Title

Social and Ecological Connectivity in Kelp Forest Ecosystems

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Publication Date

2018

UNIVERSITY OF CALIFORNIA
SANTA CRUZ

SOCIAL AND ECOLOGICAL CONNECTIVITY IN KELP FOREST ECOSYSTEMS

A dissertation submitted in partial satisfaction
of the requirements for the degree of

DOCTOR OF PHILOSOPHY

in

ECOLOGY AND EVOLUTIONARY BIOLOGY

by

Rachel Zuercher

December 2018

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Abstract

Social and ecological connectivity in kelp forest ecosystems

by

Rachel Zuercher

Connectivity between and among ecosystems is a key feature of the marine environment, taking many forms, and affecting populations, food webs, and a wide range of ecosystem processes. In the kelp forest ecosystem, connectivity with adjacent habitats and with interacting human systems shapes communities and influences ecosystem functioning. However, the identity and strength of these important connections, and their key features and consequences are not well understood. One approach for incorporating various forms of connectivity into marine ecology is through the social-ecological systems framework. By characterizing a system as having both ecological and social components, both of which are affected by external forces and entities such as adjacent ecosystems, the presence and consequences of these connections become more clear. The purpose of this dissertation was to expand our knowledge of kelp forests by characterizing and quantifying two distinct forms of kelp forest connectivity. In Chapter 1, I explore kelp forest food webs through the lens of ecosystem connectivity with adjacent coastal pelagic habitats. I synthesize existing knowledge about relevant kelp forest consumers, data on the dynamics of open ocean organisms, and information on

community responses to trophic subsidies to better understand kelp forest food webs. I then further assess the role of trophic subsidies from open ocean habitats by looking specifically at five species of kelp forest fishes in central California (Chapter 2). I use stable isotopes and traditional diet content analyses to evaluate the importance of pelagic-based energy for nearshore rockfishes, and to provide a better understanding of how the kelp forest fish assemblage accesses and uses energy sources from the open ocean. In Chapter 3, I turn to the connectivity between kelp forest ecosystems and associated social systems. The nearshore fishery is the primary commercial fishery operating in central California's kelp forests. I use a social-ecological systems framework to characterize the nearshore fishery and create a social baseline from which to better understand the connections among fishermen, fishing operations, markets, and kelp forests where the target species reside. I use fishery-dependent landings data, archival sources, information gained from interviews, and long-term ecological monitoring data to inform the research. In Chapter 4, I dig more deeply into one component of social-ecological connectivity in the nearshore fishery, combining ecological and social data sources to shed light on factors influencing the species composition of fisheries landings, a key component of the nearshore fishery and kelp forest dynamics.

The study of ecosystem connectivity and social-ecological relationships is an interdisciplinary endeavor. In this dissertation, I use a mixed methods approach to add to our understanding of kelp forest trophic connectivity and the connections between

humans and kelp forests. I draw on theory and literature from both the ecological and the social sciences, integrating ideas related to ecosystem connectivity and the human dimensions of natural resources management. I show that new and useful insights can be gained through interdisciplinary approaches that incorporate connectivity among marine habitats and with people into our concept of marine ecosystems.

This body of work is dedicated to:

The science mentors whose teaching and inspiration early in my life led me here – Lois Zuercher, Kathy Johnson, Terry Lewis, Laurie Eberhardt, Apolosi Silica, and many others.

- and -

The great plains of South Dakota where my love for ecology was born.

Acknowledgements

Advisors and Mentors

I would like to thank my committee for their encouragement and insight. A lot of time and effort goes into mentoring a graduate student, and first, I am incredibly grateful for all that Mark Carr has done for me. I thank Mark for his open-door policy, and for always taking time to provide guidance and direction to my science. I also thank him for often withholding comment and guidance, allowing me pursue the topics and questions of interest to me, to fail, and to become a more independent scientist. Mark, your enthusiasm for science and exploring the world around you have kept me going through this long process. Thank you to Pete, whose comments not only improved this dissertation, but have taught me to think more deeply about my science, and the world around us. Pete, thanks for always being ready and willing to talk. Thanks to Paul Koch for insightful questions and comments during committee meetings. Though Paul's expertise aligns with just one of my dissertation chapters, his breadth of knowledge and scientific excellence not only greatly improved all chapters my dissertation, but never ceased to amaze. And thanks to Carrie Pomeroy for taking me on. There's a lot of scholarship on the difficulties of collaborations between natural and social scientists – disciplines that emphasize two different ways of knowing and doing. Carrie guided me through, making it enjoyable and so intellectually satisfying. Sitting in meetings with both Carrie and Mark, and hearing their different thoughts, comments and questions when looking at the same graph or dataset was such a wonderful learning experience. It was this that truly taught me what it means to be an interdisciplinary scholar. Carrie, thank you for constantly pushing me to consider all angles, to re-think my assumptions, and to recognize my biases. I will miss our conversations about work and about life.

I have gotten a great deal of support from individuals at the NOAA NMFS lab and at the California Department of Fish and Wildlife. Don Pearson taught me to read otoliths, Keith Sakuma provided samples and facilitated my participation in NMFS cruises, where I learned so much about the open ocean ecosystem. John Field served as a mentor and sounding board throughout this process. At CDFW, Deb Wilson-Vandenberg and Traci Larinto generously gave their assistance and support.

RC Lab Members

Thanks to RC Lab members, past and present. To all of you, thanks for the great conversations about science, fish and life. Having a large, diverse lab has been instrumental in my education and scientific growth. To Emily Saarman, for keeping me sane on the tough days. To Dan Malone for patiently answering all my questions. To Dan Brumbaugh for his advice, guidance and insights. To Megan Sabal and Monica Moritsch for doing this by my side. To Roy Qi for always challenging me and for teaching me how to fish. And to Sarah Tepler Drobnitch for the guidance, but mostly for the distractions.

Interns

Thanks to the many interns and volunteers who gave their time and abilities to assist me with this work. As it was, I probably learned just as much from all of you as you learned from me.

Research Participants

A sincere thank you to the fishermen and fish buyers who generously took time to share their knowledge and experiences with me for chapters 3 and 4. Several fishermen in particular went out of their way on multiple occasions to ensure that I had the understanding and information needed for this research. This work would not have been possible without them. Also, I think often of the fish that were killed as part of chapter 2. I hope that the sacrifice was worth the science that it produced.

Research Support and the EEB Department

Staff of the EEB Department of UCSC's Long Marine Lab have been pivotal to my success. Thanks to Steve Clabuesch and Dave Benet for making us all better divers and boaters. Thanks to Betsy Steele and Randolph Skrovan for all they do. Thanks to HeatWave – without my custom suit with 20-mm of neoprene on the core, an always-cold person like myself would not and could not dive in central California.

For Chapter 1, thanks to my co-author Aaron Galloway for his thoughtful feedback throughout the process of writing the manuscript. For Chapter 2, thanks to Peter

Slattery for assistance in the identification of amphipods from Black Surfperch diets, and to Baldo Marinovic for help with invertebrate identification. Sincere thanks to Colin Carney of the UC Santa Cruz Stable Isotopes Lab, and to PISCO for providing data on juvenile rockfish recruitment.

Thanks to the EEB Department. It has been a wonderful academic home for the past six years. I have especially appreciated that EEB celebrates good teaching and encourages grad students to focus on classroom improvement, and that the department encourages and facilitates actionable science.

And thanks to those who provided images and graphics for this dissertation – the talented Dr. Larry Allen of CSU Long Beach, Emily Saarman, Steve Lonhart, and the Integration and Application Network (ian.umces.edu/imagelibrary/), University of Maryland Center for Environmental Science.

Funding Sources

I have been very fortunate to receive funding for this research from many sources. My stipend and tuition were provided by an NSF GRFP Fellowship (Grant Number DGE-1339067), an NSF GK-12 Fellowship (SCWIBLES, Grant Number NSF DGE-1339067), by the UCSC Earl C. Anthony endowment, and by a Wells Fargo Coastal Sustainability Fellowship. All of this generous funding allowed me the latitude to collaborate on projects outside of my dissertation research, to follow my academic interests, and to engage in service and teaching activities. It also afforded me the mental well-being that comes along with stable funding. Research funds were provided by the UCSC Ecology and Evolutionary Biology Department, Friends of Long Marine Lab, the Earl and Ethel Myers Oceanographic Trust, the Mathias Student Research Grants Program, the NSF Graduate Research Internship Program, and by UCSC Services for Transfer and Re-entry Students. I sincerely thank all of these groups, and hope that I have put the funds to good use.

Friends and Family

I have been part of an incredible community while here in Santa Cruz. You all have kept me grounded, provided intellectual and emotional support, and made the past six years so much fun. Thanks for the hikes, the camping trips, the time spent on the water, the dinners and the game nights. Thanks to the Santa Cruz marine science brewers, and to Mark Carr for the annual donation of his hop crop.

Thanks to my parents who allowed me to spend long days outside as a child. It was, in part, the desire to do that for the rest of my life that led me to this field. Thanks to Basa for the constant companionship, and for getting me up and out. And all of the thanks to Aric for believing in me. Your unending support means so, so much.

And finally, I’ll acknowledge the incredible beauty of central California that I’ve been surrounded by while completing this dissertation. Without the ocean and mountains calling, I would have finished years ago.

Introduction

Connectivity is a key feature of coastal marine ecosystems, playing a role in population dynamics, trophic interactions, and the structure and function of the ocean environment (Carr et al. 2017, Hidalgo et al. 2017). Ecosystem connectivity can take many forms: genetic connectivity, the movement of larvae and juveniles, physical connections in food webs of adjacent marine habitats, and the relationships and feedbacks between marine and human systems (Polis et al. 1997, Carpenter et al. 1999, Palumbi 2003, Cowen and Sponaugle 2009, Christie et al. 2010, Berkes 2011, López-Duarte et al. 2012). Temperate kelp forests of coastal California provide a useful example of an open marine ecosystem strongly influenced by connectivity. Ocean currents and biophysical forces physically connect kelp forests to adjacent and distant ecosystems, both in the ocean and on land (Britton-Simmons et al. 2009, Liebowitz et al. 2016). Fishing, recreation, and other human uses of kelp forests constitute strong relationships between coastal communities and nearby kelp forest ecosystems. One framework through which to incorporate this connectivity into marine ecology is by thinking of marine ecosystems as social-ecological systems (Ostrom 2009, Basurto et al. 2013, McGinnis and Ostrom 2014). The social-ecological system (SES) framework provides a way to integrate the relationships and feedbacks between kelp forests, surrounding ecosystems, and human social systems into our understanding. The SES concept reflects the fact that, although separated for the purposes of research and description, the human aspects and wide-ranging ecological aspects of a system are not separate, nor can any one be fully characterized without considering the other.

Decades of ecological research on the kelp forests of central California provides a strong foundation for my work (Miller and Geibel 1973, Pearse and Hines 1979, Carr and Reed 2016, Foster and Schiel 1985, Schiel and Foster 2015). Researchers have characterized many aspects of the biology, ecology, and biophysical dynamics of kelp forests. We know an incredible amount about the ways that kelp forest organisms survive and interact, the dynamics of kelp forest variation over space and time, and the drivers of kelp forest ecosystem function. However, there are many facets of kelp forest ecology that would benefit from explicit consideration of cross-ecosystem and social-ecological connectivity. In this dissertation, I explore connectivity, and aim to widen the lens through which we view kelp forest ecosystems: first, by looking at kelp forest food webs in the context of connectivity with adjacent coastal pelagic ecosystems, and second, by looking shoreside and explicitly including humans as members of kelp forest systems. Many researchers have considered the impact of outside stressors (Ebeling et al. 1985, Steneck et al. 2002, Reed et al. 2011), adjacent ecosystems (e.g., Foley and Koch 2010, Docmac et al. 2017), and humans (Jackson et al. 2001, Halpern et al. 2009, Foster and Schiel 2010, Carr and Reed 2015, Schiel and Foster 2015) on kelp forests. I seek to add to this literature by identifying and quantifying trophic connections between kelp forests and the open ocean, and by characterizing social-ecological connections and the factors that influence these connections in kelp forest fisheries.

In **Chapter 1**, I summarize the impact that connectivity with open ocean ecosystems has on nearshore kelp forest food webs and communities. The movement of trophic resources between and among ecosystems, referred to as cross-ecosystem subsidies, is a common phenomenon. In the marine environment, both adjacent and distant ecosystems are connected by oceanographic forces that transport nutrients, organisms, and other materials (Polis et al. 1997, Palumbi 2003, Marczak et al. 2007). Kelp forest ecosystems are one example of an open marine system that both exports and receives trophic subsidies (Bray et al. 1981, Bustamente et al. 1995, Vetter and Dayton 1998, Dugan et al. 2003, Rodríguez 2003, Foley and Koch 2010, Docmac et al. 2017, Galloway et al. 2017). Though rocky reefs are rich in internally-produced kelp-based energy, kelp forest organisms also rely on phytoplankton, and the influx of holoplankton and meroplankton from adjacent open ocean habitats. In this chapter, I seek to clarify the identity of holoplanktonic and meroplanktonic subsidies, quantify their energetic and nutrient contributions to the kelp forest, and further explore the impacts of these subsidies for individual consumers and for kelp forest communities. I review six individual subsidy organisms that are commonly advected to kelp forests on the West coast of North America, and show that these organisms from the pelagic ocean represent important resource pulses for kelp forest consumers. In addition, I summarize the characteristics of subsidies, consumers, and recipient ecosystems that provide insight into the dynamics of subsidy influx and impacts to recipient systems. Finally, I provide suggestions for quantifying the impacts of cross-ecosystem subsidies. Trophic subsidies are a major force shaping both marine and terrestrial communities and ecosystems. Quantitative information about these subsidies and their impacts on food webs will not only improve our understanding of these ecosystems, but also improve food web models and predictions of ecosystem response to change.

Building on Chapter 1, I focus my inquiry on the kelp forests of Carmel Bay. Whereas in Chapter 1 I highlight the theoretical importance of trophic subsidies from the open ocean, in **Chapter 2**, I quantify some of those impacts with a study of the feeding ecology of five species of kelp forest fishes. The study of food webs provides important information about species interactions, the roles of species within an ecosystem, and the movement of energy through the marine environment. Kelp forests, one of the most productive ecosystems in the world, are home to a nearshore fish assemblage that accesses not only energy derived from the primary production of kelp, but also energy from phytoplankton- or pelagic-based primary production (Duggins et al. 1989, Miller et al. 2011, Carr and Reed 2016). However, the relative importance of these two energy sources for kelp forest species, and how relative importance varies over time is not well known. I used a combination of stomach content analysis and carbon and nitrogen stable isotope analysis to explore the use of kelp- and phytoplankton-based carbon in central California from 2013-2016, a period that spans anomalous oceanic conditions associated with “the Blob” and El Niño (Williams et al. 2016, Joh and Di Lorenzo 2017). I show that the relative importance of phytoplankton-based carbon was higher in species that forage in the water column as opposed to on or near benthic substrates, and that $\delta^{13}C$ varies annually in those species. Further, diet contents and $\delta^{15}N$ values (i.e. trophic level) provide insight into the particular prey taxa contributing to the importance of these two energy sources, and their variability. This research advances our understanding of the importance of ecosystem connectivity in explaining the productivity of species and ecosystems, and suggests that more attention should be given to pelagic energy sources when studying nearshore food webs.

In **Chapter 3**, I shift from connectivity in the marine ecological system to the connections between marine ecosystems and the social (human) system. Fish and fisheries play significant economic, social, cultural and ecological roles in California’s coastal ecosystems and fishing communities (Pomeroy and Dalton 2003, Scholz et al. 2004, Thomson 2012). However, in the face of stressors ranging from climate change to shifts in global seafood markets, managing California’s fisheries to ensure both long-term ecosystem health and the well-being of fishing communities is challenging (Berkes et al. 2006, Sumaila et al. 2011, Pauly and Zeller 2016). The concept of fisheries as SESs has gained traction in fisheries management over the last two decades, encouraging the explicit consideration of interactions and feedbacks between ecological and social components of a fishery (Berkes 2011, Cinner 2012, Kittinger et al. 2013, Jarre et al. 2018). In Chapter 3, I characterize the nearshore fishery (the predominant commercial fishery in kelp forests of central California) as a SES, and develop a baseline description of some of its social features. Within the SES, human dimensions such as governance, economic systems, and human behavior interact with, influence, and are affected by biophysical dimensions such as marine habitats, target fish species and their ecological communities, and oceanographic dynamics. I use a mixed methods approach, guided by Ostrom's SES framework, combining literature review, archival and fishery-dependent data analysis, and semi-structured interviews to bring to light some of the important factors that influence current fishing operations and practices, and that have contributed to change in the fishery over time (Ostrom 2009). I show that flexibility, whether of fishermen to move among fisheries, to land a variety of species in the kelp forest fish assemblage, or to sell catch via different market arrangements, plays a major role in the human component of the kelp forest SES. My assessment identifies relationships between human components of the nearshore fishery and kelp forest ecosystems and factors that influence these relationships, and highlights aspects of the SES that enable adaptation in the fishery.

Finally, in **Chapter 4**, I use the insights gained in Chapter 3 to look further at some of the social-ecological interactions and relationships in nearshore kelp forest ecosystems. Despite advances in the study of SESs, challenges still exist when comparing and combining socio-cultural, economic and biophysical information sources. These data are often collected at vastly different scales and often using fundamentally different approaches. Moreover, while clear avenues exist for incorporating both ecological and economic data into the fisheries management process, standard approaches for the integration of social and cultural information are still in development (Hall-Arber et al. 2009). My research in Chapter 4 illustrates how information about fishermen and fishing operations can be combined with ecological and environmental data to explore fishery outcomes. The species composition of nearshore landings (also referred to as catch composition) is a fundamental component of the fishery SES. The composition of species removed from the kelp forest ecosystem is important when assessing the human role in the structure and dynamics of kelp forest fish assemblages and the ecosystem. Similarly, catch composition affects market opportunities and fishery supply chains, the practices of fishermen, and fishery revenue. I use multivariate analyses to explore the factors that influence nearshore fishery catch composition, showing that the permit mix that a fisherman holds, the gear they use, and the port where they land fish all strongly influence the species that fishermen land. However, the single most important predictor of a fisherman's catch composition is the identity of that fisherman. This result highlights the importance of understanding social dynamics in a fishery, and considering variation in human behavior, fishing operations, and practices when assessing a fishery system.

Through data synthesis, the collection of quantitative and qualitative information, and the use of both long-term ecological monitoring and fishery-dependent data sources, my dissertation sheds light on several forms of kelp forest connectivity, identifying and clarifying both cross-ecosystem and social-ecological linkages in kelp forest ecosystems.

Chapter 1: Coastal marine ecosystem connectivity: pelagic ocean to kelp forest subsidies

Abstract

The movement of trophic resources between and among ecosystems, referred to as cross-ecosystem subsidies, is a common phenomenon. In the marine environment, both adjacent and distant ecosystems are connected by oceanographic forces that transport nutrients, organisms and other materials. Kelp forest ecosystems are one example of an open marine system that both exports and receives trophic subsidies. Though rocky reefs are rich in kelp-based energy produced internally, kelp forest organisms also rely on phytoplankton, and the influx of holoplankton and meroplankton from adjacent open ocean habitats. In this paper, we seek to clarify the identity of holoplanktonic and meroplanktonic subsidies, quantify their energetic and nutrient contributions to the kelp forest, and further explore the impacts of these subsidies for individual consumers and for kelp forest communities. We reviewed six individual subsidy organisms that are commonly advected to kelp forests on the West coast of North America, and show that these organisms from the pelagic ocean represent important resource pulses for kelp forest consumers. In addition, we summarize the characteristics of subsidies, consumers, and recipient ecosystems that provide insight into the dynamics of subsidy influx and impacts to recipient systems.

Finally, we provide suggestions as scientists move forward with efforts to quantify the impacts of cross-ecosystem subsidies. Trophic subsidies are a major force shaping both marine and terrestrial communities and ecosystems. Quantitative information about these subsidies and their impacts on food webs will not only improve our understanding of these ecosystems, but also improve food web models, and predictions of ecosystem response to change.

Introduction

Cross-ecosystem subsidies and the movement of animals from one ecosystem to another play a fundamental role in the trophic structure of communities and the dynamics of food webs (Polis et al. 1997, Palumbi 2003, Marczak et al. 2007). While ecosystem connectivity is the rule in natural systems, not the exception, we are far from fully understanding the food web impacts of energy and nutrients that come from other ecosystems. Often termed trophic subsidies, these are donor-controlled resources (i.e. a resource with dynamics determined outside of the recipient system) that originate in one ecosystem but are moved to another (Polis et al. 1997). A subsidized system can be defined as a geographic area whose boundaries do not encompass the entire area of production that supports it (Trebilco et al. 2016). In terrestrial systems, subsidies occur predominately via rivers (Power et al. 2004, Richardson et al. 2010, Sabo and Power 2002), the movement of animals that transport and deposit nutrients derived in one ecosystem to another (e.g. birds and bats depositing guano: Anderson and Polis 1999) and animal migrations (migration-mediated subsidies: Bauer and Hoye 2014, subsidies related to fish migrations: Flecker et al. 2010). However, research on subsidies is heavily focused on prominent land-water interfaces. Salmon and other anadromous fishes link highly productive oceans with upstream watersheds (Garman and Macko 1998, Cederholm et al. 1999, Naiman et al. 2002, Moore et al. 2007). Seabirds deposit marine-derived nutrients on rocky islands and surrounding ecosystems in the form of guano, providing an influx of nitrogen and phosphorus to recipient ecosystems (Anderson and Polis 1999, Maron et al. 2006, Honig and Mahoney 2016). Carbon and nitrogen derived from riparian plants and mangroves fuel aquatic food webs below (Nakano and Murakami 2001, Wallace et al. 2015, Yeager et al. 2016). Marine macrophyte detritus creates habitat and energetic resources for detritivores, consumers and predators both in supralittoral beaches (Orr et al. 2005, Dugan and Hubbard 2016, Liebowitz et al. 2016) and in the subtidal benthos (Vetter 1994, Vetter and Dayton 1998, Britton-Simmons et al. 2012). Though there is a long history of studies describing these subsidies and their impacts in terrestrial and freshwater systems, the exploration of subsidies within and among marine ecosystems is relatively new (Gaines and Roughgarden 1985, Bustamente et al. 1995, Willson and Womble 2006, Krenz et al. 2011, Filbee-dexter and Scheibling 2016, Henschke et al. 2016, Griffiths et al. 2017, Morgan et al. 2018). This is despite the fact that in marine ecosystems, genetic material, larval and juvenile organisms, nutrients, and habitat structure move between and among ecosystems on scales that are uncommon in terrestrial counterparts. Indeed, marine systems are considered more “open” than terrestrial systems (Carr et al. 2003). The basic structure and features of the marine environment suggest that subsidies are likely much more prevalent and potentially more important than in terrestrial habitats, and that subsidies from the pelagic ocean have the potential to be widely consumed by the numerous planktivorous species present in nearshore environments (Carr et al. 2003).

Marine trophic subsidies are ubiquitous throughout the ocean environment (Willson and Womble 2006). Nutrients from rivers fuel productivity in nearshore food webs (Foley and Koch 2010, Richardson and Sato 2015); the rain of phytoplankton, zooplankton, fecal pellets and detritus (often referred to as marine snow) deliver energy to deep sea habitats (Iseki 1981, Stockton and DeLaca 1982, Alldredge and Silver 1988, Britton-Simmons et al. 2012, McClain et al. 2018); and forage fish such as menhaden undergo migrations from rearing estuaries to nearshore coastal areas, exporting large magnitudes of carbon, nitrogen and phosphorus to the marine system (Deegan 1993). These marine spatial subsidies can represent sustained and continuous nutrient and energy delivery (as in the case of marine snow to deep sea habitats), or pulses of prey lasting for short periods, with wide-ranging implications for consumer responses (Holt 2008). Yet all of these subsidies are donor-controlled, with resource availability, timing and magnitude determined by forces outside of the recipient ecosystem (Polis et al. 1997).

Especially well-studied examples of cross-ecosystems subsidies in the marine environment highlight the ecological relevance of subsidy flows between adjacent marine habitats, and from marine to terrestrial habitats. Polis and colleagues combined field surveys and stable isotopes analysis to extensively document individual, community and ecosystem-wide impacts of marine-based algal wrack and seabird guano on nutrient-poor island desert ecosystems (Polis and Hurd 1996, Anderson and Polis 1998, 1999, Spiller et al. 2010). This research traces terrestrial food web pathways of marine subsidies, finding positive community and population outcomes for terrestrial consumers. Recent experimental manipulations of beach wrack showed that subsidies increase detritivore biomass (amphipods) and predator populations (terrestrial lizards), though the mechanisms for these impacts are still being investigated (Spiller et al. 2010, Wright et al. 2013, Dugan and Hubbard 2016). Norwegian herring migration from oceanic feeding grounds to coastal overwintering and spawning areas represents a massive annual influx of energy used by benthic fish predators and crustaceans (Varpe et al. 2005). Further, investigation into effects of this subsidy on cod (herring predators in the recipient ecosystem) revealed positive impacts on population productivity from this large-scale movement of energy (Van Deurs et al. 2016). Experiments with algal detritus in subtidal habitats have shown that macrophyte detritus piles generate increased abundance of copepods and amphipods; the drift algae acts as both as a habitat to hide in and as a trophic resource (Vetter 1995, Duggins et al. 2016). Several decades of research have contributed to a rich understanding of the dynamics of kelp moving into adjacent deep sea habitats, and providing a strong foundation for studies seeking to understand the impacts of this allochthonous resource (Filbee-Dexter et al. 2018). Despite these well-described examples, our lack of knowledge of the dynamics of marine subsides, and how these dynamics link to individual and population-level responses continues to undermine a comprehensive understanding of food web dynamics.

The history of subsidies work in marine systems has, not surprisingly, focused on large inputs of energy to unproductive systems such as sandy beaches (Orr et al. 2005, Netto and Meneghel 2014, Liebowitz et al. 2016), desert island ecosystems (Polis and Hurd 1996, Spiller et al. 2010), and the deep sea, in the form of whale falls (Smith and Baco 2003) or detrital subsidies (Vanderklift and Wernberg 2008, Britton-Simmons et al. 2009, Filbee-Dexter et al. 2018). In these ecosystems with low endogenous productivity, the effect of subsidies on consumer-resource dynamics is often more evident, with recent studies finding the strongest consumer responses to subsidies in recipient habitats with low productivity (Sabo and Power 2002). Similarly, there are examples of subsidies that transport a particular limiting nutrient to systems that might otherwise support high rates of primary and secondary productivity. Phosphorus is limiting in certain mangrove and coastal nearshore systems, but cross-system subsidies deliver this nutrient with follow-on ecosystem impacts (mangroves: Adame et al. 2015; nearshore coastal environments: Deegan 1993). Lacking, however, are studies looking at the extent and impact of cross-ecosystem trophic subsidies to systems that are known for their high internal productivity.

Kelp forests in temperate coastal oceans are one of the most productive ecosystems in the world (Schiel and Foster 2015). Though literature about kelp forest subsidies exist, most focus on kelp forests as a source rather than a recipient ecosystem (Bustamente et al. 1995, Vetter and Dayton 1998, Dugan et al. 2003, Rodríguez 2003, but see Docmac et al. 2017). However, kelp forests are the recipients of trophic subsidies from a variety of sources, from adjacent rivers to the pelagic ocean (Bray et al. 1981, Foley and Koch 2010, Docmac et al. 2017, Galloway et al. 2017). These sustained or short-term pulses of energy can be predictable or sporadic, but undoubtedly have consequences for predators, trophic interactions, and community composition. The diversity of planktivores (e.g. filter-feeding invertebrates) in kelp forest ecosystems that have evolved to take advantage of the constant stream of plankton being delivered to the kelp forest highlight the role that subsidies play in community organization.

The primary productivity that fuels the incredible diversity and abundance typical of a kelp forest comes from two sources. Endogenous productivity of macroalgae (predominately kelps, but also green and red algae) and energy derived from phytoplankton through pelagic-benthic coupling both contribute to the growth and survival of kelp forest organisms (Duggins et al. 1989, Schiel and Foster 2015). Though several studies have addressed the relative importance of these two autotrophic groups, we know substantially less about the trophic importance of phytoplankton and other exogenous subsidies to kelp forests (Graham 2004, Miller et al. 2011, Koenigs et al. 2015). The most comprehensive efforts estimate that the production of giant kelp (*Macrocystis pyrifera*), the predominant macroalgae in central and southern California kelp forests, is approximately 5.5 kg m^{-2} $year^{-1}$ (Rassweiler et al. 2018). Although robust estimates of phytoplankton influx to kelp forests are not available, research suggests that coastal macrophyte production may be 5-10 times greater than phytoplankton production (Kavanaugh et al. 2009, Schiel and Foster 2015). Characterization of the spatial scales of variation in macroalgae and phytoplankton production in the complex nearshore Pacific coast environment has shown that macroalgal and phytoplankton biomass are often offset in space, and that each form of productivity exhibits spatial variation on both local and broad coastal scales (Broitman and Kinlan 2006, Kavanaugh et al. 2009, Fiechter et al. 2018). As such, the relative importance of macroalgae or phytoplankton production in a kelp forest likely varies in in space, seasonally and annually, and along shorelines

(Duggins et al. 1989). On top of this inherent variation are changing ocean conditions. Phytoplankton-based productivity and the delivery of trophic subsidies could become increasingly important in coming years. Kelp forests along portions of the California coast are currently experiencing a large-scale shift from macroalgae-dominated systems to urchin barrens with an accompanying decline in local, kelp-derived productivity (Mark H. Carr, *personal communications*).

In addition to primary production via phytoplankton, there are more episodic influxes energy and nutrients from the pelagic ocean. These trophic subsidies to the nearshore kelp forest are the topic of this review, and can be divided into two categories (Menge et al. 2015, Morgan et al. 2018): meroplanktonic organisms where recruiting larvae or juveniles can be considered a subsidy, and holoplanktonic organisms (zooplankton members of the pelagic community) that are transported to the nearshore from the open ocean, typically on ocean currents and internal waves (Shanks and Wright 1987, Carr and Syms 2006) (Figure 1.1). These trophic subsidies are not autotrophs, but are one to several trophic levels higher. As such, their energy influx reflects a larger contribution of primary production (since energy has been lost during trophic transfer to the subsidy organisms). Although specific examples of these subsidies have been documented, for almost all cases, little is known about the factors that drive variability in subsidy timing, delivery, frequency and magnitude, or their ecosystem and population-wide impacts. Recent research has highlighted the importance of relatively small-scale surfzone hydrodynamics in structuring the delivery of subsidies to the intertidal zone, and similar oceanographic dynamics likely play a role in delivery to other nearshore habitats (Shanks et al. 2017, Shanks and Morgan 2018). Though it is unlikely that each individual species representing a trophic subsidy is important to the productivity of kelp forests (relative to in-situ macroalgal production), the diversity and number of these species suggests that together, their energy inputs might be quite influential. Bray et al. (1981) assessed the diel migrations of a planktivorous kelp forest fish as a mechanism for the transport of energy from zooplankton to benthic communities. Truong et al. (2017) assessed trophodynamics on temperate reefs of Australia by constructing a food web from autotrophs to top predators using diet data and information about species' life histories. Highlighting the influence of subsidies, they conclude that the majority of fish biomass was supported by phytoplankton (largely passing through zooplankton) as opposed to macroalgae or detritus-based sources of production.

Here, we provide an integrative review on the topic of cross-ecosystem trophic subsidies from the pelagic ocean to kelp forest ecosystems. Using case studies, we highlight instances where these cross-ecosystem subsidies have been more thoroughly documented, and places where additional research would greatly improve our understanding, while emphasizing the diversity of pelagic-kelp forest subsidies that exist. Following recommendations from Richardson and Sato (2015), we provide information on the duration and magnitude of the subsidy, the nutritional value of the subsidy, and any known influences on recipient food webs and ecosystems. There are several approaches to scaling the impact of trophic subsidies to the kelp forest ecosystem. Subsidy inputs can be compared to consumer resource demand, to generation time of consumers, to productivity intrinsic to the recipient or donor ecosystems, or in relation to trophic outputs from the recipient ecosystem (Holt 2008, Yang et al. 2008). Marczak et al. (2007) show that the ratio of the energetic value of subsidy resources to equivalent energy produced within the recipient ecosystem is most related to consumer response. However, because data on resources equivalent to the diverse subsidy contributions are not available for kelp forest ecosystems, we simply present subsidy energy values for the recipient system in the case studies below. Specifically, we address three fundamental questions: 1) What is the general identity of subsidies from the open ocean to the kelp forest and what are the estimated contributions of these subsidies? 2) What do we know about how these subsidies impact kelp forest communities and ecosystem functioning? 3) What can we do to better quantify these subsidies and their impacts?

Methods

We searched the peer-reviewed literature using the Web of Science search engine (‘all years’ ending in summer 2017) for information on each of the six example subsidies discussed below. For every relevant paper identified, we looked at citations, and at papers that had cited the originally identified paper. To be included in the synthesis, the paper and data were required to meet the following qualifications: (1) the study and/or measurements must be about the taxa of interest; and (2) the study and/or measurements must be about the life phase of interest for a particular organism. Whenever possible (several categories of data did not exist for the West coast of North America), only data from the specific location of interest was used.

To estimate the energetic contribution of a given subsidy to the kelp forest, the following simple equation was used:

$$E_t = \rho E_i$$

where E_t = total energy delivered in a subsidy pulse, ρ = density of the subsidy organism in the kelp forest, and E_i = energy content of an individual subsidy organism.

While literature values of gross energy content (kcal / g or kJ / g) were available for some species, energy content was calculated from the protein, lipid and carbohydrate components of proximate composition analyses for others. The accepted values of 5.5 kcal /g (protein), 9.3 kcal / g (lipid) and 4.1 kcal / g (carbohydrates) were used in the conversion (Smith et al. 1975).

Pelagic organisms as subsidies to nearshore rocky reef habitats (holoplanktonic organisms)

On the West coast of North America, physical mechanisms including upwelling, internal waves, onshore wind waves, and tides deliver nutrients to nearshore kelp forests from the California Current ecosystem (Shanks 1995). In addition to these nutrients, oceanographic forces move animals from one marine habitat to another. Zooplankters, especially those with limited swimming ability, can be transported on currents, internal waves, and with tides to the nearshore environment (Figure 1.2 for holoplanktonic taxa representing potential kelp forest subsidies, Table 1.1 for a summary of the oceanographic forces that transport holoplankton to nearshore environments). While these drifting organisms occasionally strand on beaches, many individuals pass through or are retained in the kelp forest where they become prey for a variety of nearshore predators. We assume here that the vast majority of pelagic organisms advected to the kelp forest are consumed directly in a relatively short period of time, or enter detrital pathways, rather than surviving for longer periods of time in the nearshore environment or emigrating back to the pelagic ocean. Three examples of pelagic organisms with distinct life histories and dynamics are detailed below.

Pelagic Red Crabs (Pleuroncodes planipes)

Pelagic red crabs or “langostilla” (also known as tuna crabs) are one of approximately 200 species of Galatheoid crabs. Early life phases of red crabs exist in the plankton, followed by an adult life stage (age 2+) that is primarily benthic but includes migrations to the midwater, and a final entirely benthic adult phase (Boyd 1967, Aurioles-Gamboa 1992). Red crab densities can be extremely high in the pelagic environment, and occur with a notoriously patchy distribution (Robinson et al. 2004, Pineda et al. 2016). Patches have been observed to span up to 6 km in nearshore waters of less than 80 m depth, though efforts to estimate patch size have been not been comprehensive (Robinson et al. 2004). Echogram observations document the crabs occurring from surface waters to depths of at least 200 m, and support the well-known swarming behavior in this species (Robinson et al. 2004). Nearshore water column densities (less than 80m), predominately measured in coastal Baja range from 5 to nearly 5,000 crabs per m^2 (Robinson et al. 2004, McClatchie et al. 2016). During El Niño years when red crabs strand in Monterey Bay, expert estimates of kelp forest densities range from 5-15 individuals / m^3 (Figure 1.3). These swarms become especially conspicuous during annual stranding events to shallow water and intertidal beaches that occur in Bahia Magdalena (Baja California, Mexico) during the spring season (the end of crab’s reproductive season), and that occasionally occur in southern and central California (Glynn 1961, Aurioles-Gamboa et al. 1994, McClatchie et al. 2016). Annual stranding is well documented in Baja, but the species has a wide West coast distribution from Panama to Monterey Bay, California (Longhurst 1967, Pineda et al. 2016). It is accepted that red crabs in their pelagic life phase move with warm water to California during El Niño years, though rarely have abundances or densities been measured in California waters (Table 1.2). Apart from anecdotal evidence, little is known about the magnitude or spatial extent of the subsidy in California waters, though we do know that the frequency of occurrence can generally be predicted by El Niño conditions. The specific oceanographic forces that bring red crabs to the kelp forest are not known. Dynamics, however, are quite different in Baja where the subsidy is annually-occurring and spatially predictable.

In the center of their geographic range, pelagic red crabs play an important link between primary production and higher trophic levels, making energy from phytoplankton available to predatory vertebrates and invertebrates (Longhurst 1967, Robinson et al. 2004, Wingfield et al. 2011). An individual red crab provides an estimated 18.96 kcal (79.33 kJ) to predators (Smith et al. 1975). Using this estimate, we calculate that in nearshore California waters, energy subsidies due to the advection of red crabs from pelagic waters to the kelp forest could reach approximately 1,189.95 kJ m^{-3}. Pelagic red crabs are rich in total lipids (e.g., ~14-16% of dry weight), and they are dominated by a nutritionally valuable ω-3 essential fatty acid (20:5ω3; 9-21% of total fatty acids) (Aurioles-Gamboa et al. 2004).

Pelagic red crabs are not fast swimming, are not camouflaged, and provide a high-energy, high-protein meal. It is not surprising that many organisms prey on pelagic red crabs. The most frequent group of predators observed consuming pelagic red crabs are sea and shore birds. Gulls (*Larus occidentalis*, the western gull, in particular) seem to benefit substantially from the subsidy, both in Baja California, Mexico where the subsidy is an annual occurrence and in California where pelagic red crabs are sporadic members of the prey assemblage (Stewart et al. 1984, Aurioles-Gamboa et al. 2003). The presence of red crabs during El Niño years (which typically represent low food years for seabirds) was observed to shift roosting patterns in a population of Western gulls in California (Stewart et al. 1984). Nearshore rockfish in California also make use of pelagic red crabs during El Niño years when red crabs are available (Larson 1991). Stomach content analysis paired with analysis of fat reserves led Larson (1991) to conclude that a glut of pelagic red crabs in the nearshore prey assemblage during summer 1984 had effects at the level of individual rockfish physiology. Several species of nearshore rockfish exhibited high levels of fat reserves and high liver weights from summer 1984-spring 1985. Even the sessile black abalone (*Haliotis cracherodii*) with a typical diet of drift kelp has been observed consuming red crabs during an El Niño year in southern California (VanBlaricom and Stewart 1986).

Pelagic tunicates: Salps, doliolids and pyrosomes (Class: Thaliacea)

Together with other gelatinous zooplankton, pelagic tunicates represent a vastly understudied node in marine food webs. Pelagic tunicates refer to members of the class Thaliacea, including salps (Family: Salpidae), pyrosomes (Genus: Pyrosoma) and doliolids (Order: Doliolida). Salps are globally distributed, inhabiting pelagic habitats in all oceans except the Arctic (Lambert 2005). Thaliceans have both solitary and colonial forms, with colonial organisms reaching up to 20 m in length and solitary forms as small as several centimeters (Lambert 2005). Recent work points to the importance of both salp carcasses and salp fecal pellets as a subsidy to the deep sea, though few researchers have examined salps as a subsidy to the kelp forest (Hobson and Chess 1988, Henschke et al. 2016). While this case study looks specifically at pelagic tunicates, cnidarians and ctenophores represent a similar subsidy to kelp forest systems (though energy densities differ among the taxa).

Limited data exist that quantify the dynamics of pelagic tunicate delivery to nearshore ecosystems. However, in the pelagic environment, gelatinous zooplankton can form swarms that persist for days to months at a time, and certain oceanographic conditions transport these swarms onshore (Hereu et al. 2010, Lucas and Dawson 2014). Several groups have documented a particularly large pyrosome bloom in coastal Oregon, and noted that this increased abundance of pyrosomes coincided with increases in salp abundances in their surveys (Brodeur et al. 2018, Sutherland et al. 2018). Extremely high pyrosome densities were encountered during pelagic trawl surveys (over 200,000 kg $km^{3\ -1}$ off Vancouver Island, Washington), and corresponded with beach strandings of the organisms. Ocean conditions leading to these swarms are not well understood. Moreover, pyrosomes have been shown to subsidize diverse benthic deep sea consumers in the NE Pacific when they eventually fall to the bottom (Archer et al. 2018). Smith, Ford and Link (2016) show marked temporal variability in the abundance of gelatinous zooplankton (GZ) on the Northeast Atlantic shelf, with periods of high abundance of GZ lasting for approximately 5 years. In addition, they find a positive correlation between increased abundance of GZ and abundance of benthic scavenging fishes known to consume GZ (Smith et al. 2016).

Our lack of data makes it quite difficult to quantify the trophic importance of pelagic tunicates as a nearshore subsidy, but we can use energy estimates for individual tunicates to begin the process. Energy densities for temperate pelagic tunicates have been estimated at 4.1 kJ g^{-1} dry mass (*Salpa* spp.), 5.45 kJ g^{-1} dry mass for *Salpa fusiformis*, and 4.94 kJ g^{-1} dry mass for *Pyrosoma atlanticum* (Steimle and Terranova 1985, Davenport and Balazs 1991, Clarke et al. 1992, Wang and Jeffs 2014). Because pelagic tunicates are minimally mobile organisms, the vast majority of individuals that are delivered to the kelp forest are either consumed as prey or enter detrital food chains. Using the estimated energy content for *Salpa fusiformis*, an estimated 300 individuals m^{-3} delivered to the kelp forest (measured in the midwater zone of an

Alaskan kelp forest), and an estimated 0.24 g dry mass for an individual salp, energy from the salp subsidy could reach 392 kJ m^{-3} (Clarke et al. 1992, Pakhomov 2004). Using a 2.0 g dry weight estimate for an individual pyrosome produces an estimate of approximately 9.88 kJ $individual^{-1}$ (Davenport and Balazs 1991). Pyrosome lipid profiles are rich in 14:0 and 16:0 saturated fatty acids, 18:1 9 monounsaturated fatty acid, and 20:5 3, 22:5 6 polyunsaturated fatty acids (Davenport and Balazs 1991).

Gelatinous organisms are often considered a trophic dead-end in marine ecosystems – organisms unsuitable as prey for most predators, thus unlikely to contribute to the continued flow of carbon up the food chain. Recent work, however, points to widespread importance of gelatinous organisms, including pelagic tunicates, in the diets of many higher trophic species. Though energy content of an individual pelagic salp is significantly lower than that of a similarly-sized fish, pelagic tunicates (and other gelatinous organisms) digest extremely quickly and little energy is expended during digestion or prey capture and handling (Arai et al. 2003). Given the ease of digestion, the occasional very high densities of easily captured tunicate prey have led researchers to question the label of trophic dead-end, especially during tunicate blooms or low abundances of more energy-dense prey. Throughout marine systems, more than 47 species of fish are known to feed on pelagic salps (Kashkina 1986). In the northeastern United States, researchers estimate that spiny dogfish (*Squalus acanthias*) remove 0.3-298 g of gelatinous zooplanktors per individual annually, and posit that GZ provides important pulses of food for both spiny dogfish and several species of scavenging fishes (Smith et al. 2016). In California's kelp forests, several species of rockfish are known to consume large quantities of pelagic tunicates when particularly high abundances are present in the kelp forest (Hallacher and Roberts 1985, Hobson et al. 1996). The majority of fishes (and some invertebrates) in nearshore kelp forest systems are generalist feeders, and prey switching to pelagic tunicates in most of these species is relatively unexplored. Pulses of tunicate influx to Carmel Bay, CA kelp forests during the summers of 2015-2016 led to blue, black and kelp rockfish (*Sebastes mystinus, S. melanops and S. atrovirens*) with stomachs completely full of salps and doliolids, suggesting that these species focus their foraging on this subsidy when densities are high enough (Zuercher, *unpublished data*). During a period of uncharacteristically high salp abundance in the nearshore Alaskan kelp forest, Duggins (1981) observed 3-4 weeks in early summer where salps comprised approximately 66% of the diet of sea urchins (*Strongylocentrotus franciscanus, Strongylocentrotus droebachiensis* and *Strongylocentrotus purpuratus*).

By-the-wind-sailor (Velella velella)

A second gelatinous organism that provides a prominent subsidy to central California kelp forests is the surface-dwelling pelagic hydrozoan, *Velella velella* (hereafter Velella). Velella have a global distribution in both tropical and temperate open ocean waters, and are well known for large-scale beach strandings (Purcell et al. 2015). Indeed, reports of these large strandings account for much of the data available about Velella abundance, density and movement dynamics. During a documented mass stranding in New Zealand in October – November 2006, a subsidy of approximately 100 million individual Velella were delivered to a 6 km stretch of beach ecosystem (Flux 2008). For the almost two decades prior to the 2006 New Zealand stranding, only a few individuals per year washed up on the same beaches (Flux 2008). Kemp (1986) documented similar mass strandings on beaches around Newport, Oregon in 1981 and 1984, with only scattered stranded individuals in 1982, 1983 and 1985. To our knowledge, no abundance or density measurements have been made in kelp forest systems, however Velella must pass through forests before stranding on beaches. The delivery of Velella to the nearshore environment is pulsed, seasonal and highly variable from year to year. McGwynne (1980) measured beach deposition rates, and found highly variable delivery to beaches on the East Cape of South Africa during summer, but essentially zero deposition in the winter. Future research should address the duration of this subsidy and the frequency at which Velella are brought to nearshore systems.

Despite the wide distribution of Velella throughout tropical and temperate oceans, few have attempted to quantify its importance as a prey item in the kelp forest system. The most comprehensive work was done by Kemp (1986) in coastal Oregon. During strandings in 1984, an estimated 2573 g of ash free dry weight m^{-1} of shoreline (1223 g m^{-1} carbon, 347 g m^{-1} nitrogen) stranded on the beach. During a recent beach stranding in New Zealand, as many as 25,000 individuals m^{-2} were deposited (Flux 2008). As an individual prey item, Velella provide approximately 2.9 kJ energy g^{-1} dry mass (with an individual Velella weighing an average of approximately 0.09 g dry mass), and are likely among the gelatinous organisms that are energetically cheap for predators to capture and digest (Arai et al. 2003, Peckham et al. 2011). To our knowledge, no estimates exist for densities of Velella on the surface waters of a kelp forest, and beach densities represent the sum of all Velella that moved through the nearshore environment during a stranding without being consumed. Anecdotal evidence from pelagic waters suggests that it is not uncommon for Velella rafts to reach densities of 20 individuals m^{-2}. Using this estimate for a maximum density of individuals on the surface of a kelp forest (vulnerable to predation by kelp forest predators) during mass strandings, Velella represent an energy subsidy of 5.2 kJ m^{-2} sea surface. While relatively little is known about the lipids and fatty acids of most hydrozoans, it has been shown that the dominant fatty acid in Velella is DHA ([22:6w3] at ~28% of total fatty acids; Lopes et al., 2016). Velella also has relatively high proportion of EPA ([20:5w3] at ~8% of total FA; Rita Lopes et al. 2016). DHA and EPA are considered to be key long chain "essential" fatty acids in marine food webs because they are important for growth in many nearshore consumers, but most heterotrophs cannot synthesize these molecules de novo (Arts et al. 2001, Winder et al. 2017). The lipid contents of gelatinous zooplankton are generally known to vary greatly among taxa, on the order of ~4-12% of dry weight (e.g., Leone et al. 2015). Thus, large pulses of Velella biomass to coastal ecosystems could represent a significant input of essential fatty acids to these food webs.

Few data exist documenting the nearshore organisms that consume Velella. Like pelagic tunicates, Velella that are delivered to the nearshore system do not typically return to the pelagic ocean. Velella are either consumed, enter the detrital food chain, or are stranded where they subsidize coastal beaches. Hobson and Chess (1988) found Velella (among other pelagic hydrozoans) in the stomach contents of blue rockfish (*Sebastes mystinus*) during upwelling episodes, and it is likely that other species of kelp forest fishes consume Velella when high densities are available.

Nearshore organisms with a bipartite life history as subsidies to nearshore rocky reef habitats (meroplanktonic organisms)

Recruiting meroplanktonic organisms are the second category of cross-ecosystem trophic subsidy that must be considered as potentially influential for kelp forest food webs. Many organisms in nearshore California and California Current ecosystems live a bipartite life cycle that culminates in the kelp forest, spending a portion of their larval or juvenile life phase eating and growing in the open ocean before recruiting to adult habitat (Figure 1.2). Though extensive work has been done exploring population-level impacts of variation in their recruitment, few researchers have considered the impact of this variability on predator species that consume recruits, and on the general structure of nearshore food webs. Three examples of California kelp forest species with bipartite life histories follow.

Juvenile rockfish (Sebastes spp.)

A prominent and visible annual subsidy to the kelp forest is that of juvenile rockfish recruits. More than 60 species of rockfish (*Sebastes* spp.) inhabit rocky reef and soft bottom marine habitats off the West coast of North America. The rockfishes are a major component of nearshore, shelf and slope fish assemblages, and range from Alaska to the southern tip of Baja California, Mexico on the West coast of North America (Love et al. 2002). Like many marine fishes, rockfish have a bipartite life cycle with pelagic larval and juvenile phases. Rockfish are live-bearers (viviparous), releasing 18,000 to 2,700,000 live larval fish per female that are immediately capable of feeding, though are able to survive for a short period of time on maternal-provided energy reserves (Love et al. 2002). The larvae eat and grow in the pelagic ocean, transitioning to juveniles before recruiting to their adult habitat. The pelagic larval phase lasts for 1-6 months as larvae grow from approximately 3-7 mm to approximately 15-90 mm at settlement (Love et al. 2002). Both stomach content analyses and stable isotope data support the hypothesis that juvenile rockfish facilitate substantial cross-shelf movement of carbon and other nutrients to the nearshore environment (Bosley et al. 2014).

The duration, magnitude and frequency of the juvenile rockfish subsidy are well-documented. On the West coast of North America, upwelling dynamics, advective transport and internal waves lead to significant variability in the delivery of juvenile rockfish to the kelp forest (Carr 1991, Ainley 1993, Larson et al. 1994, Hobson et al. 2001, Caselle et al. 2010, Ralston et al. 2015). This impacts the annual availability of juvenile rockfish as a prey item and trophic subsidy to kelp forest predators. Particularly strong recruitment years (such as the mid to late 1980s, 2001-2003 and 2013) could represent a large pulse of nearshore productivity. Juvenile fish recruit to kelp forests in spring and summer months, and typically remain in the area for their adult life. Because this subsidy does not leave the kelp forest, the duration of availability of this subsidy for a given consumer can be described as the time between settlement and when a juvenile rockfish reaches a size that provides refuge from predation.

While we did not find explicit energy content estimates for post-settlement rockfish, juvenile rockfish in the pelagic environment represent an estimated 5.2-21.8 kcal g dry mass^{-1} (1.45-4.2 kcal g wet mass^{-1}) of energy (Vermeer and Cullen 1982, Perez 1994, Pelt et al. 1997, Becker et al. 2007, Glaser et al. 2015). Although highly variable in time and space, a heavy recruitment pulse can reach densities of 0.7 fish m^{-3} through the kelp forest water column, with densities in aggregations surrounding kelp plants and near the benthos much higher (Figure 1.4; Mark H. Carr, *unpublished data*). Using this estimate, pelagic energy delivered to the kelp forest in the form of juvenile rockfish could approach 23 kJ m^{-3}. Because this is such a well-studied subsidy, juvenile rockfish allow us to take a landscape ecology approach to subsidies. The majority of ecological literature, including this review, considers a subsidy to be a unidirectional flow of energy. However, we can also look at a bidirectional flow (energy in vs. energy out) and calculate the net gain or loss of energy in a given system for a meroplanktonic subsidy. We've seen that the unidirectional flow of energy represented by recruiting rockfish to the kelp forest has the potential to be quite large, but what about the energy that left the kelp forest when larvae were advected to the open ocean? Does rockfish reproduction and the subsequent dispersal and recruitment back to kelp forest represent a net loss or net gain of energy to the system? A mature female rockfish produces 125,000-1.2 million (*S. melanops*) / 16,000-640,000 (*S. caurinus*) larvae per reproductive event (Love et al. 2002). These larvae have a maternally-provided yolk sac and have an energy content of 0.345 calories (*S. melanops*) / 0.688 cal (*S. caurinus*) at birth (Dygert and Gunderson 1991). Natural mortality rate in the pelagic ocean is estimated at 0.14 day^{-1}, and the vast majority of larvae never return to the kelp forest after pelagic larval durations of 30-180 days (*S. melanops*) / 30-60 days (*S. caurinus*) (Tenera Env. Services 2000, Carr and Syms 2006, Ralston et al. 2013). Using mean fecundity and pelagic larval duration values for calculations, and with an energy content of 4.2 kcal g^{-1} for recruiting juvenile fish, we estimate that rockfish reproduction represents a net gain (in the case of *S. caurinus*) and a net loss (in the case of *S. melanops*) of energy to the kelp forest (Figure 1.5). Due to species differences, the wide range of annual larval production, and of potential pelagic larval durations, it is reasonable to consider that this reciprocal subsidy represents no net change in total annual energy for kelp forest ecosystems, though the offset timing of subsidy exit to the open ocean and arrival to the kelp forest is undoubtedly important (Takimoto et al. 2002, Sato et al. 2016).

In their pelagic environment, larval and juvenile rockfish are a major food source for seabirds and other predators (Mills et al. 2007). Becker et al. (2007) explored impacts of variation in juvenile rockfish availability for marbled murrelet (*Brachyramphus marmoratus*) reproduction, finding that murrelet productivity was positively correlated with juvenile rockfish (and krill) abundance. Post-recruitment juvenile rockfish are also an important and high-quality food source for a wide range of kelp-associated species, particularly adult rockfish and other predatory fish (e.g. lingcod, *Ophiodon elongatus*) (Hallacher and Roberts 1985, Hobson et al. 2001, Johnson 2006, Beaudreau and Essington 2007, Tinus 2012). The group of rockfish species that inhabit nearshore rocky reefs as adults recruit to several microhabitats within kelp forest systems, expanding the accessibility of juvenile rockfish prey to a large group of predators (Carr 1991, Love et al. 1991).

Juvenile Dungeness crabs (Metacarcinus magister)

The vast majority of shallow subtidal and intertidal West coast marine invertebrates have a pelagic larval phase before they recruit back to nearshore habitats. Among these is the ecologically and economically important Dungeness crab, *Metacarcinus magister*, a crustacean that that uses broadcast spawning to release meroplanktonic larvae with initially limited swimming ability. In the Pacific Northwest, juveniles complete a pelagic life phase in the plankton and settle to nearshore and estuarine habitats from March – November, with peak recruitment typically occurring in May-June (Roegner et al. 2003, 2007). Settlement of this species occurs in distinct pulses at approximately two-week intervals that last for several days (Mcconnaughey et al. 1992, Roegner et al. 2007, Shanks et al. 2010).

