## Title

Development and application of mass-balanced ecological network models for kelp forest ecosystems

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# DEVELOPMENT AND APPLICATION OF MASS-BALANCED ECOLOGICAL NETWORK MODELS FOR KELP FOREST ECOSYSTEMS

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by

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# Table of Contents

# List of Figures

# List of Tables

# Abstract

## DEVELOPMENT AND APPLICATION OF MASS-BALANCED ECOLOGICAL NETWORK MODELS FOR KELP FOREST ECOSYSTEMS

by

Rodrigo Beas-Luna

Models of ecological networks have proven to be very useful tools for understanding the structure, functions and dynamics of ecosystems. California kelp forests are highly productive and species rich ecosystems. However, the ecosystem-wide consequences of exploitation of higher tropic levels (fishes) and the effect of climate on primary producers such as the giant kelp, *Macrocystis pyrifera*, are not well understood. I develop and apply mass-balanced ecological network models, Ecopath and Ecosim, to explore separately how fishing and the dynamics of giant kelp biomass, the major primary producer in central California kelp forests, influence ecosystem functions (*e.g.*, species interactions, biomass dynamics), structure (*e.g.*, the distribution of biomass density among nodes - species or species groups) and their dynamics. Faced with the difficulty of synthesizing the information required to construct these ecological network models, I led the development and application of an online database (http://kelpforest.ucsc.edu/) to facilitate the collation, organization and accessibility of such information. It is the first online database designed specifically to inform the development of ecological network models.

To explore ecosystem-wide effects of fishing in giant kelp forests, I examine (i) the extent to which changes in species interactions and biomass of nodes caused by fishing extend across the ecological network, (ii) how these changes vary with levels of fishing mortality, (iii) how any changes vary with fishing of six different species of fishes, and (iv) when all six species are fished simultaneously. Results suggest that fished species differ markedly in the extent to which species interactions and biomass densities are altered across the ecosystem and these responses vary with different levels of fishing mortality.

I also used the models to predict the ecosystem-wide responses to different dynamics of giant kelp biomass. I test the hypotheses that different scenarios of dynamics of giant kelp biomass will influence (i) total network biomass, (ii) distribution of biomass density across nodes, (iii) temporal variation in biomass density of nodes, and (iv) how this temporal variation varies among trophic levels. Results suggest that both the mean and the variability of giant kelp biomass alter the direction and magnitude of change in total biomass of the network. The degree of variation is greater for lower trophic levels. Despite the fact that all inferences of these models are based solely on trophic interactions, they illustrate the value of ecosystem models to generate hypotheses and predictions of ecosystem responses to one or more of the changes in kelp forests.

A mi nueva familia,

Alicia y el bebé que viene en camino.

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This study would not have been possible without the sampling and associated efforts of multiple people from the PISCO and USGS long term monitoring researches. The combination of these datasets made my modeling effort one of the kind. In addition, I need to thank Mary Young for providing me the data associated with the kelp forest biomass dynamics for sub patches in central California. Thanks to her generosity, she made a whole chapter of my dissertation happened. Special thanks to Dan Malone that made all the PISCO data quarries available to me.

The design and development of the database benefited greatly from discussions with our collaborators on this project: Jarrett Byrnes, Jim Estes, John Field, Scott Hamilton, Mike Kenner, Kevin Lafferty, Phil Levin, and Dan Reed. I am grateful for data provided by the Partnership for Interdisciplinary Studies of Coastal Oceans (PISCO), Reef Check California, and the Monterey Bay National Marine Sanctuary's Integrated Monitoring Network (SIMoN). Any use of trade, product or firm names in this publication is for descriptive purposes only and does not imply endorsement by the U.S. government.

I am infinitely thankful to the army of undergraduate students and other volunteers that helped me populate the database. Particularly, Jazmin Gasca, Steven Cunningham, Philip Ericson, Laura Melroy, Jackson Winn, Hannah Nolan, Aron Kingsbook, Nathan Deakers, Anthony Martin, Roxanne Beltran, Nicolas Sarracco, Victoria Wade, Michelle Kaiser, Ian Moffitt, Alexis Walker, Paige Prentice, Cory Pickering, Andrew Kim, Max Butensky, Christine Mellon, Lindy Edwards, Hana Wilms, Alexandra Forster, Mtthew Bishop, Ryan Yuen, and many others.

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# General Introduction

Ecological network models and analyses are recognized for their value in articulating the quantitative and conceptual relationships and emergent properties of natural ecosystems, for generating plausible explanations and testable hypotheses pertaining to community structure and dynamics (Montoya *et al.* 2006, Thompson *et al.* 2012, Borrett *et al.* 2014) and predictions regarding their responses to natural and anthropogenic perturbations (Yodzis 2001, Clark *et al.* 2001). Their importance for informing management and policies has increased markedly with the advent of ecosystem-based management (EBM) approaches (*e.g.*, Field and Francis 2006). EBM requires knowledge of how the human uses of ecosystem services influence the structural (*e.g.*, diversity, composition) and functional (*e.g.*, productivity, nutrient cycling) attributes of ecosystems and how these attributes underpin their integrity and resilience. Quantitative ecosystem models based on species or functional group interaction networks that characterize the structural and functional attributes of ecosystems are key tools for understanding how human activities and environmental change influence ecosystems because they can be manipulated to forecast how entire ecosystems may respond to alternative management actions or climatic conditions. For example, models of species interactions that describe ecosystem-wide effects of anthropogenic perturbations have proven particularly insightful for informing ecosystem-based fisheries management, and for understanding the effects of seasonal forcing in freshwater ecosystems (Boit *et al.* 2012) and carbon flux in terrestrial forests (Morales *et al.* 2005).

Kelp forests along the west coast of North America are among the most species rich and productive ecosystems in the world. As such, they have long provided a variety of culturally and economically significant societal services, including valuable recreational and commercial fisheries. In addition, because of these traits and their accessibility, they have been the focus of ecological research that has generated valuable ecological insights, not limited to the marine environment. Because of these and other highly valued attributes of kelp forest ecosystems, there is growing interest in ecosystem-based approaches to managing human uses of kelp forest ecosystems, both for sustainable uses of the services they provide and their general conservation. Despite these goals and recognition of the role of ecological models to inform ecosystem-based management, very few models have been developed and applied to advance our understanding of these iconic ecosystems and inform management approaches. For example, Byrnes *et al.* (2011) used a structural equation model to explore the potential effect of increasing annual frequencies of severe storms on the diversity and complexity of food webs in forests of giant kelp. That model provided predictions of how increased storm frequencies, a phenomenon predicted by some climate change models, would reduce both the diversity and complexity of kelp forest food webs as species occupying higher trophic levels are driven to local extinction. Halpern *et al.* (2007) used a statistical model (redundancy analysis, a multivariate regression approach) to examine the relative contributions of top-down and bottom-up processes in explaining spatial and temporal variation in abundance of trophic levels in kelp forests. They concluded that top-down processes better explained variation in food web structure, suggesting the importance of over-harvesting higher level predators (but see Foster *et al.* 2006 and Steele *et al.* 2006). Other models have focused more on understanding the drivers and maintenance of alternative states (forests versus urchin barrens) of kelp forests and the consequences for species diversity (*e.g.*, Baskett and Salomon 2010). While these studies demonstrate the value of applying foodweb-based network models to understand processes that influence the structure and dynamics of ecological networks in kelp forests, they also represent the few cases in which this approach has been applied in this ecosystem.

One critical barrier to the successful implementation of ecosystem-based models is the accessibility of the substantial data they require (Tallis *et al.* 2010, Hudson and Reuman 2013). Key elements of data accessibility are that they are credible, comprehensive, relevant, well organized, thoroughly explained, easily updated and readily available at a single location online. Though there is a clear need for accessible online databases tailored for the development of ecological network models, few if any databases meet these criteria. Therefore, in the first chapter, I describe the development of the *Kelpforest Database* as an important step forward toward a simpler, more organized, and more reliable integration of the collective biological knowledge of species life histories, demographics, and interactions. My goal is to facilitate the development and use of ecological network models to inform ecosystem-based approaches to management by providing a form for accessible, quality information on kelp forest species. It is the first online database designed specifically to inform the development of ecological network models. Many of the database attributes are novel yet the structure is applicable and adaptable to other ecosystem modeling efforts. Information for each taxonomic unit includes stage-specific life history, demography, and body-size allometries. Species interactions include trophic, competitive, facilitative, and parasitic forms.

Each data entry is temporally and spatially explicit and well referenced. The online data entry interface allows researchers anywhere to contribute and access information. Quality control is facilitated by attributing each entry to unique contributor identities and source citations. The database has proven useful as an archive of species and ecosystem-specific information for the development of several ecological network models, for informing management actions, and for education purposes (*e.g.*, undergraduate and graduate training). To facilitate adaptation of the database by other researches for other ecosystems, the code and technical details on how to costumize this database and apply it to other ecosystems are freely available and located at the following link (https://github.com/kelpforest-cameo/databaseui).

Fishing is one of the most important threats to the stability and resilience of coastal marine ecosystems (*e.g.*, Jackson *et al.* 2001). Fishing directly affects the abundance of targeted species and in turn, modifies direct and indirect effects of species interactions (Cheung *et al.* 2011, Rice 2011, Frank *et al.* 2011). The removal of fished species can ultimately produce a trophic cascades and even lead to local extinctions (Sala *et al.* 1998, Pinnegar *et al.* 2000, Ling *et al.* 2009). However, understanding how fishing affects complex coastal ecosystems such as tropical coral reefs or temperate kelp forests remains very challenging. For example, several species of fishes, invertebrates and algae harvested from temperate kelp forests could potentially alter top-down and bottom-up processes, influencing the structure and functions of these ecosystems (reviewed in: Carr and Reed *in press*, Graham *et al.* 2008, Springer *et al.* 2010). However, empirical evidence of the general importance of these interactions remains unclear (Foster and

Schiel 2010, Guenther *et al.* 2012). Thus, one approach to advancing our understanding of how kelp forest ecosystems will respond to the cumulative effects of fishing is the application of ecological network models parameterized by information from experiment and long term monitoring studies.

In the second chapter, I develop and apply ecological network mass-balanced models (Ecopath with Ecosim) to characterize species interactions in kelp forest ecosystems of central California and to manipulate fishing mortality to ask: what are the ecosystem-wide effects of fishing in kelp forests? Specifically, I explore (i) the extent to which changes caused by fishing in the direction (positive, negative) and magnitude (strong, weak) of species interactions extend across the ecological network, (ii) how changes in biomass of nodes (species and species groups) vary with four levels of fishing mortality, (iii) how any changes in species interactions and biomass vary with fishing of six species of different trophic attributes (*e.g.*, trophic level and prey composition), and (iv) how these effects change when all six species are fished simultaneously. To address these questions, I assembled a network of 24 nodes (*i.e.* species or species groups with similar functional roles within the ecosystem) that included 14 commercially and recreationally fished species. Results of these analyses suggest that the extent to which interactions among species and groups are altered across the ecosystem differed markedly among these six-fished groups and with different levels of fishing mortality. For example, I found the largest and the most extended changes of species interactions and biomass distribution across nodes in the network when fishing a major piscivore, the lingcod (*Ophiodon elongatus*) and a major planktivore, the blue rockfish (*Sebastes* *mystinus*). In contrast, when fishing cabezon, kelp greenling, black rockfish and gopher rockfish, I found marginal changes, limited largely to those nodes directly interacting with these fished species. In all cases, I found a monotonic trajectory in biomass response towards a new equilibrium level. Simultaneously fishing all six species suggested a different pattern when compared to fishing one species at a time. I found a broad (*i.e.* across many nodes), large (magnitude of change) and variable response in species interactions and biomass distribution across the network. In addition, when fishing all species simultaneously, some species trajectories were not monotonic such as cabezon, gopher rockfish and octopus. In some cases, this appears to reflect an initial response to being fished themselves, then responding to the extraction of their predators or competitors. These results suggest that interactions between fished species drastically change in direction and magnitude depending on which species is being fished. Results like these are key to predicting how ecosystem-wide effects of fishing vary among the species targeted for fishing, and how they affect one another, in complex ecosystems like kelp forests. Changes in abundance (biomass) of nodes predicted by the model can inform management. For example, they predict how fishing of one species will influence the potential sustainable take of other species, and the inherent tradeoffs of fishing different species. They also inform monitoring studies designed to assess ecological responses to the establishment of marine protected areas. However, before using these results to inform policy or management, the assumptions and constraints of these models have to be considered.

Ecologists have long recognized that changes in primary production can simultaneously alter the structure (i.e. relative abundance of species, functional groups or trophic levels) and functional processes (*e.g.*, species interactions, biomass production, energy flux) of communities (*e.g.*, Oksanen *et al.* 1981, Facelli and Pickett 1991, Carpenter *et al.* 2001, Polis *et al.* 1997, Polis 1999), but that the magnitude and predictability of responses depend on a multitude of biotic and abiotic features of an ecosystem. So-called "bottom-up" processes include abiotic factors (*e.g.*, nutrient availability, temperature, light availability, environmental stressors), "top-down" processes (*e.g.*, herbivores, parasites, disease and higher level trophic processes that determine their abundance, per-capita), and disturbances can act independently or in combination to drive spatial and temporal patterns of net primary production (NPP). Moreover, the influence of these processes on NPP depends on attributes of the primary producers (plants, algae), including species composition and richness, size, age and stage structure, among others (Tilman *et al.* 1996, Polis *et al.* 1997). Furthermore, how NPP influences the structure, functions and dynamics of a community will depend on its temporal characteristics (*e.g.*, magnitude and duration of variation; Knapp and Smith 2001, Polley *et al.* 2003).

In the third chapter, I explore the ecosystem-wide responses to different dynamics of the primary production generated by the giant kelp. Specifically, I test the hypotheses that different scenarios of biomass density dynamics of giant kelp will influence (i) total network biomass, (ii) distribution of biomass density across nodes, (iii) temporal variation in biomass density of a node over the 27 year simulation, and (iv) temporal variation of biomass density of nodes and these differences will be related to trophic level (*i.e.* variation in biomass density of lower trophic levels will be greater than nodes at higher trophic levels). I identified four patches that captured the range of orthogonal combinations of mean and variance of kelp biomass density. I used the biomass density dynamics to fit the model to the giant kelp biomass density data. The results from these model simulations suggest that both the mean and the inter-annual variability of giant kelp biomass contribute to the direction (increase or decreases) and magnitude of change in total biomass of the ecological network. For example, high and constant giant kelp biomass generated the greatest change in total network biomass. Low and variable giant kelp biomass caused a decline in total network biomass. Also, I found that the highest variation concentrated in the invertebrate group. This suggests that the variability of lower trophic levels are more sensitive to kelp dynamics than higher trophic levels. Despite the fact that all inferences and results of these models are based on solely trophic interactions, and important aspects of natural communities such as competition are missing, this is an example of the value of how ecosystem models can be used to generate hypotheses and predictions of ecosystem responses to one or more of the changes in the marine environment. With this effort, I showed how mass-balanced models are useful tools to inform and generate hypothesis and predictions of ecosystem-wide responses to different sources of variation.

*citations found in the dissertation chapters

# Chapter 1

# An online database for informing ecological network models

**http://kelpforest.ucsc.edu**

## Abstract

Ecological network models and analyses are recognized as valuable tools for understanding the dynamics and resiliency of ecosystems, and for informing ecosystem-based approaches to management. However, few databases exist that can provide the life history, demographic and species interaction information necessary to parameterize ecological network models. Faced with the difficulty of synthesizing the information required to construct models for kelp forest ecosystems along the West Coast of North America, I developed an online database (http://kelpforest.ucsc.edu/) to facilitate the collation and dissemination of such information. Many of the database's attributes are novel yet the structure is applicable and adaptable to other ecosystem modeling efforts. Information for each taxonomic unit includes stage-specific life history, demography, and body-size allometries. Species interactions include trophic, competitive, facilitative, and parasitic forms. Each data entry is temporally and spatially explicit. The online data entry interface allows researchers anywhere to contribute and access information. Quality control is facilitated by attributing each entry to unique contributor identities and source citations. The database has proven useful as an archive of species and ecosystem-specific information in the development of several ecological network models, for informing management actions, and for education purposes (*e.g.*, undergraduate and graduate training). To facilitate adaptation of the database by other researches for other ecosystems, the code and technical details on how to customize this database and apply it to other ecosystems are freely available and located at the following link

(https://github.com/kelpforest-cameo/databaseui).

## 1.1 Introduction

Ecological network models and analyses are recognized for their value in articulating the quantitative and conceptual relationships and emergent properties of natural ecosystems, for generating plausible explanations and testable hypotheses pertaining to community structure and dynamics (Montoya *et al.* 2006, Thompson *et al.* 2012, Borrett *et al.* 2014) and predictions regarding their responses to natural and anthropogenic perturbations (Yodzis 2001, Clark *et al.* 2001). Their importance for informing management and policies has increased markedly with the advent of ecosystem-based management (EBM) approaches (*e.g.*, Field and Francis 2006). EBM requires knowledge of how the human uses of ecosystem services influence the structural (*e.g.*, diversity, composition) and functional (*e.g.*, productivity, nutrient cycling) attributes of ecosystems and how these attributes underpin their integrity and resilience. Quantitative ecosystem models based on species or functional group interaction networks that characterize the structural and functional attributes of ecosystems are key tools for understanding how human activities influence ecosystems because they can be manipulated to forecast how entire ecosystems may respond to alternative management actions. For example, models of species interactions that describe ecosystem-wide effects of anthropogenic perturbations have proven particularly insightful for informing ecosystem-based fisheries management, and for understanding the effects of seasonal forcing in freshwater ecosystems (Boit *et al.* 2012) and carbon flux in terrestrial forests (Morales *et al.* 2005).

However, a critical barrier to the successful implementation of ecosystem-based models is the accessibility of the substantial data they require (Tallis *et al.* 2010, Hudson and Reuman 2013). Key elements of data accessibility are that they are credible, comprehensive, relevant, well organized, thoroughly explained, easily updated and readily available at a single location online. Though there is a clear need for accessible online databases tailored for the development of ecological network models, few if any databases meet these criteria. Here, I describe an online interactive database with information (life history, demography, species interactions) required of many ecological network models and that fulfills these and other necessary criteria for expediting the development of these models.

### 1.1.1 *Why ecological network models need databases*

In a comprehensive review of ecological network models used to characterize and explore marine ecosystems, Plagányi (2007) identified four general categories of models: Minimum Realistic, Individual Based , Biogeochemical, and Aggregate System Models (Table 1.1). These four broad categories of ecological network models illustrate the diversity of information that is required of, or can be accommodated by, the various ecological network models. Other model types, such as qualitative loop analysis (Levins 1974, Dambacher *et al.* 2009) and allometric trophic network models (Boit *et al.* 2012) also benefit from such information. Despite differences in their assumptions and focal applications, all of these modeling approaches accommodate or require some of the same forms of information, such as knowledge of what species, life-stages or functional groups constitute an ecosystem. However, they differ in their requirements or ability to accommodate other forms of information including species' currencies (*e.g.*, biomass, density), distributions, life history or demographic attributes, and the manner in which species interact (*e.g.*, predation, parasitism, competition, mutualism; Table 1.1). For example, many ecological network models focus entirely on trophic interactions in their representation of species interactions, ignoring non-trophic interactions, such as competition for space (Wootton 2001) or parasitism (Lafferty *et al.* 2008). The greater the variety of information included in a database, the greater its application across the diversity of ecological network models. Much of the same types of information are also relevant to the development of single-species population models, and are useful in non-modeling contexts. For example, including knowledge of the geographic patterns of species' life history traits and interspecific interactions can help to inform the design of experimental and observational studies, or the placement of marine reserves (Gerber *et al.* 2003, Micheli *et al.* 2004, Caselle *et al.* 2011).

Table 1.1: Comparison and examples of four categories of ecosystem models (modified from Plagány 2007). “A” and “R” indicate that the model accommodates or requires information of this form, respectively. “Env”= environmental.

| Model type & examples | No. of nodes or functional groups | Currency | Life stages | Size structure | Spatial structure | Topology | Diet | Non-trophic interactions | Env. Data |
|---|---|---|---|---|---|---|---|---|---|
| Qualitative models<br>Loop Analysis | $< 10$ | Biomass | A | A |  | input |  | A |  |
| Minimum Realistic<br>GADGET[1] | 6 to 8 | Nutrients | A |  |  | input | R |  |  |
| Individual Based<br>OSMOSE[2] | 7 to 20 | Biomass | A | R | A | input | R | A |  |
| Biogeochemical<br>ATLANTIS | 20 | Nutrients | A | A | A | Input, output | R | A | R |
| Aggregate system<br>EwE[3] | $> 40$ | Biomass | A |  | A | Input, output | R | A | A |

1 Globally Applicable Area-Disaggregated General Ecosystem Toolbox

2 Object-oriented simulator of marine ecosystem exploration

3 Ecopath with Ecosim

### 1.1.2 *Shortcomings of existing online databases for ecological network modeling*

The diversity of information required by the various kinds of ecological network models is rarely organized in a form that is useful or accessible to modelers. Several well-designed online taxon-specific databases exist that collate information on species taxonomy, phylogeny, life history traits and distribution (Table 1.2). However, few of these mediate with web browsers or between multiple databases, instead referring to static species-focused summaries. Fewer still translate data requests beyond species-specific searches to permit the querying of multiple species from a common functional group. Having no online database management system (DBMS), these databases preclude the integration of different functions and information in the same process to permit simultaneous access of taxonomic, life history, distribution and ecological databases (Stein 2003). Some database management systems (*e.g.* FishBase, Sea Life Base; Table 1.2) have the potential to integrate multiple databases in their queries but do not currently do so. Furthermore, database entries do not reference their datum-specific sources, leaving attribution absent or too general and difficult to reconstruct and thereby making validation and reanalysis difficult or impossible.

More generally, few existing databases housing information relevant to ecological network models also include information on species interactions. Those that do, include only the presence of the interactions without source citations or detailed description of their nature, spatial, or temporal patterns specific to those interactions.

Hence, variation and uncertainties in interaction information are difficult to obtain and remain challenging to incorporate into ecological network models.

### 1.1.3 *Ecological network models for kelp forest ecosystems*

Kelp forests are stands of large macroalgae of the Order Laminariales that occur on temperate and boreal rocky reefs around the world and are among the most productive and diverse ecosystems in the world (reviewed by (Schiel and Foster *in press*, Mann 1973, Dayton 1985)). These species-rich ecosystems provide many ecosystem functions, including primary production, habitat for fishes, invertebrates, mammals, and birds, and nurseries for a diversity of species (reviewed by (Carr and Reed *in press*, Schiel and Foster 1986, Graham *et al.* 2008, Springer *et al.* 2010)). Kelp forests also provide humans with many services, including carbon sequestration, shoreline protection and non-consumptive recreational activities (Carr and Reed *in press*, Hlker *et al.* 2007). In particular, they support economically and culturally significant commercial and recreational fisheries (*e.g.*, Starr *et al.* 2002, Ling and Johnson 2009).

Species interactions are known to be key determinants of the structure and dynamics of kelp forests around the word such as the west coast of the United States (Carr and Reed *in press*, Estes and Palmisano 1974, Dayton 1985, Schiel and Foster 1986), North Atlantic (Johnson and Mann 1988, Steneck *et al.* 2003), Mexico (Beas-Luna and Ladah 2014), Australia and Tasmania (Ling *et al.* 2009) yet these are sensitive to anthropogenic and natural perturbations (Ebeling *et al.* 1985, Ling *et al.* 2009, Reed *et al.* 2011). Given the importance and complexity of their species interactions, kelp

Table 1.2: List of some of the most relevant marine ecological databases and their attributes to inform ecosystem models. “X” indicates available function. “Integration capability” refers to ability to link with another database.

| Database | Subject taxa | Data type | Data visualization | Data export | Integration capabilities |
|---|---|---|---|---|---|
| Algae Base | Algae | 1,2,5,6,7 | x | | |
| All about birds | Birds | 1,4,5,6,7 | x | | |
| AnAge | Multiple | 1,11 | x | | x |
| Catalog of Life | Multiple | 2 | x | | x |
| DataMares | Multiple | 2,5,6,9,10 | x | x | |
| EOL | Multiple | 1,2,3,4,5,6,7 | x | | x |
| Eurobis | Plankton | 2,5,6,10 | x | | x |
| Fish Base | Fish | 1,2,3,4,5,6,7,8 | x | | x |
| GoMexi | Multiple | 2,8,9,10 | x | x | x |
| ITS | Multiple | 2 | x | x | x |
| Kelpforest | Multiple | 1,2,3,4,5,6,7,8,9,10,11 | x | x | x |
| Sea Life Base | Multiple | 1,2,3,4,5,6,7 | x | | x |
| Sea Net | Multiple | 1,2,4,5,6,7 | x | | |
| Simon | Multiple | 1,2,3,4,5,6,7 | x | | |
| WoRMS | Multiple | 2 | x | | x |

**Data types:** 1) Life history, 2) taxonomy, 3) biometrics, 4) behavior, 5) distribution, 6) habitats, 7) photos, 8) species interactions, 9) temporal explicit data, 10) spatial explicit data, 11) references.

**Score:** Sum of number of attributes valuable for data accessibility for ecosystem modelers. These attributes provide basic information for the parameterization and validation of ecosystem models.

forest ecosystems are strong candidates for ecosystem-based management, which greatly benefits from the use of ecological network models (Springer *et al.* 2010).

Only recently, a number of ecological network models have been generated for kelp forests including Espinosa-Romero (2010), Ortiz (2010), Brynes *et al.* (2011a) and Marzloff *et al.* (2013), for the west coast of Canada, northern Chile, and southern California, respectively. In addition, theoretical multi-species models (not parameterized empirically), have enhanced our understanding of complex interactions in kelp forest systems (Baskett and Salomon 2010, Marzloff *et al.* 2011) and assemblages of sessile invertebrates on temperate rocky reefs (Dunstan and Johnson 2006). Each of these models represents local species composition and, justifiably, over-simplifies the networks of kelp forest species interactions. Model-simplification can reflect a compromise between computational power, model-sensitivity, user interests, and preconceptions, but in many cases is simply a result of a lack of accessible information about life history traits and species interactions.

In the process of our development of ecological network models for the kelp forests of the eastern Pacific I found the necessary life history, demographic, and species interaction information poorly synthesized and organized and difficult to access. For these reasons, I developed an online database to collate and freely disseminate information on species life histories, demography, and species interactions. Here, I describe the development of and rationale for the database structure, and the means of accessing the information. Our goal here is to facilitate its use and describe its potential implementation for other ecosystems. That is, although the database was constructed with a focus on kelp forests, the interface, structure, utilities and functions could be easily translated for use in any other ecosystem. Moreover, because the architecture of this database is a DBMS, it can be integrated into a more comprehensive database integrating multiple ecosystems.

## 1.2 Methods and Results

### 1.2.1 *Kelpforest Database structure*

The overarching goals of the online database, hereafter referred to as the "*Kelpforest Database*", was to create a database management system that could be conveniently populated and utilized across the community of researchers and provide users with the diversity of information required by the various types of ecosystems models. The *Kelpforest Database* consists of seven components: 1) a database management system, 2) database homepage, 3) an online data entry interface, 4) an online data entry manual, 5) graphic visualizations, 6) data export tools, and 7) a user forum for discussions, online assistance, and notification of problems. To promote and expedite adaptation of the database for modeling other ecosystems, technical information for developers is readily available, hosted at https://github.com/kelpforest-cameo/databaseui

#### 1.2.1.1 *Database management system*

The database is a relational database management system that uses MySql and PHP languages and is hosted at the University of California Santa Cruz (http://kelpforest.ucsc.edu/). The central element of the database schema is the source (*i.e.* citation) of each datum entered (Figure 1.1). This allows all possible entries and queries to be referenced to the source of that information. This reference avoids redundant entries and promotes quality control by ensuring the legitimacy of entered data. The relational database links the various data tables of the database. Taxonomic information is linked to the Integrated Taxonomic Information System (ITIS; www.ITIS.gov) to ensure that entries are standardized (*e.g.*, avoiding misspellings) and that taxonomic designations and synonyms are continuously updated.

#### 1.2.1.2 *Database website*

The database website is created using WordPress web software (wordpress.org), providing an introduction to the database that includes its purpose, information on how to access it, and up-to-date contact information. The website hosts the other components of the database (*i.e.*, data entry interface, visualization and export tools, user forum), and provides access to a sign-up form for users who wish to obtain data-entry privileges. Access to the data itself does not require registration.

#### 1.2.1.3 *Online data entry interface*

The data entry interface allows multiple users to simultaneously enter information into the database. Access to the data entry interface requires a username and password. This username is linked to every datum entered by an individual in order to provide attribution of user contributions and to simplify quality control. A "sand-

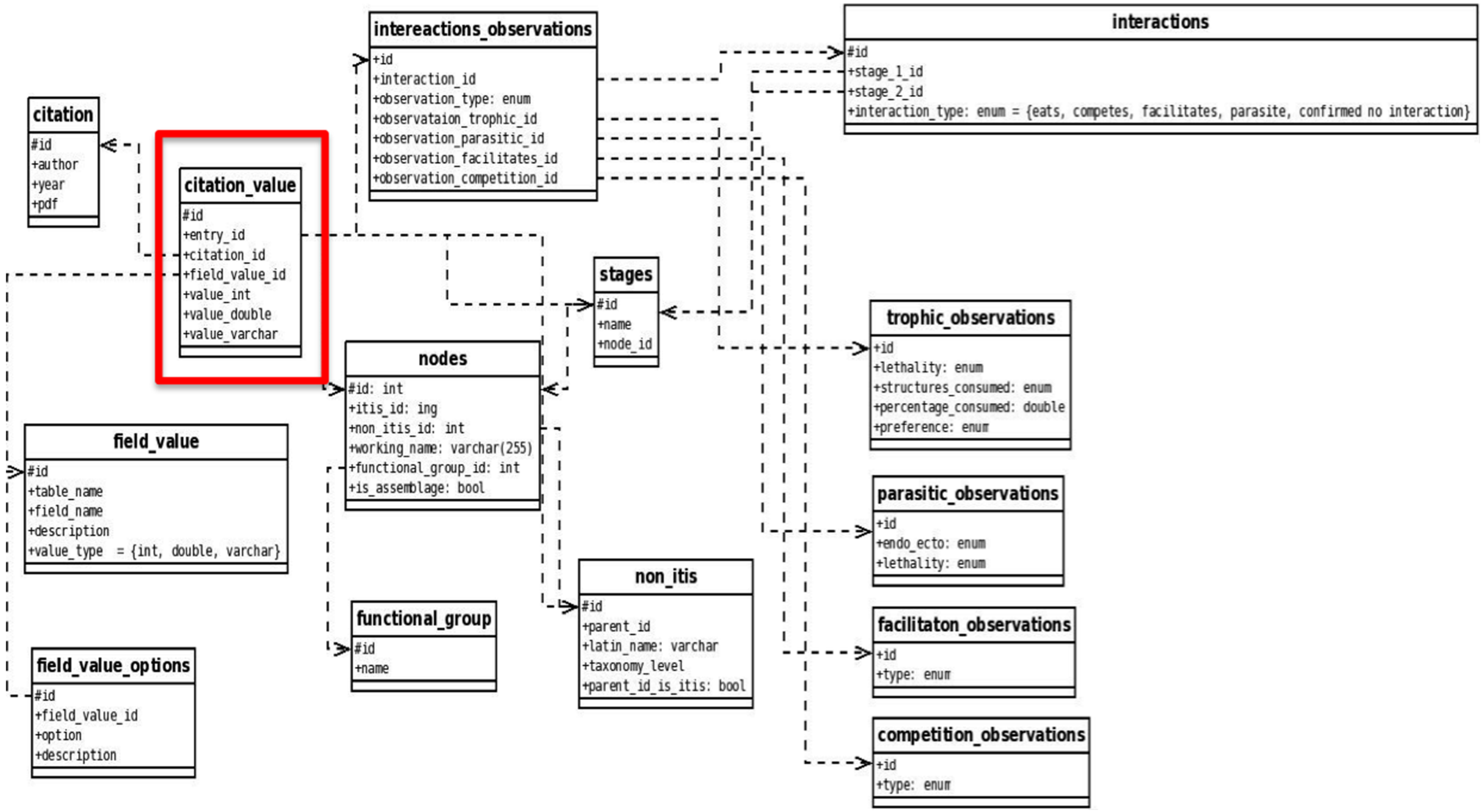

Figure 1.1: Database schema to enter, query and retrieve data for parameterizing ecological network models. The central element of the schema is the citation value table that links all entries and queries to the data source (red box). The ITIS identifier in the nodes table (red line) is used to link the *Kelpforest Database* to the ITIS database.

box" replica of the database and its data-entry interface allows individuals to practice entering data that will not be archived. Access to this "sandbox" does not require user registration.

The data entry interface provides links to three separate data entry forms: *nodes*, *interactions*, and *citations*. All forms are used to enter and look at information. The *nodes* form is used to enter information relevant to taxa (*i.e.* species, higher taxonomic units, or species groups). The *interactions* form is used to enter information characterizing interaction between nodes. The *citations* form is to enter the citation information associated with each datum that is entered. Each form contains a range of different sub forms. I, therefore, first provide an overview of each form before detailing its contents.

Within the *nodes* form, the user may list or search for existing nodes, or enter a new node. The first section of the *nodes* form indicates information that is relevant to the entire node, whereas the second section pertains to life stage-specific information. (The database distinguishes between a node's different life stages, detailed below).

The *interactions* form allows users to enter interaction information between specific life stages of two previously entered nodes. Importantly, species interactions are recorded as stage-specific observations of the interaction. That is, multiple observations of an interaction between two focal species (stages) may be recorded from different source citations or from the same citation (pertaining, for example, to different locations or time-periods). I believe such information is key to describing the breadth, spatio-temporal variation, and uncertainty in our knowledge of species interactions.

The *citations* form allows users to enter new citations and authors to which entries are to be attributed, and to list all previously entered authors and full citations. The *citations* form requires users to identify the category of the source information. That is, sources from which entries have been obtained to-date are primarily from the published peer-reviewed literature, but also include unpublished reports, theses, other online databases, unpublished datasets, and qualified personal observations. The *citations* form is directly linked to the *nodes* and *interactions* forms. Every entry requires a citation. Check boxes located next to each source citation on the list of entered source citations permit data-entry users to indicate when all its pertinent information has been extracted.

#### 1.2.1.4 *Data entry fields and manual*

All entry fields in both the *nodes* and *interactions* forms permit inclusion of the temporal and geographic information associated which each entry. Then "time stamp" sub form for individual entry fields allows users to specify whether an entry pertains to a single time point or a window of time points at daily to annual scales. Nodes and their stage-specific interactions may be specified with a geographic location, or range of locations. Location(s) can be identified using either a Google maps-based interactive interface or by entering a latitude and longitude. Nodes and interaction observations are thus geo-referenced across a range of spatial resolutions spanning regional, subregional, and within subregional scales and point locations (Figure 1.2). Regions and subregions are based on recognized biogeographic sections of the Eastern Pacific coast spanning from Baja, Mexico to the western Aleutian Islands. Polygons within each subregion reflect 20 Km sections of the coast. Each of these standardized spatial units can be identified by the user directly on the map, or from a hierarchical legend in the mapping interface.

