Advances in Models for Assessing Interactions of Forage Fish and Their Predators and Application to Ecosystem Based Fisheries Management (EBFM)

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A dissertation

submitted in partial fulfillment of the

requirements for the degree of

Doctor of Philosophy

University of Washington

2019

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Program Authorized to Offer Degree:

School of Aquatic and Fishery Sciences

University of Washington

Abstract

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Ecosystem-based fisheries management (EBFM) involves considering tradeoffs between competing objectives in fisheries management. Forage fish world-wide are an important prey source for a wide range of predators but also support profitable fisheries. These two key ecosystem roles create potential tradeoffs; exemplifying a key EBFM issue. Commonly, large ecosystem models are used to explore these tradeoffs and interactions between forage fish, fisheries, and predators. However, structural assumptions of previous models create limitations for assessing tradeoffs. In this dissertation, I advance two models of varying complexity and apply a third, for the exploration of forage fish fishery-predator interactions, and reveal insights into these interactions that previous models could not. I explore forage fish-predator interactions through a large ecosystem food-web model with high taxonomic resolution of forage fish and

their predators (Chapter 1) and potential tradeoffs of fisheries on these forage fish (Chapter 2). I also explore specific seabird-forage fish interactions through an ecological detailed seabird model (Chapter 3) and consider future avenues for EBFM implementation (Chapter 4). In the first chapter, I demonstrate that high model taxonomic resolution reveals lower ecological importance of individual forage species and lower reliance of predators on individual forage species (more generalist diets) in a large upwelling system, compared to models where species are aggregated into guilds. Though there are multiple pathways of energy flow in a system, Chapter 2 demonstrates that there are still tradeoffs to fishing forage fish, particularly large losses of non-market predators like seabirds and marine mammals. In many cases however, predator losses were only observed with increased fishing on a single forage fish species, so aggregation of forage fish species in models exaggerates tradeoffs of certain forage fish fisheries. Based on the key tradeoffs between forage fish catch and seabird conservation, in the third chapter, I demonstrate that in order to robustly apply ecologically-complex seabird models to further explore the impacts of forage fish availability on seabirds, more empirical information is needed on relationship between prey availability across a range of seabird demographic parameters. Finally, in the fourth chapter, I demonstrate that the capacity exists to apply a structured-decision making process for implementation of EBFM that explicitly addresses fishery tradeoffs. These results demonstrate the importance of constructing models around a specific question or objective to reveal insights into ecosystems that can help direct and focus future management and research.

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ACKNOWLEDGEMENTS

First and foremost I would like to thank my advisor, Dr. Timothy Essington, without whom this dissertation would not have been possible. Not only was it a perfect match in timing – Tim had funding for the exact project I wanted to do – but also a perfect match in mentorship at that time in my life. Thanks to Tim, I am a more well-rounded scientist than I was at the beginning of my dissertation. Tim was guiding but also encouraged me to think for myself – doing each in the perfect amounts that through our time together, he instilled a level of confidence in myself that I never thought was possible in a discouraging science world. Without that confidence, I'm not sure I could have tackled the projects presented in this dissertation. His consistent, unwavering confidence in my ability built up my belief in myself.

Thank you to my committee for also pushing me to be the best I could be. Dee Boersma – thank you for opening my eyes to the world of research science, providing me with countless opportunities to grow as a scientist, and for giving me my tough skin to persevere in the face of rejection. Thank you as well for always keeping me grounded in my ultimate life goal – conservation. To Phil Levin, thank you for encouraging me to look at the bigger picture and to consider it from all perspectives. Thank you also for giving me hope that the research I do is not for nothing. Chris Anderson, thank you for the countless times that your questions made me consider components of my research I would have never thought of and thus made my science that much more vigorous and strong. Thank you Ryan Kelly for being a consistent support system towards the end of my dissertation.

I would also like to thank all my collaborators on these dissertation chapters as well as on other side projects – thank you for your support, encouragement, multitude of knowledge and advice, and always being a joy to work with. Specifically (in no particular order), Bill Sydeman, Julie Thayer, Amber Szoboszlai, Jeff Hard, Alida Bundy, Lee Anderson, Ed Houde, Tony Smith, Christian Möllmann, Courtney Carothers, Leah Gerber, Jim Sanchirico, Kenny Rose, Felicia Coleman, Jonathon Grabowski, Olaf Jensen, Andre Punt, Tessa Francis, Charlotte Boyd. And thank you to Isaac Kaplan for always pushing and expanding my modeling knowledge and always making me feel like I was an invaluable contributor. Thank you to Kristin Marshall for being my rock during the Lenfest project, providing me with a strong female mentor in fisheries policy that I could learn from, and showing me, by example, how to be a good mentor to young women in our field. Thank you to the countless number of people who contributed data or information to the construction of the multiple models within this dissertation – you were all so kind and helpful.

My research was made possible by funding from the Pew Charitable Trusts, the Lenfest Ocean Program, and the Tomlinson endowment to SAFS. Thank you to Kathryn Matthews and Charlotte Hudson for their leadership within Pew/Lenfest and mentorship throughout my time working with them. Thank you to the American Fisheries Society for various travel grants to attend conferences all over North America. Also, thank you to the Ocean Modeling Forum for the opportunity to expand work in this dissertation to a broader collaboration and further research.

I would like to thank my friends from all walks of life. The people who have been a constant source of entertainment, relaxation, and advice throughout grad school and before. All my friends from undergrad and high school, thank you, I'm not going to name you here for fear I'll miss someone! I especially want to thank Abby for being my soul-sister in science and for always knowing how to best distract me when I need a break. To my friends from the penguin lab, you guided me when I first started out on this science path and provided me with invaluable advice and help as I navigated academic life; specifically, Eric Wagner, El Lee, Olivia Kane, Jeff Smith, Jack Cerchiara, Natasha Gownaris, Ginger Rebstock, Caroline Cappello, and Katie Holt. To my friends/mentors from NOAA Protected Resources – Lisa Manning, Celeste Stout, Chelsey Young, Angela Somma, Therese Conant, Maggie Miller, Jenny Schultz, Heather Austin - thank you for showing me how to stand by the science and stand strong in the face of questioning and to never waver in my principles.

To the strong women from the Essington lab that began this journey with me – thank you for being my shoulders to cry on and my constant supporters. To Megsie Siple, my forage fish partner, thank you for being my partner in crime and always boosting my confidence in my work and having the most positive, encouraging outlooks on my research. To Christine Stawitz, thank you for always lending me a hand and for reminding me that me and my work have value – your consistent optimism but realism always saw me through some low times. To Kiva Oken, thank you for being a constant, helpful mathematical guru and always making me smile with your infectious joy for quantitative science. To Halley Froehlich, for being a strong female mentor, showing me the way in grad school, being a constant, reassuring presence, and for being someone I could laugh with about random pop-culture things to keep me sane. To Pam Moriarty, thank you for being a voice of wisdom and reflection that was questioning but supportive and bettered my science as well as myself. To Emma Hodgson, my office mate, you were never too busy to listen to me and I made it through many tough times thanks to you. Your unwavering support kept me afloat. You always inspire me to push the science that I'm doing and to be a better person. To the unofficial Essington grad student, Nis Sand Jacobsen, thank you for consistent insightful comments on my research and for being my pal at many, many conferences. Additionally, for all the new members of the Essington lab, Morgan, Sean, Habib, Andy, and Elizabeth, you are the most warm, friendly people and I'm sad that I don't get more time with you. I have no doubt you will all do great things in your science careers.

To my family – Mom, Dad, Christina – I love you. Mom and Dad you always encouraged me and pushed me to be better and instilled in me a drive to never give-up, which was vital for my accomplishments in grad school. You always believed in me, so I always believed in me. And, thank you for allowing me to take a hurt seagull to a wildlife rehabilitation center when I was six and beginning a life-long love for wildlife, birds, conservation, and the ocean. Christina, thank you for being a strong, independent woman and giving me something to live up to. To my second family – the Mahers – thank you for constantly supporting me and making me feel like everything I was doing was the coolest thing ever. To my baby, Wishpoosh the cat, thank you for always being the most calming presence and always being by my side.

To Ryan, without whom, I would not have survived. You are the one bright spot whenever I am lost, scared, anxious. You remind me of what's important in life. I am forever in your debt for everything you've done for me, especially for putting up with me when I was most stressed throughout grad school. You always brought me back to a happy place. You always helped me to see the light when all seemed lost and you fueled that light – never ceasing to make me smile. I love you and hope beyond anything that all the support and love you have shown to me that I can forever repay to you.

DEDICATION

To the Great Auk and the Steller’s Sea Cow; that others do not share your fate.

INTRODUCTION

Fisheries management has begun to move away from a single-species focus towards a more holistic, place-based focus, known as ecosystem-based fisheries management (EBFM). However, the majority of fisheries are still managed around maximizing catch of a single species without considering the larger ecosystem including habitat, climate, and species interactions. This can lead to unintended direct or indirect impacts on other ecosystem components (Ecosystem Principles Advisory Panel (EPAP) 1999). These unintended impacts include, but are not limited to, the removal of non-target species or protected species as by-catch, impacts on survival or reproduction of a species due to depletion of their prey source, or destruction of essential fish habitat (Jennings and Kaiser 1998). EBFM strives to maintain all key ecosystem services that a system provides while accounting for the relationships between ecosystem components, including humans, and considering multiple societal objectives (Pikitch et al. 2004, Fogarty 2014). Though managers and scientists have long recognized that fisheries management should consider multiple ecosystem components and interconnections between them, the incorporation of many EBFM principles into current management has been limited (Skern-Mauritzen et al., 2016; Marshall et al., 2019). Despite the slow uptake, several tools exist for use in EBFM at varying levels of complexity, depending on data availability and the management questions or objectives (Smith et al. 2007), and a wide range of tools is needed to support the implementation of EBFM.

The indirect effects of forage fish fisheries on the ecosystem are a common EBFM related issue. Forage fish both support profitable fisheries (Pikitch et al. 2014) and are a main prey source for a range of valued predators (Fréon et al. 2005, Furness 2007, Brodeur et al. 2014, Szoboszlai et al. 2015). This dual role of forage fish creates potential trade-offs between the direct services forage fish provide to humans through catch and the indirect services they provide to humans through their role in ecosystems, particularly as prey for other commercially harvested fish. Multiple studies have analyzed these trade-offs and the possible impacts of forage fish fisheries on forage fish predators, using a variety of tools and techniques including large ecosystem models (Smith et al. 2011, Kaplan et al. 2013), population dynamic models (Shelton et al. 2014, Robinson et al. 2015), and observational/correlative studies (Field et al. 2010, Pichegru et al. 2010). However, there are known limitations to these studies and advances can be made so that specific tools, particularly models, are better suited for use in strategic forage fish fisheries management and EBFM.

Complex quantitative food web models are commonly used to assess ecosystem impacts of forage fish fisheries, but these models can have limitations particularly if used for analyses the model was not originally constructed to address. Any model would ideally be built to address a specific management objective or question (Starfield 1997, Rose et al. 2015). Certain large food web models have been used for multiple purposes, including quantifying the impacts of forage fish fisheries on predators (see Hannesson et al. 2009, Smith et al. 2011, Kaplan et al. 2013). However, Essington and Plagányi (2014) found that many of these models did not contain enough taxonomic resolution of forage fish or their predators to identify individual predator sensitivities to fishing, as this was not the original intent of the models. Thus, large ecosystem models could be improved to better address specific questions and objectives related to predator-forage fish fishery trade-offs. At the same time, these models are time and data intensive and may not always be the best suited for the management question at hand.

Smaller, dynamic multi-species or predator-prey models and simulations can also be used to evaluate impacts of forage fish fisheries on components of an ecosystem, from a broader perspective than traditional single-species models, but with a more focused view than ecosystem models (see for example Robinson et al. 2015, Punt et al. 2016). These models are particularly useful when data are limited or a management question is focused on only a few components of an ecosystem. However, many previous models lacked specific inclusion of predator life history traits that would impact a predator's ability to access prey (especially for non-fish predators like seabirds and marine mammals), including foraging behavior, reproductive strategy, and migration (Goedegebuure et al. 2017). Therefore focused, dynamic multi-species models could be improved for certain predators to robustly evaluate fisheries management impacts on non-fished predators.

Though these modeling tools exist to analyze impacts of forage fish fisheries and EBFM in general, very few ecosystem components (including predator-prey interactions) have been incorporated into tactical management (Skern-Mauritzen et al. 2016). However, worldwide examples do exist where ecosystem approaches to management or EBFM have occurred, including examples related to forage fish fisheries. These include the use of a large ecosystem model and management strategy evaluation to determine optimum levels of fishing on forage fish considering impacts to predator abundance (Smith et al. 2016) and harvest control rules or reference points that include consideration of forage fish predator needs (Constable et al. 2000). Additionally, structured processes for the implementation of EBFM have been proposed by multiple sources (Levin et al. 2009, Fletcher et al. 2010, Fogarty 2014). Despite the multiple efforts, implementation of EBFM is still rare and it is unclear if the management capacity exists to follow proposed processes and incorporate existing tools into processes.

One potential impediment of the use of ecosystem models for the implementation of EBFM is the absence of explicit consideration and quantification of uncertainty stemming from these models (Link et al. 2012, Rose et al. 2015). This includes parameter uncertainty (variability around input parameters) and structural uncertainty (uncertainty surrounding which ecosystem processes to model and how to represent them). Many references have noted various ways to quantify and address these types of uncertainty including fitting to data, ensemble modeling, sensitivity and perturbation analysis, Monte Carlo simulation, bounded parameterization, and model weighting (Hill et al. 2007, Fulton 2010, Link et al. 2012). However, many recent ecosystem models have no explicit assessment of uncertainty (see Essington and Plagányi 2014) and certain analyses are not practical for very large ecosystem models (Fulton 2010). Therefore, advances can be made in the methods and use of various techniques to address uncertainty.

In my thesis, I advance modeling tools of varying complexity for the exploration of forage fish fishery impacts on predators, address model uncertainty, and examine the potential for further implementation of an EBFM process. One level of complexity is a large food web model that is used to quantify the impacts of forage fish fisheries on predators in the California Current ecosystem. For this model, I apply a Monte Carlo-like approach to specifically address parameter uncertainty and structural uncertainty in predator-prey functional responses. At a more intermediate level of complexity, I also present a dynamic predator-prey model, focused on seabird predators and forage fish prey. This model can be parameterized for a range of seabird life histories, and here, I explore model performance and seabird sensitivity to fishing across variations in seabird diet specialization, foraging strategy, and productivity. This analysis reveals areas of seabird life history where parameter and structural uncertainty drastically impact model behavior. Though I develop tools within this thesis that may be useful for EBFM, pathways for incorporation of these tools into management are unclear. As a final chapter, I explore case studies of current EBFM issues and management procedures to identify pathways and barriers to the implementation of an ecosystem-based decision making process and EBFM.

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Chapter 1. DEVELOPING A HIGH TAXONOMIC RESOLUTION FOOD WEB MODEL TO ASSESS THE FUNCTIONAL ROLE OF FORAGE FISH IN THE CALIFORNIA CURRENT ECOSYSTEM[1]

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

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[1] This work has been published:
Koehn, L.E., Essington, T.E., Marshall, K.N., Kaplan, I.C., Sydeman, W.J., Szoboszlai, A.I. and Thayer, J.A., 2016. Developing a high taxonomic resolution food web model to assess the functional role of forage fish in the California Current ecosystem. *Ecological modelling*, *335*, 87-100.

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.

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 2011-2013). At the same time forage fish (small, pelagic 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 shape of this trade-off relationship 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 2004-2013 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.

METHODS

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:

$$B_i * PB_i * EE_i = C_i + \sum_{j=1}^{n} B_j * QB_j * DC_{ji} \tag{1.1}$$

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 1.1) and requires a diet matrix (DC_{ji}) (Appendix A). 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 B 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 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*), sandlance (*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, *Hypomesus 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.

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 (Figure 1.1) in order to cover the distributions of many forage fish 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.

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. 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). 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).

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*) (Equation 1.1) 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 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*, (Equation 1.1) using values provided or an assigned level of uncertainty based on data quality (see Table 1.1 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 1.2). 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 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 to 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*) (Equation 1.1), we characterized uncertainty using a uniform distribution. For consumers, we used ranges of 0.5 to 0.9, and for producers we used ranges of 0.25 to 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 can't 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 1.3). 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 1.3). 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.

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.

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 have established management plans, either by the Pacific Fishery Management Council or by state agencies, and “unmanaged” forage fish (sandlance, 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 a 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 (Csardi and Nepusz, 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).

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):

$$SURF_i = \frac{\sum_{j=1}^{S} DC_{ij}^2}{L} \quad (1.2)$$

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. 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) 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.

RESULTS

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 (Figure 1.2). 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, sandlance, 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; Figure 1.3). 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 many 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 (Figures 1.2, 1.3), most likely because of the low density of seabirds.

Food Web Model Structure

Analysis of topological graphs revealed differences in food web connections among the main managed forage fish species (Figure 1.4), 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 Figure 1.4, 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 (Figure 1.4), 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, the 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.

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 (Figure 1.5). 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 (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 (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.

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 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 & herring) 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 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 food-web 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 through 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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Table 1.1 Input parameters for food web model

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 1.2.

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

Groups	B	B CV	PB	PB CV	QB	QB CV	EE	C	C CV
Pacific Mackerel	0.49184	0.15	0.514	0.05	6	0.15	-	0.02689	0.1
Sandlance	-	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

Groups	B	B CV	PB	PB CV	QB	QB CV	EE	C	C CV
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
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

Groups	**B**	**B CV**	**PB**	**PB CV**	**QB**	**QB CV**	**EE**	**C**	**C CV**
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

Table 1.2 Data quality ranking criteria to assign parameter uncertainty

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.

Fish Biomass CV	**Data Quality Ranking Criteria**
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 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

Table 1.3 Diet data quality ranking

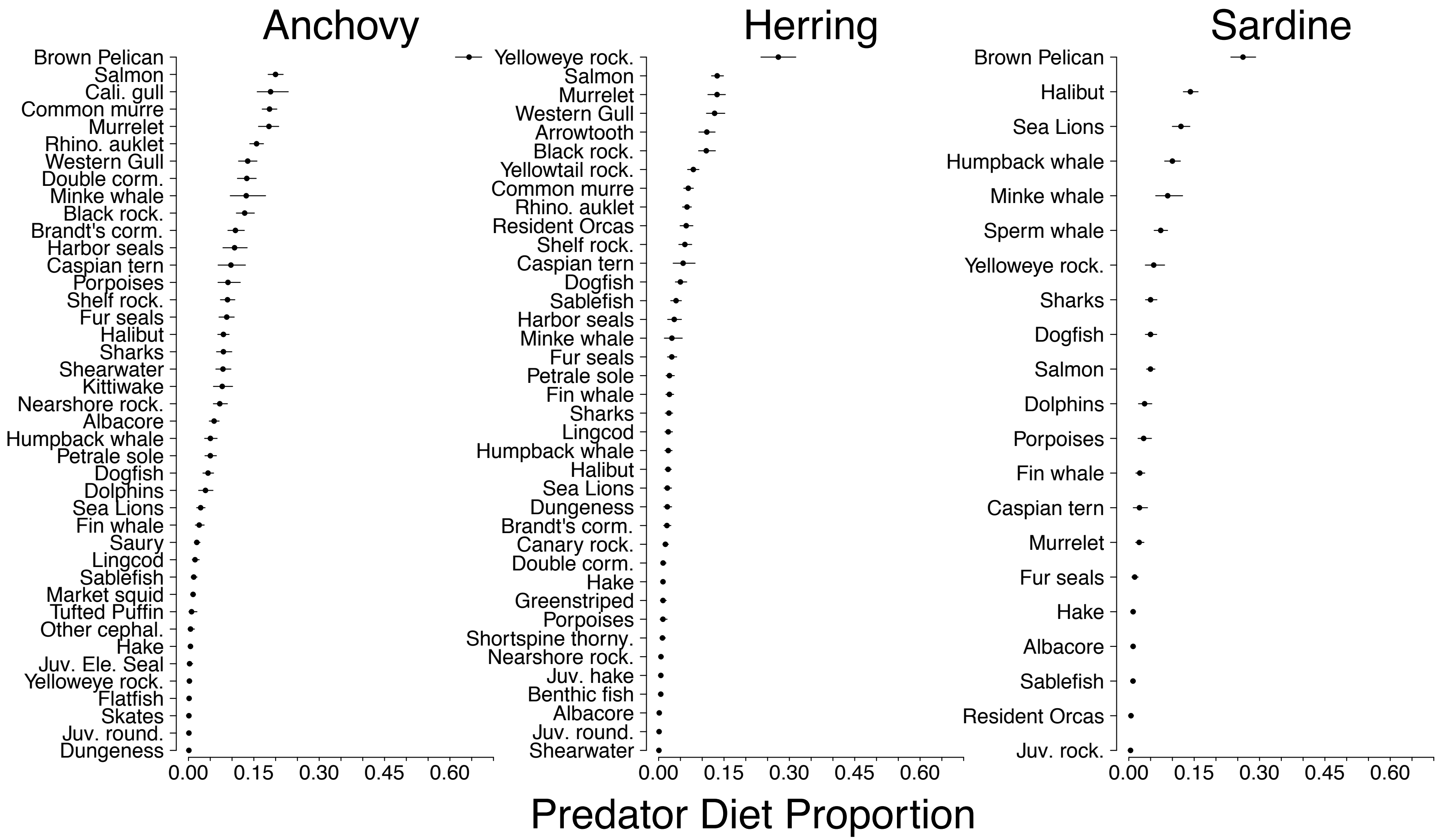
Data quality ranking criteria and relevant ranking scores for diet data for each functional group and the multiplier (related to the ranking score) needed to scale baseline diet compositions when using the Dirichlet distribution to produce relevant variability in diet distributions. To reach higher than 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

Figure 1.1 Map of model area

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).

A.)


Anchovy
Brown Pelican
Salmon
Cali. gull
Common murre
Murrelet
Rhino. auklet
Western Gull
Double corm.
Minke whale
Black rock.
Brandt's corm.
Harbor seals
Caspian tern
Porpoises
Shelf rock.
Fur seals
Halibut
Sharks
Shearwater
Kittiwake
Nearshore rock.
Albacore
Humpback whale
Petrale sole
Dogfish
Dolphins
Sea Lions
Fin whale
Saury
Lingcod
Sablefish
Market squid
Tufted Puffin
Other cephal.
Hake
Juv. Ele. Seal
Yelloweye rock.
Flatfish
Skates
Juv. round.
Dungeness
Herring
Yelloweye rock.
Salmon
Murrelet
Western Gull
Arrowtooth
Black rock.
Yellowtail rock.
Common murre
Rhino. auklet
Resident Orcas
Shelf rock.
Caspian tern
Dogfish
Sablefish
Harbor seals
Minke whale
Fur seals
Petrale sole
Fin whale
Sharks
Lingcod
Humpback whale
Halibut
Sea Lions
Dungeness
Brandt's corm.
Canary rock.
Double corm.
Hake
Greenstriped
Porpoises
Shortspine thorny.
Nearshore rock.
Juv. hake
Benthic fish
Albacore
Juv. round.
Shearwater
Sardine
Brown Pelican
Halibut
Sea Lions
Humpback whale
Minke whale
Sperm whale
Yelloweye rock.
Sharks
Dogfish
Salmon
Dolphins
Porpoises
Fin whale
Caspian tern
Murrelet
Fur seals
Hake
Albacore
Sablefish
Resident Orcas
Juv. rock.
0.00
0.15
0.30
0.45
0.60
Predator Diet Proportion

B.)

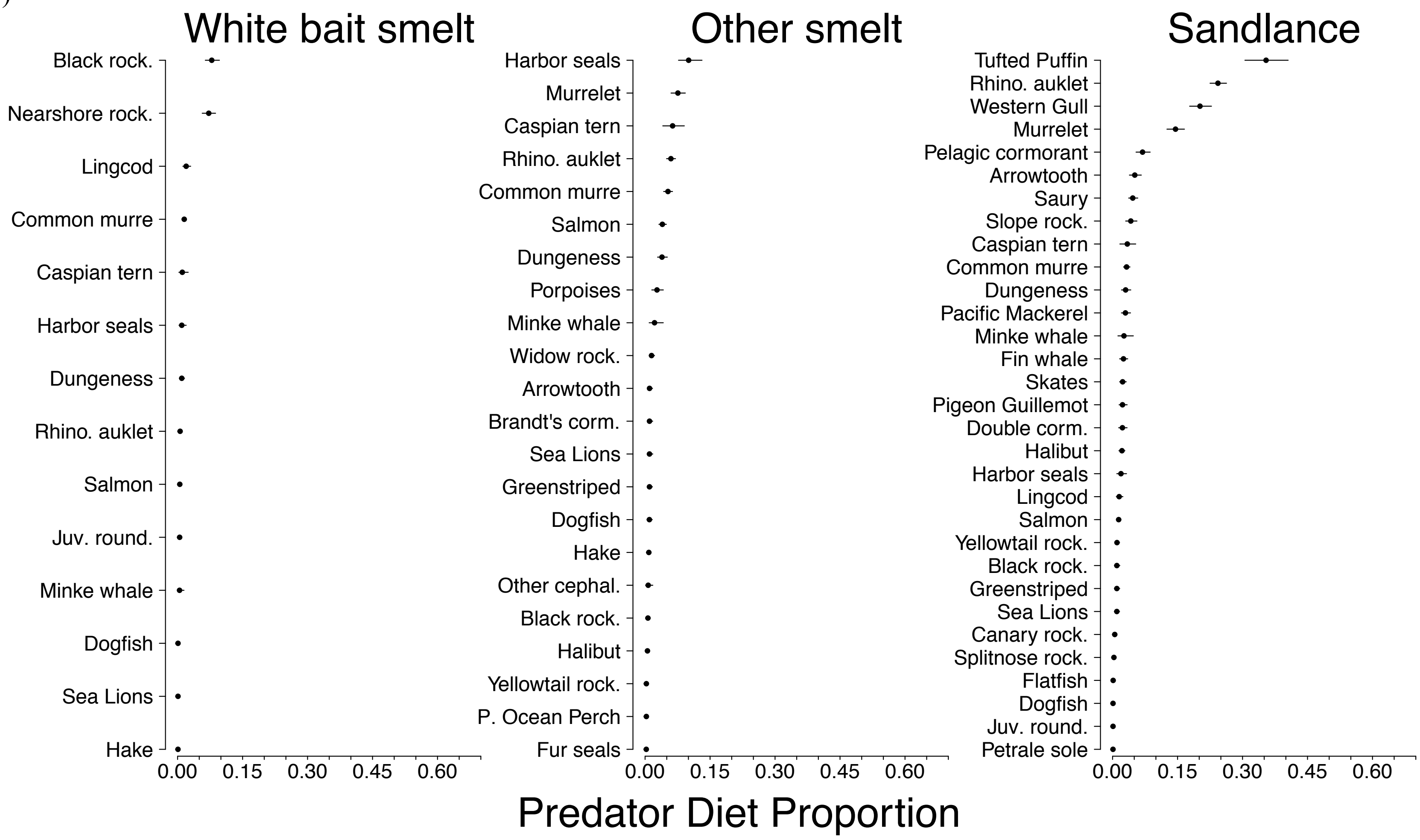
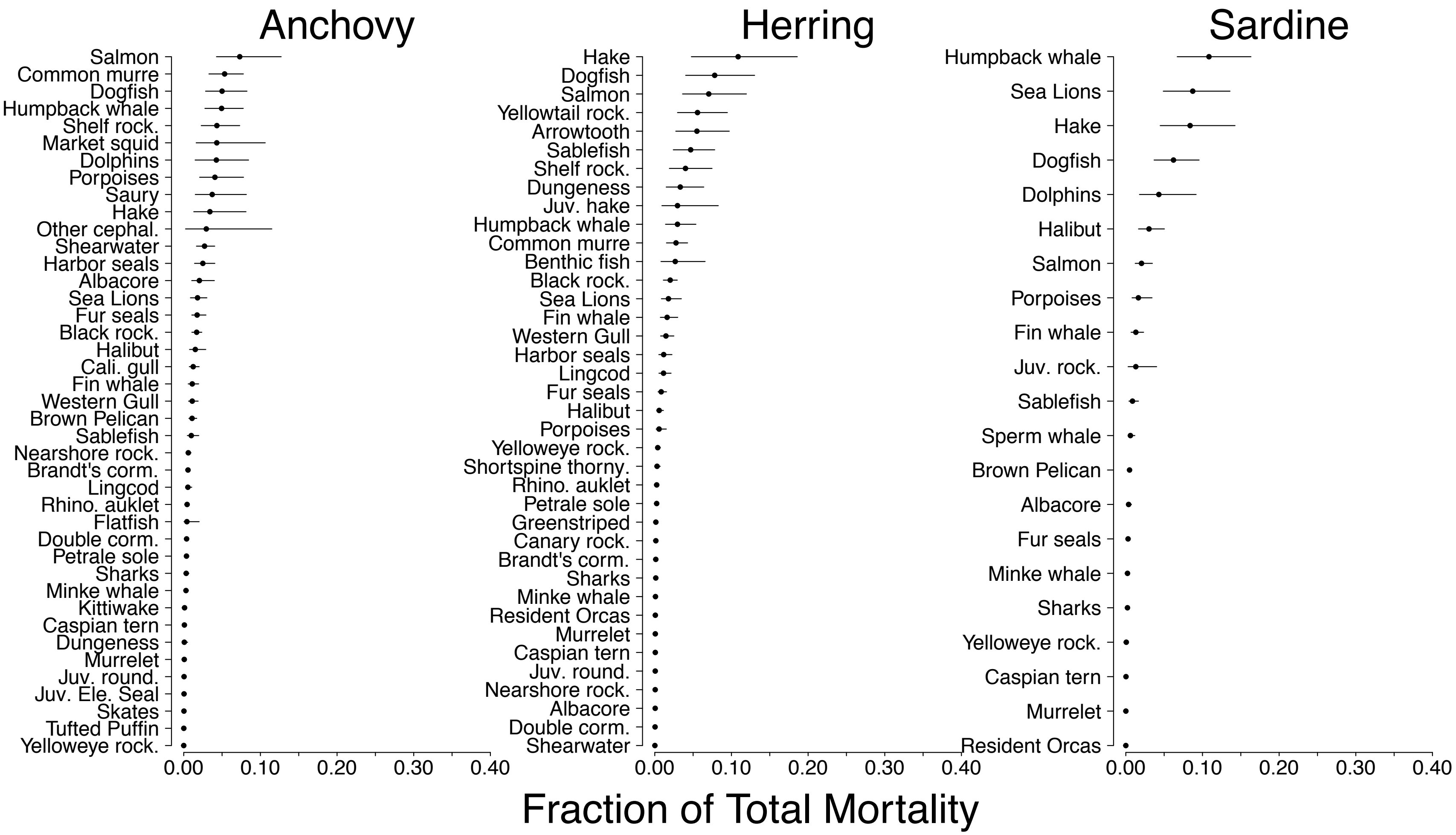


Figure 1.2 Diet proportions of predators on managed and unmanaged forage fish

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 sandlance).

A.)


Anchovy
Salmon
Common murre
Dogfish
Humpback whale
Shelf rock.
Market squid
Dolphins
Porpoises
Saury
Hake
Other cephal.
Shearwater
Harbor seals
Albacore
Sea Lions
Fur seals
Black rock.
Halibut
Cali. gull
Fin whale
Western Gull
Brown Pelican
Sablefish
Nearshore rock.
Brandt's corm.
Lingcod
Rhino. auklet
Flatfish
Double corm.
Petrale sole
Sharks
Minke whale
Kittiwake
Caspian tern
Dungeness
Murrelet
Juv. round.
Juv. Ele. Seal
Skates
Tufted Puffin
Yelloweye rock.
0.00
0.10
0.20
0.30
0.40
Herring
Hake
Dogfish
Salmon
Yellowtail rock.
Arrowtooth
Sablefish
Shelf rock.
Dungeness
Juv. hake
Humpback whale
Common murre
Benthic fish
Black rock.
Sea Lions
Fin whale
Western Gull
Harbor seals
Lingcod
Fur seals
Halibut
Porpoises
Yelloweye rock.
Shortspine thorny.
Rhino. auklet
Petrale sole
Greenstriped
Canary rock.
Brandt's corm.
Sharks
Minke whale
Resident Orcas
Murrelet
Caspian tern
Juv. round.
Nearshore rock.
Albacore
Double corm.
Shearwater
0.00
0.10
0.20
0.30
0.40
Sardine
Humpback whale
Sea Lions
Hake
Dogfish
Dolphins
Halibut
Salmon
Porpoises
Fin whale
Juv. rock.
Sablefish
Sperm whale
Brown Pelican
Albacore
Fur seals
Minke whale
Sharks
Yelloweye rock.
Caspian tern
Murrelet
Resident Orcas
0.00
0.10
0.20
0.30
0.40
Fraction of Total Mortality

B.)

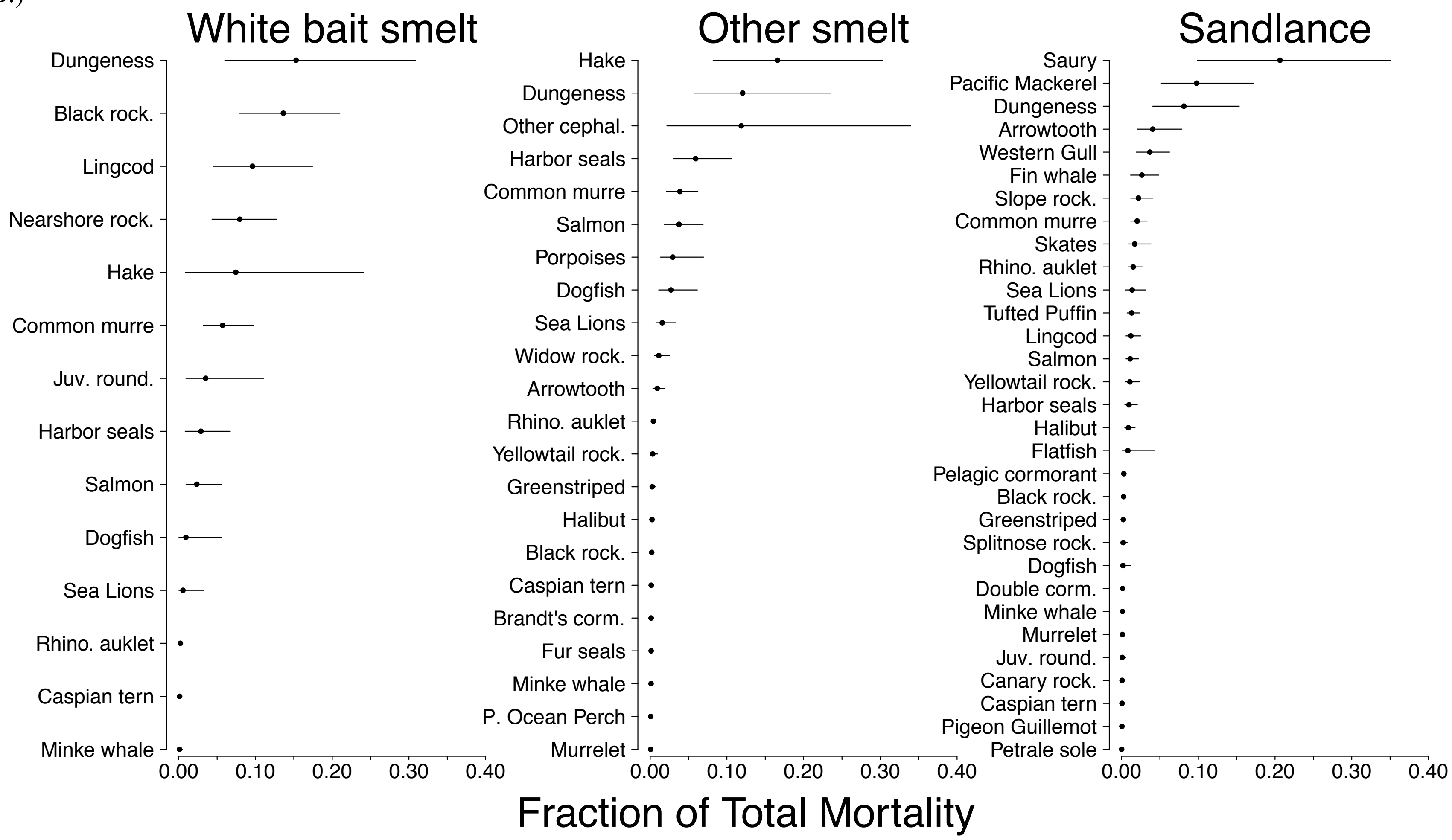


Figure 1.3 Fraction of mortality caused by different predators on managed and unmanaged forage fish

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, sandlance).

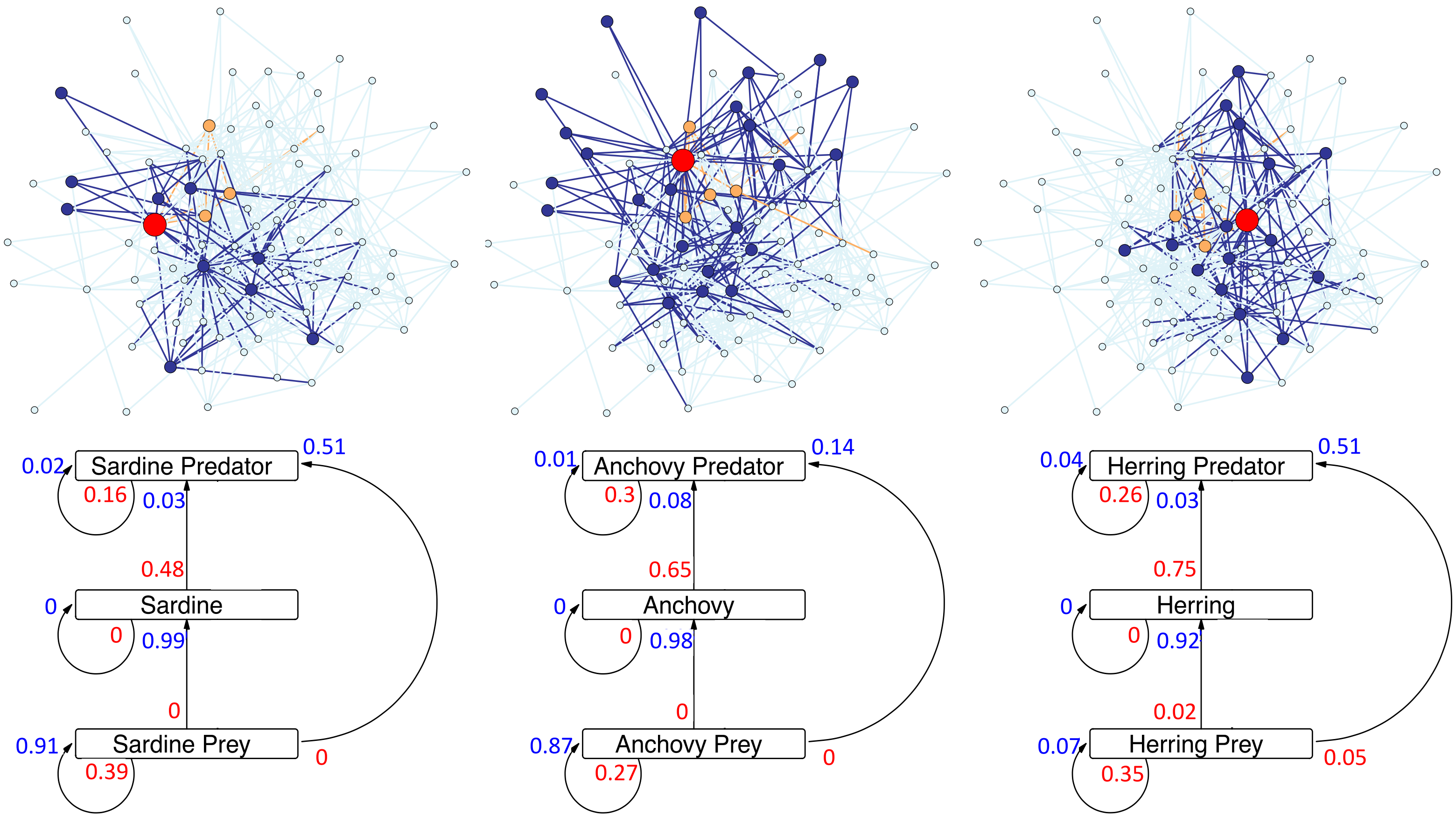


Figure 1.4 Topological graphs and energy flow diagrams for managed forage fish

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%.

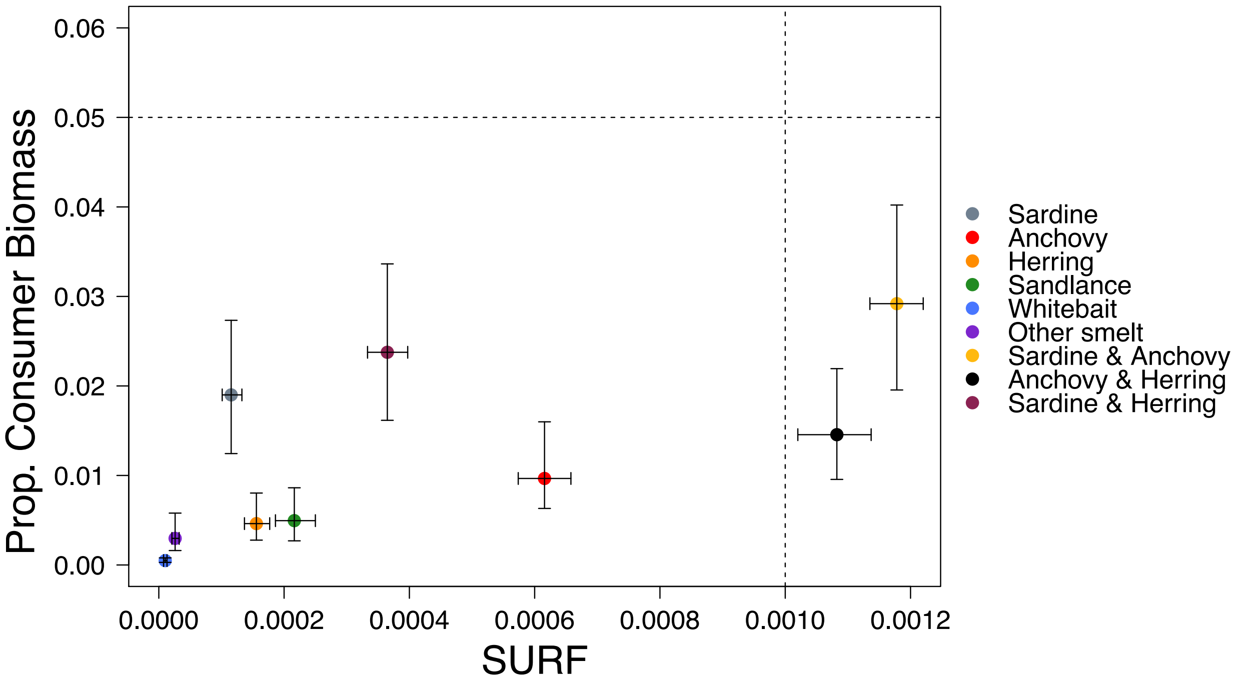


Figure 1.5 Two metrics of species ecological importance

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.

Chapter 2. TRADE-OFFS BETWEEN FORAGE FISH FISHERIES AND THEIR PREDATORS IN THE CALIFORNIA CURRENT[2]

ABSTRACT

Forage fish generate economic benefits through directed fisheries, but also generate benefits through their role as prey to other valued species (large piscivorous fish, seabirds, and marine mammals). Previous evaluations of the ecosystem consequences of forage fish fisheries used models with coarse taxonomic resolution of forage fish and their predators. Here, we quantify trade-offs between forage fish fisheries and predator fisheries, and between forage fish fisheries and species of conservation interest in the California Current, using a taxonomically detailed foodweb model and a generalized equilibrium model. We propagated uncertainty in trade-offs to forage fish fishing based on uncertainty in foodweb model parameterization and uncertainty in predator–prey functional relationships in the generalized equilibrium model. The model predicted loss in catch of some higher trophic level fisheries [mainly salmon (*Oncorhynchus* sp.) and halibut (*Paralichthys californicus*)] from fishing sardine (*Sardinops sagax*), anchovy (*Engraulis mordax*), herring (*Clupea pallasii*), or aggregated forage fish, but the lost economic revenue from predators never exceeded the economic benefit from additional forage fish catch. Predicted reductions in biomass of seabirds and marine mammals were sufficiently large that, depending on the value of these nonmarket species, consideration of nonmarket predators could tip the balance of trade-offs toward conservation of forage fish and away from harvest. This

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[2] This work has been published:
Koehn, L.E., Essington, T.E., Marshall, K.N., Sydeman, W.J., Szoboszlai, A.I. and Thayer, J.A., 2017. Trade-offs between forage fish fisheries and their predators in the California Current. *ICES Journal of Marine Science*, 74(9), 2448-2458.

work highlights specific predators [brown pelicans (*Pelecanus occidentalis*), marbled murrelets (*Brachyramphus marmoratus*), multiple other seabirds, sea lions (*Zalophus californianus*), baleen whales (Mysticeti)] that are potentially sensitive to specific forage fish fisheries in the California Current.

INTRODUCTION

A key component of ecosystem approaches to management of natural resource systems is identifying trade-offs between conflicting demands for direct services that species provide to humans vs. indirect services those species provide through their role in ecosystems (DeFries *et al.,* 2004; Leslie and McLeod, 2007). Competing demands can exist for a large variety of species in marine ecosystems where harvested organisms have key ecosystem function through habitat structuring (such as corals, Moberg and Folke, 1999), nutrient cycling (Leslie and McLeod, 2007), and/or trophic interactions (Pikitch *et al.,* 2014; Marshall *et al.,* 2016). These trade-offs create challenges in natural resource management because different management decisions will lead to changes in the allocation of benefits across societal objectives.

The management of forage fish species (i.e. small, mid-trophic level, pelagic species) exemplifies this challenge because forage fish both support profitable fisheries and are a main prey source for economically and culturally valuable predators. Moreover, these species can play key roles in structuring communities and interactions among species. Forage fish fisheries comprise ca. 25–30% of global fish landings (FAO, 2015; data from 2011–2013) with an annual catch value of $5.6 billion USD (Pikitch *et al.,* 2014) (compared to the catch value of $87.7 billion USD for all marine fisheries, Sumaila *et al.,* 2012). Forage fish landings provide multiple benefits, including food, fishmeal for agriculture or aquaculture feed, fish oil (Alder *et al.,* 2008), and bait for fisheries (Tacon and Metian, 2009). At the same time, forage species transfer energy from plankton to upper trophic levels (Cury *et al.,* 2000) and are a food source for piscivorous fishes targeted by fisheries (Overholtz *et al.,* 2000; Butler *et al.,* 2010), possibly creating trade-offs among forage fish fisheries and other fisheries. Forage fish are also a primary food source for several protected predators such as seabirds (Furness, 2003, 2007) and marine mammals (Alder *et al.,* 2008). Fluctuations in forage fish abundance can lead to changes in predator demographic traits such as adult survival (Robinson *et al.,* 2015) or reproductive success (Tasker *et al.,* 2000; Crawford *et al.,* 2006; Cury *et al.,* 2011). Given the potentially competing roles of forage fish in directed fisheries and trophic interactions, there is a need to quantify trade-offs in the exploitation of forage species to weigh the costs of potential predator losses with the benefits from direct forage fish catch.

Trade-offs have commonly been quantified using foodweb models that simulate the likely consequences of forage fish depletion on predators (e.g. Smith *et al.,* 2011; Houle *et al.,* 2013; Kaplan *et al.,* 2013; Jacobsen *et al.,* 2015), but due to structural assumptions, existing models often have limitations for assessing trade-offs. Both the magnitude and direction of responses to depleting forage fish vary across model frameworks, each of which has distinct structural assumptions (Kaplan *et al.,* 2013; Smith *et al.,* 2015). One primary structural assumption is the level of taxonomic resolution at which forage fish and their predators are represented. Foodweb models typically have multiple predators grouped into a single functional group and are not constructed with sufficient taxonomic breadth or detail to precisely capture the sensitivity of distinct predator species to depletion of forage fish (Essington and Plagányi, 2013). Some models aggregate forage fish into a single functional group rather than representing each species distinctly (Essington and Plagányi, 2013) and, therefore, may not capture predator responses that arise through depletion of individual species (Smith *et al.,* 2011). Additionally, detailed propagation of trade-off uncertainty arising from foodweb model parameter and structural uncertainty is still uncommon (Essington and Plagányi, 2013).

The California Current along the west coast of North America is a coastal upwelling ecosystem that supports multiple fished forage fish populations, including primarily Pacific sardine (*Sardinops sagax*), northern anchovy (*Engraulis mordax*), and Pacific herring (*Clupea pallasii*). As in other marine ecosystems (Pikitch *et al.,* 2014), forage fish in the California Current are a main prey source for culturally valued and protected seabirds and marine mammals including marbled murrelets (*Brachyramphus marmoratus*), humpback whales (*Megaptera novaeangliae*), and others (Szoboszlai *et al.,* 2015). Additionally, several economically and culturally valuable fish predators in this system depend on forage fish for a portion of their diet, including salmonids (*Oncorhynchus* sp., Brodeur *et al.,* 1987), California halibut (*Paralichthys californicus*, Wertz and Domeier, 1997), and albacore tuna (*Thunnus alalunga*, Glaser, 2009). These forage fish species have also supported profitable direct fisheries. The average annual ex-vessel revenue of the US catch of Pacific sardine in 2004–2013 was $13.7 million, the average annual revenue of northern anchovy catch was $1 million (Pacific Fishery Management Council [PFMC], 2014), and US revenue from herring averaged over $650,000 yearly between 2004 and 2013 (Pacific Fisheries Information Network [PacFIN], 2014).

In this study, we use a foodweb model of the California Current with high taxonomic resolution of forage fish and their predators (from Koehn *et al.,* 2016) in concert with a generalized equilibrium trade-off model (Essington and Munch, 2014) to identify the potential impacts of forage fish catch on predator fisheries and predator conservation. Specifically, we broadly sought to determine whether forage fish provide greater economic benefits as prey for other valued species or through direct harvest. To that end, we asked whether predator and fishery sensitivities to forage fish catch are variable across predators/fisheries fleets and across forage fish species. Finally, we sought to determine whether predator trade-offs to fishing forage fish are robust to uncertainty in foodweb model parameterization and generalized equilibrium model functional response assumptions.

MATERIAL AND METHODS

We used a recent foodweb model of the California Current (Koehn *et al.,* 2016) as input to a generalized equilibrium model from Essington and Munch (2014) to calculate predator responses to forage fish depletion and determine trade-offs (negative responses) and positive impacts. Briefly, the generalized equilibrium model takes information from a steady-state foodweb model (see below) to parameterize a dynamic model, so that the marginal effects of fishing forage fish can be calculated analytically and without time-intensive simulation as others have done for determining trade-offs (as in Smith *et al.,* 2011). The analytical solution first assumes the dynamic relationship that a change in abundance of a species over a change in time is a function of its abundance, growth rate, and the harvest rate it experiences. The growth rate of each species is related to prey and predator abundance. From this, we can calculate the sensitivity of equilibrium abundance to changes in catch of forage species. The advantage of the generalized linear model is that the solution is entirely analytical, allowing us to explore the sensitivity of estimated trade-offs to a wide range of alternative foodweb parameterizations.

The generalized equilibrium model of Essington and Munch (2014) presumes that each species or group in a foodweb model can be represented by the generalizable dynamic equation (as mentioned earlier):

$$\frac{dx_i}{dt} = x_i r_i(\boldsymbol{x}) - c_i \qquad (2.1)$$

where x_i is a measure of abundance of species i (here biomass), the vector $\boldsymbol{x}$ is the biomass of all species in the model, the function $r_i(\boldsymbol{x})$ is the per capita growth rate for species i given the biomass of other species (vector $\boldsymbol{x}$), and c_i is the fisheries catch of species i. The function $r_i(\boldsymbol{x})$ includes energy loss via predation and other sources, and energy gains via consumption of prey. Given this model, the marginal change in catch of any species with a change in forage fish catch equals:

$$\frac{\partial \bar{c}}{\partial c} = \{d(\boldsymbol{r}(\overline{\boldsymbol{x}})[\boldsymbol{J}_r(\overline{\boldsymbol{x}})]^{-1} + d(\overline{\boldsymbol{x}})\} \times D(\{d(\boldsymbol{r}(\overline{\boldsymbol{x}})[\boldsymbol{J}_r(\overline{\boldsymbol{x}})]^{-1} + d(\overline{\boldsymbol{x}})\})^{-1} \qquad (2.2)$$

where c is catch, $(\overline{\boldsymbol{x}})$ is a vector of equilibrium biomass values, $\boldsymbol{J}_r(\overline{\boldsymbol{x}})$ is the matrix of partial derivatives of the growth rates with respect to each state variable, and the jth column is a vector of changes in yield of all other groups given a change in yield of species j. Terms $d(\boldsymbol{r}(\overline{\boldsymbol{x}})$ and $d(\overline{\boldsymbol{x}})$ are matrices where vectors $\boldsymbol{r}(\overline{\boldsymbol{x}})$ and $\overline{\boldsymbol{x}}$ are placed on the diagonal, and terms with D of a matrix are matrices with the same diagonal as the original matrix, but off-diagonal elements are set to 0. We refer to the slope of the change in catch of a predator over a change in catch of a forage fish ($\partial c_i / \partial c_j$ in [Equation 2.2]) as S_c or the "predator catch response", and is a unitless value.

Similarly, the slope relating predator biomass for nonmarket predators (without catch) to forage fish catch is equal to:

$$\frac{\partial \overline{x}}{\partial c} = \boldsymbol{J}_r(\overline{\boldsymbol{x}})^{-1} D(\{d(\boldsymbol{r}(\overline{\boldsymbol{x}})[\boldsymbol{J}_r(\overline{\boldsymbol{x}})]^{-1} + d(\overline{\boldsymbol{x}})\})^{-1} \qquad (2.3)$$

For a change in forage fish *j*, the *j*th column of $\frac{\partial \bar{x}}{\partial c}$ is a vector of biomass changes for all other species given a change in catch of forage fish species *j*. We refer to the marginal effect on biomass to forage fish fishing as S_x or the "predator biomass response". To allow for comparisons across predators, predator biomass responses (S_x) were translated into "elasticities" (*E;* proportional change in predator biomass with a proportional change in forage catch).

The above derivations apply for any functional form for $r(\boldsymbol{x})$ (making the model generalizable), but calculating the derivatives requires that we specify a functional form. For this, we use the flexible equation used by Essington and Munch (2014). The function $r_i(x)$ is a function of the consumption of species *i* and consumption of species *i* by predators *j*:

$$r_i(\boldsymbol{x}) = GCE_i \sum_j^S \frac{f(x_j, x_i)}{x_i} - \sum_j^S \frac{f(x_i, x_j)}{x_i} - M_{0,i} x_i^{\gamma} \tag{2.4}$$

The first half of the equation represents energy gains where $f(x_i, x_j)$ represents consumption of species *j* by species *i*, and GCE_i is the gross conversion efficiency. The second half of the equation is energy losses where $f(x_i, x_j)$ is the consumption of prey *i* by species *j*. $M_{0,i}$ multiplied by the biomass of the species is the mortality of species *i* from an unspecified source and can be dictated by density dependence when γ is > 0. We define the function $f(x_i, x_j)$ as follows:

$$f(x_i, x_j) = \alpha_{i,j} x_i^{\theta_{i,j}} x_j^{\varepsilon_{i,j}} \tag{2.5}$$

where $\alpha_{i,j}$ is the search and capture rate of predator *j* on prey *i*. The parameters θ and ε can be set to account for non-linear prey-dependence (θ) (at 1 is equal to a linear functional response) and to account for predator dependence (ε) in the functional form.

We parameterized the generalized equilibrium model using parameters from the recent foodweb model of the California Current from Koehn *et al.* (2016). This foodweb model has 92 functional groups and high taxonomic resolution of forage fish (10 forage fish groups) and upper trophic predators (27 fish predators, 18 seabirds, and 15 marine mammal groups). The model extends from Vancouver Island, BC to Punta Eugenia, Mexico to capture many important predator breeding sites and the full distributional range of forage fish (specifically Pacific sardine). The model represents average ecosystem conditions during 2000–2014.

Specifically, biomass, diet, consumption, production, and catch parameters from the foodweb model are fed into the growth function [Equation 2.4] of the generalized equilibrium model. First, GCE_i is derived from the production to biomass (*P/B*) and consumption to biomass (*Q/B*) parameters from the foodweb model for each species/group. For $f(x_i, x_j)$ [Equation 2.5], $\alpha_{i,j}$ is solved for based on total per capita consumption rate of predator j on prey i, the equilibrium biomass of predator and prey (x_i, x_j), and randomly-assigned values for ε and θ (which we varied for each predator–prey pair, see below). Finally, the remaining mortality term from Equation 2.4 ($M_{0,i}$) is equal to the proportion of total mortality in a group not explicitly included via predation and fishery catch in the foodweb model.

We calculated predator responses (catch responses or biomass responses) to fishing three main forage fish from the foodweb model – Pacific sardine, northern anchovy, and Pacific herring. We also considered a second foodweb scenario where fisheries and predators can substitute freely among forage fish so that the forage fish can be considered as a single aggregate group. To do this, we combined sardine, anchovy, and herring into an aggregated forage fish group, while maintaining the same energetic and biomass properties (see Gaichas *et al.,* 2009).

We propagated uncertainty in functional response and foodweb linkages using a randomization routine where we generated 10 000 unique permutations of the generalized equilibrium model, and calculated biomass and catch trade-offs for each. First, we incorporated uncertainty in foodweb linkages by selecting for each of the 10 000 runs, one of the 500 mass-balanced randomized foodweb parameterizations from Koehn *et al.* (2016) (it was not feasible to generate more than 500, because only ~1:10 000 simulated draws met the constraint of mass balance). These 500 mass-balanced model parameterizations were found by Koehn *et al*. (2016) using a Monte Carlo approach and assigned levels of uncertainty for each parameter based on data quality rankings (mainly based on temporal and spatial scales; see Tables 1–3 in Koehn *et al.* 2016 for criteria for each quality ranking and level of uncertainty). Second, to address uncertainty in functional form, we randomly varied the parameters ε [Equation 2.4] and γ [Equation 2.5] that govern the functional form in the generalized equilibrium model, but are usually not known. For each predator–prey pair, we randomly drew unique combinations of ε_{ij} and γ_i for all 10 000 permutations. Values for ε_{ij} were randomly generated from a beta distribution (constrained to be between 0 and 1). For predator–detritus and predator–import prey pairs, ε_{ij} values were set at 1 to insure consistent sources of these diet items. Values for γ were randomly drawn from a beta distribution, constrained to be between 0 and ~0.5.

Values for θ are also usually not known, and we attempted to randomly vary θ for predator–prey pairs as well, but this led to numerical instability in solutions as is common in complex models with saturating functional response relationships. Therefore, we set $\theta = 1$ for all interactions (a linear prey response), which may be realistic for fish predators (likely no satiation effect, see Essington *et al.,* 2000), but may be less realistic for seabirds (Enstipp *et al.,* 2007; Piatt *et al.,* 2007; Cox *et al.,* 2013) and marine mammals (see Mackinson *et al.,* 2003).

In very few parameterizations (0.016%), the generalized equilibrium model predicted response magnitudes (absolute values of S_c or S_x) that exceeded 1. All of these occurred for sardine, with a total of 0.064% of all sardine predator response magnitudes exceeding 1 (0.01% of catch responses and 0.1% of biomass responses). These levels imply a greater than 1:1 dependency of predators to prey, which we deemed biologically unlikely and instead likely arose due to numerical instabilities in the inverse matrix in Equation 2.4. For this reason, we omitted slope estimates that had magnitude greater than 1 from our analysis.

We translated predator catch responses into economic values by incorporating ex-vessel price data. Price per metric ton for predatory fish came from the Pacific Fisheries Information Network (PacFIN) database (http://pacfin.psmfc.org/pacfin_pub/all_species_pub/woc_r307.php) for the year 2013 by dividing total revenue by catch. For functional groups with more than one species, we calculated an average price weighted by the catch of each species in the group. Prices per metric ton of sardine and anchovy were calculated as 10-year averages using information from the 2014 Coastal Pelagic Stock Assessment (PFMC, 2014) and were equal to \$168 and \$178, respectively, while herring price per metric ton (\$580) came from a 10-year average from PacFIN (again by dividing total revenue by total catch in metric ton). We used 10-year average prices for forage fish and only single year prices for other market fish because forage fish have higher variance in biomass between years, and biomass parameters were averaged as well (see Koehn *et al.,* 2016). Ten-year averages were used instead of the full 2000–2014 (15 years) because we lacked assessment data on all forage fish species for more recent years. We used a weighted average price based on catch to generate price for the aggregated forage group.

