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Utilizing holistic ecosystem indices to explore ecosystem structure and function and improve fisheries management strategies

A dissertation submitted in satisfaction of the requirements for the degree of Doctor of Philosophy

in

Oceanography

By

Adam James Schlenger

Committee in charge:

Professor Lisa T. Ballance, Chair
Professor Jim Leichter, Co-Chair
Professor Mark Jacobsen
Professor Veerabhadran Ramanathan
Professor Stuart Sandin
Professor Dale Squires

2017

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Chair

University of California, San Diego

2017

TABLE OF CONTENTS

Signature Page……... iii

Table of Contents……... iv

List of Figures…… v

List of Tables……. vii

Acknowledgements…… viii

Vita……..…….. x

Abstract of Dissertation……. xi

Introduction…… 1

Chapter 1 - Energy Theory and Applications for the Study of Biological Ecosystems…… 4

Chapter 2 - Temporal variability of primary production explains marine ecosystem structure and function…….. 45

Chapter 3 - Predicting Global Biomass Anomalies Under Future Climate Change……. 76

Chapter 4 - An Ecosystem-Based Modeling Approach to Fisheries Management……... 101

Conclusion…….. 138

LIST OF FIGURES

Figure 1.1 Formation of Bénard convection cells as self-organized energy dissipative structures. Cell diagram in two dimensions (Wikipedia 2009) (Left) and the relation between energy gradient (Rayleigh Number) and heat dissipation rate for conduction and conduction + Bénard convection processes (Right) (Figure from Schneider and Kay, 1994)……... 40

Figure 1.2. Diagram depicting the ecological development of ascendency through the flow of Average Mutual Information (AMI) (Figure from Ulanowicz, 2000)…….. 41

Figure 2.1. Global map of ecosystem locations differentiated by ecosystem type, selected for this study; coastal (circle), estuary (+), island (X), ocean (star), reef (*), shelf (square), and upwelling (diamond)……... 70

Figure 2.2. Relationships between ecosystem Biomass and interannual and seasonal variability in net primary production ($r^2 = 0.46$) (AIC = -2.2)…… 71

Figure 2.3. Relationships between interannual and seasonal variability in Net Primary Productivity (NPP) and primary production ($r^2 = 0.16$) (AIC = -1.67) (Top) and Respiration ($r^2 = 0.2$) (AIC = -1.78) (Bottom) estimates to measures of the log MS of interannual and seasonal variability in net primary production. Histograms as in Figure 2……. 72

Figure 2.4. Relationships between interannual and seasonal variability in Net Primary Productivity (NPP) and P/B ($r^2 = 0.15$) (AIC = -2.32) (Top), B/TST ($r^2 = 0.19$) (AIC = -8.44) (Middle), Residence Time ($r^2 = 0.14$) (AIC = -5.83) (Bottom) estimates to measures of the log MS of interannual and seasonal variability in net primary production……. 73

Figure 2.5. Relationships between interannual and seasonal variability in Net Primary Productivity (NPP) and Average Trophic Level (Top) ($r^2 = 0.22$) (AIC = -2.61) and Relative Ascendency ($r^2 = 0.49$) (AIC = 3.26) (Bottom) estimates to measures of the log MS of interannual and seasonal variability in net primary production……. 74

Figure 3.1. Maps of historical (1998-2005) seasonal variability in net primary production (NPP), calculated as the mean square (MS) of deviations between months within a year over the same period……. 93

Figure 3.2. Maps of historical (1998-2005) interannual variability in net primary production (NPP), calculated as the mean square (MS) of deviations between years……. 95

Figure 3.3. Historical Ecosystem Biomass (1998-2005) estimated using a multivariate relationship between seasonal and interannual variation in net primary production with Ecosystem Biomass. White areas represent grid cells with extremely low seasonal and/or interannual variability in net primary production (NPP) that fell outside the predictive range……... 97

Figure 3.4. Predicted seasonal variability in net primary production (NPP) (2093-2100) averaged across Institute Pierre Simon Laplace (IPSL), New Earth system model of Max Planck Institute for Meteorology (MPI), and, Community Earth System Model (NCAR) earth system models under representative concentration pathways (A) 4.5 and (B) 8.5 carbon emission scenarios…… 98

Figure 3.5. Predicted interannual variability in net primary production (NPP) (2093-2100) averaged across Institute Pierre Simon Laplace (IPSL), New Earth system model of Max Planck Institute for

Meteorology (MPI), and, Community Earth System Model (NCAR) earth system models under representative concentration pathways (A) 4.5 and (B) 8.5 carbon emission scenarios…… 99

Figure 3.6. Predicted anomalies in global Biomass from 1998-2005 to 2093-2100 under representative concentration pathways (A) 4.5 and (B) 8.5 carbon emission scenarios. White areas represent MS variability values outside the boundaries of the predictive model used to estimate Ecosystem Biomass and are indicative of areas having very low Biomass values……... 100

Figure 4.1. Schematic diagram of surface water masses and currents in the eastern tropical Pacific Ocean. STSW, Subtropical Surface Water; TSW, Tropical Surface Water; ESW, Equatorial Surface Water. Shading represents mean sea surface temperature (darker = colder) (Taken from Fielder and Talley 2006)……... 129

Figure 4.2. Species catch compositions from the base Ecopath model distributed across School Sets (A), Floating Object Sets (B), Dolphin Sets (C), and Longlines (D). The number of species fished differs between Fishing Fleets as well as their percent composition of catch……... 130

Figure 4.3. Fishing Effort estimated through the Ecopath with Ecosim Policy Optimization Routine under four management scenarios; Net Present Value (NPV), Maximize Portfolio Utility (MPU), Multiple Fishing Rights with Compete Costs, and Multiple Fishing Rights without Compete costs... 131

Figure 4.4. Distribution of total catch by species and size (Lg = large and Sm = Small) across the Net Present Value (NPV), Maximize Portfolio Utility (MPU), Multiple Fishing Rights without Compete Costs, and Multiple Fishing Rights with Compete Costs management scenarios……. 132

Figure 4.5. Estimated values of Total Catch (A), Total Cost (B), Total Value (C), Mean Trophic Level of Catch (D), and Gross Efficiency of Catch (E) under four management scenarios…….. 133

Figure 4.6. Estimated values of Biomass (A), Biodiversity (B), the ratio of Primary Production to Biomass (P/B) (C), the ratio of Primary Production to Respiration (P/R) (D), and the ratio of Biomass to Total System Throughput (B/TST) (E) under four management scenarios…… 134

Figure 4.7. Estimated values of Total Catch (A), Total Value (B), Biomass (C), and Biodiversity (D) under the Net Present Value (NPV) management scenario as policy objective weights iteratively decreased for profit and increased for biodiversity…….. 135

Figure 4.8. Estimated values of Total Catch (A), Total Value (B), Biomass (C), and Biodiversity (D) under the Maximize Portfolio Utility (MPU) management scenario as policy objective weights iteratively decreased for profit and increased for biodiversity…….. 136

Figure 4.9. Mixed trophic impact plot of the eastern tropical Pacific Ecopath model. The right column lists the species and functional groups that have an impact on the corresponding species and functional groups in the top row. Positive impacts are denoted by an open oval while negative impacts are denoted by a filled black oval. The extent of impact is denoted by the size of the oval… 137

LIST OF TABLES

Table i.1. Overview of Dissertation Chapters…….. 3

Table 1.1 (Taken from Christensen 1995): Modified list of E.P. Odum's attributes of ecological succession…… 43
.

Table 1.2: Summary of ecological systems analysis indices. See text for previse definitions and references……. 44

Table 2.1. Ecosystems included in analysis for which Ecopath models have been build and their respective publications……. 66

Table 2.2. Relationships between 8 ecosystem indices derived from Ecopath with Ecosim, and Net Primary Productivity (NPP) for 43 marine ecosystems: mean, seasonal, and interannual (see text for details). MS = mean squares and AIC = Akaike's Information Criteria……. 68

Table 2.3. Multivariate relationships between synthetic ecosystem indices and the MS of interannual and seasonal variability along with their respective model AIC values, the number of coefficients used in each model, and r-squared values…… 69

Table S2.1. Total list of synthetic ecosystem indices explored in this study and their respective units…….. 75
.

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Chapter 3 contains unpublished material with the following authors: A. Schlenger, S. Libralato. The dissertation author was the primary researcher and author of this material.

Chapter 4, in part is currently being prepared for submission for publication of the material. Schlenger, Ballance; Schlenger, Adam J. The dissertation author was the primary researcher and author of this material.

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ABSTRACT OF DISSERTATION

Utilizing holistic ecosystem indices to explore ecosystem structure and function and improve fisheries management strategies

By

Adam James Schlenger

Doctor of Philosophy in Oceanography

University of California, San Diego, 2017

Professor Lisa Ballance, Chair
Professor James Leichter, Co-Chair

The extent of anthropogenic impact on the world has reached has reached the point where humans are fundamentally disrupting the natural structure and function of entire ecosystems. The need to mitigate, restore, and protect natural ecosystems has become a critical issue throughout the world. However, the sheer scale and complexity of ecosystems makes this a difficult problem to solve. Over the past few decades, modern ecology has risen to the challenge by adopting a holistic approach to the study of ecosystems. This holistic perspective incorporates the nonlinear processes, indirect effects, and emergent properties that play a major role in ecosystem behavior. Ecosystems are hierarchal, self-organizing networks, driven by the flow of energy and material. A central focus of this viewpoint emphasizes the philosophy that the whole is more than the sum of its parts and this depiction of ecosystems has shed light on the existence of a general set of driving principles amongst a seemingly

endless sea of variables and unknowns. A holistic approach to ecology simplifies the challenges of scale and complexity to allow scientists and managers to tackle ecological issues around the globe.

Chapter 1 of this dissertation constitutes a literature review synthesizing some of the major advancements of modern ecology and the development of a holistic approach to ecosystem research. Ecosystems were placed in the context of complex adaptive systems, focusing on the important structural, functional, and mathematic properties that lead to a set of common emergent properties. The role of thermodynamics in driving ecosystem behavior is then presented along with the application of information theory to develop a conceptual framework for the interactions between components of an ecosystem and how that influences their holistic behavior. Finally, a wide variety of mathematically derived indices of ecosystem structure, function, and organizational complexity are presented. These indices represent approaches from a number of different disciplines that have been applied to the development of modern ecological theory.

Chapter 2 outlines a study aimed at identifying the major drivers of ecosystem structure and function. We used 24 synthetic ecosystem-level indices derived from trophic models, and independently-derived data for net primary productivity, to investigate drivers of ecosystem structure and function for 43 marine ecosystems distributed in all oceans of the world and including coastal, estuaries, mid-ocean islands, open-ocean, coral reef, continental shelf, and upwelling ecosystems. Of these indices, ecosystem Biomass, Primary Production, Respiration, the ratio of Biomass to Total System Throughput (sum of total energy flow into and out of an ecosystem as well as between ecosystem components), the ratio of Production to Biomass, Residence Time (mean time that a unit of energy remains in the ecosystem), Average Trophic Level, and Relative Ascendency (index of organization and complexity of a food web) displayed relationships with measures of net primary productivity (NPP). Across all ecosystems, relationships were stronger with seasonal and interannual variability of NPP as compared to mean NPP. Both measures of temporal variability were combined into multivariate predictive relationships for each ecosystem index, with r2 values ranging from 0.14 to 0.49 and Akaike's Information Criteria values from

-8.44 to 3.26. Our results indicate that despite large geographical and environmental differences, temporal variability of NPP is strongly linked to the structure and function of marine ecosystems.

Chapter 3 builds off of chapter 2 by utilizing the multi-dimensional relationship between variability in NPP and biomass to predict future changes in global biomass distributions under future climate change scenarios. Estimates of variability in NPP were calculated using output from three earth system models (ESMs) to quantify historic distributions of biomass. Similarly, these ESMs were used to quantify future estimates of NPP and subsequent biomass predicted under Representative Concentrations Pathways (RCPs) 4.5 and 8.5. Biomass anomalies between historic estimates and future predictions show very little change in mean global Biomass, but much larger localized anomalies were observed of approximately -200% to 200%. Locations displaying large regional changes include the north Atlantic, Arctic, and eastern tropical Pacific. These results provide useful information concerning which areas of the world that might be the most vulnerable at an ecosystem scale.

Chapter 4 constitutes a heuristic approach to bioeconomic modeling to optimize fishery management strategies in the eastern tropical Pacific. Linking the economic and biological components of human interactions with natural systems is a vital part of effective fisheries management. This study utilized a trophic network model of the eastern tropical Pacific to compare multi-species fishery management strategies by varying the efforts of individual fleets to optimize specific policy objectives. This approach highlights the cascading, indirect effects of fishing across an entire ecosystem and incorporates a holistic perspective to quantify their economic and ecosystem health impacts. Results of this study showed that varying management scenarios can lead to a diverse combination of economic and ecosystem health effects. This study also highlighted the potential for different management strategies to achieve similar economic results, but through alternative mechanisms with significantly different ecosystem-level impacts.

INTRODUCTION

Complexity is a word that comes with an associated stigma. It's generally tied closely with confusion, misunderstanding, and uncertainty. Humans have an innate desire to fully understand the world around them and complexity represents a barrier to that goal. As such, it is not uncommon to simplify things in order to create conceptual frameworks that make sense. It was much easier to attribute the changing of seasons to higher powers than it was to fully understand the orbital dynamics and gravitational forces of celestial bodies or to be at peace with the unknown. And while the act of simplification comes with a level of comfort through the perceived removal of uncertainty, that comfort may come at the cost of realism. As our general knowledge of the world increases and our ability to collect and interpret information rises exponentially, it's become readily apparent that the world is an incredibly complex place, whether or not we feel comfortable with the uncertainty that comes along with it.

The basis of the scientific method was built upon the simplification of conditions by creating controls, isolating variables, and reducing individual components of the natural world. However, in a world of complex systems, isolating variables is essentially impossible and the idea of control is at times laughable. In a complex system, whether it be a stock market, an ant colony, a social network, or an ecosystem, the behavior of individual components is tightly linked to their interactions with others and by removing those interactions you completely change the behavior of any one component. The shape and color of a flower would be meaningless if one doesn't consider the pollinator it's trying to attract. This represents the principle that the whole is more than the sum of its parts and this is an idea that modern ecology has embraced.

Over the past several decades a wide variety of work has been done to develop a multi-disciplinary approach to ecology that frames ecosystems in the context of complex adaptive systems. A

central theme behind this perspective lies in the treatment of ecosystems as large groups of individual components that interact nonlinearly and on a variety of spatial and temporal scales, as self-organizing to produce complex structures and behaviors, and as hierarchically organized systems. An ecosystem is comprised of interacting populations while a population is comprised of interacting individuals and so on and so forth. This holistic approach to ecology has counter-intuitively simplified their vast complexity.

Take, for example, a visit to the doctor. When a doctor wants to do a quick evaluation of your overall health, they don't look at the condition of every individual cell of your body, but instead measure your heartbeat, listen to your breathing, or take your temperature, all of which are emergent properties of the interactions of all the cells in your body. In other words, the intricate complexities of cellular and tissue function are simplified by looking at the properties of the whole. However, an essential aspect of this approach is that while our understanding and predictive power greatly increase, uncertainty can never be fully removed. Although a fast heartbeat, shallow breath, and high temperature are clear signs that something is wrong, those specific properties won't pinpoint whether it's due to an infection or high levels of stress. But that doesn't make the information any less important when it comes to identifying the right questions to ask, the next steps to take, and acting decisively to improve your health.

The same can be said of ecosystems, but instead of infections, they are vulnerable to climate change, fishing, eutrophication, species invasion, and a wide variety of other anthropogenic perturbations. While the identifications of the mechanisms behind every individual interacting component and sub-system that comprises an ecosystem is a far off goal, a holistic approach to ecology allows one to embrace our current level of uncertainty, work with it, and make decisions that are necessary to protect and improve the health of ecosystems throughout the world. Through this dissertation, I hope to provide support for the utility of taking a holistic approach to ecology. I hope to demonstrate that complexity and uncertainty are not things to be overly reduced at the cost of realism, but are instead innate attributes of the world we live in and should be embraced.

Table i.1. Overview of Dissertation Chapters.

Chapter 1. **Energy Theory and Applications for the Study of Biological Ecosystems**	
	Literature review synthesizing some of the major advancements of modern ecology and the development of a holistic approach to ecosystem research.
Chapter 2. **Temporal variability of primary production explains marine ecosystem structure and function**	
	Presents a study aimed at identifying some of the major drivers of ecosystem structure and function.
Chapter 3. **Predicting Global Biomass Anomalies Under Future Climate Change**	
	Builds off of chapter 2 by utilizing the multi-dimensional relationship between variability in net primary production and biomass to predict changes in global biomass distributions under future climate change scenarios.
Chapter 4. **An Ecosystem-Based Modeling Approach to Fisheries Management**	
	Makes the case for a heuristic approach to bioeconomic modeling to optimize fishery management strategies in the eastern tropical Pacific.

CHAPTER 1

Energy Theory and Applications for the Study of Biological Ecosystems

Introduction

Classic ecology, like many other disciplines, was founded upon a reductionist approach. Attempts to reveal the properties of nature were accomplished by separating individual components to simplify studies and to facilitate the interpretation of results (Jørgensen and Müller 2000). This method led to some of the most important scientific discoveries to date and has allowed us to learn a great deal about how life works at its most fundamental levels. However, as we gain a deeper understanding of the sheer complexity of living systems, the limitations of a reductionist approach become readily apparent. Complex systems are characterized by a high degree of independent elements that interact on multiple scales. Prevalent multi-scale linkages, nonlinear processes, and indirect effects lead to a variety of emergent properties that cannot be identified by only looking at individual components of the system (Levin 1998). A human's personality cannot be described on the basis of the properties of all the cells of the body. Global economies cannot be fully explained through the study of microeconomic transactions alone. Nor can an ecosystem be fully understood through the study of individual populations or species. The study of complex systems necessitates an additional approach to complement the limitations of reductionism. The holism perspective attempts to reveal the properties of complex systems by studying systems as a whole (Wilson 1988). This approach considers ecosystems to be more than the sum of their parts and that studying those individual parts, while still vitally important, will never be sufficient for revealing the system properties and functional patterns of interactions.

The need for a holistic approach to ecology, and complex systems in general, eventually led to the development of systems analysis. Systems analysis is the study of systems that can be thought of as groups of interacting, interdependent parts linked together by complex exchanges of energy, matter, or information (Costanza 1992). Ludwig von Bertalanffy paved the way for the discipline with the publication of *General System Theory* (1968), which argues that similar patterns of interaction can be

found in quite different systems. By studying the similarities and differences between varying types of systems at different scales and resolutions, one can develop hypotheses and test them against other systems to explore their degree of generality and predictability. The approach is inherently interdisciplinary and has been extensively applied to biotic (Hannon 1973), thermodynamic (Li and Sheraga 1988), and information systems (Haken 2006). Early application of systems analysis to ecology was pioneered by Eugene and Howard Odum, who described ecosystems as complex systems comprised of quantifiable flows of material and energy (Odum 1971). E.P. Odum published *The Strategy of Developing Ecosystems* (1969), which went on to identify predictable structural and energetic changes that take place as an ecosystem develops over time (Table 1). The qualitative framework put forth by Odum plays a fundamental role in ecosystem theory by providing directionality to ecosystem growth and development as well as touching upon the mechanisms behind those changes. Furthermore, this system analysis-based approach provides a consistent method upon which it is possible to compare the structural and functional characteristics of unique ecosystems as well as their influence on the overall health of an ecosystem.

Several decades of ecological systems analysis have resulted in the development of a variety of indices related to the emergent properties of ecosystems. These indices quantify the flows of energy or material through an ecosystem along with its structural organization. They allow one to observe how much energy moves through a system (Monaco and Ulanowicz 1997) and how it changes over time (Heymans et al. 2007). One can identify the individual pathways that energy takes and in what part of an ecosystem it is most likely to accumulate as biomass (Lindeman 1942). These indices quantify how efficiently energy is being used and how it recycles through a system (Ludovisi 2006). There are measures of overall ecosystem complexity (Jorgensen 2015), diversity (Ricotta 2002), stability (Ulanowicz et al. 2009), resilience (Rutledge et al. 1976), and scope for growth (Mageau et al. 1998). Yet, what makes these indices truly meaningful is their ability to quantify modern principles of ecological theory, such as the directionality of ecosystem development (Fath 2004). Each index provides an

important piece of information, that when fully combined, creates a narrative of holistic ecosystem behavior. The resulting narrative can be used to establish ecological baselines, identify anomalies, and help determine the mechanisms behind significant perturbations. Specific ecological features vital to ecosystem health, or those that enhance stability and resilience, can also be explored. The information derived through this approach not only advances our understanding of how ecosystems work, but provides decision makers with a flexible and effective toolset for ecosystem-based management.

Complex Systems Theory

Due to the interdisciplinary nature of systems analysis, it draws on theory developed in a number of different, yet related fields. Each discipline provides a foundation through which different indices of system analysis can be derived. But when combined into a single paradigm, a comprehensive description of ecosystem behavior at the system level can be achieved. This section will briefly introduce the sub-disciplines utilized in ecological systems analysis.

Ecosystems as Complex Adaptive Systems

What makes systems analysis applicable to ecosystems has to do with a number of properties common to all complex systems. Whether considering a human nervous system, an ant colony, the stock market, or online social systems like Facebook, they all share specific features that dictate their overall behavior:

1. They are composed of a large number of components consisting of many different types (Jørgensen and Müller 2000)
2. The components interact and react non-linearly and on different temporal and spatial scales (Allen and Starr 1983)
3. The systems organize themselves to produce complex structures and behaviors (Müller 1996)

4. Some form of heritable information allows the systems to respond adaptively to external changes (Dale 1971)
5. The structure and dynamics of these systems are effectively irreversible, and there is always a legacy of history (Layzer 1988)
6. They are hierarchically organized (Allen and Star 1983)

(1) Ecosystems are composed of individual organisms, populations, and species that all interact with each other on multiple scales. An ecosystem could even be thought of as an aggregation of individual atoms interacting and exchanging energy. (2) No matter what basic unit one considers, the complex interactions taking place in multiple dimensions commonly result in nonlinear and autocatalytic feedback processes that can amplify or degrade signals (Levin 1988). Nonlinear relationships tend to manifest themselves through threshold, limit cycle, or chaotic processes (Mandal et al. 2007). (3) These interactions also lead to organized structures and behaviors. For example, a food web is not just a random free for all of consumption and production, but rather an organized structure composed of species-specific relationships resulting in multiple trophic levels (Koestler 1978). (4) Instead of constantly forming and reforming from scratch, ecosystems are also able to adapt to external change over time through the transfer of genetic information (Abel 1998). (5) However, the evolution of ecosystems is not reversible and while the concept of irreversibility has its roots in thermodynamics and quantum physics, it is exemplified in ecosystems by things such as bifurcations (Kay 2000). (6) Finally, ecosystems are organized in a hierarchical structure composed of nested sub-systems (King 1993). A system of organelles makes a cell, a system of cells makes an organ, a system of organs makes an organism, and a system of organisms makes a population. The hierarchal structure spans from sub-atomic particles up to entire ecosystems and beyond. These fundamental characteristics of complex systems form the basis of ecological systems analysis and the indices utilized in this dissertation.

Ecosystems as Thermodynamic Systems

Thermodynamics is a discipline that deals with the relationships between different forms of energy and is the basis for the physical laws of the universe (e.g., the 1st, 2nd, and 3rd laws of thermodynamics). Early thermodynamics focused upon the transformations of one form of energy to another in order to maximize the efficiency of steam engines to perform work (Smith 1977). A variety of state variables were introduced that enables one to determine which physical and chemical reactions can be realized under which conditions (Jorgensen 2000). Due to its focus on the macroscopic flows of energy and mass, thermodynamics provides a holistic view of energetic systems from a physical perspective. However, classical thermodynamics was developed for systems in equilibrium and therefore was rarely applicable to real world dynamics (Uffink 2006). It was not until Onsager (1931) and Prigogine (1947) that thermodynamics was extended to non-equilibrium systems and its role in ecosystem structure and function was explored.

The 2nd Law of Thermodynamics states that every reaction leads to an increase in entropy or the dispersal of energy. Heat flows from an object at a higher temperature to an object at a lower temperature and not the other way. In other words, the 2nd Law of Thermodynamics says that things tend to become more disorganized or chaotic over time. However, life seems to contradict this law (Boltzmann 1886). If anything, life becomes more complex as things continuously evolve. The reason behind this apparent contradiction lies in the difference between equilibrium and nonequilibrium thermodynamics and the concept of isolation. An isolated system is one that is completely separated from the rest of the universe. These systems will degenerate over time, resulting in the elimination of all chemical/energetic gradients and reducing all chemical components to their lowest free energy, in accordance with the 2nd Law (Caratheodory 1976). Closed systems in thermodynamic equilibrium cannot perform work, and as such, cannot support life.

Non-isolated systems are not shut off from the rest of the universe and can freely exchange energy and material with outside systems. Ilya Prigogine formulated a thermodynamic description of these systems, for which he won the 1977 Nobel Prize in chemistry (Prigogene 1977). He showed that in open systems, where energy is free to flow in and out, the system will adopt a configuration that most effectively dissipates energy gradients (Figure 1). These are known as dissipative systems and they are able to obtain a low level of entropy (far from thermodynamic equilibrium) by exporting entropy outside themselves. Because these systems export entropy to the universe, the 2nd Law of Thermodynamics is still obeyed, despite the formation of organized structures. Through this perspective we can see that life, in fact, does not disobey the thermodynamic laws of the universe.

The behavior of dissipative systems has been mathematically defined and shown to be scalable (Hentschel 1991). Examples can be found throughout the world in the interactions of quantum particles (Weiss 1999), the formation of crystals (e.g., snowflakes) (Langer 1980), and RNA replication (Scott et al. 2014). Hurricanes and tornados are highly organized structures that effectively dissipate energetic pressure gradients in the atmosphere (Dekkers 2015). Even global oceanic and atmospheric circulation patterns behave as dissipative systems by redistributing energy coming from the sun (Dewar et al. 2013). Yet, some of the most efficient dissipative structures in the world are living things (Wicken 1987). A plant for example, absorbs energetic sunlight, uses it to build sugars, and ejects infrared light, a much less concentrated form of energy. Many predators feed on lipid rich (high energy) prey items, use that energy to grow, and eventually release it as heat. The behavior of dissipative systems can be scaled all the way up to entire ecosystems, which represent an aggregate of its individual components (Kay 1985). Although there are other mechanisms influencing the existence of life, the fact that living things effectively behave as dissipative systems provides us with a very useful tool by establishing a thermodynamically based directionality to ecosystem development consistent with Odum (1969).

Ecosystems as Information Systems

Information theory is a branch of applied mathematics, engineering, and computer science involving the quantification of information. It implies that a message contains a measureable amount of information and that the channel through which it is conveyed has a limited capacity or rate of transmission (Ulanowicz 2011). One of the first applications of information theory was to devise a system of coding messages so as to send them over a channel at as high a rate as possible. In other words, the goal was to get the most amount of meaning out of the least amount of transmitted data. Information theory is rooted in probability theory and statistics in that information is directly related to uncertainty (Shannon and Weaver 1949). Unfortunately, this relationship is rather unintuitive. The more uncertainty associated with a message, the more information it provides. Due to this relationship with uncertainty, strong ties have been made between information theory, thermodynamics, and the measurement of entropy (Ulanowicz and Hannon 1987).