Not only is this a pulsed subsidy, the magnitude of annual recruitment is also extremely variable. Trawl surveys off the Washington coast showed that settlement to the nearshore environment varied nearly 40-fold from year to year (1983-1988), while surveys in Oregon showed that recruitment varies by a factor of more than 1000 (Mcconnaughey et al. 1992, Shanks 2013). This extreme variation in year-class abundance is a result of interannual variation in coastal circulation, timing of the spring transition, and upwelling strength, and undoubtedly influences the nearshore food webs to which they settle (McConnaughey et al. 1992, Shanks 2013). A 12-year dataset of daily abundance of Dungeness crab megalopae in Coos Bay, OR showed a clear effect of the Pacific Decadal Oscillation phase on crab abundance with higher abundances during years of negative PDO (Shanks 2013). In addition, researchers found a negative correlation between megalopae abundance and timing of spring transition in the California Current, the shift from winter downwelling to spring upwelling (an early spring transition leads to a higher return of Dungeness megalopae), and a positive correlation between abundance and upwelling during settlement season (Shanks 2013). Likely representative of the complex oceanographic dynamics driving variability in the delivery of larvae of many nearshore species, recent work has concluded that while upwelling plays a major role in transporting the larval crabs from the open ocean to the continental shelf, internal tides and other coast-associated mechanisms transport the megalopae to their settlement habitat (Shanks 2013). Density of post-recruitment juvenile crabs also varies by habitat, substrate type, and depth. Crab densities tend to decrease as depth and distance from shore increases, and as substrate coarseness increases (McConnaughey et al. 1992). Despite an expected preference for silty or sandy habitats relative to gravel (and presumably rocky) substrates, post-larval crabs seem to use a wide diversity of habitats in years with large recruitment events (Eggleston et al. 1995, Galloway et al. 2017). One such very large recruitment event occurred off the coast of Oregon in

April 2016, with densities of new recruits exceeding 20,000 individuals per m^2 in one layer of crabs in an area where crabs were stacked up to three layers deep (Galloway et al. 2017). This observation, collected using SCUBA, was corroborated by other anecdotal observations (ROV videos, reports from fishers, intertidal observations) collected at other locations on the Oregon coast in the spring of 2016 (Galloway et al. 2017).

Crustaceans are considered to be high value prey items, and Dungeness crabs are no exception. Since we found no published energy content information for a Dungeness crab juvenile, we use an estimate of 2.37 (+/- 0.14) J $individual^{-1}$, measured for spider crab (*Hyas araneus*) megalopae (Anger and Dawirs 1982). With the extraordinarily high densities of recruits observed in nearshore subtidal habitats (estimates of 20-65,000 crabs m^{-2}), a single recruitment pulse could contribute 154 kJ m^{-2} of energy to the nearshore system, based on the high end of this observed range of densities described in Galloway et al. (2017) and the energy density estimate above (kJ). The total lipid content for Dungeness crab megalopae is very high (~15% of total dry weight) but quickly declines (e.g., ~4-5%) within a few weeks of settlement (Galloway, *unpublished data*). Similar to the pelagic red crab, Dungeness crab have relatively high essential ω-3 fatty acid content, and total lipid content of adult crabs at ~1% of total dry weight (King et al. 1990).

Though the majority of evidence for the trophic importance of Dungeness crab juveniles comes from estuarine and pelagic habitats, these observations give us insight into possible kelp forest predators. Research supports predation, including cannibalism, as the major driver of rapid declines in abundance of newly settled Dungeness crabs in the months following settlement (Armstrong et al. 1995). Of seventy demersal and pelagic fishes sampled in central California, 21 had Dungeness crab megalopae, young-of-the-year post-settlement instar, or older age class stomach contents (Reilly 1983). Many kelp forest fishes are generalist predators, limited primarily by their gape and the size of potential prey. Based on this evidence, we predict that kelp forest fishes (i.e. rockfishes in the genus *Sebastes*, surfperches of the family Embiotocidae) consume juvenile Dungeness crabs, especially during large recruitment events. In support of this hypothesis, Galloway et al. (2017) sampled black rockfish (*Sebastes melanops*) during the previously described 2016 large Dungeness crab recruitment to the nearshore, and observed that a large proportion of fish captured had eaten so many juvenile crabs that they regurgitated the megalopae at the surface. Moreover, divers observed events of cannibalism *in situ*, on the rocky reef where the initial settlement occurred; several adult Dungeness crabs were found on the rocky ledges, eating the settlers (Galloway et al. 2017, *personal observations*). A study in northern California shows Dungeness crab megalopae and post-larval instars to also be important prey for copper rockfish (*Sebastes caurinus*) (Prince and Gotshall 1972). In the estuarine environment, ample evidence supports the widespread predation on newly settled Dungeness crabs by the staghorn sculpin (*Leptocottus armatus*), a species similar to the many species of the family Cottidae in the kelp forest ecosystem (Armstrong et al. 1995). Several other fish species, wading birds, and larger crabs join the staghorn sculpin as important predators benefitting from the delivery of larval crabs to nearshore habitats (Stevens et al. 1982, Fernandez et al. 1993).

Herring (Clupea pallasii) eggs

While adult Pacific herring returning to nearshore spawning habitats are a trophic subsidy themselves, herring eggs provide a distinct, and extraordinarily rich subsidy to seagrass beds and kelp forests from California to Alaska (Fox et al. 2018). Like many pelagic fishes, herring females deposit tens of thousands of small, adhesive eggs onto subtidal vegetation, rocks, shells, and man-made structures (Watters et al. 2004). Spawning takes place in the spring months (though as early as December in California, and as late as June in Alaska), and typically happens over 3-6 weeks and in several pulses at a given location (Willson and Womble 2006). Prince William Sound spawning was highly variable during the period of 1973-1999, but seemed to have a 4-year cycle (Norcross and Brown 2000). Eggs hatch quickly in 1.5 – 3 weeks, giving predators only a short time to consume available eggs (Willson and Womble 2006).

Due to the economic and cultural importance of herring runs throughout their range, and the tight coupling between spawn and the current spawning stock biomass, the herring egg subsidy has been very well quantified by research and monitoring spanning almost a century, including the diver and aerial surveys done today (Schweigert 1993, Hay et al. 2009). Using this information, Paul et al. (1996) conducted an investigation into how the Exxon Valdez oil spill impacted the herring egg subsidy to nearshore environments in Prince William Sound. By counting eggs in adult females directly before spawning, they estimated that the approximate energy delivered to nearshore habitats (including both kelp forest and seagrass habitats) in the form of eggs (with an estimated energy content of 8.1 J energy [+/- 0.9 standard deviation] per egg) prior to the oil spill was $68 * 10^9$ kJ (Paul et al. 1996, Paul and Paul 1998). Along with this vast influx of energy, elevated levels of docosahexaenoic acid (DHA) and eicosapentaenoic acid (EPA) in consumers suggest fatty acid contributions from pelagic influx and spawning of herring which are known for their high levels of these fatty acids (Fox et al. 2014, Moss 2016).

Predation on herring spawn, particularly predation by birds, has been a focus of research for nearly 100 years (Munro and Clemens 1931, Schweigert and Haegele 2001). On the Pacific coast of North America, predation is a major source of herring egg loss with seabirds and ducks consuming a substantial proportion of annual herring spawn, including herring spawn from kelp forests. Using a fecal analysis, Using a bioenergetics model, Bishop and Green (2001) estimate that the five most abundant seabird species in Prince William Sound consumed approximately 31% of all eggs deposited in 1994. Not surprisingly, bird predation on herring eggs provides an example of population-level impacts of a cross-ecosystem subsidy. Several studies have shown depth to be an important predictor of egg mortality, providing another indication that avian predation may play an especially critical role in egg survival and are likely major benefactors of this subsidy (Norcross and Brown 2001, Schweigert and Haegele 2001). In addition to avian predation, generalist fish and invertebrate predators are common in both intertidal and shallow subtidal zones where herring eggs occur. Herring off the Norwegian coast exhibit a similar spawning pattern to fish in British Columbia, depositing eggs that are then prey for benthic fish predators such as haddock (*Malanogrammus aeglefinus*), and benthic crustaceans (Varpe et al. 2005). Using a stomach content analysis of potential fish predators, Hexagrammid fishes were estimated to consume 2-9% of herring eggs in Prince William Sound (Rooper 1996). Haegele (1993) estimated that epibenthic invertebrates spanning many taxa (though the predominant predators were crabs) consumed 3.7% of total herring eggs at several sites in British Columbia. An interesting comparison can be made between the herring eggs subsidy, and the energy-rich eggs of Cisco (*Coregonus artedi*) that bring energy from pelagic waters to nearshore benthic communities in Lake Superior (Stockwell et al. 2014). The cisco egg subsidy was shown to represent 79% of the energy consumed by whitefish (*Coregonus* *clupeaformis*; a nearshore benthic fish) in the winter months, and led to an observed increase in lipid stocks during the winter, rather than the predicted decrease (Stockwell et al. 2014).

Population and community-level consequences

Today we see calls to advance our quantitative understanding of the effects of cross-ecosystem subsidies (Richardson and Wipfli 2016). There is wide recognition that subsidies result in ecological consequences at varying levels of organization, and in general, observational and experimental approaches have shown positive consumer responses to trophic subsidies (Polis et al. 1997, Sabo and Power 2002). However, characteristics of both trophic subsidies and organisms that consume these subsidies impact the response that consumers and populations will have (Yang et al. 2008; Table 1.3). The duration of a subsidy pulse and the size of the subsidy organism relative to the size of potential consumers in the recipient ecosystem are important when predicting the influence of that subsidy. Similarly, attributes of a consumer, such as feeding mode, will determine whether it is able to exploit a certain subsidy and how that subsidy might impact individual consumers and/or the consumer population. Finally, attributes of the recipient system, for instance, what nutrients are limiting, will play a role in the consequences that result from the delivery of trophic subsidies. Importantly, spatial resource subsidies are donor controlled, meaning that the recipient can often consume all or most of the subsidy and not affect the magnitude of future subsidy inputs. In other words, subsidy source populations are decoupled from consumer dynamics in the recipient system.

Attributes of resource inputs effect ecosystem response

As the rate of delivery, timing, frequency, form (e.g. eggs vs. larvae), dispersion (i.e. patchiness), and magnitude of subsidy inputs change, the response of consumers will shift. Studying the sockeye salmon egg subsidy in aquatic systems, researchers showed that temperature and subsidy presence interact to influence predator (juvenile coho salmon) size and fatty acid composition (Smits et al. 2016). Moreover, consumer and aquatic ecosystem responses to subsidies depend on the timing of subsidy deliveries in relation to prey production in the recipient system (Sato et al. 2016). Changes in the timing of subsidy resources in relation to the life history of a consumer can lead to variation in ecosystem responses as well. For example, riparian spiders that receive subsidy resources early in development are at a disadvantage relative to those that receive subsidies closer to reproduction (Marczak and Richardson 2008). Though there have been fewer empirical studies looking at the effect of variable magnitude and frequency of subsidies, it is likely that these attributes also play a role in determining ecosystem response.

Consumer attributes influence individual and population-level effects of subsidy resources

The impact that a pulsed resource has on a consumer species will be highly dependent on the particular life history of that consumer. Long-lived predators such as kelp forest rockfishes (Genus: *Sebastes*) will be less likely to respond to a pulsed subsidy with short-term increases in abundance, but may exhibit increases in growth or reproduction, depending on the timing of subsidy availability. Larson (1991) describes a remarkable trophic subsidy of pelagic red crabs to nearshore California environments. During this period, fat and liver weights of *Sebastes* spp. increased, and the researchers posit that the subsidy-related change in food availability had impacts on reproduction. In contrast, short-lived and fast-reproducing species such as many kelp forest invertebrates might be expected to respond to abundant subsidy resources with a more rapid numerical response.

The expected consumer response to a subsidy will also depend on that consumer’s trophic level, foraging habits, behavior, and size and age class (Anderson and Polis 2004, Marczak et al. 2007, Richardson and Wipfli 2016). Because subsidies are, by nature, not always present in recipient ecosystems, few consumers specialize on individual subsidy sources of prey (Ostfeld and Keesing 2000). As a result, trophic benefits of subsidies likely accrue first to generalist consumers with the ability to switch prey types when abundant and high-quality subsidy resources are available

(Yang et al. 2008). Coutré et al. (2015) explored the use of seasonally-pulsed, high-energy trophic subsidies by juvenile sablefish (*Anoplopomo fimbria*), concluding that the fish consume high-energy subsidies when they are available, but aren't entirely reliant on this food source. However, this isn't always the case. The Dolly Varden (*Salvelinus malma*) fish exhibits unique physiological adaptations that allow it to specialize on the highly predictable subsidy of riverine salmon eggs, making them very reliant on this allochthonous food source (Armstrong and Bond 2013). Beyond generalist feeding habits, mobility will play a major role in the functional and aggregative response of a consumer to a subsidy resource. The consumer must be able to encounter and exploit the subsidy resource on the temporal and spatial scales that the resource is retained in the kelp forest and available.

Ecosystem-level effects of subsidy resources

Using a meta-analysis of 115 data sets from 32 studies of consumer responses to ecosystem subsidies, Marczak et al. (2007) make several important conclusions about consumer-subsidy interactions. First, that consumer response is significantly related to the ratio of subsidy resources to comparable resources in the recipient system, but that the strength of consumer response cannot be predicted by the productivity of the recipient ecosystem. This observation underscores the importance of quantifying subsidy inputs for kelp forest food web modeling. Second, subsidies will be more impactful in recipient ecosystems with high perimeter: area ratios, though duration of retention of the subsidy in the recipient system is also influential. Patchy distribution of kelp forests interspersed with other habitats, and the confined depth range of kelp forests (3-30 m) and rapid increase in depth with distance from shore often leads to a high perimeter: area ratio, with much of the forest directly exposed to outside influences. These broad generalizations that are beginning to emerge provide a platform for both experimental and observational studies that address subsidy impacts.

Many studies support the expectation that trophic coupling of adjacent (or otherwise spatially coupled) marine ecosystems impacts everything from predator-prey dynamics to community composition in recipient ecosystems. Evidence now suggests that subsidies can impact the distribution, relative abundance, and density of recipient species, with some subsidized marine consumers maintaining higher population densities than would exist without subsidy resources. Abyssal sharks, fishes and other organisms benefit from the infrequent but energy-rich influx from whale falls and wood falls, maintaining densities that wouldn't be possible with only the sparse resources available in the deep sea (Bennett et al. 1994, Koslow et al. 2000, McClain et al. 2018). Pulses of gelatinous zooplankton increase the abundance (with a two-year lag) of two deep water benthic detritivores (Atlantic hagfish and grenadier; Smith et al. 2016). Similarly, beach arthropods maintain significantly higher densities in areas exposed to marine-based subsidies via seabird guano, eggs and carcasses

(Polis and Hurd 1996). And in the kelp forest, foraging movements and patterns of a planktivorous damselfish (*Chromis punctipinnis*) depend on the direction of current flow that delivers plankton subsidies into the forest (Bray 1981, Kingsford and MacDiarmid 1988).

The most apparent impact that subsidies have on recipient ecosystems is their influence on trophic interactions. Subsidies can completely or partially decouple consumers from in-situ prey population dynamics, and researchers have suggested that the intensity of species interactions are influenced by subsidy delivery rates (Menge et al. 2003). However, many food web studies and models remain limited to a single-ecosystem, ignoring the impact of subsidy resources. Focusing on consequences of cross-ecosystem resource subsidies in aquatic systems, Richardson and Wipfli (2016) describe four potential functional responses of the direct consumers of trophic subsidies. These include response shapes that model prey switching, prey-swamping and/or saturation, systems where high subsidy inputs may become toxic (e.g. nutrient inputs to stream ecosystems), and the simple linear increase in consumer response as subsidy availability increases (Holling 1959). For example, predators subsidized by outside energy sources might consume fewer kelp forest prey items, thereby releasing those organisms from predation. Sea otters (*Enhydra lutris*) at Amchitka Island, Alaska undergo a drastic dietary switch from kelp forest fishes to the episodically-abundant Pacific smooth lumpsucker

(*Aptocyclus ventricosus*) and benthic invertebrates, with the subsidy resource leading to an increased foraging profitability for the otters (Watt et al. 2000). Alternately, any increase in predator abundance in response to subsidy resources could lead to increased predation on kelp forest organisms via apparent competition (Holt 1977, Schmitt 1987). In addition to this diversity of responses that might be expected from direct consumers, impacts will propagate throughout the food chain via top-down and bottom-up forces. When consumers exhibit numerical responses to pulses of subsidy resources, these population changes are likely to have follow-on effects on other prey sources, competitors, their predators, and even parasites and pathogens in the system (Ostfeld and Keesing 2000). In their review on the ecosystem-level impacts of migratory animals (a temporally predictable subsidy), Bauer and Hoye (2014) identify instances where the timing of consumer reproduction and predator-prey interactions of non-subsidy species are structured by the presence of migrants (a trophic subsidy in this case).

For further insight into the effects of pelagic subsidies on kelp forest ecosystems, we can look to several decades of work in the rocky intertidal ecosystem (Bustamente et al. 1995, Menge et al. 1997, 2003, Krenz et al. 2011). Trophic connectivity between the pelagic ocean and the intertidal zone (often termed benthic-pelagic coupling) is mediated by oceanographic currents and other physical dynamics, and can provide insights into expected pelagic – kelp forest subsidy responses. Krenz et al. (2011)

measured both larval settlement and delivery of particulates to intertidal environments on the West coast of North America, determining that subsidy dynamics are highly spatially variable, and suggesting that this plays a role in driving the observed latitudinal gradients in community structure. These "breaks" along the coast in terms of the importance of subsidies to marine ecosystems might apply to kelp forests as well. In South Africa, subtidal kelps subsidize intertidal limpet populations, allowing them to reach much higher densities than they otherwise would. Because limpets are primary space holders, increases in their density leads to follow-up impacts to community structure (i.e. subsidized limpets are able to keep the intertidal clear of understory algae) and function of the entire intertidal community (Bustamente et al. 1995). Describing subtidal-intertidal coupling, Gaines and Roughgarden (1985, 1987) showed that predation on recruiting barnacle nauplii by juvenile rockfish in the kelp forest leads to a decrease in intertidal barnacle recruitment. This decline in recruitment certainly impacts other intertidal species, and similar processes likely exist for organisms recruiting to kelp forest habitats.

Studies of consumer and ecosystem responses to subsidies in the kelp forest are rare, but increasing. In an explicit look at the role that pelagic-benthic coupling plays on the nearshore, rocky reef habitats of Chile, Docmac et al. (2017) use carbon stable isotopes to conclude that the dominant trophic pathway for kelp forest fishes is based on pelagic energy. Though further work is necessary to determine the mechanisms for the delivery of this pelagic-based energy, the results imply that subsidies are quite important. Beaudreau and Essington (2007) quantify the diet of lingcod (*Ophiodon elongatus*), an important kelp forest predator, finding that pelagic fish in the family Clupeidae (such as Pacific herring) were the second most numerically abundant prey family. In a follow-up paper, they use movement data to show that this transfer of energy from the pelagic ocean to the nearshore is prey-mediated rather than a result of lingcod foraging runs to offshore habitats (Beaudreau and Essington 2011). Hobson and Chess (1988) linked periods of summer downwelling in northern California and the influx of gelatinous zooplankters to instances of full stomachs in blue rockfish (*Sebastes mystinus*), highlighting the importance of these pulses. A recent hypothesis put forward by Trebilco et al. (2016) suggests that cross-ecosystem trophic subsidies may enable the inverted biomass pyramid structure seen in relatively pristine coral reef and kelp forest ecosystems.

How do we measure pelagic subsidies and their effects on nearshore systems?

At the most basic level, we need metrics of the timing, duration, magnitude and frequency of pelagic ocean subsidies to nearshore systems, characteristics that can directly influence impacts to individuals and populations. Consumers might evolve to use predictable subsidy resources, but not resources that come infrequently as unpredictable pulses. The timing of a subsidy might coincide with increased energy requirements for a consumer during a reproductive season, or might be less important because of a timing mismatch between the subsidy and consumer needs. A subsidy of very large magnitude over several weeks might induce a shift in foraging habitat for mobile predators, while the impacts of a shorter-term influx of smaller magnitude might remain more localized. Once a general understanding of subsidy dynamics is established, additional information is necessary to predict subsidy impacts. Data on the nutritional quality and palatability of subsidy resources for consumers, and an understanding of the likelihood that subsidy resources will be consumed is a next step. Subsequent studies can then address numerous other system attributes and factors that will influence potential ecological impacts of a subsidy resource (Table 1.3).

One of the inherent challenges to quantifying cross-ecosystem subsidies, especially those that move from the pelagic ocean to the nearshore kelp forest, is the interdisciplinary data collection involved. There is currently a mismatch between the scale at which oceanographic data relevant to kelp forests are collected (data important to understand subsidy dynamics), and the scale at which ecological data in nearshore environments are collected (data essential for understanding community and population impacts of these subsidies). Oceanographers often focus on ocean basin, large-scale processes at scales too large for observation of the movement of subsidy organisms on a weekly or monthly time frame. Kelp forest ecologists often conduct short-term experimental and observational studies at the level of the individual forest, using SCUBA transects to quantify ecosystem changes. These methods are not always suitable for observing episodic influxes or quantifying rates of delivery of subsidy organisms (especially those not easily observed), and are not always representative samples of the broader geographic significance. In addition, studies over a few years may not be long enough to capture variation in subsidies, and resulting impacts to trophic dynamics. This suggests that the development of sampling methods and designs that integrate over time, such time-lapse video equipment that can sample frequently over long periods, will be beneficial. Finally, while separating and simplifying ecosystems is extremely useful for many studies, engaging experts across traditionally-drawn ecosystem boundaries and disciplines is necessary to truly understand connectivity and the functioning of ecosystems (Saunders et al. 2015).

With many organisms that are commonly important as coastal resource subsidies to other consumers, we tend to quantify impacts in only the most visible or accessible habitats. For example, Dungeness crab recruits have been counted in many estuarine zones, but largely ignored in nearshore subtidal areas (Armstrong et al. 2003, Galloway et al. 2017). Similarly, we have a wealth of data on the dynamics of barnacle recruitment to the rocky intertidal, but no analog exists for barnacle recruitment to subtidal reefs, despite evidence for pulses of barnacle recruits large enough to impact kelp forest food webs. Understanding the diversity of settlement habitats for nearshore organisms will not only benefit our understanding of those populations, but also give insight into the spatial scale and timing at which the subsidy might be important.

As demonstrated in the six examples above, the dynamics of cross-ecosystem subsidies vary dramatically from one organism and location to another. Some organisms recruit from the open ocean to the kelp forest during downwelling conditions, while upwelling conditions bring others to the nearshore environment (Mace and Morgan 2006, Caselle et al. 2010). Certain subsidy organisms (e.g. pelagic red crabs in Monterey Bay) are found in kelp forest systems only during El Niño years when other food sources for kelp forest predators are less abundant (McClatchie et al. 2016). More work is needed to understand how the subsidies interact with each other and with other kelp forest energy sources. Does a subsidy asynchronous with intrinsic resource production stabilize consumer-resource interactions by ensuring more consistent food resources for kelp forest predators in a variable ocean environment? Or do subsidies synchronous with intrinsic production represent extra energy when the subsidy pulses arrive (i.e. do subsidies that coincide with high periods of intrinsic productivity amount to “wasted” energy)? Do subsidies always represent additional prey resources or do they sometimes simply decrease the time and energy (foraging costs) it takes for a consumer to find prey?

It is clear that our understanding of food webs could benefit from increased understanding of subsidy organisms, however the most efficient and useful time, place and method to make measurements is not always obvious. Ongoing efforts in the California Current ecosystem measure densities and relative abundance of potential kelp forest subsidy organisms while in their pelagic habitats. This is useful, but several issues arise when using these measurements to infer the realized magnitude of a subsidy. The vast majority of meroplanktonic organisms will be consumed or otherwise die before settling to nearshore habitats. In addition, complex movement of organisms in the pelagic phase of a bipartite life cycle mean that a subsidy may not be expected in nearshore environments directly adjacent to their offshore presence. To translate pelagic density measurements to nearshore densities at useful temporal scales, we need both reasonable estimates of pelagic mortality and an understanding of pelagic movement and settlement dynamics. Holoplanktonic organisms may live their entire life cycle in pelagic environments, or might be swept to nearshore habitats and represent subsidy resources, but we often lack an understanding of the oceanographic forces that determine when advection to nearshore environments will occur (but see Roegner et al. 2003). When paired with local-scale measurements of ocean conditions, and an improved understanding of the oceanographic forces that move pelagic organisms to the nearshore environment, these measurements of offshore densities (or simply presence and absence data) can prove useful for determining subsidy timing and location. As demonstrated by Morgan et al. (2018) in the surf zone and intertidal environments, measurements of abiotic forces (e.g. currents, internal waves) can alert ecologists to locations, seasons and years where subsidies might be especially influential. Understanding the patterns of heterogeneity inherent in the oceanographic conditions in kelp forest ecosystems (for instance, variable strengths of upwelling in temperate kelp forest systems plays a major role in determining deliver of pelagic materials) is a great starting point for predicting what reefs might be especially reliant on trophic subsidies (Perez-Matus et al. 2017). However, the most reliable way to measure pelagic subsidies remains obtaining estimates of the abundance and timing of these organisms in kelp forest ecosystems.

There are several widespread ways that researchers are currently quantifying organisms that represent cross-ecosystem subsidies. Ecologists along the West coast of North America routinely deploy standardized units for the recruitment of fishes or SMURFs to measure delivery of juvenile rockfish to kelp forest habitats (Ammann 2004). The Partnership for the Interdisciplinary Study of Coastal Oceans (PISCO) and Reef Check California conduct annual diver surveys in kelp forests where juvenile rockfish are counted and measured. Shanks and others commonly deploy light traps to collect invertebrate larvae (e.g. Dungeness crab larvae) as they recruit to nearshore systems, and many groups use recruitment tiles for the ongoing monitoring of invertebrate larval delivery to nearshore marine habitats (Shanks 2009, Shanks et al. 2010). However, the behaviors and physical forms of certain organisms (especially gelatinous organisms) do not lend themselves to detection by these traditional methods of recruitment monitoring. For these organisms and for more easily observed subsidies, researchers often rely on indirect measurements such as analysis of stomach contents of predators (Coutré et al. 2015, Smith et al. 2016, Eriksen et al. 2018). We can further use stomach content information to better understand the role of prey switching in consumer organisms, how a switch might correspond to the timing of a subsidy or availability of resident prey, and whether prey switching is dependent on age or size of the consumer (Hobson and Chess 1988, Watt et al. 2000). Other creative methods have been used to infer the delivery, frequency and magnitude of subsidies. Monitoring of oceanographic conditions and water chemistry measurements can illuminate likely locations and timing of the delivery of subsidies (Shanks et al. 2000, Sponaugle et al. 2002). Additional monitoring of predator diets through the use of stable isotope and fatty acid analysis allows researchers to infer use of subsidies and potential food web and community-level impacts (Stapp and Polis 2003, McMahon et al. 2016). For example, using both C and N isotopic values for two kelp forest fishes, Von Biela et al. (2016) estimate kelp-derived carbon to make up 36-89% of the diet of the benthic feeding kelp greenling (*Hexagrammos decagrammus*) and 32-65% of the more pelagic-dwelling black rockfish. Others have used stable isotopes to examine the relative importance of pelagic- versus macroalgae-derived carbon to secondary production in kelp forests ((Duggins et al. 1989, Koenigs et al. 2015, Docmac et al. 2017).

To make basic information about subsidy dynamics relevant to our understanding of the trophic ecology of recipient ecosystems, information about the energy content, proximate composition, and presence of any nutrients or molecules (e.g. certain fatty acids) that are rare or limiting in recipient systems is useful. As demonstrated with the calculations above, data to examine the energetic contributions made by subsidies and the quality of these inputs to recipient kelp forest ecosystems are not always readily available. Publication of energy content estimates from bomb calorimetry measurements or proximate composition analysis is essential to continued work on the ecology of kelp forest subsidies, and we should renew efforts to develop these basic estimates for poorly studied organisms (such as gelatinous zooplankton). Researchers should also consider the role of dietary lipids and particular fatty acids delivered with a subsidy. For example, resources that are rich in long-chain, ω-3 fatty acids are often extremely valuable prey for consumers, which cannot otherwise synthesize these ‘essential’ molecules de novo (see Arts et al. 2001, Dalsgaard et al. 2003). These nutritionally valuable resources may only be delivered to consumers in discrete intervals at certain times of the year, such as salmon returning to spawn in natal streams, delivering essential fatty acids to terrestrial river and forest food webs (Heintz et al. 2004). Van Deurs et al. (2016) traced important dietary lipids from the feeding grounds of a subsidy (Atlantic herring) to the livers of predators in the recipient ecosystem.

Finally, our understanding of the kelp forest ecosystem will improve with empirical tests of hypothesized impacts of cross-ecosystem subsidies, and with the incorporation of trophic subsidies into ecosystem models. Mesocosm (e.g. Yeager et al. 2016) and field experiments (e.g. Polis and Hurd 1996) will give us further insight into how subsidies shape and alter food webs. Efforts to simultaneously quantify subsidy delivery rates and subsidy consumption by kelp forest organisms are essential as we test the true impacts of subsidies across trophic levels, and narrow in on subsets of the food web where the largest effects might be observed (Small et al. 2013). Explicit looks at kelp forest species interactions such as competition and predation in the presence and absence of subsidy resources will highlight ecosystem-level impacts. And certainly, matching metrics of subsidy magnitude and timing with long-term ecosystem monitoring data has the potential to bring unexpected effects of subsidies to light.

Cross-ecosystem kelp forest subsidies in a changing ocean

In a changing world, the dynamics of subsidies are not static, and future environmental changes to subsidies will have implications for natural communities

(Griffiths et al. 2017). Sato et al (2016) use a field manipulation to conclude that that shifts in the timing of a pulsed subsidy to a freshwater stream ecosystem can fundamentally alter the ecosystem-wide impacts of that subsidy. In this experiment, subsidy timing affected consumer growth rates and timing of maturation, population biomass of both cutthroat trout (apex predators) and stream invertebrates (consumers), and nutrient recycling and decomposition rates (Sato et al. 2016). Similarly, there is experimental evidence that human-caused changes in predator abundance (including the introduction of non-native predators), temperature, and nutrient flux in stream systems impact the magnitude of subsidies, identity of these subsidies, and timing of their delivery (Baxter et al. 2004, Greig et al. 2012). As changes in the temperature, oxygen levels, acidity and circulation patterns in our coastal oceans continue, connectivity patterns will change, and ecosystem-wide impacts of subsidies will shift. Intensification of seasonal upwelling and/or other changes to upwelling dynamics on the West coast of North America is expected to alter dispersal pathways of larval and juvenile rockfish to the kelp forest ecosystem (Parrish et al. 1981, Bakun 1990, Rykaczewski et al. 2015, Bakun et al. 2015). Because substantial work has been done to understand patterns and processes of the juvenile rockfish subsidy, we can begin to predict how delivery to the kelp forest ecosystem might change into the future. More frequent hypoxic conditions in coastal waters are expected to impact recruitment dynamics of marine invertebrates, many of which are subsidies for nearshore predators (Powers et al. 2001, Chan et al. 2008).

Model predictions of range shifts in response to temperature increases in the ocean will shift interaction networks, and geographic patterns of subsidies, with unknown impacts for the importance of subsidies (Perry et al. 2005, Pinsky et al. 2013, Bates et al. 2014). As waters warm, ecologists predict metabolic rate increases in heterotrophs, but are unsure whether ingestion of food will keep pace (Gilbert et al. 2014, Iles 2014). No studies to our knowledge have been done on the role that trophic subsidies will play in allowing consumer ingestion to keep up with the increasing energetic demands of a changing ocean environment. In addition to these bilateral species interactions, there is the potential for impacts to propagate up or down a food web, inducing changes to multi-species interactions. This potential for trophic cascades resulting from subsidy resources has been borne out in both terrestrial and freshwater examples, with some researchers even suggesting that the rates of exogenous inputs might be key to our understanding of why trophic cascade strengths vary across ecosystem (Polis and Hurd 1996, Polis et al. 1997, Nakano et al. 1999, Baxter et al. 2005, Leroux and Loreau 2008). Finally, as more species move around the world, and invade new ecosystems, subsidy dynamics will be impacted. Invasive species can be important trophic subsidies (Quijón et al. 2017).

Following the conceptual framework presented by Larsen et al. (2016) outlining how global change might influence stream riparian subsidy dynamics and consequences, kelp forest ecologists should begin developing questions and studies that explore how changing ocean conditions will affect subsidies, trophic networks and cascades. Global climate change will impact phenology, aspects of metabolism, and the distribution of organisms, creating the possibility for spatial or temporal mismatches between consumers and subsidy delivery (Harley et al. 2006). Future studies should address the pathways and mechanisms by which global change might impact subsidy dynamics.

The topic of ecological connectivity, in the broad sense, has been embraced for its importance in conservation (Carr et al. 2017, Hidalgo et al. 2017). Ecological connectivity impacts many of the processes that shape kelp forest communities, and an understanding of this connectivity is critical for kelp forest management and predicting a system's response to management (Perez-Matus et al. 2017). For example, genetic connectivity is often used as a source of information to inform fisheries management and conservation decisions. Similarly, practitioners using spatial marine planning tools have long called for a better understanding of ecosystem connectivity and the movement of pelagic larvae and juveniles to adjacent ecosystems. The success of marine protected areas in particular relies on the ability of managers to incorporate ecological connectivity into their design (Carr et al. 2017). However, it is not common for managers to take the cross-ecosystem approach that consideration of trophic ecosystem connectivity necessitates (Loreau and Holt 2004, Massol et al. 2011, Menge et al. 2015). When estimating and measuring connectivity to ensure conservation success, trophic subsidies should not be ignored. Griffiths et al. (2017) look specifically at pelagic-benthic coupling, summarizing mechanisms by which climate change might impact physical processes and the cycling of nutrients, and ecological processes that impact consumer-resource dynamics. They also predict the directionality of response of subsidy-relevant ecological processes to nutrient loading and fishing, two notable anthropogenic pressures. As adaptive management gains prominence as a conservation tool, ongoing study into the dynamics and variability in trophic subsidies will also be essential (Hidalgo et al. 2017). It is important to note that not all subsidies are beneficial to the recipient ecosystem (Walters et al. 2008). Subsidies can be deleterious, such as in the case of natural or anthropogenic eutrophication or the movement of pollutants via organisms from adjacent ecosystems or nutrient subsidies (Brimble et al. 2009, Honig and Mahoney 2016).

Pathways of ocean connectivity and the cross-system flows of subsidy resources are not immune to human-caused disturbances and change. Bishop et al. (2017) review the ways in which sprawl of artificial structures in coastal and marine environments (e.g. marinas, seawalls, offshore energy developments) might be impacting and altering ecosystem connectivity, including the flows of trophic resources. With a meta-analysis of studies using graph theory to describe ecosystem connectivity, Saunders et al. (2015) assess the impact of habitat alteration, human-mediated species movement, overharvesting and climate change on the presence, strength and directionality of connectivity. They show that these anthropogenic stressors can impact nodes (i.e. ecosystems or populations in a connected network; in the case of habitat alteration, overharvesting or sea level rise), links (the connection between ecosystems; in the case of species introductions or altered circulation), or both (in the case of climate change).

Expanding our knowledge of the subsidies flowing from the pelagic ocean to nearshore kelp forest systems will provide insights relevant to both terrestrial and other aquatic systems. Though we focus on the kelp forest ecosystem, this is but one example where an improved understanding of the importance of cross-ecosystem subsidies will benefit understanding of ecosystem function and stability. Impacts on trophodynamics are one of the outcomes of connectivity in ecological systems, and a closer look at how the larger process of connectivity works to structure communities should remain a priority (Sheaves 2009). More work is necessary to develop a clear picture of the relative importance of endogenous vs. exogenous productivity in kelp forest and other coastal marine ecosystems. It is clear, however, that trophic subsidies are one of the forces that shape communities and ecosystems. Further research is necessary to determine the direct and indirect effects of trophic subsidies to kelp forests, and to determine the consistency of these effects among consumers and geographic locations. In addition, questions remain regarding whether subsidies impart stability or destabilize kelp forest communities and predator-prey interactions therein. There are many fruitful avenues of research exploring cross-ecosystem subsidies and their impacts, and inclusion of this important aspect of food web dynamics will surely improve our understanding of kelp forests and other coastal marine ecosystems into the future.

Tables and Figures

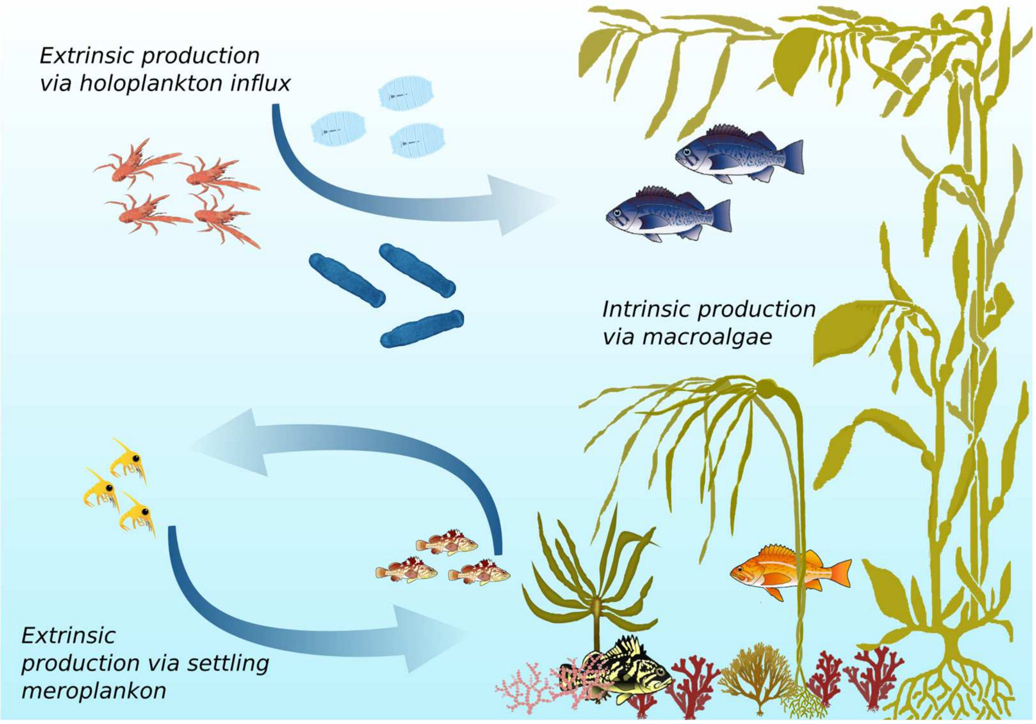


Figure 1.1. In addition to the primary production of phytoplankton, there are more episodic influxes energy and nutrients from the pelagic ocean. These trophic subsidies to the nearshore kelp forest can be divided into two categories: (1) holoplanktonic organisms transported to the kelp forest; and (2) meroplanktonic organisms settling to the kelp forest.

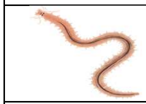
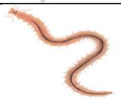
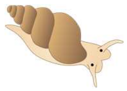
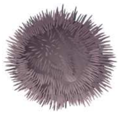
Holoplanktonic Taxa		**Meroplanktonic Taxa**	
	**Cnidaria** Class: Schyphozoa, Hydrozoa		**Cnidaria** Class: Anthozoa, Hydrozoa
	**Ctenophora**		**Bryozoa**
	**Annelida**		**Annelida** Class: Polychaeta, Echiura, Hirudinea
	**Mollusca** Class: Gastropoda, Cephalopoda		**Mollusca** Class: Gastropoda, Cephalopoda, Bivalvia, Polyplacophora
	**Arthropoda** Class: Maxillopoda Malacostraca, Ostracoda, Branchipoda		**Arthropoda** Class: Maxillopoda, Malacostraca, Chelicerata
	**Echinodermata** Class: Crinoidea		**Echinodermata** Class: Crinoidea, Echinoidea, Asteroidea, Ophiuroidea, Holothuroidea
	**Chordata (Subphylum: Tunicata)** Class: Thalicea, Appendicularia **Chordata (Subphylum: Vertebrata)** Class: Osteichthys		**Chordata (Subphylum: Vertebrata)** Class: Osteichthys

Figure 1.2. Taxonomic groups (not an exhaustive list) of the common taxa of holoplanktonic and/or meroplanktonic organisms that may serve as trophic subsidies to nearshore rocky reefs on the west coast of North America. Other phyla that likely comprise subsidies to the kelp forest include: Rotifera and Chaetognatha (holoplankton), and Porifera, Rotifera, Nemertea, Chaetognatha, Sipuncula and Brachiopoda (meroplankton).

Table 1.1. Oceanographic forces that influence the dynamics of mero- and holo-planktonic subsidy delivery.

Oceanographic forces influencing subsidy delivery to the kelp forest	**Citation**
PDO / ENSO	Cowen 1985; Lenarz et al. 1995; Field and Ralston 2005; Carr and Syms 2006; Laidig et al. 2007
Surface currents and waves	Becker 2007
Eddies and jets	Ebert and Russell 1988
Seasonal upwelling/relaxation	Menge et al. 2003; Broitman et al. 2005; Roughan et al. 2006; Wilson et al. 2008; Laidig 2010; Caselle et al. 2010; Markel 2011
Coastal fronts	Woodson et al. 2012; Ryan et al. 2014
Tides	Markel 2011
Internal waves	Woodson 2018

Figure 1.3. Pelagic red crabs on kelp (*Macrocystis pyrifera*) in coastal habitats of Monterey Bay, California in August 2015.

Table 1.2. The occurrence of pelagic red crabs in California (adapted from Lluch-Belda et al. 2005).

YEAR	LOCATION	REFERENCE
1859	Monterey Bay, CA	Stimpson 1860
1895	Monterey Bay	Boyd 1967
1941	California	Hubbs 1948
1957 - 1959	California	Longhurst 1967; Boyd 1967
1960	Monterey Bay	Glynn 1961; Boyd 1967
1969	Monterey Bay	Hardwick and Spratt 1979
1972 - 1973	Southern California Bight	Stewart et al. 1984
1978	Ensenada, CA	McLain and Thomas 1983
1982 - 1983	California	Lluch-Belda et al. 2005; Stewart et al. 1984
1984-1985	Monterey Bay	Larson 1991
1997 - 1998	California	Lluch-Belda et al. 2005
2002	California	Lluch-Belda et al. 2005
2015 - 2017	California	McClatchie et al. 2016; Sakuma et al. 2016; Connelly 2017; Carr, *personal communication*

Table 1.3. Characteristics of (a) the recipient ecosystem, (b-c) the resource inputs, and of (d) specific consumers influence the relative importance and consequences of a cross-ecosystem trophic subsidy.

(a)

RECIPIENT SYSTEM ATTRIBUTES	**RELATED CONSIDERATIONS**	**EXAMPLES**
Trophic complexity	Subsidy causing indirect impacts up or down the food chain	Bustamente et al. 1995; Polis and Hurd 1996; Maron et al. 2006
Limiting nutrients in the recipient system	Variability of nutrient limitation; whether the subsidy provides a limiting nutrient	Anderson and Polis 1999; Adame et al. 2015
In-situ productivity, baseline nutrient levels	In-situ energy production relative to energy delivered with the subsidy	Anderson and Polis 1998; Marczak et al. 2007
Perimeter to area ratio and other landscape features	Connectivity with other ecosystems; exposure to physical forces	Polis and Hurd 1996
Physical environment	The impact of temperature, geomorphology, hydrodynamics, and other physical attributes	Orr et al. 2005; Smits et al. 2016; Morgan et al. 2018; Armstrong et al. 2010

(b)

ATTRIBUTES OF SUBSIDY DELIVERY	**RELATED CONSIDERATIONS**	**EXAMPLE**
Duration	Duration of subsidy (how long it remains in the recipient system) relative to the response rate of potential consumers	
Timing	Timing relative to the timing of other prey items (i.e. when other prey is abundant or scarce) and demand by consumers in the recipient system (e.g. during periods of growth or reproduction)	Takimoto et al. 2002; McCormick 2003; Wright et al. 2013; Sato et al. 2016
Frequency	The greater the frequency, the more likely subsidies will coincide with timing of need by consumers, who will adapt foraging responses	Anderson et al. 2008; Trebilco et al. 2016
Predictability	Consumer species may have evolved to use a predictable subsidy	Armstrong and Bond 2013
Magnitude	Energy content relative to in-situ energy production; whether the subsidy is delivered in pulses	Janetski et al. 2009; Spiller et al. 2010; Marcarelli et al. 2011
Density		Moore et al. 2008
Spatial extent and evenness/patchiness	Patchiness and the spatial match or mismatch with consumers	Meyer and Schultz 1985

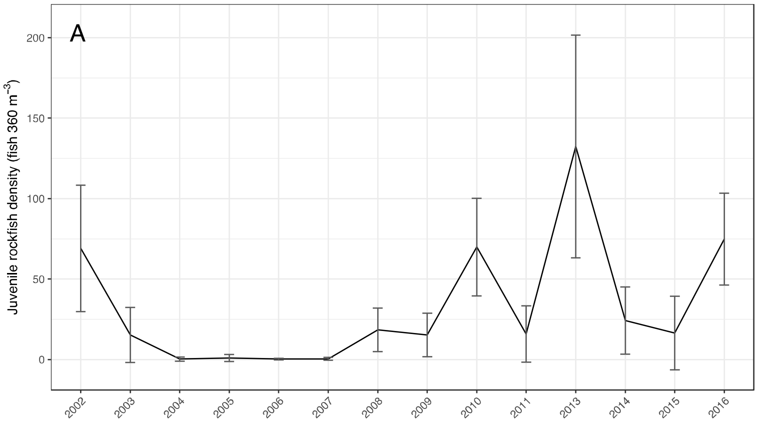
(c)

SUBSIDY ORGANISMS ATTRIBUTES	**RELATED CONSIDERATIONS**	**EXAMPLE**
Quality	Nitrogen, Carbon, lipid and energy content, content of specific fatty acids and other nutrients, bioavailability of the subsidy	Anderson and Polis 1999; Marcarelli et al. 2011; van Duers et al. 2016
Palatability, digestibility		Rodil et al. 2015; Dethier et al. 2014
Size relative to consumer size	Whether a consumer can consume the subsidy	Marczak et al. 2008
Ability to evade predators	Whether the consumer is able to capture and handle the subsidy organism	
Position in the water column	Physical location in the water column (especially relative to consumer foraging location)	Orr et al. 2005
Trophic Level		Leroux and Loreau 2008

(d)

CONSUMER ATTRIBUTES	**RELATED CONSIDERATIONS**	**EXAMPLE**
Limiting nutrients	Whether the subsidy delivers a limiting nutrient that might increase consumer growth or impact reproduction.	van Duers et al. 2016
Generation time	Generation time of the consumer relative to subsidy pulse frequency and duration	Yang et al. 2008; Holt 2008
Mobility	Ability of a consumer to access a remote subsidy	Paetzold et al. 2008; Mellbrand et al. 2011
Size	Gape width and prey size selectivity	van Duers et al. 2016
Conversion rate / assimilation efficiency		Small et al. 2013; Richardson and Wipfli 2016
Functional response to subsidy resources		Richardson and Wipfli 2016
Trophic level		Leroux and Loreau 2008
Trophic ecology (i.e. generalist or specialist)	Whether the consumer is specialized on subsidy prey or a given subsidy species	
Feeding mode		Netto and Meneghel 2014; von Biela et al. 2016
Habitat utilization		Beaudreau and Essington 2011
Anatomy and physiology		Armstrong and Bond 2013
Life history characteristics (e.g. growth rate)		Nowlin et al. 2008
Prey preference		Leroux and Loreau 2008

Temporal variability in rockfish recruitment to Stillwater Cove



Spatial variability in rockfish recruitment (2010)

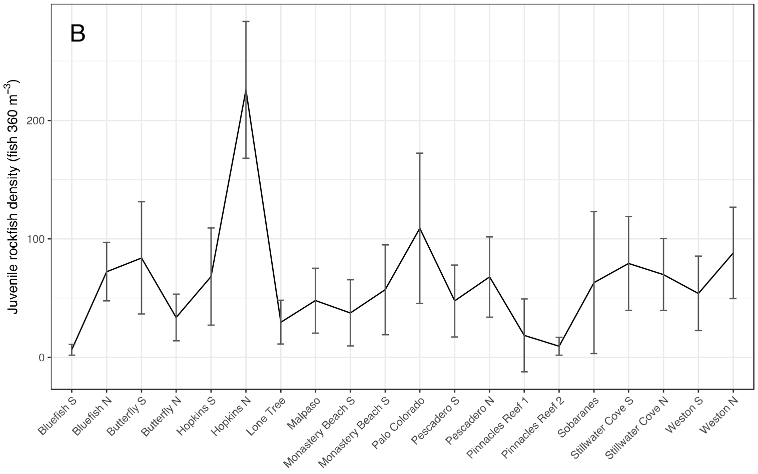


Figure 1.4. Spatial and temporal variability in the density of juvenile rockfish in the kelp forest water column. Error bars represent one standard deviation. A) Temporal variability is demonstrated with the time series of rockfish recruitment data from Stillwater Cove, Carmel Bay, California. B) Spatial variability is demonstrated with rockfish recruitment data from sites in and around Carmel Bay in 2010. For locations of sites, visit www.piscoweb.org.

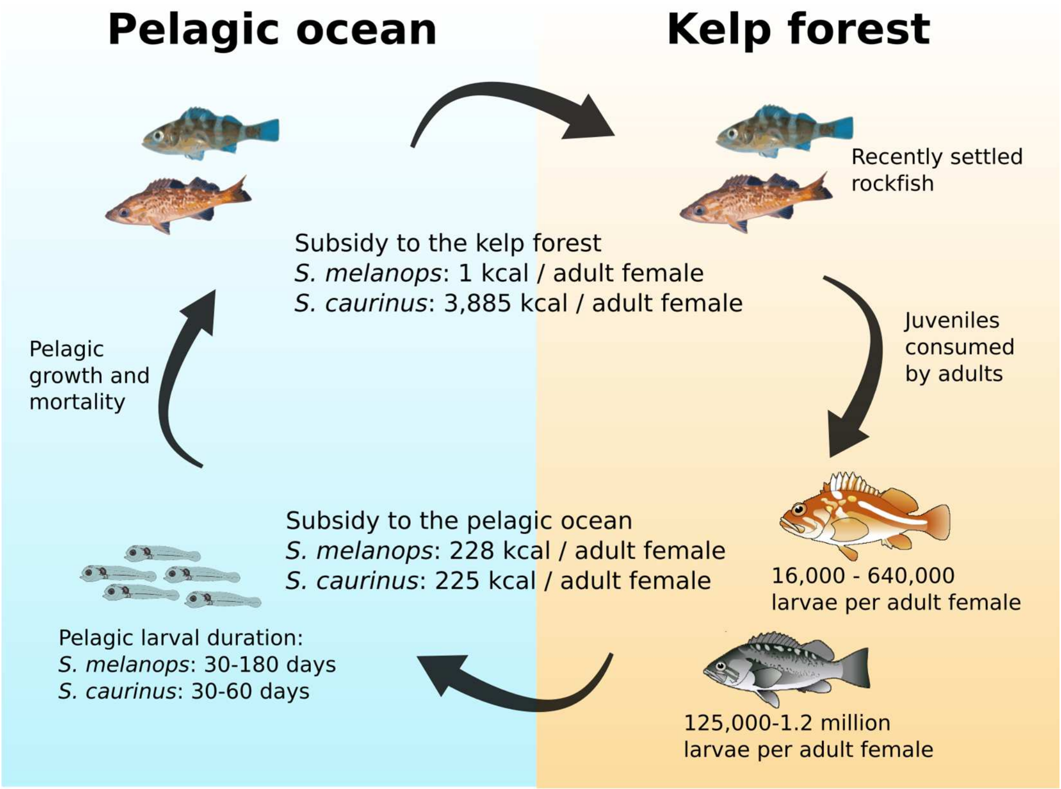


Figure 1.5. The net energy flow away from and back to the kelp forest ecosystem resulting from rockfish reproduction and the subsequent recruitment of larvae varies by species (see text for specifics regarding calculations). It is important to note that juvenile rockfish disperse widely and are not likely to return to the same kelp forest where they were born.

Chapter 2: Pelagic energy in the diets of a temperate reef fish assemblage

Abstract

The study of food webs provides important information about species interactions, the roles of species within an ecosystem, and the movement of energy through the marine environment. Kelp forests, one of the most productive ecosystems in the world, are home to a nearshore fish assemblage that accesses not only energy derived from the primary production of kelp, but also energy from phytoplankton- or pelagic-based primary production. However, the relative importance of these two energy sources for kelp forest species, and how relative importance varies over time, are not well known. I used a combination of stomach content analysis and carbon and nitrogen stable isotope analysis to explore the use of kelp- and phytoplankton-based carbon in central California from 2013-2016, a period that spans anomalous oceanic conditions associated with “the Blob” and El Niño. I show that the relative importance of phytoplankton-based carbon was higher in species that forage in the water column as opposed to on or near benthic substrates, and that carbon isotope values vary annually for those species. Further, diet contents and nitrogen isotope values (a proxy for trophic level) give insight into the particular prey taxa contributing to the importance of these two energy sources, and their variability. This research advances our

understanding of the importance of ecosystem connectivity in explaining the productivity of species and ecosystems, and suggests that more attention should be given to pelagic energy sources when studying nearshore food webs.

Introduction

The study of food webs provides important information about species interactions, the roles of species within an ecosystem, and the movement of energy through the marine environment. Kelp forests are among the most productive ecosystems in the world, supporting a diverse range of species (Schiel and Foster 2015). This productivity stems largely from two sources: dense stands of macroalgae producing energy within the kelp forest, and phytoplankton-based energy that enters the ecosystem from adjacent pelagic habitats (Duggins et al. 1989, Miller et al. 2011, Carr and Reed 2016). While some organisms feed entirely on either kelp-based or phytoplankton-based trophic pathways, many kelp forest organisms are generalist feeders that utilize both energy sources (Koenigs et al. 2015, Von Biela et al. 2016, Docmac et al. 2017).

The relative importance of these two energy sources varies among trophic level and functional groups, over time as basal resources fluctuate, with trophic structure of the ecosystem, and across oceanographic conditions. In southern California, the fish assemblage in kelp forests is receiving energy from both sources, but relying more on pelagic-based carbon (Koenigs et al. 2015). The relative proportions of the two energy sources vary by trophic level, with higher-level predators (*Paralabrax clathratus*, *Sebastes atrovirens*, and *Oxyjulus californica*) relying more heavily on kelp-based carbon. Of the fishes sampled, those in the planktivore functional guild that forage mainly in the water column (*Sebastes mystinus*, *Brachyistius frenatus*, and *Heterostichus rostratus*) consume more than 70% pelagic-based carbon (Koenigs et al. 2015). Similarly, benthic-feeding fishes in Chilean kelp forests representing a range of functional groups and trophic levels were found to rely more heavily on phytoplankton-based energy sources (Docmac et al. 2017). In contrast, several studies have found that kelp forest fish assemblages rely predominately on kelp-based carbon. On the west coast of North America, the relative contribution of kelp-based energy varies across the geographic range of two species with distinct feeding modes (*Sebastes melanops* and *Hexagrammos decagrammus*), with kelp-based contributions differing between the California Current, a seasonal upwelling system, and the Alaska Coast Current, a year-round downwelling system, apparently reflecting differences in the persistence of upwelling (von Biela et al. 2016). Similarly, the fish assemblage in Norwegian kelp forests rely on both kelp- and phytoplankton-based carbon, though kelp is dominant (Fredriksen 2003). Differences in the trophic structure of kelp forests with and without sea otters can also lead to differences in the contribution of kelp-based carbon, demonstrating that indirect effects propagated by keystone species can influence the relative importance of these two energy sources (Markel and Shurin

2015). Revealing the causes of this variation in energy source use will enable finer-scale resolution in our understanding of dietary preferences and trophic connections of economically and ecologically important nearshore fishes.

The identity of macroalgal-based carbon is relatively well-known. Canopy-forming kelps (*Macrocystis pyrifera* south of Santa Cruz, CA and *Nereocystis luetkeana* north of Monterey Bay, CA) are the dominant primary producers in kelp forests on the west coast of North America, with additional contributions from understory kelps, and benthic red and green algae (Springer et al. 2006). This energy enters the kelp forest food web through one of two pathways. Invertebrate kelp grazers serve as conduits of kelp-derived energy up the food chain, while detritivores and filter- and suspension-feeders consume drift kelp and suspended kelp particulates (Schiel and Foster 2015, Carr and Reed 2016). While phytoplankton do produce energy within the kelp forest, much of the phytoplankton-derived energy comes from primary production in the open ocean that is delivered to the kelp forest in many forms. Direct delivery of phytoplankton on currents, internal waves and other oceanographic forces provides kelp forest filter-feeders with a near-constant supply of oceanic energy. In addition, a wide diversity of trophic subsidies from the pelagic ocean (that derive their energy from phytoplankton) are delivered to kelp forests, including (but not limited to) invertebrates such as gelatinous zooplankton representing a range of trophic levels, invertebrate and juvenile fishes recruiting back to the kelp forest after a pelagic larval phase, and higher trophic level fishes that move in and out of nearshore systems (Chapter 1). These diverse pelagic subsidies result in a wide range of pathways for pelagic energy to enter kelp forest food webs and impact the many consumers that inhabit them.