To make economic response values easily comparable and interpretable, we calculated the change in fishery ex-vessel values from a \$1 change in forage fish landings. We did this for five fishery fleets: halibut (California halibut and Pacific halibut - *Hippoglossus stenolepis*), salmon (*Oncorhynchus tshawytscha* and *Oncorhynchus kisutch*), hake (*Merluccius productus)*, groundfish (multiple species, with an average price weighted by landings), and albacore. The value lost or gained was termed the "revenue response value" and was calculated as:

$$\partial V_p / \partial V_f = S_C \left(P_p / P_f \right) \tag{2.6}$$

where V_p is the predator fleet value, V_f is the forage fish value, S_c is the predator catch response, P_p is the price of 1 metric ton of predator catch ($USD/metric ton), and P_f is the price of 1 metric ton of forage fish catch ($USD/metric ton). This can be interpreted as the marginal effect of additional unit value of forage fish catch on value of predator catch.

For nonmarket predators (species that are not traded in markets so have no directly observable monetary value, such as seabirds and marine mammals), it is difficult to quantify trade-offs in economic terms because the price of an individual predator is not known or easily calculated, and there is no single widely agreed upon method for estimating these values (Mendelsohn and Olmstead, 2009; Hausman, 2012; Kling *et al.,* 2012). For this reason, we inverted the problem and instead determined the predator value where the conservation benefits of forage fish to a predator equals the value gained from additional forage fish catch. This method is similar to methods used by Hannesson and Herrick (2010) to calculate what the value of sardine would need to be to make sardine more valuable as forage compared to catch. We used the predator biomass response (S_x) of a nonmarket species along with the ex-vessel value of a forage fish fishery to determine the price per individual for a nonmarket predator that is necessary for conservation losses of the predator (due to decreases in prey) to exactly equal fishery benefits from increased catch:

$$\Delta c_f / P_f = S_x / P_p \tag{2.7}$$

where c_f is the change in forage fish catch (1 metric ton), P_f is the price of forage fish, S_x is the predator biomass response, and the unknown to be solved for is the price of the predator (P_p). We termed this price value the price equivalent point (PEP; $USD/individual), which is calculated as follows:

$$PEP = P_f \left(\frac{S_x}{W_p}\right)^{-1} \tag{2.8}$$

where W_p is the average individual weight of the predator in metric tons so that PEP values are in terms of price per individual predator. Therefore, species with large negative biomass responses will have lower PEP, meaning that relatively low nonmarket values are sufficient to tip the trade-off towards predator conservation, whereas species with small magnitude responses will have high PEP. We calculated PEP values for all direct predators of sardine, anchovy, or herring and that had a consistent negative response (95th percentiles of biomass responses were negative).

For predator catch responses, biomass responses, and revenue responses, we classified the direction of an individual predator's response based on the 95 percent quantile range (0.025 to 0.975 quantiles) of responses across the 10 000 bootstrapping runs. We classified a predator (or fleet) as having a "negative" response if the 95th percentiles of responses for that predator were negative. Similarly, a predator's response was "positive" if the 95th percentiles were only positive. Response 95th percentiles that span 0 could arise if there is no response (slope = 0) or if precision in the slope estimate is low. Therefore, these responses are inconsistent in direction across runs and are not classified as a negative or positive response.

All analyses were run in R version 3.1.2 (2014-10-31) (R Core Team, 2014).

RESULTS

Predator responses were generally robust to model parameterizations. For 35–43% of predators, the majority of model runs showed a negative response (95th percentiles were negative) in response to fishing anchovy, herring, or the aggregated group. Similarly, for 30–40% of predators, 95th percentiles of responses were all positive. Only around 25% of predators had responses that varied in direction across models runs and did depend on model parameterization. In response to fishing sardine, fewer predators (57%) had responses in the same direction across the majority of runs, and 43% had ambiguous responses.

For fished predators, there was no clear pattern in catch losses or gains across predators or across forage fish species, with increases in forage fish catch (Figure 2.1). Positive and negative catch responses to fishing forage fish were equally common across fished predators (~11–37% vs. ~26–33% of predators depending on forage fish) and were similar in magnitude (average median responses of 0.0014 and –0.0012). For a given predator, many (41%) had a consistent response to fishing only one forage fish or had divergent responses to fishing one forage fish vs. another. For example, arrowtooth flounder (*Atheresthes stomias*) had a positive response to fishing anchovy, but a negative response to fishing herring. On the other hand, four predators [specifically sharks, halibut, Pacific ocean perch (*Sebastes alutus*), and splitnose rockfish (*Sebastes diploproa*)] had directionally the same response to fishing all three forage fish species and the aggregated group (though values are small and close to zero in response to certain forage fish). Additional predators had the same directional response to fishing two forage fish species, including large declines in salmon catch and large catch gains for hake.

Although catch of certain predator fleets declined, the revenue lost from the decline was never greater than the revenue gained from fishing forage fish (Figure 2.2; as represented by the 1:1 dotted line). The majority of fleets with negative responses had losses smaller than \$0.10 in response to an additional \$1 USD increase in catch of sardine, anchovy, herring, or the aggregated forage fish group. Only the salmon fleet had larger revenue losses, with median decreases of \$0.24 and \$0.16, in response to fishing anchovy and the aggregated group, respectively.

In contrast to fished predators, seabird responses were fairly consistent in direction across all seabird species, but varied in direction by forage fish species (Figure 2.3). In response to fishing anchovy, 61% of seabird species had declines in biomass. Alternatively, in response to fishing sardine or herring, the majority of seabirds (72 and 61%, respectively) had biomass gains. When forage fish were aggregated, most seabirds (56%) again all had a negative response to fishing forage fish.

Biomass losses were commonly greater in magnitude than any biomass gains across nonmarket predators (seabirds and mammals) in response to fishing forage fish (Figure 2.3). For example, 89% nonmarket predators with negative responses to fishing anchovy had losses greater in magnitude than gains for predators with positive responses (considering median values). Similarly, in response to fishing sardine, herring, or the aggregated group, 73–100% of predators with negative responses had median losses greater than gains for other predators. Median losses ranged from –0.0002 to -0.37 compared to median positive responses of $4.4e^{-5}$ to 0.036 (all proportional changes in biomass with a proportional gain in forage fish catch). At the same time, positive and negative biomass responses were as common across nonmarket predators (~30–52% positive, ~21–55% negative). Amongst the losses, brown pelican (*Pelecanus occidentalis*) had the largest losses (in response to fishing sardine, anchovy, and the aggregated group), and mammals tended to have large losses in response to fishing sardine.

The price equivalent points (PEP) – the nonmarket value at which predator loss equals value gained in forage fish catch – were commonly smaller for seabirds than mammals (Figure 2.4). Shearwaters (*Puffinus* spp.) had the lowest PEP values, with a median value of $91 in response to fishing anchovy. In other words, if the nonmarket value exceeded $91 per individual shearwater, then the lost value of shearwaters would exceed the economic benefits of an additional metric ton of anchovy catch. Other seabirds also had low PEP values, likely from relatively large negative biomass responses, with median values ranging from $100 to $14 341. PEP values for mammals were commonly larger, ranging from a median of $600 for sea lions (*Eumetopias jubatus* and *Zalophus californianus*) (in response to sardine) to above $13 000 000 for a minke whale (*Balanoptera acutorostrata*, in response to herring). However, fur seals (*Callorhinus ursinus*) and harbor seals (*Phoca vitulina*) had lower values than a few individual seabirds in response to fishing anchovy and/or herring, and sea lions had the lowest PEP value of all predators in response to fishing sardine.

The direction of response to fishing forage fish was partly explained by the importance of forage fish in predator diets (Figure 2.5). This was most pronounced for seabirds, where negative responses to forage fish fishing were associated with higher proportions of diet consisting of forage fish. For example, among the species that declined from anchovy fishing, the median proportion of diet consisting of anchovy was 0.14 (range of 0.077–0.64). In contrast, seabirds that had either no consistent response or positive responses had diet proportions ranging from 0 to 0.7%. We observed similar patterns for marine mammal and fish predators, although there was a wider range of diet proportions among predators whose responses did not differ from 0 or were positive. Also, two mammal groups [transient and resident killer whales (*Orcinus orca*)] had negative responses to fishing a forage fish, but did not consume that forage fish (though do rely on other prey like salmon that had negative responses).

DISCUSSION

We estimated changes in predator catch or biomass in response to fishing forage fish in the California Current using a method that is generalizable, analytical, integrates over all energy flow pathways of a foodweb, and explicitly accounts for parameter uncertainty. Overall, we did not find evidence that forage fish are more valuable when left in the water to feed piscivorous fish, which are, in turn, subjected to directed fisheries. However, the nonmarket value related to the conservation of many seabirds and some marine mammals may tip trade-off scales towards certain forage fish species being more valuable left in the ocean. We found losses of predator fishery catches were variable across predators and forage fish fisheries, though there were specific predator fisheries (specifically salmon and halibut) with losses in response to fishing all or most forage fish. For unfished predators, biomass losses were larger than gains across seabirds and marine mammals, creating notable trade-offs between fisheries and conservation objectives.

Though fishing forage fish led to net economic gains for fisheries (due to the additional forage fish catch), the distribution of those gains among stakeholders was not equal, creating economic trade-offs among fisheries. Specifically, large catch losses for salmon and halibut in response to fishing forage fish led to economic losses for the salmon fleet and the halibut fishery. Fishing salmon is additionally already restricted and lowered due to ESA listings (PFMC, 2016).

Fishing anchovy, in particular, had the largest negative impact on salmon, and salmon likely have a large impact on anchovy mortality (Koehn *et al.,* 2016), so future modeling effort could further explore trade-offs between these two specific fisheries. Additionally, the magnitudes of trade-offs could change over time with any changes in market prices of species or changes in the dependence of a predator on a forage fish (Hannesson and Herrick, 2010). Certain changes could result in a switch to where forage fish are more valuable as prey than as direct catch, such as increases in predator prices and/or decreases in forage fish price.

Our results suggest that seabirds in this system likely have simpler energy flow pathways connecting them to forage fish than do piscivorous fish, making seabirds potentially higher priority for future management considerations of specific forage fish fisheries. The directions of seabird responses to forage fisheries were generally predictable based on diets, with negative responses commonly associated with feeding on a forage fish species. Additionally, seabirds that consumed mostly invertebrates, other small pelagic fish [such as sandlance (*Ammodytes hexapterus*), juvenile rockfish (*Sebastes*), smelt (*Osmeridae*), etc.], or had substantially larger diets of other forage fish considered, had positive responses. In contrast, though many fish predators with diets on a forage fish showed negative responses, others showed positive or inconsistent responses, implying that the relationship between diet and fish response direction is less consistent. There are multiple energy-flow pathways connecting fish predators to forage fish because piscivorous fish in this system have relatively generalist diets, feed at multiple trophic levels, and consume both forage fish and forage fish prey (Miller *et al.,* 2010; Koehn *et al.,* 2016). Conversely, many seabirds tend to have more specialized diets (Koehn *et al.,* 2016), creating primarily direct energy-flow pathways between seabirds and forage fish. This is corroborated by other modeling studies for this system that have shown that piscivorous fish that consume forage fish (particularly hake) do not necessarily benefit from increased forage fish abundance, likely due to competition with forage fish (see Ruzicka *et al*., 2013). The stronger relationship between seabird diet and response direction created many strong, clear trade-offs for seabirds in response to fishing anchovy and clear gains in response to fishing herring and sardine, compared to fish predators.

Alternative forage fish harvest strategies, compared to constant fishing rates, could be considered to reduce indirect impacts of fishing on predators listed under the US Endangered Species Act (ESA). Many seabirds and marine mammals that we identified to be negatively impacted by forage fish fishing are currently ESA-listed including marbled murrelets (*Brachyramphus marmoratus*), humpback whales (*Megaptera novaeangliae*), resident killer whales, Steller sea lions (*Eumetopias jubatus*), and grey whales (*Eschrichtius robustus*). Previously listed brown pelicans also had large negative responses to fishing sardine, anchovy, and the aggregated forage fish group in our model. Alternative management strategies to reduce impacts could include spatial or temporal restrictions on fishing to conserve prey for central place foragers (seabirds and some marine mammals) during critical feeding periods (Boersma *et al.,* 2015). However, our model is on a coast-wide scale, and it is unclear if fishing is localized near predators. Future modeling efforts could focus the spatial resolution and test the need and effectiveness of these strategies for minimizing indirect effects of fishing on listed predators.

Declines in nonmarket predators in general, along with their potential value, could make conservation of these species an important consideration with future forage fish management decisions. Specifically, seabird conservation may be of needed consideration with the allocation of anchovy catch, due to the negative impacts for multiple seabird species, including murres (*Uria aalge*), marbled murrelets, and brown pelicans, with anchovy fishing. Additionally, seabirds are particularly sensitive to localized prey depletion, due to small body size, correspondingly high metabolic rates, and diet specializations related to limited foraging ambits in time and space (Furness and Tasker, 2000). Models also predicted large losses for certain mammals (e.g. sea lions) in response to fishing sardine. Though sardine are managed with a cut-off rule (PFMC, 2014), which theoretically maintains prey biomass for predators at low sardine abundance, anchovy fisheries lack such a control rule, and anchovy abundance in 2011 was at ~1% of historical peak abundance (MacCall *et al.,* 2016). Anchovy was previously managed with a cut-off rule in order to account for the needs of predators (see PFMC, 1990), but this was not maintained when management of anchovy and other forage was combined into the Coastal Pelagic Species fisheries management plan (see PFMC, 2014). Our predicted losses for seabirds along with the recent decline in anchovy (as well as sardine, Hill *et al.,* 2015) in this ecosystem, emphasizes the need to explore ecosystem-based harvest rules for multiple forage fish.

Many of the PEP values calculated for seabirds, and some marine mammals, are within an order of magnitude of other attempts to quantify nonmarket values, though we do not claim to know the value of these predators. The replacement costs for murre losses following the Exxon Valdez oil spill were estimated at $274 per murre (ca. $466 today) (Brown, 1992) vs. our median estimates of $100 and $656 for fishing anchovy or herring, respectively. For another species, marbled murrelet, $4 908 883 was spent on the recovery of this federally listed species in 2014 (US Fish and Wildlife, 2014). Considering the size of the US murrelet population (~16 700 breeders, Miller *et al.,* 2012) and a ten-year life span, this would likely equate to near our median PEP value of ~$4952 per bird in response to anchovy fishing. For marine mammals, most PEP values were larger than seabird values (especially for whales) which is expected because many marine mammals are less dependent on forage fish and consume larger fish as well (Szoboszlai *et al.,* 2015; Koehn *et al.,* 2016). However, sea lion PEP value in response to fishing sardine was substantially lower than estimated by Brown (1992). The study by Brown (1992) also put marine mammals prices in the tens of thousands, similar to some of our other estimated mammal prices.

Comparing results between scenarios – forage fish individually or in an aggregated group – reveals the benefit of a taxonomically resolved model for identifying specific predator sensitivities. Many seabirds had biomass losses with increasing anchovy catch, but gains with increases in sardine and herring catch (though there were exceptions). When the forage fish were aggregated and predators were assumed to switch freely between forage fish groups, many seabirds again had losses. Therefore, aggregation in this case exaggerated the losses of seabirds, making them appear negatively impacted by the depletion of any forage fish. Alternatively, there were a few mammals and fish predators with negative responses to fishing individual forage fish, but no response to fishing the aggregated forage fish group, showing that aggregation can also mask sensitivities.

The connection between predator diets and predator response directions reveals potential use of empirical diet information as indication of forage fish importance. This result supports the use of predator diet as a metric of predator dependency on forage fish to evaluate the importance of individual forage fish (e.g. Plagányi and Essington, 2014) or to predict the impacts of forage fish fisheries on predators (e.g. Pikitch *et al.,* 2012). Therefore, empirical information could potentially be used in substitution of an ecosystem model for managers to identify sensitive predators to forage fish fishing. However, forage fish in predator diet can vary spatially and temporally (Thayer and Sydeman, 2007; Brodeur *et al.,* 2014). Many seabirds in the model have zero sardine in their diet and, thereby, positive responses to fishing sardine. But most seabird diet data came from the 1970s–1980s (Szoboszlai *et al.,* 2015) when sardine were not abundant. It is unclear if the absence of sardine in seabird diet is only a reflection of diet data temporal scale, or if seabirds do not consume sardine, possibly due to the offshore distribution of sardine (Zwolinski *et al.,* 2012). Also, diets used in the foodweb model were often averaged over time possibly dampening interannual prey importance (Koehn *et al.,* 2016). Therefore, to use diet information directly as an indicator of forage fish fishing impacts, data may need to be temporally and spatially complete.

The method we used for estimating trade-offs from fishing forage fish is based only on energy flow within a foodweb, and this and other model assumptions may impact results. First, due to instability in responses, we assumed a linear relationship between forage fish availability and predator feeding response in the generalized equilibrium model, which may be appropriate for fish (see Essington *et al.,* 2000), but less so for seabirds (Piatt *et al.,* 2007). Saturation in the functional response may reduce the magnitude of impacts (Abrams and Ginzburg, 2000), and prey-switching in the response (e.g. Holling type III functional response) may do the same (see Mackinson *et al.,* 2003). Additionally, size/age structure representation is limited. The few existing "juvenile" compartments in the model were not linked to the corresponding adult compartments (Koehn *et al.,* 2016). This could decrease bottom–up effects of removing forage fish and reduce trade-offs of forage fish fishing if juveniles of predator fish compete with, or are consumed by, forage fish (as in Houle *et al.,* 2013, Jacobsen *et al.,* 2015). Alternatively, this could increase bottom–up effects and trade-offs if there is higher predation on juveniles of predator fish after the removal of forage fish (because juvenile salmon, rockfish, and hake are alternative forage prey for many predators, see Szoboszlai *et al.,* 2015). Finally, the foodweb model only looks at average abundance and interactions at an ecosystem scale and doesn't capture ecological effects of localized depletion, which may be especially impactful on central-place foragers (Furness and Tasker, 2000). Therefore, our analysis points to species and fisheries catch that are generally likely to decline with increases in forage fish catch, but the magnitude of trade-offs may be variable.

Our economic analyses only considered ex-vessel prices, but a full cost-benefit analysis of fishing a forage fish would include all sources of revenue and costs for the entire production process from supplier to consumer. For forage fish, downstream benefits along the supply chain after ex-vessel revenue include revenue from reduction factories, fish oil factories, agriculture, aquaculture, and direct consumers (see Shepherd and Jackson, 2013). Therefore, the value of fishing forage fish could be substantially greater than the value represented by ex-vessel price. However, the total values of predators may be greater as well. Predator fish also have downstream benefits or supply chains, through processors, distributors, and consumers (see Christensen *et al.,* 2011). Nonmarket predators can have additional benefits other than existence value, including ecotourism revenue (whale watching, bird watching, etc.). Because of these additional economic benefits not considered, any potential trade-offs discussed here are only at the scale of fishers and only one part of the economic environment and cost-benefit analysis.

Our trade-off results can help direct management and conservation or focus future modeling efforts. Though response magnitudes may be over- or underestimated, future modeling efforts for all forage fish could further explore specific, individual effects of fishing revealed by our analysis. This includes the predicted economic trade-offs for salmon and halibut fisheries with forage fish fishing as well as the negative impacts across multiple seabirds with increases in anchovy catch and mammals with sardine catch. It is time and data intensive to develop models of high taxonomic resolution and run trade-off analyses for multiple species and over multiple model parameterizations. However, these efforts can save time and money in the long term by prioritizing future research and management actions, in the face of uncertainty, to the species and fisheries most impacted.

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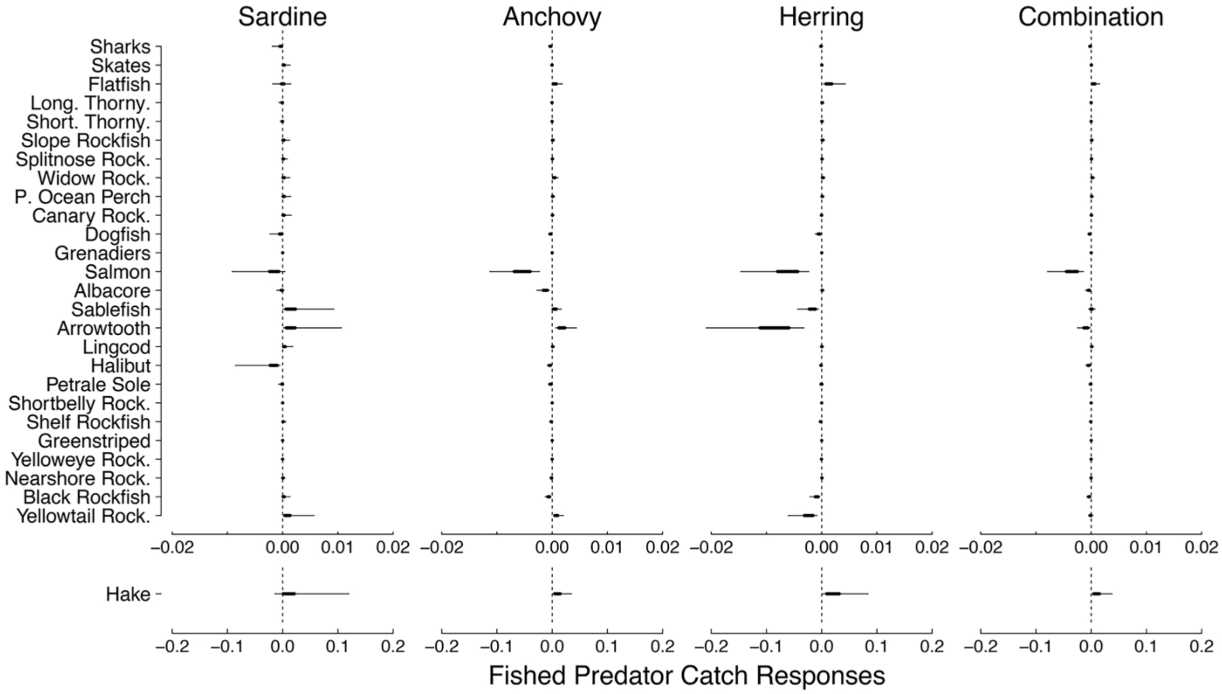

Figure 2.1 Fished predator catch responses

The effects of fishing forage fish on fished predator catches. 50th (thick line) and 95th (thin line) percentile ranges are shown for predator catch responses (the slope of the change in catch of a fished predator over a change in catch of a forage fish) in response to fishing each forage fish (sardine, anchovy, herring, and an aggregated group of sardine, anchovy, and herring) across 10 000 bootstrapping runs. Hake percentiles are wider than all other predators and are plotted on separate graphs with wider axes. A negative response means a loss in catch of the predator, while a positive response means a gain in catch.

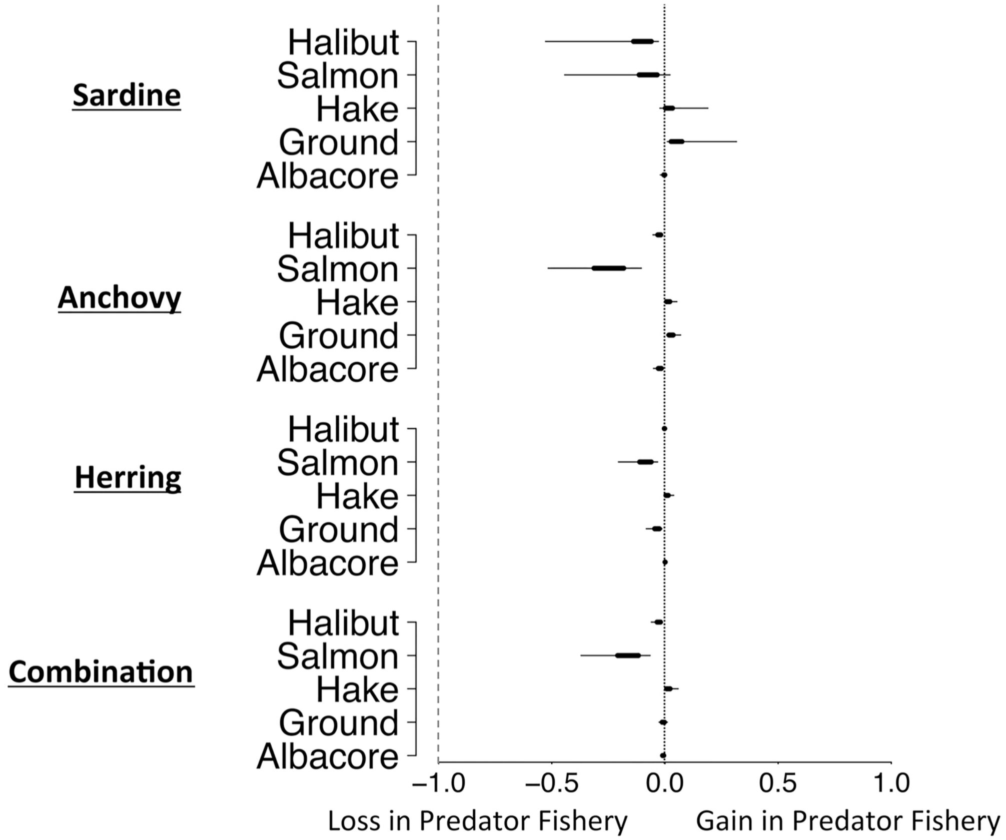

Figure 2.2 Predator fleet revenue response

The effects of fishing forage fish on predator fleet revenue. 50th (thick black line) and 95th (thin black line) percentile ranges are shown for predator fleet revenue responses (halibut, salmon, hake, groundfish, and albacore) given a $1 increase in forage fish catch (sardine, anchovy, herring, or combined group of sardine, anchovy, and herring). Values left of 0 (dotted, black line) indicate loss in catch to a predatory fishery, while values left of –$1 (dotted, gray line) indicate where losses in predator catch value exceeds the gain in forage fish value. Losses to predator fleets never exceeded gain from increased forage fish catch ($1).

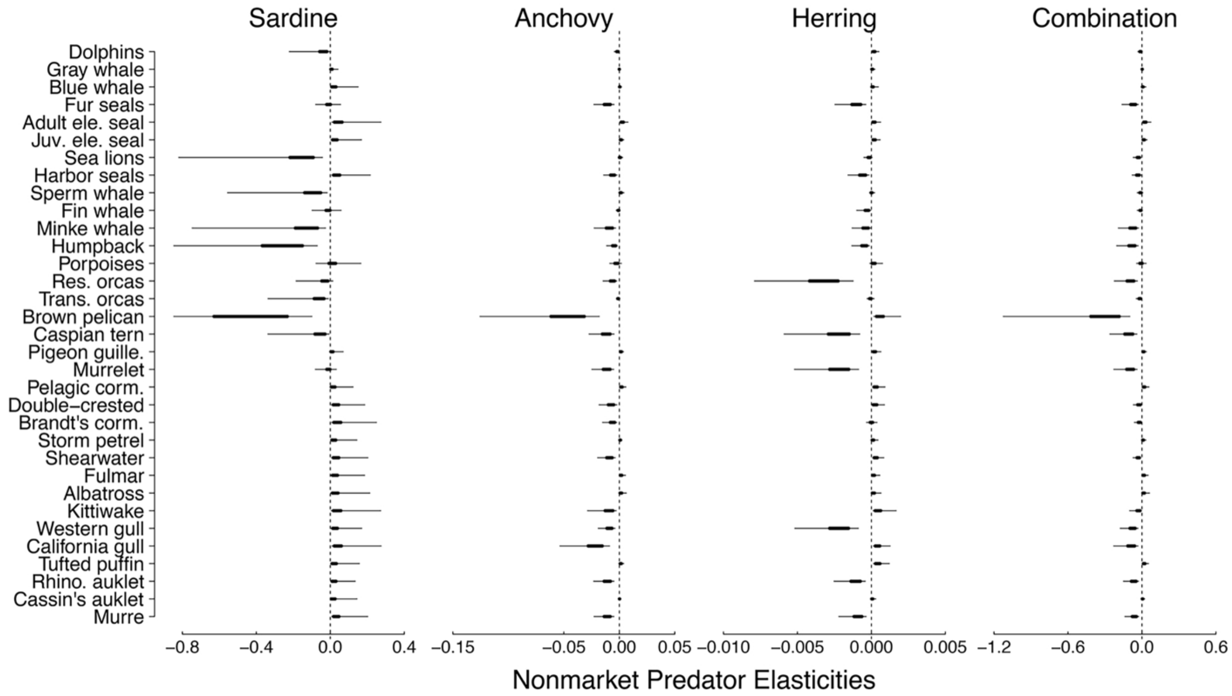

Figure 2.3 Nonmarket predator biomass responses

The effects of fishing forage fish on nonmarket predator (seabirds and marine mammals) biomass. 50th (thick black line) and 95th (thin black line) percentile ranges are shown for elasticities - proportional change in predator biomass with a proportional change in forage catch - in response to fishing sardine, anchovy, and herring separately and fishing an aggregated forage fish group (sardine, anchovy, and herring). Note the change in scale between the forage fish species/groups. Biomass losses for specific predators were commonly larger than biomass gains for other predators.

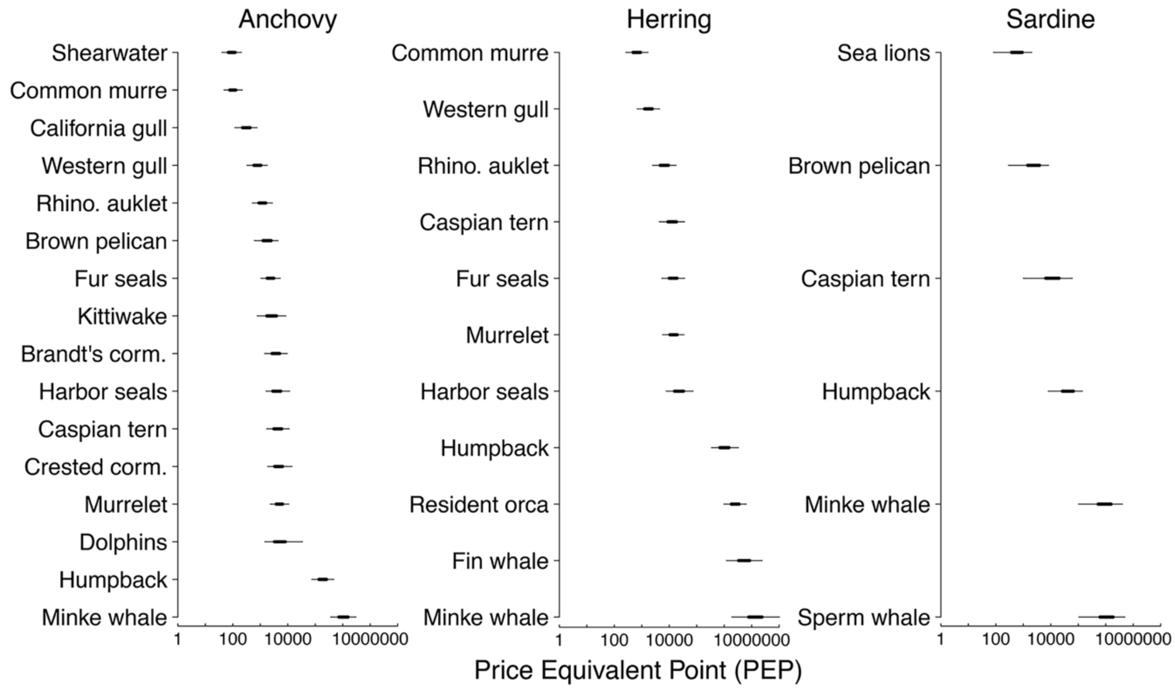

Figure 2.4 Nonmarket predator price equivalent points

Price equivalent points (PEP) that a nonmarket predator would need to cost to equal the revenue value gained from an additional 1 metric ton of sardine, anchovy, or herring catch. 50th (thick lines) and 95th (thin lines) percentiles are shown. PEP values are only listed for nonmarket predators that consume the forage fish in consideration and had negative responses (all negative 95th percentile range). Values are generally smaller for seabirds than marine mammals (but see sardine).

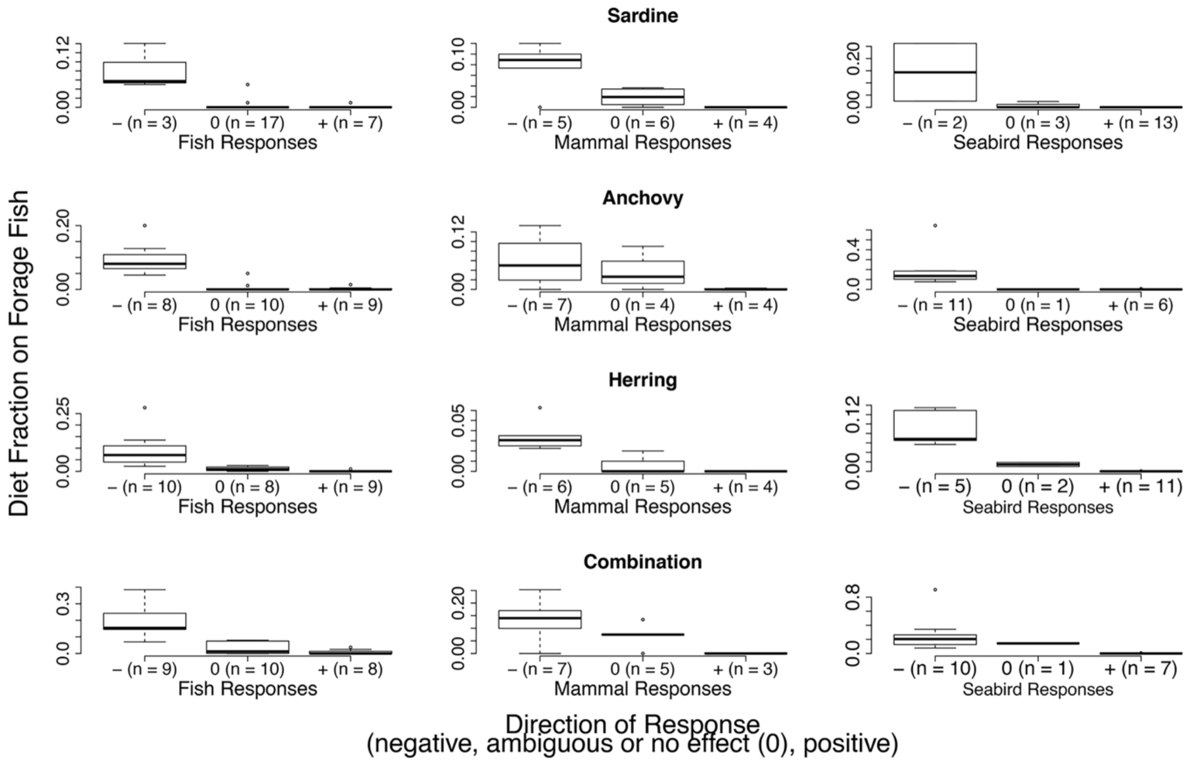

Figure 2.5 Predator responses across predator groups

Boxplots for different predator groups (fish, mammals, and seabirds) based on responses to fishing sardine, anchovy, herring, or an aggregate forage fish group ("combination" = sardine, anchovy, and herring). Predators were broken up into response groups: consistent negative responses ("–", negative 95th percentile), no effect or ambiguous responses (inconsistent,"0", 95th percentile spans zero), and consistent positive response ("+", positive 95th percentile). Negative responses were commonly associated with a wide range of non-zero diet fractions, while positive responses were almost always associated with low or zero diet on forage fish.

Chapter 3. A SEABIRD LIFE HISTORY-SPECIFIC MODEL FOR EVALUATING SEABIRD SENSIVITY TO FORAGE FISH FISHING

ABSTRACT

Changes in seabird population dynamics are commonly linked to changes in forage fish availability. Additionally, fisheries for forage fish may alter this availability, especially when forage fish populations are already low. To date, however, large models used to explore interactions between seabirds, forage fish prey, and fisheries have lacked specifics of seabird life history that make them susceptible to changes in forage fish prey. Here, we develop a general age-structured seabird model that incorporates specifics of seabird ecology, including foraging and reproductive strategy. Within the seabird model, seabird survival, reproductive success, and breeder attendance are linked to prey availability from an age-structured anchovy model. To explore model performance, we parameterized the model for two extremes of seabird life history – (1) a low fecundity, limited range, specialist and (2) a high fecundity, wide ranging, generalist. Initial parameterization of the model scenarios produced extreme model population dynamics for the restricted, specialist seabird scenario. Specifically, this seabird was unable to persist at moderate levels of fishing mortality on the anchovy prey. The extreme model behavior was mainly due to model sensitivity to functional response parameterization, particularly for breeder colony attendance and adult survival. Our model analysis, therefore, reveals areas where more empirical information is needed – on relationships between prey availability and breeders and adult survival. Also, additional processes that buffer populations during low prey availability may need to be included in the model to produce more realistic dynamics. Moving forward, for the seabird model

to be robust for investigating impacts of forage fish fisheries, additional empirical information is needed or additional exploration of parameter uncertainty within functional responses is needed.

INTRODUCTION

Forage fish (small, mid-trophic level, pelagic species) comprise valuable fisheries and provide services to the ecosystems in which they live. Around 25- 30% of all global marine landings are forage fish species (FAO 2015; data from 2011-2013) and these fisheries produce an annual revenue of $5.6 billion USD (Pikitch et al. 2014). At the same time, forage fish are the main food source for multiple predators (Szoboszlai et al. 2015) including seabirds (Furness 2003, 2007), marine mammals (Alder et al. 2008), and piscivorous fish (Overholtz et al. 2000, Butler et al. 2010). Due to this connection, changes in forage fish abundance are often correlated with changes in predator abundance (Cury et al. 2000), survival (Robinson et al. 2015), and reproductive success (Tasker et al. 2000, Crawford et al. 2006b, Cury et al. 2011).

Forage fish populations characteristically exhibit cyclic, large fluctuations in productivity and abundance. These fluctuations occur naturally, likely due to climate and oceanographic factors (Baumgartner et al. 1992, Chavez et al. 2003), but can be impacted by fishing (Beverton 1990, Essington et al. 2015). Forage fish collapses (extreme lows in abundance) may happen more often and at a greater magnitude with fishing (Essington et al. 2015), largely because management cannot respond quickly when productivity declines. Certain forage fish management strategies may help mitigate against potential negative impacts of changes in forage fish abundance or availability, and thus buffer forage fish populations for predators that depend on them. Such proposed precautionary harvest control rules often include, cut-off rules like step function rules and hockey stick rules (Pikitch et al. 2012), and marine protected areas (Boersma et al. 2015).

Due to their ecology, seabirds may be particularly susceptible to amplified, localized decreases in forage fish abundance. Specifically, seabirds are central-place foragers during the breeding season, and therefore have restricted foraging ranges due to the need to trade-off time spent foraging, time away from offspring, and their own survival (Orians and Pearson 1979, Burke and Montevecchi 2009). Additionally, small body size, specialized diet, energetic costs of flight, and other ecological traits that limit foraging range, such as diving depth (surface feeders compared to divers), likely also make specific seabird species vulnerable to drops in forage fish abundance (Furness and Tasker 2000, Piatt et al. 2007, Boyd 2012). However, seabirds have evolved alongside dynamic, naturally fluctuating prey populations and have developed traits that may help them cope with changes in prey, including early age at first breeding, larger clutch sizes, long life spans, post-fledging care, and/or flexible diets (Crawford et al. 2006a, Furness 2007, Weimerskirch 2007, Catry et al. 2013, Boersma et al 2017). Still, it is unclear how resilient seabird populations may be with changes in prey due to fishing or how this may impact seabird population sustainability long-term.

Energetic relationships between forage fish and predators and impacts of fisheries have often been studied using large ecosystem or food web models (e.g., Smith et al. 2011, Kaplan et al. 2013, Koehn et al. 2016). Though some of these models incorporate more information than purely energy flow between species (i.e. spatial distributions, climate drivers), many models lack specific information on life histories that would impact a predator’s ability to access prey (especially for non-fish predators), including foraging behavior, reproductive strategy, and migration (Goedegebuure et al. 2017). Additionally, many large models do not include enough taxonomic resolution to assess impacts of forage fish abundance on individual species (Essington and Plaganyi 2014). Certain models of intermediate complexity (MICE) have begun to incorporate some aspects of predator ecology and life history traits (for example, Punt et al. 2016; Robinson et al. 2015). However, more in-depth simulation models are needed to explore the impacts of forage fish availability on seabirds that incorporate life history traits that make seabirds susceptible to changes in prey.

Here, we present a generalized age-structured seabird model, that specifically incorporates aspects of seabird life history and ecology, that can be used to explore impacts of forage fish fisheries on seabird populations. Within the model, seabird reproduction, breeding, and survival depend on forage fish prey abundance. Our objective was to keep the model simple so that future efforts could easily re-focus the model for specific species while still incorporating details of seabird foraging strategies, prey accessibility, and productivity that likely impact seabird resilience to prey changes. We explore the application and utility of this model through two example seabird life history scenarios that span a range of plausible, realistic seabird types. We do so by fishing a modelled forage fish prey and comparing seabird populations with fished and unfished prey. The seabird and forage fish prey populations represented are generic and not specific to any one ecosystem so that the model can be tailored to specific seabird species or life history types that may be most susceptible to fishing.

METHODS

Seabird model

The seabird model is an age-structured model with yearly time steps, divided into two seasons, where reproduction and survival depend on the availability of prey (Figure 3.1). Therefore, $N_{y,s,a}$ is the number of birds at year (y), season (s) (1 = breeding or 2 = nonbreeding season), and age (a).

Survival of offspring to independence (survival to the non-breeding season) in a given year is modeled as a process of egg laying, egg and chick survival, and fledging success (chick survival to independence). To model the number of eggs laid, we wanted a function that was asymptotic to represent the limited space capacity of seabird colonies but also where at low population sizes, egg production is only limited by seabird physiology (how many eggs are they capable of laying, e.g. clutch size, the maximum number of eggs per pair).

Therefore, the number of eggs laid at the beginning of the year and breeding season ($N_{y,1,0}$) follows a von Bertalanffy relationship such that egg production is asymptotically related to the per capita egg production rate (Appendix C, Figure C1) through the following equation:

$$N_{y,1,0} = E_{max}(1 - e^{-r}) \tag{3.1}$$

Therefore, this assumes there is some maximum number (Emax) of viable eggs that can be laid (carrying capacity) based on available nesting sites, that once reached, no other eggs laid will be viable. This assumes no relaying of eggs if eggs are lost, which can occur, especially if eggs are lost near the beginning of the breeding season, but can be rare (Schreiber and Burger 2001, Boersma et al. 2013). Function r is the maximum per capita egg production rate, which is a function of the number of total breeding age seabirds in a given year and prey availability.

$$r = -(\frac{c}{2E_{max}} N_{y-1,2,a} \delta_{y,2,Br}) \; \forall a = a_b, \ldots, a_{max} \tag{3.2}$$

Where c is the clutch size of the seabird, $N_{y-1,2,a}$ is the total number of breeding adults (breeding age, a_b, to maximum age, a_{max}) at the end of the previous year (end of the non-breeding season), and $\delta_{y,2,Br}$ is a function of prey availability and is the impact of prey availability on the number of breeding age birds that attempt to breed (breeder attendance). This assumes that when prey availability is high, all seabirds will breed (lay eggs), but when prey availability is low, seabirds will skip the breeding season (less breeders will lay eggs and few birds will re-lay), waiting for more optimal breeding conditions.

The expected number of eggs that survive to fledging (surviving to the non-breeding season in first year of life, age ~6 months) is determined by the number of eggs that hatch (become chicks) and the number of chicks that fledge. The number of fledged chicks is a function of egg survival and chick survival rates in the absence of prey related affects and a function of prey availability. Therefore, the number of chicks that fledge (from the total number of eggs laid, $N_{y,1,0}$) is a random variable drawn from a binomial distribution with a fledging probability of $S_{y,E}S_{y,C}\delta_{y,1,F_c}$, where $S_{y,E}$ is the survival rate of eggs, $S_{y,C}$ is the survival rate of chicks, and $\delta_{y,1,F_c}$ is the impact of prey availability on egg and chick survival (and a function of prey availability), which will vary depending on the total number of chicks (F_c) per breeding pair. So that the total number of chicks that fledge ($N_{y,2,0}$) is equal to:

$$N_{y,2,0} = binomial(p = S_{y,C}\delta_{y,1,F_c},\ N = N_{y,1,0}) \tag{3.3}$$

All chicks that fledge are juveniles from the non-breeding season of their first year ($a = 0$, $s = 2$) to the non-breeding season of the second year ($a = 1$, $s = 2$). The number of juveniles that survive is a function of survival in the absence of prey related mortality as well as a function of prey availability. Therefore, in a given year, y, in non-breeding season ($s = 2$) and breeding season ($s = 1$), the number of juveniles surviving is equal to:

$$N_{y,s,a} = \begin{cases} N_{y,1,1} = N_{y-1,2,0}S_{y,s,J}\delta_{y,2,J} \\ N_{y,2,1} = N_{y,1,1}S_{y,s,J}\delta_{y,1,J} \end{cases} \tag{3.4}$$

Where $S_{y,s,J}$ is the bi-annual survival rate of juveniles not due to prey related impacts and $\delta_{y,s,J}$ is the impact of prey availability on juvenile survival and thus a function of prey availability.

Any juveniles that survive past the non-breeding season of their second year (*a = 1, s = 2*) are then considered "immature" until breeding age (*a* = *a*$_b$). Similar to juveniles, the annual and seasonal survival of immatures is a function of survival in the absence of prey related mortality and prey availability, such that:

$$N_{y,s,a} = \begin{cases} N_{y,1,a} = N_{y-1,2,a-1} S_{y,s,I} \delta_{y,1,NB} & \forall a = 2, \ldots, a_b - 1 \\ N_{y,2,a} = N_{y,1,a} S_{y,s,I} \delta_{y,1,NB} & \forall a = 2, \ldots, a_b - 1 \end{cases} \tag{3.5}$$

Where $S_{y,s,I}$ is the bi-annual survival rate of immatures and $\delta_{y,1,NB}$ is a function relating prey availability to survival of non-breeding seabirds.

The number of adult breeding seabirds that survive annually and seasonally is similarly modelled as a function of survival prey-independent and prey-dependent processes. Additionally, prey availability will be different for birds with offspring versus breeding age birds that either skip breeding in a year or lose offspring ("non-breeders"). Therefore, the number of breeding adults surviving to the non-breeding season is equal to:

$$N_{y,2,a} = \begin{cases} N_{y,1,a} S_{y,s,A} \delta_{y,1,B} \quad \forall a = a_b, \ldots, a_{max} & \text{if breeder} \\ N_{y,1,a} S_{y,s,A} \delta_{y,1,NB} \quad \forall a = a_b, \ldots, a_{max} & \text{if non} - \text{breeder} \end{cases} \tag{3.6}$$

Where $S_{y,s,A}$ is the bi-annual survival of adult age birds not related to prey availability and $\delta_{y,1,NB}$ and $\delta_{y,1,B}$ are functions of prey availability and are the impact of prey on survival for non-breeders and breeders, respectively.

Finally, adults surviving through the non-breeding season to the next breeding season is equal to:

$$N_{y,1,a} = N_{y-1,2,a-1} S_{y,s,A} \delta_{y,2,A} \;\; {\scriptstyle \forall a=2,\ldots,a_{max}} \tag{3.7}$$

Where the function $\delta_{y,2,A}$ is the impact of prey availability on survival for all adults in the non-breeding season (equal for all adults because there are no offspring in the non-breeding season). No seabirds survive past the maximum age (a_{max}).

Under these assumptions then, the full set of recursive equations for all state variables in the beginning of the breeding season (*s* = 1) are:

$$N_{y,1,a} = \begin{cases} N_{y,1,0} = E_{max}(1 - e^{-r}) \quad \forall a = a_b, \dots, a_{max} \\ N_{y,1,1} = N_{y-1,2,0} S_{y,s,J} \delta_{y,2,J} \\ N_{y-1,2,a-1} S_{y,s,I} \delta_{y,1,NB} \quad \forall a = 2, \dots, a_b - 1 \\ N_{y-1,2,a-1} S_{y,s,A} \delta_{y,2,A} \quad \forall a=2,\dots,a_{max} \end{cases} \tag{3.8}$$

and at the start of the non-breeding season (*s* = 2):

$$N_{y,2,a} = \begin{cases} N_{y,2,0} = binomial(p = S_{y,C} \delta_{y,1,F_C}, \; N = N_{y,1,0}) \\ N_{y,2,1} = N_{y,1,1} S_{y,s,J} \delta_{y,1,J} \\ N_{y,1,a} S_{y,s,I} \delta_{y,1,NB} \quad \forall a = 2, \dots, a_b - 1 \\ N_{y,1,a} S_{y,s,A} \delta_{y,1,B} \quad \forall a = a_b, \dots, a_{max} \quad \text{if breeder} \\ N_{y,1,a} S_{y,s,A} \delta_{y,1,NB} \quad \forall a = a_b, \dots, a_{max} \quad \text{if "non} - \text{breeder"} \end{cases} \tag{3.9}$$

The function $\delta_{y,s,l}$ is a function of prey availability and modifies survival rates, fledging rate, or breeder attendance at the colony due to prey availability in year *y*, for prey that is available for seabird life stage *l*, in season *s* and based on a defined functional response. We wanted a function that was easy to parameterize where we could adjust the shape of the relationship between prey availability and seabird demographic parameter to match variation in hypothesized functional response shapes across seabird demographic parameters (survival vs. breeding attendance, etc.). Additionally, we wanted a function where we could adjust the level of diet dependence (at which point seabirds would switch to alternative prey), and that is asymptotic so that at prey availability above some value, $\delta_{y,s,l}$ is equal to 1 (no impact of prey). Our solution was the following asymptotic, logistic function:

$$\delta_{y,s,l} = \min\left(1, \alpha + \frac{1-\alpha}{1+e^{-m\left(\left(\frac{P_{y,s,l}}{P_{0,l}}\right)-\beta\right)}}\right) \tag{3.10}$$

This logistic form suited our needs because parameters α, m, and β can be modified to change the shape of the functional relationship between prey availability ($P_{y,s,l}$) and $\delta_{y,s,l}$ depending on the life stage of the seabird (see Figure 3.2). Values of these parameters were chosen to produce functional forms similar to those hypothesized by Cairns (1987) and shown by Piatt et al. (2007) for various seabird populations at low vs. high prey availability. For fledging success, we chose parameters to match the empirical relationships revealed in the meta-analysis in Cury et al. (2011) for the relationship between reproductive success and prey availability.

Other than overall shape, α can be adjusted for diet specialization and is the lowest possible value of the impact of prey availability on a seabird demographic parameter. So that for a seabird with a generalist diet for example, $\delta_{y,s,l}$ never drops below a certain value (> 0) because a seabird will switch to an alternative prey when prey availability is low. The other parameters control: the availability of prey where the decline in the seabird parameter due to prey is most dramatically changing (β) and the rate at which the seabird parameters decline once low prey availability is reached (m). For example, β is high for juvenile survival because juveniles will likely begin to have decreases in survival at higher levels of prey than adults because juveniles are potentially less efficient foragers (less experienced). Similarly, β is high for breeding attendance as Cairns (1987) hypothesized that there would need to be substantial amounts of prey for breeders to attempt to reproduce, below which attendance would drop rapidly (higher m).

$P_{y,s,l}$ is the amount of forage fish prey biomass available to the seabird in a given season, year, and for a seabird life stage. $P_{0,l}$ is the average biomass of forage fish available (average of

$P_{y,s,l}$) across years and simulations, for each season, and that is available to each seabird life-stage when there is no fishing (similar to the methods in Punt et al. 2016). When calculating $P_{0,l}$, the first 200 years of simulation were removed to account for model stabilization.

Additionally, the functional response for chick fledging success (% fledged) is modified to account for the number of chicks per reproductive pair (Figure 3.2). We made this modification because the amount of food available to surviving chicks will increase when other chicks in the same clutch die. Similarly, seabirds that only lay one egg will have more resources to devote to their chick than seabirds that lay multiple eggs. This changes the survival probability for each chick, specifically modifying $\delta_{y,1,F_c}$ (Eq. 3.3). This assumes more prey is needed to fledge one chick when there is more than one chick total. Having one chick that fledges when there is a possibility of two, refers to percent of breeding pairs that fledge one chick if they are provisioning for two chicks; either because they started with two chicks or had three and lost one chick. Fledging one chick alone refers to the percent of breeding pairs that fledge one chick, either because they started with only one, they had two and lost one, or had three chicks and lost two. For this last scenario, prey availability must decline more compared to the other fledging scenarios, before fledging success decreases significantly, because breeding pairs need less resources since they are only raising one chick at this point.

Our model presumes that prey availability is directly related to prey population abundance. However, because seabirds are central place foragers, the actual amount available likely varies inter-annually, and this variation is likely dependent on the foraging of the seabird (diving, foraging distance, etc.). To represent local scale processes generated by interactions between fish and seabird movement and foraging variation across seabirds, we allowed for random variation in prey abundance within the model. The prey available to a seabird with a constrained foraging range will be more variable from year to year due to the lower area accessible. Therefore, to represent variation in foraging range, and processes of movement, we added lognormal error in prey availability ($P_{y,s,l}$), that can vary in variance to represent foraging type and predator and prey movement.

Forage fish model

To test the performance of the seabird model in relation to prey availability, we needed a simulated prey that exhibits realistic forage fish dynamics. An in-depth model for generic forage fish life history types was recently presented by Siple et al. (2018). We use this model to generate time series of a realistic prey populations, with and without fishing, as input for the seabird models.

The forage fish model by Siple et al. (2018) is an age-structured population model that uses recruitment deviations to create realistic forage fish fluctuations. We chose the "anchovy-like" forage fish type from Siple et al. (2018) for our simulations as its simulated population dynamics exhibit the regime-like properties typical of many forage species (Alheit et al. 2009) as well as a high degree of interannual variability (see recruitment variation parameters in supplemental information of (Siple et al. 2018)). The anchovy-like model also has recruitment deviations similar to those estimated for real anchovy and herring. These species are also commonly consumed by seabirds across the world (Weimerskirch et al. 2012; Szoboszlai et al. 2015; McLeay et al. 2009; R. Crawford et al. 2006a), so much so that seabird diets are used as indicators of their abundance (Velarde et al. 2015, Scopel et al. 2017). We used all the same initial parameterizations as Siple et al. (2018), including h (steepness) of 0.6 in the stock-recruit relationship.

To connect forage fish prey availability to the seabird model, prey biomass is needed in seasonal time steps to match modeled seabird breeding and non-breeding seasons. Therefore, within the Siple et al. (2018) model, we updated the recursive equations for the state variables biannually to account for the seasonal time step of the seabird model. Specifically, we applied a natural and fishing mortality rate twice in one year, but recruitment occurs annually (assuming anchovy only spawn once a year). Finally, we assume that seabirds are only targeting forage fish age 1+, which has been shown for certain species (Sunada et al. 1981) or used in other models (Robinson et al. 2015), but this will not impact model results since seabird populations with fishing are always compared to the populations without fishing under the same assumption.

Seabird parameters

All seabird survival rates ($S_{y,\mathrm{s,l}}$) within the seabird age structured model are stochastic and vary at the yearly and seasonal time steps. Therefore, for each year and season, a survival rate is pulled from a beta distribution, where adult, juvenile, chick, and egg survival means come from published values, and multiple values of distribution variance are tested. Ranges of adult survival rates for several seabird populations are published in Schreiber and Burger (2001) and Sæther and Bakke (2000). Values for seabirds ranged from ~0.6 to 0.97. Adult survival value less than 0.88 produced unstable model populations (populations crashed) even without impacts of prey availability. Additionally, published values likely include impacts of prey on survival. Since we model the impact of prey separately to explore the impacts of fishing on seabird populations, and also due to stabilization issues, we used an intermediate but higher adult survival rate of 0.9 The adult survival rate was used for all breeding adults as well as pre-breeding birds after their first year post fledging ("immatures"), because survival rates after this first year are near adult survival rates (Nelson 1980).

Egg and chick survival rates were collated from Nelson (1980) for seabird species. We removed outlier values that were noted by Nelson (1980) to be for populations in anomalous prey years (low prey) to try to minimize impacts of prey on these survival rates since prey impacts are incorporated elsewhere in the functional response.

Juvenile survival is not known for many seabird populations (Lewison et al. 2012) so it is difficult to identify the correct estimate to use within our model. In our seabird model, “juvenile” survival is used for seabirds in their first full year of independence (after fledging, in second half of year, and in first half, breeding season, after turning one year of age), after which they are considered immatures/non-breeders till breeding age. Reviews of seabird survival estimates, put average survival at for juveniles around 50% (Sæther and Bakke 2000, Horswill and Robinson 2015). However, values this low produced unstable populations in the absence of prey impacts and stochasticity when initializing models. Additionally, Gownaris and Boersma (2019) had magnified population declines using initial values of juvenile survival rates until these rates were increased. Juvenile seabirds are less efficient foragers than adults (Riotte-Lambert and Weimerskirch 2013, Votier et al. 2017). Therefore, low survival rates for juveniles may be more strongly influenced by prey availability than other sources. We therefore increased the mean survival rate for juveniles and made the functional response relating juvenile survival to prey availability, more severe (survival begins to decline at higher values of prey availability) than for adult survival (see above). Higher estimates of juvenile survival have been reported for certain populations in certain years (0.69-0.8; Wiens and Scott 1975, Cock and Hänel 1987, Votier et al. 2008, Payo-Payo et al. 2018, Baylis et al. 2018). So we set the mean juvenile survival at an intermediate 0.7, though there is likely a lot of uncertainty in this value.

Because variance in annual survivorship is not known for many seabird populations, we conducted sensitivity analysis across a range of plausible values. Therefore, we compared model results across scenarios with variation in variance. Higher variance was tested for egg and chick survival since reproductive success can be highly variable from year to year. Higher variance than those tested (Table 3.2) for adult and juvenile survival resulted in occasional unrealistic survival rates (based on literature listed above). This sensitivity analysis did not result in substantial variation in modeled seabird population size (confidence intervals overlapped) for most variance levels, so for other scenario testing and runs, variance was set at intermediate values (see Table 3.2).

Scenarios and Model testing

To test model performance and utility, we ran two scenarios of seabird model parameterization, to represent variation in seabird life history, as well as scenarios of fishing mortality on the prey. We ran these scenarios to test our expectations of model performance (based on general ecology), specifically that:

1. Seabird populations will be impacted by fishing but populations will persist at moderate fishing levels – based on real-world populations not having gone extinct
2. Seabirds with more specialized diets will be more sensitive to fishing than seabirds with more generalist diets
3. Seabirds with smaller foraging ranges will be more sensitive to fishing than seabirds with the ability to travel further and dive deeper
4. Variation in seabird productivity (life span, age at first breeding, clutch size) will not substantially impact seabird sensitivity to fishing, only base population sizes.

To test expectations, we parameterized the seabird model for two extremes of seabird life history (Table 3.3). These two parameterizations bound the extremes of potential scenarios in terms of accessibility to prey and impact of prey availability on life history parameters, and therefore test the model across a range of potential parameterizations. Within the two scenarios there was variation across three major life history categories – foraging, diet, and productivity. Therefore, we have two extremes: (1) a spatially restricted, low fecundity, specialist diet seabird (scenario 1), which we label the "restricted" scenario, and (2) a wider spanning, high fecundity, generalist diet seabird (scenario 2) that we label "flexible". We only picked combinations of traits that resemble life histories of real-world seabird groups, but again that bound the extremes of possibilities. Therefore, both seabird model parameterization scenarios are based on actual species but no simulated population represents a real-life seabird population. Additionally, the seabird populations modeled are assumed to represent one closed, colony specific population (no immigration, emigration). Seabird population scenarios varied based on productivity, represented by max life-span, clutch size, and age at breeding (see Table 3.3).

As mentioned above, to represent variation in foraging between our two scenarios, we used low ($\sigma_v = 0.1$) and high ($\sigma_v = 0.2$) variance in prey availability error to create seabird scenarios of wide versus limited foraging ranges. These variance values were used for prey availability for birds with offspring during the breeding season. Similarly, in the non-breeding season and for seabirds without offspring during the breeding season, we used low ($\sigma_v = 0.01$) and high ($\sigma_v = 0.05$) variance in prey availability for seabirds with wide or limited ranges. These variances are lower because seabirds are less constrained in range without offspring/when not breeding.