Entropy, in a thermodynamic sense, represents the amount of disorder or uncertainty in a system. A system can be characterized by averaging ensembles of microscopic states to yield the macrostate (Skene 2013). Entropy measures the total number of ways that a particular macrostate can be constituted microscopically. Entropy can also be considered as the amount of information needed to describe a system, which directly ties into information theory (Harte and Newman 2014). However, it is important to note that thermodynamic entropy and informational entropy are different. Not only do they have different mathematic derivations, but thermodynamic entropy specifically refers to possible thermodynamic states of a system, while informational entropy can be calculated for any probability distribution (Parrondo et al. 2015). The similarities and differences among these concepts have caused a considerable amount of confusion in the literature (Neilsen 2000). Yet, it is also this relationship that makes information theory directly applicable to biological systems. Similar to the thermodynamic development of ecosystems over time, the information content of a system also undergoes predictable changes through evolutionary history (Ulanowicz 2003). As ecosystems evolve to reach more complex and organized states, changes in the

storage and flow of information can be used to quantify ecological development in a manner also consistent with Odum (1969).

Ecological Modeling

Ecology has developing into a quantitative science and one of the most important tools in this respect is modeling. Models provide a way to describe ecosystems by integrating features of systems in an organized way through mathematics (Jørgensen and Müller 2000). A model can be considered a synthesis of elements of knowledge about a system. Significant progress has been made since the early Lotka-Volterra predator-prey models of the early 20th century. Modern models now have the ability to simultaneously solve complicated sets of equations that allow for the quantifiable synthesis of multiple system elements along with properties that emerge at the system-scale (Wu and Marceau 2002). With respect to systems analysis in ecology, trophic flow models have become a particularly effective tool (Walters et al 1997). These models structurally link trophic interactions between a network of multiple species or taxonomic groups and calculate the simultaneous movement of material or energy through the system, which cannot be done in situ. Trophic flow models can quantitatively address the processes of ecological development put forth by E.P. Odum and can be used to compare multiple ecosystems or ecosystem states (Christensen 1995). Furthermore, they can measure the influence of external perturbations and produce the system-level information necessary to understand the mechanisms behind subsequent changes (Heymans et al. 2007). Not only do these models provide an important way to test ecological theory, but they can serve an invaluable role in management and conservation strategies (Nuttall et al. 2011).

However, ecological modeling must be approached with caution. Although ecological modeling is designed to handle the complexities that make it possible to study ecosystems in a holistic fashion, that same complexity can lead to very ineffective or inaccurate models. Considering ecological models are a

synthesis of what is known about a particular system, their performance directly depends on the quantity and quality of available information (Breckling and Dong 2000). If our understanding of a system is poor, a model cannot be expected to fill the gaps. At the same time, trying to incorporate too much complexity into a model, even if the underlying data is well resolved, can result in an unwieldy and impractical model (Costanza and Sklar 1985). Therefore, a balance must be struck between accuracy and complexity that incorporates only the necessary aspects of a particular ecological process or problem to be solved. Despite how realistic and easy to use modeling may get, there will always be a certain degree of irreducible uncertainty inherent in ecological systems (Hilborn and Ludwig 1993). In order for modeling to be effective, one must have a solid understanding of those uncertainties, the way in which they influence model results, and subsequent risks associated with model based decisions (Jørgensen 1994). But when the role of uncertainty is fully addressed, a wealth of valuable information can be extracted and this is especially true for processes that cannot be measured in the field. The accuracy of local weather forecasts, for example, are limited to a 1-2 week period and are still frequently incorrect, but that does not stop people from making a multitude of decisions for their daily life based on those predictions. The true value of models depends on the questions/problems they are used to address as well as one's ability to constrain uncertainty and one's willingness to make decisions under imperfect circumstances.

Ecosystems as bioeconomic systems

Although classic ecology has sought to study natural ecosystems through the exclusion of anthropogenic influence, we now live in a world where human influence is so ubiquitous that this approach is no longer practical (Costanza 2014). This is especially true if managers and scientists are to foster the development of sustainable use of ecosystems and ecosystem services (WCED 1987). In order to achieve these goals, the interactions between ecological and social/economic systems must be characterized and understood. The field of ecological economics has existed since the mid-20th century

(Boulding 1966), where it was recognized that 'frontier economics', or growth in human welfare by material consumption, was not a sustainable ideology. The work conducted during this time sought to separate economic markets from the biophysical systems of natural resources and brought with it a fundamental change in perspective concerning how resource allocation problems should be addressed (Clark 1973). However, the field of ecological economics has made significant progress in recent years due to its incorporation into a systems framework (Costanza et al. 1997).

Economic systems are complex adaptive systems in that they share the features outlined in the previous section (Costanza et al. 1993). Their similarity to ecosystems becomes even more apparent when one considers the flow of energy and material through economies (Geogescu-Roegen 1971). When measuring the flows of an economic system as the transfer of energy and material, direct relationships can not only be drawn to ecological systems, but to the thermodynamic processes that drive their behavior (e.g., The 2nd Law of Thermodynamics) (Ayres 1998). The strong link between economic and ecological systems allows one to answer questions regarding the influence of humans on natural systems through the use of a consistent approach. The same models developed for the transfer of energy through an ecosystem can be extended to incorporate the economic components that also play a significant role (Christensen et al. 2011). As a result, it is possible to assess the feedbacks that occur between economic and ecological systems, and therefore, truly take into account the role of anthropogenic influence on the natural world (Christensen et al. 2014). There are a variety of studies that have incorporated this into a systems analysis approach (Ruth 1993, Buenstorf 2000, Hannon 2001).

Empirical Validation of Ecological Systems Analysis

The strategy of applying systems analysis to ecosystem behavior has been carried out in a number of different ecosystems related to a diverse set of objectives. Many have used this approach to characterize natural patterns of ecological change (Jorgensen 2000, Baird et al. 1995, Choi et al. 1999,

Ray 2006, Rosen 2009, Silow et al. 2011, Skene 2013). There are studies that have used it to quantify the extent of eutrophication on marine and freshwater systems (Baird and Ulanowicz 1993, Marques et al. 1997, Monaco and Ulanowicz 1997, Ludovisi 2004, Patricio et al. 2006), the effects of different fisheries on ecosystem structure and function (Arreguin-Sanchez 2002, Bundy 2005, Coll et al. 2006, Niera et al. 2004, Fulton et al. 2005, Heymans et al. 2004 and 2007, Samhouri et al. 2009), and the combined influence of multiple anthropogenic stressors (Odum 1985, Mageau et al. 1998, Libralato et al. 2002, Coll et al. 2008, Pusceddu and Danovaro 2009, Nuttall et al. 2011). Researchers have also looked into the use of systems analysis to learn more about ecosystem stability and resilience (Yodzis 1980, Pimm 1984, Jorgensen 1995, McCann and Hastings 1997, Vasconcellos et al. 1997, Perez-Espana and Sanchez 2001, Cropp and Gabric 2002, Pfisterer and Schmid 2002, Pinnegar et al 2005, Ulanowicz et al. 2009). Recently, studies have attempted to combine these systems analysis indices into standard measures of overall ecosystem health (Costanza and Mageau 1999, Xu et al. 2001 and 2004, Jorgensen and Fath 2004, Muñoz-Erickson et al. 2007, Nelson et al. 2009). These examples represent a small sample of the available literature concerning the application of systems analysis and thermodynamic principles to ecological research and management.

Ecological Systems Analysis Indices

The qualitative features of ecosystem development put forth by Odum (1969) have been improved and added upon since their introduction. Technological and computer programming advancements have enabled scientists to quantify the descriptive processes introduced decades ago (Table 2). As mentioned previously, these indices relate to a variety of ecosystem structural and functional characteristics. Some are relatively straight forward in what they measure, while others are more complex in their calculation and interpretation.

1. **Net Primary Production** – Net primary production is the amount of energy/biomass introduced to a system as a result of primary production after the subtraction of respiration from primary producers. The overall growth of an ecosystem is dependent upon the amount of energy incorporated into biomass (Pauly and Christensen 1995).

2. **Respiration** – Respiration refers to the amount of energy that leaves a system due to metabolic processes of the organisms composing it. This serves as the primary export of energy out of ecosystems (Hannon 1973).

3. **Net Production** – Net production is a system-wide measure of net production (production – respiration) aggregated over all ecosystem components. It is used to calculate how much incoming energy is retained in a system (Pradeep Ram 2003).

4. **Ratio of Net Production / Respiration** – This ratio provides a measure of ecosystem development (Odum 1969). In young ecosystems, net production is expected to be greater than respiration as the system grows and biomass is accumulated ($P/R > 1$). As an ecosystem reaches maturity, this ratio is expected to approach one because energy fixed tends to balance the energy cost of maintenance (Ryan et al. 1997, Monaco and Ulanowicz 1997).

5. **Ratio of Production / Biomass** – This ratio is another measure of ecosystem development (Odum 1969). It is calculated as the ratio of system primary production to biomass. For immature systems, production is expected to exceed respiration while biomass beings to accumulate, resulting in higher values. Lower values are expected in mature systems where the amount of biomass supported by available energy reaches a maximum and the majority of energy is used in maintenance (respiration) (Cook 1963, Winberg et al. 1972, Christensen and Pauly 1993).

6. **Ratio of System Respiration / Biomass (aka Schrödinger Ratio) -** The ratio of total system respiration to system biomass (R/B) can be considered a thermodynamic order function (Odum 1971). The ratio got its name from physicist E. Schrödinger, who applied the work of Prigogine

to biological systems, showing that they must continuously pump out disorder (entropy) to maintain their internal order as a result of the 2nd Law of Thermodynamics (Schrödinger 1944). This ratio is considered to measure the 'performance' of a self-organizing system keeping itself in a non-equilibrium condition with the environment by exporting entropy. The lower the ratio, the higher the ability to maintain the internal organization under the given thermodynamic constraints (Ludovisi 2006). In an ecological sense, respiration is a measure of entropy exported outside of the system and biomass is a measure of internal organization or complexity. Developing ecosystems will maximize the amount of biomass maintained per unit of entropy exported, resulting in lower system respiration to biomass ratios (Odum 1983, Amblard 1988, Choi et al. 1999).

7. **Total System Throughput (TST)** – TST is measured as the sum of all flows in a system (total consumption + total export + total respiration + total flows to detritus). TST represents the size of an entire system in terms of flow and changes in TST over time can be characterized as system growth (Ulanowicz 1986). It is worth noting that the gross domestic product in economic systems is calculated in the same manner.

8. **Ratio of Biomass / Total System Throughput (TST)** – Similar to the Schrödinger ratio, the ratio of biomass to TST measures the amount of biomass supported per unit of energy moving through the system. As ecosystems develop, it has been shown that they tend to maximize this ratio (Fath 2001).

9. **Connectance Index** - The Connectance index (CI) is the ratio of the number of actual links to the number of possible links in a given system. Odum (1971,1969) suggested that food chain structure changes from linear in early ecosystem development to web-like as the system matures. Much of the literature shows that mathematically, there is a hyperbolic relationship between the number of links in a network and the stability of the system (May 1973). Early research suggests

an intermediate optimum number of links. However, more recent research has found that the strength of links has a very significant effect on this relationship (McCann et al. 1998). Decreased interaction strengths allow for a system to have more links and still remain stable. This can be observed throughout nature as omnivory. While this is still an open topic of research, the general consensus seems to be that although mathematical models show decreased stability with more links (complexity), natural ecosystems incorporate structural and functional aspects that provide stability despite high complexity.

10. **System Omnivory Index** - The system omnivory index is a measure of how the feeding interactions are distributed between trophic levels. It is used to characterize the extent to which a system displays web-like features (Mcann and Hastings 1997). This index is measured as the average omnivory index (variance of the trophic level of a consumer's prey groups) of all consumers weighted by the logarithm of each consumer's food intake (Pauly et al. 1993). It is expected that system omnivory index increases with ecosystem maturity (Odum 1969).

11. **Dominance of detritus** - Dominance of detritus is measured as the proportion of the total flows in a system that originate from detritus. Odum (1969) discussed shifts in ecosystems from herbivory to detrivory dominance as the system matures. Mature systems efficiently recycle nutrients and energy through detrital pathways and back into the ecosystem, thereby maximizing the use of energy available to the system. However, this relationship must be explored further for pelagic systems that are spatially separated from many detrital pathways (i.e., large organisms sinking out of the euphotic zone).

12. **Flow Diversity** - Flow diversity is a system level property derived from information theory. It quantifies the statistical entropy estimated over all groups and is also known as Shannon's diversity index. It is a measure of the total uncertainty embodied in any given configuration of

flows. It is expected that flow diversity increases as an ecosystem matures and is consistent with expected increases in biodiversity (Weber 1989).

13. **Average Organism Size** – Average organism size is an indirect approximation of system-wide life history traits. It has been shown that the inverse of the group production/biomass ratio is a general measure of average size (Pauly and Christensen 1993a). This relationship is scaled to the system level using the total system biomass over the total system production at all trophic levels (B/P)

14. **Finn's Cycling Index (FCI)** – Finn's Cycling Index is a thermodynamically derived measure of recycling within a system. It is calculated as the proportion of the total system throughput that is recycled in the system (Finn 1976). Although it is assumed that mature systems show a higher degree of recycling than immature systems (Odum 1969), it has also been shown that system cycling responds to system stress (Baird and Ulanowicz 1993). Ulanowicz and Wulff (1991) proposed that FIC must be considered in the context of the cycling structure of the system. They found that stressed systems (Chesapeake), while they had more overall cycling (higher FCI), consisted of short/fast cycles compared to longer/slower loops in a less stressed system (Baltic). It has also been shown that the degree of storage of energy/biomass in ecosystem components plays a role in the degree of cycling (Patten 1985)

15. **Predatory Cycling Index (PCI) –** Predatory cycling index is essentially the same thing as Finn's cycling index, but calculated to exclude detritus. Detritus is generally the dominant part of cycling (Allensina et al. 2005) and the predatory cycling provides an index that is more sensitive to the rest of the food web.

16. **Nutrient Regeneration** – Nutrient regeneration is calculated as FCI – PCI and quantifies the amount of energy or material recycled through detrital pathways (Christensen 1995).

17. **Path Length** – Path length is defined as the average number of groups that an inflow or outflow passes through. Calculated as throughput / (sum export + sum respiration). Path length is expected to increase with system maturity (Baird et al. 1991).

18. **Straight Through Path Length** – Straight through path length is defined as the average path length in the network if cycles are neglected (Finn 1976).

19. **Residence Time (energy based)** – Residence time is the average time that a unit of energy remains in the system. It is measured as the total system biomass over the sum of all output (respiratory and export flows) from the system. It is assumed that residence time will increase in mature systems as energy is efficiently retained in the system (Fath 2001).

20. **Ascendency** - Ascendency is an index derived through thermodynamic and information theory that quantifies both the level of system activity and the degree of organization with which it processes energy in an autocatalytic fashion (Ulanowicz 2011). It takes into account all of the flows in a system (TST) as well as what is known as the average mutual information. The average mutual information (AMI) represents the probability that a unit of energy passes from one group to another. In a system with many groups and many links between groups, uncertainty in the flow of energy (statistical entropy) increases along with a decrease in the probability of knowing where a unit of energy will flow at any given time. Multiplying the AMI of all flows by the system size (total system throughput) gives ascendency.

With respect to ecosystem theory, it has been shown that ascendency tends to increase over time as organismal groups specialize, form niches, and the overall system complexity increases in the absence of disturbances (Ulanowicz 2003). When a system is immature, there is widespread redundancy in the flow of energy (e.g., many links between groups and many possible ways for energy to move through the system). As a system matures, biomass is accumulated, and as the competition for energy increases, redundant links disappear and a much

more linear/cyclic structure develops (Figure 3). It has been shown that ecosystems develop as to increase ascendency in the absence of disturbances (Fath 2001). It is worth noting that ascendency takes the same mathematical form as a production function in economic theory.

21. **Information Content of Flows** – This index is another name for the average mutual information component of ascendency. It measures the reduction in uncertainty that comes from knowing the relationship between two variables, or in the case of an ecosystem, between species or populations. Similar to ascendency, this index is expected to increase as ecosystems develop (Costanza and Mageau 1999).

22. **Emergy-based Ascendency** - Emergy-based ascendency is a modified way of calculating ascendency that corrects for the dominant influence of the lower trophic levels on system flow characteristics (Christensen 1994a). The regular calculation of ascendency is mainly dictated by changes in the lower trophic levels, while emergy-based ascendency is more sensitive to changes in all trophic levels. Emergy, also known as 'embodied-energy', is a way of characterizing energy that expresses all flows in terms of their solar energy equivalents (Ulgiati 1994). This is important because although the transfer of energy into the highest trophic levels may be minimal when compared to the overall flows of an ecosystem, they represent very high total energy costs that have been used to generate that flow. Emergy accounts for the energy that is lost between trophic transfers up the food chain, which usually have efficiencies of 10%. This index provides a better perspective regarding the initial amount of energy that enters a system in order to produce a specified flow of energy at higher trophic levels.

23. **Capacity** - System capacity represents the diversity of the system flows scaled by the total system throughput. It defines the maximum ascendency possible for a given system (Ulanowicz 2011). This is calculated by multiplying the total system throughput (TST) by the statistical entropy of the system (a measure of all possible system states).

24. **System Overhead** - The difference between ascendency and capacity is known as system overhead. It quantifies how much ascendency can increase. It is also a measure of the number of redundant or alternate pathways of material exchange in an ecosystem, and as such, has been suggested as a system's ability to absorb stress without dramatic loss of function (Rutledge et al. 1976). Ecosystem theory says that immature systems tend to have higher values of system overhead before autocatalysis has eliminated alternative, redundant, and less efficient pathways of material and energy transfer. Considering that system overhead provides resilience to an ecosystem while ascendency represents efficiency in energy use, it has been proposed that there is an evolutionary balance between these two indices in the presence of disturbance regimes (Ulanowicz 2011).

25. **Relative Ascendency** - Relative ascendency is a useful ratio for observing where an ecosystem is along its developmental pathway. It is measured as the ratio of ascendency to capacity and therefore has values between 0 and 1. It represents the trade-off between efficiency of flow (high ascendency) and system redundancy (system overhead) (Monaco and Ulanowicz 1997). Ecosystem theory suggests that ecosystems rarely reach a value of one due to the nature of periodic or consistent disturbances. Christensen (1995) found that relative ascendency had a very strong correlation with system maturity, but the relationship was negative. It was suggested that this has to do with the formulation of component properties and the difference between internal and external disturbances (Saint-Béat et al. 2015).

26. **Exergy** – Exergy is a concept that was introduced as a more intuitive approach to the practical applications of entropy (Wall 1986). In one sense, it serves as a classification of energy quality, or the ability for energy to do work. For example, the water flowing over the top of a waterfall is considered a high quality energy source (high exergy) because it can perform work. It can be used to run a watermill or diverted through a turbine to produce electricity. However, the energy of water hitting the rocks below is dispersed as low quality friction/heat energy. Although water

hitting the rocks has the same amount of energy as the water above (energy is not created or destroyed, 1st Law of Thermodynamics), its ability to perform work, and therefore its quality, is significantly less.

Exergy can flow through ecosystems during energetic transformations or accumulate as biochemical energy stored in organic compounds that can be used to perform work (Jorgensen 2000). When applied to a system scale, exergy is defined as the distance that a system is from thermodynamic equilibrium (Jorgensen 2015). As described before, a closed system in thermodynamic equilibrium cannot perform work and it has no exergy. Due to this definition, it is useful to think of exergy as the opposite of entropy and to reconsider the 2nd Law of Thermodynamics and dissipative systems in terms of exergy. During any thermodynamic process, the quality of energy or its capacity to do work is irretrievably lost (entropy goes up and exergy goes down) (Kay 2000). Furthermore, open living systems exposed to an exergy gradient will consume exergy (produce entropy) to maintain a nonequilibrium (organized) state.

In order to quantify the exergy of an ecosystem, one must take into account the work energy of all system components, including the living components and the work energy of information that they utilize to perform their life processes (Jorgensen 2015). While a blueprint of a house does not necessarily build the house itself, if contains information that allows for more work to be accomplished. The work energy embodied in a computer cannot directly be used for mechanical work, but it can be used to control and direct work. DNA and genomes accomplish this by providing organisms information concerning the synthesis of organic compounds and their respective role in growth, reproduction, and survival. The inclusion of information in exergy calculations serves as a fundamental link to information theory (Ulanowicz et al. 2006). In order to measure the distance between a system and thermodynamic equilibrium, it is necessary to quantify embodied information by expressing the probability that a molecule or an organism will spontaneously form under equilibrium conditions, which is dependent on genome complexity

(i.e., less likely for a complex things to form than a simple ones) (Fonseca et al. 2000). This probability is then combined with the concentration of molecules or organisms (biomass) in a system to determine its overall exergy stored in biochemical components. Due to the difficulty in quantifying all of the information provided by an individual genome, general estimates have been developed for a variety of taxa, which are used as weighting factors in the exergy calculation (Jorgensen et al. 2005). As a result, it is important to note that exergy calculated through systems analysis is an approximation of the actual exergy contained in real living systems. However, the sensitivity of this index to ecological change makes it a very useful tool (Marques et al. 1997, Pusceddu and Danovaro 2009).

27. **Specific Exergy** – Specific exergy is defined as the exergy divided by the biomass of system components (Jorgensen 2000). Specific exergy expresses the dominance of higher organisms because they carry more information per unit biomass. Therefore, specific exergy gives a better description of ecological development because it considers diversity and the conditions that lead to more complex organisms (Austoni et al. 2007).

A wide variety of quantitative indices related to ecosystem structure and function are presented here, but there is a significant amount of overlap in what these indices measure and the information they provide. Yet they all have a theoretical basis in describing the thermodynamic state of an ecosystem. As such, the most useful indices are those that best quantify the distance that an ecosystem is from thermodynamic equilibrium or the ones that are most sensitive to change in ecosystem-scale entropy. There are two major factors that best represent thermodynamic distance from equilibrium; 1) ecosystem size, which gives an idea of the total energy and material present, as well as 2) ecosystem complexity, which provides an understanding of how much information is stored in an ecosystem. Therefore, the most useful indices presented here are the ones that incorporate both of these factors, such as Exergy, Relative Ascendency, and Emergy-based Ascendency. These indices will be the most sensitive to ecosystem-scale

perturbations and provide the most information about how the overall structure and function of an entire ecosystem may change as a result.

Significance

Although the wide variety of disciplines and quantitative indices used in ecological network analysis may seem rather complex, the idea behind their application is relatively simple. If one employs modern ecological theory regarding the directionality of ecosystem development in the absence of disturbances, it may be possible to use any deviations from that behavior to learn more about why and how those changes ecologically manifest. However, while the main strategy of ecological systems analysis is straightforward, the extensive list of structural and functional processes accounted for by this method offers a level of flexibility not found in other approaches. Through the use of synthetic ecosystem indices, ecological change can be viewed from a variety of perspectives and multiple dimensions in an effort to understand the driving mechanisms. The development of a mechanistic understanding is one of the most important aspects of ecological systems analysis. Such an understanding is essential to the creation of robust predictions that can be extended outside the boundaries of statistical relationships, which will become increasingly important as our world continues to change throughout the Anthropocene.

One of the major implications that lies at the heart of complex systems analysis is the ability to extend what is learned about one system to others. The quantitative indices introduced here characterize essential ecosystem attributes, which can then be compared to systems around the world to identify universal trends in ecosystem structure and function as well as identify patterns in the sensitivity of ecosystems to external perturbations (Heymans et al. 2014). These comparisons allow one to determine how a given ecosystem might develop over time or respond to a particular disturbance based upon its unique set of system-level properties (Colléter 2015, Saint-Beat 2015). Systems analysis and the incorporation of thermodynamic and informational approaches to complex systems is a rapidly expanding

avenue of research with applications in renewable energy (Liao et al. 2011), economic systems (Rosen 2011), marketing (Goldenberg et al. 2001), urban development (Lui et al. 2014), social communication networks (Pothineni 2012), and earth systems modeling (Schellnhuber 1999). The cross disciplinary utility of a holistic approach to complex systems has the potential to further our understanding of the world around us as well as provide effective and flexible approaches to solving a variety of global problems.

"A theory is the more impressive the greater the simplicity of its premises, the more different kinds of things it relates, and the more extended its area of applicability. Therefore the deep impression that classical thermodynamics made upon me. It is the only physical theory of universal content which I am convinced will never be overthrown, within the framework of applicability of its basic concepts."

— Albert Einstein, Autobiographical Notes (c. 1940s)

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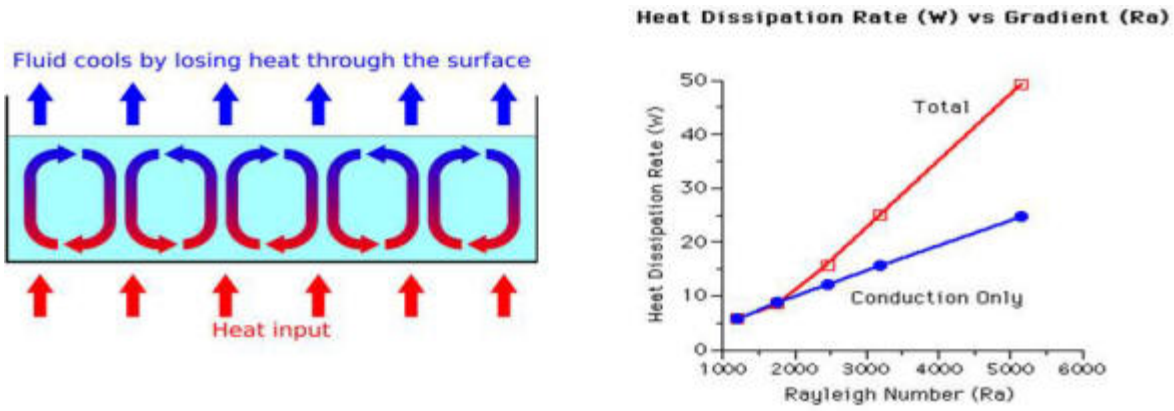


Figure 1.1. Formation of Bénard convection cells as self-organized energy dissipative structures. Cell diagram in two dimensions (Wikipedia 2009) (Left) and the relation between energy gradient (Rayleigh Number) and heat dissipation rate for conduction and conduction + Bénard convection processes (Right) (Figure from Schneider and Kay, 1994).

In the absence of major perturbations, ecosystems exhibit a propensity towards configurations of ever-greater network ascendancy.

