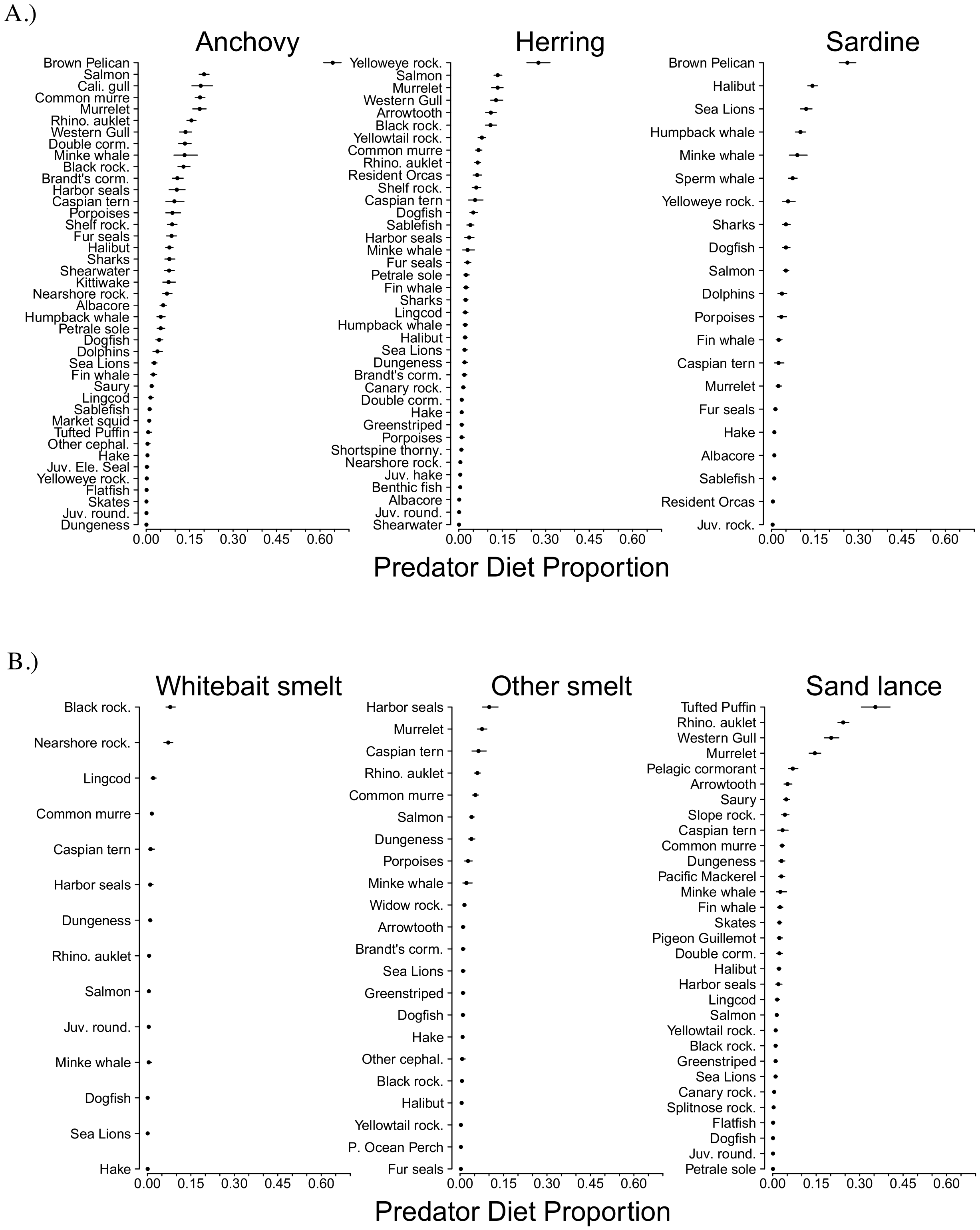

Fig. 2. Diet proportions of predators on forage fish (point = median, inner 95% percentile range) across Monte Carlo draws for (A) managed forage fish (anchovy, herring, sardine) and (B) unmanaged forage fish (whitebait smelt, other smelt, and sand lance).