Scenarios also varied in functional response in terms of diet specialization, where the seabird was specified as a specialist or generalist (see Figure 3.2). Functional forms are the same shape between the generalist and specialist for all demographic parameters impacted by prey availability. But the generalists have higher survival, breeding attendance, or fledgling success at low prey availability, compared to the specialist, to reflect that at these low levels, the generalist would switch to alternative prey and the life history parameters would not be as drastically impacted (see functional response parameters listed in Appendix C, Table S1). Within our two scenarios, we wanted to bound the extremes of specialization to test the range of seabird life history, so the impact of prey availability on the generalist at low prey levels is substantially less than the impact on the specialist at low prey.

We ran two separate scenarios of reproductive success across breeding adult age groups. In one scenario, the number of offspring lost by each age (breeding age to max age) was based on the percent of breeders in each age class; making the chance of losing offspring equal across ages. Alternatively, younger, less experienced breeders may lose offspring more easily than older, more experienced breeders. Therefore, we also ran a scenario where younger breeders (first two years of breeding) were twice as likely to lose offspring as they were in the model where offspring lost was based on the percent of birds in each age class. Model results did not vary distinctively between these two scenarios (confidence intervals overlapped), so for other model runs we used the scenario where offspring are lost equally across all age groups. But, from our sensitivity analysis, seabirds are slightly less sensitive to fishing when offspring are more often lost to inexperienced breeders than lost equally across all breeding pairs.

To test our expectations of the seabird model, we fished the modeled forage fish prey population under two realistic levels of constant fishing mortality. In all cases we compared the seabird population in the presence of fishing to that predicted without fishing. We applied constant fishing mortality rate set at two, $0.5*F_{msy}$ (the fishing mortality at which maximum sustainable yield is achieved, used in Siple et al. 2018) and a lower fishing mortality of $F = 0.25\ F_{msy}$ (see Appendix C Figure S2 for example biomass). These mortality rates were constant over time and therefore, management is not responsive to changes in forage fish biomass. This may be unrealistic for some systems but helps to establish performance of the seabird model specifically (versus the forage fish model).

We started each seabird model run at equilibrium age proportions. We then ran each seabird scenario with (1) an unfished prey and (2) a fished prey. For all results, we then compare each seabird scenario population size with a fished prey to its population size with an unfished prey population. Therefore, we express all results as the ratio of the seabird population between fished and unfished models. We refer to impacts of fishing on the seabird as the seabird "sensitivity" to fishing.

When our expectations were not met, we varied parameters within the two seabird scenarios (Table 3.3) to test model sensitivity to various parameters. Therefore, when running sensitivity analyses, a parameter is changed in both the unfished model and the fished model for comparing across like models. The seabird scenario run with initial parameterization (Table 3.3) before exploring sensitivity to changes in parameters is called the "base" parameterization or model. For sensitivity testing for functional response parameterization, we either changed responses from specialist to generalist parameterization (functional response "type") or shifted β - the "threshold prey abundance" – the prey abundance below which demographic parameters begin to decline at the fastest rate.

For model scenarios and sensitivity analyses, we calculated two metrics. (1) We calculated the mean population proportion in each simulation (compared to the unfished model population) and calculated the median and quantile values across all simulations. (2) We also calculated the probability (% of years) that a modeled seabird simulation drops below 50% of the unfished model population and the median and quantile across simulations. We ran 100 simulations of each scenario. We assume the population goes "extinct" if the entire population goes to 0 (crashes).

Likely small populations greater than 0 would also result in extinction in the real-world, but to capture all model dynamics, we let the model run till 0.

RESULTS

Under the base model parameterization, the flexible seabird predator can generally persist with moderate fishing intensity, but the restricted seabird predator cannot. On average, at low fishing intensity ($F = 0.25\ F_{msy}$), the flexible predator has population sizes around 93% of the unfished model, and at greater fishing mortality ($0.5\ F_{msy}$), this scenario maintains approximately 76% of the unfished model population size (Figure 3.3). However, the restricted predator declines to approximately 30% of the unfished model population at low fishing and goes extinct at moderate fishing of $0.5\ F_{msy}$. It is expected that a restricted, specialist would have greater sensitivity to fishing than a flexible, generalist, but crashing at a moderate level of fishing is likely extreme

We used sensitivity analysis to reveal what components of the restricted seabird parameterization were most responsible for the high seabird sensitivity to fishing. We find that the differences in model predictions are mostly due to the functional response parameters. Specifically, with generalist functional response parameterization, the seabird population is less likely to decline below 50% of unfished levels (10% of years vs. 83%, Figure 3.4A) and has higher mean relative abundance (0.74 vs. 0.25, Figure 3.4B) compared to the base scenario with specialist parameterization. Variance in prey availability has little impact on model behavior as changing variance from high to low, only slightly increases mean seabird abundance (0.28 value vs. 0.25).

Model behavior is also sensitive to parameters that increase productivity, particularly clutch size. At $F = 0.25\ F_{msy}$, increasing clutch size for the restricted scenario from 1 to 3 eggs, increases the mean relative population size for the seabird (from 0.25 with the base parameterizations to 0.73, Figure 3.4, Table 3.4). Reducing the age of initial breeding to 3 years instead of 5 years also decreases seabird sensitivity to fishing but at a more intermediate level than clutch size. Larger clutch size likely benefits modeled seabirds because there is greater reproductive success for three egg nests than one egg nests in our model (on average, 0.34 vs. 0.80 with the base model parameterization). If we shift the threshold prey abundance in the 3-egg fledging functional response (see Appendix C, Table S1), so that even more prey is needed to fledge a chick when there are multiple chicks, than clutch size has little impact on seabird sensitivity to fishing (Table 3.4).

We examined which demographic parameter in the functional response relationships are most responsible for the high seabird sensitivity to fishing. The model behavior was most sensitive to the breeding attendance functional response (Figure 3.5). At the lower constant fishing rate, setting the breeder attendance functional response to generalist, decreases seabird sensitivity to fishing (mean population 0.46) more than changing the other functional responses to generalist values (adult survival, juvenile survival, fledging survival; mean population sizes of 0.42, 0.36, and 0.25, respectively). The adult and juvenile survival functional responses have intermediate impacts on seabird sensitivity to fishing. However, if we shift the threshold prey abundance to a lower value for breeder attendance (0.1 instead of 0.3, see Appendix C, Table S1), then the adult survival functional response becomes the most impactful (Appendix C, Figure S3). Therefore, the model sensitivity is specifically related to the initial parameterization.

Though the model is most sensitive to the breeder attendance functional response, the extreme model behavior for the restricted seabird is not due to this functional response on its own. At the moderate fishing ($F = 0.5\ F_{msy}$), changing the breeder attendance to a generalist functional response does not prevent the restricted seabird scenario from going extinct (mean seabird abundance of 0, Figure S4). The same applies for changing both adult and juvenile survival functional responses separately to the generalist parameterization. Only when all three are changed to generalist functional response parameterization does the restricted seabird not go extinct with moderate fishing (Figure 3.6).

The fledging success functional response had little impact on seabird sensitivity to fishing and did not seem to contribute to model sensitivity to functional response parameterization. If we set the functional response for fledging survival (reproductive success) to the generalist type, the restricted seabird population has approximately the same probability of dropping below 50% of the unfished model as the model with all specialist responses (83% probability for both, Figure 3.5). Even at higher fishing mortality, fledging response has little impact on the model output. If we set all functional responses to the generalist parameterization except one, keeping only the specialist parameterization for the fledging functional response has almost the same result as changing all responses to the generalist parameterization (average relative populations of 0.115 and 0.124, Figure 3.6).

Seabird sensitivity to fishing was also affected by the degree of population variation in forage fish prey. Higher variation in forage fish biomass led to higher sensitivity to fishing. For both seabird life history extremes (both scenarios), as we increase the recruitment standard deviation in the forage fish model from 0.6 to 0.9, sensitivity to fishing increases (lower relative abundances, Figure 3.7). Specifically, mean seabird abundance goes from 0.25 to 0 for the restricted scenario and from 0.93 to 0.74 for the flexible seabird scenario as prey variation increases. For the restricted seabird life history, the population crashes at the highest prey variation, again signaling that parameterization for this scenario may not be realistic.

DISCUSSION

Here, we presented a model designed to test the impact of fishing forage fish prey on seabirds, that incorporates specifics of seabird ecology that make them susceptible to changes in prey. However, many of our expectations for model performance were not met; specifically that a modeled restricted, specialist seabird was unable to persist with moderate levels of fishing mortality on their prey. This was mainly caused by our parameterization of functional responses and therefore, reveals areas where empirical information could be improved to help model seabirds in the future. Our results also reveal that there are likely natural processes that buffer populations against low prey availability, that were not originally considered, but may be important for governing seabird population dynamics.

Our model analysis revealed that more empirical information is needed on the impacts of prey abundance on seabird parameters other than reproductive success, specifically breeding seabird colony attendance and adult survival. These functional responses contributed the most to the unexpected model population dynamics. As others have stated before (Cury et al. 2011, Hunsicker et al. 2011, Sydeman et al. 2017), information is needed on the relationships between predator demographic parameters and prey abundance as well as thresholds in which parameters begin to decline to accurately predict seabird-fisheries interactions. Much effort has been put forward to determine the relationship between reproductive success and prey availability across species (Furness 2007, Field et al. 2010, Cury et al. 2011), but less so for other parameters (but see: (Piatt et al. 2007, Robinson et al. 2015)), especially over a long enough time span and both within and outside of the breeding season. However, adult survival and breeding propensity are not as easy to estimate compared to reproductive success parameters (Weimerskirch 2001, Sydeman et al. 2017). It is even more difficult to relate these rates to prey availability. Our model was particularly sensitive to the breeder attendance functional response but only at certain parameterizations, so more focus is needed on determining particular prey availability levels where colony attendance by breeders begins to decline.

However, our results do support conclusions made by others that seabird population dynamics are highly impacted by changes in adult survival, but our model may reflect an extreme scenario and thus reveal additional processes that should be considered in models. Previous studies as well as life history theory suggest that even small changes in adult mortality can have large impacts on seabird population dynamics (Croxall and Rothery 1991, Nur and Sydeman 1999, Weimerskirch 2001, Furness 2003). Moreover, variation in mortality between sexes can drastically impact populations through skewing sex ratios (Gownaris and Boersma 2019).Theory also suggests that because seabirds are long-lived, adults should be less susceptible to poor environmental conditions (compared to breeding success) (Weimerskirch 2001). Within our model, adult survival decreased only at very low levels of prey availability, but possibly additional processes that buffer adults during periods of low prey availability are needed in the model as well. For instance, though modelled seabirds could skip breeding when prey was low, we did not factor in nest desertion if prey availability drops later on (though more nests would lose contents). Additionally, seabirds may migrate away from areas when conditions are poor, especially first time breeders (Crawford 1998). Including these processes in models may be needed to produce realistic population dynamics.

Incorporating additional processes may also lower model sensitivity to parameterization of the juvenile survival functional response. Specifically, almost all seabird families exhibit post-fledging provisioning to offspring (Burger 1980, Boersma et al. 2017). The modeled functional relationship between juvenile survival and prey availability could be modified to account for this additional source of prey (other than juvenile foraging alone). This would likely lower the impact of prey on juvenile survival at intermediate prey levels, changing model dynamics. But at low prey levels, adults likely can't afford to use resources to feed post-fledging offspring as adults must tradeoff their own survival with increased survival of their offspring (Trivers 1974), so this may only adjust the juvenile functional response slightly and not when prey availability has the largest impact.

Based on our model results, known relationships between prey abundance and reproductive success are likely not influencing seabird species at a population level. Our parameterization of fledging survival functional responses had little impact on simulated seabird populations. This supports conclusions by others that dynamics of seabird populations are less influenced by reproductive success compared to adult survival, juvenile recruitment, or sex ratio (Croxall and Rothery 1991, Nur and Sydeman 1999, Sæther and Bakke 2000, Gownaris and Boersma 2019). Reproductive success fluctuates substantially from year to year due to variation in environmental conditions but populations have adapted strategies to persist (Wooller et al. 1992, Weimerskirch 2001), so annual variation in reproductive success has minimal impact on overall populations. However, potentially if there are many years in a row with low reproductive success due to continuously low prey availability, this could result in population effects. Still, based on our model results, conserving prey may be more important for seabird demographics other than reproductive success, to sustain seabird populations.

Our model result that larger clutch sizes reduce seabird sensitivity to fishing supports previous conclusions about seabird adaptations to highly variable environments. Larger clutch size is likely an adaptation to buffer reproductive success against fluctuating prey availability, as seabirds with multi-egg clutches have higher variability in reproductive success than one-egg clutch species (Ainley and Boekelheide 1990). This can lead to higher chicks per egg for one-egg clutches versus multi-egg; but laying multiple eggs in highly variable environments (like upwelling ecosystems), may be beneficial over the long-term to the population (as cormorant populations with large clutches dominant many upwelling ecosystems) (Ainley and Boekelheide 1990). Our modeled prey source is highly variable, so our result that larger clutch size leads to lower sensitivity to fishing and higher population sizes supports theory that larger clutches are beneficial long-term in highly variable environments.

Constraints on foraging depth and range make certain seabirds more susceptible to changes in prey distributions, but our results suggest this may not have long-term impacts. In modeled Peruvian Booby (*Sula variegate*) and Guanay Cormorant (*Phalacrocorax bougainvilliorum*) populations, depth distribution of prey was the primary driver of foraging success, while spatial distribution was the third largest factor after prey abundance (Boyd et al. 2016). Also, Frederiksen et al. (2008) showed vulnerability to prey depletion for a seabird with limited foraging depth compared to diving seabirds in the same region. However, we modeled variation in foraging through variance in prey availability and saw little impact on model behavior. This suggests that annual variation in foraging success, similar to variability in reproductive success, may not translate to a long-term population effects, especially if years where prey are inaccessible are infrequent or not in consecutive years. And, especially if variability in foraging success impacts reproductive success more than adult survival (based on results discussed above). At the same time, we modeled these dynamic spatial foraging processes with a non-spatial model, therefore, it is difficult to tell if our model simplifications accurately capture realistic processes.

Model seabird sensitivity to fishing increased as forage fish recruitment variation increased, suggesting that seabird populations may not be resilient to larger fluctuations in prey.

Though increased recruitment variation leads to both increased maximum forage fish abundance and lower minimum abundance, greater abundance in some years may not counter the impacts of low abundance years. Prey availability impacts on demographic parameters are static at high availability, so even greater prey availability will have no additional benefit; in other words, the predator is satiated when prey are above some point. But lower prey availability results in even lower demographic parameters. Therefore, if collapses are magnified due to fishing (as predicted by Essington et al. 2015), this could substantially impact seabirds even if prey populations are allowed to rebuild.

Other simplifications were made within the model to limit model complexity but these could impact overall model dynamics. For example, we did not have seabirds relay a clutch if all nest contents were lost (which occurs, especially if lost early in the season), but can be rare (Schreiber and Burger 2001). Factoring in a process for re-laying could prevent some of the extreme model behavior seen for the restricted, specialist seabird. Though reproductive success was not a significant driver of model behavior, relaying would likely have similar impacts as larger clutch sizes as it acts as similar additional reproductive opportunity. Additionally, we did not include sex biased survival rates, which has been shown for certain populations (Gownaris and Boersma 2019). However, this would likely lead to even greater extreme model behavior as Gownaris and Boersma (2019) under-estimated declines in Magellanic penguins (*Spheniscus magellanicus*) without sex-biased survival rates. But, if not included for certain populations, such as our generalist scenario, significant impacts of a fishery could be missed. It is unclear how common sex-specific survival rates are in seabird populations, but if it is based on sexual dimorphism (males larger than females), than it may be common since most species are slightly size dimorphic (Schreiber and Burger 2001). All caveats/missing components for seabirds could be added to seabird species-specific models, building off this base model, if that component is thought to be important for a certain seabird population.

The model presented here could be used for future exploration of seabird - forage fish fishery interactions, with certain modifications. Specifically, this model could be used for management strategy evaluation on the effects of alternative forage fish harvest control rules, such as stop-loss rules or marine protected areas, on seabirds. Alternatively, the model could be tailored to a particular seabird species or population to look at impacts of current fishing practices on a potentially vulnerable species. Life history elements not included in this version of the model could be added to a species-specific model, if those components are known to be important processes for those populations (such as immigration/emigration, sex-specific survival rates, etc.). However, likely more information is needed on functional response forms for multiple seabird demographic parameters for modeling efforts to lead to robust predictions. Or, alternatively, model performance should be explored across multiple variations in functional responses (ensemble modeling) in the face of uncertainty.

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Table 3.1 Seabird model parameters and functions

Parameters and functions related to the recursive equations for the age-structured seabird model

Seabird model parameter/function	Definition
$N_{y,s,a}$	Number of seabirds in each year, y, in each season, s, and in each age, a
E_{max}	Max amount of viable eggs that can be laid based on assumptions of carrying capacity and dependent on clutch size (maximum possible eggs per pair)
$r\ (N_{y-1,2,a}\delta_{y,2,Br})$	Maximum per capita egg production rate – function of number of breeders and prey availability
c	Clutch size– total possible number of eggs laid by each breeding seabird pair
$\delta_{y,2,B}$	Impact of prey availability on the number of adult breeders in each year that will breed in the upcoming breeding season
$S_{y,E}$	Yearly survival rate of eggs not due to the impact of prey availability
$S_{y,C}$	Yearly survival rate of chicks not due to the impact of prey availability
$\delta_{y,1,F_c}$	Impact of prey availability on the fledging rate of offspring (survival to independence), that is dependent on the total number of chicks (F_c)
$\rho_{p,c}$	Probability of survival of each chick, c, for each breeding pair, p
$S_{y,s,J}$	Biannual survival rate of juveniles not due to prey related impacts
$\delta_{y,s,J}$	Impact of prey availability on the survival rate of juveniles
$S_{y,s,I}$	Biannual survival rate of immatures (not yet breeding age) not due to prey related impacts
$\delta_{y,s,NB}$	Impact of prey availability on the survival rate of non-breeding seabirds (either are not yet breeding age, did not breed that breeding season, or lost offspring)
$S_{y,s,A}$	Biannual survival rate of adults (breeding age) not due to prey related impacts
$\delta_{y,1,BA}$	Impact of prey availability on the survival rate of breeding seabirds (have offspring)
$\delta_{y,2,A}$	Impact of prey availability on the survival rate of all breeding age adults during the non-breeding season
a_b	Age at first breeding
a_{max}	Maximum age (life-span)
α	Parameter in the functional response – lowest possible value of the impact of prey availability on a life history parameter (survival or breeder attendance)
β	Parameter in functional response – point in prey availability where the decline in survival or breeder attendance is largest
m	Parameter in functional response – rate of decline in survival or breeder attendance at low levels of prey availability

$P_{y,s,l}$	Amount of forage fish prey biomass available to the seabird in year y, season s, and life stage l
$P_{0,l}$	Average $P_{y,s,l}$ in the absence of fishing

Table 3.2 Seabird survival parameters and variance

Survival parameters kept constant across all seabird scenarios. All survival parameters are stochastic across years, so values given are means within beta distributions. Multiple variance values within beta distributions were tested for model sensitivity but result confidence intervals overlapped for all variances, so one variance was used in all model results (variance in bold).

Survival rate	Mean (reference for values for specific seabirds)	Variance
Adult survival	0.9 (Schreiber and Burger 2001)	0.001, **0.005**, 0.01
Juvenile (age 1-2 survival)	0.7 (see text)	0.001, **0.005**, 0.01
Chick survival	0.75 (Nelson 1980)	0.005, **0.01**, 0.05, 0.1
Egg survival	0.7 (Nelson 1980)	0.005, **0.01**, 0.05, 0.1

Table 3.3 Seabird life history scenarios

Specific parameters/specifications for the seabird life history scenarios tested. The wording color of each scenario is the same color used in results figures for that scenario.

	Foraging	**Diet**	**Productivity**		
Scenario	Prey availability deviation	Diet specialization	Max age	Age at 1st breeding	Clutch size
1 - Restricted	High variance	Specialist	High (30)	Older (5)	Low (1 egg)
2 - Flexible	Low variance	Generalist	Low (15)	Young (3)	High (3 eggs)

Table 3.4 Seabird population sizes with variations in clutch size and fledging function response Median and 95% quantiles for the average relative seabird population sizes across all simulations for variation in fishing, ($F = 0.25\ F_{msy}$ and $F = 0.5\ F_{msy}$) for variations in clutch size and function response parameterizations for seabird scenario 1. Population sizes are also presented for a model scenario with higher β (threshold prey abundance) in the fledging functional response for 3-egg/chick nests. Clutch size impacts modeled seabird sensitivity to fishing, except when the functional response is changed so that more prey is needed to fledge a single chick in a multi-chick nest.

	Average Relative Seabird Population - Median (95% quantile)		
Fishing	Base Scenario 1	Larger clutch	Generalist response
$F = 0.25\ F_{msy}$	0.25 (0.02-0.47)	0.73 (0.62-0.81)	0.74 (0.64-0.81)
$F = 0.5\ F_{msy}$	0 (0-<0.01)	0.06 (<0.01- 0.24)	0.1 (<0.01- 0.27)
High F, Higher β in 3-chick functional response	0 (0-<0.01)	<0.01 (0- <0.01)	0.1 (<0.01- 0.27)

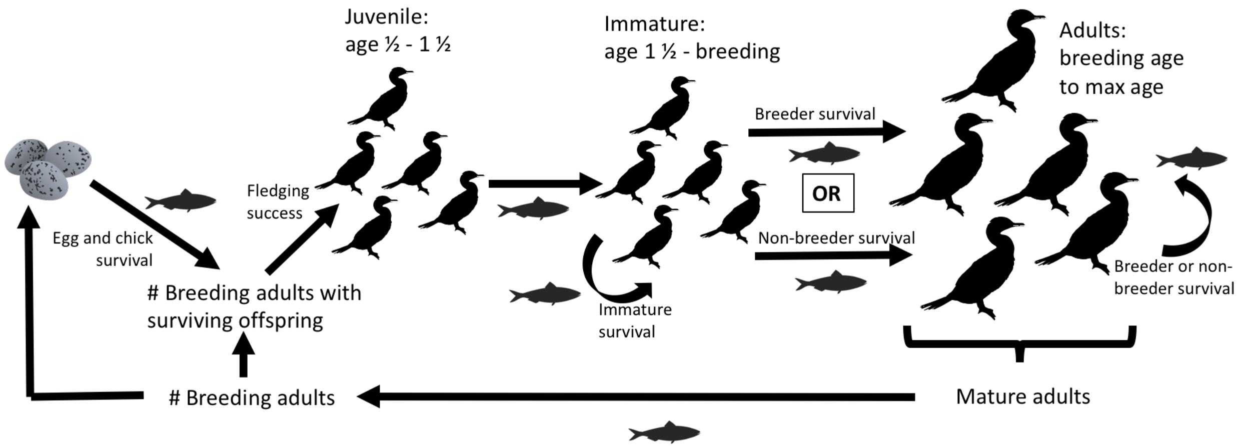

Figure 3.1 Seabird model schematic

Schematic of seabird age-structured population model. Processes (arrows) with a fish symbol denote processes that are influenced by prey availability. Therefore, survival rates are related to non-prey related mortality and prey related mortality, which vary by life stage. At the left of the schematic, the number of eggs and chicks that survive leads to the number of adults with surviving offspring which is directly related to the number of chicks that fledge (reach independence).

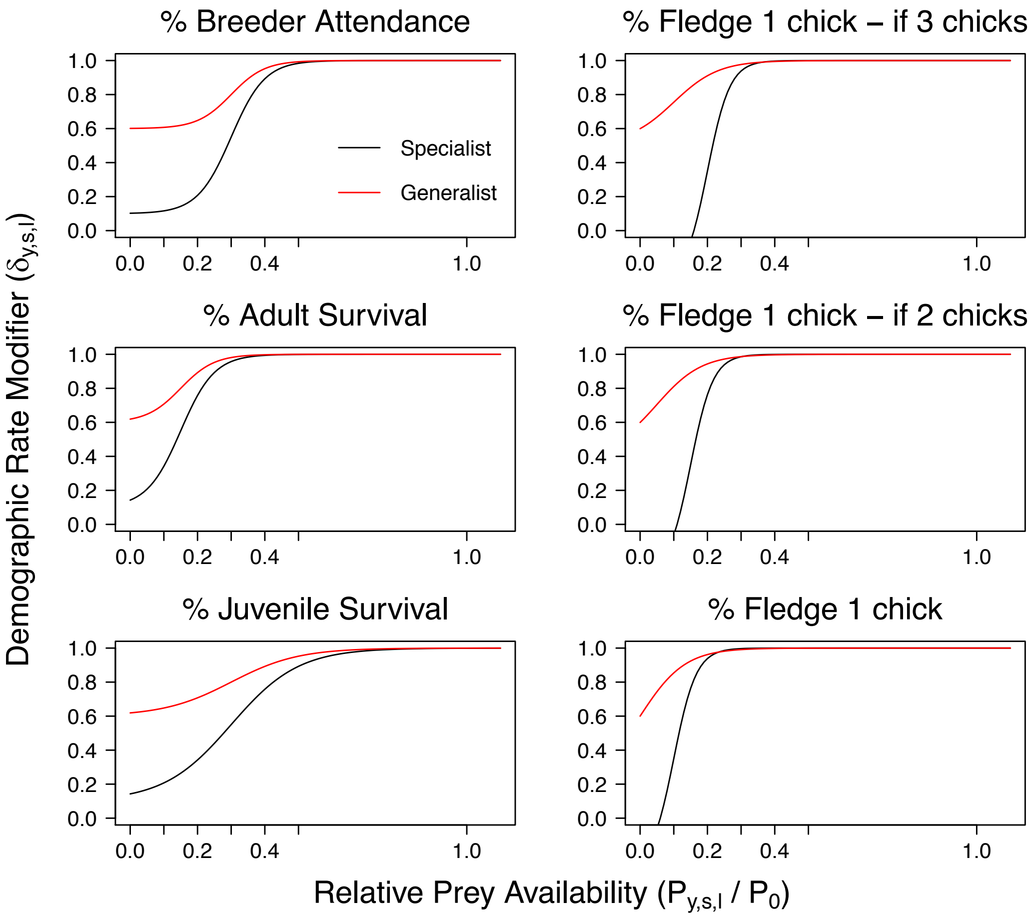

Figure 3.2 Seabird-prey functional responses

Functional responses for each demographic parameter (breeder attendance, adult survival, etc.) across two scenarios of diet specialization on forage fish prey. The proportion of prey available ($P_{y,s,l}/P_{0,y}$) is the relationship between prey in a given year, season, for a specific seabird life stage, compared to average prey availability when the prey is not fished. Then, the function $\delta_{y,s,l}$ modifies seabird demographic rates (survival, reproductive success, etc.) to adjust for prey availability impacts. Note that for the "% Fledge 1 chick – if 3 chicks" refers to percent of breeding pairs that fledge one chick when they have three chicks to feed (more constraint because need more resources to distribute among chicks). Similarly, "% Fledge 1 chick – if 2 chicks" refers to percent of breeding pairs that fledge one chick if they have two chicks; either because they started with two chicks or had three and lost one chick. Finally, "% Fledge 1 chick" refers to the percent of breeding pairs that fledge one chick, either because they started with only one, they had two and lost one, or had three chicks and lost two.

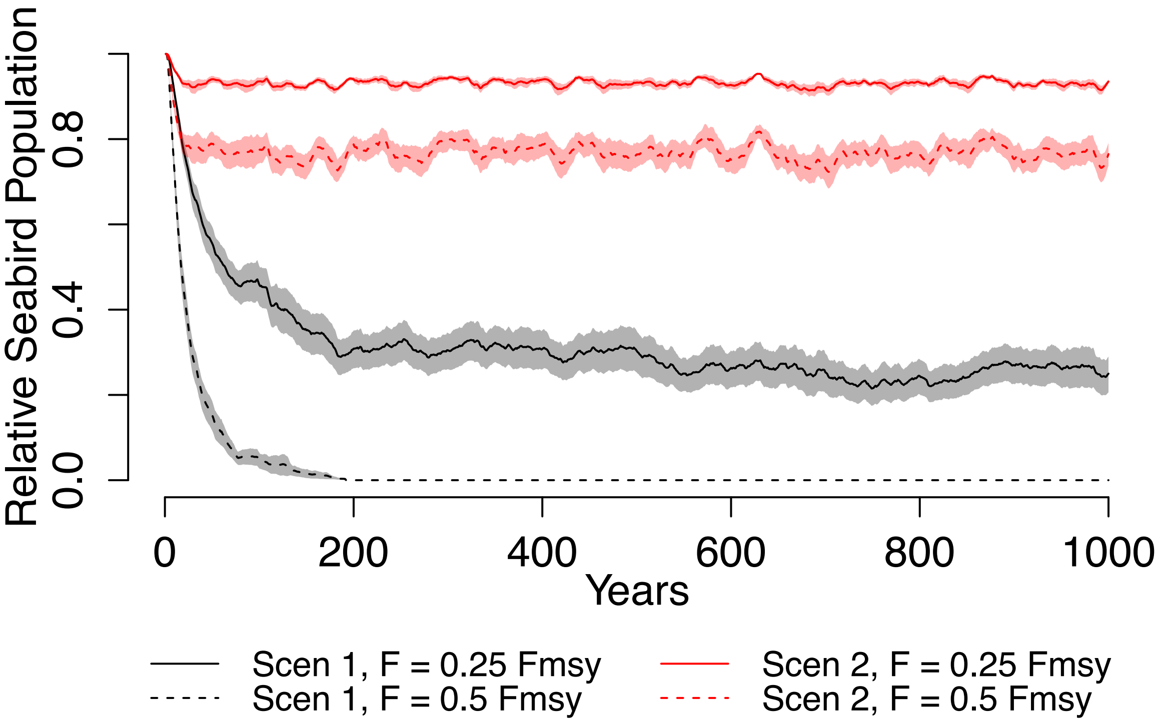

Figure 3.3 Simulated seabird scenario populations

Average simulated seabird populations (lines), relative to the unfished model, and 95% confidence intervals across simulations and under different constant fishing rates. The more restricted seabird life history scenario is presented in black ("scen 1") and the more flexible life history scenario is in red ("scen 2"). The restricted life history scenario is overly sensitive to fishing and goes extinct with moderate fishing.

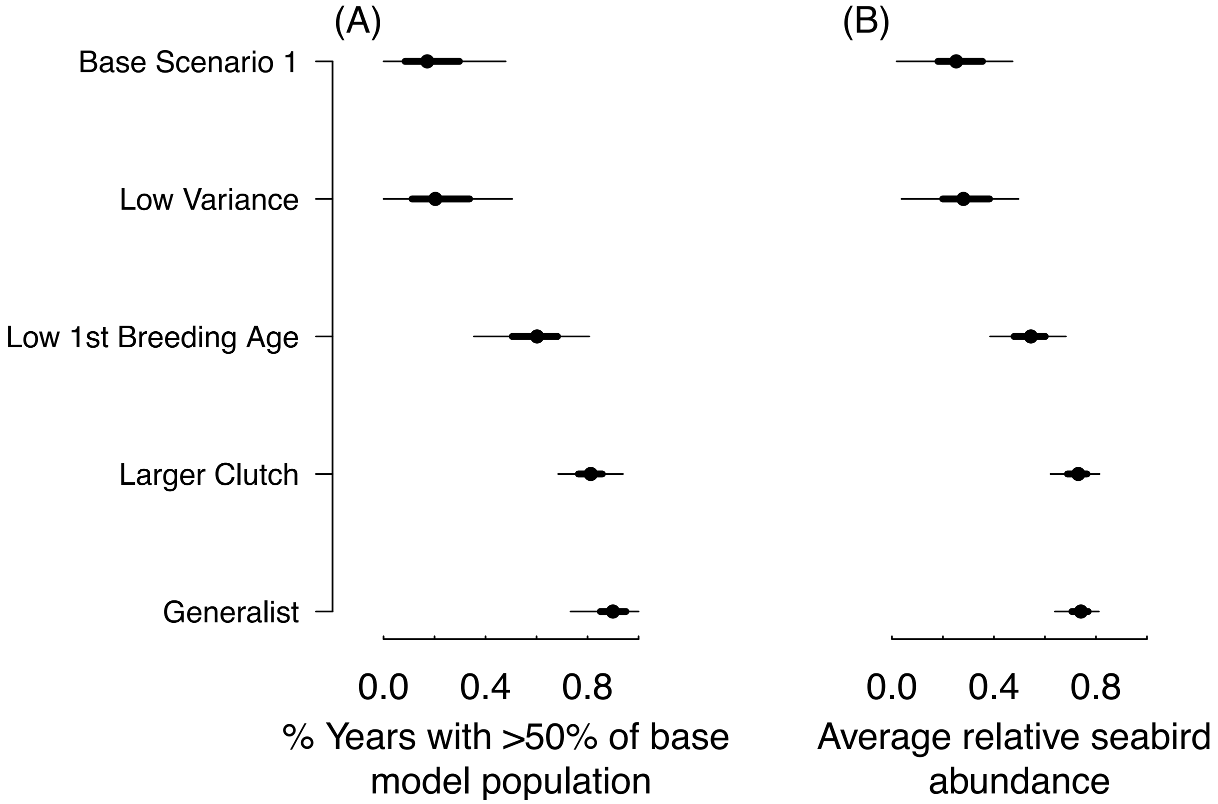

Figure 3.4 Model sensitivity to base parameterization

Median (dots), 50% quantiles (thick lines), and 95% quantiles (thin lines) for two metrics - (A) average probability that the modeled seabird population is greater than 50% of the unfished model population (percent of years with population sizes greater) and (B) average relative seabird population sizes - for sensitivity analysis of variation in scenario 1 parameterizations at F = 0.25 F_{msy}. For the sensitivity analysis, we changed each parameter/function in the scenario 1 base model (prey variability variance, clutch size, age at first breeding, and functional response type) individually to the scenario 2 value or type. The model is most sensitive to changes in the functional responses but also clutch size.

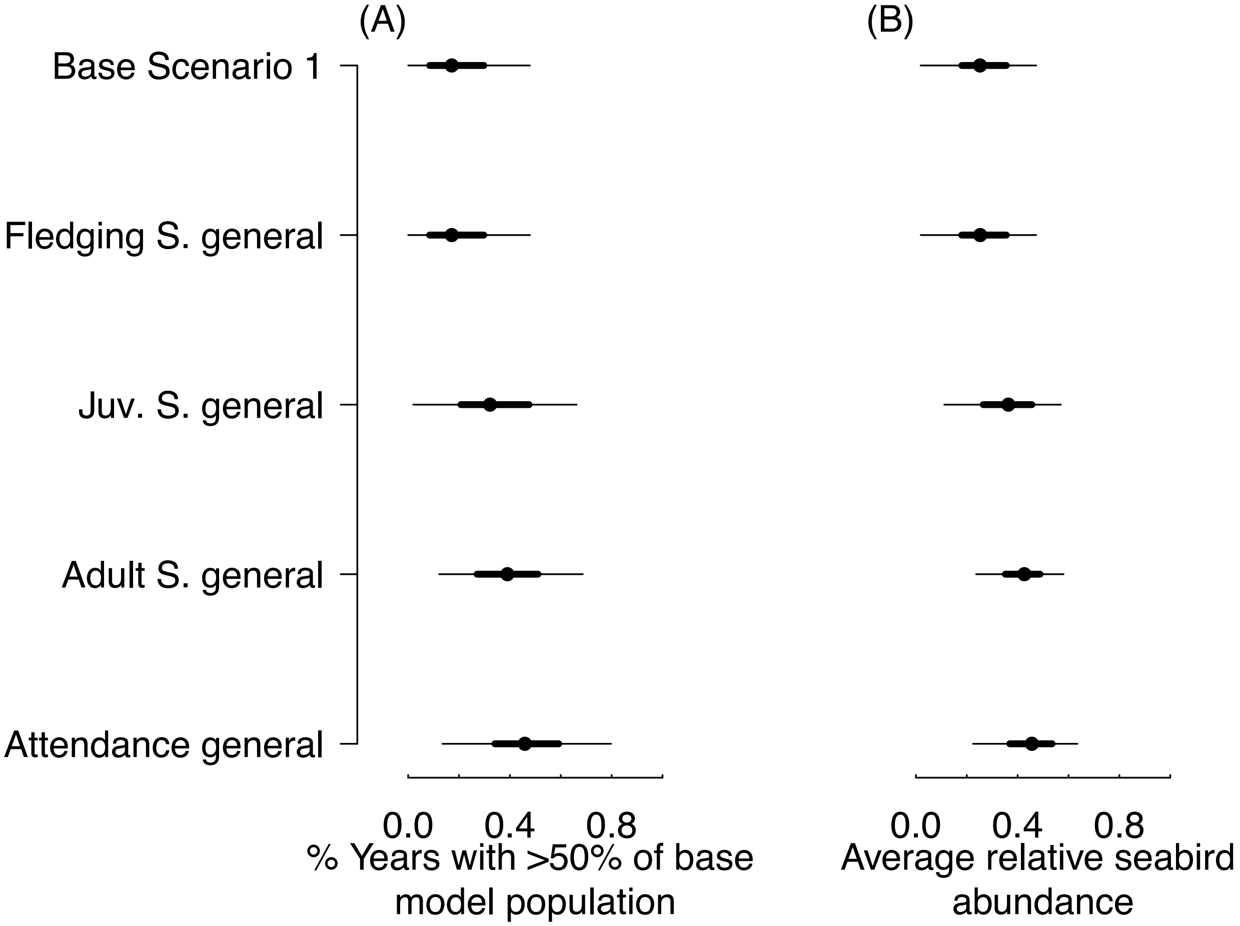

Figure 3.5 Model sensitivity to each demographic functional response

Median (dots), 50% quantiles (thick lines), and 95% quantiles (thin lines) for two metrics - (A) average probability that the modeled seabird population is greater than 50% of the unfished model population (percent of years with population sizes greater) and (B) average relative seabird population sizes - for sensitivity analysis of variation in scenario 1 functional response parameterization at F = 0.25 F_{msy}. For each variation, one functional response – either for fledging survival, juvenile survival, adult survival, or breeder attendance – is changed to a generalist response (from specialist in the base scenario 1 model). The model is most sensitive to changes in the functional response for breeder attendance at the colony.

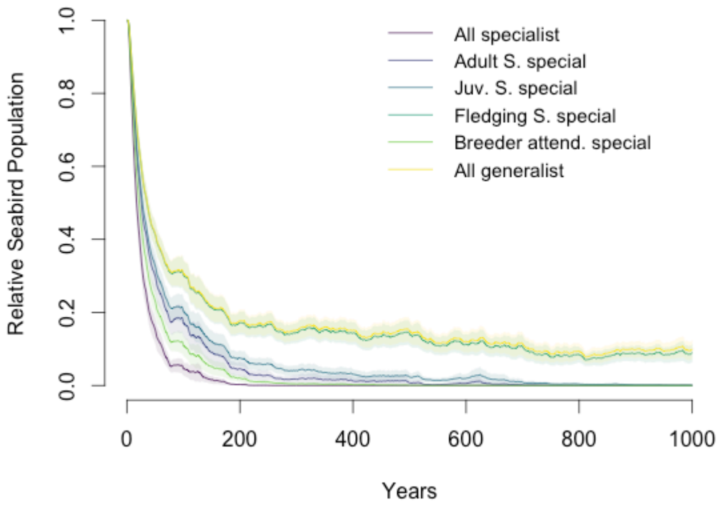

Figure 3.6 Simulated seabird scenario with variation in functional responses

Average relative seabird populations (lines, relative to the unfished model) and 95% confidence intervals for the restricted seabird life history scenario at constant fishing of F = 0.5 Fmsy with variations in functional responses. Variations shown are for the base scenario 1 model (all functional responses are specialist parameterization), switching the functional response to a generalist parameterization for all but one functional response (adult survival, juvenile survival, fledging survival, or breeder attendance), and switching all functional responses to the generalist parameterization. The specialist parameterization for the fledging response has little impact on seabird population sensitivity to fishing.

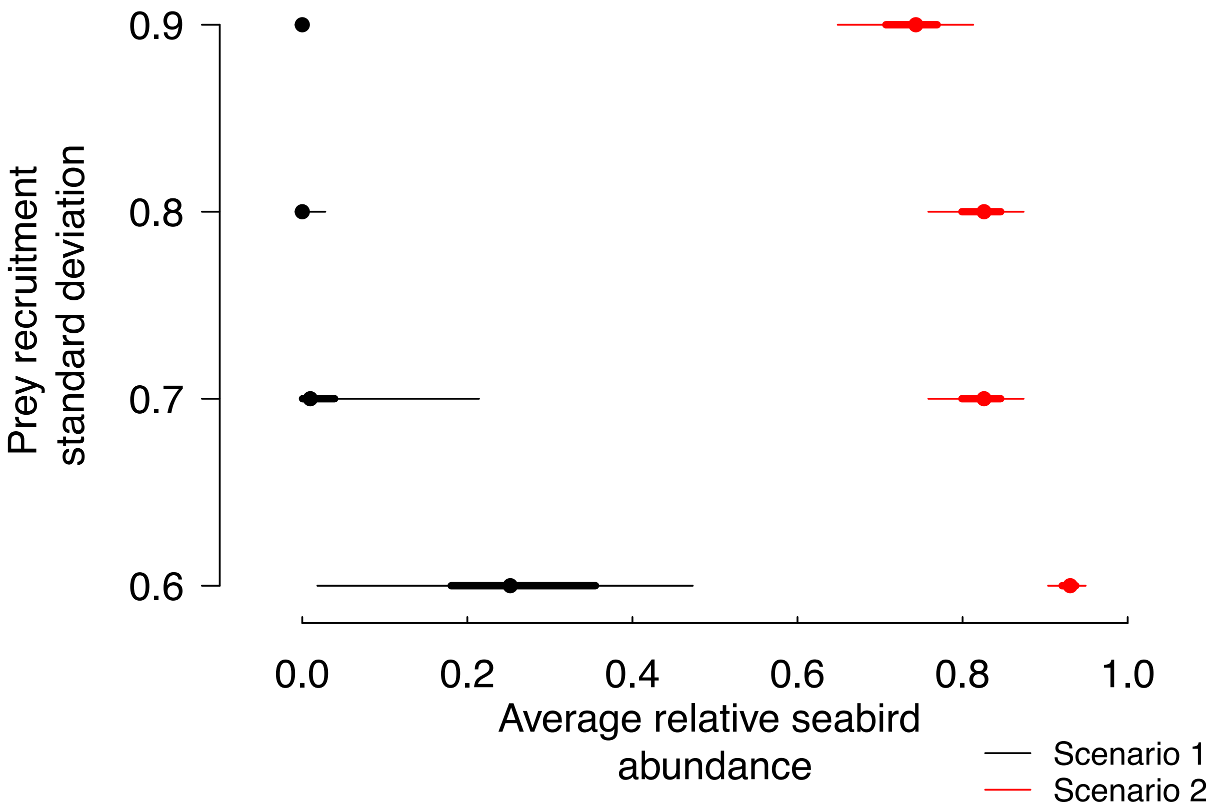

Figure 3.7 Modeled seabird sensitivty to variation in prey recruitment standard deviation Median (dots), 50% quantiles (thick lines), and 95% quantiles (thin lines) of average relative seabird population sizes for the restricted life history scenario (scenario 1) and the flexible life history scenario (scenario 2) with variation in standard deviation in forage fish prey recruitment and constant fishing of F = 0.25 F_{msy}. As forage fish recruitment variation increases, seabird population sizes decline and seabirds are more sensitive to fishing.

Chapter 4. TECHNICAL CAPACITY FOR NEXT-GENERATION FISHERY ECOSYSTEM PLANNING TO SUPPORT ECOSYSTEM-BASED FISHERIES MANAGEMENT[3]

ABSTRACT

A structured, systematic process for decision making can facilitate the implementation of Ecosystem-Based Fisheries Management (EBFM). Many such processes have been suggested, including a new process; next-generation fishery ecosystem plans, that expand upon existing fishery ecosystem plans (FEPs) by translating principles into action. Here, we assess the capacity for this recently proposed FEP process by reviewing multiple case studies from the U.S., Canada, Australia, and Europe through the lens of the steps outlined in the process and by considering how current fisheries management activity matches the proposed steps. Our review highlighted two perspectives on the current capacity for implementing a structured decision-making process like next-generation FEPs. First, across the case studies, there is activity for almost all steps in one or more regions, suggesting that the scientific and management capacity exists to conduct a structured process. This outcome suggests that barriers to implementing next generation FEPs are surmountable. Secondly, we identified situations where status quo procedures might be improved via the next generation FEP process. For example, documentation of prioritization was scarce, and steps were rarely taken as part of a holistic, fully structured and integrated process. We conclude that advancement in these areas may streamline management activity, saving time and resources while leading to improved outcomes for people and the ecosystems they depend upon.

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INTRODUCTION

Ecosystem-Based Fisheries Management (EBFM) is a holistic approach to decision making intended to improve management outcomes for people and the planet (Pikitch et al., 2004; Fogarty, 2014). Despite the promise of EBFM, the majority of fisheries are managed with a focus on maximizing sustainable catches of individual species without considering the consequences on the larger system including habitat, climate, species interactions, and cultural considerations (Pitcher et al., 2009; Travis et al., 2014; Skern-Mauritzen et al., 2016). The management of fisheries through EBFM strives to maintain multiple services that an ecosystem provides while accounting for relationships among fishery system components (Pikitch et al., 2004). Though benefits of a more holistic approach have been claimed by many (Pikitch et al., 2004; Tyrrell et al., 2011; Fogarty, 2014), incorporation of many EBFM principles into tactical fisheries management has been rare (Skern-Mauritzen et al., 2016; Marshall et al., 2019).

The lack of EBFM implementation, potential impediments, and potential tools and processes to foster EBFM implementation have been widely explored (Pikitch et al., 2004; Tyrrell et al., 2011; Patrick and Link, 2015a; Bundy et al., 2017; amongst others). Many commonly highlighted impediments to EBFM include potential short-comings of current analytical tools, such as ecosystem models (Espinoza-Tenorio et al., 2012; Hilborn et al., 2017) and multispecies and ecosystem assessments (Möllmann et al., 2013), which are considered by some to still be in their infancy (Hilborn, 2011). Critics note that empirical data needed for EBFM (including for the tools mentioned) are lacking, also that it is difficult to determine clear objectives for EBFM (compared with conventional management) (Mace, 2001), and that the resources needed for the application of EBFM are limited (FAO, 2003; Walters, 2007). The lack of long term management plans that include economic and social dimensions of fisheries is likely an impediment to EBFM as well (Bundy et al., 2017).

Essington et al. (2016) suggested that a more structured, systematic, transparent process is needed to overcome impediments and foster implementation of EBFM. Multiple step-wise, systematic decision-making frameworks for fisheries management have been proposed (FAO, 2003, 2009; Levin et al., 2009; Fletcher et al., 2010; Tyrrell et al., 2011) to improve decision-making in an ecosystem context. Many of these processes involve synthesizing ecosystem information to better assess conflicts between ecosystem components and call for extensive stakeholder involvement throughout the process for increased engagement and transparency. These processes also emphasize the identification of management objectives, prioritization of those objectives, and delineation of potential approaches for meeting objectives in a structured, step-wise manner. Some of these approaches have been adopted outside of the U.S., including in Europe (FAO, 2003, 2009) and Australia (Fletcher et al., 2010; Hobday et al., 2011). The National Marine Fisheries Service (NMFS) in the U.S. recently proposed a roadmap for EBFM (National Marine Fisheries Service, 2016), but to date there has been no wide-spread adoption of a process for implementing EBFM in the U.S.

The Lenfest Ecosystem Task Force (hereafter referred to as “task force”) recently reviewed the current state of policy, science, and decision-making processes around the globe related to EBFM, and proposed “next-generation” ecosystem plans (Essington et al., 2016) as a means for facilitating EBFM implementation. Compared to past planning documents, next generation ecosystem plans would be more strongly action-focused, as opposed to descriptions of fishery system structure and status. Fishery ecosystem plans were originally proposed as planning documents for U.S. regional fishery management councils to integrate ecosystem principles into management. However, many fishery ecosystem plans to date have been mainly descriptive in nature (see for example (Pacific Fishery Management Council, 2013)). Next generation plans would explicitly translate EBFM principles into management action (Essington et al., 2016). The recommended process for next generation ecosystem plans is founded in adaptive management, is both structured and transparent, and includes periodic reassessment and modification of strategies based on learning that ensues from implementation (Essington et al., 2016; Levin et al., 2018). Many steps in the next generation process address perceived barriers to EBFM implementation (Essington et al., 2016). However, it is not clear whether management capacity exists to implement the proposed planning process, or if there are existing barriers that would prevent future adoption. Though others have explored the frequency of incorporating ecosystem considerations into management (e.g. (Skern-Mauritzen et al., 2016; Marshall et al., 2019)), there has not been a formal evaluation to determine whether elements of a structured planning process to conduct EBFM are currently occurring in management or in what capacity.

Our objective is to assess the management and scientific capacity for such a structured decision-making process using the proposed next-generation fishery ecosystem planning process as a guiding framework (Levin et al., 2018). By evaluating how activity within current management matches this process, we can evaluate the capacity to develop next-generation fishery ecosystem plans. We specifically focus on the management and scientific capacity, as these are often identified as barriers to EBFM in general, and fishery ecosystem plans in particular. To this end, we compiled case studies in fisheries management from multiple regions that could be addressed with EBFM and are based on the expertise of the authors. We look within these case studies to assess the capacity to move towards next generation FEPs by identifying activity related to steps in the planning process. Information within these case studies can be used to specifically explore the following questions: (1) In the U.S., Canada, Australia, and Europe, where does current management activity match the proposed next-generation fishery ecosystem plan process and steps therein, in relation to specific ecosystem challenges, and which steps have been conducted? (2) For steps already taken, how does current activity deviate (if at all) from what is specifically proposed in the next-generation fishery ecosystem plan process? and (3) Across all case studies, which steps are the least commonly conducted?

METHODS

Using the recently proposed planning process from the task force (next-generation fishery ecosystem plans, Box 1, Essington et al. (2016)) as a guide, we assessed the extent to which fisheries management activity matches the proposed fishery ecosystem planning process for EBFM. For brevity, we refer to the next-generation fishery ecosystem plan process as either "ecosystem planning process" or more simply "planning process". A full description of the process can be found in Levin et al. (2018) and Essington et al. (2016). We refer to the high-level categories in the planning process such as, *Where are we now?, Where are we going?* etc. as "components" of the plan from here forward and actions within each component (bullet points in Box 1, e.g. "Develop a conceptual model", "Select and Calculate indicators," etc.) are referred to as "steps". We refer to steps for components 1-3 in short-hand (e.g. "Articulate a strategic vision" becomes "strategic vision"). For component 4, *Implement the Plan*, we used a simpler review, looking only for any evidence of putting the plan into action. Similarly, for component 5, *Did we make it?*, there is only one action, which is the definition of the component, so there are no individual steps to analyze for this component.

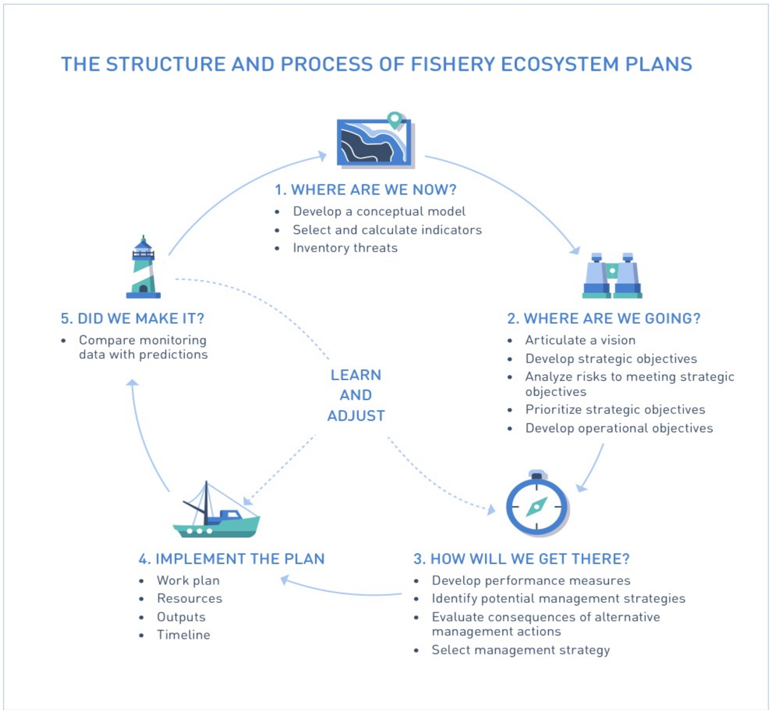

Figure 1 from Levin et al. (2018). Process proposed for developing next generation fishery ecosystem plans.

BOX 1. The planning process begins with 1. *Where are we now?* which includes understanding the current fishery system, through taking an inventory of the system or developing a conceptual model of the ecosystem, selecting and calculating indicators that represent the current status of components of the system (fish species, fisheries, predators, etc.), and taking an inventory of potential threats to the ecosystem. The next component (2. *Where are we going?*) and steps therein involve creating broad vision statements that are then broken down into several strategic objectives for multiple domains (ecological, economic, etc.). Risks to meeting the objectives are identified, prioritized and reduced to a few key objectives, and then these selected few are reconfigured and specified as measurable, achievable operational objectives. Component 3, *How will we get there?*, involves developing indicators and reference points based on objectives (targets, limits, or system states to avoid) and evaluating multiple management actions to determine which meet the objectives from component 2 based on the indicators and reference points. Then, based on this analysis, selecting one of the management strategies for implementation. Next, 4. *Implement the plan*, includes the final planning logistics of how the management action will be implemented, including potentially, work plans, timelines, etc. Management actions are then monitored overtime to see if objectives are met (5. *Did we make it?*). This can lead to changes in the development and implementation of indicators, reference points, and management strategies, as in adaptive management ("Adjust and Learn" arrows, inner loop). On a large, slower scale, the process repeats based on changes to the ecosystem (large loop).

We examined 10 case studies to determine which, if any, of the steps were taken within these current management situations. We chose each case study based on a current use of EBFM or an ecosystem approach (known management activity), a need for EBFM, or a known connection between parts of the ecosystem (species to species, species to environment, etc.). Case studies were also chosen to cover a wide range of regions in the United States, with three additional case studies from outside of the U.S. providing international perspectives. We note that other examples from these regions meet the criteria of an ecosystem approach or need for

EBFM, but we chose case studies to illustrate a range of EBFM topics. Finally, each author of this paper has expert knowledge in at least one of the case study regions, and the case study topics also reflect the expertise of the regional author. The regional experts include academics, members of government, of fishery management councils, and of U.S. regional council Scientific and Statistical Committees.

Six of the eight U.S. Fishery Management Councils are represented by the U.S. case studies, with no case studies for the Western Pacific Fishery Management Council or the Caribbean Fishery Management Council (a consequence of no task force members from these regions). Though the Western Pacific Fishery Management Council has developed FEPs, these do not differ substantially from FEPs in other case studies or from Fishery Management Plans (FMPs) (see Essington et al. (2016)), so likely another case study would add more examples but not alter our conclusions about capacity for the ecosystem planning process as a whole. The final case study regions and main management issue/topic for each region are listed in Table 4.1. From here forward, we generally refer to each case study in short-hand by either its location or key species.

Each regional expert author provided information on an individual case study. All information provided can be found in Appendix D. We collated information for each case study that highlights a specific major management question(s) or challenge(s) and how (if at all) management action around that challenge exemplifies the steps in the planning process. Each author first provided information on two main questions for an individual case study: “what is the major fishery system issue relevant to management?” and “what management actions have occurred to address that issue (if any)?”. Authors then looked specifically at each step in the process and identified if action related to the definition of those steps had occurred pertaining to the main management issue for that case study.

Additionally, we conducted searches of council and management documents and websites to explore what, if any, activities were occurring related to the individual steps in the ecosystem planning process for specific U.S. case studies. We searched council websites, NOAA science center websites, and regional integrated ecosystem assessment websites for activity related to specific steps – particularly steps within the first two components (system inventory, indicators, vision statements, objectives, etc.) that are more broadly applicable at a regional scale than other steps. We searched documents of council minutes and previous stock assessments only when it was known (through author expert knowledge) that a specific management action or plan (related to a step in the planning process) was considered at a specific meeting or in a specific assessment. Finally, we contacted regional scientists or managers (council members) when we knew there was action related to a specific step but we needed additional information to clarify what had occurred.

We identified and enumerated the case studies that included activity for each of the planning process steps and that also applied the activity to a management decision in an ecosystem context (hereafter called management activity). Management activity refers to actions taken by the councils (in the U.S.) or other governing body for international case studies (Department of Fisheries and Oceans Canada [DFO], International Council for the Exploration of the Seas [ICES] or European Union [EU] council, or Australian Fisheries Management Authority). It also refers to U.S. management authorities outside of councils (such as the Atlantic States Marine Fisheries Commission) and NOAA plans or recommended actions presented to or intended for council use (examples: Integrated Ecosystem Assessment [IEA], Chesapeake Bay fishery ecosystem plan). By “ecosystem perspective”, the action taken must be related to multiple components in the system and not focused on a single species in isolation from its environment. Such actions included those related to habitat, environment and/or climate, trophic interactions, protected species, and indigenous and traditional fisheries. We also made note of any documented presence and extent of stakeholder involvement that occurred within the management activity. By stakeholder involvement, we mean stakeholder involvement in multiple steps throughout the process and where stakeholders participate throughout the process beyond solely consultation, in a manner specifically defined by the next generation FEP planning process (Essington et al., 2016).

We determined whether each step had occurred in a binary fashion (did or did not occur) using criteria described below. This determination was made for each case study by the primary author and the author who provided the information for the case study and was reviewed by a core set of the authors. We note that in general, our benchmark for “occurrence” was based on a modest level of activity related to each step (Table 4.2). Also, activity for individual steps did not need to occur in coordination with other steps, as in a structured process (though that is the eventual goal). Criteria used to determine whether a step was completed were directly related to the definition of each step from Levin et al. (2018). We also note that management may have completed steps for other fisheries in the system, but if it is not related to the major fishery issue that is specified for that case study, we did not count that action. This may result in some variation in the number of examples for each step, but likely not the representation of capacity for the overall process across all case studies based on how we selected case studies. Finally, we only determined that a step had occurred when clear evidence existed, either through expert opinion or documentation. However, the absence of evidence for a step does not definitively confirm that activity related to that step did not occur, but at a minimum reveals the portions of the decision making process that were not documented in an accessible manner.

Our results stem directly from information found within summaries of the case studies (presented in Appendix D, steps and components are italicized). All information is reflective of management activity through the beginning of 2018.

RESULTS

Overview of Components/Process

Across all case studies, nearly all fishery ecosystem plan process components and steps were conducted in some manner in at least one region, and usually in multiple regions (Table 4.3). In most case studies, managers had conducted at least one step within each component of the process. Most case studies had management activity pertaining to components 1-4 (*Where are we now? Where are we going? How will we get there? Implement the Plan*) whereas activities for component 5 (*Did we make it?*) were absent. Management may have conducted additional relevant activities but did not document that activity in an accessible manner.

The number of steps with management activity (for components with multiple steps) varied among components, with more activity related to steps in the first component. For component 1 (*Where are we now?*) almost all case studies had activity pertaining to every step. In comparison, for components 2 and 3 (*Where are we going? How will we get there?*), most case studies had activity pertaining to fewer than half of the steps. Below we review, in turn, activities conducted related to each component.

Component 1 “Where are we now?”