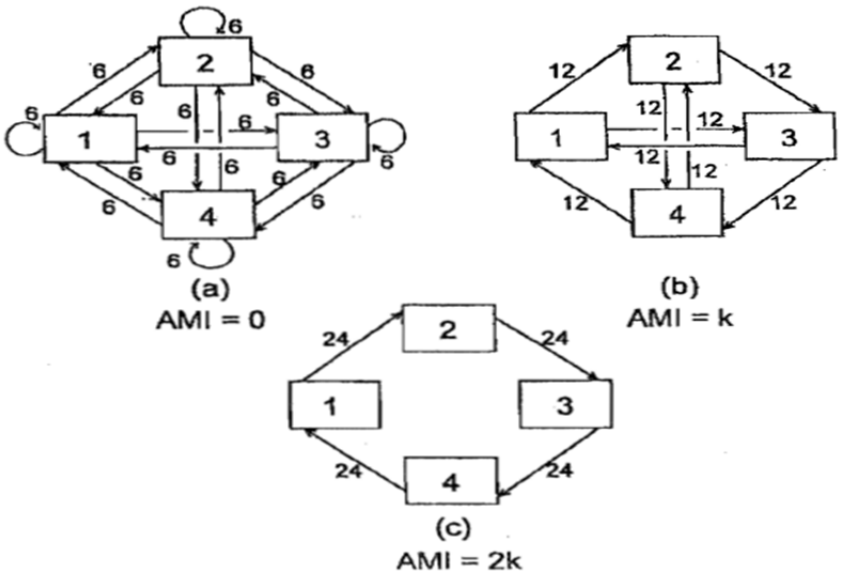


Figure 6: The increase in mutual information as flows become progressively constrained.

Figure 1.2. Diagram depicting the ecological development of ascendency through the flow of Average Mutual Information (AMI) (Figure from Ulanowicz, 2000).

Table 1.1 (Taken from Christensen 1995): Modified list of E.P. Odum's attributes of ecological succession

A tabular model of ecological succession: trends to be expected in the development of ecosystems (modified from Odum, 1969)

Ecosystem attributes	Developmental stages	Mature stages
Community energetics		
1 Gross production/community respiration (P/R ratio)	Greater or less than 1	Approaches 1
2 Gross production/standing crop/biomass (P/B ratio)	High	Low
3 Biomass supported/unit energy flow (B/E ratio)	Low	High
4 Net community production	High	Low
5 Food chains predominantly	Linear grazing	Weblike, detritus
Community structure		
6 Total organic matter	Small	Large
7 Inorganic nutrients	Extrabiotic	Intrabiotic
8 Species diversity – variety component	Low	High
9 Species diversity – equitability component	Low	High
10 Biochemical diversity	Low	High
11 Stratification and spatial heterogeneity	Poorly organized	Well organized
Life history		
12 Niche specialization	Broad	Narrow
13 Size of organism	Small	Large
14 Life cycles	Short, simple	Long, complex
Nutrient cycling		
15 Mineral cycles	Open	Closed
16 Nutrient exchange rate, with environment	Rapid	Slow
17 Role of detritus in nutrient regeneration	Unimportant	Important
Selection pressure		
18 Growth form (selection type)	For rapid growth ("r")	For feedback control ("K")
19 Production	Quantity	Quality
Overall homeostasis		
20 Internal symbiosis	Undeveloped	Developed
21 Nutrient conservation	Poor	Good
22 Stability	Poor	Good
23 Entropy	High	Low
24 Information	Low	High

Table 1.2: Summary of ecological systems analysis indices. See text for previse definitions and references.

	Index	Units
1	Net Primary Production	$g/m^2/year$
2	Respiration	$g/m^2/year$
3	Net Production	$g/m^2/year$
4	Ratio of Net Production / Respiration	-
5	Ratio of Production / Biomass	year
6	Ratio of System Respiration / Biomass (aka Schrödinger Ratio)	-
7	Total System Throughput	$g/m^2/year$
8	Ratio of Biomass / Total System Throughput	year
9	Connectance Index	-
10	System Omnivory Index	-
11	Dominance of detritus	-
12	Flow diversity	-
13	Average organism size	year
14	Finn's cycling index	-
15	Predatory cycling index	-
16	Nutrient Regeneration	-
17	Path Length	-
18	Straight-through path length	-
19	Residence time	year
20	Ascendency	-
21	Information content of flows	bits

Table 1.2: Summary of ecological systems analysis indices. See text for previse definitions and references. Continued

	Index	Units
22	Emergy-based ascendency	%
23	System overhead	-
24	Capacity	-
25	Relative ascendency	%
26	Exergy	Joules/m^2/year
27	Structural exergy	Joules/m^2/year

CHAPTER 2

Temporal variability of primary production explains marine ecosystem structure and function

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Abstract:

Understanding drivers of ecosystem structure and function is a pervasive goal in academic and applied research. We used 24 synthetic ecosystem-level indices derived from trophic models, and independently-derived data for net primary productivity, to investigate drivers of ecosystem structure and function for 43 marine ecosystems distributed in all oceans of the world and including coastal, estuaries, mid-ocean islands, open-ocean, coral reef, continental shelf, and upwelling ecosystems. Of these indices, ecosystem Biomass, Primary Production, Respiration, the ratio of Biomass to Total System Throughput (sum of total energy flow into and out of an ecosystem as well as between ecosystem components), the ratio of Production to Biomass, Residence Time (mean time that a unit of energy remains in the ecosystem), Average Trophic Level, and Relative Ascendency (index of organization and complexity of a food web) displayed relationships with measures of net primary productivity (NPP). Across all ecosystems, relationships were stronger with seasonal and interannual variability of NPP as compared to mean NPP. Both measures of temporal variability were combined into multivariate predictive relationships for each ecosystem index, with r^2 values ranging from 0.14 to 0.49. Our results indicate that

despite large geographical and environmental differences, temporal variability of NPP is strongly linked to the structure and function of

Introduction:

Ever since the inception of ecology as a field of science, a major challenge has been to understand the drivers of ecosystem structure and function [1]. Yet due to the sheer magnitude and complexity of ecosystems, the difficulties associated with quantifying all the vital processes of an ecosystem, or with conducting experiments at an ecosystem scale, this goal has remained elusive. The majority of past ecological studies attempt to focus on individual processes or to scale dynamics down to manageable scopes [2], leading to a wide variety of discoveries that apply to specific circumstances, but lack a consistent mechanistic framework applicable across ecosystems. However, modern advancements in analytical tools and data collection are slowly beginning to overcome the obstacles of complexity and scale [3]. Ecology has also expanded into a multidisciplinary field over the past few decades, whereby a diverse set of approaches to ecological questions have led to a multitude of new insights and breakthroughs [4]. These recent developments and additions to ecological thinking have opened the door for scientists to overcome the challenges of scale as well as to create a broadly applicable and consistent framework with which to explore the universal drivers of ecosystem structure and function [5,6].

Our understanding of ecosystems has come a long way from the simplified descriptions of food chains or Lotka-Volterra interactions. There is now a deeper appreciation of their vast complexity, which is characterized by a high degree of interlinked elements that interact on multiple scales. This holistic perspective incorporates the nonlinear processes, indirect effects, and emergent properties that play a major role in ecosystem behavior [7]. Ecosystems are hierarchal [8], self-organizing networks [9], driven by the flow of energy and material [10]. A central focus of this viewpoint emphasizes the philosophy that the whole is more than the sum of its parts and this depiction of ecosystems has shed light on the

existence of a general set of driving principles amongst a seemingly endless sea of variables and unknowns [11,12].

Eugene P. Odum was one of the first scientists to look at ecosystems from a holistic point of view. By observing large scale changes across ecosystems during successional events, he was able to identify general trends in productivity, biomass, and energy recycling over time [11]. He saw that ecosystems become bigger, more efficient, and more complex as they develop. The true significance of this study lies in Odum's introduction of the idea that one may not need to fully understand all of the intricate details and countless interactions of an ecosystem to predict how it will behave. Instead there may be a general set of rules or principles that drive ecosystem structure and function. Robert May and several other scientists took this a step further by identifying a number of mathematical guidelines [13] governing the behavior of model food webs that relate their structure to functional aspects of stability and resilience across multiple systems [14]. This work has led to a lot of research focusing upon the role of biodiversity in ecosystem functioning [15,16]. And more recently, scientists have developed several goal functions, or ecosystem orientors, that describe consistent multi-scale patterns of ecosystem development in terms of the flow of energy and material [17,18,19]. These goal functions are mainly derived from Odum's initial observations of ecosystem development and make use of energy accounting and the basic laws of thermodynamics.

As support for the existence of general rules governing ecosystem structure and function continue to increase, the role of energy has emerged as a central component. Energy is one of the primary unifying characteristics of all life; from cells to ecosystems. Energy availability, extraction, and efficient use serve as major evolutionary driving forces [20]. Due to this ubiquitous role, energy dynamics also provide a consistent framework for ecological comparisons [21]. This idea is certainly not new and there are entire fields dedicated to the study of energy flow and storage within individuals and even ecosystems [22,23]. Using thermodynamic principles along with biogeochemical and bioenergetic data, it is now possible to analyze how much energy enters an ecosystem in the form of primary production, flows through it, and is

stored as biomass into living organisms [24]. In particular, satellite data [25] and trophic food web models [26,3] allow for the comparison of energetic inputs, outputs, and storages of entire ecosystems. A major advantage of this approach is that complexity and detail can be synthesized into summary indices that allow for the quantification of structure and function for any given ecosystem, and these characteristics can be compared across ecosystems at a global scale.

This study set out to identify global patterns in holistic properties of ecosystems: their size, efficiency, and complexity, in order to explore the existence of universal drivers of ecosystem structure and function. We used two approaches to measure energy flow and storage: 1) Satellite-derived values of net primary production (NPP) are compared with 2) a variety of energetic attributes extracted from ecosystem models representing 43 different marine ecosystems to identify general patterns. Satellite measures of NPP and indices derived from ecosystem models serve as completely independent data sources. From these comparisons, it is possible to identify consistent ecosystem-scale characteristics across a diverse set of systems, which not only shed light on the fundamental evolutionary processes of ecosystem development, but may also provide quantitative evidence for the existence of universal principles related to ecosystem-scale energy flow.

Methods:

Satellite Data

NPP is defined in this study as the production derived from phytoplankton. Global estimates of NPP were obtained from the Centre for Environmental Data Analysis (CEDA) [27]. The CEDA derived this data from monthly estimates of carbon primary production from the Centre for the Observation of Air-sea Interaction and fluXes (CASIX) using Sea-viewing Wide Field-of-view Sensor (SeaWiFS) Primary Data [28]. The data set used in this study is comprised of monthly means of NPP in $mgC*m^{-2}*day^{-1}$ for 10 km x 10 km grid cells from 1998 to 2005. The applied NPP model incorporates a radiative transfer code, which allows for the inclusion of dissolved organic matter and suspended particulate

matter, along with measures of surface chlorophyll, photosynthetically available radiation, and sea surface temperature to calculate production [25]. The incorporation of a radiative transfer into the NPP model improves global NNP estimates by increasing the accuracy of NPP estimates in waters with high concentrations of dissolved matter and reducing the RMS between observed and predicted values to 0.23. However, moderate-resolution imaging spectroradiometer (MODIS) chlorophyll algorithms tend to overestimate dissolved organic matter in coastal waters, which can lead to an underestimation of primary production [29].

Ecosystem Models

The ecosystem models selected for this study were developed using Ecopath with Ecosim (EwE) [30,31]. EwE is a software package that comprises several modules (Ecopath, Ecosim, and Ecospace) for building mass balance as well as time and space dynamic models of ecosystems and includes a large set of diagnostics for analyzing food webs. These features plus its flexibility and user-friendly interface makes EwE one of the most widely applied modeling approaches for food web representation and scientific analysis [32,33]. We used only the Ecopath component, a platform for building ecological networks (i.e., food webs) where network components are defined as functional groups (representing species or groups of species) and the interactions between components are trophic interactions quantified using bioenergetics [34]. The major inputs for each component of the network include biomass, production and consumption rate, food preferences, unassimilated fraction, and fishing catches. Additional inputs include immigration, emigration, and biomass accumulation, while other mortality and respiration are estimated by the model. Values for these parameters typically represent yearly averages over a small subset of years. Ecopath calculates a static mass-balanced snapshot of the biomass and energy fluxes between functional groups in a food web. The mass-balance is set in a way that consumption of any given component is subtracted by all losses including bioenergetics ones (respiration, excretion), predation, eventual net migration, and mortality due to anthropogenic factors (i.e., fishing). Remaining biomass can accumulate or result in an estimate of other mortalities unexplained by the model

(summarized into the parameter Ecotrophic efficiency [34]. A data base of available EwE models is available through EcoBase [3].

Models were selected for use in this study based upon two general objectives. First, we constrained the influence of eutrophication and fishing effects. Information regarding the degree of eutrophication in ecosystem locations was provided by the World Resources Institute (WRI) [35]. The ratio of production to respiration (P/R) derived from Ecopath models represents the ratio of energy input to energy output in an ecosystem and might reflect the trophic status of a system. This was compared with WRI information in order to assure that local empirical and model-aggregated information were in agreement in spite of differences in resolution and spatial mean. Values of this ratio for systems with EwE models identified by the WRI as non-eutrophic, all fell within a range of 1-3.5, while 88.9% of all systems identified by the WRI as eutrophic had values above this range. Therefore, any systems that were identified as eutrophic by the WRI or with a ratio of production to respiration above 3.5, were not selected for this study. The impact of fishing was limited by selecting model versions where fishing mortality was at its lowest for ecosystems with multiple model versions (complete removal was not possible). For example, many ecosystems had two or more model versions representing different time periods with subsequently different commercial fishing pressures. When multiple model versions were available for different time periods, the period with the lowest fishing mortality across components was selected. Second, because model structure alters the simulated direct and indirect trophic impacts as well as subsequent energetic and organizational indices [36], models with less than 20 components (or functional groups) were considered over-aggregated and not included in this study.

Once a suite of models was selected based upon the above criteria, a principle components analysis using synthetic ecosystem indices was conducted in order to identify any obvious outliers. Five models were identified and removed using the PCA. A total of 43 Ecopath models met the requirements for inclusion (Table 1 and Fig. 1), representing ecosystems spanning 130^{o} of latitude, and including all major ocean basins and a wide variety of ecosystem types, including 13 coastal ecosystems, three

estuaries, two mid-ocean islands, five open-ocean ecosystems, one coral reef, 12 continental shelf ecosystems, and seven upwelling ecosystems.

Ecosystem Indices and definitions:

A total of 24 synthetic ecosystem indices were extracted from Ecopath models and explored (Appendix 1). Synthetic indices describing ecosystem-level properties related to macro-scale measures of ecosystem energy flow and storage as well as ecosystem structure and complexity characterize ecosystem-scale properties (combined measures of all ecosystem components), as opposed to specific properties (individual components or attributes at smaller scales within an ecosystem) [17, 18,19]. Each ecosystem index was compared with measures of mean NPP as well as seasonal and interannual variability in NPP.

Statistical Analyses

For each ecosystem, monthly estimates of NPP (mgC*m-2*day-1) per 1^{o} latitude by 1^{o} longitude grid cell were spatially averaged over a 10x10 grid cell area. Although the geographic extent of each ecosystem varied widely, we selected a 10x10 grid cell area within each ecosystem to control for those differences. The location of each sample area was chosen by using the latitude and longitude information provided by each ecosystem model to identify the ecosystem boundaries. For ecosystems that had much larger areas than 10x10 grid cells, latitude and longitude information was used to identify a central point, which was also designated as the center of the sample area. When explicit information regarding spatial dimensions of an ecosystem was missing, locations were determined by using respective maps found in model publications. Only marine cells were used for ecosystems adjacent to a coastline.

Monthly values of NPP were calculated over the period of available NPP estimates (1998 to 2005) to create time series for each ecosystem. Ecosystem indices were then compared with mean NPP (1998-2005 means) and interannual and seasonal variance in NPP. Interannual variance was calculated as the mean square (MS) of deviations between years and seasonal variance was calculated as the mean

square (MS) of deviations between months within a year. Regression models relating mean, and seasonal and interannual variability of NPP to each index were derived. In addition, due to a high degree of covariance in the MS of interannual and seasonal variability, both measures of temporal variability were simultaneously compared to each synthetic index; these are depicted in 3-dimensional plots as multivariate regression surfaces. Three-dimensional model selection between temporal variability and ecosystem indices was conducted using Akaike's Information Criteria (AIC) and comparative F-tests. AIC values used for predictive model selection ranged between -5.83 and 3.26. Random permutation tests were also conducted in order to estimate distributions of r^2 values extracted from randomly generated data sets, keeping the same polynomial models with newly fitted parameters.

The above analysis was also conducted using areas of 5x5 grid cells (5^o latitude by 5^o longitude) and 1x1grid cell (1^o latitude by 1^o longitude) to identify the influence of spatial scale. Paired t-tests were used to compare mean NPP, MS of interannual variability, and MS of seasonal variability extracted using 1x1, 5x5, and 10x10 grid cell areas. All comparisons showed that spatial resolution did not significantly influence values of NPP extracted from each ecosystem location (minimum p-value of .053). Two dimensional Kolmogorov–Smirnov tests were also used to compare the relationships between ecosystem indices with NPP data extracted at different scales. All comparisons resulted in no statistical differences between relationships observed at each scale. Therefore, we present only results based on 10x10 grid cell areas.

Results:

Of the 24 synthetic ecosystem indices explored, 8, listed below, displayed significant relationships (P value ≤ 0.05) with satellite measures of mean NPP or its variability. 1) 'Biomass' represents the total wet weight of living organisms in the system (tons/km^2). Biomass serves as a measure of energy storage in an ecosystem. 2) 'Primary Production' (PP) refers to the amount of energy entering an ecosystem to be incorporated into biomass by autotrophs in tons/km^2/year. PP serves as the major

input of energy into an ecosystem. 3) 'Respiration' refers to the amount of energy leaving the system through metabolic processes in tons/km^2 /year and constitutes the major energetic output of ecosystems. 4) 'The ratio of Production to Biomass' (P/B) is a measure of how much production is needed to support each unit of biomass within an ecosystem. Production is expected to exceed respiration in immature ecosystems as biomass begins to accumulate, resulting in higher values [37]. Lower values are expected in mature systems where the amount of biomass supported by available energy reaches a maximum and the majority of energy is used in maintenance. 5) 'The ratio of Biomass to Total System Throughput' (B/TST) is used as a measure of the amount of biomass maintained per unit of energy flowing through an ecosystem. Total system throughput represents the total flows of the ecosystem, including flows between ecosystem components and flows between the ecosystem and the exterior. The value of this ratio increases as ecosystems mature [12]. 6) 'Residence Time' is the mean time that a unit of energy remains in the system and is calculated as the total system biomass over the sum of all outputs (respiratory and export flows) from the system. Residence time is assumed to increase in mature systems as energy is efficiently retained in the system [12]. 7) 'Average Trophic Level' of the community is used to synthesize the structure of the food web and gives a general idea of system complexity. 8) 'Relative Ascendency' is an index of organization and complexity of a food web and is a useful ratio for observing where an ecosystem is along its developmental pathway. It represents the trade-off between efficiency of energy flow (high ascendency) and redundancy in energy flow (system overhead) moving from primary producers to top predators in an ecosystem context [38]. For example, a river delta would be considered a system with a low relative ascendency (high redundancy in pathways), while a single river channel would have a high relative ascendency (high efficiency of flow). Christensen (1995) found that relative ascendency had a very strong correlation with system maturity.

Mean NPP displayed weak relationships with most indices, with r^2 values below 0.1 for all but 2 of the 8 (Biomass and Average Trophic Level; Table 2). The very low r^2 associated with the relationship between mean NPP from satellite data and Primary Production from Ecopath models is due to the

inclusion of respiration in NPP calculations, which is not an input to Ecopath. Unexpectedly, temporal variability of NPP (both seasonal and interannual) had stronger relationships than mean NPP for 7 of the 8 ecosystem indices (Table 2). With one exception (Average Trophic Level), r^2 values from regression models of seasonal and interannual variability with each index were larger (1.4 to 27 times larger) than model fits with mean NPP. Furthermore, relationships between each index and seasonal and interannual variability of NPP were independent of ecosystem type or latitude (Fig. 2). R^2 values derived from multivariate relationships between both measures of variability and each ecosystem index were consistently higher than individual comparisons with either seasonal or interannual variability. R^2 values for these multivariate relationships ranged from 0.15 to 0.49 and AIC values fell between -8.44 and 3.26 (Table 3).

Comparisons of the log of Biomass with mean NPP showed a weak, yet statistically significant (P value = 0.0036), unimodal relationship ($r^2 = 0.18$, $p = .001$).Stronger relationships were identified when compared to the MS of interannual and seasonal variability ($r^2 = 0.27$ and $r^2 = 0.4$, respectively). The 3-dimensional multivariate model comparing Biomass with both modes of variability (Fig. 2) has an R-square value of 0.46. When plotting each ecosystem data point in 3-dimensional space along the predictive surface, there was no identifiable clustering of systems based upon ecosystem type or latitude.

Three-dimensional relationships between Primary Production ($r^2 = 0.16$) and Respiration ($r^2 = 0.2$) to interannual and seasonal variability displayed similar patterns to each other (Fig. 3). Both showed strong positive increases with increasing seasonal variability and only a negligible response to interannual variability. Primary Production showed a weak correlation with mean NPP (rho = 0.33, $p = 0.03$); the relationship between Respiration and mean NPP was not significant.

P/B ($r^2 = 0.15$), B/TST ($r^2 = 0.19$), and Residence Time ($r^2 = 0.14$) all displayed similar unimodal patterns when compared to interannual and seasonal variability (Fig. 4), but with P/B having an opposite trend. P/B was lowest at intermediate values of seasonal variation and higher at either extreme, while

increasing interannual variability lead to minor increases in this ratio along the entire surface. The highest values for B/TST and Residence Time were observed at intermediate levels of seasonal variability. Increasing interannual variability had a minor positive influence at low values of seasonal variability and a minor negative influence at high values of seasonal variability. These indices did not display any significant relationships with mean NPP.

The 3-dimensional relationship between Relative Ascendency ($r^2 = 0.49$) and variability (Fig. 5) displayed a unimodal, valley-shaped pattern with the lowest values extending along the line of both increasing interannual and seasonal variability. The higher values extended along this valley at either extreme of interannual variability except when seasonal variability was also at its highest. The 3-dimensional surface comparing the Average Trophic Level ($r^2 = 0.22$) of each ecosystem with variability (Fig. 5) displayed a strong positive relationship with increasing seasonal variability, while interannual variability had a negative influence. Both Relative Ascendency and Average Trophic Level did not show significant relationships with mean NPP.

Discussion:

Limitation of the Approach and Uncertainty in Ecopath Modeling

The relationships identified here, although significant, have low correlation coefficients. This is not surprising when comparing things as complex as ecosystems, which involve a myriad of interacting components and indirect effects. It is common, however, to observe low r^2 values for relationships comparing multiple ecosystems [39] because of high ecological variability observed in natural systems. The ecosystem models allow for the synthesis of ecosystem complexity, including its variability across time, permitting simple comparisons of ecosystem properties. An important drawback of this approach is that observed relationships are strongly dependent on uncertainty of models used.

Precise quantification of the uncertainty associated with Ecopath model outputs is uncommon, but past analyses indicate that model outputs are generally robust [40,41]. Since the Ecopath mass balance

constraint is used to estimate model parameters for components with missing information, Essington (2007) evaluated the sensitivity of nine Ecopath models to imprecise data inputs and the effect of the mass balance constraint on estimating missing parameters. The accuracy of Ecopath estimates of group biomass and ecotrophic efficiency (EE) (the proportion of a group's total mortality explicitly represented in the model by predation and fishing) depended mostly on the precision of input parameters and the process of mass balancing had little effect on the magnitude of output parameter prediction errors. In other words, bad data led to bad predictions. When input data had a CV of 0.05, prediction errors around these biomass and EE were approximately 10%.

The impact of uncertainty in input parameters on Ecopath model outputs has also been addressed through the incorporation of Monte-Carlo and other input parameter probability distribution methods into Ecopath and Ecosim [42]. Using this feature, other authors have found that uncertainty associated with empirical measurements for Ecopath input parameters did not significantly alter Ecosim estimates for any of the components (functional groups) [43,44,45]. In general, parameter input combinations from Monte Carlo derived models with the best fit to time series showed only slight changes from original base Ecopath model parameter inputs (averaging +/- 20%) [46,47,48]. In Parrish et al. (2011), the base model fit outperformed the best models derived from the Monte Carlo analysis [49].

The influence of parameter uncertainty on synthetic ecosystem indices was also tested in Guesnet et al. (2015) for the Bay of Biscay; an Ecopath model used in this study. Through the introduction of uncertainty to Ecopath input parameters, this study assessed how estimates of ecosystem indices derived from the original Ecopath model inputs compared to output index distributions derived from varying levels of uncertainty. All ecosystem index values derived from the original base Ecopath model fell within subsequent index distributions following the incorporation of uncertainty. Their results suggest that ecosystem indices produced by Ecopath are robust to uncertainty in original ecosystem model input parameters up to differences of 60% from true values.

Uncertainty in Ecopath model outputs aside, a major strength of our approach is the use of two independent data sets for our investigations of pattern; satellite-derived data and Ecopath model outputs. The measures of NPP that we used in our study are not used as input parameters in the construction of Ecopath models. Many of these models use in situ measurements of primary production, and while some may derive estimates of primary production from satellite data, variability in NPP is not used as an input in any way. Due to the number of ecosystem models used in this study and the consistency of global patterns identified across 8 different ecosystem indices when compared to a completely external data source, it is unlikely that the patterns found in this study are the result of a systematic error introduced through Ecopath.

Role of Temporal Variability in NPP on Ecosystem-Scale Properties

Our results provide insight into the general drivers of marine ecosystem structure and function. Total primary production is known to influence a wide variety of ecosystem-level properties including total production and biomass [50,51], and biodiversity and food chain length [52]. Few have compared the influence of temporal variation in primary production [53], but it is clearly significant. Our results show that ecosystem storage (Biomass) reaches maximum values at intermediate to high seasonal variability. Ecosystem output (Respiration) increases with seasonal variability of NPP. Ecosystem efficiency (a measure of internal recycling of energy or the amount of biomass supported by one or more energy flows, measured in this study by Residence Time, P/B, and B/TST), is also maximized at intermediate to high seasonal variability in NPP. The organizational complexity of ecosystems is strongly related to the temporal variability of NPP as well, with more efficient transfer of biomass through food chains (Average Trophic Level), and increased redundancy in pathways of biomass to top predators (Relative Ascendency) resulting from increased seasonal variability in NPP. Given that temporal variation in NPP defines optimal storage and use of energy over time by component organisms in a given ecosystem, its influence on ecosystem structure and function is perhaps not so surprising [54]. While the r^2 values for some of these relationships may seem low, when dealing with complex as ecosystems which

involve a myriad of interacting components and indirect effects it is common to observe high r^2 values for relationships comparing multiple ecosystems [39].