Each entry field also includes a comment box that allows users to clarify their input, when necessary. This is a critical element of the database. Many variables required by ecological network models are not directly available in the literature and must be calculated. The comment box allows users to describe the equations or methods that were used to derive values or standardize units from the information that was available in a given source. For example, estimates of biomass density are often derived from estimates of population size structure and density.

Data entry and standardization is facilitated by drop down menus and "mouse over" descriptions of each data entry field. In addition, the online data entry manual provides users with an overview of the database schema and the interface forms, as well as general information on data entry protocols, tips, and shortcuts.

#### 1.2.1.5 *Content*

As introduced above, there are two general categories of content that may directly or indirectly inform kelp forest ecological network models: content associated with the characterization of nodes, and content describing observations of between-node interactions.

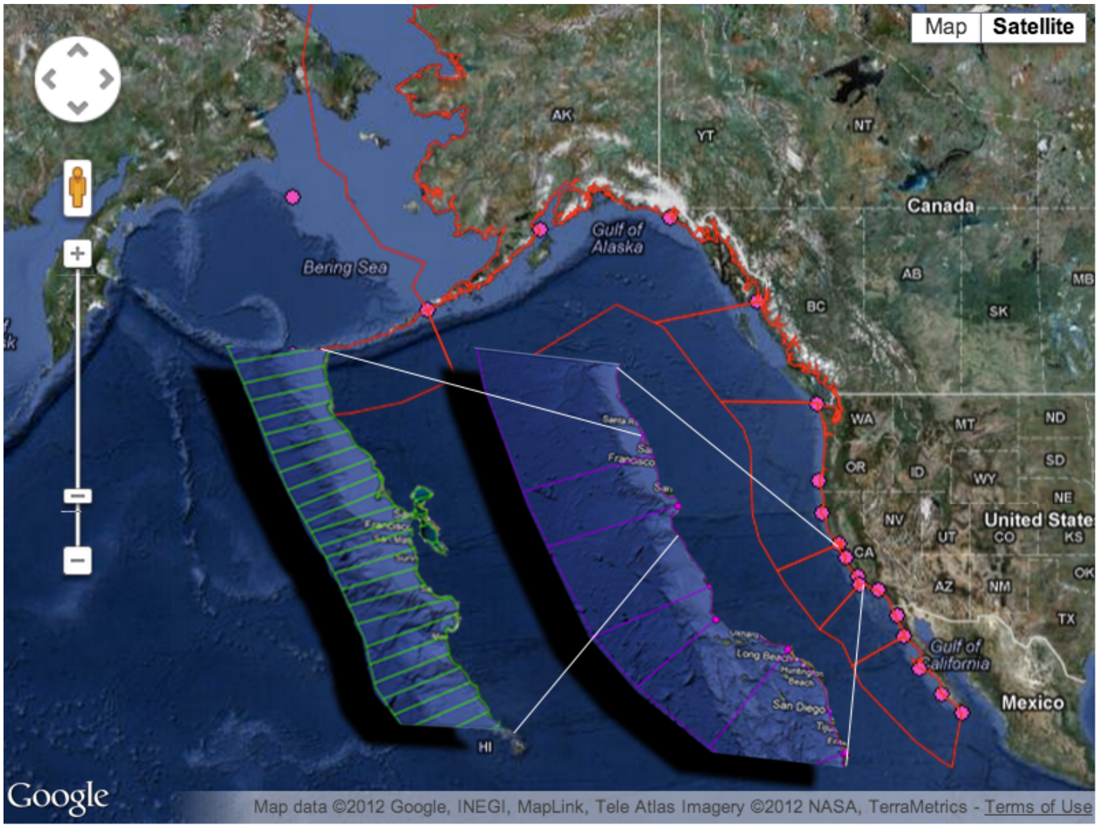

Figure 1.2: Illustration of the geographically hierarchical map interface with nested delimited regions (orange), subregions (green) and locations (purple) in the northeast Pacific. The actual interface applies Google maps to allow users to identify specific locations or regions from which data were collected in the data entry process.

***Nodes.-*** I refer to the basic taxonomic units of the database as "nodes" rather than "species" or "taxon" because these may represent differing taxonomic resolutions (species, genera, family, etc.), or aggregated assemblages of indistinguishable taxa (*e.g.*, phytoplankton). Each node is identified with a unique node identification number (nodeID), a common or "*working name*", scientific name, and is associated with an ITIS id number. ITIS is an international partnership (USA, Canada and Mexico) that provides consistent and reliable information on the taxonomy and nomenclature of species in North America. Integration with the ITIS database allows nodes to be organized in a current taxonomic hierarchy and minimizes errors associated with relic synonyms and misspelled taxon names. However, the ITIS database is not complete, some taxa or assemblages found along the eastern Pacific are absent. Our database stores these nodes separately, identifying them using the working name and the ITIS id of its most resolved taxonomic level until they become available in ITIS.

Characterization of a node includes life history traits (*e.g.*, reproductive strategy, age and size at maturity, maximum body size) and demographic information (*e.g.*, production-biomass ratios, consumption-biomass ratios, length-weight relationships, von Bertalanffy equations, biomass). This information may be specific to the ontogenetic stages of a node, or specified as "general" when stage-specificity is unknown. The number and types of stages may be customized for each node, with users choosing from an open-ended list of potential stages when stage-specific information is to be entered. Currently, animal stages include egg, larvae, juvenile, adult, and dead. Algae stages include sporophyte, gametophyte, and dead.

The database was initially populated with species lists from the Partnership for Interdisciplinary Studies of Coastal Oceans (PISCO- www.piscoweb.org), Reef Check California (http://reefcheck.org/rcca/rcca_home.php), Cailliet's *et al.* (GM *et al.* 2000), the Monterey Bay National Marine Sanctuary Integrated Monitoring Network (SIMoN- http://sanctuarysimon.org/) and a species interaction table created by Byrnes *et al.* (Byrnes *et al.* 2011b). Many other species have since been included as a result of an intensive literature search.

***Interactions.-*** Four general categories of interactions between nodes are included in the database: trophic, competitive, facilitative, and parasitic. Individual observations for all of these interaction categories are described by their observation type (*e.g.*, direct observation, diet analysis) and must be attributed to a source citation. Each interaction category also has entry fields particular to it. For example, trophic interactions may be described by their lethality, the structures consumed, and the percent of the consumer's diet that a particular resource represents. Similarly, parasitic interactions may be described as being endo- or ectoparasite, and by their prevalence and intensity. The interactions between two nodes are not assumed to be reciprocal.

***Citations.-*** Though most information in the database will likely continue to be extracted from the published, peer-reviewed literature, the demand for information with which to inform modeling efforts motivates a means for making it available that is faster than the rate at which it can be published. Thus, to accommodate unpublished data and personal observations, citations may refer to individuals who provide their contact information.

#### 1.2.1.6 *Data visualization*

A series of static and dynamic visualization tools permit real-time access and interaction with the information contained in the database. These tools query the database in real-time to produce graphics (Figure 1.3) and tables of summary statistics, interaction networks, adjacency matrices, body size frequency distributions, and interaction observation maps. These utilities rely on a combination of PHP and Mysql languages and capitalize on the capabilities of D3.js (http://d3js.org), a JavaScript library that uses HTML, SVG, and CSS to create and manipulate data-driven visualizations.

#### 1.2.1.7 *Data export*

Information in the *Kelpforest Database* is public and accessible to unregistered users through several export tools. These include database queries for tables and matrices containing information about nodes, interactions and citations, allowing users to download the data as comma-separated (CSV) files (Table 1.3). Future additions will permit registered users to query the database directly.

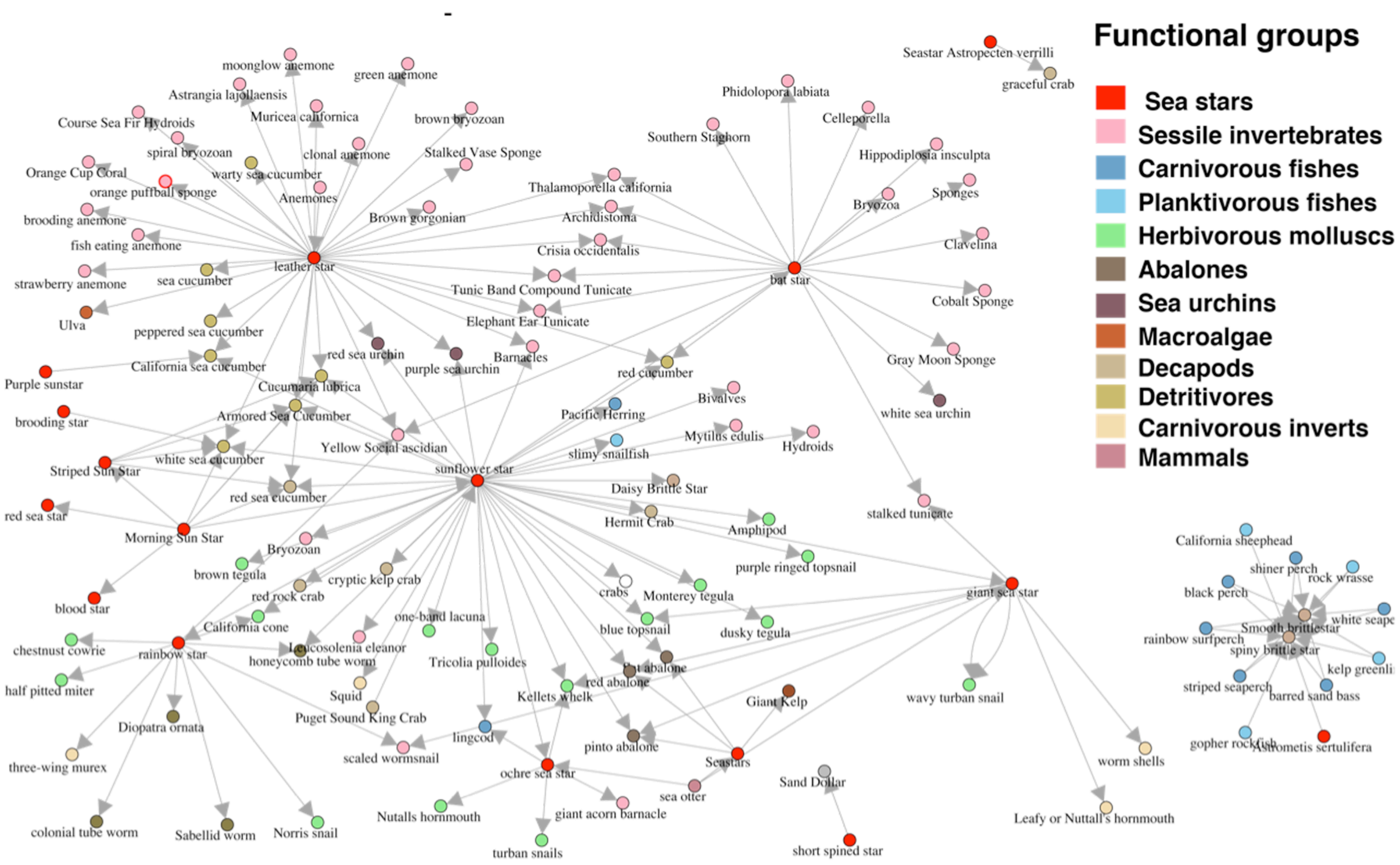

Figure 1.3: Example from the database visualization tool. Illustrated is a trophic interaction network for an assemblage of kelp forest sea stars, color-coded by functional group after Graham *et al.* (2008).

Table 1.3: Example of a csv file exported from the *Kelpforest Database*. This table identifies trophic interactions of the black and yellow (b&y) rockfish (*Sebastes chrysomelas*).

| Node 1 working name | Node 1 Stage | Node 2 working name | Node 1 Stage | type | Citations |
|---|---|---|---|---|---|
| b&y rockfish | general | crabs | general | trophic | (Larson, 1972) |
| b&y rockfish | general | tubesnout | general | trophic | (Quast, 1968) |
| b&y rockfish | general | kelp perch | general | trophic | (Robbins, 2006) |
| b&y rockfish | general | spiral bryozoan | general | trophic | (Perez, 1981) |
| b&y rockfish | general | foliate kelp crab | general | trophic | (Hines, 1982) |
| b&y rockfish | general | moss crab | general | trophic | (Hines, 1982) |
| b&y rockfish | general | sharpnose crab | general | trophic | (Hines, 1982) |
| b&y rockfish | general | cryptic kelp crab | general | trophic | (Hines, 1982) |
| b&y rockfish | general | hairy chiton | general | trophic | (Love et al. 2002) |
| b&y rockfish | general | monkeyface prickleback | general | trophic | (Love *et al.*. 2002) |
| b&y rockfish | general | rock prickleback | general | trophic | (Love *et al.*. 2002) |
| b&y rockfish | general | giant kelpfish | general | trophic | (Love *et al.*. 2002) |
| b&y rockfish | larval | copepods | general | trophic | (Love *et al.*. 2002) |
| b&y rockfish | juvenile | zooplankton | general | trophic | (Love *et al.*. 2002) |
| b&y rockfish | adult | monkeyface prickleback | general | trophic | (Love *et al.*. 2002) |
| b&y rockfish | adult | rock prickleback | general | trophic | (Love *et al.*. 2002) |
| b&y rockfish | adult | northern clingfish | general | trophic | (Love *et al.*. 2002) |
| b&y rockfish | adult | rockweed gunnel | general | trophic | (Love *et al.*. 2002) |
| b&y rockfish | adult | fluffy sculpin | general | trophic | (Love *et al.*. 2002) |
| b&y rockfish | adult | smoothhead sculpin | general | trophic | (Love *et al.*. 2002) |
| b&y rockfish | adult | striped kelpfish | general | trophic | (Love *et al.*. 2002) |
| b&y rockfish | adult | octopus | general | trophic | (Love *et al.*. 2002) |
| b&y rockfish | adult | amphipods | general | trophic | (Love *et al.*. 2002) |
| b&y rockfish | adult | polycheate worm | general | trophic | (Love *et al.*. 2002) |
| b&y rockfish | general | china rockfish | juvenile | trophic | (Love *et al.*. 2002) |
| b&y rockfish | general | squid | general | trophic | (Love *et al.*. 2002) |
| b&y rockfish | general | octopus | general | trophic | (Hallacher & Roberts, 1985) |
| b&y rockfish | general | blue rockfishes | juvenile | trophic | (Hallacher & Roberts, 1985) |

## 1.3 Discussion

Our overarching goal in developing the *Kelpforest Database* is to provide a means for expediting the process by which information is accumulated, organized and made accessible to those making and using ecological network models specific to temperate kelp forests. Its development has been greatly facilitated by collaborations involving federal agency scientists and academics from Canada, the U.S. and Mexico. As such, I believe that with similar collaborations, its framework is applicable to any ecosystem. Our description of the structure and elements of the database is meant to inform the reader of the system's capabilities, to both motivate interest in contributing to and using the information it contains, and to suggest features to consider in the development of other databases.

In our experience to date, the online presence of the *Kelpforest Database* has been one of its most important features, allowing the research community to populate and access the database simultaneously and internationally. This has greatly enhanced the rate at which the database has been populated with entries and has facilitated communication among the kelp forest research community. To date, 81 registered users across seven institutions, the majority of whom are undergraduate and graduate students, have contributed to populating the database. Thus, this database has been used as an education and training tool for human resources from different backgrounds. Through their combined effort, the database currently contains 795 nodes and 3616 interactions based on 515 citations. That said, a critical component of the database's online nature is also the online support provided to users through the online forum, webpage, manual, and data field features described above.

A second key feature adding value to the database has been its ability to accommodate a variety of data sources, including information from the literature and existing databases, as well as user-generated values (including our own field data collection to actively fill data gaps identified by the database) and values calculated by synthesis of data in the peer-reviewed and grey literature. This has both enabled users to populate the database with their own information demands, and has made the same information immediately available to other users. Thus, the database is a clearinghouse of information on species life histories, demography and species interactions that are useful not only in the development of kelp forest ecological network models, but also for a variety of other ecological applications. The database has thereby served to inform the design of observational and experimental studies at our institutions, it has been used to train students in the use and application of this tool, and promoted collaboration between research institutions.

Of course, few if any databases will ever collect all the relevant knowledge that has and is being obtained about kelp forest ecosystems. Databases need to be sufficiently flexible to not only accommodate new information as it is generated, but also to accommodate new kinds of information. For examples, as genetic information becomes increasingly available, the database could be modified to integrate this new information and enable users to explore the genetic basis of varying demographic relationships and species interactions and how variation in those variables contribute to patterns of genetic variability and structure and ecological-evolutionary feedbacks. To facilitate the expansion and evolution of this database and its adoption for other ecosystem databases, access to the code and technical details on how to customize this database and apply it to other ecosystems is freely available and located at the following link (https://github.com/kelpforest-cameo/databaseui).

I see the development of the *Kelpforest Database* as an important step forward toward a simpler, more organized, and more reliable integration of the collective biological knowledge of species life histories, demographics, and interactions. My goal is to facilitate the development and use of ecological network models to inform ecosystem-based approaches to management, to foster the sustainable management and conservation of this valuable marine ecosystem by providing a form for accessible, quality information on kelp forests species.

## 1.4 Acknowledgements

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Estes, John Field, Scott Hamilton, Mike Kenner, Kevin Lafferty, Phil Levin, and Dan Reed. I are also grateful to all the students who helped to populate the database. Particularly, Jaszmin Gasca, Steven Cunningham, and Philip Ericson at UCSC and Stephen Gosnell, who oversaw data input at UCSB. I am grateful for data provided us by the Partnership for Interdisciplinary Studies of Coastal Oceans (PISCO), Reef Check California, and the Monterey Bay National Marine Sanctuary's Integrated Monitoring Network (SIMoN). Any use of trade, product or firm names in this publication is for descriptive purposes only and does not imply endorsement by the U.S. government.

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# Chapter 2

# Predicting the ecosystem-wide effects of fishing in kelp forests of central California

## Abstract

Kelp forests along the coast of California are highly productive ecosystems that generate a number of ecosystem services, including recreational and commercial fisheries. However, the ecosystem-wide consequences of fishing on the structure and functions of these systems are not well understood. Using Ecopath and Ecosim I developed ecological network models for kelp forests of central California to refine our understanding of the major direct and indirect species interactions in this system and to inform ecosystem-based management approaches. Specifically, I explore (i) the extent to which changes caused by fishing in the direction (positive, negative) and magnitude (strong, weak) of species interactions extend across the ecological network, (ii) how changes in biomass of species and functional groups vary with four levels of fishing mortality, (iii) how any changes in species interactions and biomass vary with fishing of six species of different trophic attributes (*e.g.*, trophic level and prey composition), and (iv) how these effects change when all six species are fished simultaneously. To address these questions, I assembled a network of 24 nodes (*i.e.* species or species groups with similar functional roles within the ecosystem) that included 14 commercially and recreationally fished species. My results suggest that the extent to which interactions among species and groups are altered across the ecosystem differed markedly among these six-fished groups and with different levels of fishing mortality. For example, I found the largest and the most extended changes of species interactions and biomass distribution across nodes in the network when fishing a major piscivore, the lingcod (*Ophiodon elongatus*)

and a major planktivore, the blue rockfish (*Sebastes mystinus*). In contrast, when fishing cabezon, kelp greenling, black rockfish and gopher rockfish, I found marginal changes, limited to only nodes directly interacting with these fished species. In all cases, I found a monotonic trajectory biomass response towards a new equilibria point. Fishing all six species simultaneously suggested a different pattern when compared to fishing one species at the time. I found a broad and large mixed change in species interactions and biomass distribution across the network. In addition, when fishing all species simultaneously, some species trajectories were not monotonic such as cabezon, gopher rockfish and octopus. These results suggest that interactions between fished species drastically change in direction and magnitude depending which species is being fished. Results like these are key to predicting how ecosystem-wide effects of fishing vary among the species targeted for fishing, and how they affect one another, in complex ecosystems like kelp forests. Before using these results to inform policy or management, the assumptions of the models have to be recognized.

## 2.1 Introduction

One of the most fundamental advances in both the policy and science of resource management and conservation in the past few decades is the formal recognition of how the many services that societies derive from natural ecosystems depend upon the integrity and resilience of ecosystems in the face of natural and anthropogenic perturbations (Ostrom 2009). Ecosystem-based approaches to managing how humans interact with ocean ecosystems (Leslie and McLeod 2007) shed light on how human activities influence not only particular elements of an ecosystem, such as a species targeted by a fishery, but the integrity (*i.e.* structure and functions) and resilience of whole ecosystems (*e.g.*, Worm *et al.* 2006, Leslie and McLeod 2007, Myers *et al.* 2007, Levin and Lubchenco 2008, McLeod and Leslie 2009). Such ecosystem-based approaches require knowledge of how human uses of ecosystem services influence the structural (*e.g.*, biodiversity, species composition) and functional (*e.g.*, species interactions, productivity) attributes of ecosystems and how these attributes underpin the resistance and resilience of ecosystems to perturbations. One approach to better understand the structural and functional attributes of ecosystems and how human activities impact these traits is to construct and manipulate quantitative ecological network models to simulate and predict how ecosystems respond to human activities (Christensen and Walters 2004, Fulton *et al.* 2011). For example, modeling networks of species interactions that describe how fishing influences the structure and functional relationships of fished ecosystems has proven particularly insightful for fisheries management (Pauly, *et al.* 2000, Field *et al.* 2006, Smith *et al.* 2007, Kaplan *et al.* 2012). The development of such models requires knowledge of what species constitute an ecosystem, how those species interact with one another, and the mathematical constructs of these species interactions.

Knowledge of the structure and function of ecosystems can be generated by experiments or monitoring programs. Experiments can identify mechanisms that underline patterns and processes in natural systems. However, experiments are often limited by scale or by the number of species that can be manipulated and therefore typically do not generate comprehensive characterizations of a system and the interactions within. Monitoring programs can provide essential spatial and temporal relationships among species at large scales, but the inferred causal interactions among species responsible for these patterns are correlative and equivocal. Ecological network models in turn, have the capacity to integrate the causal mechanisms generated by experiments and the spatial and temporal patterns generated by monitoring programs to address ecosystem-scale hypotheses and processes in a cost-effective manner (Horne *et al.* 2010).

Fishing is one of the most important threats to the stability and resilience of coastal marine ecosystems (*e.g.*, Jackson *et al.* 2001). Fishing directly affects the abundance of targeted species and in turn, modifies direct and indirect effects of species interactions (Cheung *et al.* 2011, Rice 2011, Frank *et al.* 2011). The removal of fished species can ultimately produce a trophic cascade and even lead to local extinctions (Sala *et al.* 1998, Pinnegar *et al.* 2000, Ling *et al.* 2009). However, understanding how fishing affects complex coastal ecosystems such as tropical coral reefs or temperate kelp forests remains very challenging. For example, several species of fishes, invertebrates and algae harvested from temperate kelp forests could potentially alter top-down and bottom-up processes, influencing the structure and functions of these ecosystems (reviewed in: Carr and Reed *in press*, Graham *et al.* 2008, Springer *et al.* 2010). However, empirical evidence of the general importance of these interactions remains unclear (Foster and Schiel 2010, Guenther *et al.* 2012). Thus, one approach to advancing our understanding of how kelp forest ecosystems will respond to the cumulative effects of fishing is the application of ecological network models parameterized by information from experiments and long term monitoring studies.

Kelp forests are among the most species rich and productive ecosystems in the world. They provide a variety of ecosystem services, including culturally and economically important recreational and commercial uses (*e.g.*, wildlife observation, kelp harvesting, fishing) and regulating services (*e.g.*, wave attenuation and coastal protection, carbon sequestration). Their high productivity, species diversity and close proximity to shore make kelp forests a coveted resource for commercial and recreational fishing. Fishing in kelp forest ecosystems off southern and central California includes at least 30 species of finfishes and eight species of invertebrates (Table 2.1). Because fishing effort for these species varies geographically, the proportion of a species removed from highly accessible forests can be substantial. However, the indirect consequences of reducing local densities and diminishing the functional role of these species in a kelp forest are poorly understood.

To manage these fisheries sustainably and to ensure that interaction strengths and functional roles of fished species are realized in kelp forests, we need a better understanding of the ecosystem-wide consequences of fishing. Because fished species prey on, are preyed on, and compete with other species, including other species that are fished, fishing reductions in the population size of a species can cause substantial indirect effects on the relative abundance of species and functional processes throughout the ecosystem (Behrens and Lafferty 2004). Specifically, fishing of one species may affect the abundance of other fished species (*e.g.*, Ling *et al.* 2009).

One of the most commonly used ecological network models for predicting ef-

Table 2.1: Commercially and recreationally fished species associated with kelp forests in California. Southern includes Mexican border to Point Conception and central includes Point Conception to San Francisco Bay. Species fished commercially are presented for the live-fish and non-live fish fisheries separately.

| **Commercial** | | | |
|---|---|---|---|
| **Live-fish fishery** | | **Southern** | **Central** |
| blue rockfish | *Sebastes mystinus* | X | X |
| olive rockfish | *S. serranoides* | X | X |
| black rockfish | *S. melanops* | X | X |
| kelp rockfish | *S. atrovirens* | X | X |
| gopher rockfish | *S. carnatus* | X | X |
| black & yellow rockfish | *S. chrysomelas* | X | X |
| china rockfish | *S. nebulosus* | | X |
| copper rockfish | *S. caurinus* | | X |
| grass rockfish | *S. rastrelliger* | X | X |
| California sheephead | *Semicossyphus pulcher* | X | |
| cabezon | *Scorpaenichthys marmoratus* | X | X |
| kelp greenling | *Hexagrammos decagrammus* | X | X |
| monkey-faced eel | *Cebidichthys violaceus* | | X |
| California scorpionfish | *Scorpaena guttata* | X | |
| **Non-live-fish fishery** | | | |
| vermillion rockfish | *S. miniatus* | | X |
| lingcod | *Ophiodon elongatus* | | X |
| California spiny lobster | *Panularis interruptus* | X | |
| red sea urchins | *Strongylocentrotus franciscanus* | X | |
| red abalone* | *Haliotus rufescens* | | |
| turban snails | *Lithopoma undosum* | X | |
| kellets whelk | *Kelletia kelletii* | X | |
| sea cucumbers | *Parastichopus californicus* | X | |
| California yellowtail | *Seriola lalandi* | X | |
| mackerel | *Scomber japonicus* | X | X |
| * Historic commercial fishery with potential for future fishery | | | |
| **Recreational fishery (also includes all of the commercial species listed above)** | | | |
| kelp bass | *Paralabrax clathratus* | X | |
| opaleye | *Girella nigricans* | X | |
| halfmoon | *Medialuna californiensis* | X | |
| striped surfperch | *Embiotoca lateralis* | X | X |
| silver surfperch | *Hyperprosopon ellipticum* | | X |
| pile surfperch | *Rhacochilus vacca* | | X |
| rubbererlip surfperch | *Rhacochilus toxotes* | | X |
| black surfperch | *Embiotoca jacksoni* | | X |
| white seabass | *Atractoscion nobilis* | X | X |
| California halibut | *Paralichthys californicus* | | X |
| California barracuda | *Sphyraena argentea* | X | |
| ocean whitefish | *Caulolatilus princeps* | X | |
| rock scallop | *Hinnites multirugrosus* | X | |
| rock crab | *Cancer antennarius* | | X |

fects of fishing on the structure of trophic networks is the Ecopath mass balance model and the dynamic Ecosim module for Ecopath (Christensen and Walters 2004). Together, Ecopath with Ecosim can generate quantitative predictions that are based mainly on the diet composition, food consumption rates, biomass and mortality estimates. Ecopath can describe the biomass flow within and among trophic levels and how these pathways are affected by the removal of biomass by fishing (Pauly *et al.* 2000, Plaganyi and Butterworth 2004, Christensen and Walters 2004, Essington 2007). Ecopath with Ecosim is often used to address ecological questions (*e.g.*, Field and Francis 2006) and explore management and policy options (*e.g.*, Smith *et al.* 2007), including consequences of the placement of marine protected areas (MPAs) to fishing and conservation (*e.g.*, Walters *et al.* 2009).

In this study, I develop and apply Ecopath with Ecosim models to characterize species interactions in kelp forest ecosystems of central California and to manipulate fishing mortality to address the following questions. First, to what extent does fishing alter species interactions and resulting relative species biomasses beyond those species that directly interact with a fished species? Secondly, how do these results differ as fishing results in different biomass levels of a fished species? Third, how do these results vary among species of differing trophic roles (*e.g.*, piscivores, planktivores, benthic carnivores)? And finally, what is the effect of fishing multiple species simultaneously relative to the effects of each species separately? To address these questions I assembled a network of 24 functional groups (*i.e.* species with similar functional roles within the forest ecosystem) that included ten commercially and recreationally fished species (lingcod, cabezon, kelp greenling, blue, black, olive, kelp, gopher, black and yellow rockfishes), juvenile rockfishes, eight groups of invertebrates, the southern sea otter and three groups of primary producers, including the giant kelp *Macrocystis pyrifera*.

## 2.2 Methods

### 2.2.1 *Study system*

My models were designed to examine and inform finfish fisheries in forests of giant kelp, *Macrocystis pyrifera*, along the coast of central California (Figure 2.1). Giant kelp forests in central California are associated with shallow (<30m depth) rocky reefs from Point Conception (lat 34.448°, long −120.465°) in the south to Sand Hill Bluff (lat 36.976°, long −122.152°), north of Santa Cruz, in the north (Carr and Reed *in press*, Graham *et al.* 2008, Foster and Schiel 2010). Although the size and density of kelp forests in central California vary interannually (Reed *et al.* 2010), these ecosystems support persistent fish assemblages. I focused my research on this region because kelp forests are abundant, important to nearshore commercial and recreational fisheries, and the ecological data necessary to parameterize ecological network models are available. Conceptually, the spatial scale of inference of these models is one square kilometer of a continuously distributed forest (*i.e.* no explicit spatial gradients or patchiness). I assume that the modeled one square kilometer represents a typical giant kelp forest along the coast of central California.

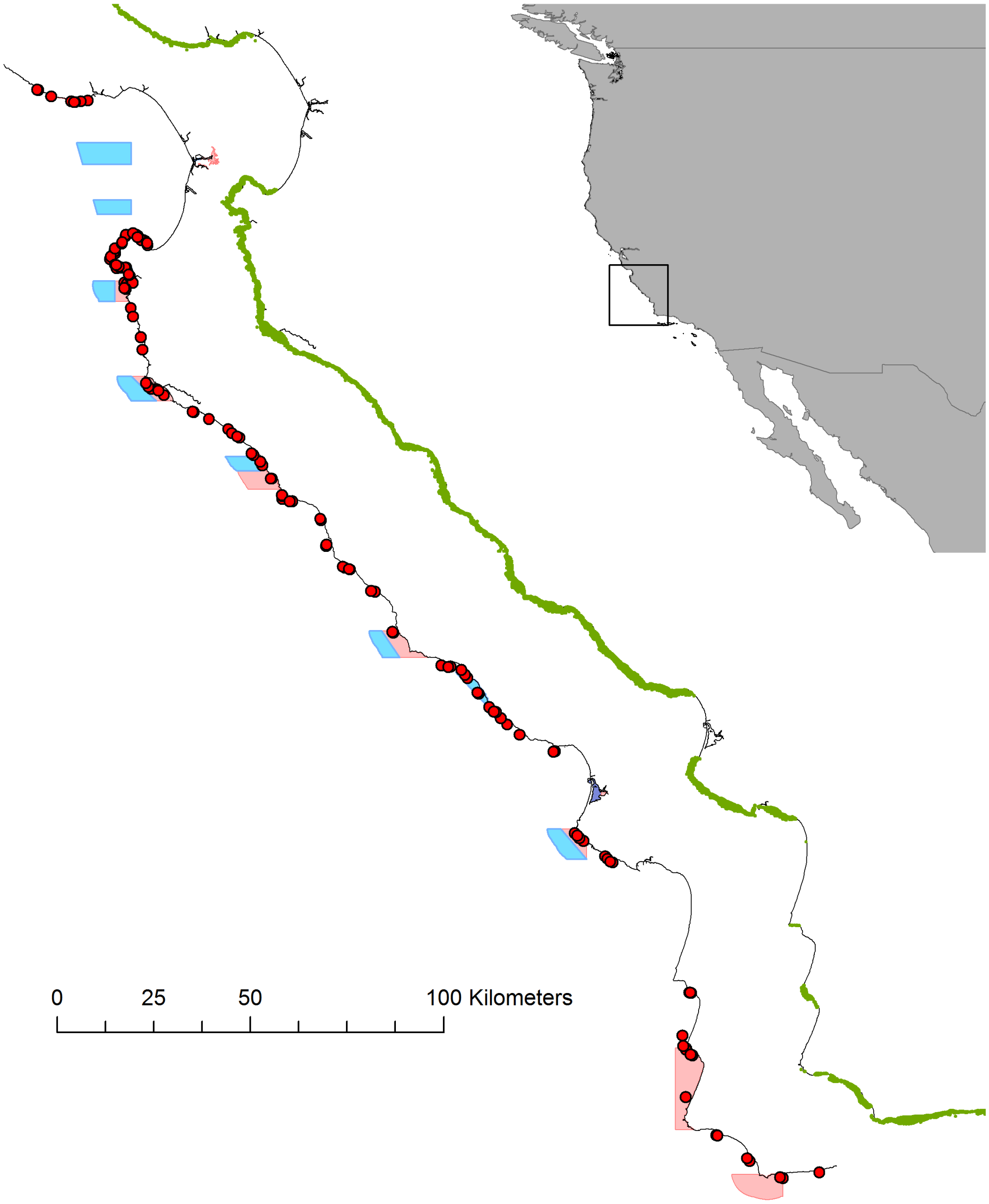

Figure 2.1: Map of central coast of California from Pigeon Point (lat 37.181888°, long −122.394°) in the north to Point Conception (lat 34.448°, long −120.465°) in the south. Kelp forests are identified by the green band along the coast. Red circles identify kelp forest sites surveyed by PISCO divers. Pink areas are State Marine Reserves and blue areas are State Marine Conservation Areas.

### 2.2.2 *Functional groups*

The models have 24 “nodes” representing individual species or aggregates of functionally similar species (*i.e.* functional groups or feeding guilds; Table 2.2). Each group is described in detail in Appendix A. These 24 species or groups were selected because of their known ecological and economic importance in kelp forests of central California. There are three functional groups of primary producers (phytoplankton, giant kelp, and understory algae), eight species or groups of invertebrates, ten species of fishes, the southern sea otter and two detrital (algae and animal) groups. Except for the juvenile rockfishes, both commercial and recreational fisheries target all of the fish groups in these models.

