Controls on the productivity of exploited ecosystems: Linking ecology and resource management

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Abstract

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Ecologists have long been striving to learn what drives the productivity of populations, communities, and ecosystems. Such an understanding can contribute to both basic science and the practical management of renewable resources, where measuring and detecting changes in productivity is still an important but challenging component of understanding and managing natural resources. Productivity integrates several basic natural processes acting on a population: mortality, growth, reproduction, and migration. This makes measuring productivity a useful tool to guide management advice and to serve as an indicator of ecological changes. However, because productivity integrates so many diverse processes, separating out contributions of different sources of variability is quite difficult, especially in large complex ecosystems. In this dissertation, I pursue four distinct lines of research related to these themes, taking a broad approach and utilizing a variety of quantitative tools. The first three chapters examine how predation influences population productivity of exploited fish populations, both exploring the performance of established methods to detect the effect of size-structured predation, while also developing novel methods and applying considerations of size-structured predation in targeted fisheries. Chapter 1 is an extensive simulation study testing detectability of a predation signal in productivity time series, the second chapter attempts to conduct a meta-analysis of predation on mid-trophic level species across the North Atlantic and North Pacific, and the third chapter uses deterministic age-structured models to examine predation by lingcod on rockfish in the California Current. The fourth chapter explores natural abiotic drivers of productivity while carefully propagating all sources of measurement error in coastal temperate rainforests of Southeast Alaska, using an exceptional dataset on forest growth following logging. These chapters all emphasize the complexities of studying drivers of productivity in ecology and resource management; however, it is also usually necessary to simplify systems and processes in order to use available data and information to answer questions and test hypotheses. We can respond to these challenges with determination and creative problem solving, and expand our understanding of how natural systems work in hopes of improving our management of the resources such systems provide.

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Introduction

Ecologists have long been striving to know what drives the productivity of populations, communities, and ecosystems. Established theories of succession postulate that ecosystem productivity is highest when the system is young, and then gradually slows as ecosystems accumulate biomass (Odum, 1969). Animal populations, as well, often grow quickly until stabilizing density-dependent factors temper growth rates (Nicholson, 1933; Turchin, 1995). However, productivity is also remarkably variable over time and space, even in so-called "equilibrium" states. For many years, scientists have recognized that processes in the physical environment and the dynamic biological community both drive fluctuations in productivity. As early as 1927, Charles Elton wrote "…a great many of the phenomena connected with numbers owe their origin to the way in which animal communities are arranged and organised, and to various processes going on in the environment" (Elton, 1927). However, in addition to its utility in basic science, productivity has also long held an important place in practical management of renewable resources, such as in commercial fisheries (Schaefer, 1954) and timber production. In such cases, an understanding of what drives changes in productivity can be used to help preserve resources for both present and future generations, in addition to elucidating fundamental ecological processes.

Today, measuring and detecting changes in productivity is still an important though challenging component of understanding and managing exploited renewable resources. Population productivity is empirically measured as the incremental change in abundance, standing stock, or any other metric of population size that occurs over a defined time interval. Consequently, productivity integrates several basic natural processes acting on a population: mortality, growth, reproduction, and migration. This makes measuring productivity a useful tool to guide management advice (Hilborn, 2001), to serve as an indicator of ecological changes, such as changing predator abundances, or to quantify ecological services, such as carbon storage in forests (IPCC, 2013). Moreover, this metric provides relatively coarse-grained information on population trends, making analysis of productivity useful in data-limited situations and enabling comparative analysis across multiple populations, taxa, or ecosystems (Link *et al.*, 2012a). Therefore, understanding productivity, how to model it, and its drivers has important implications for both natural resource management and our basic scientific understanding of how ecosystems function; however, because productivity integrates so many diverse processes, separating out contributions of different sources of variability is quite difficult (Jacobson *et al.*, 2001).

Detecting and understanding changes in productivity is particularly challenging in complex ecosystems, such as those found in coastal marine areas. In these ecosystems, a wide range of environmental, trophodynamic, and anthropogenic drivers all act simultaneously, though not necessarily synchronously, to influence productivity (Link *et al.*, 2012a). For example, trophodynamic drivers, such as predation, come from a wide diversity of species, all existing within reticulate webs of species interactions and jointly influencing a single fish population's mortality rate (Yodzis, 1998). Understanding the influence of predation on productivity therefore requires an understanding of the relative importance and functional responses of every predator species. This is further complicated by the fact that controlled experimentation is virtually impossible in these large open systems, so scientists must develop innovative methods to utilize observational data (Baum and Worm, 2009; Jensen *et al.*, 2012). For all of these reasons, to date, it has not yet been possible to quantitatively measure and compare the overall strength of predation's influence on productivity across multiple ecosystems.

An additional complication with studying the effect of predation on productivity is that predation is highly size-structured in aquatic food webs (Scharf *et al.*, 2000), whereas abundance and biomass data used to measure annual productivity are not. Ontogenetic changes in survivorship throughout species' life histories, when coupled with time-varying survival caused by temporally fluctuating predator populations, induces shifts in a population's age structure (Hsieh *et al.*, 2010) that can in turn generate complex responses in population productivity (Walters *et al.*, 2008). The responses of aggregated metrics such as population abundance and productivity ultimately depend upon the rate of change in predation and the life history traits of the prey species, such as which life stage predators target (Worden *et al.*, 2010). Further complexity arises through the vulnerability of prey species to different assemblages of predator species as they grow (Bax, 1998; Hunt Jr. and McKinnell, 2006). Population dynamics of key predators on early and late life history may not be synchronized with each other, leading to a complex temporal pattern of changing mortality rates at distinct life history stages with unknown consequences for prey production dynamics.

Another complication with modeling productivity is the difficulty in both distinguishing between and accounting for measurement error and environmental heterogeneity. Productivity cannot be measured directly; as a rate, its calculation generally requires combining multiple random variables, introducing considerable error in the observed values that can be challenging to distinguish from true biological processes (Polacheck *et al.*, 1993). This is further complicated in the case of slow-growing organisms, such as trees, where extractive sampling is generally not an option (Brown, 2002). One strategy to estimate productivity for trees is to use existing allometric equations developed from other time periods and regions to estimate total biomass from measurements of tree height and diameter, but doing so makes estimates of productivity even less certain (Phillips *et al.*, 2000; Melson *et al.*, 2011). Similar issues exist in studying population dynamics of fish, where natural mortality rates are often assumed constant and known without error, despite rarely being measured due to the logistical challenge such measurement presents (Pauly, 1980). Further clouding a formal statistical analysis of productivity is that site-specific environmental factors are crucial in dictating productivity at many management-relevant scales. This is a particularly poignant issue for trees, which cannot move to integrate environmental drivers over a wide spatial area. Therefore, accounting for measurement processes and the variable abiotic landscape can be vital to properly quantify changes in productivity.

In this dissertation, I pursue four distinct lines of research related to these questions, taking a broad approach and utilizing a variety of quantitative tools. The first three chapters examine how predation influences population productivity of exploited fish populations, both exploring the performance of established methods to detect the effect of size-structured predation, while also developing novel methods and applying considerations of size-structured predation in targeted fisheries. Chapter 1 is an extensive simulation study testing detectability of a predation signal in productivity time series, the second chapter attempts to conduct a meta-analysis of predation on mid-trophic level species across the North Atlantic and North Pacific, and the third chapter uses deterministic age-structured models to examine predation by lingcod on rockfish in the California Current. The fourth chapter explores natural abiotic drivers of productivity while carefully propagating all sources of measurement error in coastal temperate rainforests of Southeast Alaska, using an exceptional dataset on forest growth following logging.

Chapter 1. How detectable is predation in stage-structured populations? Insights from a simulation-testing analysis

ABSTRACT

The potential of predation to structure marine food webs is widely acknowledged. However, available tools to detect the regulation of prey population dynamics by predation are limited, partly because available population data often aggregate a population's age structure into a single biomass or abundance metric. Additionally, many food webs are relatively complex, with prey species subject to different assemblages of predators throughout their ontogeny. The goal of this study was to evaluate the extent to which stage-structured predation could be reliably detected from time series of total biomass of predators and prey. We simulated age-structured populations of four mid-trophic level fish species with distinct life history traits, exposed them to variable predation at different life stages, and fit production models to resulting population biomass to determine how reliably the effects of predators could be detected. Predation targeting early life history and juvenile life stages generally led to larger fluctuations in annual production, and was therefore more detectable. However, ecologically-realistic levels of observation error and environmental stochasticity masked most predator signals. The addition of predation at a second life stage sharply decreased the ability to detect the effect of each predator. We conclude an absence of detectable species interactions from biomass time series may be partly due to the interactive effects of environmental variability and complex food web linkages and life histories. We also note that predation signals are most robust for predator-prey systems where predators primarily act on mortality of sub-mature life history stages. Simulation testing can be applied widely to evaluate the statistical power of analyses to detect predation effects.

INTRODUCTION

Communities and food webs in coastal marine ecosystems are structured by the interactive effects of environmental variation and inter-specific interactions, such as predation and competition. A main challenge to date has been measuring the relative influence of these two drivers (Hunt Jr. and McKinnell, 2006). Marine populations are heavily influenced by environmental factors (Hollowed *et al.*, 2001; Chavez *et al.*, 2003; Drinkwater, 2006; Frederiksen *et al.*, 2006), but predation has been identified as a key factor in species- or community-level dynamics in several ecosystems (Harvey *et al.*, 2003; Worm and Myers, 2003; Frank *et al.*, 2005; Casini *et al.*, 2009). Discerning the importance of both abiotic controls and predator-prey interactions is important for understanding the full consequences of the targeted removal of marine life (Baum and Worm, 2009; Link *et al.*, 2010; Estes *et al.*, 2011). Considering these interspecific interactions is key because large predator species are particularly vulnerable to exploitation (Law, 2007). Therefore, if predation strongly impacts lower trophic level species, fishing can potentially have far-reaching effects on food webs.

Despite the importance of understanding the role of predation and other drivers in marine ecosystems, the impracticality of experimentation on such large scales limits our ability to draw inferences about the relative influences of these drivers. In the case of predation, an effect is often shown through a negative temporal correlation of predator and prey abundances (Worm and Myers, 2003; Frank *et al.*, 2005, 2006). While this approach is relatively simple and can be accomplished with limited data, it potentially suffers from two well-known problems. The first is the common problem of determining causality, and specifically whether predators drive prey dynamics or both populations respond in opposite directions to a shared environmental driver (Hunt Jr. and McKinnell, 2006). The second drawback is that the immediate effect of predation on prey populations is on productivity, or the population’s rate of change (Lotka, 1925), not on the state variable itself (i.e., abundance or biomass). Therefore, especially for longer-lived species, predation immediately impacts productivity, but state variables respond more slowly over time and do not directly track the changes in productivity.

An additional, as yet unconsidered problem with statistical analysis of predator and prey time series is whether predation is likely to be detectable given the nature of data often available. In most cases, the correlative approach is applied to time series of total predator and prey abundances (or biomass). These data do not include information on age or size structure and instead aggregate over predator and prey age classes. However, predation is known to be highly size-structured in aquatic food webs (Scharf *et al.*, 2000) and elsewhere (Miller and Rudolf, 2011; Middleton *et al.*, 2013), leading to variable survivorship over an individual’s life history. This result, along with time-varying survival caused by temporally fluctuating predator populations, induces shifts in a population’s age structure (Hsieh *et al.*, 2010) that causes variation in population productivity (Walters *et al.*, 2008). The responses of aggregated metrics like population abundance and productivity ultimately depend upon the rate of change in predation and the life history traits of the prey species, such as which life stage predators target (Worden *et al.*, 2010). Further complexity arises through the vulnerability of prey species to different assemblages of predator species as they grow (Bax, 1998; Hunt Jr. and McKinnell, 2006). Population dynamics of key predators on early and late life history may not be synchronized with each other, leading to a complex temporal pattern of changing mortality rates at distinct life history stages with unknown consequences for prey production dynamics.

Statistical analysis of time series of annual population productivity may provide a framework to integrate the joint effects of density dependence and other environmental drivers

(Link *et al.*, 2010, 2012a). For marine fish populations that are targeted by fisheries, annual production is often measured as the change in biomass that would have happened in the absence of fishing; it is therefore a function of the population size and quantifies the productivity in units of biomass per year (Quinn and Deriso, 1999). Basic population growth models, such as the logistic growth model, are designed to relate measures of productivity to population biomass in order to assess density dependence (Hilborn, 2001). While such density dependence explains some of the observed variation in annual production, much of the variation can be attributed to extrinsic factors, such as predation (Jacobson *et al.*, 2001; Vert-Pre *et al.*, 2013). Thus, if time series of predator abundances are available, slight modifications to standard functional forms of population growth models can be used to estimate the contribution of both predation and density dependence on production dynamics. Moreover, these models permit the estimation of standard population benchmarks used to judge the status of harvested populations and establish levels of harvest that are sustainable.

Here, we evaluated the ability to statistically measure the effect of predators on prey when the available data consist only of time series of total prey and predator biomass. Specifically, we conducted a simulation study using an age-structured model of mid-trophic level fish populations and then applied standard model-fitting procedures to the simulated data. We conducted this simulation study under a range of scenarios that we believed would dictate the ability to detect predation signals from data: the life stage targeted, the life history of the prey, the variability of bottom-up effects on the prey population, whether there is observation error, and the number of predator assemblages present (Table 1.1). We hypothesized that the detectability of a predator would depend on how strongly the predator influenced the population's productivity. Predation on adult stages was expected to be more important for longer-lived species, and predation on early life history stages was expected to be more important for short-lived species. Finally, we also examined the extent to which consideration of predation effects changes estimates of standard population benchmarks used in management.

METHODS

Approach

We developed age-structured population models to simulate data that resembled those observed for mid-trophic level fish species. Mid-trophic level species are both targets of commercial fisheries and prey of exploited upper-trophic level species. These species are therefore of interest because their productivity may be indirectly affected by fishing-induced depletion of their predators (Pikitch *et al.*, 2014). We refer to these population models as “operating models” because they represent a fuller range of ecological detail than fitted statistical models with regard to how population processes truly operate. Within these operating models, we simulated time-varying predator pressure to study the top-down effects of various hypothetical predators. The predator affected mortality at one of three specific life history stages: early life history, juveniles, and adults. Population models included fluctuations in early life history survivorship related to other environmental drivers, so that the simulated dynamics resembled those observed for real populations. We then aggregated the simulated population trajectories into total biomass to generate data that are typically used in analysis of predator-prey interaction strengths. We used these simulated data to fit statistical production models to determine how accurately top-down effects of predators are detected when only a time series describing total biomass is available. Models were discrete time with annual time steps to match the typical phenology of growth, reproduction, and mortality in these populations.

Operating models

We parameterized the age-structured population models using demographic information for four different mid-trophic level species with differing life histories: Atlantic menhaden (*Brevoortia tyrannus*), Pacific sardine (*Sardinops sagax*), California Current English sole (*Parophrys vetulus*), and Northwest Atlantic silver hake (*Merluccius bilinearis*). The primary goal in mimicking these stocks was to obtain realistic parameters across a range of life histories. Therefore, some traits specific to a species (e.g., cannibalism in silver hake; Link *et al.*, 2012b) were not modeled. The species varied in their ages at maturity, natural mortality rates, growth rates, and the strength of density dependent regulation in offspring production. Most parameter values were taken from statistical age-structured stock assessments (Table 1.2; Stewart, 2005, 2007; Hill *et al.*, 2009; Alade *et al.*, 2010; Atlantic States Marine Fisheries Commission, 2010).

We measured offspring production as the total number of fish surviving the critical early-life history period when survivorship is highly variable. We defined this as survival to age-1, and we refer to this quantity as recruitment for the remainder of this manuscript. For all species we assumed an asymptotic (density dependent) model to describe the relationship between spawning biomass and average recruitment (Beverton and Holt, 1957), and assumed lognormal variation around this relationship to capture environmental controls on recruitment. This stock-recruit relationship was defined by two parameters: recruitment at the population carrying capacity (i.e., maximum recruitment) and steepness, the ratio between recruitment when biomass is 20% of the carrying capacity and recruitment at the carrying capacity. When steepness equals one, recruitment is independent of spawning biomass, implying density dependent per-capita offspring production. When steepness equals 0.2, recruitment is linearly related to spawning biomass and per-capita offspring production is density independent. Populations with high steepness are more resilient to exploitation. To increase the ability to detect predator effects, we assumed prey populations were fished at time-invariant rates, set equal to the level that maximizes long term catches under the mean predator abundance. Fishing rates were imposed across ages based on age-specific vulnerabilities to fishing, which are commonly estimated in stock assessment models.