forage fish could meet sustainability goals for many predators by considering guilds of forage fish rather than individual species. Predator diets showed that most predators are not heavily reliant on a single forage fish species and we saw a notable degree of shared prey between forage fish and their predators. However, there were exceptions to this and some predators – mainly piscivorous seabirds – relied heavily (>10%) on individual forage fish species in their diet. On the other hand, we did not find evidence that any single forage fish was a key species (depletion would lead to widespread, substantial ecological consequences) based on two previously established criteria to determine ecological key species (the SURF index and proportion of total consumer biomass index), but some pairs of forage fish (sardine & anchovy, anchovy & her-

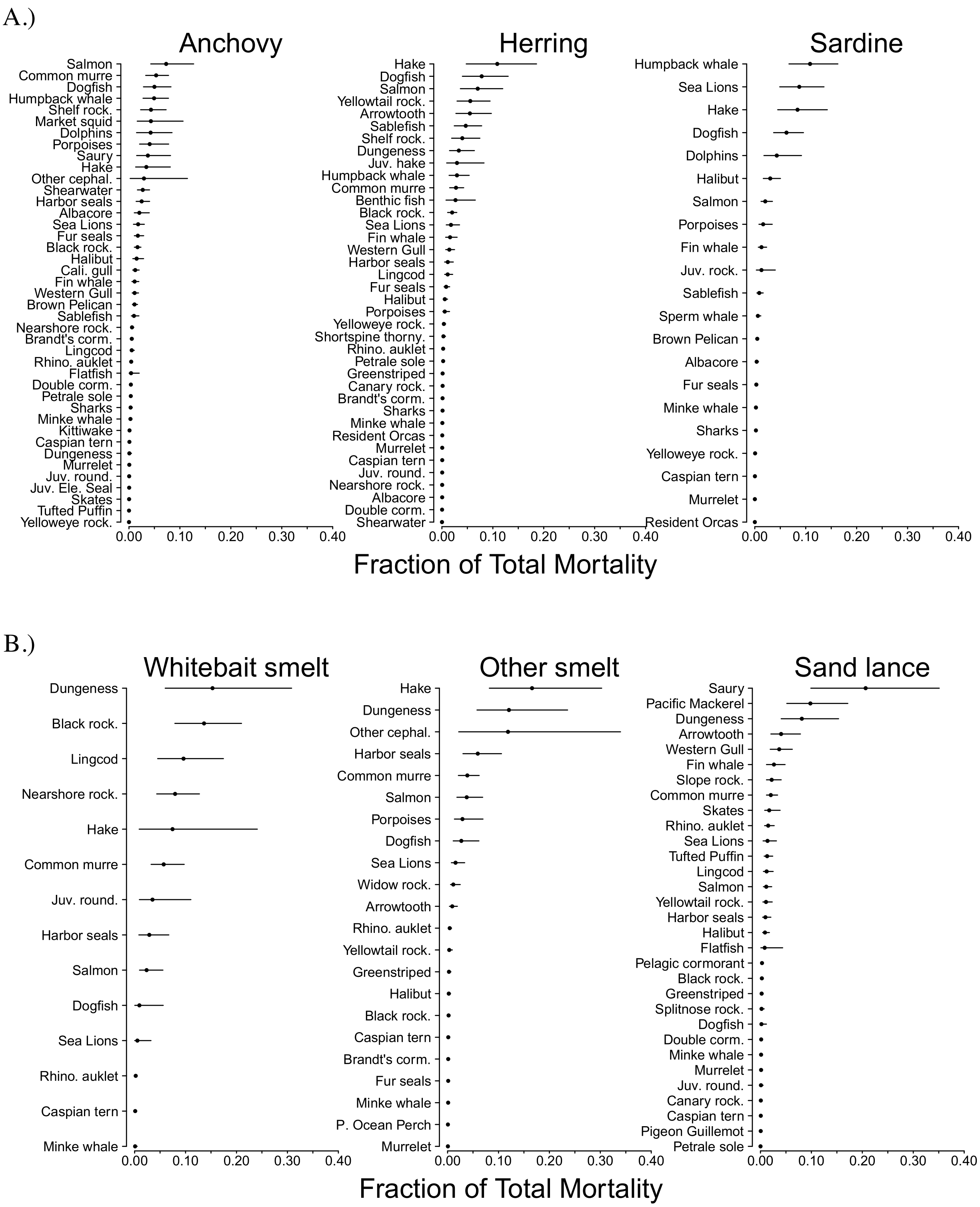

Fig. 3. Median (points and inner 95% percentile range) fractions of total mortality caused by different predators (predation mortality) across Monte Carlo draws on (A) managed forage fish (sardine, herring, anchovy) and (B) unmanaged forage fish (whitebait smelt, other smelt, sand lance).

ring) would be key if predators switched among them and these forage species had similar ecological function.

Our model revealed that mainly piscivorous seabirds, some marine mammals, and some fish might be sensitive to forage fish depletion based on diets. Common murres (*Uria aalge*), brown pelicans, marbled murrelets, and tufted puffins (*Fratercula cirrhata*) have high fractions of forage fish within their diets, particularly anchovy. Multiple species of seabirds that are dependent on forage fish currently receive or are candidates for protection under the U.S. Endangered Species Act. Marbled murrelets are listed as threatened (U.S. Fish and Wildlife, 1997), tufted puffins are being considered for listing (Hanson and Wiles, 2015), and brown pelicans were previously listed (U.S. Fish and Wildlife, 2009). These species' dependence on forage fish might have been missed if we had aggregated these species with other seabirds (e.g. Cassin's auklets (*Ptychoramphus aleuticus*) and pigeon guillemots (*Cepphus*