Table 2.2: Parameter estimates for each of the 24 nodes in the central California kelp forest ecological network model. Regular font indicates values that were input (see Methods and Appendix I). Bold values were generated by the model. See Methods for explanations of parameters. See Appendix I for description of species that constitute each of the 24 nodes.

| Group name | Trophic level ($t/km^2$) | Biomass ($t/km^2$ /year) | Production/ biomass/ year | Consumption/ biomass/ year | Ecotrophic efficiency | Production/ Consumption |
|---|---|---|---|---|---|---|
| southern sea otter | **3.01** | 0.13 | 0.15 | 101.50 | **0.00** | **0.001** |
| lingcod | **4.29** | 0.63 | 0.28 | 2.40 | **0.34** | **0.12** |
| cabezon | **3.69** | 0.12 | 0.40 | 2.00 | **0.82** | **0.20** |
| kelp greenling | **3.12** | 0.66 | 0.37 | 2.00 | **0.89** | **0.20** |
| blue rockfish | **3.33** | **14.7** | 0.21 | 1.50 | 0.60 | **0.14** |
| black rockfish | **3.38** | **3.52** | 0.30 | 1.50 | 0.40 | **0.20** |
| olive rockfish | **3.89** | **3.31** | 0.13 | 1.30 | 0.90 | **0.10** |
| kelp rockfish | **3.38** | 6.78 | 0.21 | 1.50 | **0.27** | **0.14** |
| gopher rockfish | **3.44** | 3.39 | 0.22 | 1.43 | **0.95** | **0.15** |
| black & yellow rockfish | **3.44** | 3.00 | 0.22 | 1.60 | **0.98** | **0.13** |
| juvenile rockfishes | **3.12** | **8.84** | 1.50 | 6.00 | **0.90** | **0.25** |
| octopus | **3.00** | **3.21** | 0.86 | 6.00 | 0.90 | **0.14** |
| predatory seastars | **2.90** | 0.80 | 0.52 | 2.60 | **0.00** | **0.20** |
| crabs | **2.00** | 36.00 | 1.31 | 5.00 | **0.48** | **0.26** |
| abalones | **2.00** | 2.00 | 2.00 | 10.00 | **0.78** | **0.20** |
| sea urchins | **2.00** | **8.06** | 0.50 | 10.88 | 0.80 | **0.05** |
| herbivorous mollusks | **2.00** | 20.00 | 1.00 | 8.86 | **0.53** | **0.11** |
| crustaceans | **2.00** | **9.86** | 3.41 | 25.00 | **0.90** | **0.14** |
| zooplankton | **2.18** | **14.13** | 16.50 | 62.50 | 0.80 | **0.26** |
| phytoplankton | **1.00** | 16.00 | 179.00 |  | **0.19** |  |
| giant kelp | **1.00** | 120.80 | 42.90 |  | **0.04** |  |
| understory algae | **1.00** | 27.00 | 15.00 |  | **0.43** |  |
| kelp detritus | **1.00** | 10.00 |  |  | **0.65** |  |
| animal detritus | **1.00** | 10 |  |  | **0.24** |  |

### 2.2.3 *Fished species*

I examined the effects of fishing six finfishes associated with kelp forests in central California: lingcod (*Ophiodon elongatus*), cabezon (*Scorpaenichthys marmoratus*), blue rockfish (*Sebastes mystinus*), black rockfish (*Sebastes melanops*), kelp greenlings (*Hexagrammos decagrammus*) and gopher rockfish (*Sebastes carnatus*). I use the models to explore the system-wide effects of fishing these species for four reasons. The six species differ markedly in their trophic interactions with the other nodes in the network (Table 2.3, Appendix A). All six species have had stock assessments that provide estimates critical for parameterizing the models. All six species are abundant components of the kelp forest fish assemblage and therefore targeted by both commercial and recreational fisheries.

Table 2.3: Diet matrix for the central California kelp forest ecological network. Predators are listed in column headings, prey are listed in rows. Diets were generated by the *Kelpforest Database* (Beas-Luna *et al. Submitted* ).

| **Predator** / **Prey** | sea otter | lingcod | cabezon | kelp greenling | blue rockfish | black rockfish | b & y rockfish | olive rockfish | kelp rockfish | gopher rockfish | juv. rockfishes | octopus | seastars | crabs | abalones | sea urchins | mollusks | crustaceans | zooplankton |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| southern sea otter | | | | | | | | | | | | | | | | | | | |
| lingcod | | | | | | | | | | | | | | | | | | | |
| cabezon | | 0.02 | | | | | | | | | | | | | | | | | |
| kelp greenling | | 0.05 | 0.02 | | | 0.01 | | | | | | | | | | | | | |
| blue rockfish | | 0.02 | | | | | 0.10 | | | | | | | | | | | | |
| black rockfish | | 0.05 | 0.07 | | | | | 0.02 | | | | | | | | | | | |
| olive rockfish | | 0.08 | 0.05 | | | 0.01 | 0.10 | 0.02 | | | | | | | | | | | |
| kelp rockfish | | 0.08 | 0.05 | | | 0.01 | | 0.02 | | | | | | | | | | | |
| gopher rockfish | | 0.10 | 0.05 | | | 0.01 | 0.05 | 0.02 | | | | | | | | | | | |
| black & yellow rockfish | | 0.10 | 0.05 | | | 0.01 | 0.05 | 0.02 | | | | | | | | | | | |
| juvenile rockfishes | | 0.49 | 0.14 | | 0.20 | 0.21 | 0.30 | 0.10 | 0.30 | 0.30 | | | | | | | | | |
| octopus | 0.01 | 0.02 | 0.14 | 0.10 | | 0.01 | 0.05 | 0.10 | 0.10 | 0.10 | | | | | | | | | |
| predatory seastars | | | | | | | | | | | | | | | | | | | |
| crabs | 0.64 | | 0.18 | 0.20 | | 0.10 | | 0.20 | 0.40 | 0.40 | | 0.40 | 0.10 | | | | | | |
| abalones | 0.09 | | 0.18 | | | | | | | | | 0.10 | | | | | | | |
| sea urchins | 0.20 | | | | | | | | | | | | 0.30 | | | | | | |
| herbivorous mollusks | 0.07 | | | 0.10 | | | | 0.10 | | | | 0.40 | 0.40 | | | | | | |
| crustaceans | | | 0.09 | 0.50 | 0.20 | 0.31 | 0.15 | 0.30 | 0.20 | 0.20 | 0.30 | 0.10 | 0.10 | | | | | | |
| zooplankton | | | | 0.10 | 0.60 | 0.31 | 0.20 | 0.10 | | | 0.70 | | | | | | | | 0.15 |
| phytoplankton | | | | | | | | | | | | | | | | 0.01 | | 0.05 | 0.60 |
| giant kelp | | | | | | | | | | | | | | 0.25 | 0.15 | 0.30 | 0.33 | 0.25 | |
| understory algae | | | | | | | | | | | | | | 0.25 | 0.15 | 0.19 | 0.33 | 0.20 | |
| kelp detritus | | | | | | | | | | | | | | 0.40 | 0.70 | 0.50 | 0.34 | 0.50 | 0.20 |
| animal detritus | | | | | | | | | | | | | 0.10 | 0.10 | | | | | 0.05 |

### 2.2.4 *Ecopath model*

Ecopath is a “steady state” model; the nodes and their parameters and connections among nodes, referred to as “edges”, do not change over time. The model integrates information from fisheries statistics, field surveys, stock assessments, food habits and bioenergetics into a mass balance model of an ecosystem trophic structure. The model predicts changes in the strength of impacts between species or functional groups based on the flow of biomass of species or functional groups. Ecopath is considered a “mass balance” model by assuming that the total biomass produced in the system does not change in time. Thus, as the biomass of one species or functional group changes, biomasses of other species compensate to maintain the net biomass production of the system. This compensation reveals the changes in biomass flow and species interactions. This model was developed by Polovina (1984) and made into a software suite application at the University of British Columbia (Christensen and Pauly 1992), available at http://www.ecopath.org/. It includes a series of modules where Ecopath produces a static snapshot of the net biomass production of the system.

Ecopath is based on one fundamental equation. This equation balances for each node “i” (species or functional group) in an ecosystem, where each node can be an ontogenetic stage (juvenile, adult) of a species, a species itself or a group of species that share similar functional relationships with other species in the system:

$$B_i \cdot (P/B)_i \cdot EE_i = \sum (Q/B)_j \cdot DC_{ij} \cdot B_j + C_i + BA_i + NM_i \tag{2.1}$$

where $B_i$ and $B_j$ are the biomasses of species or group $i$ and the consumers $j$ of $i$, respectively; $(P/B)_i$ is the production ($P$) biomass ($B$) ratio for $i$; $EE_i$, also known as ecotrophic efficiency, is the fraction of production of $i$ that is consumed by other species or groups in the system (the balance being assumed to contribute to detritus); $C_i$ is the fishing mortality (landings + discards) on $i$; $(Q/B)_j$ is the total food consumption per unit biomass of $j$; $DC_{ij}$ is the fractional contribution by mass of $i$ to the diet of $j$; $BA_i$ is a biomass accumulation term that describes a change in biomass over the Ecopath base reference unit time step (it is usually one year), and $NM_i$ is the net biomass migration (immigration-emigration) for $i$.

### 2.2.5 *Parameter estimates*

Parameterization of the models was supported by the availability of information from five sources. First and foremost was an online database (*Kelpforest Database*; www.kelpforest.ucsc.edu), which was created for this purpose. This database is comprised of species life history traits, demographic parameters and species interactions for kelp forest ecosystems along the west coast of North America (Beas-Luna *et al. submitted*). Species composition and density estimates were derived from three monitoring programs; (i) a large scale kelp forest monitoring program in central and southern California conducted by the Partnership for Interdisciplinary Studies of Coastal Oceans (PISCO: http://www.piscoweb.org/research/science-by-discipline/ecosystem-monitoring/kelp-forest-monitoring); (ii) a long-term kelp forest monitoring program conducted in the Santa Barbara Channel (Santa Barbara Long Term Ecological Research (SBC LTER: http://sbc.lternet.edu/); (iii) sea otter biomass and density time series were gleaned from the United States Geological Surveys Western Ecological Research Center (USGS-WERC: http://www.werc.usgs.gov/project.aspx?projectid=91). In addition, I used stock assessments and catch data for lingcod, cabezon, blue rockfish, black rockfish and gopher rockfish. These data was provided by the NOAA National Marine Fisheries Service (see Appendix A).

***B* (biomass density)** in metric tons per km$^2$ was estimated from field surveys in central California kelp forests and from the literature. Field surveys were conducted by PISCO at 30 sites sampled for various durations from 1999 to 2011. These surveys estimate both the density (number of individuals per area) and size of organisms. For each node, I used length-biomass relationships from the *Kelpforest Database* to estimate the biomass of each individual on a transect and summed individual biomasses for a total biomass per 60m$^2$ transect (reef surface). For fish, these biomasses were summed across the midwater and benthic transects. I then calculated the mean total biomass across all transects at a site (*i.e.* mean biomass per 60m$^2$ per site) and used these to calculate mean biomass density (grams per 60m$^2$) across sampling sites and years (n = 565). These mean biomass densities are presented in tons per km$^2$. Note that biomass densities of midwater fishes (*e.g.*, blue, black, olive and kelp rockfish) are probably underestimated because the two transects sample only a portion of the water column. Otherwise, biomass was gleaned from the literature using the online *Kelpforest Database*.

***P/B* (production/biomass ratio)** is measured as grams of biomass produced per gram of individual biomass per year. These are much more difficult to estimate from direct methods from empirical data. Thus, in many cases, the $P/B$ ratios where assumed to be similar to the total mortality ($Z$) (Pauly *et al.* 2000).

***Q/B* (consumption/biomass) ratios** are measured as grams of prey biomass eaten per gram of biomass per year. These values are gleaned from the *Kelpforest Database.* More specifically, I collected information from studies of consumption rates or evacuation rates when there was data on percent of body weight eaten per day.

***EE* (ecotrophic efficiency)** is the fraction of the production that is used in the system, either passed up the food web, used for biomass accumulation, migration or export. This value is dimensionless and ranges from 0 to 1. The value approaches 1 for species that experience high rates of predation.

***TL* (trophic level)** for a consumer is 1+ the weighted average trophic level of its prey. *TL* is 1 for primary producers and detritus.

***DC* (contribution of a species to the diet of its predator)** is estimated from dietary information from the literature. The diet compositions among the 14 species or groups in our model were obtained from the *species interactions* section of the online *Kelpforest Database.*

***NM* (net migration)** is the difference of immigration and emigration for each species or group and assumed to be zero in all models.

### 2.2.6 *Ecosim model*

The Ecosim module uses the "static" characterizations of biomass dynamics (*e.g.*, consumption and production ratios) and species interactions generated by Ecopath and subject them to a dynamic time-dependent equation to predict the equilibrial reallocation of biomass across the network (Walters *et al.* 1997). Ecosim uses coupled differential equations derived from the basic Ecopath equation 3.1 such that, for prey $i$ and predator $j$:

$$\frac{dB_i}{dt} = g_i \sum_j Q_{ij} - \sum_j Q_{ij} + I_i - (M0_i + F_i + e_i)B_i \tag{2.2}$$

where, $dB_i/dt$ is the growth rate (biomass) of the node $i$ during the time interval $dt$, $g_i$ is the growth efficiency, previously defined as the production $P/B$ over consumption $Q/B$, $Q_{ji}$ is the predation by node $i$ on node $j$, $Q_{ij}$ is the predation on node $i$ by node $j$, $I_i$ is the biomass migration rate, $M0_i$ is the non predation mortality, $F_i$ is the fishing mortality rate, $e_i$ is the emigration rate, and $B_i$ is the biomass of the node $i$ at the previous time step. The differential equations are solved in the Ecosim module, using an integration routine built in the software.

***Mixed trophic impacts (MTI)*** - This method is used to evaluate the direct and indirect interactions between nodes (species or groups) in the system using a Leontief matrix. MTI is used to calculate how change in biomass of one node affects the interactions of other nodes in the system:

$$MTI_{i,j} = DC_{i,j} - FC_{j,i} \tag{2.3}$$

where $DC_{i,j}$ is the diet composition term expressing how much group $j$ contributes to the diet of group $i$, and $FC_{j,i}$ is a prey composition term describing the proportion of the predation on$j$ that is due to $i$ as a predator. These values can be either positive or negative, indicating whether the change in biomass of one node causes an increase or decrease in biomass of the later, respectively.

### 2.2.7 *Model applications*

#### 2.2.7.1 *Change in species interactions caused by fishing*

To test the hypothesis that fishing causes changes in the direction and magnitude of interactions among the nodes of the kelp forest network, I compared the mixed trophic impacts (MTI) matrices with and without fishing for each of the six-fished species. I first constructed, parameterized and balanced the 24-node mass-balance model (equation 3.1) with no fishing of any species. I then did the same for each of six models that included fishing mortality for each of the six-targeted species (lingcod, cabezon, blue rockfish, black rockfish, gopher rockfish and olive rockfish). I used time series of exploitation rates generated from stock assessments (Table 2.4, Figures B.1-B.3) to calculate a mean rate of fishing mortality for each species. The changes in direction and magnitude of interactions between pairs of nodes were plotted using level plots (Sarkar 2008) to graphically depict the changes caused by fishing.

#### 2.2.7.2 *Differences among fished species in the extent to which fishing causes change in species interactions across the network*

To test the hypothesis that fished species will differ in the extent to which changes in species interactions caused by fishing extend across the network, I again applied the same mass-balance models and mixed trophic impact (MTI) matrices for each of the fished species to compare changes in the magnitude and direction of species interactions across the network. I qualitatively compared the level plots (Sakar 2008) that graphically depict the changes caused by fishing among the six fished species to contrast the extent to which changes in species interactions were manifest across the network.

Table 2.4: Parameters for the Ecopath fishing scenarios.

| Trophic level | Fished specie | Initial | Exploitation rate | Fishing removals (mt/km$^2$) | Source |
|---|---|---|---|---|---|
| 4.26 | lingcod | 0.63 | 0.09 | 0.06 | Hamel *et al.* 2009 |
| 3.68 | cabezon | 0.12 | 0.12 | 0.01 | Cope and Key 2009 |
| 3.42 | gopher rockfish | 3.09 | 0.02 | 0.06 | Key *et al.* 2005 |
| 3.34 | black rockfish | 3.70 | 0.04 | 0.13 | Sampson 2007 |
| 3.28 | blue rockfish | 38.13 | 0.04 | 1.40 | Key *et al.* 2008 |
| 3.11 | kelp greenling | 0.66 | 0.05 | 0.03 | Cope and MacCall 2005 |

#### 2.2.7.3 ***Patterns of response of species biomass to different levels of fishing mortality***

To test the hypotheses that (i) changing the rate of fishing mortality of each of the six fished species will alter the distribution of biomass across nodes in the kelp forest network, and (ii) that these responses will differ among the six fished species, I used data from the mass-balanced Ecopath model (Table B.5) to develop a biomass dynamic model, Ecosim, to simulate five different fishing mortality scenarios for each of the six fished species. The five scenarios included the mean mortality rate (X) derived from the stock assessments (Table 2.4), 0X, 0.5X, 1.5X, 2X and 3X. All of these models included the mean rate of fishing mortality for the six-fished species except the species for which mortality was manipulated. These levels of fishing mortality span the range of exploitation rates allowed under current management regimes. For each scenario, the fishing rate was applied constantly for 30 years starting in 1999, during which time each node in the network achieved a new equilibria biomass. The output of these simulations produced patterns of change in the distribution of species biomass under different rates of fishing mortality.

To characterize how different nodes responded to changes in the resulting equilibria biomass of fished species, I calculated the biomass change for each node whose biomass increased, decreased or remained the same. In addition, I compared the number of these responses by trophic level to determine how the distribution of responses across the network differed among the six-fished species.

### 2.2.8 *Effects of simultaneously fishing multiple species*

To determine how species interactions across the 24 nodes of the network respond (*i.e.* change in direction and magnitude) to the cumulative impacts of simultaneously fishing all six fished species, I generated a level plot based on differences between the mixed trophic impacts (MTI) matrices without fishing any species and simultaneously fishing all six fished species at their mean rate of fishing mortality. To determine how the distribution of biomass across the 24 nodes of the network respond to the cumulative impacts of simultaneously fishing all six fished species, I ran Ecosim with the five different rates of fishing mortality including the mean mortality rate (X) derived from the stock assessments (0X, 0.5X, 1.5X, 2X and 3X).

## 2.3 Results

### 2.3.1 *Trophic flow and structure*

Informed by estimates of species composition generated from field surveys (Appendix A), life history, demographic parameters (Appendix A and Table 2.2) and trophic interactions (Appendix A and Table 2.3) from the literature and the field, the kelp forest network model generated estimates of interaction impact and biomass production of nodes (species or species groups) such that net production and consumption of biomass across the system balanced one another (Figure 2.2). When balanced, about 64.5% of the living biomass (*i.e.* excluding detritus) was algae (giant kelp and others), 29.4% invertebrates, and 6.14% fishes. Though most of the biomass estimates are derived from empirical survey data, the value for the crustacean group was generated by the mass balance routine (Table 2.2). The model also identified trophic levels for each node in the system based on estimates of the weighted average of prey trophic levels. These trophic levels varied from 1.0 for the primary producers (algae) and detritus to 4.26 for the top predator, lingcod (Table 2.2).

One of the key features to evaluate an ecosystem model is the ecotrophic efficiency (*EE*), which is the proportion of production of a node consumed by predators or exported (Christensen *et al.* 2009). In my model, this value varied among nodes from 0.01 to 0.9 (Table 2.2). A value just above zero indicates that nodes were not consumed by any other node in the system. For example, this model assumes that there are no predators of the sunflower star, lingcod, and sea otter nodes, hence their EE values

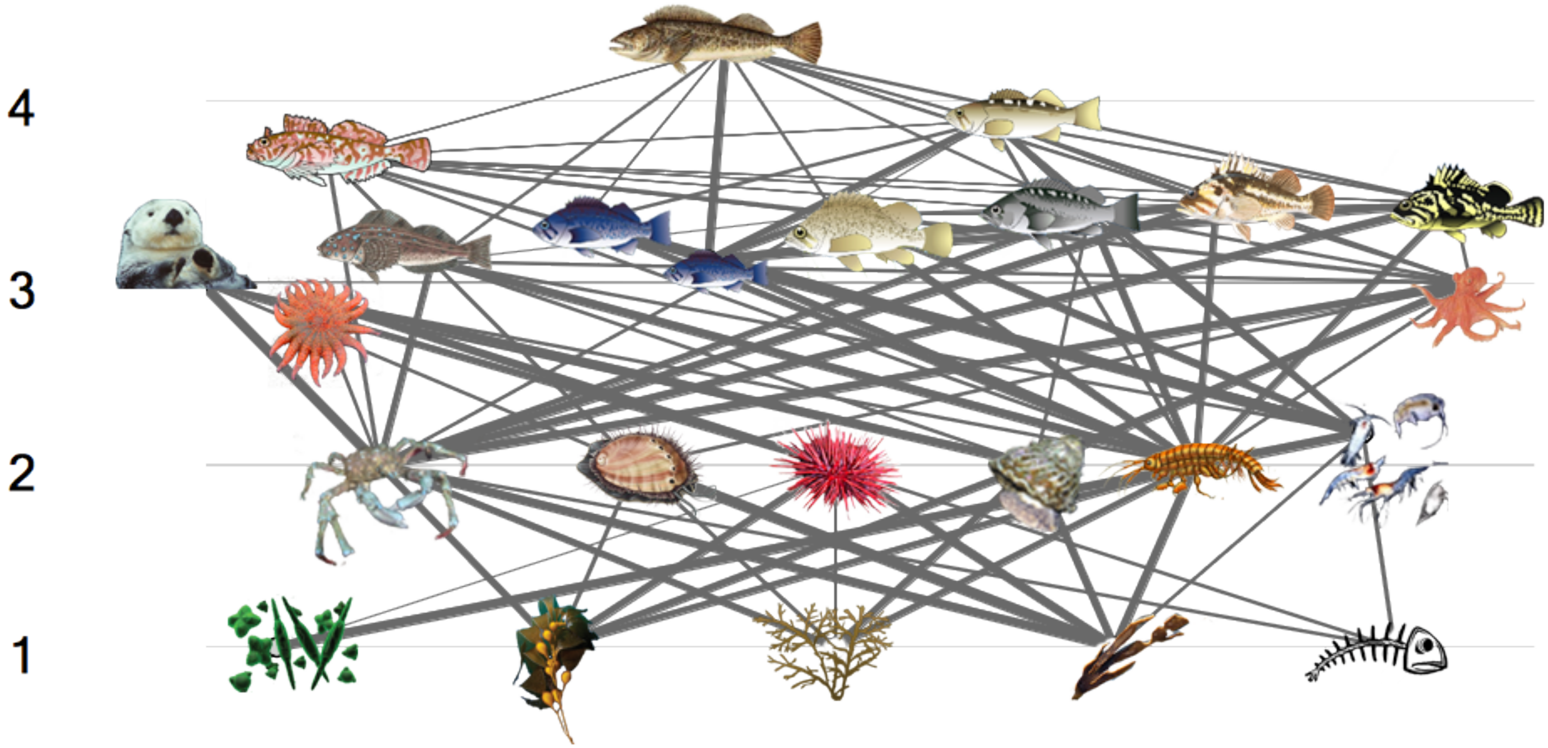

Figure 2.2: Topology of the Ecopath model for central California kelp forests. Numbers indicate trophic levels. Lines between groups represent trophic interactions weighted by the amount of biomass transferred.

of 0.00. The relatively low EE value for adult black rockfish reflects the fact that the biomass produced by this node in the model is consumed only moderately. In contrast, a value close or equal to 1 such as the 0.9 for crustaceans indicates that node is heavily preyed upon. The high EE value for crustaceans, octopus, zooplankton, urchins, and juvenile rockfishes (0.8-0.9) indicate that the biomass of these nodes is heavily consumed in the model. Also, the relatively high EE values for a few key invertebrates such as abalone and sea urchins indicate they are consumed extensively by fishes, sea otters and other predators like the sunflower star. The high EE values for all of the fishes reflect extensive predation on one another. The low EE for giant kelp (0.04), which is responsible for much of the production of kelp detritus, and higher value for kelp detritus (0.28) suggest a great amount of biomass available and that much of the consumption of kelp by higher trophic levels is through the detrital pathway. The EEs for the fished groups increased when subjected to fishing (Table B.4).

In the absence of fishing, the strengths of combined direct and indirect impacts of nodes on one another (Mixed Trophic Impact - MTI values) varied markedly in the system (Figure 2.3, Table B.1). Model estimates of MTI for most of the nodes in the model indicate marginal impacts on one another (MTI <0.1). However, some nodes like the sea otters indicated relatively strong negative effects on sea urchins, abalone, crabs and other sea otters (Figure 2.3, Table B.1). In addition, lingcod also showed a strong negative impact on cabezon and kelp greenling. The model also exposed few positive strong interactions such as the rockfish juvenile node on lingcod. A small subset of nodes, including the gopher and black and yellow rockfishes, and invertebrates, including abalone, and crustaceans, had moderate (<0.3 and >0.2) positive and negative impacts on other nodes in the system, and only the gopher and black and yellow rockfishes exhibited strong (0.4 or greater) positive and negative impacts on other nodes. These two rockfishes interacted strongly with the other fishes in the system, their prey (crabs, octopus), the algae that support their prey, and other invertebrates that interact indirectly with their prey (abalone). The sign (+/-) of many of these interactions reflect the trophic relationship of these species. For example, gopher and black and yellow rockfish, and crustaceans have a positive effect on lingcod, respectively as their prey. Black and yellow rockfish have negative impacts on cabezon as their predator, and on gopher rockfish as competitors. Thus the model suggests that these few species had particularly strong interactions across the system in the absence of fishing.

### 2.3.2 *Change in species interactions caused by fishing*

I successfully balanced separate Ecopath models that explored different rates of fishing mortality for lingcod, cabezon, kelp greenling, blue, black, and gopher rockfishes independently. I found differences in the magnitude and direction of the mixed trophic impacts when fishing the biomass of any one group at its historic mean rate (Figure 2.4a versus Figures 2.4b-g). This set of mass balanced models suggest that changes in magnitude and direction of pairwise interactions respond differently, depending on what species is fished from the system. For example, in the model where I included fishing mortality for lingcod, most interactions remained the same while only a few strong interactions change in magnitude (Figure 2.4a versus Figure 2.4b, and

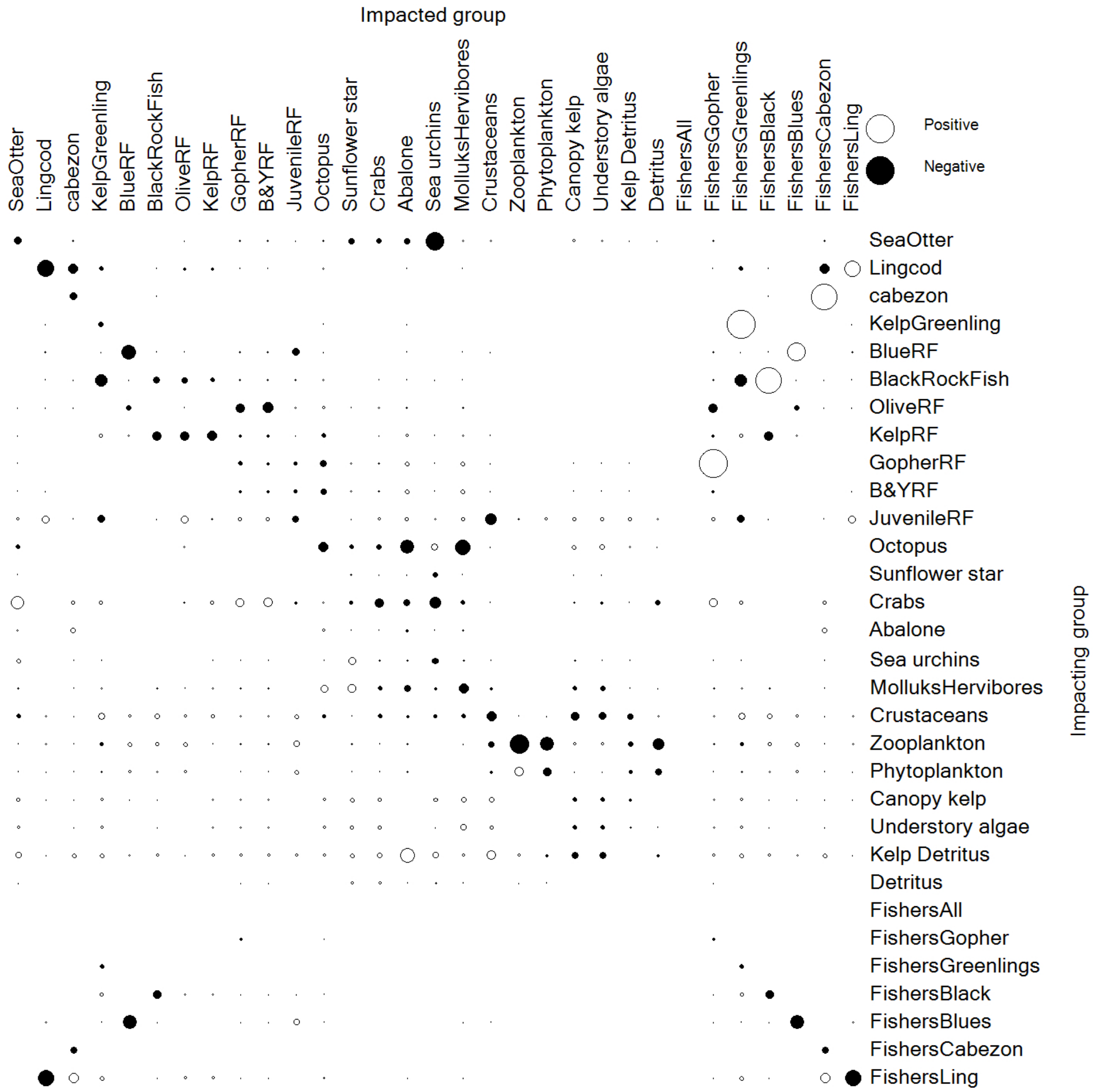

Figure 2.3: Mixed trophic impacts (MTI) plot of the central California kelp forest ecological network. The bubbles represent the the direction and magnitude of the impact. Nodes along the top of the matrix are affected by the nodes on the vertical axis. Open circles are positive interactions and solid circles are negative interactions.

Figure 2.5b). Particularly, the direct strong negative impact of lingcod on cabezon decreased (Figure 2.4a versus Figure 2.4b, Figure 2.5b). This reduction in the strength of the negative impact is manifest as a positive change in the direction of this interaction (Figure 2.4b and Figure 2.5b). Overall, the results of this model indicate that when only lingcod is fished from the system, very few pairwise effects change, and the ones that do, are mostly direct interactions with lingcod. In contrast, when species of intermediate trophic levels are fished (*e.g.*, blue, black, or gopher rockfishes), pairwise interactions change all across the network, altering both direct and indirect interactions (Figures 2.5d,e,g, respectively). Comparison among these models suggests that fishing species of intermediate trophic levels results in a greater number of changes in pairwise interactions (Figure 2.5b versus Figures 2.5d,e,g).

Fishing cabezon had similar results as fishing lingcod, though changes extended to slightly more nodes, but again largely limited to other fishes with which it interacts directly (Figures 2.5b and 2.5c). Interestingly, the model with blue rockfish fishing produced a wide spread reduction of the impact values across the network (Figure 2.5d). Models fishing cabezon, gopher and all fishes together, indicated overall increases in MTI values (Figures 2.5c,g,h). These results largely support the prediction that changes in interactions in response to fishing are largely limited to direct interactions with the fished species.

One of the few pairwise interactions that responded similarly to fishing, regardless of what species was fished, was between kelp and black rockfishes. The model indicated a reduction in the strength of this interaction from very strong to weak neg-

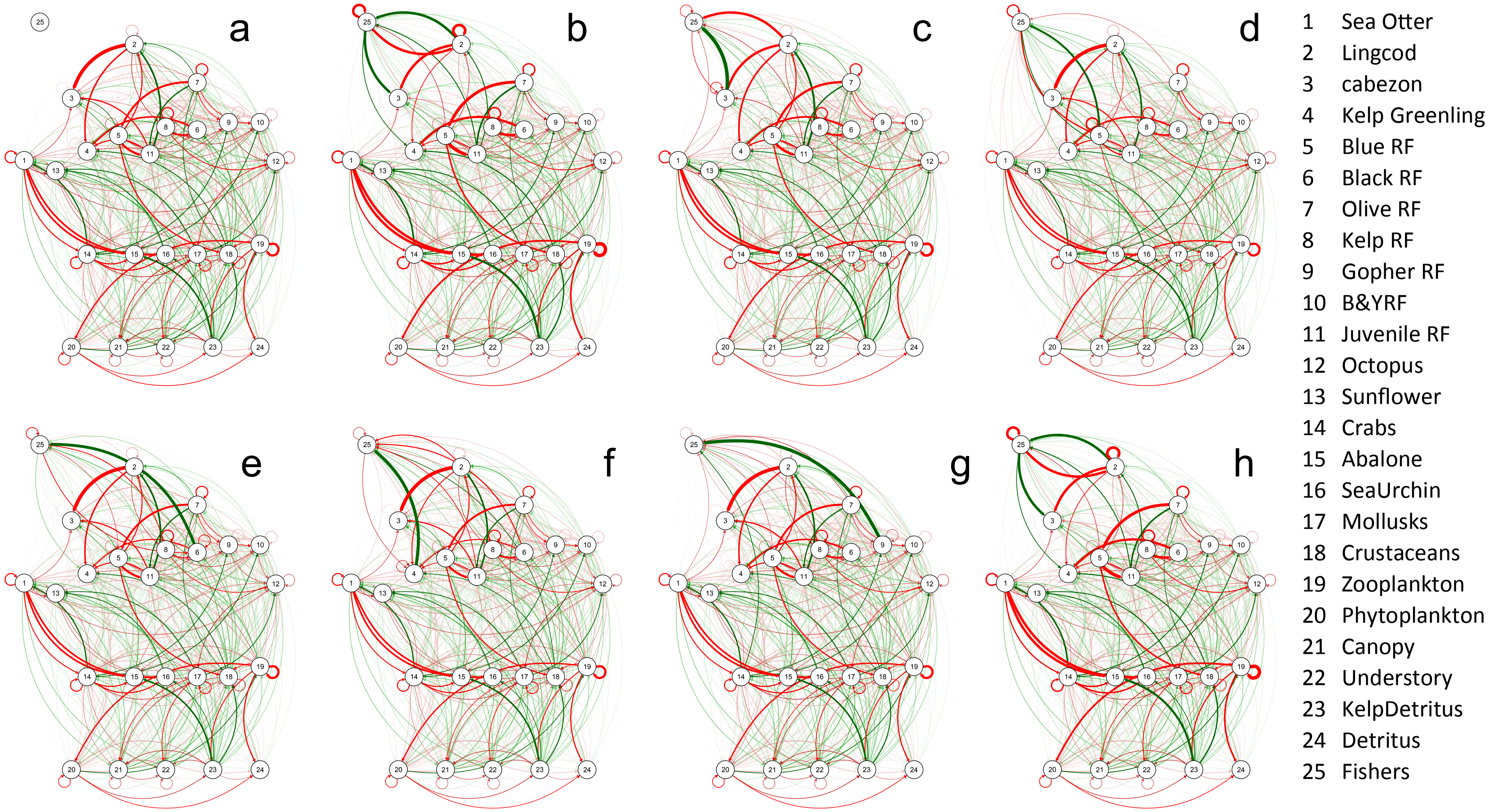

Figure 2.4: Mixed trophic impact (MTI) networks for the different fishing scenarios: No fishing (A), fishing lingcod (B), cabezon (C), blue rockfish (D), black rockfish (E), kelp greenling (F), gopher rockfish (G), and fishing all the species at once (H). Circles represent nodes identified in the legend. Red and green lines indicate negative and positive effects, respectively. Color tone scales with the magnitude of the effects.

ative (Figures 2.5c,d,e,f,g). Interestingly, only very few pairwise interactions changed their direction from positive to negative or vice versa, and the ones that did, experienced very marginal changes (*i.e.* very close to zero). Finally, these results suggest a very small change of total system throughput (*i.e.* sum of total respiration and total flows to detritus) of biomass density (t/km$^2$/year) among the different mass-balanced models (Table B.2).