Predation was modeled as an index between -1 and 1 that affected natural mortality at three life stages: before age of recruitment, between recruitment age and maturation (juveniles), and after maturation (adults). This index reflects the abundance and diet preferences of all predator species that consume the prey at a common life stage. The index was equal to 1 at maximum predator abundance, 0 at average abundance, and -1 at minimum abundance. For recruitment, if P_t is the standardized predator index in year t, S_t is the total spawning biomass at time t, α is the average number of recruits per spawner at low spawning density, and β controls the amount of density dependence in recruitment (α and β are derived from recruitment at carrying capacity and steepness, Table 1.2), then in the absence of any stochasticity, recruitment at time $t+1$, (R_{t+1}) is:

$$R_{t+1} = \frac{S_t}{1+\beta S_t}\alpha\left[1-\left(1-\frac{\alpha_{min}}{\alpha}\right)P_t\right]. \tag{1.1}$$

This formulation presumed that recruitment predation alters α, and occurs after the period of density dependent mortality. This maximized the predator's potential impact on recruitment, thereby increasing the ability of the estimation method to successfully detect the predation effect. The parameter α_{min} can take values between 0 and α, and determines the overall magnitude of the predator effect on recruitment. When α is equal to zero, the predator has the maximum influence, and the effective recruits per spawner varies between zero and 2α. In the simulations, α_{min} was chosen to produce a 50% reduction in equilibrium annual production when predators are most abundant compared to when predators are at average abundance ($P_t = 1$ compared to $P_t = 0$). Spawning biomass is a function of the number of fish in each age group a at time t, $N_{a,t}$, the weight at age a, w_a, and the maturity at age a, u_a. Using these parameters:

$$S_t = \sum_{a=0}^{A} N_{a,y} u_a w_a, \tag{1.2}$$

where A is the maximum age class modeled.

A different set of equations was used to simulate the effect of predators on juvenile or adult stages. We implemented this effect via a linear relationship between the stage-specific natural mortality rates and predator abundance. Doing so assumes predation mortality is density independent. While that may not be the case in biological populations, it is a reasonable approximation for simulation purposes because it is the most easily detectable functional form linking predation mortality to predator abundance. Here we defined juveniles as younger than the age of 75% maturity, and adults as older than the age of 75% maturity. For each stage, we decomposed natural mortality into a portion that was constant ($M1$) and a portion that fluctuated linearly with predator abundance ($M2$). We note that $M1$ can include mortality from predators, so long as that mortality is constant through time. Under these assumptions, the number of fish of age $a+1$ at time $t+1$ is:

$$N_{a+1,t+1} = N_{a,t} \exp\left[-\left(M1_a + M2_{a,t} + q_a F\right)\right], \tag{1.3}$$

where F is the fishing mortality for ages fully vulnerable to fishing and q_a is the selectivity to fishing gear for fish of age a, reflecting the fact that fisheries often target older and larger individuals. The range of $M2_a$ was chosen so that mortality due to fluctuating predator abundance varied between 25-75% of the total natural mortality rate, and the average total natural mortality rate over time was equal to the rate reported in the stock assessment. To achieve these criteria, the total natural mortality rate of fish of age a at time t, $M_{a,t}$, was:

$$M_{a,t} = M_a\left(1 + \tfrac{1}{2}P_t\right). \tag{1.4}$$

Here, M_a is the natural mortality rate for fish of age a under average predator abundance, and P_t is the standardized predator index.

We represented variation in annual predator density via an oscillating sine function. This structure provided a flexible and simple pattern of predator population decline and recovery for simulation purposes. The sine function had a period of 20 years, and in each simulation the predator index began at a random point within this period. We simulated populations for 300 years, using the first 249 years to allow populations to reach stable behavior, and then fit production models over the final 51 years. From these trajectories, we calculated observed annual production, $\widehat{AP}$, which is the total biomass the population produced in a year:

$$\widehat{AP}_t = \hat{B}_{t+1} - \hat{B}_t + C_t, \tag{1.5}$$

where $\hat{B}_t$ is observed aggregated biomass in year t and C_t is fishery catch in year t. Annual productivity is a good measure to use to detect predation because predator abundance directly influences prey productivity, not prey abundance. Only over longer time scales relative to the prey life cycle might the effects of predation on production be manifest in population abundances.

To produce a standardized metric to measure the relative importance to productivity of recruitment, and juvenile and adult growth and survival, we calculated an approximate elasticity of the population growth rate (λ) to changes in fecundity (i.e., recruitment), and growth and survival. Elasticity is the rate of change of λ with respect to a parameter, relative to the magnitude of that parameter (Caswell, 2001). To do this, we first linearized the operating model at population levels that maximized productivity under equilibrium age structure for each species and generated a biomass transition matrix at this point. The entry for the transition from age a to $a+1$ is then:

$$\exp\left[-(M_a + q_a F) + G_a\right], \tag{1.6}$$

where G_a is the instantaneous growth rate at age a, or the log of the ratio of the weights at age $a+1$ to a. The entries in the top row, representing fecundity, are the biomass of recruitment at maximum productivity multiplied by the proportion of total spawning biomass that each age class makes up. We then applied standardized calculations using left eigenvalues of the resulting biomass transition matrix to derive the elasticity for each entry (Caswell, 2001). We summed these elasticities over all of the fecundity terms, the growth and survival terms for juvenile age classes, and the growth and survival terms for adult age classes. This localized elasticity analysis allowed us to compare across life history types and ask whether common life history stages were consistently important, indicating which stages might lead to larger population responses to predation.

We considered several scenarios to understand how different variables influence the detectability of predators (Table 1.1). For all four prey species, we considered the three life stages targeted by predators (recruit, juvenile, adult), two levels of environmental stochasticitiy affecting recruitment (coefficient of variation, c.v. = 0.20, 0.66), and two levels of observation error (c.v. = 0 and 0.20) on the prey biomass and predator index. We added the environmental (non predation) stochasticity by multiplying recruitment, R_y by a log-normal random variable δ, where $\log(\delta) \sim N(-\sigma_p^2/2, \sigma_p^2)$, and σ_p is the selected standard deviation of the log for process error, related to the coefficient of variation by the formula $\sigma_p^2 = \log(cv^2 + 1)$. Observation error was included similarly, multiplying total biomass or the predator index by a random variable γ, where $\log(\gamma) \sim N(-\sigma_o^2/2, \sigma_o^2)$, and σ_o is the standard deviation of the log for observation error.

The means were adjusted from zero so that the expectation of the variables δ and γ are both one. In all simulations, the predator and prey shared a common coefficient of variation for observation error. We simulated 500 trajectories under each scenario.

Statistical model

For each scenario, we simulated age-structured data, aggregated it into an "observed" total biomass time series, and fit a logistic model to annual production (as calculated from Eq. 5) that included a term for predation:

$$\widehat{AP}_t = r\hat{B}_t\left(1 - \frac{\hat{B}_t}{K}\right) + \beta\hat{P}_t + \varepsilon_t. \tag{1.7}$$

Here, *r* is the population growth rate, *K* is the carrying capacity, $\hat{P}_{t,}\,\hat{B}_t$, and $\widehat{AP}_t$, are the observed predator population index, total prey biomass, and prey annual production respectively, at time *t*. The parameter β describes the change in prey production for a unit change in $\hat{P}$ and $\varepsilon_t \sim N(0, \sigma^2)$. We fit this model using ordinary least-squares regression. This method assumes variation about the fitted relationship is due to population processes that are not accounted for, which can sometimes be more biased than assuming variation due to errors in observed biomasses (Polacheck *et al.*, 1993). However, studies have often shown that both methods produce qualitatively similar results (Bundy *et al.*, 2012; Punt and Szuwalski, 2012). For each simulation, we also fit a single-species model that excluded the predation term, β, to determine if accounting for the predator improved fits.

We required a simple metric to assess the strength of statistical support for an estimated effect of a predator. That is, unlike some simulation testing procedures, the parameters used in the operating models are not directly estimated in the estimation models. We therefore used the *t*-value of the estimated predation coefficient, β. Because a *t*-statistic is a measure of signal to noise, the *t*-statistic provides an intuitive variable that measures the detectability of the predation effect in a system known to have an ecologically significant predator.

Multiple predators

We also explored how the detectability of predation signals changes when multiple predator assemblages prey upon populations, each predator consuming distinct life stages. We simulated biomass trajectories for populations that were preyed upon by different hypothetical predator assemblages at two life stages. For simplicity, we considered a single scenario of observation error (c.v. = 0.2) and low recruitment variation (c.v. = 0.2). We only considered predation on recruits and juveniles, because our simulation results indicated minor effects of predation on adults. To ensure that the predators were not oscillating in synchrony, we constrained the periods of the two predator assemblages. For the predator on the recruits, the period was randomly chosen in a uniform range between twice the age at maturity and 30. The predator consuming juveniles was presumed to be larger and thus longer-lived. We therefore simulated the second predator with a period randomly chosen between the period of the first predator and 30 years, again chosen uniformly at random. We did not include English sole because our analysis indicated that predation effects on recruitment could not be reliably detected.

We used these model simulations to determine whether the effect of predation on one life stage could be detected reliably when a different predator targeted a second life history stage. To that end, we first identified levels of predation in the single-predator scenario that could be reliably detected, and then, using that level of predation, evaluated whether the addition of a second predator degraded the signal of the first. We numerically estimated the magnitude of predation for both the recruit and juvenile predator that led to a statistically significant predation term in 95% of 500 simulations for each species. We then evaluated the ability of the estimation method to statistically detect the effect of this predator when a second predator also regulated that population. The statistical model with two predators estimated two predation coefficients. For these comparisons, we used the same annual recruitment and observation anomalies for the single-predator and two-predator scenarios being compared.

Application to population benchmarks for management

We evaluated whether accounting for predation in analyses of abundance data may improve estimates of population benchmarks used to sustainably manage harvested stocks. Using the single-predator simulations, we estimated two population benchmarks commonly used in management: maximum productivity (maximum sustainable yield; MSY) and the biomass associated with that productivity (biomass at MSY; B_{MSY}). We calculated the relative error of these quantities under the estimation method that accounted for predation, and the single-species method that included only density dependence. We made this calculation under average predation pressure (i.e., $P = 0$). Relative error is the difference between the estimated and true values of the quantity, standardized by the true value. We examined the distributions of the relative error for evidence of accuracy and precision in the inferred benchmark quantities as compared to their true equilibrium values. Bias might be considered “significant” when the interval for relative error of the middle 95% of simulations does not overlap zero. Precision is based on the range of the interval; when it spans two units, the range of the estimates is twice the parameter’s true magnitude.

RESULTS

Production dynamics

The simulated effect of predation on production dynamics of age-structured fish populations depended on both the life stage during which predation occurred and on the life history characteristics of the population (Figure 1.1). In general, predation targeting juvenile stages led to the largest fluctuations in biomass and production, whereas predation targeting adult stages led to the smallest fluctuations. Exceptions to these generalizations revealed the role of life history traits in dictating sensitivity to predation. For example, the species with the shortest time to maturation, the Pacific sardine, displayed larger production responses to predation during recruitment than to predation during the juvenile stage. The short duration of the juvenile life stage of this species reduced the period of exposure to fluctuating predator abundance, causing the reduced sensitivity to juvenile predators. In contrast, the longest-lived species, English sole, displayed smaller production responses to recruitment predation than adult predation. These general findings were supported by the elasticity analysis of the linearized model, which showed that changes in growth and survival at the juvenile life stage generally led to the largest changes in the population growth rate (Table 1.3). The elasticity analysis also predicted the low sensitivity of English sole to recruitment, which is attributable to the low natural mortality rate and long time to maturity (Table 1.2).

Stochastic dynamics of the four species also differed among life histories, and environmental stochasticity could sometimes overwhelm cycles generated by fluctuating predator abundances. Variation in recruitment caused annual production of hake and menhaden to show sharp inter-annual variability (Figure 1.2). In contrast, under identical magnitudes of predation, inter-annual changes in annual production and biomass were dampened in the Pacific sardine and English sole due to the relatively lower influence of recruitment on population growth (Table 1.3). For the scenarios explored here, simulations rarely produced a 25% change in English sole biomass.

Estimating single-predator effects

Fitting logistic population growth models to the simulated data showed that statistical models can only detect significant top-down trophic effects in a restricted number of cases. When there was low recruitment variation and no observation error, effects of predation on recruits and juveniles were estimated reliably (Fig 1.3). When predation targeted adults in these circumstances, detection was less consistent, but median *t*-values still reached levels needed to achieve statistical significance. Increasing recruitment variability to levels more frequently seen in mid-trophic fish populations sharply reduced the detection capability of the estimation method. Across all four species and three life stages, the absolute value of the median predation *t*-score decreased by 64%. Consequently, predation effects were only detected for some life history stages and species. A signal from a juvenile predator was reliably estimated for all species except the sardine, but predation on recruits or adults was often not detected (Figure 1.3). The addition of observation error further diminished the method's detection capability, and typically overwhelmed the true signal even when there was low recruitment variation. This decrease was particularly pronounced for English sole, possibly because English sole were least affected by recruitment variability. Therefore, inducing observation error led to a larger qualitative change in the observed dynamics. For the remaining three species, predators were only reliably detected in the presence of observation error when the deterministic model predicted very strong effects of predators on production (e.g. juveniles and sardine recruits), and when recruitment variability was low (Figure 1.3).

English sole was notable because fewer than 2.5% of predator *t*-values were statistically significant under both recruitment predator scenarios that included observation error. Under the lower recruitment c.v. of 0.20, increasing the predation magnitude to its maximum possible value caused the recruitment predator on English Sole to be statistically detected at most only 7% of the time. Because this species had the longest age to maturation, we hypothesized this could be due to delayed effects of recruitment predation on production. To test this possibility, we re-ran the statistical analysis using a 5-year moving average of the predator index in place of the observed value in a given year. This resulted in a 95% frequency of detecting a significant recruitment predator. Therefore, we infer that for longer-lived species, production is integrating predator effects over multiple years.

Multiple predators

The effect of predation was less detectable when there were different predator assemblages acting on two distinct life stages and the statistical models attempted to estimate each predator's effect (Table 1.4). Given identical observation and identical recruitment anomalies, a predation effect was detected less often when a second predator assemblage influenced mortality at a different life history stage, even when including the second predator as a covariate in the statistical model. The extent of this effect varied markedly across the prey species and life stages targeted. Silver hake experienced both the largest and smallest changes in detectability with the addition of a second predator, depending on which life history stages were affected. When predation was directed at recruits and juveniles, the recruitment predator was detected 32% less often than it was in simulations when predation only acted on recruits. In contrast, the predator on juveniles was detected 56% less often than in simulations where there was no recruitment predator. This asymmetry occurred because the estimation model incorrectly attributed too much variation in production to the juvenile predator. The detectability of predation on sardines also depended on the life stage that the initial predator targeted, though the loss in detection of the recruitment predator was greater than the loss for the juvenile predator in this case. Menhaden experienced more consistent declines in detectability between the two life stages.

Estimates for managing populations

The production models with and without predation were generally unreliable in estimating population benchmarks. Including an explicit predation term did often improve the ability of logistic growth models to accurately estimate the population benchmarks MSY and B_{MSY} under lower recruitment variability. However, there was high bias and generally low precision in the estimates regardless of whether predation was included. The models consistently overestimated MSY for all species, regardless of whether predation was accounted for in the estimation procedure (Figure 1.4). The bias in the estimates of B_{MSY} depended on the species, model, targeted life stage, and recruitment variability, but the middle 50th percentile of relative errors over all simulations contained zero in only one out of 48 cases (Figure 1.5). The estimates of B_{MSY} were nearly always lower under the model that included predation. Under low recruitment variability, these smaller estimates from the predator model were generally an improvement. Under high recruitment variability, stochasticity overwhelmed the ability of both models to accurately and reliably estimate the parameter. In order to estimate MSY and B_{MSY} you need to see annual production as a decelerating function of biomass. For that reason, we excluded simulations in which the simulated data produced a concave up relationship, but this procedure did not exclude cases where the relationship was nearly linear (i.e., second derivative approximately zero). This explains the error bars that extend orders of magnitude beyond the unbiased value. In practice, these estimation problems would be recognized by standard goodness-of-fit diagnostics.

DISCUSSION

We conducted a simulation study to assess the sensitivity of populations to predation targeting different life stages, and measured the detectability of predation when fitting population growth models to aggregate biomass data. We found that predator effects on prey populations are easily masked by other ecological or sampling processes. Further, the detectability of predation depended strongly on the life history stage that was preyed upon, as predators that targeted sub-mature life stages were generally more easily identified. However, there was no single life history stage in which predation effects were consistently most detectable. Rather, the strength of the predation signal also depended on life history features of the prey species; a short time to maturity decreased detectability of predators on juveniles, whereas a long life history meant predators impacting early life stages were unlikely to be resolved. Including predation in estimates of population benchmarks used for management has been shown to sometimes lead to more conservative estimates (Overholtz *et al.*, 2008), but we found that using production models on variable and age-structured populations that experience predation consistently leads to biased and imprecise estimates, regardless of whether predation is included in the estimation process. In addition, including predation did not lead to consistently more conservative estimates of these benchmarks.

Results of this simulation contribute new insight on the detection of top-down effects, particularly in stage-structured food webs. Traditionally, many ecologists hypothesized that trophic complexity can explain the strength of top-down influences, with such effects being weaker in speciose systems like those found in coastal marine environments (Strong, 1992). However, meta-analyses have shown that the species-specific energy conversion rate of the predator is more important than the species richness of the system in determining the strength of trophic cascades (Borer *et al.*, 2005). Moreover, the strength of trophic cascades within and among aquatic systems, both freshwater and marine, is highly variable (Shurin *et al.*, 2002). Here, our simulation results demonstrate that environmentally driven variation in productivity in marine systems is sometimes large enough that major changes in survivorship caused by predators cannot be easily resolved from typical data and production modeling tools. Detectability of predators is an additional consideration to explain the limited cases of strong top-down control in coastal marine food webs (Bundy *et al.*, 2012; Fu *et al.*, 2012; Holsman *et al.*, 2012) despite several high-profile examples of trophic cascades in these ecosystems (Worm and Myers, 2003; Frank *et al.*, 2005). More complex, non-linear time series methods (Sugihara *et al.*, 2012) might provide an improvement on production models, but these methods require lengthy time series that may not always be available.

