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Santa Barbara

Integrating Ecology and History to Understand Historical Marine Population Dynamics: A Case Study of the California Spiny Lobster

A Dissertation submitted in partial satisfaction of the

requirements for the degree Doctor of Philosophy

in Marine Science

by

Deborah Ann McArdle

Committee in charge:

Professor Hunter S. Lenihan, Chair

Professor Robert R. Warner

Professor Michael A. Osborne

Professor Paul K. Dayton

December 2008

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December 2008

Integrating History and Ecology to Understand Historical Marine Life Population Dynamics: A 120-year case study of California Spiny Lobster

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Deborah A. McArdle

Dedication

I dedicate this dissertation to Michael, William and Lulu
for their constant support

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I wish to thank my Committee members, Dr. Hunter Lenihan, Dr. Robert Warner, Dr. Michael Osborne and Dr. Paul Dayton.

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Abstract

Integrating History and Ecology to Understand Historical Marine Life Population Dynamics: A 120-year case study of California Spiny Lobster

by

Deborah A. McArdle

The extent to which exploitation may alter marine life population structure and dynamics is incompletely understood because past research overwhelmingly relies on time series that date back less than 30 years and begin long after the onset of exploitation. This study seeks to partially fill this gap with respect to the California spiny lobster, *Panulirus interruptus,* by fitting a recently developed Bayesian size-structured model to a newly assembled 120-year historical time series of catch and effort to quantify the effects of fishing on the population's size-structure and dynamics. In a little over a century, as fishing effort increased, the abundance and proportion of large-sized lobster (> 100mm carapace length) progressively declined. Severely reducing the lobster's average lifespan and size has increased the population's short-term variability, potentially diminishing the resilience of the species and the kelp forest ecosystem by compounding the effects of 'fishing down the food web.' This work also demonstrates how integrating nontraditional independent historical sources into ecological studies can help meet challenges typically posed by longer time series, including validating potentially questionable historical data points, corroborating model predictions, verifying the temporal scale of baselines, and identifying alternative anthropogenic causes for the observed or predicted ecological variability. In the lobster case study, historical sources verified

an annual catch estimate previously considered an outlier, strongly corroborated the model predictions of fishery-induced lobster population size truncation, and clarified that 1888 was a reasonable pre-exploitation baseline. Further, placing the model reconstruction within the broader historical context of marine conservation over the last 300 years illuminates how lobster conservation tactics based on outdated ecological ideas have facilitated and accelerated the size truncation of the lobster population, and may be undercutting contemporary ecosystem-based conservation measures such as reserves. This approach, which melds contemporary ecological and historical techniques, could be applied to any species to achieve a deeper and more comprehensive understanding of the history of the environment.

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Introduction

Integrating History and Ecology to Understand Historical Marine Life Population Dynamics: A 120-year case study of California Spiny Lobster

A major challenge in ecology is the description of human impacts on the environment. This task has become more complicated as awareness grows that current environments are an artifact of past human activities that significantly predate the customary temporal scale of ecological studies. Thus, there is increasing recognition that to understand the extent to which human beings have affected their surroundings, research must extend farther into the past (Jackson 1997, Swetnam et al. 1999, Myers 2000, Holm et al. 2001, Christensen et al. 2003, Pinnegar and Engelhard 2007).

Pauly (1995) described the potential consequences of continuing an ahistorical perspective as the 'shifting baseline syndrome,' in which the size of ecological change is underestimated because of incomplete historical data. The consequences of a shifting baseline could be significant; it could cause ecologists to set inappropriate reference conditions for their analyses and decision makers to underestimate conservation targets.

In attempting to better account for historical human impacts, one area of particular interest is quantifying long-term changes in marine population dynamics due to exploitation. Past work on population dynamics of exploited marine species

has overwhelmingly relied on time series that are less than 30 years and begin long after the onset of exploitation (Pinnegar and Engelhard 2007). By using short time scales, such studies may fail to reproduce the fundamental demographic changes in a population that can occur over a long history of exploitation, limiting the ability of ecologists to realistically describe and reconstruct the ecological history of exploited species.

Recent studies based on longer chronological time series have emphasized that long-term exploitation causes large-scale reductions in marine population and community abundance (Jackson et al. 2001, Grayson 2001, Roman and Palumbi 2003, Pandolfi et al. 2003, Rosenberg et al. 2005, Lotze et al. 2006). Less attention has been focused on the fact that exploitation also often truncates large size classes (Ricker 1981, Haedrich and Barnes 1997, Zwanenburg 2000, Jackson et al. 2001, Harvey et al. 2006). It is important to understand alterations in size structure because size-specific mortality can change population demographic rates; growth and other demographic traits (e.g. fecundity, egg size) are often highly size- and age dependent (Peters 1983, Schmidt-Neilson 1984, Calder 1984, Brown and West 2000).

Examining the long-term history of marine life populations requires that we obtain and evaluate data that match the temporal scales of the processes responsible for the population's variability (Ricklefs 1987, Levin 1992). However, marine ecological studies are often limited by a paucity of extended historical ecological data sets. Ecologists have recently sought to overcome this obstacle by looking for ecological information from earlier time periods in both quantitative and qualitative

historical sources (e.g. government surveys, maps, newspaper articles, photographs) (Holm et al. 2001, Pinnegar and Engelhard 2007).

In the first chapter of this work, I examine the extent to which exploitation can affect population size structure and dynamics over long temporal scales through a case study of the California spiny lobster, *Panulirus interruptus,* fishery, employing a 120-year time series of catch and effort compiled from historical government records. I gathered the data of this exceptional time series from local, state and national museums and archives. A recently developed Bayesian size structured model (Kinlan and McArdle, in prep) was fit to the time series to quantify the effects of fishing on the lobster population's size structure and dynamics over the last century. The Bayesian model framework was chosen because it allows greater flexibility than traditional statistical approaches in a study such as this, involving multiple data sets and sources of historical information. The long time frame of this study coupled with the Bayesian framework highlights the magnitude of the long-term changes in the lobster population due to exploitation. It also discusses how these changes may have lowered the resilience of both the lobster population by increasing its short-term variability (Hsieh et al. 2006, Secor 2007) and the kelp forest ecosystem by compounding the effects of 'fishing down the food web' (Pauly et al. 1998).

While studies that incorporate longer temporal time scales, like the one described in Chapter One, have demonstrated their ability to increase ecological understanding, the early data within their extended time series often creates several challenges including validating data points, corroborating model predictions of

variability, and confirming that the chosen baseline reliably represents the "natural" or pre-exploitation state (Swetnam et al. 1999, Willis and Birks 2006). Therefore, studies that cover long timeframes need to go beyond compilation and quantitative analyses (Russell 1997). They should more fully examine and understand the ecological 'history' of the population, by taking an interdisciplinary approach that integrates the fields of ecology and history. The advantages of joining the two disciplines have been recognized by ecologists, conservation biologists and historians over the last decade (Meine 1999, Dayton and Sala 2001, Ludwig et al. 1993, Holm et al. 2001, Bolster 2006). By complementing quantitative ecological studies with comparative analyses of historical documentary records, one can increase confidence in long-term ecological reconstructions.

There are only a limited number of examples of historical sources being employed to study historical ecology (Swetnam et al. 1999, Holm et al. 2001, Egan and Howell 2001, Pinnegar and Engelhard 2007). They demonstrate how history can be useful for testing predictive models, by comparing model simulations with historical records. Terrestrial ecologists have recognized the value of and utilized this approach more frequently than those studying marine systems (Russell 1997, Swetnam et al. 1999). There is now growing interest in developing and employing comparative techniques in marine ecological studies (Jackson et al. 2001, Pandolfi et al. 2003, Rosenberg et al. 2005, Lotze et al. 2006). Absent from the literature, however, is a comprehensive synthesis of historical and ecological methods.

In Chapter Two, I introduce an original five-part methodological and conceptual interdisciplinary framework for more fully integrating nontraditional historical sources into ecological studies to: 1) extend the temporal scale of quantitative analyses, 2) validate historical data points in a long time series, 3) corroborate model predictions, 4) verify the temporal scale of a study baseline, and 5) place ecological findings in historical context to interpret and explain the role of human history (e.g. economics, politics, technology, and value systems) in causing the observed or predicted ecological variability. In this chapter I also demonstrate how adding any one or combination of the elements of this approach to a quantitative analysis, (Chapter One) and thus blending different methods and data types, can extend information about population dynamics across a broader temporal scale.

I use the spiny lobster fishery case study to illustrate how these techniques can be applied to the examination of marine populations. I first review a variety of historical records to compile a unique assemblage of over 300 personal letters, oral histories, newspaper articles and government reports that describe the early history of the fishery and population. Then I validate historical data points in the time series, corroborate model predictions, and verify the temporal scale of the study's chosen reference baseline, by comparing these records to the time series and model assumptions and predictions. Finally, I demonstrate that this interdisciplinary framework facilitates the use of a triangulation methodology, which synthesizes quantitative and qualitative information collected from multiple sources by different

methods, thereby reducing the likelihood of potential bias that may arise from relying on only a single method or data source.

Chapter Three offers an in depth example of the last element of the five-part framework, placing the model reconstruction from Chapter One in historical context to identify alternative human-induced causes of the observed and predicted variability in the lobster population's structure. Recent studies propose that the trajectory of conservation may, over time, vary the temporal scale over which demographic changes occur (Conover and Munch 2002, Baskett et al. 2005). Since ecological ideas are a significant driver of conservation strategies (Worster 1994, Meffe and Carol 1997), I examine the historical interaction between marine conservation and ecological theory and practice as applied to the lobster fishery. Using the works of naturalists, ecologists and government researchers, scientific journals and reviews, I describe the historical trajectory of marine conservation, using a model describing major eras in the history of ecology and philosophical ideas about nature over the last three centuries (Worster 1994, Meffe and Carol 1997). I apply this template to the model-generated predictions of lobster population variability to identify and discuss how conservation strategies may have facilitated and accelerated the rate of change in size structure that has continued to the present.

Overall, this work addresses gaps in ecological knowledge and methodology by providing empirical data and contributing to the development of a new methodological and conceptual framework. It illustrates an approach that can move us towards a more comprehensive ecological history of marine life populations by

further broadening understanding of their long-term population dynamics, corroborating model predictions, verifying and deepening insight into the underlying causes of population variability, and placing the findings within their historical circumstances. This historical perspective also provides a frame of reference for assessing the state of contemporary marine life populations and evaluating the efficacy of measures designed to conserve them.

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Chapter One

Historical Patterns of Size-Structured Dynamics of an Exploited species: a 120-year Case Study of the California Spiny Lobster, *Panulirus interruptus*.

(Co-author: Dr. Brian Kinlan, Marine Science Institute, UCSB)

I. Introduction

Knowing a population's historical range of variability is critical to understanding and predicting population fluctuations. It is particularly important to understand variability in a population's size structure because growth and other demographic properties are often highly size dependent (Peters 1983, Schmidt-Neilson 1984, Calder 1984, Brown and West 2000).

Exploitation, even if it is not size selective, often truncates the largest and oldest size classes of a population, resulting in smaller and younger individuals becoming predominant (Ricker 1981, Haedrich and Barnes 1997, Zwanenburg 2000, Bianchi et al. 2000, Jackson et al. 2001, Harvey et al. 2006). Although the effects of size and age structure on population dynamics have long been recognized in theoretical ecology (Nisbet and Gurney 1982), and size- and age-structured models are often used in the practical assessment of exploited populations (Hilborn and Walters 1992), the wide-reaching implications of size truncation for long-term changes in dynamics of exploited species have only lately been appreciated (Birkeland and Dayton 2005, Anderson et al. 2008, Minto et al. 2008).

Size truncation can have a dramatic effect on a population's genetic and phenotypic responses, including earlier maturation and increased reproductive

investment (Rijnsdorp 1993, Heino and Godo et al. 2002, Conover and Munch 2002, Grift et al. 2003, Barot et al. 2004). Moreover, there is increasing awareness that even in the absence of adaptive or plastic responses, shifting the population to smaller and younger animals has important and predictable effects on population-level demographics and dynamics. For instance, truncating a population's size structure may negatively affect a species' reproductive success by reducing fecundity, and possibly egg and larval viability (Vallin and Nissling 2000, Berkeley et al. 2004a, Bobko and Berkeley 2004). Furthermore, even though initial ecological responses may be transient in relation to evolutionary time, shifts in size structure can be so fundamental that they alter a population's response time to perturbations and potentially lower its resilience (Hsieh et al. 2006, Secor 2007).

Few studies, however, have examined the affect of exploitation on population dynamics over long time scales Because the temporal scale observed influences whether changes are detectable (Sutherland 1981, Connell and Sousa 1983, Levin 1992), only a study employing an extended time series may reproduce fundamental changes and variability in population dynamics if exploitation has been occurring over a long time frame (Christensen et al. 2003, Jackson 1997). Long time series may also be a better means of accurately identifying the historic structure of an exploited population, providing a baseline against which to assess current conditions. If the temporal scale of study is too short, ecological models that relate to 'natural' or 'less exploited' conditions may assume erroneous starting or 'baseline' points (Rochet et al. 2000, Myers 2000, Beverton et al. 2004, Shuter and Abrams 2005) and

conservationists may fail to consider restoration targets that approach "original" conditions (Pauly 1995, Willis and Birks 2006). Because past research overwhelmingly relies on time series that are less than 30 years, and begin long after the onset of exploitation (Pinnegar and Engelhard 2007), the population dynamics of exploited species described by these studies provides only a partial understanding of the extent to which exploitation may change demographic traits and population dynamics.

Here, we demonstrate this principle through a 120-year case study of the California spiny lobster, *Panulirus interruptus*, showing that over longer timeframes, persistent exploitation can dramatically alter population structure and dynamics. We employ a newly assembled, exceptionally long historical time series of catch and effort compiled from historical government and private records. A recently developed Bayesian state spaced size structured model (Kinlan and McArdle, in prep) is fit to the time series to quantify the effects of fishing on the lobster population's structure and dynamics over the last century. A Bayesian model framework was chosen because it allows greater flexibility than traditional statistical approaches in a study such as this, which involves multiple data sets and sources of historical information (Millar and Myers 2000). The long time frame of this study coupled with the Bayesian framework highlights the magnitude of the changes in the lobster population due to exploitation.

Our examination goes beyond quantitative analyses, by employing a multidisciplinary approach that integrates ecology and history, to corroborate our

findings and assumptions. Ecologists, conservation biologists and historians over the last decade have advocated that historical and ecological data be merged for these purposes (Dayton and Sala 2001, Meine 1999, Ludwig et al. 1993, Bolster 2006) Terrestrial (Swetnam et al. 1999, Willis and Birks 2006) and to a lesser degree, marine ecologists (e.g. Jackson et al. 2001, Holm et al. 2001 Pandolfi et al. 2003, Rosenberg et al. 2005, Lotze et al. 2006, Pinnegar and Engelhard 2007) have begun to employ this method.

Here, we corroborate model predictions and assumptions, and verify the temporal scale of the chosen 'reference' baseline by comparing them to qualitative and quantitative historical records analyzed in McArdle (in prep) and (Chapter Two). The historical sources were gathered and utilized independently from model efforts and include over 300 personal letters, oral histories, newspaper articles and government reports, collected from local, state and national museums.

Our evaluation of quantitative predictions and assumptions of model-based analyses in light of historical patterns and trends demonstrates the added value of a multidisciplinary approach that combines ecology and history, by achieving a deeper understanding and more complete interpretation of the spiny lobster population's size-structured dynamics.

Finally, we discuss how changes in the lobster population's size structure and dynamics may have lowered its resilience to environmental fluctuations by increasing its short-term variability (Hsieh et al. 2006, Secor 2007). We also offer a new interpretation of the ecological implications of truncating a species' size structure; it

could compound the effects of "fishing down the food web," or the downward shifts in trophic levels and resultant trophic cascades usually attributed to a decrease in the abundance of larger species in the oceans (Pinnegar et al. 2000, Steneck et al. 2004, Frank et al. 2005). Because trophic interactions are usually size-dependent, this fundamental shift in community structure and function may occur even if large species are not depleted (Caddy et al. 1998). Intra-specific changes such as the truncation of a population's size structure alone may be enough to produce this phenomenon.

II. Materials and Methods

A. Materials

1. Focal species

This study examines the California spiny lobster, *P. interruptus.* The spiny lobster population inhabits kelp forest and inter- and subtidal rocky ecosystems in the region known as the Southern California Bight, the oceanic region from Point Conception, California to Mexico and seaward from the coast to the California Current (Daily et al. 1993). Here, we examine the lobster population only in its California range. The spiny lobster has been commercially exploited for 135 years, or approximately 27 generations. Although the California spiny lobster has supported a commercial fishery in California for over a century and the total catch has remained relatively stable over the last 25 years, the status and the history of the lobster population is largely unknown.

2. Data Sources

Fishery Time Series

Long historical data sets that encompass wide variation in abundance, fishing pressure and environmental conditions are rare. When available, they can greatly enhance our ability to understand the population dynamics of exploited species and temporal trends in fisheries (Hilborn and Walters 1992). Here, we employ >100 years of records on the California spiny lobster fishery, including three state and regional catch and effort time series that cover over a century (1888-2005) (Fig 1, 3). The lobster population experienced a variety of significant fluctuations in environmental regimes and fishing effort (e.g., closures and reductions of effort during wartime) in this period.

Catch and Fishing Effort (i.e. number of traps per year) Time Series

To examine the California spiny lobster's long-term population structure and dynamics (McArdle and Kinlan, in prep), the author compiled a 120-year time series of catch and effort in the lobster fishery from historical government records. Records of annual spiny lobster catch (lbs) came from U.S. Bureau of Fisheries reports (1888-1915) and California Department of Commercial Fisheries and Department of Fish and Game reports (1915-2005). Catch records from the early period (1888-1915) were checked to ensure that they only included California catch and not catch originating in Mexico.

Effort was measured as the number of traps fished per year. Estimates of annual trap numbers from 1888 to 1976 were compiled from federal reports first published by the U.S. Fish Commission Bureau of Fisheries (1888-1915), then the U.S. Fish and Wildlife Service (1916-1969) and finally the National Oceanographic and Atmospheric Association (1970-1976). These sources provide the annual estimate of traps (1888-1976) for the present work.

The earliest records of long data sets are often perceived as potentially unreliable. The earliest records of catch and effort came from the U.S. Fish Commission (USFC) surveys. The USFC began surveying California fisheries in 1888 by conducting annual surveys of fishermen and wholesalers.[1] The surveyors' notes assisted in validating the reliability of the early records of effort (McArdle in prep and Chapter Two). By 1919, the USFC surveyors' notes made clear that whenever possible, they combined the information they gathered with statistics from the California Department of Commercial Fisheries (CDCF).[2] More specifically they listed the CDCF's boat registration records as their source of information on the amount of effort employed in California's fisheries.[3] This was unexpected because while it was general knowledge that the CDCF had collected early catch data, there appears to be no institutional memory of their early collection of effort data. An examination of CDCF's early reports, however, uncovered that, in 1919, it initiated a mandatory boat registration program that required fishermen to provide information on both their boat and gear.[4] The discovery that the early USFC records were a result of a joint federal and state monitoring program of the fishery increased confidence in

the accuracy of the data at the beginning of the time series.[5] Newspaper reports describing the total number of traps in the lobster fishery and the number of traps per fisherman further corroborated the USFC effort data.

After 1976, there are no consistent estimates of the number of traps used in the spiny lobster fishery. For the period 1980 to 2005, the annual number of traps used in the fishery was estimated by converting the number of trap pulls, from the California Department of Fish and Game (CDFG) logbooks, into trap numbers. These estimates were corroborated using another method in which we multiplied the actual number of permitees fishing each season (1980 to 2005) by an estimate documented by fisheries-related literature of the average number of traps being used per fishermen (Shaw 1986, Odemar et al. 1975, Barsky 2001, Ventura County Star 1-6-2001, Los Angeles Times 10-7-2001, CDFG 2005). The estimates from both methods were closely aligned (For a more detailed explanation see Appendix I and Appendix I: Fig 1).

3. Data and Estimate Reliability, Verification with Historical Sources

(McArdle, in prep and Chapter Two) reviewed a variety of independent historical sources,[6] independent of sources used as priors in the model, to validate historical data points in the time series, corroborate model predictions, and verify the temporal scale of the chosen 'reference' baseline of 1888. Summaries of some of these analyses are found in the Discussion section of this paper.

B. Methods

1. Bayesian State Space Model (Biomass, Abundance, Size, Exploitation Rate)

To examine the interplay between exploitation, size structure, and population dynamics of the spiny lobster, we obtained results from a Bayesian state-space model (e.g., Millar and Myers 2000) fit to the catch and effort time series described above. This model is described and analyzed in Kinlan and McArdle (in prep), and contains a detailed description of model formulation and estimation, including sensitivity to assumptions about model structure (age vs. size), size structure, missing data, interpolation, relative uncertainty of different data sources, and priors. Here, we briefly review the basic structure of the model relevant to the estimation of abundance and size structure, and summarize the key assumptions and limitations of the approach.

The Bayesian approach provides a flexible framework to integrate diverse data sets and estimate the underlying population dynamics that best explain the observed catch and effort time series under a set of assumptions about the population dynamics. It also allows the relaxation of a number of key assumptions present in traditional likelihood-based methods. Table 1 summarizes the basic assumptions of the Bayesian state-space approach used here in comparison with two other types of models conventionally applied to catch and effort data series.

Bayesian methods have also been used to assess the Tasmanian rock lobster and the American lobster (Punt and Kennedy 1999, Chen et al. 2005). The main advantage of the Bayesian method is that it provides a valid framework for assigning

probabilities to different hypotheses using both data from the fishery and prior information from other sources. The model developed in this study includes a stochastic size-structured model (Millar and Myers 2000, Chen et al. 2005) describing the dynamics of the lobster population and fishery (referred to as population dynamics model) and a series of observational models used to relate the population dynamics models to observations made in surveys and fishery. The population dynamics model includes data, four data models, a process model and informative priors (i.e. information on lobster growth rates and length-weight relationships (Lindberg 1955, Engle 1979). Note, the information used as priors was independent from the historical sources used to corroborate the time series and model predictions.

The model framework (Fig 2) includes three components: (1) a size-structured population model and sub-models that describe the dynamics of the lobster population; (2) input data including fishery-dependent, fishery-independent data and informative priors; (3) a Bayesian estimator which fits the population model to data for estimating key parameters for the lobster population and fishery.

We used the Bayesian model to estimate lobster abundance by year and size class, average weight of legal lobsters caught by year, and true catch numbers by year. We also calculate several derived variables from the model outputs. The average annual biomass per size class was estimated by multiplying the average annual abundance of lobster per size class by the average weight for each size class (Table 2). The total annual biomass was estimated by multiplying the total annual abundance per size class by the average weight of lobster per size class and then

summing all classes. The exploitation rate was estimated by dividing annual biomass estimates by effort (i.e. number of traps). The number of traps used to calculate the exploitation rate was the actual number of traps recorded, the number of traps from the trap model (Appendix I), or the number of traps linearly interpolated from adjacent years as described in Kinlan and McArdle (in prep).

a. Length-based population dynamics model

Following Miller and Myers (2000), the state-space equation for abundance $N_{s,y}$ of lobsters in size class s at time y in years can be written as,

$$\mathbf{N_{1y} = R_y\} \ 1 \leq y \leq Y + 1}$$

$$\mathbf{N_{sy} = \psi_{s-1,y-1} * N_{s-1,y-1} * e^{-M}\} \ 2 \leq s \leq 4\} \ 2 \leq y \leq Y + 1}$$

$$\mathbf{N_{sy} = \psi_{s-1,y-1} * N_{s-1,y-1} * e^{-M} - \psi_{s-1,y-1} * C_{s-1,y-1} * e^{(-0.5) * M}\} \ 5 \leq s \leq 8\} \ 2 \leq y \leq Y + 1}$$

where R represents recruitment into size class 1, ψ_s denotes the size-specific probability of survival and growth to the next size class, and M represents size-independent natural mortality. The model domain includes Y=118 years, indexed by y = {1,2,…118}. In calendar years, this corresponds to the period from 1888 to 2005.

The length-based population dynamics model is comprised of a series of submodels or process equations (for more detail about the submodels see Appendix II).

2. Time Series Variance Analysis (Variability in Catch)

We estimated the time-lagged semivariance of the catch time series (from the fishery records) to determine the variability in catch, over a period shifting from low to high fishing pressure. The semivariance measures the degree of dissimilarity between points separated by a given lag distance in a time series and is equal to one-half of the variance of the differences between all possible points spaced at this lag distance. Contrary to the covariance, semivariance is a measure of dissimilarity (the greater the value of the semivariance the weaker the temporal association). Variogram autocorrelation ranges were plotted for sliding windows of 25 years. We only consider short-term variability so we plot average semivariance for time lags of 1-3 years. The Semivariance is divided by the total variance yielding a relative value between 0 and 1.

Semivariance is an autocorrelation statistic defined as:

$$y(h) = [1/2N(h)] \sum [z_l - z_{l+h}]^2$$

where

$y(h)$ = semivariance for distance interval class h

z_l = measured sample value point at t_l

z_{l+h} = measured sample value point at l + h; and

N(h) = total number of sample couples for the lag interval h

III. Results

A. Fishing Effort

Fishing effort (number of traps) increased exponentially in the California spiny lobster fishery over the time period studied (Fig 3a). In a little over a century, the number of traps used by the fishery increased by approximately 100%. Although catch has remained stable and shown periods of increase over the last two decades, catch per unit effort is historically low, with fishers in 2005 expending approximately 40% more effort to land a lobster biomass equal to what they landed about sixty years ago (Fig 3b).

B. Model reconstruction of changes in population structure

1. Biomass, Abundance and Escapement

Lobster biomass estimated by the Bayesian model declined by 80%, from a historic level of 9,000,000 lbs to 1,800,000 lbs from 1895 to 1915 (Fig 4). This long-term decrease in biomass occurred concurrently with increasing fishing pressure (Fig 3a). Short-term increases occurred after this decline, most notably around 1950, likely due to combination of favorable climate conditions and decreased effort during World War II. In the wartime period fishing intensity decreased significantly (~50%) throughout California and stopped completely for at least one year at the Channel Islands in Santa Barbara and Ventura counties. Numbers of lobster followed the same

general pattern as biomass (Fig 4b). After 1950, biomass and abundance again sharply declined and exhibited relatively slight variations over the next forty years (4a,b). The present biomass is estimated to be 11% - 16% of the historical baseline, or approximately an order of magnitude lower than historic levels. The model-estimated exploitation rate (the percentage of the population fished) fluctuated over time but the general direction of the trend is one of increase, with fishermen taking approximately 70% of the population's legal-sized lobsters (>83 mm CL) in 2005 (Fig 5, 6).