### 2.3.3 *Biomass change caused by different rates of fishing mortality*

To better understand the change in biomass of species due to fishing, I used a dynamic model (Ecosim) with equilibrium conditions based on the historic mean rate of fishing mortality for each of the six-fished species (*i.e.* black lines in Figures B.3-B.8). Both the number of nodes that exhibit change in biomass and the magnitude of change of a node varied markedly depending on the species fished. For example, the number nodes that changed biomass and magnitude of those changes was far greater when lingcod or blue rockfish were fished compared to cabezon or kelp greenling. (Figures B.3 and B.6 versus B.4 and B.5).

When fishing mortality was reduced, the model indicates both positive and negative changes in the biomass of the different nodes in the system (Figures B.3-B.8). For example, when fishing mortality of lingcod is reduced, the equilibrium biomass of nine species increased by the end of the 30-year model simulation (Figures 2.6, 2.7 and B.3). Fishing cabezon generated similar, but more subtle, responses (Figures 2.7 and B.4). When fishing of kelp greenling was reduced, only biomass of lingcod increased

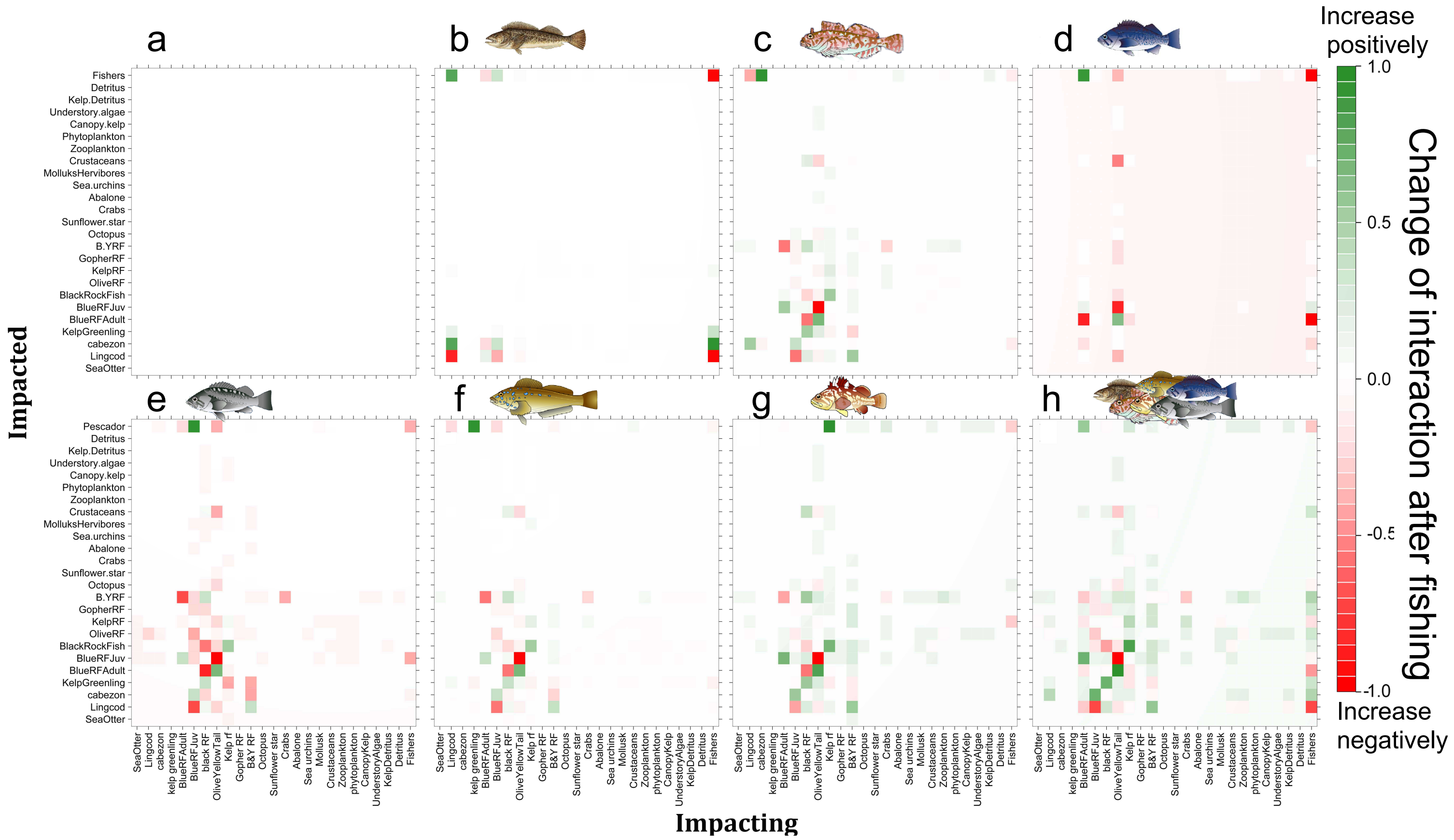

Figure 2.5: Change in magnitude and direction of mixed trophic impacts for the different fishing scenarios: No fishing (A), fishing lingcod (B), cabezon (C), blue rockfish (D), black rockfish (E), kelp greenling (F), gopher rockfish (G), and fishing all the species at once (H). Green and red tones scale with positively and negatively increasing change in magnitude of interactions. Direction of interactions, positive or negative, are indicated in Figure 2.4.

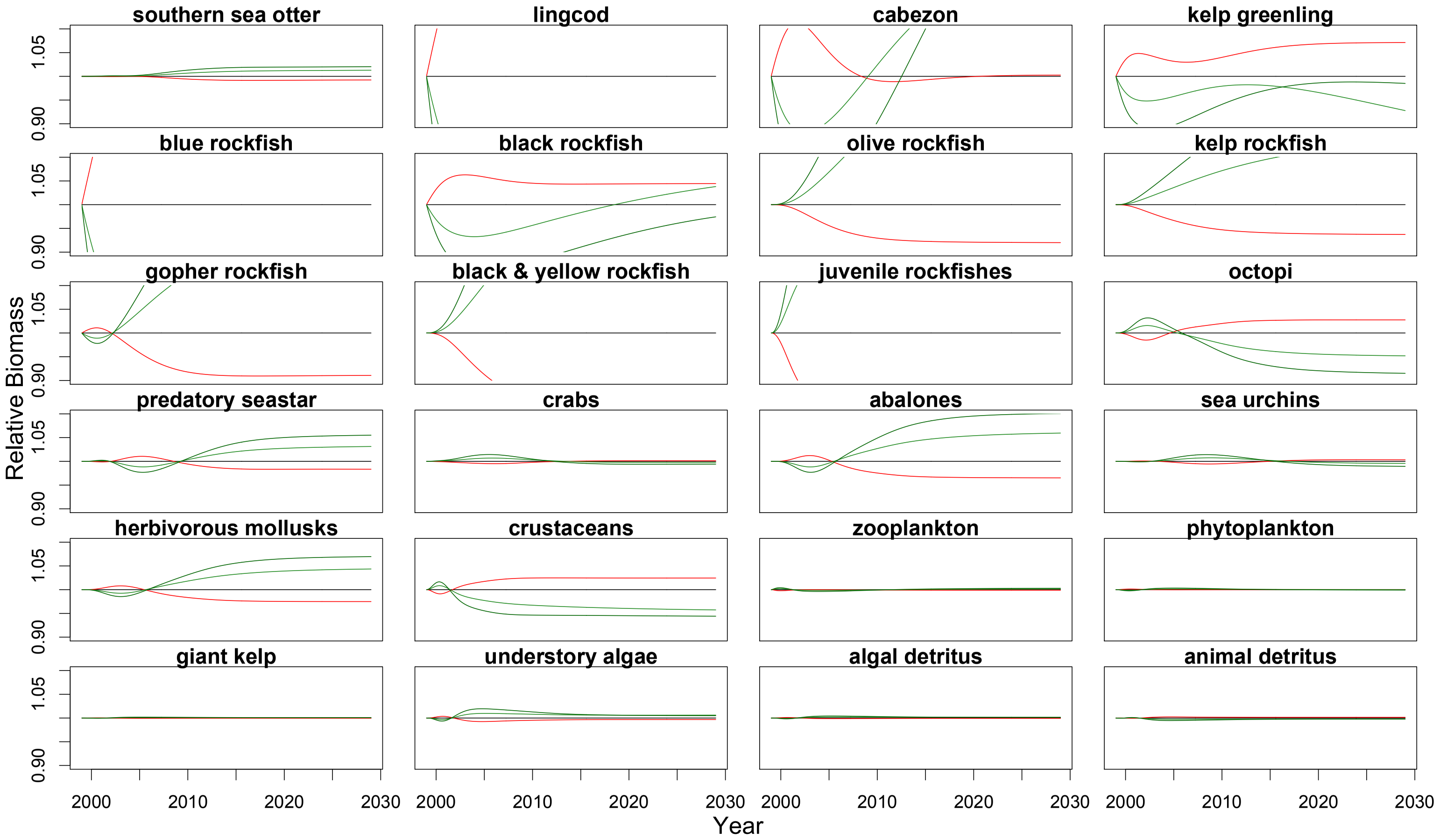

Figure 2.6: Relative biomass response of the different nodes in the ecological network after fishing all six species at five different rates of fishing mortality. Black lines represent the relative biomass at mean historical fishing rate (1x). NO fishing (red), reduced fishing by 0.5X (orange), increased fishing by 1.5X (light green), 2.0X (darker green), and 3X (darkest green).

(Figures 2.7 and B.5). However, when fishing mortality of black, blue and gopher rockfishes was reduced, the node biomasses responded variably (*i.e.* positively and negatively) further through the network (Figures 2.7 and B.6-B.8). For example, when fishing mortality of blue rockfish was reduced, biomass of nine nodes declined while three increased (Figures 2.7 and B.6).

In general, the increase of fishing mortality of higher trophic levels (*i.e.* lingcod) had an overall positive impact on the other species/groups of fish that directly interact with (Figure 2.7). This was consistent among the different fishing mortality scenarios (1.5X, 2X and 3X) and opposite among the reduced or No fishing scenarios (*e.g.* 0X, 0.5X). For instance, when I increased lingcod's fishing mortality, I found that all species of fish species/groups in the system increased their biomass except for the octopus (Figure 2.7). When lingcod was protected from fishing, the model suggested the exact opposite pattern; the biomass of all the species of fish was reduced (Figure 2.6, Table 2.5). Alternatively, when I increased fishing mortality for cabezon and kelp greenlings the changes in biomass after fishing were very small, influencing the biomass of other species very little. When I increased fishing mortality of lower trophic level fished species (*e.g.* black and gopher rockfishes), results suggest very little change of the biomass of the rest of the species/groups (Figures 2.7, B.7 and B.8). However, I found the largest changes in biomass when increasing fishing mortality of blue rockfishes (Figure 2.7 and B.6).

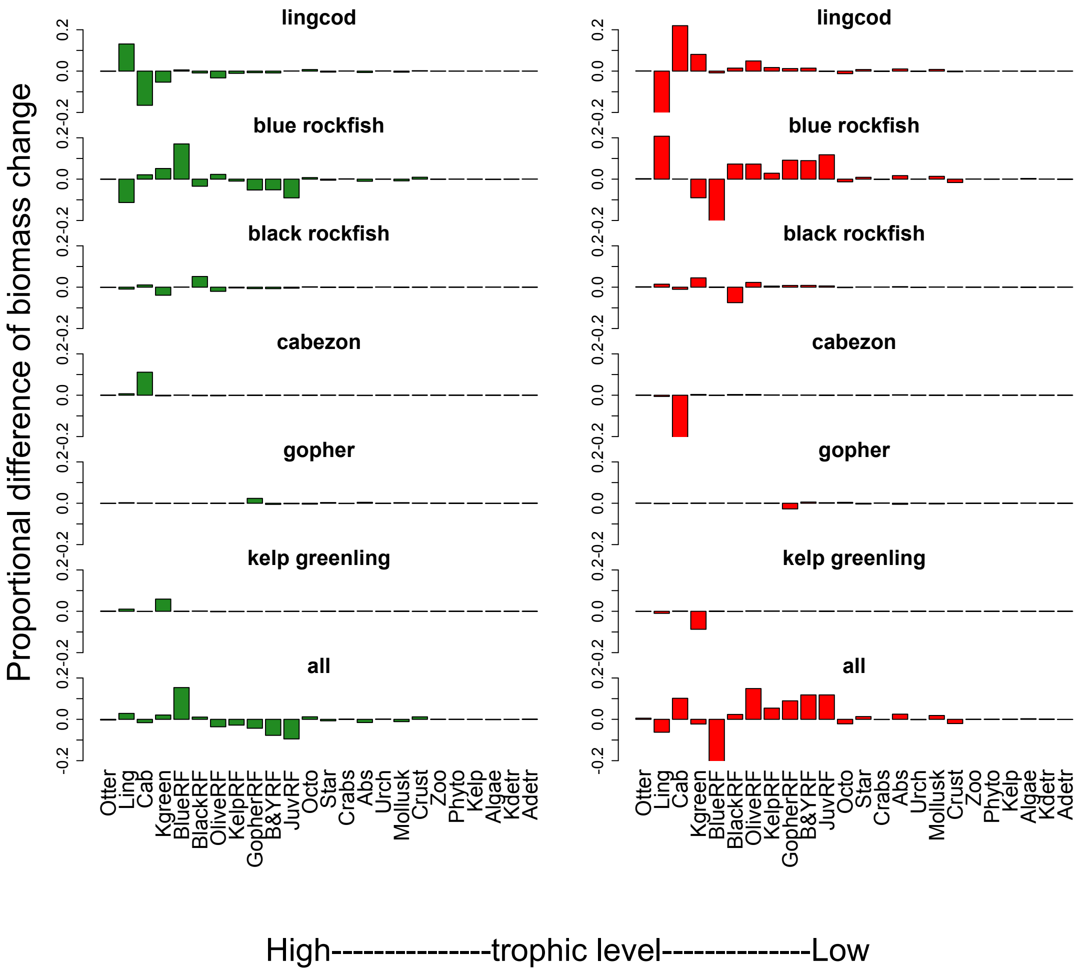

Figure 2.7: Standardized change in node biomass (log (biomass at end/biomass at start)) with (red bars) and without (green bars) fishing mortality.

Table 2.5: Change in total biomass of all nodes in the network combined when subjected to different rates of fishing mortality.

| Target species | Fishing mortality | Total biomass at start | Total biomass at end | Starting biomass/ ending biomass | Log(ending biomass/ starting biomass) | Biomass change |
|---|---|---|---|---|---|---|
| Black | NO | 368.55 | 368.64 | 1.00026 | 0.0001 | 0.10 |
| Black | 1X | 368.49 | 368.49 | 1.00000 | 0.0000 | 0.00 |
| Black | 2X | 368.43 | 368.34 | 0.99975 | -0.0001 | -0.09 |
| Black | 3X | 368.38 | 368.21 | 0.99955 | -0.0002 | -0.17 |
| Blue | NO | 369.15 | 372.58 | 1.00930 | 0.0040 | 3.43 |
| Blue | 1X | 368.49 | 368.49 | 1.00000 | 0.0000 | 0.00 |
| Blue | 2X | 367.85 | 363.91 | 0.98929 | -0.0047 | -3.94 |
| Blue | 3X | 367.22 | 359.43 | 0.97878 | -0.0093 | -7.79 |
| Cabezon | 3X | 368.48 | 368.52 | 1.00011 | 0.0000 | 0.04 |
| Cabezon | 2X | 368.49 | 368.50 | 1.00005 | 0.0000 | 0.02 |
| Cabezon | 1X | 368.49 | 368.49 | 1.00000 | 0.0000 | 0.00 |
| Cabezon | NO | 368.49 | 368.48 | 0.99996 | 0.0000 | -0.01 |
| Gopher | NO | 368.51 | 368.64 | 1.00035 | 0.0002 | 0.13 |
| Gopher | 1X | 368.49 | 368.49 | 1.00000 | 0.0000 | 0.00 |
| Gopher | 2X | 368.46 | 368.34 | 0.99965 | -0.0001 | -0.13 |
| Gopher | 3X | 368.44 | 368.19 | 0.99934 | -0.0003 | -0.24 |
| Greenlings | NO | 368.50 | 368.55 | 1.00014 | 0.0001 | 0.05 |
| Greenlings | 1X | 368.49 | 368.49 | 1.00000 | 0.0000 | 0.00 |
| Greenlings | 2X | 368.48 | 368.42 | 0.99985 | -0.0001 | -0.06 |
| Greenlings | 3X | 368.46 | 368.36 | 0.99971 | -0.0001 | -0.11 |
| Lingcod | 3X | 368.45 | 369.88 | 1.00386 | 0.0017 | 1.42 |
| Lingcod | 2X | 368.47 | 369.19 | 1.00196 | 0.0009 | 0.72 |
| Lingcod | 1X | 368.49 | 368.49 | 1.00000 | 0.0000 | 0.00 |
| Lingcod | NO | 368.51 | 368.12 | 0.99894 | -0.0005 | -0.39 |

### 2.3.4 *Effects of simultaneously fishing multiple species*

The system-wide responses of the kelp forest ecological network to the impacts of fishing all six species simultaneously revealed differences when compared to fishing only one species at a time. First, there was an overall increase in the impact of pairwise interactions (MTI values) across the network, including across all trophic levels. In addition, the model estimated the lowest total system throughput of biomass when all six species were fished (Table B.2). One of the more substantial responses was greatly increasing the strong negative effect (predation) of adult olive rockfish on juvenile rockfish (Figure 2.4a versus Figure 2.4h, and Figure 2.5h) because olive rockfish was not fished in the model. In contrast, the negative effect of olive rockfish on adult blue rockfish and kelp rockfish on black rockfish were both greatly diminished (Figure 2.5h). Likewise, the positive effect of juvenile rockfish (as prey) on lingcod was very much diminished (Figure 2.5h). All of these strong changes were only realized when multiple species were fished simultaneously. The model suggests an overall increase towards more positive interactions across the network (*i.e.* strong negative become weak negative and weak positive become strong positive).

Simultaneous fishing of multiple species has different effects on the patterns of change in biomass of nodes compared to fishing any single species. For instance, fishing all species causes changes in biomass of all nodes across the network (Figure 2.5), which occurs only rarely when fishing one species at a time (Figures B.3-B.7). Fishing any single species led to inverse changes in the biomass of nodes compared to when that species was not fished (*e.g.*, Figures 2.6 and Figure 2.7 - no fishing versus 2X fishing mortality). However, when all six species were fished simultaneously, some species did not exhibit this inverse response (*e.g.*, cabezon, kelp greenling, gopher rockfish). This is probably because those species that exhibit an inverse (positive) response to increased fishing mortality (olive, kelp, black and yellow and juvenile rockfishes) were not fished in the model and released from predation and competition with the fished species. In contrast, cabezon, kelp greenling and gopher rockfish continued to be fished, preventing the same response. The invertebrates exhibited similar responses to the presence or absence of fishing whether single or multiple species were fished. In all cases, octopus and crustaceans showed decline in biomass in response to fishing, whereas the other invertebrates increased in biomass.

## 2.4 Discussion

I developed, parameterized and balanced a series of mass-balanced models to characterize the structure and species interactions in kelp forest ecosystems in central California (Figure 2.4). This is the only instance that this form of network model has been applied to a kelp forest ecosystems. I was able to use a wealth of empirical survey data to identify the typical species composition and biomass densities of species required of the mass-balance model. I gleaned information on trophic (predator-prey) interactions from the *Kelpforest Database* (Beas-Luna *et al. submitted*) and fishing mortality rates from stock assessments and other fisheries sources. In combination, this and other information allowed me to construct an ecological network of 24 nodes comprised of individual species or species groups based on their taxonomy (*e.g.*, crustaceans) and functional similarities. I focused on incorporating the common fishes, especially six fished species, as well as the predominant primary producers, herbivores, detritivores and secondary consumers that contribute importantly as prey (*e.g.*, octopus, crabs, small crustaceans and juvenile fish) and competitors of the fishes included in the model. To simplify the models, I only included the most abundant groups in the diets of the fished species. The model balancing process generated estimates of missing values to complete the network. In this simplified representation of a kelp forest in central California, I hoped to capture the fundamental interactions and biomass flux in this system. That I was reasonably successful at this, is suggested by the degree of variability (in between 10 and 20%) of transfer efficiencies calculated by the model, which agrees in magnitude with other Ecopath models described in the literature (Field *et al.* 2006, Ortiz 2007).

I used mixed trophic impact (MTI) values to track the changes in direction and magnitude of interactions between nodes under different fishing scenarios and to test the hypotheses about the extent of changes in species interactions caused by fishing. The model revealed that the extent of changes in species interactions varied markedly depending on the species fished. The model suggests that changes in species interactions in response to fishing lingcod were largely restricted to direct interactions involving lingcod (Figure 2.5). In one sense, this was a surprising result. Lingcod are major predators in kelp forests and the magnitude and scope of their predation might suggest that they would have broad influence across the system (*e.g.*, trophic cascade). One explanation for why I did not detect broader consequences across the network could be that the abundance and diversity of other species (*e.g.*, all of the other fished species and such as kelp greenling, olive and kelp rockfishes) compensated for the reduced piscivory by lingcod and suppressed any cascading interactions among nodes in the network (Heath *et al.* 2014). An alternative explanation is that lingcod feed almost entirely on fishes and few invertebrates, and thus, perhaps their impact on other fishes in the system is dissipated across the diversity and abundance of fishes they feed on with limited impacts to particular nodes comprised of invertebrates.

In contrast to the limited effects of lingcod, the models predicted broader changes in species interactions when the other five species were fished (Figure 2.5). In part, this makes sense based on the rationale described for the limited effects of lingcod. Several of the other five species (blue, black and gopher rockfishes) feed on a much wider range of prey, including both fishes and invertebrates, hence the broader and more extended changes in species interactions. These differences are reflected in the model's assignment of these species to a lower trophic level than lingcod (Table 2.2). A medium trophic level can indicate a greater level of connectance, the actual number of links relative to the possible links in a network (Bagdassarian *et al.* 2007). Hence, it is likely that an intermediate trophic level increases the connectance value (feeding below, within and above their trophic level) and more secondary effects resulting from fishing. The other two fished species, cabezon and kelp greenling exhibited more limited changes in interactions among the other nodes (Figure 2.5). These two species are largely invertivores, kelp greenling especially feeding largely on smaller crustaceans. Although these two species are at an intermediate trophic level, the range of nodes they feed on is more limited than the rockfishes.

Of particular note is the pervasive though subtle response across nodes to the fishing of blue rockfish. The uniform pink tone across pairwise interactions in the MTI matrix (Figure 2.5) suggests a broad, though subtle increase in negative interactions (*e.g.*, predation and competition) among nodes. Blue rockfish are known as major planktivores in kelp forests, though they also feed on juvenile fishes and crustaceans (Hallacher and Roberts 1985). Because of their inordinately large biomass in the system, their predation on juvenile rockfishes and zooplankton is substantial. Removing this major conduit of planktivory may shift greater reliance of primary and higher level consumers on detrital and primary production-based trophic pathways, intensifying predation and competition across the system and possibly explaining the breadth of impacts of fishing this species. Alternatively, how changes in strength of competition between adult blue rockfish and juvenile rockfishes and other planktivores in the system plays out remains unclear. Thus, the extent to which interactions are modified in response to fishing appears to increase with the number of trophic levels a species interacts with (lingcod <cabezon and kelp greenling <blue, black and gopher rockfishes), or uniqueness of a species' functional role and abundance in the system (*e.g.*, blue rockfish). Despite the interesting patterns of response due to fishing, the changes in species interactions generated by these comparisons might be strongly influenced by my approach of creating seven separately balanced models, each of which generate separate

estimates of ecotrophic efficiency (EE) for the fished species.

The influence of fishing on the distribution of biomass across the network was very different from these patterns of response of interactions among nodes. In contrast to the limited extent to which interactions were modified when fishing lingcod, changes caused by eliminating or doubling fishing mortality altered the biomass of nodes (in opposite directions) more than any other single fished species (Figure 2.6). The breadth of responses (number of nodes and across trophic levels) was in stark contrast to the limited number of nodes for which biomass changed when fishing of cabezon and kelp greenling was terminated or doubled (Figure 2.6). Whereas fishing gopher rockfish altered biomass in several invertebrate nodes, changes node biomasses were largely limited to fishes when blue and black rockfish were fished (Figure 2.6). These patterns again suggest that the extent to which the distribution of biomass changes in response to fishing differs among species commonly targeted by fisheries in central California kelp forests.

Simultaneously fishing multiple species had a far greater impact on the number and distribution of nodes for which interactions and biomass was altered. Perhaps this was anticipated, but it was unclear a priori as to what extent changes in multiple fished species would reinforce or cancel their separate effects. Accordingly with other studies, these results suggest that fishing multiple species likely alters the structure (relative biomass of species) and function (distribution of interactions and movement of biomass through the system) more than fishing a subset of the fish assemblage (Walters *et al.* 2005). This result reinforces the importance of a multi-species approach to managing fishing in kelp forests by recognizing these combined, “cumulative”, effects of simultaneously fishing multiple species.

Application of Ecosim allowed me to explore the effects of varying rates of fishing mortality on the biomass response of other nodes in the network. With few exceptions, changes in rates of fishing mortality reinforced responses in one direction or the other (*i.e.* further decreases or increases in fishing mortality simply increased the response in the same direction and did not cause changes in direction). If true, this certainly simplifies predicted responses of the network to increases of decreases in fishing mortality of a fished species.

### 2.4.1 *Total productivity and biomass response*

In addition to lingcod, sea otters are also considered top predators of this ecosystem despite having a relatively low trophic level (3.01). This group in not subjected to any kind of exploitation in this area and thus, I did not manipulate its biomass in any of the models or simulations. I awknodlege that sea otters could be at risk of catastrophic reduction in biomass from human actives, such as disease, oil spills, etc. But at the moment, the southern sea otter populations is considered in equilibrium. However, in these mass-balanced models, I was able to reproduce important empirical observations such as the negative effect of sea otters on sea urchins and other invertebrate groups as well as its positive effect on macroalgae and detritus-dependent groups.

In their current formulation, there are important limitations to the application of mass-balanced models like Ecopath to kelp forests ecosystems. These models are constructed and based solely on trophic interactions. They have largely been applied to pelagic ecosystems, where trophic interactions are probably the strongest interactions and species compete little for other resources, like space. However, it is well known that both fishes and especially the sessile invertebrates and algae of kelp forest ecosystems also compete very strongly for space on the rocky substratum. As such, the Ecopath model may not capture important species interactions in this system and one challenge is to develop ways to incorporate these interactions into a trophic-based model. Nevertheless, when manipulating the models to simulate fishing mortality, I was able to generate predictions that were useful to compare the effect of different species/groups in the network at different levels of fishing. Importantly, model results are just that, and the predictions generated by these models are really yet another level of hypotheses that warrant examination by empirical studies, both observational and experimental, to assess their accuracy. But having generated those predictions, I now have intriguing new directions of study that are likely to reveal further insights into fishing effects that may have never been revealed in the absence of these modeling exercises.

## 2.5 Conclusion

With this model, I demonstrated how fishing different species may have markedly different direct and indirect effects on the interactions among, and biomasses of, other species in kelp forest ecosystems. Fishing multiple species simultaneously appears to alter these traits well beyond that of fishing any single species. Thus, the combination of Ecopath and Ecosim seems to be a useful tool for exploring how fishing directly and indirectly effects the structure and function of kelp forest ecosystems. With such knowledge, fisheries managers and conservation scientists can more efficiently pursue our understanding of the ecosystem-wide influences of fishing and the importance of considering these impacts among the different fished species. For example, the predicted response of fished species to fishing of other species can allow mangers to alter fishing mortality among species to distribute the relative production and yield among the fish assemblage in the forest. The predicted responses among the nodes identify species that could be monitored to determine how kelp forest ecosystems will respond to the termination of fishing within marine protected areas (MPAs). Hopefully this initial application of mass-balanced models will stimulate their further development and application to inform ecosystem-based management in kelp forest ecosystems.

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# Chapter 3

# Ecosystem-wide effects of giant kelp, *Macrocystis pyrifera*, dynamics

### Abstract

Ecologists have long recognized that changes in primary production can simultaneously alter the structure (*i.e.* relative abundance of species, functional groups or trophic levels) and functional processes (*e.g.*, species interactions, biomass production, energy flux) of communities. Our understanding of the community-wide consequences of changes in primary production has been advanced by experimental, observational and modeling. In this study, I developed and used a mass-balanced model informed with ecological time series data to simulate different biomass density dynamics. I use this model to test the hypothesis that different scenarios of biomass density of giant kelp (*Macrocystis pyrifera*) will influence (i) total network biomass, (ii) distribution of biomass density among nodes, and (iii) temporal variation in biomass density of

nodes over the 27 year simulation. I identified four patches that captured the range of orthogonal combinations of mean and variance of kelp biomass density. I used the biomass density dynamics to fit the model to the giant kelp biomass density data. The results from these model simulations suggest that both the mean and the inter-annual variability of giant kelp biomass contribute to the direction (increase or decreases) and magnitude of change in total biomass of the ecological network. For example, high and constant giant kelp biomass generated the greatest change in total network biomass. Low and variable giant kelp biomass caused a decline in total network biomass. Also, I found that the highest variation concentrated in the invertebrate group. This suggests that the variability of lower trophic levels are more sensitive to kelp dynamics than higher trophic levels. Despite the fact that all inferences and results of these models are based on solely trophic interactions, some important aspects of marine benthic communities such as competition for space or light were difficult to address in this model. However, This is an example of the value of how ecosystem models can be used to generate hypotheses and predictions of ecosystem responses to one or more of the changes in the marine environment.

## 3.1 Introduction

One longstanding goal of ecologists has been to understand the consequences of changes in primary production to the structure, functional processes and dynamics of biological communities. Ecologists have long recognized that changes in primary production can simultaneously alter the structure (*i.e.* relative abundance of species, functional groups or trophic levels) and functional processes (*e.g.*, species interactions, biomass production, energy flux) of communities (*e.g.*, Oksanen *et al.* 1981, Facelli and Pickett 1991, Carpenter *et al.* 2001, Polis *et al.* 1997, Polis 1999), but that the magnitude and predictability of responses depend on a multitude of biotic and abiotic features of an ecosystem. So-called "bottom-up" processes include abiotic factors (*e.g.*, nutrient availability, temperature, light availability, environmental stressors), "top-down" processes (*e.g.*, herbivores, parasites, disease and higher level trophic processes that determine their abundance, per-capita), and disturbances can act independently or in combination to drive spatial and temporal patterns of net primary production (NPP). Moreover, the influence of these processes on NPP depends on attributes of the primary producers (plants, algae), including species composition and richness, size, age and stage structure, among others (Tilman *et al.* 1996, Polis *et al.* 1997). Furthermore, how NPP influences the structure, functions and dynamics of a community will depend on its temporal characteristics (*e.g.*, magnitude and duration of variation; Knapp and Smith 2001, Polley *et al.* 2003).

Interest in the ecological consequences of change in NPP has gained even more attention in the face of a changing global climate. Global (Melillo *et al.* 1993), regional (Pinsky *et al.* 2013) and local changes in the magnitude of NPP have been attributed to a changing global climate and a variety of community responses, including community structure (Graham and Grimm 1990), species richness or diversity (Harley 2011), and species interactions (Blois *et al.* 2013).

Our understanding of the community-wide consequences of changes in NPP has been advanced by experimental (*e.g.*, Carpenter *et al.* 2001), observational (*e.g.*, cite) and modelling (*e.g.*, Sala *et al.* 2000) studies. Because of the difficulties inherent in well-controlled experimental and observational studies, especially at relevant spatial and temporal scales, models designed to examine community-wide response are of particular interest. However, the complexity of natural communities and the multitude of environmental factors known to influence how communities respond to changes in NPP pose serious challenges to the development, application and interpretation of models designed to identify how the structure, functions and dynamics of communities respond to changes in NPP. However, simplified models can nevertheless generate informed hypotheses and predictions that can direct studies to address these questions. Given the importance of this question and these potential contributions of models, ecologists have employed a diversity of modeling approaches.

Ecosystems for which the consequences of changing NPP on community attributes are of great interest are temperate marine kelp forests. Kelp forests are among the most species rich and productive ecosystems in the world and support a variety of ecosystem services, including culturally and economically important recreational and commercial uses (*e.g.*, wildlife observation, kelp harvesting, fishing) and regulating services (*e.g.*, wave attenuation and coastal protection, carbon sequestration). Kelps (order Laminariales) are one of three key sources of primary production in the shallow rocky reef habitats where they occur (recent reviews by Carr and Reed *in press*, Foster and Schiel *in press*). In addition to surface and subsurface canopy forming kelps, influxes of phytoplankton and production of other benthic marine algae and plants (*e.g.*, surfgrasses) contribute the primary production in these ecosystems. However, the few kelps that form surface canopies, especially the giant kelp, *Macrocystis pyrifera*, are exceptionally productive, and contribute disproportionately to NPP in these ecosystems (Reed *et al.* 2009). This NPP fuels a grazer-based trophic pathway, but more importantly, a highly productive detrital trophic pathway (Figurski 2010). This detritus, in the form of sloughing and detached blades, fronds and entire plants is also exported offshore and onshore by storms and currents to adjacent ecosystems (*e.g.*, submarine canyons, rocky and sandy intertidal zones) where it contributes to detrital pathways.