We found that predators had the largest effects when they affected survivorship of sub-mature life stages. Consequently, these predator effects were more readily detected. Studies using simple Lefkovich matrices that evaluate sensitivity of population growth rates to changes in stage-specific mortality and fecundity rates have also shown that survival at the juvenile life stage is an important driver of population growth among fish (Frisk *et al.*, 2002; Aires-da-Silva and Gallucci, 2007; Quiroz *et al.*, 2011), particularly in the presence of predators (Johnson and Jaime Zuniga-Vega, 2009), and across other taxa such as birds (Johnson and Braun, 1999), large herbivores (Gaillard *et al.*, 2000), and turtles (Crouse *et al.*, 1987). In the present study, we applied a more detailed model that included somatic growth and density-dependence, in addition to stage-specific mortality and fecundity. However, we still found the largest sensitivity to sub-mature mortality, suggesting that the earlier generalization is robust to some of the model assumptions. However, the mechanism may be slightly different in our model. In the simpler models, recruitment is directly proportional to adult biomass, so predation on juveniles eliminates individuals before they have an opportunity to reproduce, causing changes in productivity. Because recruitment steepness was relatively high in our model, recruitment into the population did not change considerably across spawner abundance. Therefore, the importance of juvenile mortality was likely a consequence of the removal of biomass and reduced somatic growth from fewer rapidly growing juveniles, rather than the loss of future reproduction. Because predators on juveniles generate larger ecological responses in the dynamics of their prey, our ability to statistically detect those predator effects is greater.

The limited response of populations to fluctuating predators on adult stages was surprising given that fishing– analogous to predation on adult life history stages– is widely acknowledged to govern marine population dynamics (Worm *et al.*, 2009). This difference between humans and other predators on marine populations likely reflects the range of variation in natural mortality that we deemed biologically plausible. We modeled the variable component of predation mortality to be between 25 and 75 percent of total natural mortality. This variable portion of natural mortality is therefore less than the adult fishing mortality when populations are fished at levels that maximize long term sustainable catch. Therefore, although the simulated adult predator and fishing fleets target similar age classes, it is less likely that a predator could induce the same changes in a population as can fishing, thereby making the predator more difficult for statistical models to detect. This has potential implications for management of harvested populations, as Fowler (1999) argues that to achieve sustainable exploitation of natural resources, we should constrain harvesting so that populations fluctuate within their natural ranges caused by environmental variability and community dynamics.

Life history traits can make populations less sensitive to varying predator populations that target certain age classes. In our simulations, English sole, a long-lived species with a low natural mortality rate, exhibited minimal inter-annual variability in annual production due to changes in recruitment, whether driven by predation or stochastic bottom-up effects. Instead, the changes compounded over time as low recruitment events led to less somatic growth and fecundity in the coming years, as there were fewer fish to grow and reproduce. When fishing pressure causes the average age of a stock to decrease by truncating older age classes, populations become more variable (Anderson *et al.*, 2008). However, species that are naturally shorter-lived could also display more variable dynamics than those that survive longer. Therefore, a long life history may be a strategy for species such as English sole that allows the population to remain relatively stable under variable conditions, as it stores recruitment gains in good years within the adult population (Warner and Chesson, 1985). For such long-lived species, using a moving average for the predator signal, as opposed to information for only one year, may improve detectability of predation effects. Carpenter & Leavitt (1991) reached similar conclusions when assessing the strength of trophic cascades, and recommended using a time scale similar to the lifespan of the top predator.

Population stochasticity can strongly influence estimates of standard population benchmarks commonly used in management of age-structured populations. Analogous simulation studies have revealed that even when natural mortality rates are stable, time series data of biomass and fishery catches have poor success in estimating the population benchmarks *MSY* and its associated exploitation rate (Punt and Szuwalski, 2012). Our results are consistent with these findings, as estimates for both B_{MSY} and MSY were generally positively biased. There are growing calls for decision-makers to consider species interactions in management of populations in both terrestrial and aquatic environments (Soule *et al.*, 2005; Estes *et al.*, 2011; Pikitch *et al.*, 2014). However, we found that regardless of whether we accounted for predation-induced variation in productivity, population benchmarks that managers often use are difficult to estimate from abundance data that is aggregated over the age structure of a population.

While predation is clearly a dominant component of mortality for most fish populations, the extent to which it drives their dynamics is still often debated. Here, we show that even if predation drives the demographic rates of the age-structured populations, we often cannot discern its effect through analysis of time series of aggregated biomass. The detectability depends on the underlying dynamics of the population and the nature of the predation. For simple biomass data of mid-trophic level species, the most robust and detectable predators are those that target sub-mature life stages. Our results therefore provide a way to identify predator-prey linkages that are more likely detectable, and can thereby direct future efforts at quantifying predator effects. For species with short life histories, predators that act on early life stages are easiest to identify, whereas for species with long life histories, predators targeting prey after recruitment but before reproductive maturity have the greatest likelihood of being distinguished. Long annual time series containing accurate age-structured data of predators and prey, as well as detailed predator diet information, allow us to detect these interactions (e.g., Tyrrell *et al.*, 2008)(e.g., Curti *et al.*, 2013); however, these rich datasets are uncommon, so we are hopeful that some intermediate level of detail may be sufficient to detect important species interactions. Developing better tools to explicitly account for observation error, in addition to process variability, may be one avenue for improvement. Population growth models that do not account for observation error should not be used to estimate management benchmarks, regardless of whether species interactions are included. When unsure, simulation testing to investigate whether one will be able to detect a specific predator of interest, in concert with the actual analysis, can ultimately yield a more complete understanding of how these populations behave.

Table 1.1. Summary of simulation scenarios

Factor	Levels
Species	Pacific sardine, Silver hake, Atlantic menhaden, English sole
Life stage targeted by predation	Recruits, juveniles, adults
Log-normal recruitment c.v.	0.20, 0.66
Log-normal observation c.v.	0, 0.20

Table 1.2. Life history parameters of the four species modeled. The variable h is the steepness of the stock-recruit relationship[1], or the ratio of recruitment at 20% of the unfished biomass to recruitment at the unfished biomass. F_{MSY} is the fully-selected fishing mortality rate that leads to a population biomass of B_{MSY} under equilibrium and average predator abundance.

	Age at 50% maturity	Average natural mortality (yr^{-1})	h	F_{MSY}
Pacific sardine	1.2	0.4	0.89	0.73
Silver hake	1.6	0.43	0.9	0.26
Atlantic menhaden	2.5	0.63	0.75	0.77
English sole	3.5	0.26	0.798	0.40

[1] $\alpha = \frac{4h}{\phi(1-h)}$ and $\beta = \frac{5h-1}{\phi R_0(1-h)}$, where R_0 is recruitment at carrying capacity, which scales the population size, and ϕ is the recruits per spawner at carrying capacity, and is derived from the age-structured model.

Table 1.3. Elasticity to changes in demographic parameters of the population biomass growth rate (λ) under a linearized matrix model at maximum productivity of the four species modeled. Elasticity is the rate of change with respect to a parameter, relative to the magnitude of that parameter.

	Juvenile growth and survival	Adult growth and survival	Fecundity
Pacific sardine	0.516	0.192	0.292
Silver hake	0.325	0.498	0.177
Atlantic menhaden	0.659	0.112	0.229
English sole	0.590	0.259	0.151

Table 1.4. Percent of simulations where the predator was detected in the single-predator scenario (columns 1 and 3) and percent of detected predators that were not detected with the addition of a second predator on a different life stage (columns 2 and 4). The ecological magnitude of the predator, and recruitment and observation deviations are the same in both cases.

	Recruitment predator		Juvenile predator	
	Single predator detection (%)	Detection loss (%)	Single predator detection (%)	Detection loss (%)
Pacific Sardine	73.2	28.4	94.4	42.2
Silver Hake	86.4	56.5	89.8	31.2
Atlantic Menhaden	89.0	34.6	95.2	32.4

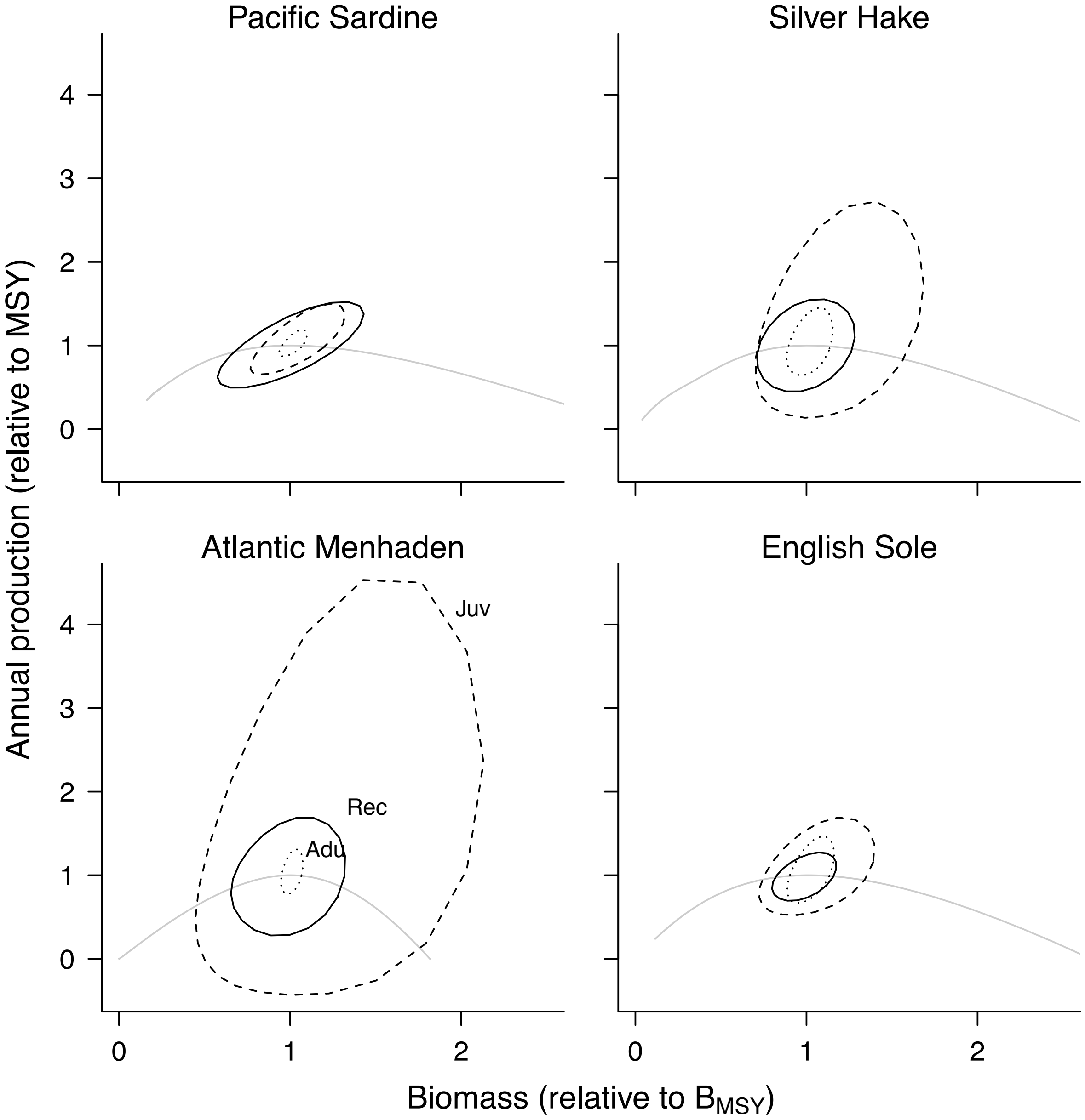

Figure 1.1. Deterministic population trajectories of four species of fish where predation targets recruits (solid), juveniles (dashed), or adults (dotted). Fishing mortality is fixed at FMSY, and the predator population (not graphed) fluctuates with a period of 20 years. Gray line is the equilibrium annual production curve under average predator abundance. MSY is maximum sustainable yield of that curve; BMSY is its associated biomass. All cycles run in a clockwise direction.

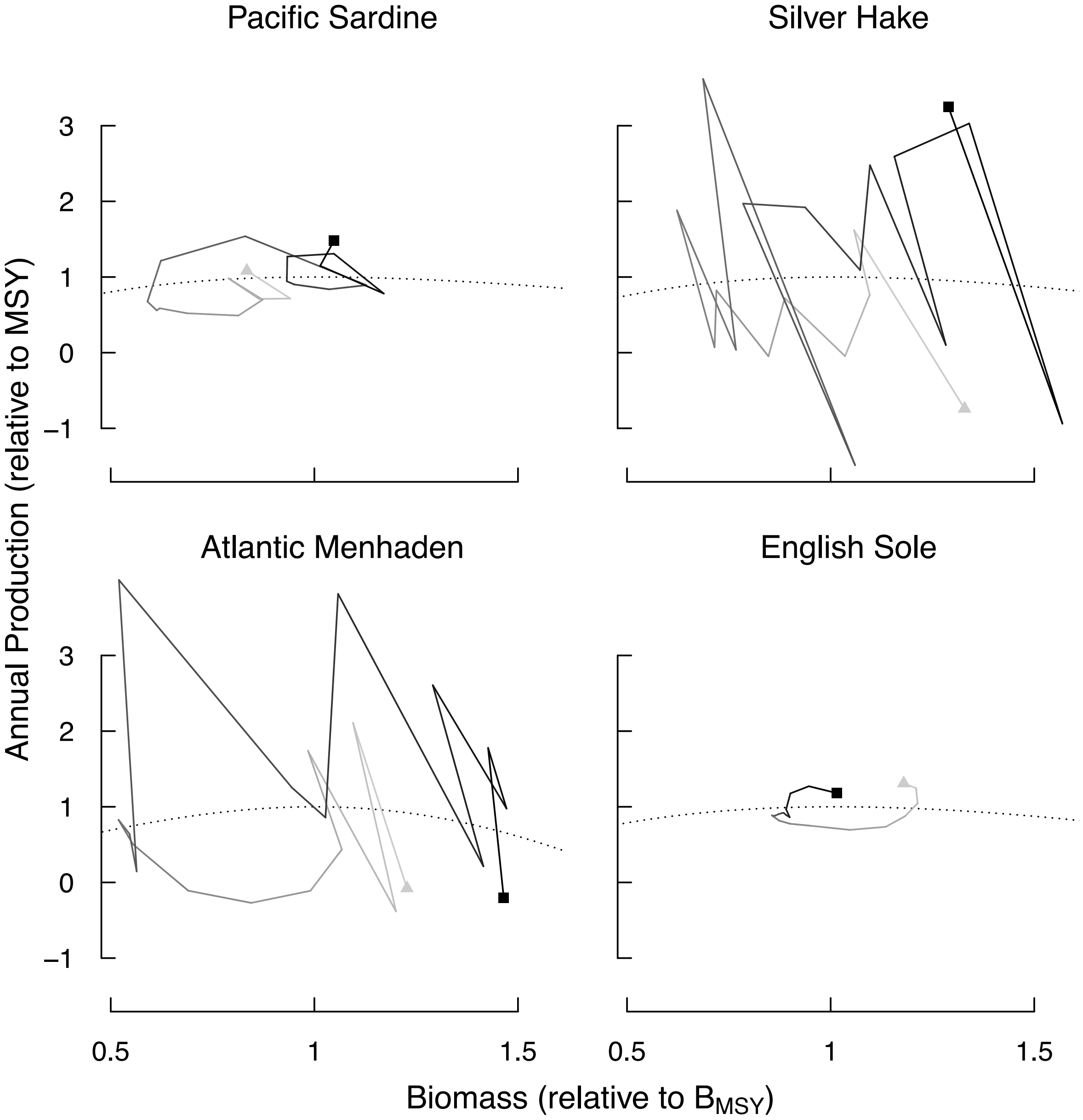

Figure 1.2. Example population trajectories with predation on recruits and lognormal recruitment deviations with a c.v. of 0.4. Trajectories begin at the gray triangle, grow darker as time progresses, end at the black square, and cover one 20-year predator cycle. Dotted line is the equilibrium annual production curve under average predator abundance. *MSY* is maximum sustainable yield of that curve; B_{MSY} is its associated biomass. Production dynamics were most variable for silver hake and Atlantic menhaden.