2. Size and Weight

The model-estimated abundance of sub-legal and small legal lobsters (size classes 2, 3 and 4) varied relatively little over the last half century compared to the early historical period, remaining relatively constant since 1960 (Fig 7). In contrast, the abundance and proportion of large-sized lobster (> 100mm CL) has progressively declined over the last century (Fig 7). The model-predicted long-term pattern of decline in large lobster follows the pattern of cumulative effort in the fishery, with fluctuations from the long-term downward trend observed at interannual and decadal timescales.

The progressive shift in size structure is evident in the decline of the predicted weight of the average legal California spiny lobster, which fell from 2.6 lbs in 1895 to 1.7 lbs in the last five years (2001-2005), with the average legal lobster becoming 35% smaller (Fig 8). See the discussion section (A) for estimates of the average legal-sized lobster weight in 1888.

C. Population Dynamics: Short-term High Frequency Variability

Time series analysis of the catch data series (total reported annual landings in pounds) reveals a substantial increase in the variance of catches over a 1-3 year time horizon (Fig 9). An increase in short-term variability (an increase in semivariance; or equivalently a decrease in autocorrelation) is evident from 1950 to 2005 compared to the years prior. The increase in short-term variability in catch is correlated with decreased abundance of large lobster (> 100mm CL, i.e. size classes 5-8) (r = -0.83, $p<0.0001$) (Fig 9).

Similar time series analysis using predicted legal-sized lobster biomass, abundance, and catch time series generated by the Bayesian model show similar patterns. We focus on the raw reported catch data here, rather than the model-predictions, to avoid any question that the trend of increased short-term variability of catch is due to a model estimation artifact.

IV. Discussion

We have demonstrated that over longer timeframes, persistent exploitation can dramatically alter size structure and the dynamics of a population. In response to a general trend of increasing exploitation, the biomass of the California spiny lobster population estimated by the Bayesian model declined by 80% (Fig 4a). This finding is consistent with past work on populations (Roman and Palumbi 2003, Rosenberg et al. 2005, Fenberg and Roy 2007) and communities (Jackson et al. 2001, Pandolfi et al. 2003, Lotze et al. 2006) of marine organisms subject to exploitation. Model

estimates of size and weight structure (Fig 7, 8) illustrate that the long-term increase in fishing mortality (Fig 5, 6) progressively "eroded" the abundance of larger size classes, resulting in a size structure composed generally of younger and smaller animals (Fig 7).

Time series analysis of the historical lobster catch data reflects a concomitant increase in the short-term variability of catch (Fig 9). Based on model results and historical observations, we suggest that the altered dynamics of California spiny lobster can be explained by population-level changes in demographic parameters arising directly from the truncation of size structure. Although a variety of other pressures, such as inter-cohort density dependence and adaptive or plastic responses at the individual level, likely play roles in producing these dynamics, we show that the historical catch-effort dynamics of lobster can be explained by a model that does not include these processes. This is important because altered size structure is a ubiquitous effect of long-term exploitation.

A. Corroboration with Historical Records

The long time series of catch and effort used in this study highlights the magnitude of the changes in the California spiny lobster population over the last 120 years. There can be complications, however, with using catch and effort data to model abundance (Hilborn and Walters 1992). One potential problem is that fishing effort is often focused on areas of the highest densities of fish, potentially biasing efforts to assess the range of total abundance. More specifically, using catch per trap as an

index of abundance as we have in this study could result in an inaccurate estimate of abundance because the number of animals caught by traps can be influenced by bait quantity and quality, time between setting and hauling, escape through the trap entrance and gear saturation (animals inside traps prevents those outside from entering) (Miller 1990, Jury et al. 2001, Ihde et al. 2006).

Thus, the scale at which catch and effort data are collected and analyzed can have important consequences for conclusions based on that data (Sutherland 1981, Connell and Sousa 1983, Levin 1992). In this study we chose to examine the lobster population at a large temporal and geographical resolution to determine changes in the lobster population over the last century statewide. As a consequence, our findings do not represent variation at finer scales. For example, as a fishery develops, both fish and the fishermen may change their spatial distribution, and aggregate catch and effort statistics may not reveal these changes (Hilborn and Walters 1992). To examine shorter-term variability, in the California spiny lobster population's structure, future studies should focus on smaller-scale spatial and temporal data.

One approach to control for such biases is to examine population abundance in fishery independent data in the field for the same timeframe to determine whether it shows similar trends. Here, we compared quantitative and qualitative information from independent historical sources to abundance and size model estimates derived from fishery-dependent catch and effort data (see Methods, Appendix I, McArdle, in prep and Chapter Two). This comparison tended to confirm the model estimates.

The available historical record is consistent with the Bayesian model's reconstruction of long-term lobster size structure (Fig 8) (McArdle in prep, and Chapter Two). The commercial California spiny lobster fishery began in 1870 and grew into a more fully developed industry by the early 1890s (McArdle in prep, and Chapter Two). Newspaper articles and government records reported that between 1895 and 1916, the weight of the average lobster caught declined from roughly three to two pounds; the frequency of very large individuals also decreased over the same time frame. These predictions generally agreed with the historical record; the 95% confidence range was 3.1 to 1.6 lbs over this period. This trend of decline in average harvested lobster size continued, despite interannual and decadal variability. By 2001, the California Department of Fish and Game estimated the average lobtster size as 1.25 to 2.0 lbs, which was consistent with a model estimate of 1.7 lbs.

Earlier model estimates of lobster size from 1888-1895 reflect considerable uncertainty, because fewer preceding years of catch-effort data exist to inform model estimates of size structure in these first few years of the time series. In the absence of historical data, size estimates from these early years might be viewed as suspect because of the wide uncertainty bounds. However, when compared to the historical record, model predictions perform well even in this early period (Fig 8). The model estimates the 1888 average weight of lobster was 5.8 lbs which was within with range documented by historical accounts of 3.5 to 6.0 lbs summarized by McArdle (in prep) (Chapter Two). Between 1888 and 2005, the model predicts that the average size of

lobster declined from 5.8 to 1.7 pounds, or 71%, reflecting the trend described in the historical accounts.

Taken together, the model estimates and historical records provide strong evidence for a substantial, rapid (<10 y) initial decline in lobster size at the onset of exploitation, followed by a continued, more gradual decline over the ensuing century. Note, however, that this study only employs a time series of commercial catch and effort; it does not consider the amount of lobster taken by the recreational fishing industry. The recreational fishery has targeted "trophy-sized" lobsters for at least half a century, making this an area that requires further investigation.

Another issue with using fishery-dependent data is that the onset of the commercial fishery may not represent the pre-exploitation or "natural" condition. Other anthropogenic or ecological disturbances may have altered the historic structure of the population before the commercial fishery began. To account for this possibility, McArdle (in prep) (Chapter Two) examined historical records for other significant ecological influences on the lobster population, including earlier fishing pressure and exploitation of other species such as sea otter (a key predator of lobster), that may have altered the lobster population before the chosen baseline (1888-1895).

This review indicated that human fishing pressure on the lobster was probably insignificant for at least a century before 1888. During the Spanish and Mexican eras (1769-1850), neither Europeans nor Native Americans were a source of substantial fishing effort. The settlers focused their commercial enterprises on cattle ranching, and social dislocation and disease decimated the Native American population.

Although the commercial lobster fishery began in 1870, it was characterized by low fishing intensity until 1895. Given the low level of human exploitation prior to 1870 and the spiny lobster's approximately 5-year generation time and 20-30 year maximum lifespan, it would be reasonable to assume that direct fishing pressure on the lobster probably had not significantly altered its population and size structure from its pre-exploitation state as of our baseline timeframe.

Determining the effect of 19th century sea otter exploitation on the California spiny lobster population structure is more complicated, in large part because it is difficult to estimate otter abundance during this era. Although it is often assumed that the otter was exterminated in California by the early to mid-1800s, the historical record reveals that the otter population remained along the coasts of Santa Barbara and the northernmost Channel Islands well into the late nineteenth century (McArdle, in prep and Chapter Two). For example, one hundred otter were taken around San Miguel and San Nicolas Islands in 1882 (Los Angeles Times 11-11-1882); the equivalent of approximately three percent of the statewide population in 2008.

While sea otter abundance was high relative to the present, it is uncertain whether it was large enough to enable it to play its functional role in the kelp forest foodweb. Altered otter population abundance could have had a significant, mainly unpredictable impact on the lobster population structure because the Southern California kelp forest food web is a diverse, complex system that includes trophic interactions among the sea otter, lobster, sea urchin and kelp (Steneck et al 2002, Graham 2004). Changing the relative numbers of any of these participants in the

foodweb could have cascading effects through the system, reducing or increasing lobster abundance.

We can nevertheless draw some reasonable inferences about the possible impact that otter had on lobster size structure near the timeframe of our reference baseline by examining historical records. In the early 1880s, two government agencies documented that lobster weighed between 3.5 and 6.0 pounds, an average of 4.75 lbs (Hittel 1882, Rathbun 1884). Given the lobster's life history characteristics, it seems improbable that this large average size was solely the product of the functional elimination of the sea otter immediately before 1880. If this were the case, lobster abundance could have been greater. That increased population size, however, probably would not account for the large average size of indivduals measured at the begining of the 1880s; to achieve that average, a significant segment of the population would have had to exceed their commonly understood growth rate. The average lobster born in the early 1870s would have had to grow in less than a decade to 4.75 lbs, a size that normally takes a lobster roughly 18-23 years to reach (Lindberg 1955, Farris and Bigsby 1972). Legal-sized lobsters grow somewhat faster, but would still normally take approximately 10.5 to 15 years to reach 4.75 pounds (Lindberg 1955, Farris and Bigsby 1972).

Overall, our use of 1888 as a baseline for the onset of commercial lobster exploitation and our reconstruction of the historical size structure of lobster since that date are both consistent with the historical record. But, whether this was the "natural" state of the lobster population, we do not know. This example illuminates the

difficulty of identifying and defining a "natural" baseline in the oceans, due to the inherent complexity of ecosystems and the long term interaction between man and the sea. To increase our ecological understanding of the history of kelp forest ecosystems, future studies may seek to identify and examine some proxy of lobster (e.g. carapace fragments in Indian middens) and sea otter abundance prior to our baseline of 120 years. For additional information on older historical lobster fishery records see (McArdle, in prep and Chapter Two).

B. Altered Population Response to Environmental Variability Due to Truncated Size Structure and Implications for Population Resilience

Our results find that the truncation of large lobster has generated increased short term variability in both lobster abundance and catch. As exploitation increased (Fig 3, 5) the number of large lobsters in the population declined (Fig 7, 8), and the short-term variability of catch increased (Fig 9). This finding is consistent with past work that has long hypothesized (Beddington and May 1977), theoretically demonstrated (Gurney and Nisbet 1980, Nisbet and Gurney 1982) and recently empirically established (Hsieh et al. 2006) that fishing increases population variability. There are two key potential mechanisms that may underlie increased variability in exploited populations (for a review see Anderson et al. 2008). First, truncation of the age structure may diminish the ability of populations to buffer environmental events by employing bet-hedging strategies (e.g. fat storage, ability to migrate, spawning over numerous seasons) and thus increase population variability.

Second, restructuring the population to one that is dominated by small young individuals may increase variability by altering size-dependent demographic parameters such as the population's intrinsic growth rate which could increase due to competitive release, increased egg output or evolutionary adaptations.

It is beyond the scope of this study to determine which mechanism is driving the lobster population's increased tracking of short-term environmental change. However, given what is known about the lobster's natural history and environmental condition, we consider how the first mechanism may be, at least, partially responsible for this change.

There has been recent recognition that the actual realized values of population-level life history parameters can be dramatically altered by exploitation-induced population level changes even when individual traits have not changed (Shuter and Abrams 2005). This is particularly true for alteration of size structure because most life history traits (e.g. growth, reproduction, and survival) are related to size. Here, we illustrate how the long-term truncation of the lobster population may relate to the population's increased response to short-term environmental variability, using an unconventional approach. We consider the change in population-averaged values of lobster demographic parameters due simply to the change in size structure (i.e. assuming no change in the values of the parameters at the level of the individual) by mapping suites of realized average demographic values at periods of low and high lobster fishing intensity into a principal components space analogous to that used by Winemiller and Rose (1992) and King and MacFarlane (2003) to depict life history

strategies appropriate for different environmental regimes. The parameters include size at 50% maturity, maximum size, fecundity, maximum age, egg size and intrinsic growth rate (Table 4).

The lobster's truncated population size-structure, increased short-term variability, and intensified fishing pressure motivate the hypothesis that exploitation has effectively caused the lobster population to effectively respond to environmental variability more as an 'opportunistic' species, in terms of life history theory. Winemiller and Rose (1992) identified three general suites of characteristics ('strategies') and the types of environmental variability under which these strategies would likely be most successful: opportunistic (high growth, short generation time, high reproductive effort, small body size, low fecundity and low investment per offspring), periodic (high growth rate, long generation time, moderate reproductive effort, large body size, high fecundity, and low investment per offspring) and equilibrium (slow growth, moderate- to long generation time, low reproductive effort, variable body size, low fecundity and high investment per offspring). All else being equal, the opportunistic suite of attributes is expected to maximize fitness in environments subject to frequent and intense disturbance, the periodic strategy in systems characterized by large-scale variation (e.g. convergence zones, gyres, coastal currents) or climatic events such as storms and El Niño and the equilibrium strategy in environments that are relatively stable.

Our findings demonstrate the magnitude of shifts in actual realized values of lobster population-level parameters simply due the altered lobster size structure (Fig

10). Exploitation has effectively shifted the California spiny lobster from being long-lived, large-bodied and slow growing (i.e. a periodic species) to short-lived, smaller and faster-growing (i.e. an opportunistic species). This shift is consistent with the lobster population's increased tracking of short-term environmental variability (Fig 9, 10). It could also indicate that the California spiny lobster population has a diminished capacity to weather environmental events making it less resilient. California spiny lobster live in a highly variable environment characterized by shifting ocean regimes, including the El Niño-Southern Oscillation (ENSO) and Pacific Decadal Oscillations (PDO) (Johnson 1960a, b and Pringle 1986), which may cause larval recruitment to fluctuate year to year. Lobster recruitment may be particularly sensitive to how fluctuating regimes affect ocean current patterns because its planktonic larvae remain in the water column for approximately ten months.

In its unfished or lightly fished state, the lobster exhibited a so-called 'periodic' life history strategy, associated with occasional large-scale disturbance (Fig 10). It now appears to behave functionally as an opportunistic species, which often exist in environments characterized by frequent disturbance (Fig 10). However, while the lobster is now subject to frequent intense disturbance due to high fishing pressure, it still faces large-scale periodic perturbations.

Lobster may have adapted to large-scale disturbances by adopting strategies of iteroparity (spawning over successive seasons) to maximize reproductive success (Murphy 1968, Chesson and Warner 1981, Warner and Chesson 1985, Orzack and Tuljapurkar 1989, Philippi, T. and Seger, J. 1989, Secor 2007). Iteroparity is a

strategy associated with long-tailed age structures. A larger number of spawning size classes can average environmental conditions over longer timeframes, and thus dampen environmental stochasticity and stabilize fish populations.

Exploitation, however, has reduced the number of years that an individual spiny lobster can spawn by over 50%, and thus diminished its capacity to hedge against unfavorable environmental events by reproducing over multiple years. Historically, a lobster could potentially spawn up to twenty times in a lifetime. They had an average life span of fifteen years, matured at approximately five years (i.e. ~65 mm CL), and were capable of spawning twice in a year (Odemar et al. 1975, Engle 1979). Now, fishers catch 70% of the new legal reproductive biomass, reducing the number of years a lobster can potentially spawn from fifteen to four to five years, the time it takes to grow from initial reproductive size (i.e. ~65 mm CL) to the legal size limit (i.e. ~83mmCL). As a result, an individual lobster that historically could spawn up to twenty times per year can now spawn only eight to ten times on average before being removed from the population.

Furthermore, as the average age of reproducing adults approaches the average time span between unsuccessful recruitment episodes, the chance of a serious recruitment failure increases. The lobster generation time has declined from an average of fifteen to five years. Ocean regime shifts caused by La Niña events (which may lead to unsuccessful recruitment episodes) occur every five to six years (Johnson 1960a.b). If there are consecutive years of environmentally-caused poor recruitment, there are now fewer mature adults producing recruits to compensate for the loss.

C. Shifting Trophic Role and Implications for Ecosystem Resilience

The value of using size-based indicators to evaluate the ecosystem effects of fishing has recently been recognized (Shin et al. 2005). It is widely recognized that exploitation can alter ecosystem function by reducing abundance and diversity (Jackson et al. 2001, Pandolfi et al. 2003, Worm et al. 2005) of large predatory species that are the top links in food webs, leading to communities disproportionately composed of smaller, shorter lived, faster growing, lower trophic level species (Jennings et al. 1998). The loss of the top trophic level is thought to have fundamentally altered food webs worldwide (reviewed in Pinnegar et al. 2000). Most past work attributes downward shifts in trophic levels to a decrease in the abundance of larger species in the oceans (Fogarty and Murawski 1998, Steneck et al. 2002, Frank et al. 2005), although the generality of these findings has been questioned (Caddy et al. 1998). The interplay of fishing, size structure, and population dynamics could produce similar ecosystem-level changes via a within-population mechanism. Direct population responses to altered size structure could mediate an intra-specific analogue to community-level changes in marine ecosystem structure known as 'fishing down the food web' (Pauly et al. 1998).

The ability of the California spiny lobster to play its functional role is highly size-dependent because large lobsters are the most adept at eating adult urchins (Tegner and Levin 1983). Fishing-induced size truncation of the lobster population has effectively eliminated a ‘large’ predator and increased the proportion of small, fast growing, low trophic species in the kelp forest community. This shift compounds

the effects of 'fishing down the food web," potentially lowering the resilience of the ecosystem and ultimately the fishery.

The southern California kelp forest community bears the imprint of fishing down the food web (For reviews see Pinnegar et al. 2000, Steneck et al. 2002). Sea urchins can have a great impact on kelp (*Macrocystis*) through overgrazing (Lawrence 1975, Pearce and Hines 1979, Harold and Pearse 1987, Tegner and Dayton 2000). Over the last two centuries, overfishing has depleted key predatory species, the sea otter (*Enhydra lutris*), and sheephead (*Semicossyphus pulcher*) which can limit sea urchin populations and prevent overgrazing of kelp (Cowen 1983, Harold and Pearce 1987, Foster and Schiel 1988, Watanabe and Harrold 1991). The depletion of top predators has left the California spiny lobster as one of the only potential urchin predators in the system. Several studies that compare fished areas and marine reserves have demonstrated the role of lobster, in trophic cascades (Babcock et al 1999, Shears and Babcock 2002, Behrens and Lafferty 2004). The truncation of the California spiny lobster population size structure has functionally altered its trophic role, limiting its ability to function as an apex predator in the southern California kelp forest ecosystems.

V. Conclusion: Implications for Restoration and Conservation

The California spiny lobster has evolved a long-lived, highly iteroparous, high fecundity life history that is well suited to withstand large scale periodic environmental fluctuations. Over a century of fishing has shifted this species from

long-lived, large-bodied, slow growing, high fecundity organisms to one that is short-lived, smaller, faster-growing, and less fecund. Between 1888 and 2005, the average size of lobster declined from 5.8 to 1.7 pounds, or 71%. Severely reducing the lobster's average lifespan and size, has increased the population's variability, potentially diminished the resilience of the species and the kelp forest ecosystem.

Restoring older age classes may require selecting areas where the entire size structure of the population is allowed to return to some point along its historic trajectory. Potential approaches for restoration and conservation of large animals include marine reserves (Kelly et al 2000, Rowe 2002, Berkeley et al. 2004b, Gaylord et al. 2005) and maximum size limits (Herrick 1893, 1909, Field 1902, Conover and Munch 2002).

In the long history of California spiny lobster conservation, both techniques were used to restore and conserve large lobster (McArdle, in prep or Chapter Three). The California Legislature passed a two-year closed season on lobster in 1909, a limited version of the California State Board of Fish Commissioner's initial request for a five-year closure. In 1913, two years after the fishery reopened, the CFC established a maximum size limit of 13 inches CL that was raised to 16 inches CL in 1917 (Fry 1928). The goal of the measure was to "protect the largest individuals," which were the "heaviest spawners."

The legislature removed the maximum size limit in 1948. For most of the last half century, measures seeking to conserve lobster have focused on safeguarding small lobster through, among other things, minimum size limits, closed seasons, and

escape ports (McArdle, in prep and Chapter Three). Recent studies, however, propose that these types of conservation measures can actually accelerate the rate of demographic changes that are potential risks to the population (Conover and Munch 2002, Baskett et al. 2005, McArdle, in prep). For instance, nineteenth century naturalists (McArdle, in prep and Chapter Three) and 21st century evolutionary ecologists (Conover and Munch 2002) have concluded that minimum size limits can be counterproductive because they tacitly allow the depletion of large animals.

Over the last decade, California and the federal government have enacted ecosystem-based conservation measures, including marine reserves that could restore older lobster age classes to historic levels. However, continuing to rely on conservation strategies such as minimum size limits could undercut the benefits of reserves. Lobster can grow larger in reserves (Kelly et al. 2000, Rowe 2002), but they often migrate out of the protected area once they reach larger sizes and are caught while departing (Rowe 2002). Outside of reserves, no measures protect large lobsters. Therefore, it is uncertain whether present day conservation measures can retain larger lobsters in the ecosystem. Future efforts should ensure that conservation measures prevent, and do not tacitly facilitate, the truncation and instability of marine life populations.

VI. References

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VII. Tables

Table 1. Underlying assumptions of the Schaefer, DeLury and Bayesian models

Model	DeLury Model assumptions (DeLury 1947)	Schaefer assumptions (Schaefer 1954)	Bayesian assumptions (Kinlan and McArdle, in prep)
Catch-Abundance Relationship	CPUE is proportional to population size	CPUE is proportional to population size	CPUE is proportional to population size
Immigration/ Emigration	Closed population[a]	Closed population[a]	Closed population[a]; size and abundance estimates robust to violation of this assumption[b]
Population growth	No growth during the fishing season (least flexible)	Density-dependent growth that is independent of age and size structure (logistic growth of total biomass)	Population biomass growth arises from interplay of individual survivorship and growth. Mean individual growth increments follow an empirical power-law regression with random year-to-year variation (most flexible)
Recruitment /Production	Recruitment or production is deterministic; that is, controlled by spawning stock size, without any environmental effects or other sources of "random" variation.	Recruitment or production is deterministic; that is, controlled by spawning stock size, without any environmental effects or other sources of "random" variation.	Recruitment/production is a log-normally distributed random variable over time; no assumptions about relation to stock size
Carrying Capacity	A constant carrying capacity or unexploited population size, at which level the population would stabilize in the absence of exploitation.	A constant carrying capacity or unexploited population size, at which level the population would stabilize in the absence of exploitation.	No fixed carrying capacity; determined by time-varying mortality, growth, and recruitment parameters estimated from catch-effort time series

[a] "Closed" refers to the fact that immigration/emigration are not explicitly modeled; sensitivity of model results to violation of this assumption depends on form of growth, mortality, and recruitment assumptions.

[b] Bayesian model estimates of abundance and size structure are less sensitive to assumptions about immigration/emigration because there is no assumed stock-recruitment relationship and growth and mortality parameterizations are more flexible. If immigration/emigration are significant, mortality, growth, and recruitment parameters will be confounded but size structure and abundance estimates will be robust unless there is systematic, large-scale (100's of km) time-varying migration of adults in specific size classes.

Table 2. Size and weight classes used in the Bayesian model.

Size Class	Carapace Length			Mean weight (pounds)
	lower bound (mm)	upper bound (mm)	midpoint (mm)	
1	0	45	22.5	0.09
2	45	70	57.5	0.45
3	70	83	76.5	0.97
4	83	100	91.5	1.69
5	100	125	112.5	3.25
6	125	150	137.5	5.97
7	150	175	162.5	9.94
8	175	200	187.5	15.41

Table 3. One- and Two-Phase Von Bertalanffy Model Comparison.

Note, DIC measures model predictive power, penalizing for model complexity (where model complexity is measured by pD, the estimated effective number of free parameters). The lowest DIC indicates the best model. DIC differences >10 are strong evidence of a difference in model performance. In this case, the DIC difference is >100, indicating the two-phase model is a much better fit even after being penalized for greater complexity.

One-Phase VBGF Model Fit (posterior mean + 1 SD)	Two-Phase VBGF Model Fit (posterior mean + 1 SD)
$k = 0.295 \pm 0.022\ y^{-1}$	$k = 1.94 \pm 0.17\ y^{-1}$
LO = 9.4 ± 2.4 mm	$k2 = 0.124 \pm 0.024\ y^{-1}$
Linf = 121.5 ± 1.6 mm	LO1 = 9.4 ± 2.4 mm
pD = 2.0	LO2 = 39.1 ± 4.6 mm
DIC = 319.99	Linf1 = 61.2 ± 1.6 mm
	Linf2 = 144.7 ± 11.8 mm
	Lswitch = 52.1 ± 5.5 mm
	pD = 4.2
	DIC = 206.7

Table 4. Parameters used in PCA for California Spiny Lobster, *Panulirus interruptus*. Maximum size in Total Length (mm TL ~ (mm CL)/0.3) was determined as the 99th percentile of the size-abundance distribution for 1888-1908 (PAST) vs. 1985-2005 (PRESENT). The parameter k from the two-phase Von Bertalanffy Growth model was determined for the same periods by calculating the average of the VBGF parameters for phase I and phase II (k1 and k2), weighted by the relative abundance of lobsters above and below the switch point (L=53.5 mm CL), and rounded to one significant figure (see Table 3). Maximum age was calculated from model estimates of total fishing and non-fishing mortality and agreed with historical reports of changes in typical maximum lifespan of lobsters over this period. Values of Size at 50% Maturity (Lindberg 1955) and Egg Size were taken from the literature and assumed not to have varied.