For component 1, almost all case studies had activity for each step, and the first step, “Taking an inventory of the system”, was accomplished through a variety of avenues. Management activity related to taking inventory and developing a conceptual model (step 1.1 in the process) was among the most commonly observed of all steps. Some examples of inventories appear as part of an existing fishery ecosystem plans, such as the Pacific Coast ecosystem plan (Pacific Fishery Management Council, 2013) and the Chesapeake Bay ecosystem plan (Chesapeake Bay Fisheries Ecosystem Advisory Panel, 2006). Other examples exist outside of ecosystem plans and include overviews of the system and its status and trends. These include the Ecosystem Status Report for the Gulf of Mexico (Karnauskas et al., 2013), Ecosystem Status Report for the Northeast Shelf Large Marine Ecosystem (Ecosystem Assessment Program, 2012), Alaska Marine Ecosystem Considerations Report (North Pacific Fishery Management Council, 2015), the DFO State of the Ocean Report (Fisheries and Oceans Canada, 2012), and the Integrated Assessments of the Baltic Sea (ICES, 2015). Additionally, most case studies with inventories also had conceptual models or used the DPSIR/DPSER (Drivers-Pressures-State-Impact or Ecosystem Service –Response) conceptual model framework (Kelble et al., 2013), either in the same document or through related activities such as Integrated Ecosystem Assessments (see the Gulf of Mexico, Northeast Pacific Sardine, and Northeast Pacific Interacting Protected Species case studies in Appendix D). As with conceptual models, activity related to “Selecting indicators” (step 1.2), and associated status and trends of indicators, were included in the system inventories or Integrated Ecosystem Assessments (IEA) for most case study regions.

Most of the discussions of threats to the ecosystem (step 1.3 in the process, "Take an inventory of threats") were also included in the system inventories (step 1.1). Inventories for most of the case studies included threats by either mentioning threats for specific ecosystem features (e.g., for specific species, habitats), by identifying potential threats when selecting and analyzing indicators (noting when indicators are near/at dangerous levels), or by including threats as major topics within the system inventories. For example, the DFO State of the Ocean Report for the Scotian shelf detailed threats such as "Ocean Acidification" and "Ocean Noise" as major chapters within the system inventory (Fisheries and Oceans Canada, 2012).

However, the breadth of threats recognized was limited. Accordingly, when conducting future inventories of threats within the process, inventories could be expanded based on specifications in the fishery ecosystem planning process. Levin et al. (2018) suggest that inventories should include more threats than those occurring in the sea (shipping, fishing, etc.), for example, pressures from the human system (changing markets) and terrestrial pressures (e.g., development and agriculture). Additionally, the planning process proposed that threats not only be identified, but that their magnitude, frequency, and spatial scale be characterized.

Component 2 "Where are we going?"

Although across case studies there is activity related to the initial steps in component 2 (Vision statements and/or Strategic objectives), there was less or no activity for later steps. Many of the case studies had activity related to developing strategic visions and strategic objectives, but few prioritized those objectives or developed more specific operational objectives. Additionally, there were few examples of risk assessments, and these risk assessments were usually disconnected from other steps. Still, across all case studies, there are examples for almost all steps in component 2.

"Vision Statements" and "Strategic Objectives" (steps 2.1 and 2.2) were derived from regional (council processes) and/or federal agencies. For example, vision statements and objectives for the Bering Sea and the Mid-Atlantic case studies were developed via regional fishery management council efforts (the Ecosystem Committee for the North Pacific Fishery Management Council [NPFMC], and a strategic planning process by the Mid-Atlantic Fishery Management Council [MAFMC]). In the New England case study, the identified strategic objective came from a legislative mandate. Specifically, the objective stemmed from the Magnuson Stevens Act requirements that councils must "minimize to the extent practicable the adverse effects of fishing on essential fish habitats (EFHs)" (Grabowski et al., 2014; New England Fishery Management Council, 2016). For the Northeast Pacific Interacting Protected Species case study, strategic objectives were listed in the killer whale and salmon recovery plan documents developed by NOAA and triggered by the Endangered Species Act (1973), again relying on objectives stemming from a federal agency.

Stakeholder involvement varied widely across case studies for activity in this component and the planning process specifically highlights the need for collaboration with stakeholders in these steps (Essington et al., 2016). For the Bering Sea and Menhaden case studies, the NPFMC and the Atlantic States Marine Fisheries Commission (ASMFC) adopted or modified vision statements (step 2.1) in response to stakeholder requests (Atlantic States Marine Fisheries Commission, 2012; North Pacific Fishery Management Council, 2014). In contrast, the vision statement and strategic objectives (steps 2.1 and 2.2) for the Mid-Atlantic case study were developed by the MAFMC with more in-depth stakeholder involvement. The development of the council's strategic plan included a large-scale outreach effort with more than 1,500 participants (Mid-Atlantic Fishery Management Council, 2012). This effort included stakeholders from commercial and recreational fisheries, environmental organizations, seafood users, scientists and researchers, and more. Other examples of vision statements and objectives for specific case studies were developed mainly by managers and/or scientists (as far as was documented; see Pacific case studies, New England case study, and others). We note here that some councils (for example, the North Pacific Fishery Management Council) may have assigned representatives to represent larger groups rather than involving large numbers of individuals.

"Risks to meeting objectives" (step 2.3) were not commonly assessed, though we found a few examples. Three case studies had explicit activities regarding risk and objectives. For one, the Alaska Groundfish Programmatic Supplemental Environmental Impact Statement (PSEIS) (National Marine Fisheries Service, 2004) analyzed risk to fishery management alternatives for various objectives. For example, one major objective identified in the PSEIS is "Avoid impacts to Seabirds and Marine Mammals," and fisheries management alternatives were analyzed for direct/indirect impacts on seabirds and marine mammals. In this case, the existing optimal yield range for the groundfish fishery resulted in no significant/negative impacts to seabirds and marine mammals, according to the PSEIS analysis.

We did not identify any case study where there was explicit "Prioritization of objectives" (step 2.4). It is possible that prioritization was conducted, but not formally expressed. Alternatively, prioritization might have been done implicitly or without a formal process. Yet, it is clear that some prioritization occurred, as many case studies had other activities that require prioritization (such as developing operational objectives). At best, prioritization was poorly documented or possibly not carried out in a systematic way.

Based on the results from this review, rarely are operational objectives developed (step 2.5) related to a specific management issue. The operational objectives that were clearly defined were either directional (e.g. improve the status of system component) or included limit or target levels for ecosystem components, as used in conventional fishery management. In both the New England Groundfish Habitat case study and Bering Sea Groundfish case study, there were operational objectives with directional goals but without specific targets, such as "…reduce impacts on spawning groundfish and on the spawning activity of key groundfish species…" (New England Fishery Management Council, 2016). For the Australian Small Pelagic Fishery case study, there were operational objectives with specific targets set for impacts on predators, including insurance that biomass of other species not be impacted by more than 70%. However, these were the only three case studies where we could identify ecosystem related operational objectives. Accordingly, the capacity may exist to develop either directional operational objectives, or objectives with specific target values, but this activity is not commonly occurring (or documented) across our case studies.

Component 3 "How will we get there?"

Across all case studies, there is activity for every step in component 3 in at least one region. However, there are some particular discrepancies between case study activity and specifications outlined in the planning process that we highlight for certain steps.

While alternative management strategies were sometimes evaluated against performance indicators, in no case was there a formal and deliberate process of identifying, evaluating, and selecting portfolios of "Performance measures" (step 3.1) based on objectives, that could be used to track success of policies. Specific performance indicators were used in management strategy evaluation, but these indicators usually did not represent the full suite of ecosystem components likely impacted by strategies. Although we counted indicators used in management strategy evaluation as completion of this step, ideally, reference points and performance indicators would be used to evaluate progress towards the operational objectives, and therefore include indicators that reflect the multiple ecosystem components contained in the operational objective(s). We suspect that this finding is related to the general lack of operational objectives noted above because indicators and reference points stem directly from desired levels identified in the operational objectives.

Most commonly, EBFM strategies chosen (“Selecting a strategy”, step 3.4) were modifications of conventional management strategies. This supports findings in Essington et al. (2016), Levin et al. (2018), and Patrick and Link (2015b) that indicate ecosystem goals can be achieved by modifying conventional strategies. All strategies chosen adjusted status quo management through either modification of estimated stock status relative to reference points by including environmental data in stock assessments or modification of catch limits via caps or cut-offs. For instance, in the Australian Small Pelagic case study, management chose a stock biomass target to diminish effects on predators. Some case studies with modifications of harvest control rules did not appear to have ecosystem operational objectives. We considered these as ecosystem strategies post-hoc because of components included, though it is unclear if these strategies were intended to have a broader ecosystem scope. For example, the strategy chosen in the Sardine case study was a harvest control rule that has a cut-off that conserves sardine when abundance is low, leaving biomass for predators, but the intended objective for the modification to the conventional management strategy was not documented. Finally, the ecosystem planning process calls for examination of a broader suite of management strategies and more novel configurations of existing management strategies or policy instruments (Essington *et al.*, 2016) than presented by many of these case studies.

Other than the modifications to conventional management mentioned above, strategies chosen were conventional strategies already in use. In both the Interacting Protected Species case study and Australian small pelagic case study, the selected strategy did not change *status quo* management. This highlights that conducting activity related to this step within a structured ecosystem planning process may not always result in a change to management. However, the process of evaluating multiple strategies may provide more confidence in the strategy selected and provide documentation that issues were considered.

Although "Selecting a strategy" (step 3.4) was one of the most commonly completed steps, the preceding steps in component 3 were not (3.2 "Identify potential management strategies" and 3.3 "Evaluate management strategies"). Thus, in some cases, activity related to step 3.4 apparently was conducted, but steps seemingly necessary for its completion may not have been done. For example, red tide is included as an additional source of mortality (modeled as extra "fishing" mortality) decoupled from natural mortality in the Gag stock assessment in the Gulf of Mexico (SEDAR, 2014, 2016). Its inclusion leads to modification of estimated stock status relative to the reference point. Thus, consideration of red tide conditions influences the estimation of stock status, and this stock status relative to the reference point impacts the management strategy chosen, e.g. allowable catch (exemplifying step 3.4 Select a Management Strategy). However, there was no formal management evaluation in which multiple strategies were assessed (steps 3.2 and 3.3).

Component 4 "Implement the Plan"

It was difficult to find evidence of specific work plans, timelines, and resources (funding, staff, etc.) required for this component (as defined in the planning process). Nonetheless, some implementation occurred. For most case studies, strategies were implemented as evidenced in subsequent fishery management plans and amendments that enacted the selected strategies (from component 3) into management. Therefore, all case studies that have activity for step 3.4, "Pick a Strategy" also have activity for component 4, *Implement the Plan* (Table 4.3).

Component 5 "Did we make it?"

We found no explicit activity for *Did we make it?* that fits the specifications of the recommended ecosystem planning process, indicating that this is an area where management can focus attention to move toward the planning process and EBFM implementation. This component specifically refers to determining if selected strategies (from step 3.4) improved the fishery system and sustainability, and if objectives are met. Addressing and answering this question requires more than monitoring the system. A specific hurdle to conducting activity addressing component 5 is the paucity of operational objectives in component 2. It is, of course, difficult to identify activities directed at evaluating strategies relative to objectives without knowing the original objectives. Additionally, many strategies were evaluated or implemented recently (e.g. Australian Small Pelagics case study management evaluation) or are currently being implemented (e.g. the area closures in the New England groundfish case study). Perhaps insufficient time has passed to evaluate these strategies applying the protocol proposed in the ecosystem planning process. We did find examples of monitoring individual indicators from *How will we get there?* (component 3), that could allow preliminary answers to *Did we make it?,* but these examples would need further evaluation and linkage to objectives to benefit future management decisions.

DISCUSSION

Our review provides two perspectives on the existing capacity for implementing a structured decision-making process for EBFM, via next-generation FEPs. On one hand, we found that, across case studies, management activity exists that follows steps in a structured process like that proposed in the ecosystem planning process. On the other hand, our review also revealed areas where management should make adjustments or initiate new actions to place activities within a more complete structured decision-making process.

Looking across all case studies, the capacity to follow a structured decision-making process exists - nearly all steps have been conducted in some manner, usually in multiple regions. We also found that activities were accomplished in numerous ways, indicating that capacity to complete each step is flexible. It is apparent that management may tailor the process to use tools already at hand and use available technical experts and capacity to meet ecosystem objectives. Though we found little evidence for activity directed to a few key steps – namely prioritization of objectives, development of operational objectives, and assessing if objectives were met – activity for these steps could be occurring (based on evidence of proceeding steps), but not in an explicit manner. As such, the capacity for management to follow the proposed process and develop next-generation ecosystem plans may be greater than indicated by this qualitative analysis.

Although we found evidence of some activity corresponding to most of the fishery ecosystem planning steps, other steps lacked activity, suggesting that barriers may still exist for transitioning to the planning process as a means to implement EBFM. First, there could be local institutional, political, or technical barriers that prevent the initiation or completion of steps. Similar barriers have been described in detail previously (Christie et al., 2007; Hilborn, 2011; Cowan et al., 2012), including the mismatch of ecological and jurisdictional scales, and costs of monitoring and resources needed for EBFM. Alternatively, or in addition, there could be a lack of incentives to engage in activity related to fisheries ecosystem planning and EBFM in general. Finally, many of the examples of steps in the case studies were narrowly focused (species or fisheries specific) and, moving forward, there could remain a lack of a coordinated effort to participate in fishery planning at an ecosystem scale. Still, across all case studies, there is activity for almost every step and management entities can learn and borrow from others for conducting individual steps in the future.

Based on our review, we identify two priority steps to enhance the implementation of EBFM via fisheries ecosystem plans.

First, efforts to implement EBFM may have greater influence on decision-making if they are integrated using an ordered, structured step-wise process such as proposed for next-generation fishery ecosystem plans (Essington et al., 2016). Couching activities within a larger planning process may streamline management planning by satisfying multiple government mandates at once and prioritizing management issues (Marshall et al., 2018). Within the case studies, activities for many steps and components were developed in isolation, via various management mandates, workshops, etc., which can lead to repeated efforts across management activities and, consequently, resource costs. For example, the Northeast Pacific protected resources case study included examples of broad visions from the salmon fishery management plan and objectives from the killer whale recovery plan. Objectives likely also exist in salmon recovery plans or documents for other protected resources under ESA or the Marine Mammal Protection Act. Although there often are objectives that address species individually, there also are objectives that overlap due to the interactions among species. We believe that placing activities within the proposed structured planning process would facilitate addressing mandates simultaneously and reduce repetitiveness across mandates.

Without placing activities within a larger planning process, steps may also be missed or addressed out of order. Several case studies illustrate the identification and evaluation of management strategies, but few provide evidence of the steps that should precede this step–articulation of operational objectives, and targets and limits therein. Specifically, within the Atlantic Menhaden case study, the Atlantic Menhaden Technical Team identified potential performance indicators (such as environmental indicators, indices of forage abundance, and prey-predator biomass ratios) and ecosystem reference points. However, the Technical Team noted that without clear statements of system goals by the Atlantic States Marine Fisheries Commission, it could not make appropriate selections from those indicator lists (SEDAR, 2015), except for setting a catch cap for menhaden within Chesapeake Bay. In the past two years the Commission has clarified its strategic (but not operational) objectives, and its Biological-Ecological Reference Point Working Group is working to select one or more models to develop reference points based on the strategic objectives (Atlantic States Marine Fisheries Commission, 2017). With hindsight, the ongoing process might have been streamlined by adopting a more structured process at the outset to articulate goals and prioritize objectives.

In contrast, the Australian small pelagic fishery (SPF) was the only case study we could identify with an example of a measurable operational objective and corresponding performance indicator and reference point to evaluate alternative management strategies. Specifically, that abundance of no more than 15% of other species or groups is impacted by more than 40%, and no species abundance is impacted by more than 70% (adopted from Marine Stewardship Council, 2014). Researchers then tested management strategies to determine which met these EBFM criteria. Accordingly, operational objectives and targets therein were identified before the evaluation of management strategies, as outlined in the ecosystem planning process.

Second, in our search for examples of each step, it was difficult to find documentation of some steps, specifically prioritizing objectives and articulating operational objectives. Therefore, additional activity related to these steps is needed to advance towards the use of structured planning and the implementation of EBFM. Leslie et al. (2015) determined that successful ecosystem-based management (EBM) projects included a defined set of specific objectives and prioritization, and EBM projects in Australia that were successful had clear operational objectives (Smith et al., 2017). Lacking prioritization, managers may fail to foresee certain risks or trade-offs and/or inefficiently allocate resources within management (Fletcher, 2005; Levin et al., 2014). Moving forward, finding examples to learn from for prioritization for EBFM may be difficult. However, the National Marine Fisheries Service has developed a framework for prioritizing fisheries species for stock assessments that includes, among other objectives, how important a target species is as a predator or prey item in its ecosystem (Methot, 2015). As management moves forward towards implementing next-generation FEPs, lessons can be learned from examples outside of EBFM such as this and tools for prioritizing objectives also exist (see Essington et al. (2016)).

Stakeholder involvement in FEP planning, while expensive (FAO, 2003; Tallis et al., 2010), is key to success in the planning process. The ecosystem planning process outlined by the Task Force calls for stakeholder participation in all steps and in more than a consultation capacity; incorporating stakeholder knowledge to describe the system and develop management strategies, including stakeholder values and needs (Essington et al., 2016). But evidence of stakeholder inclusion was limited. There are multiple potential explanations for this. First, the case study topics may not reflect stakeholder involvement occurring in regions, i.e. management may be using greater stakeholder involvement for other management issues within regions. Second, as with other steps and specifications for this process, there may be little documentation on stakeholder involvement. Nonetheless, enhanced stakeholder involvement within case study regions is beginning to emerge. For example, the recently released, Bering Sea fishery ecosystem plan outlines steps for the North Pacific Fishery Management Council to consider and incorporate local and traditional knowledge into the management process, not just through integrating it into Western science but through extensive collaboration with local and indigenous peoples at the outset (North Pacific Fishery Management Council, 2018).

CONCLUSION

Although there is currently no wide-spread use of a structured process for EBFM planning in the U.S., our analysis demonstrates that, on one hand, there is a capacity for a structured decision-making process, via next-generation fishery ecosystem plans (Essington et al., 2016), and this process is a plausible avenue for EBFM implementation. Management has conducted the majority of steps in the process and multiple tools exist to complete the steps (based on case studies and tools listed in Essington et al. (2016)). On the other hand, activity pertaining to some steps is not common (prioritization of objectives, development of operational objectives). Still, as management bodies move towards adopting the planning process there is opportunity to learn, adapt and share experiences across management regions. Also, on-going activity may be streamlined and made more effective by placing activity within an integrated decision-making process that includes prioritization and identification of specific operational objectives and appropriate performance indicators. The implementation of EBFM is not constrained by the need for new science tools; progress can be made with existing tools within a structured decision-making process.

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Table 4.1 Ten case studies evaluated

The 10 case study regions and management issues examined to evaluate management activity related to the steps in the proposed next-generation fishery ecosystem plan process.

Case Study Region	**Management Issue**
New England	Habitat area closures for improved groundfish protection
Mid-Atlantic	Butterfish and habitat-based survey availability
Mid-Atlantic/Chesapeake Bay	Needs of menhaden predators
Gulf of Mexico	Environmentally-linked mortality of gag grouper
Northeast Pacific	Pacific sardine and environmentally linked harvest control rules
Northeast Pacific/U.S. West Coast	Interacting protected species
Bering Sea	Groundfish and avoiding ecosystem overfishing
Western Scotian Shelf	Declining traditional fisheries
Eastern Baltic Sea	Cod-herring-sprat interactions
Eastern and Southern Australia	Small pelagic fishery impacts on the ecosystem

Table 4.2 Criteria for evaluating case studies

Minimum criteria used to determine if activity within each case study adhered to steps from the next-generation fishery ecosystem plan process. Minimum criteria stem from the definition of each step from Levin et al. (2018).

Component	Steps	Minimum criteria for completion
1. Where are we now?	1.1 System Inventory & Conceptual Model	A summary of multiple (at least two) components of the fishery system and connections between those multiple components.
	1.2 Select Indicators	Selected and documented indicators related to at least two system components and status and/or trend of each indicator. Indicators are selected using best practices (not add hoc indicators, see Essington et al. (2016))
	1.3 Inventory Threats	Within documentation, mention of at least two threats to the entire system or a component of the system. Does not need to be a literal list.
2. Where are we going?	2.1 Vision Statement	A broad statement about management goals or core values for a fishery system – must refer to multiple components in the system or the system as a whole (no single species).
	2.2 Strategic Objectives	Similar to vision statement but more specific. Must relate to multiple components in a system or one component's connection to other parts of the system – should relate directly to main case study topic.
	2.3 Assess Risk to Objectives	Any qualitative or quantitative evaluation of risk related to the main species/topic of the case study with reference to some other components in the system (at least one other component).
	2.4 Prioritize Objectives	Some explicit prioritization of the strategic objectives. Must mention objective related to main case study topic.
	2.5 Operational Objectives	More specific objectives that do or do not stem directly from the strategic objectives. Must contain main topic of the case study in reference to its connection to the larger system or another component in the system (not solely a single species objective). Must contain either a desired value or value to avoid or directional goal for the future. May be implied by later steps (performance measures or strategies chosen) but must be explicitly stated.
3. How will we get there?	3.1 Performance Measures	Selection of any performance measures used to evaluate potential management strategies for meeting objectives. Ideally are connected to operational objectives from component 2, but not essential.
	3.2 Management Strategies	Consideration of more than one potential management strategy.

	3.3 Evaluate Strategies	Similar to above, must have qualitative or quantitative evaluation of more than one management strategy. Evaluate based on performance measures.
	3.4 Select Strategy	A single strategy must be chosen. Reference points are used in management strategies so modifications of conventional reference points, using environmental data, count as selecting a strategy (since this will lead to a management strategy).
4. Implement the plan		Strategy selected from component 3 (How will we get there?) is currently used (or was used at one point) in management (harvest control rules, used to set quota, put in management plans or amendments, etc.). No specific evidence of planning documents/logistics needed as long as the strategy was implemented.
5. Did we make it?		Collection and evaluation of data to determine if objectives were met. Must be connected back to operational objectives from component 2 (therefore, without operational objectives, cannot be completed). Continued monitoring of status and trends of indicators without connection to objectives does not count.

Table 4.3 Activity for each step for each case study

For each case study, a check mark indicates there is management activity related to an individual step in the next-generation fishery ecosystem plan process.

STEPS	New England Groundfish	Mid-Atlantic Butterfish and Habitat	Atlantic Menhaden	Gulf of Mexico Gag Grouper	Pacific Sardine	Pacific Interacting Protected Species	Bering Sea Groundfish	Western Scotian Shelf	Eastern Baltic Sea	Australian Small Pelagics
1. Where are we?										
1.1) System inventory & Conceptual model	✔	✔	✔	✔	✔	✔	✔	✔	✔	
1.2) Select indicators	✔	✔	✔	✔	✔	✔	✔	✔	✔	
1.3) Inventory threats	✔	✔	✔	✔	✔	✔	✔	✔	✔	
2. Where are we going?										
2.1) Vision statement		✔	✔				✔	✔	✔	
2.2) Strategic objectives	✔	✔	✔		✔	✔	✔	✔	✔	✔
2.3) Assess risk to objectives						✔	✔			✔
2.4) Prioritize objectives										
2.5) Operational objectives	✔						✔			✔
3. How will we get there?										
3.1) Performance measures	✔				✔		✔			✔
3.2) Management strategies	✔				✔	✔	✔			✔
3.3) Evaluate strategy	✔				✔	✔	✔			✔
3.4) Pick strategy	✔	✔	✔	✔	✔	✔	✔		✔	✔
4. Implement the plan	✔	✔	✔	✔	✔		✔		✔	✔
5. Did we make it?										

SYNTHESIS

This dissertation presents advancements in models of varying complexity for the exploration of forage fish-predator interactions. Through these advances, it reveals insights into these interactions that previous models could not. I constructed models specifically designed to address questions surrounding forage fish, their fisheries, and impacts of these fisheries on upper trophic predators and associated tradeoffs between forage fish catch and predator conservation. These models revealed insights into the role of forage fish in ecosystems (California Current specifically) and revealed key considerations for applications of models to management. First, aggregation of species within models can over-estimate the importance of forage fish in food-webs, but also under-estimate the diet dependence and sensitivity of individual predators. Secondly, though data and time intensive to construct non-aggregate ecosystem models, this modeling effort acts as triage to identify key predator-prey interactions that likely lead to trade-offs both between fisheries and between fisheries and ecosystems. These particular interactions could then be modeled at a more focused level in order to inform management. But finally, for certain predators that are particularly sensitive to changes in prey availability, mainly seabirds, we may still be missing key information necessary to construct models that can be used to make robust management decisions. Or alternative strategies such as ensemble modeling or risk analysis are needed to address structural uncertainty within models for use in management.

Much of the concern surrounding the potential ecosystem impacts of fishing forage fish has come from papers that use food-web models with aggregated species guilds to show high reliance of groups of predators on a group of forage species (Smith et al., 2011; Pikitch et al., 2014). However, many predators are generalists (consuming multiple forage fish and other species) (Chapter 1), so when forage fish and their predators are modeled with high taxonomic resolution in a food-web model, it can reveal multiple energy flow pathways in food-webs (not "wasp-waisted", (Cury et al., 2000)), meaning that no single forage fish is key to ecosystem function (further depletion would not have wide-spread ecological impacts). Therefore, because of alternative prey and these multiple energy pathways, many predators may not have negative responses to increased fishing on an individual forage species (Chapter 2). This is not to say that there aren't predators that are sensitive to fishing forage fish, as I found many (Chapter 2), but that negative impacts and tradeoffs of fishing forage fish may not be as ubiquitous as predicted by previous studies. Therefore, managing individual forage fish fisheries to minimize tradeoffs may be more tractable.

Specifically, high taxonomic resolution models can help identify the species and fisheries most impacted by fishing forage fish and the potential greatest economic tradeoffs (Chapter 2), and therefore help focus management. In this way, ecosystem models of high taxonomic resolution can be used to prioritize predators and specific forage fish for ecosystem-based fisheries management (EBFM). For example, previous work did identify "seabirds" as dependent on forage fish and sensitive to fishing (Kaplan et al., 2013; Pikitch et al., 2014). Chapter 2 showed within the California Current system that brown pelicans specifically are the most negatively impacted of all non-market predators, with increases in forage fish fishing on anchovy and sardine causing large biomass losses. Therefore, EBFM may be needed to manage anchovy and sardine fisheries to address both fisheries and conservation objectives, but may not need to consider repercussions for all seabirds. Or similarly, we may not necessarily need EBFM to manage certain fisheries (beyond just forage fish fisheries) if there are no evident large tradeoffs.

Part of EBFM is explicitly addressing tradeoffs, but can specific results from this dissertation be incorporated into management, particularly EBFM? I showed that the capacity exists for management to employ a structured decision making process for EBFM, specifically next-generation fishery ecosystem plans (FEPs) (Chapter 4). Though models in this dissertation were not designed to be used in tactical fisheries management, the results here could be used strategically within the next-generation FEP framework. For example, Chapter 2 revealed that salmon fisheries in the California Current would likely have economic losses if fishing on anchovy increased. If one management goal is to maximize economic revenue from the salmon fishery, this result suggests that a dynamic anchovy-salmon model is needed to explore how salmon catch can be maximized given an active anchovy fishery. A management-strategy evaluation (MSE, a key step in the FEP process) could be applied to estimate the impacts of various anchovy and salmon harvest strategies on various objectives (maximize sardine catch, maximize salmon catch, etc.). Therefore, specific predator sensitivities identified could be addressed within EBFM through targeted models within the next generation FEP framework.

Seabirds were particularly sensitive to forage fish fisheries (Chapters 1,2), but we may not have enough empirical information (Chapter 3) for seabird-specific models to be used beyond informing future research. One key benefit of intermediate-complexity models is that instead of knowing consumption-growth rate functional forms, these models can incorporate functional relationships between consumption and survival, reproduction, etc., and prey; not consumption itself (Plaganyi et al., 2014). But, there are few existing quantifications of even these relationships for seabirds. Others have stated that without knowing the functional relationships between seabirds and prey availability, further modeling will not improve insight (Sydeman et al., 2017). However, there are more uses of models beyond making predictions. Our seabird model (Chapter 3) did show us what parameters/functions population dynamics were most sensitive to and therefore where we can focus future empirical research and improve data collection, to improve future modeling and understanding of populations. Additionally, model exploration of various functional form shapes and prey availability thresholds (where a demographic rate begins to decline) could help test the validity of hypothesized functional forms to constrain future modeling. This could also help narrow-down the potential lower limit of prey levels that should be avoided, by determining which thresholds lead to increased risk for seabirds. But without additional information on functional responses across a range of demographic parameters, specifically breeding propensity and adult survival, we may not be able to reproduce seabird population dynamics for making robust management predictions.

Alternatively, there are modeling approaches that could advance our use of multi-species models in management in the face of uncertainty. One tool that can be used to address structural uncertainty (uncertainty around how to represent ecosystem processes in models) is ensemble modeling – comparisons of results across a set of multiple models each with variation in ecological assumptions (Hill et al., 2007; Gårdmark et al., 2013). Running a suite of models under different assumptions of functional response shapes/thresholds (related to chapter 3) to test impacts on seabirds of various management strategies, would be one form of ensemble modeling. The goal then, would be to identify management strategies that are robust across the range of models – i.e. strategies that perform similarly and meet objectives no matter what the assumption(s). Related, another tool is quantitative risk assessment (Smith et al., 2007) – determining the probability of an undesirable outcome (for example, loss of a seabird population, Chapter 3). In the face of uncertainty about functional response shape, we could calculate the probability of reaching a specific level of seabird decline across a range of functional responses (a range of possible "realities"). Management strategies that lead to lower risk across all functional response possibilities could help managers meet objectives despite uncertainty.

Within this dissertation, I addressed model parameter uncertainty and structural uncertainty related to functional responses, but structural uncertainty encompasses ALL uncertainty surrounding which ecosystem processes to model and how to represent them. The ecological question or objective at hand helps to guide what is included in certain models, but there is still modeler discretion in what to include and how to represent it. And definitely these choices can impact results, as I showed in this dissertation with aggregation of species versus disaggregation (Chapters 1 and 2). For Chapter 3, I consulted with seabird ecologists throughout model development, but the results suggested that there were still possibly processes left out that may be needed to fully capture seabird-prey dynamics. As mentioned above, ensemble modeling can help address this uncertainty, however, researchers have noted that there could still be bias in model output based on the researchers included in the ensemble modeling process (Hill et al., 2007) and what is chosen to include in models based on those researchers expertise, background, and philosophy of modeling (complexity versus simplicity).

Therefore, for models to be useful in management, stakeholder inclusion in model development can be invaluable to the modeling process. Various stakeholders, including managers, tribes, fishers, and scientists, not just modelers themselves, should be involved from the onset of modeling projects. This group together can develop a conceptual model (a diagram of components and how they interact) that reflects each individual’s understanding of interactions and connections in a system, related to a specific management question or objective. Certain connections not thought of by certain individuals, may be deemed by other stakeholders to be key. For example, social components may not often be considered by ecological modelers. Moving forward from this, multiple models constructed as part of ensemble modeling can include various portions or subsets of the full conceptual model. Or, if there is not consensus across stakeholders on a single conceptual model, models within the ensemble could reflect various alternative conceptualizations of the system by different stakeholders (see Stier et al., 2017). Thus in total, across all models, the ensemble will reflect the full suite of relevant connections in the system and the diverse background and perspectives of stakeholders.

This dissertation as a whole suggests a path forward for explicitly accounting for forage fish fishery tradeoffs in management – for an individual forage species, determine the likely most sensitive individual predators, and develop tailored models for those forage fish-predator pairs (multispecies models, models of intermediate complexity, etc.). Others before me have suggested similar paths (Möllmann et al., 2013; Plaganyi et al., 2014). Unfortunately, we may not be at this point empirically for all predators (Chapter 3). But larger whole-ecosystem models might be useful for prioritizing which predators/relationships to collect data on or ensemble modeling or risk assessment may provide robust management advice in the face of uncertainty. Finally, models will likely only be useful to management with clear management objectives, which are often not identified (Chapter 4). Various management strategies can be tested within an ensemble of predator-forage fish models, but without objectives from management, useful performance measures cannot be specified and we cannot determine which strategies lead us to desirable outcomes. Therefore, we can build and refine models of varying complexity all we want, but we can't explicitly address tradeoffs in management, and thus implement EBFM, without direction from managers.

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APPENDIX A: CHAPTER 1 DIET TABLE

Note – certain prey\predator combinations have been removed when the row is zero for all presented predators for ease of viewing.

Invertebrate diets

Prey\Predator	Phytoplankton	Infauna	Amphipods	Epibenthic	micro-zoop	Copepods	Euphausiids	carniv-zoops
phytoplankton	0	0	0.2	0	0.75	0.8	0.9	0.03
infauna	0	0	0	0.43	0	0	0	0
amphipods	0	0	0	0.02	0	0	0	0.02
epibenthic	0	0	0	0	0	0	0	0
micro-zoop	0	0	0	0	0	0.2	0.05	0.03
copepods	0	0	0	0	0	0	0.05	0.5
euphausiids	0	0	0	0	0	0	0	0.35
carniv-zoops	0	0	0	0	0	0	0	0
small jellies	0	0	0	0	0	0	0	0.05
large jellies	0	0	0	0	0	0	0	0.02
Detritus	0	1	0.8	0.55	0.25	0	0	0
Input Consumption	0	0	0	0	0	0	0	0
Diet Quality Ranking	1	0	0	0	0	0	0.6	0.6
Dirichlet Multiplier	2000	150	150	150	150	150	1000	1000

Invertebrate diets continued

Prey\Predator	Small jellies	large jellies	pandalid shp	benthic shp	Dungeness	tanner crb	Mesopelagics	benthic fish	surf perch	Other Cephalopod
phytoplankton	0.5	0	0	0	0	0	0	0	0	0
infauna	0	0	0.25	0.4	0.4	0.792	0	0.3	0.395	0
amphipods	0	0	0.02	0.04	0.025	0	0.03	0.18	0.08	0.078
epibenthic	0	0	0.05	0.4	0.2	0.118	0	0.4	0.205	0.009
micro-zoop	0.25	0.03	0	0	0	0	0	0	0	0
copepods	0	0.3	0.1	0	0	0	0.32	0	0.25	0.072
euphausiids	0	0.6	0.2	0	0	0	0.52	0	0	0.492
carniv-zoops	0	0.02	0.03	0	0	0	0.04	0	0	0.181
small jellies	0	0.05	0	0	0	0	0.045	0	0	0.116
large jellies	0	0	0	0	0	0	0.02	0	0	0
pandalid shp	0	0	0	0	0	0	0	0.01	0.01	0.007

benthic shp	0	0	0	0	0.2	0	0	0.04	0.01	0.005
dungeness	0	0	0	0	0.005	0	0	0.01	0	0
tanner crb	0	0	0	0	0	0	0	0.002	0	0
mesopelagics	0	0	0	0	0	0	0.005	0	0	0.021
benthic fish	0	0	0	0	0.01	0	0	0	0	0
surf perch	0	0	0	0	0	0	0	0	0	0
Other Cephalopod	0	0	0	0	0.001	0	0.02	0.001	0	0.001
market squid	0	0	0	0	0	0	0	0	0	0
Sardine	0	0	0	0	0	0	0	0	0	0
Anchovy	0	0	0	0	0.001	0	0	0	0	0.005
Herring	0	0	0	0	0.02	0	0	0.005	0	0
Pacific Mackerel	0	0	0	0	0	0	0	0	0	0
Sandlance	0	0	0	0	0.03	0	0	0	0	0
White bait smelt	0	0	0	0	0.01	0	0	0	0	0
Other smelt	0	0	0	0	0.039	0	0	0	0	0.007
Saury	0	0	0	0	0	0	0	0	0	0
Juvenile rockfish	0	0	0	0	0.001	0	0	0.003	0	0.002
Juvenile hake	0	0	0	0	0	0	0	0	0	0
Juvenile flat	0	0	0	0.01	0.01	0	0	0.02	0	0.002
Juvenile round	0	0	0	0	0.002	0	0	0.002	0	0.002
Longspine Thornyhead	0	0	0	0	0	0	0	0	0	0
Flatfish	0	0	0	0	0.021	0	0	0.01	0	0
Detritus	0.25	0	0.35	0.15	0.005	0.09	0	0.017	0	0
Input Consumption	0	0	0	0	0.02	0	0	0	0.05	0
Diet Quality Ranking	0	0	0.6	0	0.6	0.2	0.6	0.6	0.2	0.2
Dirichlet Multiplier	150	150	1000	150	1000	300	1000	1000	300	300

Forage fish diet

Prey\Predator	market squid	Sardine	Anchovy	Herring	Pacific Mackerel	Sand-lance	White bait smelt	Other smelt	Saury
phytoplankton	0	0.251	0.321	0	0	0	0	0	0
infauna	0	0.001	0	0	0	0	0.044	0.003	0
amphipods	0.006	0.005	0	0.047	0.007	0.405	0.006	0.165	0.032
epibenthic	0	0	0	0.002	0.05	0	0.284	0.239	0

micro-zoop	0	0.011	0	0	0	0	0	0	0
copepods	0.017	0.307	0.124	0.195	0.145	0.232	0.012	0.159	0.045
euphausiids	0.222	0.408	0.436	0.656	0.616	0.256	0.295	0.149	0.666
carniv-zoops	0.63	0.003	0.018	0.073	0.014	0.097	0.274	0.138	0
small jellies	0.008	0.011	0.096	0.002	0.023	0	0	0.069	0
large jellies	0.075	0	0	0	0.014	0	0	0.04	0
pandalid shp	0	0	0	0	0	0	0	0	0
benthic shp	0	0	0	0	0.003	0	0	0	0
dungeness	0	0	0	0	0	0	0	0	0
tanner crb	0	0	0	0	0	0	0	0	0
mesopelagics	0	0	0	0	0	0	0	0	0
benthic fish	0	0	0	0	0.016	0	0	0	0.056
surf perch	0	0	0	0	0	0	0	0	0
Other Cephalopod	0.005	0	0.001	0	0.001	0	0	0	0
market squid	0	0	0	0	0.073	0	0	0	0
Sardine	0	0	0	0	0	0	0	0	0
Anchovy	0.01	0	0	0	0	0	0	0	0.019
Herring	0	0	0	0	0	0	0	0	0
Pacific Mackerel	0	0	0	0	0	0	0	0	0
Sandlance	0	0	0	0	0.029	0	0	0	0.047
White bait smelt	0	0	0	0	0	0	0	0	0
Other smelt	0	0	0	0	0	0	0	0	0
Saury	0	0	0	0	0	0	0	0	0
Juvenile rockfish	0.016	0	0	0	0.003	0	0	0	0
Juvenile hake	0	0	0	0	0	0	0	0	0
Juvenile flat	0.01	0	0	0	0.003	0	0	0	0
Juvenile round	0	0	0	0	0.003	0	0	0	0
Detritus	0	0	0	0	0	0	0	0	0
Input Consumption	0	0.002	0.004	0.023	0	0.01	0.085	0.037	0.135
Diet Quality Ranking	0.8	1	0.6	0.8	0.6	0.8	0.8	0.6	0.8
Dirichlet Multiplier	1500	2000	1000	1500	1000	1500	1500	1000	1500

Fish diet

Prey\Predator	Juvenile rock.	Juvenile hake	Juvenile flat	Juvenile round	Juvenile thorny	Yellow-tail Rock.	Black Rock.	Near-shore Rock.	Yellow-eye
phytoplankton	0	0	0	0	0	0	0	0	0
infauna	0.009	0	0.575	0	0	0	0	0.024	0
amphipods	0.006	0.002	0.21	0.011	0	0.002	0.006	0.002	0
epibenthic	0.022	0.006	0.2	0	0	0.005	0.03	0.072	0.178
micro-zoop	0	0	0	0	0	0	0	0	0
copepods	0.39	0.083	0	0.818	0.2	0	0	0	0
euphausiids	0.44	0.803	0	0.123	0.5	0.55	0.247	0.096	0
carniv-zoops	0.004	0.014	0	0.029	0.25	0.025	0.119	0.096	0
small jellies	0.001	0	0	0	0.05	0.06	0.02	0.134	0
large jellies	0	0	0	0	0	0.01	0.038	0.105	0
pandalid shp	0.03	0	0	0	0	0.02	0	0.001	0.091
benthic shp	0.075	0.014	0.015	0	0	0	0.041	0.223	0.009
dungeness	0	0	0	0	0	0	0	0.001	0
tanner crb	0.012	0	0	0	0	0	0	0	0
mesopelagics	0.004	0.058	0	0	0	0.05	0	0	0
benthic fish	0.003	0	0	0	0	0.01	0.025	0.029	0.141
surf perch	0	0	0	0	0	0	0	0.024	0
Cephalo-pod	0	0.001	0	0	0	0.03	0	0.01	0.006
market squid	0	0	0	0	0	0.04	0	0	0
Sardine	0.004	0	0	0	0	0	0	0	0.057
Anchovy	0	0	0	0.001	0	0	0.128	0.072	0.002
Herring	0	0.005	0	0.001	0	0.08	0.11	0.005	0.276
Pacific Mackerel	0	0	0	0	0	0	0	0	0
Sandlance	0	0	0	0.001	0	0.01	0.01	0	0
White bait smelt	0	0	0	0.005	0	0	0.08	0.072	0
Other smelt	0	0	0	0	0	0.003	0.007	0	0
Saury	0	0	0	0.011	0	0	0	0	0
Juvenile rockfish	0	0	0	0	0	0.03	0.03	0.012	0.019
Juvenile hake	0	0.012	0	0	0	0.01	0.005	0	0
Juvenile flat	0	0	0	0	0	0.005	0	0	0
Juvenile round	0	0	0	0	0	0.005	0	0.004	0
Juvenile thorny	0	0	0	0	0	0	0	0	0

Yellowtail Rockfish	0	0	0	0	0	0	0	0	0.021
Black Rockfish	0	0	0	0	0	0	0	0	0.005
Nearshore Rockfish	0	0	0	0	0	0	0	0	0.003
Yelloweye	0	0	0	0	0	0	0	0	0
Green-striped	0	0	0	0	0	0	0	0	0.003
Shelf Rockfish	0	0	0	0	0	0	0	0	0.016
Short-belly	0	0	0	0	0	0	0	0	0.012
Petrale sole	0	0	0	0	0	0	0	0	0
Halibut	0	0	0	0	0	0	0	0	0
Hake	0	0	0	0	0	0.02	0	0	0
Lingcod	0	0	0	0	0	0	0	0	0
Arrow-tooth	0	0	0	0	0	0	0	0	0
Sablefish	0	0	0	0	0	0	0	0	0
Albacore	0	0	0	0	0	0	0	0	0
Salmon	0	0	0	0	0	0	0.065	0.005	0
Grenadier	0	0	0	0	0	0	0	0	0
Dogfish	0	0	0	0	0	0	0	0.01	0
Canary Rockfish	0	0	0	0	0	0	0	0	0.002
Pacific Ocean P.	0	0	0	0	0	0	0	0	0.003
Widow Rockfish	0	0	0	0	0	0	0	0	0.01
Splitnose Rockfish	0	0	0	0	0	0	0	0	0.01
Slope Rockfish	0	0	0	0	0	0	0	0	0.008
Shortspine thorny.	0	0	0	0	0	0	0	0	0
Longspine Thorny.	0	0	0	0	0	0	0	0	0
Flatfish	0	0	0	0	0	0.025	0.01	0.005	0.127
Detritus	0	0	0	0	0	0	0	0	0
Input Consump.	0	0	0	0	0	0.01	0.03	0	0
Diet Quality	0.6	0.8	0	0.6	0	0.8	0.6	0.6	0.4
Dirichlet Multiplier	1000	1500	150	1000	150	1500	1000	1000	500

Fish diet continued

Prey\Predator	Greenstripe	Shelf Rockfish	Shortbelly	Petrale sole	Halibut	Hake	Lingcod	Arrowtooth	Sablefish
phytoplank	0	0	0	0	0	0	0	0	0
infauna	0	0.003	0	0	0.002	0.003	0	0.001	0.02
amphipods	0.003	0.005	0.06	0.004	0	0	0	0.001	0.001
epibenthic	0.057	0.05	0	0.14	0.019	0.004	0.05	0.02	0.05
micro-zoop	0	0	0	0	0	0	0	0	0
copepods	0.005	0.02	0.071	0	0	0	0	0	0
euphausiids	0.144	0.5	0.828	0.003	0	0.709	0.003	0.07	0.074
carniv-zoops	0.352	0.01	0.041	0	0	0.021	0.009	0.001	0.01
small jellies	0	0	0	0	0	0	0	0	0.04
large jellies	0	0	0	0	0	0	0	0	0.025
pandalid shp	0.375	0.05	0	0.01	0.017	0.007	0.01	0.041	0.015
benthic shp	0.007	0.01	0	0.2	0.018	0.021	0.01	0.002	0.002
dungeness	0	0	0	0.003	0.017	0	0.05	0.002	0.001
tanner crb	0	0	0	0	0.001	0	0	0.001	0.002
Meso-pelagics	0.014	0.08	0	0	0	0.084	0.004	0.004	0.025
benthic fish	0	0.03	0	0.124	0.018	0.005	0.25	0.009	0.05
surf perch	0	0	0	0	0.004	0	0.001	0	0
Other Cephalopod	0.013	0.005	0	0.005	0	0.041	0.145	0.005	0.075
market squid	0	0.005	0	0	0.064	0.001	0.005	0	0.006
Sardine	0	0	0	0	0.14	0.01	0	0	0.01
Anchovy	0	0.09	0	0.05	0.08	0.005	0.015	0	0.012
Herring	0.01	0.06	0	0.025	0.022	0.01	0.022	0.11	0.04
Pacific Mackerel	0	0	0	0	0.058	0	0	0	0
Sandlance	0.01	0	0	0.001	0.022	0	0.015	0.051	0
White bait smelt	0	0	0	0	0	0.001	0.02	0	0
Other smelt	0.01	0	0	0	0.005	0.009	0	0.01	0
Saury	0	0	0	0	0	0.005	0.004	0	0.003
Juvenile rockfish	0	0.015	0	0.001	0	0.004	0.01	0.002	0.03
Juvenile hake	0	0.03	0	0.001	0.01	0.048	0	0.188	0.018
Juvenile flat	0	0.005	0	0.02	0.01	0	0.025	0.013	0.003
Juvenile round	0	0.005	0	0	0.01	0	0.027	0.003	0.025

Juvenile thorny	0	0	0	0	0	0	0	0	0.05
Yellowtail Rockfish	0	0.002	0	0	0.002	0	0.008	0.001	0.002
Black Rockfish	0	0	0	0	0	0	0.002	0	0
Nearshore Rockfish	0	0	0	0	0	0	0.001	0	0.001
Yelloweye	0	0	0	0	0	0	0	0	0
Greenstripe	0	0	0	0	0	0	0.001	0	0
Shelf Rockfish	0	0.002	0	0	0.001	0	0.006	0.001	0.002
Shortbelly	0	0.001	0	0	0.001	0	0.005	0.001	0.02
Petrale sole	0	0	0	0	0.001	0	0.006	0.002	0
Halibut	0	0	0	0	0	0	0	0	0
Hake	0	0	0	0	0.185	0	0.103	0.377	0.2
Lingcod	0	0	0	0	0	0	0	0	0.001
Arrowtooth flounder	0	0.005	0	0	0.004	0	0	0	0.001
Sablefish	0	0	0	0	0.002	0	0	0	0
Albacore	0	0	0	0	0	0	0	0	0
Salmon	0	0	0	0	0.018	0	0.001	0.001	0.002
Grenadiers	0	0	0	0	0	0	0	0	0.01
Dogfish	0	0	0	0	0	0	0.001	0	0.004
Canary Rockfish	0	0	0	0	0	0	0.001	0	0
Pacific Ocean P.	0	0	0	0	0	0	0	0	0
Widow Rockfish	0	0.001	0	0	0.001	0	0.005	0.001	0.001
Splitnose Rockfish	0	0.001	0	0	0.001	0	0	0.001	0.001
Slope Rockfish	0	0	0	0	0	0	0	0	0.001
Shortspine thornyhead	0	0	0	0	0	0	0	0	0.015
Longspine Thornyhead	0	0	0	0	0	0	0	0	0.015
Flatfish	0	0.015	0	0.415	0.067	0.011	0.184	0.06	0.046
Skates	0	0	0	0	0	0	0	0	0.001
Sharks	0	0	0	0	0	0	0	0	0
Detritus	0	0	0	0	0.014	0	0	0	0.04

Input Consump.	0	0	0	0	0.185	0	0.001	0.02	0.05
Diet Quality Ranking	0.6	0.6	0.6	0.6	0.8	0.8	0.6	0.6	0.6
Dirichlet Multiplier	1000	1000	1000	1000	1500	1500	1000	1000	1000

Fish diet continued

Prey\Predator	Alba-core	Sal-mon	Grenadiers	Dog-fish	Canary Rockfish	Pacific Ocean Perch	Widow Rockfish	Splitnose Rockfish	Slope Rockfish
phytoplankton	0	0	0	0	0	0	0	0	0
infauna	0	0	0.15	0	0	0	0	0	0
amphipods	0	0.01	0.05	0.003	0.001	0.032	0.035	0.021	0.016
epibenthic	0	0	0.15	0.04	0	0.005	0	0.001	0.021
micro-zoop	0	0	0	0	0	0	0	0	0
copepods	0	0.03	0	0	0	0	0.002	0.002	0
euphausiids	0.003	0.16	0	0.23	0.92	0.771	0.3	0.76	0.712
carniv-zoops	0.003	0.18	0	0.005	0.008	0.069	0.2	0.175	0.053
small jellies	0	0.01	0	0	0.001	0	0.32	0	0
large jellies	0	0.002	0	0.05	0	0	0.04	0	0.005
pandalid shp	0	0	0.01	0.015	0.03	0.015	0.001	0	0.074
benthic shp	0	0	0.04	0.015	0	0	0	0.001	0.011
dungeness	0	0	0	0.03	0	0	0	0.001	0
tanner crb	0	0	0	0	0	0	0	0	0
mesopelagics	0.001	0.008	0.05	0	0.018	0.059	0.035	0.01	0.053
benthic fish	0	0.003	0.05	0.07	0	0.01	0	0.001	0
surf perch	0	0	0	0.001	0	0	0	0	0
Other Cephalopod	0.034	0.001	0.3	0.04	0	0.02	0.005	0.002	0.013
market squid	0.008	0.03	0	0.02	0	0.01	0	0	0
Sardine	0.01	0.05	0	0.05	0	0	0	0	0
Anchovy	0.059	0.2	0	0.045	0	0	0	0	0
Herring	0.001	0.135	0	0.05	0.015	0	0	0	0
Pacific Mackerel	0	0	0	0	0	0.005	0	0	0
Sandlance	0	0.014	0	0.001	0.005	0	0	0.003	0.042
White bait smelt	0	0.005	0	0.001	0	0	0	0	0
Other smelt	0	0.04	0	0.01	0	0.003	0.015	0	0
Saury	0.051	0.022	0	0.01	0	0	0	0	0

Juvenile rockfish	0.001	0.055	0	0.02	0	0	0.02	0	0
Juvenile hake	0.077	0.01	0.05	0.02	0	0	0	0	0
Juvenile flat	0	0.01	0	0.02	0	0	0.002	0	0
Juvenile round	0	0.01	0	0.013	0	0	0.002	0	0
Juvenile thorny	0	0	0	0	0	0	0	0	0
Yellowtail Rockfish	0	0	0	0.001	0	0	0	0	0
Black Rockfish	0	0	0	0	0	0	0	0	0
Nearshore Rockfish	0	0	0	0	0	0	0	0	0
Yelloweye	0	0	0	0	0	0	0	0	0
Greenstriped	0	0	0	0	0	0	0	0	0
Shelf Rockfish	0	0	0	0	0	0	0	0	0
Shortbelly	0	0	0	0.001	0	0	0	0	0
Petrale sole	0	0	0	0.001	0	0	0	0	0
Halibut	0	0	0	0	0	0	0	0	0
Hake	0	0	0	0.155	0	0	0.02	0	0
Lingcod	0	0	0	0.013	0	0	0	0	0
Arrowtooth flounder	0	0	0	0.002	0	0	0	0	0
Sablefish	0	0	0	0	0	0	0	0	0
Albacore	0	0	0	0	0	0	0	0	0
Salmon	0.001	0	0	0	0	0	0	0	0
Grenadiers	0	0	0	0	0	0	0	0	0
Dogfish	0	0	0	0	0	0	0	0	0
Canary Rockfish	0	0	0	0	0	0	0	0	0
Pacific Ocean Perch	0	0	0	0	0	0	0	0	0
Widow Rockfish	0	0	0	0	0	0	0	0	0
Splitnose Rockfish	0	0	0	0	0	0	0	0	0
Slope Rockfish	0	0	0	0	0	0	0	0	0
Shortspine thornyhead	0	0	0	0	0	0	0	0	0
Longspine Thornyhead	0	0	0	0	0	0	0	0	0
Flatfish	0	0.005	0	0.06	0	0	0.003	0	0
Detritus	0	0	0.15	0.004	0	0	0	0	0

Input Consumption	0.75	0.01	0	0.005	0.002	0	0	0.023	0
Diet Quality Ranking	0.8	1	1	0.6	0.8	0.6	0.8	0.6	0.6
Dirichlet Multiplier	1500	2000	2000	1000	1500	1000	1500	1000	1000

Fish diet continued

Prey\Predator	Shortspine thornyhead	Longspine Thornyhead	Flatfish	Skates	Sharks
phytoplankton	0	0	0	0	0
infauna	0.05	0.16	0.778	0.022	0
amphipods	0.05	0.03	0.053	0.01	0
epibenthic	0.057	0.2	0.131	0.12	0.004
micro-zoop	0	0	0	0	0
copepods	0	0	0.007	0	0
euphausiids	0	0	0.005	0.048	0.012
carniv-zoops	0.01	0	0.001	0.005	0
small jellies	0.005	0.01	0	0	0
large jellies	0	0	0	0	0
pandalid shp	0.058	0.01	0.009	0.01	0
benthic shp	0.151	0.25	0.013	0.28	0
dungeness	0	0	0	0.05	0.003
tanner crb	0.168	0.1	0	0.01	0
mesopelagics	0.037	0.1	0	0.029	0.013
benthic fish	0.05	0.05	0	0.02	0.013
surf perch	0	0	0	0.001	0
Other Cephalopod	0.025	0.05	0	0.06	0.16
market squid	0	0	0	0.025	0.012
Sardine	0	0	0	0	0.05
Anchovy	0	0	0.001	0.001	0.08
Herring	0.009	0	0	0	0.024
Pacific Mackerel	0	0	0	0	0.055
Sandlance	0	0	0.001	0.023	0
White bait smelt	0	0	0	0	0
Other smelt	0	0	0	0	0
Saury	0.006	0	0	0	0.02
Juvenile rockfish	0.05	0.015	0	0.012	0
Juvenile hake	0	0	0	0	0.05
Juvenile flat	0	0	0	0.05	0
Juvenile round	0	0	0	0.01	0.004
Juvenile thorny	0.05	0	0	0	0
Yellowtail Rockfish	0	0	0	0.004	0.003
Black Rockfish	0	0	0	0.001	0.001

Nearshore Rockfish	0	0	0	0	0
Yelloweye	0	0	0	0	0
Greenstriped	0	0	0	0	0
Shelf Rockfish	0.002	0	0	0.007	0.003
Shortbelly	0.002	0	0	0.022	0.002
Petrale sole	0	0	0	0.005	0.001
Halibut	0	0	0	0	0.005
Hake	0.131	0	0	0.024	0.22
Lingcod	0	0	0	0	0.005
Arrowtooth flounder	0.001	0	0	0.005	0.004
Sablefish	0	0	0	0.006	0
Albacore	0	0	0	0	0.003
Salmon	0	0	0	0	0.013
Grenadiers	0.005	0	0	0	0
Dogfish	0	0	0	0	0.01
Canary Rockfish	0	0	0	0	0
Pacific Ocean Perch	0	0	0	0	0
Widow Rockfish	0	0	0	0.003	0.002
Splitnose Rockfish	0.002	0	0	0.005	0.002
Slope Rockfish	0.001	0	0	0.002	0.001
Shortspine thornyhead	0	0	0	0	0
Longspine Thornyhead	0.01	0	0	0	0
Flatfish	0.008	0.005	0	0.11	0.02
Skates	0	0	0	0	0.001
Sharks	0	0	0	0	0.012
Porpoises	0	0	0	0	0.015
Humpback	0	0	0	0	0
Minke	0	0	0	0	0
Fin	0	0	0	0	0
Sperm whale	0	0	0	0	0
Harbor seals	0	0	0	0	0.005
Sea Lions	0	0	0	0	0.02
Juv. Nor. Ele. Seal	0	0	0	0	0
Adult Nor. Ele. Seal	0	0	0	0	0.03
Detritus	0	0.02	0	0	0
Input Consumption	0.06	0	0	0.02	0.124

Diet Quality Ranking	0.6	0.8	0.6	0.8	0.6
Dirichlet Multiplier	1000	1500	1000	1500	1000

Seabird diet

Prey\Predator	Comm. Murre	Cassin auklet	Rhino-ceros auklet	Tufted Puffin	Califor. gull	West. Gull	Black-legged kittiwake	Alba-tross	North. Fulmar
Phytoplank.	0	0	0	0	0	0	0	0	0
infauna	0	0	0	0.011	0	0.005	0	0.001	0
amphipods	0	0.019	0	0.004	0.004	0	0	0	0.022
epibenthic	0	0.005	0	0	0	0.005	0	0	0
micro-zoop	0	0	0	0	0	0	0	0	0
copepods	0	0.393	0	0.004	0	0	0	0	0.022
euphausiids	0.008	0.393	0.093	0.051	0	0.008	0.012	0	0.022
carniv-zoops	0	0.005	0	0	0	0	0	0.003	0
small jellies	0	0	0	0	0	0	0	0	0
large jellies	0	0	0	0	0	0	0	0	0
pandalid shp	0	0.008	0	0	0	0	0	0	0
benthic shp	0	0	0	0	0	0	0	0	0
dungeness	0	0	0	0	0	0.001	0	0	0
tanner crb	0	0	0	0	0	0	0	0	0
Meso-pelagics	0.011	0	0	0.084	0	0.032	0.016	0.001	0
benthic fish	0.089	0	0	0	0	0.002	0	0	0
surf perch	0.043	0	0	0	0	0.003	0	0	0
Other Cephalopod	0.019	0.001	0.01	0.009	0.135	0.011	0	0.161	0.352
market squid	0.117	0	0.058	0.006	0.243	0.1	0.394	0	0.066
Sardine	0	0	0	0	0	0	0	0	0
Anchovy	0.186	0	0.156	0.007	0.187	0.136	0.077	0	0
Herring	0.068	0	0.065	0	0	0.129	0	0	0
Pacific Mackerel	0	0	0	0	0	0	0	0	0
Sandlance	0.032	0	0.244	0.355	0	0.202	0	0	0
White bait smelt	0.015	0	0.006	0	0	0	0	0	0
Other smelt	0.053	0	0.06	0	0	0	0	0	0
Saury	0	0	0.056	0.082	0	0.176	0	0.026	0
Juvenile rockfish	0.204	0	0.14	0.339	0	0.075	0	0	0.015

Juvenile hake	0.064	0	0.002	0	0	0.035	0	0	0
Juvenile flat	0.032	0	0	0	0	0.005	0	0	0
Juvenile round	0.026	0	0.007	0.041	0	0	0	0	0
Salmon	0.023	0	0.084	0	0	0.047	0	0	0
Detritus	0	0	0	0	0	0	0	0	0
Input Consumption	0.01	0.176	0.021	0.007	0.43	0.029	0.5	0.807	0.5
Diet Quality Ranking	1	0.8	1	0.2	0.4	0.6	0.4	0.4	0.4
Dirichlet Multiplier	2000	1500	2000	300	500	1000	500	500	500

Seabird diet continued

Prey\Predator	Shear-water	Leach's S. Petrel	Brandt's cormorant	Double crested cormorant	Pelagic cormorant	Marbled murrelet	Pigeon Guillemot	Caspian tern	Brown Pelican
phytoplankton	0	0	0	0	0	0	0	0	0
infauna	0.027	0.01	0.009	0	0.002	0	0	0	0
amphipods	0.002	0.02	0	0	0	0	0	0	0
epibenthic	0.002	0.002	0	0	0	0	0	0	0
micro-zoop	0	0	0	0	0	0	0	0	0
copepods	0	0.001	0	0	0	0	0	0	0
euphausiids	0.066	0.297	0	0	0	0.145	0	0	0
carniv-zoops	0	0	0	0	0.005	0.034	0	0	0
small jellies	0	0	0	0	0	0	0	0	0
large jellies	0.002	0.218	0	0	0	0	0	0	0
pandalid shp	0	0	0	0	0.005	0	0	0	0
benthic shp	0	0	0	0	0.003	0	0	0	0
dungeness	0	0	0	0	0	0	0	0	0
tanner crb	0	0	0	0	0	0	0	0	0
mesopelagics	0.002	0.297	0.033	0.012	0.002	0	0	0	0
benthic fish	0	0.001	0.03	0.029	0.388	0	0.384	0.059	0
surf perch	0	0	0.046	0.367	0	0.011	0.005	0.185	0
Other Cephalopod	0.096	0.035	0.012	0	0.002	0	0.026	0	0
market squid	0.183	0	0.01	0	0	0.109	0	0	0
Sardine	0	0	0	0	0	0.024	0	0.025	0.262
Anchovy	0.08	0	0.107	0.134	0	0.184	0	0.097	0.644
Herring	0.001	0	0.019	0.01	0	0.135	0	0.057	0
Pacific Mackerel	0	0	0	0	0	0	0	0	0.022