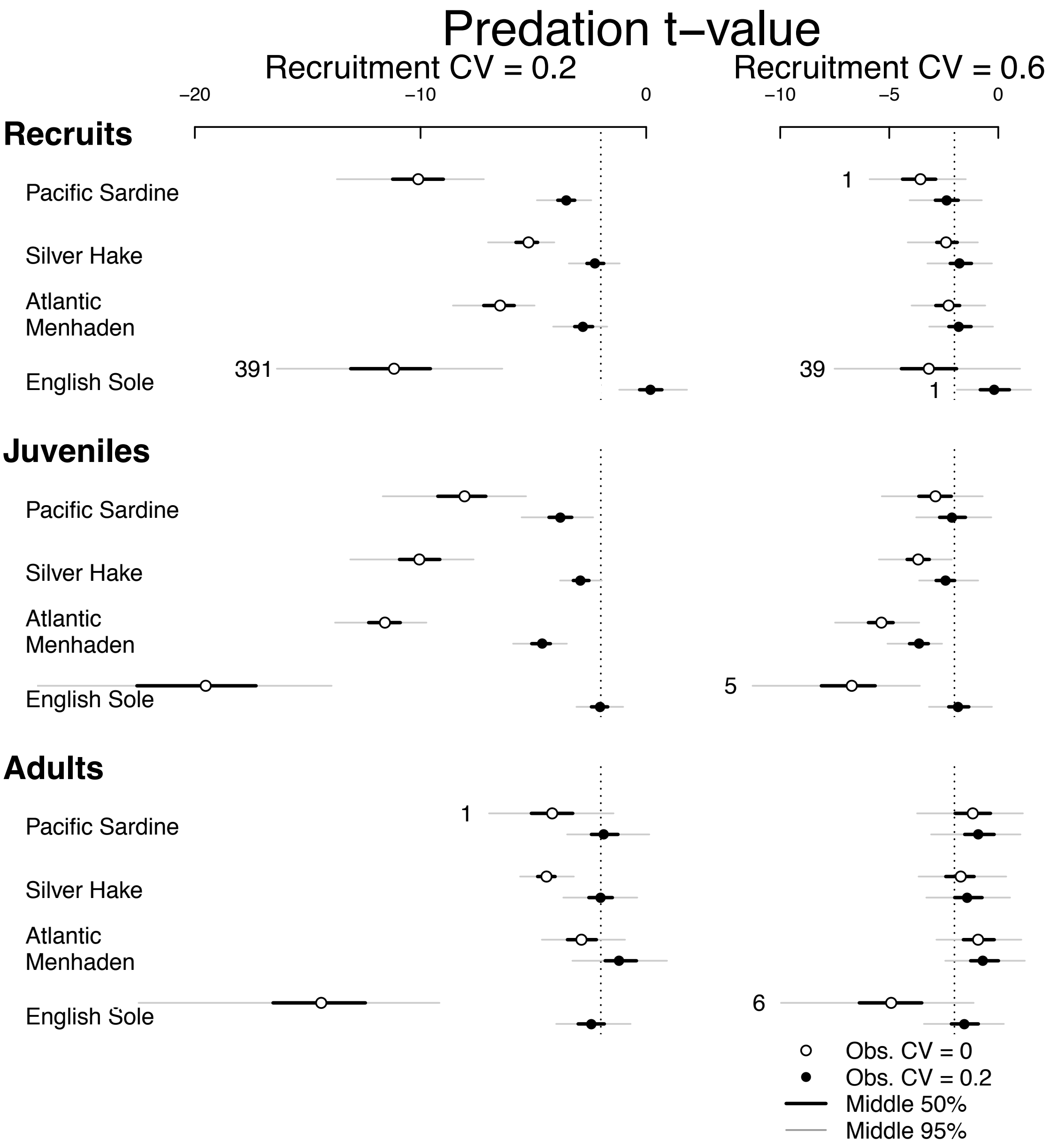

Figure 1.3. Ranges of *t*-values for the predation term in logistic population growth model under different scenarios. Predation targets recruits, juveniles, or adults of one of four species. Points are placed at the median with dark lines representing the middle 50% of simulations and light lines representing the middle 95%. Models are fit to 51 years of data. The vertical dotted line is the critical value for a *t*-test with $\alpha = 0.05$. Numbers indicate how many cases were excluded due to negative estimates of *K*.

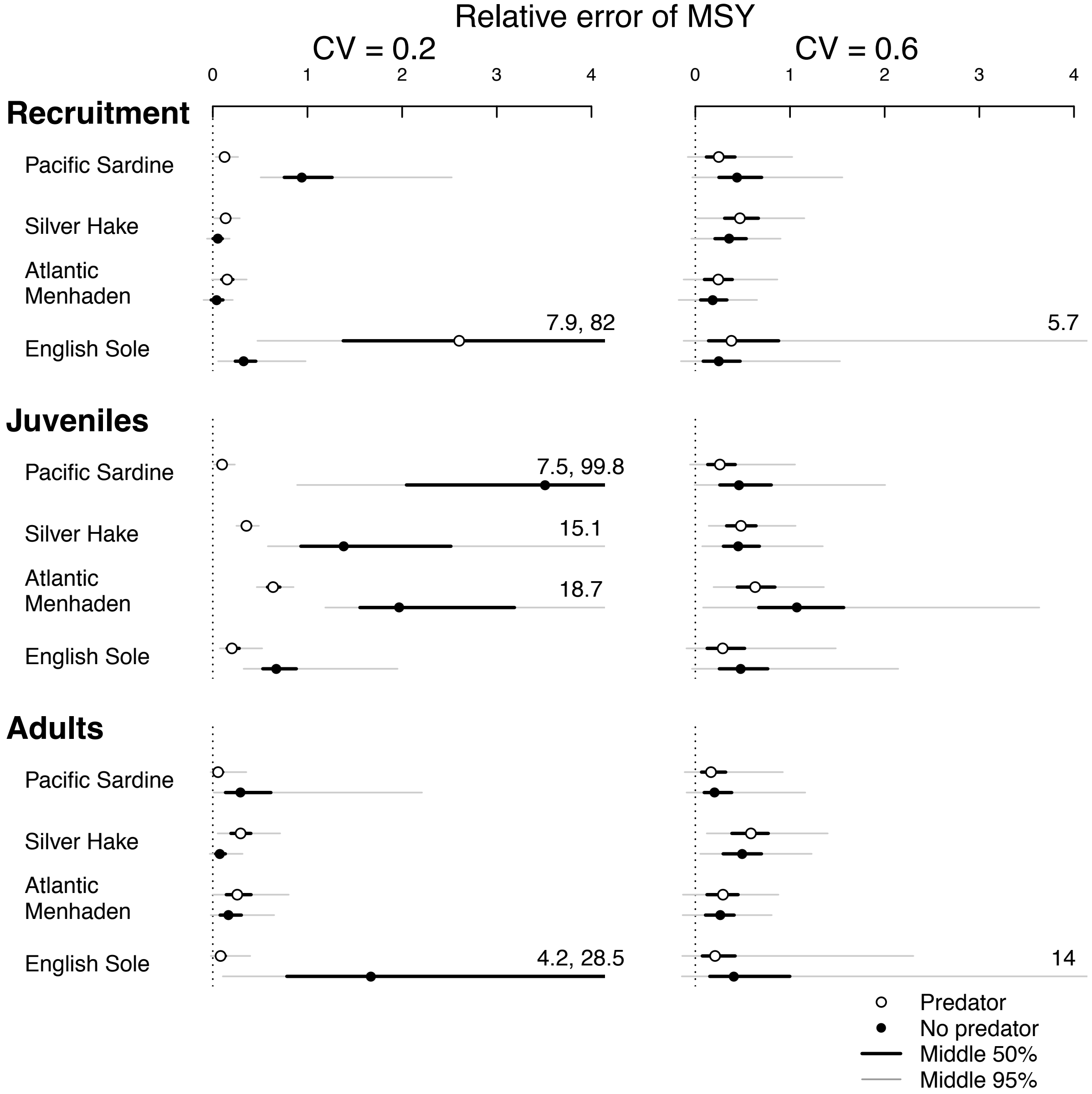

Figure 1.4. Relative error of *MSY* compared to equilibrium value under average predator conditions. Numbers indicate endpoints of the 95% and, if appropriate, 50% quantiles when those quantiles extend beyond plot bounds. Predator model (open circles) includes a linear effect of the observed predator signal in addition to the biomass. The model without predators (closed circles) does not include this parameter. Vertical line indicates an unbiased estimate. Observation error c.v. is 0.2.

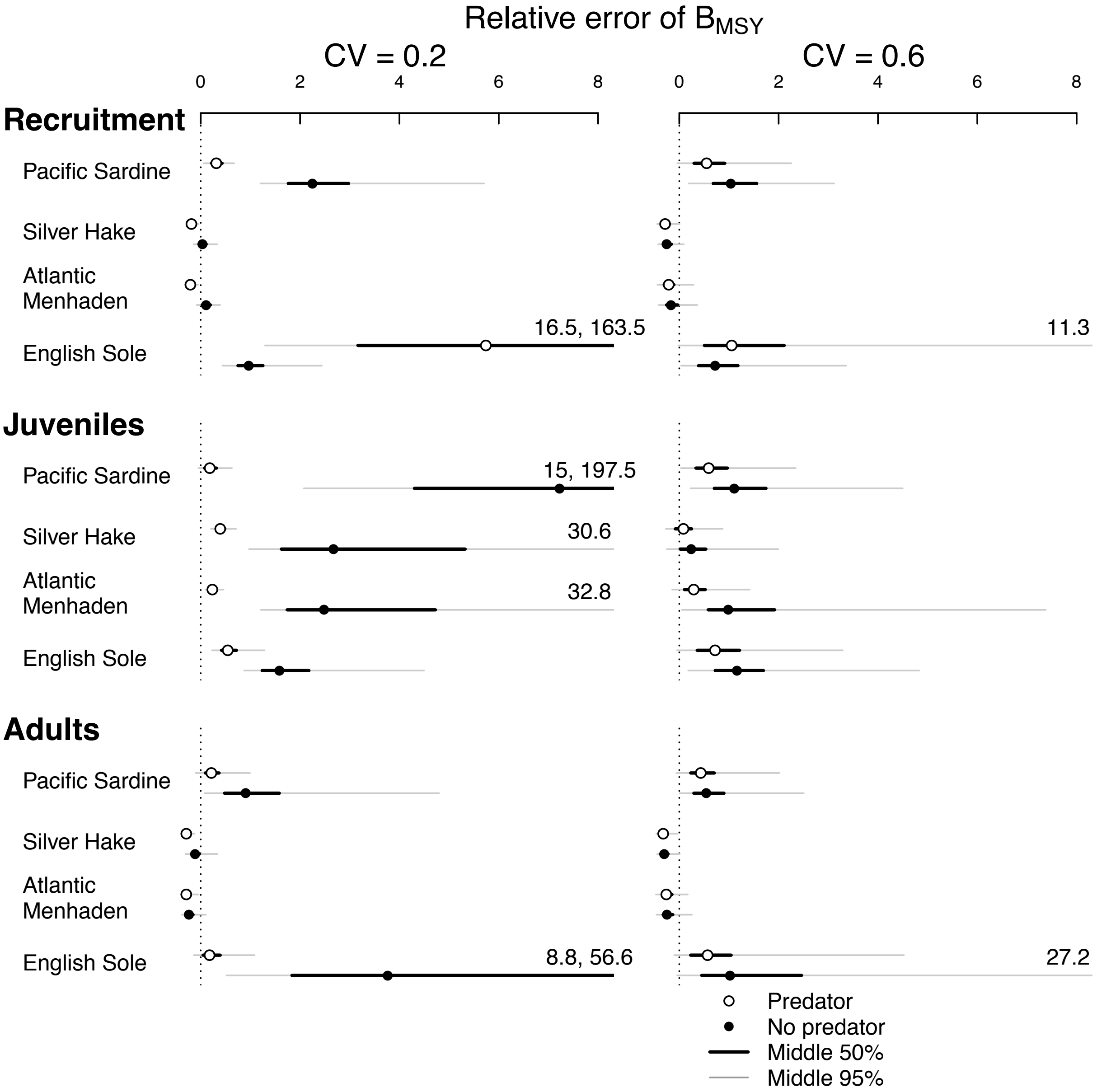

Figure 1.5. Relative error of *B_{MSY}* compared to equilibrium value under average predator conditions. Numbers indicate endpoints of the 95% and, if appropriate, 50% quantiles when those quantiles extend beyond plot bounds.

Chapter 2. Variability and stability in predation landscapes: a cross ecosystem comparison on the potential for predator control in temperate marine ecosystems

ABSTRACT

The importance of predator consumption in shaping population, community, and ecosystem scale processes is an active area of study. In general, it is thought that when food webs have multiple top predators, fluctuations in any single population have only a small influence on variability of the guild at large, meaning that predator diversity stabilizes the predator landscape that prey experience. The degree to which this phenomenon occurs depends on the how populations within the predator assemblage vary. The greatest dampening of variability occurs when populations vary asynchronously, consistent with compensatory dynamics, while the least dampening occurs when populations vary synchronously, possibly in response to a shared environmental driver or similar exploitation history. We utilized a database of biomasses of (mainly) commercial fish species across ten large marine ecosystems paired with information on diet composition and feeding rates to develop a novel multi-component index of predation that allowed us to ask two main questions. First, how diverse are sources of predation in large marine ecosystems. Second, based on synchrony of the assemblages, how much does diversity stabilize variability in the predation landscape. We found that the predator assemblages were only moderately diverse; approximately one-third of the assemblages had a single predator group that accounted for over half of all predation. Abundances of predator populations within these assemblages generally varied independently of one another (neither synchronous nor asynchronous), implying an intermediate stabilizing effect of predator diversity on predation mortality. However, we also observed ecosystems with both synchronous and asynchronous predator assemblages.

Assemblages that are either synchronous or that have low diversity have a greater potential to vary dramatically and induce large-scale changes throughout the system. Quantifying and understanding this potential can help identify systems where precautionary management of predators may be particularly valuable.

INTRODUCTION

Understanding what drives the population- and community-scale consequences of predator-prey interactions is a key question in ecology. The strength of predation control and trophic cascades is remarkably variable among systems, even within a system type (Shurin *et al.*, 2002). For example, both predation (Swain and Benoît, 2015) and climate (Rose, 2004) have been implicated in the slow population growth rate of Atlantic cod (Gadus morhua) in two nearby ecosystems. Food webs characterized by strong predator control tend to have dynamics that are non-linear, hard to understand, and unpredictable (Pace *et al.*, 1999). Management of these food webs is difficult due to their susceptibility to dramatic community shifts and unpredictable responses to anthropogenic or other exogenous perturbations, making such ecosystems important to identify (Estes *et al.*, 2011).

One way to examine the strength of predator control in a community is to quantify the extent to which changes in predator abundances induce changes in prey dynamics (MacArthur, 1955; Paine, 1980). Mechanistically, this means that prey vital rates (principally, natural mortality) exhibit changes through time in response to changes in the predator landscape. The strength of predator control then depends both on how much the predator landscape varies through time and how sensitive prey vital rates are to such variations (Essington and Hansson, 2004). In complex speciose systems, ecologists often predict that prey should experience a relatively constant rate of predation because prey are subject to a diverse assemblage of predators whose temporal dynamics are not synchronized, diminishing the influence of fluctuations in a single population (Power, 1992; Polis and Strong, 1996). This stability in the predator landscape reduces the strength of control caused by any single predator (Strong, 1992). However, diverse predator landscapes do not render dramatic community shifts impossible if exploitation or any other driver suddenly depletes the entire guild of predators at once (Baum and Worm, 2009).

The degree to which diversity dampens fluctuations of the entire predator assemblage, potentially decreasing susceptibility of prey to predator control, depends on the extent to which predator population dynamics are synchronized (Fig. 2.1). When predators are strong competitors, reduction of one predator (i.e. due to an exogenous driver) can lead to increases in others, resulting in *asynchronous* populations (Gonzalez and Loreau, 2009) and strongly stabilizing predator landscapes experienced by prey populations (sometimes referred to as compensatory dynamics or functional complementarity). When predator populations fluctuate independently of each other, statistical averaging implies that as species are added to the system, their fluctuations become more likely to balance each other out (Doak *et al.,* 1998), resulting in an intermediate level of stabilization. Finally, if predator populations exhibit similar responses to a shared exogenous driver or experience a similar history of exploitation, predator populations will be *synchronous* (Baum and Worm, 2009), which will weaken the effect of predator species richness on stabilization of predator landscapes.

There is some evidence supporting the hypothesis that less diverse predator assemblages are associated with stronger predator control of prey populations. The dominance of predator control in marine systems, as measured by a negative correlation between adjacent trophic levels, has been found to be associated with lower predator diversity (Frank *et al.,* 2006; Boyce *et al.,* 2015). However, work across system types on trophic cascades (i.e., separated by two trophic levels) has found no relationship between species richness at any trophic level and the strength of top-down control (Borer *et al.*, 2005). Lindegren *et al.* (2016) found evidence supporting the hypothesis of functional complementarity in predators in the Southern California Current, and concluded that this stabilized predation intensity and contributed to the observed strong linear effect of environmental drivers on ecosystem dynamics. There remains a need to take a comparative cross-system examination (Link *et al.*, 2012a) that explicitly explores the mechanism by which predator diversity could stabilize variability of predator assemblages, thereby decreasing the strength of predator control.

To understand linkages among predator diversity, stability, and predator control, we first must develop time series composed of meaningful metrics of predation intensity that account for the different roles each predator species plays. To date, metrics of predation have generally taken one of two approaches. Both approaches are easy to compute and understand, yet also have key weaknesses. The first approach is to sum the abundances of all piscivorous species (e.g., Frank *et al.*, 2005; Lucey *et al.*, 2012; Lindegren *et al.*, 2016). This approach acknowledges that each prey species is eaten by a diverse assemblage of consumers, and the ability to partition predation by predator species allows the testing of hypotheses regarding connections between predator diversity and top-down control. However, it ignores the fact that some predators are relatively minor consumers (i.e., comprise a small amount of predation mortality) while others might be more important, either due to higher consumption rates, feeding preferences, or higher levels of habitat overlap. The second approach is to take a single species that is thought to be particularly important and track only its abundance (e.g., Worm and Myers, 2003; Holsman *et al.*, 2012; Minto and Worm, 2012). This acknowledges the outsized importance of key predator species, but ignores secondary predators that may consume significant prey biomass. Most importantly, it prevents any examination of functional complementarity or diversity-stability relationships because it only considers one predator population. New metrics are needed to bridge the divide between these two endpoints.