	Sizeat50%	MaxSize	Growth(k)	Fecundity	MaxAge	Eggsize
PAST	216 mmCL	967 mmCL	r=0.1	1000000	30 y	0.69
PRESENT	216 mmCL	322 mmCL	r=1	100000	7 y	0.69

VIII. FIGURES

Figure 1. California spiny lobster fishery annual landings (lbs), 1888-2005.

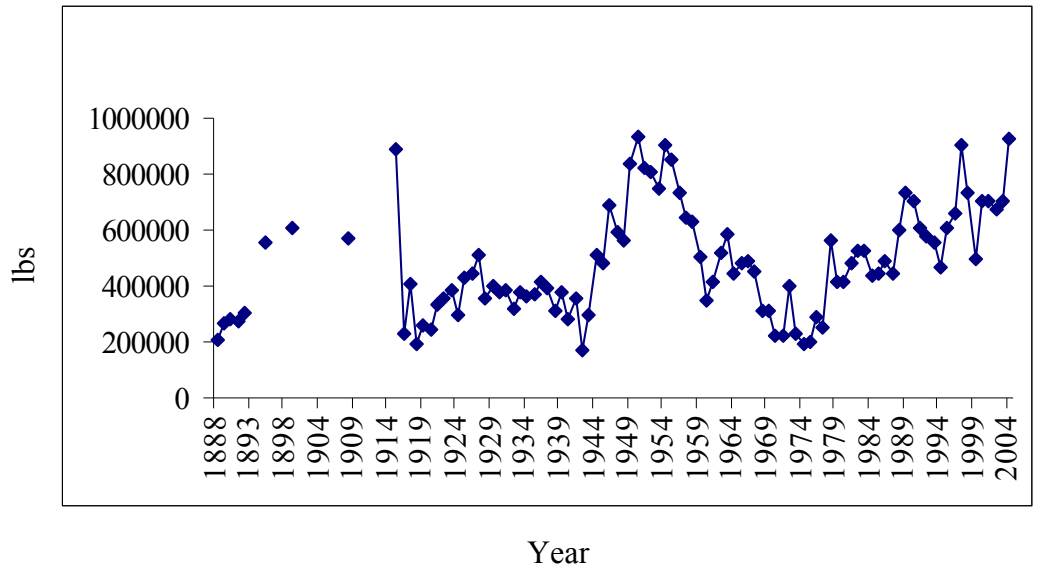


Figure 2. Flowchart of the Bayesian model framework. See *Methods* for summary of model, Appendix II and Kinlan and McArdle (in prep) for a fuller model description and results.

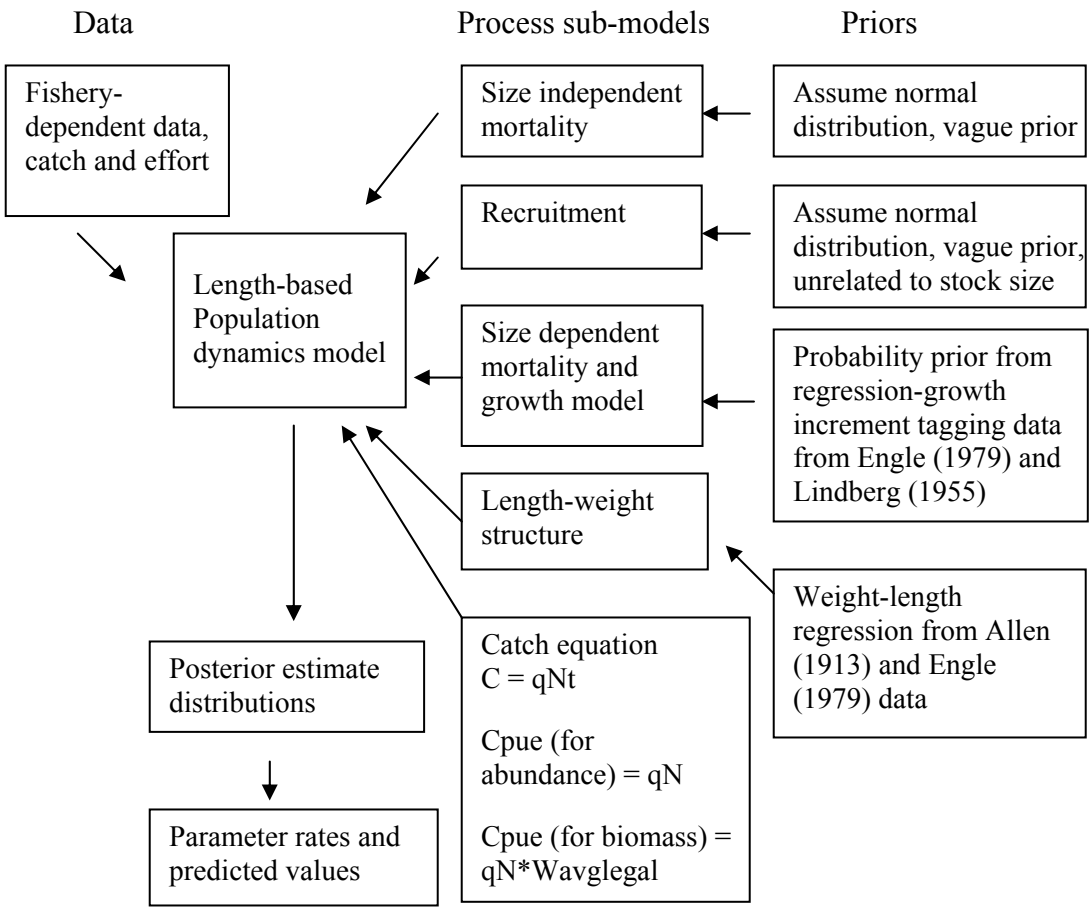
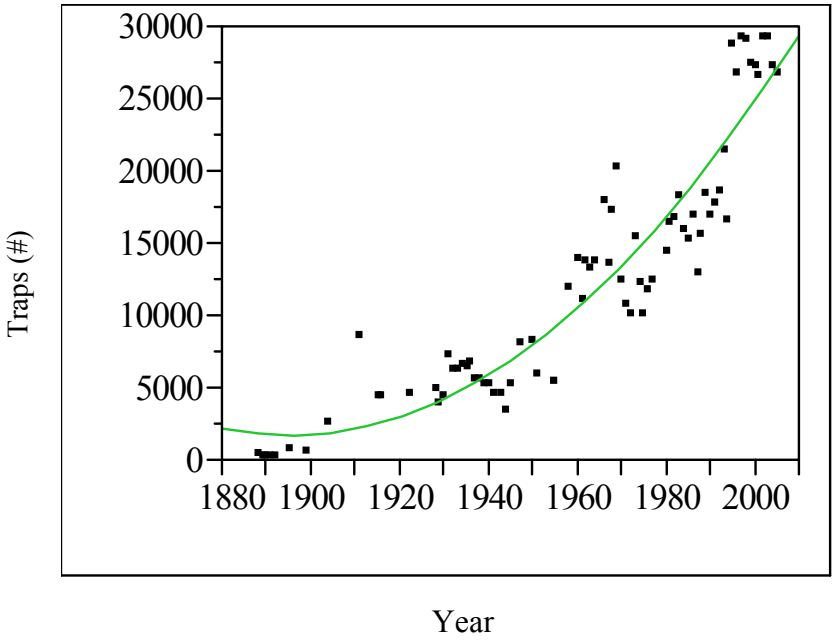


Figure 3. (a) Effort in the California spiny lobster fishery effort (trap #) by year, 1888-2005 (Polynomial fit degree 2, R^2: 0.88, p: 0.0001). (b) Catch per unit effort (catch per trap) and catch (lbs), of the California spiny lobster fishery, 1888-2005.

a.



b.

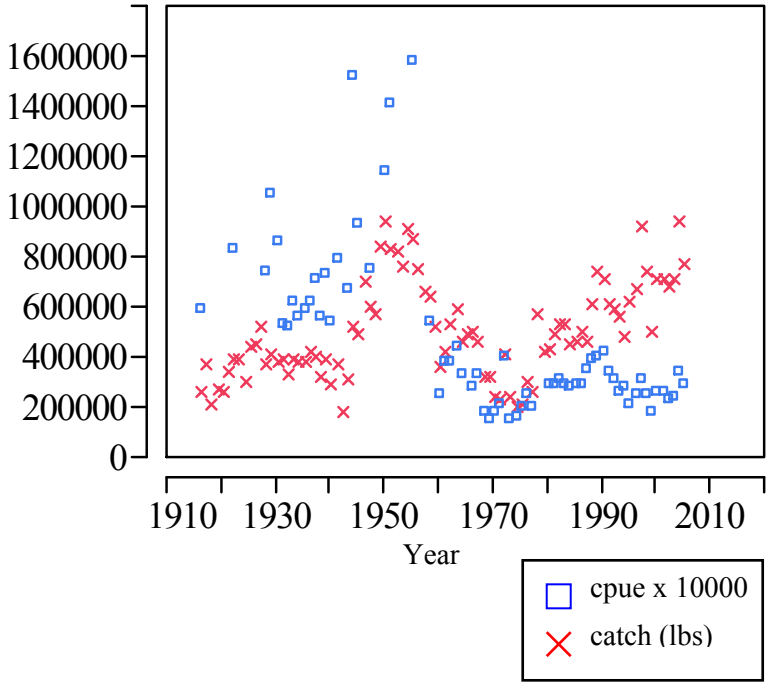
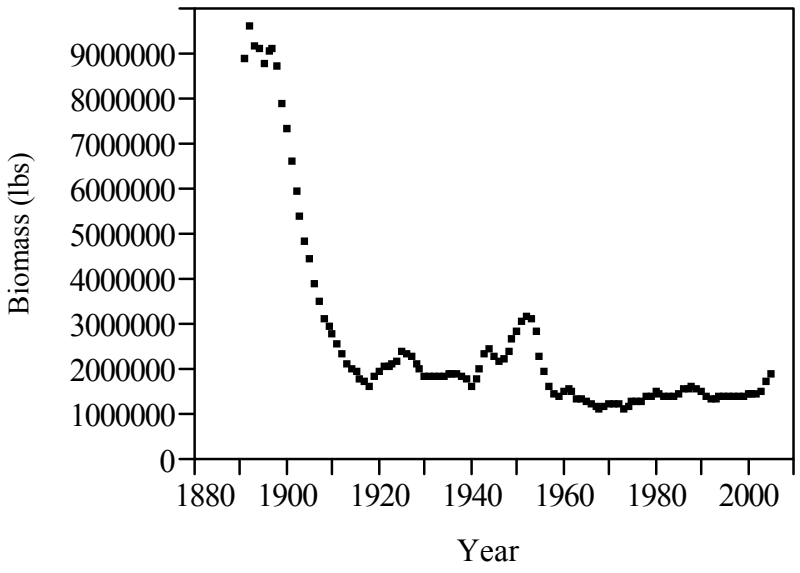

1600000
1400000
1200000
1000000
800000
600000
400000
200000
0
1910
1930
1950
1970
1990
2010
Year
cpue x 10000
catch (lbs)

Figure 4. (a) Model-estimated California spiny lobster biomass (pounds) versus time, 1895-2005. (b) Model-estimated California spiny lobster abundance (numbers of individuals) versus time, 1895-2005. Points represent medians of posterior distributions from the Bayesian model.

a.



b.

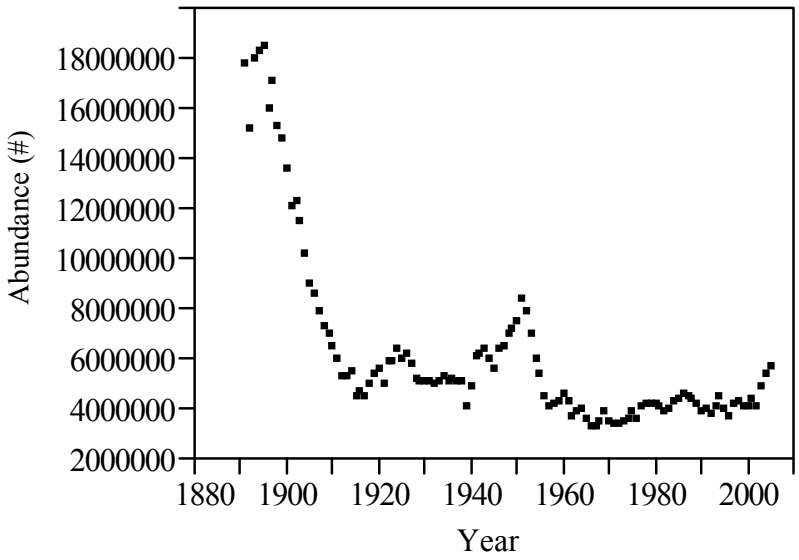

18000000
16000000
14000000
12000000
10000000
8000000
6000000
4000000
2000000
Abundance (#)
1880
1900
1920
1940
1960
1980
2000
Year

Figure 5. Annual exploitation rate (F), fraction of the population biomass fished, of the California spiny lobster fishery, 1895-2005. F is calculated as a ratio of catch biomass to median legal-sized population biomass using medians of posterior distributions for these parameters from the Bayesian model.

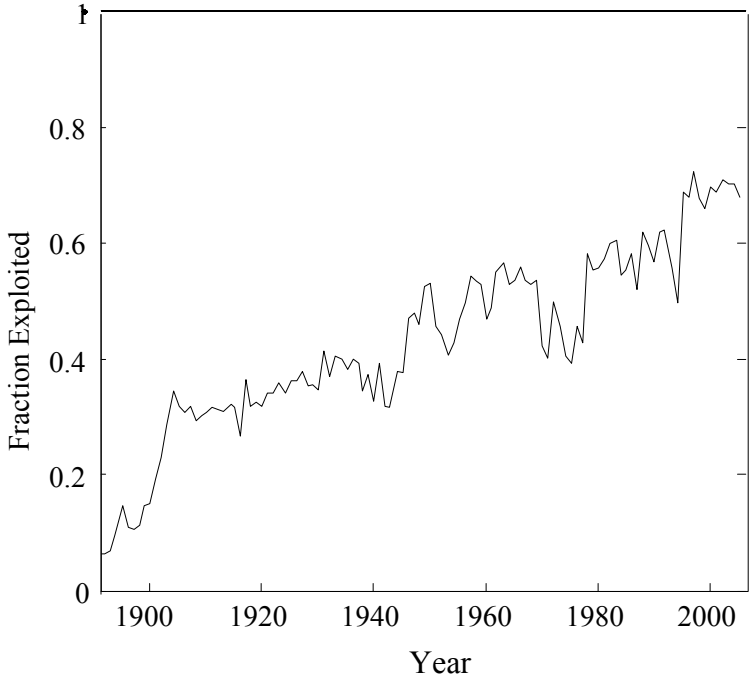


Figure 6. Model-estimated annual total abundance of legal-sized lobsters and escapement in the California spiny lobster, 1895-2005. Lines represent medians of posterior distributions from the Bayesian model.

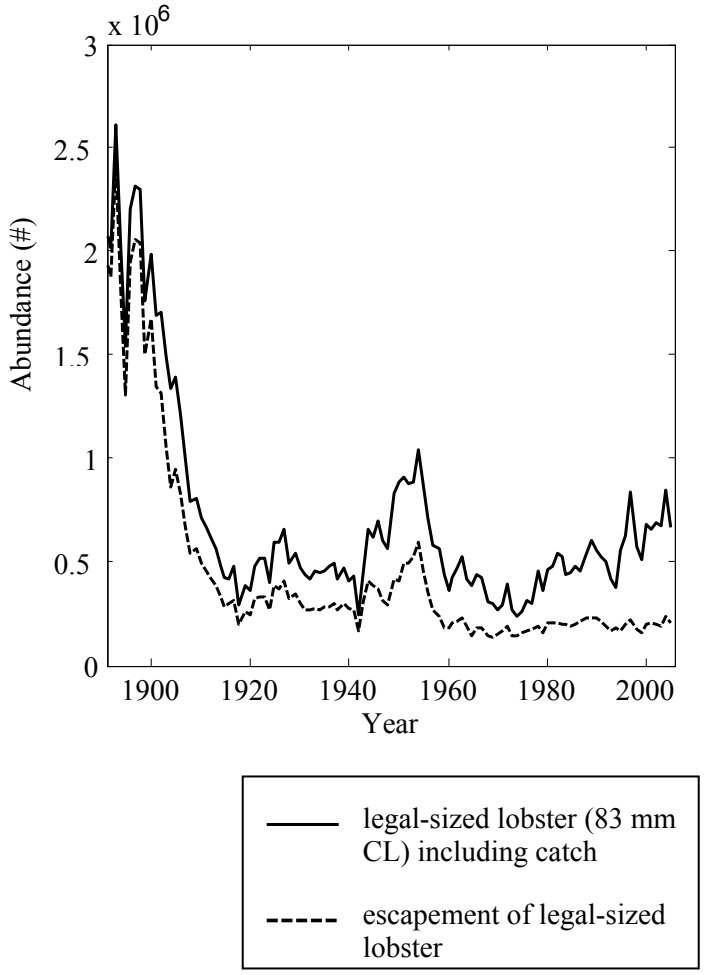


Figure 7. Abundance per size class by carapace length (CL) of the California spiny lobster, 1895-2006. (Legal-sized lobster are 83mm CL). Lines represent medians of posterior distributions from the Bayesian model.

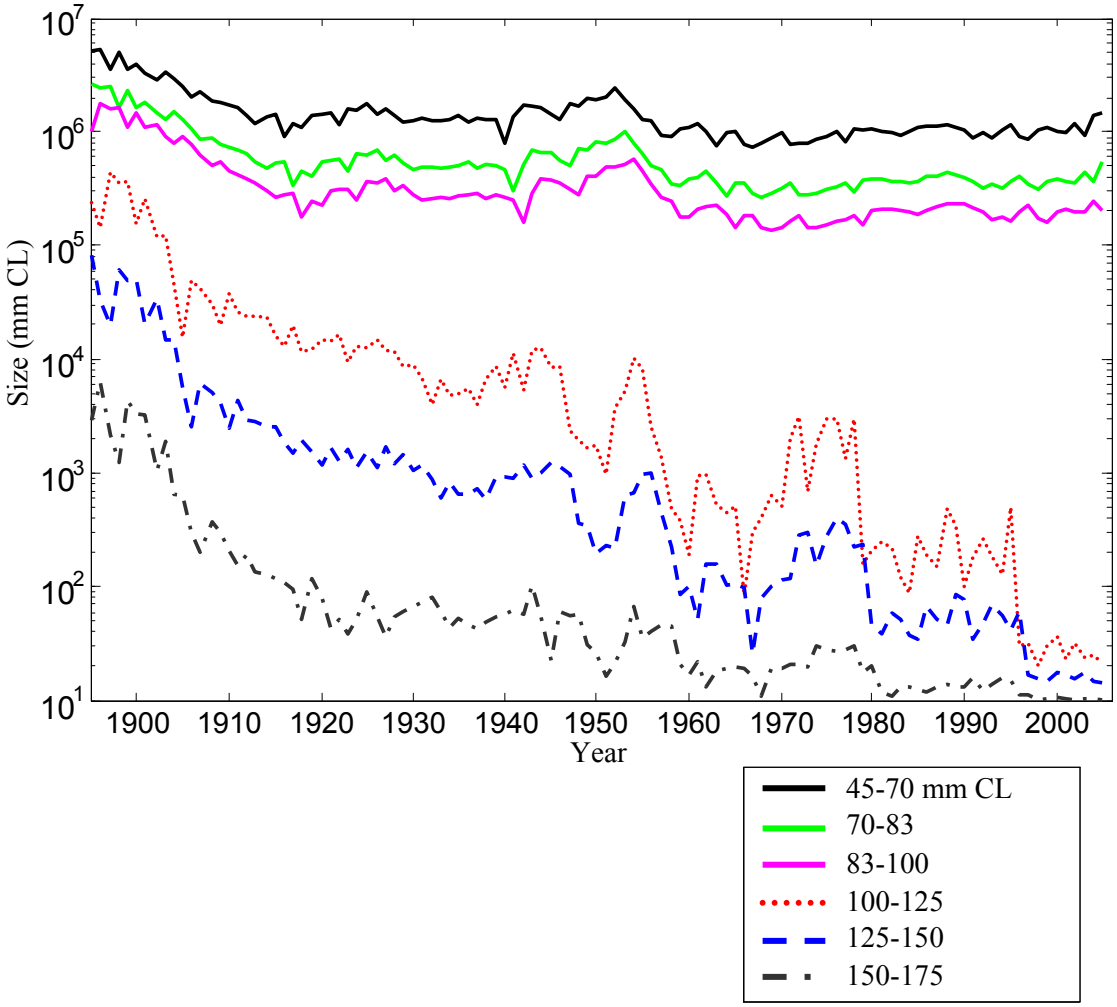


Figure 8. The model-predicted average weight of the California spiny lobster (lbs), 1895-2006.

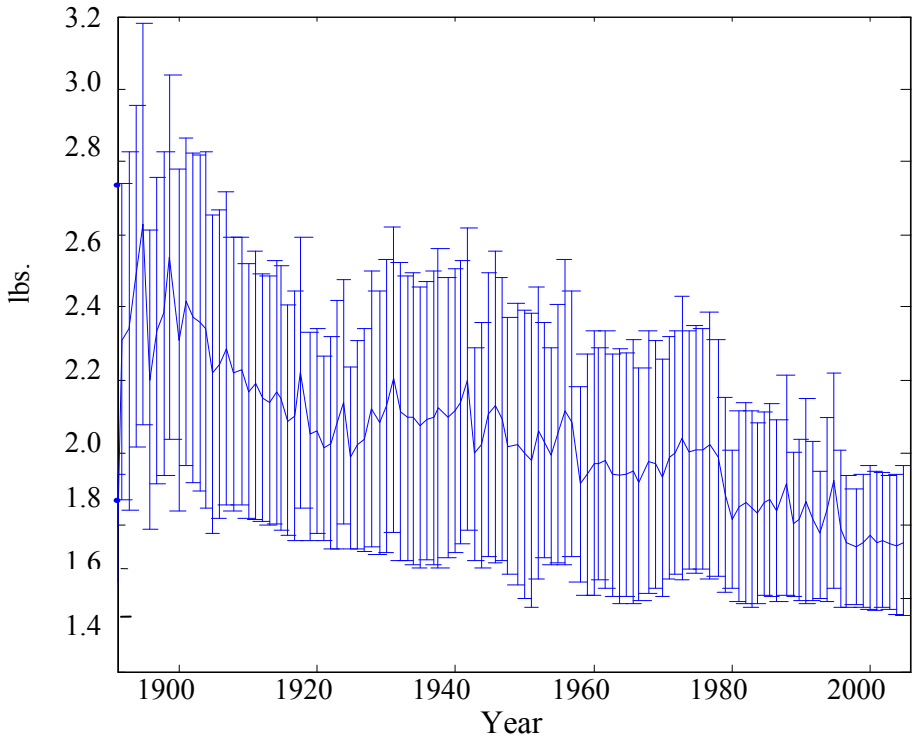


Figure 9. Short term (1-3 year time horizon) variability in catch with time overlaid on the abundance of large lobster (> 100mm CL, i.e. size classes 5-8)

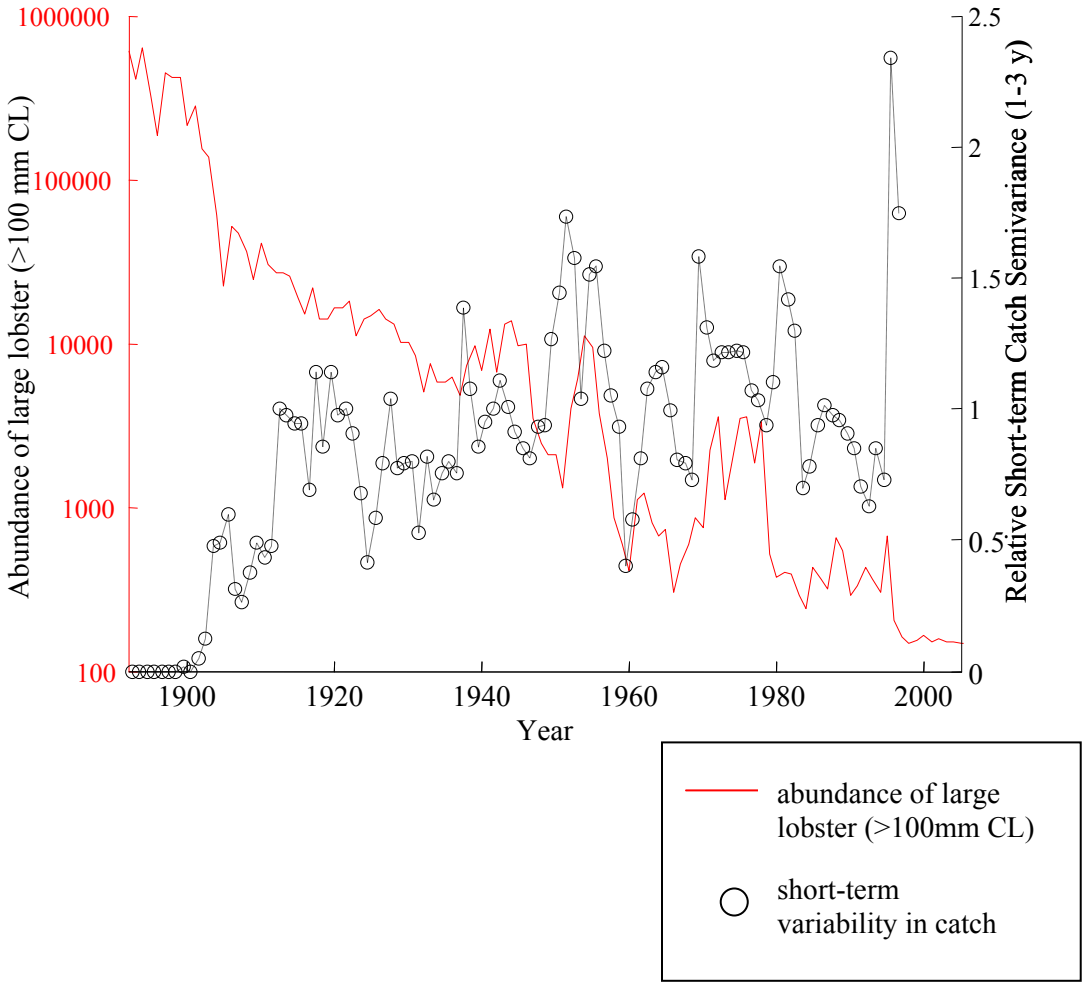


Figure 10. Bivariate plot of standardized scores from the significant principal components analysis (PCA) on six life history traits of 42 marine species, and the California spiny lobster. Life history traits included are size at 50% maturity, maximum size, growth, fecundity, maximum age and egg size. The lobster's past traits come from estimates made between 1888-1970 and present traits from 1970-2005. Over the time series, the lobster has effectively changed from functioning as a periodic to an opportunistic strategist. This figure is modified from King and MacFarlane (2003) Fisheries Management and Ecology 10:249-264, Figure 1. Several species are removed from the original graph to make it readable. The PCA is based on the model of Winemiller and Rose (1992)