Sandlance	0	0	0	0.023	0.069	0.145	0.023	0.033	0
White bait smelt	0	0	0	0	0	0	0	0.011	0
Other smelt	0	0	0.01	0	0	0.075	0	0.064	0
Saury	0.048	0	0	0	0	0	0	0	0.033
Juvenile rockfish	0.02	0.119	0.456	0.111	0.362	0.088	0.182	0	0.022
Juvenile hake	0.001	0	0	0	0	0	0	0.002	0
Juvenile flat	0	0	0.113	0.003	0.002	0	0.167	0.002	0
Juvenile round	0.005	0	0.005	0	0	0	0.02	0	0
Salmon	0	0	0	0.003	0	0	0	0.386	0
Detritus	0	0	0	0	0	0	0	0	0
Input Consumption	0.467	0	0.148	0.309	0.16	0.049	0.193	0.078	0.017
Diet Quality Ranking	0.6	0.6	0.6	0.6	0.6	0.6	0.6	0.2	0.6
Dirichlet Multiplier	1000	1000	1000	1000	1000	1000	1000	300	1000

Marine mammal diet

Prey\Predator	Orcas (transient)	Orcas (residential)	Porpoises	Hump-back	Minke	Fin	Sperm whale	Harbor seals
phytoplankton	0	0	0	0	0	0	0	0
infauna	0	0	0	0	0	0	0	0
amphipods	0	0	0	0	0.009	0	0	0
epibenthic	0	0	0	0	0.003	0	0	0.02
micro-zoop	0	0	0	0	0	0	0	0
copepods	0	0	0	0	0.009	0.01	0	0
euphausiids	0	0	0	0.3	0.511	0.78	0	0
carniv-zoops	0	0	0	0	0.004	0.01	0	0
small jellies	0	0	0	0	0.005	0	0	0
large jellies	0	0	0	0	0	0	0	0
pandalid shp	0	0	0	0	0	0	0	0
benthic shp	0	0	0	0	0	0	0	0
dungeness	0	0	0	0	0	0	0	0.02
tanner crb	0	0	0	0	0	0	0	0
mesopelagics	0	0.013	0.04	0	0	0.05	0.033	0.04
benthic fish	0	0.031	0.025	0	0	0	0	0.05
surf perch	0	0	0	0	0	0	0	0.025
Other Cephalopod	0	0.056	0.345	0.005	0.031	0.05	0.602	0.025

market squid	0	0	0.14	0	0	0	0	0.025
Sardine	0	0.005	0.034	0.1	0.089	0.025	0.074	0
Anchovy	0	0	0.09	0.05	0.133	0.025	0	0.105
Herring	0	0.063	0.01	0.023	0.031	0.025	0	0.035
Pacific Mackerel	0	0.019	0.001	0	0.004	0	0	0
Sandlance	0	0	0	0	0.027	0.025	0	0.02
White bait smelt	0	0	0	0	0.004	0	0	0.01
Other smelt	0	0	0.027	0	0.022	0	0	0.1
Saury	0	0	0.022	0	0.027	0	0	0
Juvenile rockfish	0	0	0.002	0.023	0.004	0	0	0.01
Juvenile hake	0	0	0	0	0.018	0	0	0.01
Juvenile flat	0	0	0	0	0	0	0	0
Juvenile round	0	0	0.01	0	0	0	0	0.01
Juvenile thorny	0	0	0	0	0	0	0	0
Yellowtail Rockfish	0	0.002	0.006	0	0	0	0.018	0.008
Black Rockfish	0	0	0.002	0	0	0	0.004	0.002
Nearshore Rockfish	0	0.002	0.001	0	0	0	0.003	0.001
Yelloweye	0	0.002	0	0	0	0	0	0
Greenstriped	0	0	0.001	0	0	0	0.004	0.001
Shelf Rockfish	0	0.001	0.005	0	0	0	0.014	0.006
Shortbelly	0	0.001	0.004	0	0	0	0.012	0.005
Petrale sole	0	0	0	0	0	0	0	0.01
Halibut	0	0.013	0	0	0	0	0.022	0
Hake	0	0.025	0.125	0	0	0	0.045	0.1
Lingcod	0	0.038	0	0	0	0	0.022	0.018
Arrowtooth flounder	0	0.005	0	0	0	0	0	0.01
Sablefish	0	0.019	0.005	0	0	0	0.033	0
Albacore	0	0.001	0	0	0	0	0	0
Salmon	0	0.251	0.02	0	0.018	0	0	0.075
Grenadiers	0	0.013	0	0	0	0	0.029	0
Dogfish	0	0.013	0.003	0	0	0	0.022	0
Canary Rockfish	0	0	0	0	0	0	0.002	0.001
Pacific Ocean Perch	0	0	0.001	0	0	0	0.004	0.001

Widow Rockfish	0	0.001	0.004	0	0	0	0.012	0.005
Splitnose Rockfish	0	0	0.001	0	0	0	0.011	0.001
Slope Rockfish	0	0	0.001	0	0	0	0.007	0.001
Shortspine thornyhead	0	0	0	0	0	0	0.004	0
Longspine Thornyhead	0	0	0	0	0	0	0	0
Flatfish	0	0.031	0.016	0	0	0	0	0.2
Skates	0	0.013	0.003	0	0	0	0.022	0
Sharks	0.002	0.001	0.001	0	0	0	0	0
Porpoises	0.004	0	0	0	0	0	0	0
Humpback	0.02	0	0	0	0	0	0	0
Minke	0.001	0	0	0	0	0	0	0
Fin	0.022	0	0	0	0	0	0	0
Sperm whale	0.002	0	0	0	0	0	0	0
Harbor seals	0.002	0	0	0	0	0	0	0
Sea Lions	0.022	0	0	0	0	0	0	0
Juv. Nor. Ele. Seal	0	0	0	0	0	0	0	0
Adult Nor. Ele. Seal	0.005	0	0	0	0	0	0	0
Fur seals	0.001	0	0	0	0	0	0	0
Blue whale	0.052	0	0	0	0	0	0	0
Gray whale	0.105	0	0	0	0	0	0	0
Dolphins	0.011	0	0	0	0	0	0	0
Detritus	0	0	0	0	0	0	0	0
Input Consumption	0.75	0.383	0.055	0.5	0.05	0	0	0.05
Diet Quality Ranking	0.4	0.6	0.4	0.6	0.2	0.6	0.6	0.4
Dirichlet Multiplier	500	1000	500	1000	300	1000	1000	500

Marine mammal diet continued

Prey\Predator	Sea Lions	Juv. Nor. Ele. Seal	Adult Nor. Ele. Seal	Fur seals	Blue whale	Gray whale	Dolphins
phytoplankton	0	0	0	0	0	0	0
infauna	0	0	0	0	0	0.017	0
amphipods	0	0	0	0	0	0.637	0
epibenthic	0.005	0	0.047	0	0	0.018	0

micro-zoop	0	0	0	0	0	0	0
copepods	0	0	0	0	0	0	0
euphausiids	0	0	0.004	0	0.517	0.001	0
carniv-zoops	0	0	0.01	0	0	0.009	0.042
small jellies	0	0.017	0.012	0	0	0	0
large jellies	0	0	0	0	0	0	0
pandalid shp	0	0	0	0	0	0	0
benthic shp	0	0	0	0	0	0	0
dungeness	0	0	0	0	0	0	0
tanner crb	0	0	0	0	0	0	0
mesopelagics	0.02	0.046	0	0.013	0	0	0.203
benthic fish	0.02	0.037	0	0.006	0	0	0.012
surf perch	0.01	0.003	0	0	0	0	0.003
Other Cephalopod	0.11	0.126	0.228	0.109	0	0	0.212
market squid	0.11	0.259	0.002	0.041	0	0	0.076
Sardine	0.12	0	0	0.014	0	0	0.037
Anchovy	0.028	0.003	0	0.087	0	0	0.039
Herring	0.02	0	0	0.03	0	0	0
Pacific Mackerel	0.015	0	0	0	0	0	0.022
Sandlance	0.01	0	0	0	0	0	0
White bait smelt	0.001	0	0	0	0	0	0
Other smelt	0.01	0	0	0.003	0	0	0
Saury	0.01	0	0	0.03	0	0	0.002
Juvenile rockfish	0.13	0.023	0	0	0	0	0.025
Juvenile hake	0.09	0.1	0	0	0	0	0.097
Juvenile flat	0.012	0.003	0	0	0	0	0.02
Juvenile round	0.01	0.02	0	0.005	0	0	0
Juvenile thorny	0	0	0	0	0	0	0
Yellowtail Rockfish	0.006	0	0.002	0.011	0	0	0
Black Rockfish	0.001	0	0	0.003	0	0	0
Nearshore Rockfish	0.001	0	0	0.002	0	0	0
Yelloweye	0	0	0	0	0	0	0
Greenstriped	0.001	0	0	0.002	0	0	0
Shelf Rockfish	0.005	0	0.001	0.009	0	0	0
Shortbelly	0.004	0	0.001	0.007	0	0	0

Petrale sole	0	0	0	0	0	0	0
Halibut	0	0	0	0	0	0	0
Hake	0.09	0	0.043	0.101	0	0	0
Lingcod	0.01	0	0	0	0	0	0
Arrowtooth flounder	0	0	0	0	0	0	0
Sablefish	0.01	0	0	0.011	0	0	0
Albacore	0	0	0	0	0	0	0
Salmon	0.03	0	0	0.038	0	0	0
Grenadiers	0	0	0.006	0	0	0	0
Dogfish	0.01	0.021	0.008	0	0	0	0
Canary Rockfish	0.001	0	0	0.001	0	0	0
Pacific Ocean Perch	0.001	0	0	0.002	0	0	0
Widow Rockfish	0.003	0	0.001	0.008	0	0	0
Splitnose Rockfish	0.004	0	0.001	0.007	0	0	0
Slope Rockfish	0.001	0	0.001	0.004	0	0	0
Shortspine thornyhead	0	0	0	0	0	0	0
Longspine Thornyhead	0	0	0	0	0	0	0
Flatfish	0.02	0	0	0.003	0	0	0
Skates	0.01	0.014	0.008	0	0	0	0
Sharks	0	0	0	0	0	0	0
Detritus	0	0	0	0	0	0	0
Input Consumption	0.061	0.329	0.625	0.454	0.483	0.319	0.21
Diet Quality Ranking	0.6	0.4	0.6	0.6	1	0.2	0.4
Dirichlet Multiplier	1000	300	1000	1000	2000	300	500

APPENDIX B: CHAPTER 1 FUNCTIONAL GROUPS

FOOD WEB MODEL FUNCTIONAL GROUPS AND PARAMETERS

This appendix includes information on each functional group in the food web model and the data sources for parameters for each species and functional group.

BENTHIC CONSUMERS **Benthic Infauna** The benthic infauna functional group consists mainly of polychaetes, bivalves, small crustaceans, echinoderms and other organisms that feed directly or indirectly on the organic matter on the sea floor. This group is equivalent to the benthic infauna group in Field (2004). Parameters of PB, QB, EE, and diet quantities were borrowed from Field (2004) from the 1990's California Current Ecopath model. Biomass was solved for in the model.

Amphipods

This group consists of all amphipods including gammaridae, caprellidea, and hyperiidea (not separating benthic and pelagic amphipods) and is equivalent to the group in Field (2004). PB, QB, EE, and diet information all came from Field (2004) and biomass was solved for in the model.

Epibenthic infauna

This group is made up of larger benthic organisms that live above the sediments and are somewhat to very motile. This includes: holothuroids, asteroids, ophiuroids, crinoids, brachyurans (NOT Dungeness or Tanner), anomurans, mysids, isopods, cumaceans, mollusks (primarily gastropods). This group is equivalent to the group in Field (2004). PB, QB, EE, and diet information all came from Field (2004) and biomass was solved for in the model.

Pandalid shrimp

The pandalid shrimp group contains *Pandalus jordanii*, *P.platyceros*, *P. borealis* and other, uncommon pandalid species, same as Field (2004). PB, QB, EE, and diet information all came from Field (2004) and biomass was solved for in the model. For yield, pink shrimp landings for the U.S. in 2013 of 31567 MT came from the PacFIN database, giving a yield density of 0.105 MT/km^2 (PacFIN, http://pacfin.psmfc.org/pacfin_pub/all_species_pub/woc_r307.php). Pandalid shrimp catch in Canada was very small in 2013, only amounting to 0.41 mt (Invertebrate catch data Fisheries and Oceans Canada, Science Branch)

Benthic shrimp

This group consists mainly of Crangon species but others as well including: Eualus, Daridea, and Calocaris species. This group is equivalent to the Field (2004) benthic shrimp group. PB, QB, EE, and diet information all came from Field (2004) and biomass was solved for in the model.

Dungeness crab

Dungeness crab (*Cancer magister*) PB, QB, and EE were borrowed from Field (2004). Density was solved for in the model.

Dungeness crab yield for the most recent season available was compiled from communication with experts from the Department of Fish and Wildlife. This included Heather Reed from WDFW that reported 18,523,645 lbs of Dungeness crab in Washington for 2012-2013 (WDFW unpublished data), Peter Kalvass at CDFW that reported 23,517,326 lbs in California in 2011-2012 (https://nrm.dfg.ca.gov/FileHandler.ashx?DocumentID=55686&inline=true), and Kelly Corbett that reported 18,203,385 lbs of Dungeness harvest in Oregon in 2012-2013 (ODFW unpublished data). This gave a total of 27,326 MT of catch in the US West Coast. Yonis (2010) listed Dungeness crab harvest in Canada by area up to 2008. The 2008 Dungeness harvest in area E (West coast of Vancouver island) was 699.3 MT. The final total is 28025.68 MT or a density of 0.0928 MT/km^2.

Dungeness crab diet was constructed based on two main sources, Stevens et al. (1982) and Gotshall (1977), however, we mainly used Stevens as the Gotshall diet was only reported in frequency of occurrence. Field (2004) used these same studies and came up with a base diet of: "...40% infauna (presumably dominated by bivalves), 20% epibenthic fauna, 20% benthic shrimp, 2.5% amphipods, 10% forage fish, 2% small flatfish, 1% juvenile flatfish, 0.2% juvenile roundfish, 0.1% juvenile rockfish, 0.1% cephalopods, 0.1% rex sole, 1% benthic fishes and 2.5% fisheries offal." Using this as a starter, the 10% forage fish was broken up using information from primarily Stevens, where the majority was given to sand lance and other smelt. This led to 4% other smelt, 0.5% whitebait smelt, 3.4% sandlance, 2% herring, and 0.1% anchovy.

Tanner crab

Chionoecetes tanneri (Tanner crab) parameters (PB, QB, and EE) were taken from Field (2004) as well as diet information. Density was solved for in the model. Though Field has a very small discard catch amount (0.0004 mt/km^2) in the 1990's California Current model, we did not find any recent estimates of yield, and this yield is substantially lower than yield of other species.

PLANKTONIC COMMUNITY

Phytoplankton Parameters of PB, QB, EE, and diet information were borrowed from Field (2004) from the 1990's California Current Ecopath model. Biomass was solved for in the model.

Microzooplankton

This group is made up of small protozoans (gymnodiniods, dinoflagellates, ciliates, and nanoflagellates). Field considered this whole group to be heterotrophic (autotrophs are in phytoplankton group/primary producers). This group is equivalent to Field's microzooplankton group and PB, QB, EE, and diet information were taken from Field (2004). Density was solved for in the model.

Copepods

Includes all developmental stages of copepods – furcilia, calyptosis, megalope, zoea, nauplii, trocophores. Copepods include: *Pseudocalanus* spp., *Calanus marshallae, Centropages abdominalis, Acartia longiremis*, *A. hudsonica, Paracalanus parvus, Ctenocalanus vanus,* and *Calanus pacificus.* PB, QB, EE, and diet are taken from Field (2004) and density was solved for in the model based on consumption by predators.

Euphausiids

This group consists of all life stages of euphausiid species, mainly *Euphasia pacifica, Thysanoessa spinifera*, *Nyctiphanes simplex*, and *T. longipes*. This group is equivalent to Field's group, parameters (PB, QB, and EE) and diet are taken from Field (2004), and density was solved for in the model.

Macrozooplankton

This group includes pasiphaid, seregestid and other pelagic shrimps, chaetognaths, pelagic polychaetes, and other non-gelatinous carnivorous zooplankton. It also includes crab megalopae since this life stage is more pelagic than benthic like the adult stage. Some species in this group include: *Pasiphaea pacifica, P. tarda, Sergestis similes, Saggitta elegans*, and *Eukrohnia hamate*. PB, QB, EE, and diet information was taken from Field (2004) and this group is equivalent to the macrozooplankton group in the Field model. Additionally, density was solved for in the model.

Gelatinous herbivores

This group consists of all filter-feeding urochordate herbivores, mostly salps, doliolids, and larvaceans, pteropods (including the snail *Limacina helecina*) and is identical to the Field (2004) gelatinous herbivore group. PB, QB, EE, and diet were taken from Field (2004) and density was solved for in the model.

Gelatinous carnivores

This group is primarily cnidarians (hydrozoans and scyphozoans), ctenophores, and heteropods and is identical to the Field (2004) gelatinous herbivore group. PB, QB, EE, and diet were taken from Field (2004) and density was solved for in the model.

LARGE INVERTS

Cephalopod The cephalopod group contains all cephalopoda (octopoda, teuthida, etc.) other than market squid (*Doryteuthis opalescens*). Therefore, a range of life history dynamics are included in this group, but many diet studies only specify cephalopod species to the class (cephalopoda), making it difficult to split up this group further as well as difficult to split it up as much as we did (separating market squid). PB, QB, and EE parameters were borrowed from Field (2004) and density was solved for in the model.

Diet mainly came from the Ruzicka et al. (2007) EwE model. Because this group mostly represents small cephalopods being consumed by predators, and not the larger predatory cephalopods (jumbo squid and Humboldt squid), we began with the “small squid” diet from Ruzicka et al. 2007 Ecopath model and market squid diet information (similar sized species). Ruzicka work showed large consumption on euphausiids and macrozooplankton. Market squid diet from Karpov and Cailliet (1979) also showed large consumption on euphausiids, copepods, and other crustaceans. Taking forage consumption and weighting by biomass of available forage, led to a diet of 7.8% amphipods, 1% epibenthic fauna, 7.2% copepods, 46.1% euphausiids, 18.1% macrozooplankton, 11.6% small jellies, 0.7% pandalid shrimp, 0.5% benthic shrimp, 2.1% mesopelagic fish, 0.1% cephalopods, 1.2% sardine, 1.1% anchovy, 0.7% herring, 0.7% other smelt, 0.8% juvenile rockfish, 0.2% juvenile flatfish, 0.2% juvenile roundfish. However, because cephalopod biomass is being estimated by top down balancing, consumption by others on cephalopods led to a very large biomass of cephalopods and thus, a large predation mortality of cephalopods on forage species. Again, because this group mainly represents small squids eaten by predators, consumption on forage is probably less than originally assumed for this group. We therefore removed consumption on sardine and herring (only small portions in the Ruzicka data, no information in the market squid diet) and lowered consumption on anchovy to

0.5%. The remaining consumption percent was allocated to euphausiids since Karpov and Cailliet (1979) attribute close to 66% of the diet as euphausiids.

LOWER TROPHIC FISH

Mesopelagic fish The mesopelagic fish group was borrowed from Field (2004), including mainly myctophids but also argentinids, gonostomatids, photichthyid, bathylagids, stomiatids. However, dragonfish were removed from this group as a large percent of myctophid mortality is from dragonfish consumption. Biomass for this group was set at 3 million MT from personal communication with Pete Davison and information in a recent report (Davison et al. 2013). PB, QB, EE, and diet values were taken from Field (2004).

Benthic fish

This group is identical to the Field (2004) benthic fish group and as Field mentions, this is a "catch-all" of benthic species. The group includes eelpouts (*Zoarcidae*), snailfish (*Cyclopteridae*), poachers (*Agonidae*), sculpins (*cottidae*), tomcod (*Microgadus proximus*), and spotted ratfish (*Hydrolagus colliei*). PB, QB, EE, and diet values were taken from Field (2004) and top-down balancing was used to determine the density of this group.

Surfperch

Surfperch (*Embiotocidae*) was added as an additional functional group in comparison to the Field (2004) model mainly as a prey item for upper trophic seabird predators. Surfperch parameters of PB, QB, and EE were taken from the Harvey et al. (2010) Puget Sound Ecopath model. Density was determined in the model. Diet for surfperch fish was also taken from Harvey et al. (2010). The functional groups in the diet of surfperch from the Puget Sound model were copepods, small crustaceans, shrimp, other grazers, predatory gastropods, mussels, barnacles, infaunal bivalves, soft infauna, and deposit feeders, that were translated into functional groups in this model of benthic infauna, epibenthic fauna, amphipods, copepods, pandalid shrimp, and benthic shrimp. This led to a final diet of 39.5% benthic infauna, 8% amphipods, 20.5% epibenthic fauna, 25% copepods, 1% pandalid shrimp, and 1% benthic shrimp.

FORAGE "FISH"

Market squid

There are no reliable sources of biomass for market squid (*Doryteuthis opalescens*). Because of this, biomass was estimated in the model using top-down balancing and an EE of 0.8. We recognize the potential problems of using top-down balancing to estimate market squid biomass, given that many diet studies only identify "cephalopod" in diets and not higher taxonomic resolution, but without a more reliable estimate, we used predator consumption to estimate density. Recent Canada catch is 0 mt according to Fisheries and Oceans Canada, Science Branch. For the U.S. and Mexico, the 2014 Coastal Pelagic stock assessment from the PFMC lists landings for both regions, leading to a 10-year average of 80,630 mt (0.267 mt/km^2) for 2004-2013 (PFMC 2014b). This led to a total yield in 2013 of 104282 mt. The PB value of 2.75 and QB value of 10 are borrowed from the cephalopod functional group in Field (2004).

Diet for market squid was a combination of Brodeur et al. (1987), Karpov and Cailliet (1979), and Miller (2006), though more weight was given to the Miller study because it's the most recent of the three. Mainly, the older studies showed a larger consumption on juvenile and adult fish than the more recent Miller study, which only had consumption on larval fish. The final diet became 0.6% amphipod, 1.7% copepods, 22.2% euphausiids, 63% macrozooplankton, 0.8% small jellies, 7.5% large jellies, 0.5% cephalopods, 1% anchovy, 1.6% juvenile rockfish, and 1% juvenile flatfish.

Sardine

Over the past 10 years, Pacific sardine (*Sardinops sagax*) biomass has decreased from around 1 million mt to around 600,000 mt (Hill et al. 2012). Because of this trend, we used an average biomass from the past 10 years (2003-2012) to calculate sardine biomass. This came to a total biomass of 978,632 mt (Hill et al. 2012). Stock assessments for sardine cover the whole distributional range of sardine from Canada to Mexico so we did not need to increase this biomass to include the whole domain. This led to a final model density of 3.241 mt/km^2. For yield, we also used a 10-year average, for a total average catch of 147,219.8 mt (PFMC 2014b). This again covers the whole range and includes catch for Canada and Mexico.
PB for sardine was set at 0.515, from the natural mortality rate of 0.4 used in the sardine stock assessment and a 10-year average fishing mortality rate of 0.115. The QB value of 5 was borrowed from the sardine group from Field (2004).

For sardine diet, two studies had repeated data for stomach contents –Miller (2006), and Emmett et al. (2005), though Miller (2006) had one extra sample for June 2000 that wasn't included in the Emmett study. These diet studies ranged from the coast of Washington to Northern California and consisted of samples collected in the early 2000s. For each study, samples from the same year (either 2000 or 2002) were averaged and then a total average was found for each study. Since there is repeat information between Emmett et al. and Miller, data was not averaged between the two studies but both were considered when constructing the overall sardine diet since there was extra information in each (either extra sample or taxonomic information). These two studies were compared to the diet for sardine from the Field (2004) Ecopath model. These sources considered led to an overall diet estimate of approximately 25% phytoplankton, 0.1% benthic infauna, 0.5% amphipod, 1% microzooplankton, 31% copepods, 41% euphausiids, 0.3% carnivorous zooplankton, and 1% small gelatinous jellies.

Anchovy

The original estimate for anchovy (*Engraulis mordax*) biomass came from Orsi et al. (2007) that calculated a coastal summer anchovy density for the California Current (from Northwest Vancouver island South) of 1333 individuals/km^2. At 50 grams per individual and a total Ecopath domain of 302,000, this leads to a density of around 0.05 mt/km^2.
Using this value in the Ecopath model led to an unbalanced model due to high consumption by predators on anchovy. Even after adjusting consumption rates of predators on anchovy, the model was still not balanced.

Egg surveys conducted by Fissel et al. (2011) found a spawning stock biomass (SSB) for the central subpopulation of anchovy to be 159370.3 mt. Extrapolating to a total biomass for the population using proportion at age, weight at age, and exponential growth led to a total of 186714.632 mt for the central subpopulation (population from San Francisco, CA to the southern extent of the model in Baja). I assumed that SSB included all mature adults. Since anchovy mature at 2 years of age, calculating total biomass led to the addition of age 1 fish. This is already greater metric tonnes than just using the Orsi estimate and only represents part of the model domain. Because anchovy biomass is highly variable, we used a 10-year average (2000-2009) of SSB/total biomass for the Southern anchovy stock biomass. This equaled 445017.49 mt South of San Francisco.

There additionally exists a northern subpopulation in Oregon and Washington (PFMC 2011). McClatchie (2009) has density estimates for the entire US West Coast using acoustic data but, we were cautioned by the author to not use these densities, as it is preliminary data and not meant to be used for biomass estimation. Furthermore, Fissel et al (2011) states that the central (Southern CA) subpopulation is the “largest of the North Pacific subpopulations” and yet densities from McClatchie would lead to larger populations in the North, which seems implausible.

Therefore, we used the Orsi et al. (2007) density of 1333 individuals per km^2 to calculate a total biomass for the Northern subpopulation. The total area from San Francisco, CA to the Northern extent of the model is equal to 127600 km^2, and at 50 grams per individual and a density of 0.06665 mt/km^2, this leads to a total biomass of 8504.54 mt in the North. Adding this to the total biomass from the South (445017.49) leads to 453522.028 mt in the whole Ecopath range (302,000 km^2). This translates to a density of approximately 1.502 mt/km^2.

Total catch data came for the Coastal Pelagic Stock assessment (PFMC 2011). Similar to biomass, we used a 10-year average (2000-2009) for Mexico and U.S. catch. Canada catch was basically 0 for the time series. This led to a total catch biomass of 11675.7 mt.
For the other parameters, a QB of 6 was used which is equivalent to the QB for the forage fish group in Field (2004). The PB was taken from MacCall (1973) that found an instantaneous mortality rate of 1.09 (natural mortality rate of 1.06). These values were used by Lindegren et al. (2013) in the stage-structured model for anchovy. EE was solved for in the model since all other parameters were provided.

Diet was calculated based on three sources: Brodeur et al. (1987), Tam et al. (2008) (N. Humboldt Ecopath model), and Miller (2006). We began with the diet information from Brodeur et al. (1987), however, 59% of the diet contents were unidentified. Because of this, we used the diet percentages from Tam et al. (2008) from the N. Humboldt current to break up the unidentified 59% into functional groups based on these percentages. Careful attention was paid to the difference in functional group composition between this model and the N. Humboldt model. Additionally, diet information from Miller was used. This study had two samples from 2002 (June and August), and only 1 from 2000. The 2002 diets were averaged first and than this was averaged with the 2000 sample. Any unidentified percent was split up into the identified groups based on percentages of what was identified. Finally, the two diets (one based on Brodeur/Tam, and one based on Miller) were averaged. Any values less than 0.001 (0.1%) were removed and the final diet was scaled to have a sum of 1. This led to an approximate diet of 32% phytoplankton, 12% copepods, 44% euphausiids, 2% macrozooplankton, 10% gelatinous herbivores, 0.1% cephalopod, and 0.4% input or other.

Herring

The Pacific herring (*Clupea pallasii*) biomass estimate is a rough estimate using the densities from Hay and McCarter (1997).These authors suggest max densities of 10, 0.8, and 2 t/km^2 for BC, Washington/Oregon, and North/Central California, respectively. Using these densities for the area from shore to 200 m (herring are near shore), leads to approximately 46,000 mt in the U.S. and 149,000 mt in Canada. This is higher than would be expected from the 2012 DFO assessment (DFO 2012) for herring but without another source, we use this estimate for a density of 0.662 mt/km^2. Initial balancing attempts with lower density estimates led to unbalanced models for herring based on large consumptions of herring by predators in the North.

Additionally, there are estimates for herring in BC (DFO 2014) and San Francisco (Greiner et al. 2014) that give a total spawning stock biomass of 84,249 for those two regions. Extrapolating up to a total biomass from spawning stock biomass using numbers at age and a mature age of 3 gives approximately 95,000 mt. Using the density from Hay and McCarter (1997) for WA and OR gives an additional biomass of 53,600 for a total of 148,632 mt. Though this is less than the estimate using Hay and McCarter (1997) alone, it is close and does not include any herring outside of San Francisco in California. For balancing, we will use a biomass of 200,000 mt. Herring catch biomass comes from PacFIN for 2013. Catch data for herring was obtained from publicly available groundfish trawl summary documents (that included information on herring) for 1997 to 2013 maintained by Fisheries and Oceans Canada.

The herring PB value of 1.6 and the QB value of 7.489 came from the Puget Sound Ecopath model (Harvey et al. 2010).

Herring diet came from two main sources: Brodeur et al. (1987) and Miller (2006). Both studies included samples from off the Washington and Oregon coasts, with Brodeur consisting of data from the early 1980s and Miller using samples from the early 2000s. Each study had multiple samples, and we found the average diet for each study before averaging the two studies together. For Miller, two samples were taken in 2002 and only 1 in 2000, so the 2002 samples were averaged before averaging with the 2000 sample. In the end, the diet for herring was approximately 5% amphipods, 0.2% epibenthic fauna, 20% copepods, 66% euphausiids, 7% carnivorous zooplankton, 0.2% small gelatinous herbivores, and 2% input consumption for "juvenile" fish (sand lance and sculpin) that we assumed were actually larval fish not juvenile fish based on herring size.

Pacific Mackerel

Pacific mackerel (*Scomber japonicas*) biomass estimate is a 10-year biomass estimate from the

2011 stock assessment (Crone et al. 2011). This stock assessment includes the stock in the Southern half of the domain in Baja California. The 10-year average leads to a total biomass of 148,535.4 mt and a density of 0.492 mt/km^2. Total catch was calculated in a similar way, taking a 10-year average catch for both the U.S. and Mexico from the 2011 assessment. This led to a catch density of 0.0269 km/mt^2. The PB value of 0.514 came from the adding together the natural mortality used in the 2011 stock assessment (0.5) and the fishing mortality from the assessment of 0.014. The QB value of 6 is the general mackerel QB from Field (2004).

Pacific mackerel diet came from Brodeur et al. (1987) and Miller (2006). Though the Miller study is more recent, sample sizes were larger for the Brodeur study. Any “unidentified”, general “osteichthyes”, or general “decapod” from Brodeur, were broken up based on the percentages of identified groups that fit into those categories. The same was done with the data from Miller. For most prey items, we averaged the Miller percentage with Brodeur. However, if there was zero of a certain prey group in one study, this was noted but a direct average wasn’t used. This was done because the “unidentified” percentages were so high that there is a large chance that any “0” was not a true zero. This led to the following final diet: 0.7% amphipods, 5% epibenthic fauna, 14.5% copepods, 61.5% euphausiids, 1.4% macrozooplankton, 2.3% small jellies, 1.4% large jellies, 0.3% benthic shrimp, 1.6% benthic fish, 0.1% cephalopod, 7.2% market squid, 3% sand lance, 0.3% juvenile rockfish, 0.3% juvenile flatfish, and 0.3% juvenile roundfish.

Sandlance

Sandlance (*Ammodytes hexapterus*) is an important forage fish in the diets of many species. However, biomass estimates are unavailable for these species. Therefore, we used top-down balancing to estimate density in the model using an EE of 0.8. The PB value of 1 came from an analysis by Gunderson (1997). The QB value of 3.65 is from the Aleutian Islands model (Aydin et al. 2007).

Sandlance diet came from publications by TW Miller and RD Brodeur. Diet information from Miller and Brodeur (2007) is duplicated in Miller’s dissertation thesis which also has additional information not included in the publication (Miller 2006). Using both studies and percent mass diet information from these studies that included data on samples from 2002, we were able to develop a reasonable diet composition for sandlance. This included 40.5% amphipod, 23.25 copepod, 25.6% euphausiid, 9.7% macro zooplankton, and 1% input consumption (mainly fish eggs and fish larvae). Though there was 2.7% unidentified material in Miller (2006), this was broken up amongst the identified groups based on percent identified.

Whitebait smelt

For whitebait smelt (*Allosmerus elongatus*), we used a crude biomass estimate using density from the Columbia River plume Ecopath model. Ruzicka et al. (2007) estimates density of whitebait smelt to be 0.00281 mt/km^2 based on BPA and GLOBEC trawl survey data. Using this density and a model domain out to 1200 m depth (extent of whitebait), this leads to 24,000 mt. We then multiply the 24,000 mt by 15 based on a comparison of BPA nighttime predator data and the sardine stock assessment and the 2008 Miller Freeman cruise (J. Ruzicka, Oregon State University, Newport OR); see the updated Atlantis model for further descrption (Kaplan et al. 2014). The PB value of 1.6 came from a combination of the estimate used for forage fish in Field (2004) and the estimate used by Ruzicka et al. (2007). The QB value of 6 is a general forage fish consumption value from Field (2004). There is no fishery for whitebait smelt in the model domain.

Diet data for whitebait smelt came from two main studies: Wakefield (1984) and Miller (2006). Information in Miller (2006) is also presented in Miller and Brodeur (2007) but in more detail for individual species. Wakefield (1984) looked at stomach contents for 13 specimens off the coast of Oregon. Miller (2006) had four separate samples of 38,51,60, and 41 whitebait smelt off the coast of Northern California and in Oregon. For the Miller study, the two samples from 2000 and the two samples from 2002 were averaged before the years were averaged. Both Miller (2006) and Wakefield (1984) were used in the final diet but Wakefield diet had approximately 16.7% "osteichthyes" which was not averaged with Miller, instead Miller fish percentages were used. Additionally, all fish identified were assumed to be larval (based on whitebait size) and therefore, included in input consumption. The final diet became 4% benthic infauna, 0.6% amphipods, 28% epibenthic fauna, 1.2% copepods, 29.5% euphausiids, 27% carnivorous zooplankton, and 8.5% input consumption (fish larvae).

Other smelt

This group includes all other osmeridaes (other than whitebait smelt), including surf smelt (*Hypomesus pretiosus*), night smelt (*Spirinchus starksi*), and eulachon (*Thaleichthys pacificus*). Abundance/biomass is unknown for these species so density was solved for in the model by top-down balancing using an EE of 0.8. The PB value of 1.5 and the QB value of 6 are the general PB, QB values for the forage fish group from Field (2004).

The smelt group diet is a combination of diet of surf smelt, night smelt, and eulachon. Surf smelt diet was available from Brodeur et al. (1987) and Miller (2006) and night smelt diet came from

Wakefield 1984 and eulachon diet from Gulf of Alaska studies, specifically Wilson et al. (2009) and Pearsall and Fargo (2007). Averaging the diets for these three species led to a final diet of 0.3% infauna, 16% amphipods, 24% epibenthic fauna, 16% copepods, 15% euphausiids, 14% macrozooplankton, 7% small jellies, 4% large jellies, and 4% fish eggs/larva (input consumption).

Saury

The biomass for saury (*Cololabis saira*) came from a density of 0.31 mt/km^2 from Smith et al. (1970). This density was multiplied by an area of 1.12x10^6, the total pelagic area from 1200 meters out (Kaplan et al. 2014). The PB value of 1.6 comes from the Alaska Gyre Ecopath model for the same species. The QB value of 3.65 comes from the Japan Ecopath model (Zhang et al. 2004). This PB and QB are therefore from different systems but for the same species in similar ecosystems.

Two main diet studies exist for Saury in the California Current, Brodeur et al. (1987) and Miller (2006). Though both studies were used, a large percent of the diet was “unidentified” in the Brodeur study (60-80%) and additionally 11-18% classified only as “osteichthyes”. For both studies, we debated if consumption on juvenile sandlance, juvenile anchovy, and juvenile sculpin may actually be consumption on larval stages, but decided that saury size is large enough that they could be consuming juvenile stages. For Miller (2006) because there were two samples from 2002, these were averaged before averaging with the 2000 sample. Diet was constructed using this average and information from Brodeur et al. (1987). Because of the large unidentified percentages, we used the base percentages and extrapolated up to a total of 1 using the base percentages. All of this together led to a diet of 3.2% amphipods, 4.5% copepods, 66.6% euphausiids, 5.6% benthic fish, 2% anchovy, and 4.7% sandlance.

JUVENILE FISH GROUPS

Juvenile Rockfish

This groups consists of juveniles of any and all rockfish species in the California Current, where juveniles are approximately ages 0-2 or the size that can be consumed by a seabird. Production and consumption values were borrowed from Field (2004). Diet was also taken from Field (2004). Biomass was solved for in the model through top-down balancing, using an EE of 0.8.

Juvenile Hake

Biomass for juvenile hake (*Merluccius productus*) was solved for by the model (assuming an EE value of 0.8) since this group was mainly included to be prey for multiple predator species, including adult hake. This group is meant to represent biomass of age 0 and 1 juvenile hake. PB and QB values were taken from other Ecopath models in nearby systems (Ainsworth et al. 2002; Aydin et al. 2007). We found a range of potential values for both, PB = 1.061-2.67 and QB = 5.31-6.98, and taking these ranges to be the 5th and 95th percentiles, we found the mean of the range based on a lognormal distribution. This led to a PB of 1.75 and a QB of 6.1.

Diet for juvenile hake came from two different Buckley data sets: Buckley et al. 1999 and unpublished Buckley diet data (T.W. Buckley, unpublished data) for hake for multiple size classes. Using only predator sizes of 20 cm or less, we calculated a diet of 0.2% amphipods, 0.6% epibenthic fauna, 8% copepods, 80% euphuasiids, 1.4% carnivorous zooplankton, 1.4% benthic shrimp, 6% mesopelagic fish, 0.1% cephalopods, 1% juvenile hake (cannibalism), and 0.5% herring.

Juvenile Flatfish

This includes juvenile life stages of starry flounder (*Platichthys stellatus*), Pacific sanddab (*Citharichthys sordidus*), Slender sole (*Lyopsetta exilis*), Pacific sand sole (*Psettichthys melanostictus),* Butter sole (*Isopsetta isolepis*), Rock sole (*Lepidopsetta bilineata*), English sole (*Parophrys vetulus)*, Petrale sole (*Eopsetta jordani*), Dover sole (*Microstomus pacificus)*, Rex sole (*Glyptocephalus zachirus*), and any other Pleuronectiformes species. This group was borrowed from the Field (2004) model. PB, QB, EE, and diet were all borrowed from Field (2004) and biomass was solved for in the model based on top-down balancing.

Juvenile Roundfish

This group includes juvenile life stage of sablefish (*Anoplopoma fimbria*) and lingcod (*Ophiodon elongatus*) species. This group was borrowed from the Field (2004) model. PB, QB, and EE were all borrowed from Field (2004) and biomass was solved for in the model based on top-down balancing. Diet was borrowed from Field (2004) with a few adjustments for the new forage fish groups. Using the diet from Field (2004) and information from the diet study by Brodeur et al. (1987) on consumption of specific forage fish, the diet became: 1.1% amphipods, 81.8% copepods, 12.3% euphasusiids, 2.9% macrozooplankton, 0.1% anchovy, 0.1% herring, 0.1% sandlance, 0.5% whitebait smelt, and 1.1% saury.

Juvenile Thornyhead

This group included juvenile ages of shortspine and longspine thornyhead species

(*Sebastolobus*). This group was borrowed from the Field (2004) model. PB, QB, EE, and diet were all borrowed from Field (2004) and biomass was solved for in the model based on top-down balancing.

PREDATORY FISH

Canada catch was only for the British Columbia fishery, with landings and catch data extracted from the Fishery Operations System (FOS) maintained by Fisheries and Oceans Canada (DFO) for 2007-2014. For all Canada catch, catch was summed over DFO catch areas 3C and 3D and half of area 5A for the most recent year available. Mexican catch came from CONAPESCA (2015) and see Ainsworth et al. 2011 for data methods. Additionally, when estimates of biomass in Canada were not known, U.S. estimates were extrapolated up using the same scaling factors as the Atlantis California Current model (Kaplan et al. 2014). These scaling factors were decided based on distribution of species.

Yellowtail rockfish

Biomass for yellowtail rockfish (*Sebastes flavidus*) came from the data moderate assessment by Cope et al. (2013), which gave a US biomass of 143,384 mt. According to Love (1996) Yellowtail extend from the Aleutian island to San Diego, CA. Because the biomass from the stock assessment does not include the Canada portion of the model and the full distribution of Yellowtail, we extrapolated the 143,384 mt by multiplying the U.S. density by total area in the Canada portion of the model. This led to a total biomass in the model domain of 164,639 mt or a density of 0.545 mt/km^2. Total yield was 1,376.33 mt from the stock assessment and 2,783 mt from Canada (Fisheries and Oceans Canada) for a total yield density of 0.0138 mt/km^2. QB and PB parameters were taken from the Field (2004) EwE model.

There are two main diet studies for yellowtail rockfish in the California Current: Lee (2002) and Brodeur and Pearcy (1984). Both of these studies together cover close to the full range of the domain, with Lee (2002) hitting Northern California to Washington and Brodeur and Pearcy using diet samples from Monterey California to Vancouver Island. There were substantial differences in these studies, with Lee showing euphausiids as a large percent of yellowtail diet and Brodeur and Pearcy attributing a higher percent to general osteichthyes. Field (2004) used these same two studies to construct the diet of yellowtail for his model as well as Pereyra et al. (1969), Lorz et al. (1983), and P.A. Livingston (pers. Comm). We began with the Field (2004) diet but had slight variations based on separating forage fish species and averaging Lee (2002) based on month/season in which samples were collected and based on things we observed in the same studies that Field (2004) used. This led to a final diet of 0.2% amphipods, 0.5% epibenthic fauna, 55% euphausiids, 2.5% carnivorous zooplankton, 6% small jellies, 1% large jellies, 2% pandalid shrimp, 5% mesopelagic fish, 1% benthic fish, 3% other cephalopods, 4% market squid, 8% herring, 1% sand lance, 0.3% other smelt, 3% juvenile rockfish, 1% juvenile hake, 0.5% juvenile flatfish, 0.5% juvenile roundfish, 2% hake, 1.5% small flatfish, and 2% input consumption.

Black Rockfish

The 2006 stock assessment for Black rockfish (*Sebastes melanops*) gave a biomass of 30,363 mt in the United States (Wallace et al. 2008). According to Love (1996), Black rockfish inhabit waters from Alaska to Central California. We therefore assumed no biomass in Baja and extrapolated to find a Canadian biomass. Since the U.S. stock assessment split biomass up into North and South, we used both the North and the total overall densities to extrapolate into the Canada area. This gave a range of potential densities in the entire model domain from 0.115 to 0.1333 mt/km^2. Because each parameter was later turned into a probability distribution from which multiple Ecopath model parameters were pulled, this range was used as the 95% confidence interval of that distribution. Based on that range and a lognormal distribution, the mean value that would produce that confidence interval was 0.124 mt/km^2. For yield, we took the total catch from the U.S. 2006 assessment plus the minimal catch from Canada (only area 5A, 0.0023 mt) for a total yield density of 0.003 mt/km^2. Both PB and QB parameters were borrowed from Field (2004) and were equal to 0.129 and 2.01, respectively.

Diet for black rockfish came from Brodeur et al. (1987), Steiner (1978), and diet for the general “black rockfish” group from Field (2004). We mainly relied on the Brodeur study for black rockfish diet since the Steiner study was only from one year (1976-1977) that was notably a “warm” phase year and a PDO shift year. We also used data from Gladics (2012) and Hallacher and Roberts (1985) but only qualitatively since raw diet data was presented in percent number or counts. All together, we calculated a final, overall diet to be 0.6% amphipods, 3% epibenthic fauna, 25% euphuasiids, 12% carnivorous zooplankton, 2% small jellyfish, 4% large jellyfish, 2.5% benthic fish, 13% anchovy, 11% herring, 1% sandlance, 8% whitebait smelt, 0.7% other smelt, 3% juvenile rockfish, and 0.5% juvenile hake.

Nearshore Rockfish

This rockfish group contains Blue Rockfish (*Sebastes mystinus*), Kelp greenling (*Hexagrammos decagrammus*), Brown Rockfish (*Sebastes auriculatus*), Copper Rockfish (*Sebastes caurinus*), Greenspotted Rockfish (*Sebastes chlorstictus*), and Cowcod (*Sebastes levis*). For biomass, blue rockfish biomass came from the 2007 stock assessment (age 1+ biomass; Key et al. 2008) and kelp greenling from the 2005 assessment (Cope and MacCall 2005). Brown rockfish biomass came from Cope et al. (2013) assessment (mature male and female biomass) and Copper biomass also came from Cope et al. (2013) and is again just mature male and female biomass. Greenspotted biomass came from Dick et al. (2011). Finally, cowcod biomass came from Dick (2013) but was only for Southern California Bight and was scaled up by a factor of 3.8 to include all of California and Mexico and 231 mt was added to included the stock north of Point Conception (note this was also only mature male and female biomass). All biomass other than cowcod was only for the United States. Biomass was scaled up in two ways: 1. Dividing by the area in the US alone, assuming the density is the same through out the domain and 2. Scaling up by a factor of 1.36. Not adjusting cowcod, this led to a range for the entire group density of 0.077-0.0833 mt/km^2. Because each parameter was later turned into a probability distribution from which multiple Ecopath models were pulled, this range was used as the 95% confidence interval of that distribution. Based on that range and a lognormal distribution, the mean value that would produce that confidence interval was 0.0801 mt/km^2. Yield was taken from each assessment as well as from Fisheries and Oceans Canada for blue rockfish, kelp greenling, Copper and greenspotted, and minimal catch from Mexico (CONAPESCA 2015) for a total yield density of 0.00169. Blue rockfish has the highest biomass in this group and the PB value was based off of this species. The PB value of 0.158 is the average natural plus fishing mortality for males and females from the Key et al. stock assessment. The QB of 2.01 was borrowed from Field (2004).

Nearshore rockfish diet came from multiple sources (many used by Field 2004). These included Brodeur et al. (1987), Steiner (1978), and Stein and Hassler (1989) (and citations within Stein and Hassler). Combining these studies with the diet that Field previously estimated for this group, that included Black rockfish, we estimated a general diet, trying to remove any consumption that was mostly from black rockfish and not the others. Scaling so that the diet would total to 1, this led to a diet of 2.4% benthic infauna, 0.2% amphipods, 7% epibenthic fauna, 9.6% euphuasiids, 9.6% carnivorous zooplankton, 13.4% small jellies, 10.5% large jellies, 0.1% pandalid shrimp, 22% benthic shrimp, 0.1% Dungeness crab, 7% anchovy, 0.5% herring, 7% white bait smelt, 1.2% juvenile rockfish, 0.4% juvenile roundfish, 0.5% salmon, 1% dogfish, and 0.5% small flatfish.

Yelloweye rockfish

Yelloweye rockfish (*Sebastes ruberrimus*) are both present in the United States and Canada, and are rarely seen South of Central California according to Love (1996). US biomass came from the 2011 stock assessment (Taylor and Wetzel 2011) and was scaled up to include Canada by multiplying by a factor of 1.24 leading to a total biomass density of 0.00898 mt/km^2. The PB value of 0.0505 was taken from the U.S. stock assessment using an average male and female mortality (natural and fishing). QB was borrowed from the Field (2004) shelf rockfish group and equals 2.2. Yield is low for yelloweye with 11.39 mt from the U.S. and 1.91 from Canada for a total yield density of 0.000044 mt/km^2.

Only one main study was found for Yelloweye rockfish diet in the California Current; York (2005) that looked at only 9 stomach samples from Washington to Northern California in 2003-2004. Additionally, a large part of the diet in York (2005) was only specified to the family or genus level (*Sebastes, Clupeidae, Pleuronectiformes,* etc.). However, Field (2004) also cited diet information from a dissertation by Steiner (1978). We combined Steiner (1978) with York (2005) to give a more comprehensive diet. Because rockfish were not identified at the species level, we broke up the total rockfish percent by the biomass proportion of rockfish species in the domain. For forage fish, other than a large portion of herring in York (2005) stomachs, Steiner (1978) identified anchovy in the diet and we assumed that a portion of the identified clupeidae is sardine. These two studies led to a final diet of 17.8% epibenthic fauna, 9% pandalid shrimp, 0.9% benthic shrimp, 14% benthic shrimp, 0.6% cephalopod, 6% sardine, 0.2% anchovy, 27.5% herring, 1.9% juvenile rockfish, 2% yellowtail rockfish, 0.5% black rockfish, 0.3% nearshore rockfish, 0.3% greenstriped rockfish, 3% slope rockfish, 0.2% canary rockfish, 0.3% pacific ocean perch, 1% widow rockfish, 1% splitnose rockfish, 0.8% shelf rockfish, and 12.6% flatfish.

Greenstriped rockfish

Biomass for Greenstriped rockfish (*Sebastes elongatus*) comes from the West Coast Groundfish Bottom Trawl Survey (WCGBTS) from NOAA Northwest Fisheries science Center, based on methods in (Bradburn et al. 2011) with a swept area estimate of 17,378 mt. Greenstriped are present in Canada and Mexico also, so we multiplied the total US biomass by 1.7 (ratio of 0-200m habitat in the whole model, divided by 0-200m habitat in U.S. waters, Kaplan et al. 2014) to extrapolate up. This gave a final density of 0.098 mt/km^2. For yield, the 2009 stock assessment (Hicks et al. 2009) had a total catch of 9.2 mt while the Canada catch data showed a total catch of 28.59 mt for a total yield density of 0.00013 mt/km^2. QB and PB parameters were taken from Field (2004) from the shelf rockfish functional group.

Diet was mainly taken from York (2005), which looked at 51 greenstriped stomachs from

Washington to N. California. This was supplemented with information from Shaw (1999) that found mainly pandalid shrimp in the stomachs of Greenstriped rockfish, then euphausiids, and then trace amounts of fish species. This led to a final diet of 0.3% amphipods, 6% epibenthic fauna, 0.5% copepods, 14% euphausiids, 35% carnivorous zooplankton, 38% pandalid shrimp, 0.7% benthic shrimp, 1.5% mesopelagic fish, 1% herring, 1% sandlance, and 1% smelt.

Shelf Rockfish

This group includes Bocaccio (*Sebastes paucispinis*), Vermillion (*Sebastes miniatus*), Chilipepper (*Sebastes goodei*), Stripetail (*Sebastes saxicola)*, Gopher (*Sebastes carnatus)*, and China rockfish (*Sebastes nebulosus*). Bocaccio U.S. biomass came from the 2011 stock assessment (Field 2011) and Canada biomass came from the 2012 DFO assessment for all of British Columbia (Stanley et al. 2012) and was cut in half to get an approximate biomass for in the model domain. Finally, bocaccio biomass was multiplied by 1.36 to extrapolate into Baja. All other species in this functional group only had biomass estimates for the U.S. (Chilipepper – Field 2007; Stripetail – the West Coast Groundfish Bottom Trawl Survey (WCGBTS) from NOAA Northwest Fisheries science Center, based on methods in (Bradburn et al. 2011), Gopher – Key et al. 2005; China – Cope et al, 2013 only mature male and females, Vermillion –MacCall 2005) and all of these were increased by a factor of 1.7 to account for biomass in Canada and Baja. For yield, Bocaccio yield was taken from the stock assessment for the U.S. and from Fisheries and Oceans Canada data for Canada (38.4 mt). Yield for all other species were taken from their respective assessments, except for Vermillion, which has an updated yield in the PacFIN database. With additional catch from Canada for these species, total catch was 0.00153 mt/km^2.

Shelf rockfish PB was calculated for this group using the Field (2004) PB for this group (0.125) and the Chilipepper natural and fishing mortality from the stock assessment (total of 0.185) and finding the weighted average based on biomass for a final PB of 0.159. The QB value of 2.2 was borrowed from Field (2004).

Diet was taken from Field (2004) with adjustments due to changes in species composition of the group. Diet was adjusted based on information in Steiner (1978), Phillips (1964), and Shaw (1999). Chilipepper and stripetail consume mainly euphausiids and these two species make up the largest amount of biomass in this group so euphausiid consumption was increased. Any consumption on larger fish species is due to Bocaccio rockfish consumption. Consumption on other rockfish species was broken up based on biomass availability of those rockfish species and a total consumption on rockfish fraction. This led to a diet of 0.3% infauna, 0.5% amphipods, 5% epibenthic fauna, 2% copepods, 50% euphausiids, 1% carnivorous zooplankton, 5% pandalid shrimp, 1% benthic shrimp, 8% mesopelagic fish, 3% benthic fish, 0.5% cephalopods, 0.5% market squid, 9% anchovy, 6% herring, 1.5% juvenile rockfish, 3% juvenile hake, 0.5% juvenile flatfish, 0.5% juvenile roundfish, 0.2% yellowtail rockfish, 0.2% shelf rockfish (cannibalism), 0.1% shortbelly, 0.5% arrowtooth flounder, 0.1% widow rockfish, 0.1% splitnose rockfish, and 1.5% small flatfish.

Shortbelly Rockfish

Shortbelly rockfish (*Sebastes jordani*) was separated into it's own group because of its large biomass and difference in diet from the other shelf rockfish. Biomass came from the 2007 US stock assessment (Field et al. 2007), and extrapolated up for biomass in Canada and Baja by a factor of 1.7. For the U.S., yield was set at zero because there was zero catch and a zero harvest rate in 2005 in the last year of data from the assessment. For Canada, catch was low at 0.0075 mt, leading to a total yield density of 2.48E-08 mt/km^2. The PB value of 0.1 was taken from the stock assessment and is equal to the natural mortality for shortbelly rockfish since harvest rate was near zero. The QB value of 2.2 was borrowed from Field (2004) and is the general shelf rockfish QB.

Diet for Shortbelly mainly came from Chess et al. (1988). Chess gave diets for 190 Shortbelly rockfish off the coast of Central California, and separated diet by length (99-160 mm, 161-200 mm, and 201-272 mm). All together, Shortbelly seem to be only consuming euphausiids, copepods, macrozooplankton, and amphipods. Percentages of these were weighted based on the lengths given, using information on length at age and numbers at age. This led to a final diet of 83% euphausiids, 7% copepods, 6% amphipods, and 4% macrozooplankton.

Petrale sole

Petrale sole (*Eopsetta jordani*) biomass came from the 2013 Haltuch et al. stock assessment and was scaled up by a factor of 1.58 (closer in shore than other species that were scaled up by a factor 1.7) (see Kaplan et al. 2014). U.S. yield also came from the Haltuch et al. (2013) assessment and with the addition of 472 mt of catch from Canada, the total catch density was 0.0054 mt/km^2. The PB value of 0.32 is equal to the 2013 harvest rate plus the average male and female natural mortality rate, again from Haltuch et al. (2013). Finally, the QB value of 1.7 is borrowed from Field (2004).

For Petrale sole diet, we began with the diet from Field (2004) (that used Kravitz et al. 1976) and information from Wakefield (1984). The Wakefield (1984) study noted changes in consumption based on petrale sole size, where smaller individuals consumed larger amounts of mysids, sculpins and recently settled flatfish, and larger individuals consumed more juvenile pleuronectiformes and crangon shrimp. We did consider this shift and numbers at age/weight at age when constructing the final diet. Additionally, Kravitz et al. (1976) noted an importance of anchovy in the diet. Other forage fish in the diet noted in the stock assessment for petrale sole were herring and sandlance. Diet information was also taken from Pearsall and Fargo (2007) for Petrale diet in the Hecate strait, which suggested consumption of mainly benthic/epibenthic fauna, shrimp, and herring in the Winter and no fish in the summer diet at all. Adjusting the original Field (2004) diet based on information from these other sources gave a final diet of 0.35% amphipods, 14% epibenthic fauna, 0.25% euphausiids, 12.4% mesopelagic fish, 0.45% cephalopod, 5% anchovy, 2.5% herring, 0.1% sand lance, 0.1% juvenile rockfish, 0.1% juvenile hake, 2% juvenile flatfish, and 41.5% other flatfish.

Halibut

This group contains both Pacific and California Halibut (*Hippoglossus stenolepis* and *Paralichthys californicus*) though there are differences between the two species. For California Halibut biomass, we used an estimate of 18,000 mt from the Maunder et al. (2011) California Department of Fish and Wildlife assessment. We doubled this value, since 18,000 was only for Northern and Sourthern California, for a total C. Halibut biomass of 36,000 mt. For Pacific Halibut, Stewart et al. (2012) estimated 849 million net lbs of age 2+ halibut (equal to 1,131 million lbs rough weight) from the Bering Sea to California. Based on this and 2012 survey catches, close to 2% of this total was in U.S. waters and 13.2% in British Columbia (but only 14.2% of the BC total is in the model domain) (*pers. comm.*, I. Stewart, IPHC, Seattle,WA). This leads to a total of 19,909 mt of Pacific halibut in the model domain. For yield, Stewart et al. (2012) had Pacific halibut catch for Oregon, Washington, and BC. California halibut yield came from Maunder et al. (2011) and is both recreational and commercial yield. Recreational yield was in numbers and was translated to metric tonnes using an average weight of 2.58 kg per fish from Reed and Maccall (1988). In addition, catch for these species in Canada totaled 191 mt for a total yield density of 0.0032 mt/km^2.

A PB value for California Halibut came from MacNair et al. (2001) and was equal to 0.545 (average male and female). Pacific halibut was assumed to have a similar PB to arrowtooth flounder, for a PB of 0.335. Based on biomass proportions of both species, this led to a PB of

0.47. The QB value (2.12) was also taken from arrowtooth flounder (Field, 2004).

Final halibut diet came from a weighted average of California and Pacific halibut diets, weighting by biomass in the model domain. Pacific halibut diet came from Field (2004), who used diet information from Yang (1995) noting that this is from the Gulf of Alaska and consisted of a large consumption of hake (~45%). The 15% forage fish consumption for pacific halibut was split into 6% sandlance, 6% herring, 1.5% eulachon (other smelt), and 1.5% anchovy (assumed to be similar to capelin consumption in GOA), based on the info given by Field (2004) and Yang (1995). California halibut constitutes a much larger total percent of halibut in the model domain, at 64%. Diet for California halibut came from Wertz and Domeier (1997) that breaks up % volume consumption by different length groups of C. halibut. Diets for different length groups were averaged but values adjusted qualitatively if a prey item was only present in one or two length groups' diets. Using these two diets and 64% California halibut and 36% Pacific halibut (biomass weights), the following diet was constructed: 0.2% benthic infauna, 1.9% epibenthic infauna, 1.7% pandalid shrimp, 1.7% benthic shrimp, 1.7% Dungeness crab, 0.06% tanner crab, 1.8% benthic fish, 0.4% surf perch, 6% market squid, 14% sardine, 8% anchovy, 2.2% herring, 6% pacific mackerel, 2.2% sand lance, 0.5% other smelt, 1% juvenile flatfish, 1% juvenile roundfish, 0.2% yellowtail rockfish, 0.1% slope rockfish, 0.1% shortbelly rockfish, 0.1% petrale sole, 20% hake, 0.3% arrowtooth flounder, 0.2% sablefish, 0.1% widow rockfish, 0.1% splitnose, 7% other flatfish, and 1.4% input consumption. Rockfish consumption was determined by splitting up total rockfish consumption based on biomass available.