In addition to their function as a source of primary production, kelps influence the structure and interactions among species by creating habitat structure that extends through the water column from the rocky reef to the surface. That habitat is used and partitioned by benthic invertebrates, contributing to overall diversity of the kelp forest community (Watanabe 1984, Coyer 1985, 1987, Karr 2012) and provides a nursery function for rocky reef fishes (reviewed by Carr and Syms 2006). Its presence also alters water flow and the delivery of zooplankton to planktivorous fishes (Bray 1981) and sessile invertebrates (Arkema 2009). Giant kelp competes with subsurface macroalgae for light and with both macroalgae and benthic sessile invertebrates for space on the surface of the reef, and indirectly facilitates sessile invertebrates through its competition with macroalgae (Arkema *et al.* 2009).

Factors known to influence the standing biomass and productivity of individuals and forests of giant kelp include those that influence light availability (water depth, turbidity, geomorphology, competition with other algae), water temperature (Beas-Luna and Ladah 2014), nutrient availability (Jackson 1977), large scale currents and small-scale turbulence (as they influence rates of delivery of nutrients to the forest and surface of the kelp), wave disturbance that constrains the size and longevity of individual plants and entire forests (Reed *et al.* 2010) and grazing rates of herbivores (Dayton 1985, Davenport and Anderson 2007) and their predators (Davenport and Anderson 2007). Turbidity and water clarity vary geographically and at local scales (among forests) depending on plankton concentrations (phytoplankton and zooplankton), the friability of the rocky substratum (*e.g.*, sandstone versus granite) and proximity to and timing of freshwater runoff. The different life stages of surface canopy-forming kelps (*e.g.*, giant kelp) and subsurface canopy-forming kelps (*e.g., Pterygophora*) compete with one another and with lower lying foliose brown, red and green algae for light (Reed and Foster 1984, Dayton *et al.* 1984, Clark *et al.* 2004, Arkema *et al.* 2009) and space (Ambrose and Nelson 1982). Currents influence rates of delivery of nutrients to and within forests, and these sources of nutrient delivery to individual plants interact with the size (area), shape and density of forests (Jackson 1984, 19998, Jackson and Winant 1983, Gaylord *et al.* 2007). Wave disturbance varies geographically (*e.g.*, north and south of Point Conception) and locally, depending on the direction of ocean swell, aspect of the coastline, slope and topographic variation (*i.e.* relief) of the rocky substratum (Figurski 2010). Local and regional wave climates can be chronic or associated with episodic events, such as storms associated with El Nino (Dayton and Tegner 1984, Dayton *et al.* 1992, Ebeling *et al.* 1985, Graham *et al.* 1997, Edwards 2004, Edwards and Estes 2006). Grazing rates of herbivores, especially sea urchins, can have dramatic effects on the standing biomass of kelps (Ebeling *et al.* 1985, recently reviewed by Carr and Reed *in press*, Foster and Schiel *in press*). Water temperature likely influences physiological processes, but most importantly is a well-established proxy for nutrient availability (Dayton *et al.* 1999). Water temperature and nutrient concentrations vary spatially at geographic scales (Edward and Estes 2006) and at smaller scales, among forests, depending on proximity to areas of coastal upwelling (Broitman and Kinlan 2006). Warmer ocean waters generally have lower nutrient concentrations (Dayton *et al.* 1999). Warmer surface waters cause vertical stratification of the water column, preventing colder, nutrient-rich waters from being delivered to forests. In particular, vertical stratification prevents coastal upwelling or causes upwelling to deliver low nutrient water (Auad *et al.* 2006). Critically, all of these factors and processes that, separately and in combination, influence both the standing biomass and productivity of giant kelp forests, vary in space and time at multiple spatial and temporal scales. The consequence is that forests show great differences in both their mean and variation in biomass and productivity.

I develop and use a popular mass-balanced ecological network model, Ecopath with Ecosim, to test the hypotheses that different scenarios of biomass density dynamics of giant kelp will influence (i) total network biomass, (ii) distribution of biomass density across nodes, (iii) temporal variation in biomass density of a node over the 27 year simulation (*i.e.* variation in biomass density of lower trophic levels will be greater than nodes at higher trophic levels).

## 3.2 Methods

### 3.2.1 *Study system*

Forests of giant kelp, *Macrocystis pyrifera*, in central California are associated with shallow (<30m depth) rocky reefs from Point Conception (lat 34.448°, long −120.465°) in the south to Sand Hill Bluff (lat 36.976°, long −122.152°), north of Santa Cruz (Figure 3.1; Graham *et al.* 2008, Foster and Schiel 2010, Carr and Reed *in press*). The size (areal extent) and density (number of plants per reef area) of kelp forests in central California exhibit strong interannual variation (Edwards 2004, Reed *et al.* 2010). Forests and sub-patches within forests vary markedly in both the mean and variance in biomass density. Although these spatial scales of variability are well recognized, how these dynamics influence the structure and function of these forests is not understood. Based on a previously developed relationship between biomass density and NPP for giant kelp (Reed *et al.* 2008), I used biomass density as a proxy for giant kelp NPP. Kelp forests in central California support both commercial (*e.g.*, the "livefish" fishery) and recreational fishing (Chapter 2). Therefore, to more realistically simulate species interactions (including fishing) and the distribution of biomass density among nodes in the network model, I include fishing mortality for six finfishes for which I have fishery statistics (Chapter 2).

### 3.2.2 *Functional groups*

The model has 24 "nodes" representing individual species or aggregates of taxonomically or functionally similar species (*i.e.* functional groups or feeding guilds; Table 3.1). Each group is described in detail in Appendix A. These 24 species or groups were selected because of their known ecological and economic importance in kelp forests of central California. There are three functional groups of primary producers (phytoplankton, giant kelp, and understory algae), eight species or groups of invertebrates, ten species of fishes, the southern sea otter and two detrital (algae and animal) groups. Except for the juvenile rockfishes, both commercial and recreational fisheries target all of the fish groups in these models.

### 3.2.3 *Ecopath model*

I developed an Ecopath "steady state" model. The model integrates information from fisheries statistics, field surveys, stock assessments, food habits and bioenergetics into a mass balance model of an ecosystems trophic structure. The model predicts changes in the effects between species or functional groups based on the flow of biomass of species or functional groups. The model considers a conceptual area of one square kilometer of a kelp forest with no explicit spatial gradients or patchiness. I assume that the modeled one square kilometer represents kelp forests throughout the central coast

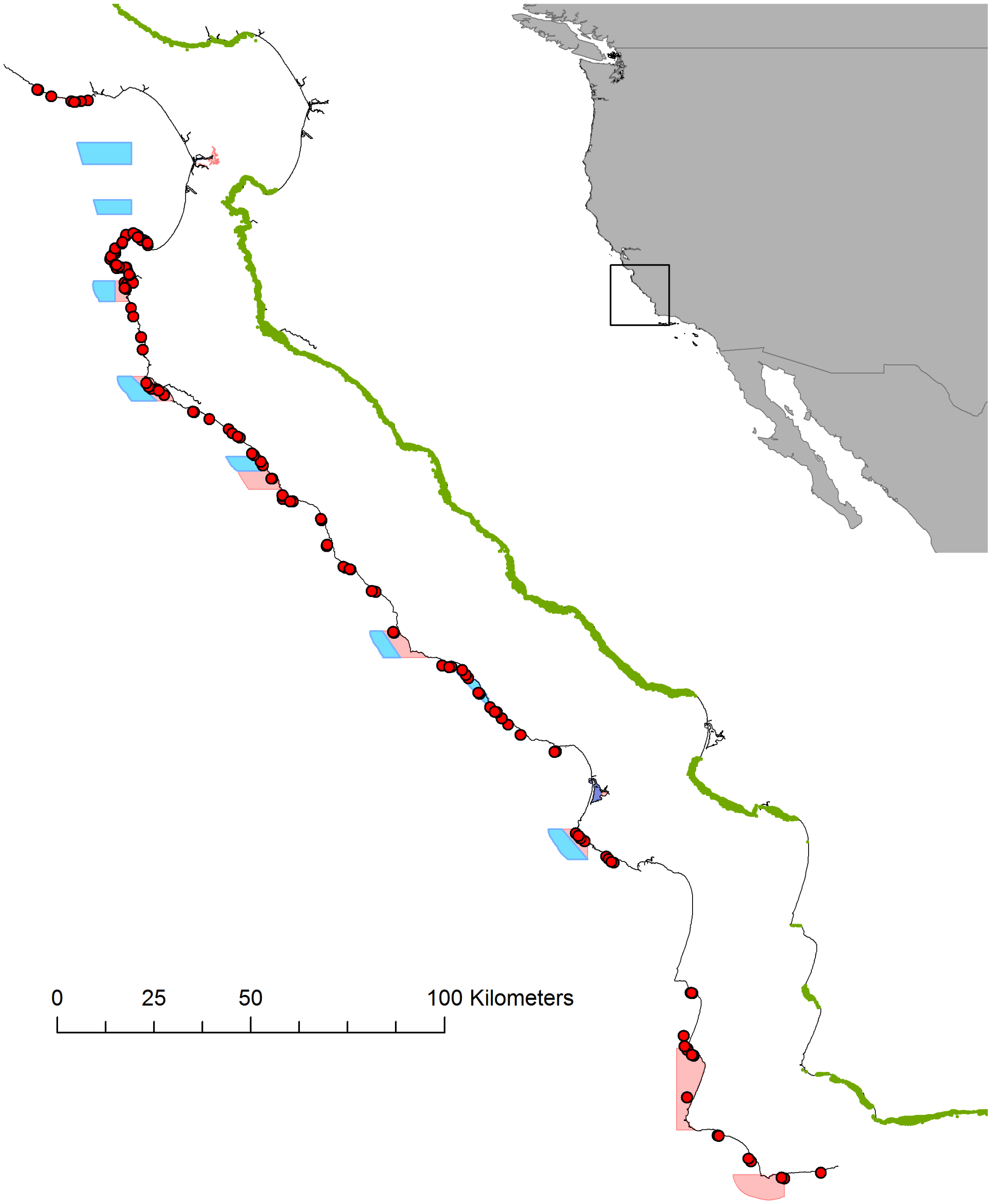

Figure 3.1: Map of central coast of California from Pigeon Point (lat 37.181°, long −122.394°) in the north to Point Conception (lat 34.448°, long −120.465°) in the south. Also shown is the network of Marine Protected Areas and sites surveyed by PISCO divers for estimates of fish density and sizes, which were used to estimate Biomass. Red areas are reserves and blue are conservation areas. Green color represents spatial distribution of giant kelp.

Table 3.1: Best fit parameter estimates for the mass-balanced model based on Monte Carlo simulation results after 100 trials. Original SS=182.8, Best SS=148.1.

| Group name | Biomass | Production/ biomass | consumption/ biomass | Ecotrophic effciciency |
|---|---|---|---|---|
| sea otter | 0.141 | 0.137 | 86.097 | 0.222 |
| lingcod | 0.613 | 0.257 | 2.276 | 0.479 |
| cabezon | 0.132 | 0.343 | 2.198 | 0.917 |
| kelp greenling | 0.666 | 0.293 | 1.440 | 0.561 |
| blue rockfish | 41.252 | 0.210 | 1.444 | 0.520 |
| black rockfish | 3.495 | 0.248 | 1.318 | 0.558 |
| olive rockfish | 5.416 | 0.144 | 1.218 | 0.823 |
| kelp rockfish | 7.272 | 0.207 | 1.512 | 0.292 |
| gopher rockfish | 3.392 | 0.229 | 1.462 | 0.633 |
| black & yellow rockfish | 2.467 | 0.197 | 1.611 | 0.999 |
| juvenile rockfishes | 8.151 | 1.489 | 5.898 | 0.937 |
| octopus | 2.486 | 1.031 | 5.027 | 0.819 |
| predatory seastars | 0.820 | 0.605 | 2.440 | 0.086 |
| crabs | 37.237 | 1.159 | 5.134 | 0.426 |
| abalones | 1.693 | 2.256 | 10.308 | 0.610 |
| sea urchins | 7.081 | 0.462 | 12.100 | 0.635 |
| herbivorous mollusks | 20.867 | 1.021 | 9.018 | 0.424 |
| crustaceans | 11.145 | 3.651 | 24.972 | 0.880 |
| zooplankton | 19.131 | 17.552 | 54.020 | 0.716 |
| phytoplankton | 14.665 | 160.118 | 0.000 | 0.270 |
| canopy kelp | 103.158 | 49.331 | 0.000 | 0.041 |
| understory algae | 29.582 | 16.706 | 0.000 | 0.378 |

study region. Ecopath is considered a “mass balance” model by assuming that the total biomass produced in the system does not change in time. Thus, as the biomass of one species or functional group changes, biomasses of other species compensate to maintain the net biomass production of the system. This compensation reveals the changes in biomass flow and species interactions. This model was developed by Polovina (1984) and made into a software suite application at the University of British Columbia (Christensen and Pauly 1992), available at http://www.ecopath.org/. It includes a series of modules where Ecopath produces a static snapshot of the net biomass production of the system.

Ecopath is based on one fundamental equation. This equation balances for each node “i” (species or functional group) in an ecosystem, where each node can be an ontogenetic stage (juvenile, adult) of a species, a species itself or a group of species that share similar functional relationships with other species in the system:

$$B_i \cdot (P/B)_i \cdot EE_i = \sum (Q/B)_j \cdot DC_{ij} \cdot B_j + C_i + BA_i + NM_i \tag{3.1}$$

where $B_i$ and $B_j$ are the biomasses of species or group $i$ and the consumers $j$ of $i$, respectively; $(P/B)_i$ is the production ($P$) biomass ($B$) ratio for $i$; $EE_i$, also known as ecotrophic efficiency, is the fraction of production of $i$ that is consumed by other species or groups in the system (the balance being assumed to contribute to detritus); $C_i$ is the fishing mortality (landings + discards) on $i$; $(Q/B)_j$ is the total food consumption per unit biomass of $j$; $DC_{ij}$ is the fractional contribution by mass of $i$ to the diet of $j$; $BA_i$ is a biomass accumulation term that describes a change in biomass over the Ecopath base reference unit time step (it is usually one year), and $NM_i$ is the net biomass migration (immigration-emigration) for $i$.

### 3.2.4 *Parameter estimates*

Parameterization of the models was supported by the availability of information from five sources. First and foremost was an online database (*Kelpforest Database*; www.kelpforest.ucsc.edu), which was created for this purpose. This database is comprised of species life history traits, demographic parameters and species interactions for kelp forest ecosystems along the west coast of North America (Beas-Luna *et al. submitted*). Species composition and density estimates were derived from three monitoring programs; (i) a large scale kelp forest monitoring program in central and southern California conducted by the Partnership for Interdisciplinary Studies of Coastal Oceans (PISCO: http://www.piscoweb.org/research/science-by-discipline/ecosystem-monitoring/kelp-forest-monitoring); (ii) a long-term kelp forest monitoring program conducted in the Santa Barbara Channel (Santa Barbara Long Term Ecological Research (SBC LTER: http://sbc.lternet.edu/); (iii) sea otter biomass and density time series were gleaned from the United States Geological Surveys Western Ecological Research Center (USGS-WERC: http://www.werc.usgs.gov/project.aspx?projectid=91). In addition, I used stock assessments and catch data for lingcod, cabezon, blue, and black, olives and yellow rockfishes provided by the NOAA National Marine Fisheries Service (see Appendix A).

***B* (biomass density)** in metric tons per $km^2$ was estimated from field surveys in central California kelp forests and from the literature. Field surveys were conducted by PISCO at 30 sites sampled for various durations from 1999 to 2011. These surveys estimate both the density (number of individuals per area) and size of organisms. For each node, I used length-biomass relationships from the *Kelpforest Database* to estimate the biomass of each individual on a transect and summed individual biomasses for a total biomass per 60m$^2$ transect (reef surface). For fish, these biomasses were summed across the midwater and benthic transects. I then calculated the mean total biomass across all transects at a site (*i.e.* mean biomass per 60m$^2$ per site) and used these to calculate mean biomass density (grams per 60m$^2$) across sampling sites and years (n = 565). These mean biomass densities are presented in tons per km$^2$. Note that biomass densities of midwater fishes (*e.g.*, blue, black, olive and kelp rockfish) are probably underestimated because the two transects sample only a portion of the water column. Otherwise, biomass was gleaned from the literature using the online *Kelpforest Database.*

***P/B* (production/biomass ratio)** is measured as grams of biomass produced per gram of individual biomass per year. These are much more difficult to estimate from direct methods from empirical data. Thus, in many cases, the $P/B$ ratios where assumed to be similar to the total mortality ($Z$) (Pauly *et al.* 2000).

***Q/B* (consumption/biomass) ratios** are measured as grams of prey biomass eaten per gram of biomass per year. These values are gleaned from the *Kelpforest Database.* More specifically, I collected information from studies of consumption rates or evacuation rates when there was data on percent of body weight eaten per day.

***EE* (ecotrophic efficiency)** is the fraction of the production that is used in the system, either passed up the food web, used for biomass accumulation, migration or export. This value is dimensionless and ranges from 0 to 1. The value approaches 1 for species that experience high rates of predation.

***TL* (trophic level)** for a consumer is 1+ the weighted average trophic level of its prey. *TL* is 1 for primary producers and detritus.

***DC* (contribution of a species to the diet of its predator)** is estimated from dietary information from the literature. The diet compositions among the 14 species or groups in our model were obtained from the *species interactions* section of the online *Kelpforest Database.*

***NM* (net migration)** is the difference of immigration and emigration for each species or group and assumed to be zero in all models.

### 3.2.5 *Ecosim model*

The Ecosim module uses the “static” characterizations of biomass dynamics (*e.g.*, consumption and production ratios) and species interactions generated by Ecopath and subject them to a dynamic time-dependent equation to predict the equilibrial reallocation of biomass across the network (Walters *et al.* 1997). Ecosim uses coupled differential equations derived from the basic Ecopath equation 3.1 such that, for prey $i$ and predator $j$:

$$\frac{dB_i}{dt} = g_i \sum_j Q_{ij} - \sum_j Q_{ij} + I_i - (M0_i + F_i + e_i)B_i \tag{3.2}$$

where, $dB_i/dt$ is the growth rate (biomass) of the node $i$ during the time interval $dt$, $g_i$ is the growth efficiency, previously defined as the production $P/B$ over consumption $Q/B$, $Q_{ji}$ is the predation by node $i$ on node $j$, $Q_{ij}$ is the predation on node $i$ by node $j$, $I_i$ is the biomass migration rate, $M0_i$ is the non predation mortality, $F_i$ is the fishing mortality rate, $e_i$ is the emigration rate, and $B_i$ is the biomass of the node $i$ at the previous time step. The differential equations are solved in the Ecosim module, using an integration routine built in the software.

### 3.2.6 *Characterization of giant kelp biomass density dynamics*

To characterize the spatial and temporal dynamics of kelp biomass density, I used time series (1985 to 2010) of kelp biomass density that were generated from Landsat images of kelp canopy cover in central California (Young, *unpublished data*) and an empirically derived relationship between canopy density and total kelp biomass density (Cavanaugh *et al.* 2010). Young *et al.* (unpublished data) defined kelp sub-patches based contiguous aggregations of Landat pixels with common dynamics, resulting in one or more sub-patches of kelp within a single forest. I calculated the annual mean and coefficient of variation (CV) of biomass density from 1985 to 2010 (years as replicates) for each of 168 sub-patches from central California. I used this information to identify four sub-patches that characterize the range of mean and CV in biomass density of sub-patches. These biomass density values were used in the Ecosim model to simulate each of four scenarios of biomass density dynamics: low mean with low CV (“low constant”), low mean with high CV (“low variable”), high mean with low CV (“high constant”), high mean with high CV ("high variable").

### 3.2.7 *Model application*

I used the results from the Ecopath and Ecosim simulations described above to test the hypotheses that different scenarios of biomass density dynamics of giant kelp will influence (i) total network biomass, (ii) distribution of biomass density across nodes, (iii) temporal variation in biomass density of a node over the 27 year simulation (*i.e.* variation in biomass density of lower trophic levels will be greater than nodes at higher trophic levels).

#### 3.2.7.1 *Response of total network biomass density to scenarios of giant kelp dynamics*

To characterize the change in total biomass density of the network for each of the four scenarios of kelp biomass dynamics, I ran Ecopath with Ecosim simulations for 27 years and calculated the total biomass change (difference between beginning and ending total biomass) for each of the four scenarios.

#### 3.2.7.2 *Response of biomass density distribution among nodes to scenarios of giant kelp dynamics*

To characterize the change in distribution of biomass density among the 24 nodes of the network for each of the four scenarios of kelp biomass dynamics, I ran Ecopath and Ecosim simulations for 27 years and calculated the standardized proportionate change in biomass density (log [ending node biomass divided by beginning node biomass]) for each of the four scenarios of kelp dynamics.

#### 3.2.7.3 *Response of temporal variation in biomass density of nodes to scenarios of giant kelp dynamics*

To characterize how temporal variation in biomass density of each of the 24 nodes of the network respond to the four scenarios of kelp biomass dynamics, I ran Ecopath and Ecosim simulations for 27 years and calculated the coefficient of variation (CV) using years as replicates. I then compared the CVs of each node across the four scenarios to see how they varied in response to the kelp dynamics.

## 3.3 Results

I successfully balanced the 24-node Ecopath mass-balanced network model that represents key interactions of a kelp forest in central California (Table 3.1). The kelp forest network model generated estimates of impacts and biomass production of nodes (species or species groups) such that net production and consumption of biomass across the system balanced one another (Figure 3.2). When balanced, about 64.5% of the living biomass density (*i.e.* excluding detritus) was algae (giant kelp and others), 29.4% invertebrates, and 6.14% fishes. For more details of the Ecopath results (*e.g.*, trophic flow and structure), see Chapter 2.

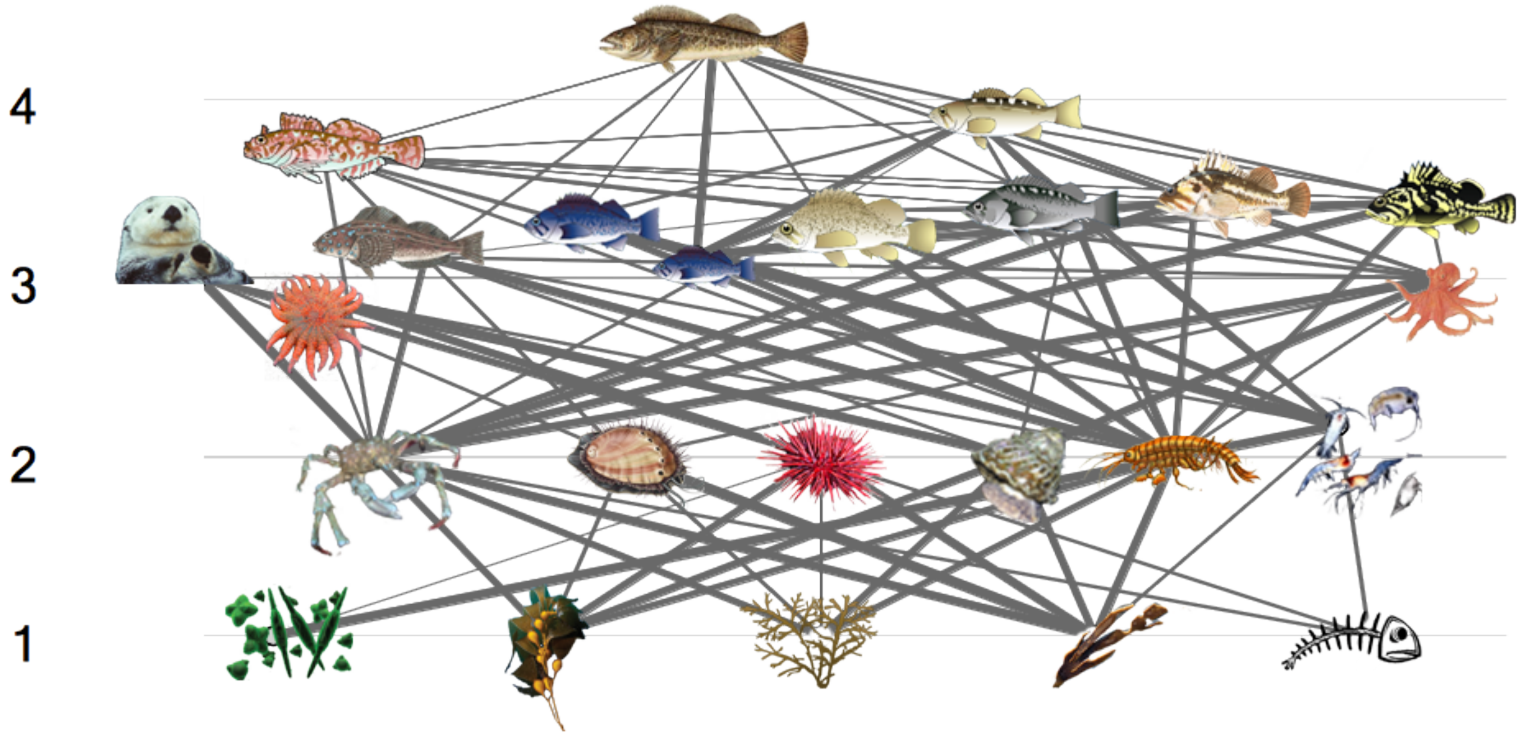

Figure 3.2: Topology of the Ecopath model for central California kelp forests. Numbers indicate trophic levels. Lines between groups represent trophic interactions weighted by the amount of biomass transferred.

### 3.3.1 *Giant kelp biomass density dynamics in central California*

Comparison of the annual mean and variance (CV) of kelp biomass density among the 168 sub-patches, between 1984 to 2011, identified four patches that captured the range of orthogonal combinations of mean and variance of kelp biomass density. Sub-patches ranged in kelp biomass density from 11 kg/900m$^2$ to 1900 kg/900m$^2$. Interannual variance (CV) in kelp biomass density of sub-patches ranged from 0.3 to 3.3 (Figure 3.2). Across the 168 sub-patches that constitute all forests in the central California study region, the mean biomass density of giant kelp was 514 kg/900m$^2$ and the mean CV was 0.98. The four patches selected to represent the four kelp dynamic scenarios (Figures 3.1 and 3.3) were: low constant biomass (74 kg/900m$^2$, 0.55), low variable biomass (15 kg/900m$^2$, 3.3), high constant biomass (1900 kg/900m$^2$, 0.3), high variable biomass (547 kg/900m$^2$, 1.67). Each sub-patch exhibits a characteristic biomass density dynamic (Figure 3.4). For example, the two sub-patches with the highest variance exhibit a large increase in kelp biomass density in the early 90s, although the two differ from one another by an order of magnitude (Figures 3.4b and 3.4c). The two sub-patches with low variance exhibit little change in biomass density over the entire period from 1985 to 2010 (Figures 3.4a and 3.4d).

### 3.3.2 *Response of total network biomass density to giant kelp dynamics*

Percent change in total network biomass density (excluding giant kelp) differed among the four scenarios of mean biomass density and variance in giant kelp . The giant

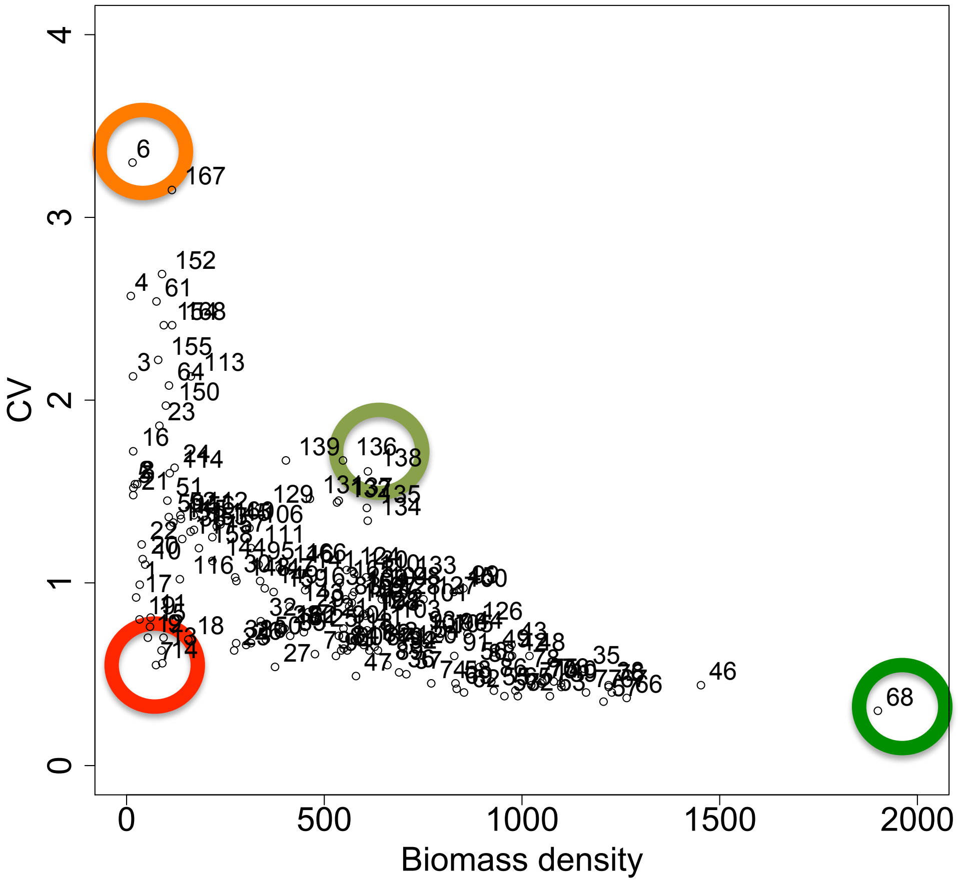

Figure 3.3: Identification of the variation in kelp canopy biomass at different sub-patches of kelp forests in central California. Biomass estimates based on LandSat images and diver estimates of frond densities. Colored circles indicate the kelp patched selected to used in the dynamic model.

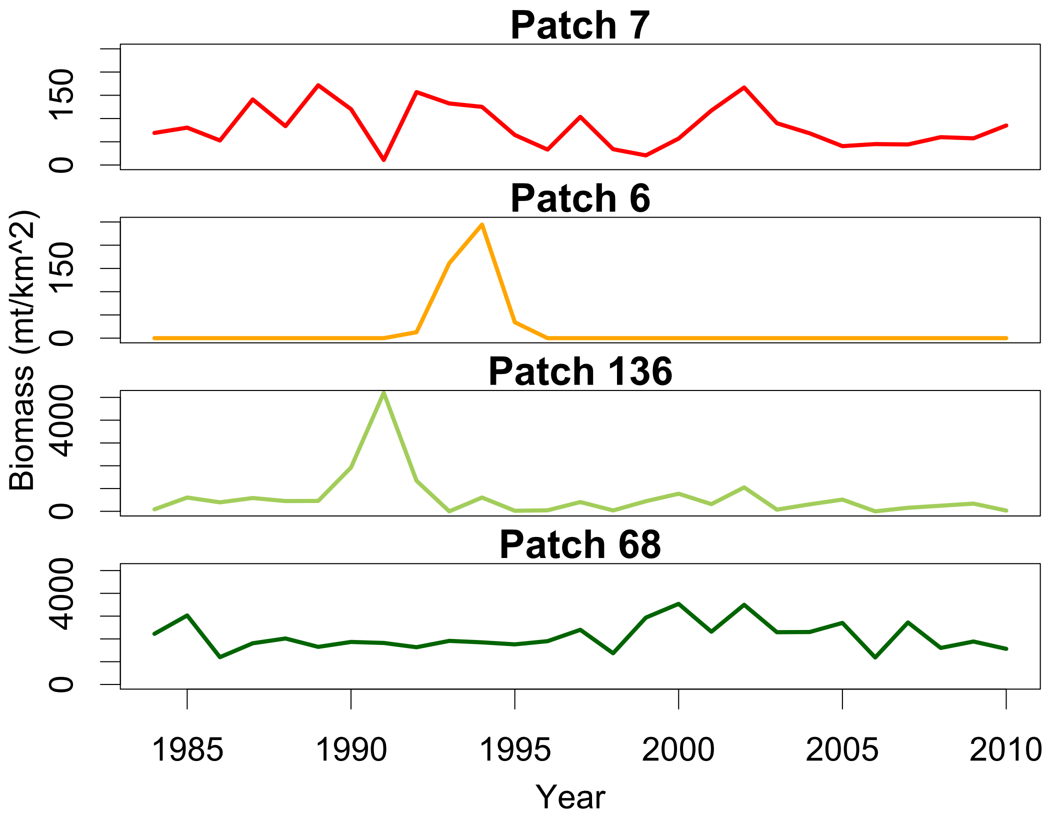

Figure 3.4: Canopy kelp (*Macrocystis pyrifera*) biomass dynamics for sub-patches with extreme dynamics in central California.

kelp biomass scenario with high variable biomass predicted only a small increase in total network biomass (1%). The total network biomass increased from 247 t/km$^2$ to 250 t/km$^2$. Similarly, the scenario with low constant kelp biomass also shows a marginal change of 2%. This scenario caused a slight increase from 247 to 251 t/km$^2$. The low variable kelp biomass scenario predicted the only negative change in total network biomass of 13%. The model predicted a biomass decline from 247 to 216 t/km$^2$. In contrast, the scenario with high biomass/low CV predicted a 174% increase in total biomass of the network; from 247 to 677 t/km$^2$. Thus, the greatest response, reflecting a marked increase in network biomass, was observed for the scenario with a consistently high biomass density of kelp. In contrast, total network biomass declined with highly variable low biomass density of kelp. Neither low biomass density with low variance nor high biomass density with high variance resulted in an appreciable change in total network biomass density. This result suggests that even though the amount of giant kelp biomass density is important, the effect of CV is relevant, especially when the biomass is low.