While support for the influence of temporal variability in NPP on single properties of ecosystems (as opposed to indices that synthesize the state of an entire ecosystem) can be found throughout the literature, there is very little evidence for its influence on holistic ecosystem structure and function. For example, temporal variability in NPP drives the switch from small- to large-bodied planktonic communities [55], strongly impacts fisheries yield [56], and is positively correlated with the trophic level of fisheries at a global scale [53]. However, this study quantifies the underlying *holistic* dynamics of energy flow related to a variety of ecosystem properties at a macro scale, with the hope of combining previously qualitative observations with modern ecological theory. More importantly, we identified consistent global patterns across a variety of holistic ecosystem traits from extremely different ecosystems all related to a single variable, which has not been reported in the literature previously. This work shows that variability in NPP simultaneously influences a variety of ecosystem-level characteristics of energy flow that can be related to ecosystem efficiency, complexity, and scope. Very few individual variables have such far reaching consequences for holistic ecosystem structure and function. Furthermore, variability in NPP can be easily measured from satellites. As such, the identification of this relationship allows for a broad understanding and potential prediction of global ecosystem dynamics using minimal resources.

One potential mechanism explaining the influence of temporal variability of NPP on ecosystem structure and function may be related to functional diversity (the number of functionally disparate species within an ecosystem), which tends to be maximized under regimes of intermediate disturbance [57]. While stable conditions can favor species-specific competitive advantages, disturbance can allow for the coexistence of competing species (i.e., an increase in functional diversity) [58]. Temporal variability in NPP can be thought of as change from a climatological mean and, in this way, analogous to a disturbance [54]. These subsequent changes allow for the coexistence of several energy pathways that are an

expression of high functional diversity [59], which in turn influences ecosystem biomass [60]. The strong positive relationship we found between Relative Ascendency, a measure of the number of diverse paths leading from primary producers to apex predators in a food web, and temporal variability in NPP provides support for this concept. The results of this study build upon previous literature linking biodiversity to ecosystem functioning [16] by exploring the underlying energetic processes and identifying a potential mechanistic framework.

Conclusion

The field of systems ecology is progressing towards a consistent approach to understand and predict ecosystem structure and function [61] and the use of overarching synthetic indices, emergent properties of ecosystem-scale energy flow have played a primary role in that advancement [5,6,17,19]. By using completely independent data sources (satellite measures of NPP and synthetic indices of structure and function from trophic food web models) this study builds upon past theoretical and empirical work by quantifying the role of ecosystem-scale energy input in explaining patterns of ecosystem structure and function. Our results highlight the utility of applying macro-scale dynamics of energy flow to understand and predict complex ecosystem behavior. These patterns are consistent across a wide range of temperatures, latitudes, and marine ecosystem types; linking diverse ecosystems together in a way that has not been previously identified. Results of this study imply that despite complex evolutionary histories, species compositions, or environmental conditions, the temporal dynamics of NPP influence ecosystem properties in a way that is common to all marine ecosystems. While more research needs to be conducted in order to truly identify the causal relationships behind these emergent ecosystem properties, energy flow and accounting provides a framework with which to potentially begin quantifying those mechanisms and this approach takes a step forward in that direction.

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Table 2.1. Ecosystems included in analysis for which Ecopath models have been build and their respective publications.

Ecosystem	**Type**	**Ocean Basin**	**Reference**
Corsica	Coastal	Mediterranean	Albouy et al. 2010
Hudson Bay	Coastal	Atlantic	Hoover 2009
NC Adriatic Sea	Coastal	Mediterranean	Coll et al. 2007
NE Ionian Sea	Coastal	Mediterranean	Piroddi et al. 2010
North Aegean Sea	Coastal	Mediterranean	Tsagarakis et al. 2010
Norway	Coastal	Atlantic	Falk-Petersen 2004
Prince William Sound	Coastal	Pacific	Okey and Pauly 1999
Sinaloa	Coastal	Pacific	Salcido-Guevara 2006
Sri Lanka	Coastal	Indian	Haputhantri et al. 2008
Aleutians	Coastal	Pacific	Guénette et al. 2006
British Columbia Coast	Coastal	Pacific	Preikshot 2007
Grand Banks of Newfoundland	Coastal	Atlantic	Bundy et al. 2000
Grand Banks of Newfoundland	Coastal	Atlantic	Heymans 2014
Gulf of Nicoya	Estuary	Pacific	Wolff et al. 1998
Port Phillip Bay	Estuary	Southern Ocean	Fulton and Smith 2002
Strait of Georgia	Estuary	Pacific	Preikshot 2007
Prince Edward Islands	Island	Atlantic	Gurney et al. 2014
Virgin Islands	Island	Atlantic	Opitz 1993
Central Atlantic	Ocean	Atlantic	Vasconcellos 2004
Eastern Tropical Pacific	Ocean	Pacific	Olson and Watters 2003
North Atlantic	Ocean	Atlantic	Vasconcellos 2004
North East Pacific	Ocean	Pacific	Preikshot 2007
Western Tropical Pacific	Ocean	Pacific	Godinot and Allain 2003
Looe Key	Reef	Atlantic	Venier 1997
Bay of Biscay	Shelf	Atlantic	Ainsworth et al. 2001

Table 2.1. Ecosystems included in analysis for which Ecopath models have been build and their respective publications. Continued.

Ecosystem	**Type**	**Ocean Basin**	**Reference**
E. Berring Sea	Shelf	Pacific	Trites et al. 1999
Eastern Scotian Shelf	Shelf	Atlantic	Bundy 2005
Gulf of St. Lawrence	Shelf	Atlantic	Morissette and Hammill 2006
Gulf of Thailand	Shelf	Indian	Christensen 1998
High Barents	Shelf	Atlantic	Blanchard and Pinegar 2002
Low Barents Sea	Shelf	Atlantic	Blanchard and Pinegar 2002
North Sea	Shelf	Atlantic	Christensen 1992
SE Shelf Australia	Shelf	Southern Ocean	Bulman et al. 2002
Tasmania	Shelf	Southern Ocean	Watson et al. 2013
West Coast Greenland	Shelf	Atlantic	Pedersen and Zeller 2001
West Coast Scotland	Shelf	Atlantic	Heymans et al. 2011
Benguela	Upwelling	Atlantic	Watermeyer et al. 2008
Cape Verde	Upwelling	Atlantic	Stobberup et al. 2004
Central Chile	Upwelling	Pacific	Neira Arancibia 2013
Morocco	Upwelling	Atlantic	Stanford et al. 2001
Northwest Africa	Upwelling	Atlantic	Morissette et al. 2010
South Benguela (Watermeyer)	Upwelling	Atlantic	Watermeyer et al. 2008
W. Coast Sabah	Upwelling	Atlantic	Garces et al. 2003

Table 2.2. Relationships between 8 ecosystem indices derived from Ecopath with Ecosim, and Net Primary Productivity (NPP) for 43 marine ecosystems: mean, seasonal, and interannual (see text for details). MS = mean squares and AIC = Akaike's Information Criteria.

Index	Proxy for	Mean NPP		MS of Seasonal Variability		MS of Interannual Variability	
		AIC	r^2	AIC	r^2	AIC	r^2
Biomass	Energy Storage	-1.912	0.19	-2.21	0.398	-2.012	0.267
Primary Production	Energy Input	-1.596	0.1	-1.664	0.158	-1.566	0.072
Respiration	Energy Output	-1.696	0.09	-1.823	0.197	-1.728	0.157
Production/Biomass (P/B)	Energy Use Efficiency	-2.318	0.014	-2.412	0.143	-2.331	0.071
Biomass/Total System Throughput (B/TST)	Energy Use Efficiency	-8.393	0.028	-8.505	0.17	-8.427	0.102
Residence Time	Energy Recycling	-5.824	0.009	-5.911	0.133	-5.852	0.08
Relative Ascendency	Structural Complexity	3.673	0.008	3.471	0.189	3.432	0.221
Average Trophic Level	Structural Complexity	-2.67	0.263	-2.417	0.006	-2.476	0.063

Table 2.3. Multivariate relationships between synthetic ecosystem indices and the MS of interannual and seasonal variability along with their respective model AIC values, the number of coefficients used in each model, and r-squared values.

Index	3D Model AIC	# Model Coefficients	Degrees of Freedom	r-squared
Biomass	-2.2	5	38	0.46
Primary Production	-1.67	3	40	0.16
Respiration	-1.78	3	40	0.20
Production/Biomass (P/B)	-2.32	5	38	0.15
Biomass/Total System Throughput (B/TST)	-8.44	5	38	0.19
Residence Time	-5.83	5	38	0.14
Relative Ascendency	3.26	9	34	0.49
Average Trophic Level	-2.61	3	40	0.22

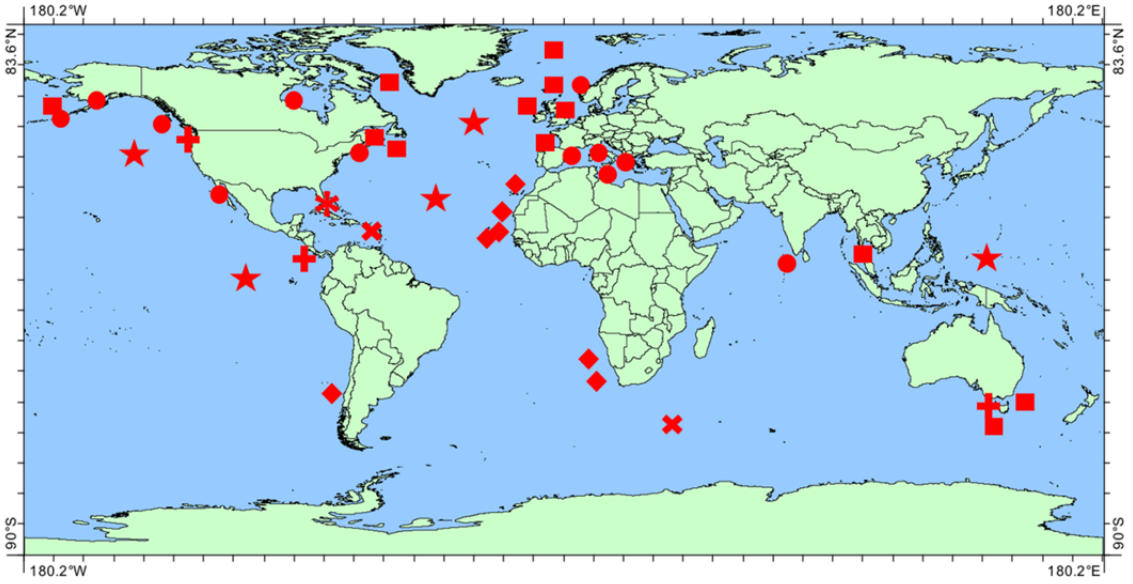


Figure 2.1. Global map of ecosystem locations differentiated by ecosystem type, selected for this study; coastal (circle), estuary (+), island (X), ocean (star), reef (*), shelf (square), and upwelling (diamond).

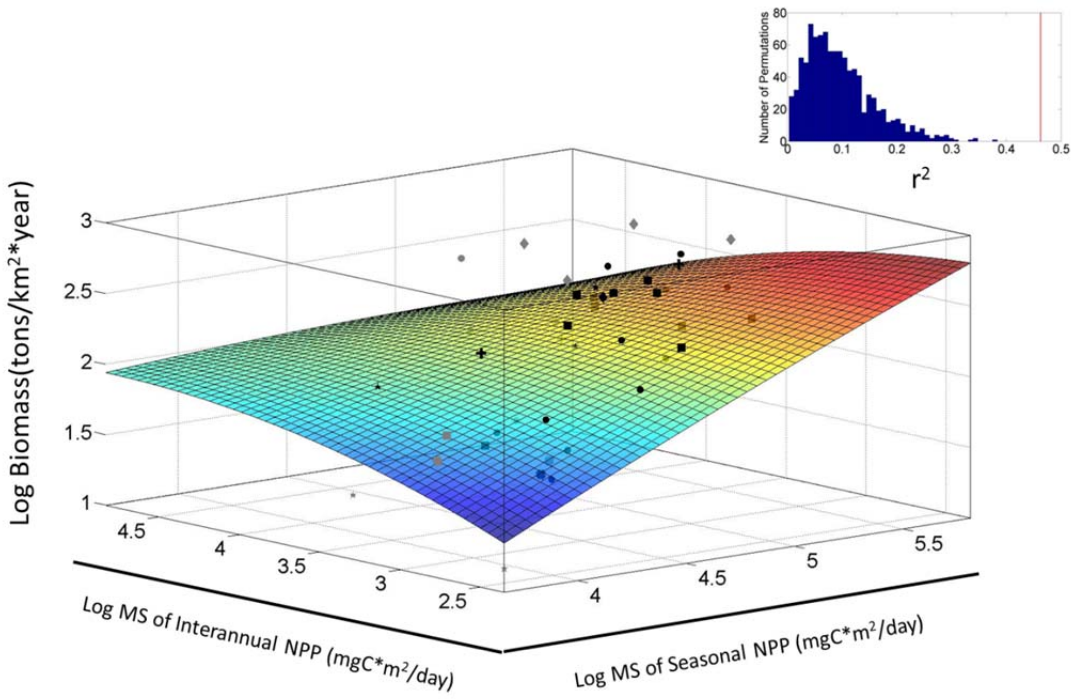


Figure 2.2. Relationships between ecosystem Biomass and interannual and seasonal variability in net primary production ($r^2 = 0.46$) (AIC = -2.2). Ecosystems (n=43) located in higher latitudes ($\leq -30^o$ and $\geq 30^o$) (black) and ecosystems located in lower latitudes ($\geq -30^o$ and $\leq 30^o$) (gray) are separated by ecosystem type; coastal (circle), estuary (+), island (X), ocean (star), reef (*), shelf (square), and upwelling (diamond). Histogram (top right) depicts r^2 distributions from a random permutation of model fits using randomized coefficients with the red line representing the model fit of the original data.

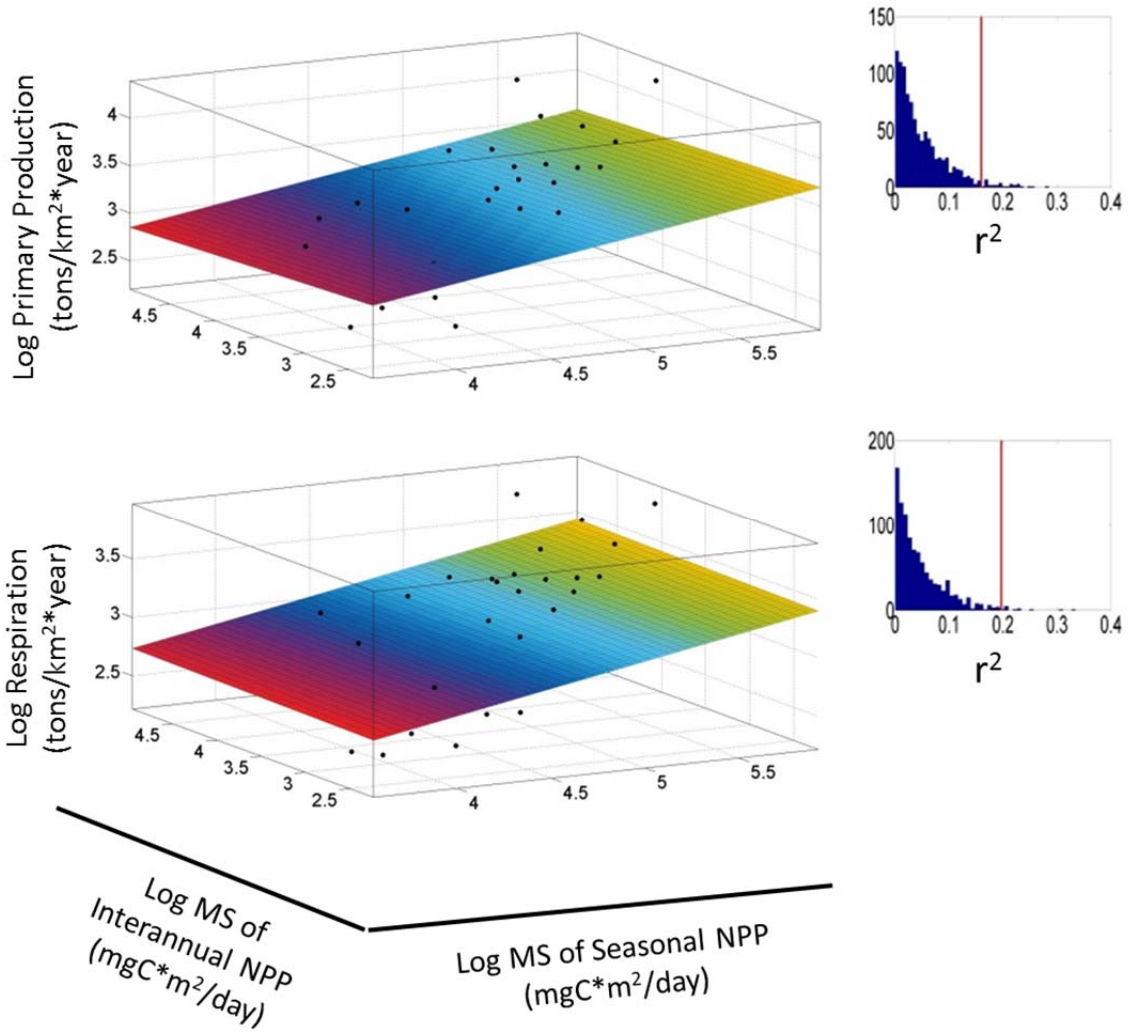


Figure 2.3. Relationships between interannual and seasonal variability in Net Primary Productivity (NPP) and primary production ($r^2 = 0.16$) (AIC = -1.67) (Top) and Respiration ($r^2 = 0.2$) (AIC = -1.78) (Bottom) estimates to measures of the log MS of interannual and seasonal variability in net primary production. Histograms as in Figure 2. Black dots denote ecosystem (n=43) locations in variable space.

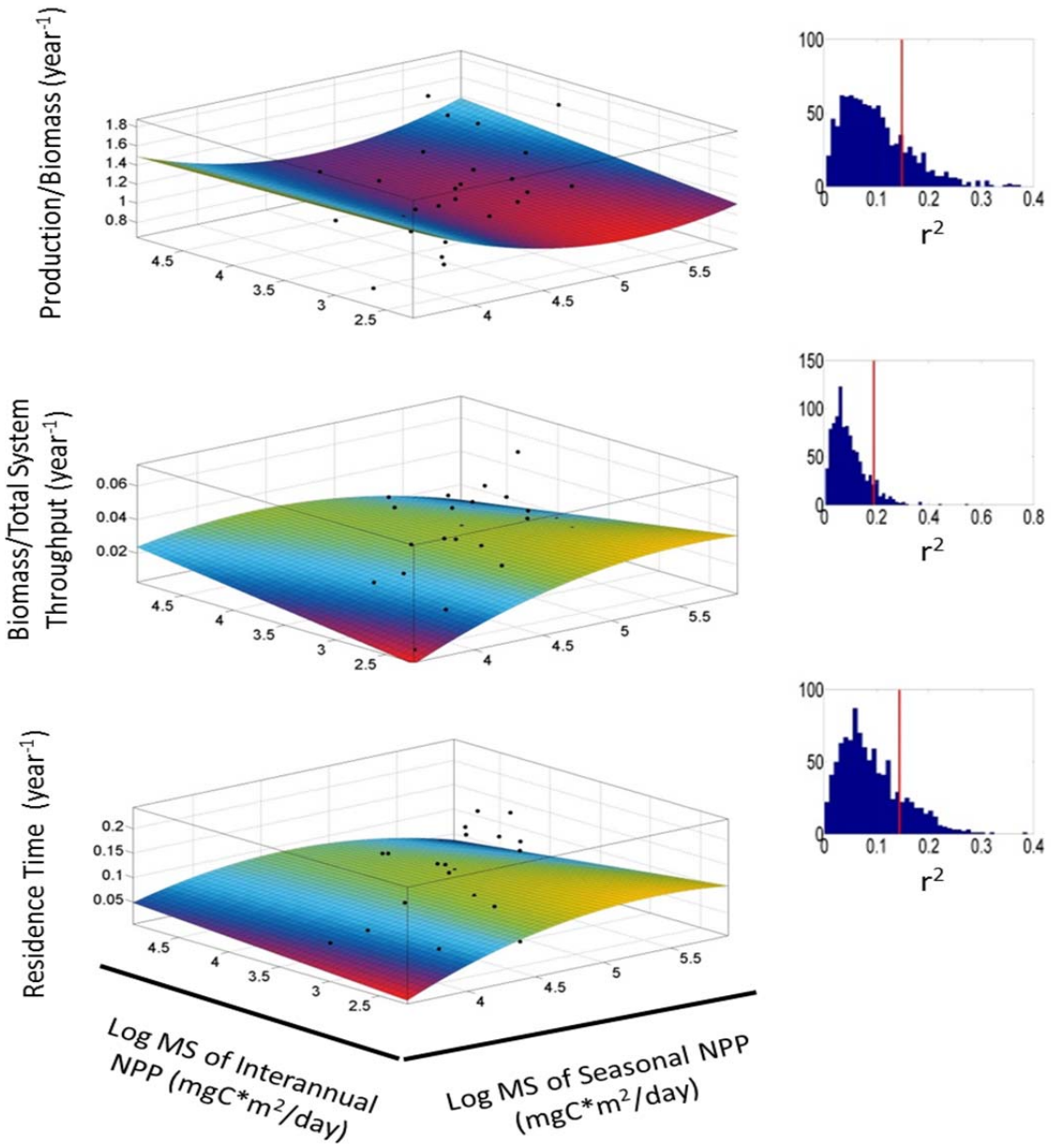


Figure 2.4. Relationships between interannual and seasonal variability in Net Primary Productivity (NPP) and P/B (r^2 = 0.15) (AIC = -2.32) (Top), B/TST (r^2 = 0.19) (AIC = -8.44) (Middle), Residence Time (r^2 = 0.14) (AIC = -5.83) (Bottom) estimates to measures of the log MS of interannual and seasonal variability in net primary production. Histograms as in Figure 2. Black dots denote ecosystem (n=43) locations in variable space.

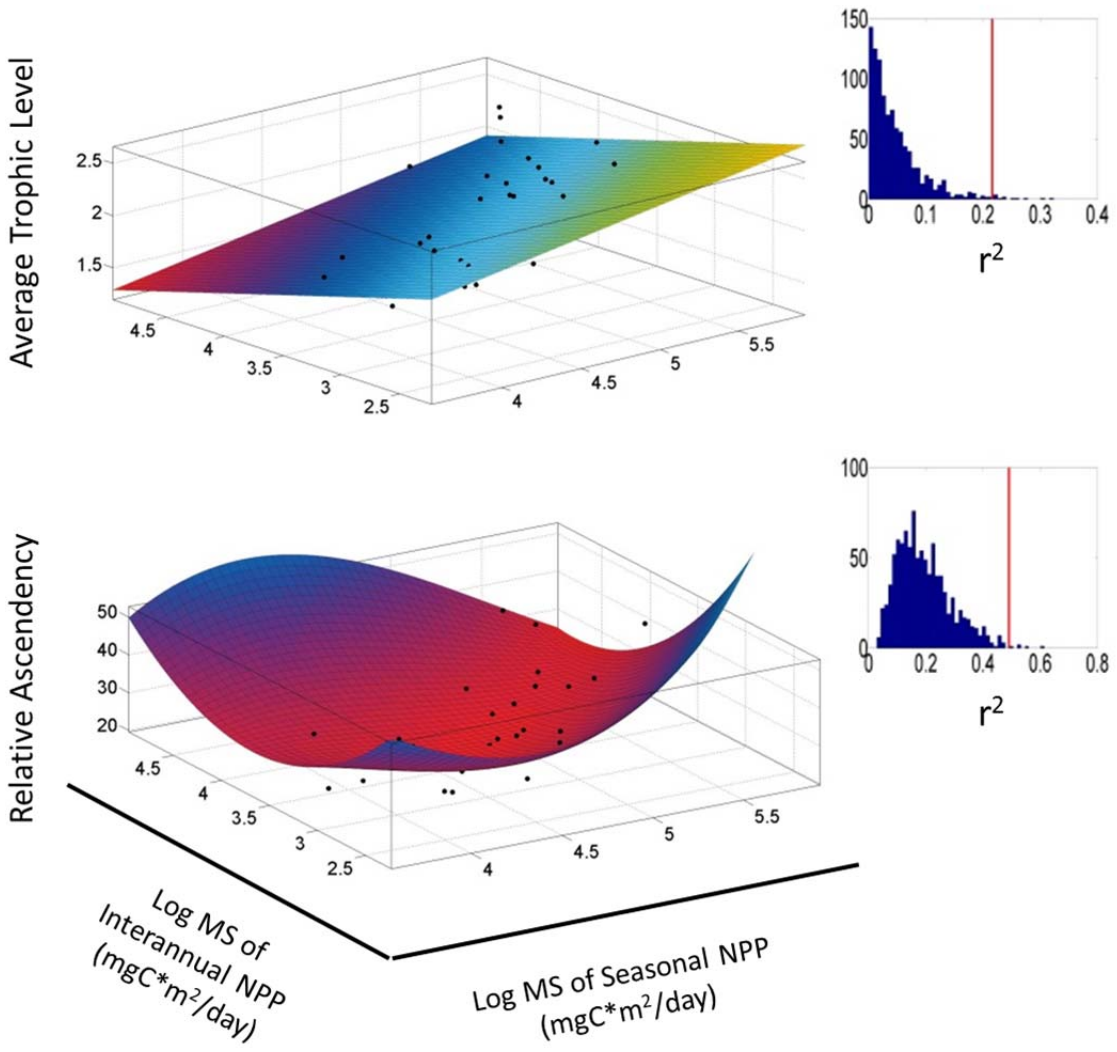


Figure 2.5. Relationships between interannual and seasonal variability in Net Primary Productivity (NPP) and Average Trophic Level (Top) ($r^2 = 0.22$) (AIC = -2.61) and Relative Ascendency ($r^2 = 0.49$) (AIC = 3.26) (Bottom) estimates to measures of the log MS of interannual and seasonal variability in net primary production. Histograms as in Figure 2. Black dots denote ecosystem (n=43) locations in variable space.

Table S2.1. Total list of synthetic ecosystem indices explored in this study and their respective units.

	Index	Units
1	Biomass	$g/km^2/year$
2	Net Primary Production	$g/km^2/year$
3	Respiration	$g/km^2/year$
4	Primary Production	$g/km^2/year$
5	Ratio of Net Production / Respiration	-
6	Ratio of Production / Biomass	year
7	Ratio of System Respiration / Biomass (aka Schrödinger Ratio)	-
8	Total System Throughput	$g/km^2/year$
9	Ratio of Biomass / Total System Throughput	year
10	Connectance Index	-
11	System Omnivory Index	-
12	Dominance of detritus	-
13	Flow diversity	-
14	Average organism size	year
15	Finn's cycling index	-
16	Predatory cycling index	-
17	Nutrient Regeneration	-
18	Path Length	-
19	Straight-through path length	-
20	Residence time	year
21	Ascendency	-
23	Average Trophic Level	-
24	System overhead	-
25	Capacity	-
26	Relative ascendency	%

CHAPTER 3

Predicting Global Biomass Anomalies Under Future Climate Change

Introduction:

Understanding and predicting ecological responses to future climate change is of vital importance when it comes to properly managing and conserving ecosystem services. Climate change is expected to fundamentally disrupt the current structure and function of ecosystems, leading to large scale shifts in spatial and temporal ecological processes (Mooney et al. 2009). These effects are likely to be amplified by anthropogenic perturbations such as intensifying land use, pollution, and overharvesting of biological resources (Myers et al. 2013). While many ecological studies focus on how these changes may influence local processes at small scales, which allows for more controlled experiments and the isolation of target variables, this approach excludes the ability to address entire ecosystems as a whole. Due to issues associated with large-scale interactions, indirect/nonlinear consequences, and cascading effects, understanding local and population level effects of climate change is strengthened through a global understanding of the mechanisms that drive ecosystem-level changes (Cabré et al. 2014, Lefort et al. 2014). Many of the ecosystem-scale effects of climate change, such as shifting sea surface temperatures and carbon cycling, have the potential to significantly impact species-specific interactions, range distributions, and regional biodiversity levels (Parmesan and Yohe 2003, Araújo et al. 2005). This requires not only an understanding of global environmental changes along with predictive capabilities, but also a way to link them to local processes or target species of interest (Walther et al. 2002, McHamon et al. 2011).