The (non-cryptic) nearshore fish assemblage in central California is dominated by rockfishes in the genus *Sebastes*. They are ecologically important as meso-predators with diverse diets. Rockfish occupy habitats from the kelp forest canopy, to the midwater environment, to benthic cracks and crevices of the rocky reef. They are mobile, but typically have small home-ranges, making them vulnerable to changes in the local prey assemblage (Love 2002, Freiwald 2012). In this paper, I focus on four species of nearshore rockfish to represent a diversity of trophic strategies, foraging habitats, and feeding morphologies across the genus: Blue Rockfish (*Sebastes mystinus*), Black Rockfish (*S. melanops*), Kelp Rockfish (*S. atrovirens*) and Black-and-Yellow Rockfish (*S. chrysomelas*). While all four rockfishes are generalist predators with overlapping diets, studies over the last 40 years show interspecies diet variation (Love and Ebeling 1978, Hallacher and Roberts 1985, Hobson and Chess 1988, Lea et al. 1999, Hobson et al. 2001). I also include the demersal Black Surfperch (*Embiotoca jacksoni*) as a species that is not expected to prey on pelagic species coming into the kelp forest. The five fishes sampled range from planktivorous to piscivorous, have a range mouth sizes, and forage in different locations throughout the water column, giving some species (e.g. Blue Rockfish) more access to prey entering the kelp forest from the open ocean (Table 2.1).

While we know a substantial amount about the diet of these five nearshore fishes, a species' food habits and trophic niche are not necessarily static over time. Kelp forest prey assemblages vary on seasonal, annual and decadal scales, as does prey abundance. The relative abundance of phytoplankton- and macroalgal-derived energy in the kelp forest varies with the strength of upwelling and with oceanographic cycles such as the El Niño-Southern Oscillation (ENSO) (Bell et al. 2018). Furthermore, predator population sizes vary over time, altering predator-prey interactions (Stephens et al. 1984). Fish respond to these shifts with changes in diet composition and richness, and in the way that the diet of one predator overlaps with another (Lee and Sampson 2009, Gladics et al. 2014). As such, revisiting diet studies done in the 1980s and 1990s will serve to update and add to the diet information, and better understand if and how rockfish diet has changed over time. The first objective of this study is the characterize the diet of these five nearshore fishes from 2013-2016, a period of much oceanographic variability. Though 2013 did not see strong El Niño or La Niña conditions, a major shift occurred when 2014 brought "The Blob" ocean conditions to the west coast of the United States (Williams et al. 2016, Joh and Di Lorenzo 2017). Warm water temperatures of 2014 persisted through 2015, a year with strong El Niño conditions, before the ocean returned to more average conditions in 2016.

Ecologists use two dominant methods to study the food habits of fish: traditional stomach content analysis and the analysis of biomarkers, including stable carbon and nitrogen stable isotopes (in addition to direct observations of feeding in field or laboratory environments). To develop a deeper understanding of kelp forest trophic relationships, I combine these two methods. While stomach content analyses can give very high-resolution information about diet composition (even to the prey species level), there are well-known limitations of this method. Often partial digestion and mastication lead to ambiguous prey identifications and an abundance of unidentified prey material (Baker et al. 2014). In addition, stomach content analyses tend to underestimate the importance of soft-bodied prey items such as gelatinous zooplankton that digest quickly (Hyslop 1980, Arai et al. 2003). Further, a stomach content sample is a snapshot in time, and does not capture temporal diet variability. Extrapolating annual diet from this type of data is problematic.

Stable isotopes have become a standard method to integrate the temporal variability that is often lost with stomach content analysis, and to quantifying trophic relationships. The stable carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) value of a given organism reflect the prey items that it has consumed (after accounting for trophic fractionation due to predator metabolism). Trophic position can be determined by comparison to known $\delta^{15}N$ values from organisms at the base of the food web, while $\delta^{13}C$ values provide insight into the primary producer from which consumed energy came (kelp or phytoplankton in this case). Here I explore the relative contribution of phytoplankton- versus macroalgae-derived carbon (characterized by more ^{13}C-enriched values relative to phytoplankton) in the diet of nearshore fishes. I hypothesize that the five focal species will differ in the relative importance of these two carbon sources in their diet. Further, I expect that relative importance can be predicted by a species' predominate foraging location in the water column, with species foraging higher in the water column relying more heavily on phytoplankton-derived carbon.

Though analysis of bulk carbon and nitrogen isotopes is a coarse method for identifying prey species, it does provide explicit information about trophic level. I predict that species with larger gapes will feed on species with higher tropic levels, leading to wider-gaped species themselves occupying higher trophic levels. To further assess trophic interactions, diet content analysis will provide information about individual taxa contributing to a fish species' isotope signature. I expect that the identity of prey items contributing to the importance of phytoplankton-based energy will differ among species.

Bulk isotope values reflect the diet of a fish over the time period determined by the turnover of the tissue sampled. Muscle tissue of adult kelp forest fishes with a slow turnover time largely dependent on growth, likely integrates diet over at least one year (Perga and Gerdeaux 2005, Weidel et al. 2011). Alternately, liver tissue with a turnover rate that depends more on metabolism gives diet information that reflects a shorter period of time, likely approximately 6 months (Perga and Gerdeaux 2005, Miller 2006, Kim et al. 2012). This difference allows me to test whether trophic level or relative carbon contributions vary seasonally and/or annually. I hypothesize that there is temporal variability in pelagic carbon contribution and in trophic level, but that these patterns differ by species, especially as related to two prominent subsidies from the open ocean to the kelp forest. Juvenile rockfish exhibit strong variability in recruitment strength, virtually absent in some years, and recruiting in dense aggregations in others (Caselle et al. 2010, Ralston et al. 2012). Because juvenile rockfish are a high-protein and high energy prey item recruiting from the pelagic environment, I expect that adult fish will switch to a diet heavier in fish and show corresponding shifts in $\delta^{13}C$ and $\delta^{15}N$ during large recruitment years. For fish that forage on the influx of pelagic prey such as gelatinous zooplankton, the relative importance of macroalgal-based carbon versus phytoplankton-based carbon, and trophic level of those species will vary annually (since magnitude of pelagic prey influx varies by year) and seasonally (because upwelling dynamics influence delivery of pelagic carbon). I do not expect to see these seasonal and annual changes in Black Surfperch, a non-piscivore that forages near the benthos or Black and Yellow Rockfish, a benthic invertivore.

Methods

Study Area

I collected all fish samples in kelp forests of southern Monterey (36º38'N, 121º55'W) and Carmel Bays (36º33'N, 121º56'W) in central California where a narrow shelf positions kelp forests in close proximity to open ocean habitats. Collection site depth ranged from approximately 5-20 m, and took place within 350 m of shore. Surface water temperatures in the region range from approximately 13° - 16° C, and kelp forests here experience strong, seasonal upwelling in the spring and early summer months (Graham and Largiert 1997, Pennington and Chavez 2000). The hard benthic substrate across both bays is granitic and reefs are interspersed with sandy patches. Fish were collected in kelp forests representing a wide range of swell and wave exposure.

Relative importance of phytoplankton-based carbon to nearshore fishes

I used both stomach contents and stable isotope ratios to examine the relative importance of phytoplankton-based carbon in the diets of nearshore fishes. Stomach content samples were collected in the years 2013 to 2016, and muscle tissue for stable carbon isotope analysis was collected from 2014 to 2016 (fin tissue was also collected and compared with muscle tissue, Supplementary Figure 2.1). Fish samples were collected during daylight hours using either hook and line gear (squid bait was excluded from stomach content analysis), spear on SCUBA, or were salvaged from the local recreational fishery. Species, total length, and location of capture were recorded for all fishes sampled. To limit variation in diet due to ontogenetic dietary or habitat shifts, only fishes 22 cm and larger (20 cm and larger for Black-and-Yellow Rockfish) were included in this analysis.

Non-lethal sampling for stomach contents using gastric lavage was done when lethal sampling for other tissues was not required. Gastric lavage was performed using a 100 mL syringe attached to a 20-cm section of flexible polyethylene tubing (Hartleb and Moring 1995). The flexible tubing was inserted into the fish's stomach after it was anesthetized using MS-222. Seawater was then pumped into the stomach until water forced back through the esophagus was free of prey items. Prey items were collected with a mesh sieve, then immediately preserved in 95% ethanol. Fish that showed any signs of regurgitated stomach contents or stomach extrusion upon capture were excluded from the study. Fish sampled for stable isotopes were euthanized immediately following capture (excepting those salvaged from recreational fisheries) and put directly on ice. A 2 cm^3 section of anterior dorsal muscle was removed from each rockfish. All stable isotope samples were immediately frozen.

Stomach Content Analysis

Prey items and partial prey items were enumerated and identified to the lowest taxonomic level possible using a dissecting scope. Because many prey items could not be identified to species, I aggregated most prey into broad taxonomic groups. Bryozoan species (e.g. *Membranipora* spp.) found encrusting kelp were quantified as bryozoans. After sorting, prey items were blotted dry and weighed. Only stomachs with identifiable prey items were included in the analysis. For stomachs that contained identified prey items, unidentified material was sorted and weighed (to contribute to total weight), but excluded from subsequent analysis. I identified stomach contents from a total of 117 Kelp Rockfish ($\bar{x}$ total length ± SD; 30.7 ± 3.1 cm), 112 Black-and-Yellow Rockfish (27.3 ± 3.0 cm), 72 Black Rockfish (30.9 ± 2.9 cm), 64 Blue Rockfish (30.5 ± 4.4 cm), and 11 Black Surfperch (30.3 ± 3.4 cm). The percentage of empty stomachs for all years and all species was relatively high at 45.8%, though stomachs with very little prey material were categorized as empty due to the potential that stomach contents were regurgitated during hook-and-line capture. Cumulative prey curves generated using the vegan package in R and following Cailliet (1996) indicated that our sampling was sufficient to characterize diet by rockfish species (Supplementary Figure 2.2; Oksanen et al. 2016, R Core Team 2018). For each prey item, prey-specific abundances (by weight and number), frequency of occurrence (FO) and the prey-specific index of relative importance

(PSIRI) were calculated following Brown et al. 2011. Prey-specific abundance was calculated as

$$\%PX_{i,j} = \frac{\sum_{j=1}^{n} \%X_{i,j}}{n_i}$$

where i is a given prey item in stomach sample j, n_i is the total number of stomachs containing prey i, X is either the number (N) or weight (W), and PX is the prey-specific number or weight. Percent PSIRI values were calculated as

$$\%PSIRI_i = \frac{\%FO_i(\%PN_i + \%PW_i)}{2}$$

$\%FO_i$ was calculated as the number of stomach samples containing prey i divided by the total number of stomach samples.

Stable Isotope Sample Preparation and Analysis for Muscle Tissue

To examine basal carbon sources for each fish sampled, I measured $\delta^{13}C$ of muscle tissue for 60 Kelp Rockfish ($\bar{x}$ total length ± SD; 31.3 ± 2.5 cm), 57 Black-and-Yellow rockfish (27.6 ± 2.9 cm), 59 Black Rockfish (31.5 ± 2.7 cm), 52 Blue Rockfish (30.5 ± 3.7 cm), and 20 Black Surfperch (30.0 ± 3.9 cm). All tissue samples were dried for 48 hours in a Labconco FreeZone 4.5 lyophilizer. Lipid extraction was not done for muscle tissue, as the C:N ratio for those samples were found to be less than 3.5 (Pinnegar and Polunin 1999, Post et al. 2007, Markel and Shurin 2015). Dried samples were pulverized and homogenized with a ceramic mortar and pestle before a 0.5 mg portion of each sample (weighed to the nearest 0.001 mg) was placed in a tin capsule for analysis. I used a Carlo-Erba 1108 elemental analyzer coupled to an isotope ratio mass spectrometer (ThermoFinnigan Delta Plus XP IRMS) at the University of California Santa Cruz Stable Isotope Laboratory to analyze all samples for $\delta^{15}N$, $\delta^{13}C$, %N and %C. Data are reported in standard delta notation (‰) relative to the standards Vienna Pee Dee Belenmite for carbon and atmospheric N_2 for nitrogen, as:

$$\delta X = \left[\left(\frac{R_{sample}}{R_{standard}}\right) - 1\right] * 1000,$$

where X is either carbon or nitrogen, and R is the ratio $^{13}C/^{12}C$ or $^{15}N/^{14}N$ (Peterson and Fry 1987). Five percent of samples were run in duplicate with a mean difference between duplicate samples of 0.07 ± 0.07‰ for $\delta^{13}C$, 0.12 ± 0.12‰ for $\delta^{15}N$, and 0.1 ± 0.39 for C:N ratio. For duplicate samples, means were used in subsequent analyses.

Mixing models

I developed two-source Bayesian mixing models using the package simmr in R to estimate the proportion of carbon from each of two sources: kelp and phytoplankton (Parnell et al. 2010, Parnell and Inger 2016, R Core Team 2018). Inputs to mixing models include mean and standard deviation of isotope values for primary producers, mean and standard deviation of isotope values for the focal species of nearshore fish, trophic level estimates for each fish species, and the mean and standard deviation of trophic discrimination factors. I used the commonly-cited 1.0 ± 1.0‰ δ^{13}C, allowing error in these estimates to propagate through the model (Vander Zanden and Rasmussen 2001, Post 2002, Elsdon et al. 2010). No priors were used to inform the mixing models.

Because primary producers in nearshore marine systems exhibit large temporal variability in isotopic value, primary consumers were used as baseline trophic species to integrate this variation and represent an average baseline value (Parnell et al. 2010, Kurle and McWhorter 2017). Isotopic values for giant kelp vary seasonally, between distal and proximal blades, and by depth, in addition to variability seen among kelps and other kelp forest algae (Fredriksen 2003, Foley and Koch 2010, Drobnitch et al. 2017, Supplementary Figure 2.3). For example, for a study in southern California, Page et al. (2013) used macroalgae δ^{15}N values of 7.9-8.7‰, while kelp that I sampled in central California ranged from 5.5-13.9‰ (median: 9.1‰, mean: 9.1 ±

1.7‰). Kelp Isopods (*Idotea resecata)*, which graze directly on giant kelp, were used as a proxy in mixing models to represent macroalgae. They were collected haphazardly from a boat in kelp forests of Carmel Bay in June 2014, June and September 2015, and July 2016. *I. resecata* samples were acidified following drying to eliminate inorganic carbon (Carabel et al. 2006, Jaschinski et al. 2008). Per Carabel et al. (2006), samples were not washed with deionized water following acidification. Pelagic-grazing pyrosomes (used as a proxy in mixing models to represent phytoplankton) were collected in mid-water trawls in open ocean environments at the mouth of Monterey Bay (Site 1: 36° 44.77' N, 121° 59.87' W; Site 2: 36° 35.95' N, 122° 3.5' W) in April-May 2016 (Perissinotto et al. 2007). Whole pyrosomes were dried, crushed and weighed for isotopic analysis.

Feeding morphology and trophic level of nearshore fishes

To measure trophic level of each fish species, the same fish samples described in the previous section were sampled for δ^{15}N. Trophic position was estimated from δ^{15}N data according to the following equation:

$$TL_{consumer} = \lambda + (\delta^{15}N_{consumer} - (\delta^{15}N_{macroalgal\ end\ member} * a$$
$$+ \delta^{15}N_{phytoplankton\ end\ member} * \beta))/\Delta,$$

where end members (at the reference trophic level) are the primary consumers described above (and so, $\lambda = 2$), Δ is the δ^{15}N trophic enrichment factor from prey to predator, α is the proportion of macroalgal-based prey eaten by the consumer, and β is the proportion of phytoplankton-based prey eaten by the consumer, with α and β summing to one. Based on others' experiments on non-herbivorous fishes, I used a value of 3.4‰ as the nitrogen isotope trophic enrichment factor (Vander Zanden and Rasmussen 2001, Post 2002, Sweeting et al. 2007, Elsdon et al. 2010). A one-way analysis of variance (ANOVA) followed by pairwise Tukey's honest significant post-hoc tests was used to test for a difference in trophic level among species. The stomach content analysis described in the previous section was used to interpret and contextualize trophic level results.

Temporal variability in the trophic ecology of the nearshore fish assemblage

To test whether the contribution of pelagic carbon and/or trophic level of fish species varied on an annual or seasonal basis, samples were collected over four years and during both upwelling (April-July) and non-upwelling seasons (Jan-Mar, Aug-Dec). Stomach content samples were collected in 2013 (July – November), 2014 (June – October), 2015 (April – September) and 2016 (March – September). Samples for stable isotope analysis were collected in 2014 (June-October), 2015 (May-September) and 2016 (March-September). I assumed that muscle tissue has a one-year turnover time, and that liver tissue has a six-month turnover time. Upwelling and non-upwelling seasons were categorized to reflect the diet consumed rather than the months sampled (i.e. turnover time was considered when categorizing a sample as either "upwelling" or "non-upwelling"). Because diet content analysis captures what a fish consumed in the previous 48 hours, I used wind speed and direction data from the National Data Buoy Center Station 46042 (36.785° N, 122.398° W) to categorize upwelling at a higher temporal resolution. Wind speeds of greater than 5 meters per second in the southerly direction, and sustained for at least 4 days prior to the day of sampling were categorized as upwelling (García-Reyes et al. 2014). All other conditions were categorized as non-upwelling.

Because muscle tissue integrates diet over a long time period (estimated at one year), seasonal differences in carbon contribution and trophic level were tested using the more metabolically-active liver tissue. Livers have a higher lipid content, and because lipid synthesis leads to lower values of $\delta^{13}C$, lipids were extracted from a subset of liver samples (Kelp Rockfish, n = 23; Black-and-Yellow Rockfish, n = 24; Black Rockfish, n = 21; Blue Rockfish, n = 19) by accelerated solvent extraction using petroleum ether. Samples measured after lipid extraction reflect carbon assimilation more accurately (Kiljunen et al. 2006). The $\delta^{13}C$ and C:N values from liver samples analyzed both before and after lipid extraction were used to generate arithmetic lipid correction equations to mathematically normalize samples that did not undergo lipid extraction (Sweeting et al. 2006; see Supplementary text, Supplementary Figures 2.4-

2.5 and Supplementary Table 2.1 for details). Lipid-extracted liver samples were analyzed for $\delta^{13}C$, while livers that had not undergone lipid extraction were analyzed for $\delta^{15}N$, %N and %C. Liver tissue sample sizes were as follows: Kelp Rockfish (n=35), Black-and-Yellow Rockfish (n=35), Black Rockfish (n=35), Blue Rockfish (n=32), Black Surfperch (n=5). Differences between isotope values and season or year were tested with two-sample t-tests (season) or a one-way ANOVA followed by pairwise Tukey's honest significant post-hoc tests (year).

To test for a correlation between rockfish recruitment and changes in diet metrics, recruitment indices for juvenile rockfish were obtained from the Partnership for the Interdisciplinary Study of Coastal Oceans (PISCO, *unpublished data*). Recruitment anomalies were calculated based on the long-term average density of all species of juvenile *Sebastes* (less than 10 cm total length) across Carmel Bay sites on benthic and midwater fish surveys. Because these surveys take place before some species (i.e. the Kelp, Gopher, Black-and-Yellow Rockfish complex) migrate from kelp canopies deeper into the kelp forest, the data used do not reflect the annual influx of these species. The majority of species that are captured in the PISCO survey data are Black Rockfish, Blue Rockfish, and Olive Rockfish (*Sebastes serranoides*). For more information on PISCO methods, see www.piscoweb.org. To clarify how juvenile rockfish might be impacting isotopic values of adult nearshore fishes, stable carbon and nitrogen isotopes were measured for three life phases of juvenile rockfish: pelagic juveniles, newly recruited juveniles (arrived in the kelp forest from the pelagic ocean less than 3 days prior), and kelp forest juveniles. Pelagic juveniles were collected in mid-water trawls in open ocean environments at the mouth of Monterey Bay in April and May (see methods in Ralston et al. 2013), newly recruited juveniles were captured with SMURFs (for details on this method, see Ammann 2004), and kelp forest juveniles were captured in Carmel Bay, CA, on SCUBA with BINCKE nets (for details on this method, see Anderson and Carr 1998).

I used a multivariate statistical approach (Permutational Analysis of Variance; PERMANOVA) paired with ordination analyses to look at diet content differences among *Sebastes* spp., and for seasonal and interannual variability for individual species. PERMANOVA analyses were performed in PRIMER 6 with untransformed data to test for differences in the diet contents for each rockfish species among years and between seasons. A Type III sum of squares was used to account for the unbalanced design in my data (Clarke and Gorley 2006). Similarity percentages (SIMPER) were used to examine pair-wise comparisons between species and years, and to explore the prey species driving differences shown in the PERMANOVA results. These relationships were plotted and visualized using an ordination analysis with Bray-Curtis dissimilarity used to quantify distance.

Results

Relative importance of phytoplankton-based carbon to nearshore fishes

The relative importance of pelagic-based carbon in a kelp forest fish's diet was predicted by foraging location in the water column. Mixing models using the primary consumers kelp isopods and pyrosomes as end members (Figure 2.1) revealed that pelagic-based carbon contributed approximately 50% to the benthic foraging Black-and-Yellow Rockfish and Kelp Rockfish, with these more demersal species relying essentially equally on macroalgal- and phytoplankton-based carbon sources (Figure 2.2). Pelagic-based carbon was more important for mid-water feeding Black (~ 60%) and Blue (~ 64%) Rockfishes, which have lower δ^{13}C values than the other the fishes sampled. As expected based on previously collected diet information, Black Surfperch rely predominately (~ 60%) on kelp-derived carbon. In addition, all pairwise comparisons of δ^{13}C values differed between species (ANOVA, $p < 0.001$), with the exception of Kelp and Black-and-Yellow Rockfish ($p = 0.17$) (Figure 2.3).

The most important prey items identified in stomach contents with the prey-specific index of relative importance (PSIRI) also varied as predicted with species' position in the water column (Table 2.2; See Supplementary Table 2.2a-b for PSIRI information at lower taxonomic resolution and Supplementary text for species-level stomach content identifications). Despite interspecies differences in the contribution of pelagic-based carbon, several prey items identified as important in the PSIRI analysis were the same for all four *Sebastes* spp. For example, fish was the most important prey item for Kelp and Black Rockfishes, and within the top five for Blue and Black-and-Yellow Rockfishes. The ways that prey fish, especially juvenile rockfish, are contributing to the isotopic composition of adult rockfish depends on the life phase and trophic ecology of that prey fish. Newly recruited juvenile rockfish residing in the kelp canopy and water column, and likely more vulnerable to predation by Blue or Black Rockfishes, were found to have a more pelagic carbon isotope signature from their larval feeding in the open ocean (Figure 2.4). Conversely, juvenile rockfish that had been in the nearshore habitat for several weeks, and resided closer to the benthos where Kelp and Black-and-Yellow Rockfish forage, had a more macroalgal-based carbon signature. Isopods (predominately *I. resecata*) that live on kelp fronds and within the kelp canopy played a large role in the diet of Black Rockfish, likely contributing to the ~40% macroalgal-based carbon in their diet (see Supplementary Table 2.3 for information on isotope values of common prey items). Amphipods, a taxon generally abundant in microhabitats throughout the water column, were more important to Kelp Rockfish. Black-and-Yellow Rockfish rely on hard-bodied benthic invertebrates on the reef surface such as Brachyuran crabs, shrimps and other arthropods, in addition to octopus (likely *Octopus rubescens)*. Blue Rockfish rely on prey found in the water column, including tunicates, cnidarians, fish, and bryozoan-encrusted kelp. Notably, tunicates (predominately pelagic salps) were among the five most important prey taxa for three of the four *Sebastes* spp. (excluding the benthic

Black-and Yellow Rockfish). Black Surfperch stomachs showed that amphipods were the most important prey item, with prey species from that category found in 100% of stomachs sampled. Other benthic invertebrates such as small crabs, shelled gastropods, shrimps, isopods, and polychaetes were also common in Black Surfperch diets.

Feeding morphology and trophic level of nearshore fishes

Baseline $\delta^{15}N$ for isopods and pyrosomes were 9.7 ± 1.2‰ and 8.8 ± 1.0‰, respectively (Figure 2.1). Because both of these organisms are primary consumers grazing directly on macroalgae (isopods) and phytoplankton (pyrosomes), this difference reflects a baseline difference between nearshore and offshore systems (Foley and Koch 2010). Using these baseline values to scale trophic level calculations, I determined that trophic level in the nearshore fish assemblage was predicted by feeding morphology, with wider-gaped rockfishes occupying higher trophic levels. Maxillary length (a measure of mouth gape) for rockfishes ranges from Black-and-Yellow at the largest (40.2 mm), to Kelp (38.8 mm), Black (37.3 mm), then Blue Rockfish at the smallest (30.7 mm) (Roberts 1979). As predicted, there was a positive, linear relationship between isotopic estimates of trophic level from fish muscle and mean adjusted maxillary length of a rockfish species ($p < 0.01$, $R^2 = 0.93$). However, Black Surfperch have a much smaller gape than any of the rockfishes, yet fill the highest trophic level of the species measured, followed by Black-and-Yellow Rockfish, Black and Kelp Rockfishes (not different, ANOVA, $p = 0.62$), and Blue Rockfish (Figure 2.5). A linear relationship was also found between fish total length and the trophic level of that individual fish for both Kelp Rockfish ($p = 0.02$; $R^2 = 0.08$) and Black-and-Yellow Rockfish ($p < 0.001$; $R^2 = 0.23$) (Supplementary Figure 2.6).

Temporal variability in the trophic ecology of the nearshore fish assemblage

Differences in diet among the four rockfishes (as quantified using prey-specific abundance by number in a stomach sample) were consistent across sampling years, with the exception of 2015 when Black, Blue and Kelp Rockfishes all exhibited more similar diet compositions than each species exhibited with the other years (Figure 2.6). The 2015 diet is distinguished from the other years by the importance of crab megalopae and zoea, tunicates, Brachyuran crabs, and the relative unimportance of fish (including juvenile rockfish) and cephalopods (Supplementary Figure 2.7). The importance of tunicates in rockfish diet increased from 2013-2015 before decreasing again in 2016. Crab megalopae and zoea spiked in importance in 2015, though are relatively unimportant in other years. The importance of fish showed an opposite pattern to that of tunicates with high importance in 2013 and 2014, a drastic decrease in 2015, and subsequent increase in 2016 (Supplementary Figure 2.7). This aligns with an index of juvenile rockfish recruitment for the Monterey Bay area (including

Carmel Bay) from 1999 to 2016 where 2013 had the highest recorded recruitment, recruitment decreased from 2013-2015 before increasing again to moderate recruitment in 2016 (Figure 2.7). Interestingly, for the most strongly benthic-associated of the fish sampled, Black-and-Yellow Rockfish and Black Surfperch, diet remained static across the sampling years, with a heavy reliance on benthic invertebrates driving the similarity.

Mixing models indicated that Black and Blue Rockfishes rely more heavily than the other species on pelagic-based carbon. As such, I expected that $\delta^{13}C$ and $\delta^{15}N$ of liver tissue from these two species would vary seasonally and annually as the influx of pelagic prey changed. In fact, $\delta^{15}N$ of Black, Blue and Kelp Rockfish liver tissue dropped in 2015 (ANOVA, $p \leq 0.01$), a year of anomalous oceanographic conditions, and potentially the result of a diet more reliant on lower trophic-level, pelagic-based prey (such as crab megalopae). It then increased again in 2016 for Kelp and Black Rockfishes ($p \leq 0.01$). This pattern was not seen in Black-and-Yellow Rockfish, a fish not shown to rely on midwater pelagic influx, though they did exhibit an increase in trophic level in 2016 (Figure 2.8a). Black, Kelp and Black-and-Yellow Rockfish showed a seasonal difference in $\delta^{15}N$, occupying a lower trophic level in upwelling season (t-test, $p < 0.04$; Figure 2.8b). The only species with $\delta^{13}C$ values that varied by year was the Blue Rockfish (Figure 2.9a). Blue Rockfish $\delta^{13}C$ trended less negative from 2014-2015 ($p = 0.08$) before dropping significantly from 2015-2016 ($p < 0.001$).

None of the species showed significant seasonal variability in $\delta^{13}C$ values (Figure 2.9b).

Discussion

Phytoplankton-based carbon from gelatinous organisms and recruiting fish subsidizes the kelp forest fish assemblage

My results show that carbon derived from pelagic primary production plays a major role in the nearshore fish assemblage in the Monterey Bay area of central California. The relative importance of phytoplankton-based carbon differs by species, and that importance can largely be determined by predominate foraging location in the water column. Black Surfperch and Black-and-Yellow Rockfish forage near the benthos and rely more heavily on macroalgal-based carbon (major prey items are Brachyuran crabs and octopus for Black-and-Yellow Rockfish and amphipods for Black Surfperch). Black and Rockfish and Blue Rockfish are known mid-water foragers, and thus encounter and exploit pelagic sources of energy more frequently. However, Blue Rockfish diet can be distinguished by a lack of benthic invertebrates and the relative unimportance of fish as prey, and Black Rockfish utilize both of these taxa. Black Rockfish and Kelp Rockfish diets overlap substantially, though Kelp Rockfish (a more demersal forager) consumes more macroalgal-derived carbon.

Results from the diet content analysis give insight into taxa contributing to the pelagic signal. Gelatinous organisms that typically live in the open ocean are advected to the kelp forest during downwelling or relaxation events. Though tunicates (both salps and pyrosomes) were the most common gelatinous organisms observed, both cnidarians and ctenophores were also identified. I expect that many of the prey items classified as ‘unknown’, and thus excluded from further analysis also fall into the category of gelatinous organisms. These prey items digest quickly, and are likely underestimated in the PSIRI results. Suspension and filter-feeding organisms such as benthic tunicates, barnacles, and bryozoans likely consume substantial phytoplankton-based energy that is then passed up the food chain to nearshore fishes, though they also consume suspended algal particulates (Miller and Page 2012). Previous studies have found Thaliaceans (pelagic salps) to be important prey categories for Blue Rockfish, especially during upwelling, but that they are not typically consumed by Kelp, Black and Black-and-Yellow Rockfish (Hallacher and Roberts 1985, Hobson and Chess 1988). My results suggest that the importance of salps as prey for the nearshore fish assemblage extended beyond Blue Rockfish during certain conditions. Finally, recruiting juvenile rockfish and crabs represent an influx of pelagic energy into the kelp forest. The juvenile life phase makes both rockfish young-of-the-year and crab megalopae vulnerable to predation, especially during years of high recruitment (such as 2013 and 2014 for juvenile rockfish when adults seem to shift toward fish as prey items). Notably, though recently recruited rockfish exhibited a more pelagic $\delta^{13}C$

signature than those juvenile rockfish that had lived for several weeks or months in the kelp forest, even the recently recruited rockfish showed some macroalgae signal. This suggests that the carbon contribution of a newly recruited juvenile rockfish to an adult rockfish predator is not entirely pelagic-based. A wide variety of benthic organisms contribute to the macroalgal signal detected in adult rockfishes. Brachyuran and anomuran crabs, isopods, amphipods, benthic shrimps, and juvenile fish that have transitioned to a kelp forest diet all move kelp-based carbon up the food chain. Black-and-Yellow Rockfish forage almost entirely on benthic organisms, and might be expected to have a stronger macroalgal signal. However, octopus, an important prey item has $\delta^{13}C$ values indicating use of phytoplankton-based energy (Supplementary Table 2.3).

It is possible that a portion of the $\delta^{13}C$ signal interpreted as pelagic instead reflects use of red algae. A wide diversity of red algae reside in California kelp forests, and likely provide food for benthic invertebrates via direct grazing and through detrital pathways. A sample of red algae from Carmel Bay (n = 5) collected in September 2015 had $\delta^{13}C$ values that were more ^{13}C-depleted than those typically reported for phytoplankton ($\delta^{13}C$: -28.9 ± 5.0‰, $\delta^{15}N$: 7.5 ± 0.8‰) (Zuercher, *unpublished data*). These are consistent with values measured in Norwegian kelp forests where two multi-species groups of red algae were analyzed, one group with $\delta^{13}C$ values ranging from -18.9 through -22.3‰, and another group with even lower values of -32.9

through -34.4‰ (Raven et al. 2002, Fredriksen 2003). This could explain why Black Surfperch, with a diet of predominately benthic kelp-feeding organisms yielded mixing model results showing a contribution of 40% phytoplankton-based carbon.

Trophic level of kelp forest rockfishes

As hypothesized, feeding morphology (measured by maxillary length) showed a positive relationship with trophic level for the rockfishes. However, this pattern did not hold for the Black Surfperch. The relatively high trophic level of Black Surfperch is seemingly not explained by stomach contents identified in this study, or information on diet in the literature (Schmitt and Coyer 1982, Holbrook and Schmitt 1984). A more in-depth look into the species composition of amphipods in Black Surfperch diets showed that very few individuals were from taxa known to forage on decomposing organisms (and thus occupying higher trophic levels). Further investigation is needed to uncover the prey items contributing to the high trophic levels measured here.

The trophic levels estimated here using muscle tissue are comparable to those reported by Page et al. (2003) for Blue and Kelp Rockfishes collected in kelp forests of southern California. Similarly, trophic level results for Gopher Rockfish (*S. carnatus*) correspond to the level reported here for and Black-and-Yellow Rockfish, a morphologically and ecologically-similar species. However, absolute trophic level results should be interpreted with care, as there are no experimentally-determined estimates for trophic enrichment for adult rockfishes or Black Surfperch to my knowledge. Trophic enrichment factors (TEFs) can vary by species, location and tissue type, and trophic level calculations are sensitive to changes in the TEF constant used. Future studies would benefit from species-specific, experimentally-determined TEFs.

The only fish that did not exhibit a seasonal shift in trophic level was the Blue Rockfish. All others occupy a lower trophic level during upwelling season. This is contrary to the expectation that trophic level would increase during upwelling-mediated pulses of rockfish recruitment. However, the seasonal shift may not be related to rockfish diet at all. This could be due to a seasonal decrease in baseline $\delta^{15}N$ values of *Macrocystis* during upwelling season that is only reflected in species that have more macroalgal-dominated diets (Foley and Koch 2010). Blue Rockfish use less macroalgal-based carbon than any of the other species, and as such, a seasonal baseline shift in *Macrocystis* is perhaps not reflected.

2015: an anomalous year for Sebastes spp. diet

Black, Kelp and Blue Rockfishes shifted away from juvenile rockfish as prey in 2015, a low recruitment year compared to 2013, 2014 and 2016. Interestingly, though 2015 was a low recruitment year for the time period addressed in this study, it was a moderate recruitment year compared with very low recruitment in 2005-2008 and 2011-2012. In these very low recruitment years, adult rockfishes likely rely even less on fish as prey, and more heavily on kelp forest invertebrates and any pelagic subsidies that might be available. The switch seen in this study from fish to an assemblage of pelagic prey items (including tunicates, crab megalopae and zoea) was not accompanied by a corresponding decrease in $\delta^{13}C$ reflecting a more pelagic carbon-heavy diet, except in Blue Rockfish. Perhaps the loss of pelagic carbon from energy-rich recruiting rockfishes is not fully compensated for by pulses of pelagic organisms during El Niño conditions. However, I did find a downward shift in trophic level in 2015 as may be expected with a switch from fish to gelatinous invertebrates in 2015. This downward shift was not seen in Black-and-Yellow Rockfish, a species that forages near the benthos (and thus likely encounters gelatinous zooplankton less frequently) and does not rely heavily on fish in their diet. However, because the trend for all rockfishes (including Black-and-Yellow Rockfish) was a decrease in $\delta^{15}N$ in 2015, a shift in baseline $\delta^{15}N$ in either the nearshore or offshore systems in that year could be at least partially responsible. Foley and Koch (2010) showed 3‰ changes in the $\delta^{15}N$ values of *Macrocystis pyrifera* (giant kelp) between samples collected in spring to early summer and those collected in late summer to winter, suggesting that it is possible that the apparent decrease in trophic level reported here is actually a result of a baseline shift. Moreover, while the shift from fish to pelagic salps and other pelagic prey in 2015 is also supported in the diet content data, there are other possible drivers of the shift toward more phytoplankton-derived carbon. Kelp production typically declines during El Niño events (such as 2015), potentially limiting kelp-based carbon in the entire system. Similarly, kelp production declines for ecological reasons, such as the shift from a kelp forest state to a barrens state caused by herbivore outbreaks occurring in central California starting in approximately 2015. These shifts highlight the role that both energy sources play in maintaining the high productivity (i.e. high increase in biomass of an organism per unit time and space) of kelp forest fish assemblages in a highly variable marine environment.

Significance beyond central California

The mixing model results presented here are consistent with findings of similar studies done in other regions of California (Page et al. 2013, Koenigs et al. 2015, von Biela et al. 2016). Despite differences in upwelling dynamics between central and southern California, kelp forest fishes seem to access pelagic-based carbon in similar relative proportions. Accessing energy from pelagic primary producers is not uncommon for fish dwelling in nearshore marine ecosystems. Stable isotopes and stomach content methods have revealed that the majority of fish residing in mangrove habitats rely predominately on external sources of energy, and salt marsh infauna have been shown to receive large dietary contributions from phytoplankton-based sources (Igulu et al. 2013). However, despite being ecologically connected to pelagic ecosystems, higher trophic levels in the nearshore Dutch Wadden Sea rely predominately on benthic primary production, emphasizing that the relative contribution of these components is context and system dependent (Christianen et al. 2017).

I selected species for this study that typify different attributes, such as foraging habitat in the water column, and feeding morphology. Though these five fishes coexist in central California, kelp forest fish assemblages throughout the world typically support a set of species in the same function guilds (i.e. planktivores, generalist demersal predators, and invertivores). I expect that the results presented here for the central California nearshore fish assemblage are representative of others around the globe.

Conclusions

The kelp forest ecosystem is known for extremely high productivity as a result of accessing both benthic and pelagic sources of energy, and the diet of nearshore kelp forest fishes highlights this benthic-pelagic coupling. Though the focal rockfishes in this study spend their entire adult lives in the kelp forest ecosystem, productivity (i.e. growth) of these species depends quite heavily on donor-controlled resources coming from the pelagic ocean. My results show that species' behavioral (habitat affinity in the water column) and morphological traits contribute to variability in the contributions of these two energy sources. Moreover, my results imply that the contributions of carbon sources not only vary by consumer species, but also as production of phytoplankton (and subsequent influx of energy to the kelp forest) and macroalgae change.

This study has advanced our understanding of the importance of ecosystem connectivity in explaining the productivity of species and ecosystems. Marine ecosystems are constantly changing, and food webs follow suit. Changes to habitat structure, such as is occurring on the west coast of the United States through the loss of giant kelp, and variation in circulation patterns will likely drive further changes in the importance of phytoplankton-based energy to the nearshore fish assemblage. Whether the ability to access more than one basal energy source infers resilience and/or stability on the kelp forest ecosystem remains unanswered. Using two energy sources could exacerbate stress in years of low productivity or could buffer against this stress. To truly understand how kelp forest communities function, we must give more attention to dynamics of pelagic energy sources, the conditions that lead to changes in the influx of this energy to the nearshore environment, and the ecosystem-level consequences of these changes.

Tables and Figures

Table 2.1. Blue Rockfish inhabit the water column and are planktivorous, while Black Rockfish, also an active-swimming, midwater fish, tend to be piscivorous. Kelp Rockfish are demersal with a broad diet, and Black-and-Yellow Rockfish and Black Surfperch are largely benthic invertivores. Gape width differs by species as well, with small-mouthed Blue Rockfish constrained to smaller prey, and Black, Kelp, and Black-and-Yellow Rockfishes able to consume larger crabs, octopus and fishes.

Species	**Functional guild**	**Foraging location**	**Maxillary length (i.e. gape width)**
Blue Rockfish	Planktivore	Midwater	30.7 mm
Black Rockfish	Piscivore	Midwater	37.3 mm
Kelp Rockfish	Generalist predator	Midwater/Benthos	38.8 mm
Black Surfperch	Small invertivore	Midwater/Benthos	Unknown; smaller than Blue Rockfish
Black-and-Yellow Rockfish	Benthic invertivore	Benthos	40.2 mm

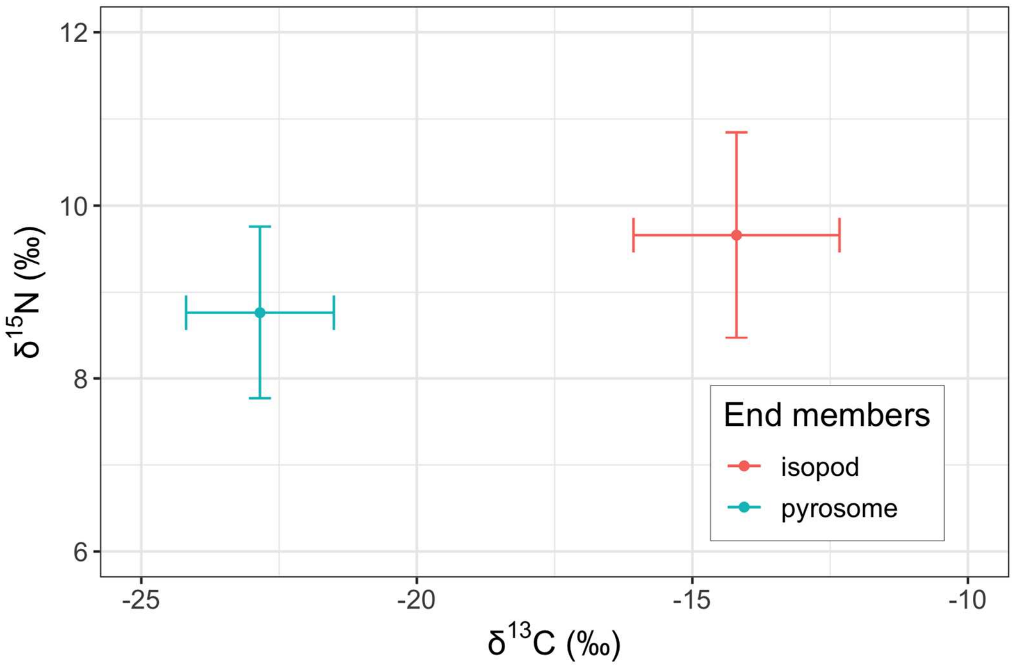


Figure 2.1. Primary consumers were used as end members for a phytoplankton-based food chain (primary consumer – *Pyrosoma atlanticum*) and macroalgal-based food chain (primary consumer – *Idotea resecata*). Biplot shows mean values with error bars representing the standard deviation. Mean δ^{13}C value (± SD) for pyrosomes was -22.9‰ ± 1.3‰, and for kelp isopods was -14.2‰ ± 1.9‰. Mean δ^{15}N value (± SD) for pyrosomes was -9.7 ± 1.2‰, and for kelp isopods was 8.8 ± 1.0‰, reflecting a nearshore-offshore baseline difference.

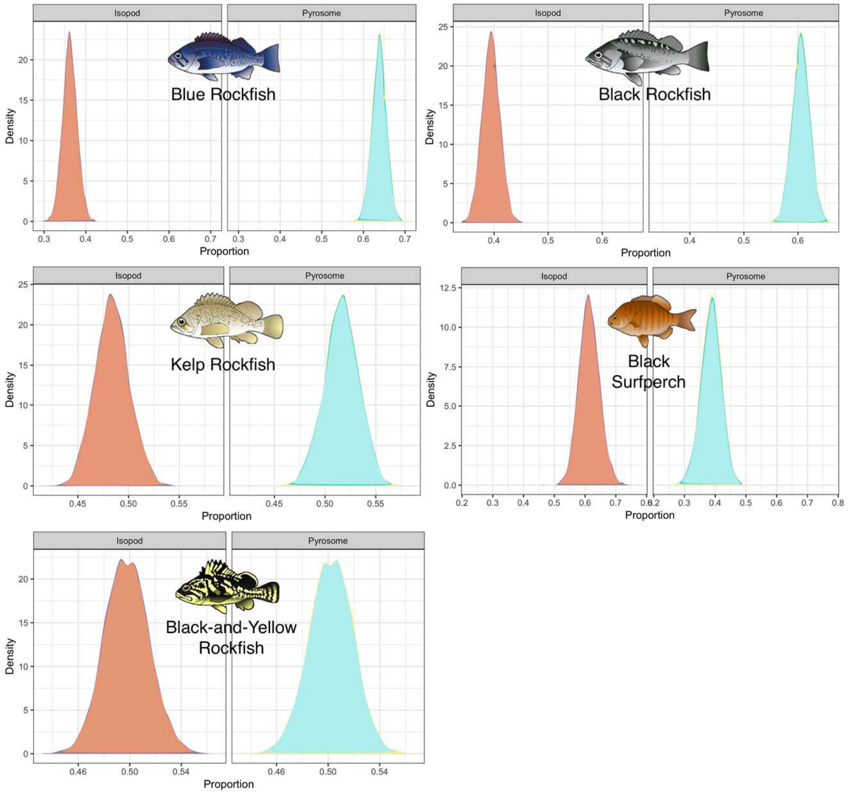


Figure 2.2. Proportional contributions of macroalgal- (Kelp Isopod) and phytoplankton-based (Pyrosome) carbon in the diets of kelp forest fishes. Results are posterior probabilities based on a two-source Bayesian mixing model using $\delta^{13}C$ values derived from muscle tissue.

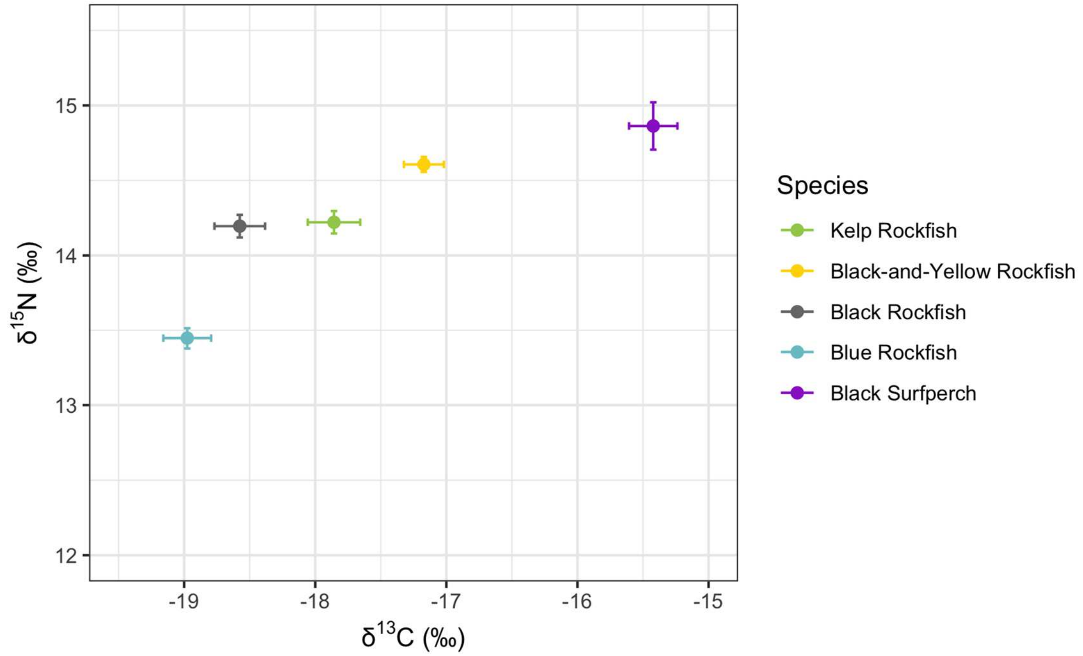


Figure 2.3. δ^{13}C and δ^{15}N for muscle tissue of all study species ($\bar{x}$ ± SE). Pairwise comparisons showed that δ^{13}C values of all species were significantly different from others (ANOVA, $p < 0.001$), with the exception of Black-and-Yellow and Kelp Rockfishes ($p = 0.167$). δ^{15}N values of all species were significantly different from others ($p < 0.001$; Black and Black-and-Yellow Rockfishes, $p < 0.05$), with the exception of Kelp and Black Rockfishes ($p = 0.62$).

Table 2.2. Diet composition of four species of nearshore *Sebastes* rockfish (a-c, e) and Black Surfperch (d) by percent frequency of occurrence (%FO), percent prey-specific number (%PN), percent prey-specific volume (%PV) and percent prey-specific index of relative importance (%PSIRI). Diet data with prey categorized at a higher taxonomic resolution can be found in Supplementary Tables 2.2a-b.

***a. Sebastes mystinus*, Blue Rockfish (mid-water forager)**

Prey Category	%FO	%PN	%PW	%PSIRI
Tunicate	20.31	82.37	74.95	15.98
Algae	28.13	51.10	47.10	13.80
Fish	26.56	43.31	48.71	12.22
Cnidarian	17.19	66.74	68.40	11.61
Bryozoan (incl. algae encrusted with *Membranipora* spp.)	14.06	62.17	58.35	8.47
Other or unidentified arthropod	15.63	28.03	23.19	4.00
Cephalopod	6.25	52.08	72.57	3.90
Crab megalopa / zoea	9.38	52.10	25.42	3.63
Brachyuran crab	4.69	50.00	57.77	2.53
Amphipod	10.94	30.17	0.63	1.68
Ctenophore	1.56	90.90	84.46	1.37
Caridean shrimp	4.69	44.44	13.77	1.36
Polychaete	3.13	50.00	5.60	0.87
Mollusc (excluding Cephalopoda)	1.56	50.00	5.60	0.87
Copepod	1.56	33.33	0.81	0.27

***b. Sebastes melanops*, Black Rockfish (mid-water forager)**

Prey Category	%FO	%PN	%PW	%PSIRI
Fish	55.56	69.95	82.32	42.30
Isopod	31.94	46.26	42.31	14.15
Tunicate	11.11	83.39	63.56	8.16
Cephalopod	8.33	62.78	97.11	6.66
Other or unidentified arthropod	22.22	30.04	16.13	5.13
Amphipod	16.67	31.46	10.36	3.48
Crab megalopa / zoea	11.11	35.70	14.18	2.77
Polychaete	6.94	37.33	37.52	2.60
Mollusc (excluding Cephalopoda)	5.56	43.59	37.28	2.25
Barnacle	2.78	33.33	68.93	1.42
Ctenophore	1.39	100.00	100.00	1.39
Brachyuran crab	4.17	31.33	33.18	1.34
Cnidarian	2.78	38.33	4.68	0.60
Caridean shrimp	4.17	24.44	2.00	0.55
Krill	4.17	20.51	1.89	0.47
Anomuran crab	1.39	50.00	13.35	0.44
Bryozoan (incl. algae encrusted with *Membranipora* spp.)	1.39	50.00	0.11	0.34
Copepod	1.39	33.33	12.31	0.32
Algae	2.78	3.78	2.83	0.09

***c. Sebastes atrovirens*, Kelp Rockfish (demersal forager)**

Prey Category	%FO	%PN	%PW	%PSIRI
Fish	36.75	47.07	71.72	21.83
Amphipod	48.72	38.99	19.31	14.20
Tunicate	14.53	82.50	74.71	11.42
Other or unidentified arthropod	29.91	27.95	33.14	9.14
Caridean shrimp	32.47	27.75	28.17	9.08
Brachyuran crab	13.68	44.50	58.30	7.03
Isopod	33.33	21.66	18.91	6.76
Cephalopod	10.26	36.77	71.82	5.57
Crab megalopa / zoea	18.80	38.38	15.38	5.05
Barnacle	3.42	39.09	46.23	1.46
Mollusc (excluding Cephalopoda)	7.69	23.36	10.83	1.31
Anomuran crab	2.56	32.32	32.29	0.83
Polychaete	4.27	25.58	4.42	0.64
Cnidarian	1.71	18.95	22.11	0.35
Algae	3.42	14.91	1.91	0.29
Copepod	1.71	26.85	0.20	0.23
Krill	0.85	33.33	0.04	0.14
Bryozoan (incl. algae encrusted with *Membranipora* spp.)	1.71	5.32	0.27	0.05

***d. Embiotoca jacksoni*, Black surfperch (demersal forager)**

Prey Category	%FO	%PN	%PW	%PSIRI
Amphipod	100.00	70.86	15.45	43.15
Brachyuran / Anomuran crab	100.00	5.55	5.94	5.74
Other or unidentified arthropod	45.45	14.88	3.60	4.20
Mollusc (excluding Cephalopoda)*	100.00	4.87	2.80	3.83
Algae	81.82	4.71	2.24	2.84
Isopod	90.91	4.78	1.14	2.69
Polychaete	81.82	2.78	3.65	2.63
Tunicate	9.09	4.31	11.88	0.74
Echinoderm	45.45	0.49	0.91	0.32
Leptostraca	18.18	2.00	0.81	0.26
San crab (Hippidae)	9.09	0.55	4.45	0.22
Caridean shrimp	36.36	0.32	0.59	0.17
Porifera (sponge)	18.18	0.29	1.50	0.16
Megalopa / zoea	9.09	0.18	1.51	0.08

** All prey items in the 'Mollusc (excluding Cephalopoda)' category for Black Surfperch were small, shelled gastropods*

***e. Sebastes chrysomelas*, Black-and-Yellow Rockfish (benthic forager)**

Prey Category	%FO	%PN	%PW	%PSIRI
Brachyuran crab	44.64	60.34	61.15	27.12
Cephalopod	25.00	63.10	80.29	17.92
Other or unidentified arthropod	22.32	51.74	54.35	11.84
Caridean shrimp	20.54	56.99	46.96	10.67
Fish	18.75	45.77	57.81	9.71
Anomuran crab	12.50	50.68	60.18	6.93
Mollusc (excluding Cephalopoda)	10.71	39.98	34.44	3.99
Polychaete	8.04	41.20	34.18	3.03
Echinoderm	4.46	44.00	43.63	1.96
Tunicate	1.79	70.00	55.97	1.12
Algae	5.36	22.68	9.44	0.86
Bryozoan (incl. algae encrusted with *Membranipora* spp.)	3.57	39.58	3.47	0.77
Amphipod	6.25	21.34	1.14	0.70
Cnidarian	1.79	45.00	32.71	0.69
Barnacle	1.79	47.78	22.88	0.63
Isopod	1.79	35.00	18.78	0.48
Nematode	0.89	50.00	17.08	0.30

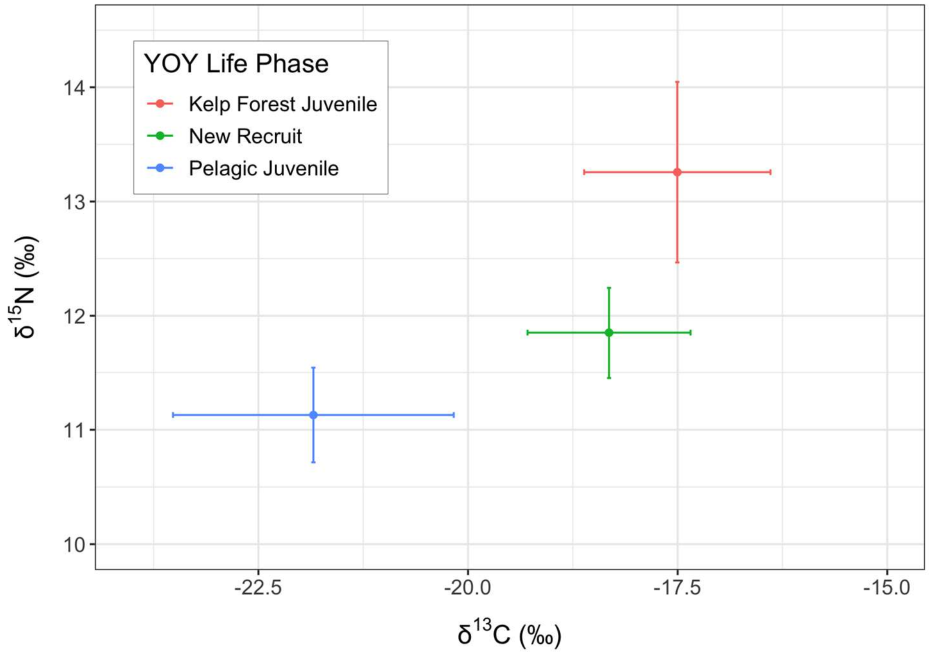


Figure 2.4. Carbon and nitrogen isotopic values ($\bar{x} \pm$ SD) for juvenile rockfish (YOY) muscle tissue (Pelagic juveniles: Blue Rockfish and the KGBC Complex (*Sebastes atrovirens, Sebastes carnatus, Sebastes chrysomelas, Sebastes caurinus);* New Recruits: KGBC Complex and the OYT Complex (*Sebastes flavidus, Sebastes serranoides*); Kelp Forest Juveniles: KGBC Complex, OYT Complex, and Blue Rockfish. Pairwise comparisons confirm that the δ^{13}C of pelagic juveniles is lower than both other life phases ($p < 0.01$), which are not different from each other ($p = 0.051$). The well-known baseline difference in δ^{15}N between nearshore and offshore marine environments (approximately 1‰) is partially responsible for the differences in δ^{15}N among life phases. However, with a 1‰ correction, δ^{15}N of pelagic juveniles are still significantly different from kelp forest juveniles ($p < 0.001$).