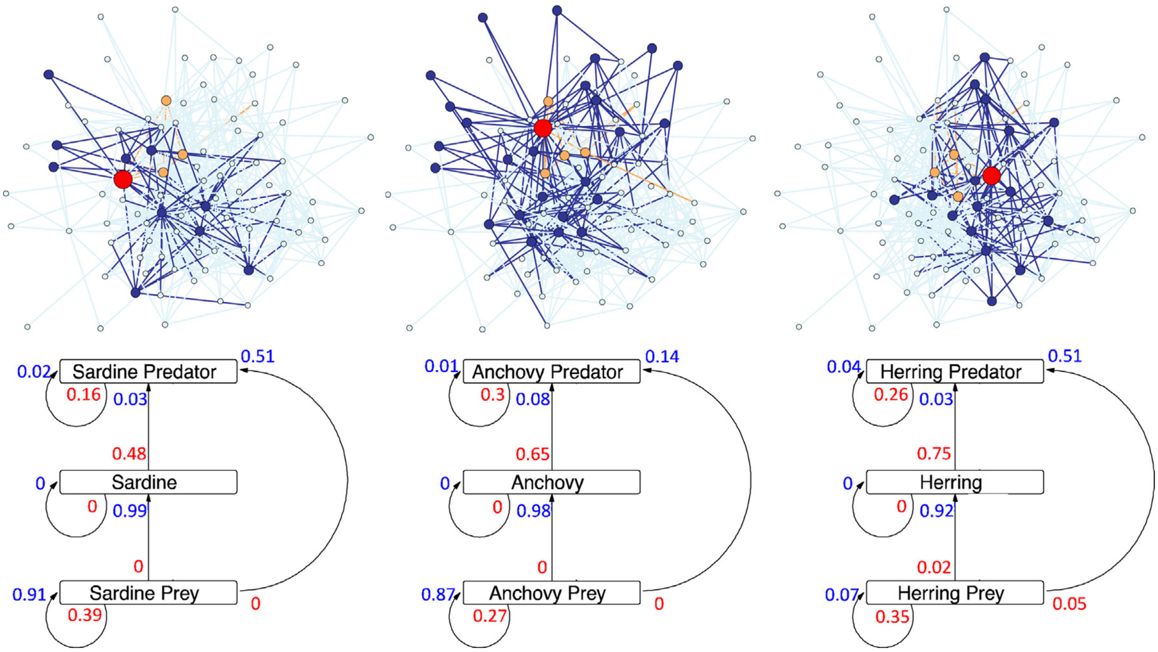

Fig. 4. Topological graphs (top) for each forage fish (in red, same order as bottom graphs), forage fish predators (blue), forage fish prey (orange) and all other functional groups in the model (light blue) for diet proportions and predation mortality fractions greater than 5%. Energy flow diagrams (bottom) show diet fractions in blue and predation mortality proportions in red. Predators of forage fish and prey of forage fish were aggregated using methods similar to Gaichas et al. (2009) and only included for diet fractions and predation mortality fractions greater than 5%.

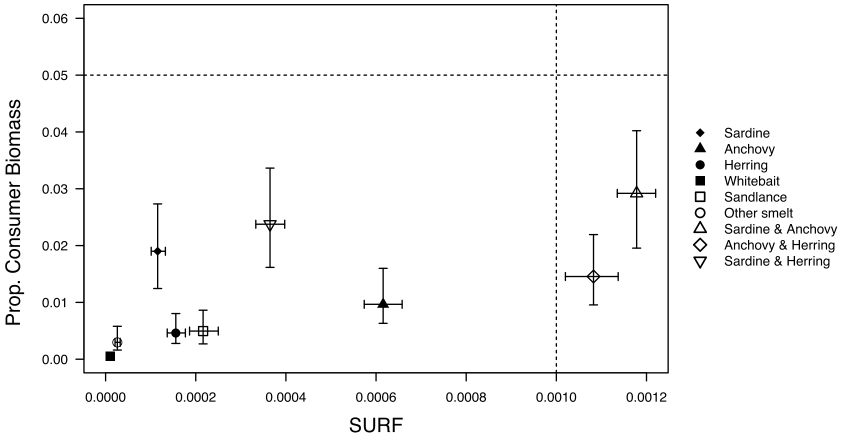

Fig. 5. Median values (with inner 95% percentile range) for two metrics of species importance – proportion of consumer biomass (Smith et al., 2011) and SURF (Supportive Role to Fishery ecosystem, Plagányi and Essington, 2014) – for nine forage fish functional groups, including individual species and pairs of forage fish (anchovy & herring, sardine & anchovy, and sardine & herring). Dotted lines are thresholds for each metric above which a species is considered "key", which equal 0.05 for proportion of consumer biomass and 0.001 for SURF (values come from Smith et al., 2011 and Plagányi and Essington, 2014). No single species is key based on either metric but two pairs of forage fish (anchovy & sardine and anchovy & herring) are key based on the SURF index.

columba)) that are less dependent on forage fish, as other models have (Field, 2004; Kaplan et al., 2013). These diet dependencies can translate into population responses of seabirds (lower reproductive success or survival) with reductions in prey abundance below threshold values (Furness, 2007; Cury et al., 2011; Robinson et al., 2015). Some marine mammals have high consumption of sardine, possibly because sardines are generally distributed further offshore than many other forage species (Zwolinski et al., 2012). In contrast, few fish predators had large diet proportions of forage fish (exceptions were salmon (*Oncorhynchus* spp.), arrowtooth flounder (*Atheresthes stomias*), halibut (*Hippoglossus stenolepis* and *Paralichthys californicus*), lingcod (*Ophiodon elongatus*), black rockfish (*Sebastes melanops*), and near-shore rockfish (*Sebastes* spp.)), which is consistent with the notion that many piscivorous fish tend to be generalist predators. However, it is unclear if marine fish exhibit prey switching responses with changes in prey availability (Rindorf et al., 2006).