In this study, we take a unique comparative database of multispecies abundances and predator feeding habits and consumption rates across ten large marine ecosystems in North America and Europe (Table 2.1). We use the database to quantify species richness in marine predator assemblages associated with individual prey species, and the frequency and extent to which predator diversity may stabilize the predator landscape experienced by prey. We create a novel multi-component index that assesses predator assemblages from the perspective of different prey populations and then: 1) quantify whether and in what cases predation tends to come from a small or large number of consumers, and 2) quantify whether populations within predator assemblages are synchronous (consistent with a similar fishing history or other shared driver), asynchronous (consistent with compensatory dynamics), or independent (consistent with statistical averaging).

METHODS

We combined published static food web models (Christensen and Pauly, 1992) with abundance information from surveys and stock assessments across ten large marine ecosystems in North America and Europe to create a multi-component index of predation on mid-trophic level species and to quantify how the index and its components have varied through time. First, we developed a multi-component index of predation. Second, we examined this index at the mass-balance model equilibrium biomasses (static analysis), and third, across the time series of biomasses (dynamic analysis). Ecosystems from across the Atlantic and Eastern Pacific all varied in their length and intensities of exploitation, latitude, and perceived major drivers of community structure and dynamics. For a list of ecosystems and prey species included and the food web models used, see Table 2.1. Abundance information is from the database compiled in Fu *et al.* (2012).

Developing the predation index

First, we developed a predator index that is unique to each prey species. The simplest estimate of an index of predation might merely sum the abundances of all predators that are known to consume a given prey species. The ideal estimate would explicitly quantify each predator's contribution to natural mortality every year, which requires spatially explicit time series of abundance, feeding rate, and diet composition, which we are unlikely to ever fully resolve. Here, we attempt to find a middle ground that captures more complexity than a simple sum, but still makes a number of simplifying assumptions that allow us to calculate the index for multiple prey species across many ecosystems.

Our predator index is a weighted sum of predator abundances where the weighting factors are determined by values from static food web models of the predator consumption rates and diets. Specifically, the weights are calculated as the product of consumption rate per unit biomass and the fraction of predator diet that consists of the prey. Both inputs come from a static food web model based on a distinct time period relative to our abundance time series. In the predator index for prey j, the weighting factor of predator i $W_{i,j}$ is written as:

$$W_{i,j} = QB_i D_{i,j} \tag{2.1}$$

where QB_i is the annual consumption to biomass ratio (a single quantity) of predator i, and $D_{i,j}$ is the fraction of predator species i's diet that prey species j makes up. Some food web models divided species into juvenile and adult stages, but our time series of abundance data did not. We therefore averaged the weights for the juvenile and adult life stages based on their relative biomasses in the static model. When prey species were divided into juvenile and adult stages, we quantified predation on the juvenile stage because predation tends to be more important and detectable when it targets younger ages (Oken and Essington, 2015). Although juvenile functional groups in food web models tend to be more data-poor, we note that we use diet information of groups *consuming* juveniles, not the actual juvenile diets or consumption rates (unless the juveniles are themselves predators).

We selected mid-trophic level species within a system as prey species. Experts from each ecosystem used in the analysis had initially classified all species in the system based on taxonomic grouping and size, among other characteristics (Fu *et al.*, 2012). In general, we selected as prey any functional group that contained forage fish, clupeids, and gadids and pleuronectids that were classified by experts as “small,” as well as any other species or species groups that were thought to be key for transferring energy from low to high trophic levels.

Static analysis

First, we calculated the predation index at the biomasses associated with the static model equilibria. To do this, we multiplied the weights in equation 2.1 by the baseline biomasses from the static models, an approximation of species’ relative abundances in the ecosystem. Therefore, the contribution of predator functional group *i* to the static predator index for prey group j, $P_{i,j}^*$ is:

$$P_{i,j}^* = W_{i,j} B_i^* \tag{2.2}$$

where $B_{i,}^*$ is the static model biomass of functional group *i*. Furthermore, the total predator index for prey group j, P_j is the sum of $P_{i,j}$ over all predators *i*.

Using the static predation index that included all or most species in the ecosystem, we examined how comprehensively the subset of species for which we had time series data quantified predation mortality. To do so, we checked which predator functional groups contained at least one predator species found in the abundance time series, and calculated what fraction of predation mortality those functional groups made up.

We also used these static calculations to assess the hypothesis that predation is distributed diffusely among many different species. One key advantage to using the static calculations for this analysis was that we were able to include all predators, even those not included in the abundance time series. We ranked predators in descending order of the $P_{i,j}^*$ and then compared the proportion of predation mortality attributable to the top ranked and second ranked predator for each prey species.

Dynamic analysis

We then examined how the predator index and its component parts varied through time. We again used the weights from equation 2.1 to calculate the predator index, but used the time series of predator biomasses instead of the single value in the static food web model. In addition, the time series data had more taxonomic detail than the food web models. When several species were part of the same predator functional group in the food web model, they were included as separate components in the index, but all received the same weight that was calculated for that predator functional group. This assumes that all species within a functional group have grossly similar diets and consumption rates. The contribution of predator species i_k within functional group i to the predator index for prey group j, at time t, $P_{i\_k,j}(t)$, is:

$$P_{i_k,j}(t) = W_{i,j} B_{i_k,j}(t) \tag{2.3}$$

Once again, the total dynamic predator index, $P_j(t)$ is the sum over all predator species of the $P_{i\_k,j}(t)$. Missing biomass estimates were imputed by linearly interpolating between the two most adjacent years with biomasses. If no earlier (or later) years had estimates for a single species, the value from the first (or last) year with information was inserted.

We measured the degree of synchrony or asynchrony of a predator guild (Fig. 2.1) using the variance ratio. The variance ratio is commonly used to test for compensatory dynamics (Gonzalez and Loreau, 2009), and can be interpreted as a metric of correlation in a multivariate dataset (as opposed to bivariate). The variance ratio of the predator index for prey group j, VR_j was:

$$VR_j = \frac{Var[P_j(t)]}{\sum_{predators\, i_k} Var[P_{i,k,j}(t)]} \tag{2.4}$$

where the variances of each predator species or assemblage are calculated over time. The variance ratio is equal to one when the components are, on average, statistically independent (i.e., pairwise covariances of all predator populations sum to zero), less than one when components are, on average, asynchronous (i.e., negative sum of covariances, consistent with compensatory dynamics), and greater than one when components are, on average, synchronous (i.e, positive sum of covariances, consistent with a shared driver).

We then examined how the variance ratio was related to diversity (species richness) of the predator guild. We used species richness as a metric of diversity because the expected value of the variance ratio is directly proportional to the number of components over which it is calculated, if average pairwise correlation among the species remains constant with the addition of more predator populations. Deviations from this expected relationship would signify stronger or weaker correlations among predator species within the assemblages. We also recalculated the variance ratio and species counts for a subset of the original guild of predator species: the minimum number of predators that account for at least 90% of the average, over time, of the total dynamic predator index (which we refer to as the “core” predator species). In this way, we accounted for the majority of predation, but when there were many rare or unimportant predators, they did not inflate the diversity metric.

Because population dynamics are inherently noisy, it was important to determine the probability of the observed variance ratios occurring by chance alone. To do so, we bootstrapped each weighted biomass time series for each predator species under the null assumption that predator populations are independent (i.e., an expected variance ratio of one, consistent with the statistical averaging hypothesis), and then, for each bootstrap iteration, recalculated the variance ratio of the assemblage. If the observed variance ratio falls in the tails of the distribution of bootstrapped variance ratios, this is evidence that the predator populations are not statistically independent, and either display synchrony or asynchrony. To account for the serial nature of the time series data, we used phase scrambling, a parametric bootstrap method that resamples the phases of the empirical Fourier transform while keeping fixed the moduli, thereby maintaining the mean and spectral characteristics of the time series. This is an effective method for statistics such as the variance ratio that are independent of statistical location (Davison and Hinkley, 1997; Solow and Duplisea, 2007). When a single species dominates the predator index, but there are still many component species, the null distribution of the variance ratio tended to become extremely tightly centered about one; the variance of the sum and the sum of the variances are both nearly equal to the variance of the dominant species. Therefore, for ease in plotting the distributions, we only bootstrapped the variance ratios of the core predator species that accounted for the top 90% of predation. This had no qualitative impact on results beyond the aforementioned cases.

All analysis was done in R version 3.3.0 (R Core Team, 2016). Bootstrapping was done with the boot package (Canty and Ripley, 2016).

RESULTS

We first sought to determine whether the predator species for which we had time series of abundance accounted for a sizable fraction of the baseline mortality. For over one-half of prey (15/26), we had time series data for at least one predator species within functional groups accounting for 50% or more of the of total predation mortality (Fig. 2.2). Key predators that usually lacked time series data were marine mammals and gelatinous zooplankton. Whales and seals accounted for 89% of predation on Barents sea Atlantic herring, and seals accounted for 81% of predation on Eastern Bering Sea Pacific herring. In every prey group in both the Gulf of Maine and Georges Bank, gelatinous zooplankton accounted for greater than 70% of predation mortality. This was because the consumption to biomass ratio of gelatinous zooplankton in the model was two to three orders of magnitude greater than that of predatory fish. This caused gelatinous zooplankton to consume a large biomass of forage fish, even though forage fish represented only a small diet fraction, and furthermore meant that gelatinous zooplankton were the chief consumers of forage fish.

The number of predation sources varied widely among species and systems; the components of the predator indices were not always distributed among many species (Fig. 2.3,2.4). Based on the static analyses, over 50% of predation came from a single predator functional group for approximately one-third (9/26) of the prey groups (Fig. 2.3). Five of those nine functional groups were composed of a single species, underscoring that predation mortality can come from a small number of species. The North Sea tended to have predation that was most evenly distributed, with no predator group accounting for more than a quarter of the total in any prey group. Based on the dynamic analyses, four prey functional groups had a single predator account for at least 90% of the average total predator index (which only includes predators for which there is time series data, Fig. 2.4). These were Baltic Sea sprat (Atlantic cod are the predator), both sand lance and other small pelagics in the Eastern Scotian Shelf (Grey seals), and Pacific herring in the Gulf of Alaska (Arrowtooth flounder).

Across ecosystems, there was no overall tendency for predator populations to be either synchronous or asynchronous (Fig. 2.5). A consistent pattern of synchrony or asynchrony across assemblages is indicated by a positively or negatively sloping relationship between the variance factor and species richness. However, we saw no significant slope in the relationship between the variance factor and species richness (all species slope = -0.006, $P = 0.298$; core species slope = -0.020, $P = 0.404$). Furthermore, the mean of both sets of variance ratios was approximately one (1.03 and 0.99 for all predators and core predators, respectively), indicating an even balance between synchronous and asynchronous assemblages.

Bootstrapping confirmed that there was generally insufficient evidence to reject the null hypothesis that predator populations vary independently. When we bootstrapped components of the predator index under the null assumption that populations are independent (i.e., forced the theoretical variance ratios of the bootstrapped assemblages to be one), the observed variance ratios usually fell well within the distribution of bootstrapped variance ratios (Fig. 2.6). In 18 out of 26 assemblages, the observed variance ratio was within the middle 90% of the bootstrapped distribution. When predator species are independent of one another, there is an intermediate stabilizing effect of predator diversity on the total predator index; the data do not provide consistent cross-system support for further stabilization through asynchrony and compensatory dynamics.

Predator assemblages that did show evidence for either synchrony or asynchrony were clustered within a few ecosystems (Fig. 2.6). Of the eight non-independent predator assemblages, four came from the Eastern Bering Sea, where all four variance ratios were less than one (asynchronous), and four came from the North Sea, where all four variance ratios were greater than one (synchronous). Thus, exceptions to the pattern of independence among predators tended to occur by ecosystem rather than by prey functional group. This is likely in part because predator assemblages on different prey functional groups in the same ecosystem were composed of the same set of biomass time series, only weighted differently.

DISCUSSION

We developed a novel index of predation to study the potential for predator control across marine ecosystems. We find evidence of many cases across systems of low predator richness, so that although the food webs were complex, predator guilds on individual prey are not always so, potentially leading to higher variability of the predator landscape. On the other hand, for prey where predation is distributed across several predators, we find that predator populations tend to vary independently of one another, implying that the diversity of predator assemblages leads to an intermediate level of stabilization on the total amount of predation that populations at lower trophic levels experience. However, this is not uniformly the case. We observe one system (North Sea) where predator populations are synchronous and thus predator diversity will only minimally dampen variability in the total predation. This synchronicity could be due to a similar fishing history or a shared response to an environmental driver. We also find one system (Eastern Bering Sea) where predator populations are asynchronous, a pattern consistent with the hypothesis of compensatory dynamics. Therefore, while the idea of statistical averaging can largely explain characteristics of predator assemblage variability, there are few universal rules in ecology, and understanding individual communities will always be crucial. In cases when predation variability is not dampened by predator diversity, whether due to synchrony among predators or low diversity, prey populations should be more susceptible to predator control.

There is a rich literature linking diversity, stability, and ecosystem functioning, particularly in terrestrial ecosystems (e.g., May, 1973; Tilman, 1996; Doak *et al.*, 1998; McCann, 2000; Gonzalez and Loreau, 2009), but less in marine ecosystems where empirical evidence is harder to obtain because of the difficulties of experimentation in such large connected systems (Naeem, 2006). However, a small number of studies have looked for evidence of compensatory dynamics in individual marine ecosystems (Duplisea and Blanchard, 2005; Shackell and Frank, 2007; Gifford *et al.*, 2009; Lindegren *et al.*, 2016). They have generally found mixed results, and their varying methodologies likely make the studies only grossly comparable (e.g., accounting for serial autocorrelation, see Solow and Duplisea, 2007). One large terrestrial study found that compensatory dynamics are rare across natural systems (Houlahan *et al.*, 2007); however, a similar examination over marine ecosystems has yet to be undertaken. Here, we also found that compensatory dynamics are likely to be the exceptional case, and extend the results of Houlahan (2007) to both marine ecosystems, and ecosystems with long and varying histories of exploitation, which have long since left their "natural" state.

There is some empirical evidence that stronger predator control on prey populations is correlated with less diverse and higher latitude systems, though establishing the actual driver is challenging because many factors, including diversity, covary with latitude (Frank *et al.*, 2006, 2007; Boyce *et al.*, 2015). Establishing evidence for (or ruling out) potential mechanisms by which a particular factor could influence trophic control is an important step in determining which variable actually drives trophic control. This work offers a mechanism for predator diversity to govern predator control: more diverse predator assemblages could reduce the strength of predator control by temporally stabilizing the total amount of predation that prey species experience through statistical averaging, but generally not through compensatory dynamics. Therefore, if we assume that diversity and latitude are correlated (Hillebrand, 2004), predator diversity could cause observed spatial variation in trophic control.

While our predator index is a significant improvement over past efforts that either gave all weight to one predator, or equal weight to all predators, the new index has limitations. In particular, the weights, based on static food web models, are constant and do not accurately quantify the predator assemblages when predators display non-linear functional responses. This becomes most apparent for systems that have undergone major reorganizations, such as those that experienced the collapse of Atlantic cod. When there is a narrow range of predator and prey biomasses, most functional responses can be approximated as linear over the observed values. However, major changes generally induce a wider range of observed biomasses, causing the linear approximation to break down. For a prey density initially in the middle section of a type III functional response (typical of generalists like most marine predators), our linear assumption will overweight the predator if prey abundance increases dramatically and underweight the predator if prey abundance decreases. This means that when non-linear functional responses are accounted for, the predator index will be less variable. If the incorrect weightings are proportional across predators, the relative importance of a predator species would be unaffected, but the variances may still be incorrect. Unfortunately, time series of ecosystem information necessary to parameterize a functional response curve are only available in a small number of cases (Szoboszlai *et al.*, 2015). This makes accounting for such complexities while also maintaining a comparative approach challenging, underscoring the utility of the snapshot food web models (Pikitch *et al.*, 2014).

The Eastern Scotian Shelf is an example of a system where the use of a static food web model led to inconsistent results. The time series of biomasses used in the dynamic analysis indicated that grey seals account for an overwhelming amount of predation throughout the time period (Fig. 2.4). However, using the equilibrium biomasses in the food web model, as we did in the static analysis, seals account for only 15% (Northern sand lance) and 2% (Small pelagics) of the predation. Thus, the model biomass for the reference years (1995-2000) does not match our available seal biomass, even for that same time period, perhaps due to new assessments of seal biomass that have become available since construction of the model. It is also likely that such a substantial change in biomass has been associated with changes in consumption patterns.

The findings of this study contribute to our understanding of the linkage between food web composition and the potential for predator control. Previous evidence has shown that predation can play a crucial role in population dynamics in complex marine systems. In the Southern Gulf of St. Lawrence, predation is thought to be a key factor preventing demersal fish populations from recovering following collapse due to overfishing (Swain and Benoît, 2015). This underscores the importance of understanding and predicting more nuances in the relative strength of predator control. We found that, in general, variability of predation mortality should be somewhat stabilized in diverse predator assemblages, potentially decreasing the strength of predator control in such systems. However, when examining predator assemblages from the perspective of specific prey, we found that marine predator assemblages are not uniformly diverse, and systems are therefore not automatically buffered from predator control. Because of this, understanding whether a given prey species or system is likely to experience predator control requires specific knowledge of the food web, an important step in implementing an ecosystem-based approach to fisheries management. As trophic cascades resulting from strong predator control can be major hurdles towards sustainable resource management, predator populations and assemblages in low diversity systems should be managed with particular precaution, avoiding both sudden decreases (e.g., overfishing) or increases (e.g., rapid mammal reintroductions) in predator populations, as high variability in individual populations may have far-reaching consequences for the community.