Hake

For hake (*Merluccius productus*) biomass, because the species' biomass has increased substantially over the last years, a 10-year (2004-2013) average biomass was used to represent the system in a steady state. Data for biomass came from (Hicks et al. 2014). This led to a total biomass of 2,429,248 mt. Additionally, the yield used is a 10-year average yield from the stock assessment giving a final yield density of 0.95 mt/km^2. These estimates represent the full geographic range of Hake. The PB value came from the natural mortality used in the 2013 stock assessment plus a 10-year average (2012-2003) of fishing mortality (average of 0.2) for a total mortality of 0.41. The QB value came from the balanced version of the Field (2004) 1990 model (QB = 1.95), versus the original QB value that Field (2004) cites of 2.43.

For diet, data from T. Buckley (Alaska Fisheries Science Center, unpubl. data) has diet by size (10 cm increments from 0 to 70 cm) for multiple years from the 1960s through 1990s (see work in Buckley and Livingston 1997). Since this functional group represents year 2 and older hake, we used diet for sizes 20 cm to 70 cm, and broke up the diet as: 20 cm = year 2, 30 cm = year 3, 40 cm = years 4-9, and 50-70 cm = years 10+ (based on information from Beamish 1979 of size at age). We averaged diets for sizes 50 cm and greater for a general diet for hake 10 years of age and greater. Then, using information on growth and the Von Bertalanffy growth function, we calculated numbers at age (see Kaplan et al. 2014) and then we determined QB at age. Using QB at different ages/sizes, we weighted the diets. Data from Buckley that were labeled "prickle squish deep" were determined to be mostly mesopelagic species. Unidentified fish was broken up based on the percentages of identified fish. Final diet became 0.3% infauna, 0.4% epibenthic fauna, 71% euphausiids, 2% carnivorous zooplankton, 0.7% pandalid shrimp, 2% benthic shrimp, 8% mesopelagic fish, 0.5% benthic fish, 4% cephalopods, 0.1% market squid, 1% sardine, 0.5% anchovy, 1% herring, 0.1% whitebait smelt, 0.8% other smelt, 0.5% saury, 0.5% juvenile rockfish, 5% juvenile hake (cannibalism), and 1% flatfish. Consumption on herring is potentially higher but was lowered for balancing and may only be high in the northern part of the model domain. For consumption on herring, we also consulted other hake diets including Brodeur et al. (1987), Buckley et al. (1999), Miller and Brodeur (2007), Livingston and Alton 1982, Livingston 1983, Rexstad and Pikitch 1986, Tanasichuk et al. 1991, and Buckley and Livingston 1997. We also consulted these studies for separation of general smelt in the diet into our two smelt groups.

Lingcod

The lingcod (*Ophiodon elongatus*) biomass was a combination of U.S. biomass from the Hamel et al. (2009) stock assessment and Canada biomass from the 2011 DFO assessment. According to Love (1996), South of Point Conception lingcod abundance is low, so we assumed no lingcod in Mexico. U.S. yield came from the 2009 stock assessment and Canada catch came from the Fisheries and Oceans Canada data (422 mt) leading to a total yield density of 0.0036 mt/km^2. The PB value of 0.295 is the male and female average natural mortality from the 2009 assessment, plus the 2008 fishing mortality. The QB of 2.4 was borrowed from Field (2004).

Extensive lingcod diet data exists for the San Juans for multiple size classes of Lingcod (Beaudreau and Essington 2007). However, this region is technically outside the domain of the model. Field (2004) cites additional diets from Steiner (1978) and Wakefield (1984). A recent study by Tinus (2012) gives lingcod diet on the coast of Oregon. Because of its location and recent time period, the diet was mainly weighted towards Tinus (2012). Rockfish consumption was not identified at the species level, therefore, we broke up consumption into the individual rockfish groups based on biomass availability. Final diet became 5% epibenthic fauna, 0.3% euphuasiids, 0.9% carnivorous zooplankton, 1% pandalid shrimp, 1% benthic shrimp, 5% Dungeness crab, 0.4% mesopelagic fish, 25% benthic fish, 0.1% surf perch, 14.5% cephalopods, 0.5% market squid, 1.5% anchovy, 2.2% herring, 1.5% sand lance, 2% whitebait smelt, 0.4% saury, 1% juvenile rockfish, 2.5% juvenile flatfish, 2.7% juvenile roundfish, 0.8% yellowtail, 0.2% black rockfish, 0.1% nearshore rockfish, 0.1% greenstriped, 0.6% shelf rockfish, 0.5% shortbelly, 0.5% petrale sole, 10% hake, 0.1% salmon, 0.1% dogfish, 0.1% canary rockfish, 0.5% widow rockfish, 18.4% flatfish, and 0.1% input consumption.

Arrowtooth flounder

Arrowtooth flounder (*Atheresthes stomias*) biomass came from the 2007 U.S. stock assessment (Kaplan and Helser 2007). U.S. biomass was than multiplied by a factor of 1.22 to extrapolate into Canada, but only near shore (out to about 550 m). Total catch for the U.S. came from Kaplan and Helser (2007), and total Canada catch was 7,947 mt for a total yield density of 0.0342 mt/km^2. From the same stock assessment, using average male and female natural mortality and the most recent fishing mortality, led to a PB of 0.264. The QB value of 2.12 was taken from Field (2004).

For Arrowtooth flounder diet, we began with diets from Buckley et al. (1999), Yang (1995), and Gotshall (1969). Buckley et al. looked at stomach contents for 380 arrowtooth in 1989 and 1992 from Oregon to Vancouver Canada. Yang (1995) evaluated arrowtooth diet in the Gulf of Alaska and Gotshall (1969) looked at diet of 425 arrowtooth back in the 1960s. Based on the original diet compositions from these studies, as well as the Field (2004) composite of these studies, we constructed our original estimate of diet for arrowtooth, noting that Yang (1995) data is from outside the model domain. Buckley et al. showed a large consumption on hake while Yang (1995) showed a large consumption on Pollock in Alaska. A few other groups seemed to be more present in the diet of arrowtooth further North including cephalopods, benthic fish, salmon, and sablefish. Also, because no specific rockfish species were specified by species (just general *Sebastes*), we broke up the proportion of rockfish in the diet by the weighted proportion of rockfish in the system, keeping in mind that any values less than 0.1% were assumed negligible. Additionally, the composite diet of the three studies used by Field were compared to the Buckley et al. raw diet data and slight adjustments were made based on our observations and adjusting for Buckley et al. being the most recent study in the domain. After considering these three studies and Field (2004) composite diet, there were still some questions on forage fish in the diet, particularly a large percent (30%) given to total forage fish by Field that seemed to mainly consist of herring. Therefore, we also looked at additional diet information from Canadian technical report on Diet Composition and Habitat Fidelity for Groundfish Assemblages in Hecate Strait (Pearshall and Fargo, 2007). This showed less herring consumption then Buckley et al. Averaging the Pearshall and Fargo arrowtooth diet summary with the previous diet for arrowtooth led to slightly less consumption on herring (15%), more on euphausiids, tanner crab, benthic fish, cephalopod, hake, and sand lance. This level of consumption on herring was till too high to support population sizes of arrowtooth, and we determined that a diet percent of 11% was more realistic given that the other studies were for the very Northern end of the model (Gotshall 1969 though old, was the only California study and had 0% consumption on herring). There was also a lot of uncertainty surrounding the proportion of hake diet that was adult hake vs. juvenile hake. Using percentages created in the Atlantis model (Kaplan et al. 2014), we assumed it was about 1/3 consumption on juvenile and 2/3 consumption on adult hake. In the end, all sources considered, this led to an overall diet of 0.1% benthic infauna, 0.1% amphipods, 2% epibenthic fauna, 7% euphausiids, 0.1% carnivorous zooplankton, 4.1% pandalid shrimp, 0.21% benthic shrimp, 0.21% Dungeness crab, 0.1% tanner crab, 0.4% mesopelagic fish, 0.9% benthic fish, 0.5% cephalopod, 11% herring, 5.1% sand lance, 1% other smelt, 18.8% juvenile hake, 1.34% juvenile flatfish, 0.3% juvenile roundfish, 0.14% yellowtail rockfish, 0.1% slope rockfish, 0.1% shortbelly, 0.2% petrale sole, 37.7% hake, 0.1% salmon, 0.1% widow rockfish, 0.1% splitnose rockfish, 6% flatfish, and 2% for input consumption (dragonfish, prickleback, other near shore species not represented in the other groups).

Sablefish

For the United States, sablefish (*Anoplopoma fimbria*) biomass came from 2011 assessment (Stewart et al. 2011). Canada biomass came from the 2004 DFO assessment (Haist et al. 2004). Sablefish do extend into Mexican waters but abundance higher North of Mendocino and thus lower south (Bradburn et al. 2011). Total catch came from the 2011 U.S. stock assessment and 213 mt from Canada for a total yield density of 0.025 mt/km^2. The PB value of 0.1095 is the average natural mortality for males and females and fishing mortality rate from 2010 from the U.S. stock assessment. The QB value of 2 was taken from Field (2004).

Sablefish diet came from mainly two studies: Laidig et al. (1997) and Buckley et al. (1999). We also cross-referenced our final diet with the final diet used by Field (2004). Finally, we also looked at recent information published in Brodeur et al. (2014). Some of these diet studies have extensive consumption of thornyhead by Sablefish. Field (2004) notes that a large portion of this is possibly net-feeding by sablefish on thornyheads. Therefore, thornyhead in the diet was down-weighted. Unlike other diet studies, Laidig identified some rockfish in the diet at species level, including splitnose, shortbelly, copper, darkblotched, and pacific ocean perch. Species level fractions were used when known and the remaining "rockfish" consumption was broken up into the other rockfish groups based on biomass availability. New information from Brodeur et al. (2014) showed an increase in hake consumption in recent years and less consumption on rockfish and herring. All this considered, the final diet became 2% infauna, 0.1% amphipods, 5% epibenthic fauna, 7.4% euphausiids, 1% carnivorous zooplankton, 4% small jellies, 2.5% large jellies, 1.5% pandalid shrimp, 0.2% benthic shrimp, 0.1% Dungeness crab, 0.2% tanner crab, 2.5% mesopelagic, 5% benthic fish, 7.5% other cephalopods, 0.6% market squid, 1% sardine, 1.2% anchovy, 4% herring, 0.3% saury, 3% juvenile rockfish, 1.8% juvenile hake, 0.3% juvenile flatfish, 2.5% juvenile roundfish, 5% juvenile thornyhead, 0.2% yellowtail, 0.1% nearshore rockfish, 0.15% shelf rockfish, 2% shortbelly, 20% hake, 0.1% lingcod, 0.1% arrowtooth flounder, 0.2% salmon, 1% grenadiers, 0.4% dogfish, 0.13% widow rockfish, 0.12% splitnose, 0.1% slope rockfish, 1.5% shortspine thornyhead, 1.5% longspine thornyhead, 4.6% flatfish, 0.1% skates, 4% input consumption, 5% fishery offal.

Albacore tuna

A stock assessment for albacore tuna (*Thunnus alalunga*) from the International Scientific Committee for Tuna and Tuna-like Species in the North Pacific Ocean (2011) gave a total North Pacific stock estimate of 850,000 mt. Based on U.S. catch of 14,000 mt and Canada catch of 6,500 mt, and assuming that this catch is sustainable, leads to an estimate of 128,125 mt out to the Economic Exclusion Zone (EEZ). Because the Ecopath model (in comparison to the new Atlantis model) only goes out to the 2,000 meter isobath, we divided this total biomass by the total area in the Atlantis model (1,340,000 km) to reach a reasonable density for inside the model domain (0.0956 mt/km^2). Though albacore migrate out of the domain, we modeled this by adjusting the diet composition instead of adjusting biomass. Total catch also came from the International Scientific Committee for Tuna and Tuna-like Species in the North Pacific Ocean (2011). Total yield for the U.S., Mexico, and Canada came from the same report as biomass, for a total catch of 19,536 mt, divided by a larger model domain (1,340,000 km^2) and divided by 4, because albacore are only in the domain for a quarter of the year and the catch extends out across a larger domain in the quarter of the year. This gave a final total yield density of 0.00364 mt/km^2.

The PB value of 0.36 and the QB value of 7.3 are borrowed from Field (2004).
Diet comes from the percent mass values given in Sarah Glaser's dissertation from UC San

Diego (Glaser 2009). This study summarized diet data from 371 albacore stomachs in the California Current in 2005 and 2006. The main prey items by weight were hake, anchovy, and saury. Since albacore tuna are only present in the ecosystem for a quarter of the year, 75% of the diet was classified as "input consumption" to represent the prey being consumed by these predators that is not in the domain (not represented by the model). The other 25% was broken down as follows: 0.3% euphausiids, 0.3% carnivorous zooplankton, 0.1% mesopelagic fish, 3.5% cephalopod, 0.8% market squid, 1% sardine, 6% anchovy, 0.1% herring, 5% saury, 0.1% juvenile rockfish, 7.5% juvenile hake, and 0.1%.

Salmon

Our salmon group contained both Chinook (*Oncorhynchus tshawytscha*) and Coho (*Oncorhynchus kisutch*) salmon (the most abundant species in the model domain). Abundance was calculated by assuming that total abundance was equal to escapement to the ocean and was calculated to try to represent total amounts in the ocean (not in estuaries, rivers, etc). Coho adult biomass for the United State came from 2013 Review of Ocean Salmon Fisheries (PFMC 2014a) and for Canada from the Pacific Salmon Commission Joint Coho Technical Committee periodic report (PSC-JCTC 2013) (via personal communication with Laurie Weitkamp). This gave a total adult coho biomass of 4426.61555 mt when using an average weight of 5.2 lbs. We then estimated the number of coho smolts by taking the adult biomass and a survival rate at sea of 0.104 (Quinn et al. 2005) and working backwards. This gave 360.9 mt of smolts, for a coho total biomass of 4787.5 mt. Chinook salmon adult at sea biomass for U.S. and Canada came from data used in Ward et al. (2013). Using the 2010 estimates and a weight estimate of 8.1 lbs per salmon, this gave a total adult biomass of 24,185.79 mt. Again, working backwards and using a survival rate of 3.1% (Quinn et al. 2005), this led to a smolt biomass of 8,668.7 mt. Coho and Chinook adult and smolt biomass combined was calculated to be 37,642 mt and a density of 0.1246 mt/km^2. The PB of 1.76 was found by taking numbers used in Harvey et al. (2010) for different life stages of Chinook and coho and weighting by biomass of each (adult chinook, juvenile Chinook, adult coho, and juvenile coho). The QB value of 5.3 came from Field (2004). Total yield came from the same sources as biomass (PFMC 2014a, Ward et al. 2013) for a total yield of 7,660.84 mt or a density of 0.025 mt/km^2.

For Coho diet, data came from Brodeur et al (1987). Chinook diet came from multiple sources including Brodeur et al. (1987), Hunt et al. (1999), Thayer et al. (2014), and Merkel (1957) and with additional consideration of Gladics (2012) and Ruzicka et al. (2007). Coho and Chinook diets were averaged together by weighting the average by biomass. All diets showed extensive consumption on euphausiids and other large zooplankton, anchovy, and herring, as well as sardine further South. Final diet became 1% amphipods, 3% copepods, 16% euphausiids, 18% carnivorous zooplankton, 1% small jellies, 0.2% large jellies, 0.8% mesopelagic fish, 0.3% benthic fish, 0.1% cephalopods, 3% market squid, 5% sardine, 20% anchovy, 13.5% herring, 1.4% sand lance, 0.5% whitebait smelt, 4% other smelt, 2.2% saury, 5.5% juvenile rockfish, 1% juvenile hake, 1% juvenile flatfish, 1% juvenile roundfish, 0.5% small flatfish, and 1% input consumption.

Macrourids

This group consists of all grenadiers (*Macrouridae*). PB and QB values were borrowed from Field (2004). Biomass is a combination of Giant grenadier and Pacific grenadier biomass from the West Coast Groundfish Bottom Trawl Survey (WCGBTS) from NOAA Northwest Fisheries science Center, based on methods in (Bradburn et al. 2011). Together, these two species make up 91% of the grenadier biomass in the California Current (according to information in Field 2004). The trawl survey gives a total biomass for these species of 73,449 mt. This value was divided by a smaller domain area (just U.S. only: 201,586 km^2) to arrive at a final density of 0.364 mt/km^2, assuming that the density is constant throughout the domain. For yield, PacFIN from 2013 gave a total yield of 90 mt. Canada yield of grenadiers is given to be about 20 mt, for a total model yield density of 0.00036 mt/km^2.

Diet for macrourids was taken from the Field (2004) balanced diet composition. This included 15% benthic infauna, 5% amphipods, 15% epibenthic fauna, 1% pandalid shrimp, 4% benthic shrimp, 30% cephalopods, 5% mesopelagic fish, 5% benthic fish, 5% hake, and 15% detritus.

Dogfish

The dogfish functional group contains both Spiny dogfish (*Squalus acanthias*) and Brown catsharks (*Apristurus brunneus*) though the large majority of biomass is Spiny dogfish. The Spiny dogfish estimate came from the 2011 stock assessment (Gertseva and Taylor 2011) for a total U.S. estimate of 215,988 mt. Brown cat shark biomass came from the NWFSC trawl surveys, suggesting 9,961 mt. Scaling up both dogfish and brown catshark biomass to the entire domain by taking the densities in the U.S. and applying them to a Canada total area of 29,500 km^2, gives a final density for the entire group of 0.859 mt/km^2. Total catch came from taking a 10-year average of catch in the United States for a total of 1,780.6 mt (Gertseva and Taylor, 2012). Canada catch from Fisheries and Oceans Canada totaled 268.7 mt for dogfish and cat sharks. This led to a final yield density of 0.0047 mt/km^2. We assumed no Mexican catch since

Bradburn et al. 2011 stated that dogfish are rare south of Point Conception. The PB value of 0.0694 came from natural mortality and fishing mortality from the 2011 assessment. For QB, Field cites a range of 2.5-5. Using a lognormal distribution and taking 2.5 to 5 as the 95% confidence interval, this led to an average QB of 3.61 with a CV of 0.21 to be used when pulling parameters from distributions to create multiple Ecopath models.

Diet came from mainly Brodeur et al. (1987) and Bigman (2013), with some additional information from Brodeur et al. (2009) (though there may be overlap between the Brodeur studies). There is also dogfish diet available in Miller (2006) but over 80% of the diet was unidentified, so we did not include this study in our final diet. We also considered the diet for Dogfish from the Field (2004) model though this diet included data from regions outside the model domain (mainly Puget Sound). The Brodeur diet studies included dogfish taken off the coasts of Washington and Oregon while the Bigman study was located in California. This was important to consider since the Bigman thesis had very little herring in the diet (and substantially more anchovy and sardine) versus the substantial amount of herring in the diet in Washington/Oregon. Combining these two regions into a single diet gave a final diet of 0.3% amphipods, 4% epibenthic fauna, 23% euphuasiids, 0.5% carnivorous zooplankton, 5% large jellies, 1.5% pandalid shrimp, 1.5% benthic shrimp, 3% Dungeness crab, 7% benthic fish, 0.1% surf perches, 4% cephalopod, 2% market squid, 5% sardine, 4.5% anchovy, 5% herring, 0.1% sandlance, 0.1% whitebait smelt, 1% other smelt, 1% saury, 2% juvenile rockfish, 2% juvenile hake, 2% juvenile flatfish, 1.25% juvenile roundfish, 0.1% yellowtail rockfish, 0.1% shortbelly rockfish, 0.1% petrale sole, 15.5% hake, 1.25% lingcod, 0.2% arrowtooth flounder, 6% small flatfish, 0.4% detritus, and 0.5% input consumption.

Canary rockfish

The biomass for Canary rockfish (*Sebastes pinniger*) in the United States came from the 2011 stock assessment (Wallace and Cope 2011). To extrapolate into Canada, we multiplied by a factor of 1.24. We did not extrapolate into Mexico because Canary rockfish are rare south of Central California. For catch, the 2010 catch from the 2011 assessment was used for the U.S. and Canada catch totaled 576.7 mt for a total yield density of 0.0022 mt/km^2. The PB value of 0.113 and the QB value of 1.66 were borrowed from Field (2004).

For Canary rockfish diet, we used the diet estimates from Field (2004) with slight modifications for changes in functional groups (i.e. forage fish grups) and modifications from new data from York (2005) for diet off the coast of Washington. Other than York, Field (2004) used all the diet studies that we had access too (Lee 2002; Brodeur et al. 1987) plus additional NOAA food habits that had more information about herring in Canary diet. However, euphausiids made up by far the largest percent by weight in the diets of Canary rockfish in all studies. This led to a final diet of 0.1% amphipods, 92% euphausiids, 0.8% carnivorous zooplankton, 0.1% small jellies, 3% pandalid shrimp, 2% mesopelagic fish, 1.5% herring, and 0.5% sand lance.

Pacific Ocean Perch

For Pacific Ocean Perch (*Sebastes alutus*), biomass for the United States came from the Hamel and Ono (2011) stock assessment. For Canada, in the 2001 DFO assessment for Pacific Ocean Perch by Schnute et al. report, the AFSC trawl estimates gave an estimate of 5,000 mt (Schnute et al. 2001). These two sources leads to a total biomass around 30,500 mt.

Pacific ocean perch yield in the U.S. from the stock assessment was set at 140.94 mt/km^2. Canada catch in the 2013/2014 season according to the Fisheries and Oceans Canada data was substantially larger than in previous years. Therefore, we used the 2012/2013 season catch data of 575.5 mt (2013/2014 catch was almost double this). Using these estimates, the total yield density became 0.0023 mt/km^2.

For the PB value, we came up with a range of plausible values based on natural mortality from the US stock assessment (Hamel and Ono, 2011) and fishing mortality from both the U.S. and Canada. The Canadian fishing mortality was substantially larger and led to the upper value of the range (0.0558-0.082). Because we later need distributions for each parameter to pull multiple Ecopath models from, we used this range as the 95% confidence interval in the lognormal distribution for Pacific Ocean Perch PB. Based on this confidence interval, the mean was calculated to be 0.0689 with a CV of 0.246. The QB value of 2.07 was borrowed from Field (2004).

The main Pacific Ocean Perch diet study was Brodeur and Pearcy (1984) that included stomach contents for 73 POP in 1980 from Vancouver Island to Monterey California. Field (2004) uses this study in combination with Livingston (pers. Com.) to construct POP diet. Because Field (2004) has all the same data as us, plus more, we used mainly his diet for POP for our model. Based on this, the diet became 3% amphipod, 0.5% epibenthic fauna, 77% euphausiids, 7% carnivorous zooplankton, 1.5% pandalid shrimp, 6% mesopelagic fish, 1% benthic fish, 2% cephalopod, 1% market squid, 0.55% pacific mackerel, and 0.3% smelt (specifically eulachon). Field (2004) had 1% forage fish, and according to Livingston (pers. Com.) cited by Field, this is mostly mackerel, though follow-up communication with Field clarified that this is also eulachon (pers. comm. J. Field).

Widow Rockfish

Widow rockfish (*Sebastes entomelas*) biomass comes from the 2011 stock assessment (He et al. 2011). We assumed that the density in the U.S. was the same in Canada and scaled biomass up based on the density in the U.S. and the total Canada area in the domain. This led to a total biomass density of 0.259 mt/km^2. U.S. catch data also came from the He et al. (2011) stock assessment and data from Canada gave a total yield density of 0.0051 mt/km^2. The PB value of 0.1287 came from natural mortality and fishing mortality from the stock assessment and the QB value of 2.2 was borrowed from Field (2004).

For Widow rockfish, we used the same diet as Field (2004) since he used all the same studies that we are aware of for widow rockfish, including Lee (2002) and Adams (1987). Field also used personal communication information from Livingston that helped to identify forage fish in Widow diet. Using Field's diet, this led to a diet of 3.5% amphipods, 0.2% copepods, 30% euphausiids, 20% carnivorous zooplankton, 32% small jellies, 4% large jellies, 0.1% pandalid shrimp, 0.5% cephalopods, 0.015% forage fish which we determined was osmerid smelt from the Livingston pers. Comm., 3.5% mesopelagic fish, 2% hake, 2% juvenile rockfish, 0.2% juvenile roundfish, 0.2% juvenile flatfish, and 0.3% small flatfish.

Splitnose rockfish

Biomass for Splitnose (*Sebastes diploproa)* rockfish in the United States came from the 2009 stock assessment (Gertseva et al. 2009). To extrapolate into the whole domain, U.S. biomass was multiplied by a factor of 1.36. U.S. total catch from the 2009 stock assessment was 149 mt, plus additional catch from Fisheries and Oceans Canada data of 215.2 mt, led to a final yield density of 0.0012 mt/km^2. For PB, we borrowed the value of 0.06 from Darkblotched rockfish. This seems reasonable since the stock assessment uses a natural mortality of 0.048. The QB of 1.91 was borrowed from the Field (2004) rockfish group that splitnose was grouped with in the previous model.

Splitnose rockfish diet came from Brodeur and Pearcy (1984), the same study used by Field (2004). This diet study looked at the stomach contents of 62 splitnose rockfish from Vancouver Island in BC to Monterey in California in 1980. The largest portion of splitnose diet by weight is euphausiids. The final diet was 2% amphipods, 0.1% epibenthic fauna, 0.2% copepods, 76%

euphausiids, 17.5% carnivorous zooplankton, 0.1% benthic shrimp, 0.1% Dungeness crab, 1% mesopelagic fish, 0.1% benthic fish, 0.2% cephalopods, 0.3% sand lance, and 2.2% input (dragonfish). Note, dragonfish was included in mesopelagic fish in the Field (2004) model but due to the great consumption of dragonfish on other mesopelagics, they were removed from the mesopelagic group in this updated model.

Slope Rockfish

This rockfish group includes Darkblotched (*Sebastes crameri*), Blackgill (*Sebastes melanostomus*), Aurora (*Sebastes aurora*), Rougheye (*Sebastes aleutianus*), and Sharpchin (*Sebastes zacentrus)* rockfish, all of which have stock assessments (Field and Pearson 2011; Cope et al. 2013; Gertseva and Thorson 2013; Hamel et al. 2013; Hicks et al. 2013). All of these were extrapolated up by a factor of 1.36 except for darkblotched biomass, which was multiplied by 1.24. The final density for this group was 0.23 mt/km^2. Total catch came from both these U.S. stock assessments and data from Fisheries and Oceans Canada, for a total yield density of 0.003 mt/km^2. The PB value of 0.0645 is a weighted average of PBs for each species. The QB value of 1.91 is borrowed from Field (2004) from the darkblotched rockfish group.

Diet was adopted from Field (2004) who looked at Shaw (1999) and Brodeur and Pearcy (1984). We also looked at additional diet for sharpchin rockfish from York (2005). From these three studies, there was diet for rougheye, splitnose, darkblotched, and sharpchin (x2). Based on biomass of each species, final diet was a weighted average of the diet for the species individually. Scaling to 1, this led to a final diet of 1.6% amphipods, 2.1% epibenthic fauna, 71% euphuasiids, 5.3% carnivorous zooplankton, 0.5% large jellies, 7.4% pandalid shrimp, 1.1% benthic shrimp, 5.3% mesopelagic fish, 1.3% cephalopods, 4.2% sand lance.

Shortspine Thornyhead

Shortspine thornyhead (*Sebastolobus alascanus*) biomass came from the 2013 stock assessment for shortspine (Taylor and Stephens 2013) and was scaled up by 1.36 for the entire domain since estimates for Mexico and Canada are unknown. This gave a total density of 1.098 mt/km^2. U.S. yield from the stock assessment was 911 mt, while Canada catch totaled 146.6 mt. No catch was assumed for Mexico based on data from CONAPESCA (2015). The total yield density was set at 0.0035 mt/km^2. The PB value of 0.0545 comes from natural mortality and fishing mortality from the 2013 stock assessment and the QB value of 0.47 was borrowed from Field (2004).

Diet information for shortspine thornyhead can be found in Buckley et al. 1999. Field (2004) used this diet information as well as information from Jacobson and Vetter (1996). We used the diet from Field (2004) and modified it using information from Buckley et al. (1999) on forage fish consumption. Shortspine diet consisted of 5% benthic infauna, 5% amphipods, 6% epibenthic fauna, 1% carnivorous zooplankton, 0.5% small jellies, 6% pandalid shrimp, 15% benthic shrimp, 17% tanner crab, 2.5% cephalopods, 4% mesopelagic fish, 5% benthic fish, 0.85% herring, 0.6% saury, 5% juvenile rockfish, 5% juvenile thornyhead, 0.21% slope rockfish, 0.17% shortbelly rockfish, 13% hake, 0.1% arrowtooth flounder, 0.5% grenadiers/macrourids, 0.2% splitnose rockfish, 0.1% shelf rockfish, 1% longspine thornyhead, 0.8% flatfish, and 6% fishery offal. Rockfish percentages came from taking a total rockfish percentage and splitting it up best on amount of biomass of each rockfish group and removing any values less than 0.1%.

Longspine Thornyhead

The 2013 assessment (Stephens et al. 2014) for Longspine Thornyhead (*Sebastolobus altivelis)* gave a total biomass of 68571 mt. This amount was multiplied by 1.36 to extrapolate to the entire domain out to 1200 m. The total density was 0.309 mt/km^2. The total catch for the U.S. in 2012 (from the 2013 stock assessment) was 912 mt. Canada catch totaled 17.56 mt. No catch was assumed for Mexico based on data from CONAPESCA (2015). This led to a total yield density of 0.0031 mt/km^2. The stock assessment also gave natural mortality and exploitation mortality for a total PB of 0.1213. QB was taken from Field (2004). Diet was also taken from Field (2004) and included 16% benthic infauna, 3% amphipods, 20% epibenthic fauna, 1% small jellies (gelatinous herbivores), 1% pandalid shrimp, 25% benthic shrimp, 10% tanner crab, 10% mesopelagic fish, 5% benthic fish, 5% cephalopod, 1.5% juvenile rockfish, 0.5% small flatfish, and 2% detritus.

Flatfish

This group contains all pleuronectiforms other than halibut and petrale sole, including: Starry flounder (*Platichthys stellatus)*, Pacific sanddab (*Citharichthys sordidus)*, Slender sole (*Lyopsetta exilis)*, Deepsea sole (*Embassichthys bathybius*), English sole (*Parophrys vetulus*), Dover sole (*Microstomus pacificus*), and Rex sole (*Glyptocephalus zachirus)*. Dover sole biomass came from the 2011 stock assessment (Hicks and Wetzel 2011), both slender sole and English sole biomass came from the 2013 'Data moderate' stock assessment (Cope et al. 2013), Pacific sanddab biomass came from the 2013 assessment (He et al. 2013), slender sole and deepsea sole biomass came from the West Coast Groundfish Bottom Trawl Survey (WCGBTS) from NOAA Northwest Fisheries science Center, based on methods in (Bradburn et al. 2011), and starry flounder biomass came from the 2005 assessment (Ralston 2005). We multiplied all flatfish biomass by 1.36 to scale up for the whole domain. This led to a total density of 3.57 mt/km^2, most of which is dover sole. For flatfish with assessments, total U.S. catch came from the assessments outlined above. For all others, catch information came from PacFIN for 2013. Canada catch came from Fisheries and Oceans Canada for a total catch in Canada of 1,535.8 mt. Mexico catch came from CONAPESCA (2015) with a total of 190 mt. All together, this led to a total yield density of 0.049 mt/km^2.

For the PB value, we used information from Harvey et al. (2010) on PB values for piscivorous vs. small mouthed flatfish. Based on this, all of the flatfish in this group are small mouthed except for Pacific sanddab. Weighting by biomass and using a PB of 0.467 for piscivorous and a PB of 0.345 for small mouthed, leads to a PB of approximately 0.35. The QB value of 2 was borrowed from Field (2004) from the small flatfish group.

Flatfish diet was constructed by weighting the diets of rex sole, dover sole, English sole, and other small flatfish by biomass of each species/group of species. Diets for these 4 species/group of species came from Field (2004). Dover sole diet was constructed based on Buckley et al. (1999), Gabriel 1978; Pearcy and Hancock 1978; Gabriel and Pearcy 1981, and Wakefield (1984). Dover sole by far has the highest abundance in this group and these diets led to the majority of the flatfish group diet being benthic infauna. Other diet resources included Kravitz et al. (1977) for English sole and other flatfish diet, and again Pearcy and Hancock (1978) and Wakefield (1984) had diets for additional flatfish species as well. In the end, the diet for the entire flatfish group was 78% benthic infauna, 5% amphipods, 13% epibenthic fauna, 0.7% copepods, 0.5% euphausiids, 0.1% carnivorous zooplankton, 0.9% pandalid shrimp, 1.3% benthic shrimp, 0.1% anchovy, and 0.1% sand lance. Again, any values of less than 0.1% were considered negligible and removed.

Skates

The skate functional group includes Big skate (*Raja binoculata*), Longnose skate (*Raha rhina)*, Sandpaper skate (*Bathyraja kincaidii*), Bering skate (*Rhinoraja interrupta*), Roughtail skate (*Bathyraja truchura*), and California skate (*Raja inornata*). For this group, longnose skate is the only species with a stock assessment. Gertseva and Schirripa (2007) estimate longnose skate biomass of 71,217 mt. This value was scaled up by a ratio of big skate plus longnose plus sandpaper (the three most commons species) to longnose, using data on occurrence from the West Coast Groundfish Bottom Trawl Survey (WCGBTS) from NOAA Northwest Fisheries science Center, based on methods in (Bradburn et al. 2011). This value was then multiplied by a factor of 1.36 to extrapolate into Canada and Mexico. Total yield consists of landings from the 2007 stock assessment for longnose skate, catch for Big skate, longnose skate, and sandpaper skate from Canada (160 mt) and Mexican catch from CONAPESCA (2015) of 110.8 mt for a total yield density of 0.0039 mt/km^2. The PB value of 0.2216 is equal to natural mortality plus fishing mortality from the 2007 assessment for longnose. The QB value of 2 was borrowed from Field (2004).

There exists skate diet information for longnose skate, big skate, and sandpaper skate. For longnose, we used diet information from Robinson (2006) from Monterey Bay and Davenport CA and from Wakefield (1984) from the Oregon Coast. For Big skate, diet came Wakefield (1984) from the Oregon coast. For Sandpaper skate, we used information from Wakefield (1984) and Rinewalt et al. (2009) (though mainly the Rinewalt study was used because it was more recent). First, an average diet was found for each species. Big and Longnose skates are more common than sandpaper skate, so the diets for the species were than averaged together with less weight to the sandpaper diet, assuming 45% longnose and 45% big skate and only 10% sandpaper (suggested by Field, 2004). Then, this final diet was compared to the final skate diet from Field (2004) which used similar studies, and small adjustments were made based on any substantial differences between the two. The final diet used consisted of: 2.2% infauna, 1% amphipods, 12% epibenthic fauna, 4.8% euphausiids, 0.5% macrozooplankton, 1% pandalid shrimp, 28% benthic shrimp, 5% Dungeness crab, 1% tanner crab, 2.9% mesopelagic, 2% benthic fish, 0.1% surf perch, 6% cephalopod, 2.5% market squid, 0.1% anchovy, 2.3% sand lance, 1.2% juvenile rockfish, 5% juvenile flatfish, 1% juvenile roundfish, 0.4% yellowtail rockfish, 0.1% black rockfish, 0.7% slope rockfish, 2.2% shortbelly rockfish, 0.5% petrale sole, 2.4% hake, 0.5% arrowtooth flounder, 0.6% sablefish, 0.3% widow rockfish, 0.5% splitnose rockfish, 0.2% shelf rockfish, 11% flatfish, and 2% input consumption. Rockfish percentages were calculated based on total rockfish consumption by skates, split up using the biomass proportions of each rockfish group. However, more diet was allocated to shortbelly rockfish since this species was specifically identified in stomachs of skates. Stripetail and splitnose rockfish were also specifically identified in diets but at fewer amounts than shortbelly.

Sharks

The shark functional group includes Thresher (*Alopias* sp.), Blue (*Prionace glauca*), Soupfin (*Galeorhinus galeus*), Mako (*Isurus oxyrinchus*), Brown (*Carcharhinus milberti*), and Great white sharks (*Carcharodon carcharias*). Biomass is extremely uncertain for this group and there are no stock assessments for the majority of these species. Blue shark has been assessed (Kleiber et al. 2009) but for a domain much larger than the domain of this model. Thresher, Blue, and Mako sharks have the highest landings of all species in this group, ranging from 95-424 mt from 2001-2011. We first used the high end of the range to calculate a reasonable biomass. Assuming 424 mt are taken sustainably, and assuming an average stock productivity of 0.055 (NOAA Fishery Management Plan 2011), this leads to a total of 7,700 mt. Multiplied by a factor of 1.7 scales this amount up to the entire domain for a total biomass of 13,200 mt. We then divided by the total Atlantis model domain of 1,340,000 km^2 instead of the Ecopath domain because pelagic sharks can be found outside our Ecopath model domain. This gives a final density of 0.0098 mt/km^2. However, based on shark catch in Mexican waters, this biomass level is too small to sustain a fishery of 3,525 mt a year (density of 0.0027 mt/km^2) with production levels of sharks. Therefore, because biomass for sharks is very uncertain, we had the model calculate shark biomass based on an EE value of 0.75. For yield, any species with catch reported in PacFIN (Thresher, Blue – though catch equaled 0 mt for 2013, Mako, and Soupfin) was summed and added to the total from Mexico of 3,525 mt (CONAPESCA 2015; Ainsworth et al. 2011) and the small amount of catch from Canada for blue shark (0.068 mt) for a total yield density of 0.0027 mt/km^2. The PB value of 0.18 and the QB value of 2.8 are borrowed from the shark group from Field (2004).

Shark diet is available for a few species in this group – Blue shark, Thresher shark, Shortfin mako shark, and Soupfin shark. Diet for blue shark, thresher shark, and shortfin mako came most recently from Preti et al. 2012. Additional Blue shark diet came from Tricas 1979, Harvey 1989, and Miller 2006, Thresher diet from Preti et al. 2001 with additional information on sardine consumption from Emmett et al. 2005 and Soupfin diet from Brodeur et al. 1987. Without knowledge on proportional biomass, diet could not be weighted by species abundance. Therefore, diet was simply averaged over the four species. In addition, the diet from the Field (2004) model was consulted and compared against. Finally, since rockfish in shark diet was unknown at the species level, total rockfish consumed by sharks was broken up based on available biomass of each rockfish group. The final diet for sharks became 0.4% epibenthic, 1.2% euphausiids, 0.25% Dungeness, 1.3% mesopelagic, 1.3% benthic fish, 16% cephalopods, 1.2% market squid, 5% sardine, 8% anchovy, 2.4% herring, 5.5% pacific mackerel, 2% saury, 5% juvenile hake, 0.4% juvenile roundfish, 0.3% yellowtail rockfish, 0.1% black rockfish, 0.25% shelf rockfish, 0.2% shortbelly, 0.1% petrale sole, 0.5% halibut, 22% hake, 0.5% lingcod, 0.4% arrowtooth flounder, 0.25% albacore, 1.25% salmon, 1% dogfish, 0.2% widow rockfish, 0.2% splitnose rockfish, 0.1% slope rockfish, 2% flatfish, 0.1% skates, 1.2% sharks, 1.5% porpoises, 0.5% harbor seals, 2% sea lions, 3% elephant seals, 12.4% input consumption. See

Brown and Anderson (2005), SharkTrust report White Shark Studies at the Farallon Islands: Fall 2005 for consumption on marine mammals.

SEABIRDS

Converting Abundances: Similar to how seabird biomass was handled by Kaplan et al. (2014), when any seabird estimates were presented as total breeding population estimates, we used the estimates directly (e.g. Carter et al. 1992). When data was presented as nest counts instead, these counts were multiplied by 1.67 to account for breeding birds that were not present during the count. This multipler came from estimates for Common Murre (Sydeman et al. 1997a), and has been applied to other species in other studies (Carter et al. 1992; Naughton et al. 2007).
Total counts for the majority of the seabird functional groups were breeding population estimates only. Therefore, these were converted to a total population estimate by multiplying the abundances by conversion factors to account for non-breeding, immature, fledged (juvenile) individuals. Conversion factors were calculated using stable age distributions from age-structured models and by taking estimates of juvenile survival rates and adult age at maturity (taken from Birds of North America Online, Poole 2005). Abundances were then converted to biomass by multiplying by average weight for each species, which were taken from Hunt et al. (2000). This assumes that immature, juvenile individuals are approximately the same weight at mature adults. See methods in Kaplan et al. 2014.

For seabird diet, most studies are for prey items delivered from adults to chicks. Though for some species, what adults feed chicks is likely to be what adults eat themselves, diets for both "chicks" (adults feeding chicks) and adults (nonbreeding) were used when the data was available.

Common murre

Common murre (*Uria aalge*) abundance information came from a variety of sources for the model domain. Coastal British Columbia murre counts came from Hipfner (2005), with counts from the early 2000s. Washington counts came from the updated Catalog of Washington Seabird Colonies (Jenkerson and Pearson 2012). The Washington count was multiplied by a conversion factor of 1.6 to extrapolate rough colony counts to total breeding bird counts. Oregon counts came from the Oregon Seabird Colony Database (U.S. Fish and Wildlife, 2013), with many counts from in the 2000s. Finally, California counts came from multiple sources, mainly Carter et al. (1992), with updates for Gualala Point Island (Garcia-Reyes et al. 2013) Southern Farallon Island (Warzybok and Bradley 2011), and Castle Rock (Jaques 2007). Breeding abundance was then adjusted to total abundance as described above and converted to biomass (see above).

Multiple PB values were compiled that ranges from 0.05-0.13 (Birds of North America, Poole 2005). Based on these values, we calculated what the mean and standard deviation of a lognormal distribution would be to produce a 95% confidence interval with this range. This produced a mean of approximately 0.084. QB was calculated using information from Hunt et al. (2000) on daily energy needs (kj) and weight, assuming an average prey density of 5 kj/grams and adjusting for the portion of prey not digestible. QB calculations are similar to use in Harvey et al. (2010).

Many diet studies exist for Common Murre along the West coast of the United States and Common Murre diet had one of the highest pedigrees of seabird diets. Of all the diet studies on Common Murre, we included all within the model domain. This included: Baltz and Morejohn 1977; Matthews 1983; Ainley et al. 1996b; Sydeman et al. 2001, 2009; Hamel 2009; Gladics 2012; Schrimpf et al. 2012 (though there is data overlap between the two Sydeman studies). Each study was separated based on location (state) and life stage (chick or adult). Most studies were for chick diet (parent's returning from foraging and feeding chicks), but the Ainley et al. 1996b and Baltz and Morejohn 1977 studies were for adult diets in California. Therefore, adult and chick diets were averaged (50/50) for an overall California diet. A few studies were presented in percent mass, but the majority was presented in percent number. These were translated to rough percent mass equivalents by using prey weight from Cassin's auklet diet information and assuming fish weight at about 5 grams. Final diet was a weighted average based on the biomass in each state, with the majority of common murres located in California (approximately 56%) and then Oregon (approximately 41%). Any consumption on "unknown smelt" was broken up into whitebait smelt and other smelt groups based on the proportions of identified smelt in the diet. The final diet became 0.8% euphausiids, 1.1% mesopelagic fish, 8.9% benthic fish, 4.3% surf perch 1.9% cephalopods, 11.7% market squid, 18.6% anchovy, 6.8% herring, 3.2% sand lance, 1.5% whitebait smelt, 5.3% other smelt (including eulachon), 20% juvenile rockfish, 6.4% juvenile hake, 3.2% juvenile flatfish, 2.6% juvenile roundfish (small lingcod), 2.3% salmon (probably juvenile leaving rivers/estuaries and entering the ocean), and 1% input consumption. There were additional small amounts of consumption on other species, including some sardine, but these values were negligible and led to errors in the model. Many of these diets came from the 2000s and therefore accurately represent the sardine consumption by murres (not very much because sardine are too far off shore) compared to other diets that were taken from a period when sardine was not abundant.

Cassin's Auklet

Breeding pair counts for Cassin's auklet (*Ptychoramphus aleuticus*) in British Columbia came from Rodway (1991) giving an estimate for Triangle Island in 1989. This abundance was multiplied by two to increase from number of pairs to number of individuals. Cassin's auklet counts for Washington came from the 1989 Catalog of Washington Seabird Colonies (Speich and Wahl 1989). Oregon counts came from the Oregon Seabird Colony Database (U.S. Fish and Wildlife, 2013), with one count from 2008 and the other from 1967. Finally, California counts came from multiple sources, mainly Carter et al. (1992), with updates for Castle Rock (Cunha 2010), Southest Farallon Island (Warzybok and Bradley 2011), and Ano Nuevo island (Hester et al. 2013). Baja colony counts come from Wolf et al. (2006).

Multiple PB values were compiled that ranges from 0.2185-0.25 (Lee et al. 2007, cited in Schreiber and Burger 2001). Based on these values, we calculated what the mean and standard deviation of a lognormal distribution would be to produce a 95% confidence interval with this range. This produced a mean of approximately 0.234. QB was calculated using information from Hunt et al. (2000) on daily energy needs (kj) and weight, assuming an average prey density of 5 kj/gram and adjusting for the portion of prey not digestible. QB calculations are similar to use in Harvey et al. (2010).

Diet data for Cassin's auklet was separated by region and by life stage (chick or adult). For B.C. chick diet, Vermeer (1985) and Bertram et al. (2009) were used. California diet came from Sydeman et al. (2001), Ainley et al. (1996a), Adams et al. (2004), and Abraham and Sydeman (2004) with Ainley et al. having both chick and adult data. The diets for B.C. were presented in percent mass but many of the studies for California were presented in percent number. Therefore, we used known weights of different prey items from Sydeman et al. (2001) and data from J. Thayer to scale the percent number diets to approximate percent masses. Then, all chick diets were averaged for B.C. and for California separately and then averaged together using a weighted average of number of individuals in each region. Finally, adult diets were factored in. Cassin's auklets are mainly planktivorous, with the majority of their diet being euphausiids and copepods, with which being more prevalent in the diet changing between years. The final diet for Cassin's auklets became 1.9% amphipods, 0.5% epibenthic fauna, 39% copepods, 39% euphuasiids, 0.5% carnivorous zooplankton, 0.8% pandalid shrimp, 0.15% cephalopods, and 17.5% input consumption (mainly fish larvae and eggs not captured by the functional groups in this model and not specified at a species level).

Rhinoceros auklet

Breeding pair counts for Rhinoceros auklet (*Cerorhinca monocerata*) in British Columbia came from Rodway (1991), giving an estimate for Triangle Island in 1989. This abundance was multiplied by two to increase from number of pairs to number of individuals. Washington counts came from the updated Catalog of Washington Seabird Colonies (Jenkerson and Pearson, 2012). The Washington count was multiplied by a conversion factor of 1.6 to extrapolate rough colony counts to total breeding bird counts. Oregon counts came from the Oregon Seabird Colony Database (U.S. Fish and Wildlife, 2013), with many counts from 2008. Finally, California counts came from multiple sources, mainly Carter et al. (1992), with updates for Castle Rock (Cunha, 2010), Southeast Farallon Island (Thayer and Sydeman 2007), and Ano Nuevo Island (Hester et al., 2013).

Multiple PB values were compiled that ranges from 0.1-0.14 (Sydeman and Thayer pers. Com., Morrison et al. 2011). Based on these values, we calculated what the mean and standard deviation of a lognormal distribution would be to produce a 95% confidence interval with this range. This produced a mean of approximately 0.119. QB was calculated using information from Hunt et al. (2000) on daily energy needs (kj) and weight, assuming an average prey density of 5 kj/gram and adjusting for the portion of prey not digestible. QB calculations are similar to use in Harvey et al. (2010).

Similar to common murre, there is also substantial diet information for Rhinoceros auklet, but mainly for chicks (adults feeding chicks). The few studies for adult diets came from Baltz and Morejohn 1977; Sorensen et al. 2009, and though the Baltz and Morejohn study is older, it was used to represent adult diet in California. Thayer et al. 2008 has diets for rhino. auklet for multiple locations in the domain including California and British Columbia. Additional B.C. diet can be found in Hedd et al. 2006, Burger et al. 1993 and Bertram et al. 2002. Diet for rhino. auklets in Washington came from mainly Pearson et al. 2012 (unpublished data) and Leschner (1976). Diet was separated by location (state/country) and life stage (adult/chick). Any percent number data was roughly scaled to percent mass data based on known weights of prey. For adult diets and chick diets separately, diets for different locations were averaged together using a weighted average of the proportion of biomass in each region. Finally, adult and chick diets were averaged together. This led to a final diet of 9% euphausiids, 1% cephalopod, 5.75% market squid, 15.6% anchovy, 6.5% herring, 24% sand lance, 0.5% whitebait smelt, 6% other smelt, 5.6% saury, 14% juvenile rockfish, 0.2% juvenile hake, 0.7% juvenile roundfish, 8.4% salmon, and 2% input consumption.

Tufted puffin

Breeding pair counts for Tufted Puffin (*Fratercula cirrhata*) in British Columbia came from Rodway (1991), giving an estimate for Triangle Island in 1989. This abundance was multiplied by two to increase from number of pairs to number of individuals. Washington counts came from the updated Catalog of Washington Seabird Colonies (Jenkerson and Pearson, 2012). The Washington count was multiplied by a conversion factor of 1.6 to extrapolate rough colony counts to total breeding bird counts. Oregon counts came from the Oregon Seabird Colony Database (U.S. Fish and Wildlife, 2013), with many counts from the late 2000's (2008-2010). Finally, California counts were mainly all from Carter et al. (1992), though there was one update for Southeast Farallon Island from Warzybok and Bradley (2011).

PB came from taking the male and female survival estimates from Morrison et al. (2011) and averaging the two estimates for a final PB of 0.065. QB was calculated using information from Hunt et al. (2000) on daily energy needs (kj) and weight, assuming an average prey density of 5 kj/gram and adjusting for the portion of prey not digestible. QB calculations are similar to use in Harvey et al. (2010).

The only diet study for Tufted Puffin is Vermeer (1979) that examined 22 puffin stomachs in August 1977 and 35 puffin stomachs in August 1978, all at Triangle Island, B.C. Puffin diet in this study consisted of 10-25.2% saury, 59.8-44.9% sandlance, 7.8-3.6% juvenile rockfish, 0-2.6% rabbitfish (*Chimaera* monstrosa) 0-4.6% gonatid squid, 0-36.4% blue throat argentine, 0-2.6% juvenile sablefish, and 0-2.5% clubhook squid. Though the blue throat argentine made up a large portion of the diet in one year (36.4%), this year was known to be an anomalous year (personal communication Julie Thayer) and does not represent the average tufted puffin diet and was down weighted. Additionally, Gjerdrum et al. (2006) reported bill load percent mass for Tufted puffins in Triangle island in 2000 that showed consumption mainly on sandlance, rockfish (juvenile), and squid.

Because the Vermeer and Gjerdrum studies only represent Tufted puffin diet in British Columbia and other percent mass studies were not found for the rest of our model domain, Rhinoceros auklet diet for California was used as a proxy for puffin diet in California. Since only a small portion of the total puffin population breeds in California (~2%) and we weighted the final diet by proportion in each region, this seems a reasonable assumption. California auklet adult diet came from Baltz and Morejohn (1977) and chick diet came from Thayer et al. (2008) and both were scaled to percent mass based on data from Julie Thayer. These studies showed large consumption on anchovy and juvenile rockfish.

Finally, no studies were found for the diet of adults in the North end of the model where the majority of biomass for these birds exists. Personal communication with Mark Hipfner and analysis in Williams et al. (2008) suggests that adults are probably feeding on prey at a lower trophic level, mainly large krill. Therefore, using information from Alaska Tufted puffin adult diet (Baird 1991) that also shows a large consumption on krill, final diet was adjusted to have a larger consumption of euphausiids. Based on all this, final diet became 1% infauna, 0.4% amphipods, 0.4% copepods, 5% euphausiids, 8% mesopelagic fish, 1% cephalopods, 0.5% market squid, 0.7% anchovy, 35% sand lance, 8.2% saury, 34% juvenile rockfish, 4% juvenile roundfish, 0.7% input consumption (other fish that are very near shore and not represented by the model).

California gull

The majority of California Gulls (*Larus californicus*) breed inland, with the breeding season beginning in February, but are present on the coast from late summer till February (Mason et al., 2007). However, there is a breeding colony in San Francisco Bay of approximately 46,000 individuals (Josh Ackerman, pers comm.). Abundance estimates for the rest of the domain came from regional density estimates extrapolated to the model domain area. These densities came from multiple sources –Burger 2003; Mason et al. 2007; McClatchie 2009; Ainley and Hyrenbach 2010. These densities were converted to biomasses and than reduced to account for the portion of the year that California Gulls are not in the domain. This was added to the count from the San Francisco colony.

Multiple PB values were compiled that ranges from 0.08-0.21 (Schreiber and Burger 2001). Based on these values, we calculated what the mean and standard deviation of a lognormal distribution would be to produce a 95% confidence interval with this range. This produced a mean of approximately 0.135. QB was calculated using information from Hunt et al. (2000) on daily energy needs (kj) and weight, assuming an average prey density of 5 kj/gram and adjusting for the portion of prey not digestible. QB calculations are similar to use in Harvey et al. (2010).

For California gull diet, not very many diet studies exist for this species. Baltz and Morejohn (1977) report on diet of five California gulls in Monterey Bay in the 1970s. This diet consisted of only anchovy, market squid, clubhook squid, and amphipods. An additional study by Collis et al. (2002) showed a similar diet of California gulls on the lower Columbia River, with the addition of some salmonid consumption, but the locations of this study were outside the domain of our model. Therefore, we based the diet of California gull on the Baltz and Morejohn study with low certainty in the final values. Also, because the majority of these gulls are migrating out of the domain to breed, we made 43% of the diet input consumption in order to represent the time/biomass not in the domain year round and therefore account for prey not being consumed in the domain. Information on migration timing was taken from Mason et al. (2007). With 43% diet as input consumption, the rest of the final diet consisted of: 0.4% amphipods, 13.5% cephalopods, 24% market squid, and 19% anchovy.

Western/Glaucous-winged gull

These two species were grouped into one group because they often inter-breed, creating hybrid offspring. Western gull or Glaucous-winged gull (*Larus occidentalis* and *Larus glaucescens*) abundances for British Columbia came from Vermeer and Irons (1991). Washington counts came from the updated Catalog of Washington Seabird Colonies (Jenkerson and Pearson, 2012). The Washington count was multiplied by a conversion factor of 1.6 to extrapolate rough colony counts to total breeding bird counts. Oregon counts came from the Oregon Seabird Colony Database (U.S. Fish and Wildlife, 2013), with the majority of abundances from 2001-2012 but some from the 1990s and 1980s. California abundances were mainly from Carter et al. (1992) (more than half), but there were updates for some colonies from Eigner et al. (2010), Garcia-Reyes et al. (2013) for Gualala Point Island, Warzybok and Bradley (2011) for Southeast Farallon Island, Saenz et al. 2006, Acosta et al. 2010 for Alacatraz Island, and Hester et al. (2013) for Ano Nuevo Island. Additional counts from Southern California came from multiple studies from PRBO (Robinette and Acosta 2011; Robinette et al. 2012; Robinette et al. 2013). Baja abundances are from Wolf et al. (2006).

Multiple PB values were compiled that ranges from 0.1-0.17 (Schreiber and Burger 2001). Based on these values, we calculated what the mean and standard deviation of a lognormal distribution would be to produce a 95% confidence interval with this range. This produced a mean of approximately 0.132. QB was calculated using information from Hunt et al. (2000) on daily energy needs (kj) and weight, assuming an average prey density of 5 kj/gram and adjusting for the portion of prey not digestible. QB calculations are similar to use in Harvey et al. (2010).

For diet, one study with percent mass exists for Western gull (Hunt and Butler 1980) that looked at regurgitations in the 1970's on Nicolas, Prince, and Santa Barbara islands in the Channel Islands. There were three years of samples for each island. Additionally, Hunt and Butler had percent frequency of occurrence (FO) data for these same islands and Anacapa island, for 1975-1977 combined. The percent FO data probably overlaps with the percent mass and even though there is an extra island, it's a similar location and percent mass is more informative.

The percent mass data showed that a large percent of Western gull diet is anchovy and market squid (18% and 17% respectively). Additional prey items were garbage, saury, detritus (sea lion), juvenile rockfish, juvenile hake, mesopelagic fish, cephalopods, euphausiids, molluscs (other than cephalopods), and topsmelt silverside. Additionally, there was around 20-23% unidentified fish and around 2% “other”.

There is additional percent mass data for Glaucous-winged gull. Vermeer (1982) has a sample of 129 regurgitations from Triangle, Vancouver, and Florencia islands, and Starlight reef from 1980. The study also had additional percent mass information but not from within the study domain. This study showed large predation on sandlance and saury, followed by herring, more unidentified fish, and salmon.

Since there was still a large subset of unidentified fish, I also looked at a percent number study from the Farallon islands by Ainley and Boekelheide (1990). This study looked at regurgitations, scat, and pellets. Most of this study was very general, separating diet out into Fish, Euphausiids, Invertebrates, Birds, Garbage, and Unidentified. However, they also broke out the fish species in Western gull diet, with about 39% juvenile rockfish, 21% cusk-eels, 12% hake, and 11% midshipmen (mesopelagic). To distribute the remaining “unidentified” fish, I used a combination of splitting out the remaining proportions to the species in each study based on biomass and by splitting up the unidentified based on the Ainley study. They also broke up the invertebrates somewhat, but without mass, this is difficult to include and doesn’t add anything that’s missing. Also, all invertebrates present in Ainley are in the groups benthic infauna and epibenthic fauna, percents of which were determined in the Hunt et al. percent mass study.
Creating ranges of possible diet values from these studies and scaling up to 1, led to the following diet: 0.5% benthic infauna, 0.5% epibenthic fauna, 0.8% euphausiids, 0.1% Dungeness, 3% mesopelagic fish, 0.2% benthic fish, 0.35% perch, 1% other cephalopod, 10% market squid, 13.5% anchovy, 13% herring, 20% sandlance, 17.5% saury, 7.5% juvenile rockfish, 3.5% juvenile hake, 0.5% juvenile flatfish, 5% salmon, almost 3% input consumption from near shore species not represented in the model.

Petrels

The Petrels group is mainly a Leach’s storm petrel (*Oceanodroma leucorhoa*) group. British Columbia estimates for Leach’s storm petrel came from Rodway (1991). Petrel counts for Washington came from the 1989 Catalog of Washington Seabird Colonies (Speich and Wahl 1989). Oregon counts came from the Oregon Seabird Colony Database (U.S. Fish and Wildlife, 2013), with about half of the counts coming from 2008 or later, and the other half coming from the 1960s-1980s. The majority of California abundances came from Carter et al. (1992) and Baja abundances from Wolf et al. (2006).

Multiple PB values were compiled that range from 0.063-0.213 (Schreiber and Burger 2001). Based on these values, we calculated what the mean and standard deviation of a lognormal distribution would be to produce a 95% confidence interval with this range. This produced a mean of approximately 0.124. QB was calculated using information from Hunt et al. (2000) on daily energy needs (kj) and weight, assuming an average prey density of 5 kj/gram and adjusting for the portion of prey not digestible. QB calculations are similar to those used in Harvey et al. (2010).

Petrel diet was based on Wiens and Scott (1975), Vermeer and Devito (1988), and Schuiteman (2006). Wiens and Scott cite unpublished data that shows petrel diet consisting of 44% hydrozoans (gelatinous carnivores), 38% euphausiids, 9% “other” crustaceans, 1% cephalopods, and 8% “other” fish.

An additional percent occurrence study from Vermeer and Devito (1988), had additional diet data, however, this study was done in Queen Charlotte’s Island, B.C., substantially far North of the northern end of our Ecopath domain. However, based on this study, it seems that the 9% crustacean from the Wiens and Scott study should be split among amphipods and euphuasiids. Additionally, the Vermeer and Devito study show a large amount of predation on mesopelagics, so possibly the 8% other fish is only mesopelagics.

Additionally, Schuiteman (2006) gives diet data as number of occurrences of each diet item. We took total counts from this study and using weights of fish from Cassin’s auklet diets, transformed these counts numbers into approximately percent mass. Combining all three studies together and separating out “unidentified” fish into the identified fish species, this led to a final diet of 0.1% infauna, 2% amphipods, 0.2% epibenthic fauna, 0.15% copepods, 30% euphausiids, 22% large jellies (hydrozoans), 30% mesopelagic fish, 0.1% benthic fish, 3.5% cephalopods, and 12% juvenile rockfish.