No single forage fish species met either criteria for being a "key" species (SURF or proportion of consumer biomass); meaning that dynamic models would generally not predict widespread ecological effects from depleting individual forage fish species. We note that the models used to generate threshold values for the criteria were never as taxonomically detailed as the model described here (see Plagányi and Essington, 2014), so additional testing of the criteria is needed to see if their predictions hold for more taxonomically complex food web models. The absence of any single forage fish being designated "key" was likely due to the broad distribution of predator feeding among many prey items. However, we did identify ecologically plausible forage fish functional groups consisting of pairs of species that would be deemed "key", if the species were a single, combined functional group from the perspective of predators (i.e. predators could readily switch between these species according to their relative abundance). We considered groupings to be plausible if the two forage fish had overlapping spatial distributions and if they co-occurred in predator diets (with spatial overlap, these may also be plausible pairings for fisheries because of shared gears for these species). Among the three main forage fish species, sardine & anchovy and anchovy & herring were the most plausible pairings. Sardine is the most offshore of the three species, anchovy are intermediate, and herring are the most near shore (Zwolinski et al., 2012). Additionally, herring are mainly concentrated in the Northern half of the model domain (Zwolinski et al., 2012), anchovy occur in the full North-South range of the model (Checkley et al., 2008), and sardine occur in the full North-South range of the model; spawning in the South off of California and migrating North in summer, but being mainly concentrated in the Southern half in low population years (see Checkley et al., 2008). These distributional gradients are evident in the estimated diet fractions for predators, where some predators feed substantially on either sardine & anchovy (e.g. brown pelican, halibut, minke whales (*Balaenoptera acutorostrata*)) or anchovy & herring (e.g., salmon, western gull/glaucous-winged gull *Larus occidentalis* and *Larus glaucescens*), but few predators have a high diet proportion of both sardine & herring.

Though the above criteria of key species did not suggest large ecological effects of depletion of a single forage fish species, other characteristics not captured adequately by these methods, could lead to ecosystem effects. For example, quality of food (e.g. size, energy content) has been linked to predator population dynamics through effects on vital rates, notably reproductive success (see review in Österblom et al., 2008). Also, many predators are central-place foragers (return to a central, home base, usually to feed young, between foraging trips), specifically seabirds and some marine mammals. Because of this, abundance of forage fish near breeding colonies or haul out sites at specific times of the year can limit reproductive success (Furness and Birkhead, 1984; Lewis et al., 2001), and may be more important than the overall abundance used in these criteria. Therefore, certain forage fish may have been identified as key if smaller regions were considered (not the entire California Current), specifically when considering forage fish that are more localized to only part of our larger domain (i.e. higher concentrations of herring in Northern portion, specifically British Columbia). At a broader scale, distributional shifts of forage fish in the South Benguela ecosystem have been linked to reduced survivorship of African penguins (*Spheniscus demersus*) (Robinson et al., 2015), and shifts have occurred for certain forage fish in the California Current (Brodeur et al., 2006; Fiedler et al., 1986).

The food web model revealed widespread intraguild predation (Polis et al., 1989) at multiple levels of the food web, showing this food web does not have structural characteristics of a "wasp-waisted" system, which makes it difficult to predict impacts of forage fish depletion. Intraguild predation, where species both consume and compete with their prey, was common. Forage fish predators both consumed forage fish and shared prey of forage fish, while forage fish prey often predated on each other. Much of the overlap in diet between forage fish and predators was due to consumption of euphausiids, while overlap between forage fish and prey was due to consumption on phytoplankton. Therefore, there are many pathways through which energy can flow. This is in contrast to characterization of forage fish in other upwelling systems (Cury et al., 2000), where food webs are "wasp-waisted", whereby a small number of planktivorous forage fish dominate the mid-trophic level of food webs and energy flow to predators is concentrated through those species. However, models to describe these systems have not been taxonomically detailed (see Essington and Plagányi, 2014), and it has been suggested that no eastern boundary upwelling system is wasp-waisted (Fréon et al., 2009). Other studies of specifically the Northern California Current food web also showed that this system does not appear to have structural characteristics of a wasp-waisted system and noted the importance of euphausiids as prey for multiple trophic levels (Miller et al., 2010; Ruzicka et al., 2012). Miller et al. (2010) characterized the system as having "bottom-up omnivory" (bottom-up control with organisms feeding at multiple trophic levels) and our results support this conclusion. Intraguild predation could lead to complex responses of components of the food web to forage fish depletion and these indirect food web linkages make it difficult to predict the effects of species removal in complex food webs (Yodzis, 2000).