### 3.3.3 *Response of the distribution of biomass density among nodes to giant kelp dynamics*

Responses in total biomass density described above were generally consistent across the nodes of the network (Figure 3.5a,b,c,d). Biomass density of most nodes declined in both low mean kelp biomass density scenarios (Figure 3.5a,b), and most nodes increased in biomass density in both high mean kelp biomass density scenarios, regardless of their CV (Figure 3.5c,d). In addition to the marked differences in the direction (increase or decrease) of change in biomass density across nodes, the redistribution of biomass density among nodes varied as well. Both low mean giant kelp biomass density scenarios predicted very similar distributions of change in biomass density among nodes (Figure 3.5a,b). However, between these two scenarios (with different CVs), several of the invertebrates (*e.g.*, seastars, crabs, abalone, mollusks, crustaceans) showed marked differences in their declines relative to other nodes in the network (Figure 3.5a,b). Similarly, the distribution of changes in biomass density among nodes was similar between the two scenarios with mean high giant kelp biomass density (Figure 3.5c,d). However, again, several nodes exhibited differences in their changes relative to other nodes in the network between these two scenarios of different CVs (*e.g.*, blue rockfish, black and yellow rockfish, juvenile rockfishes, crabs, abalone, sea urchins). Given the strong differences in direction of change between the low and high mean giant kelp biomass densities, and the differences in some nodes based on different CVs, these results suggest that both mean kelp biomass density and CV contributed to overall differences in the distribution of responses across the nodes of the network to the four scenarios of kelp dynamics.

### 3.3.4 *Temporal variation in biomass density of nodes*

The Ecosim simulations characterize the short-term dynamics of biomass density of nodes (*i.e.* trajectories to their new equilibrial biomass densities) in response to the four different scenarios of giant kelp dynamics (Figure 3.6). The low constant kelp

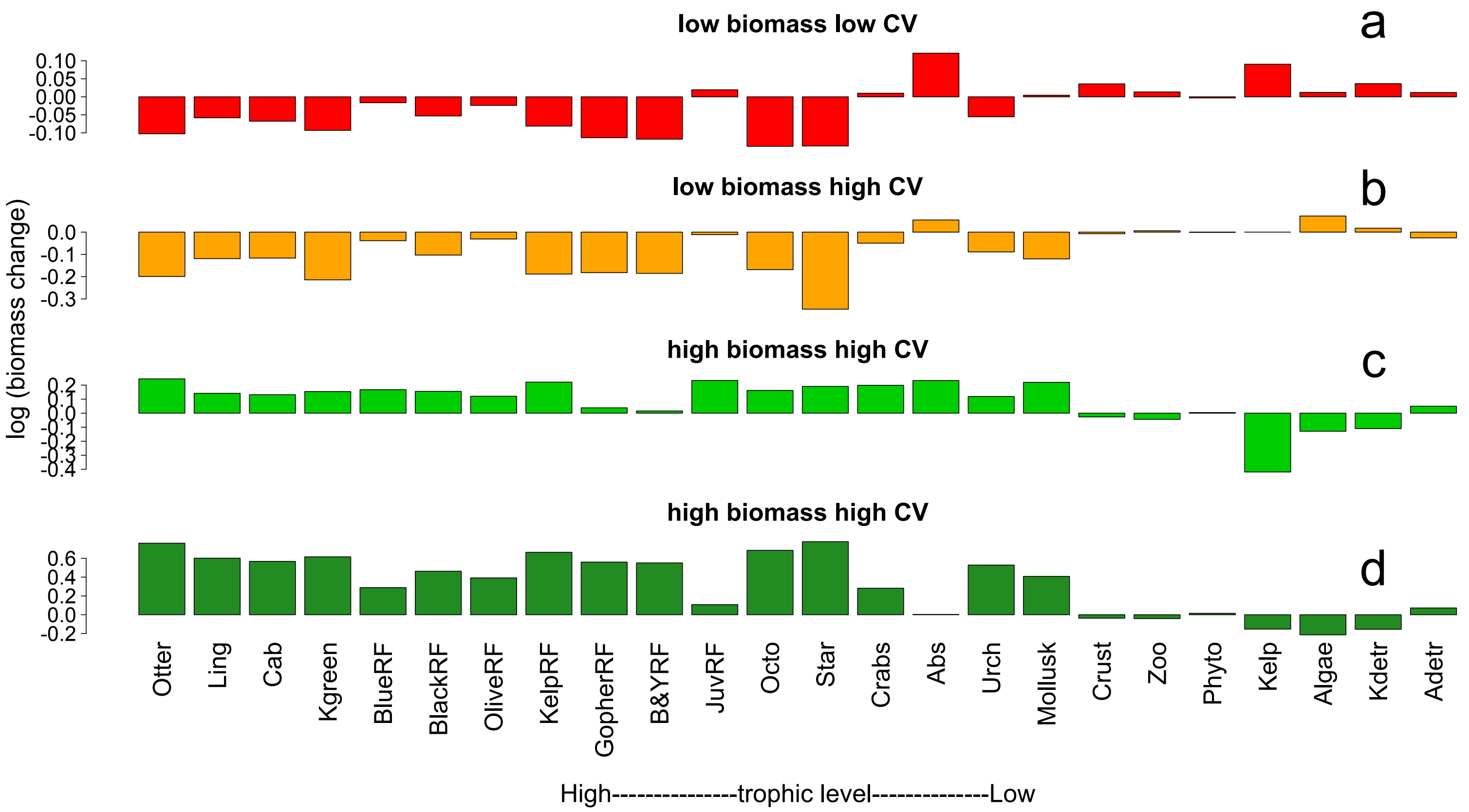

Figure 3.5: Standardized change in node biomass (log (biomass at end/biomass at start)). Low biomass and low variance (red bars), low biomass and high variance (orange bars), high biomass and medium variance (light green bars), and high biomass and low variance (dark green bars).

biomass and the high constant kelp biomass scenarios both exhibited low average node CVs (0.2 and 0.3, respectively; Figures 3.7a,b). The low variable kelp biomass scenario exhibited the next highest variation in node biomass (mean CV= 0.54; Figure 3.7c) and the high variable kelp biomass scenario exhibited the greatest variation in node biomass (mean CV= 1.03, Figures 3.7d). These differences among scenarios are stronger at lower trophic levels, and dampened at higher trophic levels (Figures 3.6 and 3.7). Only three nodes (phytoplankton, zooplankton and understory algae) responded marginally to the variation of the giant kelp biomass density.

## 3.4 Discussion

Kelp forests along the west coast of North America are among the most productive and diverse ecosystems in the world. The giant kelp *Macrocystis pyrifera* is the greatest source of primary production and standing biomass in these temperate rocky bottom coastal ecosystems, whose primary production is consumed directly by grazers, fuels an extremely productive detrital pathway, and constitutes biogenic habitat for invertebrates, fishes, birds and mammals. As such, processes that influence the spatial and temporal variation in the abundance (density and biomass) and productivity of giant kelp has received great attention by benthic ecologists, as well as the consequences of those dynamics to the structure and functions of kelp forest ecosystems (reviewed by Graham *et al.* 2008, Carr and Reed *in press*, Schiel and Foster *in press*). The results of this modeling exercise suggest that change in the dynamics of giant kelp biomass den-

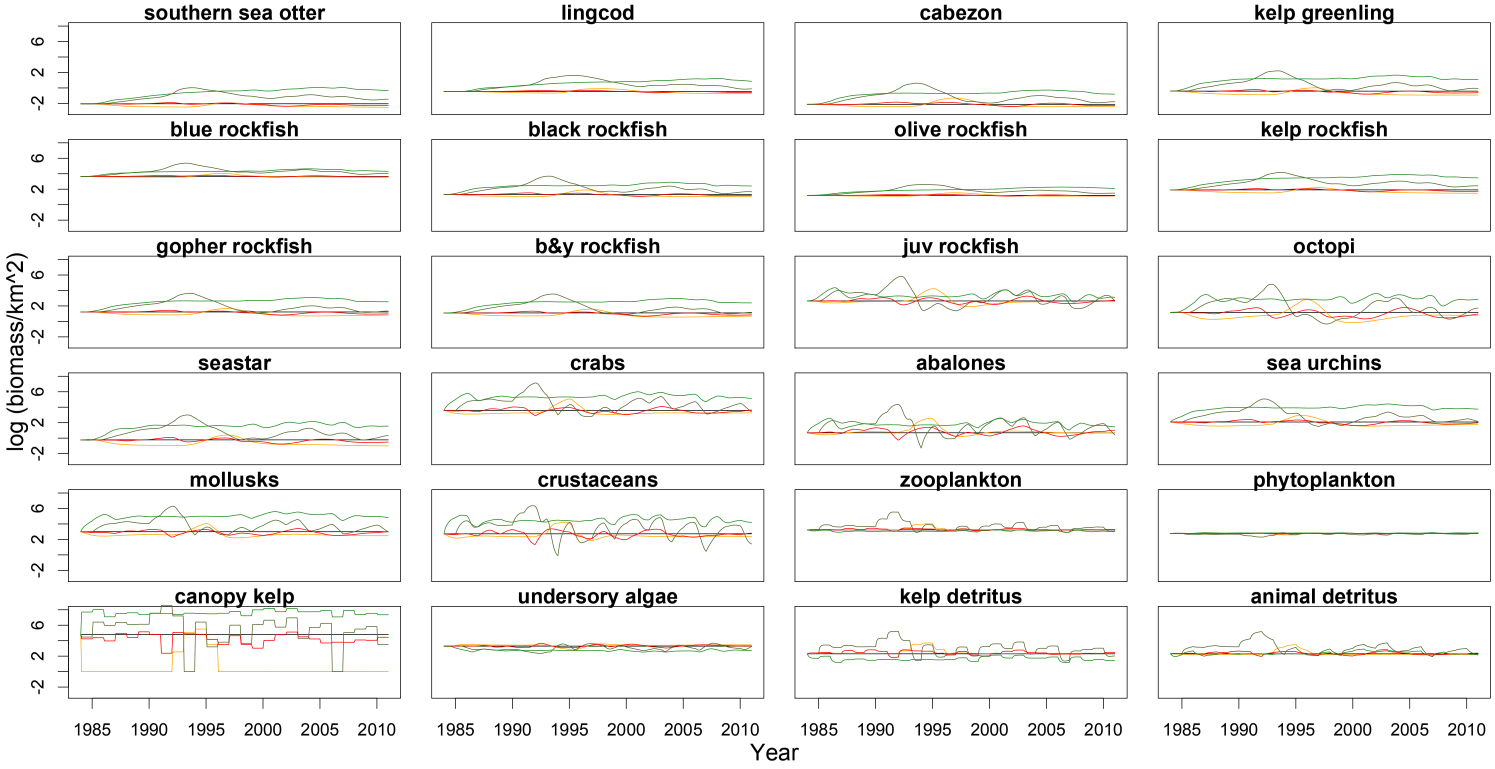

Figure 3.6: Biomass response of the different nodes in the ecological network after fitting the kelp biomass time series for different sub-patch dynamics. Low biomass and low variation (red), low biomass and high variation (orange), high biomass and medium variation (light green), and high biomass and low variation (dark green).

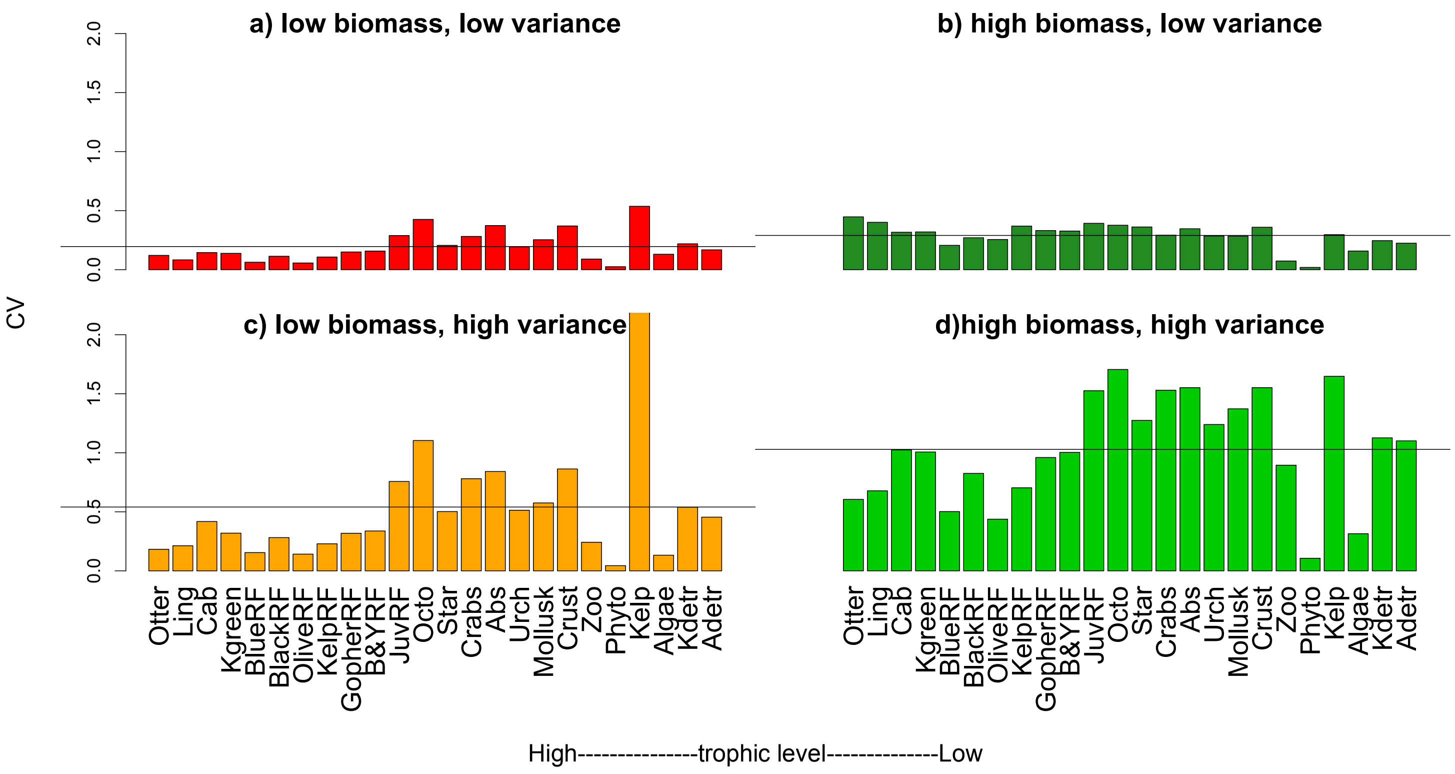

Figure 3.7: Temporal coefficient of variation (CV) of biomass density for each node in the kelp forest ecological network. Low biomass and low variation (red bars), low biomass and high variation (orange bars), high biomass and high variation (light green bars), and high biomass and low variation (dark green bars). The mean CV across nodes for each simulation is indicated with a black line.

sity influence (1) the direction (increases or decreases) and magnitude of change in total biomass of the ecological network (excluding giant kelp itself), (2) how that biomass is distributed across nodes of the network, and (3) the temporal variation in biomass of nodes. Thus, kelp dynamics likely influence the structure (total and relative biomass density of nodes), functional relationships (*i.e.* relative rates of movement of biomass among nodes) and dynamics of kelp forest ecosystems.

The results of this modeling exercise suggest that both the mean and interannual variability of standing biomass density of giant kelp contribute to the overall relationship between kelp dynamics and the direction (increases or decreases) and magnitude of change in total biomass of the ecological network (excluding kelp itself). These predictions corroborate Reed *et al.* (2011) empirical results indicating that differences in the year-to-year frequency of storm disturbance between southern and central California giant kelp forests were the major determinant of both standing biomass density and net primary production (NPP) of giant kelp forests, which are likely to underpin the total biomass of the network. My results suggest that neither mean nor variation in biomass density of kelp separately is most important, but that their combined effects determine the total biomass density of the network. However, the model does suggest that interannual variation is most important at low mean biomass, which also might shed light on why interannual variation is particularly important in limiting NPP of central California forests that also have lower mean annual standing biomass (Reed *et al.* 2011).

The results of this model also predict that different kelp dynamics result in differences in how biomass is distributed across nodes of the network. While many nodes exhibited similar responses in both direction (increases or decreases) and relative magnitude to different scenarios of kelp dynamics, some nodes varied markedly in their direction or relative magnitude of change. These changes in the structure of the network in response to changes in kelp dynamics were also predicted in the only other modeling study of this relationship. Using structural equation modeling, Byrnes *et al.* (2011) found that frequencies of disturbance currently experienced by kelp forests in southern California help maintain the complexity of food webs (*i.e.* the number of nodes in the network), but that increasing storm frequency could reduce food web complexity. The reduced complexity resulted from local extinction of nodes at higher trophic levels, reflecting responses of higher levels of the network to changes at the bottom of the network. In contrast, the results of my models did not exhibit local extinctions of any node, nor disproportionate changes at any particular trophic level. Rather, the change in network structure (*i.e.* the relative biomass across nodes) was contributed to by nodes at higher and lower tropic levels. Thus, responses of the network were more complex and do not lead to predictable changes among trophic levels in this study.

The “short-term” (albeit 30-year) dynamics of nodes also differed among the scenarios of kelp dynamics and this relationship was largely driven by the variability (CV) of the kelp itself. Whether high or low kelp biomass, lower CV of nodes was associated with lower CV of kelp biomass density. In contrast to the complex responses of distribution of biomass among nodes, which was mixed among trophic levels, the response of temporal variation of nodes was stronger among lower trophic levels and more dampened at higher trophic levels. The presumably reflects the stronger, more direct interaction between kelp and the grazers and detritivores in the system relative to the less direct interaction between kelp and higher trophic levels. This pattern would have been magnified had I incorporated more direct interactions between giant kelp and the understory algae, which are known to compete strongly for both light and space on the reef surface (*e.g.*, Reed and Foster 1984, Reed 1990).

While the results of this model suggest that kelp dynamics influences several attributes of kelp forest ecosystems, and is a useful tool for exploring these relationships, the structure of mass balance models has shortcomings for these benthic ecosystems. In their present form, including the model applied in this study, mass balance models only consider trophic interactions. However, non-trophic interactions are known to be very important in these forest ecosystems (reviewed in Carr and Reed *in press*, Schiel and Foster *in press*). Kelp is a major source of biogenic structure and it competes with both algae and invertebrates for space on the reef surface. These additional, complex interactions are not captured in mass balance models. One key advancement in the application of these models for kelp forest ecosystems will be creative ways to capture these additional interactions.

Several studies have identified the effect of increasing or decreasing the diversity of primary producers and its effects on grazer communities (Knoops *et al.* 2009, Hawes *et al.* 2006). Other studies have focused on how change in abundance or biomass of primary producers can lead to a bottom-up trophic cascades (Kagata and Ohgushi 2005, Scherber *et al.* 2010). In this study, I found that the effect of increasing or decreasing biomass density of a key primary producer on the structure and function of an ecosystem will depend on the dynamics (both mean and variance) of the primary producer. For example, I found that high biomass density of giant kelp could have positive or negative effects on other species in the community, but the effect will depend on the variability of that biomass. These results suggest that exploring the separate and combined effects of both mean and variance in biomass of primary producers is critical to advancing our understanding of the influence of primary production on the structure, functions and dynamics of ecosystems.

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# Appendix A

# Characterization of the 24 nodes that constitute the California kelp forest ecological network model

The majority of information used to parameterize the model came directly or were derived from the *Kelpforest database* hosted at www.kelpforest.ucsc.edu. The *Kelpforest* database includes spatially explicit natural history, demographic and species interaction information for species associated with kelp forests in the northeastern Pacific Ocean. The database was designed to parameterize ecological network models (Beas-Luna *et al. submitted*). Biomass density estimates for many of the groups were extracted from an unpublished online database of SCUBA surveys conducted by the Partnership for Interdisciplinary Studies of Coastal Oceans (PISCO; http://data.piscoweb.org/DataCatalogAccess/DataCatalogAccess.html).

With three out of the four basic parameters (Biomass, Production Biomass ratio, Consumption Biomass ratio, Ecotrophic Efficiency) informed by external information, the mass balance model, estimated the fourth parameter in the balancing procedure. For each group below, I identify the sources of externally derived parameter estimates.

### Southern sea otter (*Enhydra lutris nereis*)

The southern sea otter is a marine mammal and an apex predator in central California kelp forests. They range from Año Nuevo Island to just south of Point Conception and San Nicolas Island. The average adult sea otter weighs 45 kg, with an average length of 148 cm (Reeves 2002). Its diet consists primarily of invertebrates such as sea urchins, mollusks and crustaceans (Tinker 2012). *Enhydra lutris* is currently on both the federal and state Endangered Species lists, thus making their population dynamics and range expansion of great interest. I used mean sea otter biomass density estimates (0.154 mt/km$^2$) based on USGS sampling sites in central California from 1985 to 2013 (USGS-WERC 2013, http://www.werc.usgs.gov/project.aspx?projectid=91).

Production/biomass/year (0.15) and consumption/biomass/year (101.5) are from Ainsworth *et al.* (2002). Sea otter diet (Table 2.3) were derived from Tinker *et al.* (2008).

### Lingcod (*Ophiodon elongates*)

Lingcod is a carnivorous, primarily piscivorous, fish, with few predators (*e.g.*, pinnipeds) in central California kelp forests. Their distribution ranges from the Shumagin Islands, Alaska to Baja California, Mexico (Beaudreau 2009). The average length of an adult lingcod is 152 cm (Eschmeyer 1983) and they can live up to 36 years (Love 2011). Lingcod is targeted by both commercial and recreational nearshore fisheries in central California. It has been harvested on the U.S. west coast for over a century. Lingcod was declared overfished in 1999 and declared rebuilt in 2005, several years ahead of schedule due in part to the species high level of productivity (Hamel *et al.* 2009). In California, commercial fishing was more important historically, but has been surpassed in recent years by recreational catches as deeper water habitats have been closed to fishing. Most of the catch is recreational over the past ten year. Mean biomass density (0.627 mt/km$^2$) was calculated from unpublished PISCO SCUBA surveys, conducted at sites in central California from 1999 through 2010. I used the average ($\sim$0.2) of the natural mortality (M) for females (0.32) and males (0.18), based on the 2009 fishery status report

(Hamel *et al.* 2009). Production/biomass/year (0.28) and consumption/biomass/year (2.4) were derived from Preikshot (2005). Prey includes rockfishes (adult and juvenile), cabezon, forage fish, and benthic invertebrates (Tinus 2008, Beaudreau 2009).

### Cabezon (*Scorpaenichthys marmoratus*)

Cabezon are a carnivorous fish that inhabits rocky reefs along the Pacific coast from southern Alaska to central Baja California, Mexico (fishbase.org). Juvenile cabezon feed almost exclusively on small crustaceans. Adults prey on crabs, small lobsters, mollusks (abalone, squid, octopus), small fish (including rockfishes), and fish eggs. In preying on abalone, cabezon have a unique ability to prey smaller animals off of rocks, consume them and regurgitate the shell when done (Love 2011). Its predators include other piscivorous fishes, various marine birds (*e.g.*, cormorants, pigeon guillemots, sooty shearwaters, etc.), harbor seals and sea otters (Love 2011). Cabezon play a similar role to that of lingcod, as adults both species are preyed only by pinnipeds, and juveniles are important prey for other piscivorous fishes. Mean biomass density of cabezon (0.12 mt/km$^2$) was calculated from unpublished PISCO SCUBA surveys, conducted at sites in central California from 1999 through 2010. I used the production/biomass/year of 0.4 reported in Cope and Key (2010). I used a consumption/biomass/year of 2.0 generated in the balancing procedure of the model. Commercial interest in cabezon was generally low but has become lucrative in the live-fish fishery since late 1990s. The importance of the cabezon fishery is reflected in the fact that it is now managed as its own separate harvest group with specific regulations for both sport and commercial fishing. I averaged the reported natural mortality of approximately 0.25 $yr^{-1}$ for females and 0.3 $yr^{-1}$ for males for this group (Pascual and Iribarne 1993).

### Kelp greenling (*Hexagrammos decagrammus*)

Kelp greenling range from La Jolla, California in the south to the Aleutian Islands, Alaska in the north. Mean biomass density (0.6 mt/$km^2$) was calculated from unpublished PISCO SCUBA surveys, conducted at sites in central California from 1999 through 2010. Production/biomass/year (0.3) was derived from Cope and MacCall (2005) and consumption/biomass/year (1.5) was based on Houk (2006) and adjusted in the balancing procedure. Their diet consists primarily of small crustaceans, but such other items as octopus, brittle star fragments, small fish, fish eggs, urchin eggs, chitons, polychaetes, algae, small snails, and small abalones can be found in their stomachs (Burge and Schultz 1973, Houk 2006).

### Blue rockfish (*Sebastes mystinus*)

Blue rockfish are primarily zooplanktivores found from Alaska to Baja California (Love 2011). Blue rockfish can reach up to 53 cm in length and weigh up to 1.8 kg (Love 2011). Their maximum age is recorded at 43 years (Laidig *et al.* 2003). Juveniles are prey to many piscivorous fishes including all rockfishes that inhabit central California kelp forests (Hallacher and Roberts 1985) However, for this model, I have created a separate functional group, “juvenile rockfishes”, that includes blue young-of-the-year and juveniles. Other rockfishes, lingcod and California sea lions consume adults of this group. Blue rockfish adults, prey upon organisms in the water column such as crustaceans, gelatinous zooplankton, arrow worms and polychaetes (Hobson and Chess 1988). Blue rockfish biomass density is the highest of all fish groups in central California kelp forests. Mean biomass density (38.13 mt/km$^2$) was calculated from unpublished PISCO SCUBA surveys, conducted at sites in central California from 1999 through 2010. The production/biomass/year (0.21) and the consumption rate/biomass/year (1.5) were adapted from Field (2004).

### Black rockfish (*Sebastes melanops*)

This is one of the most common mid-water species in the kelp forests of central California. Their distribution ranges from Santa Barbara, California in the south, to Amchitka Island, Alaska to the north (Love 2011). Mean biomass density (3.7 mt/km$^2$) was calculated from unpublished PISCO SCUBA surveys, conducted at sites in central California from 1999 through 2010. Production/biomass/year (0.3) and the consumption rate/biomass/year (1.5) ratios where adapted from Field (2004) in the balancing procedure of this model. Black rockfish have increasingly become important fished species in the recreational catch in this area. Black rockfish juveniles prey principally upon copepods, gammarid, and caprellid amphipods, however, sixteen other prey items have been identified (Studebaker and Mulligan 2009). Adult black rockfishes prey mainly on juvenile rockfishes, euphausids and polychaetes (Hallacher and Roberts 1985).

### Olive rockfish (*Sebastes serranoides*)

Olive rockfish can be found in the mid-water column of the kelp forests from northern California to Baja California. These fish are fairly sedentary, measure up to 0.5 m in length and have a life span of 25 years (Love 2011). They prey mostly on juvenile fish, octopus, squids, and other planktonic and benthic invertebrates (Hallacher and Roberts 1985). Mean biomass density (4.9 mt/km$^2$) was calculated from unpublished PISCO SCUBA surveys, conducted at sites in central California from 1999 through 2010. Production/biomass/year (0.13) and the consumption rate/biomass/year (1.3) were used based on Harvey *et al.* (2012) for the "rockfish group" and adapted to this model during the balancing procedure. Olive rockfish are common in recreational catches from Commercial Passenger Fishing Vessels (CPFV) in central California. They are rarely found in commercial fishing catches. Not only they are very common in central California kelp forests, but also exhibit a rather different diet from other rockfishes (*i.e.*, generalist predators including fish, benthic and water column invertebrates) and thus, a unique component in the model.

### Kelp rockfish (*Sebastes atrovirens*)

Kelp rockfish are among the most abundant shallow-dwelling reef fishes in central California (Hallacher and Roberts 1985). Its distribution and abundance are strongly related with the presence of *Macrocystis pyrifera* from Baja California, Mexico in the south to Santa Cruz, California in the north (Foster and Schiel 1985). Kelp rockfish are important to the recreational and nearshore live-fish fishery along the central California coast. Principal diet includes juvenile rockfishes and small mollusks, crustaceans and zooplankton (Hallacher and Roberts 1985). Mean biomass density (6.7 mt/km$^2$) was calculated from unpublished PISCO SCUBA surveys, conducted at sites in central California from 1999 through 2010. Production/biomass/year (0.21) and consumption/biomass/year (1.5) were based on Harvey *et al.* (2012) for the "rockfish group" and adapted to this model during the balancing procedure.

### Gopher rockfish (*Sebastes carnatus*)

Gopher rockfish range from northern Baja California, Mexico in the south to northern California (Love 2011). They are closely related to black-and-yellow rockfish. They can reach lengths of up to 39.6 cm (Love 2011) and live for up to 30 years (Bloeser 1999). Adult fish have a diet of benthic crustaceans (crabs, shrimps, mysid shrimps, isopods and gammarid amphipods) and fishes, some squids, octopus, snails, polychaetes, brittle stars and fish eggs (Hallacher and Roberts 1985, Loury 2011). Gopher rockfish were a minor component of the commercial and recreational rockfish fishery since at least the late 1960s, but recently make up about 50% of the estimated take of the shallow nearshore rockfishes and 6% of all nearshore rockfish species combined (Key *et al.* 2005). Mean biomass density (3.09 mt/km$^2$) was calculated from unpublished PISCO SCUBA surveys, conducted at sites in central California from 1999 through 2010. Production/biomass/year (0.22) and consumption/biomass/year (1.43) were based on (Harvey *et al.* 2012). Natural mortality (M) was estimated as the average of males (0.32) and females (0.18), based on the 2009 Status Report by Key *et al.* (2005).

### Black and yellow rockfish (*Sebastes chrysomelas*)

Black and yellow rockfish are closely related to the gopher rockfish. In fact, Narum *et al.* (2004) classified them as “incipient species”. They are found from Cape Blanco, Oregon to central Baja California, Mexico, and reach lengths of 38.7 cm, while living up to 30 years (Love, 2011). Competition between black and yellow rockfish and gopher rockfish is thought to be the cause of their relative depth stratification (Larson 1980); black and yellow rockfish are shallower than gopher rockfish. Black and yellow rockfish feed primarily on benthic organisms: crab and shrimp, but also feed on fishes, gammarid, isopods, amphipods, snails, chiton octopuses, hydrozoans, bryozoans and kelp fragments (Hallacher and Roberts 1985). Black and yellow rockfish is an important portion of the live fish fishery in central California. Mean biomass density (2.55 mt/km$^2$) was calculated from unpublished PISCO SCUBA surveys, conducted at sites in central California from 1999 through 2010. Production/biomass/year (0.22) and consumption/biomass/year (1.6) were based on Harvey *et al.* (2012) and Field (2004).

### Juvenile rockfishes

The juvenile rockfishes group is comprised by the juveniles of blue rockfish, the olive-yellow tail (OYT) complex, and the kelp, gopher, and black and yellow complex (KGB), and black rockfish. I selected these two complexes of juvenile rockfishes because they are the most abundant groups that recruit in kelp forests in central California (Carr 1991). The biomass of this group is one of the primary driving mechanisms in the model because they are a large source of biomass that is consumed by all of the fishes in the model, especially in the spring and summer (Hallacher and Roberts 1985). Interannual variation in recruitment rates (number per year) appears to correlate with oceanic processes such as upwelling, sea surface temperature (SST), and sea level anomalies (Caselle *et al.* 2010, Ralston *et al.* 2013). In my attempt to link juvenile rockfish to the adult groups suggested by Walters *et al.* (2010), I found a series of difficulties. Specifically, I found the multistanza approach to influence the dynamics of the Ecosim runs and found as the system never started in an stable equilibrium. Production/biomass/year (0.31) and consumption/biomass/year (4.3) were based on Ainsworth *et al.* (2002), Field (2004), and Harvey *et al.* (2012). The mean biomass density of 1.045 mt/km$^2$ was estimated using multi stanza calculations in previous models parameterized with PISCO survey data. The most preferred prey for juvenile rockfish in this model is zooplankton and small crustaceans. They are prey items for all the groups of fishes in this model. Finally, I separated this functional group from the adult groups to explore the effect of fishing, species interactions and climate variation on the different life stages.

### Octopus

There are two well distinguished species of octopus in the kelp forests of central and southern California, *Octopus bimaculatus* and *O. rubescens* (Graham 2004). These organisms are voracious gastropod predators, and represent the highest trophic level of invertebrates in this model. They prey on large crustaceans, crabs, sea urchins and abalones (Ambrose 1986). The natural mortality rate (M) of octopus is close to or greater than 0.5 (Hatanaka 1979). This high mortality rate might reflect the short lifespan (even in the case of males), rapid growth rate and high rates of consumption of octopus by many demersal fishes. I used a biomass density for this group of 1.2 mt/km$^2$, production/biomass/year ratio of 0.86, and consumption/biomass/year ratio of 2.9 (Harvey *et al.* 2012).

### Predatory seastars

In the model, this group is composed principally by *Pycnopodia helianthoides*, the sunflower star. This group of asteroids is considered very important in the structure and dynamics of kelp forests in central California (Herrlingler 1983). Predation by these seastars can produce mosaics of ephemeral patches free of herbivores and this can have a significant effect on rates of primary production of the system (Duggins 1983). The diet of this group includes mollusks, crustaceans, sea urchins, crabs and animal detritus (Herrlingler 1983, Shivji *et al.* 1983). Mean biomass density (0.8 mt/km$^2$) was calculated from unpublished PISCO SCUBA surveys, conducted at sites in central California from 1999 through 2010. Production/biomass/year (0.52) and consumption/biomass/year (2.6) were based on Harvey *et al.* (2012).

### Crabs

Crabs are important trophic links in kelp habitats and can influence food web dynamics by acting as algal and animal detritivores, grazers, primary consumers, and as a key food source for secondary consumers (Hines 1982). This group combines the different species from the genus *Cancer* and the species of the family Majidae. These crabs feed on giant kelp, understory algae, sessile invertebrates, and algal and animal detritus. Mean biomass density (36 mt/km$^2$)was estimated using PISCO density and length-weight relationships generated with field collections for this project. Production/biomass/year (1.312) was based on Harvey *et al.* (2012) and consumption/biomass/year (5.00) was based on Ainsworth *et al.* (2002).

### Abalones (***Haliotis spp.***)

Abalones, *Haliotis spp.*, are mobile algal detritivores and benthic grazers closely associated with kelp forests. In central California, they are so heavily preyed on by the southern sea otter, and they have not supported a commercial fishery for decades. Since 1997, recreational take has been terminated in central California. Abalone diet includes kelp, understory algae, and algal detritus. The biomass density was estimated from PISCO subtidal densities and size-weight estimations (Rogers-Bennett *et al.* 2007). The production/biomass ratio (1.9 years$^{-1}$) and consumption/ biomass ratio (12.7 years$^{-1}$) reported by Espinosa-Romero *et al.* (2011) was increased to 2.0 years$^{-1}$ and reduced to 10 years$^{-1}$, respectively, in the balancing process of this model.

### Sea urchins

Along the coast of central California, sea urchins such as *Strongylocentrotus purpuratus* and *Mesocentrotus* (formally *Strongylocentrotus*) *franciscanus*, are thought to be very important grazers in kelp forest ecosystems. These are voracious herbivores of the giant kelp, *Macrocystis pyrifera.* They can weaken the holdfast, releasing the entire sporophyte from the substratum, thereby causing export of kelp biomass out of the system. Mean biomass density (2.79 mt/km$^2$) was calculated from unpublished PISCO SCUBA surveys, conducted at sites in central California from 1999 through 2010, combined with length-weight equations provided by Sarah Teck (Table A3) and adjusted to the model in the balancing procedure. Production/biomass/year (0.4) and consumption/biomass/year (10.8) rates were adjusted from Harvey (2012).