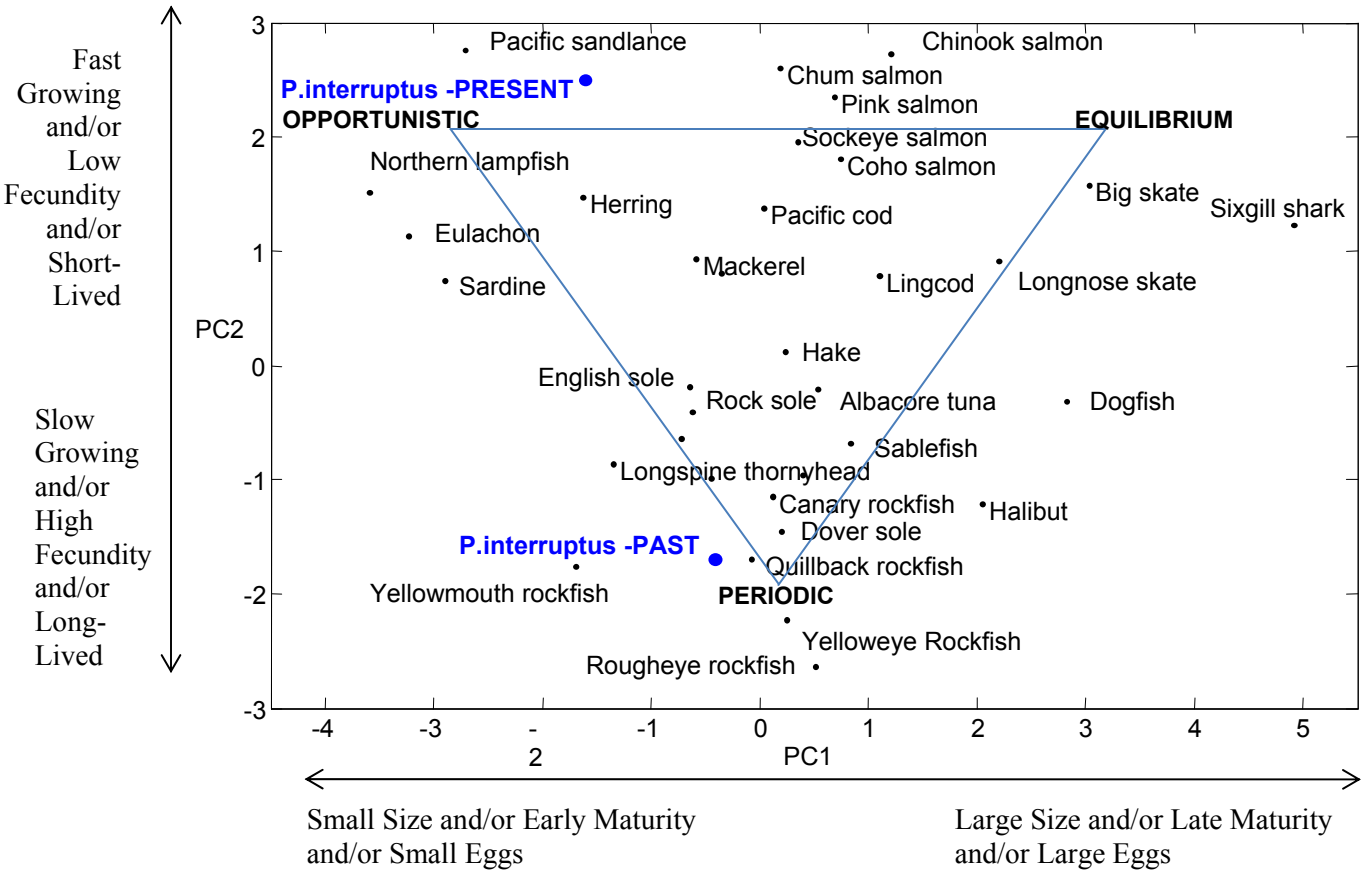
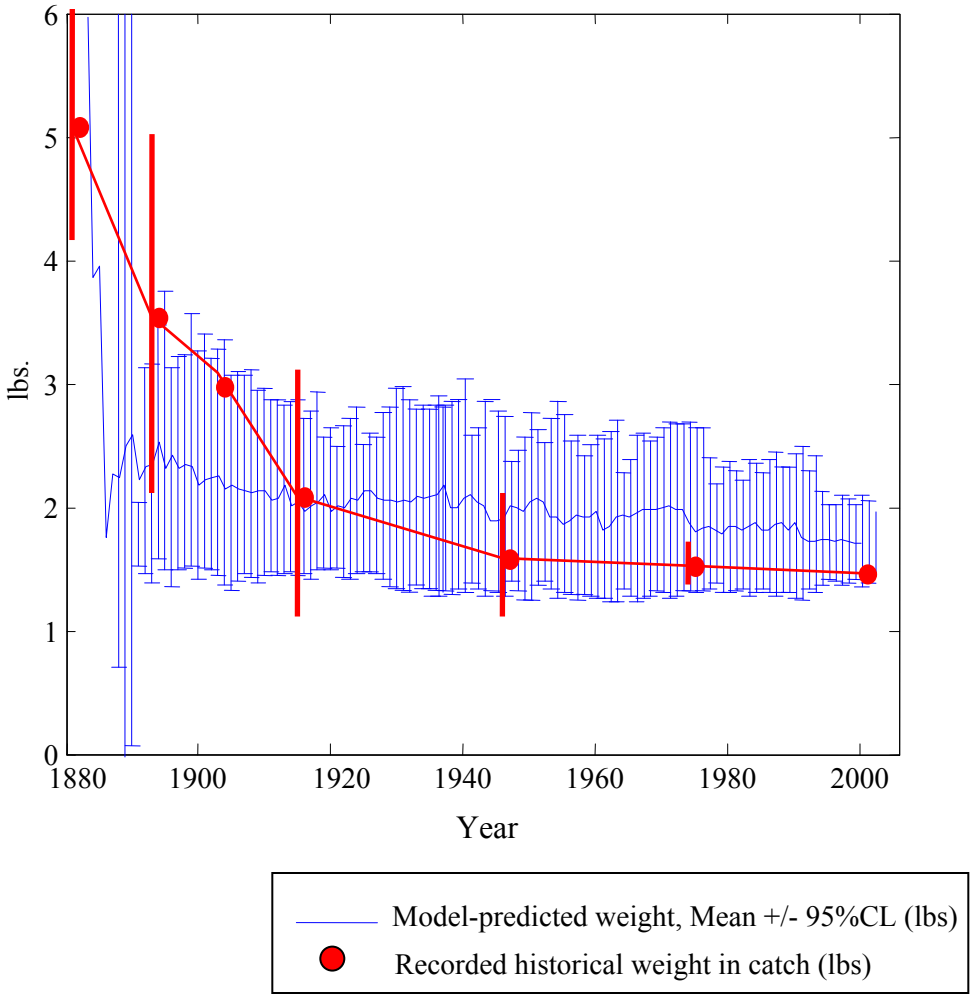

Fast Growing and/or Low Fecundity and/or Short-Lived
Slow Growing and/or High Fecundity and/or Long-Lived
PC2
PC1
Pacific sandlance
Chinook salmon
Chum salmon
P.interruptus -PRESENT
Pink salmon
OPPORTUNISTIC
EQUILIBRIUM
Sockeye salmon
Northern lampfish
Coho salmon
Herring
Pacific cod
Big skate
Sixgill shark
Eulachon
Mackerel
Lingcod
Longnose skate
Sardine
Hake
English sole
Rock sole
Albacore tuna
Dogfish
Sablefish
Longspine thornyhead
Canary rockfish
Halibut
Dover sole
P.interruptus -PAST
Quillback rockfish
Yellowmouth rockfish
PERIODIC
Yelloweye Rockfish
Rougheye rockfish
Small Size and/or Early Maturity and/or Small Eggs
Large Size and/or Late Maturity and/or Large Eggs

Figure 11. The model-predicted compared to the historical record average weight of the California spiny lobster (lbs), 1880-2006. Lines represent medians of posterior distributions from the Bayesian model, with Markov-Chain Monte Carlo 95% confidence intervals (see Appendix II). Dotted line indicates range of reported lobster weights from survey of the historical record.



Chapter Two

A Framework Integrating History and Ecology to Extend, Verify and Interpret Ecological Baselines, Time Series and Model Predictions

I. Introduction

There is an increasing awareness that to understand the full extent to which humans have affected the environment, the temporal scale of ecological studies should extend further into the past (Jackson 1997, Swetnam et al. 1999, Myers 2000, Holm et al. 2001, Christensen et al. 2003, Pinnegar and Engelhard 2007). There is growing recognition that current terrestrial and marine ecosystems are artifacts of human activities that occurred much longer ago than previously realized. Recent studies based on longer chronological time series have found that today's terrestrial landscapes bear the imprint of human hunting and agricultural practices dating back millennia (Bonnicksen, T. M. 2000, Grayson 2001, Deneven 2005). For instance, the current structure of forests and prairies throughout the U.S. is in part a product of pre-Columbian Native Americans using fire to clear areas for planting and to flush game.

Similarly, evidence of early human exploitation appears in the composition and function of contemporary marine ecosystem. The present reduced abundance and diversity of species in ecosystems ranging from kelp forests to coral reefs reflects thousands of years of fishing. Many individual species (Roman and Palumbi 2003, Rose 2004, Rosenberg et al. 2005, MacKenzie and Myers 2007) and some communities (Jackson et al. 2001, Pandolfi et al. 2003, Jennings and Blanchard 2004, Lotze et al. 2006) are only a fraction of their prehistoric size.

It is important to know the historic structure of an exploited population, community or ecosystem because it provides a baseline against which to assess current conditions. The consequence of a shifting baseline could be significant. Ecological models that relate to 'natural' or 'less exploited' conditions may assume erroneous starting or 'baseline' points and conservationists may fail to consider restoration targets that approach "original" conditions.

While studies incorporating longer temporal time scales have demonstrated their ability to increase ecological understanding, the early data within their extended time series often creates several challenges including validating specific points, corroborating model predictions of variability, and confirming that the chosen baseline reliably represents the "natural" or pre-exploitation state. Therefore, methods are needed to that go beyond compilation and quantitative analyses (Russell 1997). They should more fully examine and understand the ecological 'history' of the population, by taking an interdisciplinary approach that integrates the fields of ecology and history. The advantages of joining the two disciplines have been recognized by ecologists, conservation biologists and historians over the last decade (Meine 1999, Dayton and Sala 2001, Ludwig et al. 1993, Holm et al. 2001, Bolster 2006).

A limited number of review articles and books offer examples of historical sources being employed to study historical ecology (Swetnam et al. 1999, Holm et al. 2001, Egan and Howell 2001, Pinnegar and Engelhard 2007). Absent from the literature, however, is a comprehensive synthesis of historical and ecological methods

to achieve the goal of extending ecological history. Here, a new five-part methodological and conceptual interdisciplinary framework is introduced for more fully integrating nontraditional historical sources into ecological studies to: 1) extend the temporal scale of quantitative analyses, 2) validate historical data points in a time series, 3) corroborate model predictions, 4) verify the temporal scale of study baselines, and 5) place ecological findings in historical context to interpret and explain the role of human history (e.g. economics, politics, technology, and value systems) in causing observed or predicted ecological variability. This work will also demonstrate that adding any one or more of the elements of this approach to a quantitative analysis can lead to a deeper, more comprehensive, and better informed understanding of the history of the environment.

To illustrate the application and value of the five components of this framework, I employ a case study of the southern California spiny lobster, *Panulirus interruptus,* based on personal letters, oral histories, maps, newspaper articles and government reports gathered from local, state and national museums.[7] Spiny lobster populations occur in kelp forest and inter- and subtidal rocky ecosystems in the oceanic region known as the Southern California Bight, which extends from Point Conception, California to Mexico and seaward from the coast to the California Current (Daily et al. 1993). While the species has supported a commercial fishery in California for 135 years, relatively little is known about its ecological history.

II. Five-Part Methodological and Conceptual Interdisciplinary Framework

Next, I use a case study of the California spiny lobster to illustrate how to more fully integrate nontraditional historical sources into ecological studies to extend the temporal scale of quantitative analyses, validate historical data points in a time series, corroborate model predictions, verify baselines, and place ecological findings in historical context to identify additional anthropogenic explanations for the observed or predicted ecological variability.

A. Long Time-Series and Quantitative Analyses

The temporal scale observed influences whether and which ecological changes are detectable (Sutherland 1981, Connell and Sousa 1983, Levin 1992). Most analyses are based on time series that are relatively short, starting long after human beings began to impact the environment. A problem with employing short time series is they may fail to identify fundamental human-induced long-term changes and variability in the environment. Long time series, when available, can avoid this pitfall and greatly enhance our understanding of long-term interactions between humans and environmental variability.

Compiling an extended time series is a challenge in part because of the paucity of long historical ecological data sets. Ecologists have recently sought to overcome this obstacle by utilizing both quantitative and qualitative (e.g. government surveys, maps, photographs, etc) historical documentary information (Egan and Howell 2001 and Pinnegar and Engelhard 2007). While it is often difficult to find

long quantitative time series, nontraditional records can extend back over considerable time frames. For example, terrestrial ecologists have found consistent records of vegetation cover dating back to the early 19th century in General Land Office surveys (Egan and Howell 2001). Marine studies have relied on detailed records of fishery catches and effort in financial records (Ravier and Fromentin 2001) and ships logbooks (Rosenberg et al. 2005), some of which extend back hundreds of years.

The author compiled a 120-year time series of catch and effort in the lobster fishery from historical government records to examine the California spiny lobster's long-term population structure and dynamics (McArdle and Kinlan, in prep and Chapter One). Records of annual spiny lobster catch (lbs) were collected from U.S. Bureau of Fisheries reports (1888-1915) and California Department of Commercial Fisheries and Department of Fish and Game reports (1915-2005). Catch records from the early period (1888-1915) were checked to ensure that they only included California catch, excluding catch originating in Mexico. Estimates of fishing effort measured by the number of traps fished per year from 1888 to 1976 were compiled from federal reports first published by the U.S. Fish Commission Bureau of Fisheries (1888-1915), then the U.S. Fish and Wildlife Service (1916-1969) and finally the National Oceanographic and Atmospheric Association (1970-1976).

The earliest records in long data sets are often perceived as potentially unreliable. The earliest catch and effort data in the lobster time series came from the U.S. Fish Commission (USFC) surveys. The USFC began surveying California

fisheries in 1888 by conducting annual canvases of fishermen and wholesalers.[8] The surveyors' notes assisted in verifying the reliability of the quantitative entries in these records.

By 1919, the USFC surveyors' notes explain that whenever possible, they routinely combined the information they collected with catch and effort statistics from the California Department of Commercial Fisheries (CDCF).[9] In 1924, federal agents listed the CDCF's boat registration records as their source for tallying effort in California's fisheries stating, "Statistics on persons, boats, and gear were taken from the State's registration lists."[10] This was surprising because, while it was common knowledge that the CDCF had gathered early catch data, it appears that the CDFC's early effort data collection program had disappeared from institutional memory. Nevertheless, an examination of CDCF's early reports revealed that, in 1919, it began a mandatory boat registration program that required fishermen to provide information on both their boat and gear.[11] The discovery that the early USFC records were a product of combined federal and state monitoring increased confidence in the accuracy of the data at the beginning of the time series.[12]

Kinlan and McArdle (in prep) fit a Bayesian state spaced size structured model to the time series to quantify the effects of fishing on the lobster population's size structure and dynamics over the last century. The Bayesian model framework allows greater flexibility than traditional statistical approaches in a study such as this, which employs multiple data sets and sources of historical information.

The combination of the long time series with the Bayesian model revealed the full extent to which exploitation had dramatically altered the lobster population (McArdle and Kinlan in prep or Chapter One). In a little over a century, fishing effort measured by the number of traps increased by 100%. Although the model-estimated exploitation rate (the percent of the population fished) fluctuated, it also generally increased over time. By 2005, fishermen were taking approximately 70% of the total of the legal-sized lobsters (>83 mm CL). As fishing effort increased, the population's abundance and structure changed. Biomass declined by 80%, from a historical baseline of 9,000,000 lbs to 1,800,000 lbs. and size structure transitioned to one composed generally of younger and smaller animals. As the proportion of larger lobster decreased, their average weight declined, with the average weight of legal lobster falling from 5.8 to 1.7 lbs. These long-term shifts in the lobster's population structure and dynamics were large enough to potentially increase the variability and unpredictability of abundance and catches, and diminish its resilience. The truncation of the population's size structure may have also lowered kelp forest ecosystem resilience by functionally removing a key predator – large lobster

B. Validation of historical data points in time series

Validating the accuracy of apparently "exceptional" specific data points in long time series can often be a challenge. Researchers who do not access relevant qualitative historical sources may exclude these points from their analyses as outliers

or anomalies, thereby failing to realistically describe and reconstruct a population's historic variability.

One data point in the time series of spiny lobster catch is exceptional and thus potentially an excludable outlier. In 1904, the U.S. Bureau of Fisheries' survey reported that the fishery landed 1,078,065 lbs of lobster (see Chapter One: Fig 1). It is possible that this catch estimate is unreasonably high or even the product of a recording or typing error. This is a facially plausible theory because the reported 1904 catch represents an unprecedented increase in landings over a five-year period. Landings rose 471,065 lbs. between 1899 and 1904. Before this, the largest increase in five years was 279,744 lbs. (1890-1895). The 1904 estimate is also exceptional because it is the largest recorded catch of spiny lobster over the history of the fishery, with later catches reaching highs of only ~ 900,000 lbs (i.e. 1950, 1955, 1997, 2004).

Government fisheries reports that occasionally accompany surveys can aid in validating such potentially anomalous historic fisheries data points. The U.S. Fisheries Bureau began surveying fisheries in 1883, and in addition to providing quantitative statistics, they often described the fisheries and placed them in a historical context.

The U.S. Fish Commission and the U.S. Census Bureau surveys of U.S. fisheries of 1904 and 1908 listed the 1904 spiny lobster catch as 1,078,065 lbs. While surveyors from both agencies pointed out the high catch of 1904, they did not consider it inaccurate. Instead, they simply acknowledged that it was "an abnormal catch," noting that it was well above the average pounds landed per year.[13] The

surveyors explained that the underlying cause of the surge was increased fishing efficiency and spatial expansion of the fishery writing, "The increase in catch is chiefly due to the use of gasoline boats employed on new fishing grounds among the Santa Barbara Islands." And, "These boats carry double the crew… and make quick trips." [14] The Federal Surveys also listed the amount of effort expended by the fisheries annually. By reviewing this information, we learn that not only did fishing efficiency increase dramatically from1899 to 1904, fishing effort (number of traps) quadrupled.

Local newspaper articles are another source for verifying general trends like those described in the government records containing lobster catch data. Newspapers can be a rich resource because they were usually published daily, typically filled with details, and, through at least the first half of the twentieth century, concerned with the "progress" or development of local and national natural resource-based industries and markets. Southern California newspaper reporters confirmed the marked increase in efficiency and effort within the spiny lobster fishery at the turn of the century. The Santa Barbara News-Press reported that by 1900, "gasoline-powered boats began being employed in the [lobster] fishery" around the Channel Islands.[15] In the beginning, these gasoline-powered boats were used primaily as "pickup boats that departed Santa Barbara and San Pedro for the Channel Islands" to collect lobsters "from island-based fishermen at the camps."[16] The new engine technology allowed fishermen to shuttle between the Channel Islands, and San Pedro and Santa Barbara more frequently, quickly and consistently. The new boats also allowed fishermen to

expand their efforts to previously lightly or never exploited areas such as San Nicolas Island.

By 1904 fishermen from San Pedro and Santa Barbara were catching lobster around the islands of Anacapa, Santa Barbara, Santa Rosa and Santa Cruz, and San Nicolas.[17] When the 1904 season opened, a Los Angeles Time article documented this spatial increase in effort describing how, "For days past, weeks past, the little lobster sloops have been clearing away with huge deckloads of lobster traps to…almost every island for the channel to leave camps of lobster fishers."[18]

Newspaper articles can also contextualize the fishery trends documented in other records. Southern California newspapers illuminate the force driving the growth of the Channel Islands lobster fishery at the turn of the century – increased national appetite for this resource. Fishermen initially focused their efforts on local lobster populations in the Los Angeles and Santa Barbara regions to fulfill this rising demand. By 1903, some local populations began showing signs of depletion, including at Catalina Island and San Pedro, both of which the Los Angeles Times declared were "fished out."[19] Fishermen from the Los Angeles region shifted their efforts to the Channel Islands to try to meet the continued growth in demand; in 1904, fishermen landed 73% of the southern California lobster catch in Santa Barbara and Ventura counties.

Newspaper reports corroborate the U.S. Census Report's characterization of the 1904 lobster catch as "abnormal." Newspapers documented a dramatic increase in fishing pressure at the Channel Islands, resulting in uncommonly large catches

leading up to 1904. Lobster catches had grown so large that by 1903 even seasoned Santa Barbara fishermen were concerned. One pioneer of the fishery warned in a 1903 Santa Barbara Daily Press article that the amount of lobster caught was too great and that the "crawfish" was "doomed to extermination" because "hundreds of tons of the crustacean have been secured at the expense of the future supply."[20] In 1904 there were reports of bi-weekly trips yielding "the prodigious catch of 3 tons of live lobsters." Also in 1904,"Over one tiny wharf of one fishing Company, a ton of lobsters passes every day to markets of Los Angeles, the Coast and the East."[21] That same year, Captain Swansen, a Swedish fishermen who ran lobster traps to the Channel Islands, similarly reported in a Los Angeles Times article that lobster were "being taken out at the rate of a ton a day." He was so troubled by the dramatic increase in fishing pressure that he declared "unless the laws are made stricter, lobsters will become almost extinct on this Coast." [22]

In sum, historical records, including federal reports and numerous newspaper articles, show that the lobster catch of 1904 was extraordinary. Growing demand drove increased effort, culminating in an exceptional year. The corroboration of this data point with multiple independent historical sources increases our confidence that the high catch estimate was not an outlier. Far from being an anomaly that should be disregarded, the 1904 catch enhances our understanding of the historic range of variability in spiny lobster population dynamics.

C. Corroboration of model estimates and trends with historical records

One component of any ecological analysis is assessing the relative level of confidence in the results, or parameter estimates (Hilborn and Walters 1992). There are a myriad of statistical tests of certainty. An interdisciplinary approach used less frequently compares model-generated predictions and trends to historical sources. Studies that employ this technique can increase confidence in model parameters.

1. General Trends - Decrease in the lobster biomass and size from 1890 to 1915

General trends described by a model (Chapter One) can be confirmed by reviewing historical records for the presence of established and predictable patterns. Fisheries biologists have identified a consistent progression in species abundance and size during the early phases of a fishery. Fisheries typically follow a trajectory beginning with a phase of exploration and initiation, transitioning to a development phase characterized by rapid market expansion, increasing exploitation, and spatial expansion, leading to declining profits, waning resource availability and repeated proposals for restoration and conservation (Hilborn and Walters 1992).

Lobster fisheries have historically traversed these stages. As early as 1909, naturalist and lobster expert Francis Herrick described the development phase of a lobster fishery as a predictable three-stage trajectory: "(1) Period of plenty- lobsters are large, abundant, cheap; pots and fishermen few. (2) Period of rapid expansion- greater supplies each year to meet the growing demand; lobsters in fair size and of moderate price. (3) Period of real decline- fluctuating yield with a tendency to

decline; a rapid extension of fishing areas; multiplication of fishermen, pots and fishing gear of all kinds; decrease in the size of all lobsters caught, and steadily increasing prices." [23]

The following examination of the historical record shows that the California spiny lobster fishery passed through these classic stages of early fisheries growth. From 1870 to 1915 the fishery moved from the initiation to the development phase; a transition typically characterized by decreases in population biomass and average individual size – the same pattern predicted by the Bayesian model.

a. Initiation and Exploration Phase (1870-1890)

Historical accounts indicate that the period from 1870 to 1890 encompassed the initiation and exploration phase of the California commercial spiny lobster fishery. Beginning in 1870, a small number of Chinese and Caucasian fishermen focused their efforts on the Santa Barbara area. The Chinese caught lobsters in coastal tidal regions and on the east coast of Santa Cruz Island. They sun-dried the tails and then shipped them in 300-pound bags to San Francisco's Chinatown markets, where a large portion of the catch was exported to China.[24] In the 1870s, Italian immigrant Andrea Larco initiated the live lobster market. He sold live lobsters for ten cents each in Santa Barbara and shipped bagfuls north on coastal steamers to the San Francisco market.[25]

By 1880, the fishery was still relatively primitive and still centered in Santa Barbara. Total Southern California landings for that year were 90 tons, with 85% of

the catch coming from the Santa Barbara/Ventura area.[26] Lobsters remained extremely abundant; a single person could make near shore "catches aggregating 500 pounds…in the short space of two hours."[27] In 1882, a published federal government review recognized that while lobster was "one of the most notable crustaceans of the San Francisco market,"[28] overall "markets were still small."[29] Five years later, there was still "no regular market."[30]

b. Development Phase (1890 to 1915)

The California spiny lobster fisheries' began to transition into a development phase in the early 1890s. The market expanded rapidly, leading to increased fishing effort and efficiency, and exploitation of new grounds. With more fishing pressure came more competition, waning resource availability, steadily rising prices and repeated calls for conservation measures.

(1). Market Expansion and Infrastructure Creation

The key conditions required for the initiation of a fishery's development phase are the presence of sufficient market demand and an infrastructure adequate to process, sell and transport larger catches (Hilborn and Walters 1992). Newspaper articles and government reports document that both of these conditions were met for the lobster fishery between 1890 and 1915.