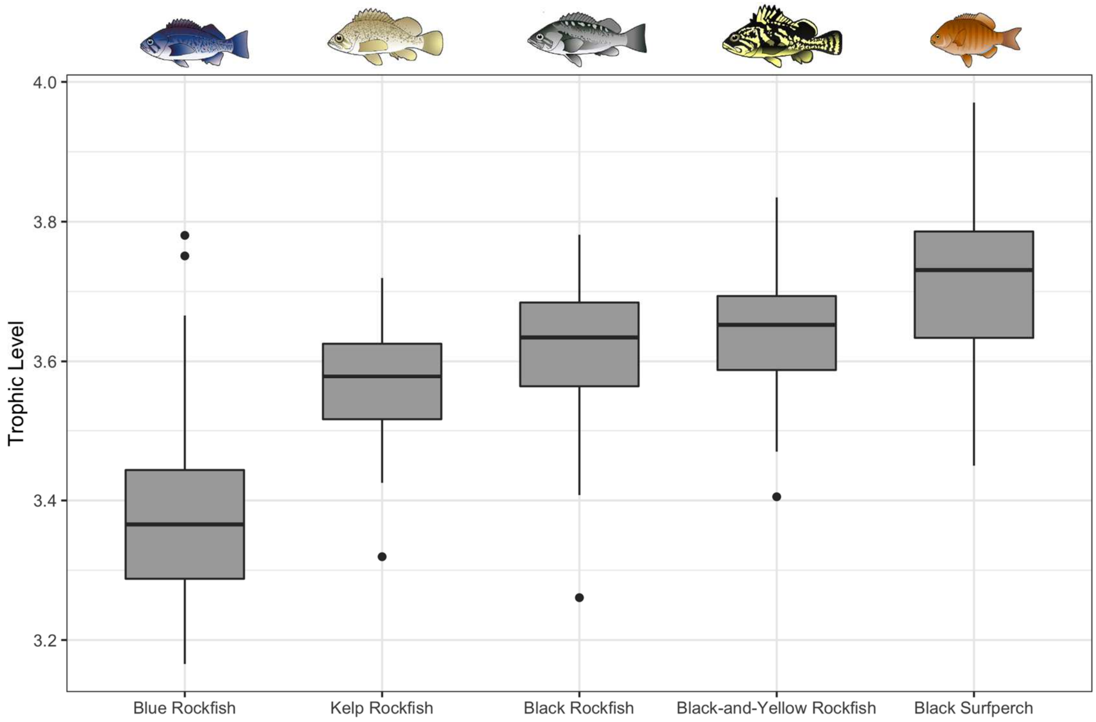


Figure 2.5. Trophic level as calculated using muscle tissue with Kelp Isopods and Pyrosomes as end members (trophic level 2). Boxplots depict the median (bold line), first (25th) quantile (lower hinge), third (75th) quantile (upper hinge), maximum (upper whisker), minimum (lower whisker), and outliers (black dots). There is no difference between Black Rockfish and Black and Yellow Rockfish ($p = 0.62$) or Black Rockfish and Kelp Rockfish (0.06). All other pairwise comparisons are significant ($p < 0.001$, except Black Surfperch and Black-and-Yellow Rockfish, $p = 0.02$).

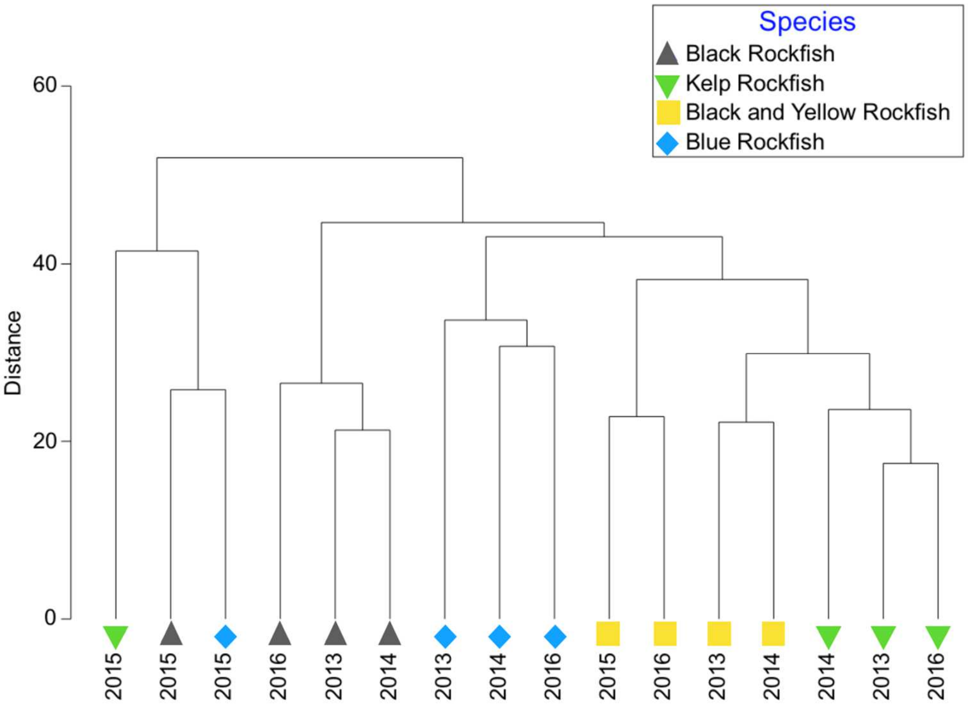


Figure 2.6. Results from ordination analyses revealed that the diets of Kelp, Black and Blue Rockfish were more similar to each other in 2015, than to diets more typical for each species in other years.

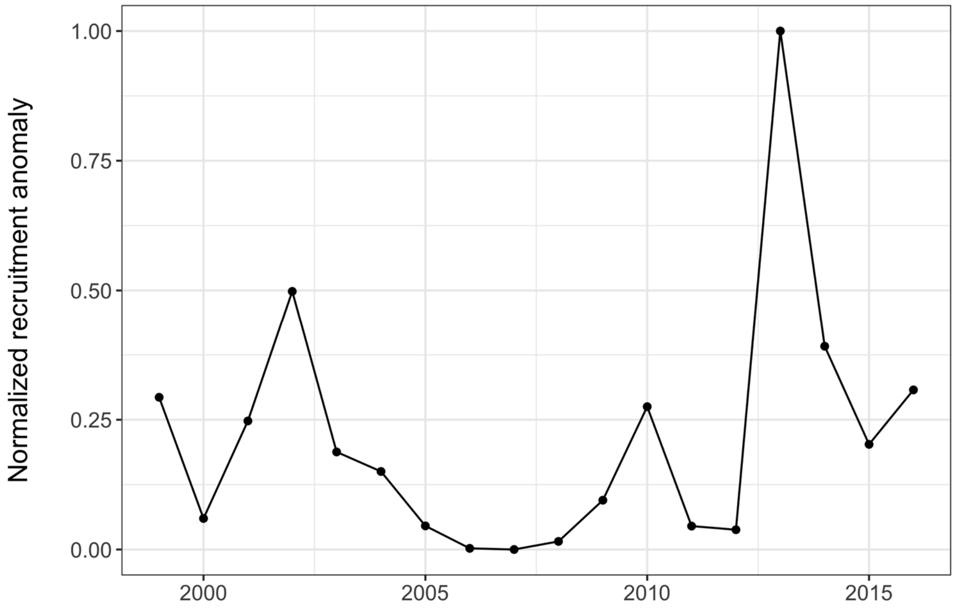
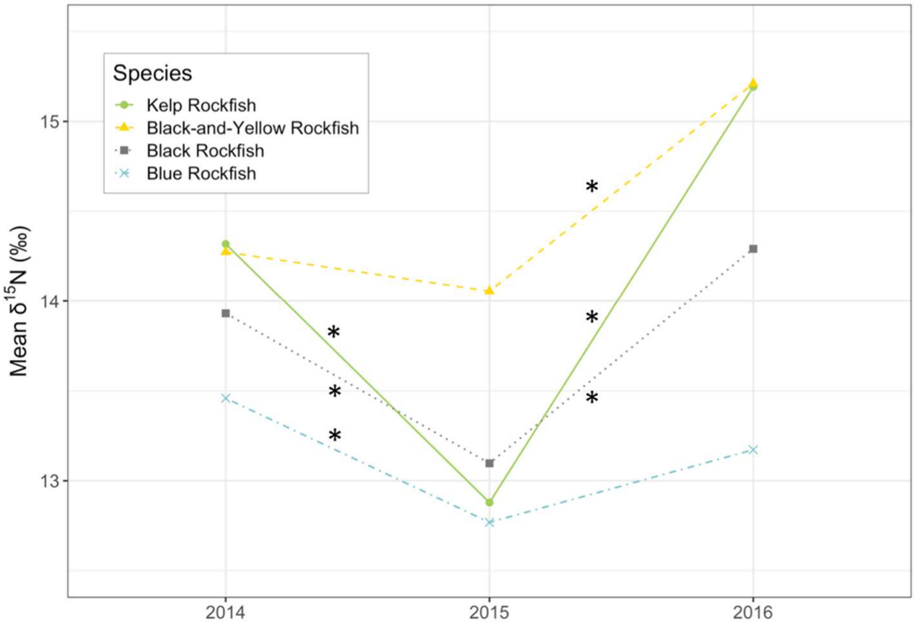


Figure 2.7. The rockfish recruitment anomaly (normalized to a 0-1 scale) for 1999 to 2016 for PISCO sites in Monterey and Carmel Bays.

(a)


Species
Kelp Rockfish
Black-and-Yellow Rockfish
Black Rockfish
Blue Rockfish
Mean δ15N (‰)
15
14
13
2014
2015
2016
*
*
*
*
*
*

(b)

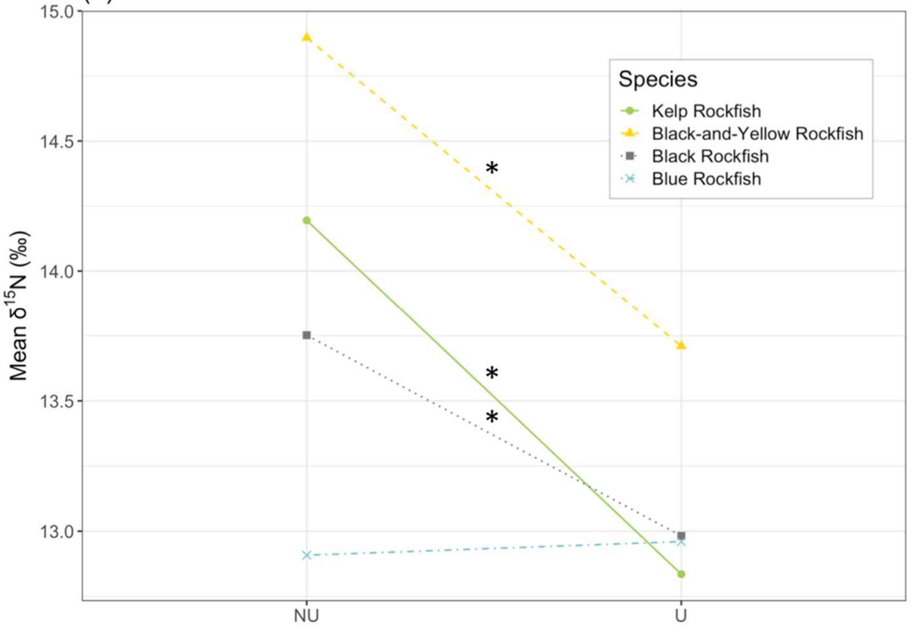
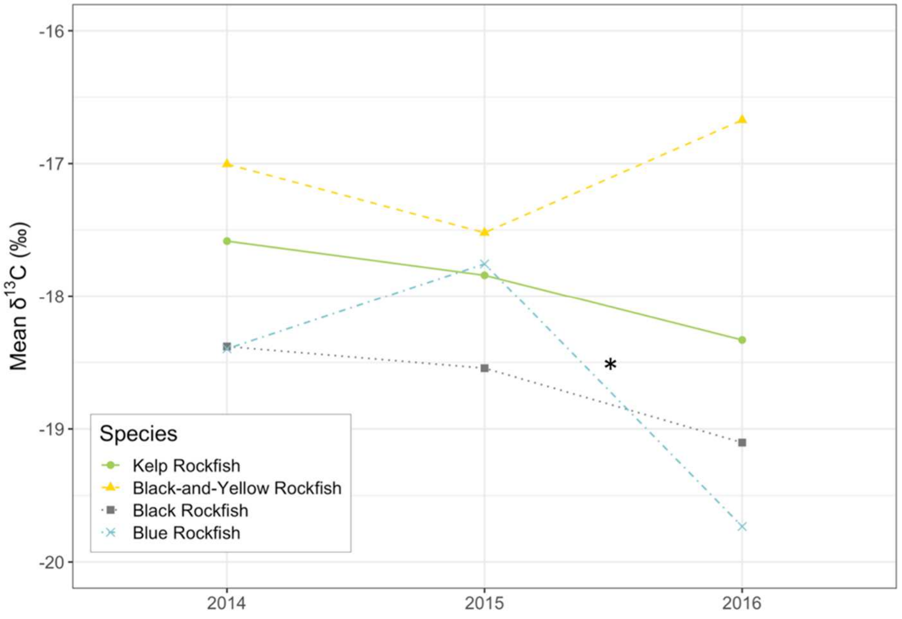

Species
Kelp Rockfish
Black-and-Yellow Rockfish
Black Rockfish
Blue Rockfish
Mean δ15N (‰)
15.0
14.5
14.0
13.5
13.0
NU
U
*
*
*

Figure 2.8. (a) Liver tissue samples of all species with the exception of Black-and-Yellow Rockfish showed a pattern of significantly decreasing $\delta^{15}N$ values from 2014-2015, then increasing again from 2015-2016. (b) All species except Blue Rockfish had lower $\delta^{15}N$ values (i.e. occupied lower trophic levels) during upwelling season (April-July). A '*' signifies significance between points to the left and right ($\alpha = 0.05$).

(a)


-16
-17
-18
-19
-20
Mean $\delta^{13}C$ (‰)
2014
2015
2016
*
Species
Kelp Rockfish
Black-and-Yellow Rockfish
Black Rockfish
Blue Rockfish

(b)

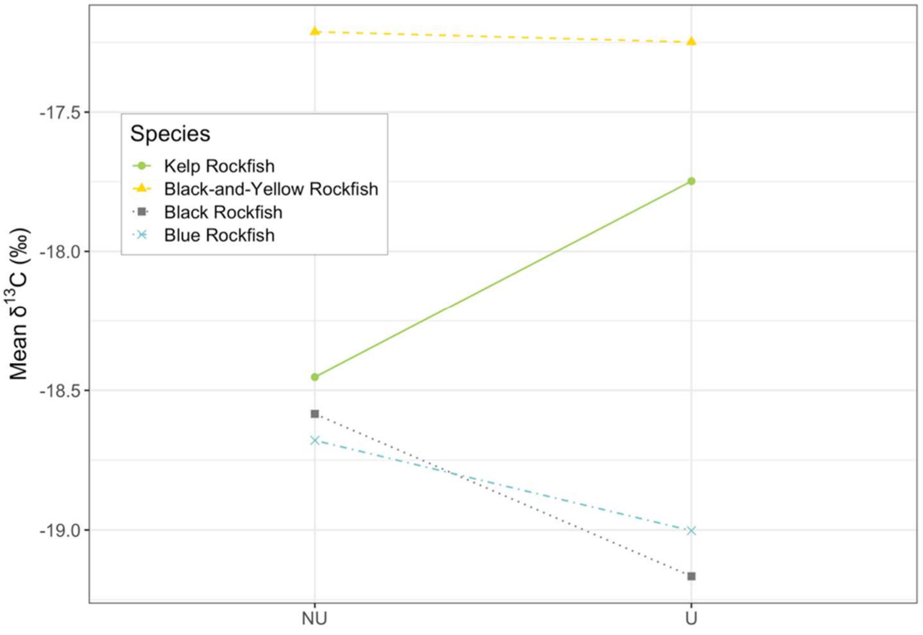

-17.5
-18.0
-18.5
-19.0
Mean $\delta^{13}C$ (‰)
NU
U
Species
Kelp Rockfish
Black-and-Yellow Rockfish
Black Rockfish
Blue Rockfish

Figure 2.9. (a) Mean $\delta^{13}C$ of liver tissue samples for Blue Rockfish showed a significant decrease in $\delta^{13}C$ from 2015-2016. (b) $\delta^{13}C$ values did not change seasonally for any species (Upwelling – April-July; Non-upwelling – all other months) A '*' signifies significance between points to the left and right ($\alpha = 0.05$).

Chapter 3: Central California's nearshore fishery as a social-ecological system

Abstract

Fish and fisheries play significant economic, social, cultural and ecological roles in California's coastal ecosystems and fishing communities. However, in the face of stressors ranging from climate change to shifts in global seafood markets, managing California's fisheries to ensure both long-term ecosystem health and the well-being of fishing communities is challenging. The concept of fisheries as social-ecological systems (SESs) has gained traction in fisheries management over the last two decades, encouraging the explicit consideration of interactions and feedbacks between ecological and social components of a fishery. Here I characterize the nearshore fishery (the predominant commercial fishery in kelp forests of central California) as a SES, and develop a baseline description of some of its social features. Within the SES, human dimensions such as governance, economic systems, and human behavior interact with, influence, and are affected by biophysical dimensions such as marine habitats, target fish species and their ecological communities, and oceanographic dynamics. I use a mixed methods approach, guided by Ostrom's SES framework, combining literature review, archival and fishery-dependent data analysis, and semi-structured interviews to bring to light some of the important factors that influence

current fishing operations and practices, and that have contributed to change in the fishery over time (Ostrom 2009). I show that flexibility, whether of fishermen to move among fisheries, to land a variety of species in the kelp forest fish assemblage, or to sell catch via different market arrangements, plays a major role in the human component of the kelp forest SES. My assessment identifies relationships between human components of the nearshore fishery and kelp forest ecosystems and factors that influence these relationships, and highlights aspects of the SES that enable adaptation.

Introduction

Fish and fisheries play significant economic, social, cultural and ecological roles in California's coastal ecosystems and fishing communities (Pomeroy and Dalton 2003, Scholz et al. 2004, Thomson 2012). However, in the face of stressors ranging from climate change to shifts in global seafood markets, managing California's fisheries to ensure both long-term ecosystem health and the well-being of fishing communities is challenging (Berkes et al. 2006, Sumaila et al. 2011, Pauly and Zeller 2016). The Magnuson-Stevens Fisheries Conservation and Management Act at the federal level and the Marine Life Management Act at the state-level require fisheries managers to consider the impact of regulatory actions on fishing communities, and to minimize adverse impacts to the extent possible while still achieving conservation outcomes

(MSA National Standard 8, Buck 1995, NOAA 2006, Weber et al. 2018). This has been particularly challenging due to a lack of baseline socio-economic information characterizing fishing communities, and a lack of integration of social and cultural understanding into the fisheries management process (Clay and McGoodwin 1995, Clay and Olson 2008). In some cases, this stems from a lack of data or lack of attention to socioeconomic information. However, detailed landings and permit records for California's fisheries provide a unique resource for furthering understanding of the socio-economics of fishing communities and the role and relevance of particular fisheries. In these data-moderate or data-rich cases, development of a fishery's social baseline is essential for managers attempting to understand the cumulative impacts of previously adopted regulatory changes and the implications of future management decisions (NMFS 2007, Thomson 2010, Pomeroy 2018).

In addition to improved information about social, cultural and economic aspects of California's fisheries, fisheries management will benefit from a clearer understanding of the interdependencies between social and biophysical systems (Pomeroy 1999, Hall-Arber et al. 2009, McClanahan et al. 2009). The concept of a social-ecological system (SES), has gained traction in fisheries management over the last two decades (Berkes 2011, Cinner 2012, Kittinger et al. 2013, Jarre et al. 2018). Moreover, recent efforts to move away from single-species management to more comprehensive, ecosystem-based management has encouraged the explicit consideration of interactions and feedbacks between ecological and social components of a fishery (Mahon et al. 2008, McClanahan et al. 2009). Within a SES, human dimensions such as governance institutions, economic systems, and human behaviors interact with, influence, and are affected by biophysical components such as marine habitats, target fish species and their ecological communities, and oceanographic dynamics. Interactions among diverse SES components influence outcomes in the SES, leading to a complex adaptive system that incorporates feedbacks, nonlinearities, and emergent properties (Berkes and Folke 1998, Levin et al. 2013). The SES concept implies that, although separated for the purposes of research and description, the human aspects and ecological aspects of a system are not separate, nor can either one be fully characterized without consideration of the other.

Approach and Objectives

Ostrom's SES framework, developed particularly for common pool resource systems such as wild-capture fisheries, provides a structure for identifying important variables in both the biophysical and social realms, recognizing potential interactions among these variables, and exploring external drivers influencing the system (Ostrom 2009, Basurto et al. 2013, McGinnis and Ostrom 2014). I use a mixed-methods approach, guided by the Ostrom SES framework, to characterize one of California's fisheries, the nearshore fishery, as a SES, and develop a baseline description of some of its social aspects. By characterizing the fishery as a SES, I bring to light some of the important factors that influence current fishing operations and practices and that have contributed to change in the fishery over time. I seek to describe (a) the demographics of fishery participants; (b) fishing operations and practices including those for transporting and selling catch; and (c) patterns in fishery landings and activity (Pomeroy et al. 2018). I then explore the impact of two notable regulatory interventions – implementation of restricted access and establishment of marine protected areas – on two measures: the amount and species composition of landings. Finally, I discuss several major conclusions that emerge from viewing the nearshore fishery through the lens of SES theory.

Methods

I combine literature review, fishery landings data analysis, and semi-structured interviews, to characterize and create a social baseline for central California's present-day nearshore fishery. Data sources (detailed below) included information collected by the California Department of Fish and Wildlife (CDFW) on fishery landings and first receiver purchases, associated permits, fishing licenses, and vessel registration, along with semi-structured interviews of current and former fishermen, fish buyers and fishery managers involved in the nearshore fishery. Because actual landings (as indicated by fishery landings data) are a function of multiple ecological, technological, social, economic and regulatory factors in this and other fisheries, qualitative data from interviews and literature review were employed to provide context and explain patterns in the landings and permit data.

Study System

California's nearshore fishery: management context and history

California's nearshore fishery (as defined by the CDFW) has a relatively short, but rich history (CDFW 2002, Wilson-Vandenberg et al. 2014; Figure 3.1). Although nearshore finfish were targeted by many groups prior to the 1980s, the fishery as currently defined started in the 1980s with the growth of a valuable market for live groundfish (i.e., fish sold live to retailers and consumers) (Pomeroy and Beck 1999, Starr et al. 2002). As individuals who had fished commercially, and some who had not, became involved in the live fish fishery, participation swelled into the late 1990s due to high price per pound being paid for live fish (Pomeroy and Beck 1999). In response to this rapid increase in commercial nearshore fishing activity, growing concern from the public, the scientific community, and advocacy groups led to regulatory discussion and action in the mid to late 1990s (Tegner and Dayton 1997, Starr et al. 2002; Supplementary Figure 3.1). In 1998, California's Marine Life Management Act (MLMA; California Fish and Game Code Sections 7060- 7090), which included the Nearshore Fishery Management Act (MLMA Section 3) was enacted, requiring the development of a Nearshore Fishery Management Plan (FMP) by 2001 for ten species of concern (shallow nearshore species in Table 3.1; Leet et al. 2001, Weber et al. 2018). This legislation also required that fishermen[1] targeting these species in state waters have an (initially unrestricted) nearshore fishery permit and established minimum size limits and commercial trip limits in the interim (Leet et al. 2001). In 2000, the permit became restrictive with a moratorium on the issuance of new permits, and a control date for a future restricted access program was established. As the Nearshore FMP was being developed, the Pacific Fisheries Management Council (PFMC) was working to more tightly regulate both the commercial and recreational sectors of the groundfish fishery in federal waters to protect overfished species, notably by closing Rockfish Conservation Areas, depth-based closures that vary by region, to commercial and recreational groundfish fishing.[2] This put nearshore stocks (in state waters) at risk from both a growing commercial fishery and increased recreational fishing pressure inshore as deeper waters were closed. Shortly thereafter, the PFMC split the rockfish species into nearshore, shelf, and slope complexes to allow more complete catch accounting by species. In 2002, the California Fish and Game Commission adopted the Nearshore FMP, covering

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[1] The term "fisherman" is the preferred, non-gender specific term to refer to anyone in California who fishes.

[2] Federal and state regulatory authority overlap on the management of groundfish species in California. NOAA National Marine Fisheries Service (NMFS) and the Pacific Fishery Management Council (PFMC) at the federal level, and the CA Department of Fish and Wildlife (CDFW) and the Fish and Game Commission at the state level all play roles in the management of groundfish species. Most of the nineteen species managed as the nearshore complex are also included in the federally-managed groundfish complex.

nineteen nearshore species, including nine additional species to be managed under a new Deeper Nearshore Species Fishery Permit (deeper nearshore species in Table 3.1). Due to widespread concern that all or some of the nearshore species had the potential to become overexploited, a restricted access program was implemented, resulting in a decline in the number of statewide permits from 1,127 in 1999-2000 to 505 in 2002-2003 (permits are issued for the period starting on April 1 and ending on March 31 the following year; Starr et al. 2002).

Implementation of the Nearshore FMP coincided with the process to develop a network of MPAs in California state waters, with MPAs established on rocky reef habitats overlapping substantially with habitat of species managed under the Nearshore FMP. In addition, the Nearshore FMP split the state into four management regions for the shallow nearshore species (Table 3.1), each with a regional capacity goal (i.e., a target number of nearshore permittees for each region). Nearshore fishery permits are assigned to one of four permit regions: North (Oregon-California border to Cape Mendocino), North-central (Cape Mendocino to Año Nuevo), South-central (Año Nuevo to Point Conception) and South (Point Conception to the California-Mexico border), and permittees are allowed to land shallow nearshore fish in the region for which their permit is designated. To acquire a permit in the fishery after 2003, a fisherman had to purchase two permits, and retire one. In contrast, the fishery for deeper nearshore species (Table 3.1) was managed using a statewide rather than a regional structure. Deeper permits were entirely non-transferrable until recently, and no capacity goal for the fishery was set. Species-specific total allowable catches (TAC) and associated TAC-based trip limits allocated to nearshore fishermen are determined by the PFMC for rockfishes in the genus *Sebastes*, and by the CDFW for Sheephead, Cabezon and Greenlings (published annually in the California Commercial Fishing Digest) (see NFMP 2002, Wilson-Vandenberg et al. 2014). Since 2003, results of stock assessments for nearshore species have enabled increases in trip limits for all nearshore rockfishes. Trip limits for California Sheephead have remained stable, while those for Greenlings increased during the 2003 to 2015 period, and those for Cabezon decreased from 2003 to 2006, then increased from 2006 to 2017. Over time, access to the fishery has changed. With substantial input from the fishing community, the CDFW approved two changes in permit transferability rules in April 2018 (California Code of Regulations Section 150(g), Title 14). These changes allowed fisherman to become permitted in the nearshore fishery by purchasing one transferrable permit (rather than two), and made deeper nearshore permits fully transferrable (also on a 1:1 basis).

This study focuses on the two central regions of the shallow nearshore fishery which span the area from Cape Mendocino in the North to Point Conception in the South. From North to South, within the central regions, port areas include Fort Bragg, Bodega Bay, San Francisco, Monterey, and Morro Bay, each of which includes many smaller ports and other landing sites across the region (Figure 3.2). The analysis addresses the period from 1999 (the first year that a nearshore permit was required) to 2015, with the majority of time series analyses spanning the period from 2003 to 2015, since permit structure in the nearshore fishery changed dramatically following the implementation of restricted access in 2002. Though a permit purchased or renewed in 2003 is valid from April 1, 2003 – March 31, 2004 (note that the fishery is closed from March 1 – April 30), I consider this to be a 2003 permit.

Central California's nearshore fish assemblage

The present-day nearshore fishery complex includes nineteen species from several functional guilds in the kelp forest. While Blue, Black, and Olive Rockfishes are midwater schooling species, Black-and-Yellow, Gopher and China Rockfishes (among others) are strongly benthic-associated. The complex includes planktivores, invertivores, piscivores, and generalist predators. Within this broad range, there are several attributes of the complex that are especially relevant to the fishery's SES. Most of the nearshore species (i.e. *Sebastes* rockfishes) are slow-growing and slow to mature, making them especially vulnerable to fishery overharvest (Love et al. 2002). In addition, species in the nearshore complex are relatively sedentary, making them vulnerable to localized fishing pressure (Freiwald 2012). Nearshore rockfishes are also susceptible to barotrauma, injury and/or death related to a rockfish's inability to quickly release gas from its swim bladder while being ascended from depth (Jarvis and Lowe 2008). This is especially relevant for the live fish component of the nearshore fishery, as the prevalence of serious barotrauma injury limits the depth at which nearshore fishermen wishing to sell their catch live operate. Finally, these nineteen species are not the only members of the kelp forest fish assemblage. Notably, lingcod (*Ophiodon elongatus*) and members of the surf perch family (Embiotocidae) also reside in the kelp forest, and are landed by nearshore and other fishermen.

Data Sources

<u>CDFW fisheries landings and permit data</u>

CDFW collects a wide range of data related to commercial fisheries, including the nearshore fishery, which it archives and manages through the Commercial Fisheries Information System (CFIS). Each time a commercial fisherman lands his/her catch, he or the first receiver (dockside buyer) is required to complete a landing receipt (commonly referred to as a fish ticket). Information on this ticket includes the name and license number of the fisherman, date of landing, the geographic area where fish were captured (assigned to a 10 minute latitude by 10 minute longitude block), each species of fish landed along with the weight and ex-vessel price per pound, an identification number for the first receiver purchasing the catch, and the condition of the landed species (e.g. live, dead with head off, dead with head on) (Supplementary Figure 3.2). In addition, CDFW maintains a database of licensed fishermen, fish receivers and businesses, individuals and vessels with state-issued fishery permits, and registered vessels[3].

For the CFIS data analysis, I considered fishermen to be participants in central California's nearshore fishery if they held either a North-central or South-central nearshore permit (transferrable or non-transferrable), or if they held a deeper nearshore permit (which is not managed regionally) and made landings at sites within the study region (i.e., between Cape Mendocino and Point Conception). Individuals located in the central coast region and permitted in the deeper nearshore fishery that made no landings of nearshore species in a given year were excluded from the analysis. Fish were considered to be landed live if the corresponding fish ticket entry specified the condition code as "6" for live catch. If any other condition code was used, or if the data were missing (approximately 27% of nearshore landings from 2003-2015 had no condition code listed which is considered to mean a whole, dead fish), the catch was considered dead. For clearer interpretation of landings data analyses, and because confidentiality rules prohibit the publication of data from fewer than three individual fishermen, categories (bins) were created for several variables.

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[3] A fish license refers to a state-issued commercial fishing license, not specific to any fishery. A fishery permit refers to access to an individual fishery, and may be associated with an individual or a vessel. A fish receiver license is required for anyone who purchases or receives fish for commercial purposes. Commercial fishermen who handle only their catch are also required to have a fish receiver license. The CFIS database excludes federal fishery permits, including those associated with the federal West Coast Groundfish FMP.

Gear was binned into the following major categories: Hook-and-Line, Longline, Trawl, Gillnet, Pot/Trap, Other Net (e.g., Purse Seine, Fyke Net), and Other (e.g., Spear, Diving) (Supplementary Table 3.1). There are many instances, especially prior to 2003, when fish were reported by species group (i.e., “market category”) rather than individual species. For the species-specific price analysis, any fish categorized only by an unspecific market category was considered an unknown rockfish and excluded. Kelp and Rock Greenlings were grouped together as “Greenling”, and California Sheephead, Monkeyface Prickleback, and California Scorpionfish (which are not commonly landed in central California) were excluded. For other analyses, nearshore fishes were grouped into categories based on ecological and fishery characteristics (Supplementary Table 3.2). Following CDFW convention, ports were grouped into the following port areas for analysis: Fort Bragg, Bodega Bay, San Francisco, Monterey, and Morro Bay (Supplementary Table 3.3). Prices for all analyses were adjusted to 2015 dollars to account for inflation using the Bureau of Labor Statistics’ Consumer Price Index for the United States.

Few nearshore species move further than the distance among several reef patches (Freiwald 2012). As such, variation in reef-to-reef fishing impact is important when assessing ecological impact. However, using state-collected landings data to characterize the spatial distribution of fishing activity at an ecologically-relevant resolution is difficult. While block-level (10 minutes by 10 minute cell) data are collected on where fish are captured, these data are often not considered to accurately reflect actual catch sites (Mason 2010). Despite this challenge, using the landings data to map fishing effort across the central region provides insight into the distribution of nearshore fishing pressure among reefs. I use port of landing as a proxy for the area fished based on literature review and interview data indicating general operations and practices in the fishery.

A variety of summary statistics were used to characterize the fishery using CFIS data. To explore the role that the implementation of restricted access and establishment of MPAs played in species composition of landings, I used a permutational multivariate analysis of variance (PERMANOVA) with proportion data before and after a management event. I followed this with a similarity percentage (SIMPER) analysis to identify the individual species driving any significant PERMANOVA results. All analyses of the landings data were done in R (R Core Team 2018).

Interviews: protocol and analytical approach

To inform the development of semi-structured interview protocols for fishermen, buyers and fishery managers, I first conducted archival data analysis and discussions with experts. Following these efforts, a semi-structured interview format was designed and used to gather information on six topics: (1) commercial fishing background and experience; (2) nearshore fishery operations and practices; (3) spatial and temporal distribution of nearshore fishing; (4) catch composition and any temporal changes in catch composition; (5) the nearshore fishery supply chain; and (6) experiences with and opinions about nearshore fishery management. The flexible interview format enabled a conversation with each participant that covered each topic while allowing the interviewee to determine the depth and direction of the discussion based on their experience and knowledge.

Interviews were conducted with 5 North-central fishermen, 11 South-central fishermen, 2 to 3 buyers from each region, and 2 state fishery managers with extensive knowledge and experience related to the nearshore fishery. Because several interviewees didn't hold nearshore permits in 2015, they accounted for 17% of 2015 shallow nearshore permittees in the South-central region and 19% in the North-central region. Initial interview participants were selected based on their current activity in the fishery, knowledge of the history of the fishery, and involvement in nearshore fishery management and research, with additional participants identified using a snowball sampling approach (Goodman 1960). Thirteen of the sixteen fishermen interviewed were continually permitted in the nearshore fishery from 1999 to 2015. The average age of study participants at the time of their interview was 60 for the South-central region and 62 for the North-central region. Fisherman interviewed made up more than 8% of total pounds landed of shallow and deeper nearshore species in 2015 in the South-central region, and 4% in the North-central region. Interviews were conducted in places convenient and comfortable for participants, at ports along the central coast, from February 2017 to September 2018. Interviews typically lasted from 60 to 90 minutes. All interviews were conducted pursuant to a human subjects research protocol approved by the University of California Santa Cruz Institutional Review Board.

Whereas some interviews were recorded (with participant consent), others were not. I transcribed recorded interviews verbatim and handwritten notes from unrecorded interviews to be used for qualitative data analysis. Transcriptions and notes were then classified using interviewee attributes (e.g. permit region), and coded for analysis and as a rigorous way to ensure that all information pertinent to a given topic was considered. The coding hierarchy had eight major themes corresponding to research questions. These were broken down further into sub-themes (Table 3.2). This structure allowed for the comparison and synthesis of different viewpoints and experiences relating to a given topic. All organization and analysis of interview data was done using NVivo v.10 (NVivo 2014). From this analysis, I developed a conceptual model of the nearshore fishery SES to facilitate understanding, and to provide information and context on the human dimensions (i.e. social, cultural and economic components) of the fishery.

Results

Today's Nearshore Fishery

Insights from the literature review, archival data analysis and interviews were combined to generate a conceptual model of today's nearshore fishery. The nearshore fishery SES includes the focal nearshore species; the physical marine environment that influences these species (e.g., oceanographic dynamics and habitat); the associated ecological system (e.g., kelp forest predators and prey resources); fishermen, their operations, and practices; fish businesses, supply chains and markets associated with the nearshore fishery; coastal communities where fishermen live and/or launch and land vessels; the governance system related to nearshore fishing; and interactions among all of these (Bodin and Tengo 2012, Zador et al. 2017; Figure 3.3). The conceptual model highlights connections and overlaps with the wider live fish fishery (an informal way to refer to nearshore finfish and other species such as California halibut, sablefish, lingcod, and thornyhead species that are sold live) and additional California fisheries, such as the federal groundfish fishery. It also emphasizes the role of formal state and federal governance in the fishery in contrast to some small-scale fisheries that are heavily influenced by informal governance and rules (but see Pomeroy and Beck 1999). Finally, the model underscores coupling between focal aspects of the fishery (i.e., permittees, focal fish species) and the associated supply chain and food system.

Fishery participants

Participation has changed markedly since the state's designation of the nearshore fishery in 1999. The implementation of restricted access in 2003 resulted in a sharp decline in the number of nearshore permittees and the pounds of fish landed (Figure 3.4). After 2003, the number of nearshore permittees declined gradually as non-transferrable permits retired with individual fishermen (a permit in the fishery is assigned to an individual rather than a vessel), and as new participants entered into the fishery by purchasing two transferrable permits, retiring one. However, permit turnover (i.e., entry of new individuals into the fishery) has not kept pace with this gradual attrition, contributing to an aging fleet. The average age of a shallow nearshore permittee increased from just over 43 in 1999 to nearly 55 in 2015 (with a similar pattern seen in the deeper nearshore fleet), with very few participants under age 40 in the fishery (Figure 3.5). Part of the reason for the lack of fishery turnover is likely the high cost of a nearshore permit which can easily exceed $50,000. Nearly all nearshore fishery permittees are male, as has been the case since the state began requiring permits. In the two central regions combined, 0.9% of shallow nearshore permittees were female in 2003 and 3.8% in 2015. The low number of female permittees does not mean that women do not play an important role in fishing operations (whether fishing or providing shoreside support), however little information is available to characterize this role. Interviewees variously reported fishing alone or with one additional crewman. Most nearshore permittees live in the same region where they land their catch. In 2015, all nearly all nearshore fishermen indicated a residential address located in the region for which they are permitted (North-central region: 97% in 2003, 100% in 2015; South-central region: 90% in 2003, 98% in 2015).

Fishery practices and operations

Fishing practices and operations include how and where people fish, the vessels and gear used for catching and transporting fish, the supply chains and markets that make fishing economically viable, and the social and environmental context that enables fishing to occur (Pomeroy et al. 2018). Participation in the nearshore fishery requires a unique gear and skill set to target, catch, and sell shallow-water groundfish found in the region's temperate, kelp forest ecosystems. The nearshore fishery's SES exhibits local and regional diversity across California's central coast, and operations, fishing practices, and supply chains vary within and among ports.

<u>Nearshore vessels and fishing gear</u>

Mean vessel size and size distribution in the nearshore fishery remained nearly constant from 1999 to 2015 with an average of 8.5 m (± 3.2); mean length of vessels engaged in the shallow component of the nearshore fishery from 2003 to 2015 was 8.1 ft (± 3.1), relatively small for a commercial fishery in California (vessel size distribution in Figure 3.6). Because most nearshore fishermen participate in other fisheries, many nearshore vessels are configured for multi-fishery use. Interview data suggest that there is a trade-off between deck space for equipment and gear (for both nearshore fishing and for other fisheries), and having a boat that can be safely maneuvered in very shallow water (< 3 m) where nearshore species such as the Grass Rockfish are found. Some fishermen interviewed reported that larger-than-ideal vessels are often used in the nearshore fishery so that the same vessel can accommodate other fisheries. In contrast, others fish from a kayak or very small skiff that allows shallow water access.

The nearshore fishery is a multi-gear fishery, with fishermen relying predominantly on fixed gear including hook-and-line, fish traps, stick gear, and set longlines, although fishermen targeting deeper nearshore species can use any gear. Stick gear consists of a line attached to a surface float to mark the gear, and to a 1-3 m PVC pipe fit with rebar (for weight) which sits on the sea floor with 5-12 hooks. Stick gear is deployed from the vessel, and allowed to soak for 1-2 hours (typically while other sticks are deployed) before it is retrieved. Hook-and-line fishing is the predominant mode of nearshore fishing both in the shallow and deeper sectors, though set longlines also are used in the deeper sector (Figure 3.7). Set longline configurations in the nearshore fishery consist of up to 150 hooks in the water with no more than 15 hooks per line. Traps are more commonly used in the South-central region where

~36% of nearshore permittees have a trap endorsement (Figure 3.8), ~11% of permittees make at least 70% of their landings with trap gear, ~44% use primarily hook and line, ~10% use primarily stick gear, and an additional ~36% use a mix of gears. In the North-central region, only ~4% of permittees make at least 70% of their landings with trap gear, ~41% primarily use hook-and-line gear, ~22.5% use stick gear, and ~32.5% use a mix of gear types.

Many factors influence a fisherman's gear use decisions. First, there have been gear restrictions in the shallow nearshore fishery since 2003 that prohibit the use of nets (with the exception of dip nets), limit nearshore fishermen to 150 hooks per vessel and 15 hooks per line, and require that fishermen using traps qualify for and purchase an annually-renewed trap endorsement that is tied to a shallow nearshore permit. Further, deck space on the vessel for storing and transporting gear; whether a person fishes with a crewmember to assist in deploying and retrieving gear; maneuverability of a vessel in shallow, rocky waters; the presence of predators such as harbor seals that will prey upon hooked or trapped fish; and whether one intends to sell a fish live or dead all play in to fishermen's gear configuration. In this predominantly live fish fishery, many participants use gear to reduce injury and stress to the fish, with all interviewees reporting a typical mortality rate of less than 5%. Nearshore fishermen use deck space on their vessels for "live wells," or aerated tanks for keeping fish alive during the transit to shore (and often to market as well), and often use hypodermic needles to puncture a fish’s swim bladder after it ascends from depth (to alleviate some symptoms of barotrauma).

Spatial and temporal distribution of nearshore fishing

Fishermen landing in the Morro Bay port area accounted for 67% of central region landings (by weight) in 2003 and 62% in 2015 (Figure 3.9). Whereas the importance of Morro Bay as a nearshore fishery port remained relatively unchanged over the study period, landings in the Fort Bragg and Monterey port areas have fluctuated. Fort Bragg port area landings were highest from 1997 to 2000 (18-28%), before decreasing to 11% in 2015. Similarly, Monterey port area landings were at their highest from 1998 to 2002, dropped thereafter to a period low of 5% in 2007, then increased to nearly 14% of study area landings in 2015. All other port areas accounted for less than 10% of central coast nearshore landings over the 1995-2015 period.

At a finer scale, nearshore fishing depth is limited by federal Rockfish Conservation Areas (RCAs), and fishermen often operate directly on rocky reefs with kelp cover, sometimes in water as shallow as 2 m. Most nearshore fishermen only fish day trips for nearshore species rather than several day or overnight trips. As such, most permittees fish on reefs within a few hours trip from launch sites. Finally, in areas where larger ($\bar{x} \approx 13.5$ m in 2015) commercial passenger fishing vessels (CPFVs) operate, there is little spatial overlap between these and shallow nearshore fishermen, as CPFVs tend to fish deeper. More overlap is likely between CPFVs and commercial deeper nearshore operations.

Like many fisheries, the nearshore fishery is seasonal, both due to regulations (with a March-April closure) and because fishing activity in shallow, nearshore waters from small vessels is sensitive to (and constrained by) weather and ocean conditions (e.g., seasonal fog, winter storms). Fishing activity varies by month, with landings and ex-vessel revenue highest in the summer months when marine conditions in central California tend to be more favorable for nearshore fishing (Figures 3.10).

Nearshore fishery markets and supply chain

The seafood supply chain in the nearshore fishery takes five major forms (Figure 3.11). Ports in more populated areas have established dockside receiving stations operated by seafood companies as part of a larger fishing port infrastructure. For example, many fishermen in the Morro Bay port area sell to a dockside buyer who then holds live fish until transport to either the Los Angeles or the San Francisco urban area for sale in restaurants, fish markets, or grocery stores. In places without a resident live fish buyer such as Monterey, fish buyers from urban areas visit periodically to buy fish. In these cases, fishermen coordinate with other fishermen and these mobile buyers to ensure that sufficient fish are available when a buyer visits and that fish aren’t held too long (risking mortality) before being sold. In the case of Monterey, there is a resident market to purchase fresh fish (nearshore fish not kept alive) for direct sale to consumers. In addition to grocery stores, fish markets, and restaurants, a subset of nearshore fish landed on the central coast is sold as whole fish or fillets to consumers at farmer’s markets or directly to local restaurants (fishermen who hold a first receiver permit can sell catch directly to a restaurant). Some fishermen transport their own catch to grocery stores or wholesalers in urban areas. This requires owning or having access to a pickup truck, a trailer, or another platform with aerated tanks, but enables fishermen to operate in less populated areas (e.g., Big Sur, small ports in the North-central region) where buyers and markets are not always present. Finally, in some locations (e.g., Half Moon Bay), local regulations, infrastructure, and consumer demand enable fishermen with a fisherman’s retail permit to sell their catch off the boat or at the docks directly to the public.

The availability of markets for both fresh fish and live fish is central to viability of the nearshore fishery. Interviews with both fishermen and buyers suggest that several factors influence the ex-vessel price of fish. In the case of live fish, some species are worth more per pound when they are under a certain size. Cabezon sells for a higher price per pound when it weighs less than four pounds, and many fishermen, especially those seeking to meet their cabezon trip limit, throw back large cabezon (and other nearshore species). In summer months when many people are fishing, markets occasionally become flooded with live nearshore fish. Several interviewees suggested that prices sometimes drop slightly during these times, though it is not common. Ex-vessel prices also increase slightly for some fishermen in the weeks prior to Chinese New Year celebrations. Despite markets in the past favoring brightly colored fish (e.g., red rather than brown fish), no one interviewed for this project agreed that color influences fish price today.

Fisherman are paid more on average for a live fish than for a fresh dead fish (Figure 3.12). A t-test comparing the price of live versus dead fish by species in 2015 indicates that live fish of most species had a significantly higher price than dead fish. The one exception was Kelp Rockfish, for which there was no significant difference in price between live and fresh dead ($p = 0.60$). The significantly higher price for most species likely contributed to the fact that, annually, 74% to 84% of nearshore fish was landed and sold live from 2003 to 2015. In addition to condition (i.e., live vs. dead), species itself is also an important determinant of price in the nearshore fishery (Figure 3.13). Interviews suggest that this is because some species are simply less hearty than others, harder to keep alive, or lose their color and become a lower quality product when kept in a tank. When sold live, there was a significant difference in price among all species with the exception of the Blue Rockfish and the Black Rockfish ($p = 0.13$) and the Gopher Rockfish and the Black-and-Yellow Rockfish ($p = 1.00$). When sold fresh dead, price among species tended to be much more similar.

Overall, while the market favors live Cabezon and Grass, Brown (Bolina), Gopher, Copper, and Black-and-Yellow Rockfishes, fishermen typically are paid less for Blue, Black, Kelp, and Olive Rockfishes.

Prices in the nearshore fishery increased steadily from 1999 to 2007, and have decreased slightly since then (Figure 3.12). There was a significant positive correlation between price and year for live ($R^2 = 0.72$, $p = 0.04$), but not for dead fish ($R^2 = 0.69$, $p = 0.09$), and a significant effect of condition (i.e., live vs. dead) on the regression between price and year (ANCOVA: $p < 0.001$). The overall price increase over time has worked to maintain ex-vessel value in the nearshore fishery despite the decrease in landings following the implementation of restricted access (Figure 3.4). All fisherman interviewed agreed that they had no problem selling the nearshore fish that they landed, and that price for nearshore species was stable. Fishermen suggested that the market would support an increase in landings, but that too many entrants into the fishery could cause prices to decline.

Nearshore landings and fishery activity

Although the number of permittees in the fishery in 2015 still exceeded CDFW fishery capacity goals for the South-central and North-central regions, not all of these permittees were actively participating fishery (there is no requirement to make landings to keep the permit). Here, I define an active nearshore fisherman as any permittee that made at least one landing in a given year. From 2003 to 2015 an average of 87% (South-central shallow), 82% (North-central shallow) and 46% (deeper nearshore permittees making at least one landing in a central region port) were actively fishing (Figure 3.14). Although these percentages have fluctuated over time, the overall pattern has been a relatively constant proportion of permittees making landings, with a notably smaller proportion of deeper nearshore than shallow nearshore permittees active in the fishery. Among active fishermen, the distribution of pounds landed annually by an individual is notably skewed toward fewer landings, especially in the deeper nearshore fishery (Supplementary Figures 3.3a-b).

As expected for a fishery managed as a complex of nineteen species, most nearshore trips have landings of multiple species. Overall nearshore species composition of landings differed between the South-central and North-central regions in recent years, with North-central fishermen landing more Blue Rockfish and Black Rockfish and South-central fishermen landing a larger proportion of ‘Other Shallow Rockfish’ (Black-and-Yellow Rockfish, Gopher Rockfish, Kelp Rockfish, China Rockfish) (Figure 3.15). Moreover, species composition of landings (both regions combined) has shifted over time, with Cabezon accounting for a decreasing proportion of landings and other shallow rockfish species accounting for an increasing proportion of landings (Figure 3.15). Fishermen also landed species managed separately from the nearshore species on the majority of their trips (Figure 3.16). Most commonly, federally-managed shelf and slope rockfishes and other groundfish species such as lingcod (which is sometimes described as an incidental or bycatch species in the nearshore fishery, but is also a target species to sell on both live and fresh fish markets), are landed on the same trip as nearshore species, although this varies by port complex (Supplementary Figure 3.4). Across both regions, fishermen reported that annual landings of an individual species are influenced by a variety of factors including regulatory restrictions, price, and weather (which influences whether fishermen are able to fish in very shallow water). Nearshore permittees are allotted two-month trip limits (often referred to as quotas by fishermen) for Cabezon (set by the state), Greenlings (Kelp and Rock; set by the state), and the complexes of Minor Shallow Nearshore Rockfishes and Minor Deeper Nearshore Rockfishes (set by the PFMC). Though several interviewees reported that these trip limits can be limiting, this doesn’t seem to be the case for the majority of nearshore fishermen. Over the time period from 2004 to 2015, no more than 60% of active permittees landed at least 90% of their two-month trip limit for any species group (Figure 3.17). Likely due to its high price, more permittees fish their full Cabezon trip limit than their full trip limits of rockfish species. A similar pattern was seen for Greenlings until 2014 when a substantial trip limit increase (statewide commercial total allowable catch increased from 3,400 pounds to 55,400 pounds, and individual trip limits increased from 125 pounds to 950 pounds annually) made that species much less limiting for fishermen. Interviews suggest that for active nearshore fishermen, weather is the main factor keeping them from reaching trip limits. Additionally, several fishermen indicated that increasing *Sebastes* trip limits in recent years make nearshore fishing a more attractive (relative to other fisheries) and economically viable option for them. It is important to note that the nearshore fishery is subject to in-season closures if all fishermen fished their full two-month trip limit to ensure that the statewide total allowable catch is not exceeded. The most recent in-season closure to occur was for Greenlings in 2009.

Permit data suggests, and interviews support, that having a mix (sometimes referred to as a "portfolio") of fisheries is important for the economic viability of many nearshore fishermen, and that the particular fishery mix of nearshore fishermen varies within and among regions. The landings data indicate strong connections between the shallow and deeper components of the nearshore fishery, as a high percentage of shallow permittees also hold deeper permits in both regions (Figure 3.18), with the federally-managed fixed gear groundfish fishery (for shelf rockfishes, slope rockfishes, and sablefish), and with open access fisheries for other nearshore finfish (Tables 3.3a -3.3b). Less prominent connections among the nearshore, Dungeness crab, salmon, and California halibut fisheries also are evident.

Changes in the nearshore fishery: before and after management actions

Shifts in the species composition of nearshore landings emerged in the landings data analysis and throughout interviews with fishermen as a major change in the fishery over time. To evaluate management interventions as a potential driver of these patterns, I compared the periods before and after two notable management actions: implementation of restricted access (2003) and establishment of marine protected areas (MPAs), which overlap substantially with nearshore fish habitat, through the state's Marine Life Protection Act process (South-central: September 21, 2007, North-central: May 1, 2010 and December 19, 2012).

Species composition of landings in both regions combined remained remarkably constant through the implementation of restricted access in the nearshore fishery ($p = 0.24$), despite the decline in total pounds landed (Figures 3.19 - 3.20). While many fishermen reported that MPA establishment concentrated nearshore fishing effort in areas that remained open, at the resolution of port area, pounds of nearshore species landed did not differ before and after MPAs in the Morro Bay ($p = 0.47$), Monterey ($p = 0.15$) or Fort Bragg ($p = 0.54$) areas (Figure 3.19). Changes following MPA establishment in the number of annual pounds landed per individual and number of annual landings per individual were seen only in the Morro Bay port area where, on average, individuals landed more pounds and made more nearshore trips following MPA establishment (Table 3.4). However, notable shifts in species composition of landings occurred with the establishment of MPAs in these port areas (Figure 3.21). In the Morro Bay port area, the species make-up of fisheries landings changed significantly (PERMANOVA, $p = 0.03$), with other shallow nearshore species (38.6%) and Cabezon (35.9%) accounting for the largest percent contribution to the change. Similarly, species make-up of landings in the Monterey port area changed significantly (PERMANOVA, $p = 0.03$), with major contributions to the change from other shallow nearshore species (36.2%), Blue Rockfish and Black Rockfish (24.8%), and Cabezon (14.7%). Finally, species make-up did not change significantly in the Fort Bragg port area (PERMANOVA, $p = 0.12$).

Discussion

Flexibility in the nearshore fishery contributes to fishery viability

Despite the significant decline in pounds landed following the change to restricted access, overall ex-vessel revenues for those who have remained in the fishery have rebounded, and fishery participants interviewed expressed optimism about the future of the nearshore fishery in central California. This suggests that the ability of the nearshore fishery to remain economically viable has depended at least in part on the presence of a high price-per-pound live fish market. This low-volume, high-price-per-pound fishery is in line with ecological sustainability in a fishery that targets long-lived species that are slow to mature. In addition, supply chain diversity in the nearshore fishery has contributed to nearshore economic viability. Fishermen are able to sell a high value product (live fish) when possible, but have access to fresh fish and fillet markets when live buyers aren't available or when conditions don't allow for keeping fish alive. This allows nearshore fishermen to sell catch under conditions that vary in time and space. Though the presence of both live and fresh fish markets were not explicitly built into the design of the nearshore fishery management system, this case study provides a salient example of ways that policy interventions in food systems (in addition to fisheries management) can influence fishery outcomes. There has been increasing attention given to alternative marketing strategies in fisheries, and growing interest in locally-caught fish. These direct marketing options, which are often started or promoted by non-governmental organizations, and which vary among ports on the central California coast, influence the nearshore fishery SES. Interviews with fishermen in ports where direct marketing to consumers and other alternative arrangements exist suggest that these options enable the viability of nearshore fishing operations.