### Herbivorous mollusks

This group represents the many species of small gastropods, excluding juvenile abalones, found in kelp forests in central California. The group includes snails and limpets of the genus *Chlorostoma, Calliostoma, Ceratostoma, Diodora, Lithopoma, Megathura, Mitra, Tegula*, and others. The diet of this group includes giant kelp, understory algae (including both suc-canopy forming kelps and red foliose algae) and kelp detritus. Mean biomass density (20 mt/km$^2$) and production/biomass/year ratio (1.0) ratios were adapted from Preikshot *et al.* (2005). Consumption/biomass/year ratio (8.86) was adapted from other grazers (Harvey *et al.* 2012).

### Crustaceans

This group includes the myriad species of small ($<$ 2 cm in length) crustaceans associated with giant kelp, understory algae, and kelp detritus. The group is comprised of species in such families as Caprellidae, Gammaridae, Tanaidae and the order Isopoda.

Mean biomass density was generated by the model balancing, but I set the ecotrophic efficiency at 0.9 as this group is an extremely important prey of adults of many fishes and juveniles of all fishes in kelp forests in central California (*e.g.*, Burge and Schultz 1973, Hallacher and Roberts 1985). Mean biomass density (6.93 mt/km$^2$) was estimated by our model. Production/biomass/year (3.41) and consumption/biomass/year (25.0) ratios were adapted from Harvey *et al.* (2012).

### Zooplankton

This group is principally represented by copepods, larvaceans, euphausid furcilia, zoea, chaetognaths, ctenophores, crab megalops, small medusa and barnacle cyprids and nauplii. The diet of this group includes other zooplankton, phytoplankton and both forms of detritus. Mean biomass density (22.0 mt/km$^2$) was estimated by the model. Ecotrophic efficiency was set to (0.8) as the group of a very important diet item for most of the fished species. Production/biomass/year (16.5) and consumption/biomass/year (62.5) were adapted from Field (2004), personal communication (J. Field), and unpublished data from Baldo Marinovic at UC Santa Cruz.

### Phytoplankton

This group represents all photosynthetic primary producers in the water column inside kelp forests in central California. Diatoms are the dominant taxon in this group. Mean biomass density (16.0 mt/km$^2$) was adjusted from Ainsworth *et al.* (2002). The production/biomass/year (179.0) was adapted from Espinosa-Romero *et al.* (2011).

### Giant kelp (*Macrocystis pyrifera*)

The network model only considers giant kelp, *Macrocystis pyrifera*, as the canopy-forming kelp in central California. Although other canopy-forming kelps occur in central California (*e.g.*, *Nereocystis luetkeana, Egregia menziesii*) the model focuses on giant kelp because of its predominance in the area, its great productivity, and role as a major source of biogenic habitat structure (reviewed by Graham *et al.* 2007, 2008, Foster and Scheil 1985, Carr and Reed *in press*). Mean biomass density (120.8 mt/km$^2$) was calculated using PISCO average frond density for all sites in central California and transformed to biomass density using the relationship between density and foliar standing crop (FSC: dry kg m$^2$) for *Macrocystis pyrifera* individuals and *M. pyrifera* fronds in Reed *et al.* (2009). The production/biomass/year (42.9) was adapted from Harvey *et al.* (2012).

### Understory algae

This group represents the short primary producers (algae) within the kelp forest. This group includes the sub-canopy kelps (*e.g.*, *Eisenia arborea, Pterygophora californica, Laminaria spp.*). It also represents understory brown, red and green algae, including the coralline algae. However, the parameter estimations for mean biomass density (27.0) used in this model was based on density data from unpublished PISCO SCUBA surveys, conducted at sites in central California from 1999 through 2010, transformed to biomass density using Reed *et al.* (2009) relationship for macroalgae collected on "swath" surveys. Table 2.2 lists the biomass for 16 species of understory macroalgae in the kelp forest. The mean biomass for each species was used to calculate the mean biomass of all species (16.001 mt/km$^2$). Production/biomass/year (15.0) was based on Harvey *et al.* (2012) for benthic macroalgae.

**Algal and animal detritus**

In most ecosystems, everything that dies go to the detritus loop. In nature, the detrital pathway feeds back into the system as nutrients for primary producers, planktivores, and detritivores. In this model, I have split this group into algal detritus and animal detritus to explore the effects of these two different pathways and the fate of the material in the kelp forests of central California. All energy that is not consumed in the model by other functional groups is directed to the two detritus functional groups. Parameters for this group are estimated by the model despite the fact that wet biomass can be determined from in situ estimates of percent cover (Figurski 2010): Wet biomass = (0.959 + 27.492 ($\sin^{-1}$ square root Cover/100) )$^2$; $R^2 = 0.874$, $P < 0.000001$.

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# Appendix B

# Supplemental material

Table B.1: Model estimates of the combined direct and indirect impacts (Mixed Trophic Impacts) that nodes in rows have on nodes in columns.

| **Impacted**<br>**Impacting** | sea otter | lingcod | cabezon | kelp greenling | blue rockfish | black rockfish | olive rockfish | kelp rockfish | gopher rockfish | black & yellow rockfish | juvenile rockfish | octopus |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| sea otter | -0.254 | -0.008 | -0.081 | -0.020 | 0.010 | 0.015 | 0.006 | -0.019 | -0.071 | -0.071 | 0.020 | -0.073 |
| lingcod | 0.000 | -0.073 | -0.946 | -0.424 | 0.003 | -0.060 | -0.040 | -0.157 | -0.087 | -0.087 | -0.001 | 0.103 |
| cabezon | 0.000 | 0.014 | -0.022 | -0.019 | 0.003 | -0.050 | -0.004 | -0.016 | -0.006 | -0.006 | 0.001 | -0.002 |
| kelp greenling | 0.002 | 0.043 | -0.027 | -0.031 | 0.000 | 0.006 | -0.004 | -0.012 | -0.008 | -0.008 | -0.003 | -0.027 |
| blue rockfish | 0.012 | -0.267 | 0.180 | 0.155 | -0.081 | -0.088 | -0.041 | 0.011 | -0.094 | -0.094 | -0.553 | 0.028 |
| black rockfish | -0.007 | -0.022 | 0.069 | -0.436 | 0.024 | 0.042 | -0.039 | -0.093 | -0.057 | -0.057 | -0.064 | 0.045 |
| olive rockfish | 0.007 | 0.148 | -0.090 | -0.079 | -0.561 | 0.051 | -0.341 | 0.000 | -0.211 | -0.211 | 0.310 | -0.006 |
| kelp rockfish | 0.016 | -0.014 | -0.017 | 0.186 | 0.073 | -0.488 | -0.090 | -0.311 | -0.139 | -0.139 | -0.034 | -0.191 |
| gopher rockfish | -0.015 | 0.057 | -0.037 | -0.038 | -0.021 | -0.010 | 0.012 | -0.010 | -0.056 | -0.056 | -0.049 | -0.133 |
| black & yellow rockfish | -0.014 | 0.061 | -0.038 | -0.039 | -0.022 | -0.010 | 0.013 | -0.009 | -0.053 | -0.053 | -0.044 | -0.121 |
| juvenile rockfish | 0.039 | 0.430 | -0.311 | -0.369 | -0.038 | 0.049 | 0.121 | -0.070 | 0.104 | 0.104 | -0.128 | 0.008 |
| octopus | -0.087 | 0.031 | 0.005 | 0.019 | -0.016 | -0.003 | 0.029 | 0.014 | 0.023 | 0.023 | 0.016 | -0.245 |
| predatory seastars | -0.021 | 0.002 | 0.007 | -0.003 | 0.001 | 0.005 | 0.001 | -0.001 | 0.006 | 0.006 | 0.001 | -0.014 |
| crabs | 0.360 | 0.037 | 0.074 | 0.092 | -0.014 | -0.010 | -0.010 | 0.076 | 0.247 | 0.247 | -0.046 | 0.069 |
| abalones | 0.053 | 0.003 | 0.169 | -0.007 | -0.001 | -0.009 | 0.002 | -0.006 | -0.008 | -0.008 | 0.002 | 0.066 |
| sea urchins | 0.118 | -0.010 | -0.023 | -0.025 | -0.003 | -0.001 | -0.003 | -0.016 | -0.025 | -0.025 | -0.002 | -0.035 |
| herbivorous mollusks | -0.058 | -0.009 | -0.029 | 0.057 | -0.011 | -0.060 | -0.008 | 0.034 | -0.047 | -0.047 | -0.010 | 0.218 |
| crustaceans | -0.097 | 0.100 | -0.030 | 0.212 | 0.083 | 0.153 | 0.074 | 0.098 | 0.045 | 0.045 | 0.123 | -0.094 |
| zooplankton | -0.029 | 0.057 | -0.072 | -0.124 | 0.177 | 0.104 | 0.067 | -0.022 | -0.052 | -0.052 | 0.128 | -0.011 |
| phytoplankton | -0.021 | 0.039 | -0.045 | -0.064 | 0.111 | 0.070 | 0.044 | -0.009 | -0.029 | -0.029 | 0.083 | -0.011 |
| canopy kelp | 0.090 | 0.029 | 0.020 | 0.086 | 0.013 | 0.014 | 0.013 | 0.049 | 0.049 | 0.049 | 0.016 | 0.065 |
| understory algae | 0.082 | 0.025 | 0.024 | 0.078 | 0.009 | 0.007 | 0.009 | 0.046 | 0.049 | 0.049 | 0.010 | 0.074 |
| kelp detritus | 0.166 | 0.071 | 0.097 | 0.120 | 0.065 | 0.066 | 0.043 | 0.074 | 0.077 | 0.077 | 0.066 | 0.081 |
| detritus | 0.033 | 0.007 | 0.004 | 0.003 | 0.008 | 0.005 | 0.002 | 0.006 | 0.023 | 0.023 | 0.002 | 0.005 |

Table B.1 Continued

| Impacted<br>Impacting | predatory seastars | crabs | abalones | sea urchins | herbivorous mollusks | crustaceans | zooplankton | phytoplankton | canopy kelp | understory algae | kelp detritus | detritus |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| sea otter | -0.150 | -0.209 | -0.232 | -0.519 | 0.045 | 0.048 | 0.003 | -0.003 | 0.071 | 0.063 | 0.041 | 0.041 |
| lingcod | -0.014 | 0.009 | -0.042 | 0.003 | -0.044 | 0.024 | 0.000 | -0.001 | 0.002 | 0.005 | -0.002 | -0.002 |
| cabezon | 0.001 | 0.002 | -0.015 | -0.001 | 0.002 | 0.002 | 0.000 | 0.000 | -0.001 | -0.001 | 0.000 | 0.000 |
| kelp greenling | 0.002 | 0.001 | 0.015 | -0.001 | 0.009 | -0.009 | 0.000 | 0.000 | 0.001 | 0.000 | 0.001 | 0.000 |
| blue rockfish | -0.003 | 0.018 | -0.006 | 0.008 | -0.007 | -0.049 | -0.019 | 0.019 | 0.015 | 0.014 | 0.019 | 0.011 |
| black rockfish | -0.001 | -0.011 | -0.018 | 0.012 | -0.007 | -0.011 | 0.000 | 0.000 | 0.008 | 0.008 | 0.004 | 0.002 |
| olive rockfish | -0.005 | 0.020 | -0.012 | -0.018 | -0.008 | 0.033 | 0.011 | -0.012 | -0.012 | -0.012 | -0.014 | -0.013 |
| kelp rockfish | 0.010 | 0.014 | 0.099 | -0.016 | 0.042 | -0.032 | -0.002 | 0.002 | -0.003 | -0.007 | 0.002 | -0.002 |
| gopher rockfish | 0.027 | -0.040 | 0.071 | -0.004 | 0.078 | 0.001 | 0.004 | -0.003 | -0.015 | -0.017 | -0.006 | 0.005 |
| black & yellow rockfish | 0.024 | -0.037 | 0.065 | -0.004 | 0.071 | 0.002 | 0.003 | -0.003 | -0.014 | -0.015 | -0.006 | 0.005 |
| juvenile rockfish | 0.015 | 0.036 | 0.052 | 0.033 | 0.067 | -0.275 | -0.038 | 0.042 | 0.069 | 0.056 | 0.071 | 0.023 |
| octopus | -0.112 | -0.107 | -0.316 | 0.171 | -0.396 | 0.039 | 0.004 | -0.004 | 0.114 | 0.138 | 0.038 | 0.020 |
| predatory seastars | -0.066 | 0.016 | 0.030 | -0.148 | -0.057 | 0.009 | 0.001 | -0.001 | 0.024 | 0.022 | 0.009 | -0.006 |
| crabs | -0.105 | -0.280 | -0.244 | -0.326 | -0.149 | -0.051 | -0.003 | 0.004 | -0.066 | -0.092 | -0.036 | -0.146 |
| abalones | -0.029 | -0.034 | -0.063 | -0.034 | -0.041 | 0.001 | 0.000 | 0.000 | 0.012 | 0.012 | -0.006 | 0.007 |
| sea urchins | 0.226 | -0.060 | -0.060 | -0.170 | -0.040 | -0.024 | -0.002 | 0.002 | -0.047 | -0.021 | -0.026 | 0.013 |
| herbivorous mollusks | 0.242 | -0.124 | -0.162 | -0.089 | -0.281 | -0.086 | 0.000 | 0.002 | -0.142 | -0.171 | -0.029 | 0.025 |
| crustaceans | -0.002 | -0.104 | -0.061 | -0.086 | -0.113 | -0.251 | -0.028 | 0.014 | -0.207 | -0.175 | -0.139 | 0.043 |
| zooplankton | -0.052 | -0.034 | -0.064 | -0.012 | 0.013 | -0.173 | -0.579 | -0.410 | 0.069 | 0.063 | -0.148 | -0.326 |
| phytoplankton | -0.029 | -0.026 | -0.042 | -0.003 | 0.001 | -0.067 | 0.251 | -0.246 | 0.031 | 0.029 | -0.096 | -0.193 |
| canopy kelp | 0.116 | 0.090 | -0.007 | 0.111 | 0.154 | 0.139 | -0.008 | 0.006 | -0.128 | -0.128 | -0.062 | -0.012 |
| understory algae | 0.092 | 0.102 | 0.003 | 0.024 | 0.164 | 0.104 | -0.007 | 0.005 | -0.112 | -0.116 | -0.053 | -0.016 |
| kelp detritus | 0.121 | 0.133 | 0.430 | 0.185 | 0.082 | 0.279 | 0.068 | -0.072 | -0.180 | -0.172 | 0.000 | -0.082 |
| detritus | 0.080 | 0.072 | -0.025 | -0.048 | -0.020 | -0.013 | 0.021 | -0.020 | -0.001 | -0.004 | -0.010 | 0.000 |

Table B.2: Summary statistics for the different Ecopath models.

| Models | Total system throughput $t/km^2/year$ | Sum of all production $t/km^2/year$ | Mean trophic level of the catch | Net system Production $t/km^2/year$ | Total biomass $t/km^2$ | PP/Biomass |
|---|---|---|---|---|---|---|
| Fishing gopher rockfish | 18264.21 | 8954.408 | 3.437059 | 6863.05 | 332.8959 | 25.38728 |
| No fishing | 18264.15 | 8954.408 | - | 6863.05 | 332.8959 | 25.38728 |
| Fishing cabezon | 18264.14 | 8954.408 | 3.689733 | 6863.05 | 332.8959 | 25.38728 |
| Fishing kelp greenling | 18264.12 | 8954.408 | 3.117647 | 6863.05 | 332.8959 | 25.38728 |
| Fishing lingcod | 18264.09 | 8954.408 | 4.289766 | 6863.05 | 332.8959 | 25.38728 |
| Fishing black rockfish | 18264.02 | 8954.408 | 3.375257 | 6863.05 | 332.8959 | 25.38728 |
| Fishing blue rockfish | 18262.75 | 8954.408 | 3.330588 | 6863.05 | 332.8959 | 25.38728 |
| Fishing all spp combined | 18262.58 | 8954.408 | 3.325952 | 6863.05 | 332.8959 | 25.38728 |

Table B.3: Best fit parameter estimates for mass-balanced model based on Monte Carlo simulation results after 100 trials. Original SS=182.8, Best SS=148.1.

| Group name | No fishing | Fishing lingcod | Fishing cabezon | Fishing kelp greenlings | Fishing blue rofkcfish | Fishing black rockfish | Fishing gopher | Fishing all |
|---|---|---|---|---|---|---|---|---|
| sea otter | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 |
| lingcod | 0.000 | **0.339** | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | **0.339** |
| cabezon | 0.616 | 0.616 | **0.824** | 0.616 | 0.616 | 0.616 | 0.616 | **0.824** |
| kelp greenling | 0.689 | 0.689 | 0.689 | **0.841** | 0.689 | 0.689 | 0.689 | **0.841** |
| blue rockfish | 0.084 | 0.084 | 0.084 | 0.084 | **0.259** | 0.084 | 0.084 | **0.259** |
| black rockfish | 0.263 | 0.263 | 0.263 | 0.263 | 0.263 | **0.380** | 0.263 | **0.380** |
| olive rockfish | 0.500 | 0.500 | 0.500 | 0.500 | 0.500 | 0.500 | 0.500 | 0.500 |
| kelp rockfish | 0.274 | 0.274 | 0.274 | 0.274 | 0.274 | 0.274 | 0.274 | 0.274 |
| gopher rockfish | 0.700 | 0.700 | 0.700 | 0.700 | 0.700 | 0.700 | 0.700 | 0.700 |
| black & yellow rockfish | 0.700 | 0.700 | 0.700 | 0.700 | 0.700 | 0.700 | 0.700 | 0.700 |
| juvenile rockfish | 0.800 | 0.800 | 0.800 | 0.800 | 0.800 | 0.800 | 0.800 | 0.800 |
| octopus | 0.900 | 0.900 | 0.900 | 0.900 | 0.900 | 0.900 | 0.900 | 0.900 |
| predatory seastars | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 |
| crabs | 0.373 | 0.373 | 0.373 | 0.373 | 0.373 | 0.373 | 0.373 | 0.373 |
| abalones | 0.581 | 0.581 | 0.581 | 0.581 | 0.581 | 0.581 | 0.581 | 0.581 |
| sea urchins | 0.800 | 0.800 | 0.800 | 0.800 | 0.800 | 0.800 | 0.800 | 0.800 |
| herbivorous mollusks | 0.214 | 0.214 | 0.214 | 0.214 | 0.214 | 0.214 | 0.214 | 0.214 |
| crustaceans | 0.900 | 0.900 | 0.900 | 0.900 | 0.900 | 0.900 | 0.900 | 0.900 |
| zooplankton | 0.800 | 0.800 | 0.800 | 0.800 | 0.800 | 0.800 | 0.800 | 0.800 |
| phytoplankton | 0.894 | 0.894 | 0.894 | 0.894 | 0.894 | 0.894 | 0.894 | 0.894 |
| canopy kelp | 0.031 | 0.031 | 0.031 | 0.031 | 0.031 | 0.031 | 0.031 | 0.031 |
| understory algae | 0.363 | 0.363 | 0.363 | 0.363 | 0.363 | 0.363 | 0.363 | 0.363 |
| kelp detritus | 0.234 | 0.234 | 0.234 | 0.234 | 0.234 | 0.234 | 0.234 | 0.234 |
| detritus | 0.544 | 0.544 | 0.544 | 0.544 | 0.546 | 0.544 | 0.544 | 0.546 |

Table B.4: Ecotrophic Efficiency (EE) for the different fishing scenarios. Bold numbers represent an increment from no fishing to fishing for the different models.

| Group name | Biomass | Production/ biomass | Consumtion/ biomass | Ecotrophic efficiency |
|---|---|---|---|---|
| sea otter | 0.141 | 0.137 | 86.097 | 0.222 |
| lingcod | 0.613 | 0.257 | 2.276 | 0.479 |
| cabezon | 0.132 | 0.343 | 2.198 | 0.917 |
| kelp greenling | 0.666 | 0.293 | 1.440 | 0.561 |
| blue rockfish | 41.252 | 0.210 | 1.444 | 0.520 |
| black rockfish | 3.495 | 0.248 | 1.318 | 0.558 |
| olive rockfish | 5.416 | 0.144 | 1.218 | 0.823 |
| kelp rockfish | 7.272 | 0.207 | 1.512 | 0.292 |
| gopher rockfish | 3.392 | 0.229 | 1.462 | 0.633 |
| black & yellow rockfish | 2.467 | 0.197 | 1.611 | 0.999 |
| juvenile rockfish | 8.151 | 1.489 | 5.898 | 0.937 |
| octopus | 2.486 | 1.031 | 5.027 | 0.819 |
| predatory seastars | 0.820 | 0.605 | 2.440 | 0.086 |
| crabs | 37.237 | 1.159 | 5.134 | 0.426 |
| abalones | 1.693 | 2.256 | 10.308 | 0.610 |
| sea urchins | 7.081 | 0.462 | 12.100 | 0.635 |
| herbivorous mollusks | 20.867 | 1.021 | 9.018 | 0.424 |
| crustaceans | 11.145 | 3.651 | 24.972 | 0.880 |
| zooplankton | 19.131 | 17.552 | 54.020 | 0.716 |
| phytoplankton | 14.665 | 160.118 | 0.000 | 0.270 |
| canopy kelp | 103.158 | 49.331 | 0.000 | 0.041 |
| understory algae | 29.582 | 16.706 | 0.000 | 0.378 |

Table B.5: Empirical time series used in the Ecosim module.

| Name | southern sea otter | lingcod | cabezon | kelp greenling | blue rockfish | juvenile rockfishes | black rockfish | olive rockfish | kelp rockfish | gopher rockfish | black & yellow rockfish | sea urchins | giant kelp |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| pool | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 | 11 | 16 | 21 |
| code | | | | | | | | | | | | | |
| type | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 |
| 1999 | 0.129 | 0.470 | 1.250 | 0.660 | 3.300 | 0.100 | 3.703 | 0.828 | 6.780 | 0.309 | 2.530 | 2.790 | 120.00 |
| 2000 | 0.120 | 0.037 | 0.807 | 0.426 | 5.017 | 0.027 | 0.279 | 0.403 | 3.298 | 0.362 | 1.285 | 1.417 | 142.42 |
| 2001 | 0.116 | 0.605 | 0.979 | 0.517 | 5.500 | 0.108 | 2.139 | 1.250 | 10.229 | 1.426 | 1.522 | 1.678 | 130.30 |
| 2002 | 0.118 | 1.001 | 0.844 | 0.446 | 22.660 | 0.259 | 3.384 | 2.489 | 20.367 | 3.126 | 2.216 | 2.444 | 175.10 |
| 2003 | 0.119 | 1.636 | 0.915 | 0.483 | 13.920 | 0.169 | 4.251 | 2.113 | 17.290 | 2.668 | 2.084 | 2.298 | 79.78 |
| 2004 | 0.118 | 2.812 | 1.093 | 0.577 | 18.585 | 0.050 | 3.056 | 1.818 | 14.877 | 3.399 | 2.683 | 2.959 | 146.81 |
| 2005 | 0.126 | 1.020 | 0.636 | 0.336 | 11.657 | 0.003 | 1.672 | 0.967 | 7.913 | 3.103 | 2.324 | 2.563 | 167.69 |
| 2006 | 0.130 | 0.758 | 0.836 | 0.441 | 19.607 | 0.001 | 2.715 | 1.631 | 13.346 | 2.241 | 2.081 | 2.295 | 51.37 |
| 2007 | 0.130 | 0.734 | 0.650 | 0.343 | 6.351 | 0.000 | 2.355 | 0.764 | 6.252 | 1.921 | 1.699 | 1.874 | 136.44 |
| 2008 | 0.119 | 0.402 | 0.864 | 0.456 | 3.968 | 0.001 | 2.093 | 0.478 | 3.911 | 1.689 | 1.867 | 2.059 | 145.06 |
| 2009 | 0.115 | 0.507 | 0.619 | 0.327 | 4.290 | 0.032 | 2.843 | 0.450 | 3.682 | 1.734 | 0.951 | 1.049 | 183.05 |
| 2010 | 0.112 | 0.321 | 0.234 | 0.124 | 7.715 | 0.000 | 1.071 | 0.792 | 6.481 | 1.281 | 0.978 | 1.079 | 118.20 |
| 2011 | 0.116 | 0.511 | 1.201 | 0.634 | 7.000 | 0.012 | 3.709 | 0.513 | 4.198 | 1.314 | 1.816 | | 49.25 |

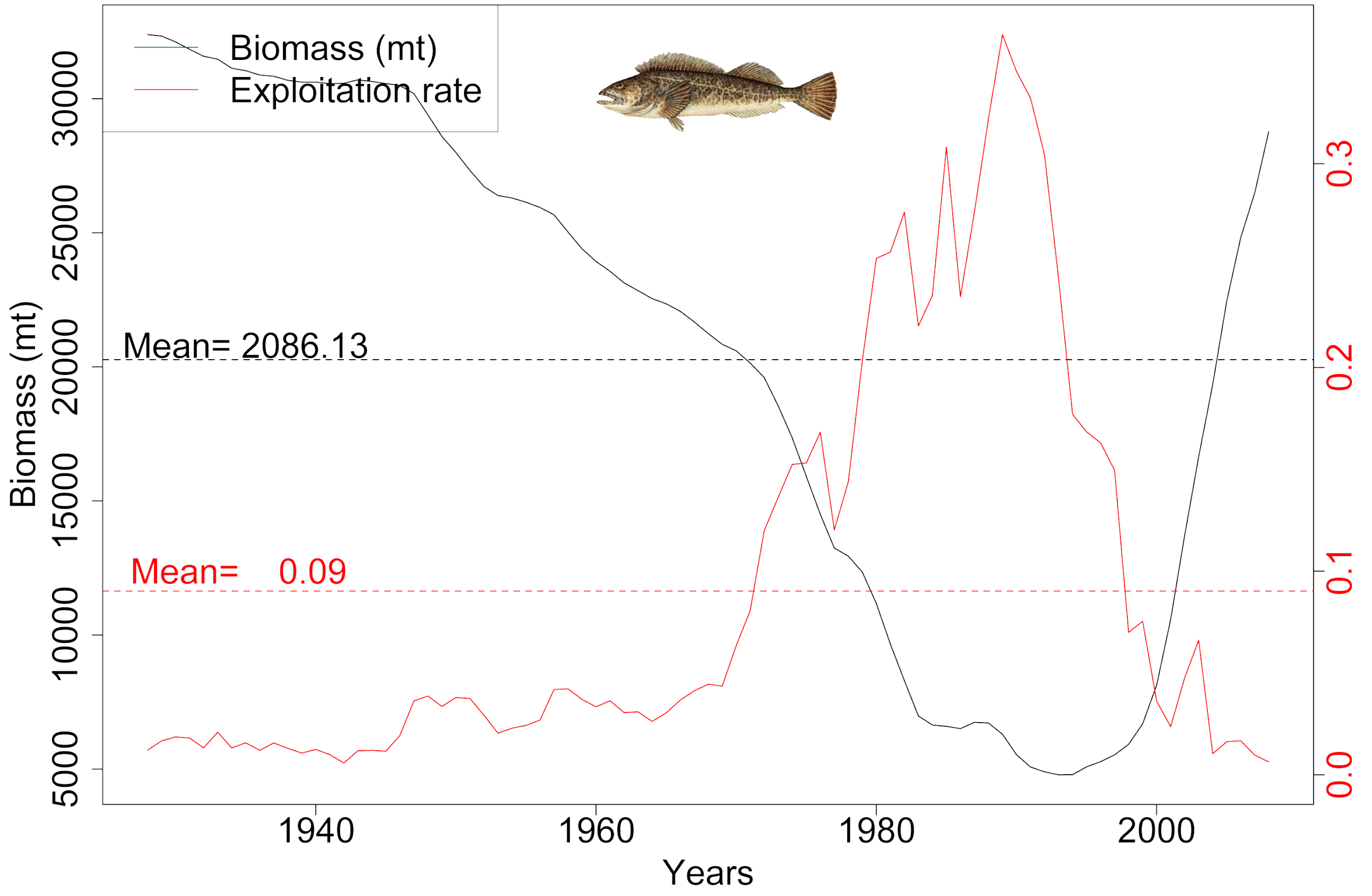

Figure B.1: Time series of biomass and exploitation rate of lingcod (*Ophiodon elongatus*). Exploitation rate is fishing mortality as a proportion of biomass. Black and red horizontal dashed lines are mean biomass and exploitation rate, respectively. Data source: Hamel *et al.* 2009.

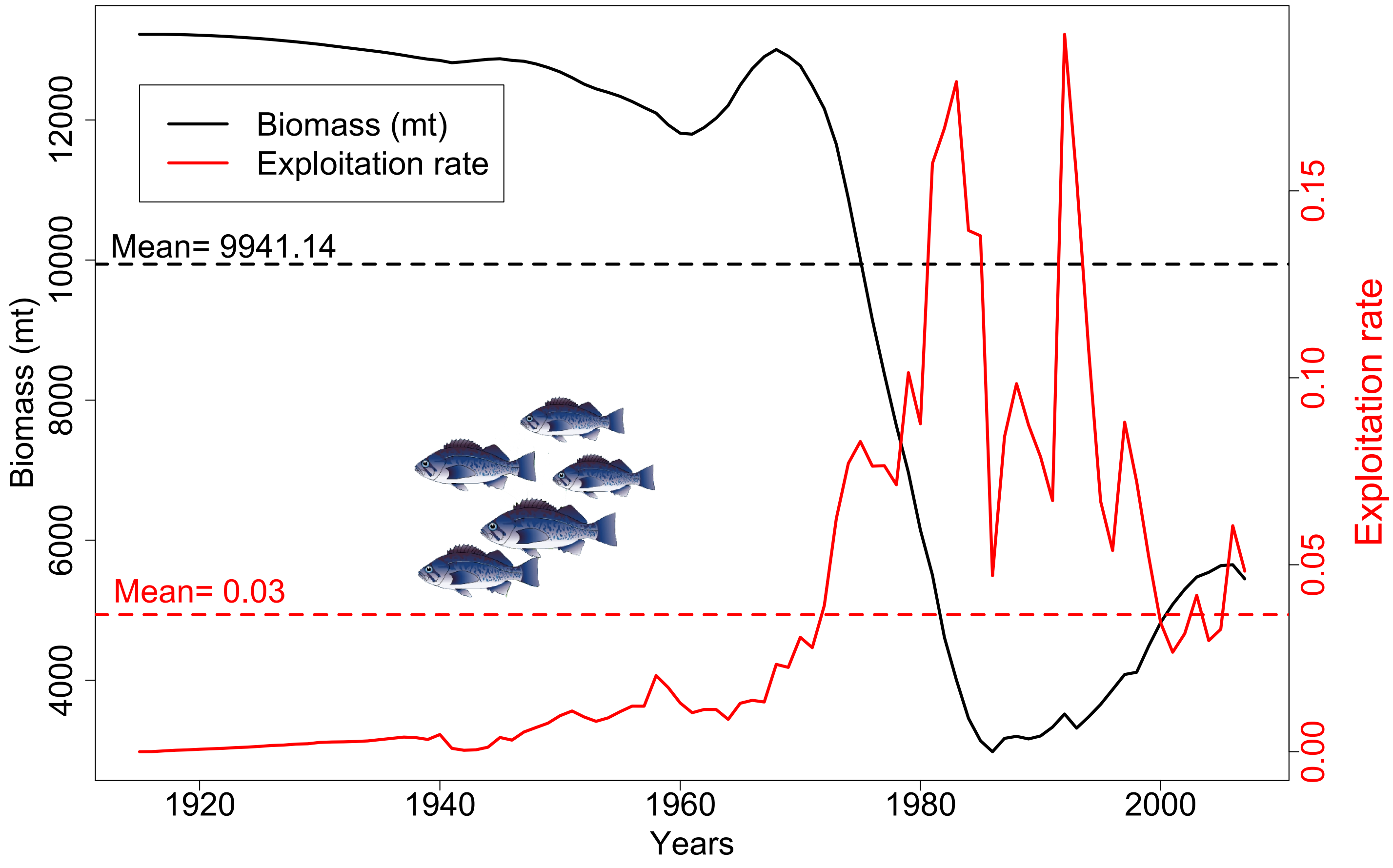

Figure B.2: Time series of biomass and exploitation rate of blue rockfish (*Sebastes mystinus*). Exploitation rate is fishing mortality as a proportion of biomass. Black and red horizontal dashed lines are mean biomass and exploitation rate, respectively. Data source: Key *et al.* 2008.

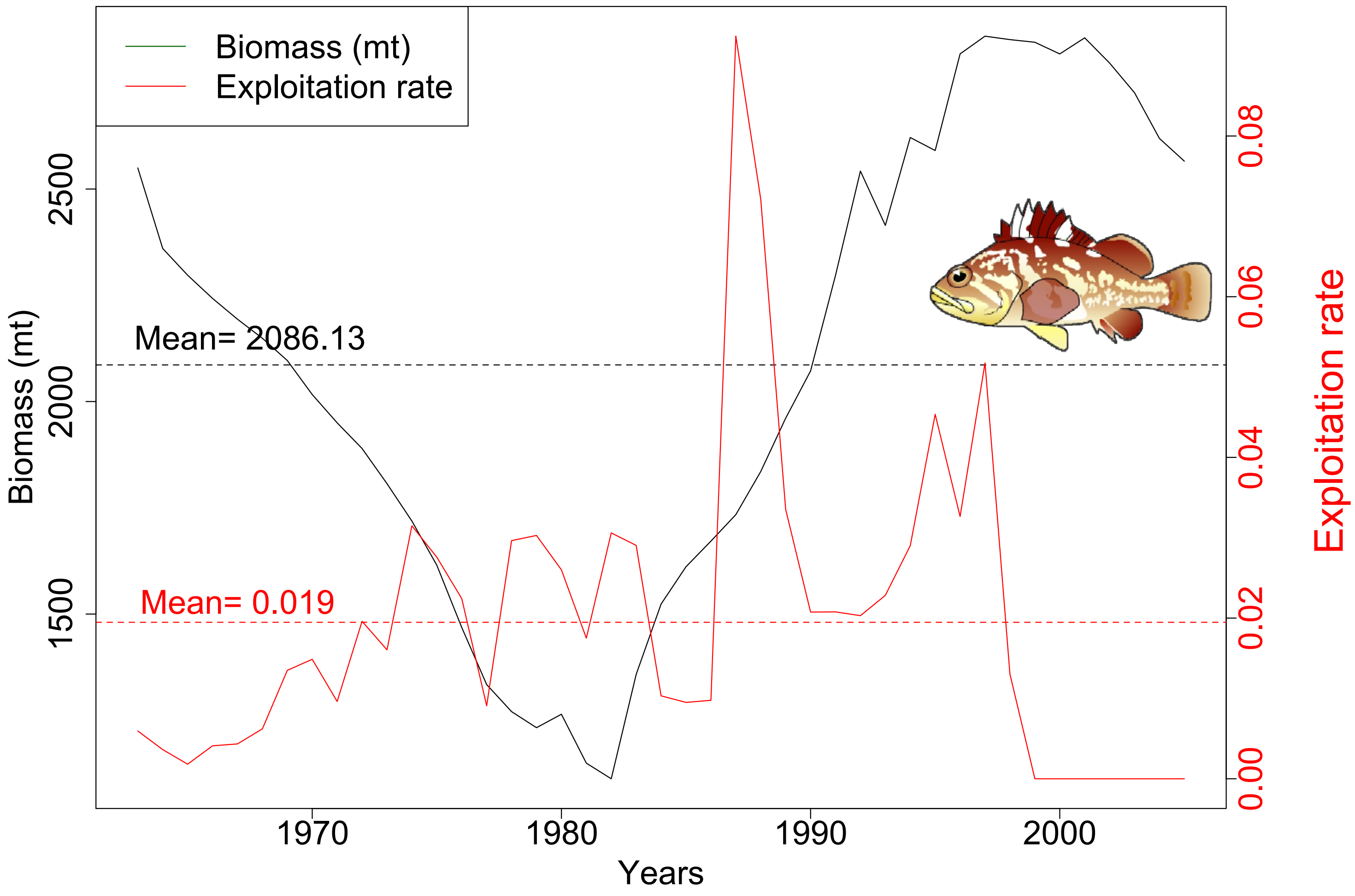

Figure B.3: Time series of biomass and exploitation rate of gopher rockfish (*Sebastes carnatus*). Exploitation rate is fishing mortality as a proportion of biomass. Black and red horizontal dashed lines are mean biomass and exploitation rate, respectively. Data source: Key *et al.* 2005.