While many assessments of the ecological effects of climate change (e.g., changes in trophic interactions, abundance, distributions, and the ecosystem-scale shifts that occur as a result) have centered around envelope models, a promising new approach to predict large-scale impacts involves using relationships between ecosystem-scale properties and environmental conditions as mechanism-based, predictive tools in modeling simulations (Kerr et al. 2007, Russell et al. 2012). This approach may offer new insights into the drivers of species richness, ecosystem biomass, and functional diversity patterns as well as provide a framework for investigating the effects of future climate change on global gradients in

these properties (Gotelli et al. 2009). A potentially valuable and under-utilized step in this direction involves applying ecosystem-scale perspectives to earth system models (ESMs) in order to simulate ecosystem responses to climate change at a global scale. ESMs generally consist of a number of individually coupled models that account for the physical processes that simulate the interactions between the physical climate, the biosphere, and the chemical components of the atmosphere and ocean. A variety of ESMs have been developed over the past few decades and have been used to broaden our understanding of the mechanisms behind carbon cycling, vegetation distribution, regional climate oscillations (e.g., El Niño–Southern Oscillation (ENSO), North Atlantic Oscillation (NAO), Pacific Decadal Oscillation (PDO)), historical climate events, and expected future changes (Heavens et al. 2013). ESMs are particularly useful in understanding climate variability, how human activities impact it, and developing possible mitigation actions against future climate change (Flato 2011).

ESMs provide a unique opportunity to predict future ecosystem-scale changes. Through the use of a mechanistic approach to assessing the role of shifting environmental conditions on ecosystem-level properties, it is possible to infer subsequent impacts on biotic abundance, distributions, and diversity at smaller scales. This study combines output from ESMs with an ecosystem-level relationship between net primary production (NPP) to total Ecosystem Biomass to predict global changes in future biomass distribution.

Methods:

A statistical relationship between NPP and total Ecosystem Biomass was developed by Schlenger et al. (Schlenger et al., Chapter 2, this dissertation). This study used 43 marine ecosystems distributed in all oceans of the world and including multiple ecosystem types to compare quantifications of ecosystem-scale energy input, output, and storage with satellite-derived data of net primary production (NPP) (Smyth 2005) from the same locations, calculated as the amount of primary production incorporated into an ecosystem after accounting for loses from respiration. Estimates of ecosystem energy flows were

calculated using Ecopath with Ecosim (EwE). EwE estimates "Biomass", essentially a metric that can be used to represent energy storage, for all species and functional groups in an ecosystem, which when summed together, provide a value for "Ecosystem Biomass". Ecosystem Biomass was compared with the mean values of NPP as well as measures of temporal variability for each ecosystem location. Mean NPP and temporal variability in NPP was calculated for each 1^o latitude by 1^o longitude grid cell. Temporal variability was also broken down into two components: seasonal and interannual. Interannual variability was calculated as the mean square (MS) of deviations between years (1998-2005) and seasonal variability was calculated as the mean square (MS) of deviations between months within a year over the same period. When compared to Ecosystem Biomass, relationships were stronger with seasonal and interannual variability of NPP as compared to mean NPP. Due to a high degree of covariance in the MS of interannual and seasonal variability, both measures of temporal variability were simultaneously compared to Ecosystem Biomass using a multivariate model to improve predictive power. The resulting multivariate regression (Eq 1.) uses both modes of variability to predict Ecosystem Biomass and had an r-squared value of 0.46. The relationship displayed a pattern of increasing Ecosystem Biomass with higher seasonal variability, while interannual variability played a smaller role.

$$Ecosystem\ Biomass = -5.512 + 1.46 * (I\ Var) + 1.932 * (S\ Var) - 0.3075 * (I\ Var) * (S\ Var) - 0.07 * (S\ Var)\text{^}2$$

Equation 1. Relationship between Ecosystem Biomass and temporal variability in Net Primary Production. I Var = interannual variation; S Var = seasonal variation.

This study 1) used output from ESM's to predict temporal variability in NPP and 2) applied the above multivariate relationship to estimate future changes in Ecosystem Biomass on a global scale. Three ESMs were used to back-calculate historical and predict future seasonal and interannual variability in NPP. These models included the Institute Pierre Simon Laplace (IPSL) model, the New Earth system

model of Max Planck Institute for Meteorology (MPI), and the Community Earth System Model (NCAR). These ESM's and their role in estimating global Ecosystem Biomass are detailed below.

Earth System Models

The IPSL model is constructed around a physical core that incorporates atmosphere, land-surface, ocean, and sea-ice components (Séférian et al. 2012). It also accounts for biogeochemical processes through the modeling of stratospheric and tropospheric chemistry, aerosols, terrestrial, and oceanic carbon cycle dynamics. IPSL has been used to simulate and analyze a number of processes including tropical climate variability, climate change projections, paleo climates, and the impact of ice sheet melting on Atlantic meridional overturning (Dufresne et al. 2013). However, this model, along with many others, has trouble predicting mixed layer depths along with precise biogeochemical dynamics in deep layers.

The MPI model consists of several coupled circulation models for the atmosphere and ocean along with components for land/vegetation and marine biogeochemistry (Maier-Reimer et al. 2005). It is been used to predict future climate variations, specifically looking at changes in the carbon cycle and the role of dynamic vegetation (Giorgetta et al. 2016). Prediction errors tend to manifest themselves in precipitation bias and surface SST due to the insufficient representation of stratocumulus.

The NCAR model includes a wide range of coupled systems incorporating interactive carbon-nitrogen cycling, global dynamic vegetation and land use change, marine biogeochemistry, and atmospheric aerosols along with general atmospheric-ocean circulation and land/sea ice components (Hurrell et al 2013). This model has been used to simulate pre-industrial control conditions as well as long-term future projections under various representative concentration pathway (RCP) scenarios (Kay et al. 2015). However, biases such as a double intertropical convergence zone, an excessive tropical water cycle, and insufficient ocean ventilation in some areas exist.

Each of these three models were used to simulate historic (1998-2005) and future (2093-2100) distributions of NPP, calculated at monthly intervals, using two RCP scenarios for future predictions;

RCP 4.5 and RCP 8.5. (Detlef van Vuuren et al. 2011). RCP's were created to provide information consistent with climate change scenario literature for climate models and integrated assessment models to use for standardized simulations. In total, a set of four pathways were created that lead to radiative forcing levels of 8.5, 6, 4.5, and 2.5 W/m^2 by the end of the century. RCP 4.5 was developed by the Global Change Assessment Model (GCAM) team at the Pacific Northwest National Laboratory's Joint Global Change Research Institute and is a stabilization scenario in which total radiative forcing is stabilized shortly after 2100, without overshooting the long-run radiative forcing target level. RCP 8.5 was developed using the Model of Energy Supply Systems and their General Environmental Impact (MESSAGE) model and the Integrated Assessment Framework by the International Institute for Applied Systems Analysis (IIASA), which is characterized by increasing greenhouse gas emissions continuously over time up to high levels by 2100. CO_2 concentrations stabilize at 650 ppm in RCP4.5 and continuously rise to 1370 ppm in RCP8.5 with effects on ocean NPP described elsewhere (Pachauri R 2014).

Simulations

For each ESM, output of NPP was used to calculate both seasonal and interannual variability in NPP from 1995 to 2005 per individual 1^o latitude by 1^o longitude grid cell. These estimates were then averaged together across all three models to produce a map of seasonal and a map of interannual variability in NPP for all years combined. Ecosystem Biomass estimates from 1995 to 2005 were calculated for each grid cell by combining values of seasonal and interannual variability in NPP from each average map into the multivariate equation (Eq. 1) relating temporal variability in NPP to Ecosystem Biomass, resulting in a single map of Ecosystem Biomass for all years combined. Similar maps of seasonal and interannual variability in NPP were created using future projections of NPP (2093-2100) under RCP 4.5 and 8.5 scenarios. From these, average maps of seasonal and interannual variability in NPP across all three ESMs as well as future estimates of Ecosystem Biomass were also created using the same procedure for each scenario. Ecosystem Biomass anomalies over the 100 year period were

calculated by subtracting future Ecosystem Biomass means from historical means for each individual grid cell under both RCP scenarios.

Results:

In general, the three climate models displayed similar patterns of seasonal variability in NPP, with increased variability, relative to other areas, in the temperate zones as well as in upwelling regions (Figure 1). MPI simulations displayed noticeably higher values in these regions. Lower seasonal variability was observed in the mid-ocean gyres while the arctic showed intermediate values of seasonal variability for the IPSL and MPI simulations, but higher values under NCAR. Averaging seasonal variability in NPP across the three models resulted in geographically distinct patterns of high seasonal variability in the temperate zones, intermediate in the arctic, and low variability in the mid-ocean gyres (Figure 1D).

Interannual variability in NPP displayed slightly different patterns between climate models (Figure 2). IPSL showed the highest values along the equatorial Pacific and North Atlantic. MPI showed higher interannual variability in the north Pacific, equatorial Pacific, and Southern Ocean while NCAR also had higher values along the equatorial Pacific as well as along upper and lower temperate zones. Mid-ocean gyres displayed lower interannual variability across all three models, but IPSL also resulted in lower values in the Arctic and Southern Oceans in contrast with the other two models. Averaging all three models together resulted in high interannual variability along the equatorial Pacific, intermediate values within temperate zones, and lower values in the mid-ocean gyres and Arctic polar regions.

Historical Ecosystem Biomass (1998 to 2005) displayed consistent patterns of known global biomass distribution (Figure 3). Ecosystem Biomass was highest in temperate zones and upwelling

regions, intermediate along the edges of mid-ocean gyres as well as the Arctic ocean, and lowest within the mid-ocean gyres. Estimated values of temporal variability in NPP of some regions fell outside the predictive range of the multivariate relationship between variability and Ecosystem Biomass. Therefore we do not report those values here (represented as white areas in Figure 3). These areas were generally associated with extremely low seasonal and/or interannual variability in NPP.

Seasonal variability in NPP from 2093 to 2100 under carbon emission scenarios RCP 4.5 (Fig 4A) and RCP 8.5 (4B) displayed changes from historical estimates that were consistent with each other. In general, seasonal variability in NPP decreased within and along the edges of mid-ocean gyres (most noticeably in the north Atlantic) as well as upwelling regions in the Indian Ocean and along West Africa. However, seasonal variability in NPP increased and shifted eastward along the equatorial Pacific. The RCP 8.5 scenario showed the same patterns and trends, but to a larger extent.

Interannual variability in NPP from 2093 to 2100 under carbon emission scenarios RCP 4.5 (Fig 5A) and RCP 8.5 (5B) also showed changes from historical estimates that were consistent with each other. Similar to seasonal variability, interannual variability decreased within and along the edges of mid-ocean gyres (also most noticeably in the North Atlantic). The Arctic Ocean displayed decreasing values along mid-longitudes, but increased at lower longitudes. Interannual variability also increased and shifted eastward along the equatorial Pacific, similar to changes in seasonal variability of NPP.

Ecosystem Biomass anomalies between the present (1998-2005) and future (2093-2100) obtained from Representative Concentration Pathways RCP4.5 (Figure 6A) and RCP8.5 (Figure 6B) emission scenarios displayed highly localized spatial differences across the world within each scenario. Total (global) Ecosystem Biomass in the world's oceans did not change, with mean anomalies of -5.4e-05 % for RCP4.5 and -1.94e-04 % for RCP8.5, but the distribution of Ecosystem Biomass changed significantly in many regions. Ecosystem Biomass anomalies ranged from approximately -200% to 200% depending on

location. The Arctic, north Atlantic, and eastern tropical Pacific in particular displayed significant Ecosystem Biomass anomalies associated with climate change. Patterns were qualitatively consistent between the three climate models. Generally, Ecosystem Biomass anomalies had similar spatial trends over 100 years between scenarios, with the RCP8.5 displaying an overall larger magnitude.

Discussion:

Overall results of this study show that very little change in total Ecosystem Biomass at a global scale may take place due to future climate conditions, but significant regional changes in the distribution of Ecosystem Biomass across the world may occur. Historical estimates of temporal variability in NPP from all three ESMs were generally geographically consistent, despite differences in magnitude. The MPI model resulted in higher values of both seasonal and interannual variability than the other two models, mainly in the Southern Ocean. However, these differences were minimized by averaging all three models together. The resulting averaged maps of seasonal and interannual variability reflect known climate patterns, with higher seasonal variability in temperate and upwelling regions (Cermeno et al. 2006, Lutz et al. 2009), and higher interannual variability in areas subject to longer term climate processes, such as El Niño , NAO, and PDO (Rousseaux and Gregg 2015). When these maps of temporal variability were combined to predict historical distributions of Ecosystem Biomass, the resulting map accurately reflected known areas of high biomass across the world (Watson et al. 2015). With respect to future changes in temporal variability of NPP under RCP 4.5 and 8.5 scenarios, there was generally little observable change from historical values for seasonal and interannual variability, respectively, over the majority of the globe. Yet in the areas that did show noticeable differences, maps of both modes of temporal variability displayed an expansion of low variability zones associated with mid-ocean gyres as well as an eastward shift in variability along the equatorial Pacific. Both of these changes are consistent with the predicted effects of climate change (Polovina et al. 2008, Cai et al. 2014). However, the combined effects from

changes in both seasonal and interannual variability amplified large regional changes in Ecosystem Biomass under both RCP scenarios.

The cumulative change in total Ecosystem Biomass (Ecosystem Biomass anomalies summed up across all grid cells) under the RCP 4.5 and 8.5 scenarios displayed almost no change over a 100 year period from historical estimates. However, large local and regional changes in Ecosystem Biomass were observed. The Arctic and eastern tropical Pacific displayed significant increases in Ecosystem Biomass anomalies associated with climate change while the north Atlantic displayed significant decreases. Ecosystem Biomass surrounding mid-ocean gyres also decreased along with the expansion of decreased temporal variability within these regions. Trends in Ecosystem Biomass were consistent between RCP scenarios, but with RCP 8.5 showing an overall larger magnitude. Yet, there were a few areas that showed opposite trends between scenarios, such as off the west coast of Brazil and Australia. While it is possible that these opposite changes are the result of poor modeling resolution for some of the ESMs, they could also be representative of threshold or bifurcation like behaviors, which are a common aspect of ecosystem behavior (D'Souza et al. 2015).

Results of this research agree with similar studies applying output from ESMs to predict future changes in ecosystem production and Biomass distribution. Cabre et al. (2014) used output from 16 Coupled Model Intercomparison Project Phase 5 models to assess large scale changes in sea surface temperature, stratification, nutrient concentrations, and primary productivity (PP), which is related to the amount of biomass entering an ecosystem through primary producers. Maps of PP anomalies show similar patterns to Ecosystem Biomass changes found in this study, with decreasing trends in the north Atlantic and east Indian ocean as well as increasing trends in the Arctic and west Indian ocean. Lefort et al. (2014) used IPSL output combined with a marine biogeochemistry and ecosystem models to predict changes in pelagic biomass across the world's oceans. They identified similar spatial trends in biomass anomalies across epipelagic, migrating community, and mesopelagic biomasses. And Jones et al. (2014)

used the same approach taking output from Coupled Model Intercomparison Project Phase 5 models to predict changes in the biomass of meiofauna, macrofauna, and megafauna of seafloor organisms, in which very similar patterns to surface biomass changes from other studies were also found. However, a major difference between this study and previous results in the literature involves opposite trends concerning the eastern tropical Pacific. Results of this study show increases in biomass throughout this region, while other studies displayed decreases or no change, excluding the biomass of the migratory community predicted in Lefort et al. (2014). These differences could potentially derive from the role of using average values of NPP versus temporal variability in NPP in estimating community biomasses.

Changes in Ecosystem Biomass predicted by this study should not be taken as absolute changes in biomass distributions, but as indicators of ecosystem-scale change. Climate change has been shown to expand or reduce the range of many mobile species (Davis et al. 2005). Therefore, these simulations can be used to potentially map the spatial extent of those changes as well as which species are likely to exhibit shifts. For example, results of this research indicate that the north Atlantic may not support as much biomass in the future as it currently does, possibly leading to the potential emigration of apex predators like whales, dolphins, or tuna. More importantly, these maps can be used to assess the relative vulnerability of specific ecosystems to future climate change. Areas representing the largest changes in temporal variability of NPP, and subsequent Ecosystem Biomass, (e.g., the Arctic, north Atlantic, or eastern tropical Pacific) may experience the highest degree of ecological stress. Species living in such areas may not be able to adapt fast enough or to the degree necessary to survive under these new conditions. Little is known regarding the speed at which organisms can adapt to shifts in external conditions (Hoffmann and Sgro 2011).

Due to the high reliance of this study on modeling output, uncertainty regarding results should be given careful consideration. The predictive model using Ecosystem Biomasses taken from EwE models in Schlenger et al. (in prep) is founded upon relationships that have evolved on an evolutionary time scale.

In other words, each food web model essentially represents a distribution of life history traits that have optimally evolved under a variability regime respective of that location. The optimization and emergence of those life history traits due to natural selection occur over hundreds, thousands, or millions of years. With respect to the global climate scenario simulations, the variability regime associated with each ecosystem is rapidly changing over a 100 year time period. In an evolutionary sense, this is an extremely short time period and it is unlikely that the distribution of life history traits of organisms comprising each ecosystem, and subsequent ecosystem-level biomass, will change fast enough to optimize under these new variability regimes. As such, it is possible that the multivariate relationship between Ecosystem Biomass and temporal variability in NPP may not hold the same shape or may potentially breakdown under previously unseen modes of variability brought on by climate change. Furthermore, each ESM used in this study includes certain biases that may influence the estimated distributions of variability in NPP. Although averaging three models together may help minimize these biases, they should not be ignored.

While this quantitative exercise demonstrates the potential magnitude of ecosystem-scale change resulting from future scenarios of climate change through the use of an emergent property of ecosystem structure and function (biomass vs temporal variability), more work needs to be done to identify the underlying mechanisms relating these attributes. However, this study contributes to the use of a macro/holistic ecological perspective by utilizing global patterns in a single variable (temporal variability of NPP) to predict large-scale patterns in ecosystem processes. The strength of this approach is that it synthesizes a variety of physical, chemical, and biological variables that are extremely difficult to simultaneously predict or measure, into ecosystem-scale emergent properties that are much easier to work with. In conjunction with output from ESMs, a variety of useful information can be derived to not only strengthen our understanding of the ecological effects of climate change, but provide managers and decision makers with the tools necessary to mitigate those changes.

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Figure 3.1. Maps of historical (1998-2005) seasonal variability in net primary production (NPP), calculated as the mean square (MS) of deviations between months within a year over the same period, using output from (A) Institute Pierre Simon Laplace (IPSL), (B) New Earth system model of Max Planck Institute for Meteorology (MPI), and (C) Community Earth System Model (NCAR) models as well as a map of (D) average seasonal variability derived from all three.

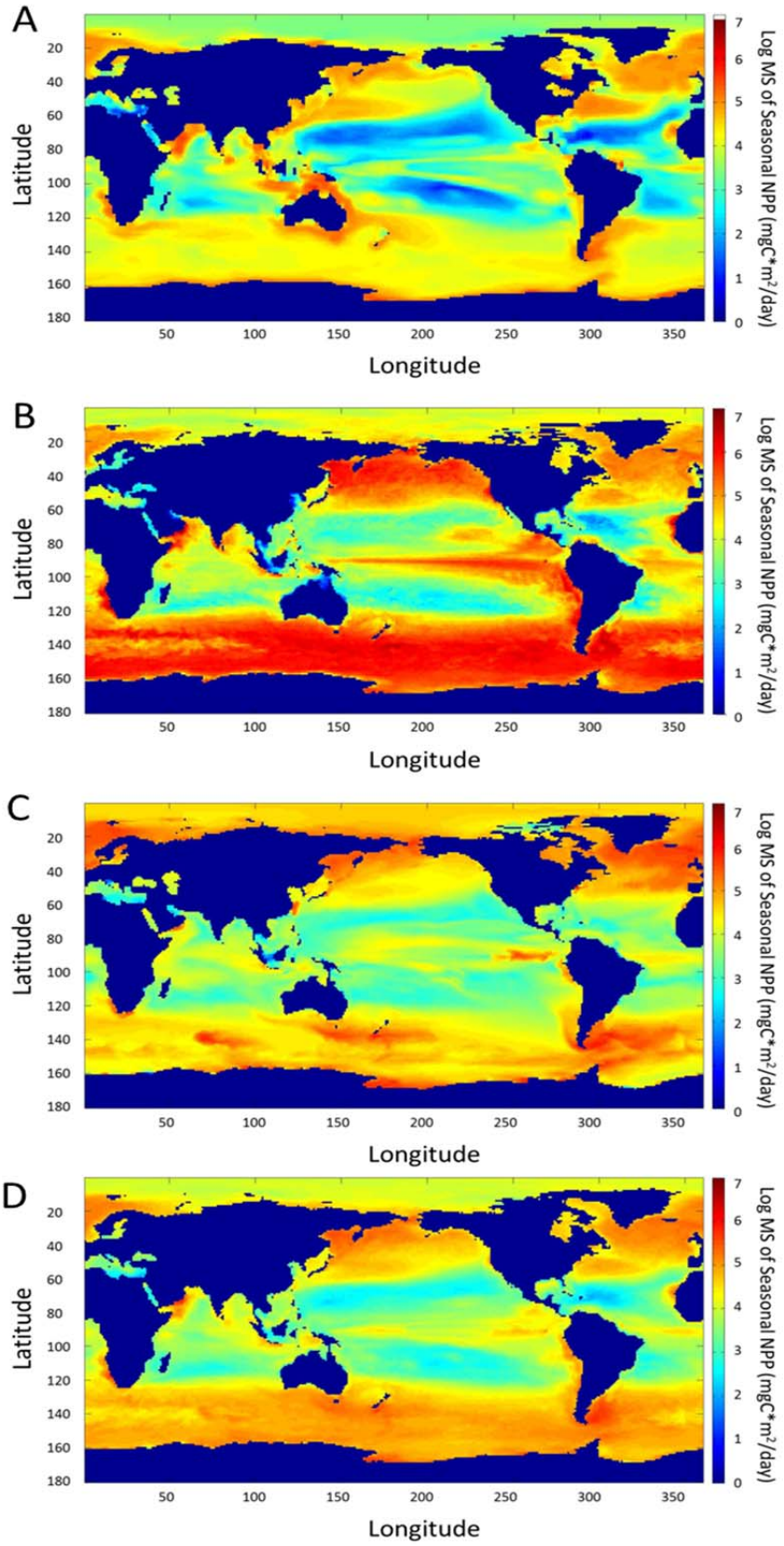
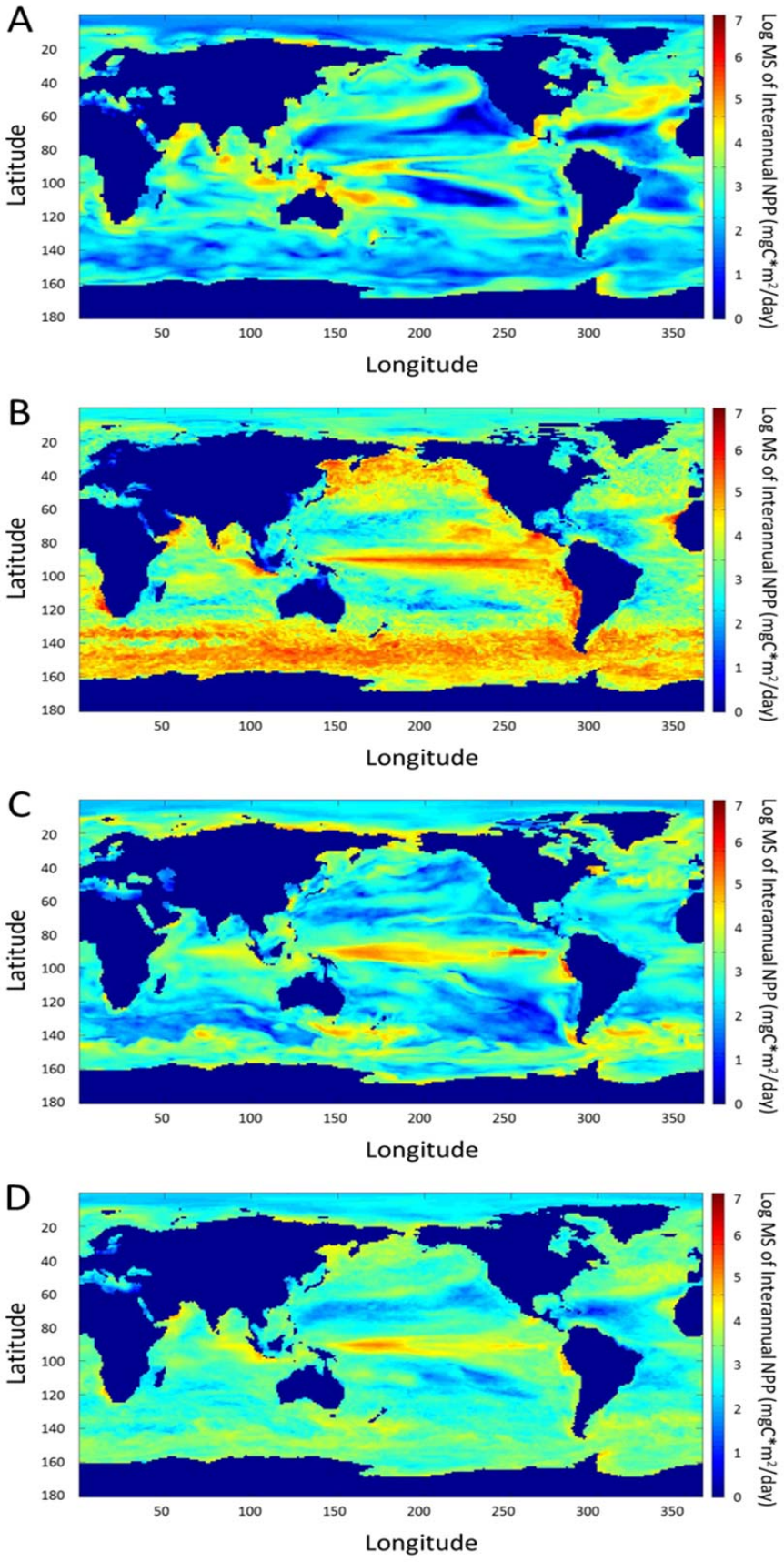

A
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C
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Latitude
Longitude
Log MS of Seasonal NPP (mgC*m²/day)
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140
160
180
50
100
150
200
250
300
350
0
1
2
3
4
5
6
7

Figure 3.2. Maps of historical (1998-2005) interannual variability in net primary production (NPP), calculated as the mean square (MS) of deviations between years, using output from (A) Institute Pierre Simon Laplace (IPSL), (B) New Earth system model of Max Planck Institute for Meteorology (MPI), and (C) Community Earth System Model (NCAR) models as well as a map of (D) average seasonal variability derived from all three.