The ability to move among fisheries is pivotal for full-time fishermen. Though the majority of California fisheries are managed under some form of restricted or limited access, most nearshore fishermen are able to access a mix of restricted access and/or open access fisheries. This has been especially important in the nearshore fishery, as regional management restricts individuals' ability to shift effort to another region to maintain a viable business. Many factors influence this flexibility and an individual participant's fishery mix. In the nearshore fishery, relatively small vessels and fixed gear configurations make it difficult for most fishermen to switch to large-vessel, gear intensive fisheries such as the market squid or groundfish trawl fisheries. However, some fishermen own or fish multiple vessels, allowing them access to fisheries that require a different vessel or gear set than is used in the nearshore fishery. The majority of permittees interviewed for this research began fishing in California prior to the implementation of restricted access in the nearshore and other fisheries. As such, many of them retain permits in now-restricted access fisheries. Some discussed making strategic landings before a fishery moved to a restricted access arrangement, implying that having access to a mix of fisheries is quite important. Despite some nearshore fishermen having the ability to shift among restricted access fisheries, the fishery mixes reported here (Tables 3.3a – 3.3b) highlight the strong connections between nearshore and both open access groundfish and other finfish not managed under a restricted access arrangement. Nearshore is a multi-species fishery and fishermen use a range of vessel sizes and gear configurations, giving them more options for maintaining a fishery mix with nearshore and the set of non-nearshore, open access species such as lingcod, surfperches, albacore, and others. Finally, it is not uncommon for nearshore fishermen to also work outside of the fishing industry (Pomeroy and Beck 1999). The nearshore fishery provides an example of how small-scale fisheries can operate in concert with, and potentially benefit from the presence of, larger-scale, higher-volume fisheries.

Further work should address the way that changes in management in these other California fisheries impact permittees' reliance on the nearshore fishery, and influence nearshore fishery operations. Results of the fishery mix analysis highlight the importance of several California fisheries that face uncertain futures on California's central coast. Ongoing salmon population declines stemming largely from water and habitat issues in upstream habitat and the potential for more frequent and/or longer closures of the Dungeness and rock crab fisheries due to harmful algal blooms will almost certainly impact the fishery mix of nearshore participants (Yoshiyama et al. 2000, Katz et al. 2013, McCabe et al. 2016).

Fishing practices and operations

I identified the primary factors that influence where, when and how a nearshore permittee fishes for nearshore species. Using interview data to qualitatively rank these factors in importance, my research indicates that regulatory restrictions such as MPA and RCA closures, weather, and opportunities in other fisheries play major roles. In some locations, especially those ports that do not have a regularly visiting mobile buyer or a resident buyer for live fish, the availability of local demand also plays a role. Because this work focuses on just the geographic area covered by the two central management regions of the shallow nearshore fishery, I was unable to fully assess the role of changes to harvest allowances (e.g. total allowable catches, two-month trip limits) that are set either statewide or for regions that do not fully overlap with nearshore management regions. Further work should look more explicitly at changes in nearshore trip limits and resulting the consequences, and also at the changes in trip limits in interacting fisheries.

Many fishermen who participated in this study and in others reported impacts from MPA establishment (especially in the South-central region) such as concentration of nearshore fishing effort in areas that remain open, and the loss of access to "bad weather spots" (spots where nearshore fishing is still possible in bad weather) that limits the seasons in which fishermen can target nearshore species. However, in contrast to common expectations, landings at the port area level did not significantly decrease following MPA establishment. More research is necessary to assess local-scale impacts of MPAs such as changes in fishing distribution relative to individual reefs, and the factors that have affected people's decisions to remain in the fishery or leave it. Because many of the nearshore species are also part of the federal groundfish fishery (categorized as Minor Shallow Nearshore and Minor Deeper Nearshore Species), there is some fishery observer coverage of the nearshore fishery. The relatively small size of nearshore fishermen's vessels limits their capacity to take observers; however, the observer data that do exist could be used to improve understanding of fishing operations at a finer spatial scale.

Species composition of nearshore landings has changed over time and varies by port area. These temporal and geographic changes in the mix of species landed is of particular importance when assessing ecological impacts of fishing and the ecological health of the fishery (Pellowe and Leslie 2017). Significant shifts from one species to another in the nearshore fishery has the potential to influence kelp forest communities and predator-prey relationships within those communities. Moreover, understanding species-level impacts (and how they have changed over time) in coastal areas open to fishing can improve our ability to interpret results of long-term monitoring of California's MPAs.

Challenges to developing a social baseline for the nearshore fishery

While it is straightforward to identify nearshore permittees for the two central management regions from 2003 to 2015 in the CDFW landings data, it is more difficult to isolate data for deeper nearshore permittees with landings at central region ports. Because I could only analyze data for deeper nearshore fishermen who made landings at central region ports in a given year, I was unable to include inactive permittees who may have been active in other central coast fisheries, and was only able to estimate activity in the deeper nearshore fishery at the statewide level. Further work should focus on deeper nearshore fishermen to better understand the implications of statewide management in the deeper nearshore fishery (as opposed to the regional management in the shallow nearshore fishery) on fishermen's mobility, fishing activity, and fishing income.

Another challenge to characterizing the human dimensions of the nearshore fishery is the presence of fishermen with a distinct sociocultural heritage that influences their fishing practices and operations, but who are not represented in the interview data collected in this study. In both the South-central and North-central management regions, Vietnamese and other culturally Asian fishermen are permitted and active in both the nearshore and deeper nearshore fisheries. Interviews conducted for this project and previous work suggests that, especially in the deeper nearshore fishery, Vietnamese fishermen tend to fish differently from other sectors of the fishery (Orbach 1983). Future studies could focus on describing these sub-sectors of the nearshore fishery and comparing and contrasting fishing practices and operations. In addition, others have suggested that fishery practices and operations differ between the two central and both the Southern and Northern management regions. The prevalence of California Sheephead and California Scorpionfish in Southern California landings changes the make-up of the Southern nearshore fishery, and dramatically higher landings of Black Rockfish in Northern California make that region unique. Additional efforts to extend this characterization of fishery participants, practices and social-ecological relationships to the entire state would be useful.

Finally, it is difficult to fully understand the nearshore fishery SES without considering the recreational fishery for nearshore species. Fortunately, data on landings, species composition, and spatial distribution of effort exist for CPFVs (commercial passenger fishing vessels or charter boats). However, though surveys are conducted to characterize recreational fishing from private vessels, by spear divers, and by shore-based anglers, these data are not as comprehensive as commercial landings data. The recreational sector is allocated a larger proportion of the total allowable catch for nearshore species than the commercial fishery and, as such, understanding fishing impacts on the nearshore fish assemblage and kelp forest ecosystems will be difficult without additional recreational fishery information.

Adaptive management in the nearshore fishery

As with other fisheries that provide local jobs, generate local revenue, and produce local seafood for consumers, the nearshore fishery is an important part of a larger fishery system that contributes to the social and economic well-being of California fishing communities. As noted by a nearshore permittee in the North-central region, aging nearshore participants fish less often, making it difficult to keep buyers coming to a place so that fishing opportunities exist for the next generation. The aging of the nearshore fleet, an unintended consequence of restricted access, was a concern expressed by many nearshore permittees. Restricted access and restrictive trip limits were put in place following concerns that the fishery could become ecologically unsustainable. Since then, managers have assessed both the resource and the fishery, and with considerable input from fishermen, have revisited and scaled-back management decisions. Recent changes in the permit transferability rules increase likelihood that older fishermen will sell their permits, better enabling new participants to enter the fishery. This change, along with gradual increases in nearshore species trip limits may lead to increases in both effort and landings. However, because both federal and state agencies have the ability to adjust two-month trip limits (even by making in-season changes), the fishery has a built-in safety mechanism to protect the resource if effort increases more than the ecological system can sustain.

Another unintended consequence of management is the regulatory discard of fish by individuals without the appropriate permit – for example, shallow nearshore species discarded by deeper permittees and vice versa. Data collected by the West Coast Groundfish Observer program (which only has approximately 5% coverage in California's nearshore fleet) suggest that this is not uncommon (National Marine Fisheries Service NWFSC 2008). For example, in the 0-10 fathom depth range, 41.8% of Treefish (a deeper nearshore species) caught on observed trips in 2007 was discarded. Only 1.9% of Treefish caught in the 10-20 fathom depth zone, where deeper nearshore permittees are more likely to fish, was discarded. Similarly, fewer Gopher Rockfish, a shallow nearshore species, were discarded in shallow waters (14.4%) relative to deeper waters (28.2%). Although combining the nearshore and deeper nearshore permits to limit these discards has not yet been formally considered, the move to full transferability of deeper nearshore permits opens the possibility that more fishermen can hold both permits, thus eliminating their need to discard a subset of nearshore species. The information presented here can provide a useful characterization of the 'before' state with which to measure and assess changes resulting from the permit transferability change.

Conclusions

The results presented here contribute to the development of a social baseline for central California's nearshore fishery, consistent with the recently released MLMA Socioeconomic Guidance (Pomeroy et al. 2018). Management changes, environmental variability and climate change, and shifts in market dynamics occurring now and in the future will influence interactions between the social and ecological components of the nearshore fishery SES. The information presented here can be used in future management analyses to build understanding about the impacts and implications of recent changes in nearshore fishery management, changes in the kelp forest ecosystem, and how the nearshore fishery might be impacted by further environmental, regulatory, market or technological changes in other, related fisheries (e.g., salmon, Dungeness and rock crab, or federally managed groundfish). This assessment of the nearshore fishery also provides a bright spot in small-scale fisheries, where SES characteristics enable adaption of nearshore participants in the face of a changing fisheries landscape.

Tables and Figures

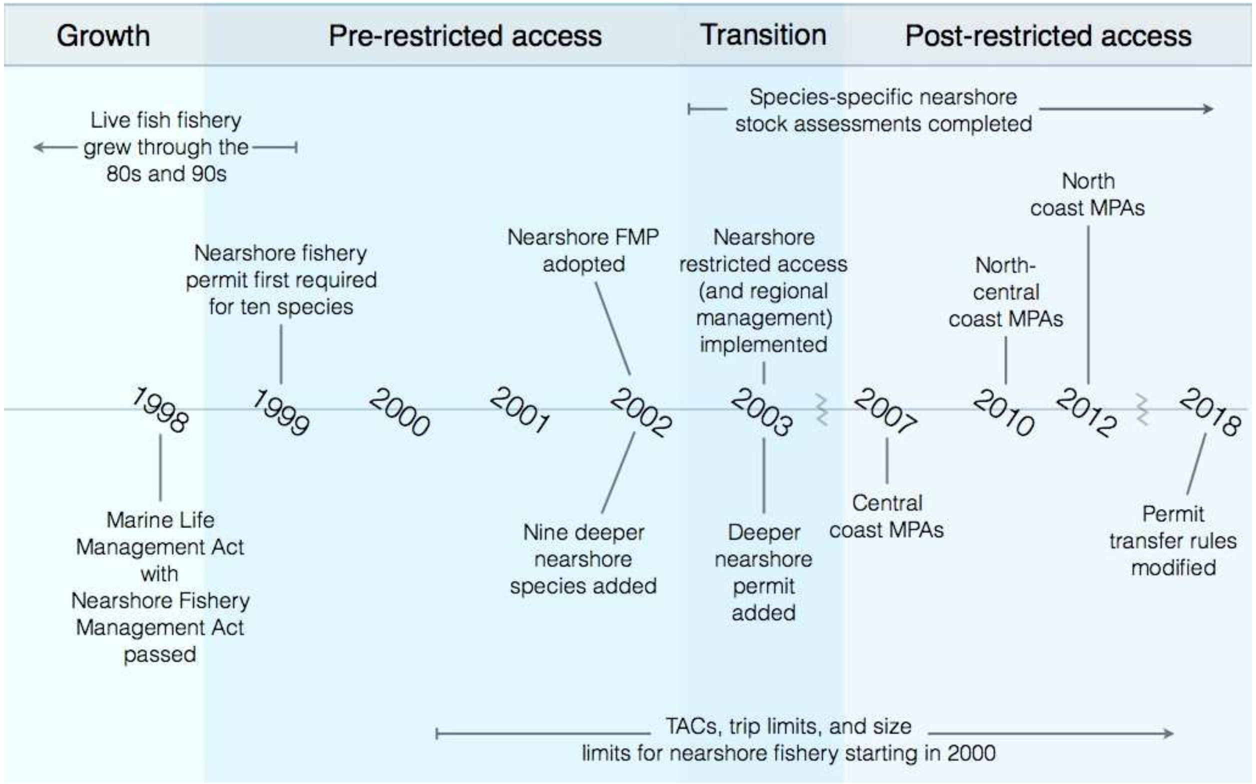


Figure 3.1. Timeline of selected events in the history of California's nearshore fishery.

Species	Permit Category	Geographic range	Common depth range (m)	Max Age
Black-and-Yellow Rockfish *(Sebastes chrysomelas)*	Shallow	Cape Blanco, OR – Isla Natividad (central Baja California)	Intertidal - 18	30
Cabezon (*Scorpaenichthys marmoratus)*	Shallow	Sitka, AK – Punta Abreojos (central Baja California)	Intertidal – 30	19
California Scorpionfish (*Scorpaena guttata)*	Shallow	Santa Cruz, CA – Gulf of California, Mexico	18 - 110	21
California Sheephead (*Semicossyphus pulcher)*	Shallow	Monterey Bay, CA – Gulf of California, Mexico	Intertidal – 90	53
China Rockfish *(Sebastes nebulosus)*	Shallow	Kachemak Bay, AK – Redondo Beach, CA (common to Northern CA)	3 - 128	79
Gopher Rockfish *(Sebastes carnatus)*	Shallow	Cape Blanco, OR – Punta San Roque (southern Baja California)	12 – 80	30
Grass Rockfish (*Sebastes rastrelliger)*	Shallow	Yaquina Bay, OR – Bahia Playa Maria (central Baja California)	Intertidal - 46	23
Kelp Greenling (*Hexagrammos decagrammus)*	Shallow	Attu Island, AK – La Jolla, CA	Intertidal - 130	25
Kelp Rockfish (*Sebastes atrovirens)*	Shallow	Albion, CA – Islas san Benitos (central Baja California)	Shallow subtidal - 21	25
Rock Greenling (*Hexagrammos lagocephalus)*	Shallow	Aleutian Islands, AK – Point Conception, CA	Intertidal - 80	11
Black Rockfish (*Sebastes melanops)*	Deeper	Amchitka Island, AK – Huntington Beach, CA (rare in Southern CA)	Shallow subtidal - 55	50

Blue Rockfish (*Sebastes mystinus)*	Deeper	Sitka Strait, AK – Punta Santa Tomas (northern Baja California)	Shallow subtidal - 90	44
Brown Rockfish (*Sebastes auriculatus)*	Deeper	Prince William Sound (northern Gulf of AK) – Bahia Tortugas (southern Baja California)	Shallow subtidal - 120	34
Calico Rockfish (*Sebastes dallii)*	Deeper	San Francisco, CA – Bahia de Sebastian Vizcaino (central Baja California)	60 - 120	12+
Copper Rockfish (*Sebastes caurinus)*	Deeper	Northern Gulf of AK – Islas San Benito (central Baja California)	Shallow subtidal – 100	50
Olive Rockfish (*Sebastes serranoides)*	Deeper	Southern Oregon – Islas San Benitos (central Baja California)	Shallow subtidal - 120	30
Quillback Rockfish (*Sebastes maliger)*	Deeper	Kenai Peninsula, AK – Anacapa Passage (Southern CA); common AK to Northern CA	Shallow subtidal – 274	95
Treefish Rockfish (*Sebastes serriceps)*	Deeper	San Francisco, CA – Isla Cedros (central Baja California)	Shallow subtidal - 60	23
Monkeyface Prickleback (*Cebidichthys violaceus)*	No permit required	Southern OR – Bahia San Quintin (northern Baja California)	Intertidal - 3	18

Table 3.1. Species managed under the Nearshore fishery management plan (i.e., “nearshore species”) with basic ecological attributes (Nearshore FMP 2002, Love et al. 2002, Love 2011).

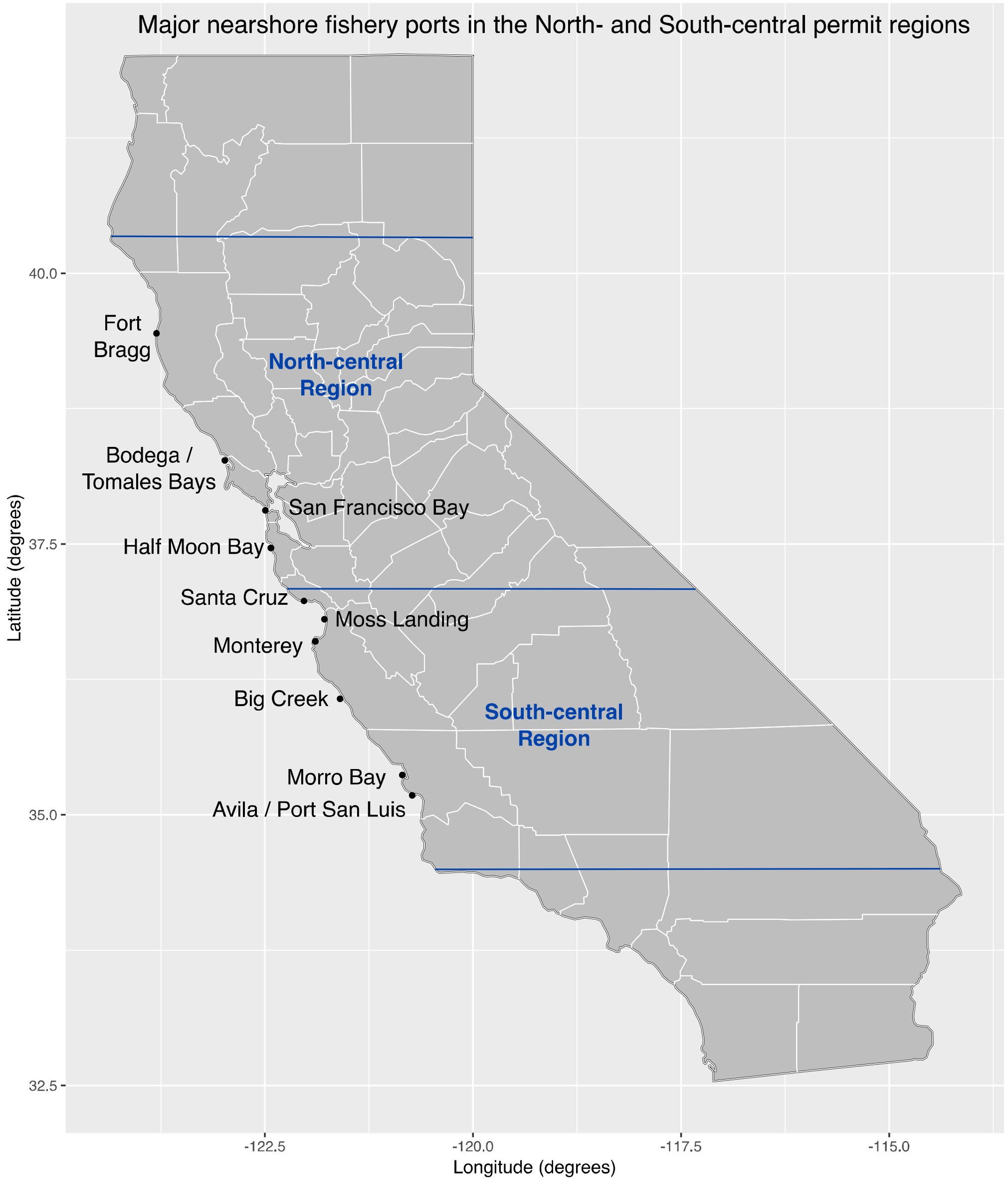


Figure 3.2. North- and South-central permit regions as defined by the Nearshore FMP with labels at some of the more commonly-used nearshore landing sites.

NODE
Cultural or societal role of fishing
Ecology -
Changing biophysical conditions
Fish abundance or distribution
Species composition of catch
Fishing operation -
Distribution of effort
Gear
Vessel
Management -
Limited entry; permits
Management in other fisheries
Marine protected areas
Participation in management
Market and supply chain
Nearshore fishery history
Fisheries mix; interacting fisheries
Recreational fishery

Table 3.2. Hierarchy of themes (or Nodes in NVivo) used to code interview data.

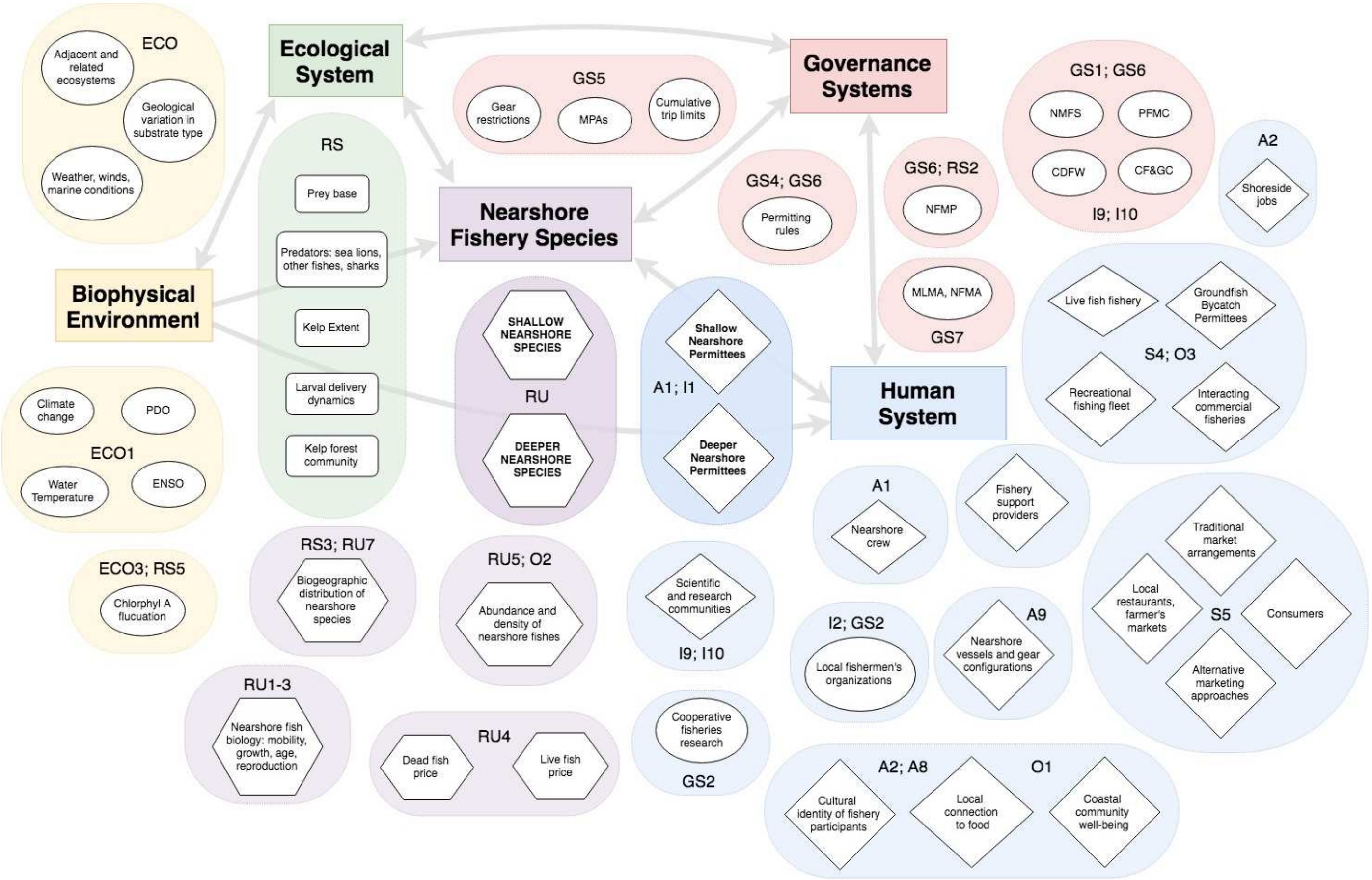


Figure 3.3. Conceptual map of central California's nearshore fishery. Codes are suggested links to Ostrom's SES framework (Ostrom 2009, Vogt et al. 2015).

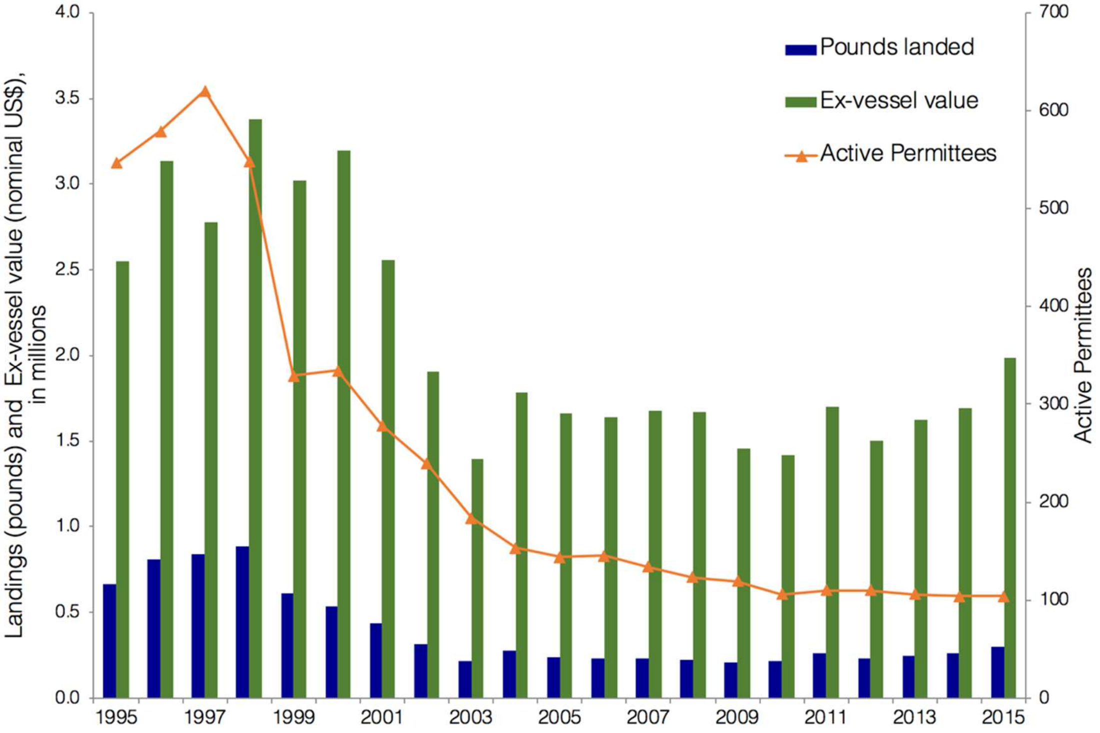


Figure 3.4. Interannual patterns in the number of deeper and shallow nearshore permittees, the annual pounds landed, and the ex-vessel value of the fishery for ports in the South-central and North-central management regions from 1999 to 2015.

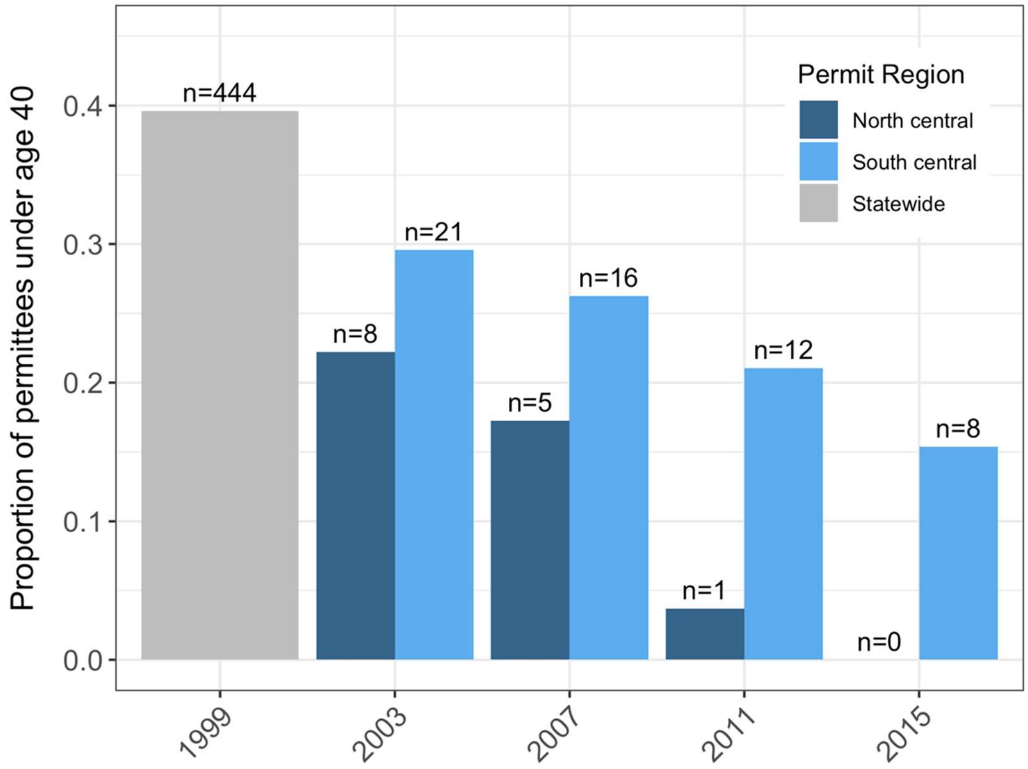


Figure 3.5. The proportion of shallow nearshore permittees under 40 in 1999 (before regional management was enacted, so data are statewide), and subsequent years (North-central and South-central regions).

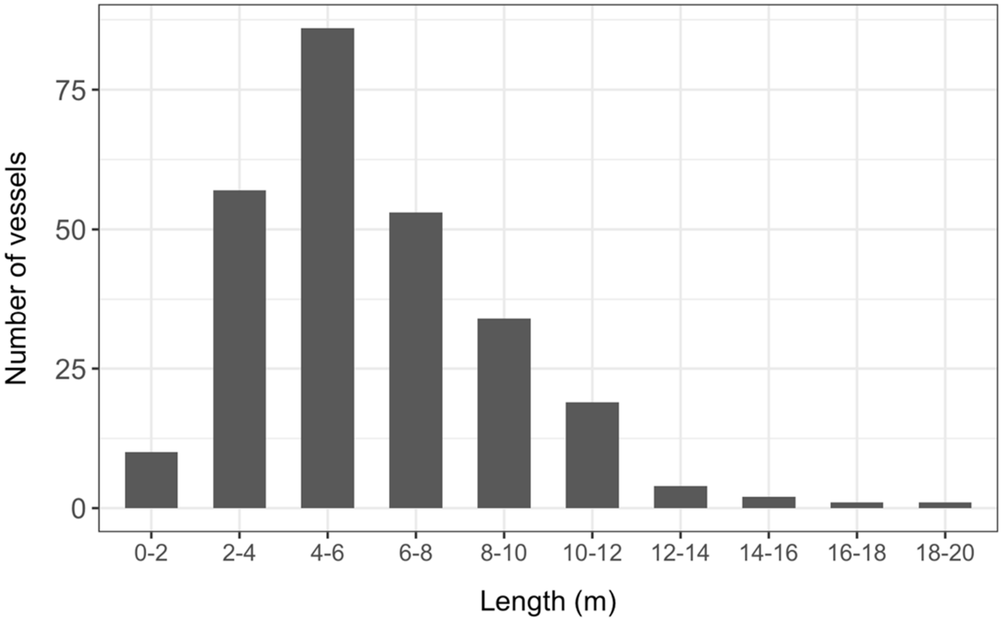


Figure 3.6. The size distribution of nearshore vessels landing in central regions in 2015.

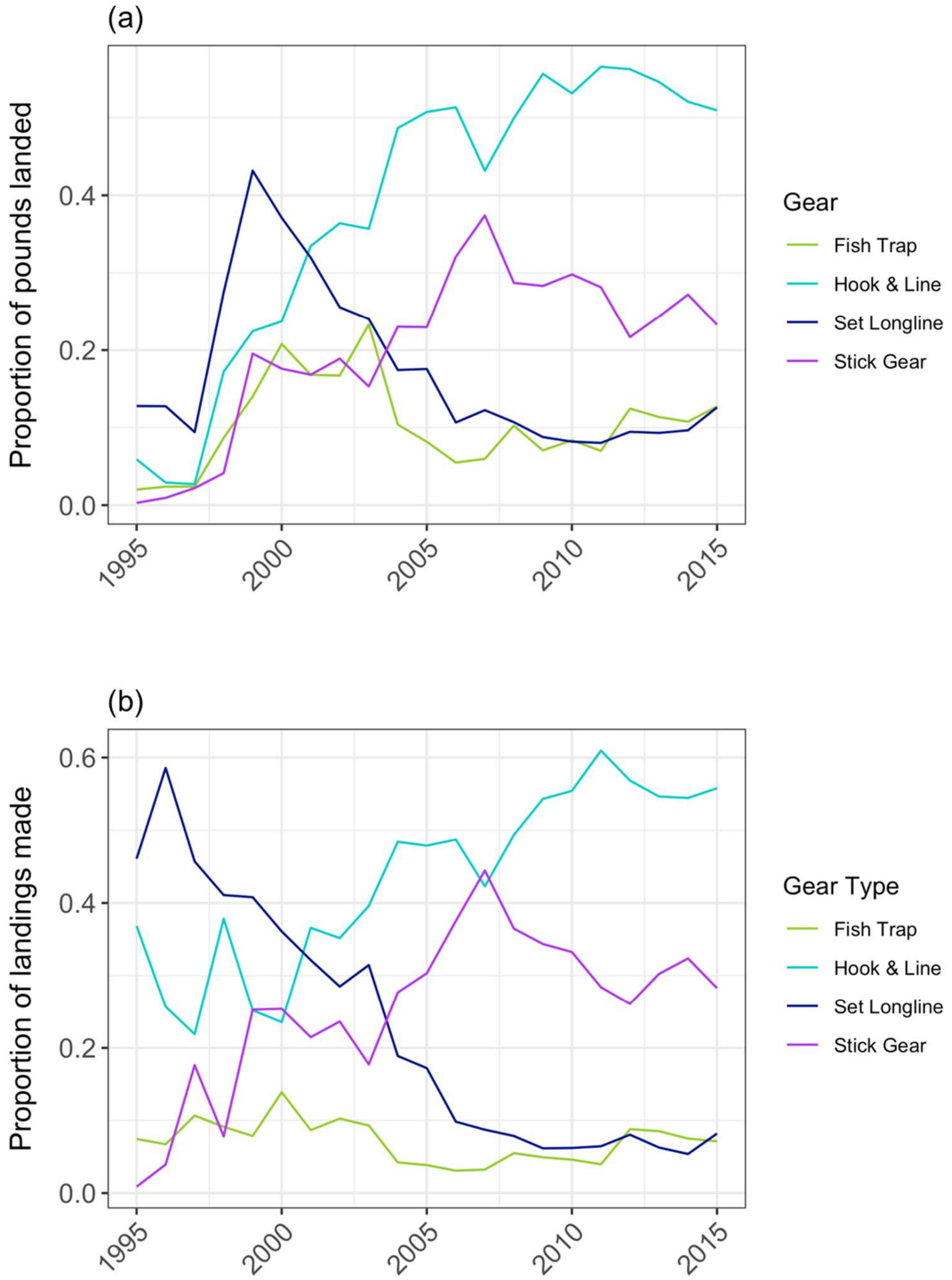


Figure 3.7. Interannual trend in gear use as (a) the proportion of total pounds landed, and (b) the proportion of total landings (by number) in the central regions of

California’s nearshore fishery. Note that it is not possible to fully characterize the use of “stick gear”. Here, the “stick gear” category is gear reported on a fish ticket as “Vertical Hook & Line/Portuguese Longline”.

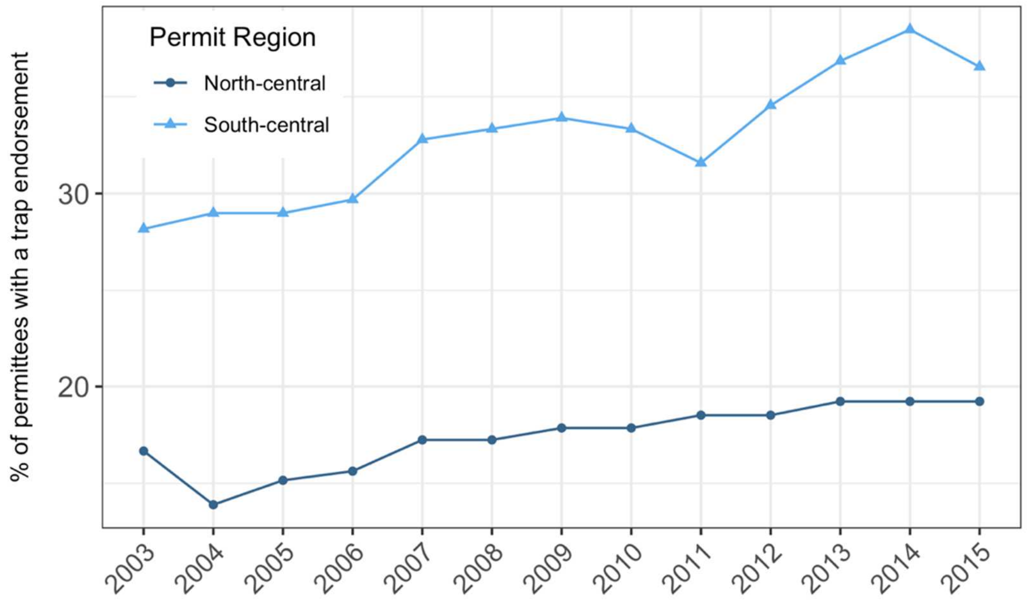


Figure 3.8. Interannual trends in the percentage of shallow nearshore permittees that also hold trap endorsements. Non-transferrable and transferrable designations are combined for both the fishery permit and the trap endorsements.

Figure 3.9. Geographic distribution of fishing effort in 2015 for the two central regions of California's nearshore fishery at the spatial resolution of port region.

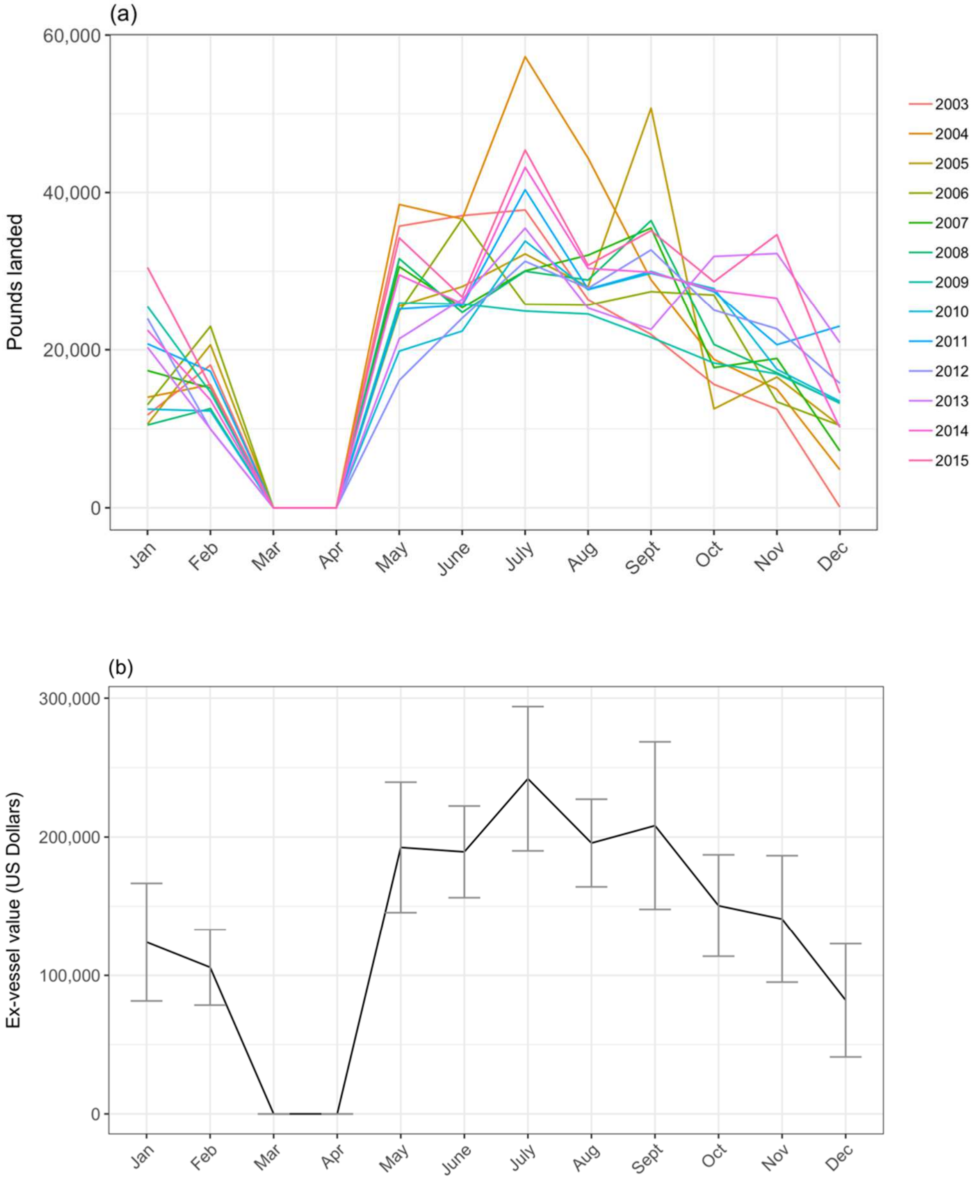


Figure 3.10. Seasonal trends in (a) the total pounds landed by month, and (b) the mean ($\pm 1\ SD$) ex-vessel value of landings in the combined shallow and deeper nearshore fishery in central region ports by month. The fishery is closed in March and April.

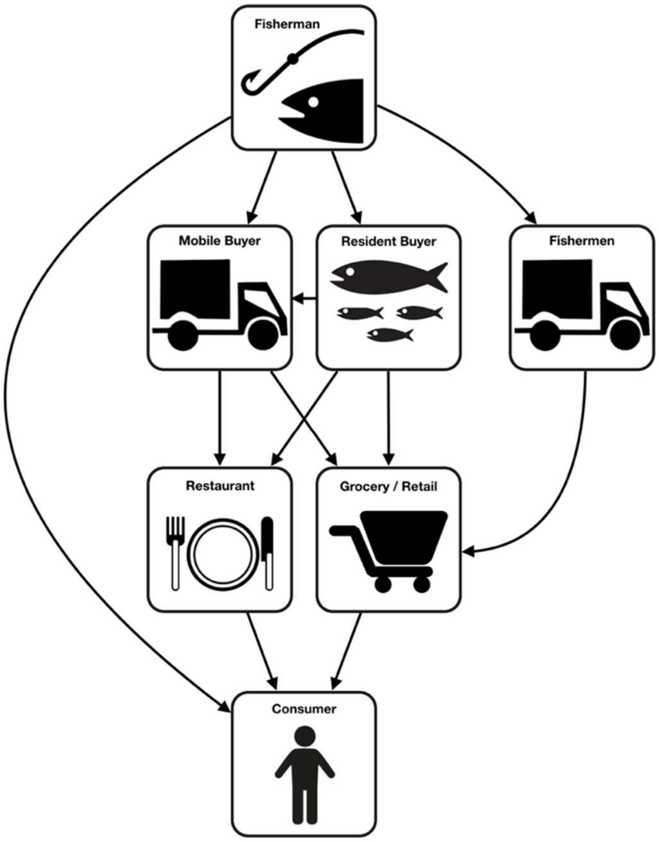


Figure 3.11. Major supply chains for nearshore catch in the central regions of California. A small portion of nearshore catch is also consumed rather than sold. Adapted from marketyourcatch.org.

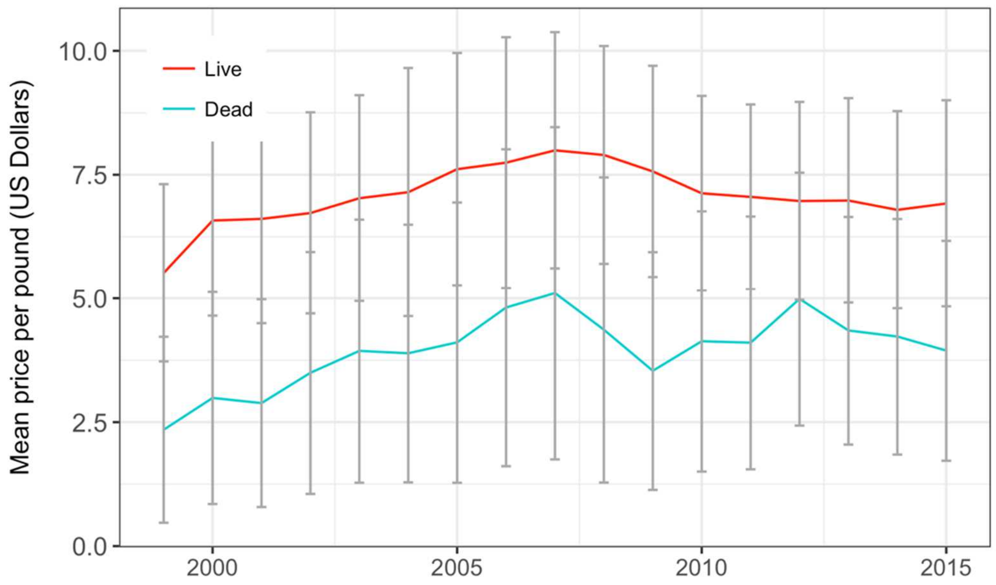


Figure 3.12. The interannual trend in mean price per pound ($\pm\ 1\ SD$) of nearshore landings in central region ports (all species combined) from 1999 to 2015. Landings with a price of $0 reported on the landings receipt were excluded.

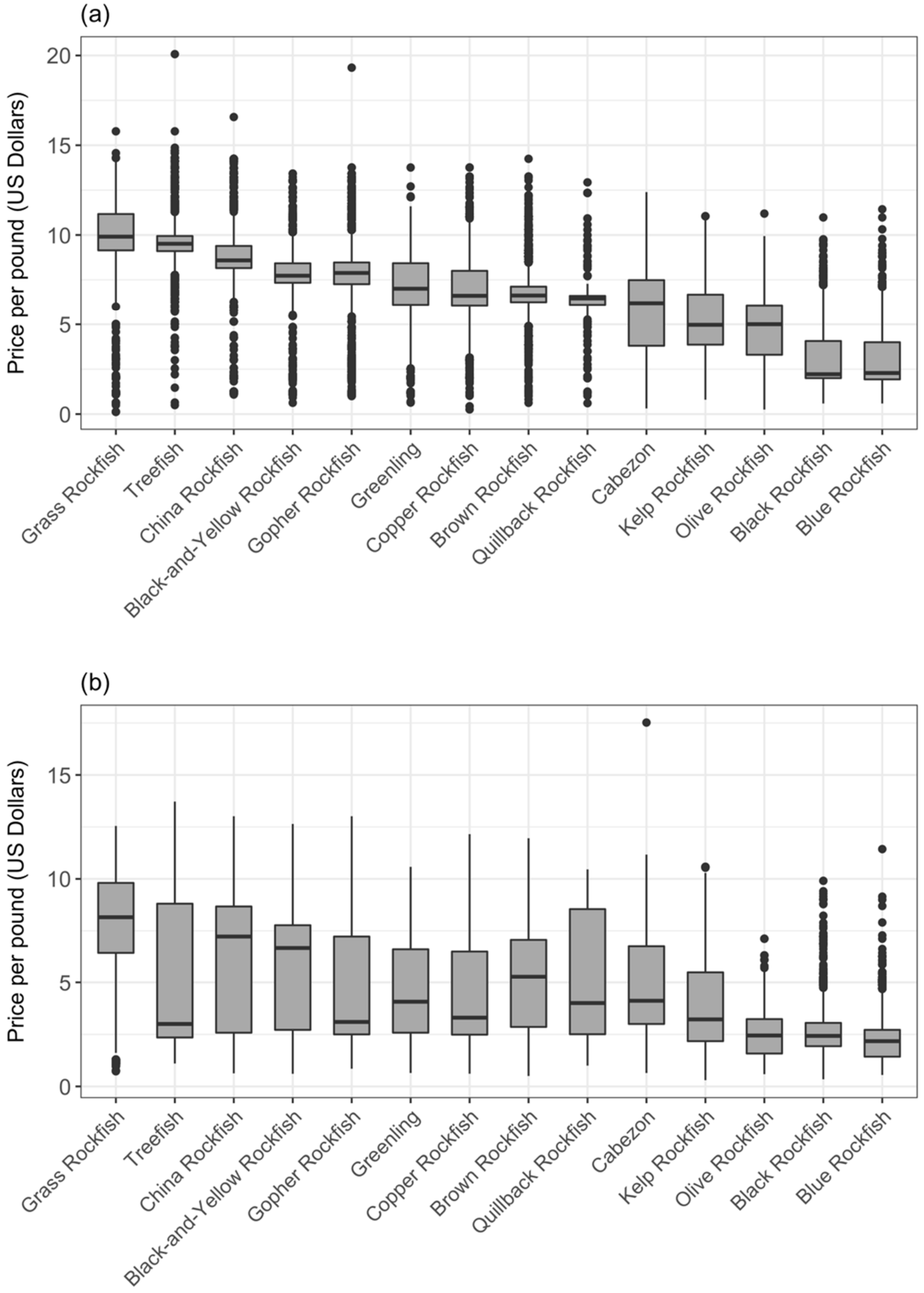


Figure 3.13. Price per pound of nearshore landings by species aggregated over years 2003 to 2015 for (a) fish sold live, and (b) fish sold fresh dead. Boxplots depict the

median (bold line), first (25th) quantile (lower hinge), third (75th) quantile (upper hinge), maximum (upper whisker), minimum (lower whisker), and outliers (black dots). Landings with a price of $0 reported on the landings receipt were excluded.

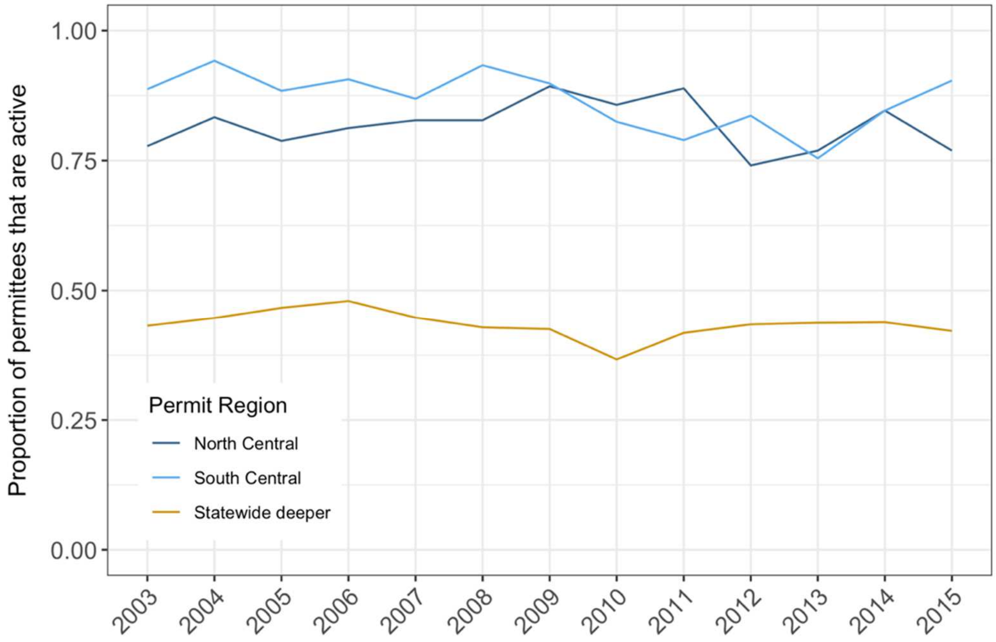


Figure 3.14. Interannual trends in the proportion of nearshore permittees that were active (made at least one landing of nearshore species) in each year 2003 to 2015. Data for deeper nearshore permittees is statewide.

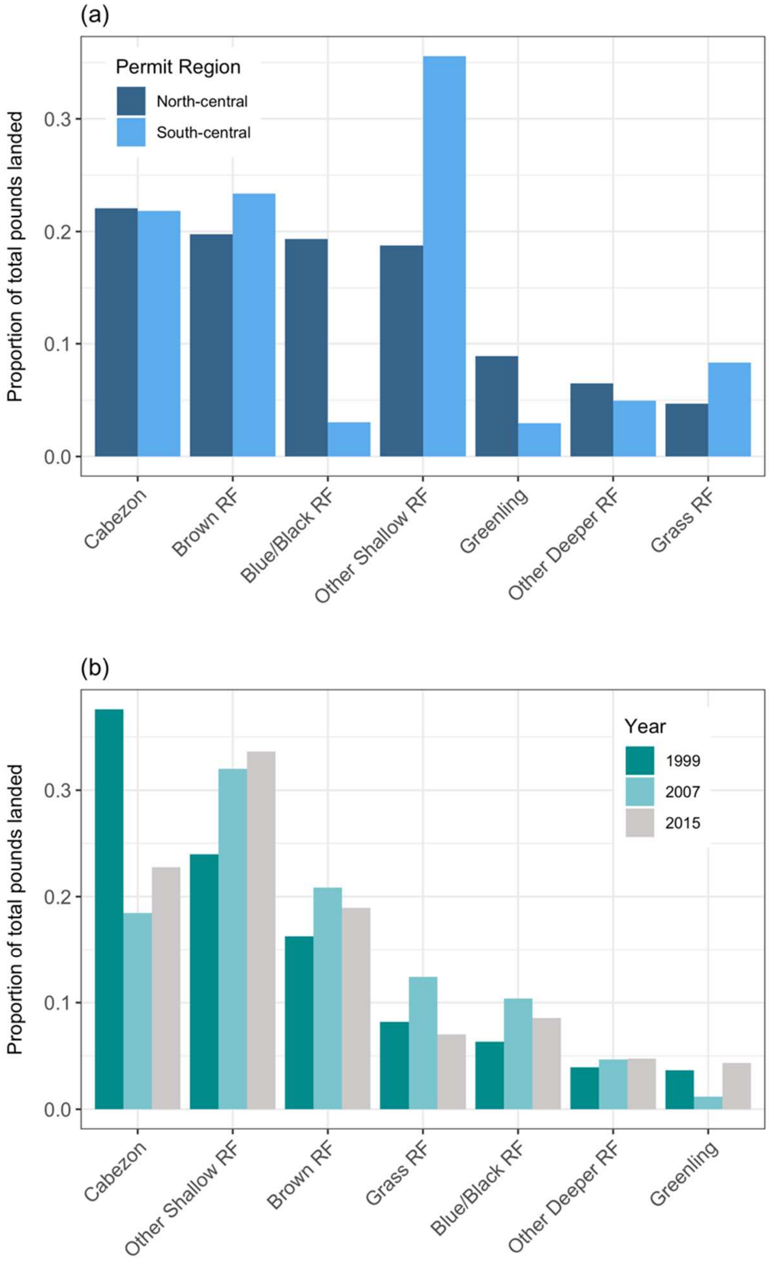


Figure 3.15. Species composition of nearshore landings for (a) the North-central and South-central permit regions in 2015, and (b) the years 1999, 2007 and 2015 for the North- and South-central regions combined.