Before 1890, east coast American lobster fed the nation's hunger for this "toothsome dainty." Demand for lobster rose across the country during this time

frame, including in the growing cities of the Great Plains. American lobster populations declined drastically after 1890. The Los Angeles Times repeatedly reported on the plight of the eastern lobster, which was "growing scarce" and "about to disappear," particularly in Massachusetts.[31] California spiny lobster filled the void. According to one federal government fisheries expert, "the crawfish was regarded as a fair substitute and met with a ready sale at good prices" on the east coast because "the true lobsters were very scarce."[32] The potential for growth seemed limitless, with one Los Angeles Times reporter explaining how, in 1893, there was "an unlimited field for the crawfish-catcher in this channel and on the shores of the Channel Islands."[33] Market observers thought that spiny lobster could "supply all present demands" because they were "found in great abundance along southern California shores" and were "extremely numerous."[34]

A crucial piece of the infrastructure necessary for the development of the fishery was already present before the opening of the national market. The first crosscountry rail line connecting Los Angeles to the east coast was the Sante Fe system, completed in 1885. The railroads were an essential element of the production system that would ultimately support a larger lobster fishery. Before they appeared there was no reliable form of transportation to supply markets east of the Rocky Mountains. Railroads linked the product with markets from coast to coast.

One of the first attempts to supply California spiny lobster to the east coast and interior was to ship it in refridgerated railroad cars. Live and boiled lobster were packed in layers of ice and sent to various parts of the country, including towns in

interior California, Iowa, Kansas, Nevada, New Mexico, and Arizona.[35] In 1893, iced spiny lobster was shipped as far east Chicago and Philadelphia. These efforts, though, proved to be only moderately successful.

It would take the cannery industry to truly trigger the development phase of the California spiny lobster fishery. In 1894, the Catalina Conserving Company opened in San Pedro, where it laid the groundwork for and charted the course of the fishery during the next three decades. The Catalina Conserving Company created a production system that included a holding area to store recently caught lobster, a packing facility, and a canning factory. The company also utilized the latest fishing technology, purchasing a fast, gasoline-powered schooner, the "Lizzie Bell. W.," that could gather and transport much greater loads of lobster than older vessels.[36]

This marked the beginning of a new era. During the early years of the development phase, fishermen were limited to catching lobster near their homeport because they used either simple rowboats or sailboats. Gasoline-powered schooners enabled the San Pedro fishers to travel farther and faster. Fishing effort now expanded to include the northern Channel Islands, as evidenced by the Catalina Conserving Company's copyrighted label, describing the canned contents as "a California product" that were "caught about the islands."[37]

The Catalina Conserving Company dropped off small boats and crews to gather lobsters, usually on Santa Cruz Island. The crews lived in camps "to secure their spot." [38] Fishermen would store the daily catches in holding pens until they were transferred in sacks to the gasoline powered schooner every few days. The "pick-up

boat" directly transported the loads aproximately sixty miles from the island to the San Pedro plant, where the lobster was canned, then put on railroad cars and shipped across the country.

In 1897, the Los Angeles Times accurately predicted that although the Catalina Conserving Company only "operated on a small scale," it promised "material development." [39] The company and the industry grew rapidly. In only a few years, new competitors had established five more canning plants in San Diego, San Pedro and Santa Barbara, and at least ten gasoline-powered schooners were transporting lobster catches from the Channel Islands to ports in San Pedro and Santa Barbara.

(2). Increasing fishing effort

As markets grew and transportation developed, effort increased. In 1880, there were only a few fishermen working in the primitive fishery.[40] By 1912, 200 men were engaged in the industry.[41] The number of traps being used in the fishery increased, from 260 to 4255 between 1888 and 1917.[42] By 1911, each fisherman was also using more traps to catch lobster, causing one lobster fishery biologist to recommend that fishermen be limited to 25 traps each. [43]

(3). Spatial expansion

Consistent with the typical pattern of early fisheries growth, the lobster fishery also expanded spatially. A fold-out map from the 'Report of the U.S. Commission of

Fish and Fisheries‘ shows that during the exploration phase in 1888, lobster fishing grounds in southern California were primarily off the coastal mainland and the east end of Santa Cruz Island.[44] Numerous newspaper articles document the expansion of the fishery as it developed over the next decade.

At the beginning of the development phase, the canning industry initially focused its fishing at the Channel Islands, with “nearly all of the product packed by the Catalina Conserving Company com[ing] from Santa Cruz Island.”[45] By the end of the 1890s, lobster cannery fishing camps had expanded from the east side of Santa Cruz to include the southeast and south of the island.[46]

In 1904, an article about the lobster fishery in the Los Angeles Times characterized the lobster populations at Catalina Island and San Pedro as “fished out.”[47] The next year the fishery and camps had expanded to the islands of San Clemente, Anacapa, San Nicolas, Santa Barbara and Santa Rosa Islands. By 1906, fishermen were catching lobster at the more remote and less accessible island of San Miguel. Fishermen explained that they had rapidly expanded the area they fished because “boats now go from 50 to 100 miles for 5 to 10 percent of the catch they could make within 2 hours run of San Pedro a few years ago.”[48]

As the fishery grew around the Channel Islands, plans were made to enlarge it to include new lobster grounds in Mexico.[49] Lobster canning factories considered this neccesary because “the abundance of product in those waters” was far greater than along the coast [of California] where lobsters for years have been sought by fleets of fishing boats.” A seasoned fishermen explained to The Santa Barbara Morning Press

that "Crawfish have to be shipped from the coast of Mexico to supply the demand."[50] In less than a decade, southern California's lobster industry had expanded throughout the Channel Islands into Mexican waters. Grounds that once contained lobster populations that were "extremely numerous" and "in sufficient abundance to supply all present demands" were now so "limited" that they could no longer meet the "enormous demand."[51]

(4). Waning resource availability, steadily increasing prices

Shortly after the turn of the century, the lobster fishery entered the next predictable phase of its development. As effort intensified and the resource waned, its price rose.

In 1907, government officials, reporters and fishermen expressed concern about the rise in the price of spiny lobster over the preceding decade. Articles in the Los Angeles Times and Santa Barbara Morning Press surmised that lobster had shifted from being so "common and so cheap that anybody could afford them" to a high value "table delicacy"[52] "A dozen years ago the markets could hardly give them away" but now the price was "extremely high."[53]

Many surmised that the inflated prices were the product of a depleted lobster population. In a 1906 meeting that brought fishers together in Monterey to talk about resource conservation, California Fish and Game Deputy Commissioner Pritchard declared, "No fair-minded market man will attempt to deny that the crawfish are being rapidly cleaned out….The price is steadily going up and crawfish are getting

scarcer every month. " According to the California Board of Fish Commissioners, "Although there were practically the same number of camps engaged in the capture of crawfish, "the market prices have been unusually high," and there has been an "extreme lightness of the catch of legal-sized fish."[54]

During this time period, the Los Angeles Times reported that because the supply was "decreasing with the shocking speed," many crawfishermen were "quitting the business."[55] The "number of legal-sized fish now caught hardly justifies the cost of operating traps."[56] However, for those few who were willing and able to invest in newer boats and venture farther off shore, the business remained a "paying proposition" because of the higher price.[57] For instance, Captain George McGuire, owner and operator of both a gasoline-powered schooner and fishing camps, admitted to the Santa Barbara News Press that while many lobstermen were failing, he was still making a profit by fishing "where crawfish are plentiful," including the relatively new fishing grounds found at San Miguel Island.

(5). Repeated restoration and conservation proposals

The lobster fishery also experienced the final stage of typical fishery development – repeated efforts to restore and conserve the species.

The first management measures applied to the lobster fishery were minimum size limits and spawning season closures. The intent was to protect small lobsters and allowing lobster spawn a few times before they were caught (McArdle, in prep and Chapter Three). These regulations began in 1894, before significant decreases in

supply became apparent. Several counties passed local ordinances that imposed a closed season, which prohibited the sale and capture of lobsters from May 15 to July 15, and a minimum 'weight' limit that prohibited the capture of lobster of less than one pound. The next year, 1895, the state adopted these restrictions. One Federal Fish Commission fisheries expert praised the "commendable foresight" of the California fish commissioners for predicting that the continued "unrestricted capture of the crawfish would greatly reduce the production, and have taken measures to avert, as long as may be, a diminution in the supply."[58]

Four years later, the predicted shortfall in production caused by fishing was becoming a reality, starting in Santa Barbara County. Fishing intensity had increased at Santa Cruz Island to the point where in 1899 just one canning company was reportedly taking "from twenty-five to thirty tons of lobsters per week"[59] Motivated by a desire to reduce the increasing pressure on the lobster population, the Santa Barbara County Board of Supervisors responded by shortening the fishing season from ten to seven months, making the County's closed season much longer than the one prescribed by the State law.

Over the next fifteen years, government officials and fishermen continued to call for increased regulation of the lobster fishery, as it became increasingly apparent that the supply was waning. In response, the state legislature passed a series of progressively more restrictive laws to regulate the lobster fishery in an effort to maintain and restore the lobster population. By the turn of the century, the season was closed between April 1st and August 15th and there was a minimum size limit of nine

and one-half inches. Over the next several decades, the duration of the spawning season and the minimum size limit were altered a number of times.

In 1903, some also began to suggest measures that would protect large-sized lobster. According to naturalist Francis Herrick, larger older lobster produced more eggs, so by "legalizing the capture of the large adult animals," "the great source of eggs themselves-the large producing adults" was destroyed (McArdle, in prep and Chapter Three).[60] In 1897, Herrick recommended two complimentary approaches to protect the larger lobsters, maximum size limits and areas closed to fishing. Assuming the areas were closed for at least five years, this would give the population time to create a class of mature lobsters. Maximum size limits would shield the large lobster from catch when the protected areas reopened.

In 1903, there were repeated demands for an even more restrictive measure – a temporary absolute closure. The California State Board of Fish Commissioners recommended at least a two-year closed season to replenish this "most important shellfish," which was beginning "to show signs of great depletion, if not extermination."[61] The following year, Captain A. Larco, the pioneer fisherman of the Santa Barbara channel, explained to the Santa Barbara Morning Press that "a closed season of at least two years" was needed because "if the taking of crawfish can be stopped for that length of time, the stock will have opportunity to replenish."[62] In 1904, another prominent Santa Barbara lobster boat captain told the Los Angeles Times that unless the laws were made stricter, "lobsters will become almost extinct on this Coast;" a "closed season two or three years long should be declared." [63]

Others, like California Fish Commissioner Pritchard, presumably relying on Herrick's research and recommendations, argued for a longer five-year closure to restock the "crawfish" population.[64]

The Legislature considered even a two-year closure too restrictive, choosing instead to add one month to the 1906 closed season.[65] The push for a complete closure, however, continued. Two years later, a Santa Barbara Morning Press headline reported that, Senator-Elect Roseberry "Takes Up the Fight" to pass a bill that would close the lobster fishery for three or four years. Roseberry explained that the "crawfish" of California "were rapidly becoming depleted" and that a three or four year closed season would serve to "restore their wonted numbers."[66] At approximately the same time, the State Board of Fish Commissioners repeated their earlier request for a two-year closure in their preliminary report of 1907-08.[67] In 1909, these efforts culminated with the legislature, "after much discussion," enacting a two-year closure of the California spiny lobster fishery.

During the closure, Mexican sources supplied the market. When the fishery reopened in 1911, the legislature imposed a shorter time limit on the season, reducing it to five months, while it relaxed the minimum size limit from nine and one-half inches to nine inches.

Shortly after the fishery reopened, concerns about the health of the fishery and the lobster population resurfaced. An article in the Santa Barbara Morning Press warned, "How many thousand crawfish were taken from the waters of the Santa Barbara Channel yesterday, the first day of open season, will never be known; but it

is certain that the number was enormous, and it is certain that there will be few of these delicate Pacific lobsters left to stock the beds for another year."[68] That same year, The Los Angeles Times reported that County Supervisor H.J. Doulton "strongly" advocated "action toward the restriction of crawfish business in the Santa Barbara Channel."[69] A year later, Bennet Allen, a researcher contracted by the California Fish and Game to study the lobster population, concluded that although the two-year closure was successful, as "spiny lobsters were very plentiful this 1911-1912 season," the "the benefit will be short-lived because of the depletion of the supply."[70] A continuance of the heavy catch of last season must inevitably make it necessary to again impose a closed period of two years or more, to enable the fishery to again rehabilitate itself." He also noted that Santa Catalina Island had recently "become so depleted by intensive fishing that the fishery is no longer profitable there."

Evidently responding to these calls for another closure, in 1913 the legislature shortened the season slightly. The legislature heeded Herrick's advice to protect large lobster and established a maximum size limit of thirteen and one-half inches, in addition to the pre-existing minimum size limit.[71] In 1917, the legislature adjusted the size limits, significantly relaxing the maximum limit to 16 inches and tightening the minimum limit to ten and a half inches.

2. Quantitative Corroboration of Parameter Estimates –Decrease in Lobster Size (1880 to 1915)

Historical records can also be employed to verify the magnitude and direction of changes in parameters estimated by a model. I illustrate this technique by comparing estimates of changes in average individual lobster size generated by the Bayesian model (McArdle and Kinlan, in prep and Chapter One) with size reports from multiple independent historical sources.

The Bayesian model predicted that California spiny lobster size declined during the development phase of the lobster fishery, from 1895 to 1915. Historical accounts from multiple newspapers and government reports generally support this finding. Historical records show that the average size of lobster caught began to decline shortly after the onset of the fishery's development phase in 1890. The 1894 U.S Fisheries Bureau survey of the Pacific Coast estimated that, "The average weight of those [spiny lobster] sold in San Francisco" had decreased to between "2 and 4 lbs."[72] Although the average size of lobster caught was decreasing, large lobster remained a significant portion of the catch for at least the next five years. Lobster weighing as much as seven pounds were "common," and ten to twelve pound animals "cannot be rare."[73] Newspaper articles reported catches that included many lobster that were "over twelve pounds each."[74]

Shortly after the turn of the century, a government surveyer estimated that the average spiny lobster now weighed an average of "3 pounds."[75] Although this average was similar to that of just a few years prior, the California State Board of

Fish Commissioners and a few experienced fishermen noted the "extreme lightness of the catch of legal-sized fish [lobster]" [76] The source of their concern may have been the recognizable disappearance of the largest animals from the catch. By 1911, spiny lobster weighing over ten pounds, evidently a considerable share of the population during the 1890s, were "very uncommon." The large end of the size spectrum appears to have been reduced to the four to six pound range, which were "not infrequently met with."[77] Moreover, "Many of the lobsters caught were under the regulation size," nine and one-half inches, and had "to be thrown from the traps back into the waters by the fishermen."[78] Five years later, in 1916, a Wells Fargo Messenger newsletter that described "California's Crawfish Industry" estimated that the average lobster's weight was then between one and three pounds.[79]

Thus, according to historical accounts, the weight of the average lobster caught declined by approximately 33% from 1895 to 1916, falling from roughly three to two pounds, with a concomitant decrease in the frequency of very large individuals. The Bayesian model predicted a similar, somewhat smaller decline during the same time frame of about 20%, from an average of approximately 2.6 to 2.1 pounds.

Model estimates of lobster size from the earlier period of 1888-1895 reflect considerable uncertainty, because fewer preceding years of data exist to inform model estimates of size structure. However, when compared to historical records, the model estimates appear more reliable (see Chapter One: Fig. 11). Between 1888 and 1894, the model predicts that the average size of lobster declined from 5.8 to 2.6 pounds, or

56%. This reflects the trend described in the historical accounts. Reports of spiny lobster size began with an 1880 U.S. Bureau of Fisheries survey, which stated that "average-sized individuals" weighed approximately "three and one half pounds to four pounds."[80] An 1882 report on the Commerce and Industries of the Pacific Coast of North America stated that spiny lobster or, "crawfish," sold in "the San Francisco market" typically weighed "4 to 6 pounds."[81] Most of the spiny lobster sold in San Francisco at the time were caught in the Santa Barbara region, where a local historian confirmed that there were many "crayfish, of a large size"[82] Combining these records, we could approximate the average weight of a lobster caught in the early 1880s to be 3.5 to 6.0 lbs. The Bayesian model estimated that lobster caught in 1888 weighed an average of 5.8 lbs, in good agreement with historical records. Furthermore, historical records document that the average size of legal lobster fell to 3.0 lbs by 1894, only slightly more than the 2.6 lbs estimated by the model.[83]

D. Validating the Temporal Scale of the Chosen Baseline

Understanding "original" or pre-exploitation historic conditions is a fundamental requirement of any effort to determine the magnitude of changes in populations, communities and ecosystems after the onset of exploitation, identify realistic starting points for ecological models, or set baseline targets for restoration (Willis and Birks 2006).

In terrestrial ecology, the classic norm for American pre-exploitation conditions was the state of a site just prior to 1492, or before European-American

settlement. The idea that 1492 was a pre-exploitation state stemmed mainly from the assumption that "the entire Western hemisphere was in a natural condition, free from human influence, when discovered by Columbus" (Callicott 2002). Ecologists believed that there were so few pre-Columbian inhabitants of North America that they could not have had a significant ecological impact. Aldo Leopold advanced the similar idea that if landscapes were restored to the condition that existed when "our ancestors first arrived," they would be in their "original" state (Meine 1999). This suggestion became an accepted guideline for restoration.

Marine ecologists have traditionally taken a different, shorter-term view, assuming conditions just prior to the development phase of a fishery represent the pre-exploitation state. Thus, until recently, few historical marine ecological studies dated back further than the 1940s. In the late 1990s, marine historical ecology recognized that in some cases baselines for study and restoration may need to extend back to Columbus' arrival (Jackson 1997).

Recently, determining "original" conditions before human impacts has become more complicated. In both marine and terrestrial systems, studies have shown that the pre-Columbian condition may be an inappropriate reference condition for ecological analyses or restoration efforts. Contrary to earlier assumptions, Native Americans had the capacity to dramatically alter both terrestrial and marine environments (e.g. Wing and Wing 2001, Jackson et al 2001, Pandolfi et al. 2001). Thus, the identification of pre-exploitation conditions may require studies that extend their temporal scale back to prehistoric periods.

One can evaluate the extent to which a selected baseline represents a true pre-exploitation condition, and determine whether it should be extended father back in time, by reviewing historical records near and before the chose time period. A wide range of historical sources provide evidence of pre-settlement conditions. These include traditional written sources, such as early explorer accounts, maps, missionary reports and Native American accounts and biographies (Egan and Howell 2001). Less conventional sources include archaeological remains, genetic analyses, dendrology and oral, written, or anecdotal evidence (reviewed by Swetnam et al. 1999, Egan and Howell 2001, Pinnegar and Engelhard 2007).

The spiny lobster case study illustrates how archaeological findings and early explorer accounts can be used to verify whether a chosen historic baseline realistically represents a pre-exploitation state. I focus on four specific questions that test the chosen reference point, the advent of the modern commercial lobster fishery in 1888. These questions could also be applied to existing or future studies.

1. Was exploitation before the chosen reference point significant enough to call into question this baseline?

2. Were there significant ecological and environmental influences on the lobster population, including exploitation of other species that undercut the chosen baseline?

3. Assuming exploitation or the environmental context had a significant impact, where in the historical trajectory did important shifts occur?

4. If an earlier point in the time line more accurately represents the "original" state, does the chosen baseline remain a reasonable approximation of the pre-exploitation state?

1. Rationale for initial choice of 1888 as a reference point

Government reports and newspaper articles establish that in 1888, the California spiny lobster population was not in a pre-exploitation state. As described in above, the commercial fishery for California spiny lobster began eighteen years earlier, in 1870.

2. Question 1: Was exploitation before the chosen reference point significant enough to call into question this baseline?

The lobster fishery was in an initiation phase characterized by low levels of fishing intensity from 1870 to the 1890s. Historical records describe the California spiny lobster as being abundant during this time period, as described in prior sections.

Although fishing was limited in scale during this initiation phase, extending the baseline back approximately twenty years could increase our understanding of the lobster population's pre-exploitation state. The average or maximum lobster size might have been particularly sensitive to initial unaccounted for exploitation. Historical records, however, are consistent with predictions of initial lobster size structure from the Bayesian model (see Chapter One: Fig. 11).

Moreover, it would be difficult to expand the time series quantitatively back to a reference point earlier than 1880, because there is little documentation of lobster

catch or effort before this date. The government did not document lobster landings until 1888. Pre-1888 government fisheries export records could be an alternative source of information, given that Chinese fishermen exported most of their lobster catch to China from 1870 to 1880; but unfortunately, these records do not specifically identify spiny lobster. Cargo manifests of the Pacific Coast Steamship Company, which transported lobster from Santa Barbara to San Francisco at the onset of the fishery, are another possible source of information. However, according to historians familiar with this topic, the ship cargo manifests were usually discarded due to their perceived unimportance.[84]

By the 1890s the fishery had entered the development phase. At the beginning of this period, local newspaper reports suggest that lobster were still highly abundant. Santa Barbara was “wriggling with lobster" in 1893.[85] Similarly, the Los Angeles Times said that there was an “unlimited field for the crawfish catcher in this channel and on the shores of the Channel islands because “it flourishes in the Santa Barbara channel."[86] The lobster population appears to have remained robust until 1895, when concerns regarding declines first started. This is seven years after 1888, the point chosen for the reference condition. Thus, the 1888 baseline appears to reasonably represent conditions approximately prior to the onset of commercial exploitation.

Nevertheless, the assessment of the validity of this baseline could be extended further back into time. It appears that lobster fishing began in some form centuries before the 1870 advent of the commercial fishery. Is there evidence for a dramatically different population and size structure at some earlier time? To answer

to this question, I examine archaeological and historical records from prehistory to 1888.

Lobster Fishing in Pre-history (10,000-12,500 B.P. – 500 B.P.)

Native Americans began fishing along the southern California coast approximately 10,000-12,500 years ago, relying heavily on marine shellfish (Erlandson 1994, Rick et al 2001). Shellfish remains in Native American middens are mostly of rocky intertidal taxa, such as the California mussel, abalone, barnacles, urchins and gastropods (Rick et al 2001, Colten 2001). Although lobster occupy the same habitats as these animals, lobster remains are conspicuously absent from the middens. This is likely a preservation effect; lobster shells are thought to be too delicate to remain intact over long periods of time (Johnson 2008, Glassow 2008). Although archaeologists regularly find crustacean claw and carapace fragments in middens, none have undertaken the difficult task of determining the extent to which lobster remains contribute to the composition of these fragments.

Lack of midden evidence notwithstanding, spiny lobster was a significant enough presence within the Chumash environment to have several native names. The mainland Santa Barbara Chumash called lobster *wuluwul*.[87] The island Chumash called it *anaxcici*.[88] The Chumash also had access to the materials needed to make fishing nets, such as dip nets that could trap lobster in small rock pools. Rick et al. (2001) found almost 2000 pieces of woven seagrass cordage in a midden on San Miguel Island, that may be fragments of fishing line or nets (Connolly et al. 1995).

In short, there is circumstantial evidence from a variety of sources that

prehistoric Native Americans probably fished spiny lobster. Using prehistory as a baseline for study, however, would be problematic because there is no quantitative information on the number or size of individuals that were caught. Since lobsters range well into subtidal depths, it is probably reasonable to assume that pre-historic shoreline and near-shore fishing was negligible in the context of region-wide lobster population dynamics.

Lobster fishing after European Contact and Settlement (1542-1870)

Native Americans had occupied the Santa Barbara Channel region at least 10,000 years before the Spanish arrived in 1542. Between 600 B.C. and 1150, they had organized into villages of up to several hundred people each. As early as 750, these villages formed a complex trading network in the Santa Barbara Channel region within which they exchanged many products, including shellfish (Bowser 2001). This trade network remained intact until the Spanish moved the Native Americans out of their villages and into the missions.

Native American population and trade growth apparently resulted in greater pressure on marine life (Glassow 2001), including marine mammals, large fish and shellfish (Erlandson et al. 2004). There is, nevertheless, no evidence that Native Americans had depleted lobster populations by the onset of the "Spanish Era" (1769-1822). To the contrary, there are anecdotal accounts indicating lobster remained plentiful at the moment of European contact. For example, Spanish missionary explorer (1769–1774) Fray Juan Crespi noted the presence of "Much… lobsters…and many other fish" in Santa Barbara, Spanish and Indian villages.[89]

Spanish exploration of California began with Cabrillo's voyage, fifty years after Columbus arrived on the shores of the New World. Accounts from European explorers who followed Cabrillo's expedition provide a valuable source of information prior to and during the early Spanish settlement period. For instance, in 1602, Spanish merchant and explorer Sebastian Vizcaino documented the presence of lobster in San Diego Bay where he admired "a great variety of fish, as oysters, muscles [sic], [and] lobsters."[90]

By the end of the seventeenth century, Spain had formally colonized California. Between 1769 and 1823, the Spanish founded twenty-one Franciscan missions throughout the state, dedicated in part to converting the Native Americans to Christianity. As the Spanish settled in and expanded their influence over California, they were largely rancheros, and did not develop or take part in commercial fishing, except for marine mammals (Johnson 2008). Native Americans conducted most of the fishing during the "Spanish Era." Thus, in 1774, Fray Francisco Palou wrote that because the "beach Indians" were successful fishermen, "the missionary fathers have asked [the colonial government] for a canoe and a net" so that "the new Christians" could expand their fishing activities in support of the Spanish community.[91]

During the "Spanish Era," Native Americans were able to take a wide diversity of fish, in large quantities, with little effort. Western European writers observed abundant catches in Native American villages, and reported that Native Americans would often give them excessive amounts of fish as a gift. Although these accounts include few details relevant to choosing a baseline, such as the species

fished, the amount taken, and methods employed, it appears that lobster was part of the catch. In 1792, a biologist traveling with English explorer, Vancouver reported that Indians had devices that resembled lobster traps (Hudson and Blackburn 1982). Given the history of the Southern California Native Americans during the Spanish Era, though, it seems unlikely that Native American fishing would have had anything more than a minimal impact on the lobster population. As the Spanish absorbed the mainland tribes into the missions, Old World disease epidemics, starvation, disruption of island society by increased foreign contacts, and the disappearance of economic exchange with mainland villages decimated the Native American population. Over time, the population dropped from approximately 18,500 in the eighteenth century to just a few thousand by the 1820s.[92]

In 1821, Mexico won its independence from Spain and assumed sovereignty over Alta California, which remained part of Mexico until 1850. Like in the preceding era, the Mexicans' "work was exclusively on the ranches." [93] Some grew crops, but the mainstay of the 'rancho' was the hide and tallow trade. In 1824, the Chumash revolted against the newly established Mexican government, further reducing the Indian population and essentially guaranteeing that they would have no more than a negligible impact on lobster.