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Latitude
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Log MS of Interannual NPP (mgC*m2/day)
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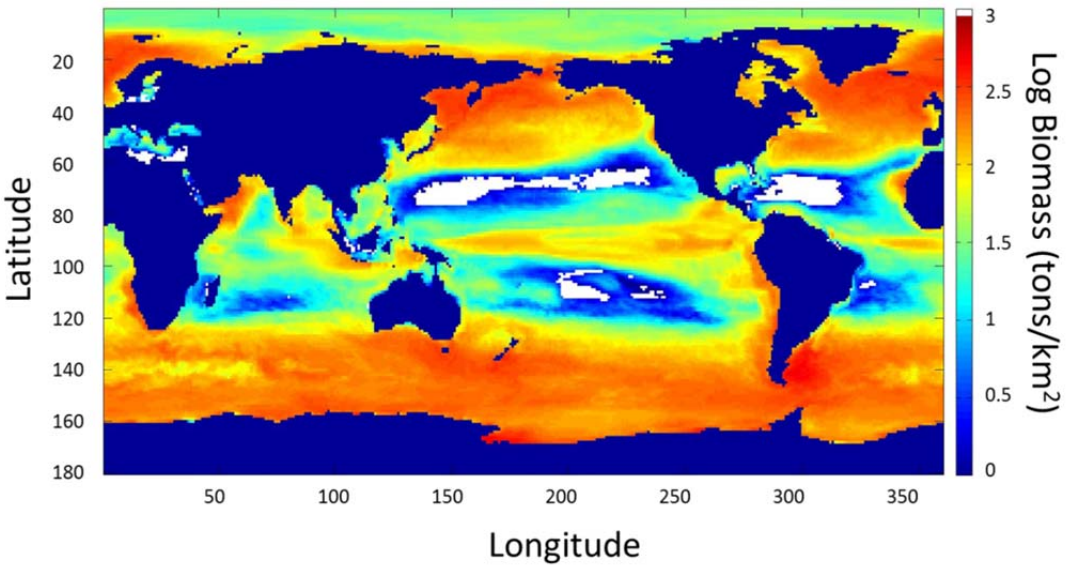


Figure 3.3. Historical Ecosystem Biomass (1998-2005) estimated using a multivariate relationship between seasonal and interannual variation in net primary production with Ecosystem Biomass. White areas represent grid cells with extremely low seasonal and/or interannual variability in net primary production (NPP) that fell outside the predictive range.

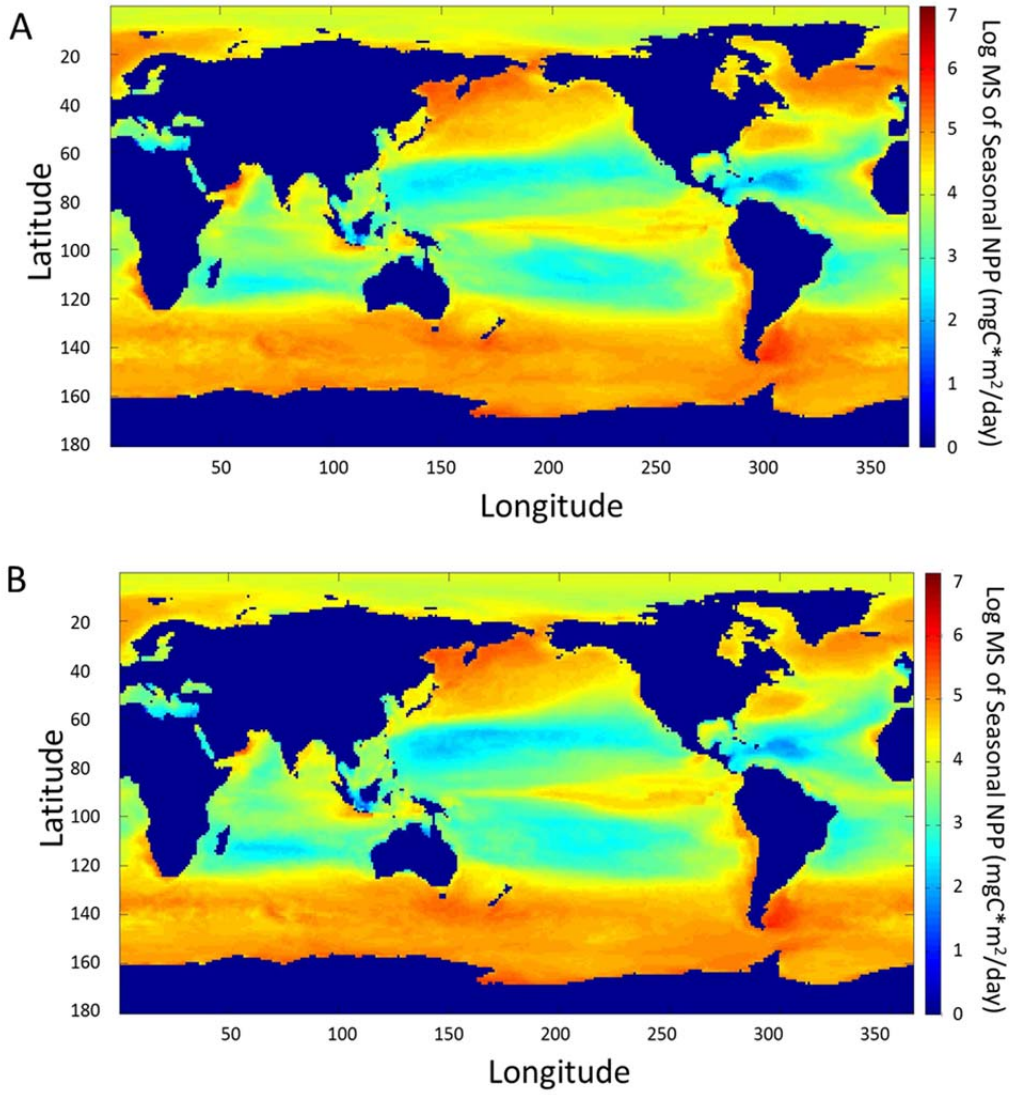


Figure 3.4. Predicted seasonal variability in net primary production (NPP) (2093-2100) averaged across Institute Pierre Simon Laplace (IPSL), New Earth system model of Max Planck Institute for Meteorology (MPI), and, Community Earth System Model (NCAR) earth system models under representative concentration pathways (A) 4.5 and (B) 8.5 carbon emission scenarios.

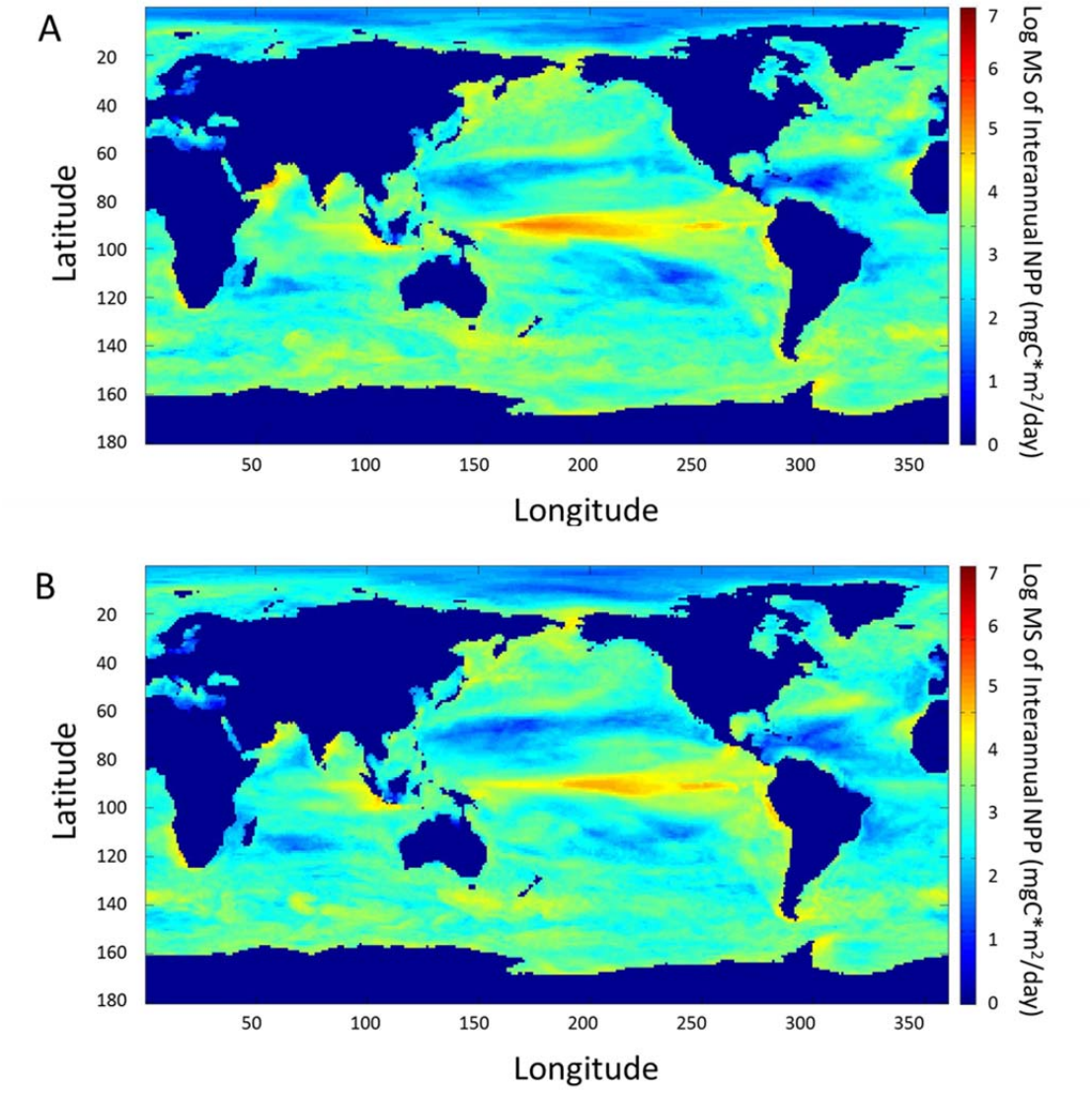


Figure 3.5. Predicted interannual variability in net primary production (NPP) (2093-2100) averaged across Institute Pierre Simon Laplace (IPSL), New Earth system model of Max Planck Institute for Meteorology (MPI), and, Community Earth System Model (NCAR) earth system models under representative concentration pathways (A) 4.5 and (B) 8.5 carbon emission scenarios.

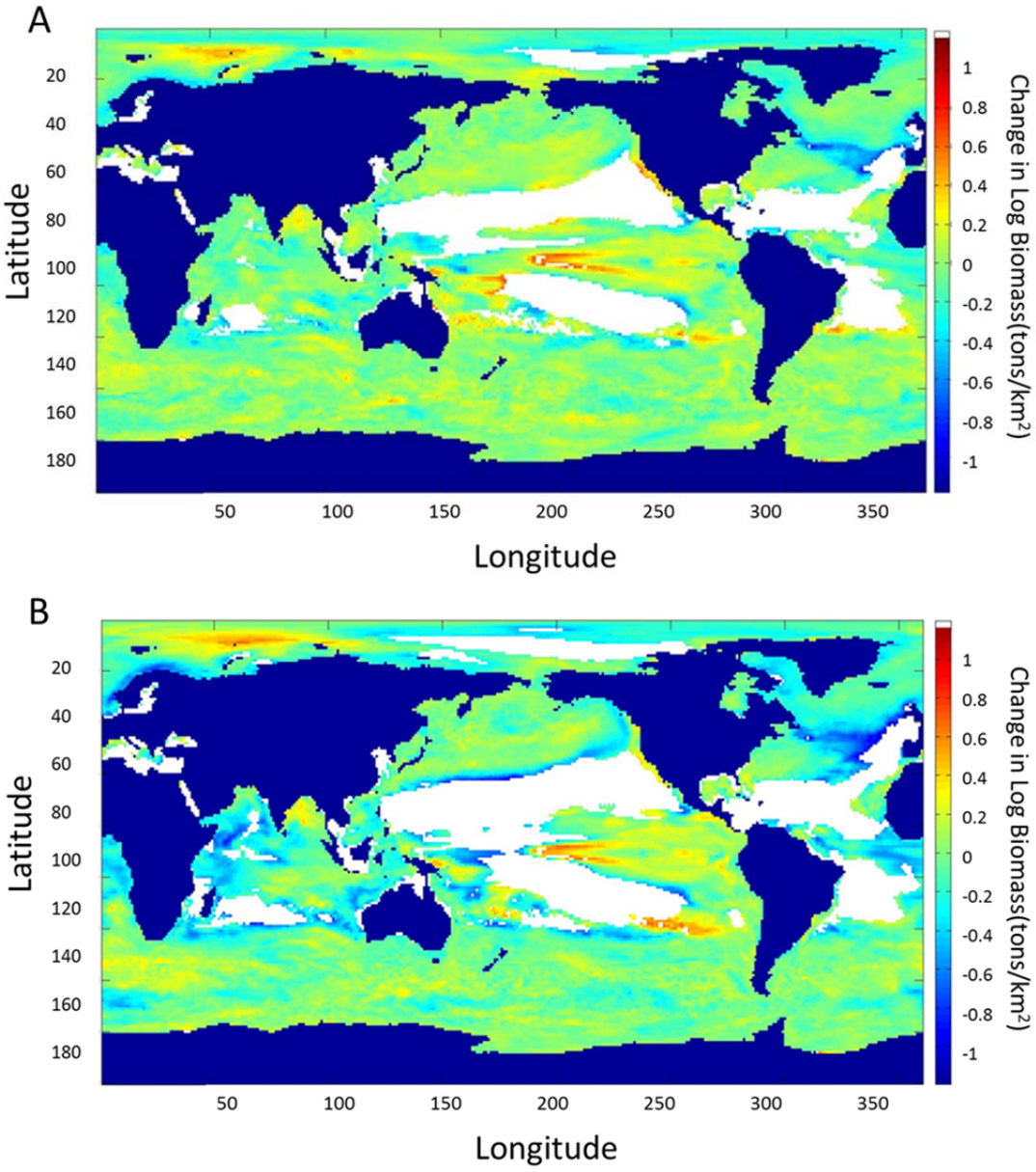


Figure 3.6. Predicted anomalies in global Biomass from 1998-2005 to 2093-2100 under representative concentration pathways (A) 4.5 and (B) 8.5 carbon emission scenarios. White areas represent MS variability values outside the boundaries of the predictive model used to estimate Ecosystem Biomass and are indicative of areas having very low Biomass values.

CHAPTER 4

An Ecosystem-Based Modeling Approach to Fisheries Management

An Ecosystem-Based Modeling Approach to Fisheries Management

Introduction:

The extent of anthropogenic impact on the world has reached such a scale that we are now fundamentally disrupting the natural structure and function of entire ecosystems (Myers et al. 2013). Whether through eutrophication, fishing, pollution, development, climate change, or synoptic combinations of multiple perturbations, our influence on natural systems occurs across a variety of spatial and temporal scales. Along with a higher understanding of our impact on the world around us, scientists are beginning to place increased importance on ecosystem-scale dynamics such as regime shifts, trophic cascades, and bifurcations (Patten 2014). This perspective stems from the need to place individual species or populations in context of the greater system that they are a part of. As a result, the term ecosystem-based management (EBM) has gained significant traction over the past few decades (Long et al. 2015).

The purpose of EBM is to identify key natural and anthropogenic pressures on ecosystems, account for their cumulative impact, and address trade-offs across multiple objectives for a given ecosystem (Pikitch 2004). EBM addresses the physical, biological, social, and economic complexities of managing natural resources (Patrick and Link 2015). This approach is now a major objective in a variety of large management organizations like the National Oceanic and Atmospheric Administration (NOAA), North Pacific Marine Science Organization (PICES), International Council for the Exploration of the Seas (ICES), Food and Agriculture Organization (FAO), and the United Nations Environment Program (UNEP). One of the key advantages of EBM is that it can take into account the indirect, nonlinear interactions that take place within ecosystems, which traditional management strategies generally do not incorporate (Link 2002). A major consideration for excluding these interactions from traditional management efforts was to reduce complexity associated with additional variables and therefore increase prediction accuracy. However, the indirect effects associated with complex system dynamics can

frequently be greater than direct effects and excluding these components often leads to ambiguous or conflicting results (Wootton 2002).

Despite the need for a more comprehensive understanding of ecosystem structure and function in developing management frameworks, there are a wide variety of challenges associated with these efforts including limited data availability, environmental stochasticity, and limited management resources (Fogarty 2014). Fortunately, there are a number of approaches aimed at tackling these issues (Patrick and Link 2015). One of the most powerful and widely used methods is ecosystem modeling (Collie et al. 2014). Ecosystem models provide an effective way to organize and quantify our knowledge of ecosystem processes, identify the importance of ecosystem connections not easily measured in situ, and project alternative future ecosystem states resulting from various management decisions. While data availability, uncertainty, and complexity are all still important factors that need to be addressed, ecosystem modeling provides a high degree of flexibility because diverse models can be specifically designed to address a range of targeted questions and management strategies (Playgani et al. 2012). Furthermore, a major advantage of this approach lies in the use of 'gaming' to test how a model responds to a variety of theoretical situations, which in turn gives the user an idea of what's mathematically possible given the underlying structural organization of the model components. This is extremely useful because while it's not possible to set up ecosystem-scale experiments to test these situations, gaming could provide valuable insight into the potential natural responses of ecosystems under novel conditions.

Major components still missing from many ecosystem models are terms to incorporate feedbacks between natural and anthropogenic systems. One way to describe and predict human interactions with ecosystems is through economics (Thébaud et al. 2014). Economics provides a framework with which to model anthropogenic influence based upon the financial drivers that are thought to govern decision making. Just as it is unrealistic to predict population abundance outside of the context of an ecosystem, it may be unrealistic to predict the behavior of ecosystems without including anthropogenic effects that have major impacts on species abundance or distributions (Levin et al. 2012). Over the past decade, the

need to include anthropogenic impacts into ecosystem models has resulted in a wide variety of bioeconomic models aimed at quantifying human and ecosystem interactions (Nielson et al. 2017), mainly with respect to marine ecosystems. These efforts include modeling frameworks such as Integration of Spatial Information for Simulation of Fisheries (ISIS-FISH), Impact Assessment Models (IAM), Fleets and Fisheries Forecast Model (FCUBE), Atlantis, and Ecopath with Ecosim (EwE). EwE is among the most widely used ecosystem models across the world (Colléter et al. 2015) and provides a number of economic and policy management routines that enable comprehensive exploration of alternate management strategies and their ecosystem impacts.

This study utilizes an Ecopath with Ecosim (EwE) model of the eastern tropical Pacific (ETP) to heuristically assess the role of fishing fleet effort in the development of management targets. This approach allows for the optimization of economic and ecosystem health objectives by exploring ecosystem behavior within the mathematical constraints of a food web network structure. Through the use of multiple management scenarios, this study aims to identify the major interactions and feedbacks linking human and ecological systems, as well as to quantify potential tradeoffs in management policy design. By considering various fisheries management frameworks in both an ecosystem and bioeconomic context, it is possible to investigate the important indirect effects and nonlinear behaviors that drive the dynamics of complex systems so that effective and efficient management can occur.

Methods:

Ecopath with Ecosim Model of the eastern tropical Pacific

Study Area

The ETP is defined in this study by a polygon that roughly circumscribes oceanic waters between the coastal region of San Diego to the east, Hawaii to the west, and the coast of central Peru and portions

of central America to the south. Broadscale surface circulation in the region is driven by the North and South Equatorial Currents (NEC, SEC), which are forced to the west by trade winds, while the North Equatorial Countercurrent flows eastward between the NEC and SEC (Fiedler and Talley 2006). The three principal surface water masses of the ETP include Tropical Surface Water, Subtropical Surface Water, and Equatorial Surface Water. The ETP also supports high productivity driven by vertical nutrient flux to the euphotic zone along zonal divergences at the Costa Rica Dome (Fiedler and Talley 2006) and through zonal advection from coastal upwellings (Owen & Zeitschel 1986). Annual changes in wind-driven circulation show distinct winter and summer seasonal patterns (Fiedler and Talley 2006). The surface waters of the ETP are subject to El Niño Southern Oscillation (ENSO)-related variability, which occurs approximately every two to seven years (Wang and Fiedler 2006) and the Pacific Decadal Oscillation, which occurs approximately every 20-30 years (Schneider and Cornuelle 2005).

Original ETP EwE Model

EwE is an ecosystem modeling software platform that has been constructed and extended on for almost twenty years (Pauly et al. 2000). It was developed in order to address ecological questions, evaluate ecosystem effects of fishing, explore management policy options, and model the effects of environmental changes. The foundation of the EwE suite is an Ecopath model, which creates a static mass-balanced snapshot of the organisms in an ecosystem and their interactions, represented by trophically linked biomass 'pools'. The biomass pools consist of a single species, or species groups representing ecosystem guilds. Ecopath data requirements are relatively simple, and data are often available from stock assessments or ecosystem studies (e.g., biomass estimates, total mortality estimates, consumption estimates, diet compositions, fishery catches). Ecosim extends the Ecopath model by providing a dynamic simulation capability at the ecosystem level using a system of differential equations that express biomass flux rates between pools as a function of time.

Olson and Watters (2003) created a trophic mass-balance model of the ETP pelagic ecosystem using Ecopath and analyzed the system's behavior through time with Ecosim. The model incorporates 38 species or speices guilds (functional groups of species), which include principal exploited species (e.g., tunas and marlins), functional groups (e.g., sharks and cephalopods), protected species (e.g., sea turtles and dolphins), and species that reside in the system for only part of the year (e.g., Pacific bluefin tuna and baleen whales). Model parameters were derived using average estimates from a small subset of years (1993-1997), a common approach in constructing trophic mass-balance models. They also fitted a balanced version of the model to historical time series of catches per unit effort during a period from 1961-1998. Biomass estimates of commercially fished species predicted by the model closely matched observed abundances (Olson and Watters 2003).

Climate forcing was also included to simulate ENSO - scale variability (Watters et al. 2003). Climate forcing of phytoplankton was focused on large phytoplankton under the assumption that the biomass of small producers (picoplankton) was relatively stable under ENSO-induced sea surface temperature (SST) oscillations, which is consistent with observations (Bidigare and Ondrusek 1996, Landry et al. 1996). An empirical model relating SST in the NINO3 region, an area of the ETP to the south of Mexico, to surface chlorophyll was used to create a time series of large phytoplankton biomass under the influence of ENSO variability. Two additional empirical models were used to simulate an increase in predator recruitment (for all predatory fish species excluding sharks) following warm events, also consistent with observations (Maunder and Watters 2002). These empirical recruitment models relate physical forcing to the survival of small fishes and the egg production by large fishes. Both predator recruitment models provided relatively good estimates when compared with empirical stock assessment data (Olson and Watters 2003).

Model Updates

We updated the Olson and Watters (2003) EwE model of the ETP in a number of ways.1) We downloaded the most recent software version for this study (EwE version 6.4.3), which incorporates new features regarding ontogenetic life stages and fish egg production. 2) We then implemented the multi-stanza routine, included in the recent EwE software version, which refers to the individual treatment of multiple life stages and enables users to separate ontogenetic life stages of organisms with varying trophic requirements. Population growth and mortality estimates linking ontogenetic life stages for each species was taken Fishbase.org (Froese and Pauly 2017). Dividing some species into multiple life stages also required a slight rebalancing of diet interaction strengths, which was done by lowering the diet fraction of prey species that had unrealistic predation mortalities, as a result of the multi-stanza inclusion, and redistributing those fractions among all other prey in the diet. This was done in an iterative fashion until population estimates agreed with historic time series. 3) Recent versions of EwE also include a fish egg production routine that ties into the multi-stanza components. We transcribed the original egg production function developed by Olson and Watters (2003) into this routine, which was built into the original ETP model as a forcing function. 4) After adjusting the ETP model to incorporate the new routines introduced to EwE, we then updated time series of fishing effort and species abundance, used to fit the original model, with the most recent years of available data using technical reports provided by the Inter-American Tropical Tuna Commission (IATTC) and NOAA along with the inclusion of additional time series for marlin, skipjack, and albacore (Minte-Vera 2014, Aires-da-Silva et al. 2015, Kolody et al. 2016, ISC 2016). 5) Updated time series were then used to parameterize trophic vulnerabilities, which represent interaction strengths between model groups, by utilizing the EwE time series fitting routine. This routine automatically calculates vulnerability parameters that result in the lowest Akaike's information criterion (AIC) value across all species when comparing hindcast estimates to historic time series.

Model Uncertainty

Model uncertainty was addressed during the original ETP model development by conducting a sensitivity analysis to identify the most important parameters and by fitting model projections to multi-

species time series (Watters et al. 2003). In the updated version of the ETP model used for this study, over-fitting was avoided through the use of AIC criteria to adjust sensitive model parameters and time series data of ecosystem components were updated along with the inclusion of additional time series for certain species and fishing effort. The degree of origin and quality of each parameter developed for the updated model was also characterized using the Ecopath model pedigree values. Pedigree values are qualitative categorizations of input parameter confidence, which then feed into probability distribution methods to address uncertainty. Pedigree values for input parameters are used to set confidence intervals for a Monte-Carlo analysis to assess potential output parameter distributions. The overall pedigree value of the ETP model was a 0.613, which is in the top 88% of overall pedigree values calculated across a sample of 50 EwE models during a study conducted in Morissette (2007).

Fishing Fleets

'Fishing Fleets' is a term used by EwE to characterize the different trophic impacts of fishing in a given ecosystem. Fishing Fleets are used to define separate fishing entities and respective fishing methods that target unique compositions of species. The Fishing Fleets incorporated into this model include three types of purse seine fishing methods as well as longlines (Fig.1). The purse seine methods include Floating Object Sets, Dolphin Sets, and School Sets. Floating Object Sets involve fishermen setting nets around floating objects (e.g., logs, seaweed, or artificial rafts). Dolphin Sets target groups of both dolphin and tuna while School Sets involve fishermen setting nets around free-swimming schools of fish. The ETP model also includes longlines, which involve the use of a main line with baited hooks attached at intervals by means of branch lines. Due to the unique catch compositions and trophic impacts of these fishing methods (Olson and Watters 2003), they are each defined as individual Fishing Fleets in the model. Each Fleet is treated as a separate economic industry with respective catch, costs, and profit calculations. 'fishing effort' is also defined individually for each Fleet (IATTC.org). Fishing effort for

purse seine Fleets is defined as the number of sets per year, while the effort for longlines is defined as the number of hooks per year.