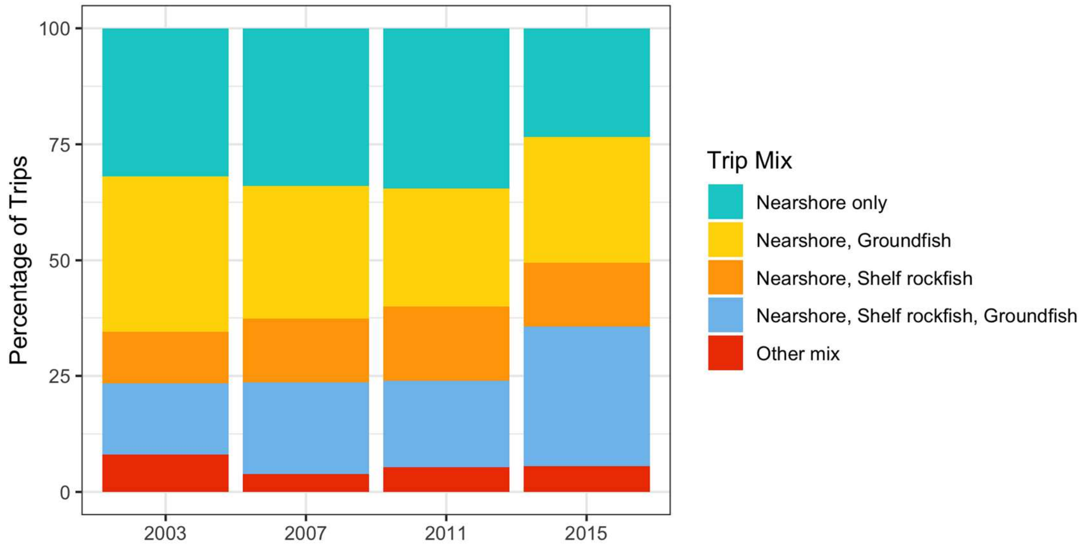


Figure 3.16. The landings mix on trips made by nearshore permittees (shallow and deeper) where nearshore species were landed. All mixes that make up more than 1% of annual trips from 2003 to 2015 are included. Four years are shown for visual assessment of change over time. The groundfish category includes all groundfish species that are not part of the shelf rockfish, slope rockfish or nearshore rockfish groups.

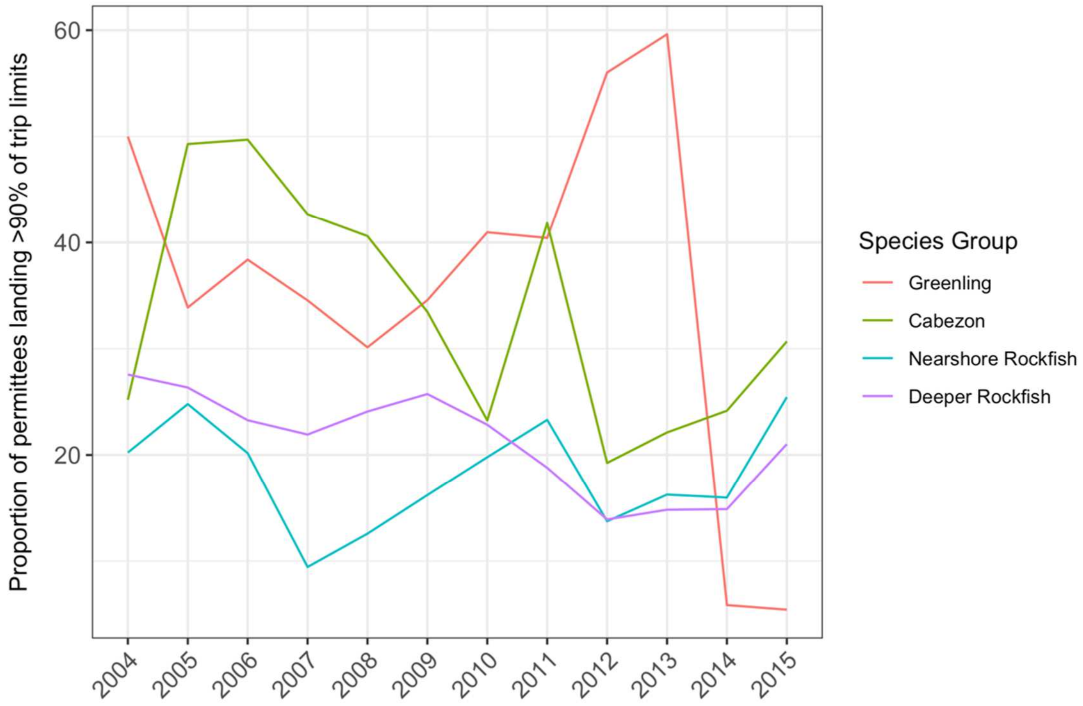


Figure 3.17. Proportion of central region nearshore permittees that land at least 90% of their annual trip limits for a given species group in a year-long period (2-month trip limits were summed for the year). Cabezon, Greenling and Nearshore Rockfish data comes from North-central and South-central permittees that made at least one landing of shallow nearshore species in a given year. Deeper Rockfish data comes from statewide deeper permittees that made at least one landing of a deeper nearshore species in a given year.

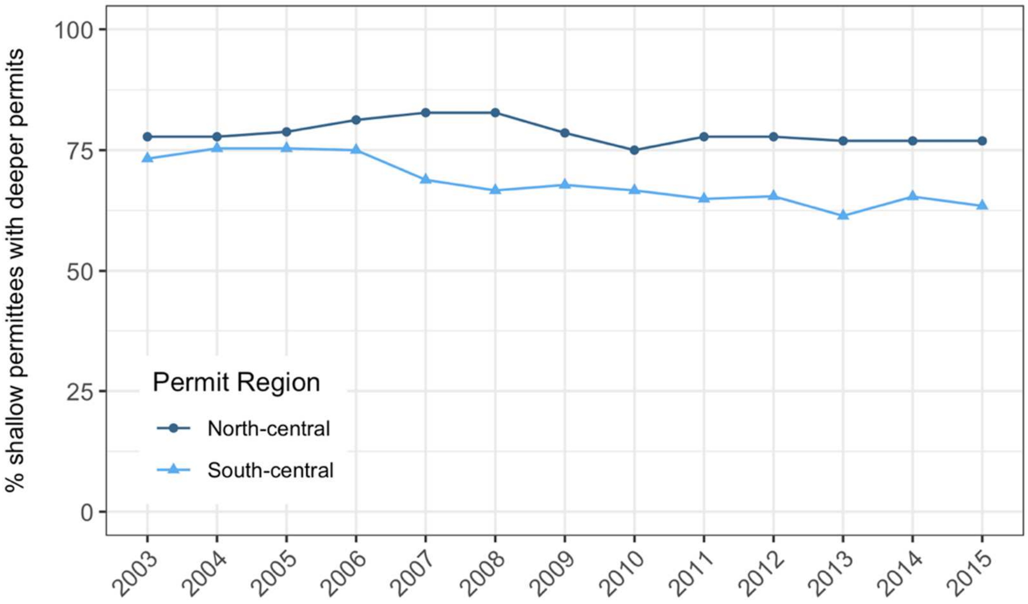


Figure 3.18. The percentage of shallow nearshore permittees in the North- and South-central permit regions that also hold deeper nearshore permits.

Table 3.3a. The top ten fishery mixes of nearshore permit holders (1999 to 2002) who made landings of nearshore species in central ports. Values are the percentage of fishermen with a given fishery mix for that year. '—' denotes mixes that were not identified or are not within the top ten for a given year. Years with '*' had fewer than ten mixes identified. HMS = Highly Migratory Species complex. 'Nearshore' refers to both shallow and deeper nearshore species. 'Groundfish' includes all groundfish species not included in other categories in this table.

Fishery Mix	**Percentage of nearshore fishermen (%)**			
	1999	**2000**	**2001**	**2002***
Nearshore, Groundfish	39.5	26.9	29.7	35.9
Nearshore, Salmon, Groundfish	7.6	6.6	9.5	13.7
Nearshore	7.0	10.7	9.5	6.0
Nearshore, Urchin, Groundfish	6.5	4.7	4.1	8.5
Nearshore, Groundfish, Other finfish	5.9	7.5	9.5	16.2
Nearshore, Groundfish, Surfperch	5.4	4.2	2.7	—
Nearshore, Salmon, Groundfish, Halibut	4.3	—	—	—
Nearshore, Groundfish, Halibut, HMS	3.2	—	2.7	—
Nearshore, Groundfish, Halibut	3.2	7.1	6.1	6.8
Nearshore, Salmon, Groundfish, HMS	2.7	—	—	—
Nearshore, Salmon, Dungeness crab, Groundfish	2.7	—	—	—
Nearshore, Groundfish, HMS	2.7	4.7	4.1	6.8

Nearshore, Salmon	—	3.8	—	—
Nearshore, Salmon, Groundfish, Halibut, HMS	—	2.8	—	2.6
Nearshore, Groundfish, Other finfish, Surfperch	—	2.8	—	—
Nearshore, Salmon, Groundfish, Sablefish	—	—	4.7	3.4
Nearshore, Groundfish, Sablefish	—	—	2.7	—
Nearshore, Groundfish, Halibut, HMS, Other finfish	—	—	2.7	—

Table 3.3b. The top ten fishery mixes of shallow and deeper nearshore permit holders following the implementation of restricted access (2003 to 2015) who made landings of nearshore species in central ports. Values are the percentage of fishermen with a given fishery mix for that year. '—' denotes mixes that were not identified or are not within the top ten for a given year. Years with '*' had fewer than ten mixes identified. HMS = Highly Migratory Species complex. 'Nearshore' refers to both shallow nearshore species. 'Groundfish' includes all groundfish species not included in other categories in this table.

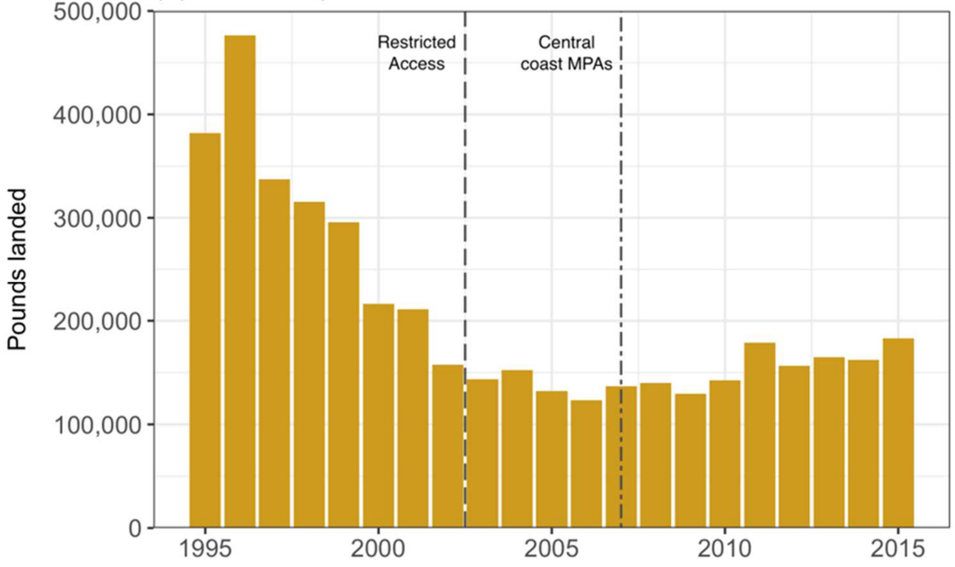
Fishery Mix	**Percentage of nearshore fishermen (%)**												
	2003	**2004***	**2005***	**2006**	**2007**	**2008***	**2009**	**2010**	**2011***	**2012***	**2013**	**2014***	**2015***
Deeper nearshore, Nearshore, Groundfish	30.9	31.1	33.3	21.0	20.7	25.5	19.0	15.2	26.1	23.5	26.8	29.3	27.3
Deeper nearshore, Nearshore	10.9	4.9	—	6.5	5.2	—	—	—	8.7	5.9	5.4	—	9.1
Nearshore, Groundfish	10.9	16.4	17.5	12.9	17.2	13.7	5.2	13.0	6.5	9.8	7.1	7.3	9.1
Deeper nearshore, Groundfish Halibut	9.1	9.8	—	—	5.2	5.9	13.8	—	—	—	—	—	—

Deeper nearshore, Nearshore, Salmon, Groundfish	9.1	9.8	12.3	—	10.3	7.8	6.9	—	—	—	5.4	7.3	—
Deeper nearshore, Salmon, Groundfish	7.3	9.8	8.8	4.8	5.2	7.8	—	—	—	—	7.1	—	—
Deeper nearshore, Groundfish	5.5	11.5	10.5	9.7	12.1	21.6	13.8	15.2	17.4	19.6	17.9	17.1	18.2
Deeper nearshore, Nearshore, Groundfish, Other finfish	5.5	6.6	7.0	6.5	5.2	5.9	13.8	13.0	13.0	15.7	7.1	17.1	15.9
Deeper nearshore, Nearshore, Urchin, Groundfish	5.5	—	—	—	—	—	—	—	—	—	—	—	—
Nearshore, Urchin, Groundfish	5.5	—	—	—	—	—	—	—	—	—		7.3	—
Deeper nearshore, Nearshore, Groundfish, Surfperch	—	—	5.3	—	—	—	—	—	—	—	5.4	—	—
Deeper nearshore, Salmon, Groundfish, Halibut	—	—	5.3	8.1	—	5.9	8.6	6.5	—	7.8	5.4	—	—
Deeper nearshore	—	—	—	6.5	—	—	—	—	—	—	—	—	—
Deeper nearshore, Nearshore, Groundfish, Halibut	—	—	—	4.8	—	5.9	5.2	10.9	6.5	—	—	—	—

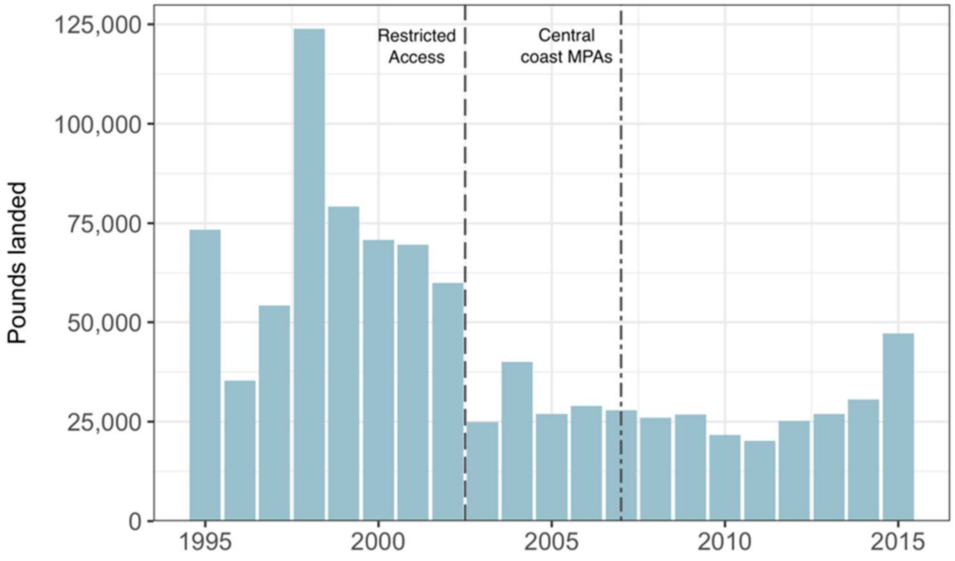
Deeper nearshore, Nearshore, Salmon, Dungeness crab, Groundfish, Sablefish	—	—	—	4.8	—	—	—	—	—	—	—	—	—
Deeper nearshore, Nearshore, Salmon, Groundfish, Halibut	—	—	—	4.8	5.2	—	—	—	—	—	—	—	—
Deeper nearshore, Salmon, Dungeness crab, Groundfish	—	—	—	4.8	6.9	—	—	—	—	—	—	—	—
Nearshore	—	—	—	4.8	—	—	8.6	—	6.5	5.9	7.1	7.3	6.8
Deeper nearshore, Nearshore, Salmon, Groundfish, Sablefish	—	—	—	—	6.9	—	—	—	—	—	—	—	—
Deeper nearshore, Nearshore, Salmon	—	—	—	—	—	—	5.2	—	—	—	—	—	—
Deeper nearshore, Groundfish, Halibut, Other finfish	—	—	—	—	—	—	—	6.5	6.5	5.9	—	—	6.8
Deeper nearshore, Nearshore, Groundfish, Halibut, Other finfish	—	—	—	—	—	—	—	6.5	—	—	—	—	—

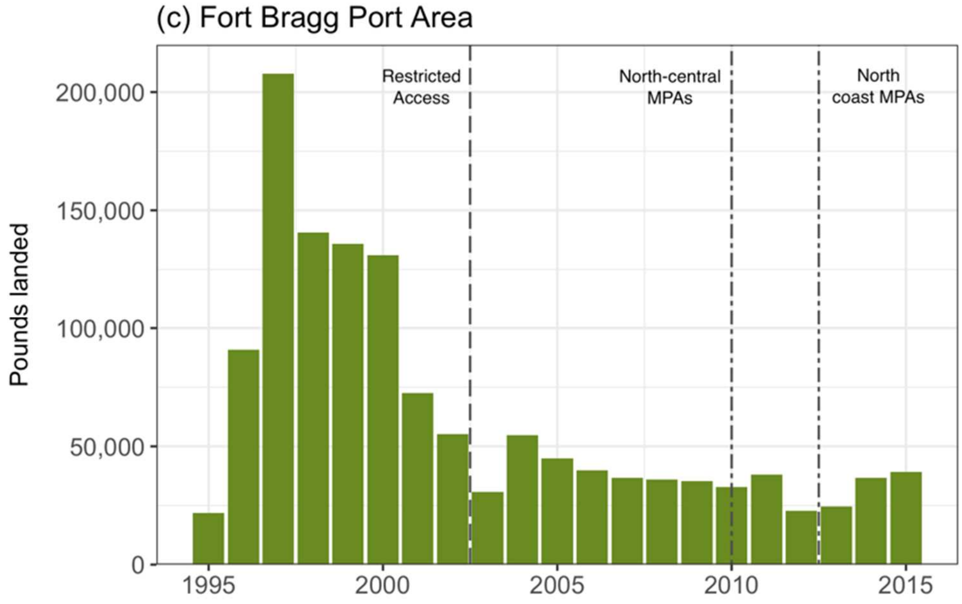
Deeper nearshore, Nearshore, Salmon, Dungeness crab, Groundfish, Sablefish	—	—	—	—	—	—	—	6.5	—	—	—	—	—
Nearshore, Urchin, Groundfish	—	—	—	—	—	—	—	6.5	8.7	—	—	—	—
Deeper nearshore, Nearshore, Salmon, Groundfish, HMS, Other finfish	—	—	—	—	—	—	—	—	—	5.9	—	—	—
Nearshore, Salmon	—	—	—	—	—	—	—	—	—	—	5.4	—	—
Deeper nearshore, Nearshore, Groundfish, Sablefish	—	—	—	—	—	—	—	—	—	—	—	7.3	—
Deeper nearshore, Nearshore, Groundfish, Other finfish, Surfperch													6.8

(a) Morro Bay Port Area



(b) Monterey Bay Port Area





Figures 3.19. Total landings for the shallow and deeper sectors of the nearshore fishery from 1995 to 2015 for (a) Morro Bay, (b) Monterey, and (c) Fort Bragg port areas, the three port areas making up the largest proportion of central coast landings.

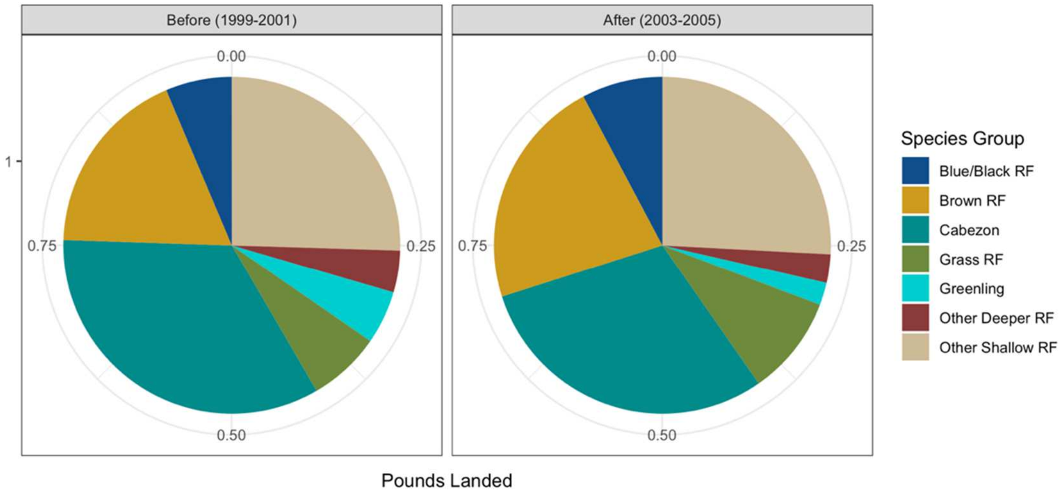
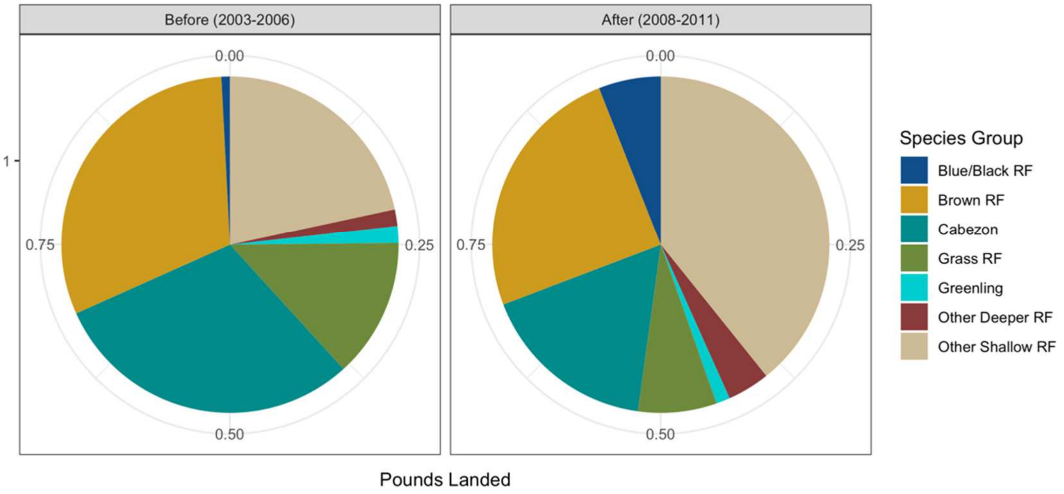


Figure 3.20. Species composition of landings in the three years before (1999-2001) and after (2003-2005) restricted access permits were required to participate in the nearshore fishery. 2002 is excluded as a year that was potentially anomalous due to anticipation of restricted access implementation.

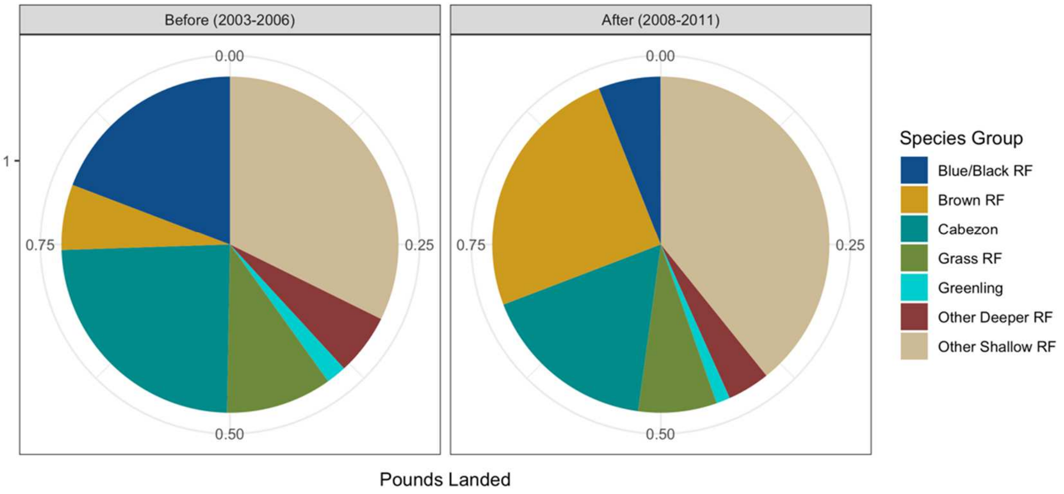
Table 3.4. The average (± *SD*) number of annual pounds landed and annual number of nearshore trips (as estimated by the number of distinct nearshore landings in the CFIS data) pre- and post-MPA establishment (Monterey and Morro Bay, pre: 2003-2006, post: 2008-2011; Fort Bragg, pre: 2007-2009, post: 2013-2015) for shallow and deeper nearshore fishermen. For Morro Bay, Welch's two sample t-tests were used to account for unequal variance.

Port Area	**Annual pounds landed per fisherman**			**Number of annual landings per fisherman**		
	Pre-MPA	Post-MPA	t-test	Pre-MPA	Post-MPA	t-test
Fort Bragg	1586 ± 1440	1647 ± 1668	$p = 0.82$ t(127) = 0.22	21 ± 21	18 ± 18	$p = 0.37$ t(127) = 0.90
Monterey	998 ± 1134	1214 ± 1189	$p = 0.20$ t(197) = 1.29	13 ± 17	17 ± 21	$p = 0.15$ t(197) = 1.43
Morro Bay	1943 ± 1899	2815 ± 2441	$p < 0.001$ t(381.55) = 4.30	24 ± 25	44 ± 42	$p < 0.001$ t(321.09) = 6.08

(a) Morro Bay



(b) Monterey



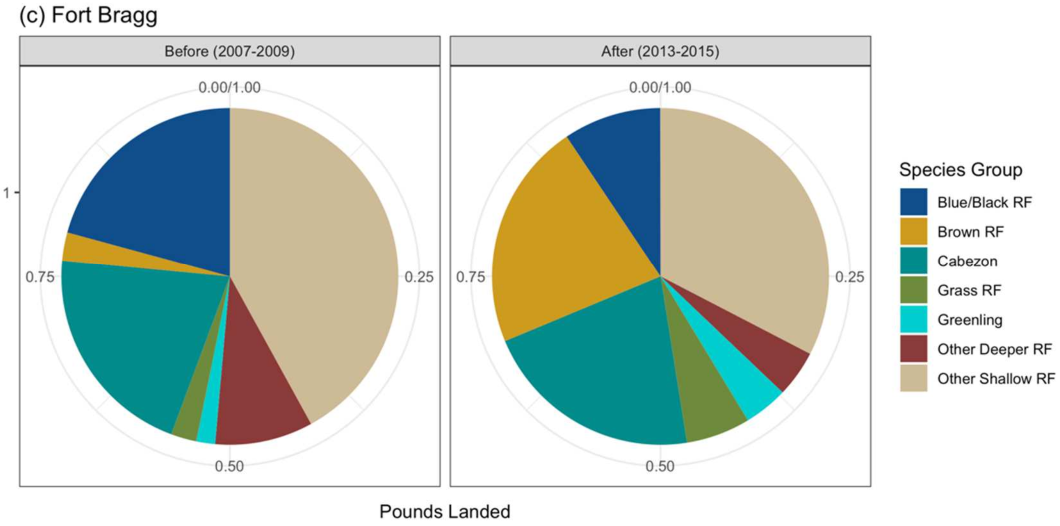


Figure 3.21. Species composition of landings in the three years before and after MPAs were established in (a) Morro Bay, (b) Monterey, and (c) Fort Bragg port areas. The year that MPA restrictions went into effect is excluded.

Chapter 4: Social and biophysical factors influencing catch composition in central California's commercial nearshore fishery

Abstract

Despite advances in the study of fishery social-ecological systems, challenges still exist when comparing and combining socio-cultural, economic and biophysical information sources. These data are often collected at vastly different scales and often using fundamentally different approaches. However, as fisheries management continues to shift from single-species approaches to more holistic, ecosystem-based approaches, both biophysical and socio-economic considerations and data sources are necessary to inform decision-making. With this research, I illustrate how information about fishermen and fishing operations can be combined with ecological and environmental data to explore and better understand fishery outcomes. The composition of species removed by a fishery from the kelp forest ecosystem is essential when assessing the environmental impacts of fishing, and also important for understanding market opportunities for fishermen, fishery operations, and variation in fishery revenue. Here I use multivariate analyses to explore the factors that influence the species composition of nearshore landings, showing that the permit mix that a fishery participant holds, the gear they use, and the port where they land fish all

strongly influence the species that fishermen land. However, the single most important predictor of a fisherman's catch composition is the identity of that fisherman. This result highlights the importance of understanding social dynamics in a fishery, and considering variation in human behavior, fishing operations, and practices when assessing a fishery system.

Introduction

The last several decades have seen a shift from single-species models and fisheries management approaches to ecosystem-based fisheries management (EBFM) (Link 2002, Pikitch et al. 2004, Crowder et al. 2008). With the shift toward this more systems-wide management approach, many definitions and conceptions of EBFM have emerged (Arkema et al. 2006). Some take a more ecology-centric approach, variously emphasizing the management of marine ecosystems rather than species (with humans treated as stressors on, rather than a component of, the ecosystem), the inclusion of all species in a food web, and the biophysical dynamics of a system (Link 2002, Cury 2004, Pikitch et al. 2004). Focusing more on relationships and process, Hilborn (2004) calls for an ecosystem approach that emphasizes "the interactions between fish, fishermen, and government regulators and concentrates on incentives and participation with user groups." Similarly, Jennings (2004) discusses the importance of recognizing multiple objectives in EBFM: protecting natural ecosystems in a way that will allow future generations to continue to benefit from fishery-based ecosystem services, and maintaining fisheries that meet the needs of society today. However, as many have noted, fisheries management is the management of people who exist in complex communities with social, economic and governance institutions, not the management of fish (Campling et al. 2012). To this end, some take a more interdisciplinary approach to defining EBFM, emphasizing management objectives that include socioeconomic goals, connections within social-ecological systems, and relevant governance institutions (De Young et al. 2008, Christie et al. 2009, Berkes 2012). Regardless of the definition used, EBFM calls for both biophysical and socio-economic considerations and data sources.

Despite advances in the study of social-ecological systems, challenges remain when comparing and combining socio-cultural, economic and biophysical information. These data are often collected at vastly different spatial and temporal scales, and often using fundamentally different scientific approaches. Moreover, while clear avenues exist for incorporating both ecological and economic data into the fisheries management process, standard approaches for the integration of social and cultural information are still in development (Burdge et al. 2003, National Marine Fisheries Service 2007, Pomeroy et al. 2018).

Climate change and the accompanying changes in distribution and abundance of fished species, variable ocean dynamics, and global market shifts suggest a changing commercial fisheries landscape in California. To deal with this ever-present uncertainty in California's fisheries, an adaptive approach to EBFM is being pursued by state and federal regulatory institutions (Pacific Fishery Management Council 2013). California's commercial nearshore fishery (characterized in Chapter 3 of this dissertation) provides a case study for one such fishery where advances in management's ability to incorporate new data types could improve EBFM outcomes. Though aspects of single-species management are an essential part of the nearshore management scheme (e.g., total allowable catch-based trip limits for specific nearshore species derived from single-species stock assessments), other aspects of management take a decidedly ecosystem-based approach. The fishery is managed as a complex of nineteen interacting species that rely on similar habitats, have many of the same ecological and biological characteristics, and are influenced by similar environmental phenomena. Marine protected areas (MPAs) that focus on habitats and wider kelp forest ecosystems are part of the management approach detailed in the Nearshore Fisheries Management Plan. In fact, California's nearshore fishery is highlighted in early literature on EBFM for the precautionary approach taken in the face of ecological uncertainty (Pikitch et al. 2004). Building on that history, my research explores how information about fishermen and their fishing operations can be combined with ecological and environmental data to explore fishery outcomes relevant to adaptive management.

The species composition of nearshore landings (also referred to as catch composition) is a fundamental component of the fishery's social-ecological system. The composition of species removed from the kelp forest ecosystem is important when assessing the environmental impacts of fishing, and changes in kelp forest communities. Similarly, catch composition affects and is affected by the fishery's human system, including fishing practices, market opportunities and supply chains, and revenue to fishermen. Species composition of landings in the nearshore fishery varies over both space and time, and specific management interventions likely have played a role in this variability (see Chapter 3). Landings data show that catch composition was different before and after the implementation of restricted access, and (in some ports) before and after MPA establishment. Interviews with fishermen suggested that species composition is influenced not only by fisheries management, but also by ex-vessel price per pound of individual species and by weather. Here, I take a comprehensive approach to understanding the various socio-economic and biophysical factors that influence catch composition in the nearshore fishery.

Based on results from Chapter 3, I hypothesize that increasing ex-vessel price (paid to the fisherman) of a nearshore species (which itself stems in part from market preferences and species' biological attributes) will have a positive effect on the proportion of that species in a fisherman's nearshore catch. Second, because the fishery is divided into two sub-sectors, shallow and deeper nearshore, and because permittees do not necessarily have access to both sets of species, I expect that that the nearshore permit mix that a fisherman holds (shallow permit, deeper permit or both) will play a major role in a fishery participant's catch composition.

Many fishermen cited weather as the main factor influencing where they could or would fish in the nearshore. Because some species live in shallower habitats that are more dangerous to access during high winds or high swell, I expect that poor weather will decrease the proportion of these shallow species (e.g., Grass Rockfish, Black-and-Yellow Rockfish) in the landings. Most of the shallow nearshore species in the fish assemblage are strongly kelp-associated. As such, I expect that fishermen with access to both shallow and deeper species will land a higher proportion of shallow species in years with above average kelp biomass. Finally, variability in net primary productivity may influence ecological communities, potentially affecting larval production and survival of fish in central California. However, because nearshore species are not known to migrate out of central California in search of favorable conditions, and since there is no evidence to suggest interspecies differences in the nearshore assemblage response to changes in net primary productivity, I do not expect that this biophysical driver will influence nearshore catch composition.

In addition to these environmental variables, localized variability in fish abundance and distribution likely influences nearshore catch composition. Using high-resolution ecological data (collected by the Partnership for Interdisciplinary Studies of Coastal Oceans; PISCO) and commercial fishery landings data, I assess the correlation between landings in the nearshore fishery and the relative abundances of nearshore species in kelp forests. I hypothesize that biogeography (i.e., which species are present and abundant in which port areas) of the nearshore rockfishes contributes to the spatial variation in landings shown in the previous chapter. However, because of market forces such as consumer preference, and the constraints of fishing operations, I do not expect that temporal shifts in species composition of the fish assemblage will correspond to shifts in the species composition of nearshore landings.

Methods

Study system

California's nearshore fishery is a small-scale commercial fishery operating in coastal waters over rocky reef habitats. The restricted access fishery includes nineteen species of nearshore finfish that permittees target with hook-and-line, trap, and longline gear, predominately for sale in the live fish market. The history of the nearshore fishery, characteristics of the social system, and important ecological attributes of nearshore species are detailed in Chapter 3. Here I focus on contemporary changes in the nearshore fishery during the time period following the implementation of restricted access in 2003 and ending in 2015 (the last year for which data are currently available). As such, management structure in the fishery has remained relatively constant, with the notable exception of MPA establishment.

CDFW fisheries landings and associated data

A variety of independent variables that might affect catch composition were chosen based on insights from interviews with fishermen, and nearshore fishery summary statistics calculated using CDFW's Commercial Fisheries Information System (CFIS) landings data. Social and economic attributes of the fishery and nearshore participants were derived using data from CFIS. Biophysical data were accessed through public sources. Descriptions, geographic scale and sources of data are summarized in Table 4.1.

Analytical approach

I first used a linear regression analysis to assess the influence of mean price paid to a fisherman for a live fish of a given species on the proportion of that species in a participant's catch composition. Due to the potentially confounding effects of regulations related to California's diverse commercial fisheries, only permittees with both shallow and deeper nearshore permits (enabling them to land any nearshore species) were included in this analysis. Landings were excluded when the unit price recorded in the CFIS database was zero. Price was adjusted to 2015 dollars to account for inflation using the Bureau of Labor Statistics' Consumer Price Index for the United States.

Next, I explored the relationships between socio-economic attributes of permittees, characteristics of fishing operations, and biophysical variables, and the response variable of catch composition using permutational multivariate analysis of variance (PERMANOVA) and non-metric multidimensional scaling (NMDS). Data for these analyses were extracted from the CFIS database for all permittees in the North-central and South-central regions of the shallow nearshore fishery, and the permittees in the deeper nearshore fishery that made landings in central region ports (Cape Mendocino to Point Conception). Landings made in the year 2003 were excluded from this analysis because landings made from January to April in that year occurred before restricted access was implemented. Replicates were individual fishermen for a given year (n = 1372), and their catch composition was calculated based on the annual weight of each species landed. Replicates with missing data for any of the explanatory variables derived from the CFIS data were excluded. Replicates that listed catch by the market categories "nearshore rockfish group" (n = 20), "deeper nearshore rockfish group" (n = 17), or "blue/black rockfish group" (n = 7) were excluded. Market category “Bolina group” was re-categorized as Brown Rockfish, and category “Gopher group” was re-categorized as Gopher Rockfish (Leet et al. 2001). California Scorpionfish, Calico Rockfish and Rock Greenling were present in fewer than 20 observations, and were excluded from the analysis. Finally, kelp extent data were only available for the Monterey and Morro Bay port areas. As such, a separate model for just these South-central ports was run to test the affect of kelp extent. In this model, Quillback Rockfish were also excluded since fewer than 10 landings of this species were made from 2004 to 2015 in the South-central region.

I developed PERMANOVA models using PRIMER 6.0 and a Type III sum of squares to quantify the effect of each of the focal variables detailed in Table 4.1 on nearshore catch composition (Anderson 2001). One model was run with all variables with the exception of PISCO abundance data; a second was run also excluding the permittee variable. Post-hoc pairwise comparisons were conducted to determine significance between levels of the categorical variables tested. I then used NMDS to better understand the relationships among different levels of these variables and species in the nearshore fish assemblage. This allowed me to visualize the similarities in catch composition among port areas (Fort Bragg, Bodega Bay, San Francisco, Monterey, and Morro Bay), permit mixes (shallow, deeper, or both), and predominant gear types (hook-and-line, longline, trap, stick or mixed gears). NMDS analysis was conducted using the vegan package in R, with Bray-Curtis dissimilarity to calculate distance matrices (Bray and Curtis 1957, Oksanen et al. 2016, R Core Team 2018). Variation in catch composition was reduced to 1, 2, and 3 axes, and stress values were used to determine the best model. A stress value below 0.2 indicated that the NMDS ordination represented the original data well. When stress values of multiple models were below 0.2, the model with fewer axes was chosen. Convex hull ellipses were used to visualize 95% confidence intervals around data centroids.

Finally, I directly compared long-term ecological monitoring biomass data derived from PISCO SCUBA surveys with fishery-dependent landings data to explore the relationship between ecological relative abundance of species and the proportion of that species in nearshore landings. The match, M, between nearshore biomass and annual fishery landings biomass was calculated as

$$M_i = (mean\ pounds\ landed_{i,j} - mean\ PISCO\ biomass_{i,j}) \,/\, (mean\ PISCO\ biomass_{i,j} + mean\ pounds\ landed_{i,j})$$

where *i* is a nearshore species, and *j* is a year from 2004 to 2015. Due to ecological data constraints, this analysis is limited to the Monterey port area where PISCO data have been collected nearly continuously from 2004 to 2015. Ecological data were collected at Monterey Bay, Carmel Bay and Big Sur sites (for more information, see www.piscoweb.org). Because California Sheephead, Quillback Rockfish, Monkeyface Prickleback, California Scorpionfish, Calico Rockfish, and Rock Greenling are not often recorded in PISCO surveys or landed on the central coast (leading to many zeros in the dataset), these species were excluded from the analysis. A Mantel test was used to test for a correlation between the matrix representing the similarity in ecological relative abundance between years, and the matrix representing the similarity between catch composition between years.

Results

I found a positive linear relationship between average live price per pound paid to a permittee for a given species and the proportion of that species in the permittee's nearshore catch composition ($p = 0.001$, $R^2 = 0.03$; Figure 4.1). However, the low percentage of variance explained by price indicates that catch composition proportions were not well explained by price alone.

All variables tested in the PERMANOVA model, with the exception of the number of annual small craft advisory days ($p = 0.94$) and net primary productivity ($p = 0.34$), significantly affected catch composition in the full model (Table 4.2). Overall, the model explained approximately 72% of the total variance in catch composition. The factor accounting for the highest proportion of variance explained (PERMANOVA:

$R^2 = 0.33$, $p < 0.001$) was permittee (fish license ID in the CFIS database). This variable represents the identity of an individual fisherman, his/her particular social, cultural and economic characteristics, along with experience and skill, which likely influences behavior and associated outcomes. A second PERMANOVA model excluding the permittee variable allowed me to explore the importance other variables, some of which are not independent from permittee (e.g. vessel length for an individual permittee is associated with that person; Table 4.2, results in parentheses). In the second model, which in total explained 54% of the variance in catch composition, permit mix (PERMANOVA: $R^2 = 0.35$ $p < 0.001$), port area (PERMANOVA: $R^2 = 0.13$, $p < 0.01$), and gear type (PERMANOVA: $R^2 = 0.04$, $p < 0.001$) were the top predictors. All post-hoc pairwise comparisons among permit mixes, gear types and port areas were significant ($p \leq 0.001$).

An NMDS analysis of 92 central coast nearshore fishermen in 2015 revealed distinct clusters based on several variables that were identified as predictors of catch composition in the previous analysis. Reducing catch composition to two axes (i.e., two dimensions) represented sufficient variance in catch composition among individual fishermen (stress = 0.13). Visualized with ellipses that represent the 95% confidence interval around the data centroid, catch composition of a fisherman's landings cluster by the nearshore permit mix that the fisherman holds (shallow, deeper, or both) (Figure 4.2). Notably, the centroid of catch compositions for permittees with both permits is closer to the centroid of those with shallow rather than deeper permits. All species, with the exception of Treefish, group in ordination space with the permit required to catch them, with deeper species assigned negative values on NMDS axis 1 and shallow species assigned positive values. Though on the negative side of NMDS axis 1, Treefish falls closer to the centroid of data for individuals holding both permits or only shallow permits despite the fact that it is managed in the deeper nearshore fishery. Neither a deeper or shallow nearshore permit is required to land Monkeyface Prickleback, however that species clusters with the shallow nearshore species.

Fishermen predominantly using trap, stick, or mixed gears cluster with shallow nearshore species on NMDS axis 1, while those using predominantly hook-and-line and longline gear fall on the more negative side of axis 1 with deeper nearshore species (Figure 4.3). Bodega Bay and San Francisco port areas, both in the North-central management region, cluster with deeper nearshore species, whereas Monterey and Morro Bay port areas, in the South-central management region, cluster with shallow nearshore species (Figure 4.4). Interestingly, the Fort Bragg port area in the North-central management region clusters with Monterey and Morro Bay port areas.

Comparison of the species assemblage of nearshore fishes in Monterey port area waters and catch composition of nearshore fishermen who landed their catch in the

Monterey port area identified nine species that are landed either more or less than would be expected by the relative observed abundances of those species in the nearshore environment (Figure 4.5). Cabezon, Gopher Rockfish, Black-and-Yellow Rockfish, and Grass Rockfish are landed in a higher proportion than they are seen in PISCO surveys throughout the time series. Blue Rockfish, Black Rockfish, Kelp Rockfish, Copper Rockfish, and Treefish have higher relative abundances in the marine environment than they do in nearshore catch compositions in various years of the time series. However, species such as Copper Rockfish and Kelp Rockfish vary substantially over time. A Mantel test revealed that similarity matrices of species relative abundance between years and catch composition between years (calculated using Bray-Curtis similarity) were more correlated than would be expected by chance ($p = 0.02$, $R^2 = 0.09$).

Discussion

The single best predictor of catch composition was the permittee catching and landing the fish. This result highlights the importance of exploring and accounting for social and cultural, as well as economic, aspects of a fishery – including its participants – when seeking to understand basic fishery characteristics such as catch composition (Pomeroy et al. 2018). Participants in a given fishery often represent diverse backgrounds, perspectives, values and goals, practices, and economic contexts (Miller and Van Maanen 1979, Smith and Hanna 1993, Hall-Arber et al. 2009). A fishery managed as a multi-species complex, such as the nearshore fishery, often has even more potential for a wide range of fishing practices and styles than does a single-species fishery (Boonstra and Hentati-Sundberg 2016). As such, management measures affect individuals differently, and may lead to distinct outcomes among participants. In the PERMANOVA model presented here, the permittee variable is a proxy for many things, including some of the other variables in the model (e.g. vessel length, permit mix, gear), and some things for which no data were available (e.g. nearshore fishery background and knowledge). In the second model (run without the permittee variable), permit mix, which relates to regulatory measures explains 35% of the variance in catch composition. However, vessel length and gear used, which are also associated with an individual, explained a relatively low proportion of the variance in species composition (1% and 4% respectively), suggesting that there are additional mechanisms by which an individual's fishery practices influence catch. A person's background, knowledge, skills and experience likely play a major role. Looking forward, permittee turnover in this multi-species fishery has the potential to influence fishery outcomes even if total landing volume does not change.

Fishermen with access to all nineteen nearshore species (i.e., those holding both shallow and deeper nearshore permits) tend to land a higher proportion of shallow species. This is in part due to the higher price typically paid for many of the shallow species. Though clustering by gear type likely indicates fishermen's preference for gear based on the species they target, it is important to note that species landed does not necessarily equate to species captured. For example, nearshore trap fishermen with only shallow permits may be compelled to throw back deeper nearshore species, such as Black or Brown Rockfish caught in traps due to regulations. However, because approximately 75% of shallow permittees also hold deeper nearshore permits, gear clusters likely indicate successful targeting of higher price-per-pound, shallow species using trap and stick gear.

Species composition data for the nearshore fish assemblage is patchy in space and time on the central California coast. As such, I was not able to statistically test the influence of ecological abundance of nearshore fishes on catch composition across the study region. However, port area, which explains 13% of the variance in catch composition in the second model, may at least partially reflect spatial variability in species composition. Black Rockfish and Quillback Rockfish are more abundant in the North-central region, whereas California Sheephead are rarely seen north of Monterey Bay. These biogeographic patterns of nearshore fishes undoubtedly account for some of the explained variance attributed to port area. However, the Fort Bragg port area clusters with South-central port areas and shallow nearshore species in ordination space. This suggests that biogeographic patterns in fish distribution and abundance are only part of what makes port area important. Fort Bragg is an active commercial fishing port with essential infrastructure and sufficient landings volume to support a mobile live fish buyer. Mobile buyers also visit Monterey area ports, and a resident live fish buyer operates in Morro Bay. This is not the case at landings sites in the Bodega Bay port area. Since shallow nearshore species tend to be most valuable when landed live (which is not always the case for deeper nearshore species), these differences in fish market infrastructure potentially contribute to the distinct clusters seen among ports. Finally, access to productive kelp forest habitats in shallow water (typically less than 20 m to facilitative keeping the fish alive for sale) that are open to fishing and within several hours of a landing site differs among port areas, and likely contributes to differences in species composition among ports.

Overall, environmental factors explained less of the variance in catch composition than did factors related to the human dimensions of the fishery. The minimal variance explained by the estimates of net primary productivity support my hypothesis predicting that catch composition of the mostly sedentary nearshore fish assemblage is likely not impacted by large-scale environmental factors. The Pacific Decadal Oscillation, PDO, is another large-scale environmental driver known to impact ecological communities. However, because the response variable in this model was annual catch composition, including a variable in the model for annual PDO index was redundant with the year variable. As such, it was not possible to isolate the importance of the PDO, though the phase of the PDO may have contributed to the variance in catch composition explained by year. It is also possible that local-scale biophysical factors such as kelp extent have more of an influence on catch composition than was determined here. Variability in kelp extent occurs at the scale of individual reef areas, whereas landings data for individual fishermen are available by port of landing. Landings data are reported by 10 x 10 minute blocks, a coarser spatial resolution than ecological data, and are considered insufficiently reliable for use in such analyses. A fisherman that I classified to the Monterey port area could be landing fish anywhere from Año Nuevo to the Big Sur coast. This broad spatial scale of fishery-dependent observations may limit the ability to detect the influence of local-scale biophysical factors. Fishermen report that weather plays a major role in where and when they fish for nearshore species, with high wind days precluding them from fishing in shallow waters that become dangerous to fish in during high wind and wave conditions. However, the annual number of days with wind exceeding 20 knots (a metric similar to that of small craft advisory days issued by the National Weather Service) did not explain any of the variance in catch composition. This could be because most fishermen simply do not fish on those days rather than shifting effort to deeper water nearshore species, or that there are sufficient shallow nearshore fishing grounds that remain protected during high wind and/or swell conditions. Issues of scale of data collection could also be influencing this result. Data on wind speed were provided by the National Buoy Data Center, and most wind observations are made significantly farther offshore than nearshore fishermen operate. As such, it is possible that these data do not reflect the actual number of days that nearshore fishermen were unable to access places where shallow nearshore species are typically caught.

Results of the analysis assessing the relationship between PISCO and CFIS data support what is known regarding price by species in the nearshore fishery (see Chapter 3). The four species landed much more frequently than they are observed in ecological monitoring are among the highest value species by price, and the species landed in relatively low proportions despite high abundances in central California kelp forests are among the species with the lowest mean price. Results of the Mantel test, though significant, suggest that interannual changes in a species' relative abundance in the kelp forest do not explain interannual changes in catch composition well. Based on the null hypothesis that fishermen are landing species in equal proportions to their relative abundance in the kelp forest, it would be expected that the R^2 value of the Mantel test would be much higher than was found. These results emphasizes the important role that consumer preferences, markets, and supply chains play in determining fishery outcomes. Interviews conducted with nearshore fishermen suggested that consumers prefer live fish that look and act healthy. Fishermen reported that the difficulty in keeping certain species alive and healthy during transfer from their vessel to a fish buyer, then to a final place of sale keeps the price of species such as Kelp Rockfish, Black Rockfish and Blue Rockfish lower. In a port such as Monterey where the majority of nearshore catch is sold live, these consumer preferences in the live market influence catch composition. It follows that food systems are important to consider when assessing the ecological role of fishing. In the EBFM literature, fish are almost universally looked at as a natural resource as opposed to food, a distinction which seems to inform the specific human dimensions considered in the management process. In fact, consumer preferences, diversity in supply chains and the distribution of seafood in a given fishery, and more recently consumer-directed campaigns for environmental and social sustainability in fisheries have the potential to affect both human and ecological aspects of fishery systems (Olson et al. 2014, Kittinger et al. 2015). Further research on aspects of the nearshore fishery food system could prove beneficial in the adaptive management of the fishery.

Successful EBFM will integrate multiple interdisciplinary concepts and theories, diverse approaches to research and data collection, and multiple ways of knowing. As such, this field is a fertile ground for cross-pollination across disciplines. These analyses provide several examples of ways that ecological and socio-economic data can be combined to provide a more comprehensive understanding of fishery outcomes. Further research on the human dimensions of California’s many fisheries, and more explicit consideration of the diversity of individual fishing operations and practices should inform management decisions in the future.

Tables and Figures

Table 4.1. The variables tested for their effect on the species composition of nearshore landings.

*Due to data constraints in port areas of the North-central nearshore management region, the kelp extent variable was only tested for Monterey and Morro Bay port areas.

Variable / Factor	**Description**	**Scale**	**Source**
Year	The year in which landings took place.	NA	CFIS data; year column
Port	The port area where a permittee landed the majority of their catch in a given year	One designation for each permittee in each year	CFIS data: port_name column, binned according to CDFW convention (see Chapter 3)
Permittee	Unique ID of the fisherman holding a nearshore permit	NA	CFIS data: fish_license column
Nearshore activity	The percentage of a fisherman's total annual landings that are nearshore species	The calculation of this variable included all commercial fishery landings made in California by a given fisherman	CFIS data

Gear	Each permittee is characterized as H&L (at least 70% of nearshore landings are H&L), Longline (70% longline), Pot/Trap (70% pot/trap), Stick (70% stick) or Mixed Gear for a given year	The calculation of this variable included all landings by a fisherman of nearshore species in California for a given year	CFIS data: gear_name column, binned as detailed in Chapter 3
Vessel length	Length of the vessel used for nearshore landings (if there were multiple vessels for one fishermen in one year, lengths were averaged)	NA	CFIS data: length column in the vessels spreadsheet
Permit mix	For each year, whether a permittee had a shallow permit only, a deeper permit only, or both	NA	CFIS data: permit column in the permits spreadsheet
Small craft advisory days	Annual number of days with wind speeds exceeding 20 knots per hour	One value per year for each port region	NOAA National Data Buoy Center. Fort Bragg area: 46014; Bodega Bay Area: 46013; San Francisco Bay Area: 46026; Monterey Bay area: 46092 (2005-2015), 46042 (2004); Morro Bay Area: 46011

Net primary productivity	Annual mean estimates for primary productivity derived from satellite-collected chlorophyll A measurements	One annual mean value for each port region (all measurements within each region in a given year were averaged)	Primary Productivity, Aqua MODIS, NPP, Global, 2003-present, EXPERIMENTAL (Monthly Composite), NOAA NMFS SWFSC ERD
Kelp extent*	Percentage of the 2004-2015 mean kelp extent for each year based on LandSat data collected in Quarter 3 (when the max annual kelp extent typically occurs)	Data were averaged across the lat/long that encompass port areas for the South-Central nearshore fishery region. LandSat data were collected for 30 by 30 m blocks.	Bell et al (*in press*); Santa Barbara Coastal LTER (http://sbc.lternet.edu/cgi-bin/showDataset.cgi?docid=knb-lter-sbc.74)
PISCO species abundance	PISCO SCUBA counts for all nearshore species, including only fish above the minimum size limit for that species	All PISCO sites in the Monterey Bay, Carmel Bay and Big Sur area were averaged	Mark H. Carr, PISCO

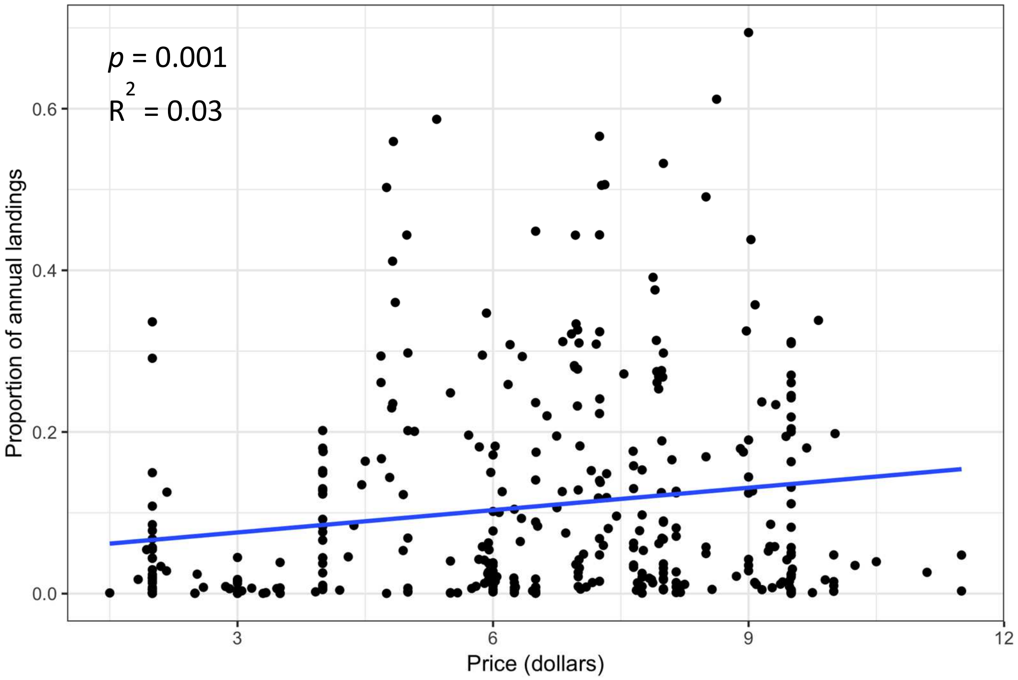


Figure 4.1. The correlation between average price per pound paid to a fisherman for a given species and the proportion of that participant's total nearshore landings comprised of that species in 2015. Each point represents the 2015 landings of a single species by an individual fisherman.

Table 4.2. Results from a PERMANOVA analysis with 999 permutations testing the effect of biophysical and socio-economic variables on catch composition. Data is for 2004 to 2015 with 1372 observations. *df* = degrees of freedom, MS = mean squares, Pseudo-*F* = *F*-value by permutation. Values in parentheses are results from a PERMANOVA model excluding the permittee variable. *The kelp extent variable was run in separate model using only data from the South-central permit region (n = 874).