Thus, it appears that during the fifty to possibly one hundred years prior to the 1870 onset of the California spiny lobster fishery, the lobster population was subjected to little fishing pressure. The European settlers focused their commercial enterprises on cattle ranching not fishing, while disease and social dislocation quickly

overwhelmed the Native Americans. Consequently, given the approximately 5 year generation time and 20-30 year maximum lifespan of the California spiny lobster, it would be reasonable to assume that lobster population and size structure were close to a pre-exploitation state in 1870.

3. Questions 2 and 3: Were there significant ecological and environmental influences on the lobster population, including exploitation of other species, that undercut the chosen baseline? If so, what was their timing?

Finally, we consider whether any pre-1888 ecological events could have caused the lobster's population abundance and size structure to be uncharacteristic of its pre-exploitation state. It is well known that sea otters play this role in kelp forests and that they were heavily exploited in the 18th and 19th centuries. I examined both secondary and primary sources to determine the extent to which hunters had depleted sea otter in southern California, prior to the onset of the lobster fishery and by our 1888 reference point. I focused on records related to the Santa Barbara region, the area where the lobster fishery originated.

Determining the effect of 19th century sea otter exploitation on the California spiny lobster population structure is complex. Sea otter hunting began in southern California during the Spanish Era, in the late-1700s, and in Santa Barbara around 1786.[94] After five years, "the project proved unsatisfactory," so it ceased. The industry began again in Santa Barbara in 1802. It is often assumed that the sea otter was exterminated in California by the early to mid-1800s. The historical record reveals, however, that although the sea otter population in California was

significantly reduced by the late 1800s, it was much higher than has been commonly assumed in some regions such as the Santa Barbara coast and northernmost Channel Islands. According to historical records, sea otter were still "found in considerable numbers" in both the Santa Barbara Channel and around the islands lying off the coast in 1876, six years after the initiation of the lobster fishery.[95] Three years later, the sea otter population was considered large enough to support a hunting industry of "more importance than people generally suppose" on both "the islands and coasts of Santa Barbara."[96] By the early 1880s, historical records indicate that hunters had likely reduced the sea otter's range to the Channel Islands, although they were still found there in relatively high abundance. For example, one hundred otter were taken around San Miguel and San Nicolas Islands in 1882.[97] This would be the equivalent of taking approximately three percent of the statewide population in 2008.

While it is certain that there was a sea otter population at the Channel Islands during the 1880s, it is uncertain whether the otter population was large enough to enable it to play its functional role in the kelp forest foodweb, which could have had a significant, largely unpredictable impact on the lobster. The southern California kelp forest food web is a diverse complex system with trophic interactions among the sea otter, lobster, sea urchin and kelp (for reviews see Pinnegar et al. 2000 and Steneck et al 2002). Consequently, it is difficult to draw conclusions about how altered abundance of sea otter would affect lobster population structure. Altering any component of the foodweb could have cascading effects through the ecosystem, reducing or increasing lobster abundance.

Nonetheless, the historical record provides some insight into whether the otter was affecting lobster size structure near our chosen baseline of 1888. In the early 1880s, the surveyors from two government agencies documented that the average lobster weighed between 3.5 and 6.0 pounds, an average of 4.75 lbs.[98] Considering the lobster's life history characteristics, it is unlikely that this large average size was due to the functional elimination of the sea otter between 1876 and 1880.

To achieve the sizes measured in 1880 and 1881, a significant segment of the lobster population would have had to grow considerably larger within less than a decade. This is unlikely because lobsters generally take 7-8 years just to reach a legal size (83 mm CL), at which they weigh approximately 1.5 pounds (Allen 1913, Lindberg 1955, Engle 1979). From that point, adult lobsters only grow on average 3.75 mm per year (Odemar et al 1975, Engle 1979). Thus, it would take a lobster roughly 18-23 years from birth to reach the 4.75 lbs average (122.5 to 139.0 mm CL) (Lindberg 1955, Farris and Bigsby 1972). It is also unlikely that the high proportion of large-sized lobster present in the population in the early 1880s would have been the product of the growth of legal-sized lobster (83.0 mm CL) in this period because it would take approximately 10.5 to 15 years for a legal-sized lobster to grow to 4.75 pounds (Lindberg 1955, Farris and Bigsby 1972).

4. Question 4: To what extent is the chosen baseline a reasonable approximation of the pre-exploitation state?

The historical record indicates that fishing pressure on the California spiny lobster was probably insignificant for at least a century before 1888. Thus, our use of 1888 as a baseline for the onset of commercial lobster exploitation and our reconstruction of the historical size structure of lobster since that date are both consistent with the historical record. However, whether 1888 repesents the "original" state of the lobster population, is uncertain. To deepen our understanding of the history of kelp forest ecosystems, future studies may seek to examine some proxy of lobster (e.g. carapace fragments in Indian middens) and sea otter abundance that represents an earlier time period.

Other ecological factors like ocean temperature and productivity changes may have impacted the pre-exploitation state, but there is no evidence that major climate cycles (e.g., ENSO and PDO) behaved fundamentally differently during the mid-to-late 19th century period than they have in the past century.

E. Placing Observations and Estimations in a Historical Context

Historical documents can also supply a context for deepening our understanding of environmental variability. Changes over time in economics, politics, technology, value systems, and scientific and philosophical ideas can explain, individually or in combination, ecological trends predicted by a model or observed in the field. Moreover, history that illuminates these potential underlying reasons for ecological findings may be an important verification tool and, depending on whether the variability is of natural or anthropogenic origin, point towards possible improvements

in conservation measures.

In 'People and the Land Through Time,' Russell (1997) discusses several examples where the contemporaneous, relevant historical record offered explanations for ecological events. One was the observed increase in fire frequency in the U.S. during the mid- to late nineteenth century. Using historical records from railroad lines and various agencies including the U.S. Forest Service, Olson (1971) determined that there were more fires during this period due to the proliferation of railroads, which ignited vegetation along the rail lines. Russell also describes how Cramp (1963) discovered that the dramatic drop in Peregrine falcon abundance in the 1940s was due to a political activity. During World War II, the English killed falcons and other birds of prey to prevent them from interfering with an important wartime communication method – the passenger pigeon.

The California spiny lobster case study further illustrates the utility of combining historical research with ecological findings. McArdle (in prep) (Chapter Three) reviewed primary and secondary sources that described the history of ecology and conservation starting in the 18th century to determine whether scientific and philosophical ideas contributed to the decline in lobster size structure described in the beginning of this paper. Recent research proposes that the course of conservation may, over time, speed demographic changes, such as population size structure (Conover and Munch 2002, Baskett et al. 2005). Since ecological ideas are a significant driver of conservation strategies (Worster 1994, Meffe and Carol 1997), the author examined the historical interaction between marine conservation and

ecological theory and practice. Using the works of naturalists, ecologists and government researchers, scientific journals and reviews, the author found that some current lobster conservation tactics are based on ecological ideas that originated up to three centuries ago. These tactics appear to have facilitated and accelerated the historic rate of changes in lobster size structure. They are also probably undercutting contemporary ecosystem-based conservation measures designed in part to sustain the lobster population's size structure; suggesting that altering or removing these outmoded tactics may improve lobster conservation.

III. Conclusion

The spiny lobster case study demonstrates the efficacy of the five-part framework. Using nontraditional historical sources, this method assisted in compiling a longer time series for quantitative analyses, validating specific potentially questionable historic points in the data set, corroborating model predictions by comparing results to established historical paradigms, verifying that the baseline choice reasonably represents the "natural" condition, and providing possible explanations for ecological findings by considering them in historical context.

The framework can also have a broader benefit by facilitating the application of triangulation methodology. Triangulation synthesizes quantitative and qualitative information collected from multiple sources by different methods to increase confidence in or refute study findings. Relying on multiple sources and techniques reduces the likelihood of potential bias that can exist when depending on a single

source or method. Here, four different historical techniques incorporating both quantitative and qualitative information from different sources corroborated the Bayesian model predictions regarding the lobster population early in the history of the fishery. Each step in the analysis moved the study towards a more comprehensive ecological history of the lobster by further confirming the results, deepening insight into their underlying causes, broadening understanding of the lobster's ecology, and placing the findings within their historical circumstances.

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Chapter Three

The Ecological Underpinnings of Marine Conservation (1700 to 2008): Why Outdated Ideas May Tacitly Facilitate the Depletion of Large Animals

I. Introduction

For most of human history, man believed that the seas were limitless. Uncertainty has replaced the certainty of inexhaustibility. Recent studies reveal that marine populations are indeed exhaustible. Numerous marine species (Jackson et al. 2001, Pandolfi et al. 2003, Roman and Palumbi 2003, Rosenberg et al. 2005, Lotze et al. 2006) began showing signs of overexploitation centuries ago. Long-term persistent exploitation has severely reduced the abundance (Food and Agriculture 2000, National Marine Fisheries Service 2002) and size of individuals in many populations (for a review see Fenberg and Roy 2007). These structural changes have in turn altered ecosystem composition and function, the consequences of which are largely unknown (Fogarty and Murawski 1998, Steneck et al. 2004, Frank et al. 2005). Although this reshaping of the oceans occurred relatively quickly by evolutionary standards, it could take much longer for it to revert to a prior state (Conover and Munch 2002, Heino and Godo 2002, Law 2007).

Given the degraded state of the oceans, it is imperative that new conservation strategies succeed. To accomplish this, we must examine the path that led us here, since the past influences "what we do and why we do it" (Meine 1999). However, the

history of the marine environment remains largely uninvestigated, and histories of human interaction with the sea are scarce (Bolster 2006). Those marine historiographies that describe the origins and course of man's assumptions and knowledge about how the sea functioned often focus on the history of fisheries science. They portray the first century of marine history as a continuing search for a coherent and generally accepted theoretical explanation for the causes of finfish fluctuations (McEvoy 1986, Smith 1994, Taylor 1999, Lackey 2003). Because of this scientific uncertainty, the common perception is that marine conservation originated in common sense and, for much of its history, consisted of a series of disconnected efforts to control the unpredictable seas.

Histories of terrestrial conservation, however, have established that changing general ecological theories and cultural philosophical ideas have interacted to produce a coherent history (Worster 1994, Meffe and Carol 1997, Pickett and Ostfeld 1997). Terrestrial conservation originated in the ecological "studies" and philosophy of eighteenth and nineteenth century naturalists who studied and applied biology, zoology, botany and geology (Worster 1994, Farber 2000, Dayton and Sala 2001). Furthermore, over the last three centuries naturalists and later scientists have posited and contested six dominant principles that have directly influenced conservation: whether and the extent to which ecological systems are closed, self-regulated, exist in equilibrium, follow deterministic succession, subject to environmental disturbance, and are influenced by humans (Worster 1994, Pickett and Ostfeld 1997). Studies examining the interaction between the history of ecology and philosophy find that

terrestrial conservation has followed a path that traces generally the trajectory of these principles. A model with three conservation "ethics," Romantic, Resource Conservation and Evolutionary-Ecological, marks this path (Meffe and Carol 1997). These "ethics" incorporate and apply the ecological theories and assumptions, and the larger society's cultural norms and philosophical views prevailing during each era (Oelschlaeger 1991, Worster 1994, Callicott 1997, Pickett and Ostfeld 1997).

This study tests the efficacy of this conservation "ethic" model to describe the historical pattern of marine conservation. It uses the conservation history of the California spiny lobster, *Panulirus interruptus* and the American lobster, *Homarus americanus* as case studies. Lobsters are useful for this purpose because they were some of the first stocks recognized as requiring conservation because they were exhaustible. While many nineteenth century naturalists were debating whether this was true for finfish, most had already concluded that invertebrates like oysters, crab and lobster were exhaustible. Even Thomas Huxley, the naturalist who famously claimed that "all the great sea-fisheries are inexhaustible," was an early advocate of invertebrate conservation. As such, studying invertebrates like lobster allows for an analysis of the origins of marine conservation as well as the path that it traversed. This provides a template against which other species can be compared to historicize marine conservation.

Finally, I apply this template to a model-generated reconstruction of California spiny lobster population variability over 120 years (McArdle and Kinlan, in prep and Chapter One), to identify and discuss how the interaction between

ecological ideas and conservation strategies may have facilitated and accelerated the rate of decline in the California spiny lobster population's size structure that has continued to the present. I discuss how the lobster population's conservation regime continues to include tactics that originated and were questioned over a century ago. Continued reliance on conservation strategies grounded on outmoded ecological models could be partially responsible for the present depleted state of large lobster (McArdle and Kinlan in prep and Chapter One), and could undercut new better-informed ecosystem-based strategies.

This study's findings will contribute to both the established historiography on the history of ecology, ongoing work in historical ecology, and the emerging literature on marine environmental history. It also introduces the concept of "conservation crossroads" to improve the understanding and resolution of contemporary marine conservation issues.

II. Methods

The scientific rationale and assumptions underlying conservation goals for the lobster were first and most thoroughly developed on the East Coast for the American lobster. Since experts studying the California spiny lobster were well aware of these efforts and viewed them as a starting point for their own work, I examined the rationale and assumptions underlying conservation goals for both species for the first three eras; thereafter I only examined the spiny lobster. I reviewed archives at local, state and national museums, compiling personal letters,

oral histories, local and state newspaper articles and government reports, tracing the history of the science and conservation of the American and California spiny lobster. I then evaluated these sources against a conceptual model that coupled major ecological principles with three philosophical conservation eras: Romantic, Resource Conservation, and the Evolutionary-Ecological.

III. Findings

The origins of marine conservation stretch back centuries, to the ideas of naturalists such as Bacon, Linnaeus, Lyell and Darwin. Naturalists and later scientists persistently evaluated existing, and developed new, marine conservation measures through the lens of their era's ecological understanding and philosophical views of nature generally, the oceans specifically, and man's relationship to both.

Lobster conservation has generally followed this pattern, for the last 150 years. Historical ecological ideas held that the marine environment was closed, self-regulated, in equilibrium, changed through deterministic successions, and rarely experienced environmental or anthropocentric disturbances. The view shifted to one in which marine systems were rarely if ever closed, often regulated by external events, infrequently maintained equilibrium, seldom followed deterministic successions, and commonly experienced disturbances including those driven by humans. Philosophical views of man's relationship to the sea also shifted from a primarily anthropocentric and mechanistic worldview to one that was biocentric and cognizant of the ocean's inherent complexity. As these ecological and philosophical

assumptions shifted, marine conservation followed suit, moving from production-based single-species to ecosystem-based approaches.

While the original three-era model fit the history of lobster conservation well, it did not disclose its full trajectory. To identify the roots of lobster conservation, I extended the original model's view back one hundred years, adding the Inexhaustibility era (Fig 1). To explain changes in lobster conservation between 1870 and 1970, I subdivided the Resource era into the Resource Progressive Conservation and Resource Scientific Conservation eras. Thus, the extended model includes five eras, Inexhaustibility, Romantic, Resource Progressive Conservation, Resource Scientific Conservation, and Evolutionary-Ecological. Lobster conservation fit the expanded model in all but the Romantic era.

A. The Inexhaustibility Ethic (1700-1880)

Many of the ecological and philosophical ideas that drove marine and lobster conservation for well over a century originate from eighteenth century natural historians during the Age of Reason. They viewed nature from an anthropocentric and mechanistic perspective as a closed, fixed system that was in a perpetual state of equilibrium, and impervious to either environmental or anthropogenic influences.

Reflecting on the mechanistic philosophy of Descartes and Newton, naturalists viewed nature as a smooth functioning machine consisting of immutable, replaceable parts that they could mathematically describe, predict and control. The Swedish naturalist, Carl Linnaeus, was one the most famous exponents of this

perception, presenting this model of nature in *The Oeconomy of Nature* (1749). Linnaeus saw "the hand of God in nature" (Worster 1994). God fashioned a "Grand Design" composed of separate organisms living in isolation from environmental variability, with fixed and independent qualities, and adapted to their environment at their creation. A species' characteristics and patterns were not a product of historical evolutionary processes, they simply occurred.

Linnaeus reasoned that God benevolently created this state of balance or "rational order and harmony" by assigning every plant and animal a peculiar food, geographical range, and minimum and maximum rates of reproduction. Thus, the Creator arranged a system of differential reproduction rates by which the "harmless and esculent animals" reproduced vastly more than their predators so that numbers of both would remain relatively stable. Creatures created only to be "miserably butchered by others" were essential to the plan of Providence, since they kept "a just proportion amongst all the species" and prevented "any one of them increasing too much, to the detriment of men, and other animals" (Worster 1994).

Linnaeus perpetuated the anthropocentric view espoused earlier by Francis Bacon that, "The world is made for man, not man for the world." According to Linnaeus, the, "treasures of nature" seemed "intended by the Creator for the sake of man" and "subservient to his use." It was man's responsibility to use and improve nature by increasing its productivity, while avoiding becoming "mere idle spectators."

Some naturalists saw a potential flaw in this reasoning because there were already well-known examples of man seriously diminishing the number of other species. Linneaus' followers answered by relying on their understanding of natural history and belief in God's benevolence. They rationalized that the Creator's plan did not provide humans with the capacity to eliminate another species because, to their knowledge, no plant or animal had become extinct even though humans had been exploiting nature for millennia.

The naturalists' conclusion that it was impossible for humans to alter the Creator's grand scheme was consistent with the prevailing faith in the Western World; nature was for man's use and was essentially inexhaustible (Nash 1967). Although preservation was part of God's design, conservation was usually "left to Providence." There is little readily available information regarding the application of these principles to the marine world during this era. As for the lobster, historical records, if they exist, would likely focus on European commercial fisheries, which began in the eighteenth century. American commercial lobster fisheries did not start until the 1840s. Nevertheless, these ecological and philosophical ideas influenced naturalists and lobster conservationists throughout the next century.

B. The Romantic-Preservation Ethic (1820-1920)

The early nineteenth century saw the rise of Romanticism. Artists, intellectuals, naturalists and the public showed increasing interest in nature. Figures such as Emerson, Whitman and Thoreau were influential in the American

movement. Romantics sought to redefine how nature functioned and man's place in the "Grand Design." They saw nature as a system of interconnected relationships that if disturbed would disrupt the equilibrium of the whole. Individual organisms were not like the gears and screws of a clock that man could remove and replace without altering their identity or interfering with the clock's timekeeping. In contrast to the eighteenth century anthropocentric view that man should and could dominate and transform nature for his own purposes, some Romantics began to believe that man should learn to accommodate himself to the natural order.

Romantics' appreciation for wilderness led to concern about its disappearance from the American landscape. The population of the United States was growing rapidly and new technologies enabled species extraction at rates and geographic scales previously unimaginable. Naturalists, in contrast to their forbearers, could see the changes in terrestrial landscapes within the course of their own lifetimes. By the 1830s, concern over the loss of wilderness led some Romantics to question whether society could continue to leave conservation in the hands of the Divine Engineer (Nash 1967). They asked society to preserve, as Thoreau stated, "a certain sample of wild nature" so at least some portions of nature were not degraded and could function holistically.

Romantics were also enamored by the sea. Its seeming unchanging character provided an "eternal reference" against which they compared their temporary existence (Corbin 1994). Viewing the ocean from the shore, they were unable to recognize any degradation of marine flora or fauna. The ocean appeared

timeless, immutable, and impervious to man. Because of this myth of a timeless ocean, Romantics did not generally express concern over the loss of marine wilderness nor call for the ocean's preservation. Thus, the oft-described debate in histories of conservation between "preservationists" and utilitarian "conservationists," is conspicuously absent in nineteenth and early twentieth century marine historical records and marine conservation does not fit the original ethics model during this era. In contrast to terrestrial conservation, the generally accepted wisdom passed down from the naturalists of the Age of Reason remained the dominant ethic applied to marine life. Human beings could do virtually nothing to disrupt the balance of the sea. Conservation of the sea, for the first half of the nineteenth century, remained in the hands of Providence.

It would take approximately 150 years for the ecological ideas that Romantics proposed to influence marine conservation.

C. The Resource-Progressive Conservation Ethic (1880-1920)

1. Ecological Ideas

In the nineteenth century, naturalists began to see nature in a different light. In contrast to Linnaeus's static model, the new ecological model described nature as dynamic. The "Grand Design" was not composed of organisms with fixed qualities, adapted to their environment the moment they were created. Rather, a species' characteristics were changeable and the result of historical evolutionary processes. Jean-Baptiste Lamarck and especially Charles Darwin pioneered this idea. In his

Origin of the Species (1859), Darwin surmised that nature evolves through competition among and within species, with selective breeding producing new species of organisms. This occurred through a mechanism that Darwin described as 'survival of the fittest,' an idea that he grounded on principles in Reverend Thomas Malthus' *An Essay on the Principle of Population* (1798). Malthus wrote that populations tend to 'increase at a geometrical ratio.' Darwin explained that the 'struggle for existence' checks this potential growth. Only a very small number of the offspring of any species survive this competition to maturity. Nature favors these survivors possessing variations that enhance their ability to compete, resulting in new species better adapted to the environment. Thus, the balance of nature was no longer due to God's benevolence; it was a result of "constant warfare" or a struggle to survive.

Although Darwin viewed most characteristics as being changeable, he and Malthus believed that species fecundity was fixed. In this way, his ideas echoed those of eighteenth century naturalists.

The historical approach taken by naturalist Charles Lyell in his *Principles of Geology* (1830) inspired Darwin. Based on the geological and paleontological record of species extinction in man's presence, Lyell recognized and drew broad attention to the fact that man could disturb the balance of nature by diminishing the number of species. This long-term perspective made Lyell one of the first naturalists to diverge from the belief that the "Creator's plan" did not provide humans with the capacity to eliminate other species. However, unlike the

Romantics, Lyell did not regret this ecological disorder. To Lyell, man was just another predator, acting according to natural law. Furthermore, compared to the environmental changes wrought by geological forces, man's impact on nature appeared negligible (Worster 1994).

Lyell also influenced naturalists on both sides of a growing debate during this era over the accuracy of the basic assumption from the Inexhaustibility Ethic that marine species were invulnerable to man's exploitation. The typical response to those who first suggested that marine life was exhaustible reflected eighteenth century naturalists' confidence in nature's capacity to overcome man's exploitation. A review of the "Report on the fisheries of Norfolk, especially crabs, lobsters, herrings, and the broads," authored in part by well-known and influential British naturalist Frank Buckland, explained how those who first claimed that marine life was exhaustible were "laughed at as visionaries, or scouted as false prophets to whom none should listen" (The London Quarterly Review 1877). Overfishing was impossible because of "the prodigious powers of reproduction with which fish and crustaceans are endowed."

Approximately fifty years later, prominent British naturalist Thomas Huxley repeated this argument during his inaugural address to the 1883 United Kingdom Fisheries Exhibition. In support of his well-known and influential proclamation, "all the great sea-fisheries are inexhaustible," he claimed that fish could multiply at such an enormous rate that the quantity caught was relatively unimportant (Huxley 1884). Huxley also reflected the latest thinking, echoing Lyell by asserting that fishing had

no appreciable effect on total mortality or nature's balance given the overwhelming magnitude of environmental disturbances.

During the Fisheries Exhibition and over the next few decades numerous naturalists challenged the inexhaustibility position (for a review of these debates see Smith 1994). Buckland, like Huxley, incorporated Lyell's concepts into his argument, arguing that the "destructive power of man" was "insignificant, when, it is compared with the destructive agencies which nature created" (Bompas 1885). In the case of migratory finfish like herring, "nothing that man has done, or is likely to do" will have "any appreciable effect" on their abundance.

Huxley and Buckland, however, did not believe that the plentitude of marine life always counterbalanced man's impact. Lobster and other near-shore marine invertebrates, such as oyster and crab, were vulnerable to "overfishing" and therefore exhaustible (Buckland 1875, Great Britain Commission on Crab and Lobster Fisheries 1877). Six years before Huxley's famous speech, Buckland requested restrictions on lobster fishing in Norfolk England to prevent a collapse of the fishery (Great Britain Commission on Crab and Lobster Fisheries 1877, The London Quarterly Review 1877). Unbeknownst to most, Huxley had extended Buckland's order to restrict crab and lobster fishing the same year he gave his Fisheries Exhibition address (Huxley 1900). Huxley believed that invertebrates were vulnerable to overfishing because, unlike finfish in the major fisheries, they were non-migratory and confined to limited areas (Collins 1904).

Huxley and Buckland's agreement that lobster were vulnerable to overfishing is not surprising since by the time Huxley gave his Fisheries Exhibition speech, the decline of lobster fisheries was a well-worn theme, depleted in every location where there was a commercial fishery - Scotland, England, Norway, and Newfoundland (Herrick 1893). Concern was also mounting in the U.S. about the potential for an American lobster collapse. Commercial interest in the American lobster started around 1820. Large-scale production began in Maine during the 1850s and expanded rapidly over the ensuing decades. By the turn of the century, a U.S. Fish Commissioner expressed his unease about the growth and continuing viability of the lobster fishery to Huxley. He also quoted Huxley for the proposition that lobster were exhaustible stating, "Why, even Professor Huxley, the distinguished apostle of the theory that man's influence on the free-swimming ocean fishes is nil, concedes that some species [e.g. lobster and other near-shore invertebrates] …are liable to serious depletion through over-fishing" (Collins 1904).

At the same time, the United States Fish Commission (USFC) was also aware of the California spiny lobster's potential exhaustibility. A small-scale coastal commercial fishery began during the 1870s. By 1890, the fishery had shifted from an initiation to a development phase that was characterized by larger scale production (McArdle, in prep and Chapter Two). It had also become one of the most lucrative commercial fisheries in Southern California. In 1890, a USFC survey of California marine life resources concluded that the California spiny lobster was also "in danger of extermination from overfishing" (Herrick 1909). The California State Board of

Fish Commissioners (CBFC) likewise warned the Governor in 1905 that the fishery was showing signs of great depletion, if not extermination (California State Board of Fish Commissioners 1907).

2. Philosophical Ideas

During this era, nineteenth century naturalists continued to embrace an anthropocentric worldview similar to that of the Inexhaustibility Ethic. In a twist on this old idea, species once valued out of respect for God's plan to make them subservient to man's needs, were now deemed worthy only when their lives were transformed into "resources" that supported the new market economy, and in turn advanced society by improving the material quality of life. Naturalists' view of nature as a provider of "resources" was at least partly a product of the Progressive Movement during the last quarter of the nineteenth century (Hays 1959). Progressives' overarching goal was to reform and regulate large businesses and corporations. A secondary and related goal was to manage the nation's public "natural resources" in a manner that ensured they were fairly distributed and sustained in perpetuity.