Economic and Ecosystem Indices

Economic Indices

The indices used to assess economic impacts include Total Catch, Total Value, Total Cost, Mean Tropic Level of Catch, and Gross Efficiency of Catch. Total Catch represents the total biomass in tons/km^2/year of fish caught. Total Value is the summation of off-vessel price multiplied by the value of each species across all Fleets. Total Cost, is measured as a percentage of the total revenue spent on effort-related costs. Default values of Total Cost were used from the original ETP model, which include a constant 20% effort-related cost. Mean Trophic Level of Catch is an average measure of trophic level derived from Ecopath estimates of diet composition. Gross Efficiency of Catch is defined as the ratio of catch to net primary production of the system and represents the amount of catch supported per unit of primary production.

Ecosystem Indices

Ecosystem indices used here include Biomass, Biodiversity, Biomass/Total System Throughput (B/TST), Primary Production/Biomass (P/B), and Primary Production/Respiration (P/R). Biomass represents the wet weight of living organisms defined by the system in tons/km^2 and is used to quantify energy storage in an ecosystem. Biodiversity, calculated through the use of a modified Kempton's Q (Ainsworth and Pitcher 2006), is an index that describes the slope of the cumulative species-abundance curve between the 10th and 90th percentiles, in which a more even distribution of biomass across species leads to higher values of ecosystem Biodiversity. P/B is a measure of how much production is needed to support each unit of Biomass within an ecosystem. Lower values are expected in mature systems where the amount of biomass supported by available energy reaches a maximum and the majority of energy is used in maintenance (respiration) (Winberg et al. 1972). This index is considered a measure of ecosystem

efficiency. B/TST is similarly a measure of ecosystem efficiency, and represents the amount of Biomass maintained per unit of energy flowing through an ecosystem and it has been shown that ecosystems tend to maximize this ratio as they develop (Fath 2001). TST represents the total energy flows within an ecosystem, including flows between ecosystem components and flows between the ecosystem and the exterior. P/R relates the energy inputs to the outputs of an ecosystem and provides a measure of ecosystem development (Odum 1969). As an ecosystem reaches maturity, this ratio is expected to approach one because energy fixed tends to balance the energy cost of maintenance (Ryan et al. 1997, Monaco and Ulanowicz 1997). It is important to note that the calculation of many of these indices encompasses all components and respective energy flows in the ecosystem. As a result, small changes of only a few of those components, such as target fish species, lead to very small changes in the overall value of several indices.

Policy Optimization Routine

The fishing Policy Optimization Routine in Ecosim was used to identify what levels of fishing effort, distributed across Fishing Fleets, satisfies multi-criterion objective policies that incorporate weightings for economic, employment, mandated rebuilding of a species, ecosystem structure, and biodiversity, formally described in Walters et al. (2002). The Policy Optimization Routine utilizes the Davidson-Fletcher-Powell (DFP) nonlinear method to repeatedly test alternate fishing efforts of each defined Fleet over specific time periods in order to iteratively improve the objective function with respect to pre-defined weightings set by the user. This procedure uses a conjugate-gradient method, which tests alternate parameter values to approximate the objective function locally as a quadratic function of the parameter values that progresses towards the solution in a stepwise manner (Ecopath.org). In order to avoid the optimization procedure prematurely terminating at local maxima, instead of global, the routine was conducted using both original base model and random initial fishing efforts and carried out at least 10 times per management scenario (defined below).

When determining the respective optimal fishing efforts of each Fleet, or the fishing effort that reaches a target solution, users have the flexibility to quantify the weight of five or more policy objectives. 1) Net Present Value is defined as the difference between the value of catch (off-vessel revenue) and the cost of fishing, to determine Fleet profitability. 2) Social Benefits is expressed through the number of jobs supported by each Fleet and calculated as the number of jobs relative to the catch value for each individual Fleet. 3) Mandated Rebuilding refers to maintaining species or species groups at abundances required by various statutes. 4) Ecosystem Structure places importance on maximizing ecosystem health, as defined by Odum (1969), whereby ecosystem maturity corresponds to ecosystem health, and mature ecosystems are dominated by large, long-lived organisms. This is quantified by the ratio of ecosystem biomass to ecosystem production, which is indicative of average organism longevity. 5) Biodiversity is defined as Kempton's Q. For each of these policy objectives, weightings are defined by the user, which are then incorporated by the DFP nonlinear method to calculate optimal fishing efforts per Fleet. In this paper, we focus only on the Net Present Value and biodiversity objective weightings.

Management Scenarios

This study used the Policy Optimization Routine to compare and contrast a variety of management scenarios in order to assess the economic and ecosystem health impacts of each approach. Four individual management conditions (defined below) were simulated in this analysis 1) Maximize Net Present Value (NPV), 2) Maximize Portfolio Utility (MPU), 3) Multiple Fishing Rights (MFR) without compete costs, and 4) MFR with compete costs. For each of the management scenarios, a discount of 4% was applied to the value of future catches to represent current economic interest rates adjusted for inflation. A 4% discount is the EwE default value, however, a variety of discount values were explored and it was shown that changes in this variable did not influence the Policy Optimization Routine results under our search conditions until unrealistic values were reached. Full weight was put on the NPV Policy Objective to maximize profit for each management scenario. Each simulation was run over a 100-year period to allow the ecosystem to fully reach a new equilibrium. Economic and ecosystem health indices were extracted at

year 100. While equilibrium conditions were generally reached within the first 10-20 years, 100 years was chosen as a precautionary period to fully allow for species with slow generation times to reach equilibrium. Output from each management scenario was also compared with the base model as well as simulations where all fishing was removed from the system. fishing effort is presented as relative to the base model values. Relative changes in fishing effort less than one are treated as fractional differences

In the maximize NPV scenario, fishing efforts were selected to maximize the discounted profit derived from all fisheries summed together (off-vessel price of catch - costs of fishing), which is the default policy optimization setting. Under this scenario, all Fleets are treated as a single entity, in that some Fleets could potentially operate at a loss in order to maximize the overall profit of all Fleets combined. This approach tends to exploit the most profitable species and may also remove species/groups that compete with or prey upon target species (Christensen and Walters 2004).

The MPU scenario is a risk-averse management strategy that incorporates diminishing returns on catch and accounts for the role of uncertainty in policies that result in significant departures of biomass from the Ecopath base model (Christensen and Walters 2004). In other words, the optimization algorithm penalizes fishing efforts that lead to drastic changes in the biomass of any group in order to address the increased uncertainty of predictions derived from 'extreme' scenarios, which can be considered as large changes in biomass across multiple groups. Similar to NPV, all Fishing Fleets in MPU are treated as a single entity.

MFR treats each Fleet as a separate economic entity (i.e., individual revenue, costs, and profit) and identifies Fleet-specific fishing efforts that satisfy policy optimization objectives (Ecopath.org). MFR ensures that individual Fleets do not continuously operate at a loss (negative profit) and attempts to maximize profit under the policy objective weightings. If for some reason a Fleet passes into negative profit during a simulation, through competition with other Fleets or changing ecosystem conditions, the optimization procedure will be reduce its fishing effort until effort-related costs decrease enough to result

in positive profit or it will subsequently be removed from the system (similar to competition between species or functional groups). Multiple Fishing Fleets tend to have a wide variety of direct and indirect effects on each other and the ecosystem, whereby the success of one Fleet may be at the detriment of another (e.g., bycatch or competition). The EwE policy optimization scheme can quantify these direct and indirect costs by running multiple simulations and iteratively removing individual Fleets in order to calculate their respective influence on all other Fleets and species groups. From this, the equilibrium gains in income achieved by remaining Fleets are a direct estimate of the income losses caused by a removed Fleet if it were to remain in the system. The loss of income for a Fleet that is directly or indirectly caused by another Fleet is defined as a compete cost. These compete costs, which are usually treated as externalities, can then be directly incorporated into the policy optimization search in order to maximize profit across all Fleets under those constraints. In this analysis, fishing efforts were derived from MFR simulations with and without compete costs included.

Management Tradeoffs

The tradeoffs between maximizing profit and maximizing ecosystem biodiversity Policy Objective weights were also explored under two of the management scenarios; NPV and MPU. Under each of these management scenarios, the Policy Optimization Routine objective function weightings were iteratively increased or decreased over the course of 11 simulations run for 100 years. The weights for profit maximization started at 1 (full weight) and decreased to 0 at a rate of 0.1. Simultaneously, biodiversity weights started at 0 and increased to 1 at a rate of 0.1. The sequential change in fishing effort and respective Total Catch, Total Value, Biomass, and Biodiversity indices were then compared across simulations.

Results:

Management Comparisons

Target fishing effort output varied across each management scenario (Fig. 3), with fishing efforts (relative to the original base Ecopath values) ranging from 0 to 10 times (x) higher than the base model fishing effort. Base model fishing effort values were 9943, 4098, and 7087 sets per year for Floating Object Sets, School Sets, and Dolphin Sets respectively, as well as 165 million hooks per year for Longlines. The NPV scenario resulted in all Fleets increasing effort by approximately 3x from the base model effort, excluding Dolphin Sets, which dropped by about 0.5x. The MPU scenario had the most even distribution of effort across Fleets and the smallest change from base model values, with efforts ranging from 0.5x-2x. Both MFR scenarios led to significant changes in Fleet efforts with Dolphin Sets effort dropping to 0. Floating Object set effort increased to approximately 10x when compete costs were included, but dropped to 0 when compete costs were not included. Both School Sets and Longline effort increased during MFR scenarios, with no compete costs leading to a noticeably higher increase of each.

The proportion of specific species caught varied in response to Fleet-effort combinations under different management scenarios (Fig. 4). Generally, the species with the highest catch included skipjack, large yellowfin, large bigeye, and small yellowfin respectively. Yellowfin tuna were mainly caught by Dolphin Sets and School Sets, skipjack largely caught by Floating Object Sets and School Sets, and large bigeye were primarily caught by Longlines. With respect to each management scenario, skipjack tuna comprised the largest proportion of catch across all scenarios, excluding MPU, in which yellowfin tuna made up the highest catch. A larger proportion of yellowfin tuna catch is consistent with an increase in Dolphin Sets and a decrease in Floating Object Set effort observed in the MPU scenario. Total catches of yellowfin tuna were comparable across most scenarios, but significantly decreased under MFR with no compete costs, which is also consistent with a decrease in Dolphin Sets and an increase in Floating Object Set effort.

Economic indicators varied across management scenarios (Fig. 5). NPV management had the highest Total Catch, Total Value, and Gross Efficiency of Catch, although these came with a marginally

higher Total Cost. The Mean Trophic Level of Catch was intermediate, compared to other scenarios, representing a comparatively mixed distribution of catch across trophic levels. MPU and both MFR scenarios had similar Total Value and Total Cost, but differed in Total Catch and Gross Efficiency, with the MFR including compete costs having slightly higher values for each. Mean Trophic Level of Catch varied across scenarios; with MFR without compete costs having the highest Mean Trophic Level of Catch of all scenarios due to an increase in Longline effort, which had higher catches of upper trophic level species, such as large bigeye, albacore, and large yellowfin. MFR with compete costs had the lowest Mean Trophic Level of Catch. In general, all management scenarios had higher Total Catch, Total Value, and Total Cost, and Gross Efficiency of Catch values than the base model, while Mean Trophic Level of Cath displayed both lower and high values.

Ecosystem health indicators responded differently to specific scenarios (Fig. 6), leading to unique combinations of positive or negative effects. For example, the MPU scenario had the highest value of Biodiversity and lowest P/R of the four management scenarios, representing a more complex and mature ecosystem respectively. However, this scenario also had the lowest values of Biomass and B/TST along with the highest P/B, which represents a less efficient ecosystem in terms of the amount of Biomass supported per unit of energy entering and flowing through the system. The NPV scenario similarly had values representative of a less efficient system, but also had lower Biodiversity and higher P/R, meaning that all measures of ecosystem health were impacted more negatively under this management scenario. MFR with compete costs had comparatively positive measures of ecosystem Biomass, efficiency, and Biodiversity, but ecosystem maturity was lower. The higher estimate of Biomass under this scenario was primarily attributed to a major increase in cephalopod Biomass at lower trophic levels. Finally, MFR without compete costs had intermediate values of Biomass, efficiency, and maturity indicators, but had the lowest Biodiversity of all scenarios.

Tradeoffs

NPV

Varying policy optimization objective weights between profit and biodiversity under the NPV management scenario led to a variety of fishing effort per Fleet combinations as weights shifted away from profit onto biodiversity. Floating Object Sets, Dolphin Sets, and School Sets did not show any distinct pattern, while Longlines displayed a noticeable declining trend with decreased weight on profit, suggesting that it played the biggest role in determining Biodiversity. The lack of any discernable trends across the other Fleets suggest that there are a variety of Fleet-effort combinations that reach similar Policy Optimization Routine goals. Total Catch and Total Value did not display any significant trend as Policy Optimization Routine weights varied from profit to biodiversity, however, both Biomass and Biodiversity showed a steady increase as the Optimization weights shifted to biodiversity (Fig. 7). The lower x-axis of this figure depicts the weight on profit (iteratively decreasing from left to right), while the upper axis depicts the weight on biodiversity (iteratively increasing from left to right).

MPU

Varying Policy Optimization Objective weights between profit and biodiversity under the MPU management scenario led to more distinct patterns in fishing effort across Fleets when compared to the NPV trade-off scenario. The patterns for School Sets and Floating Object Sets displayed concave shapes with highest efforts at intermediate weightings of both profit and biodiversity. Dolphin Sets and Longline efforts showed an opposite convex shape with lowest efforts occurring at intermediate weightings of profit and biodiversity. Total Catch and Total Value displayed similar concave shapes as School Set and Floating Object Set effort (Fig. 8), each reaching their highest values at intermediate weights of both profit and biodiversity. Biomass and Biodiversity both showed steep increases as weight on profit moved from 1 to 0.7 before gradually decreasing as the weight on profit dropped to 0. Similar to the NPV tradeoff scenario, the lower x-axis of this figure depicts the weight of profit (iteratively decreasing from

left to right), while the upper axis depicts the weight on biodiversity (iteratively increasing from left to right).

Discussion:

This study represents a heuristic approach to utilizing a trophic network model of the ETP to compare multi-species fishery management strategies by varying the fishing efforts of individual Fleets to optimize specific policy objectives. This method highlights the cascading, indirect effects of fishing across an entire ecosystem and incorporates a holistic perspective to quantify their economic and ecosystem health impacts. Results of this study show that varying management scenarios (e.g., NPV, MPU, MFR) could potentially lead to a diverse combination of economic and ecosystem effects. This study also highlights the potential for different management strategies to achieve similar economic results, but through alternative mechanisms with subsequently different ecosystem-level impacts (i.e., ecosystem maturity, efficiency, complexity, etc.). Furthermore, tradeoffs between profit or biodiversity optimizations under different management scenarios are nonlinear and it may be possible to increase one objective without decreasing the other within this modeling framework, leading to potentially flexible management approaches. This nonlinear behavior is in agreement with similar studies conducted with other ecosystem models (Okey and Wright 2004)

However, changes in a variety of the ecosystem and economic indices presented here displayed only very small differences between scenarios, in terms of absolute numbers. These small differences may be a product of their quantification, in that they incorporate measures of biomass and energy from all components within the ecosystem, and therefore changes to only a few of those components have a very small influence on ecosystem-level changes. Whether that means that these different management strategies have only minor ecosystem-level impacts or if those small changes lead to much more

significant species-specific impacts is much harder to determine as very little research has been done quantifying the extent of change in these ecosystem indices and their impact on management targets (Christensen and Walters 2004, Okey and Wright 2004). Yet, the strength of this analysis lies in the inclusion of complex interactions among ecosystem components and Fleets that allow for the identification of economic and ecosystem feedbacks, which cannot be quantified through single species approaches to fishery management. As such, the value of these results lies in the qualitative comparisons across management scenarios, the base model, and simulations with fishing effort completely removed. Another major advantage of this approach is that one can explicitly choose a desired economic and/or ecosystem objective and then manage to achieve that goal.

Mechanisms of Optimal Management

Management scenarios

The management scenario comparison highlights the possibility of achieving similar economic objectives under different strategies that optimize distinct ecosystem impacts. For example, MPU as well as MFR with and without compete costs all had consistent overall values and similar catch, but their ecosystem impacts were highly variable. MPU management results in a more mature and structurally complex ecosystem, MFR with compete costs leads to a larger and more energetically efficient ecosystem, and MFR without compete costs displayed intermediate ecosystem health values, but at lower Biodiversity. While NPV had the highest economic performance in terms of Total Catch and Total Value, it resulted in the largest negative ecosystem impacts in terms of ecosystem size, complexity, efficiency, and development. Approaching management strategies using this perspective provides a potentially high degree of flexibility that may allow decision makers to choose a system of management that best suits their ecosystem objectives, while still attaining desired economic targets. Similarly, varying management scenarios led to significantly different Fleet efforts, which in turn determine Fleet sizes and social benefits

in the form of jobs. Therefore, it may also be possible to meet the same economic goals through a variety of individual Fleet sizes, which may have important impacts on bycatch management policies.

Management Tradeoffs

NPV

The profit versus biodiversity tradeoff analysis under the NPV management scenario resulted in nonlinear relationships between economic and ecosystem health indicators. In general, Total Catch and Total Value showed very little change as Policy Objective weights moved from profit to biodiversity. However, Biomass and Biodiversity were much more responsive to changes in objective weights. Increased weight on biodiversity led to a larger and more structurally complex ecosystem, as indicated by changes in ecosystem indices, consistent with the removal of fishery pressure as weight on profit decreased. These results suggest that it may be possible to increase these ecosystem characteristics without sacrificing economic outputs. Patterns in economic and ecosystem indices seem to be most consistent with the trend in Longline effort as Policy Objective weights shifted from profit to biodiversity, indicating that the Longline fishery might have a comparatively higher impact on ecosystem health than other fisheries and, therefore, play a more important role in management.

MPU

Results of the tradeoff analysis under the MPU scenario suggested that full weight on the profit objective led to a lower economic performance (Total Catch and Total Value) than intermediate weights, while full weight on biodiversity led to lower ecosystem health (Biomass and Biodiversity) than at intermediate weights. Surprisingly, both Biomass and Biodiversity had higher values at a profit weight of 0.7 and biodiversity weight of 0.3 as compared to increased weights on biodiversity. A potential reason for the concave patterns observed is that the MPU scenario includes a penalty in the policy optimization algorithm that occurs when the Biomass of ecosystem components are pushed far away from the original ecosystem state, as described in the methods section. In other words, this management scenario takes into

account the assumed uncertainty of ecosystem predictions associated with significant shifts from the original ecosystem structure (Ecopath.org). The purpose of this penalty is to reduce risk around policy targets that lead to significant perturbations to the ecosystem and to promote more conservative management strategies. Under this framework, information can be used to provide managers with a better understanding of how to achieve economic and ecosystem objectives while reducing the risk of significantly disrupting ecosystem dynamics.

Complexity and Indirect Effects

One of the major advantages of an ecosystem-based approach to fisheries management is that it incorporates the indirect effects representative of a complex system (Wootton 2002). Food webs are detailed with vast networks of interactions resulting in diverse sets of positive and negative feedbacks along with threshold and bifurcation responses to perturbations (Levin 1998). Fishery management programs that only utilize single species models lose these important dynamics, which drive ecosystem-scale processes that subsequently impact target species populations (Hallowed et al. 2000). By removing individual species from this context and treating them as separate entities, natural processes cannot be fully replicated and this may lead to significantly inaccurate predictions. Figure 9 represents a Mixed Trophic Impact plot for the ETP model, which is a Leontiff matrix generated through EwE. This plot represents the impact that a change in the Biomass in one group has on all other groups in the ecosystem and provides a visual representation of the positive and negative indirect effects that link together all components of the ecosystem (Christensen and Pauly 1992). From this plot, it is possible to see that changes in any one species can have cascading effects that reverberate through the ecosystem, leading to nonlinear responses that single species models would be unable to account for.

Ecosystem Modeling

The inclusion of multi-species fishery management strategies have been strongly advocated by a variety of scientific and government institutions and the development of multi-species fishery models are

more frequently being used to fulfill this role (Link and Browman 2014). These models allow for the simultaneous estimation of major ecosystem processes and interactions among species that cannot be measured directly in situ (Latour et al. 2003) and have been shown to outperform single species models in longer term projections (Hollowed et al 2000). There are a variety of ecosystem modeling approaches meeting these requirements, such as multi-species models (MSP), virtual population analysis, aggregate system models (EwE), and multi-species bioenergetic models (MSBE). Each modeling approach comes with a set of advantages and disadvantages depending on the question being addressed. EwE is particularly useful in quantifying, projecting, and exploring ecosystem-scale flow of energy along with the indirect effects of complex trophic interactions (Coll et al. 2015). Multi-species models, in general, allow for the exploration of alternate ecosystem states, the identification of vital gaps in uncertainty, and an increased understanding of nonlinear network behavior.

Despite these advantages, the uncertainty regarding quantitative predictions from multi-species models requires an in-depth exploration in order to identify parameters and emergent properties most affected (Thorpe et al. 2015). One of the difficult balances for these models to achieve involves tradeoffs between model complexity and uncertainty (Collie et al. 2014). Modeling ecosystem processes inherently requires the incorporation of a wide variety of environmental factors, ecosystem components, and variability in time or space. While this approach technically leads to a much more realistic and accurate representation of an ecosystem, uncertainty across parameters has the potential to propagate and distort model predictions (Link et al. 2012). Many models reduce complexity by simplifying non-vital dynamics, but at the cost of realism. The most effective multi-species models tend to be those that find a target balance between parameter uncertainty and model complexity, which yields the lowest overall uncertainty in model predictions.

Despite the challenges associated with uncertainty, not all of the important uses of multi-species modeling lie in their quantitative predictions. A major strength of this study is the use of ‘gaming’ to explore alternative ecosystem states and behaviors resulting from various management strategies

(Essington 2007). Simply understanding what is possible in the confines of a mathematical network structure provides valuable insight into potential natural responses to ecosystem-level perturbations (Link 2012). Furthermore, the true utility of this method lies in its incorporation into a multi-faceted approach to EBM. Through the combination of a suite of models and analyses, it is possible to fully utilize the advantages each, while employing other models to supplement respective disadvantages.

Conclusion

Through the use of an ecosystem-based approach to fisheries management, this study shows that NPV, MPU, and MFR with and without compete costs provide potentially distinct combinations of economic and ecosystem impacts. While the NPV scenario resulted in the highest Total Catch and Total Value, it coincided with a decrease in Biomass, Biodiversity, P/R, P/B, and B/TST. However, MPU and MFR with and without compete costs resulted in very similar Total Catch and Total Value, but with combinations of positive and negative changes in ecosystem indices associated with each scenario. These results suggest that it might be possible to manage for specific ecosystem-level properties while maintaining comparable fishery outputs. These results are further supported by the tradeoff comparisons between NPV and MPU scenarios where it was shown that economic and ecosystem indices do not linearly change with Policy Optimization weights on profit and biodiversity. Through the use of ecosystem modeling, this study provides support for the existence of flexible management strategies that can be applied to situations where specific aspects of ecosystem structure and function need to be prioritized over others. While these results apply specifically to the ETP model used here and the mathematical constraints associated with its construction, the observed qualitative ecosystem responses to fisheries management can be compared across multiple trophic network models of ecosystems to identify how underlying model structure influences ecosystem-scale behavior to anthropogenic perturbations.

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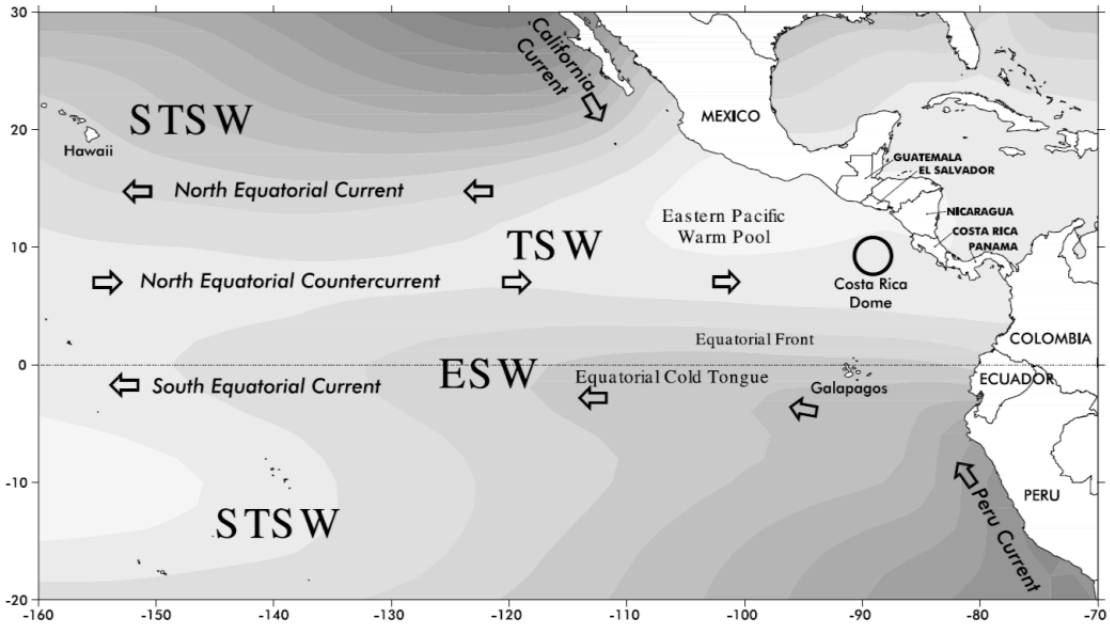


Figure 4.1. Schematic diagram of surface water masses and currents in the eastern tropical Pacific Ocean. STSW, Subtropical Surface Water; TSW, Tropical Surface Water; ESW, Equatorial Surface Water. Shading represents mean sea surface temperature (darker = colder) (Taken from Fielder and Talley 2006).