Table 2.1. Ecosystems, prey species, and food web models used

Ecosystem	Region code	Prey functional groups	Food web model
North Sea	NORT	Atlantic herring, Lesser sandeel, Norway pout, Common sole, Whiting	(Mackinson and Daskalov, 2007)
Barents Sea	BS	Atlantic herring, Capelin	(Blanchard *et al.*, 2002)
Baltic Sea	BALT	Atlantic herring, Sprat	(Harvey *et al.*, 2003)
Western Scotian Shelf	WSS	Atlantic herring, Other pelagics	(Araújo *et al.*, 2011)
Eastern Scotian Shelf	ESS	Northern sand lance, small pelagics	(Bundy, 2004)
Gulf of Maine	GoM	Commercial pelagics, Other pelagics	(Link *et al.*, 2006)
Georges Bank	GB	Commercial pelagics, Other pelagics	(Link *et al.*, 2006)
Hecate Strait	HS	Pacific herring, Flatfish	(Ainsworth *et al.*, 2002)
Gulf of Alaska	GoA	Pacific herring, Walleye Pollock, Capelin	(Aydin *et al.*, 2002)
Eastern Bering Sea	EBS	Pacific herring, Walleye pollock, Capelin, Yellowfin sole, Pacific sand lance	(Aydin *et al.*, 2002)

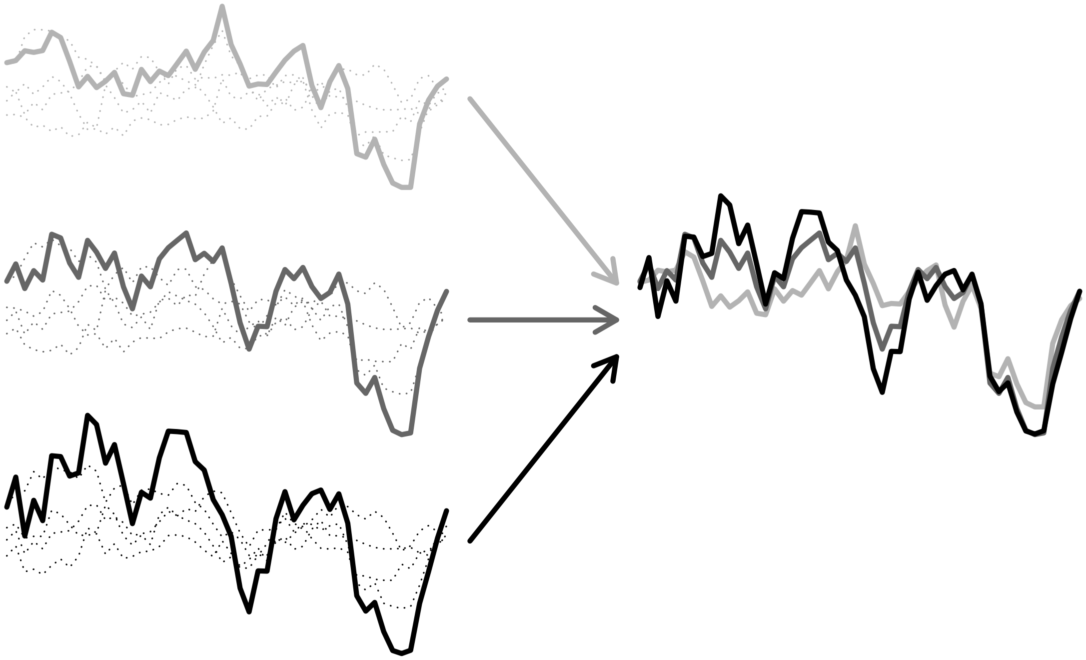

Figure 2.1. Schematic of how synchrony mediates the stabilization effect of diversity. Multiple time series of predator abundance (dotted lines), all with a mean of zero, sum together into a single predator index (solid line). Component species can be either synchronous (black, most variable sum), statistically independent (dark gray, moderately variable), or asynchronous (light ray, least variable). The three different cases all have identical random generator seeds, and only differ in the correlation structure of the component species.

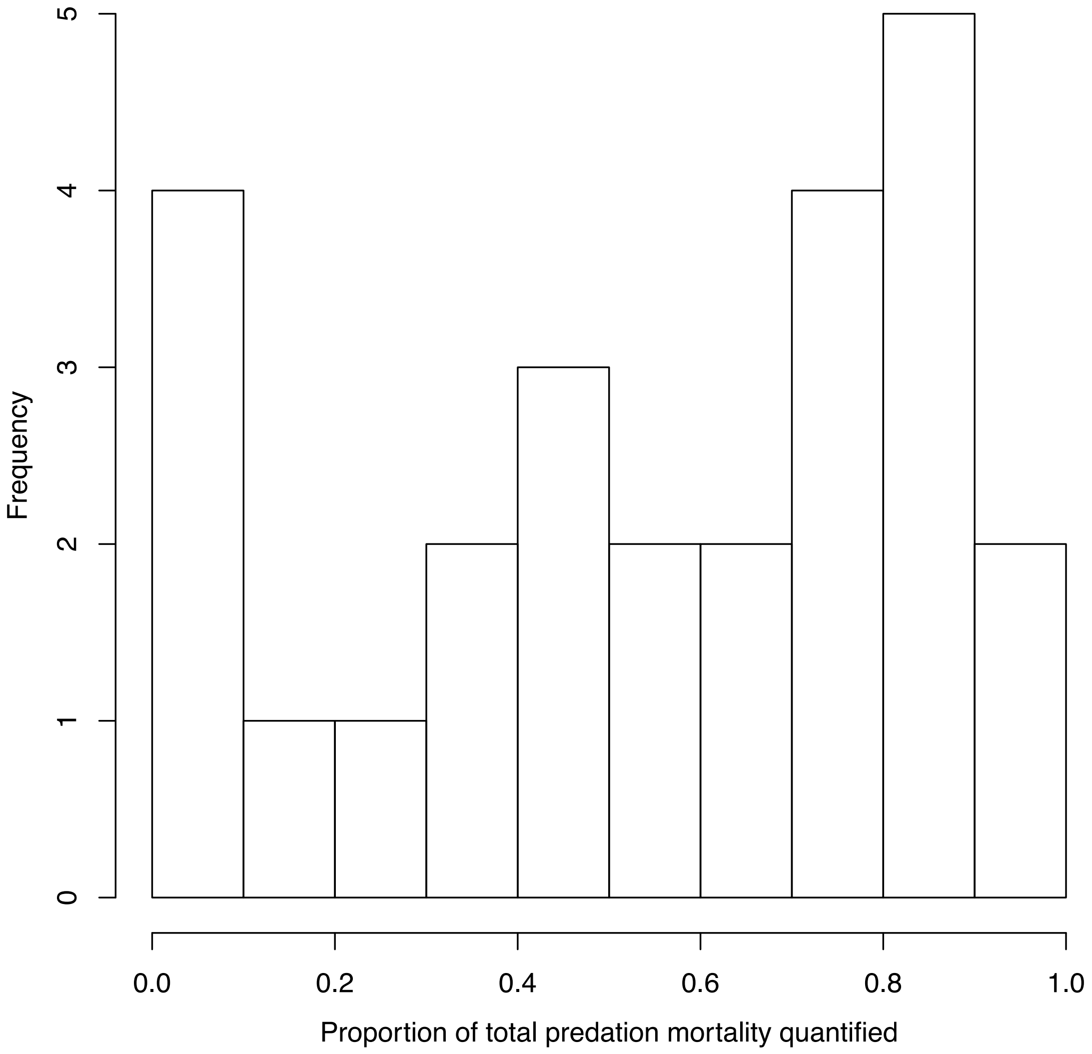

Figure 2.2. Histogram of proportion of predation mortality accounted for by the available time series data, where total predation is based on all functional groups in the mass-balance model.

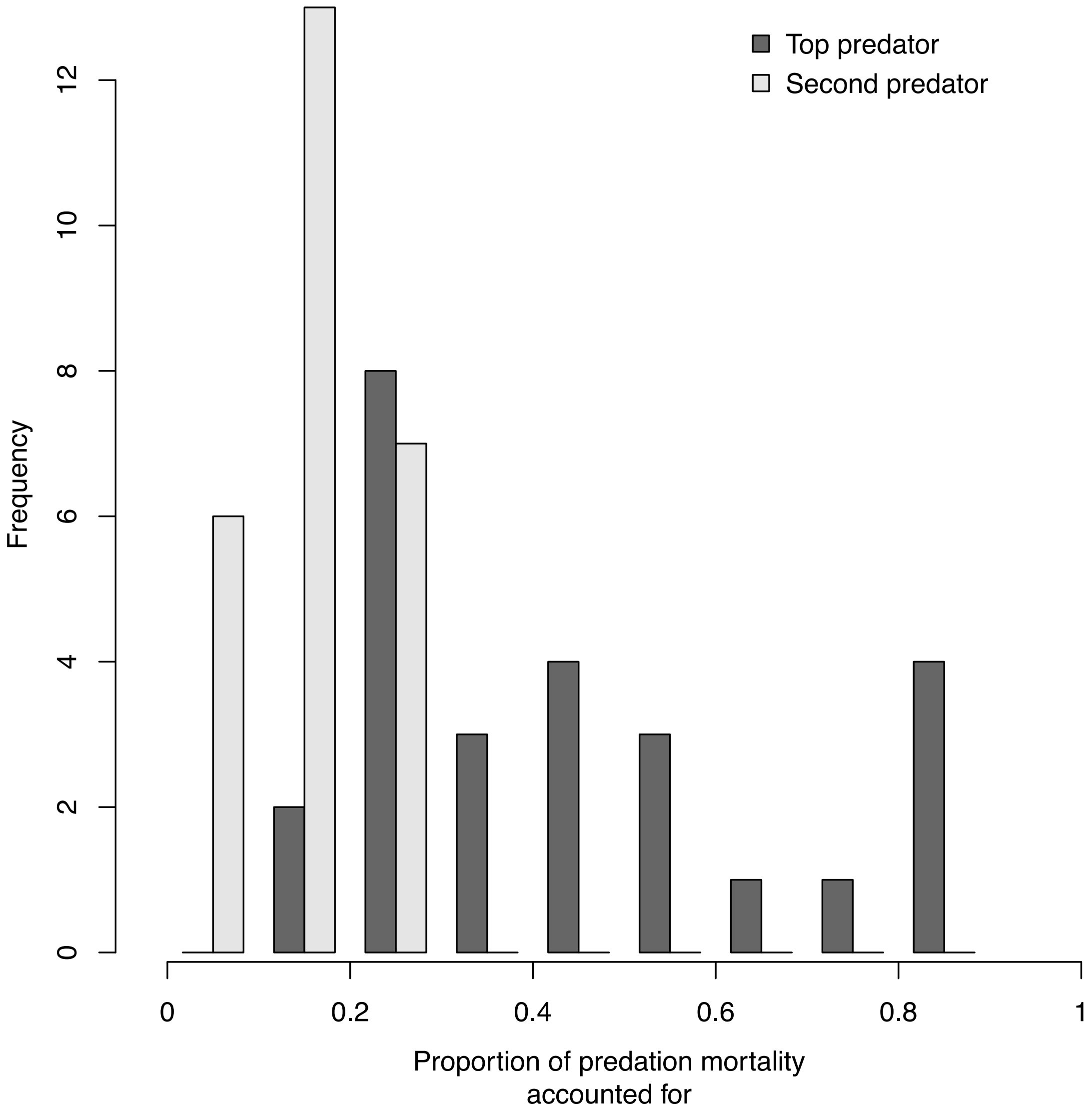

Figure 2.3. Histogram of proportion of predation mortality accounted for by most important predators. Number one most important predator is in dark gray and second-most important predator is in light gray.

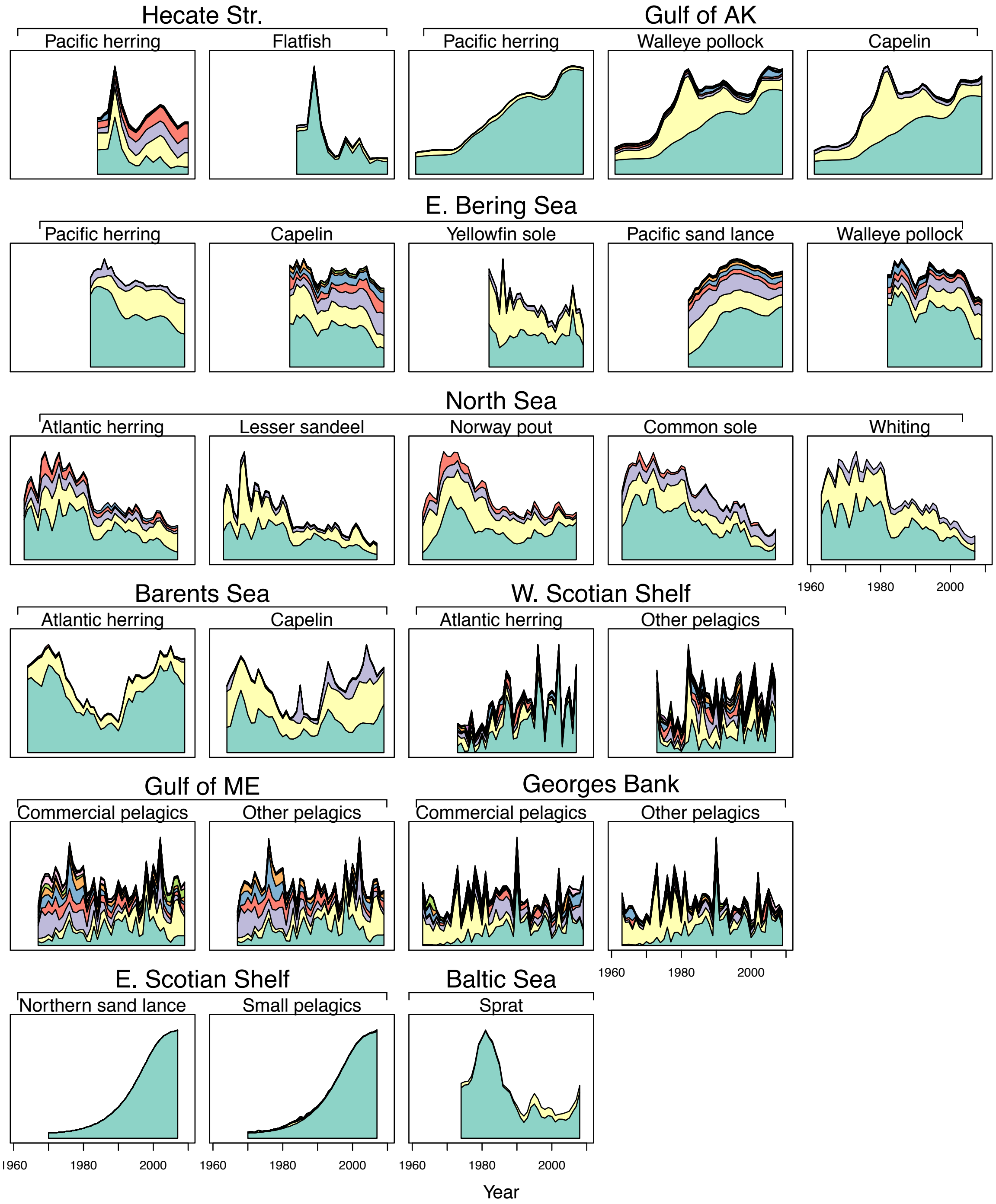

Figure 2.4. Predator index for all prey species in all regions. Each color slice represents a different predator species. For simplicity, only the top ten predators are included in the visual representation. These species make up at least 90% of the total index, and an average of 99%. See appendix for predator species labels.