Gifford Pinchot was a major architect of the Progressive conservation ideology. A naturalist who served as President Theodore Roosevelt's Chief Forester, Pinchot based his conservation blueprint on the philosophy of utilitarianism originating from 18th century philosopher Jeremy Bentham (Bentham 1823, Hays 1959, Katz 1997). Bentham premised his theory on the belief that an

action's "utility" is measured by the extent to which it creates pleasure or reduces pain. The morally correct course is the one that maximizes the pleasure of those human beings affected by it. Utilitarian political economists reinterpreted Bentham's original idea by strictly defining pleasure or utility in economic terms (Katz 1997).[99]

Thus, the ethically proper action became the one that maximizes the economic wellbeing of those human beings affected by it. Following this reasoning, the greatest good or benefit comes to a society when species become 'resources' that by definition produce monetary gain. Those who managed natural resources from this point of view called themselves 'Conservationists.

3. Marine Conservation and the Philosophy of Progressive Utilitarianism

The 'natural resource' philosophy that grew out of the Progressive movement guided both federal and state agencies in setting goals for and measuring the effectiveness of conservation policies. Consequently, their efforts to conserve marine life were focused primarily on production, not preservation.

The influence of progressive ideology is evident in the early history of the United States Fish Commission (USFC), established in 1880 to study and manage marine resources. The USFC contracted with natural historians Dr. George W. Field, a biologist at the Massachusetts Institute of Technology and a Massachusetts Fish Commissioner and Professor Francis Hobart Herrick, a professor at Western Reserve University in Ohio, to provide the scientific underpinnings for its goals of sustaining and expanding the American lobster fishery. Two of Herrick's works remain the

most comprehensive studies on the general biology of the American lobster, *The American Lobster, A study of its Habits and Development* (1893) and *The Natural History of the American Lobster (1909)*. After reviewing a draft of Herrick's major work on lobster biology in 1892, a U.S. Fish Commissioner wrote in a letter to Herrick that he was anticipating Herrick's lobster study not just because it would provide important scientific results, but also because it could have a significant positive economic impact on the fishery (McDonald 1892).

Herrick recognized the potential economic benefits of his research, explaining in a later publication that because larger lobster produced more eggs they could be "worth nine times as much as the smaller; in other words, in the course of [allowing the animal to live an additional] twelve years its value to the fishery has been increased by 800 per cent" (Herrick 1909). In 1904, another Fish Commissioner similarly asked Field to investigate the Massachusetts lobster fishery to learn how it could "better advantage" consumers, fishermen and dealers (Collins 1904). Field also described the purpose of this study in utilitarian terms, "how to permit the production of the greatest possible number of lobster eggs" and to market "the maximum quantity of lobster meat" to meet "market demands" (Collins 1904).

In 1870, the California legislature created the CBFC to restore and preserve fish in California waters. Like the USFC, the CBFC institutionalized the philosophical goals of utilitarianism. According to the first Director of the CBFC's Department of Commercial Fisheries, the economic benefits of commercial fisheries "could be greatly extended" with "proper conservation" (Scofield 1916). Reflecting

this utilitarian perspective, the CBFC did not embrace Romantic 'preservationist' ideas, which had apparently penetrated into views of the ocean by the turn of the 20th century. [100] The CBFC would not follow "the eastern centers of radicalism, where some weaned themselves away from the practical aspects of the problem to chase the chimera of sentiment." Protecting nature for preservationist reasons was "sentimental," "ultra-aesthetic," and aimed at setting "the rod in its corner for all time," and thereby conflicted with their goals of promoting social progress and economic welfare (Hedderly 1916). Naturalists working for the CBFC also aimed to meet the utilitarian goal of providing "wise, consistent conservation"of the lobster to "benefit the consumer" (Allen 1913).

4. The Integration of Ecology, Philosophy, and Conservation

The origins of 'formal' marine conservation arose at least in part, from the recognition that the lobster population was exhaustible. In accordance with the utilitarian ethic of the era, policy makers and most naturalists judged the health of marine life populations by their ability to sustain commercial fisheries. This anthropocentric production-oriented focus, coupled with a mechanistic view of nature, instigated a reliance on two single-species approaches to conservation – size limits and artificial propagation. Naturalists developed and evaluated the efficacy of these measures based on the ecological understanding of their time.

5. Lobster Conservation

Size Limits

Buckland reasoned that lobster were exhaustible because man could disrupt lobster populations by taking the breeding stock. Overfishing was by definition the taking of immature fish and fishing at inappropriate seasons. Buckland, therefore, argued for measures that allowed small lobster to spawn several times before being caught. He first recommended one such restriction, minimum size limits, in 1877 (Great Britain Commission on Crab and Lobster Fisheries 1877, The London Quarterly Review 1877). This was one of the first measures to conserve lobster. This conservation measure was based, in part, on the idea of eighteenth and nineteenth century naturalists such as Linnaeus, Malthus and Darwin, that lobster fecundity was fixed and that lobster lived in isolation from their environment. Thus, if lobster had two or three opportunities of adding to the piscine population before being removed, the population would return to equilibrium regardless of environmental influences (The London Quarterly Review 1877). As invertebrates like lobster were some of the first species subject to widespread conservation, this represents an example of the origins of institutionalized marine conservation based on generally applicable ecological principles. Shortly thereafter, minimum size limits were instituted on the east coast American lobster fishery and the California, Australian, French and Mexican spiny lobster fisheries.

Herrick disagreed with Buckland's reasoning that protecting immature and spawning lobster could restore equilibrium to their populations. Herrick criticized

this technique because it did not embody the current state of ecological knowledge, namely Darwin's law of survival (Herrick 1909). According to Herrick, the most egregious error was the belief that if female lobsters were able to reproduce only a few times, there would be enough eggs to sustain the population and the fishery. This assumed that a large proportion of the huge numbers of eggs that lobsters produced survived to sexual maturity. Herrick explained the fault in this logic to the 1897 National Fishery Academy, "In the animal kingdom the production of a large number of eggs points, not to a greater number of survivals and consequent abundance of the species, but to a greater destruction of young, which makes a large number of eggs a necessity in order to maintain the species even at equilibrium." Herrick pointed to his discovery that while lobster produced between 3,000 and 100,000 eggs each, most of these eggs did not survive to maturity. Thus, protecting only the young "egg lobsters" would not produce enough animals to replace the lobsters taken by fishing.

Herrick also found that larger older lobster produced more eggs, so by "legalizing the capture of the large adult animals," "the great source of eggs themselves-the large producing adults" were destroyed (Herrick 1909). Herrick's collegue Field similarly asserted that minimum size limits put a premium on the capture of large lobster "through tacitly specifying that only adults above the breeding age shall be killed" (Field 1902). Instead of maintaining population equilibrium, the minimum size method of "protection" would result in population decline.

Herrick and Field grounded their claims on practical knowledge, not just theory. By 1902, traditional policies were uniformly failing to protect large lobster.

According to Field minimum size limits had not "prevented the continued rapid decline" in "the average size of the lobster caught" throughout New England and the Maritime Provinces (Field 1902). By 1909, Herrick described the mechanism by which lobster size declined as a predictable three-stage trajectory: "(1) Period of plenty- *lobsters are large*, abundant, cheap; pots and fishermen few. (2) Period of rapid expansion- greater supplies each year to meet the growing demand; *lobsters in fair size* and of moderate price. (3) Period of real decline- fluctuating yield with a tendency to decline; a rapid extension of fishing areas; multiplication of fishermen, pots and fishing gear of all kinds; *decrease in the size of all lobsters caught*, and steadily increasing prices [emphasis added]" (Herrick 1909).

Consistent with the model, Herrick and Buckland based their conservation proposals on the prevailing ecological concepts. They understood fertility as fixed and independent of the environment. Thus, if lobster were allowed to reach their egg producing potential by protecting either small or large animals, the population would follow its predetermined path back to equilibrium regardless of other external influences. The sole "problem was to aid nature in restoring and maintaining equilibrium of the number of species" (Herrick 1909).

Artificial Propagation

Progressive conservationists recognized, like Lyell, that man could exhaust nature. However, they believed they could use science to overcome any manmade imbalance. Viewing nature mechanistically, they believed that if they understood

the laws governing nature's "parts," or in this case individual species, they could actively manipulate, improve and supplement them.

Hence, while naturalists were evaluating whether and how to restrict fishing activities, they were also attempting to counterbalance fishing pressure by artificially enhancing natural productivity. The tool that they relied upon most heavily was progressive scientific agriculture, the roots of which lie in eighteenth century English agriculture and forestry. Imported to America in the mid-nineteenth century, the initial goal of progressive scientific agriculture was to improve the productivity of virgin forests. Thus, the third chief of the Division of Forestry, Bernhard E. Fernow, described the problem with unmanaged forests was they produced only a fraction "of the useful material which it is capable of producing" and took "two to threefold the time which it would take under skillful direction" (Fernow 2000). Conservationists employing scientific agriculture believed they could eliminate this inefficiency by skillfully planting, cultivating and harvesting forests like farmers managed agriculture crops. Foresters replaced large old trees that they viewed as stagnant with younger faster growing trees, converting the country's vast expanses of old growth "mixed up messes" into stands of "thrifty" young trees, or "vigorous producers of wood fiber in perpetuity" (List 2000).

After starting with forests, conservationists progressively applied scientific agricultural methods to terrestrial wildlife, fresh water fish, and ultimately marine life. Marine conservationists attempted to supplant and cultivate marine populations by 'seeding the crop,' using two artificial propagation techniques. They either

'seeded' the ocean by spreading eggs and larvae, or they 'replanted' mature animals from one geographic location to another. Marine naturalists explicitly and routinely referred to shallow water invertebrate populations, including lobster, as crops. To Herrick, the depleted state of lobster populations at the turn of the century was a result of man "continually gathering in the wild crop" while bestowing "no effective care upon the seed" (Herrick 1909). Naturalists studying California spiny lobster saw the results in forestry as the benchmark against which they would measure their efforts to artificially propagate the species. And they were convinced they would succeed because "Exactly the same principles apply to conservation of our fish as to the conservation of our forests" (Allen 1913).

U.S. federal and state agencies adopted these techniques during this era and placed a high priority upon and invested a significant proportion of their funding on the artificial propagation of lobster (Goode 1886, Towle 2001). This task proved much more difficult than naturalists predicted. The USFC attempted five times from 1874 to 1889 to acclimatize the eastern American lobster on the west coast, with thousands of animals transported across the continent in special box cars, designed at great expense. One Fish Commission expert summarized the outcome, "No positive results … appeared" (Smith 1896). By 1911, attempts to rear the California spiny lobster also "proved futile" (Allen 1913).

Herrick was one of the naturalists employed in the artificial propagation endeavor. Applying Darwin's ecological ideas, he explained that lobster hatcheries were "not very encouraging" when "analyzed in the light of the law of survival"

(Herrick 1909). Lobster had evolved a survival strategy to spawn vast numbers of eggs because only a very small number of them survived to maturity. The common practice of hatching and raising fry was not likely to achieve the utilitarian goal of providing "material aid to fisheries" because it at that point it was not feasible to raise sufficient eggs and larvae to overcome the higher mortality rates. Although Herrick and others thought that artificial propagation would ultimately be successful, the effort was suspended after several fruitless decades.

D. Resource-Scientific Conservation Ethic (1920-1970)

1. Ecological Ideas

By the middle of the twentieth century, the investigation of nature was no longer the sole province of natural historians observing and describing general patterns from which they derived ecological ideas. Underpinned by the basic relationships between species and their environment deduced by the naturalists, ecology became a specialized discipline searching for principles grounded on the scientific method. Eugene Warming, Frederic Clements, Eugene Odum, Charles Elton, Joseph Connell, and Robert McArthur, among others, charted the original course for this emerging discipline.

Ecologists realized that not only did individual species evolve over time to adapt to their environment, so did the communities of species within which they lived. Communities changed in composition and complexity through a process of succession. The first organisms to dominate the system modified the environment in

ways that were ultimately detrimental to themselves and favorable to new species. Over time, the number of species increased until the community reached a predetermined climax, or mature ecosystem, state, at which point its composition and function became relatively stable or in equilibrium. Climate was the primary determinant of climax community composition, undercutting the prevailing belief that species existed in isolation from their environment. While this idea of a preset equilibrium state resulting from succession may appear to embrace the traditional "balance of nature" concept, it was different from the static order described by eighteenth and nineteenth century naturalists. To Odum, in particular, nature's equilibrium fluctuated around a single homeostatic point, resulting from species within an "ecosystem" evolving to work together to make their surrounding environment increasingly suitable as a habitat. The primary example of succession was the transition from grassland to hardwood forest.

Community succession was analogous to the growth of populations described by the study of population dynamics at the time (Royce 1972). Population composition was thought to proceed through a predictable pattern of logistic growth, represented by an S-shaped curve. The initial stage of growth was approximately exponential because the population had low biomass and was composed of young animals. As it increased to a critical density, competition for essential resources slowed and eventually stopped growth. When the population reached this equilibrium state, its composition would have succeeded from primarily fast growing young to slow growing old animals.

2. Philosophical Ideas

Many twentieth century naturalists continued to embrace the utilitarian and mechanistic view of nature. Michael Graham summarized this prevaling utilitarian view of the sea in the well known publication, *The Fish Gate,* (1943) stating, "The fishing industry must work with nature just as agriculture must work with the soil and weather, and as mechanics must fulfill the dreams of the designers of their machines.

3. Interaction of ecology, philosophy and conservation

Some conservationists aimed to preserve climax communities (e.g. old growth forests), or at least allow them to remain in a relatively undisturbed state. At the same time, however, scientists and conservationists recognized the utility of communities or populations in earlier successional stages composed of smaller, faster growing plants or animals. Some ecologists, including Clements, in accord with the Resource Conservation Ethic, attempted to determine how to create these more productive states by "carefully and skillfully" reversing succession in communities and populations.

Marine conservationists, continuing their single species approach to conservation, applied succession theory to populations not communities. In the 1950s, Schaefer proposed a model that would produce a maximum sustainable yield (MSY), by reverting marine populations to a less mature successional stage (Schaefer 1954a, b). [101] The MSY model assumed that density dependent competition kept the size of an unfished population at equilibrium.[102] As fishing mortality increased, the

population and the average size of the fish decreased. This resulted in more space and food for the remaining fish, and increased growth and survival rates. The logistic model predicted that the maximum productivity or MSY occurred when fishing held the population to approximately half of the initial equilibrium size. At this point the fishing removal rate was the same as the reproduction rate. Because enough spawners were left to supply young, the resource woud exist in perpetuity and the population would eventually reach a new equilibrium. Reminiscent of the original Progressive foresters who replaced virgin forests with more productive, younger crops, marine scientists sought to produce younger, faster growing fish populations that were more productive than at their original equilibriuMarine conservationists held up MSY as the standard for managing fisheries throughout the middle of the twentieth century. The California Department of Fish and Game (CDFG) repeatedly stated that it was necessary to set MSY as a target to successfully conserve and enhance California spiny lobster productivity (CDFG 1965, Mitchell et al. 1969, Duffy 1973, Odemar et al. 1975). They believed that a "harvest" targeted at MSY was "consistent with sound conservation practices" and would "increase and/or sustain the fishery for maximum utilization" (CDFG 1965). Despite this aspiration, the CDFG was never able to estimate an MSY for spiny lobster. Consequently, the CDFG continued to rely on conservation measures from the previous era, including minimum size limits and closed seasons.

The view of nature progressing towards an equilibrium or climax state dominated the mindset of ecologists over the rest of the twentieth century. Likewise,

despite persistent criticism that the MSY model did not incorporate contemporary ecological ideas,[103] it remained, with various extensions and revisions, a mainstay of marine conservation.

E. Evolutionary-Ecological Ethic (1970-present)

1. Ecological Ideas

In the last quarter of the twentieth century, ecologists began to question whether nature existed in a state of equilibrium. They realized that the scale at which they observed nature influenced whether it appeared stable or not (Sutherland 1981, Connell and Sousa 1983). If their observations were over sufficiently large scales, ecosystems and populations often appeared stable and balanced, but at limited or small scales they seemed unstable. Many ecologists concluded that nature did not march towards a state of perpetual stability*;* instead, it remained dynamic, shifting between states of equilibrium and disequilibrium (Drury and Nisbet 1973, Collin and Slayter 1977, Pickett and White 1985, Botkin 1990).

Ecologists also verified and began to quantify the influence of the environment on populations, communities and ecosystems over all temporal and spatial scales. They no longer assumed that competition over limited resources was the exclusive mechanism maintaining nature's structure and balance. Environmentally driven disturbances, ranging from fires to large-scale climatic events, also influenced community and population structure.[104] However, even though the environmental events driving ecological structure were highly variable and

unpredictable, they did not, as the Progressives believed, generate an assemblage of "mixed up messes." To the contrary, ecological studies repeatedly demonstrated that ecosystems were networks of interrelated and interdependent species, produced by long evolutionary processes and adapted to this environmental stochasticity.

As ecologists' perception of nature changed, so did their view of lobster. They began to realize that the environment, including large-scale climatic events, highly influenced lobster populations (McLeese and Wilder 1958, Dow 1969, Flowers and Saila 1971, Aiken and Waddy 1986). California spiny lobster researchers proposed that ocean temperature and changing current regimes affected larval recruitment and in turn population abundance (Johnson 1960a,b, Pringle 1986). Studies also found that California spiny lobster populations were intricately connected to and dependent upon other species living in their ecosystem (e.g. Tegner and Levin 1983).

2. Philosophical Ideas

The discovery of the magnitude of nature's complexity led ecologists and institutions to formally acknowledge that uncertainty was an inherent component of ecology that improved scientific knowledge could help to reduce, but not eliminate (Ludwig et al. 1993, Food and Agriculture Organization 1995, United Nations 1995, Dayton 1998). Nature's persistent uncertainty diminished the faith in man's ability to control nature. Recurring marine life conservation failures contributed to this waning belief.

3. Integration of Ecology, Philosophy and Conservation

These new perspectives took conservation in the direction of an Ecological-Evolutionary Ethic. The recognition that animals were components of an intricate interdependent web, not disaggregated assortments of "natural resources," revealed the inefficacy of basing conservation on single species approaches. The foundations for this contemporary idea trace back to Aldo Leopold. Educated in the Pinchot tradition of utilitarian resource-based conservation, Leopold initially argued for using traditional single species techniques based on scientific agriculture to conserve wild "game" (Callicot 1992). By the 1940s, though, he realized that conservation must aim for something more comprehensive than a maximum sustained flow of desirable products garnered from a single species. Leopold asserted that, even from a purely anthropocentric perspective, conservationists could only sustain "yields" if their practices did not undermine the ecological interactions that enabled the ecosystem to function properly. Because the degradation or elimination of any species, even one with no obvious economic value, could potentially reduce the viability of the whole ecosystem, conservationists needed to ensure the integrity of nature in its entirety.

Ecosystem approaches to conservation embody the ecological-evolutionary ethic. But they reversed the order of conservation priorities, starting first with the ecosystem rather than the targeted species. The goal now was to maintain the ability of the system to retain its diversity of structure and function, and adapt through long-term evolutionary processes. This would consequently sustain the system's

ability to produce resources. To ensure against uncertainty, the strategies chosen to achieve these ends also included precautionary measures (Ludwig et al. 1993, National Marine Fisheries Service 1999, National Research Council 1999, Pew Oceans Commission. 2003, U.S. Commission on Ocean Policy 2004).

Over the last decade, California and the federal government have enacted three conservation measures that institutionalize the Ecological-Evolutionary Ethic. These ecosystem-based approaches all apply to the California spiny lobster. First, the California's Marine Life Management Act of 1999 shifted California marine conservation away from the traditional single-species focus by recognizing that maintaining the health of marine ecosystems was a key to maintaining productive fisheries. The same year, the Marine Life Protection Act required the state to establish a network of no-take marine protected areas to protect and sustain marine life populations and ecosystem integrity, and to preserve species and habitat diversity for its commercial and intrinsic value. In the last ten years, a network of marine reserves was established around the Southern California Channel Islands, nine of which prohibit commercial fishing. These reserves added to the handful of other no-take reserves established prior to 2002 (McArdle 1997).

IV. Discussion

This case study historicizes marine invertebrate conservation by examining case studies of the California spiny and American lobster conservation. It shows that lobster conservation followed a complex but coherent trajectory through five

discernible conservation ethics: Inexhaustibility, Romantic Preservation, Resource-Progressive Conservation, Resource-Scientific Conservation and Ecological-Evolutionary. This framework provides historians, conservation biologists and ecologists with a new template against which to compare the conservation of other marine species to determine where they fall along the history of ecological ideas and conservation ethics.

This study also concurs with others that find the ecology has not progressed through a consistent series of paradigm shifts (Worster 1994). Rather, as each new model of marine life emerged, it built on and incorporated some of the old theories. The related conservation ethics crossed paths, converging and diverging over time. This historical perspective could illuminate when conservation measures unknowingly converge at an ethical and ecological crossroads, potentially producing strategies at cross-purposes that may undermine well-intentioned and currently informed efforts.

The California spiny lobster is a species that lies at the center of such a conservation crossroads. Conservation of the species is located at the intersection of eighteenth and twenty-first century ecological models of nature. In the last decade state and federal agencies have enacted lobster conservation measures in California embodying the twenty-first century ecological-evolutionary ethic. These holistic approaches consider the lobster as an interdependent and interconnected species within the kelp forest ecosystem, whose removal may negatively affect other species and possibly degrade the system's integrity. Nevertheless, current

conservation strategies continue to employ methods based on eighteenth and nineteenth century models that treat the lobster as an independent species isolated from its environment. These measures seek to protect small lobster through, among other things, minimum size limits, closed seasons, and escape ports.

Nineteenth century naturalists argued that measures like those in existence today, designed solely to protect small animals, were ineffective because they assumed that a large proportion of lobster eggs survived to sexual maturity. They also concluded that minimum size limits were counterproductive because they tacitly allowed the depletion of large animals, which could reduce population viability. Studies over the ensuing century have repeatedly indicated that, although naturalists had an incomplete understanding of the large lobster's role in maintaining populations and ecosystems, they accurately predicted that there would be negative consequences if large lobster were depleted. Over 150 years of persistent exploitation has reduced the California spiny lobster weight from an average of 5.8 to 1.7 lbs. or 71%, from 1888 to 2005 (McArdle and Kinlan, in prep and Chapter One). Effort and the exploitation rate in the spiny lobster fishery have increased steadily, with fishers now taking 70% of the new legal biomass each year. Following the 'classic' progression described by Herrick in 1909, generally as effort and exploitation have increased, the number of individuals surviving to old age and large size has decreased.

Present day ecological-evolutionary theory explains the potential consequences of failing to recognize when ecological ideas and resulting

conservation measures are at one of these historical crossroads. It demonstrates the extent to which conservation measures that altered spiny lobster population composition may undermine the species and the ecosystem. Reducing the proportion of large animals in a population may increase its vulnerability to collapse, because there are fewer adult age classes to buffer its ability to ride out environmental change (Stearns 1976, Chesson and Warner 1981, Hsieh et al. 2006, Secor 2007). For instance, the California spiny lobster evolved a long-lived, highly iteroparous, high fecundity life history to withstand environmental fluctuations by averaging reproductive success over many seasons. However, the current spiny lobster generation time has declined from five to twenty years to five to eight years. Ocean regime shifts caused by La Niña events, predicted to lead to unsuccessful recruitment episodes (Johnson 1960 a, b, Pringle 1986), occur every five to six years. As the average age of reproducing adults decreases towards the average time span between unsuccessful recruitment episodes, the chance of a serious recruitment failure increases. Because truncated populations more closely track short-term environmental variability, as the lobster population now does (McArdle and Kinlan, in prep and Chapter One), they may be less resilient.

Depleting large lobster may also diminish ecosystem viability because they are unable to perform their role as an apex predator in the kelp forest ecosystem (For reviews see Tegner and Dayton 2000, Pinnegar et al. 2000, Steneck et al. 2002).

Finally, the alteration of one life history trait such as size structure can lead to changes in other traits such as individual growth rates. Due to competitive release,

smaller sized fish, including lobster often grow faster than larger fish. This change may lead to a phenotypical response, in which smaller-sized fish mature earlier because less competition for nutrition during the juvenile phase may indicate favorable conditions for early breeders. These plastic changes can occur over a relatively brief time scale and are in principle, easily reversible. However, if lobster that produce at a younger age gain a selective advantage, the respective changes to life history traits (i.e. smaller size structure and younger age at maturity) will begin to reflect changes in the underlying genetic determinants (Rochet et al. 2000, Law 2000, Hutchings 2005). Such evolutionary changes will be difficult to reverse. Conservation strategies, such as minimum size limits, may initiate such a trajectory because they ensure, "the harvest of larger fish" (Conover and Munch 2002).

In the long history of California spiny lobster conservation, several attempts were made to protect large lobster. The California Legislature passed a two-year closed season on lobster in 1909, a limited version of the CBFC's initial request for a five-year closure (California Board of Fish Commissioners 1907). Herrick originally recommended five-year closures to allow lobster to spawn repeatedly and create a class of mature large lobsters. It is uncertain if the CBFC's goal was to specifically replenish large lobster, although this was their rationale for closing the crab fishery for two years the same year (California Board of Fish Commissioners 1907). In 1913, two years after the fishery reopened, the CBFC established a maximum size limit (13 inches carapace length to "protect the largest individuals," which were the "heaviest

spawners," and for unknown reasons raised the limit from 13 to 16 inches carapace length in 1917 (Fry 1928). In 1948, the legislature removed the maximum size limit.

V. Conclusion

This review establishes that changing general ecological theories and cultural philosophical ideas have interacted to produce a coherent history of invertebrate marine conservation. Marine conservation traversed five eras, Inexhaustibility, Romantic, Resource Progressive Conservation, Resource Scientific Conservation, and Evolutionary-Ecological. By documenting this established pattern, this work provides a template against which other species can be compared to further historicize marine conservation.