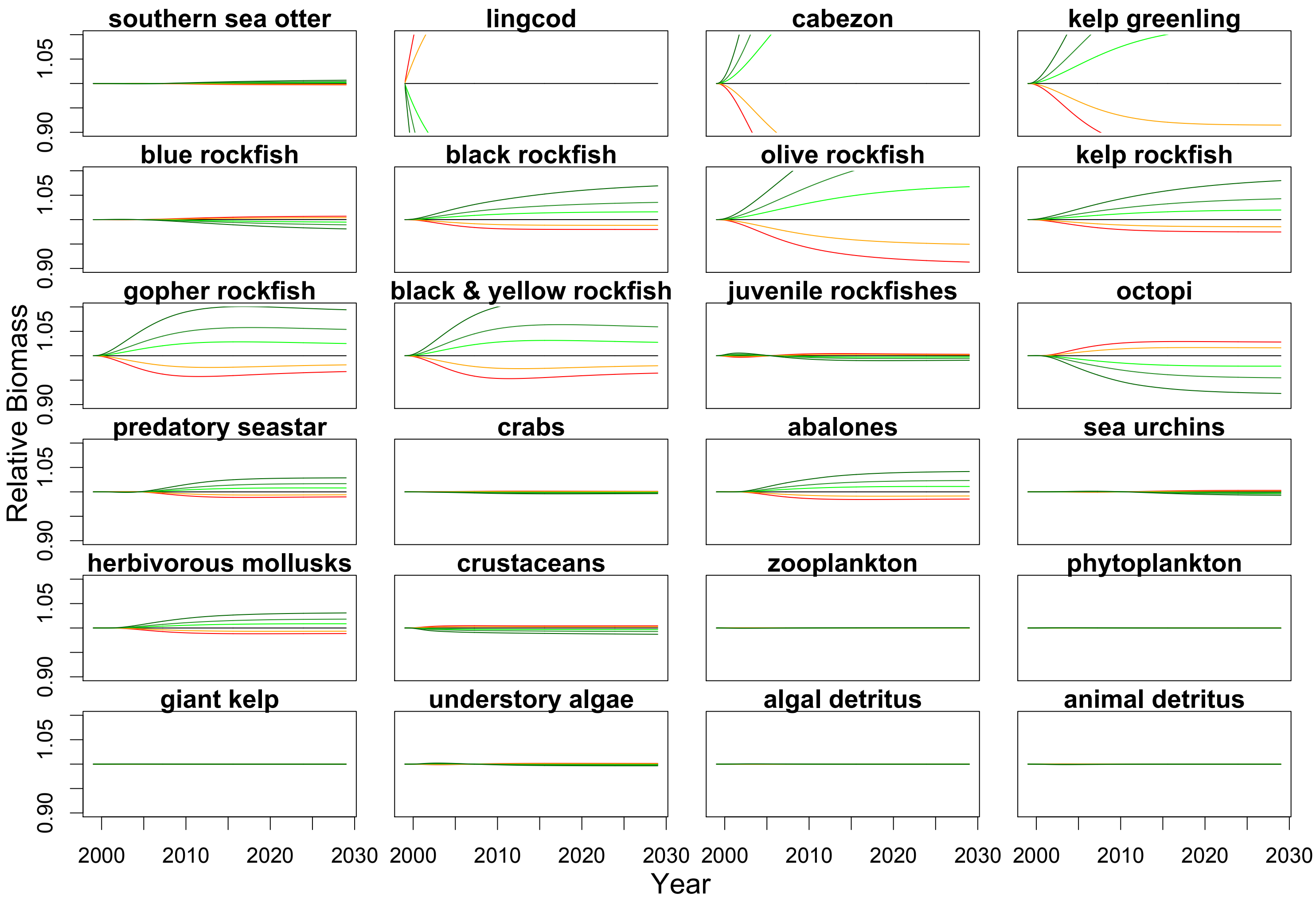

Figure B.4: Relative biomass response of the different nodes in the ecological network after fishing **lingcod** at five different rates of fishing mortality. Black lines represent the relative biomass at mean historical fishing rate (1x). NO fishing (red), reduced fishing by 0.5X (orange), increased fishing by 1.5X (light green), 2.0X (darker green), and 3X (darkest green).

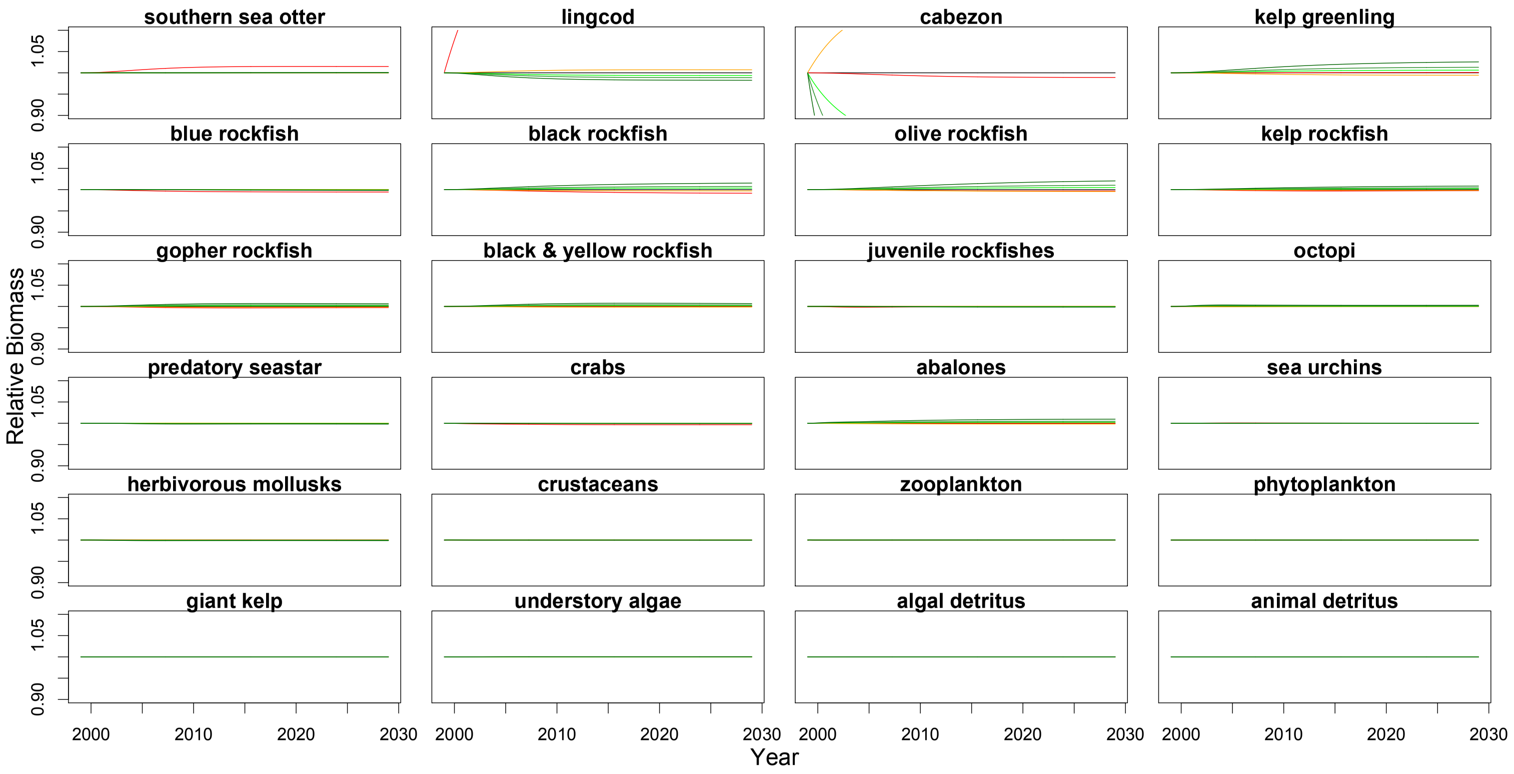

Figure B.5: Relative biomass response of the different nodes in the ecological network after fishing **cabezon** at five different rates of fishing mortality. Black lines represent the relative biomass at mean historical fishing rate (1x). NO fishing (red), reduced fishing by 0.5X (orange), increased fishing by 1.5X (light green), 2.0X (darker green), and 3X (darkest green).

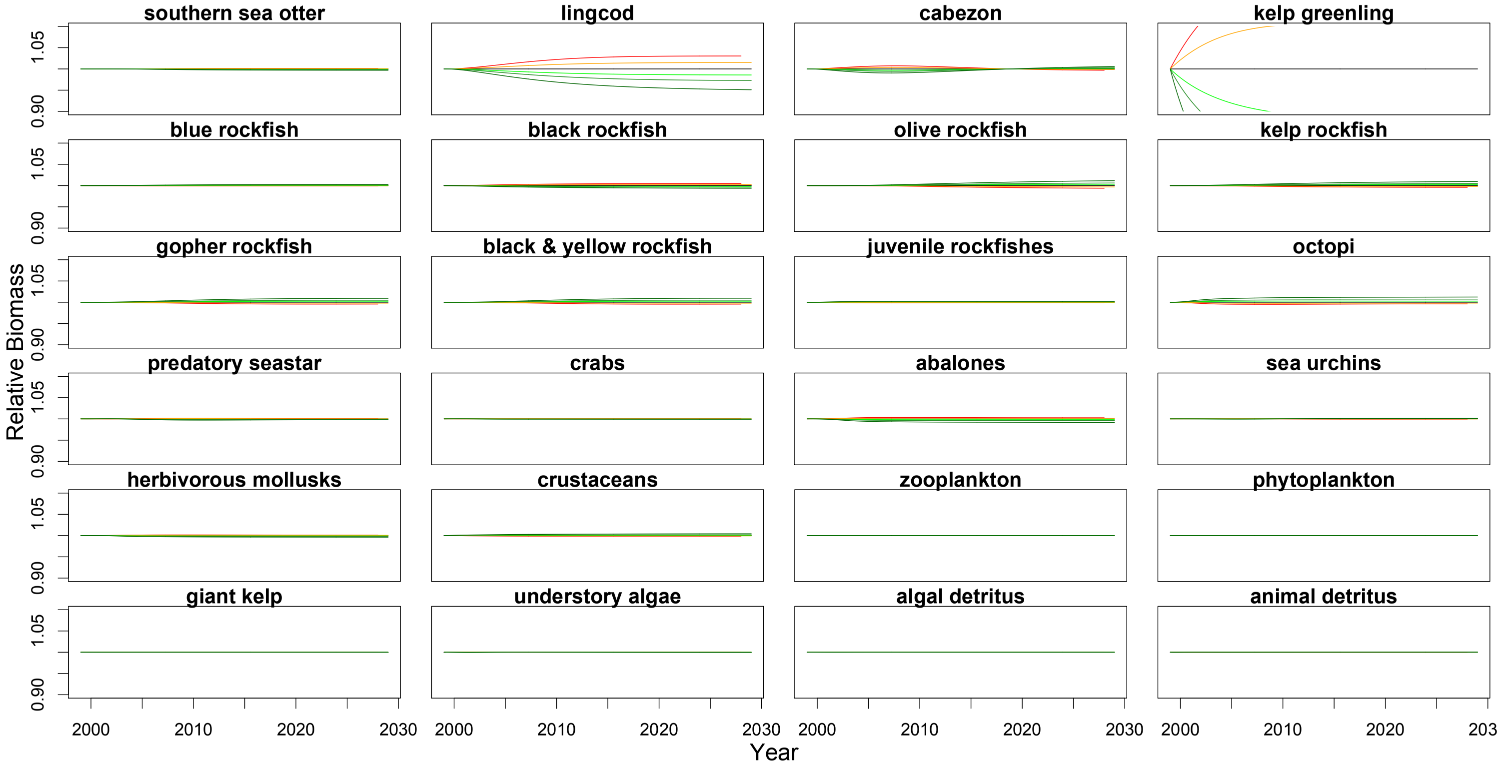

Figure B.6: Relative biomass response of the different nodes in the ecological network after fishing **kelp greenling** at five different rates of fishing mortality. Black lines represent the relative biomass at mean historical fishing rate (1x). NO fishing (red), reduced fishing by 0.5X (orange), increased fishing by 1.5X (light green), 2.0X (darker green), and 3X (darkest green).

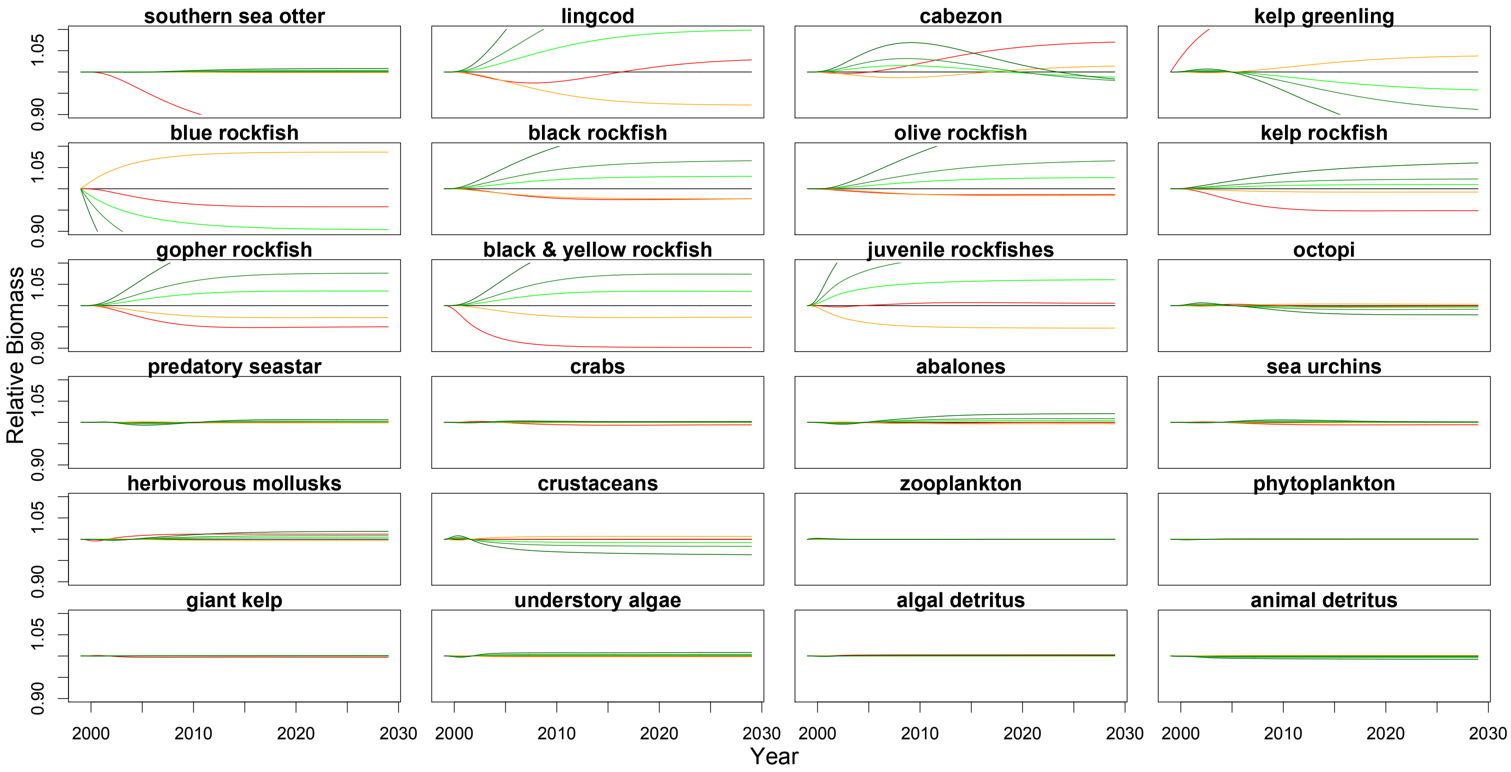

Figure B.7: Relative biomass response of the different nodes in the ecological network after fishing **blue rockfish** at five different rates of fishing mortality. Black lines represent the relative biomass at mean historical fishing rate (1x). NO fishing (red), reduced fishing by 0.5X (orange), increased fishing by 1.5X (light green), 2.0X (darker green), and 3X (darkest green).

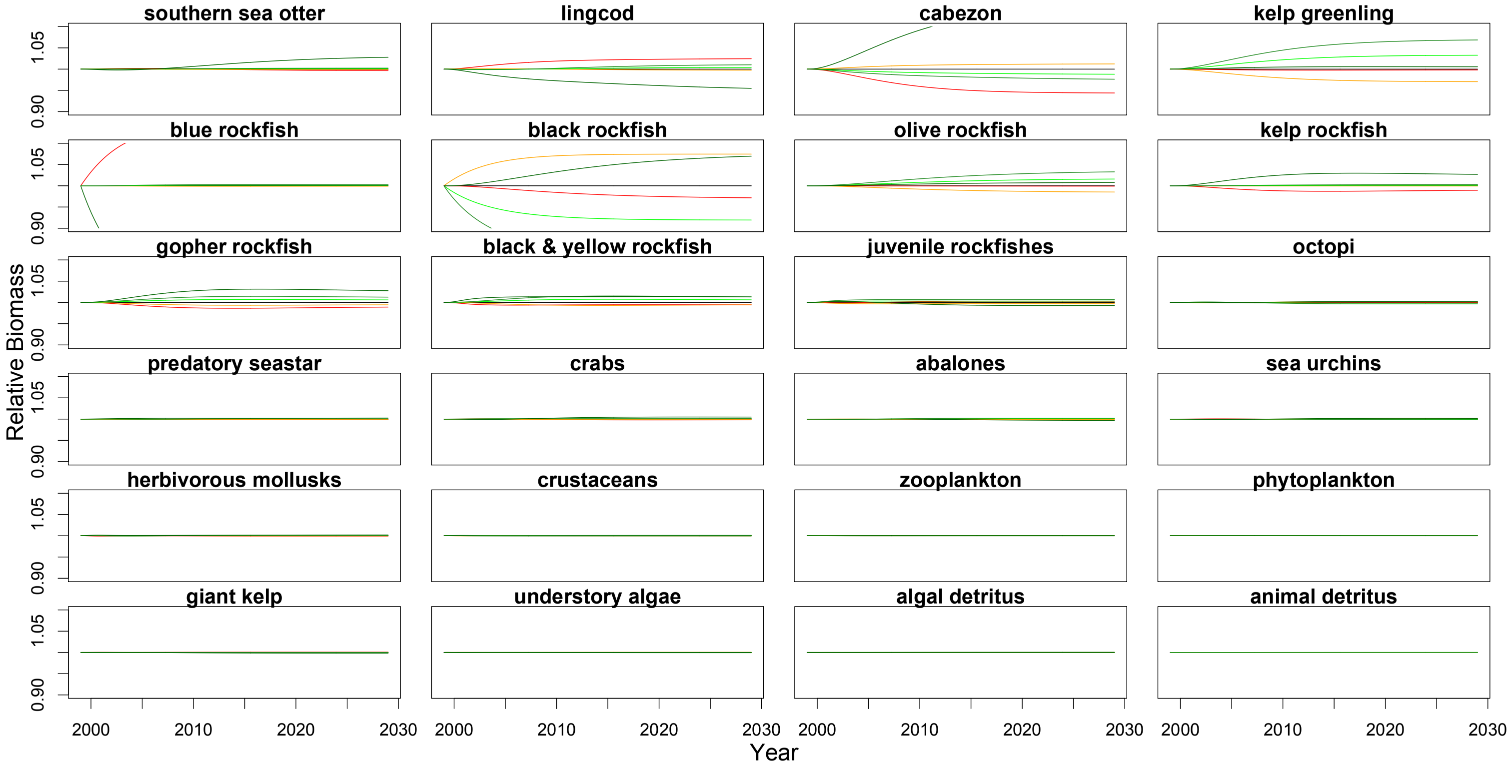

Figure B.8: Relative biomass response of the different nodes in the ecological network after fishing **black rockfish** at five different rates of fishing mortality. Black lines represent the relative biomass at mean historical fishing rate (1x). NO fishing (red), reduced fishing by 0.5X (orange), increased fishing by 1.5X (light green), 2.0X (darker green), and 3X (darkest green).

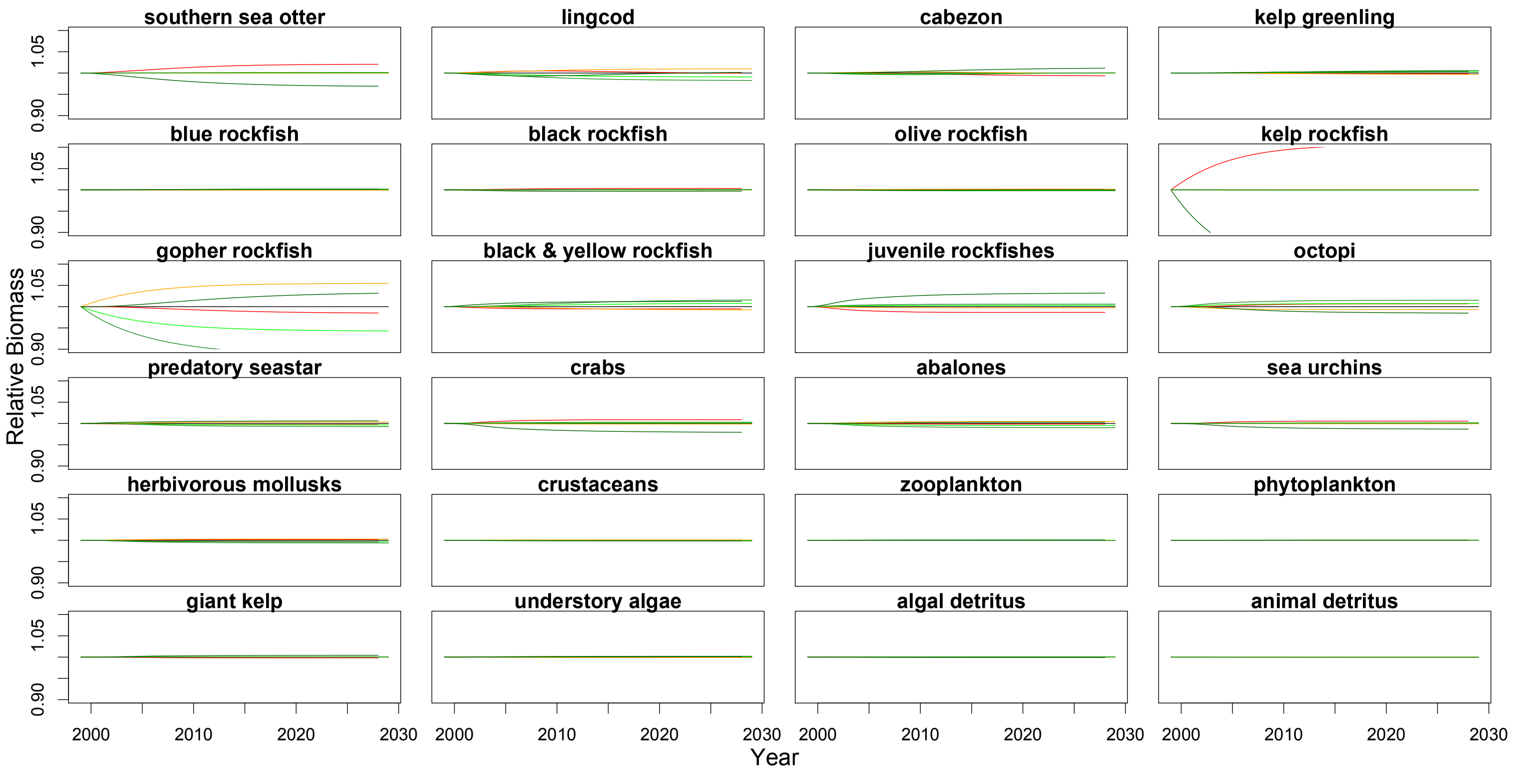

Figure B.9: Relative biomass response of the different nodes in the ecological network after fishing **gopher rockfish** at five different rates of fishing mortality. Black lines represent the relative biomass at mean historical fishing rate (1x). NO fishing (red), reduced fishing by 0.5X (orange), increased fishing by 1.5X (light green), 2.0X (darker green), and 3X (darkest green).

Table B.6: Weigt/density understory algae relationships modified from Reed *et al.* (2009) to estimate biomass density.

| **Taxon** | **Dry mass estimation** | $r^2$ |
|---|---|---|
| Pterygophora californica (adult: stipe$\geq$ 20cm long; $\geq$ 7mm wide ) | dry mass ($gm^{-2}$)= 36.12 * density | 0.88 |
| Eisenia arborea (adult: split stipe) | dry mass ($gm^{-2}$)= 71.85 * density | 0.82** |
| Cystoseira osmundacea (adult: diameter $\geq$ 10cm) | dry mass ($gm^{-2}$)= 13.85 * density | 0.48** |
| Laminaria farlowii (adult: blade width $\geq$ 15cm) | dry mass ($gm^{-2}$)= 21.64 * density | 0.92 |

Table B.7: Biomass density of fish estimated from PISCO data from sites in central California.

| Code | Common name | n | Biomass t/km$^2$ | Standar error |
|---|---|---|---|---|
| | | 565 | 0.000 | 0.000 |
| ACOR | Coralline Sculpin | 565 | 0.000 | 0.000 |
| AFLA | Tubesnout | 565 | 0.137 | 0.022 |
| AOCE | Wolf Eel | 565 | 0.868 | 0.327 |
| APFL | Penpiont Gunnel | 565 | 0.000 | 0.000 |
| ASAN | Kelp Gunnel | 565 | 0.000 | 0.000 |
| ATHE | Grunion, Topsmelt or Jacksmelt | 565 | 0.011 | 0.006 |
| BATH | Ronquils | 565 | 0.000 | 0.000 |
| BFRE | Kelp Surfperch | 565 | 0.170 | 0.030 |
| BLEN | Blennies | 565 | 0.000 | 0.000 |
| BOTH | Lefteyed flounders | 565 | 0.009 | 0.008 |
| CAGG | Shiner Surfperch | 565 | 0.015 | 0.013 |
| CITH | Sanddabs | 565 | 0.000 | 0.000 |
| CLIN | Kelpfishes and Fringeheads | 565 | 0.000 | 0.000 |
| CNUG | Mosshead warbonnet | 565 | 0.000 | 0.000 |
| COTT | Sculpins | 565 | 0.001 | 0.000 |
| CPUN | Blacksmith | 565 | 0.038 | 0.010 |
| CSAT | Black Croaker | 565 | 0.000 | 0.000 |
| CSOR | Pacific Sanddab | 565 | 0.000 | 0.000 |
| CSTI | Speckled Sanddab | 565 | 0.000 | 0.000 |
| CVEN | Swell Shark | 565 | 0.104 | 0.070 |
| CVIO | Monkeyface Eel | 565 | 0.000 | 0.000 |
| EJAC | Black Surfperch | 565 | 2.017 | 0.135 |
| ELAT | Striped Surfperch | 565 | 4.838 | 0.219 |
| EMOR | Northern Anchovy | 565 | 0.288 | 0.227 |
| EWAL | Masked prickleback | 565 | 0.000 | 0.000 |
| GIBB | Kelpfish | 565 | 0.003 | 0.001 |
| GMAE | Northern Clingfish | 565 | 0.000 | 0.000 |
| GMOR | California Moray | 565 | 0.007 | 0.007 |
| GNIG | Opaleye | 565 | 0.225 | 0.097 |
| GOBI | Gobies | 565 | 0.000 | 0.000 |
| HANA | Spotfin Surfperch | 565 | 0.000 | 0.000 |
| HARG | Walleye Surfperch | 565 | 0.015 | 0.015 |
| HCAR | Rainbow Surfperch | 565 | 0.566 | 0.080 |
| HDEC | Kelp Greenling | 565 | 3.318 | 0.163 |
| HELL | Silver Surfperch | 565 | 0.008 | 0.004 |
| HFRA | Horn Shark | 565 | 0.000 | 0.000 |
| HLAG | Rock Greenling | 565 | 0.031 | 0.008 |
| HROS | Giant Kelpfish | 565 | 0.000 | 0.000 |
| JZON | Longfin Sculpin | 565 | 0.000 | 0.000 |
| KSEI | Six-spot Prickleback | 565 | 0.000 | 0.000 |
| LCON | Kelp Goby, Halfblind Goby | 565 | 0.005 | 0.001 |
| LLEP | bay goby | 565 | 0.000 | 0.000 |
| OCAL | Senorita | 565 | 1.832 | 0.225 |
| OELO | Lingcod | 565 | 6.079 | 0.879 |
| OPIC | Painted Greenling | 565 | 0.506 | 0.025 |
| OTRI | snubnose sculpin | 565 | 0.000 | 0.000 |
| OYT | olive or yellowtail rockfish | 565 | 4.960 | 0.317 |

Table B.7 Continued

| Code | Common name | n | Biomass $t/km^2$ | Standar error |
|---|---|---|---|---|
| PATR | sharpnose surfperch | 565 | 0.000 | 0.000 |
| PCAL | california halibut | 565 | 0.435 | 0.311 |
| PCLA | kelp bass, calico bass | 565 | 0.071 | 0.028 |
| PFUR | white surfperch | 565 | 0.107 | 0.030 |
| PHOL | Gunnels | 565 | 0.001 | 0.000 |
| PTRI | thornback | 565 | 0.025 | 0.018 |
| RALL | stripefin ronquil | 565 | 0.000 | 0.000 |
| RHYP | smooth ronquil | 565 | 0.000 | 0.000 |
| RNIC | Blackeye Goby | 565 | 0.075 | 0.008 |
| RSTE | Starry Skate | 565 | 0.000 | 0.000 |
| RTOX | rubberlip surfperch | 565 | 0.833 | 0.176 |
| RVAC | Pile Surfperch | 565 | 2.078 | 0.207 |
| SACA | Spiny dogfish | 565 | 0.449 | 0.319 |
| SATR | kelp rockfish | 565 | 6.775 | 0.331 |
| SAUR | brown rockfish | 565 | 0.007 | 0.002 |
| SCAL | pacific angel shark | 565 | 0.093 | 0.093 |
| SCAR | gopher rockfish | 565 | 3.091 | 0.152 |
| SCAU | copper rockfish | 565 | 0.591 | 0.083 |
| SCHR | black and yellow rockfish | 565 | 2.553 | 0.125 |
| SDAL | calico rockfish | 565 | 0.000 | 0.000 |
| SDIP | spitnose rockfish | 565 | 0.000 | 0.000 |
| SENT | widow rockfish | 565 | 0.005 | 0.003 |
| SHOP | squarespot rockfish | 565 | 0.000 | 0.000 |
| SMAR | cabezon | 565 | 1.204 | 0.091 |
| SMEL | black rockfish | 565 | 3.703 | 0.342 |
| SMIN | vermilion rockfish | 565 | 2.831 | 0.230 |
| SMYS | blue rockfish | 565 | 38.127 | 2.570 |
| SNEB | china rockfish | 565 | 0.047 | 0.012 |
| SPAU | bocaccio | 565 | 0.117 | 0.034 |
| SPIN | canary rockfish | 565 | 0.118 | 0.029 |
| SPUL | california sheephead | 565 | 1.804 | 0.201 |
| SRAS | grass rockfish | 565 | 0.284 | 0.046 |
| SROS | rosy rockfish | 565 | 0.000 | 0.000 |
| SSAG | pacific sardine | 565 | 0.012 | 0.009 |
| SSAX | stripetail rockfish | 565 | 0.000 | 0.000 |
| STICH | Pricklebacks | 565 | 0.000 | 0.000 |
| STRE | treefish | 565 | 0.192 | 0.026 |
| SYNG | pipefish | 565 | 0.000 | 0.000 |
| SYRI | Manacled sculpin/Kelp clingfish | 565 | 0.000 | 0.000 |
| TCAL | pacific electric ray | 565 | 0.003 | 0.003 |
| TSEM | leopard shark | 565 | 0.047 | 0.038 |
| ZROS | pink surfperch | 565 | 0.000 | 0.000 |

Table B.8: Time series of sea urchin biomass density (t/km2) estimated by the average of PISCO site in central California.

| Year | Red Urchin | Purple Urchin | Both |
|---|---|---|---|
| 1999 | 0.85 | 1.70 | 2.55 |
| 2000 | 0.48 | 2.90 | 3.38 |
| 2001 | 0.03 | 4.15 | 4.17 |
| 2002 | 0.07 | 1.90 | 1.97 |
| 2003 | 0.39 | 2.32 | 2.71 |
| 2004 | 0.14 | 2.17 | 2.31 |
| 2005 | 0.07 | 0.81 | 0.88 |
| 2006 | 0.46 | 1.29 | 1.75 |
| 2007 | 0.60 | 2.62 | 3.22 |
| 2008 | 0.46 | 3.45 | 3.91 |
| 2009 | 0.36 | 4.16 | 4.52 |
| 2010 | 0.11 | 2.11 | 2.22 |