Source	***df***	**MS**	**Pseudo-*F***	**R^2**	***p***
Permittee	184	6037.2 (--)	9.15 (--)	0.33 (--)	0.001 (--)
Year	10	3914.5 (4655.7)	5.93 (3.34)	0.01 (0.01)	0.001 (0.001)
Permit mix	2	13558 (330,000)	20.55 (238.64)	0.25 (0.35)	0.001 (0.001)
Port	3	3035.9 (46,596)	4.60 (33.39)	0.09 (0.13)	0.001 (0.001)
Gear	4	2814.2 (196,35)	4.27 (14.07)	0.01 (0.04)	0.001 (0.001)
Vessel length	1	5276.4 (39,090)	8.00 (28.01)	0.01 (0.01)	0.001 (0.001)
Price	1	6099.5 (1868.3)	9.25 (1.34)	0.01 (< 0.001)	0.001 (0.2)
Nearshore activity	1	3657.1 (10,488)	5.54 (7.51)	< 0.01 (< 0.01)	0.002 (0.001)

Kelp extent*	1	1833.4 (9131.7)	3.25 (1.64)	0.01 (< 0.01)	0.01 (0.1)
Net primary productivity	1	796.64 (1033.1)	1.21 (0.74)	< 0.001 (0)	0.34 (0.61)
Small craft advisory days	1	113.71 (658.3)	0.17 (0.49)	0 (0)	0.94 (0.78)
Residuals	1161	--	--	0.28 (0.46)	--

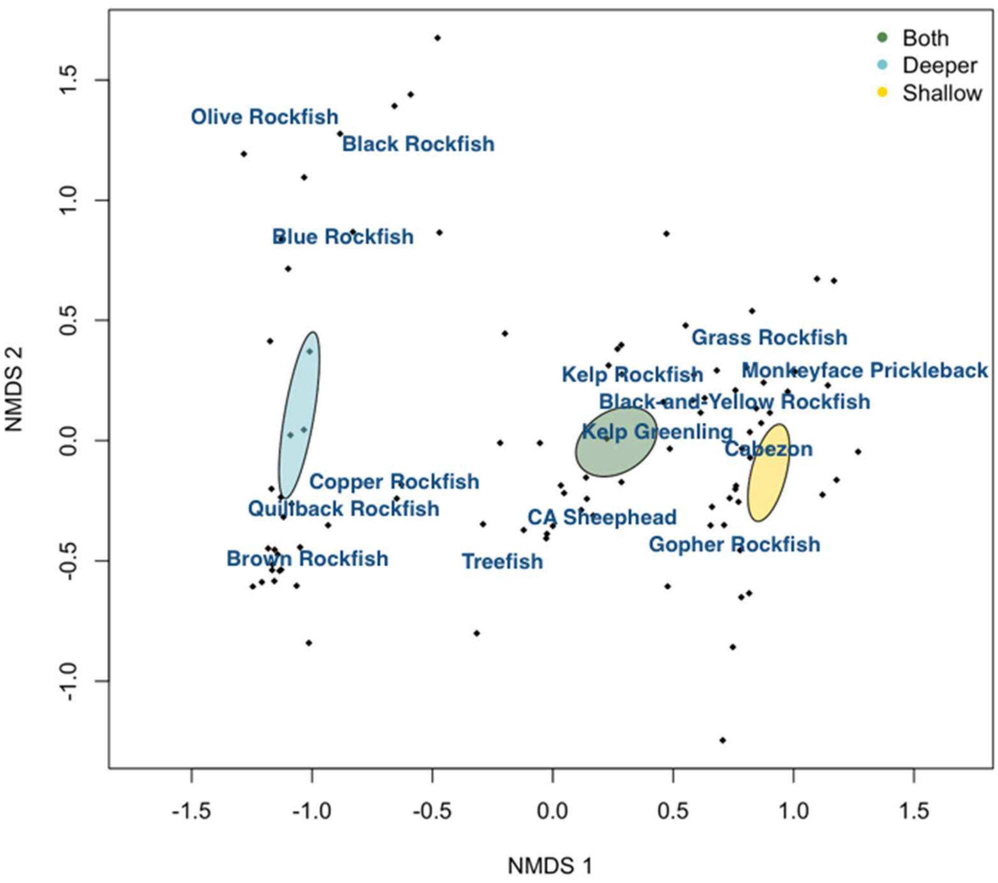


Figure 4.2. NMDS plot showing the relationship between permit mix and catch composition. Each point represents the catch composition of a fisherman in 2015. Ellipses represent the 95% confidence interval around the centroid of the nearshore permit mix that a fisherman has (shallow permit, deeper permit or both permits).

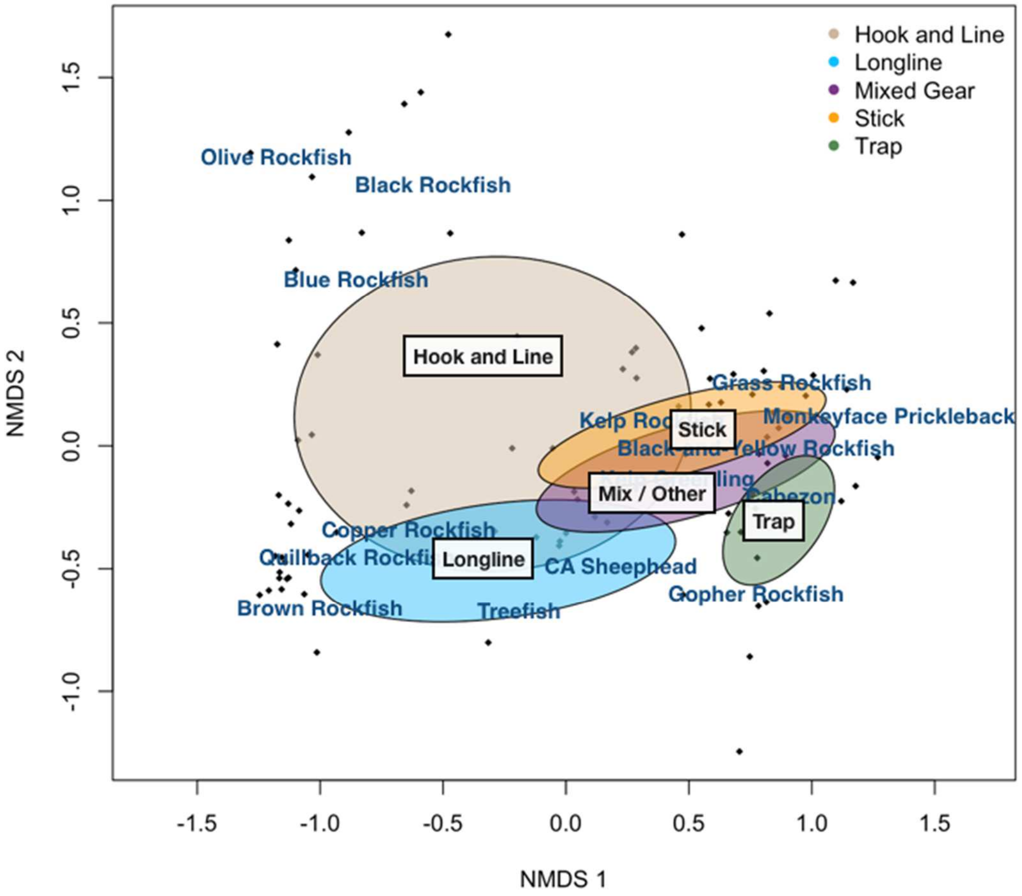


Figure 4.3. NMDS plot showing the relationship between predominant gear type used by a fisherman and their catch composition. Each point represents the catch composition of a fisherman in 2015. Ellipses represent the 95% confidence interval around the centroid of the major gear type of a fisherman in 2015.

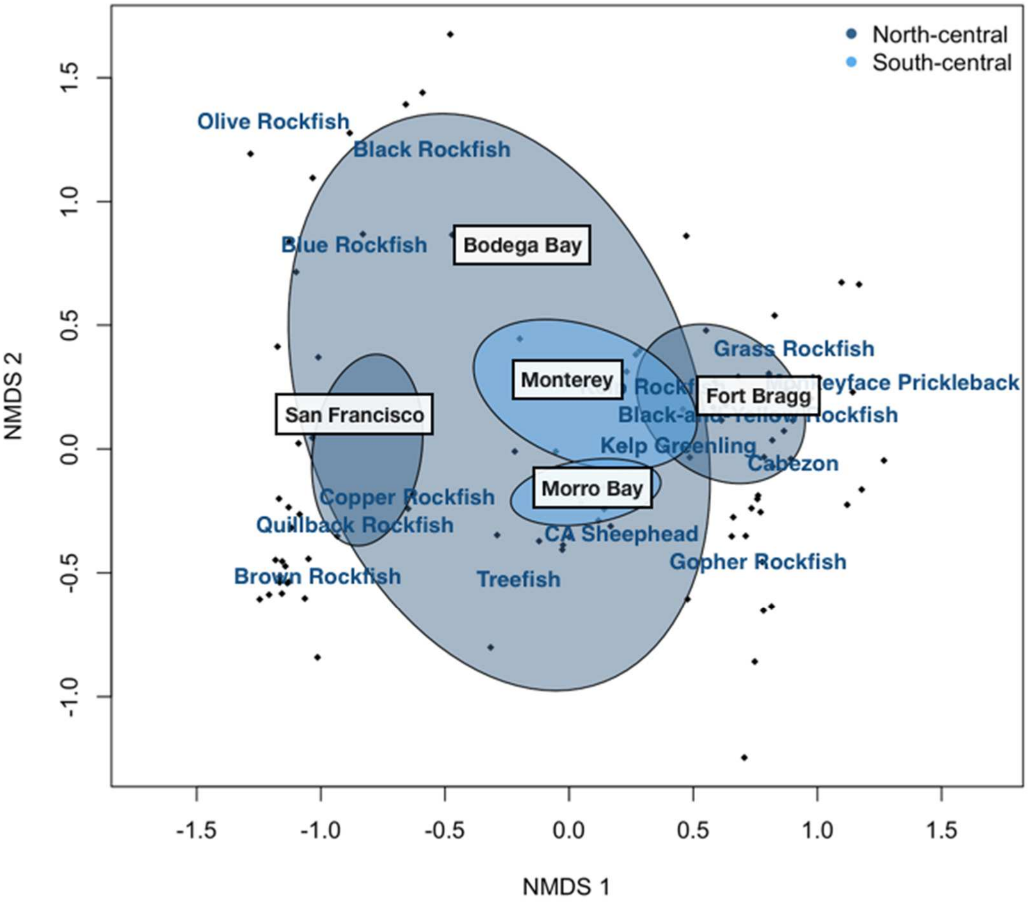


Figure 4.4. NMDS plot showing the relationship between predominant port of landing of a fisherman and their catch composition. Each point represents the catch composition of a fisherman in 2015. Ellipses represent the 95% confidence interval around the centroid of the port area where a fisherman made the majority of his/her landings in 2015.

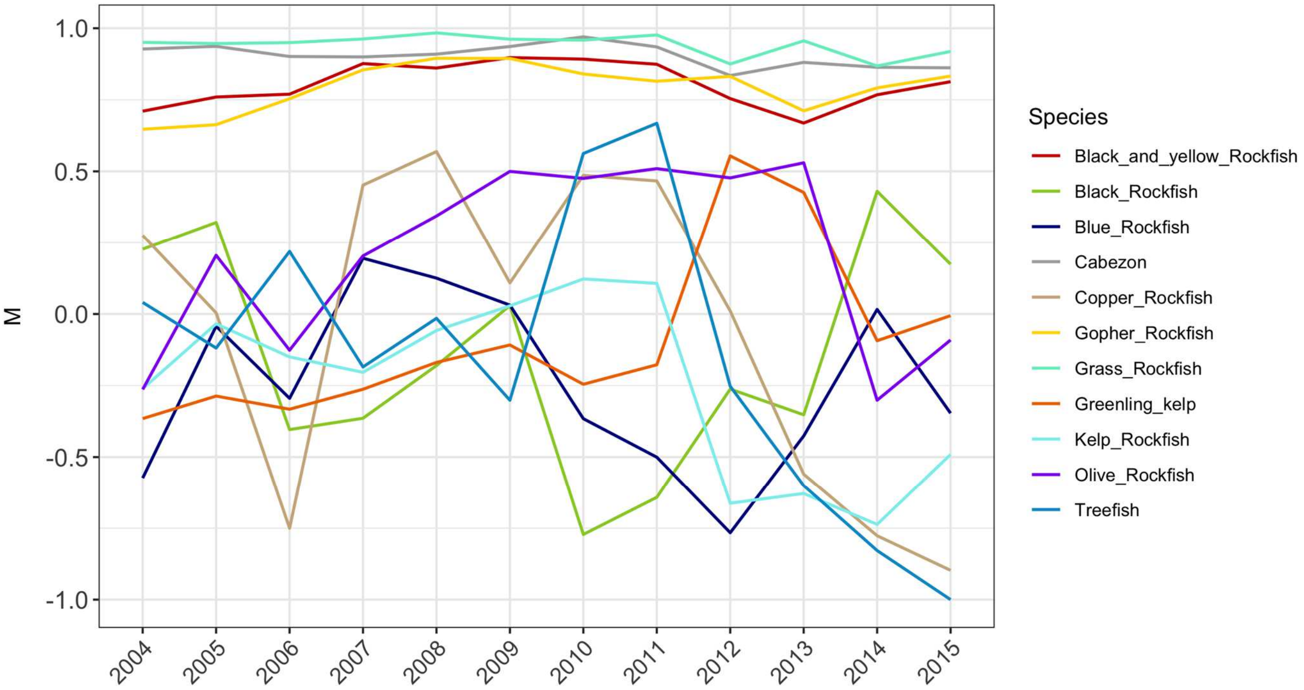


Figure 4.5. The relative match (M) between the proportion by biomass of a species in the nearshore fish assemblage and the proportion by pounds landed of that species in nearshore fishery landings. A positive number indicates that the species makes up a larger proportion of annual fishery landings than would be expected based on biomass. A negative number indicates the opposite.

Conclusion

Assessing kelp forest food webs and the trophic ecology of nearshore fishes through the lens of ecosystem connectivity yielded several major results. In Chapter 1, I identify a suite of factors that may influence the effect that trophic subsidies have on an ecosystem, synthesize what is known about subsidies to kelp forests and, importantly, summarize the gaps in our knowledge and how we can begin to fill them. Chapter 2 showed that the nearshore fish assemblage inhabiting kelp forests of central California uses trophic resources (energy and nutrients), in many cases more prominently than kelp-based energy. It also showed that variation in habitat affinity and feeding morphology across the fish assemblage leads to differences in the relative use of pelagic resources. This knowledge can be extended to other nearshore fish assemblages, and can inform our predictions of changes to food webs as the climate changes.

My ideas for work on the human dimensions of the nearshore fishery and kelp forest system were shaped by literature on social-ecological systems theory, common pool resource management, and ecosystem-based fisheries management. In Chapter 3, I highlight connections, relationships and feedbacks among ecology, human behavior, governance institutions, and economics. The research supports the need for fisheries managers to consider by ecological and human dynamics, and to incorporate both fishery systems and associated food systems into management approaches. Chapters 3 and 4 together provide one example of ways that ecological and social data can be combined to generate insights into the factors that influence fishery outcomes that would not be possible without this interdisciplinary integration. This work highlights both the challenges of working across these different forms of data, and the benefits of doing so.

Like most science, my dissertation research leaves more questions unanswered than it provides answers for. There are several particularly fruitful avenues of research both on cross-ecosystem subsidies in the marine environment, and on nearshore social-ecological systems. Although I show that kelp forest fishes access and use both kelp- and pelagic-based energy sources, many of the particular dynamics of trophic subsidy species are still unknown. Research to determine the drivers of trophic influx from the open ocean and to further characterize the variability in this influx will be useful. Moreover, my work on fish assemblages suggests that these coastal pelagic subsidies to kelp forests ecosystems may be even more significant when considering the great diversity and abundance of invertebrate planktivores in this ecosystem. These questions are particularly relevant for gelatinous zooplankton that I show to play a substantial role in nearshore food webs, but that we know very little about. Moreover, it is unknown whether the diversity of energy resources accessed by the nearshore fish assemblage imparts stability and resilience to the system, or makes it more vulnerable. Following my synthesis of the factors that influence subsidy impacts, experiments and field studies to observe and test the consequences of trophic subsidies on individuals, species, communities will expand our understanding of the ways that ecosystems assemble and function.

The nearshore fishery characterization that I presented contributes to a baseline and an entry-point for future research on the role and relevance of the nearshore fishery in coastal communities, and on the wider kelp forest social-ecological system. However, this is but one component of the kelp forest SES in central California. Further work on other kelp forest-associated fisheries, the social and economic aspects of recreation in and around kelp forests, and the diverse ways that humans interact with and are influenced by kelp forests will continue to build our understanding of the connectivity between nearshore marine systems and coastal communities. Building on conclusions from Chapters 3 and 4, further research should characterize the relationships among state and federal fisheries in California, the social and ecological impacts of market flexibility and alternative marketing approaches, and the widespread consequences, both intended and unintended, of fisheries management interventions. Addition research could also explore the ways that social-ecological systems thinking can inform efforts to mitigate and adapt to the ecological and social manifestations of a change global climate. The continued development of creative methods to combine disparate data types and to conduct research that spans disciplinary boundaries will teach us more about the role of connectivity, and enrich our understanding of the natural world.

Appendices

Appendix 1: Supplemental material for Chapter 2

Fin versus muscle tissue $\delta^{13}C$ *and* $\delta^{15}N$

Numerous studies have found that tissues sampled by non-lethal means can be substituted for muscle tissue (Kelly et al. 2006). To determine whether this was the case for kelp forest rockfishes, both muscle and fin tissues were analyzed from a subset of adult rockfish samples ($n = 20$). Though $\delta\ ^{15}N$ values do not differ between the two tissue types ($p = 0.09$), $\delta\ ^{13}C$ values were significantly different ($p < 0.001$) (Supplementary Figure 2.1). As such, fins were not used for further analyses.

Species-level stomach content identifications

The following species-level stomach content identifications (not reported in other tables) were made. PSIRI tables with prey taxa at a finer taxonomic resolution than is presented in Table 2.2 can be found in the Supplementary Tables 2.2a-b.

Kelp Rockfish**:** *Semibalanus balanoides, Balanus glandula, Cancer antennarius, Pugettia productus, Hemigrapsus oregonensis, Cancer jordani, Pleuroncodes planipes, Peprilus tricanthus, Idotea resecata, Octopus rubescens, Pyrosoma atlanticum.*

Black-and-Yellow Rockfish**:** *Pugettia dalli, Petrolisthes spp., Mimulus foliatus, Cryptolithodes typicus, Pugettia richii, Cancer jordani, Cryptolithodes sitchensis, Scyra acutifrons, Cancer oregonensis, Pugettia product, Lophopanopeus bella, Haplogaster cavicauda, Herbstia parvifrons, Loxorhynchus sp., Cancer antennarius, Alpheus clamator, Pandalus danae, Idotea resecata, Octopus rubescens, Tonicella lineata, Pyrosoma atlanticum, Strongylocentrutus purpuratus.*

Black Rockfish**:** *Panulirus interruptus, Engraulis mordax, Anarrhichthys ocellatus, Idotea resecata, Octopus rubescens, Pyrosoma atlanticum.*

Blue Rockfish**:** *Anarrhichthys ocellatus, Octopus rubescens, Pyrosoma atlanticum.*

Black Surfperch**:** *Amphipods: Elasmopus, Quadrimaera, Eusiroidea, Isaeidae, Photis, Gammaropsis, Protomedeia, Columbara, Ampithoe, Phoxocephalidae, Heterophoxus, Dissiminassa, Orchomenella, Podocerus, Ampelisca lobate, Tiron, Polycheria. Isopods: Limnoria. Decapoda: Pugettia sp., Alpheus spp., Crangon spp., Heptacartus. Leptostraca: Nebalia spp. Gastropoda: Epitonium.*

Liver sample lipid normalization

I found a significant negative relationship between C:N and $\delta^{13}C$ values of intact lipid samples, suggesting that lipid in liver samples was leading to values of $\delta^{13}C$ that were depleted relative to samples with a lower lipid content ($p < 0.01$, $R^2 = 0.29$). To control for the impact of lipid content, I compared isotope values from samples run prior to and after undergoing lipid extraction. Values for both carbon and nitrogen isotope ratios differed in intact versus lipid extracted liver samples ($\delta^{13}C$: $p < 0.001$; $\delta^{15}N$: $p < 0.001$) (Supplementary Table 2.1). I fit two linear models, one for samples with C:N below 10.9 (Equation 1) and another for samples with C:N above 10.9 (Equation 2), determined with a break-point analysis, to describe the relationship between C:N values of intact liver samples, and the difference between $\delta^{13}C$ values of lipid intact and lipid-extracted livers (Supplementary Figure 2.4). The residual mean square error of two linear equations was lower than that of a negative exponential fit, the best fitting nonlinear model. The equations generated were used to mathematically normalize samples that did not undergo the lipid extraction process.

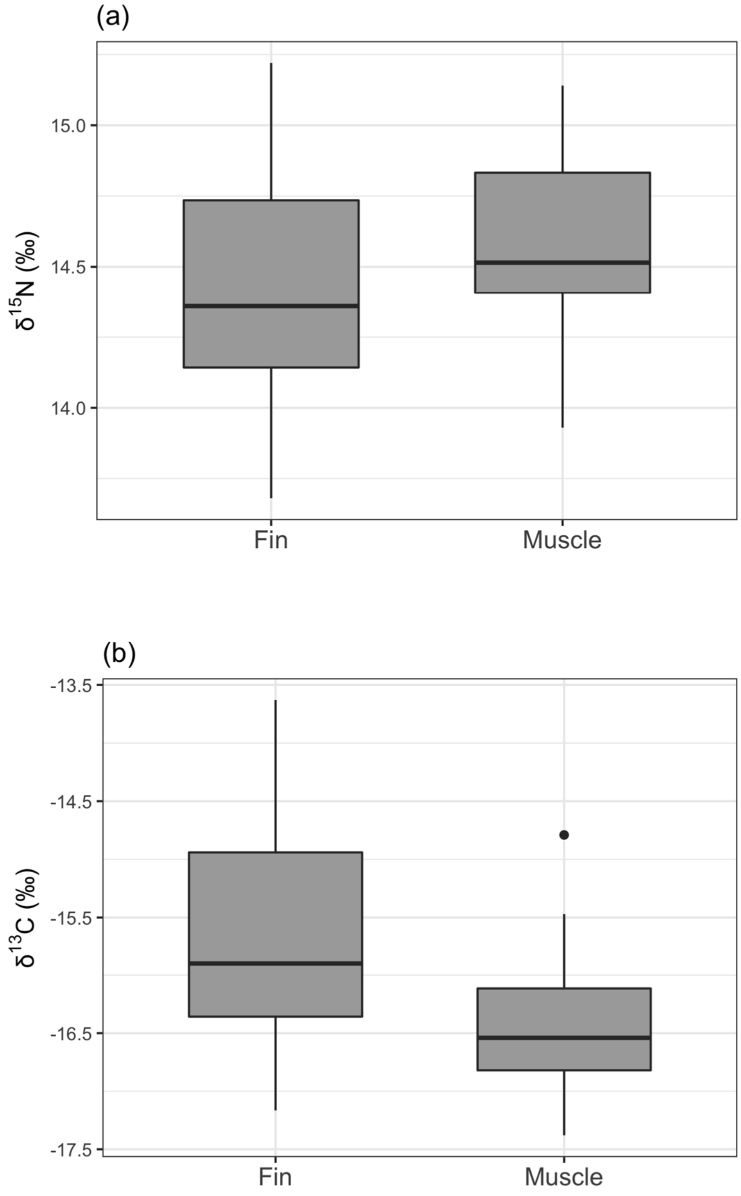
Equation 1 (for samples with C:N < 10.9).

$$d^{13}C_{normalized} = d^{13}C_{intact} - (-0.3363 * C{:}N_{intact} \ + \ 0.5882)$$

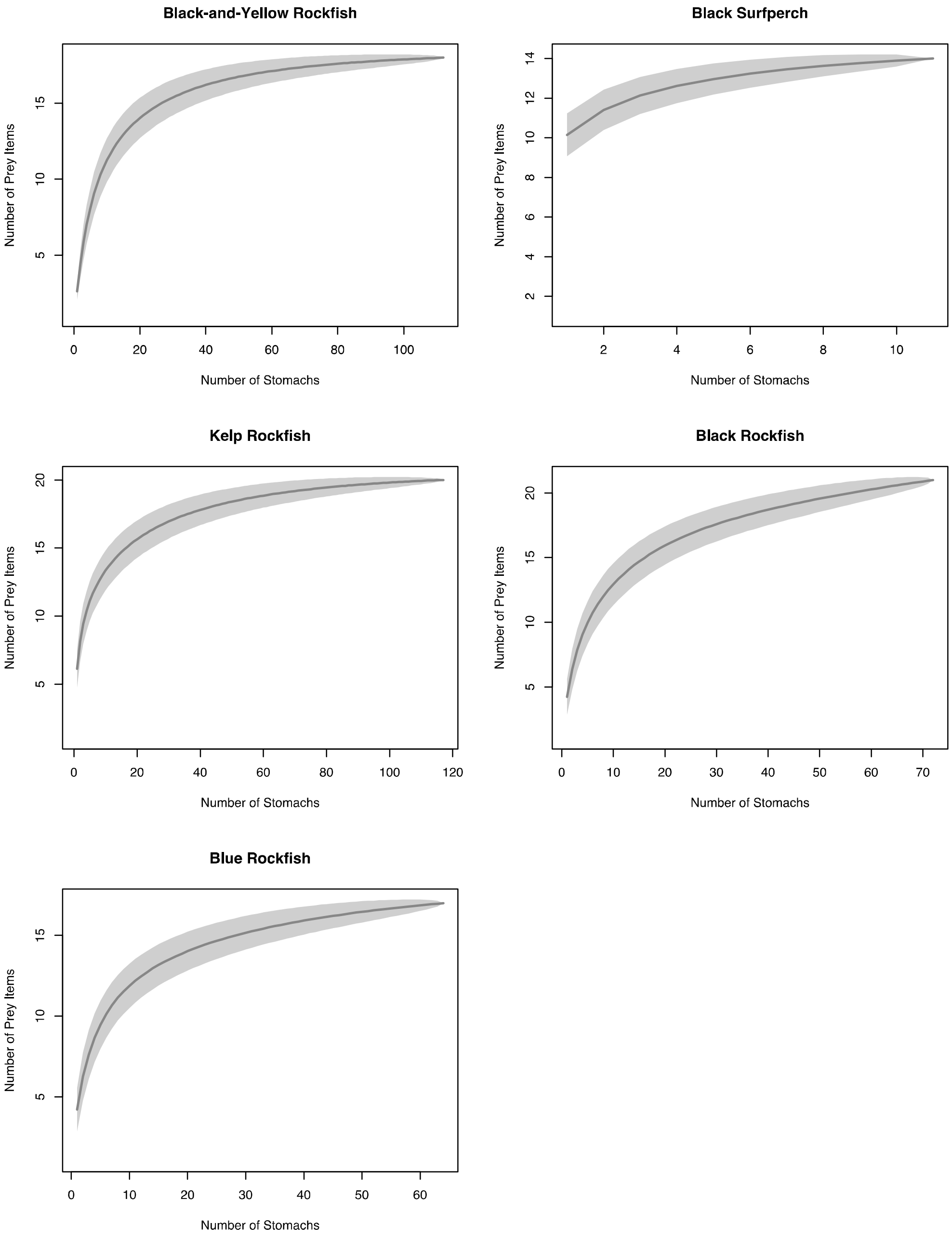
Equation 2 (for samples with C:N > 10.9).

$$d^{13}C_{normalized} = d^{13}C_{intact} - (-0.0621 * C{:}N_{intact} \ + \ -2.4030)$$

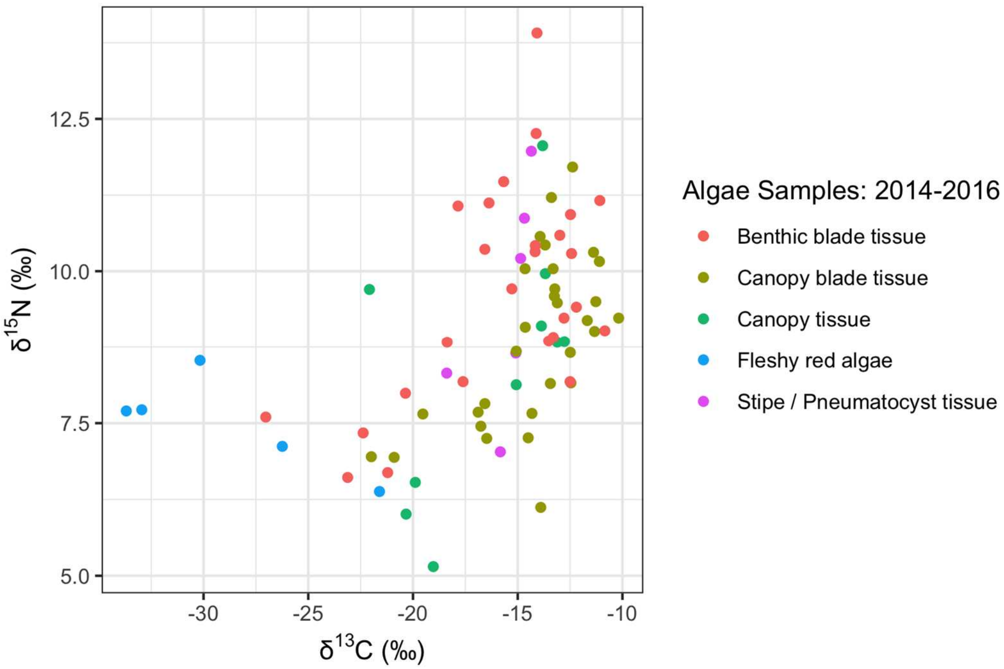
Following lipid-extraction on a subset of liver samples and arithmetic normalization of the remaining samples, $\delta^{13}C$ still differed between muscle and liver tissue for an individual fish (paired t-test, $p < 0.001$), with liver tissue exhibiting consistently lower $\delta^{13}C$ values relative to muscle tissue (Supplementary Figure 2.5).



Supplementary Figure 2.1. (a) $\delta^{15}N$ values did not differ between fin and muscle tissue (paired T-test, $p = 0.13$); (b) $\delta^{13}C$ values for fin tissue were significantly less depleted than $\delta^{13}C$ of muscle tissue ($p < 0.001$).



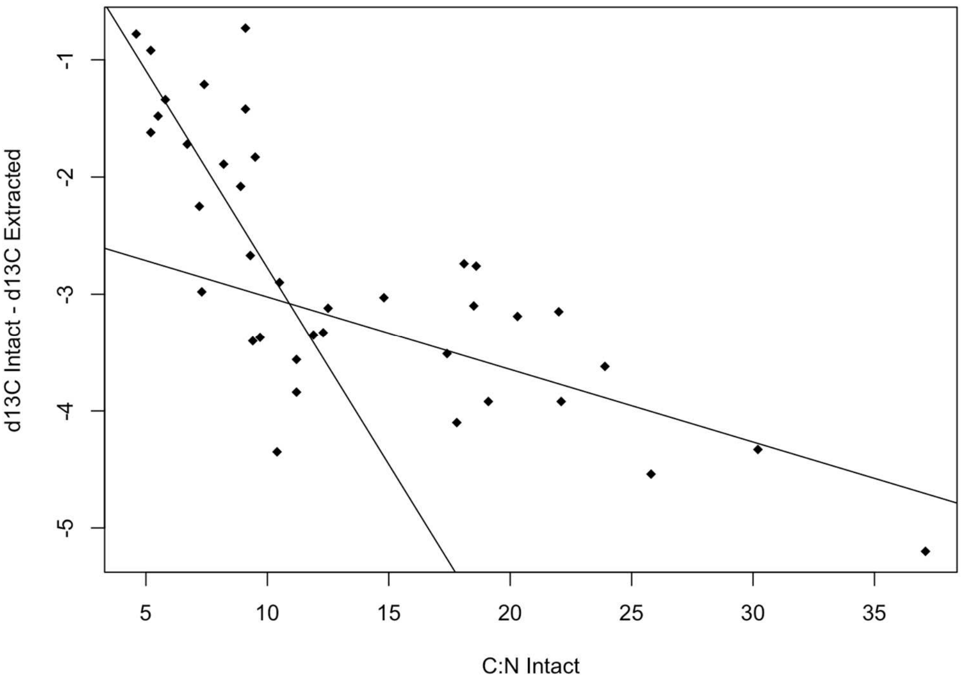
Supplementary Figure 2.2. Cumulative prey curves, generated using the specaccum function in R, indicate that sampling was sufficient to characterize diet by species.



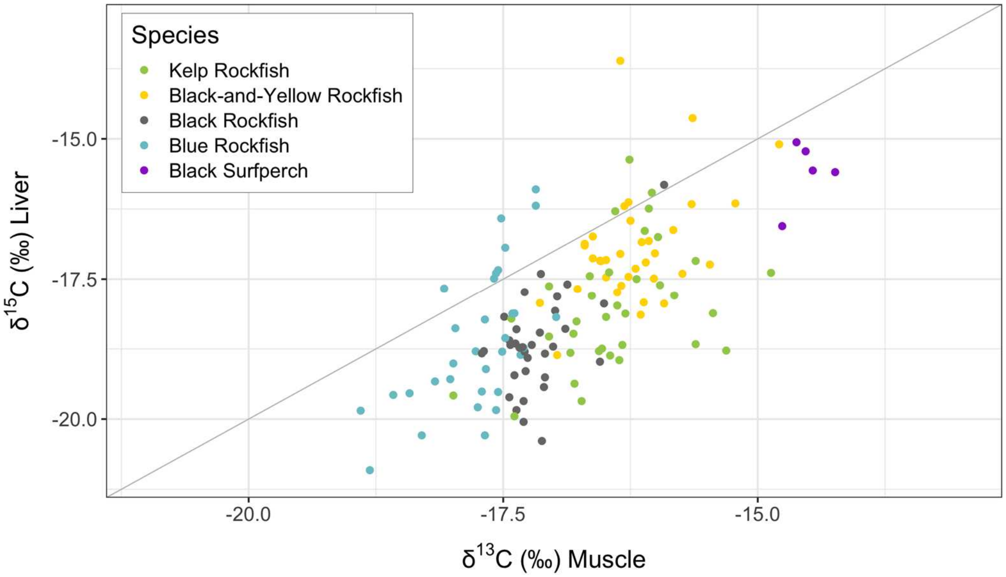
Supplementary Figure 2.3. *Macrocystis* displays substantial variability in both $\delta^{13}C$ and $\delta^{15}N$ values. Red algae is a ^{13}C-depleted source relative to *Macrocystis.*

Supplementary Table 2.1. Comparisons between lipid-intact and lipid-extracted liver samples for mean δ^{13}C (± SD) and mean δ^{15}N (± SD). p values are indicated as follows: ‘ns’: $p > 0.05$, ‘*’: $p < 0.05$, ‘**’: $p < 0.01$, ‘***’: $p < 0.001$.

Species	**n**	**δ^{13}C (‰)**		**p**	**δ^{15}N (‰)**		**p**
		Lipid-intact	**Lipid-extracted**		**Lipid-intact**	**Lipid-extracted**	
Kelp Rockfish	12	-21.4 ± 0.8	-18.3 ± 1.2	***	13.8 ± 1.4	14.2 ± 1.0	*
Black and Yellow Rockfish	14	-19.5 ± 1.1	-17.4 ± 0.7	***	14.4 ± 0.8	14.6 ± 0.5	*
Black Rockfish	11	-22.4 ± 1.0	-20.0 ± 1.3	***	13.5 ± 0.8	14.0 ± 0.8	*
Blue Rockfish	9	-21.7 ± 0.8	-19.2 ± 1.4	***	13.0 ± 0.3	13.2 ± 0.3	*



Supplementary Figure 2.4. Negative linear relationships between the difference in δ^{13}C value of an intact sample and the δ^{13}C value of that sample following extraction, and the C:N of the intact sample with a break point at 10.9. These relationships were used to develop lipid normalization equations for samples that did not undergo lipid extraction.



Supplementary Figure 2.5. δ^{13}C values for liver tissue (following either lipid extraction or mathematical normalization) were still significantly lower than values for muscle tissue (paired t-test, $p < 0.001$). The line represents an exact match between δ^{13}C values for the two tissue types.

Supplementary Table 2.2a. Diet composition of four species of nearshore *Sebastes* rockfishes by percent frequency of occurrence (%FO) and percent prey-specific index of relative importance (%PSIRI). Phyla are in bold font (with the exception of algae which is a combination of two phyla: Rhodophyta and Heterokontophkya).

	Kelp Rockfish		**Black and Yellow Rockfish**		**Black Rockfish**		**Blue Rockfish**	
Prey Type	**%FO**	**%PSIRI**	**%FO**	**%PSIRI**	**%FO**	**%PSIRI**	**%FO**	**%PSIRI**
NEMATODA	0.00	0.00	0.89	0.30	0.00	0.00	0.00	0.00
CTENOPHORA	0.00	0.00	0.00	0.00	1.39	1.39	1.56	1.17
ANNELIDA: Polychaeta	4.27	0.64	8.04	3.03	6.94	2.60	3.13	0.87
ALGAE	3.42	0.29	5.36	0.86	2.78	0.09	28.13	13.80
BRYOZOA	1.71	0.05	3.57	0.77	1.39	0.35	14.06	8.47
CNIDARIA	1.71	0.35	1.79	0.69	2.78	0.60	17.19	11.61
CHORDATA								
Tunicata	14.53	11.42	1.79	1.12	11.11	8.16	20.31	15.98
Vertebrata: Actinoptyrigii	36.75	21.83	18.75	9.71	55.56	42.30	26.56	12.22
ECHINODERMATA	0.00	0.00	4.46	1.95	0.00	0.00	0.00	0.00
MOLLUSCA								
Non-Cephalopod Molluscs	7.69	1.31	10.71	3.99	5.56	2.25	1.56	1.17
Cephalopoda	10.26	5.57	25.00	17.92	8.33	6.66	6.25	3.90

ARTHROPODA								
Unidentified	11.11	4.27	6.25	2.88	6.94	2.89	4.69	1.43
Chelicerata	0.00	0.00	0.89	0.05	0.00	0.00	0.00	0.00
Crustacea								
Unidentified	10.26	2.78	7.14	2.49	2.78	0.55	6.25	2.33
Maxillopoda								
Cirripeda	3.42	1.46	1.79	0.63	2.78	0.23	0.00	0.00
Copepoda	1.71	0.23	0.00	0.00	1.39	0.32	1.56	0.27
Malacostraca								
Euphausiacea	0.85	0.14	0.00	0.00	4.17	0.47	0.00	0.00
Isopoda	33.33	6.76	1.79	0.48	31.94	14.15	0.00	0.00
Amphipoda	48.72	14.20	6.25	0.70	16.67	3.48	10.94	1.68
Decapoda								
Unidentified	5.13	1.09	5.36	3.46	8.33	1.13	3.13	0.20
Unidentified shrimp	3.42	0.41	0.00	0.00	5.56	0.50	1.56	0.04
Unid. mature crab	0.85	0.60	5.36	2.96	0.00	0.00	0.00	0.00
Crab megalopa/zoea	18.80	5.05	0.00	0.00	11.11	2.77	9.38	3.63
Anomura	2.56	0.83	12.50	6.93	1.39	0.44	0.00	0.00
Brachyura	13.68	7.03	44.64	27.12	4.17	1.34	4.69	2.53
Caridea	32.48	9.08	20.54	10.67	4.17	0.55	4.69	1.36
Achelata: Palinurdiae	0.00	0.00	0.00	0.00	1.39	0.05	0.00	0.00

Supplementary Table 2.2b. Diet composition of four species of nearshore *Sebastes* rockfishes by percent frequency of occurrence (%FO) and percent prey-specific index of relative importance (%PSIRI). Phyla are in bold font (with the exception of algae which is a combination of two phyla: Rhodophyta and Heterokontophkya.

	Kelp Rockfish		**Black and Yellow Rockfish**		**Black Rockfish**		**Blue Rockfish**	
Prey Type	**%FO**	**%PSIRI**	**%FO**	**%PSIRI**	**%FO**	**%PSIRI**	**%FO**	**%PSIRI**
NEMATODA	0	0	0.89	0.30	0	0	0	0
CTENOPHORA	0	0	0	0	1.39	1.39	1.56	1.37
ANNELIDA								
Polychaeta	4.27	0.64	8.04	3.03	6.94	2.60	3.13	0.87
ALGAE	3.42	0.29	5.36	0.86	2.78	0.09	28.13	13.80
BRYOZOA	1.71	0.05	3.57	0.77	1.39	0.35	14.06	8.47
Unidentified	1.71	0.05	0.89	0.11	1.39	0.35	6.25	2.75
Membranipora spp.	0	0	2.68	0.65	0	0	7.81	5.72
CNIDARIA	1.71	0.35	1.79	0.69	2.78	0.60	17.19	11.61
Scyphozoa	0	0	0	0	0	0	1.56	1.56
Chrysaora sp.	0	0	0	0	0	0	1.56	1.56
Hydrozoa								
Unidentified	0.85	0.16	0.89	0.23	1.39	0.07	9.38	5.34
Siphonophorae	0	0	0	0	1.39	0.52	0	0
Unidentified	0.85	0.19	0.89	0.46	0	0	6.25	4.70
CHORDATA								
Tunicata	14.53	11.42	1.79	1.12	11.11	8.16	20.31	15.98

Unidentified	44.16	3.30	0	0	6.94	5.85	15.63	11.56
Pyrosomida	0.85	0.55	0.89	0.89	1.39	0.07	6.25	1.67
Doliolida	0	0	0	0	1.39	1.37	0	0
Salpida	8.58	7.58	0.89	0.23	2.78	0.88	3.13	2.75
Vertebrata								
Actinoptyrigii	36.75	21.83	18.75	9.71	55.56	42.30	26.56	12.22
Sebastes spp.	11.11	7.49	4.46	2.69	11.11	8.50	3.13	1.72
Unidentified fish	22.22	10.24	13.39	5.42	38.89	26.58	23.44	9.63
Non-*Sebastes* fish	6.84	4.09	2.68	1.61	9.72	7.22	1.56	0.88
ECHINODERMATA	0	0	4.46	1.95	0	0	0	0
Ophiuroidea	0	0	3.57	1.71	0	0	0	0
Echinoidea								
Strongylocentrutus purpuratus	0	0	0.89	0.25	0	0	0	0
MOLLUSCA								
Bivalvia	0	0	0	0	4.17	2.11	0	0
Cephalopoda	10.26	5.57	25.00	17.92	8.33	6.66	6.25	3.90
Octopoda								
Octopus rubescens	6.84	4.52	23.21	17.47	5.56	4.49	3.13	2.70
Decapodiformes	0	0	0	0	2.78	2.18	1.56	0.39
Unidentified	3.42	1.03	1.79	0.45	0	0	1.56	0.80
Polyplacophora	0	0	4.46	2.09	0	0	0	0
Gastropoda	5.98	1.00	6.25	1.70	1.39	0.13	0	0
Unidentified	1.71	0.31	0.89	0.20	0	0	1.56	1.17
ARTHROPODA								
Unidentified	11.11	4.27	6.25	2.88	6.94	2.89	4.69	1.43
Chelicerata	0	0	0.89	0.05	0	0	0	0
Crustacea								

Unidentified	10.26	2.78	7.14	2.49	2.78	0.55	6.25	2.33
Maxillopoda								
Cirripeda	3.42	1.46	1.79	0.63	2.78	1.42	0	0
Copepoda	1.71	0.23	0	0	1.39	0.32	1.56	0.27
Malacostraca								
Euphausiacea	0.85	0.14	0	0	4.17	0.47	0	0
Isopoda	33.33	6.76	1.79	0.48	31.94	14.15	0	0
Unidentified	23.93	3.12	0	0	18.06	6.24	0	0
Idotea resecata	10.26	3.64	1.79	0.48	16.67	7.91	0	0
Amphipoda	48.72	14.20	6.25	0.70	16.67	3.48	10.94	1.68
Unidentified	6.84	1.90	0.89	0.06	2.78	0.24	1.56	0.007
Gammaridae	41.88	12.20	4.46	0.53	13.89	3.25	9.38	1.68
Caprellidae	1.71	0.10	0.89	0.12	0	0	0	0
Decapoda								
Unidentified	5.13	1.09	5.36	3.46	8.33	1.13	3.13	0.20
Unid. shrimp	3.42	0.41	0	0	5.56	0.50	1.56	0.04
Unid. crab	0.85	0.60	5.36	2.96	0	0	9.38	0
Unid. megalopa/zoea	18.80	5.05	0	0	11.11	2.77	9.38	3.63
Anomura	2.56	0.83	12.50	6.93	1.39	0.44	0	0
Porcellanidae	0	0	4.46	3.33	0	0	0	0
Diogenidae	1.71	0.77	0.89	0.26	0	0	0	0
Paguridae	0	0	5.36	1.70	0	0	0	0
Lithodidae	0	0	2.68	1.09	0	0	0	0
Munidae	0.85	0.06	0	0	0	0	0	0
Hapalogastridae	0	0	0.89	0.54	0	0	0	0
Unidentified	0	0	0	0	1.39	0.44	0	0
Brachyura	13.68	7.03	44.64	27.12	4.17	1.34	4.69	2.53

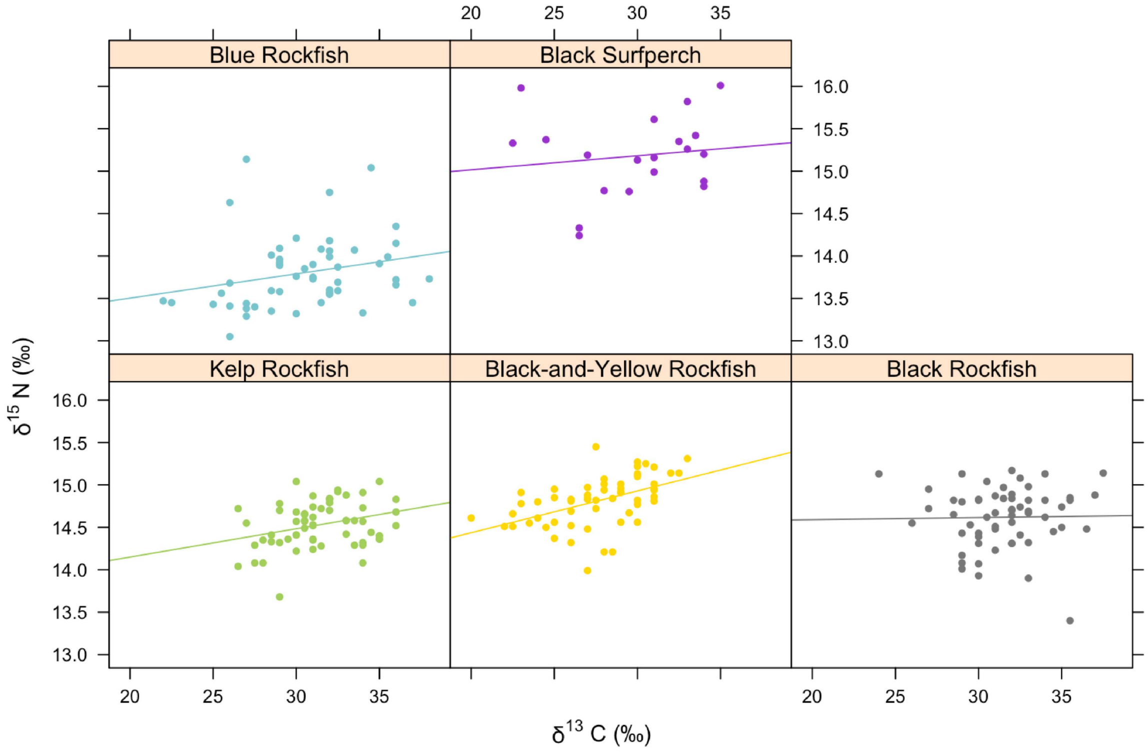
Epialtidae	1.71	1.29	10.71	3.89	0	0	0	0
Majidae	1.71	0.17	15.18	6.49	1.39	0.46	0	0
Xanthidae	0.85	0.24	4.46	1.95	0	0	1.56	0.58
Cancridae	5.13	3.37	19.62	7.63	1.39	0.37	1.56	0.79
Unidentified	6.84	1.95	16.96	7.15	2.78	0.51	1.56	1.16
Caridea	32.48	9.08	20.54	10.67	4.17	0.55	4.69	1.36
Unidentified	27.35	6.63	15.18	6.58	4.17	0.55	4.69	1.36
Alpheoidea	1.71	0.65	6.25	3.86	0	0	0	0
Pandalidae	4.27	0.95	0.89	0.23	0	0	0	0
Atyoidea	0.85	0.85	0	0	0	0	0	0
Achelata	0	0	0	0	1.39	0.05	0	0
Palinuridae	0	0	0	0	1.39	0.05	0	0

Supplementary Table 2.3. Isotope values ($\bar{x}$ ± SD) for prey items of nearshore, kelp forest fishes in California.

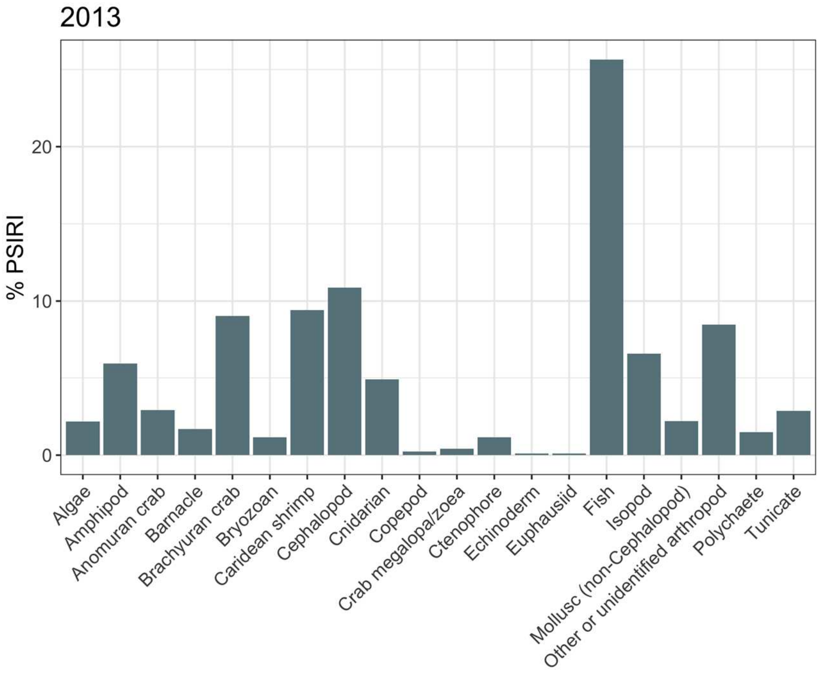
Species	**n**	**$\delta^{13}C$ (‰)**	**$\delta^{15}N$ (‰)**	**Location**	**Data source**
Amphipod (multiple species)	5	-16.2 ± 0.7	9.0 ± 1.2	Carmel Bay, CA	Zuercher
Kelp Amphipod (*Peramphithoe humeralis*)	5	-12.4 ± 0.6	8.7 ± 0.4	Southern California	Koenigs et al. 2015
Sebastes YOY pelagic	39	-21.5 ± 1.8	11.1 ± 0.5	California Current, outside Monterey Bay	Zuercher
Sebastes YOY new recruit	16	-18.3 ± 1.0	11.9 ± 0.4	Carmel Bay, CA	Zuercher
Sebastes YOY kelp forest	79	-17.5 ± 1.1	13.3 ± 0.8	Carmel Bay, CA	Zuercher
Sebastes jordani YOY	5	-17.1 ± 0.3	13.8 ± 0.2	Gulf of the Farallones (from bird diet contents)	Sydeman et al. 1997
Idotea resecata	16	-14.2 ± 1.9	9.7 ± 1.2	Carmel Bay, CA	Zuercher
Idotea resecata	10	-12.7 ± 1.5	10.5 ± 1.2	Southern California	Koenigs et al. 2015
Krill	5	-20.2 ± 0.3	11.2 ± 0.5	California Current, outside Gulf of the Farallones	Sydeman et al. 1997

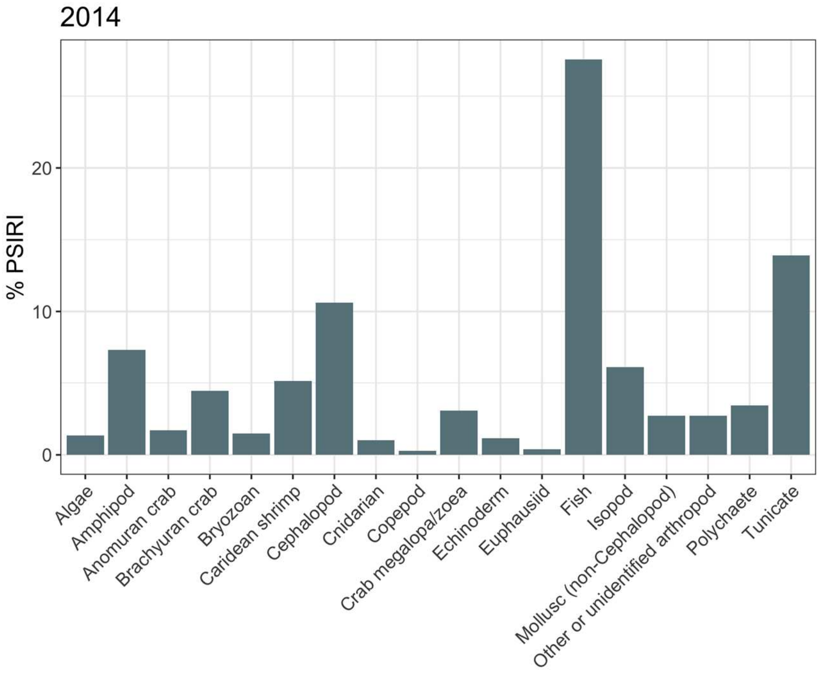
Octopus rubescens	14	-18.3 ± 1.0	12.7 ± 0.5	Carmel Bay, CA	Zuercher
Pugettia richii	5	-14.7 ± 1.4	9.7 ± 1.0	Carmel Bay, CA	Zuercher
Scyra acutifrons	3	-14.8 ± 1.2	11.2 ± 0.4	Carmel Bay, CA	Zuercher
Salpa spp.	12	-22.3 ± 1.8	9.2 ± 0.6	Carmel Bay, CA	Zuercher
Ctenophore	7	-18.9 ± 1.1	12.4 ± 0.2	Carmel Bay, CA	Zuercher
Pyrosome	15	-22.9 ± 1.3	8.8 ± 1.0	California Current, outside Monterey Bay	Zuercher
Hydrozoan (*Obelia* sp.)	5	-18.1 ± 0.6	11.6 ± 1.0	Southern California	Koenigs et al. 2015
Cancer productus/ antennarius	15	-15.1 (0.2 SE)	13.9 (0.2 SE)	San Simeon and Monterey Bay, CA	Newsome et al. 2009
Strongylocentrotus purpuratus	6	-17.0 (0.4 SE)	9.3 (0.2 SE)	San Simeon and Monterey Bay, CA	Newsome et al. 2009
Chlorostoma spp. (snails)*	12	-14.3 (0.3 SE)	10.4 (0.2 SE)	San Simeon and Monterey Bay, CA	Newsome et al. 2009

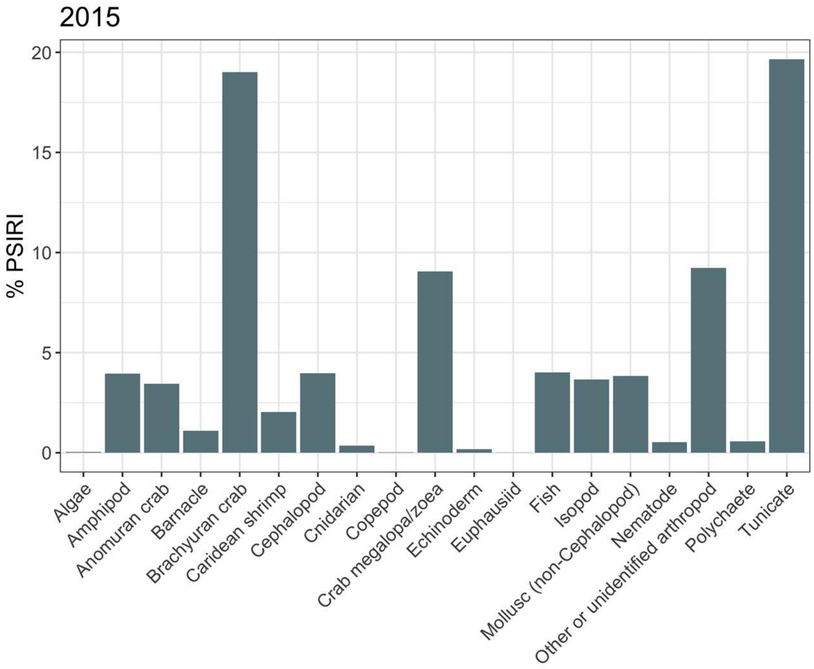
* Snail species include *Chlorostoma funebralis, C. pulligo, C. brunnea*, and C. *montereyi.*

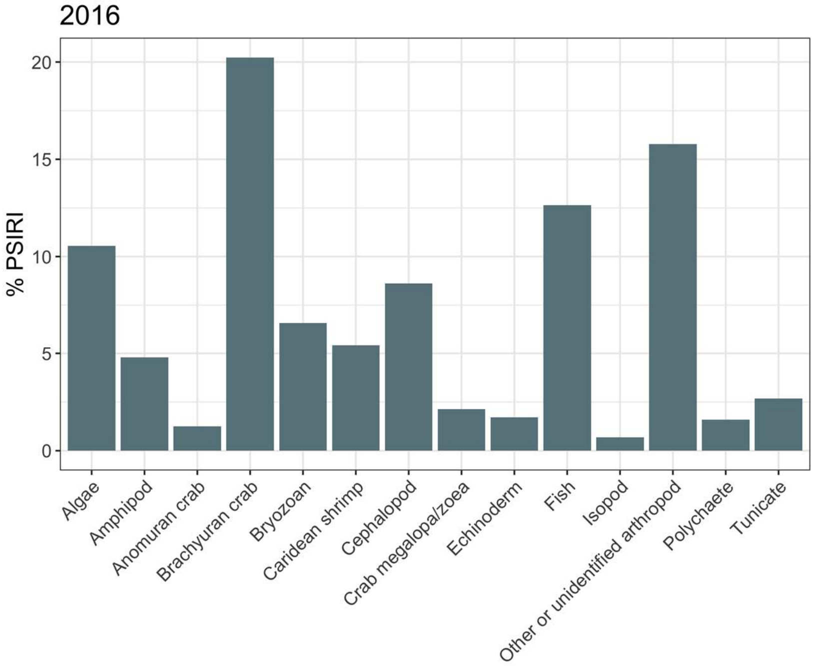


Supplementary Figure 2.6. Total length as a predictor of δ^{15}N (i.e. trophic level) as measured using muscle tissue. The slope of linear regressions for Kelp Rockfish ($p = 0.02$; $R^2 = 0.08$) and Black-and-Yellow Rockfish ($p < 0.001$; $R^2 = 0.23$) are significantly different from zero.