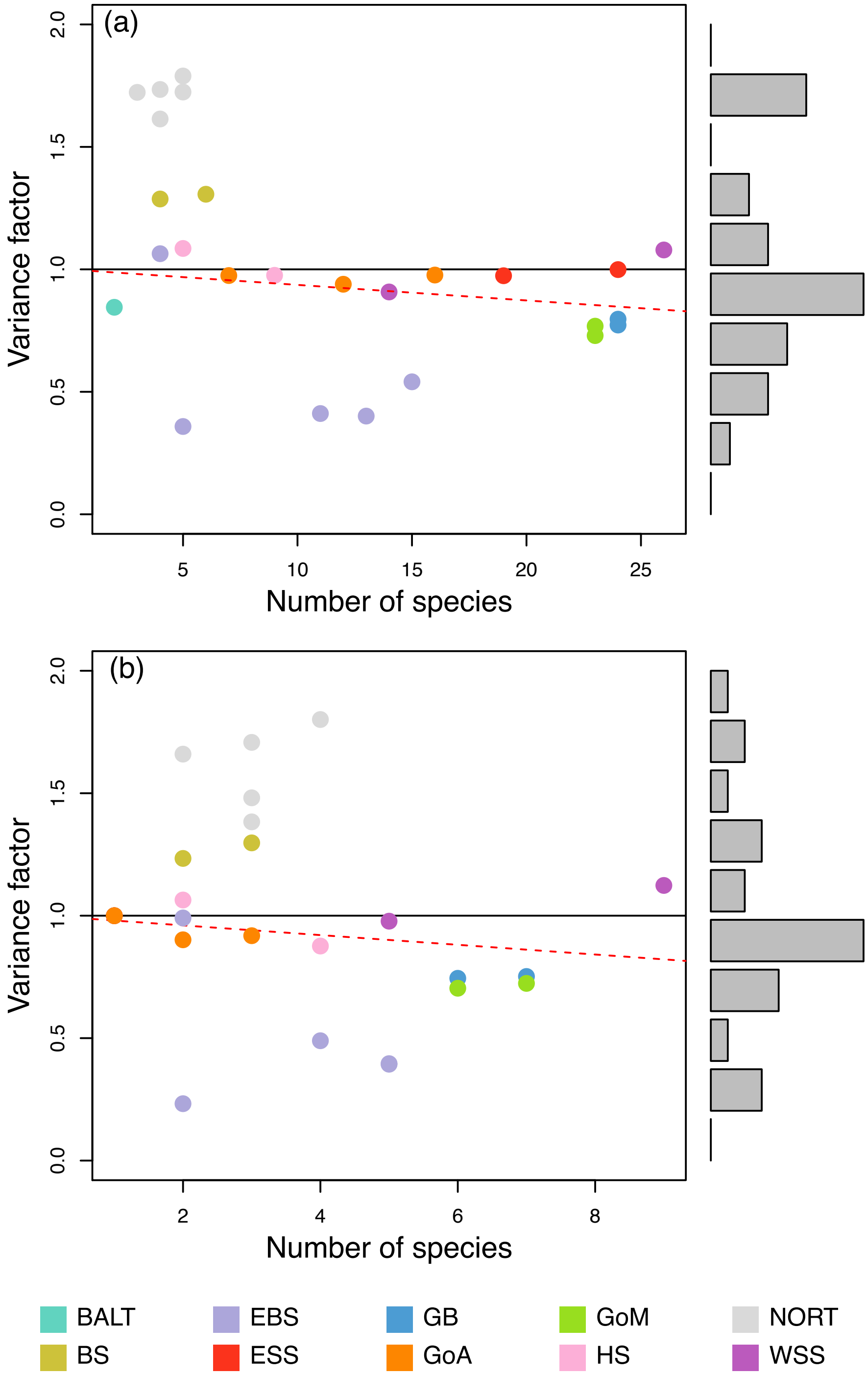

Figure 2.5. Variance factor of predator index versus species richness for (a) all predator species and (b) the minimum number of species to account for 90% of the total predator index (i.e., core species only). Black horizontal line is at 1. Red dashed line is best-fit linear model forced to go through (1,1). Note four points are over-plotted in panel (b) at (1,1). Bars on the right-hand side are histograms aggregated over species richness. See table 4.1 for region codes.

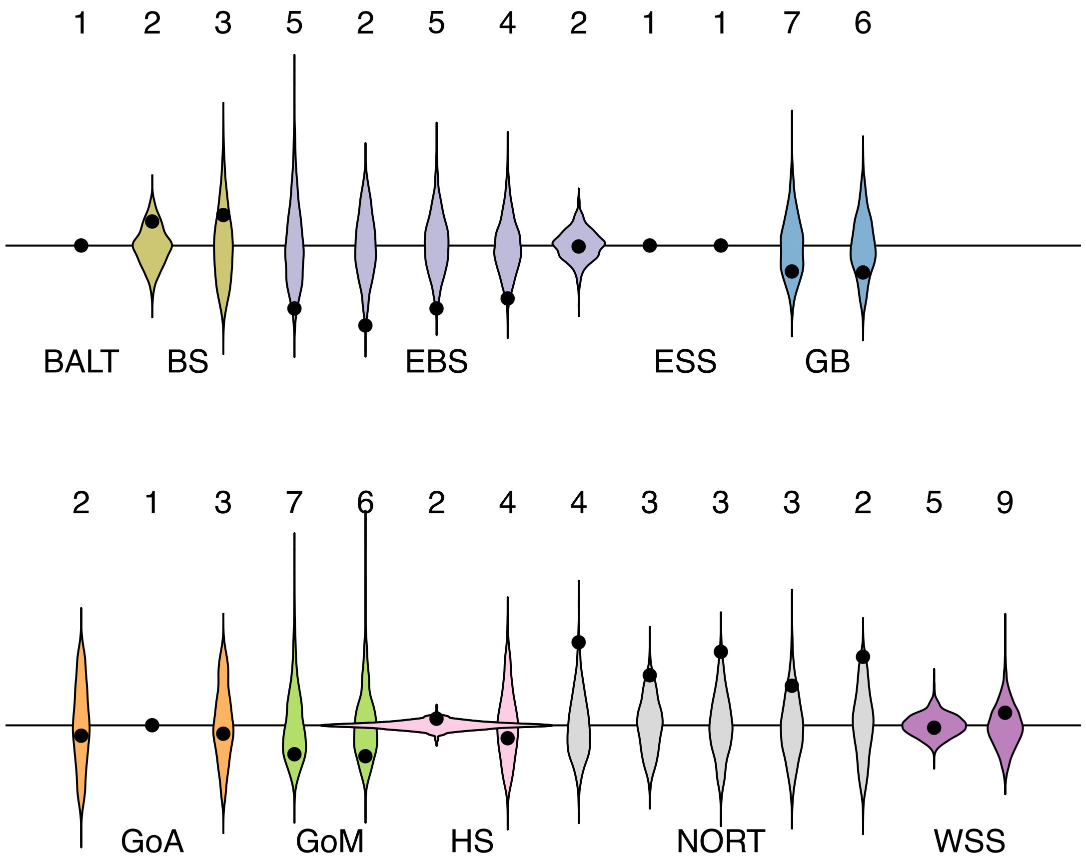

Figure 2.6. Distribution of bootstrapped variance factors along with observed variance factors (points) for core species. Distributions are under the null assumption that predator populations are independent. Horizontal line is where the variance factor equals one, the theoretical mean of the distributions. Numbers on top indicate number of predators. Points without distributions have one predator that accounts for >90% of predator index, and thus the variance factor must equal one. Points in the tails of the distributions indicate evidence for synchronous (above) or asynchronous (below) predator assemblages. See table 4.1 for region codes.

Chapter 3. Evaluating the effect of a selective piscivore fishery on rockfish recovery within marine protected areas

ABSTRACT

Although ecosystem-based fisheries management is often associated with tradeoffs between conflicting demands for ecosystem services, the holistic ecological considerations the approach promotes may sometimes lead to novel solutions that benefit both conservation and fisheries. Directed fishing on large piscivorous fish can reduce predation on prey and thereby benefit those populations, but incidental take of prey species in these fisheries may negate or even reverse the benefit. Whether benefits from reduced predation outweigh the costs of increased fishing will depend on the relative strength of each mortality source and the sensitivity of the population to mortality at different life stages. In the California Current, predatory lingcod (Ophiodon elongatus) populations recovered rapidly from fishing exploitation over the past two decades, while recovery of some rockfish species (Sebastes spp.) has been slow, mainly because of low natural rates of population growth. One management tool has been the adoption of rockfish conservation areas (RCAs) that prohibit bottom contact fishing gear. Because lingcod also inhabit RCAs, fishers have been unable to catch their sustainable lingcod quotas. Therefore, we explored the conditions under which opening RCAs to a selective lingcod fishery might permit rockfish recovery despite the potential bycatch. We developed a joint equilibrium model of the two populations and analyzed scenarios to assess the sensitivity of the model's predictions to key uncertainties. The model suggests a wide range of fishery and ecological conditions under which a lingcod fishery may not harm rockfish populations. However, a sensitivity analysis indicated that the range of fishing scenarios where rockfish are not harmed is highly sensitive to assumptions regarding the nature of the trophic linkage between lingcod and rockfish. We

conclude that consideration of trophic interactions may reveal new fishing opportunities that meet both ecological and human goals, but precise predictions of the outcomes will require more detailed models and adaptive management.

INTRODUCTION

There is a push in fisheries management to consider the whole social-ecological system rather than individual fish populations when making decisions and setting regulations (Levin *et al.*, 2009). This ecosystem-based approach to fisheries management acknowledges the effects of decisions on multiple interacting species and on the people who utilize such species (Arkema *et al.*, 2006). In some cases, such as forage fish management, thinking at a larger system-wide scale leads one to potentially fish less intensively than would be done using a single-species paradigm to protect predator populations (Cury *et al.*, 2011; Pikitch *et al.*, 2014). However, when there are asymmetric predator-prey interactions where the top-down effect greatly exceeds the bottom-up effect, managers may be presented with a different set of policy choices to conserve the mid-trophic level species (Marshall *et al.*, 2015), and these choices may not necessitate less fishing overall.

One tool that has resulted from embracing a multi-species framework in the management of both aquatic and terrestrial populations is the harvest of predators to assist prey populations. Culling predators has been proposed both to increase productivity and yield of exploited prey (Flaaten and Stollery, 1996; Bowen and Lidgard, 2013) and to help conserve endangered prey species (Beamesderfer *et al.*, 1996; Williams, 2014). The basic principle of culling is that reducing predator populations reduces natural mortality rates, which in turn increases the population growth rate (Reynolds and Tapper, 1996). When the management goal is simply to maintain the current level of population productivity, rather than to enhance it, reducing natural mortality through culling predators means that populations may be able to sustain higher harvest rates, irrespective of whether the population is a target species. However, it is important to consider that the success of culling programs has been highly variable (Reynolds and Tapper, 1996; Bowen and Lidgard, 2013) and rests on a thorough understanding of the ecosystem in which the predator-prey interaction exists (Yodzis, 2001).

Subscribing to an ecosystem-based approach to fisheries management also includes ensuring the social and economic health of fishing communities (Arkema *et al.*, 2006). Fishery catches can sometimes be constrained by the incidental bycatch of species of conservation concern, rather than by the amount of fishing effort that target species can sustain (Hall *et al.*, 2000). As a result, these fisheries remain under-utilized due to catch restrictions for the non-target species (O'Keefe and DeCelles, 2013). In response, technical gear modifications are often engineered that rely on behavioral or morphological differences between target and non-target species (Lomeli and Wakefield, 2012). While considering predatory and competitive interactions among species is a vital component of ecosystem-based fisheries management (Pikitch *et al.*, 2004), so too is developing creative solutions to reduce restrictions that have arisen due to bycatch, as doing so allows us to sustain both biological communities and fishing communities alike (Graham *et al.*, 2007).

Models can illuminate important dynamics relevant to policy development and generate new questions for future policy-relevant exploration, but it is first necessary to identify an appropriate level of model complexity for the question at hand. Simple equilibrium-based age- or stage-structured matrix models can inform management and conservation decisions by identifying key life stages sensitive to changing survival rates that warrant more conservation attention (Caswell, 2001). Age structure is particularly important in the context of ecosystem-based fisheries management because fish often change trophic levels considerably throughout their ontogeny, serving as prey during juvenile life stages and becoming predators as adults (Scharf *et al.*, 2000), when fish are also subject to commercial fisheries (Law, 2007; Fisher *et al.*, 2010). However, these equilibrium matrix models generally only consider individual populations. As a result, complex whole-ecosystem models are often used instead to account for tradeoffs among competing objectives and to consider indirect ecological effects resulting from management choices (Pauly *et al.*, 2000; Fulton *et al.*, 2011). In contrast, models of intermediate complexity that have higher resolution for only a specific component of the ecosystem can more easily and effectively answer many of these same questions, with only a minimal loss of detail (Plagányi *et al.*, 2014). That is, simpler mathematical models continue to serve as useful conservation tools to identify influential processes, but we must advance the models so that they link dependent populations and account for both antagonistic and synergistic species interactions.

In the California Current ecosystem, many groundfish populations were depleted by overfishing that occurred in the 1980s and 1990s, leading management to establish closed fishing areas along the coast, called rockfish conservation areas (RCAs). However, not all species have been recovering at the same rate. For example, lingcod (*Ophiodon elongates*), a productive piscivorous species, recovered quickly once management responded (Hamel *et al.*, 2009), whereas some of the slower growing long-lived rockfish species (*Sebastes spp.*) have been increasing in abundance more gradually (PFMC (Pacific Fishery Management Council), 2014). Both lingcod and rockfish occupy similar habitat on rocky reefs (Tissot *et al.*, 2007), and juvenile rockfish are frequently found in the diets of lingcod in the San Juan Islands (Beaudreau and Essington, 2007), which lie slightly inland of the federally managed area of which the RCAs are a part. There is demand for lingcod as a target species, but the RCAs limit the development of a lingcod fishery. As a result, in 2013, fishers only caught 28% of the allowable limit for lingcod off the coasts of Washington and Oregon (Somers *et al.*, 2014). Opening of the RCAs to a commercial lingcod fishery would likely lead to some incidental mortality of adult rockfish because of their shared habitat (Tissot *et al.*, 2007). However, if gear, such as a trap, is sufficiently selective towards lingcod morphology and behavior, the reduction in lingcod predation on juveniles due to the fishery's "culling" of lingcod may compensate for the incidental mortality of adult rockfish. Therefore, opening the RCAs to a lingcod fishery could lead to potential gains for fishing communities without harming the ecosystem they depend upon, but there is a need to better understand the dynamics of how the rockfish and lingcod populations interact.

Here, we construct a trophically linked age-structured equilibrium-based model to explore the possible implications to rockfish populations of opening RCAs to a selective lingcod fishery. The simple equilibrium model allows for rapid evaluation of many alternative scenarios to explore under which conditions rockfish populations are most successful in ultimately attaining high abundances. While equilibrium models do not quantify recovery rates, they do quantify the long-term abundance we might expect following recovery. Thus, high abundances at equilibrium can only occur if recovery also occurs. We analyze this model under a range of fishing and ecological conditions to understand the full spectrum of possible population responses to the management change based on key uncertainties about dynamics of lingcod and rockfish. We seek to answer two main questions: 1) under what scenarios might reduced predation on juvenile rockfish compensate for the bycatch of adult rockfish by the hypothetical lingcod fishery and 2) what model parameters are most influential in determining the answer to the first question. We acknowledge that further empirical research and modeling work will be necessary to fully evaluate a potential lingcod fishery within RCAs for implementation; here we attempt to show the fishery's theoretical plausibility and direct future research by identifying key parameters and processes that are highly uncertain, highly influential, or both, and that therefore warrant further exploration.

METHODS

We constructed linked age-structured models for rockfish and lingcod and evaluated them at equilibrium conditions to calculate the level of rockfish bycatch that could be sustained in a directed lingcod fishery without reducing rockfish female spawning biomass, under a range of potential lingcod harvest intensities (Figure 3.1). Because of the high uncertainty in the trophic relationship between lingcod and rockfish, as well as unknown size selectivity of potential fishing gear, we use this model primarily as a platform to conduct an extensive sensitivity analysis on input parameter values to identify the conditions under which calculated equilibrium rockfish biomass is equivalent to 1) currently estimated unfished levels and 2) the management target of 40% of the unfished biomass. We used equilibrium model conditions to permit rapid evaluation of alternative parameterizations, and thereby provide insight into how populations might respond under different conditions and illuminate key ecological and fishery parameters that can have major influence on the population dynamics.

Model Structure

Because lingcod are highly opportunistic generalist predators, we assume here that lingcod predation affects rockfish populations, but that rockfish abundance does not affect lingcod population growth rates. We therefore first calculated the lingcod equilibrium properties under different fishing rates, and use that to adjust demographic parameters in an age-structured rockfish model. The initial step was to calculate the equilibrium lingcod age structure-per-recruit in numbers-at-age. Because lingcod are highly sexually dimorphic (Hamel *et al.*, 2009), we model the two sexes explicitly and assume the sex ratio at birth is 0.5. Then $L_{a+1,s}$, the lingcod per recruit of age $a+1$ and sex s is modeled as:

$$L_{a+1,s} = L_{a,s}\exp[-(M_s^l + v_{a,s}^l F)], \tag{3.1}$$

where $L_{a,s}$ is the number of fish of age a and sex s, M_s is the natural mortality rate of sex s, $v_{a,s}$ is the relative vulnerability to fishing gear for fish of age a and sex s, F is the mortality rate from fishing for ages that are fully vulnerable to the fishery ($v_{a,s}$=1), and the superscript l denotes parameters that relate to lingcod. For simplicity, $v_{a,s} = 0$ or 1 (i.e., a "knife-edge" curve where each age class is either fully vulnerable or not). For the final age class, or "plus group", we divided the quantity in equation 1 by $1 - \exp\left[-\left(M_s^l + v_{n,s}^l F\right)\right]$ where n is the plus group age (20). This process leads to a matrix of the equilibrium lingcod age-structure as a function of the fishing rate, $L(F)$.