Many of the ecological and philosophical ideas that continue to underpin lobster conservation stem from eighteenth century natural historians during the Age of Reason. These include tactics, such as minimum size limits, that originated and were questioned over a century ago. Such conservation strategies, grounded on outmoded ecological models, facilitated the truncation of the California spiny lobster population. They have also, ironically, produced a population that resembles one prescribed by traditional utilitarian forestry conservation, one that consists primarily of small and fast growing animals (McArdle and Kinlan, in prep and Chapter One). This altered population structure has potentially diminished the resilience of this species and the kelp forest ecosystem.

The lobster population now stands at conservation crossroads where conservation measures grounded on old and new ideas of nature intersect. Continued reliance on outdated measures may undercut new better-informed ecosystem-based strategies. For instance, marine reserves are an ecosystem-based strategy that could restore older age classes to historic levels, and in so doing increase the likelihood of conservation success. However, while lobster may grow larger in reserves (Kelly et al. 2000, Rowe 2002, they often migrate out of the protected area and are caught upon departure (Rowe 2002). Thus, without measures to protect large lobster outside of reserves, even contemporary conservation measures may not restore large-sized lobster to the population. To ensure the success of future efforts to conserve marine life populations, we must avoid unconsciously relying on outmoded ecological ideas and conservation ethics.

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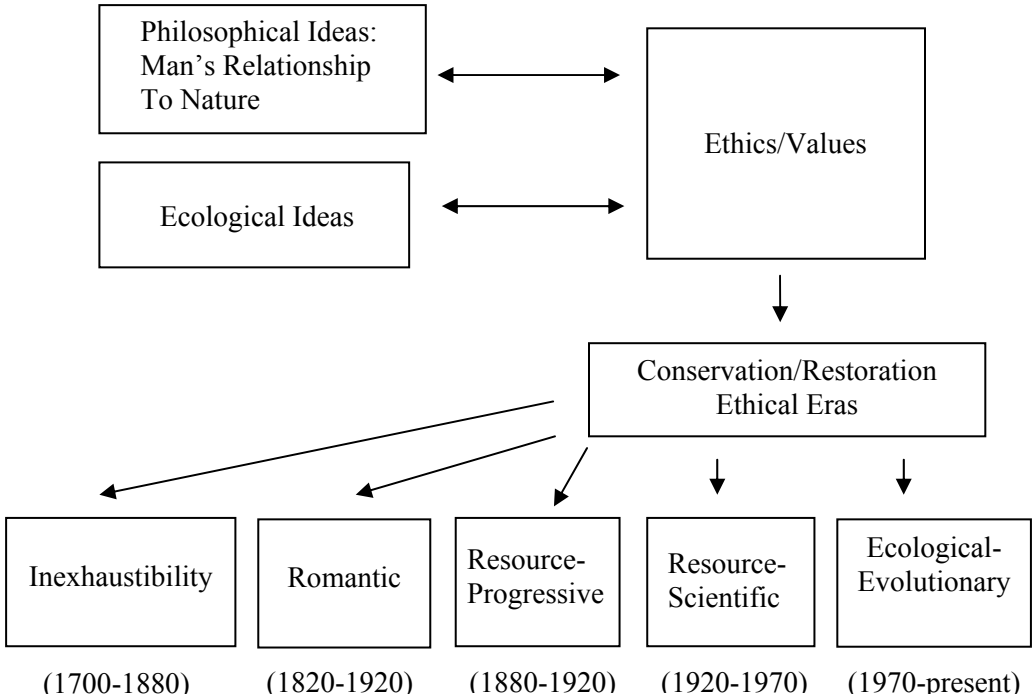
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VII. Figures

Figure 1. A conceptual model of the trajectory of conservation eras in relationship to philosophical ideas, ecological ideas, and ethics and values over the last three centuries (1700 to 2008).



Appendix I: Chapter One

Estimation of Trap Numbers used in the California spiny lobster fishery (1980-2005)

After 1976, there are no regular estimates of the number of traps employed in the spiny lobster fishery. For the period 1980 to 2005, the annual number of traps used in the fishery was estimated by converting the number of trap pulls, from CDFG logbooks, into trap numbers (Method 2). These estimates were compared to a different estimate (Method 1) made by multiplying the actual number of permitees fishing each season (1980 to 2005), from CDFG logbooks, by an estimate of the average number of traps being used per fishermen documented in the literature (Odemar et al. 1975, Shaw 1986, CDFG 2001, Ventura County Star 1-6-2001, Los Angeles Times 10-7-2001, CDFG 2005).

The resulting continuous annual time series of trap numbers estimated by Method 2 is not radically different from the one obtained simply by interpolating in Method 1 (Fig 1), but has the advantage of combining all available data in a consistent way. We used the time series of estimated adjusted total number of traps from Method 2 to calculate CPUE for input to the Bayesian model.

Method 1. Estimation using literature estimates of average traps per fishermen

In 1970, the CDFG initiated a logbook system that required fisherman to submit monthly records of their catch, catch location and amount of gear. Annual logbook summaries include this information as well as the number of fishermen that bought lobster permits and the number of permitees that actually fished each year. It is important to distinguish between the two because the number of fishermen that

actually fishing during a season is usually less than the number that buy permits. To get an average estimate of fishing effort, the actual number of permitees fishing each season was multiplied by an estimate of traps per active fisherman documented in the literature. For 1980-1990, it was estimated that each fisherman used an average of 100 traps a year (Odemar et al. 1975, Shaw 1986) and from 1990-2005, they used 100-300 traps or an average of 200 traps (CDFG 2005). Some annual logbook summaries were either incomplete or unavailable, creating missing data points. As a first approximation of the missing data, we linearly interpolated the missing values from adjacent years, resulting in our original estimated trend of fishing effort (Fig 1).

Method 2. Estimation using logbook records of trap pulls (1980-2005)

Closer inspection of the logbook summaries revealed that in addition to the missing data points, some of the recorded data points were inconsistent (e.g., for 1993, the number of permits dropped precipitously and rose back the next year). Also, the permitting system changed over the period from 1993-1997 such that lobster crew members were required to obtain different permits than boat operators (prior to that both crew and operators had the same type of permit). Original hardcopy logbooks permitted correction of some of these errors[105], but in an attempt to obtain a consistent estimate of traps for all years we developed a "consensus trap estimate" (Method 2) based on multiple sources of data.

First, we calculated the mean ratio (41.3%) of the number of crew member permits (Ncrew) to the total number of permits (Ntotal_permits) for the period after

the transition to separate crew/operator permits (1997-2005). We used this proportion to predict the division of permit types from 1980-1995 as follows:

$$\text{Noperators} = \max(\,[\text{Ntotal_permits} - (0.413 * \text{Ntotal_permits})],\ \text{Nsubmitting_logbooks}) \quad (1)$$

$$\text{Ncrew} = \text{Ntotal_permits} - \text{Noperators} \quad (2)$$

We used least-squares linear regression to model the number of permittees landing lobster (NLanding_Lobster) as a function of Noperators and Nsubmitting_logbooks, using only the period 1998 – 2005 after the permit system transition. The regression explained >99% of the variance in Nlanding_lobster. We used the resulting prediction expression to estimate Nlanding_lobster from 1980-1990. For 1980 and 1981, the prediction of Nlanding_lobster was slightly higher than the number of predicted operator permits, so the estimated number of operator permits was raised for those years (1980: 186→193 and 1981: 220→230). The estimated number of crew permits was decreased by a corresponding amount. Encouragingly, this approach improved consistency in the logbook submission compliance numbers for 1980-1990 (mean ± 1 SD = 95.3% ± 0.6%), which had previously incorporated some anomalous values.

Next, we assumed the following relationships among number of reported traps (Ntraps_reported), number of trap pulls reported (Ntrap_pulls_reported), and number of traps reported per permittee:

$$\text{Ntraps_Reported} = \frac{\text{Ntrap_pulls_reported}}{24\ \text{wks/season} * \text{Npullspertrapperweek}} \quad (3)$$

Ntraps_Reported_per_fisherman = Ntraps_Reported / Nsubmitting_logbooks (4)

For each of the time periods where we had both Ntraps_reported and Ntrap_pulls_reported, we solved for Npullspertrapperweek in equation (3). We then adjusted the value of this parameter seeking to maximize continuity with the pre-1980 data series (based on 1976-1977 trend of effort, and considering increase in catch, projected number of traps in 1980 is ~ 14400), and on literature values of Ntraps_reported_per_fisherman (~100 in 1980's and ~200 in 1990's-present [Odemar et al. 1975, CDFG 2005]). This resulted in a predicted value of pulls/trap/week of 1.3. Inserting this value into equation (3), we obtained an adjusted "consensus" value of the number of reported traps.

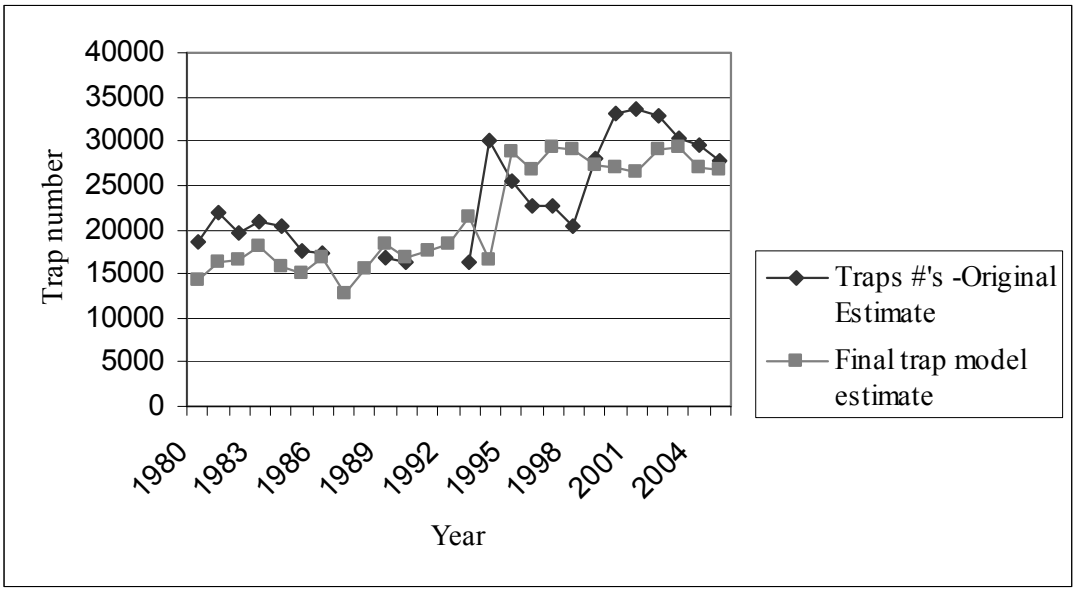
We further adjusted for "casual" fishermen prevalent during the 1993-1997 period when the fishery was being considered for limited entry (K. Barsky, pers. comm. 2007). We assumed that the average number of traps per fishermen was ¼ that of the other periods, based on anecdotal evidence and continuity with points on either side of this period in the time series:

> Adjusted Trap Estimate = (Nsubmitting_logbooks/0.953) *NtrapsReportedperFisherman+MAX([Nlanding_lobster-(Nsubmitting_logbooks/0.953)],0)*20

Lastly, we linearly interpolated to find the number of fishermen submitting logbooks and landing lobster for 1987 and trap pulls, number of fishermen submitting logbooks, number of operators, and number landing lobster for 1988, 1991, 1992. We used these interpolated values as inputs into equations (3) and (4) above to

produce adjusted trap estimates for those years. It is important to note here that the interpolated number of trap pulls were not used as input to Bayesian model; they were only used to show the pattern of trap numbers in the fishery and to derive the exploitation rate.

Figure 1. Estimates of trap numbers used in the California spiny lobster fishery using an original trap estimate from historical records (Method 1) and the final trap estimate (Method 2) from 1980-2005.



Appendix II: Chapter One

The Bayesian model

The model framework (Fig 2) includes three components: (1) a size-structured population model (see Methods) and submodels that describe the dynamics of the lobster population; (2) input data including fishery-dependent, fishery-independent data and informative priors; (3) a Bayesian estimator which fits the population model to data for estimating key parameters for the lobster population and fishery.

A. Process Equations (Sub-models)

The length-based population dynamics model is comprised of a series of submodels or process equations:

Recruitment

Because of the notorious difficulty of estimating stock-recruitment relationships accurately, we assume 'recruitment' is merely the input of individuals into size class s=1 in each year necessary to produce the observed catch in subsequent years, once lobsters have achieved legal size. Thus recruitment is given a vague normal prior and assumed to be stochastic and independent of spawning stock in any given year (u is the mean and $\sigma 2$ is the standard deviation of the parameter):

$Ry \sim \text{LogNormal}(\mu recruits, \sigma 2 recruits)$

Size-independent mortality

This is assumed constant and given a vague lognormal prior (u is the mean and $\sigma 2$ is the standard deviation of the parameter):

$M \sim \text{LogNormal}(\mu M, \sigma 2M)$

Size-dependent probability of mortality and growth

These are indistinguishable from the perspective of our observations on catch and effort, and so we combine these effects into a "growth and survival" probability *psi*[s,y]. A prior on this probability was established by the following procedure by fitting a regression of the form dL = B0 * exp(-L*B1) to growth increment data from tagging studies by Engle (1979) and Lindberg (1955). Then, for a fixed value of B1, the probability of transitioning from one size class to the next as a function of B0 was calculated. A Uniform prior was established on the annual value of B0, B0[y], restricting it to the range of the observed data (20 to 40 mm). In this manner, the transition from one size class to the next is tied to a natural expression of the growth function, but the model is allowed substantial flexibility in the 'growth parameter', which effectively accounts for size-specific mortality in conjunction with growth.

The Bayes procedure begins with these prior probabilities and revises them based upon observations. The changed probabilities are posterior probabilities. This process estimates the probability that a randomly selected lobster from this population will be in age class X, given any year.

Size structure

The model tracks the abundance of lobsters in 8 size classes indexed by s = {1, 2, … 8}, with bins defined by lower (Llower) and upper (Lupper) bounds on carapace length (CL) (Table 2). The average weight of lobsters in each size class was approximated by using the midpoint of the upper and lower length bins (Lmid) and the weight vs. length regression from Engle (1979; ln W = ln a + b ln L, a = .00063, b = 3.098).

Stock-recruitment relationship

We assume that CPUE is linearly related to the abundance of legal-sized lobster by a constant of proportionality q, the catchability, such that:

CPUE[y] = q x Nlegal[y],

where,

$$N_y^{legal} = \sum_{s=4}^{8} N_{s,y}$$

Because there are two measures of effort used in the input data (number of traps and number of trap pulls), we estimate separate catchabilities q=qT and q=qTP for the two sets of observations on catch per unit effort (catch per trap and catch per trap

pull). These quantities are linked because the associated CPUE values are assumed to reflect the same underlying abundance of lobsters, albeit with different constants of proportionality qT and qTP. We used estimates of catchability that minimized the residuals over the time series.

Additional Comments about Recruitment, Growth, and Mortality

The interaction among processes of recruitment, growth, and mortality is extremely difficult to untangle from non-size-specific catch and effort data alone. We give each of these processes a natural definition in this model, but recognize that the available data are unlikely to allow the model to truly separate these processes. This problem is common in estimation of state-space models of population dynamics, and is known as non-identifiability. To avoid this issue, we do not draw any inferences from these parameters, but rather focus on the size-structured estimates of abundance, which are more robust because they are directly related to catch data in each year. We also address the growth process in more detail using a separate model (see Appendix III).

B. Observation Equations

Catch in pounds is assumed to be a fixed parameter (i.e., with no observation error). CPUE is used as an index of abundance and is defined on a lognormal observation error model.

Appendix Three: Chapter One

The California Spiny Lobster Growth Curve

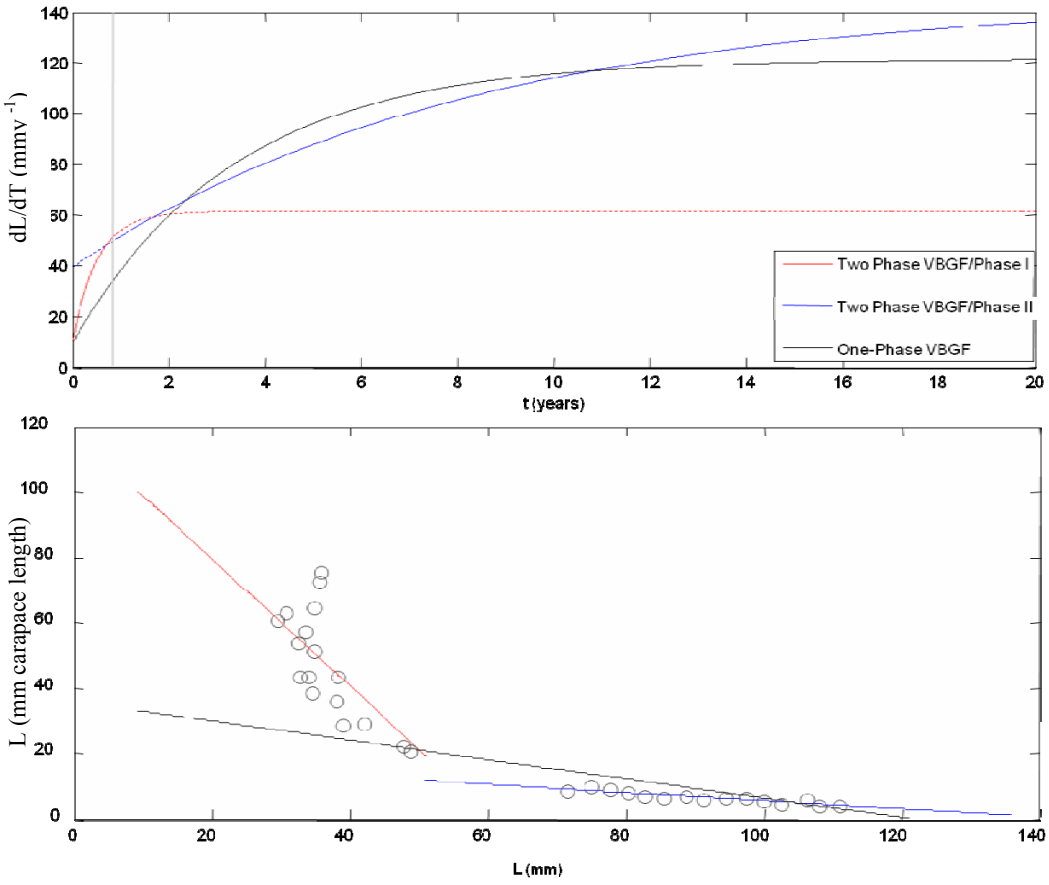
In organisms with indeterminate growth, one of the most important and general demographic changes expected to result from truncation of size structure is an increase in population-averaged values of individual growth rates; in the absence of other regulating factors, this translates directly into an increase in the biomass intrinsic growth rate of the population. Our results support the operation of this mechanism in the lobster population.

Although this qualitative finding is expected for any organism in which growth rate decreases with size, specific aspects of crustacean growth may accentuate this phenomenon. Like most other species, small lobsters grow faster than larger lobster, exhibiting high specific growth rates. However, growth rates of species with exoskeletons have two components, size increase at molt and frequency of molt. Because lobster growth occurs almost entirely during molt periods and smaller lobster molt more frequently, smaller lobsters grow extremely fast relative to larger lobster (Engle 1979, Cobb and Caddy 1989).

We reasoned that this growth pattern could not be explained by a smooth exponential decrease in growth rate such as that employed in the standard von Bertalanffy growth function (VBGF). The Bayesian model on which we relied for our analysis (Kinlan and McArdle, in prep) avoided the issue of growth model selection by using an empirical power function regression relationship derived from a large database of growth increment data under a variety of environmental and habitat

conditions (see Methods). This allowed the model flexibility to account for differences in growth among time periods, such that any given cohort was not constrained to follow a single VBGF throughout its lifetime. This was desirable for model fitting, but given the mechanistic underpinnings of the VBGF we also conducted an analysis of a smaller set of growth trajectories at a single site over several years of similar environmental conditions (Lindberg 1955) to test the hypothesis that lobsters undergo a distinct shift in annual growth. Initial analyses confirmed that a standard VGBF did not provide an adequate fit to growth trajectories across the entire life cycle; rather, there appeared to be a rapid change in the slope of growth rate vs. length around the length at which reproductive maturity is attained (Table 3). Based on this observation we compared the single VBGF model fit with a two-phase model, which allowed for two sets of VBGF parameters in two life cycle phases and estimated the switch point length separating these phases (Fig 1). Comparison of information criteria for the two model fits (Table 3) indicated that the two-phase version more realistically describes the pattern of lobster growth increments. Because the estimated switch point is just below the legal size limit, but well below the maximum size of lobster in an unexploited population, this pattern of growth would be expected to enhance the response of lobster population dynamics to size structure truncation.

Figure 1. One phase versus two phase fitted von Bertalanffy growth curves and associated parameters. Data on length and growth rates from Lindberg (1955). For model fit and model comparison statistics, see Table 3. Model selection criteria indicated that the two-phase model was most appropriate.



ENDNOTES

[1] Wilcox, W.A. 1907. The Commercial Fisheries of the Pacific Coast States in 1904. Bureau of Fisheries Department. Doc. No. 612. U.S. Government Printing Office, Washington D.C.

[2] Sette, O. 1926. U.S. Department of Commerce, Bureau of Fisheries. Report of the United States Commissioner of Fisheries for the fiscal year 1925. U.S. Government Printing Office, Washington, D.C., 335.; Sette, O. 1928. U.S. Department of the Interior, Fish and Wildlife Service. Fishery Statistics of the United States. 1924,1925. Statistical Digest No. 1. U.S. Government Printing Office, Washington, D.C., 452-453; Fielder, R.H. 1942. U.S. Department of the Interior, Fish and Wildlife Service. Fishery Statistics of the United States. 1939. Statistical Digest No. 1. U.S. Government Printing Office, Washington, D.C. Footnote 8 on page 158.

[3] Sette, O. 1928. U.S. Department of the Interior, Fish and Wildlife Service. Fishery Statistics of the United States. 1924,1925. Statistical Digest No. 1. U.S. Government Printing Office, Washington, D.C., 419.

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[6] The primary sources were located in collections at the National Archives, the Huntington Museum, the San Diego, Los Angeles and Santa Barbara Historical Societies, the Santa Cruz Island Foundation, the Chinese Historical Society of Southern California, the Wells Fargo Museum, the California Fish and Game Library, the Los Angeles Times, the Santa Barbara News Press, the Santa Barbara Morning Press and a variety of other archives.

[7] The primary sources were located in collections at the National Archives, the Huntington Museum, the San Diego, Los Angeles and Santa Barbara Historical Societies, the Santa Cruz Island Foundation, the Chinese Historical Society of Southern California, the Wells Fargo Museum, the California Fish and Game Library, the Los Angeles Times, the Santa Barbara News Press, the Santa Barbara Morning Press and a variety of other archives.

[8] Wilcox, W.A. 1907. The Commercial Fisheries of the Pacific Coast States in 1904. Bureau of Fisheries Department. Doc. No. 612. U.S. Government Printing Office, Washington D.C.

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[99] Utilitarian conservationists had broader goals than monetary gain. They believed that by making nature more productive they were contributing to cultural

advancement. When nature was unused, and plants and animals left in a natural state it was a symbol of stunted cultural development. The roots of this idea lie, in part, in the ideas of philosopher John Locke who compared the cultural value of cultivated land in England to the vast amount of uncultivated land in America, "Despite the richness of American soil, it lacked the value and productivity of the land of the advanced nations, because the land lay unused, fallow, uncultivated, as waste." (Katz 1997). At the turn of the century, U.S. forestry chief Bernhard Fernow echoed Locke by describing how forestry played a role in advancing society, "The history of woodlands has been the same in all parts of the world, progressing according to the cultural development of the people…only in a highly civilized nation and in a well settled country does the conception of the relation of forests to the future welfare of the community lead to rational treatment of forests…" (Fernow 2000).

[100] Individual naturalists probably held views about utilitarianism that were more nuanced. For instance, Francis Herrick based his conservation recommendations solely on their ability to increase the lobster's productivity and hence, economic utility. However, he was broad-minded and his interests in natural history were wide-ranging. In his inaugural address at Case Western Reserve University, he reviewed the 500-year history of biology and shortly thereafter, published a 350- page biography of John James Audubon. In the latter work, Herrick seems to diverge from traditional anthropocentric utilitarian views, by referring to Thoreau as a sage.

[101] The theory of optimum or maximum catch has origins in the work of mainly a few people, Baranov (1916 and 1925), Russel (1931), Hjort, Jahn and Ottestad (1933), Thompson and Bell (1934) and Graham (1935). For a review of this history see, Smith, T.D. 1994. Scaling fisheries: the science of measuring the effects of fishing, 1855-1955. Cambridge University Press, Great Britain.

[102] The idea of an equilibrium between births, growth, natural deaths, and rate of fishing can be traced back to Petersen (1894, 1903), but the quantitative dynamic concept was developed by Baranov (1918, 1925), Thompson (1916, 1917, 1919, 1936, 1937) and Thompson and Bell (1934). The theory was extended by Russell (1931), Buckmann (1932), Hjort, Jahn and Ottestad (1933), Graham (1935), Ricker (1940, 1954, 1958), Beverton and Holt (1957), Schaefer (1943, 1954, 1957), Chapman (1961,1964) and Gulland (1964). For a review of this history see, Smith, T.D. 1994. Scaling fisheries: the science of measuring the effects of fishing, 1855-1955. Cambridge University Press, Great Britain.

[103] The concept of a maximum sustainable yield often failed because it did not take into account contemporary ecological understanding. The model assumed that population dynamics were soley a function of density dependence and ignored the impact of the environment. The model also assumed that there was a harvestable surplus that could be removed from a population without deleterious effects. It did not consider that reducing 'surplus production' of one species could affect the community of other species in the ecosystem and in turn ultimately affect the species originally fished. For some critiques of MSY see Larkin, P.A. 1977. An epitaph for the concept of maximum sustainable yield. Transactions of the American Fisheries Society

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[104] By the turn of the century some naturalists, such as Johan Hjort (1914) recognized that fluctuations in ocean temperature could affect populations by reducing larval survival rates. However, marine conservation did not generally embody this view until this era.

[105] The total number of permitees landing lobster in 1993 was found to be 281, more than the number of recorded permits (n=271; K. Barsky, California Department of Fish & Game, October 2007, pers. comm.). The recorded number of permits was replaced with a value (n=449) linearly interpolated from the 1990 to 1994 trend, which was relatively consistent except for the anomalous value in 1993.