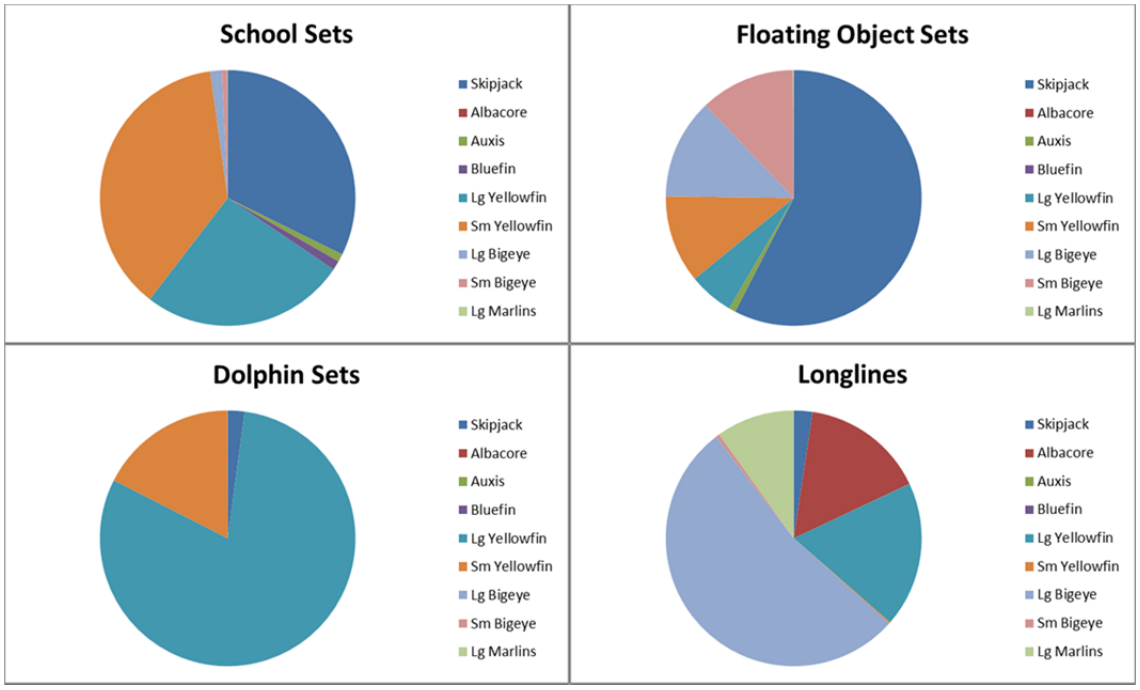


Figure 4.2. Species catch compositions from the base Ecopath model distributed across School Sets (A), Floating Object Sets (B), Dolphin Sets (C), and Longlines (D). The number of species fished differs between Fishing Fleets as well as their percent composition of catch.

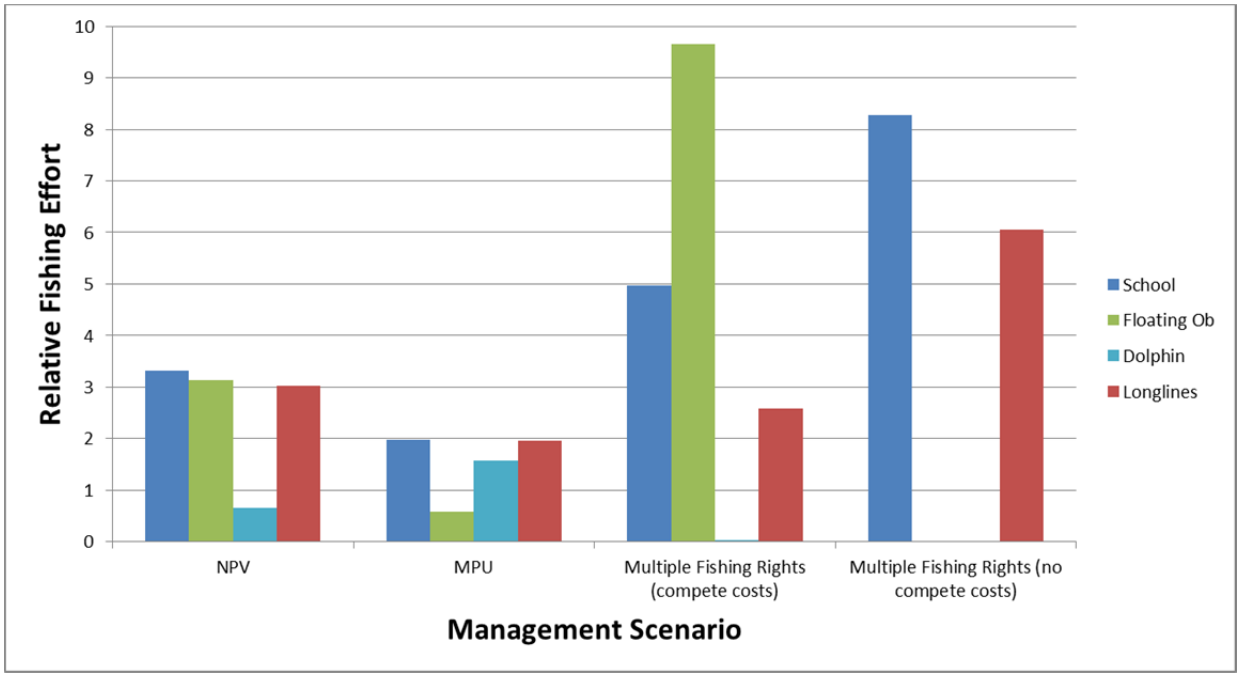


Figure 4.3. Fishing Effort estimated through the Ecopath with Ecosim Policy Optimization Routine under four management scenarios; Net Present Value (NPV), Maximize Portfolio Utility (MPU), Multiple Fishing Rights with Compete Costs, and Multiple Fishing Rights without Compete costs. Fishing Effort is shown for the School Set, Floating Object Set, and Dolphin Set Fleets as well as the Longlines. Effort is relative to original base model values.

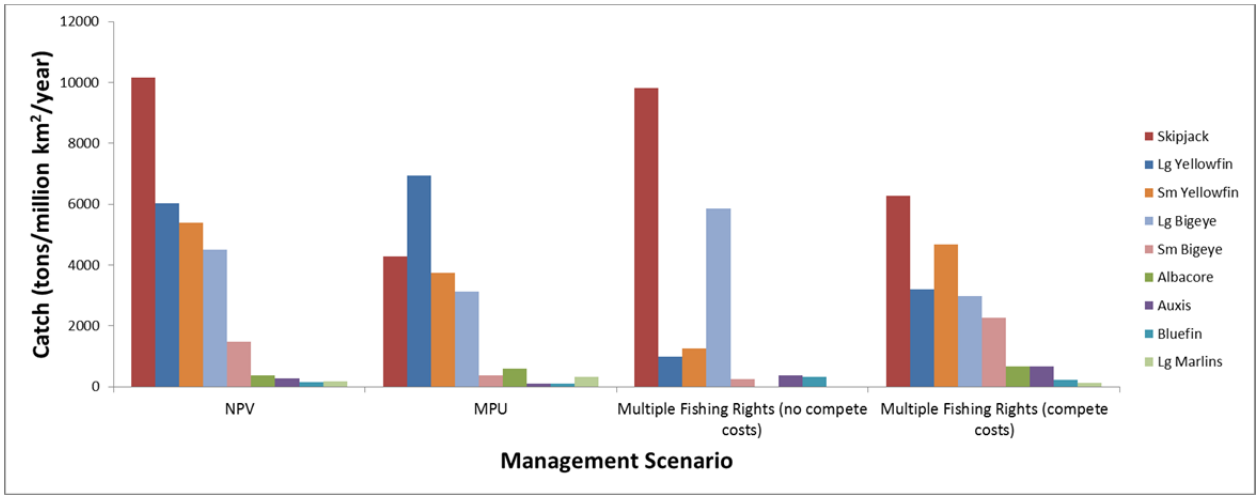


Figure 4.4. Distribution of total catch by species and size (Lg = large and Sm = Small) across the Net Present Value (NPV), Maximize Portfolio Utility (MPU), Multiple Fishing Rights without Compete Costs, and Multiple Fishing Rights with Compete Costs management scenarios.

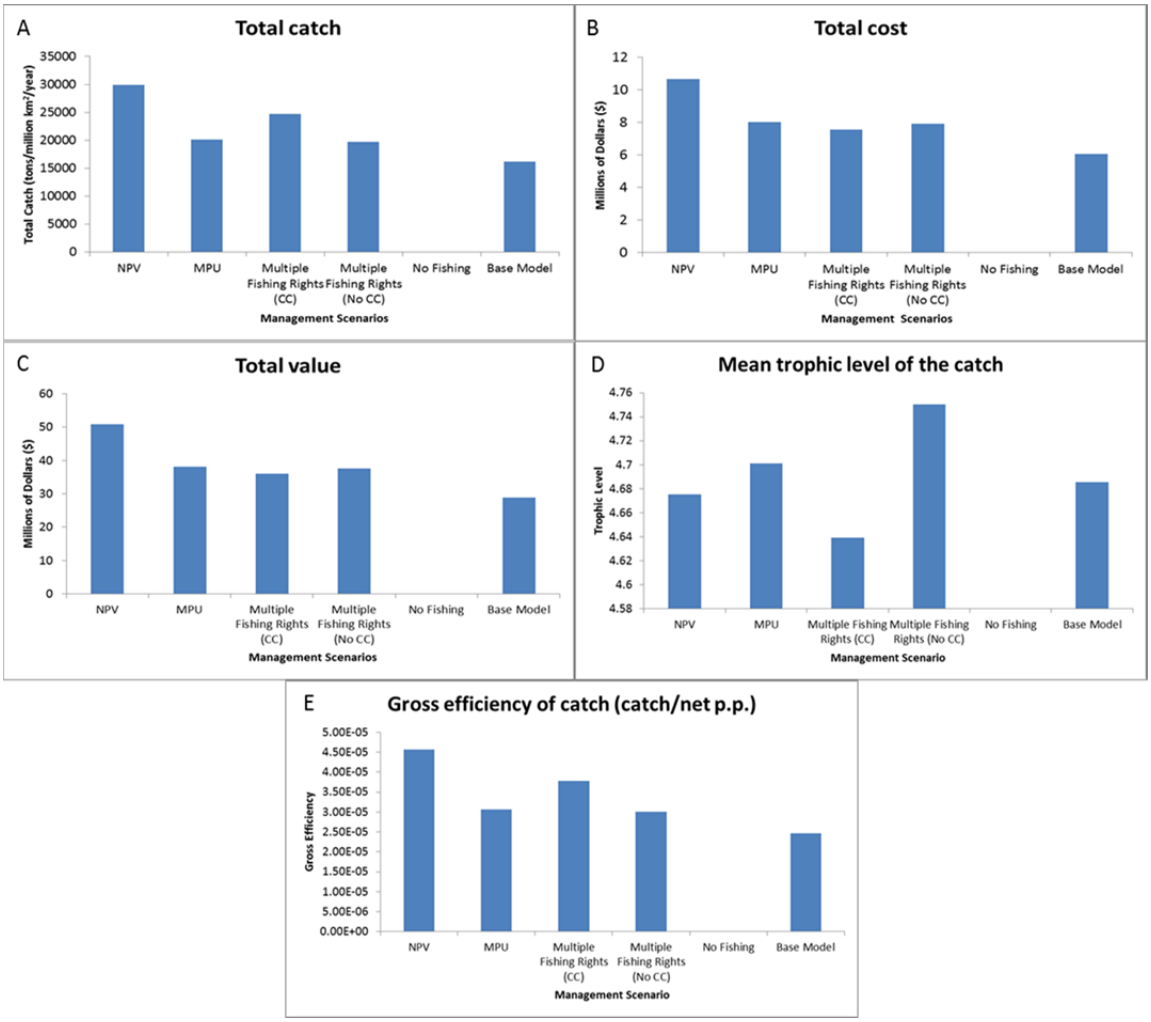


Figure 4.5. Estimated values of Total Catch (A), Total Cost (B), Total Value (C), Mean Trophic Level of Catch (D), and Gross Efficiency of Catch (E) under four management scenarios, Net Present Value (NPV), Maximize Portfolio Utility (MPU), Multiple Fishing Rights with Compete Costs (CC), Multiple Fishing Rights without Compete Costs (CC), as well as comparisons with the base model and all fishing removed.

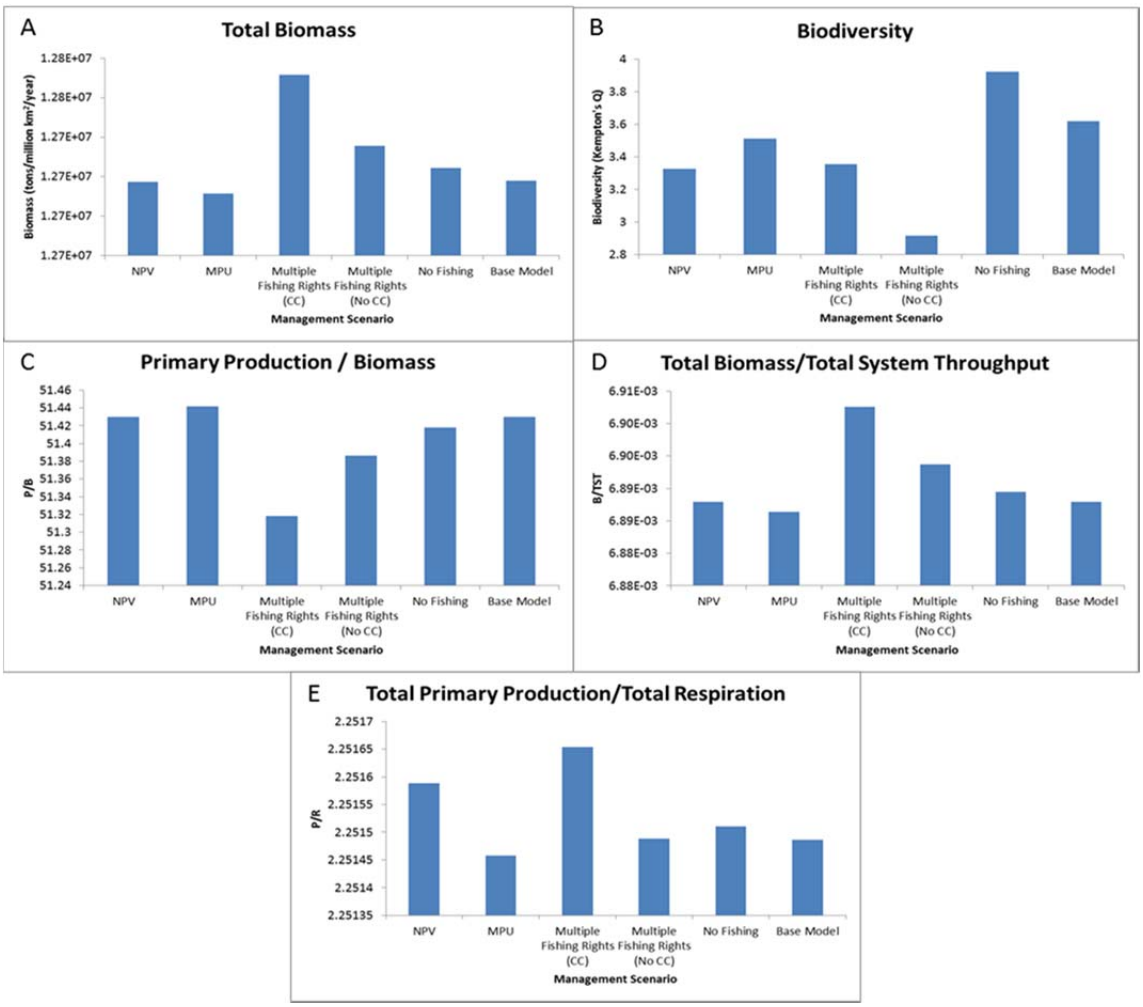


Figure 4.6. Estimated values of Biomass (A), Biodiversity (B), the ratio of Primary Production to Biomass (P/B) (C), the ratio of Primary Production to Respiration (P/R) (D), and the ratio of Biomass to Total System Throughput (B/TST) (E) under four management scenarios, Net Present Value (NPV), Maximize Portfolio Utility (MPU), Multiple Fishing Rights with Compete Costs (CC), and Multiple Fishing Rights without Compete Costs (No CC), as well as comparisons with the base model and all fishing removed.

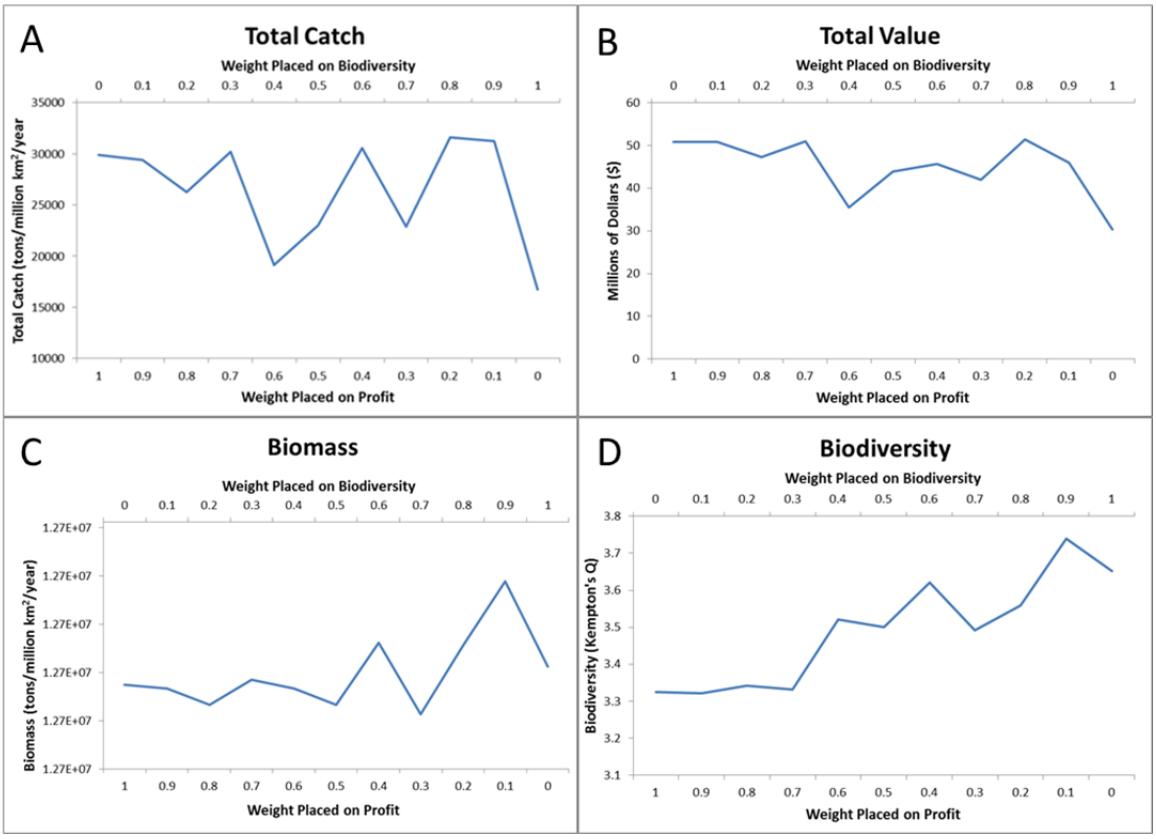


Figure 4.7. Estimated values of Total Catch (A), Total Value (B), Biomass (C), and Biodiversity (D) under the Net Present Value (NPV) management scenario as policy objective weights iteratively decreased for profit and increased for biodiversity.

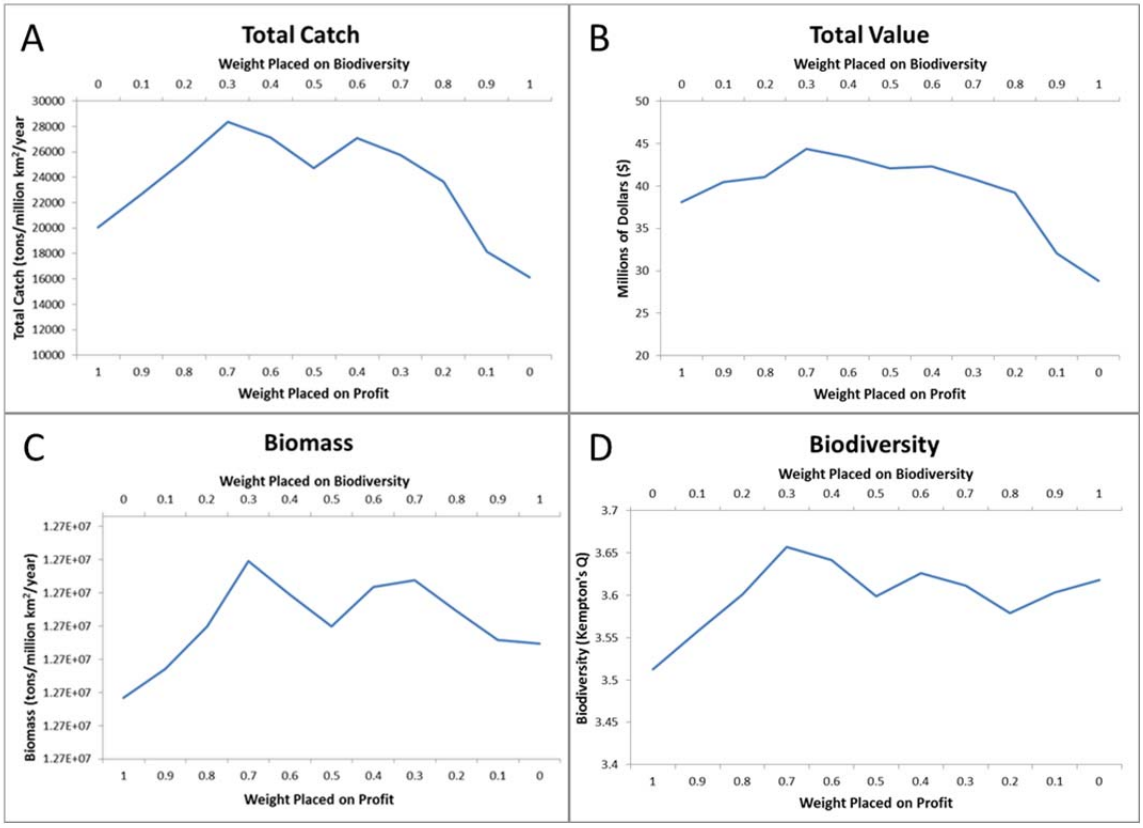


Figure 4.8. Estimated values of Total Catch (A), Total Value (B), Biomass (C), and Biodiversity (D) under the Maximize Portfolio Utility (MPU) management scenario as policy objective weights iteratively decreased for profit and increased for biodiversity.

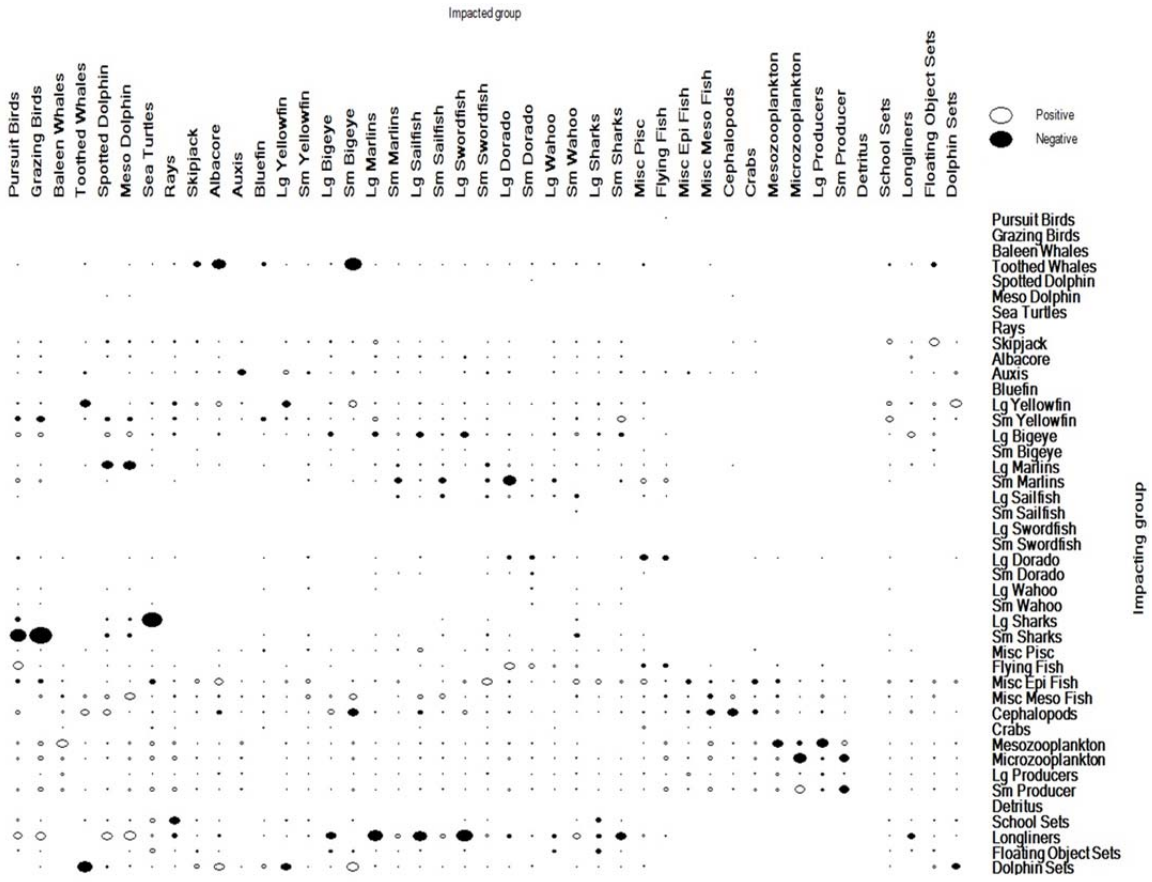


Figure 4.9. Mixed trophic impact plot of the eastern tropical Pacific Ecopath model. The right column lists the species and functional groups that have an impact on the corresponding species and functional groups in the top row. Positive impacts are denoted by an open oval while negative impacts are denoted by a filled black oval. The extent of impact is denoted by the size of the oval.

CONCLUSION

Throughout this dissertation, the reader is introduced to a broad base of work representing the theory behind complex systems and a holistic approach to ecology, the use of that theory in identifying universal patterns in ecosystem structure and function, an exploration of the role of climate change on emergent ecosystem properties, and a heuristic approach to using holistic ecological methods to optimize management strategies. As this dissertation moved from theory to application, a comprehensive understanding of modern ecology and examples of its utility are presented.

An overarching goal of this work was to provide readers with alternative approaches to the challenges of complexity and scale in ecology. While our ability to understand the mechanisms linking every component and process that comprise ecosystems is a very far off goal, it should not inhibit our ability or willingness to tackle the myriad of issues facing ecosystems in today's world. That by taking a step back and viewing ecosystems as functional units, significant advancements in ecological understanding can be achieved. More importantly, the study of complex systems is an inherently multi-disciplinary field, whereby lessons learned from distinct systems can be effectively applied to each other. As such, insight into the behavior of natural ecosystems can be derived through a better understanding of seemingly unrelated complex systems, like social networks or stock markets. This cross disciplinary thinking has the potential to spur creative problem solving by linking consistent structural, functional, and mechanistic properties of complex systems and allow people to approach problems from a variety of angles and perspectives.

However, uncertainty is an innate property of complex systems and something that can never be fully removed, which represents a unique approach to their study that deviates from traditional scientific methods. Uncertainty in complex systems cannot be isolated and controlled for, but instead needs to be treated as its own variable. Sources of uncertainty need to be identified, constrained, and their influence

on system dynamics needs to be clearly defined wherever possible. A holistic approach to ecology is one that fully embraces uncertainty as part of the system.

As humans learn more about the world and information increases at a rate never seen before, our ability to accurately model and simulate natural dynamics will increase alongside, but that does not mean that the issues facing ecosystems will conveniently follow the same timeline. Holistic ecology represents a promising course of action to do what we can with the information currently available to us. Similar to how a doctor should never refuse to help someone due to the sheer complexity of human biology, we must adopt the same perspective when protecting natural ecosystems for generations to come.