2013
% PSIRI
0
10
20
Algae
Amphipod
Anomuran crab
Barnacle
Brachyuran crab
Bryozoan
Caridean shrimp
Cephalopod
Cnidarian
Copepod
Crab megalopa/zoea
Ctenophore
Echinoderm
Euphausiid
Fish
Isopod
Mollusc (non-Cephalopod)
Other or unidentified arthropod
Polychaete
Tunicate


2014
% PSIRI
0
10
20
Algae
Amphipod
Anomuran crab
Brachyuran crab
Bryozoan
Caridean shrimp
Cephalopod
Cnidarian
Copepod
Crab megalopa/zoea
Echinoderm
Euphausiid
Fish
Isopod
Mollusc (non-Cephalopod)
Other or unidentified arthropod
Polychaete
Tunicate


2015
% PSIRI
0
5
10
15
20
Algae
Amphipod
Anomuran crab
Barnacle
Brachyuran crab
Caridean shrimp
Cephalopod
Cnidarian
Copepod
Crab megalopa/zoea
Echinoderm
Euphausiid
Fish
Isopod
Mollusc (non-Cephalopod)
Nematode
Other or unidentified arthropod
Polychaete
Tunicate


2016
% PSIRI
0
5
10
15
20
Algae
Amphipod
Anomuran crab
Brachyuran crab
Bryozoan
Caridean shrimp
Cephalopod
Crab megalopa/zoea
Echinoderm
Fish
Isopod
Other or unidentified arthropod
Polychaete
Tunicate

Supplementary Figure 2.7. Across the four rockfish species sampled (species combined), fish is the most important prey item in 2013 and 2014, but becomes very unimportant in 2015 (a low *Sebastes* recruitment) year, before increasing again in importance in 2016.

Appendix 2: Supplemental material for Chapter 3

Robert Dyer/Telegram-Tribune

DWINDLING STOCKS: Sam Smith, left, of Morro Bay and Tim Slattery of Cayucos fish in Morro Bay near commercial vessels.

Alarm sounds over fisheries depletion

NORTH COAST

By Glenn Roberts Jr.
Telegram-Tribune

Members of the Cambria Fishing Club, concerned that there aren't enough fish in the sea, are asking for stricter regulations to protect the shrinking populations of rockfish and cabezon.

Rockfish are a staple catch for commercial fishermen, said club president Dr. Mal Stock. But the resource is being depleted.

"(The Central Coast) was the best fishing along the whole coast of California as late as 1991. It's been overharvested — it's been pillaged."

It will take years for the resource to rebound, said Stock, who for years wrote a fishing column for a national magazine.

So the group is trying to do something about it.

In January, the fishing club sent out letters to local legislators in hopes of turning the tide on the fishery depletion.

"Our plea is for the enactment of statewide regulations this year to control the explosive exploitation of the California near-shore fisheries," the letter states.

The commercial rockfish catch in 1996 was up nearly 1 million pounds from the catch reported in 1989, according to the letter.

The club recommends banning the shipment of live, edible ocean fish by land vehicles; setting a minimum size limit of 1 foot in length for rockfish catches; limiting the catch, per boat, of live ocean rockfish; and curbing the length of the commercial rockfish season.

Bob Hardy, a marine biologist for the state Department of Fish and Game, said the state Legislature sets most of the state's fishing regulations.

The rockfish catch on the West Coast has been fairly stable from 1986 to 1994, according to a National Marine Fisheries Service study, averaging 35,000 metric tons of fish per year.

But the catch does not necessarily reflect the actual population of the resource.

Fishermen may be moving to new spots after fish populations at other locations become scarce. In this way, the reported yields may appear level while the resource suffers.

"In this particular case I think that there can be some pretty severe depletion of (the near-shore fishery)," he said.

There are no size or quantity limits on the commercial catch of rockfish and cabezon.

"There is some likelihood that those regulations will be pursued. We recognize that the ability of the fishermen to deplete these resources is real."

★ A recent practice of catching live rockfish in traps is a particularly nasty threat to the fishery, Stock said.

Live rockfish can sell for ten ^{4}times more money than dead fish, and the live market calls for smaller, immature fish, Stock said.

"They're keeping the smaller ones — there is a tremendous restaurant demand for them. They're really depleting the fishery."

The live fish are very popular in Asian markets and restaurants, Hardy agreed.

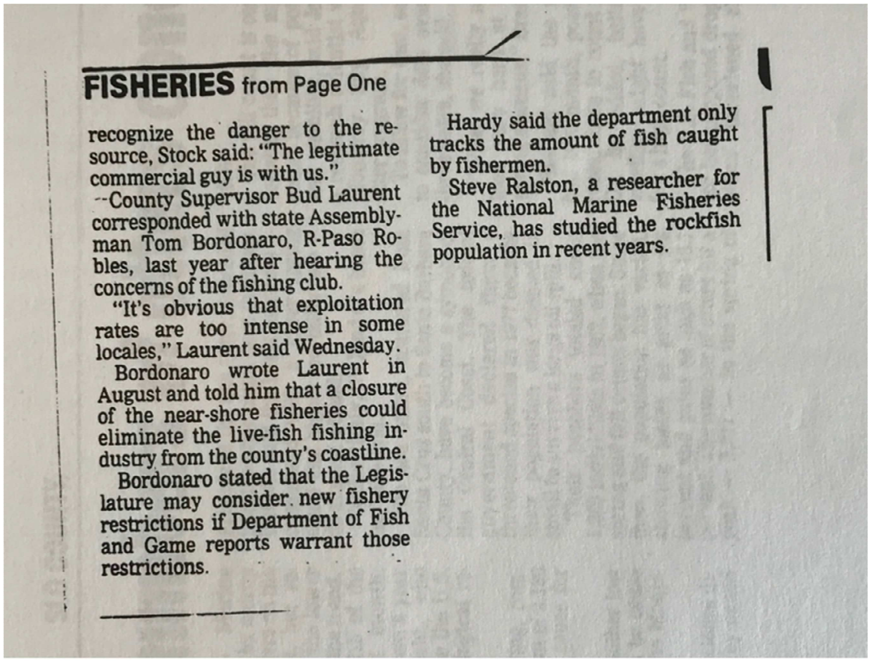
Stock worries that the rockfish may not be around for the next generation since they are being harvested before they reach spawning age.

Jack Breglio, chairman of the Cambria Fishing Club's political action committee, said the key to a solution is a continued dialog with commercial fishing representatives and local legislators.

"We have a common problem I think. I hope we can catch it before it's too late," he said.

Responsible commercial fishermen also

Please see **FISHERIES, Back Page**



FISHERIES from Page One

recognize the danger to the resource, Stock said: "The legitimate commercial guy is with us."

--County Supervisor Bud Laurent corresponded with state Assemblyman Tom Bordonaro, R-Paso Robles, last year after hearing the concerns of the fishing club.

"It's obvious that exploitation rates are too intense in some locales," Laurent said Wednesday.

Bordonaro wrote Laurent in August and told him that a closure of the near-shore fisheries could eliminate the live-fish fishing industry from the county's coastline.

Bordonaro stated that the Legislature may consider new fishery restrictions if Department of Fish and Game reports warrant those restrictions.

Hardy said the department only tracks the amount of fish caught by fishermen.

Steve Ralston, a researcher for the National Marine Fisheries Service, has studied the rockfish population in recent years.

Net profit

Local fishermen are catching on to the lucrative market for live fish

Bill Lovejoy/Sentinel phot

SC Sentinel 3/7/99 p. A1, A16

Asian markets pay top dollar for the live catch

By ROBIN MUSITELLI
Sentinel staff writer

MOSS LANDING — Kurt Solomon's business is for folks who like to see their dinner swimming moments before they eat it.

Solomon deals in live fish — thornyheads, cabezon, lingcod and the various kinds of rockfish that are sold primarily to Asian markets and restaurants in San Jose.

It's a hot market, relatively new to the Monterey Bay, where fishermen are able to double and triple their per-pound profits.

Solomon traded a career in carpentry for his fishing gig five years ago. He established a live fish operation at Moss Landing last year.

Solomon Live Fish is a family affair: his wife Donna runs the office; his son John and brother Weston work in the business, too.

Solomon figures the market has lots of growing room. Within a year, Solomon plans to expand his three-tank operation on K Dock to 25 tanks in a new building across the street.

Statewide, the market for live fish is growing, too. Last year, the haul was nearly a million pounds, an increase of 95 percent since 1989. Right now, most of the live fish mar-

Please see LIVE FISH — BACK PAGE

Kurt Solomon has been providing live fish to San Jose fish markets, from his business in Moss Landing, for five years.

A-16 – Sunday, March 7, 1999 – Sentinel

Live fish

Continued from Page A1

kets are in larger urban areas like San Francisco and Los Angeles, with fishermen outside those cities filling the demand.

The primary reason for the market's growth is financial. Fishermen can get $4.50 a pound for a live gopher cod. Dead, it's worth $1 a pound.

"Live fish is a very brisk market," said Lt. Tim Olivas of the state Department of Fish and Game. "There's a lot of money involved in it."

Solomon buys fish from about 40 different fishermen — about 25 of them regulars. Last year, the company paid about $445,000 for live fish, Donna Solomon said.

The fish are hooked, caught in baskets or trapped and then tossed into a boat's holding tanks. Often, an observer from the state Department of Fish and Game tags along on the boat to monitor the catch and to sample the size of the fish.

On shore, the fish are weighed and sorted. Then they'll go into one of Solomon's three tanks or will be loaded into tanks on the truck, bound for market.

The fisherman are paid $2 to $7.50 a pound. Solomon adds an additional $1 a pound when he sells the fish.

During the summer, height of the live-fish season, Solomon buys and sells up to 7,000 pounds a week.

The fishermen don't catch salmon — those are readily available from salmon farms. Nor do they catch albacore. "Albacore have too much energy" and are difficult to keep alive in tanks, Solomon said.

The occasional oddball fish or sea creature hauled up is sold to the Monterey Bay Aquarium.

This past week, the company's tanks had about 400 pounds of thornyheads, which are rockfish that look like giant goldfish. They're prized for their golden hue, and their red-snapper like taste, Solomon said.

They're also an easy fish to take live, he said. Unlike most saltwater fish, the thornyheads have no air bladders. That means they can be brought to the surface quickly without their air bladder inflating and their eyes popping out, Solomon said.

Other fish caught for the live market have to be "bled," which involves poking them with a needle behind the gills to let the air out of their air bladders, Solomon said.

"All our fishermen carry needles with them," he said. "They do it right on the spot."

Until this year, the live-fish market was relatively unregulated, and many environmentalists complained that it targeted fish whose numbers are in decline, such as the thornyheads.

A 1994 Fish and Game report looked at the rockfish market and found that the size of the fish being taken off the shores of California was decreasing — a sign that the fish are being taken at a higher rate than the ocean produces them.

One variety, bocaccio, declined from a total catch of 10 million pounds in 1981 to 2 million in 1988.

Although the live fish market comprised only a small portion of the total, the report found that fishermen going for live fish were working the nearshore regions that are also rockfish nurseries.

They also were taking youngsters that had yet to reproduce; it turns out, the smaller fish were the ideal size for a dinner plate.

Spurred by the findings, Assemblyman Fred Keeley, D-Boulder Creek, sponsored legislation, the Marine Life Management Act, which puts management of marine fisheries into the hands of Fish and Game rather than the state Legislature. Keeley said the goal was to allow Fish and Game officials to identify problems before they occurred rather than react to depleted fisheries.

One of the first requirements of the Marine Act was that the Fish and Game Commission adopt a management plan for nearshore rockfish, including Dover sole, thornyhead and sablefish.

The commission also imposed new size restrictions designed to allow fish to reproduce before they can be taken, and limits on catches. Fishermen new to the live-fish market are allowed a maximum of 1,000 pounds a month. Established fishermen are allowed 2,000 pounds each month, Solomon said.

Solomon said his practices are more stringent than the Fish and Game rules. The company requires that fish weigh at least 1 pound, a size Solomon figured would allow the fish a chance to reproduce before they are taken. Nor do the fishermen who sell to Solomon work the nearshore nurseries, Donna Solomon said.

"We felt that we wanted to keep this fishery going and continue it for quite a long time," she said. "We all got into it for a future and a career."

Substitutes

Continued from Page A1

Some are credentialed teachers while others have emergency credentials, which only allow them to teach part

Online voting

Continued from Page A1

polling places instead of traditional ballots. Initial reaction from voters was positive, and it took election officials minutes — instead of the normal hours — to tally the results.

"Brazil last year had the world's largest closed (computer) network for conducting elections. Why is it that America lags behind?" asked Warren Slocum, San Mateo County clerk and registrar of voters.

Slocum is among nearly two dozen voting officials, elections experts, technology company representatives, security experts, voting groups and legislators invited to attend the first scheduled meeting of the Internet Voting Task Force on March 17. In an invitation letter mailed Tuesday, Jones said he hopes the group will meet for six months, or as long as necessary to complete its study.

"The task force will be charged with developing a feasibility study that will address security, accessibility, public acceptance, electronic voter registration and the impact such a system would have on the initiative process," Jones wrote.

In an interview, the Republican secretary of state said he expects Internet voting to become a reality in California one day.

"I may not see it in my tenure, but, yes, I think at some point you will see Internet voting. But we do have a lot of research to do to make sure we are secure and that the system has integrity — that is the number one concern that I have," he said.

Some Internet voting advocates have complained that California hasn't moved quickly enough toward what they view as an inevitable future of easy, online voting from personal computers in homes, offices, libraries and elsewhere. But skeptics have voiced strong concerns

FALL 1998 VOL. 17, NO. 3

SAVE OUR SHORES
SANCTUARY WATCH

Dedicated to Preserving the Coastal and Marine Environment of the Monterey Bay National Marine Sanctuary

Expensive Tastes

BY ROBIN CROWN, MARINE ADVOCATE

Rockfish in a tank awaits its invitation to dinner.

At local restaurants, heavy-bodied rockfish swim in murky aquariums, waiting to become part of somebody's remarkably fresh meal. These fish and other species are part of a growing trend driving what's known as the live fishing industry.

Live fish are prized for their flavor and the prestige that accompanies serving them. Prices for these fish are four to ten times higher than for dead ones. The large profits have attracted increasing numbers of commercial fishers, and the number of live fish taken in California every year has grown dramatically. In 1997 about 1.2 million pounds of live fish were caught by 855 licensed fishers—compared to only 52,000 pounds by 77 fishers in 1989.

Live fish that are sought include 66 nearshore species, such as rockfish, greenling, and cabezon. These fish are usually bottom dwellers living in an area between 10 and 40 feet deep, up to about a mile from shore. Commercial fishers are allowed to take these fish with hooks or traps, and there is no limit on number or size. Forty percent of the catch is taken within or near the Sanctuary.

One of the consequences of the rush to capture fish live is the fact that the rockfish population appears to be declining. Scientist Bob Hardy of the California Department of Fish and Game is worried about the sustainability of the rockfish population at the current rate of harvest. "Both commercial and sportfishers," he says, "have commented that there are fewer out there." Because plate-sized fish are sought, immature fish are taken and consequently rockfish breeding is inhibited.

Commercial and sportfishers compete for the same prey. The sportfishing industry, worth $40 to $80 million annually, is also important to California's economy. We should aim to maintain a sustainable commercial live-fishing industry while satisfying the needs of recreational fishers, without adversely impacting the environment.

What is being done about this situation? Early in this legislative session, state Senator Mike Thompson of Sonoma introduced Senate Bill 1336, which would restrict the size of eleven species of nearshore fish taken (about 80 to 90 percent of the catch) and put limits on traps. This bill would establish

(cont'd on p. 2)

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CALENDAR

Saturday, September 19, 9am to noon
14th Annual International Coastal Cleanup Day. Call 647-4259 to find out how you can help.

Saturday, September 19, 11am to 5pm
Shark Festival and Sanctuary Celebration at the Santa Cruz wharf. Celebrate the Monterey Bay National Marine Sanctuary's sixth birthday and honor one of its most interesting inhabitants—the shark! Live music, bay cruises, commemorative ceremonies, plus more than 40 educational and entertaining booths. For more information call 429-3477, or check www.santacruzwharf.com

Wednesday, September 30
The last **Save Our Shores Sunset Cruise** of 1998 (see sail announcement on p. 3).

Thursday, October 1, 6:30 to 9:30pm
SOS Ocean Outreach Training. Eight-hour training program for volunteers who want to save our shores but can't invest 50 hours in training (see story on p. 5). First session will be held at Sleepy Dragon Book Bistro (at the Santa Cruz Harbor near the Crow's Nest). Second session will be on Sunday, October 4, at the Save Our Shores Marine Sanctuary Center.

Saturday and Sunday, October 3 & 4
Monterey Bay Bird Festival at Elkhorn Slough Reserve. Field trips, workshops, exhibits. Call 831-728-5939 for more info.

Saturday, October 17, 4 to 6pm
Northern Sanctuary Outreach Open House. Held at the Half Moon Bay Board Shop, 3032 N. Cabrillo Highway, Half Moon Bay (see box at right).

Sunday, November 8, 5:30pm
Between the Tides: Dining to Save Our Shores. SOS is delighted to present Dr. Carl Safina, noted author, and Julie Packard, renowned director of the Monterey Bay Aquarium, as featured guests at a gala event to be held at Seascape Resort. Reservations required; seating is limited (see story on p. 7). ~

Expensive Tastes *cont'd from front page*

a Rockfish Research and Management Act that would result in a sustainable rockfish population while optimizing the number of fish taken. It would also require the Department of Fish and Game to create a nearshore fisheries management plan.

In the Assembly, Assemblyman Fred Keeley of Santa Cruz and Monterey authored a similar bill (AB1241), one that would also create a change in the way fisheries are managed in California. Instead of requiring new legislation every time a fishery is in crisis, it would give Fish and Game the power to manage fish populations through fish management plans. In August, AB1241 passed the Assembly and moved to a Senate committee. At that point, SB1336 was folded into AB1241 and passed by the Senate; it proceeded to the governor's desk for his signature (as of September 1).

Members of the Conservation Working Group of the Sanctuary Advisory Council were informed of these live-fishing issues during a presentation in May by councilmember Chet Forrest. The Department of Fish and Game also spoke to the council on this topic during the August 7 meeting in Cambria.

What you can do:
Write to Governor Pete Wilson immediately, urging him to sign AB1241. The bill points to the fact that "there is increasing pressure being placed on these [nearshore] fish from recreational and commercial fisheries, that many of these fish species found in the near-shore waters are slow growing and long lived, and that, if depleted, many of these species may take decades to rebuild." It is critical that action be taken now to assure a sustainable fishing industry in California.

For more information on the Live Fishing Industry, contact SOS for a public information packet. ~

Earth Share of California

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Visit our Website: **www.saveourshores.org**

NORTHERN SANCTUARY OPEN HOUSE

Check out SOS's brand new Northern Sanctuary office, located at the Half Moon Bay Board Shop, 3032 N. Cabrillo Highway in Half Moon Bay. Funding for the office has been supplied by a generous grant from the Gabilan Foundation Fund (via the Peninsula Community Foundation).

Come meet John Kucera, our new Northern Sanctuary outreach coordinator, as well as other Save Our Shores staff and volunteers. Enjoy hors d'oeuvres, spirits, and music as we celebrate the opening of our new office on Saturday, October 17, 4 to 6pm.

Going [illegible]

By John Griffith

PART II

John Griffith

Shoppers crowd Lun Sang Market, a live fish shop in San Francisco's Chinatown. (After a shopkeeper screamed "No picture!" our author leaned on a parking meter, trying to look innocent as he shot this photo from the waist.)

The price of a parking meter on San Francisco's Stockton Avenue buys a trip to Hong Kong. Walk sidewalks full of jostling shoppers in Chinatown, and at the 1200 block you find a string of stores that sell the product of the fastest growing, widest open, out-of-control commercial fishery on the West Coast. Bubbling aquariums hold live greenling, lingcod, and rockfish. Floors are lined with cardboard boxes of live frogs and turtles; wire cages keep ducks, chickens, and chuker partridge.

They're like pet stores where everything dies.

"No Pictures" say signs on the walls. Proprietors nervously eye tall, white strangers. Asking questions is worthless. Nobody wants to speak English. Animal rights groups are suing these guys. Seeing food die offends their sensibilities.

The cash register of the Vallejo Market has a sheet of plastic stretched over it, smeared with bloody fingerprints. Like a murder scene, blood-spatter tracks arc across the walls. The severed head of a lingood lying on a pile of ice pops its gills at a shopper. Now that's a fresh fish.

It's an Asian thing. It makes perfect sense: Given the choice, seafood diners select the freshest product, and nothing is fresher than alive. It's cultural: cellophane-wrapped dissections versus live fish. Asians are better able to deal with the fact that something had to die for dinner. They cook their live fish in steamers. The fish pop open and cook up entirely different than dead fish do. Culinary quality is notably better. It's worth trying before criticizing.

THE WHITE VAN

A white van with only spray paint graffiti on its sides pulls in front of the Vallejo Market on Stockton. They set a digital scale on the sidewalk, put a tote on it, and start pitching live fish from a box of sea water in the truck. A man inside puts his hand on a camera lens before a reporter can fire off a shot.

"I believe that there's some less-than-up-and-up things going on," says Kimberly McKee-Lewis, a San Diego-based biologist with the California Department of Fish and Game (CDFG). Besides traditional buyers in ports, much of the product comes through family operations that market their own catch to eliminate middleman profit leakage.

"It's the white van syndrome," says McKee-Lewis. "Anonymity is great for the fishery. They don't want to be known. They want to get business done and get it done as quickly and with the least amount of resistance as possible."

There is an above-board fishery too. West Coast fishery managers get their data from licensed buyers, and the information is troubling. They can only guess at the amount of missing data because the family operations do not cooperate.

They work at all hours from beaches and coastal bluffs. McKee-Lewis says that they speed away when spotted. If intercepted, without a warden present for a show of force the unmarked mobile operators refuse field biologists' requests to sample catches. They decline to speak English. If cornered, they protest that they have a delicate product that suffers from additional handling.

BALLISTIC RISE, BALLISTIC FALL?

The live-fish business in California started going ballistic six years ago. It's grown fast in Oregon in the past year. Demand is huge. Supply is not. Hook-and-line fishing for rockfish and like species is the last open-access fishery on the coast. For the $50 price of a license, Oregon and California sport anglers are flooding into the world of commercial fishing. The action is close to shore, using little boats, kayaks, even surfboards. It's a major moneymaker, and a major headache for fisheries managers who know they're years behind the curve in managing this fishery. It has relatively no regulation.

If it breathes, consumers want it. They'll take everything—the smaller the better, putting the crunch on fish stocks before they've had time to spawn. They pay premium prices for little fish because they fit nicely on platters and in steamers.

"What I see down here is ugly," says Bill Dawson, owner of Seafood Suppliers, at Pier 33 in San Francisco. Dawson wants no part of the live-fish business. "They're raping the resource. I think it's already shot in the ass."

Catch per unit of effort has crashed in many former California near-shore hotspots, making sporties who aren't joining the commercial fishery angry. Biologists lack long-term data to make convincing arguments to limit the fishery, and nobody can agree on how.

"What used to be economic protection isn't there anymore. Now there's economic incentive," says Bob Hardy, marine biologist with the CDFG in Morro Bay.

Before, it was not worth fooling around on reefs and wash rocks to catch maybe 100 pounds of 30-cent dead fish. But with ex-vessel prices up to $9.00 per pound for live grass bass *(Sebastes rastrelliger)* depending on market proximity, a lot of skiff owners

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In direct response to the dwindling salmon market, those working closely in the seafood industry estimate that within 3 years a majority of salmon fishermen will either be unemployed or actively pursuing different employment opportunities. It is imperative, therefore, that salmon fishermen begin working collectively and cooperatively to develop new salmon markets worldwide.

United Salmon Association's agenda is to establish a strong membership for the purpose of aggressively marketing wild-caught salmon. Through a united effort we can save our industry, not just for next season, but for decades to come.

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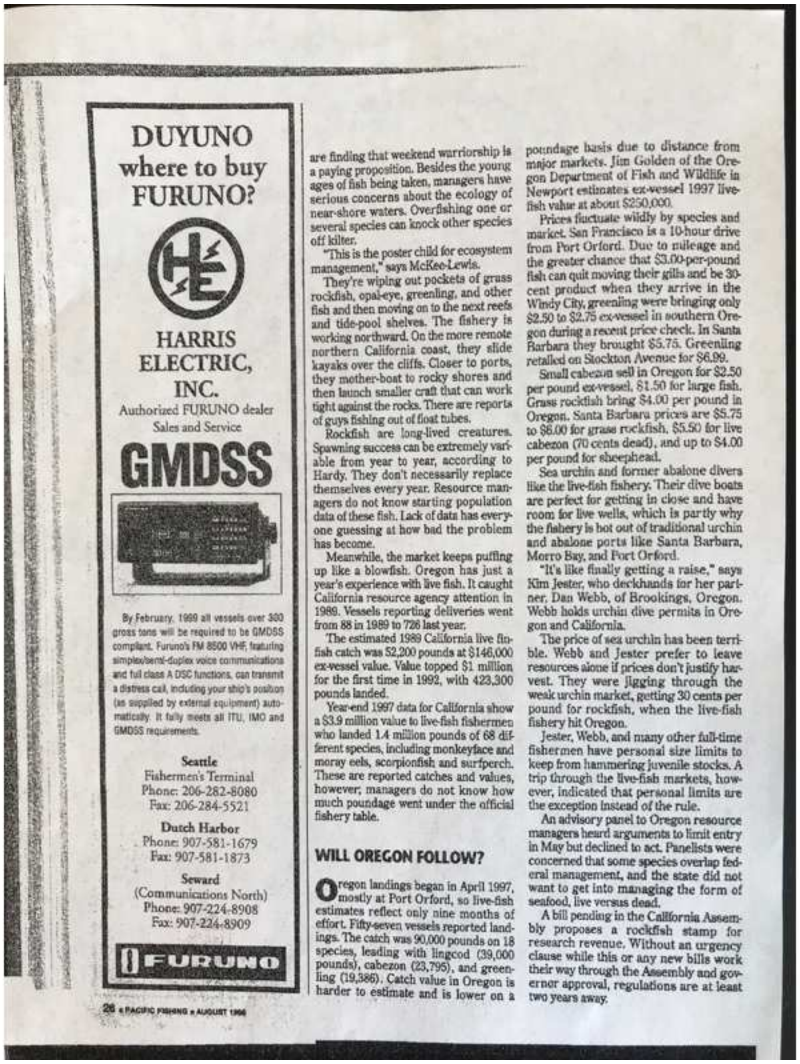

are finding that weekend warriorship is a paying proposition. Besides the young ages of fish being taken, managers have serious concerns about the ecology of near-shore waters. Overfishing one or several species can knock other species off kilter.

"This is the poster child for ecosystem management," says McKee-Lewis.

They're wiping out pockets of grass rockfish, opal-eye, greenling, and other fish and then moving on to the next reefs and tide-pool shelves. The fishery is working northward. On the more remote northern California coast, they slide kayaks over the cliffs. Closer to ports, they mother-boat to rocky shores and then launch smaller craft that can work tight against the rocks. There are reports of guys fishing out of float tubes.

Rockfish are long-lived creatures. Spawning success can be extremely variable from year to year, according to Hardy. They don't necessarily replace themselves every year. Resource managers do not know starting population data of these fish. Lack of data has everyone guessing at how bad the problem has become.

Meanwhile, the market keeps puffing up like a blowfish. Oregon has just a year's experience with live fish. It caught California resource agency attention in 1989. Vessels reporting deliveries went from 88 in 1989 to 726 last year.

The estimated 1989 California live finfish catch was 52,200 pounds at $146,000 ex-vessel value. Value topped $1 million for the first time in 1992, with 423,300 pounds landed.

Year-end 1997 data for California show a $3.9 million value to live-fish fishermen who landed 1.4 million pounds of 68 different species, including monkeyface and moray eels, scorpionfish and surfperch. These are reported catches and values, however; managers do not know how much poundage went under the official fishery table.

WILL OREGON FOLLOW?

Oregon landings began in April 1997, mostly at Port Orford, so live-fish estimates reflect only nine months of effort. Fifty-seven vessels reported landings. The catch was 90,000 pounds on 18 species, leading with lingcod (39,000 pounds), cabezon (23,795), and greenling (19,386). Catch value in Oregon is harder to estimate and is lower on a poundage basis due to distance from major markets. Jim Golden of the Oregon Department of Fish and Wildlife in Newport estimates ex-vessel 1997 live-fish value at about $250,000.

Prices fluctuate wildly by species and market. San Francisco is a 10-hour drive from Port Orford. Due to mileage and the greater chance that $3.00-per-pound fish can quit moving their gills and be 30-cent product when they arrive in the Windy City, greenling were bringing only $2.50 to $2.75 ex-vessel in southern Oregon during a recent price check. In Santa Barbara they brought $5.75. Greenling retailed on Stockton Avenue for $6.99.

Small cabezon sell in Oregon for $2.50 per pound ex-vessel, $1.50 for large fish. Grass rockfish bring $4.00 per pound in Oregon. Santa Barbara prices are $5.75 to $6.00 for grass rockfish, $5.50 for live cabezon (70 cents dead), and up to $4.00 per pound for sheephead.

Sea urchin and former abalone divers like the live-fish fishery. Their dive boats are perfect for getting in close and have room for live wells, which is partly why the fishery is hot out of traditional urchin and abalone ports like Santa Barbara, Morro Bay, and Port Orford.

"It's like finally getting a raise," says Kim Jester, who deckhands for her partner, Dan Webb, of Brookings, Oregon. Webb holds urchin dive permits in Oregon and California.

The price of sea urchin has been terrible. Webb and Jester prefer to leave resources alone if prices don't justify harvest. They were jigging through the weak urchin market, getting 30 cents per pound for rockfish, when the live-fish fishery hit Oregon.

Jester, Webb, and many other full-time fishermen have personal size limits to keep from hammering juvenile stocks. A trip through the live-fish markets, however, indicated that personal limits are the exception instead of the rule.

An advisory panel to Oregon resource managers heard arguments to limit entry in May but declined to act. Panelists were concerned that some species overlap federal management, and the state did not want to get into managing the form of seafood, live versus dead.

A bill pending in the California Assembly proposes a rockfish stamp for research revenue. Without an urgency clause while this or any new bills work their way through the Assembly and governor approval, regulations are at least two years away.

The CDFG isn't waiting. McKee-Lewis is on a team to identify what information is needed to craft a management plan. Stronger data make legislative approval more likely.

Past assemblies passed bills that limited trap fishing south of Pt. Arguello. In 1996, two California Senate bills went into effect to limit the number of hooks used per vessel and to establish weekend closures in designated areas. Otherwise, the near-shore hook-and-line fishery is open access.

Unlike California, the Oregon Fish and Wildlife Commission has much more rulemaking authority over its department. And although no action came in May, the department is considering options including limited entry, gear restrictions, and fish size and area limits, according to Golden.

ROADS TO SUSTAINABILITY?

Despite the current gloomy situation from an ecological perspective, Hardy thinks that with proper management the fishery could become sustainable. Fish are landed carefully to give them the best chance of survival, including thornyheads brought up from considerable depth. With proper management, there would be little waste because unwanted or disallowed catches can be released.

Citing the difficulty of gathering sound data from so many varied habitats and species, McKee-Lewis recommends dramatic changes in landing requirements. "In a perfect world, I would like to see certified weight stations used exclusively to significantly improve enforcement and sampling capabilities," she says.

If politics were not a factor, McKee-Lewis's ideal management plan would include an observer program, logbooks, and independent stock assessment of near-shore target species. An experimental gear permit requirement would also control the fishery long enough for California managers to assemble needed data to determine if any aspects of the new fishery would have a deleterious effect on near-shore ecosystems. Traditional management options such as minimum sizes, seasonal closures, and area closures would also have to be incorporated as appropriate.

"Unfortunately, many of these suggestions for achieving sustainable fisheries are not necessarily palatable to many of our stakeholders," McKee-Lewis says.

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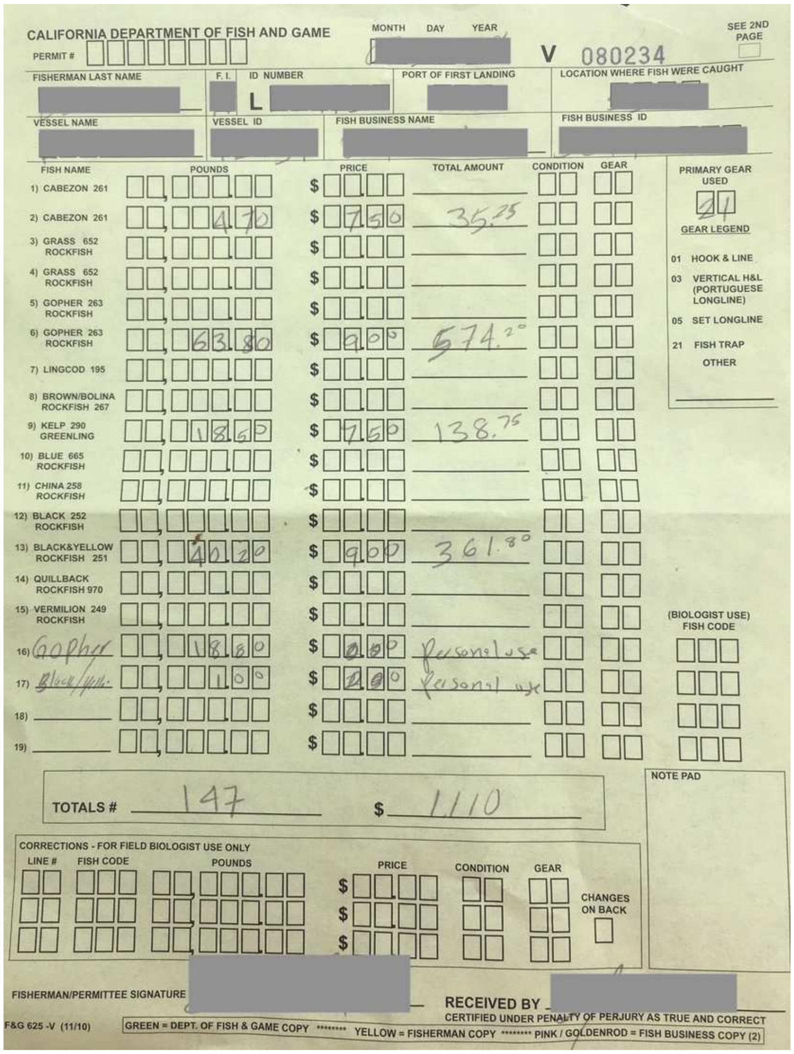
PACIFIC FISHING • AUGUST [illegible] • 27

Supplementary Figure 3.1. News articles illustrating concern from the science and environmental advocacy communities during the "boom era" of the live fish fishery (which included many of the nearshore species).



CALIFORNIA DEPARTMENT OF FISH AND GAME

PERMIT #

MONTH DAY YEAR [redacted]

V 080234

SEE 2ND PAGE ☐

FISHERMAN LAST NAME [redacted]

F. I. [redacted]

ID NUMBER L [redacted]

PORT OF FIRST LANDING [redacted]

LOCATION WHERE FISH WERE CAUGHT [redacted]

VESSEL NAME [redacted]

VESSEL ID [redacted]

FISH BUSINESS NAME [redacted]

FISH BUSINESS ID [redacted]

FISH NAME	POUNDS	PRICE	TOTAL AMOUNT	CONDITION	GEAR
1) CABEZON 261		$			
2) CABEZON 261	4.70	$ 7.50	35.25		
3) GRASS 652 ROCKFISH		$			
4) GRASS 652 ROCKFISH		$			
5) GOPHER 263 ROCKFISH		$			
6) GOPHER 263 ROCKFISH	63.80	$ 9.00	574.20		
7) LINGCOD 195		$			
8) BROWN/BOLINA ROCKFISH 267		$			
9) KELP 290 GREENLING	18.50	$ 7.50	138.75		
10) BLUE 665 ROCKFISH		$			
11) CHINA 258 ROCKFISH		$			
12) BLACK 252 ROCKFISH		$			
13) BLACK&YELLOW ROCKFISH 251	40.20	$ 9.00	361.80		
14) QUILLBACK ROCKFISH 970		$			
15) VERMILION 249 ROCKFISH		$			
16) Gopher	18.80	$ 0.00	Personal use		
17) Black/yell.	1.00	$ 2.00	Personal use		
18)		$			
19)		$			

PRIMARY GEAR USED 21

GEAR LEGEND

01	HOOK & LINE
03	VERTICAL H&L (PORTUGUESE LONGLINE)
05	SET LONGLINE
21	FISH TRAP
	OTHER

(BIOLOGIST USE) FISH CODE

TOTALS # 147 $ 1,110

NOTE PAD

CORRECTIONS - FOR FIELD BIOLOGIST USE ONLY

LINE # FISH CODE POUNDS PRICE $ CONDITION GEAR

CHANGES ON BACK ☐

FISHERMAN/PERMITTEE SIGNATURE [redacted]

RECEIVED BY [redacted]

CERTIFIED UNDER PENALTY OF PERJURY AS TRUE AND CORRECT

F&G 625 -V (11/10)

GREEN = DEPT. OF FISH & GAME COPY ******** YELLOW = FISHERMAN COPY ******** PINK / GOLDENROD = FISH BUSINESS COPY (2)

Supplementary Figure 3.2. A landing receipt ("fish ticket") form for nearshore fishing in 2018. Receipts are filled out and submitted to CDFW for every fish landing made.

Gear Bin	**Gear Type (as listed on fish ticket)**
Hook and Line	Hook and Line, Mooching (salmon), Troll (albacore), Jig/Bait (albacore), Live bait, Troll (salmon), Troll (groundfish or other fish)
Longline*	Set Longline, Vertical Hook and Line / Portuguese Longline
Gillnet	Set Gillnet, Drift Gillnet, Trammel Net
Pot/Trap	Fish Trap, Crab or Lobster Trap, Prawn Trap, Traps Seattle Type (Sablefish), Entrapping
Other Net	Dainish/Scottish Seine, Lampara Net, Hook Net Crab – Rings, Brail/Dip Net or A-Frame, Shrimp Net Chinese Type, Dip Net A Frame, Fyke Net, Drum Seine, Purse Seine, Beach Seine
Trawl	Bottom Trawl, Single-rigged Trawl, Trawl Net, Beam Trawl, Double-rigged Trawl, Midwater Trawl, Trawl with Roller Gear, Trawl – Footrope less than 8 inches in diameter, Trawl – Footrope greater than 8 inches in diameter, Selective flatfish trawl – small footrope
Other	Unknown, Diving, Spear, Diving/Hooks (Sea Urchins), Miscellaneous, Hand Pump, Harpoon/Spear

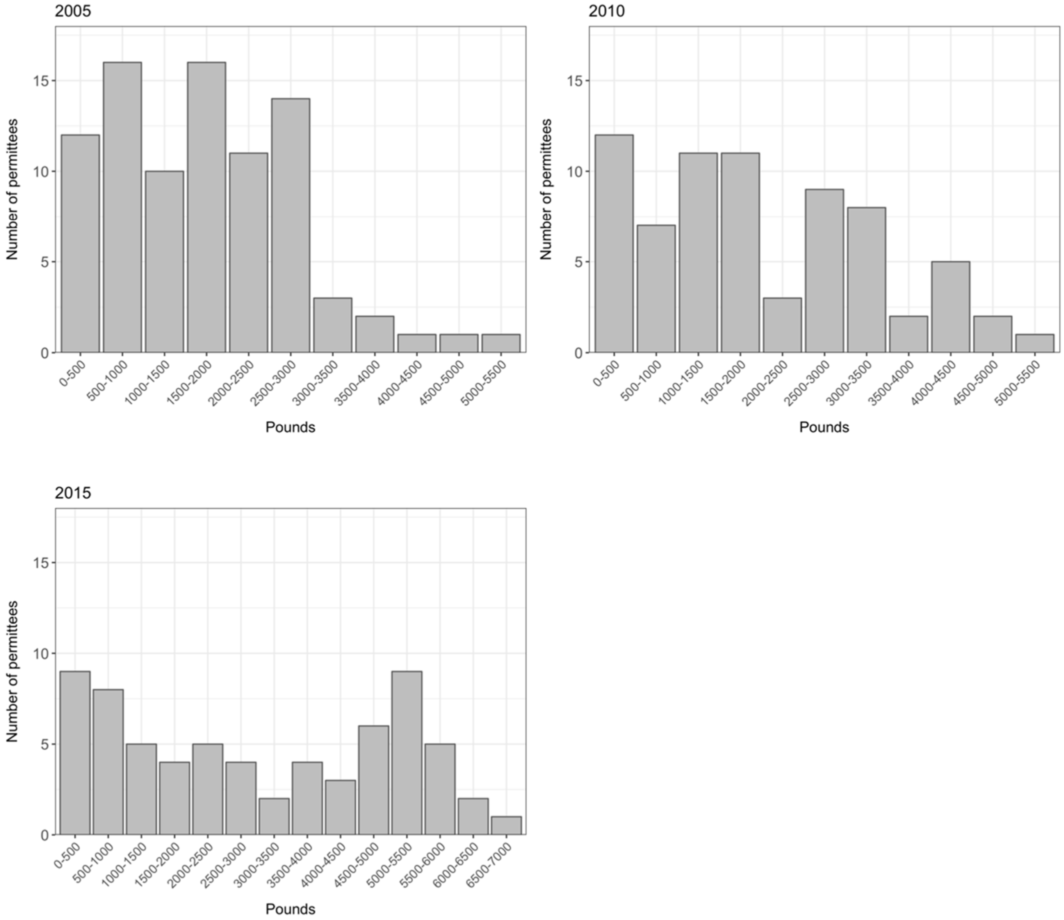
Supplementary Table 3.1. Gear was grouped for all analyses into the categories described in the table above. *Vertical Hook and Line / Portuguese Longline was categorized as “Stick Gear” in some analyses.

Species Group	**Species**
Blue / Black Rockfish	Blue Rockfish, Black Rockfish, Black/Blue Rockfish group
Other Shallow Rockfish	Kelp Rockfish, Gopher Rockfish, Gopher Rockfish group, Black-and-Yellow Rockfish, Nearshore rockfish group, China Rockfish
Cabezon	Cabezon
Greenlings	Kelp Greenling, Rock Greenling
Brown Rockfish	Brown Rockfish, Bolina Rockfish group
Other Deeper Rockfish	Copper Rockfish, Olive Rockfish, Calico Rockfish, Deeper nearshore rockfish group, Quillback Rockfish, Treefish, Copper Rockfish (whitebelly)
Other Nearshore	California Scorpionfish, Monkeyface Prickleback, California Sheephead

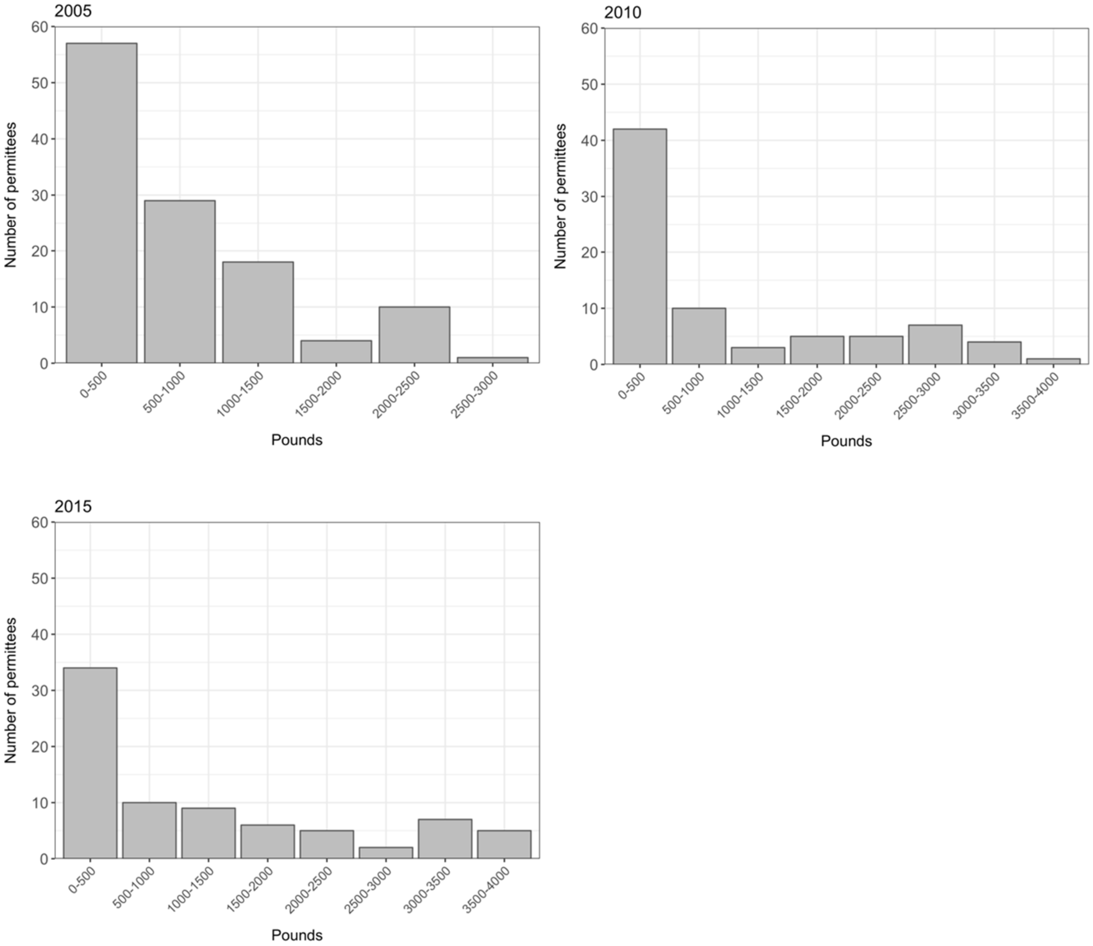
Supplementary Table 3.2. Species (and species designations in the CFIS landings data) were grouped into bins for several analyses throughout the paper.

Port Region	Port of Landing (as listed on fish ticket)
Fort Bragg	Fort Bragg, Point Arena, Albion, Westport, Little River, Elk, Centerville, Shelter Cove
Bodega Bay	Bodega Bay, Tomales Bay, Inverness, Marconi Cove, Dillon Beach, Marshall, Bolinas, Drake's Bay, Point Reyes, Timber Cove, Stewart's Point
San Francisco	San Francisco, Berkeley, Oakland, China Camp, Vallejo, Alameda, Rodeo, Emeryville, Richmond, Pinole, South San Francisco, San Francisco Area, Sausalito, Campbell, Redwood City, Newark, Alviso, Petaluma, Pacifica, Princeton-Half Moon
Monterey	Santa Cruz, Moss Landing, Monterey, Big Sur, Mill Creek, Big Creek, Lindsay
Morro Bay	Morro Bay, Atascadero, Avila/Port San Luis, San Simeon, Moonstone Beach

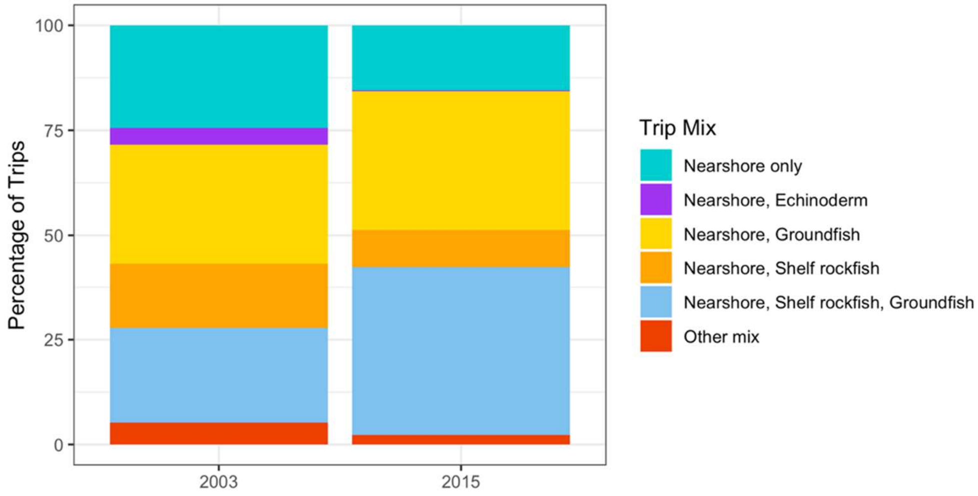
Supplementary Table 3.3. Ports were grouped into port area for all analyses as described in the table above. Port areas follow CDFW convention for port area groupings, with the exception of Shelter Cove. CDFW groups Shelter Cove into the Eureka port area. However, all other landing sites in the Eureka port area fall into the North permit region which is not included in this analysis. As such, Shelter Cove is grouped with Fort Bragg which is in the North-central permit region.



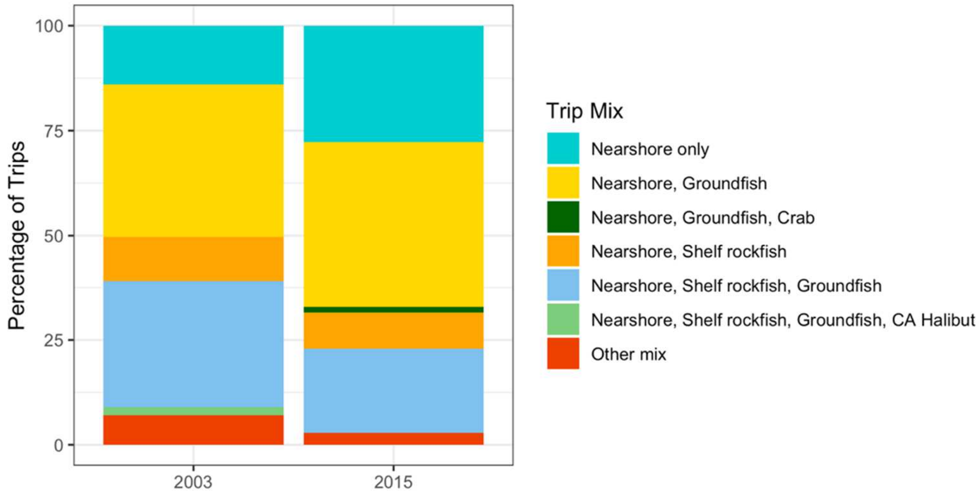
Supplementary Figure 3.3a. The distribution of total annual landings of shallow nearshore species by active shallow nearshore permittees for central permit regions in 2005, 2010 and 2015.



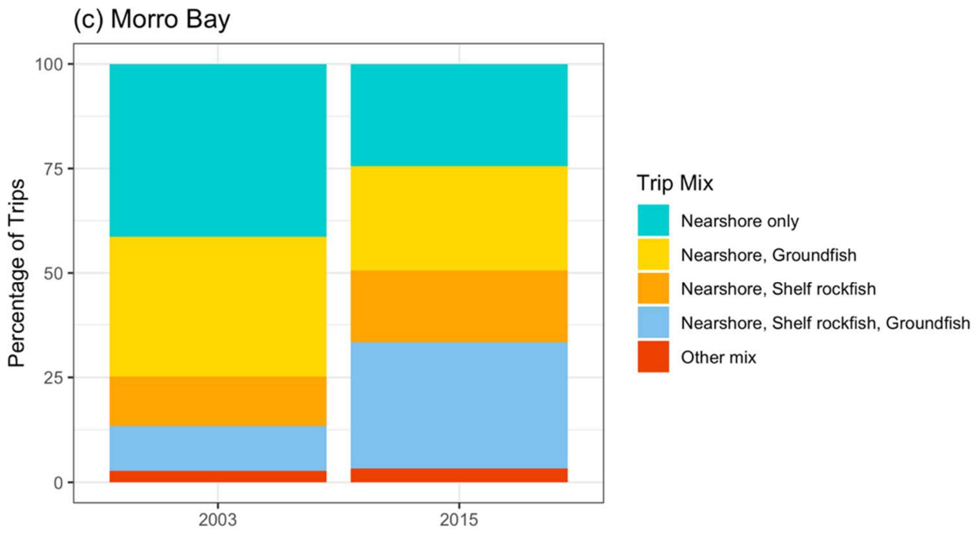
Supplementary Figure 3.3b. The distribution of total annual landings of deeper nearshore species by active deeper nearshore permittees for central region ports in 2005, 2010 and 2015.



(a) Fort Bragg



(b) Monterey Bay



Supplementary Figure 3.4. The landings mix on trips made by nearshore permittees (shallow and deeper) where nearshore species were landed in (a) Fort Bragg, (b) Monterey Bay, and (c) Morro Bay port areas. All mixes that make up more than 1% of annual trips from 2003 to 2015 are included. Two years are shown for visual assessment of change over time. The groundfish category includes all groundfish species that are not part of the shelf rockfish, slope rockfish or nearshore rockfish groups.

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