Despite this complexity, we identified specific species that mainly have only direct linkages with forage fish. Namely, piscivorous birds were particularly dependent on forage fish, are not preyed upon by other forage fish predators, and do not have much overlapping diet preferences with forage fish. Groups such as these might show more predictable negative responses to depletion of forage fish because of these attributes.

The model described here is the first Ecopath foodweb model for the entire spatial domain of the California Current Ecosystem (British Columbia, Canada to Baja California). Though other models have been constructed for the Northern U.S. portion (Field, 2004; Ruzicka et al., 2007), distributions of many species considered, including forage fish and their predators, extend for the entire California Current region, either for the entire year or through-out the year (i.e. migrations). For example, sardine spawn in the Southern portion of our model domain but adults migrate North in the summer (Checkley et al., 2008). Additionally, many predator species migrate from one portion of the domain to another depending on season or expand their distribution when not breeding. For example, male California sea lions (*Zalophus californianus*), Pacific hake (*Merluccius productus*), and many seabirds undergo seasonal latitudinal migrations (Odell, 1981; Tyler et al., 1993; Agostini et al., 2006). Because this model integrates these spatio-temporal phenomenon, the model does not capture dependencies that occur at finer scales

All models suffer from the limitations of data availability to parameterize them, and the model presented here is no exception. Predation on forage fish can vary across space and time (Brodeur et al., 2014; Ainley et al., 1996; Thayer and Sydeman, 2007). Though we attempted to incorporate diet studies from multiple locations for all species, these data were not available for every species. Additionally, the abundance and availability of specific forage fish species varies annually, seasonally, and on decadal scales (Brodeur et al., 2003; Litz et al., 2014) and many diet studies span only a single year and/or single season (usually summer) (Szoboszlai et al., 2015). Consequently, there may be seasonal dependencies that are not well resolved in this food web model. Our model also does not resolve the size structure of all feeding interactions between forage fish and predators due to data limitations. Finally, many of the diet studies were conducted during time periods when sardine were relatively scarce but anchovies were abundant. We therefore may have underestimated the contribution of sardine (and overestimated the contribution of anchovy) for those predators that could switch between the two, and potentially underestimated SURF for sardine (overestimated for anchovy) because SURF relies mainly on predator diet proportions (Plagányi and Essington, 2014).

Model development requires trade-offs between model breadth and detail (Walters, 1986), leading to trade-offs in potential uses of the model. Here, we emphasized taxonomic resolution of forage fish and predators, but sacrificed detail on spatial components of the model and temporal differences in parameters (specifically diet) at both yearly and seasonal time scales. We also sacrificed taxonomic resolution of lower trophic species (zooplankton and phytoplankton), which may have led to some amount of the intraguild predation between forage fish and their predators for similar prey. Additionally, environmental processes, such as climate variability, are widely known to govern productivity of forage fish species (Chavez et al., 2003; Schwartzlose et al., 1999) but are not accounted for in this model. Regardless of these limitations, this model overcomes specific limitations that were previously identified for other ecological models.

Our food web model was conducive to describing the trophic interactions of forage fish in this ecosystem, describing the diversity of predators that feed upon them, and for identifying species that are likely to be most sensitive to forage fish depletion based on diets (namely piscivorous seabirds), due to the taxonomic richness of forage fish and predators in the model. By starting with high taxonomic breadth, we were able to analyze food web connections through individual species interactions, but also aggregate species in different combinations as needed for alternative perspectives. Building a model with this level of breadth is data intensive, but allows for more thorough identification of predators most dependent on forage fish species. At the same time, high taxonomic breadth of individual forage fish lowered the apparent "key-ness" value of individual forage species compared to more aggregated models that combined multiple forage fish into a single compartment Finally, because of the complexity in food web dynamics revealed here, such as intraguild predation and the lack of wasp-waisted structure, trade-offs between forage fish fisheries and predators are not clear and identification of these will require additional modeling or empirical study

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.ecolmodel.2016.05.010.

Data deposition: Data reported in this paper and R codes are available at https://github.com/koehnl/CalCurFoodWebModel ECOMOD.

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