Brandt’s cormorants

Brandt’s cormorant (*Phalacrocorax penicillatus*) abundance for British Columbia came from Siegel-Causey and Litvinenko (1993). Washington counts came from the updated Catalog of Washington Seabird Colonies (Jenkerson and Pearson, 2012). The Washington count was multiplied by a conversion factor of 1.6 to extrapolate rough colony counts to total breeding bird counts. Oregon counts came from the Oregon Seabird Colony Database (U.S. Fish and Wildlife, 2013), with all counts coming from 2003-2012. For California, only very little abundance from Carter et al. (1992) was used as many colony counts were updated by other sources. New abundances came from Capitolo et al. (2011), Capitolo (2006), Capitolo et al. (2004), Jaques (2007) for Castle Rock, Garcia-Reyes et al. (2013) for Gualala Point Island, Warzybok and Bradley (2011) for Southeast Farallon Island, Saenz et al. 2006; Acosta et al. 2010 for Alacatraz Island, and many more colonies in Eigner et al. (2010). Additional counts from Southern California came from multiple studies from PRBO (Robinette and Acosta 2011; Robinette et al. 2012; Robinette et al. 2013). Baja abundances are from Wolf et al. (2006).

A PB of 0.26 came from the Biology of Marine Birds (Schreiber and Burger, 2001). QB was calculated using information from Hunt et al. (2000) on daily energy needs (kj) and weight, assuming an average prey density of 5 kj/gram and adjusting for the portion of prey not digestible. QB calculations are similar to use in Harvey et al. (2010).

There are three main diet studies for Brandt's cormorant – Ainley et al. (1981), Baltz and Morejohn (1977), and (Sydeman et al. 1997b), spanning the whole range of the domain from Canada, Oregon, to California/Baja. We also qualitatively looked at Yakich (2005), however this data was presented in % occurrence which is difficult to translate into diet information needed for Ecopath.

There was only one sample of 13 brandt's cormorant stomachs in Canada (Ainley et al., 1981) and only one sample of 29 chick regurgitations from Oregon (Ainley et al., 1981). All other samples were from California. The California studies were averaged before averaging with the other locations, paying attention to time of the year that data was collected. We also looked at how often a prey item was occurring, taking into consideration how many birds are in each region. There are more BRCO's in Oregon/California than Canada/Washington (around 87 thousand vs. 1.4 thousand). Therefore, for example, herring was the largest amount of the diet in Vancouver Island, but basically nonexistent else where, so the lower value was used. Another example is market squid, where a lower value was used because it was only present substantially in 1/11 samples and is only really abundant in central California. This led to potential ranges for diet values for a lot of prey items, leading us to choose the middle of the road value for many and allowing the probability distribution to encompass the whole range. Yakich (2005) found a similar diet composition as the other California studies, included a large presence of juvenile flatfish in the diet and anchovy. This study had less rockfish consumption than the other studies, but assuming that rockfish are the largest of the prey consumed by Brandt's cormorant, they may be more important in terms of mass than revealed by percent occurrence data.

There are a few prey species that are very near shore and not accounted for in our model, most notably blacksmith and senorita (around 4% and 1%). These were included in input consumption for Brandt's cormorant diet. Additionally, even though data for these studies were all presented in % number, all prey are relatively the same size, except for isopods, in which case a lower value was used (due to the lower weight). In the end, the final diet became: 0.8% benthic infauna, 3.3% mesopelagic fish, 3% benthic fish, 4.6% surf perch, 1.2% cephalopod, 1% market squid, 11% anchovy, 2% herring, 1% other smelt, 46% juvenile rockfish, 11.3% juvenile flatfish, 0.5% juvenile roundfish, and 15% input consumption (species that are too near shore).

Double-crested cormorants

Double-crested cormorant (DCCO, *Phalacrocorax auritus*) colonies in British Columbia are all located in the interior (Carter et al. 1995) and are therefore not included in the abundance used in the model. Washington counts came from the updated Catalog of Washington Seabird Colonies (Jenkerson and Pearson, 2012). The Washington count was multiplied by a conversion factor of 1.6 to extrapolate rough colony counts to total breeding bird counts. Oregon counts came from the Oregon Seabird Colony Database (U.S. Fish and Wildlife, 2013), with the majority of counts coming from the 2000s. For California, abundance estimates came mainly from updated sources with a few from Carter et al. (1992). New abundances came specifically from Capitolo (2006), Capitolo et al. (2004), Jaques (2007) for Castle Rock (match abundances from Capitolo), and Warzybok and Bradley (2011) for the Southeast Farallon Island. Additional counts from Southern California came from multiple studies from PRBO (Robinette and Acosta 2011; Robinette et al. 2012; Robinette et al. 2013). Baja abundances are from Wolf et al. (2006).
A PB of 0.15 came from the Biology of Marine Birds (Schreiber and Burger, 2001). QB was calculated using information from Hunt et al. (2000) on daily energy needs (kj) and weight, assuming an average prey density of 5 kj/gram and adjusting for the portion of prey not digestible. QB calculations are similar to use in Harvey et al. (2010).

For DCCO, many studies were outside of the domain. However, Ainley et al. (1981) had samples from three areas within the domain – Isla San Martin in Baja, Mexico, Farallon Island, and San Miguel island in the Channel islands – in the 1970's. These samples are percent number and not percent mass but all prey items are small fish. These samples were averaged, but then values and ranges were adjusted based on how often the prey item appeared (in how many locations) and if there was that item made-up a large percent of the diet in all locations or just one. A large percent of DCCO diet is made up of near shore species that are not represented by our model and are therefore input consumption species. There was specifically a large amount of White croaker. This led to a diet of 1.1% mesopelagic fish, 3% benthic fish, 37% surf perch, 13% anchovy, 1% herring, 2.2% sand lance, 11% juvenile rockfish, 0.4% juvenile flatfish, 0.3% salmon (probably juvenile), and 31% input consumption (gunnels, croaker, prickleback, stickleback, goby, wrasse).

Pelagic cormorants

British Columbia abundance for Pelagic cormorants (*Phalacrocorax pelagicus*) mainly came from Siegel-Causey and Litvinenko (1993), with an update for Barkley Sound in 2007 from Carter et al. (2007). Washington counts came from the updated Catalog of Washington Seabird Colonies (Jenkerson and Pearson, 2012). The Washington count was multiplied by a conversion factor of 1.6 to extrapolate rough colony counts to total breeding bird counts. Oregon counts came from the Oregon Seabird Colony Database (U.S. Fish and Wildlife, 2013), with the majority of counts coming from the 2000s. California abundances were mainly from Carter et al. (1992) (more than half), but there were updates for some colonies from Eigner et al. (2010), Garcia-Reyes et al. (2013) for Gualala Point Island, Warzybok and Bradley (2011) for Southeast Farallon Island, Saenz et al. 2006; Acosta et al. 2010 for Alacatraz Island, and Hester et al. (2013) for Ano Nuevo Island. Additional counts from Southern California came from multiple studies from PRBO (Robinette and Acosta 2011; Robinette et al. 2012; Robinette et al. 2013). Baja abundances are from Wolf et al. (2006).

A PB of 0.15 was borrowed from the Double-crested cormorant functional group. QB was calculated using information from Hunt et al. (2000) on daily energy needs (kj) and weight, assuming an average prey density of 5 kj/gram and adjusting for the portion of prey not digestible. QB calculations are similar to use in Harvey et al. (2010).

The only diet study/sample that fit in the domain for pelagic cormorants was from Ainley, Anderson, and Kelly (1981) and was a sample of 199 pelagic cormorants from South Farallon Island in the 1970's. In this study, the majority of the prey were juvenile rockfish, followed by various benthic fish, mainly cottidae (sculpins). However, we note that this ratio has recently switched with a higher consumption of sculpin than juvenile rockfish according to an unpublished study from Ano Nuevo island in 2000-2007 (J. Thayer and A. Doty), and use unpublished data from this study to readjust consumption of sculpin and rockfish. Additionally, most of the prey of pelagic cormorants is small fish, except for 3.5% (by number) benthic shrimp and unidentified shrimp and trace amounts of benthic infauna (polychaetes and brittle stars). Pandalid shrimp weigh between 1-20 grams (see Butler 1964), and assuming all shrimp weigh about this and fish the size of anchovy weigh about 68 g, this makes shrimp weight about 15% of fish weight. This was used to adjust the percent number data for the non-fish species in pelagic cormorant diet.

Though the samples from the same study but in the North (Mandarte Island) are out of the domain, they were considered here because there was no other information of diet in the North range of the California current for Pelgaic cormorants. After California (where 43% of PECO breed), the next highest biomass proportion is 26% in Canada. Therefore, this Northern diet should be considered. For just California and Canada, Canada represents 37.5 of the population and California holds 62.5% of the population. However, the Canada study is also outside of the domain (East side of Vancouver island). Therefore, we weighted information in the Canada study at 26%, and weighted data from the California study by 74%. Using this weighting scheme and information on sculpin:rockfish ratios in pelagic cormorant diet from unpublished data, the diet became: 0.2% benthic infauna, 0.5% carnivorous zooplankton, 0.5% pandalid shrimp, 0.3% benthic shrimp, 0.15% mesopelagic fish, 36% benthic fish (sculpin), 0.15% cephalopod, 6.5% sandlance, 34% juvenile rockfish, 0.2% juvenile flatfish, and 15% input consumption (near shore species not in the model). Pelagic cormorants tend to forage near shore (pers. Comm. Julie Thayer, Farallon Institute), so this large percent of input consumption is reasonable. Though the other cormorants seem to be feeding on anchovy, herring, and pacific mackerel, we could not find any consumption of those groups by pelagic cormorants.

Marbled murrelet

The British Columbia Marbled murrelet (*Brachyramphus marmoratus,* MAMU) abundance estimate came from a combination of Burger (2003) and the COSEWIC (2012a) Marbled Murrelet assessment (2012), using the middle of the range of these two. For Washington, Oregon, and California, a total abundance for 2010 came from Miller et al. (2012).
Multiple PB values were compiled that ranges from 0.07-0.19 (Cam et al. 2003, Birds of North America Online – Poole 2005). Based on these values, we calculated what the mean and standard deviation of a lognormal distribution would be to produce a 95% confidence interval with this range. This produced a mean of approximately 0.121. QB was calculated using information from Hunt et al. (2000) on daily energy needs (kj) and weight, assuming an average prey density of 5 kj/gram and adjusting for the portion of prey not digestible. QB calculations are similar to use in Harvey et al. (2010).

Burkett (1995) summarized multiple studies that identified prey items of marbled murrelets, many of which were only observational studies. For the observational studies, the following prey items were observed at the following frequencies:

Herring	7

Sand lance	10
Anchovy	7
Osmeridae	3
Sardine	1
Euphausiid	4
Market squid	1
Juv. Scorpaenidae	3
Californian needlefish	1
Shiner perch	1

In addition to the observation studies that Burkett (1995) summarizes, they also summarize a few studies with count and percent number values. Half of these studies however, come from Langara island, which is far North outside of the Ecopath domain. Another study from Barkley Sound, which is near shore but still in the domain. Therefore, the diet was based mainly on the observational studies (that span a wide range of locations), but also with consideration of the Barkley sound data, and qualitatively consideration of the Langara Island data.

Burkett (1995) cited a paper by Carter that determined for marbled murrelets that 71.2% by weight of prey items are fish and the other 28.7% are invertebrates. However, recent studies have begun to show increasingly more euphausiids in the diet of marbled murrelets (see Norris et al. 2007). It was also brought to our attention that MAMU diet in the North of our model domain may be drastically different then the diet of MAMU in California. Therefore, we weighted diets based on population abundance for each region, with about 44% of marbled murrelets in California, and 56% further North. We took California diet information from a stable isotope analysis by Becker et al. (2007) and Northern diet from the diets summarized by Burkett (1995), and using the weights by area, determined a diet estimate of 11% market squid, 14.5% sand lance, 18% anchovy, 13.5% herring, 7.5% other smelt, 14.5% euphausiids, 1% perch, 5% input consumption or other (white croaker, nettle fish – too near shore), 9% juvenile rockfish, and 3.5% mysid shrimp (carnivorous zooplankton).

Pigeon guillemot

Pigeon guillemot (*Cepphus Columba*) British Columbia abundance estimate came from Ewins et al. (1993) (cited by Birds of North America Online – Poole 2005). Washington counts came from the updated Catalog of Washington Seabird Colonies (Jenkerson and Pearson, 2012). The Washington count was multiplied by a conversion factor of 1.6 to extrapolate rough colony counts to total breeding bird counts. Oregon counts came from the Oregon Seabird Colony

Database (U.S. Fish and Wildlife, 2013), with many counts from 2008 but extending back into the 1990s and 1980s. Finally, California counts were mainly all from Carter et al. (1992), though there were updates for Gualala Point Island (Garcia-Reyes et al. 2013), Southeast Farallon Island (Warzybok and Bradley, 2011), Alcatraz Island (Saenz et al. 2006; Acosta et al. 2010), Ano Nuevo Island (Hester et al., 2013), and many more colonies from Eigner et al. (2010) from Point Reyes to central California. Additional counts from Southern California came from multiple studies from PRBO (Robinette and Acosta 2011; Robinette et al. 2012; Robinette et al. 2013). A PB of 0.2 came from the Biology of Marine Birds (Schreiber and Burger, 2001). QB was calculated using information from Hunt et al. (2000) on daily energy needs (kj) and weight, assuming an average prey density of 5 kj/gram and adjusting for the portion of prey not digestible. QB calculations are similar to use in Harvey et al. (2010).

Within the model domain, Pigeon guillemot diet data came from percent number studies by Sydeman et al. 1997b and Sydeman et al. 2001. The majority of prey items were all small fish/cephalopods that are likely close in weight and therefore, we assumed percent number to be representative of percent mass. There was a trace amount of polychaetes (benthic infauna), but this probably represents 0% of the diet because when considering mass, this would be very small compared to fish and cephalopod mass.

The studies showed a large consumption on juvenile rockfish and cottidae (sculpins – benthic fish). Weighting more recent data (1990s) higher, this would lead to greater consumption on cottidae than rockfish. Personal communication with Julie Thayer corroborates this. Additionally, there were two diet studies outside the model domain; Cyra (1982) for Protection Island in Washington and Drent (1965) for Mandarte Island in Bristish Columbia. Using these studies to supplement (since the other Sydeman studies are only for California), and weighting by the proportion of birds in each major region with diet data (California, Washington, and British Columbia), this led to a diet of 38% benthic fish (cottidae), 0.5% surf perch, 2.6% cephalopod, 2.2% sandlance, 18% juvenile rockfish, 16.6% juvenile flatfish, 0.2% juvenile roundfish, and 19% input consumption, mostly because many of these birds are foraging very near shore.

Caspian tern

Caspian tern (*Sterna caspia*) counts for Washington came from the 1989 Catalog of Washington Seabird Colonies (Speich and Wahl, 1989). Oregon counts came from the Oregon Seabird Colony Database (U.S. Fish and Wildlife, 2013), with counts coming from 2001/2005. Finally, California counts came Carter et al. (1992) with no recent updates.

Multiple PB values were compiled that ranges from 0.09-0.13 (Schreiber and Burger, 2001). Based on these values, we calculated what the mean and standard deviation of a lognormal distribution would be to produce a 95% confidence interval with this range. This produced a mean of approximately 0.109. QB was calculated using information from Hunt et al. (2000) on daily energy needs (kj) and weight, assuming an average prey density of 5 kj/gram and adjusting for the portion of prey not digestible. QB calculations are similar to use in Harvey et al. (2010).

Many of the Caspian tern diet studies come from outside of the model domain in rivers and estuaries. The final diet is an attempt to reconcile this but we do recognize that these values have low certainty and this is reflected in the pedigree of this diet and the Monte Carlo routine. Diets were available for two states, Washington and Oregon, and we found the average of each state and then found a weighted average between the Washington and Oregon diets based on the percent of total Caspian Tern biomass in each state. Washington diets came from Smith and Mudd (1978) for Grays Harbor and Thompson et al. (2002) for Commencement Bay. Diets from Washington mainly consisted of smelt, perch, sculpin (*cottidae*) salmon, and herring. Diet for Oregon came from Roby et al. (2002) and mainly consisted of salmon, perch, anchovy (engraulidae), smelt, and sand lance. Weighting the Washington diet by 42% and the Oregon diet by 58% gave a final diet of 6% benthic fish, 18% perch, 2.5% sardine, 10% anchovy, 6% herring, 3.3% sand lance, 1.1% white bait smelt, 6% other smelt, 0.2% juvenile flatfish, 39% salmon, and 8% input consumption.

Brown pelican

Brown pelicans (*Pelecanus occidentalis*) breed in the Southern range of the model domain in California and Baja, Mexico. Abundance for Southern California and the West coast of the Baja peninsula came from Anderson et al. 2013 by taking the full count for the Southern California bight plus half the count from the Southern Baja-Pacific (13,245 breeding pairs, 26,490 individuals). Additional abundance for colonies further north came from Carter et al. (1992). We did not scale numbers up to reflect juveniles as this is extremely unknown but our final density is similar to that in the Atlantis model (Kaplan et al. 2014). Using a mean male-female brown pelican mass from Hunt et al. (2000) of 3,057 grams, the final density became 0.00027 mt/km^2. A PB of 0.2 came from the Biology of Marine Birds (Schreiber and Burger, 2001) and was cited to be “circa” or around 0.2. QB was calculated using information from Hunt et al. (2000) on daily energy needs (kj) and weight, assuming an average prey density of 5 kj/gram and adjusting for the portion of prey not digestible. QB calculations are similar to use in Harvey et al. (2010).

Currently, the only diet data available for Brown Pelican comes from a table in the 1983 Brown Pelican Recovery Plan (Gress and Anderson 1983, U.S. Fish and Wildlife). The table summarizes diet data from (Gress et al. 1980) that looked at diet of pelicans breeding in the Southern California Bight in 1972-79. This study contributed a HUGE portion of the diet to anchovy (92.4%), which makes sense during this time period (no sardine present). Though the table breaks down diets based on percent number, all prey items are similar sized fish species. Other prey items included saury, juvenile rockfish, pacific mackerel, topsmelt, white croaker, surfperches, and black smith.

Aditionally, Velarde et al. (2013), compared the proportion of sardine in Brown Pelican diet to the proportion of anchovy in the diet. This showed potentially more weight to sardine, though it was quite even. This study also mentioned that 83% of Brown Pelican diet is anchovy/sardine. Additionally, information from Harvey and Gress (2007) presented by Harvey in Ainley et al. (2014), gives percent composition of anchovy and sardine for Brown pelican diets in 1991,1992,1996,2002,2004, and 2005. Using an average percent composition from this, gives a sardine/anchovy diet of around 71% anchovy and 29% sardine. Therefore, using the non-anchovy, non-sardine diet composition from the Gress et al. (1980) source and making 83% of the diet sardine/anchovy from Velarde and finally, breaking that 83% based on the diet percentages from Harvey and Gress (2007), this gives the final diet of 26% sardine, 64% anchovy, 2% pacific mackerel, 3% saury, 2% juvenile rockfish, and 2% input consumption (species not in the model such as white croaker and top smelt).

MIGRATORY BIRDS

Biomass estimates for migratory birds (black-legged kittiwake, albatross, northern fulmar, and shearwaters) were calculated by taking region specific densities (abundance/area) and extrapolating to entire areas in the model domain. We tried to use densities from the period of May to June if they were available. If specific regional densities did not exist, we used densities from the 2008 California Current Ecosystem Survey (McClatchie 2009). Because these species are only present in the system for part of the year, we could lower biomass to represent the amount of time the species spend outside the domain. Instead, we made a proportion of their diets "input consumption" based on the amount of time these species are not in the domain to account for food consumed outside of the system in the months these birds are not present.

Black-legged kittiwake

Black-legged kittiwake (*Rissa tridactyla*) density for Britich Columbia came from Burger (2003) and was used to calculate a total abundance for the BC region. Mason et al. (2007) has a density estimate for kittiwakes in Southern California in January. This was used for S. California and an average density from the same source was used for the rest of the model domain. Using an average individual bird weight from Hunt et al. (2000) this led to a total biomass of 38.46 mt. Multiple PB values were compiled that range from 0.07-0.12 (Schreiber and Burger, 2001). Based on these values, we calculated what the mean and standard deviation of a lognormal distribution would be to produce a 95% confidence interval with this range. This produced a mean of approximately 0.093 with a CV of 0.16. QB was calculated using information from Hunt et al. (2000) on daily energy needs (kj) and weight, assuming an average prey density of 5 kj/gram and adjusting for the portion of prey not digestible. QB calculations are similar to use in Harvey et al. (2010).

According to multiple sources (Harrington 1975; Briggs et al. 1987; Gaston and Jones 1991; Richardson et al. 2003; Nysewander 1983) documented in Birds of North America online, kittiwakes are present in the model domain about half the year, leaving their breeding grounds in Alaska in September and returning to Alaska in March-April. Because of this migration, 50% of the diet was attributed to input consumption, since 50% of prey kittiwakes need in a given year is taken from outside of the domain. The rest of the kittiwake diet consists of anchovy, mesopelagic fish, market squid, and euphausiids, based on information from Baltz and Morejohn (1977) and some information on diet from Alaska from Suryan et al. (2002). Based on this, the final diet becomes 50% input consumption, 1.2% euphuasiids, 1.6% mesopelagic fish, 40% market squid, and 8% anchovy. Recognizing that most of this data came from one study with a sample size of eight, leads us to have low certainty in this data when running the Monte Carlo simulation.

Albatross (Black-footed and Laysan)

Density for albatross (mainly Black-footed and Laysan, *Phoebastria nigripes* and *Diomedea immutabilis*) came mainly from McClatchie (2009) and the 2008 California Current Ecosystem Survey. However, there were a few more specific regional densities. COSEWIC (2006) estimated an abundance of 2500 albatross in the waters off British Columbia. In central California, densities for the marine sanctuaries came from Ainley and Hyrenbach (2010). Finally, Baja density estimates came from Wolf et al. (2006). Note that birds in Baja breed in the Hawaiian archipelago and are therefore different from the albatross in the northern part of the domain. Using average weight from Hunt et al (2000) this led to an overall biomass of 226.9 mt. Multiple PB values were compiled that range from 0.01-0.1 for black-footed and Laysan (Schreiber and Burger 2001; Veran et al. 2007; VanderWerf and Young 2011; Lebreton and Veran 2013). Based on these values, we calculated what the mean and standard deviation of a lognormal distribution would be to produce a 95% confidence interval with this range. This produced a mean of approximately 0.04 with a CV of 0.7. QB was calculated using information from Hunt et al. (2000) on daily energy needs (kj) and weight, assuming an average prey density of 5 kj/gram and adjusting for the portion of prey not digestible. QB calculations are similar to use in Harvey et al. (2010).

Diet for albatross is available in Gould et al. (1997) for the Pacific Ocean from the early 1990's. This study location is East of our Ecopath domain (middle of the Pacific), creating diets made up of potentially species that Albatross would not encounter closer to shore, but possibly only on the outer limit of our model.

In addition, there is diet information in the USGS report for Albatross (Arata et al. 2009), and a thesis by Bisson (Bisson 2008) that shows these birds are consuming a lot of fishery offal, scavenging off of driftnet fisheries in the Pacific. The large diet proportions on neon flying squid and pomfret from the Gould study were due to these being the species used as bait in a nearby fishery. However, according to the authors, black-footed albatross are still consuming mostly cephalopods, regardless of the neon flying squid bait. On the other hand, fish and squid are equally important in Layson diet.

It is difficult to determine how much fishery offal these birds are consuming overall. When around fishing boats, they are consuming around 40-65% based on Gould et al. and the Bisson thesis. Additionally, these species are migratory and based on personal communication with Bill Sydeman and information from the Birds of North America online (Poole 2005), albatross are in the domain completely for 5 months of the year, in transition (50% in the domain) for 2 months, and only a few left in the domain (10%) for the other 5 months. Migration and offal consumption considered, this led to a final diet of 0.1% infauna, 0.3% large zooplankton, 16% cephalopods, 2.6% saury, and 80% input consumption (around 20-30% offal).

Northern Fulmar

Northern fulmar (*Fulmarus glacialis*) density values came from a mixture of sources: Burger (2003) for British Columbia, McClatchie (2009) for Washington, Oregon, and Northern Calfornia, Ainley and Hyrenbach (2010) for the central California sanctuaries, and Mason et al. (2007) for Southern California. Using average individual weight from Hunt et al. (2000), the overall biomass for Northern fulmar was 72.6 mt.

Multiple PB values were compiled that range from 0.03-0.06 (Schreiber and Burger, 2001;

Dunnet et al. 1963). Based on these values, we calculated what the mean and standard deviation of a lognormal distribution would be to produce a 95% confidence interval with this range. This produced a mean of approximately 0.04 with a CV of 0.21. QB was calculated using information from Hunt et al. (2000) on daily energy needs (kj) and weight, assuming an average prey density of 5 kj/gram and adjusting for the portion of prey not digestible. QB calculations are similar to use in Harvey et al. (2010).

The two main diet studies for Northern Fulmar (NOFU) are Baltz and Morejohn (1977) that examined 3 NOFU diets in 1974 in Monterey Bay, CA and Hills and Fiscus (1988) that examined 28 NOFU diets in 1976 near Clallam and Grays Harbor counties. Both studies were percent number studies, however, other than the juvenile rockfish, most of the prey should weigh similar amounts and therefore, these diets can be considered basically as percent mass studies. From these studies, NOFU were eating mostly cephalopod, including 29.6% market squid in the Baltz and Morejohn study. The only prey items that were not cephalopods were juvenile *Sebastes* (assumed to be juvenile) and unidentified fish. Donnelly-Greenan (2012) also notes the high consumption on cephalopods but only includes information on consumption of cephalopods by fulmars (no other prey items). Additionally, Northern Fulmars are migratory and only in our model domain for approximately half of the year (based on information in Cogswell 1977; Morgan et al. 1991). Therefore, 50% of the diet was allocated to input consumption. The other 50% was broken up as 2.2% amphipods, 2.2% euphausiids, 2.2% copepods, 35% other cephalopods, 6.6% market squid and 1.5% juvenile rockfish.

Shearwater (Sooty and Pink-footed, *Puffinus griseus* and *Puffinus creatopus*)

Of all migratory birds, shearwaters are the most abundant in the domain. Regional density estimates came from a variety of sources: for British Columbia, year-round density estimates came from Burger (2003), for Washington and Oregon, densities from North and South of the Columbia plume (not in the plume) came from Zamon et al. (2014), for Southern Oregon to the Northern boundary of the California sanctuaries, we used the density from McClatchie et al. (2009), for the California sanctuaries, density came from Ainley and Hyrenbach (2010), and finally, for California (south of the sanctuaries), density came from Mason et al. (2007). There were no density estimates for Baja, so the density from Mason et al. (2007) for Southern California was extrapolated into Baja as well. Using an average individual mass from Hunt et al. (2000), the final biomass was approximately 1,098.2 mt.

The PB value of 0.07 came from Biology of Marine Birds (Schreiber and Burger, 2001). QB was calculated using information from Hunt et al. (2000) on daily energy needs (kj) and weight, assuming an average prey density of 5 kj/gram and adjusting for the portion of prey not digestible. QB calculations are similar to use in Harvey et al. (2010).

Baltz and Morejohn (1977) provide diets for both Sooty and Pink-footed shearwaters in Monterey bay for 1974/75. Gould et al. (2000) also provides diets for Sooty Shearwater in the North Pacific. Both are not exactly in the domain, but both were included assuming that these birds forage within the domain occasionally and because these are close and similar to our model domain. Based on the shearwater diets from Baltz and Morejohn, shearwaters are consuming mostly anchovy, market squid, and euphuasiids. However, these are percent numbers studies so in terms of percent mass, we would assume euphuasiid percentage to not be as high. Gould et al. (2000) had high consumption on saury and cephalopods (probably because of the distance from shore).

Field (2004) cites two other studies for shearwater diets – Wiens and Scott 1975; Chu 1984. Wiens and Scott attribute the majority of shearwater diet to anchovy (80%). Chu found that for May to June, the main prey item was juvenile rockfish. For July to September, anchovy and market squid were the most important. Chu also mentions predation on euphausiids, polychaetes, juvenile lingcods, and other cephalopods. The overall diet was constructed based on this information however; I could not find access to the Chu study for further data.

Additionally, shearwaters are migratory and only present in the model for about half the year, though a few linger year round. Based on personal communication with Bill Sydeman, we assumed 100% of shearwaters in the domain for 5 months, 50% of shearwaters in the domain for 2 months (book-ending the 5 months of 100% where birds are entering and leaving), and 10% of shearwaters in the domain for 5 months. This led to 46% of the diet being input consumption for the amount of time not in the domain. The rest of the diet was estimated to be approximately: 2.7% benthic infauna, 0.15% amphipods, 0.2% epibenthic fauna, 6.6% euphausiids, 0.2% large jellies, 0.15% mesopelagics, 9.6% cephalopods, 18% market squid, 8% anchovy, 0.1% herring, 4.8% saury, 2% juvenile rockfish, 0.1% juvenile hake, and 0.5% juvenile roundfish.

MARINE MAMMALS

Transient orcas

Transient orcas (*Orcinus orca*) in the California Current are part of the West coast transient stock that ranges from California to Southeastern Alaska (Allen and Angliss, 2010). Transient and resident populations have been split into separate functional groups in the model due to their drastic differences in diets, with transients consuming mainly mammals and residents being primarily fish eaters. According to Allen and Angliss (2010), there are 324 individual transients in the West coast stock. At an average weight of 2,280.5 kg, this leads to a total biomass of 807 mt and a density in the model domain of 0.00267 mt/km^2. Migration out of the model domain is handled by specifying a percent of the diet as input consumption that is representative of the amount of time the whales spend out of the model domain. The PB value of 0.025 came from the Gulf of Alaska model (Aydin et al. 2007), while the QB also came from the GOA model but was multiplied by 4/3 as described in Harvey et al. (2010).

For transient whale diet, Field (2004) cited Pauly et al. (1996). Additional qualitative data can be found in Hunt et al. (2000) and Barrett-Lennard et al. (1995). These studies give transient whale diet of mainly pinnipeds and additionally, porpoises and baleen whales. Transient orca consumption on other species has been noted for grey whales (Green et al. 1992) and seabirds (Ford et al. 1998) (though consumption on seabirds is small when diet is mass-based). Though many studies have given counts and observations about transient killer whale diet and prey, it is difficult to break up observations into an overall diet by mass. We complied the species that the literature said are consumed by transients and broke up the total diet based on biomass of prey. Additionally, transient killer whales are transient and are assumed to be in our model domain only about 25% of the time. Therefore, 75% of the diet was set as input consumption, 0.15% sharks, 0.4% porpoises, 2% humpback whale, 0.1% minke whale, 2.2% fin whale, 0.2% sperm whale, 0.2% harbor seals, 2% sea lions, 0.5% adult northern elephant seals, 0.1% fur seals, 5% blue whales, 10% grey whales, 1.1% dolphins.

Residential orcas

For resident orca (*Orcinus orca*) biomass, census data came from Ellis et al. (2011) and Carretta et al (2013). Based on these estimates, we concluded that all 87 southern residents are in the model domain in the winter and only about 58 of the northern residents reside in the domain during winter. With a mass of 2,280.5 kg from Hunt et al. (2000), this leads to a total density of 0.0011 mt/km^2. All southern residents migrate out of the domain in summer, while about half of the northern residents are in the domain in winter, and migrate out in summer. These migrations were incorporated into the model by specifying a certain percentage of the diet as input consumption (being consumed outside the model). The PB value of 0.025 came from the Gulf of Alaska model (Aydin et al. 2007), while the QB also came from the GOA model but was multiplied by 4/3 as described in Harvey et al. (2010).

For resident orca whale diet, diet was taken from an amalgamation of mainly observation studies (Ford et al. 1998; Ford and Ellis 2006; Pauly et al. 1998) in addition to information presented in Field (2004). Field cites multiple studies and states: "In the Bering Sea, Orcas were observed to prey on sablefish, arrowtooth flounder and halibut off of longlines, while ignoring pollock, cod, grenadier, rockfish and thornyheads (Dahlheim 1995, Yano and Dahlheim 1995)". Finally, Hunt et al. (2000), partitions non-transient orca diet into 1:1:4 squid:forage fish:other fish according to Field (2004). With all these studies, we broke up diet based on given general percentages and total number of observed feedings on each prey item. Our final diet became 1.3% mesopelagic fish, 3% benthic fish, 5.6% cephalopods, 0.5% sardine, 6% herring, 1.8% mackerel, 0.2% yellowtail rockfish, 0.2% nearshore rockfish, 0.15% yelloweye, 0.2% shelf rockfish, 0.1% shortbelly, 1.3% halibut, 2.5% hake, 3.8% lingcod, 0.5% arrowtooth flounder, 2% sablefish, 0.1% albacore tuna, 25% salmon, 1.3% grenadiers, 1.3% dogfish, 0.1% widow rockfish, 3% flatfish, 1.3% skates, 0.1% sharks, and 38% input consumption (due to amount spent outside of the model domain). Rockfish consumption was not known at a species level and therefore total rockfish consumption was broken up based on available biomass.

Porpoises

The porpoise group includes Dall's porpoise (*Phocoenoides dalli*), Harbor porpoise (*Phocoena phocoena*), Pacific white-sided dolphin (*Lagenorhynchus obliquidens*), Risso's dolphin (*Grampus griseus*), and the Northern Right Whale dolphin (*Lissodelphis borealis*). Abundance in the United States came from the 2012 Marine Mammal Stock Assessment Report (Carretta et al. 2013). For the rest of the model domain, Dall's, Harbor, and Northern Right Whale Dolphin were assumed to not inhabit Mexican waters. Risso's and Pacific white-sided dolphin were assumed to have the same density in Mexico as in the U.S. For Canada, abundances were added to Harbor, Dall's, Northern right whale, and Pacific White-Sided assuming the same densities as the U.S. Risso's dolphin was assumed to not inhabit Canadian waters. Finally, Carretta et al. (2013) showed distributions for each species off the coast. These were used to adjust biomass for the percent of each species residing within the 2000 meter isobaths. For Dall's porpoise, approximately 50% are in the domain, 75% for Pacific White sided Dolphin, 50% for Risso's dolphin, 50% for Northern Right Whale dolphin, and 100% for Harbor porpoises. Note that the Harbor porpoise biomass does not include individuals in the Puget Sound (outside of the domain). The final biomass for the porpoise group using mass from Hunt et al. (2000) was 8006.21 mt and a density of 0.0265 mt/km^2.

A PB of 0.07 for the group is the corresponding PB for Harbor Porpoise and comes from Field

(2004). This is an appropriate PB as Harbor porpoise are the second most abundant species in the group. QB was calculated for each species based on information from Hunt et al. (2000). Then, a weighted average for QB was calculated using biomass proportions for each species out of the entire group. This led to a QB of 36.52.

Diets are known for Harbor porpoise, Pacific white-sided dolphin, and Dall's porpoise. Final diet was averaged for these species and weighted by biomass abundance of each species (25%, 45%, 30% respectively). Only harbor porpoise diet was percent mass and percent number. Dall's and Pacific white-sided diets were both percent frequency of occurrence but were used because no other diets could be found and harbor porpoise diet alone would not fully represent this entire group. Harbor porpoise diet data was from California from two studies Sekiguchi 1995 and Toperoff 2002. Pacific white-sided dolphin diet data came from Washington and California from Stroud et al. (1981). Finally, Dall's porpoise data is for Washington and California from Stroud et al. (1981), Norris and Prescott (1961), and Walker et al. (1998). For rockfish in the diet, since rockfish was not identified at a species level, total consumption on rockfish was broken up into the individual functional groups based on available biomass. Harbor porpoise show high consumption on anchovy, market squid, spotted cusk eel, and sardine (to a lesser extent). Pacific white-sided dolphin diet consisted mainly of cephalopods (including market squid), with additional consumption on hake and anchovy. Dall's porpoise diet mainly consisted of anchovy, hake, and cephalopods as well. The weighted average final diet became 4% mesopelagic, 2.5% benthic fish, 34.5% cephalopod, 14% market squid, 3.4% sardine, 9% anchovy, 1% herring, 0.1% mackerel, 0.8% other smelt, 1.9% whitebait smelt, 2.2% saury, 1% juvenile roundfish, 0.6% yellowtail, 0.1% black rockfish, 0.1% nearshore rockfish, 0.1% yelloweye, 0.1% greenstriped, 0.9% shelf rockfish, 12.5% hake, 0.5% sablefish, 2% salmon, 0.3% dogfish, 0.1% canary, 0.1% pacific ocean perch, 0.4% widow, 0.1% splitnose, 0.1% slope rockfish, 1.6% flatfish, 0.2% skates, 0.2% sharks, and 5% input consumption (mainly jack mackerel).

Humpback

Because Humpback whale (*Megaptera novaeangliae*) biomass has increased substantially over the last 10 years, an average biomass was used in order to adjust for this increasing trend in an assumed steady state. First, for the British Columbia population, DFO (2009) gives an abundance estimate of 2,145 individuals in 2006 and states that the population grew over the period of 1992-2006 at a rate of 4.1%. Based on this growth rate and the 2006 estimate, we back calculated what the population would have been for the 9 years previous to 2006 and calculate the 10-year average (including 2006). This gave a 10-year average BC population abundance of approximately 1,802 individuals. Similarly, for the, there was a U.S. total estimate of 2,043 whales in 2008 (Calambokidis et al. 2009; Carretta et al. 2013), with a rate of increase equal to 7.5% per year. Using this growth rate and 2,043 individuals, we calculated backwards to find the abundance in the previous 9 years. We than found the 10-year average (including 2008), which was equal to 1,508 individuals. Adding together BC and US and using a mass from Hunt et al. (2000), this gave a biomass of 100,639.611 mt. Finally, the distribution in the MMSA (Carretta et al. 2013), showed approximately 75% of the Humpback population in the model domain (between shore and the 2000 mt isobaths). Therefore, we multiplied the biomass by 0.75 for a final biomass of 75,479.71 and a density of 0.25. Humpback whales winter down South, outside of the model domain (Carretta et al. 2013). This was handled by adjusting the diet of Humpback to include a proportion of outside consumption instead of adjusting the overall biomass. PB and QB values were both taken from Field (2004) who used a PB of 0.0377 and QB of 7.58. Recent diet for any baleen whales is rare.

The most in depth diets come from information from the 1920s summarized by Clapham et al. (1997) for Humpback, Fin, and Sei whales off the California coast. For Humpback, stomach contents for 253, 67, 421, 356, 166, 40, and 17 whales were analyzed for the years 1920-1926. These samples showed large consumption of anchovy, sardine, euphausiids, and herring, however, were only reported in percent number not percent mass. There is additional humpback diet data from scat samples from Kieckhefer (1992) for very small sample sizes. This study showed a large diet of euphausiids with qualitative information on consumption of “small schooling fish, presumably pacific herring, northern anchovy, and juvenile rockfish”. Also, Field (2004) cites Rice (1963) that found that 149 humpback whales primarily consumed anchovy (64%) and euphausiids (36%), though this was during a time that sardine were not present in the ecosystem. Based on the percent number data from Clapham et al (1997) and additional qualitative information from the other sources, this leads to an overall diet of 60% euphausiids, 1% cephalopod, 20.5% sardine, 9.5% anchovy, 4.5% herring, and 4.5% juvenile rockfish where forage fish percentages were calculated based on availability, so a weighted percent based on biomass. Also, since humpback whales migrate out of the system for approximately half the year, breeding in Hawaii and off the coast of Mexico (Carretta et al., 2013), 50% of consumption was attributed to input consumption (outside the domain), cutting all the other consumptions in half (30% euphausiids, 0.5% cephalopod, 10% sardine, 5% anchovy, 2.25% herring and 2.25% juvenile rockfish).

Minke

The abundance of Minke whales (*Balaenoptera acutorostrata*) came from the 2012 MMSA (Carretta et al. 2013), giving a total of 478 whales in the domain. However, based on the distribution provided in the MMSA out to the 2000 m isobath, Minke whales can be found further offshore than the 2000 meter isobath, and it was assumed only around 50% reside in the model domain. Along with mass from Hunt et al. (2000), this led to a total biomass of 1,569 mt. The PB of 0.0511 came from the Gulf of Alaska Ecopath model (Aydin et al. 2007). For QB, using information on daily energy consumption and mass from Hunt et al. (2000) and a prey density of 5 kj/gram, this led to a QB of 8.69.

There is not extensive information for Minke whale diet in the California Current, and therefore, diet from Alaska Ecopath models (Aydin et al. 2007) was mainly used for Minke whale diet. Additional information came from studies used by Field (2004) and personal communication with Szymon Surma (UBC). Information summarized in Field (2004) and the Alaska Ecopath models states that consumption is mainly on small crustaceans (krill), other plankton, and small schooling fish.

When translating the Alaska diet into a corresponding diet for Minke whales in the California Current, consumption on capelin was split into anchovy, sardine, juvenile rockfish, saury, and mackerel. Because this diet came from another ecosystem, the pedigree was low (uncertainty high). Final diet scaled to equal 1 became 0.9% amphipods, 0.3% epibenthic fauna, 0.9% copepods, 51% euphausiids, 0.4% large zooplankton, 0.5% small jellies, 3% cephalopods, 9% sardine, 13.3% anchovy, 3% Herring, 0.4% mackerel, 2.7% sand lance, 0.44% whitebait smelt, 2.2% other smelt, 0.44% juvenile rockfish, 1.8% juvenile hake, 1.8% salmon, and 5% input consumption. Minke whales in California to Washington are considered somewhat “resident” and little information is known about any movement (Carretta et al. 2013), so no migration was included in diet proportions.

Fin whale

Fin whale (*Balaenoptera physalus*) abundance came from the 2012 MMSA with a total of 3,044 individuals (Carretta et al. 2013). However, based on the distribution presented in the stock assessment, based on visual approximation, only 25% of population resides in the domain (within the 2000 m isobaths). Using 25% and a mass from Hunt et al. (2000), this leads to a total biomass of 42,304 mt. A PB value of 0.0377 came from Field (2004) and the QB value of 6.52 came from the Gulf of Alaska Ecopath model (Aydin et al. 2007).

Similar to other baleen whales, diet information for Fin whales is sparse, though all studies show the majority of consumption on euphausiids and secondly, forage fish. Data from the 1920s summarized by Clapham et al. (1997) shows 92/141 stomachs containing euphausiids and

45/141 containing sardine. Data from the 1950s (when no sardine were present) from Rice (1963) show 90% of the diet being euphausiids and only 10% anchovy. Combining percent number data from Clapham et al. (1997), some additional data from Flinn et al. (2002) from the 1960s, and percent mass general diet composition from Pauly et al. (1998), this gives 80% large zooplankton, that we classified as 78% euphausiid, 1% copepod, and 1% carnivorous zooplankton. Additionally, Fin diet included 5% mesopelagic fish, 5% cephalopod, 2.5% sardine, 2.5% anchovy, 2.5% herring, and 2.5% sand lance.

Sperm whale

Sperm whale (*Physeter macrocephalus*) abundance came from Carretta et al. (2013) with a total abundance in the U.S. of 971 whales. Assuming the same density in Canada, leads to an addition of approximately 111 individuals in Canada. Using an average male and female mass from Hunt et al. (2000) leads to a total biomass of 22,093 mt. However, according to the distribution in Carretta et al. (2013), only approximately 25% of these whales are residing within the model domain (within the 2000 m isobath). Therefore, we multiply this biomass by 0.25 and divide by the domain area for a final density of 0.018 mt/km^2. We assumed no migration for Sperm whales since they are found year-round off the coast of California (Dohl et al. 1983; Barlow 1995; Forney et al. 1995). Both PB and QB were borrowed from Field (2004) using a PB of 0.021 and a QB of 6.609.

Sperm whale diet is based on Clapham et al. (1997) and diet from Field (2004), who used the Clapham study as well as data from Rice (1963) and Kajimura and Loughlin (1988). All studies show a large consumption of cephalopods (squid and octopus). Based on these studies, Field (2004) assumed a diet of 65% squid/cephalopod and 35% fish. For the most part we followed the diet that Field (2004) determined, with some adjustments for new functional groups, percent number information from Flinn et al. (2002), and that many of the diet studies for sperm whales were done during environmental regimes of low sardine abundance. Additionally, rockfish consumption was based on the total rockfish consumption from the Field diet, partitioned out based on biomass of each rockfish functional group in the model domain. The final diet for sperm whales was 3.3% mesopelagic (including ragfish), 60.2% cephalopod, 7.4% sardine, 1.8% yellowtail, 0.4% black rockfish, 0.3% nearshore rockfish, 0.4% greenstriped rockfish, 1.4% slope rockfish, 1.2% shortbelly rockfish, 2.2% halibut, 4.5% hake, 2.2% lingcod, 3.3% sablefish, 3% grenadiers (macrourids), 2.2% dogfish, 0.2% canary rockfish, 0.4% pacific ocean perch, 1.2% widow rockfish, 1.1% splitnose rockfish, 0.7% shelf rockfish, 0.4% shortspine thornyhead, and 2.2% skates.

Harbor seals

Harbor seal (*Phoca vitulina*) abundance from the U.S. came from Carretta et al. (2013) excluding harbor seals in inland Washington waters (Puget Sound, etc.). We estimated harbor seal abundance in Canada to be about 15,000 individuals based on a total B.C. abundance of 105,000 (with the majority, about 65,000, of seals being in inland waters) (DFO 2010). The DFO report also estimates about 2.6 harbor seals per km of shoreline, not inside the Strait of Georgia, leading to about 15,000 seals on the West coast of Vancouver Island. For the Baja abundance, we used the density from Southern California and extrapolated into Mexico (this used area from the Atlantis model, Kaplan et al. 2014). Using an average of male and female mass from Hunt et al. (2000), this led to a final biomass of 5,926.5 mt and a density of 0.0196 mt/km^2. The PB value of 0.08265 was borrowed from Field (2004) and the QB value of 24.594 was taken from Harvey et al. (2010).

Multiple diet studies exist for harbor seals but mainly near shore and some in estuaries outside of our model domain. We began with diet studies from San Francisco bay, close to our model region, including Torok 1994 and Gibble 2011. We also included the diet that Field (2004) used for Harbor seal based on information from National Marine Fisheries Service (NMFS) (1997). Like Field, we tried to interpret an equivalent harbor seal diet for our domain based on the data from outside the domain (including the NMFS information). We broke up the total forage fish consumption from Field into our individual functional groups based on the number of occurrences of prey items in the NMFS data. Additionally, since consumption on rockfish was not given at a species level, total consumption was broken up into the individual rockfish groups based on available biomass of those groups. With Field's data as a base, we determined overall harbor seal diet to be 2% epibenthic fauna, 2% Dungeness crab, 4% mesopelagic fish, 5% benthic fish, 2.5% surfperch, 2.5% cephalopods, 2.5% market squid, 10.5% anchovy, 3.5% herring, 2% sand lance, 1% whitebait smelt, 10% smelt, 1% juvenile rockfish, 1% juvenile hake, 1% juvenile roundfish, 0.8% yellowtail, 0.2% black rockfish, 0.1% nearshore rockfish, 0.1% greenstriped, 0.6% shelf rockfish, 0.5% shortbelly, 1% petrale sole, 10% hake, 1.8% lingcod, 1% arrowtooth flounder, 7.5% salmon, 0.1% canary, 0.1% Pacific ocean perch, 0.5% widow, 0.1% splitnose, 0.1% slope rockfish, 20% flatfish, and 5% input consumption.

Sea lions

The sea lion functional group includes both California sea lions (*Zalophus californianus*) and Steller sea lions (*Eumetopias jubatus*). The magnitude of California sea lions in the California

Current and consumption of forage fish, particularly sardine, led to substantial balancing problems. However, when accounting for sex ratios along with male versus female weights, we were able to balance the original model.

Steller sea lion biomass came from two sources: for the US, from Allen and Angliss (2012) and for Canada, Olesiuk (2009). For the Canada abundance, only the portion of the population occurring inside the model domain was used. Based on biomass from Hunt et al. (2000), this led to approximately 5,600 mt of Steller sea lion in the model. For California sea lion abundance in the United States, we used the total count from Carretta et al. (2013) of 297,760 sea lions (which was calculated based on pup counts scaled up by 4.317). For abundance in Baja, counts were taken from Lowry and Maravilla-Chavez (2005), which gave pup counts by colony in 2000. Only including colonies within our model domain, again these pup counts were converted to total abundance by multiplying by 4.317. This gave a total population for Baja of 43,373 sea lions. Additionally, because these total counts include all ages and sexes of sea lions, we proportioned out total counts to pups, juveniles, sub-adult males, males, and females based on proportions from Boveng (1988). Using different weights for each group, a total biomass for California sea lions became 24,214 mt. Adding this to the total Steller biomass, this leads to a density of 0.0987 mt/km^2.

The PB and QB parameters also had to be adjusted in order to balance the model, but the final values are reasonable values for sea lions. The PB of 0.076 is a weighted (Steller versus California sea lion) PB from the Puget Sound Ecopath model (Harvey et al. 2010). The QB value of 15.1 is borrowed from the Hecate strait model (Ainsworth et al. 2002). Though this is lower than the QB used in other models (Gulf of Alaska, Puget Sound, Columbia plume), it is reasonable and leads to a balanced model. In addition, high uncertainty was put on this parameter when creating the probability distribution and running Monte Carlo simulations for this value. Steller diet came mainly from Riemer et al. (2011). Though diet in this study is presented in percent frequency of occurrence, it is more comprehensive then some other studies for Steller that either have very small sample sizes (1 sea lion) or just reported diet compositions in “salmonid” versus “non-salmonid”.

For California sea lion diet, we began with percent mass diet from Weise and Harvey (2008). We also supplemented this diet by looking at the recent study by Orr et al. (2011) that includes frequency of occurrence data. Other diet studies exist for California sea lions but these look at only certain components of the diet (just hake and rockfish or just market squid in the diet).

Additionally, the Farallon Institute has recent data on California sea lion from 2010 and 2013 (we averaged diet between the two years) (Hassrick et al. 2014). Using mainly Weise and Harvey (2008) and data from the Farallon Institute, we determined an average diet for California sea lion that was composed of mainly rockfish, hake, cephalopods (market squid or others), and sardine. Because rockfish in diets are not identified at the species level, total adult rockfish consumption (thought most consumption is on juvenile rockfish for sea lions), was split up based on proportion of biomass available of each rockfish group. Finally, Steller and California sea lion diets were averaged using a weighted average with a 10%/90% (Steller/California) split based on biomass. The final diet became 0.5% epibenthic fauna, 2% mesopelagic fish, 2% benthic fish, 1% surf perch, 11% cephalopods, 11% market squid, 12% sardine, 2.8% anchovy, 2% herring, 1.5% mackerel, 1% sand lance, 0.1% whitebait smelt, 1% other smelt, 1% saury, 13% juvenile rockfish, 9% juvenile hake, 1.2% juvenile flatfish, 1% juvenile roundfish, 0.6% yellowtail, 0.1% black rockfish, 0.1% nearshore rockfish, 0.1% greenstriped, 0.5% shelf rockfish, 0.4% shortbelly, 9% hake, 1% lingcod, 3% salmon, 1% dogfish, 0.1% canary, 0.1% pacific ocean perch, 0.2% widow, 0.4% splitnose, 0.1% slope rockfish, 2% flatfish, 1% skates, and 6% input consumption (some salmon consumed in the Columbia river, outside the domain, and other nearshore species).

JUVENILE northern elephant seals

Juvenile Northern elephant seals (*Mirounga angustirostris*) and adult elephant seals were split into two groups because each has quite different migration patterns. Again, instead of adjusting for absence from the system in the biomass parameter, input consumption was added to the diet to represent the amount of prey that both these groups are consuming when not in the system and thus reflecting migration. All things considered, there biomass values are related to each other, which is understandable.

The total northern elephant seal population is estimated at around 124,000 individuals (Carretta et al., 2013). According to Condit et al. (2014), the majority of females give birth to their first pup at the age of 4, but males don’t reach sexual maturity until 5. Based on this, we calculated a range of biomass values for juveniles, with the low end assuming 4 years olds are not “juveniles” and the high end assuming that 4 year olds are included in the juvenile biomass pool. Working backwards and using survival rates for all ages (1-16 years old) from Condit et al. (2014), we were able to calculate the proportion by number and proportion by weight for ages 1-3 and 1-4. This led to two estimates, 41% of the population are ages 1-3 and 55% are ages 1-4. Using these two percentages, the total population size of 127,000, and an average juvenile weight of 192.57 kg (Le Boeuf et al. 1996), this led to a range of biomasses from 10,027 mt to 13,451 mt.

The PB value of 0.31 is the average juvenile (ages 1-4) mortality rate from Condit et al. (2014). The QB value of 14.76 is the same as the adult elephant seals for lack of a better estimate. The only available diet for juvenile Northern elephant seals comes from Sinclair 1994 and was reported in percent frequency of occurrence. Without other available data, the final diet for juvenile elephant seals was given a low pedigree. Diet from this study mainly consisted of cephalopods and hake. Juveniles, like adults, migrate out of the domain for a part of the year. Movement mainly came from Le Boeuf et al. (1996) and depends on the age of the elephant seal. In summary, juveniles from weaning to age 2 are in the domain year round. Ages 3 and 4 are more complicated because females can start to breed at age 3 but don't necessarily. I ended up with a range of possible values where the lower ranges is assuming seals are only juveniles until age 3 and are in the model domain 75% of the time. The upper range assumes that seals are juveniles until age 4 and 50% of the seals ages 3 and 4 are in the domain 100% of the time and 50% are only in the domain 50% of the time. In terms of diet, this leads to around 33% of diet coming from outside the model domain and being classified as input consumption. In addition to this input consumption, diet was set at 1.7% small jellies, 4.5% mesopelagic fish, 3.7% benthic fish, 0.3% surf perch, 12.6% other cephalopods, 25.9% market squid, 0.3% anchovy, 2.3% juvenile rockfish, 10% juvenile hake (assumed juvenile), 0.3% juvenile flatfish, 2% juvenile roundfish, 2% dogfish, and 1.4% skates.

ADULT northern elephant seals

See the juvenile elephant seal group for explanation on why the two groups were split and how the proportion of juveniles versus adults was calculated. Based on these proportions, 45-59% of elephant seals are adults, depending on when maturity is reached at age 4 or age 5. Based on these proportions and that adults weigh 363 kg, this led to a range of biomass values of 20,745.45 mt to 27,199.59 mt. The PB value of 0.2276 is the average adult mortality (ages 5-15) for males and females from Condit et al. (2014). The QB value of 14.76 was calculated using information on daily energy needs and prey density from Hunt et al. (2000).

The only available diet for Northern elephant seals comes from Antonelis et al. 1994 and Antonelis et al. 1987 and was reported in percent frequency of occurrence. Without other available data, the final diets for Northern elephant seal were given a low pedigree. These diets showed a large consumption of cephalopods and hake. Additionally, based on information from Le Boeuf et al. 2000, Le Boeuf and Laws 1994, and Robinson et al. 2012, adult Northern elephant seals are outside of the model domain for approximately 7 1⁄2 months of the year. Based on this, 62.5% of diet was allocated to input consumption. Additionally, though diet studies included consumption on general rockfish, because it is unknown what specific rockfish species are being consumed, diet on rockfish was allocated to rockfish groups based on available biomass of each rockfish group. In the end the final diet became 5% epibenthic fauna, 0.4% euphuasiids, 1% large zooplankton, 1.1% small jellies, 22.8% cephalopods, 0.2% market squid, 0.15% yellowtail rockfish, 0.1% shelf rockfish, 0.1% shortbelly rockfish, 4% hake, 0.6% grenadiers, 0.7% dogfish, 0.1% widow rockfish, 0.1% splitnose rockfish, 0.1% slope rockfish, 0.04% shortspine thornyhead, 0.04% flatfish, 0.8% skates, and 62.5% input consumption.

Fur seals

Much of the information on fur seals (*Callorhinus ursinus*), including migration and sex ratios came from Rolf Ream (NOAA National Marine Mammal Laboratory, pers. Correspondence). According to Ream, about 75% of females (mature females, 4+ years) from the Pribilof and Bogoslof islands in Alaska, migrate to the California current. A smaller portion of males and other female age classes migrate as well. Communication from Rolf Ream included information that Olesiuk (2012) estimated that 27% of yearlings (or young of the year, pups), 40% of juveniles ages 1-3, and 9% of 4 year old males, all migrate. All together, this represents about 52% of the entire Pribilof and Bogoslof populations. They migrate to the California current (including Canada), beginning in January, and begin to leave in May or early June. Also Ream gave the following table:

population component	proportion
pups (1:1 m:f)	0.223481
yearlings (1:1 m:f)	0.11174
2yo (1:1 m:f)	0.089392
3yo FEMALE	0.038439
3yo MALE	0.035757
4+ FEMALE	0.372466
4+ MALE	0.128725

Assuming that 27% of pups, with a sex ratio of 1:1, migrate, 40% of all other juveniles migrate, 75% of females 4+ migrate, and 9% of males 4+ migrate, and using Pribilof and Bogoslof population counts from the Alaska MMSA (Allen and Angliss 2013) and weights for different sexes and different ages from Rod Towell (NOAA National Marine Mammal Laboratory), this leads to 1,832.42 mt of fur seals from Alaska migrating into the domain.

Additionally, there is a population of fur seals in California on San Miguel and Farallon islands. The 2012 MMSA gives 9,968 individual fur seals on San Miguel island. Also, from the 2013 stock assessment (Carretta et al. 2014) and information from fish and wildlife (Dewar 2012) (http://www.fws.gov/refuges/refugeupdate/SepOct_2012/Farallon-Refuge.html), led us to conclude that there is a population size of approximately 720 individuals on the Farallons. Using the same weights and sex ratios as information from Alaska, this leads to 543.53 mt in California.

The final density of fur seals in the model was calculated to be 0.00787 mt/km^2. Also, around 55% of that density leaves the model domain for 5 out of 12 months each year. This movement is reflected in the diet for fur seals, where a proportion of the diet is set as input consumption for prey that is consumed when the seals are outside the model domain.

The PB value of 0.091 came from Field (2004) using a Siler life history table. The QB value of 52.04 came from information on daily energy requirements from Hunt et al. (2000), using a similar method to Harvey et al. (2010) for seabird and marine mammal QBs.

For fur seal diet, Antonelis and Fiscus (1980) and Walker and Jones (1993) presented diets as percent volume and were therefore, the main studies we considered. We also considered Stroud and Fiscus (1981) information though this was presented in frequency of occurrence. Field (2004) also used additional diet studies for fur seals. As with many studies, consumption on rockfish was not specified at the species level and therefore, total consumption on rockfish was broken up into individual groups based on total biomass of each rockfish group. We arrived at the final diet by averaging percent volume studies, factoring in qualitatively the frequency of occurrence data (mainly adding in species not found in the diets of the other studies), and factoring in Field’s interpretation of the diet. The frequency of occurrence study (Stroud and Fiscus 1981) had additional salmon and smelt in the diet, amongst other species. All studies showed large consumption on cephalopods and hake. This led to a final diet of 1.3% mesopelagic fish, 0.6% benthic fish, 10.9% cephalopods, 4% market squid, 1.4% sardine, 8.7% anchovy, 3% herring, 0.3% other smelt, 3% saury, 0.5% juvenile roundfish, 1% yellowtail, 0.3% black rockfish, 0.2% nearshore rockfish, 0.2% greenstriped, 0.9% shelf rockfish, 0.7% shortbelly, 10% hake, 1% sablefish, 4% salmon, 0.1% canary, 0.2% pacific ocean perch, 0.8% widow, 0.6% splitnose, 0.4% slope rockfish, 0.3% flatfish, and 45% input consumption (because fur seals migrate into the domain and are outside the domain for a large part of the year, see information above).

Blue whale

Blue whale (*Balaenoptera musculus*) abundance throughout the domain comes from sources for the U.S., Canada, and Mexico. For the United States, Carretta et al. (2013) cites an estimate of 2,497 individuals. For Mexico, Calambokidis and Barlow (2004) estimate 1,012 individuals and a recent COSEWIC (2012b) report for Canada estimates 250 individuals. Using mass estimates for males and females from Hunt et al. (2000) this led to a total biomass of 386,187 mt. However, according to the distribution in Carretta et al. (2013), only approximately 50% of the individuals reside within the 2000 meter isobath. Therefore, we cut the biomass in half for a final biomass of 193,093.25 mt. The PB value of 0.05 is a general baleen whale PB. The QB value of 5.5 came from using parameters in Hunt et al. (2000) and assuming a prey density of 4 kj/gram.

Diet for blue whales came from two studies, Fiedler et al. 1998 and Croll et al. 2005, both of which are from off the coast of California. Both studies show a diet consisting of only euphausiids, including all the main species (Thysanoessa spinifera, Euphausia pacifica, and Nyctiphanes simplex). Because all euphausiids are in one functional group in this model, blue whale diet becomes 100% euphausiids. However, because blue whales migrate out of the domain, we adjusted this biomass to represent the proportion of prey being consumed outside vs. inside the domain. Oleson et al. (2007) monitored blue whale calls off the coast of California for four years, showing the presence of whales from April to January. Based on the abundance of calls in each month (see Figure 4 in Oleson et al. 2007), we assumed 10% of the population present in May, 50% in June, 100% from July through November, 50% in December, 10% in January, and 0% in February, March, and April. This led to around 52% of the diet being consumed within the model domain, and 48% consumed outside (input consumption).

Gray whale

Gray whale (*Eschrichtius robustus*) abundance numbers come from the 2012 Marine Mammal Stock Assessment Report (Carretta et al. 2013). This assessment gave a total abundance of 19,126 individuals, and using an average (male and female average) of 15,372 kg, this gives a total biomass of 293,995 mt. Gray whales feed in the Chukchi, Beaufort, Northwestern Bering seas in summer and fall, and migrate South into the model domain (Southern California and Baja) to breed in the Winter (Carretta et al. 2013). We did not adjust biomass to deal with this migration but instead adjusted the diet composition to represent a proportion of feeding occurring outside the model domain.

A PB of 0.037 was taken from Field (2004). QB was also taken from Field (2004) but adjusted by multiplying by 4/3 to account for prey consumed but no digested (see Harvey et al. 2010 for more details on QB calculation).

Gray whale diet predominately came from studies used in Field (2004) and the balanced diet from the 1990s Ecopath model, observation data from Darling et al. 1998 from Vancouver island, count data from Avery and Hawkinson 1992, and information from the Alaska Ecopath models (Aydin et al. 2007). All sources show large consumption of amphipods. As mentioned above, gray whales are migratory and extend into Mexico for a part of the year and in Alaska feeding grounds for another part of the year. According to information in the Marine Mammal stock assessment (Carretta et al. 2013) and Pike (1962), we assumed approximately 32% of the year, gray whales are outside the model domain, leading to 32% input consumption of diet. This comes from the quarter of the year they are in Alaska, the 30% of the population extending into Mexico (outside of the model domain), and approximately 120 individuals that are in the domain year round. With 32% input consumption, the other diet values become 1.7% infauna, 64% amphipods, 1.7% epibenthic, 0.07% euphuasiids, and 1% large zooplankton.

Dolphins

The dolphin group consists of both long-beaked (*Delphinus capensis*) and short-beaked common dolphins (*Delphinus delphis*) as well as the Bottlenose dolphin (*Tursiops truncates*). Abundance data for the U.S. for bottlenose dolphin came from Carretta et al. (2013). The U.S. density for bottlenose was used to extrapolate into Mexico for a total bottlenose abundance of 1481. For long-beaked common dolphin, Carretta et al. (2013) gave an estimate of 107,016 individuals in the U.S. and this was used to extrapolate into Mexico as well (based on density) for a total of 152,334 individuals. Short-beaked common dolphin U.S. abundance came from Carretta et al. (2013) as well and this density was used to extrapolate into Mexico for a total of 458,089 individuals. Based on distributions from Carretta et al. (2013), only around 25% of short-beaked common dolphins reside in the domain and around 50% of bottlenose dolphins reside in the domain (within the 2000 m isobath). Therefore, we adjusted abundance estimates to reflect this. Based on weights from Hunt et al. (2000), we calculated a total biomass of 21,527.37 mt and a density of 0.0713 mt/km^2.

We found a range of possible PB values (Reilly and Barlow 1986; Christensen et al. 2009) and used this as the 95% confidence interval for the distribution of PB values to be used when running Monte Carlo runs. The range of 0.03-0.15, using a lognormal distribution, led to a mean PB of 0.0756 and a CV of 0.489. The QB value of 32.33 came from a weighted average of QBs for each species based on parameters from Hunt et al. (2000) and using a prey density of 5 kj/gram.

Diet for both short-beaked common dolphin and long-beaked common dolphin came from the thesis “Food habits of common dolphin (Delphinus delphis and D. capensis” (Osnes-Erie 1999), which had percent number diet information for both species in California from 1983-1992 and 1975-1993, respectively. For bottlenose dolphin diet, Walker (1981) analyzed 9 stomachs in Southern California. We found a weighted average diet for the three species by weighting by biomass present in the domain (there is a large abundance of short-beaked common dolphins but many of them reside outside the model domain). Final percentages to weight diets by were 42.6% short-beaked common dolphin, 56.7% long-beaked common dolphin, and 0.6% bottlenose dolphin. This led to final diet of 4% carnivorous zooplankton, 20% mesopelagic fish, 1.2% benthic fish, 0.3% surf perch, 21% cephalopods, 7.5% market squid, 3.7% sardine, 3.9% anchovy, 2.2% mackerel, 0.2% saury, 2.5% juvenile rockfish, 9.7% juvenile hake, 2% juvenile flatfish, and 21% input consumption (medusa fish, barracuda, ridgeheads, hatchetfish, queenfish, ribbonfish, drums, eels, etc.).

Further Considerations

Any diet values that were less than 0.1% in the original Ecopath model were assumed to be negligible and were removed to help with balancing. Some values less than 0.1% remain due to changes in diets when species are migratory (original were >0.1% before removing a certain percent for migration) or because summing to 1 led to values slightly less than 0.1% (began at 0.1% or greater).

Diets were averaged over multiple years when data for multiple years were available, specifically for recent data (2000-2014). This was done to avoid anomalous years weighting the diet.

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APPENDIX C: CHAPTER 3 SUPPLEMENTARY

Supplemental Figures and Tables

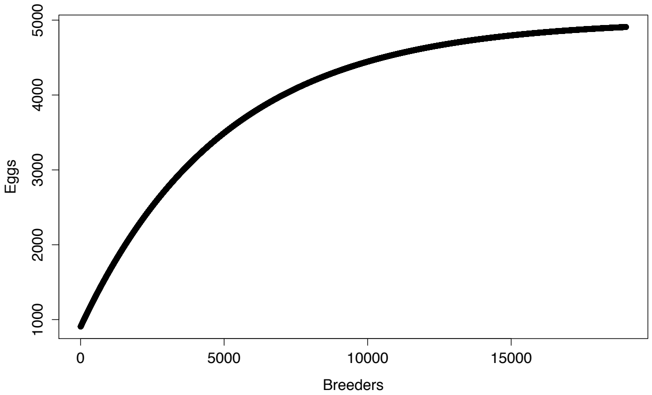

Figure S1. Von-Bertalanffy relationship between number of seabird breeders and number of viable eggs laid.

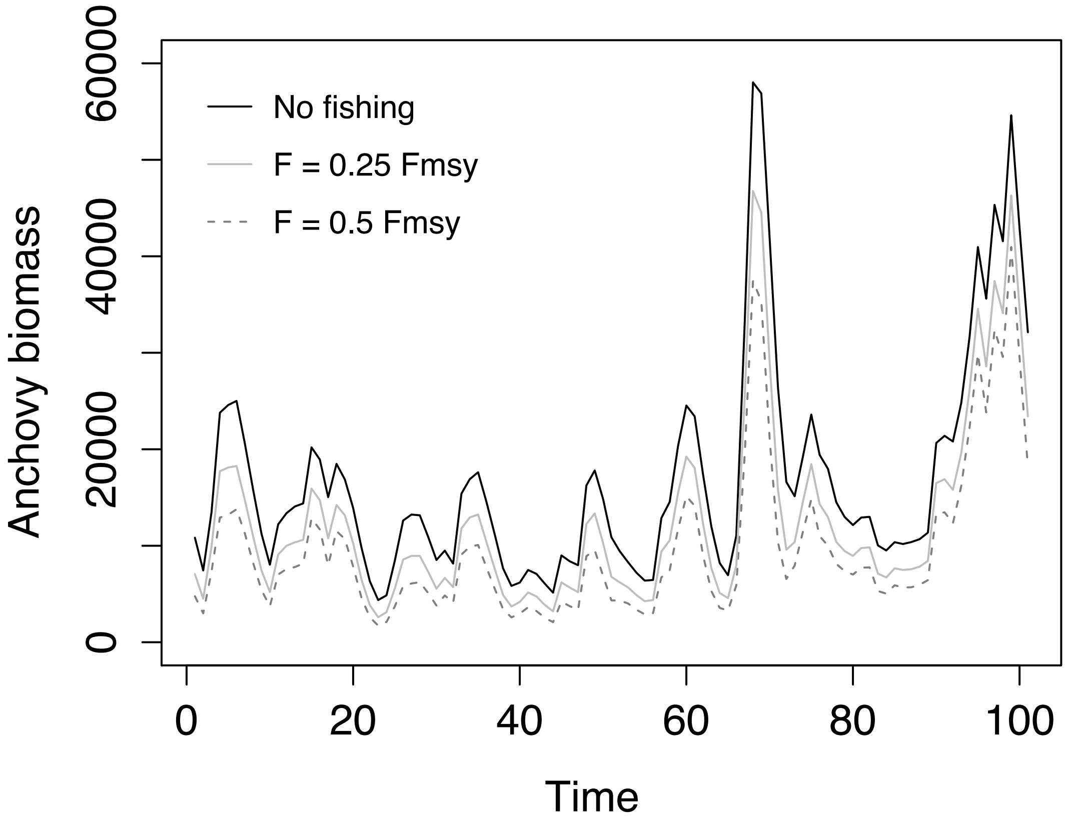

Figure S2. Example time series of anchovy prey biomass for 100 years under different levels of constant fishing.

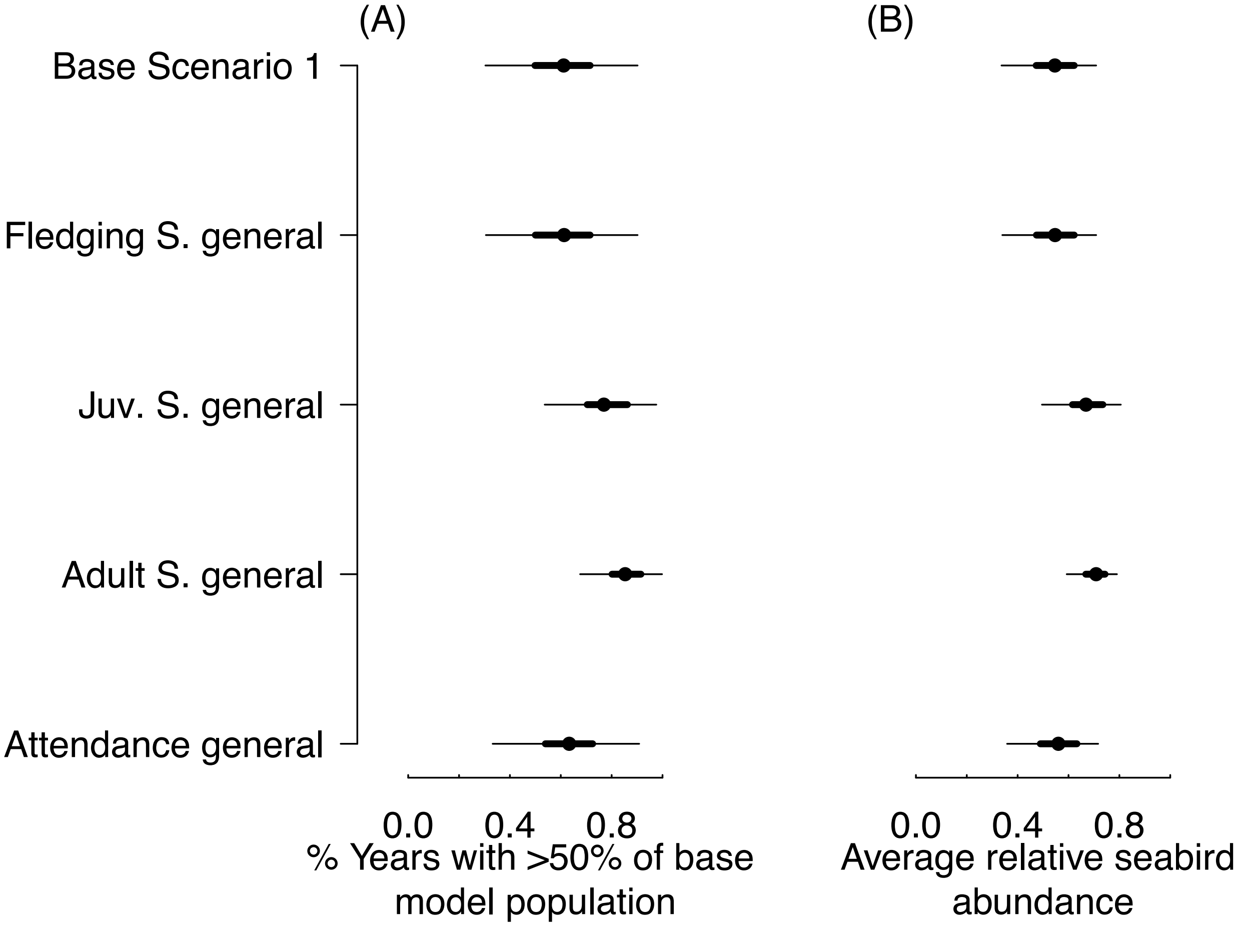

Figure S3. Median (dots), 50% quantiles (thick lines), and 95% quantiles (thin lines) for two metrics - (A) average probability that the modeled seabird population is greater than 50% of the unfished model population (percent of years with population sizes greater) and (B) average relative seabird population sizes - for sensitivity analysis of variation in scenario 1 functional response parameterization at F = 0.25 F_{msy} when the prey abundance threshold (β in the functional response, Table S1) is shifted for breeder attendance (colony attendance of breeders decreases at lower prey availability). For each variation, one functional response – either for fledging survival, juvenile survival, adult survival, or breeder attendance – is changed to a generalist response (from specialist in the base scenario 1 model). The model is most sensitive to changes in the functional response for adult survival after changing the initial parameterization of the breeder attendance functional response.

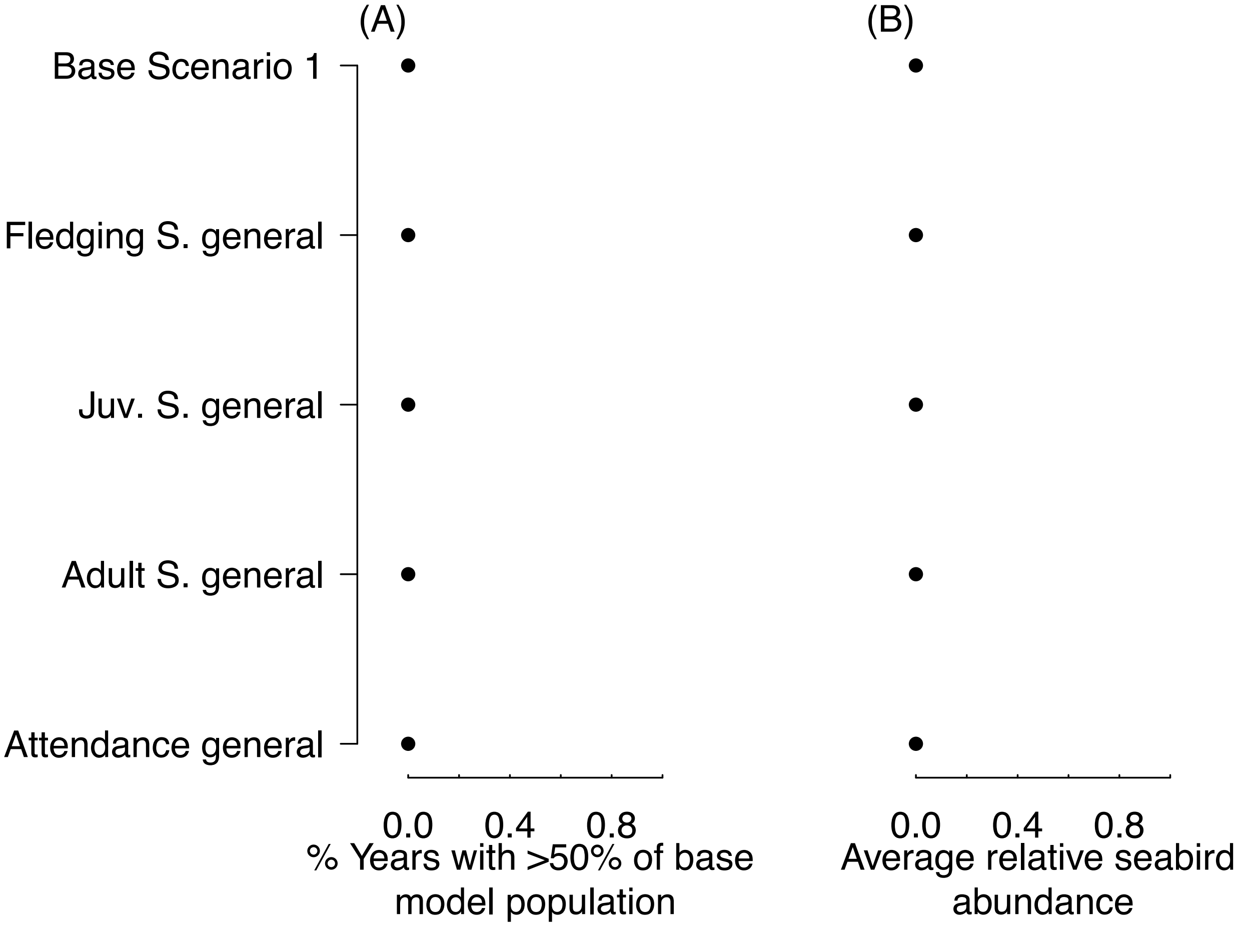

Figure S4. Median (dots), 50% quantiles (thick lines), and 95% quantiles (thin lines) for two metrics - (A) average probability that the modeled seabird population is greater than 50% of the unfished model population (percent of years with population sizes greater) and (B) average relative seabird population sizes - for sensitivity analysis of variation in scenario 1 functional response parameterization at $F = 0.5\ F_{msy}$. For each variation, one functional response – either for fledging survival, juvenile survival, adult survival, or breeder attendance – is changed to a generalist response (from specialist in the base scenario 1 model). Scenario 1 (restricted seabird) goes extinct at this level of fishing no matter what demographic parameter functional response is switched to the generalist parameterization.

Table S1. Input values for parameters α, β, and m that control the shape of the functional response between prey availability and various life history parameters. These values also vary across scenarios based on if a seabird scenario has a generalist or specialized diet preference for anchovy prey.

Life History Parameter	**Functional response type**	**α**	**m**	**β**
Breeder attendance	Generalist	0.6	20	0.3
	Specialist	0.1	20	0.3
	Impact at lower prey level scenario	0.1, 0.6 (specialist vs. general)	20	0.1
Adult survival	Generalist	0.6	20	0.15
	Specialist	0.1	20	0.15
Juvenile survival	Generalist	0.6	10	0.3
	Specialist	0.1	10	0.3
One chick survival/fledging with three chicks	Generalist	0.51	15	0.1
	Specialist	-0.3	30	0.2
	Impact at higher prey level scenario	-0.3	30	0.5
One chick survival/fledging with two chicks	Generalist	0.41	15	0.05
	Specialist	-0.3	30	0.15
Solo chick survival/fledging	Generalist	0.2	15	0
	Specialist	-0.3	30	0.1

APPENDIX D: CHAPTER 4 CASE STUDY SUMMARIES

Australia and Small Pelagic Fishery Impacts on the Ecosystem

The small pelagic fishery (SPF) in Eastern and Southern Australia is managed by the Australian Fishery Management Authority (AFMA) and is comprised of commercial mid-water and bottom trawl fisheries targeting four low- to mid-trophic level species (Australian sardine *Sardinop sagax*, blue mackerel *Scomber australasicus*, jack mackerel *Trachurus declivis*, and redbait *Emmelichthys nitidus*). A constellation of factors led AFMA to review the SPF harvest strategy in 2013, in order to determine target and limit reference points for the SPF that consider impacts on predators and the food web. These factors included public concern about a factory trawler brought in by a license holder (quota owner) to fish SPF and its impact on predators, protected species, the ecosystem, and other fisheries (Tracey et al. 2013). This coincided with a heightened public awareness about the trophic impacts of fishing "forage fish" due to publications such as the Lenfest report (Pikitch et al. 2012) and the Marine Stewardship Council (MSC) criteria for assessing the sustainability of low trophic fisheries to account for trophic impacts (MSC 2014).

For this case study, activity pertaining to steps in the Lenfest process began in the second component, *Where are we going*. In Australia, ecological risk assessment is used to inform management of all federally-managed (and many state-managed) fisheries and a comprehensive risk assessment was completed for the SPF fishery in 2007 (Daley et al. 2007). Note that the ecological risk assessment focuses on the effects of fishing and not other potential stressors (e.g. climate change). This risk assessment is similar to the step, *assess risk to objectives* (step 2.3) in the Lenfest process. One step in the risk assessment process is the selection of objectives, therefore, the step, *develop strategic objectives* (step 2.2) was also conducted through the risk assessment process. However, the risk assessment was not conducted in connection to the AFMA review and objectives were distinct from the operational objective determined later on.

The AFMA review of the harvest policy met our criteria for 2.5, *developing an operational objective*, and all steps in component 3 (*How will we get there*). The review of the SPF harvest strategy was undertaken by a group of fishery scientists and involved considerable interaction with AFMA and with stakeholders in the fishery, in the initial design phase and during the course of the review. The scientific group suggested using MSC criteria as objectives/performance indicators for the review and this was endorsed by the Resource Assessment Group for the fishery and by AFMA management. Adopting MSC criteria was seen as adopting a credible international standard. The criteria for determining acceptable impact are that: *(1) No other species abundance is impacted by more than 70% and (2) The abundance of no more than 15% of other species or groups is impacted by more than 40%.* These criteria are specific *operational objectives* (step 2.5), and also contain *performance indicators* (step 3.1).

The scientific group then used an existing Atlantis ecosystem model (Smith et al. 2015) to evaluate management strategies that would meet these operational objectives and performance indicators; (steps 3.2 *identifying potential management strategies* and 3.3 *evaluating, management strategies*). The analysis concluded that harvest rates that achieved a target stock size of B50 (50% of unexploited biomass) met the performance criterion (Smith et al. 2015) and no changes were made to the harvest strategy because the B50 strategy was the status quo strategy (step 3.4, *select a strategy* and component 4, *Implementation*).

Eastern Baltic Sea and Cod-Herring-Sprat Interactions

Eastern Baltic Sea fisheries are mainly focused on demersal cod (*Gadus morhua*) (bottom/pelagic trawling, gillnets) and pelagic forage fish, herring (*Clupea harengus*) and sprat (*Sprattus sprattus*). A main EBFM topic is centered around the strong ecological interactions between cod and forage fishes (Casini et al. 2008). Specifically, (1) cod top-down predation on sprat and herring (Köster et al. 2001) and (2) sprat and herring predation on cod eggs (Köster et al. 2001; Neumann et al. 2017). Furthermore, there is competition for zooplankton food between sprat and herring (Möllmann et al. 2005). All species, but especially cod, are strongly dependent (mainly recruitment) on the physical oceanographic environment (Köster et al. 2017). Recent environmental conditions have resulted in distribution changes leading to a spatial mismatch of species interactions (Casini et al. 2016; Orio et al. 2017). Analytical assessments of Eastern Baltic cod are presently not conducted due to deficient input data and rapidly changing environmental conditions (Eero et al. 2015).

Activity for component 1, *Where are we now*, is well represented for the Baltic Sea case study. System inventories for the Baltic Sea have been conducted within different International Council for the Exploration of the Sea (ICES) initiatives, matching step 1.1 in the process of *developing a system inventory*. The ICES/HELCOM (Baltic Marine Environment Protection Commission – Helsinki Commission) Working Group on Integrated Assessments of the Baltic Sea (WGIAB) conducted "Integrated Trends Assessments (ITAs)" of the various sub-systems of the Baltic Sea. These assessments include multivariate analyses of time-series encompassing abiotic (nutrients, hydrography, fishing pressure) as well as plankton (phyto- and zooplankton) and fish (pelagic and demersal) time-series (step 1.2, *selecting and calculating indicators*). Results for assessments for the Central Baltic are published in Möllmann et al. (2009) and analyses for multiple sub-systems are contained in Diekmann and Möllmann (2010), which are irregularly updated within WGIAB. Threats to the system (related to step 1.3, *inventory threats*) are included in the discussion of trends in indicators in Diekmann and Möllmann (2010), but not as an explicit list of threats as the step suggests.

A *vision statement* and *strategic objectives* (steps 2.1 and 2.2) can be found in the Common Fisheries Policy (CFP) and the Marine Strategy Framework Directive (MSFD). The Common Fishery Policy of the European Union (EU) (reformed in 2014) has the broad goal that, "Fish stocks should be brought up to healthy levels and be maintained in healthy conditions," (European Commission [EC] 2013), a statement similar to that developed in step 2.1, articulating a strategic vision. More specifically (similar to *strategic objectives*, which are developed in step 2.2), the CFP strives to develop ecosystem-based fisheries management by applying an MSY approach: "Fish stocks should be exploited at maximum sustainable yield levels. These levels can be defined as the highest catch that can be safely taken year after year and which maintains the fish population size at maximum productivity." A common multi-annual plan has been established by the EU for the stocks of cod, herring and sprat in the Baltic Sea and the fisheries exploiting those stocks. The plan implicitly accounts for multi-species management goals by defining F_{MSY} ranges (EC 2016), however, presently not defined for Eastern Baltic cod. In addition minimum levels of spawning stock biomass are set for conservation purposes. Overall though, management of Baltic fish stocks can still be considered single-species.

One potential effort that would exemplify an ecosystem example of step 3.4 (*selecting a management strategy*), was previous efforts within ICES to evaluate and use multi-species F_{MSY}'s for cod, sprat, and herring. However, the multispecies F_{MSY}'s are presently not used as a management strategy due to uncertainties inherent in multispecies model and cod input data (ICES 2013). On the other hand, there are management strategies chosen (step 3.4 *select a strategy*, and component 4, *Implementation*) to estimate biological reference points by considering shifting predation and growth for herring and sprat. This is done by incorporating predation mortality parameters from a stochastic multi-species model into stock assessments (ICES 2015). Therefore, this is a management strategy with an ecosystem consideration, though still from a single species perspective, and without a full management-strategy evaluation approach (other steps in component 3).

Western Scotian Shelf and declining traditional fisheries

There are several ecosystem considerations for the Western Scotian Shelf fisheries, which include fisheries for groundfish, pelagic fish and invertebrates. Groundfish are harvested as part of a multi-species groundfish fishery, mostly targeting pollock (*Pollachius virens*), haddock (*Melanogrammus aeglefinus*) and cod (*Gadus morhua*). Cod is primarily caught as bycatch now, due to its low abundance. Herring (*Clupea harengus*) are prey for many groundfish, seabirds, and mammals, the main forage fish species in the area, and are over-fished. The main invertebrate fisheries are for scallop (*Placopecten magellanicus)* and American lobster, with some by-catch of groundfish, especially flatfish, in the former. Currently, there is a decline in traditional groundfish fisheries and herring stocks are depressed, but invertebrate stocks (scallop and lobster) are doing well.

Fisheries and Oceans Canada (DFO) uses Integrated Fisheries Management Plans (IFMPs) to guide the conservation and sustainable use of marine resources. An IFMP is developed to manage the fishery of a particular species in a given region. It combines the best available science on a species with industry data on capacity and methods for harvesting that species, and includes social, cultural and economic objectives. The latter can reflect the aboriginal right to fish for food and social and ceremonial purposes, and recognize the economic contribution that the fishing industry makes to Canadian businesses and many coastal communities. Ultimately, the economic viability of fisheries depends on the industry itself. However, the department is committed to managing the fisheries in a manner that helps them be economically successful while using the ocean's resources in an environmentally sustainable manner.

Activity pertaining to steps in component 1, *Where are we now*, are all encompassed in Fisheries and Oceans Canada State of the Ocean Reports for Canadian marine regions. The State of the Ocean Report for the Scotian Shelf, including the western Scotian Shelf, covers a range of topics including ocean acidification, climate change and its effects on ecosystems, habitats and biota, at-risk species, marine habitats and communities, and more. This report also uses the Drivers-Pressures-State-Impact-Response (DPSIR) conceptual model framework (Kelble et al. 2013) to identify indicators (http://www.dfo-mpo.gc.ca/oceans/publications/soto-rceo/2012/scotian-ecossais-eng.html), thus taking an *inventory of the system* and *developing a conceptual model* (step 1.1). Activity related to *selecting and calculating indicators* (step 1.2) is included both in the State of the Ocean reports as well as the Ecosystem Status and Trends Report for the Gulf of Maine and Scotian Shelf (Worcester and Parker 2010) as time series data. Additionally, though not an explicit list of threats as step 1.3 in the process suggests (*inventory threats*), many of the major topics covered through-out the State of the Ocean Report are threats to the system (ocean acidification, ocean noise, etc.).

A *vision statement* as well as *strategic objectives* (steps 2.1 and 2.2 in *Where are we going*), exist for the Scotian Shelf region. Specifically, within the DFO Regional Oceans Plan for the Maritimes Region (that includes the Scotian Shelf) there is the following broad vision statement (step 2.1 articulate a strategic vision) for the region: "*Healthy marine and coastal ecosystems, sustainable communities and responsible use supported by effective management processes,"* (DFO 2014). Each individual species or fishery in this case study (herring, groundfish, lobster, and scallop), has an IFMP with specific goals or objectives (step 2.2 *developing strategic objectives*). Within the lobster management plan for example, there are goals related to broader ecosystem impacts including: "Control unintended incidental mortality of North Atlantic right whales," and "Manage area disturbed of bottom habitat," (DFO 2011). Overarching all fisheries in the region are a list of conservation and social objectives (see list in DFO 2013), that include "Respect Aboriginal and treaty rights to fish".

Bering Sea Groundfish and Avoiding Ecosystem Overfishing

One EBFM consideration for the Bering Sea region revolves around the groundfish fishery and the 2 million metric ton removal cap on the fishery. Main Bering Sea fisheries consist of high-volume walleye pollock (*Gadus chalcogrammus*) fisheries, and other groundfish fisheries, including Pacific halibut (*Hippoglossus stenolepis*), sablefish (*Anoplopoma fimbria*) and Pacific cod (*Gadus macrocephalus*). Many of these fisheries are rationalized as ITQs or cooperatives and the fleet is socially heterogeneous consisting of non-Alaska residents, non-indigenous Alaska residents, and indigenous Alaska residents. Most groundfish fisheries also are conducted by multiple commercial sectors defined by gears or vessel characteristics. Species use across sectors has generated recent controversy. For instance, the bycatch of Chinook salmon (*Oncorhynchus tshawytscha*) and halibut in the trawl sector might reduce returns and opportunities for subsistence, recreational and directed commercial fisheries for these species. Because of the total cap on groundfish removals at 2 million metric tons per year, high quotas for pollock will reduce opportunities for fisheries in other groundfish sectors.

Activity related to all steps in component 1, *Where are we now*, is present in the Ecosystem Considerations Report for the Alaska Regions (Bering Sea/Aleutian Islands, Gulf of Alaska, and Arctic). The goal of this annual report is to provide an ecosystem context for fishery management decisions. This report stems from the groundfish FMPs (Arctic, Bering Sea/Aleutian Islands, and Gulf) (North Pacific Fishery Management Council [NPFMC], 2015a) and contains ecosystem assessments, similar to *taking a system inventory* (step 1.1). The report also includes ecosystem status and trends and indicators (using the DPSIR conceptual model framework) for each region in Alaska, leading to indicators similar to what would be selected and calculated in step 1.2 (*selecting and calculating indicators*). Finally, the Ecosystem Considerations reports mention individual threats through-out, specifically anomalies in indicators, such as warm ocean conditions, or some new/emerging potential problems in the "Hot Topics" section, which relate to step 1.3 (*inventory threats*), but without a full comprehensive, explicit list.

Additionally, a Fishery Ecosystem Plan (FEP) for the Bering Sea is currently in development, which also is an example of step 1.1, *developing a system inventory*, and the FEP includes selected indicators and specific ecosystem threats (steps 1.2 and 1.3) as well. The Bering Sea FEP also calls for increased stakeholder involvement by outlining steps to consider and incorporate local and traditional knowledge (LTK) into the management process, not just through integrating it into Western science but through collaboration with local and indigenous peoples from the beginning (NPFMC 2018, pre-draft).

For component 2, *Where are we going*, there is activity for almost all steps for the Bering Sea. For Alaska fisheries, there is a broad ecosystem vision statement (step 2.1 *articulate a vision statement*) that states:

> "*Vision Statement – The Council envisions sustainable fisheries that provide benefits for harvesters, processors, recreational and subsistence users, and fishing communities, which (1) are maintained by healthy, productive, biodiverse, resilient marine ecosystems that support a range of services; (2) support robust populations of marine species at all trophic levels, including marine mammals and seabirds; and (3) are managed using a precautionary, transparent, and inclusive process that allows for analyses of tradeoffs, accounts for changing conditions, and mitigates threats*," (NPFMC 2014).

This statement was developed by the Ecosystem Committee for the North Pacific Fishery Management Council, brought on partly by input from stakeholders that the council did not previously have a vision statement or ecosystem objectives (pers. Comm. Bill Tweit). Additionally, for more specific strategies/goals (step 2.2 *develop strategic objectives*), the Groundfish FMP has multiple high level ecosystem related objectives that stem from the 45 objectives from the Alaska Groundfish Programmatic Supplemental Environmental Impact Statement (PSEIS), including: "*Preserve food web*" and "*Incorporate ecosystem-based considerations into fishery management decisions, as appropriate*." In line with the Lenfest process step of *assessing risk to objectives* (step 2.3), the PSEIS also (National Marine Fisheries Service [NMFS] 2004) includes assessments of risk for all objectives. However, there was no evidence of then *prioritizing those objectives* (step 2.4). Within the PSEIS and Groundfish FMP, there are more specific operational objectives, including "*Maintain or adjust current protection measures as appropriate to avoid jeopardy of extinction or adverse modification of critical habitat for ESA-listed Steller sea lions*", examples of activity pertaining to step 2.5 (*develop operational objectives*). There are also both strategic and operational objectives described in each iteration of the Bering Sea/Aleutians Island groundfish FMP (see NPFMC 2017) (many of which stem from the PSEIS objectives).

There is activity related to all steps in component 3, *How will we get there*, due to various reviews of, and continued use of, the 2 million mt cap on the groundfish fishery. An OY (optimum yield) of 2 million mt was originally selected from three primary alternative strategies for the groundfish fishery in January of 1984, as part of amendment 1 to the Bering Sea, Aleutian Islands (BSAI) groundfish FMP (49 FR 397) (NPFMC 2016). In this and multiple subsequent reviews of the cap, multiple strategies and variations on the cap were suggested and evaluated (steps 3.2 and 3.3, *identify potential management strategies* and *evaluate strategies*). These subsequent reviews included the General Accounting Office (GAO) report (GAO 1991), the review of the F40% reference point (Goodman et al. 2002), and the 2004 PSEIS (NMFS 2004).

As a more in depth example, the PSEIS includes multiple performance measures for various ecosystem metrics (and implied desired directions for those metrics) (step 3.1 *developing performance indicators and reference points*). Based on these measures, four alternative harvest management policies for groundfish were considered, similar to the selection of multiple strategies as outlined by step 3.2 (*identify potential management strategies*) and the strategies were evaluated based on the performance metrics (step 3.3 *evaluate consequences of alternative management actions*). The Council selected the strategy, and continued use, of a system-wide cap of 2 million metric tons on groundfish catch (NPFMC 2015b) (step 3.4 *select a strategy*, and component 4, *Implementation*). Acceptable Biological Catch (ABCs) are set for each stock separately, and then Annual Catch Limits (ACLs) are set so that they all total ACLs don't sum to above 2 million (only partially based on the ecosystem state). This cap was put into place in order to limit fleet capacity and avoid ecosystem overfishing (NPFMC 2015b). The OY (optimum yield) of 2 million mt value was chosen based on 85% of historical annual summed MSY estimates (1.4 to 2 million mt) (NPFMC 2015b). This cap has been triggered in multiple years, leading to reductions in catch limits, and exploitation rates are thereby commonly less than single-species maximum sustainable yield for most species.

Northeast Pacific and Interacting Protected Species

Pacific salmon fisheries on the US West Coast primarily target Chinook (*Oncorhynchus tshawytscha*), Coho (*Oncorhynchus kisutch*), and Pink Salmon (*Oncorhynchus gorbuscha*) and 17 populations are ESA listed. Potential EBFM related conflicts between fisheries and marine mammals center on Chinook salmon, southern resident killer whales (*Orcinus orca*), and pinnipeds (primarily harbor seals [*Phoca vitulina*] and California sea lions [*Zalophus californianus*]). Southern resident killer whales are listed as endangered under the U.S. Endangered Species Act, and pinnipeds are protected by the Marine Mammal Protection Act. Since its inception in 1972, many protected pinnipeds on the West Coast have been increasing rapidly. The effects of pinniped and killer whale predation on Pacific salmon are not currently addressed by management. Salmon and killer whales are iconic in the Pacific Northwest and both have high non-monetary value.

Activity related to all steps in component 1 (*Where are we now*) of the process can be found in documents highlighting either council or NOAA efforts for this region and mammal-salmon interactions. The Pacific Council's Fishery Ecosystem Plan serves as an *inventory for the system* (step 1.1) and provides general information on direct and indirect interactions between fisheries and marine mammals on the West Coast. The FEP also mentions the importance of salmon in the diets of endangered killer whales (PFMC 2013a). NOAA's Integrated Ecosystem Assessment (IEA) for the California Current includes salmon and marine mammals as key ecosystem components, with multiple indicators for each, thus showing activity related to step 1.2, *developing and calculating indicators*. The IEA also includes a conceptual model for the system. Finally, certain threats are mentioned throughout the IEA report (similar to threats that would be listed in step 1.3, *inventory threats*) related to specific indicators, such as threats of ship strikes and fisheries gear entanglements for cetaceans (Levin et al. 2013). The risk analyses portions of the IEA reports also mention threats, but there is never an explicit list of threats in the report.

There is less activity related to component 2, *Where are we going*. The Pacific Council's Salmon Fishery Management Plan does not have specific objectives for managing salmon fisheries relating to their importance as prey to marine mammals. However, protected species in marine waters are managed by NOAA Fisheries, and there are broad level objectives/goals (*strategic objectives*, step 2.2) stemming from the killer whale recovery plan (mandated by the Endangered Species Act). These objectives include: "Ensure adequate habitat to support a recovered population of Southern Resident killer whales. Habitat needs include sufficient quantity, quality, and **accessibility of prey species**," (NMFS 2008). Related to step 2.3 (*assess risk to objectives*), there is a recent Environmental Impact Statement (EIS) for salmon populations that qualitatively considers the impacts of fishing on killer whales and pinnipeds (NMFS 2017, and likely previous EIS's as well).

Activities related to component 3, *How do we get there*, stem from work by NOAA Fisheries and the Department of Fisheries and Oceans (DFO) Canada, which convened an independent scientific review panel to evaluate the effects of salmon fisheries on southern resident killer whales (Hilborn et al. 2012). The panel reviewed science that suggested that southern resident killer whale survival and fecundity rates were correlated with indices of Chinook abundance (Hilborn et al. 2012, Ward et al. 2009). From this, a possibly strategy of closing all ocean fishing on Chinook was simulated, (3.2 and 3.3 *selecting potential management strategies* and *evaluating these strategies*). A salmon population model was used to assess the strategy of closing all ocean fishing, and concluded that even complete cessation of fishing would increase Chinook abundance by a maximum of 25 percent. The panel concluded that the effects of this small change in Chinook abundance would be difficult to predict, and would likely not translate to increased prey (or survival or fecundity) for killer whales. Instead, Chinook abundance is more strongly influenced by freshwater habitat and ocean conditions than by fishing mortality. Therefore, the no fishing strategy was not pursued (step 3.4 *select a strategy*).

Northeast Pacific Sardine and Environmentally-Linked Harvest Control Rules

The Pacific sardine (*Sardinops sagax*) fishery was the largest in terms of catch for any of the species included in the PFMC CPS (Coastal Pelagic Species) FMP in the California Current system, till the closure of the fishery in 2015. Potential EBFM topics related to sardine stem from the importance of sardine as prey for predators and the relationship between sardine abundance and oceanic conditions. Sardine are prey for predatory fish in the west coast groundfish, salmon, halibut, and migratory species (including albacore) fisheries, leading to potential trade-offs between fisheries. Sardine are also prey for other marine species, including protected marine mammals and seabirds. Additionally, sardine recruitment is related to ocean conditions, with specifically higher recruitment in warm ocean conditions (related to the Pacific decadal oscillation) (Jacobson and MacCall 1995).

Again, activity related to all steps in component 1, *Where are we now*, can be found in documents from council or NOAA efforts. The Pacific Coast Fishery Ecosystem Plan summarizes information on the entire California Current ecosystem and includes information on Pacific sardine (PFMC 2013a), thus acting as a *system inventory* (step 1.1). Additionally, the Integrated Ecosystem Assessment (IEA) for the California Current includes status and trends of indicators related to environment (temperature) and coastal pelagic species (similar to indicators that would be produced by step 1.2 *selecting and calculating indicators*) and includes a conceptual model for the system (Levin et al. 2013). As mentioned in the previous case study, threats to the system are listed throughout portions of the IEA report (step 1.3 *inventory threats*) but not as an explicit list.

Related to component 2, *Where are we going*, there is activity for only step 2.2, *developing strategic objectives*. Within the FEP, there is a summary of ecosystem goals across FMPs and one broad goal or objective for Coastal Pelagic species (including sardine) is to "Provide adequate forage for dependent predators" (PFMC 2013a).

All of component 3, *How will we get there*, is exemplified by work surrounding the Pacific sardine harvest control rule. Because sardine recruitment is related to oceanic conditions, the harvest control rule for Pacific sardine includes a temperature predictor to set catch based on the relationship between sardine recruitment and sea surface temperature. In the early 2010's, stock assessment scientists in the SSC determined that the previously used temperature predictor (temperature off Scripps pier) was deficient (McClatchie et al. 2010, Lindegren et al. 2012).

Work by McClatchie et al. 2010 showed an alternative relationship between California Cooperative Oceanic Fisheries Investigations (CalCOFI) sea surface temperature and sardine productivity. Therefore, the Pacific Fishery Management Council convened a workshop to determine new potential management strategies (PFMC 2013b). This workshop included members of the SSC, the PFMC CPS Advisory subpanel and management team, and other scientists. Similar to step 3.2 (*identify potential management strategies*), the members identified multiple strategies for a sardine harvest control rule including using the previous temperature indicator (from off the Scripps pier), the new temperature indicator (CalCOFI temperature), and various levels of a "cutoff" value to protect the stock at low levels (close fishery if stock drops below this level). Then, Hurtado-Ferro and Punt (2014) performed a management strategy evaluation using the strategies identified in the 2013 workshop (step 3.3 *evaluate consequences of alternative management actions*). They used an age-structured population model of Pacific Sardine as the operating model and evaluated strategies based on performance criteria (indicators), such as variance of catch, mean catch, spawning stock biomass, and more. These performance criteria or indicators are similar to what would be produced in step 3.1 (*defining indicators and performance measures*) (see Hurtado-Ferro and Punt 2014 for all criteria and strategies). After the MSE was reviewed, the council chose the control rule that included the use of CalCOFI temperature (see PFMC 2014a, b) and a 150,000 mt cut-off (exemplifying step 3.4 *select management strategy,* and component 4, *Implementation*).

Moving forward, there is no formal re-evaluation of the temperature-recruitment relationship from year to year, but there is monitoring of these indicators within the stock assessments and this can show when/if there is any deviation from the pattern. This acts as continued monitoring of the strategy, similar to component 5 of the process. However, component 5 particularly focuses on monitoring strategies in terms of meeting the objectives identified in component 2, and there were no explicit operational objectives that could be identified for this case study.

Gulf of Mexico and Environmentally-linked Mortality of Gag Grouper

This case study focuses on the EBFM topics surrounding Gag grouper in the Gulf of Mexico and increased mortality of Gag during red tide events. Gag grouper is a 2nd-level priority species (designated as overfished or undergoing overfishing or in need of an assessment) in the Gulf of Mexico and one of the more important reef fish species exploited in the eastern Gulf (second only to red grouper). Harmful algal blooms or red tide events in the West Florida Shelf likely cause increased mortality for gag grouper. Particularly, a severe event in 2005 coincided with a sharp decline in gag grouper abundance indices. However, the mechanism behind how red tide causes mortality in gag is not known (direct toxicity or indirect impact) (Southeast Data, Assessment, and Review [SEDAR] 2014).

Activity related to all steps in component 1, *Where are we now*, can be found in the Ecosystem Status Report for the Gulf of Mexico (Karnauskas et al. 2013, 2017). The status report summarizes components of the fishery system (step 1.1 *develop a system inventory*). This report also has activity related to step 1.2, *select and calculate indicators*, by including status and trends for individual species, fisheries and environmental components and indicators such as data on trends of red tide events. The status report was part of the Integrated Ecosystem Assessment work for the Gulf of Mexico and a Driver-Pressure-State-Ecosystem Service-Response (DPSER) conceptual model was used to select indicators that "reflect the status of key drivers, pressures, states, ecosystem services, and responses in the ecosystem," (Kelble et al. 2013). Finally, the status report also lists a number of stressors including oil spills, hurricanes, and more, similar to step 1.3 (*inventory threats*), though not as an exhaustive explicit list as the step specifies.

Because of the mortality caused by red tide in 2005, an additional source of mortality was added to the Gag grouper stock assessment in the Gulf of Mexico (SEDAR 2014), thus exemplifying step 3.4, *select a management strategy*, with an ecosystem consideration. Red tide was modeled as a fishing fleet “discard” removal of Gag (vs. a “directed fishing mortality”), doubling mortality predicted in the previous assessment. Therefore, this strategy modified the estimated stock status relative to the reference point using ecosystem information, modifying the management strategy (step 3.4 *select a strategy*) based on ecosystem information, and was then put into practice for gag grouper (component 4, *Implementation*). There is also ongoing work by the Integrated Ecosystem Assessment working group on red tide severity indices that could be used as covariates in the stock assessment model (SEDAR 2014), but are not currently used. Finally, there is continued monitoring of red tide events, but not in connection to Gag mortality, which would be needed to exemplify component 5 of the process, *Comparing monitoring data with predictions*.

Mid-Atlantic Butterfish and Habitat-based Availability

One approach to establishing EBFM in the Mid-Atlantic centers on butterfish (*Peprilus triacanthus*), primarily a bycatch species, and how butterfish bycatch caps have historically constrained the longfin inshore squid (*Doryteuthis pealeii)* fishery (prior to the 2014 butterfish assessment). There is a high degree of habitat overlap between butterfish and squid and technical measures, e.g., minimum mesh size, have only been partly successful in reducing bycatch. The butterfish stock was determined to be overfished in the 2003 stock assessment, but the trends in the 2003 assessment conflicted with trends observed in the follow-up assessment in 2009. One problem with the stock assessment of butterfish is that the degree of overlap between the stock and the trawl survey frame (i.e., the region from which random trawl locations are drawn) is variable depending on environmental conditions. The 2009 stock assessment resulted in a determination that fishing mortality rates had been extremely low in recent years and could not account for the apparent decline in butterfish biomass. Nevertheless, the biological reference points estimated from the 2009 assessment were rejected by the assessment review panel (Northeast Fisheries Science Center [NEFSC] 2010). As a result, the industry was faced with a situation in which it was widely acknowledged that fishing mortality rates on butterfish were extremely low, yet the rebuilding plan continued to call for tight caps on butterfish bycatch in the squid fishery. This example of a technical interaction is common in conventional management but is highlighted here because it led to incorporation of environmental habitat models and data in the stock assessment and management of butterfish.

Activity for Component 1, *Where are we now*, can be found in the Mid-Atlantic Fisheries Management Council's (MAFMC) Ecosystem Approach to Fishery Management (EAFM) Guidance Document (MAFMC 2016). This document includes specific information on butterfish and climate and has summaries of system components, creating an inventory similar to step 1.1 (*system inventory*). The guidance document includes trends in indicators such as temperature and landings, which is the same as step 1.2, *selecting and calculating indicators*. It also contains multiple conceptual models linking climate, habitat, species, and more in the Mid-Atlantic (http://www.mafmc.org/s/EAFM_Guidance-Doc_2017-02-07.pdf, MAFMC 2016). Additionally, a list of threats to the system (step 1.3, *inventory threats)* can be found within the Northeast region U.S. Ecosystem status report (https://www.nefsc.noaa.gov/ecosys/) under "stressors and impact", including water contaminants, climate change, and fishing gear impacts.

Activity related to a few steps in Component 2*, Where are we going*, can be found within the Mid-Atlantic Fishery Management Council [MAFMC] Strategic Plan (MAFMC 2013). Work to *articulate a strategic vision* (step 2.1) and *develop strategic objectives* (step 2.2) that broadly relate to the case study topic was completed in 2013 and presented in the MAFMC Strategic Plan. The final vision statement says: "*Healthy and productive marine ecosystems supporting thriving, sustainable marine fisheries that provide the greatest overall benefit to stakeholders,*" (MAFMC 2013). This vision, other goals, and a comprehensive strategic plan were developed through the Council's "Visioning and Strategic Planning Project". This project was initiated at a time when all MAFMC managed fisheries were rebuilt and no longer overfished, which promoted flexibility to cultivate the Council's management strategies (MAFMC 2012). This planning strategy included a "large-scale stakeholder outreach effort" (MAFMC 2012) with input from more than 1,500 stakeholders through surveys, port meetings (roundtable sessions), and position letters (MAFMC 2012). Stakeholders included commercial and recreational fisheries, environmental organizations, seafood users, scientists and researchers, and the public at large.

Finally, the inclusion of environmental data in the most recent butterfish stock assessment (Adams et al. 2015) led to selection of a single-species harvest control rule with an ecosystem consideration (step 3.4, *selecting a management strategy*). Due to the potential mismatch in spatial occurrence of the butterfish stock and trawl surveys to estimate abundance, attributable to environmental conditions (leading to low stock estimates), there was a specific "Term of Reference" for the stock assessment in 2014 that required the assessment scientists to consider oceanographic factors and include them in the assessment model if possible. Through an academic-industry-NOAA collaborative process, key environmental drivers of butterfish spatial distribution were identified and used to estimate the annual overlap between the stock and the trawl survey. Specifically, bottom temperature was used to define the availability of butterfish to the NEFSC trawl survey by measuring overlap between their thermal habitat and the trawl survey frame. This thermal niche model estimated annual availability of butterfish to the trawl survey but, in the end, a constant availability (from the model) was incorporated into the assessment because there was relatively little interannual variability in availability (range: 62-75% of butterfish habitat overlap with the survey frame). The 2014 assessment concluded that the stock is not overfished and that overfishing is not occurring, and led to the implementation of the current harvest control rule (Component 4, *Implementation*).

Mid-Atlantic/Chesapeake Bay: Supporting Needs of Menhaden Predators

Atlantic menhaden (*Brevoortia tyrannus*) constitutes the biggest fishery in the Mid-Atlantic and has been referred to as "the most important fish in the sea," highlighting its role in supporting predators in the coastal ecosystem. A filter-feeder, menhaden also is believed to contribute to combatting eutrophication (Gottlieb 1998, Dalyander and Crecco 2010). As an important fishery and key forage species, management of Atlantic menhaden is at the core of developing EBFM in the Chesapeake Bay and coastal Mid-Atlantic region.

Activity more than a decade ago related to Component 1, *Where are we now?*, is documented in a Chesapeake bay FEP. The FEP includes information on Atlantic menhaden and conceptual models of major elements of the ecosystem (Chesapeake Bay Fisheries Ecosystem Advisory Panel 2006). As such, it serves as an *inventory for the system* (step 1.1). This FEP and publications that followed (Houde 2011; Maryland Sea Grant 2011) also recognize many threats to the system, including accelerated eutrophication and related hypoxia, invasive species, and fishing pressure. The FEP includes sections on major ecosystem issues and concerns in Chesapeake Bay, addressing step 1.3 (*inventory threats*). Additionally, the Ecosystem Status Report for the Northeast Shelf Large Marine Ecosystem (Ecosystem Assessment Program 2012) provides a relevant system inventory on a broader regional scale that includes indicators (informing step 1.2, *selecting and calculating indicators*) and documentation of additional threats to the ecosystem.

In the past decade, there has been interest and activity directed toward developing an explicit menhaden management plan with ecosystem reference points that accounts for menhaden's important role in the mid-Atlantic coastal ecosystem. In this regard, there is activity related to initial steps in Component 2, *Where are we going?*. Step 2.1 is to *develop a strategic vision* for the system and the strategic vision for the menhaden fishery. The vision emphasizes maintaining a valuable and sustainable menhaden fishery while avoiding damage to the ecosystem and its menhaden-dependent predators. Broad objectives for the fishery were expressed in the most recent stock assessment (SEDAR 2015). It addressed strategic objectives for step 2.2 (*develop strategic objectives*). The updated goal, provided in Amendment 3 to the FMP (ASMFC 2017), is to,

> "*…manage the Atlantic menhaden fishery in a manner which equitably allocates the resource's ecological and economic benefits between all user groups. The primary user groups include those who extract and utilize menhaden for human use, those who extract and utilize predators which rely on menhaden as a source of prey, and those whose livelihood depends on the health of the marine ecosystem. Pursuit of this goal will require a holistic management approach which allocates the resource in a method that is biologically, economically, and socially sound in order to protect the resource and those who benefit from it.*"

For Component 3, *How will we get there?,* there is ongoing activity for two steps, *identify potential management strategies* (step 3.2) and *select a management strategy* (step 3.4). Recent management of Atlantic menhaden has relied on modeling its age-specific predation mortality based on a Multispecies Virtual Population Analysis (SEDAR 2015). This single-species harvest control rule/strategy, with an ecosystem consideration, is a component of the management strategy for the coast-wide menhaden fishery. For Chesapeake Bay, the management strategy is to cap menhaden landings (SEDAR 2015), a measure aimed at reducing the likelihood of localized depletion of menhaden (ASMFC 2005), and exemplifies the Task Force's step 3.4 (*selecting a management strategy*). The initial menhaden cap for Chesapeake Bay was 87,120 mt, which was lowered to 51,000 mt in ASMFC's most recent action (ASMFC 2017), a strategy intended to benefit menhaden's predators and the recreational fishery that targets important predators, e.g., striped bass.

The ASMFC Atlantic Menhaden Technical Team and its Biological-Ecological Reference Points (BERP) working group identified performance indicators for menhaden, including environmental indicators, indices of forage abundance, and prey: predator ratios (Appendix E in SEDAR 2015). The BERP's work led the ASMFC to develop ecosystem objectives (ASMFC memorandum 2015). Fundamental objectives such as "sustain menhaden to provide for predators" were identified (exemplifying step 2.2, *developing strategic objectives*). The BERP also adopted explicit objectives provided by the ASMFC's Menhaden Board and an inclusive set of performance indicators. The BERP is developing ecosystem reference points

(ERPs) for menhaden, activity specified in the Task Force's step 3.1 (*developing performance indicators and reference points*). The BERP is charged to formally recommend an ERP by 2019 (ASMFC 2017).

The Atlantic menhaden case study, while centered on a single species, exemplifies how concerns about its management address FEP goals in the Chesapeake Bay and the broader coastal zone. In this regard, a recently developed, coast-wide ecosystem model demonstrates how management decisions related to selection of ERPs for menhaden could resonate throughout the predator community in the mid-Atlantic region (Buchheister et al. 2017). Ongoing work by ASMFC and its BERP working group illustrate how the process now underway includes many activities embodied in the components and steps of the FEP process recommended by the Task Force.

New England and Habitat Area Closures for Improved Groundfish Protection

The multispecies groundfish fishery is one of the most ecologically and economically important finfish fishery in the Gulf of Maine. This fishery incudes as targets iconic species like cod (*Gadus morhua*) and haddock (*Melanogrammus aeglefinus*). The Gulf of Maine cod stock has been assessed as both overfished and that overfishing is still occurring, though fishermen continue to find large amounts of cod. Therefore, there is tension between management and fishermen, and fishermen want greater access to catch and certainty in catch levels in the future (3-5 years out). Emergency actions shutting down the groundfish fishery and the annual assessments are causing the industry both severe economic hardship and inducing high levels of stress. There is specific ongoing EBFM activity surrounding the groundfish fishery (including cod) and habitat.

There is activity related to all steps in component 1, *Where are we now*. The Ecosystem Status Report of the Northeast Shelf Large Marine Ecosystem (Ecosystem Assessment Program 2012) was completed in 2012 and contains descriptions of components of the fishery system, thus serving as a *system inventory*, as is specified in step 1.1. Additionally, the status report contains time-series data on components and indicators (integrative ecosystem measures), similar to step 1.2 (*selecting and calculating indicators*). Finally, the updated Northeast status report (see Mid-Atlantic case study) includes a section on stressors, again acting as an example of an *inventory of threats* to the system (step 1.3), though not as an explicit list.

Strategic objectives (step 2.2), as well as more specific *operational objectives* (step 2.5), from component 2, *Where are we going*, exist for this case study. Step 2.2 is to *develop strategic objectives* and the New England Fishery Management Council (NEFMC) adopted a specific strategic objective from the Essential Fish Habitat (EFH) mandate – "describe and identify essential fish habitat for the fishery based on the guidelines established by the Secretary under section 305(b)(1)(A), minimize to the extent practicable adverse effects on such habitat caused by fishing, and identify other actions to encourage the conservation and enhancement of such habitat," (NEFMC 2016; Grabowski et al. 2014). Based on this objective, more specific objectives (step 2.5 *develop operational objectives*) were identified related to EFH and on-going work on groundfish habitat in the NEFMC's Omnibus Habitat Amendment 2. Specifically:

> *"The first groundfish-specific purpose of this amendment is to improve protection for juvenile groundfish and their habitats (Purpose D). Success at younger ages can have positive productivity benefits for managed resources, and therefore action is needed to protect the habitats important for juvenile groundfish, particularly for commercially*

valuable species. A second groundfish-specific purpose of this amendment is to identify seasonal closed areas in the Northeast Multispecies FMP that would reduce impacts on spawning groundfish and on the spawning activity of key groundfish species, because the protection of spawning fish is needed to sustainably manage stocks (Purpose E)" (NEFMC 2016).

Additionally, activity related to all the steps in component 3, *How will we get there*, can be found in the recent Omnibus habitat amendment 2 for New England, centered around groundfish habitat. A management strategy evaluation process was used to evaluate various fisheries closures that may impact groundfish habitat based on the objectives above. Specifically, a Swept area seabed impacts model (SASI) was developed to evaluate different gear-types in terms of adverse effects on fish habitat (Omnibus Habitat Amendment 2 Appendix D; Grabowski et al. 2014). The SASI model highlighted areas vulnerable to fishing gear and this information was paired with analyses on juvenile habitat and adult spawning habitat of cod and other groundfish. Based on this information, a Closed Area Technical Team identified *potential management strategies* (step 3.2) in the form of possible alternative closed areas (see Habitat Omnibus Amendment II Volume 3). The alternative spatial management strategies were then evaluated (step 3.3 *evaluate consequences of alternative management strategies*) based on performance indicators such as overlap with EFH, unique habitat features, and species diversity indices. These indicators are examples of the type of performance indicator that would be chosen in step 3.1 (*develop performance indicators and reference points*). The alternative spatial management strategies were then voted on by the council (Grabowski per. Comm.). As of September 2016, the amendment documents were submitted to NMFS GARFO for review, thus a management strategy has been chosen (step 3.4 *select management strategy*) by the council. In January of 2018, most of the amendment was approved by NMFS and was published in the federal register in April 2018 (83 FR 15240).

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VITA

Laura Elizabeth Koehn was born in Bellingham, WA where she frequented the many lakes, forests, and beaches around Northwest Washington. She first dove into Biology in freshman year at Sehome High School in Bellingham. She graduated with a Bachelors in Science from the University of Washington in 2011, double majoring in Biology: Ecology, Evolution, and Conservation and Applied and Computational Mathematical Sciences. Her undergraduate research was with Dr. P. Dee Boersma studying Magellanic penguins; and in Fall 2012, she spent a field season at Punta Tombo, Argentina studying this species. She continued her studies at the University of Washington in Winter 2013 in pursuit of her PhD. In 2018 she was a John A. Knauss Sea Grant Fellow. Her doctoral work focuses on the ecological interactions of forage fish and implications to management.