The rockfish population model only includes females, as females generally determine a fish population's ability to persist (Hixon *et al.*, 2013). Lingcod consumption was halved to adjust for this simplification. We calculated the equilibrium female rockfish age structure scaled to lingcod recruitment by fixing the ratio of recruitment between the two groups. Then apply a similar equation as above:

$$R_{a+1} = R_a\exp[-(M^r + v_a^r bF)] - Q_a(L, R, F), \tag{3.2}$$

where $R_1 = \phi/2$ and ϕ is the ratio of rockfish recruits to lingcod recruits, the r superscript denotes parameters that relate to rockfish, and Q_a is the consumption of age a rockfish per lingcod recruit. We define this vector as $R(F)$. The variable b is the gear selectivity efficiency, or, more explicitly, the fraction of lingcod fishing mortality that fully-selected rockfish experience; it describes how effectively the fishing gear avoids rockfish. When $b = 1$, the mortality rates of rockfish and lingcod are equal, implying that the gear is indiscriminate between groups. For well-constructed gear, $b << 1$. For the plus group, age class n, equation 2 becomes:

$$R_n = \frac{R_{n-1}\exp[-(M^r+v_{n-1}^r bF)]-Q_{n-1}(L,R)-Q_n(L,R)}{1-\exp[-(M^r+v_n^r bF)]}. \qquad (3.3)$$

Equations 3.2 and 3.3 assume that populations are not subject to any other fishing mortality; that is, they are closed populations within no-take marine reserves. Also, they presume that mortality from lingcod occurs after other natural mortality and after fishing. A scenario with constant recruitment that is independent of spawning biomass explored sensitivity to the assumption that populations are closed. Sensitivity to the assumption regarding the order of mortality was tested using numerical methods, and results were nearly indistinguishable between the model with lingcod mortality occurring after other mortality sources and the model with all mortality occurring simultaneously. We then calculated total rockfish spawning biomass per rockfish recruit to use in a stock-recruit function and ultimately evaluate the impact of lingcod fishing on rockfish populations. We calculated this as $[R(F)' W^r]/(\phi/2)$. Here, W^r is a vector of rockfish weights at age, and the apostrophe denotes the transpose of a vector.

We needed to account for size-selective vulnerability of rockfish for each age class of lingcod, using existing information on prey size spectra of lingcod. To do this, each age class of lingcod for both sexes was assumed to have a diet size spectrum that was represented by a unique gamma probability distribution with quantiles that increased linearly with lingcod size. These distributions were integrated over length bins determined by the length-at-age of each rockfish age class (see supplementary materials for equation). This assigned the relative vulnerability of each age class of rockfish to predation by each age and sex of lingcod. The area in each length bin was normalized so that the sum over all rockfish age bins was one. We then used the probabilities from these bins to populate an array *D* that gives the preference of lingcod of each age and sex to consume rockfish of each age, relative to the lingcod's overall preference to consume rockfish. In this way, *D* is an array of two *r* x *l* matrices (one for each lingcod sex) where *r* is the number of rockfish age classes and *l* is the number of lingcod age classes, and each column of *D* sums to one. For details, see supplementary materials.

We calculated lingcod consumption of rockfish, *Q(R, L)*, using two distinct functional responses that represent two end-point scenarios. The first was where the lingcod per-capita consumption was independent of rockfish density (heretofore referred to as "saturating"). The second was a linearly increasing response, where lingcod per capita consumption is directly proportional to rockfish density (i.e., Hollings type I). These two simple cases bracket a range of other more complex and realistic lingcod consumption patterns, but we expect results from those cases to fall intermediate to our two endpoints. For the simpler method with a saturating response, we define *P* as a vector that represents the proportion of lingcod consumption that is composed of rockfish, by lingcod age, and define *C* as a matrix of total lingcod annual per capita consumption by lingcod age and sex. Then to calculate consumption of rockfish per lingcod recruit, *Q*, we calculate:

$$Q_{a_r} = \frac{\sum_s \sum_{a_l=0}^{l} D_{a_r,a_l,s}\ 0.5\ C_{a_l,s}\ P_{a_l} L_{a_l,s}(F)}{W_{a_r}^{r}}. \qquad (3.4)$$

where the subscript *s* denotes sex, the division is elementwise, and the one-half appears to account for consumption of female rockfish only. The result of equation 3.4 is a vector with *r* elements, one for each rockfish age class.

For the type I functional response where lingcod diets adapt to changing rockfish abundances, we needed to adopt a separate functional response for each combination of lingcod and rockfish age classes. We assumed the per capita consumption of rockfish increases linearly with rockfish abundance at each rockfish age class (per lingcod recruit). To set the slope of this relationship, we assumed that, when summed over all rockfish age classes, the total per capita consumption passes through the origin and is equal to the value at the saturating functional response when rockfish are at the unfished biomass. In addition, lingcod preference towards each rockfish age class was weighted by the diet size spectra. We therefore assumed that:

$$Q_{a_r} = R_{a_r}(F) \sum_s \sum_{a_l=0}^{l} \frac{D_{a_r,a_l,s}\, 0.5\, C_{a_l,s}\, P_{a_l} L_{a_l,s}(F)}{\sum_{i=0}^{r} D_{i,a_l,s} R_i(0) W_i}, \tag{3.5}$$

where w_a^r is the weight of age *a* rockfish. In this case, the vector *Q* must be calculated sequentially for each rockfish age class, and cannot be done in a single calculation as in (3.4). In addition, the unfished condition, *R(0)*, must be calculated numerically by solving a system of non-linear equations. To accomplish this, we used the package nleqslv in R (Hasselman, 2015). For a derivation of equation 3.5, see supplementary materials. Note that *P* now represents the diet proportions at the unfished biomass. The actual diet proportion now scales with the rockfish population. However, the values within *P* remain unchanged.

To examine different levels of density-dependence in the stock-recruit relationship, we examined rockfish spawning biomass instead of rockfish spawners-per-recruit. Because we fixed the ratio of recruitment between the two groups, there is only one free stock-recruit relationship between the two species groups. We briefly tested sensitivity to this assumption (see supplementary materials), but in general keep the constant ratio because it allows us to calculate the equilibria analytically and therefore explore model outcomes over a wide range of parameters and scenarios. We varied rockfish density-dependence through the steepness parameter (*h*) in the Beverton-Holt stock-recruit relationship. A steepness of one indicates that recruitment is independent of spawning biomass, and a steepness of 0.2 indicates density-independent per capita recruitment. We fixed the unfished recruitment to one in all cases, as this simply scales the size of both populations, but does not influence dynamics of the system. We calculated rockfish female spawning stock biomass (*SSB*) from spawners per recruit (*R*) using the following formula:

$$SB(F) = \frac{4hR(F) - (1-h)R(0)}{5h-1}. \tag{3.6}$$

Baseline Parameterization

Demographic parameters (Table 1) were obtained from the most recent stock assessments for lingcod (Hamel *et al.*, 2009) and yelloweye rockfish (Taylor and Wetzel, 2011). Yelloweye rockfish (*S. ruberriumus*) is an overfished rockfish species with major habitat overlap with lingcod (Tissot *et al.*, 2007), and with similar demographic characteristics to other slow-growing rockfish species, such as canary rockfish (*S. pinniger*). For both lingcod and rockfish, total length at age, S_a, was modeled with a parameterization of the Von Bertalanffy growth function:

$$S_a = S_\infty - (S_\infty - S_1)\exp[-K(a-1)], \tag{3.7}$$

where S_∞ is the asymptotic length, S_1 is the length at age 1, and K is the growth rate parameter. For lingcod, this relationship was sex-specific. For rockfish, we decreased the length of the youngest age class to 10cm, as these young rockfish are particularly vulnerable to predators and their size is not well-estimated in the stock assessment because there are no data to inform it. Rockfish weight-at-age was taken directly from the age-structured stock assessment, which models weight in kilograms as an allometric scaling of length (supplementary materials table 1). Because we are partitioning rockfish natural mortality into lingcod and non-lingcod sources, the overall stock assessment natural mortality rate would over-estimate M^r, which we assume to come from non-lingcod sources only. Therefore, non-lingcod natural mortality of rockfish was set to 0.043 yr^{-1}, so that the weighted average of total natural mortality over ages 10 and above under the baseline scenario would be approximately equal to the total natural mortality rate used in the stock assessment (0.046). Age 10 was chosen as the cutoff because that is the age at which most stock assessment indices of abundance have greater than 50% selectivity (Taylor and Wetzel, 2011). Lingcod consumption rates are based on Beaudreau & Essington (2009), and then corrected using their reported Q_{10} temperature coefficient of 1.9 for the lower temperatures found on the continental shelf as compared to Puget Sound (6 versus 9°C). The function for lingcod consumption for sex s, measured in kilograms per capita per year, was:

$$C = a_{c,s} W^{b_{c,s}}, \tag{3.8}$$

where weight-at-age in kilograms for lingcod was calculated using the allometric scaling of length-at-age $a_{w,s} S^{b_{w,s}}$.

Remaining model parameters were known with considerable uncertainty, and form the basis for the extensive sensitivity analysis that followed model construction. However, baseline values were selected. Lingcod were considered vulnerable to the fishery at 60 cm, which is near 50% selectivity for the commercial trawl fishery (Hamel *et al.*, 2009). Rockfish were considered vulnerable at 25 cm, a smaller size than the lingcod, because we assume fish are captured by the gear at 25 cm, and, unlike lingcod, no captured rockfish survive due to barotrauma (Parker *et al.*, 2006). This is somewhat close to the inflection point of yelloweye selectivity curves in Washington, which is around 40 cm for both the trawl and recreational fisheries; note there is currently no trap fishery for rockfish. The lingcod diet size spectra are gamma distributions where the 5th and 95th quantiles increase linearly with lingcod size (Figure 3.2). The slopes of these two quantiles define the size spectra. Baseline slopes are from the total lingcod diet described by Beaudreau & Essington (2007). All reported slopes are with respect to standard length for rockfish, which were obtained from total lengths based on Echeverria & Lenarz (1984). The recruitment ratio, ϕ, was tuned so that the ratio of unfished biomasses of demersal rockfish species to lingcod approximately matched the ratio in the California Current (Kaplan *et al.*, 2014). The rockfish diet fraction of adult lingcod, *P*, was approximately based on the California Current mass-balance model (Koehn *et al.*, in review). While our model is parameterized for large slow-growing rockfish species, we assume that their relative abundance within the rockfish guild is similar to their relative abundance within the rockfish component of lingcod diets, so that using information on the whole rockfish clade is a reasonable simplification. However, the large slow-growing rockfish modeled here likely make up a smaller fraction of lingcod diets than their relative abundance among all rockfish, as some rockfish remain small their entire lives. Therefore, in the baseline model we used a slightly (one percentage point) smaller diet proportion than Koehn *et al.* (in review), and then explored a range of possible values. In addition, the diet proportion was assumed to increase linearly for the first six lingcod ages modeled, beginning at 0, as young lingcod likely eat relatively less rockfish than older lingcod.

The full set of parameters explored is listed in Table 3.1. The model was built and analyzed in R version 3.1.1 (R Core Team, 2016).

RESULTS

The different parameterizations consistently show that when fishing is conducted at low enough intensities and with minimal incidental catch of rockfish, opening marine protected areas to a selective lingcod fishery (i.e., low gear selectivity efficiency) may actually enhance equilibrium population levels of vulnerable rockfish populations (Figure 3.3), indicating that populations will ultimately recover to higher levels. Equilibrium biomass is maintained at the level it will eventually reach in the absence of fishing along a contour line defined by lingcod fishing intensity and relative gear selectivity for the two species. The maintenance line curves downward, indicating that rockfish biomass levels would be unchanged by either high fishing effort with low bycatch or with low harvest intensity and less selective fishing gear. In other words, to increase fishing effort while also sustaining rockfish populations in the long-term, it is necessary to improve species selectivity of the lingcod fishing gear. However, the relationship is nonlinear; incrementally increasing fishing intensity when effort is low requires a larger improvement in gear than undergoing the same incremental increase while fishing efforts are already high. The fishing mortality that leads to maximum sustainable yield for lingcod is 0.15 yr^{-1} (Hamel *et al.*, 2009), which intersects the unfished contour at a gear selectivity efficiency of 0.08. Thus under the base case of our model, lingcod populations can be fully utilized while maintaining eventual equilibrium rockfish populations at unfished levels if rockfish fully-selected fishing mortality remains below 0.004 yr^{-1} (the product of 0.15 and 0.08), and there is no other rockfish harvest.

Away from the unfished rockfish biomass, the isoclines for biomasses that are greater than the unfished level are not monotonic (Figure 3.3). This is because there are actually two contours where equilibrium rockfish biomass is equal to the unfished level: 1) the downward sloping curve that is plotted in black and 2) the y-axis, where fishing mortality is zero and populations are by definition unfished. Contour lines for different relative biomasses cannot intersect, so the lines for the higher biomass levels must curve downward instead of intersecting the y-axis. Essentially, when the fishing gear selects almost perfectly for lingcod, increasing fishing intensity at low levels decreases predation mortality more than it increases fishing mortality, and rockfish populations actually benefit. For biomasses above the unfished level, there is an extremely small range of low fishing intensities where rockfish biomass can be maintained at a constant level by increasing the fishing intensity *and* making less selective gear.

However, target levels in the California Current are 40% of the unfished biomass, and populations are currently well below that target.

The stock-recruit relationship, or amount of density-dependence, has no bearing on the unfished rockfish biomass contour, but does influence how the equilibrium rockfish spawning biomass changes as fishing conditions move away from those that result in unfished biomass (Figure 3.3a,c vs. 3.3b,c). Recruitment at the unfished rockfish biomass is defined to be the same for the two relationships; recruitment only differs at other biomasses. A highly density-dependent population (i.e., steepness ≈ 1, recruitment is constant) is more resilient and maintains a biomass near the unfished level under a wide range of fishing conditions because recruitment to the population remains high even when spawning biomass is low. With less density-dependence (i.e., steepness << 1), fishing can greatly reduce (or increase) the rockfish population's reproduction rate, leading to larger changes in equilibrium spawning biomass resulting from more incremental shifts in fishing conditions. This occurs because recruitment responds strongly to changes in spawning biomass caused by fishing. Understanding the stock-recruit relationship therefore has important implications for management targets, which are set at 40% of the unfished biomass. If the population displays high density-dependence, there is a wider range of fishing scenarios that will lead to rockfish biomasses at or above target levels.

Including a functional response where lingcod eat more rockfish when rockfish are more abundant leads to major differences, particularly at low fishing efforts ($F <$ ca 0.2), in both the unfished biomass contour and the entire rockfish spawning biomass surface. (Figure 3.3c,d vs 3.3a,b). Although the model assumes that lingcod consume the same mass of rockfish in the absence of fishing for both scenarios, the age structure of the consumed rockfish differs. Under the saturating functional response, lingcod eat large masses of juvenile rockfish, which are of optimal size, though not necessarily abundant. When the lingcod respond to relative rockfish abundance, the lingcod consume more large rockfish despite their suboptimal size. Therefore, under the saturating functional response, fishing lingcod better improves survival probabilities for the small juvenile rockfish that are crucial for population growth. However, it is notable that the total unfished rockfish spawning biomass is approximately three times greater with the type I functional response because fewer individuals are consumed in this case, thus resulting in a lower natural mortality rate. For simplicity, remaining results from the sensitivity analysis are presented assuming a saturating functional response, but only the unfished biomass contour is examined. Behavior away from the unfished contour showed similar tendencies to the base case, and including a type I functional response produced similar changes to those described above.

The model was highly sensitive to changes in parameters related to how much rockfish lingcod consume (diet fractions and size spectra, Figures 3.4a,b). When rockfish comprise a larger fraction of lingod diets, lingcod fishing has a greater benefit to rockfish. Therefore, fishing lingcod while maintaining a constant species selectivity of the gear is more likely to have neutral to positive impacts on rockfish populations when lingcod consume high volumes of rockfish. Increasing the slope of the 95th quantile of the gamma distribution for lingcod diet size spectra led to a larger area where rockfish populations decline. Increasing these slopes generally increases the average size of rockfish that lingcod consume. Lingcod have a larger impact on rockfish, and thus rockfish are less likely to be harmed by a lingcod fishery, when lingcod select younger smaller fish because those fish have not yet had many opportunities to reproduce. Rockfish populations are sensitive to changes in juvenile survival. Therefore, in cases where lingcod strictly eat smaller rockfish, the benefits to rockfish of the lingcod fishery (predator culling) are more likely to outweigh the costs (bycatch).

The sensitivity analysis showed that while varying size selectivity of the fishing gear on both rockfish and lingcod does influence rockfish biomass, the changes in the unfished biomass contour are small, implying that size-selectivity of fishing gear need only be known approximately to understand impacts of the potential fishery on rockfish populations (Figure 3.5). Results demonstrated that selecting a wider range of lingcod sizes tends to slightly benefit the rockfish populations, as doing so results in removing more potential predators from the water, essentially increasing the fishing effort (Figure 3.5a). However, such a change in the fishing gear would likely increase the range of rockfish sizes selected, as well, which would hamper rockfish recovery (Figure 3.5b).

Changing the ratio of recruitment (and therefore total abundance) between rockfish and lingcod led to less dramatic changes than altering diets, but more substantial changes in rockfish dynamics than shifting gear selectivity (Figure 3.4c). It is also notable that the unfished contour line moves more as the relative abundance of lingcod increases. Although the current ratio of demersal rockfish to lingcod biomass is ca. 9 (Kaplan *et al.*, 2014), the analysis here explores dynamics of the unfished system, where rockfish are fully recovered, and the ratio is thus likely to be greater. Decreasing the relative abundance of lingcod in the system decreases the range of scenarios where rockfish populations would benefit from the lingcod fishery due to reduced predation (i.e., the contour line falls at lower fishing mortality rates and gear selectivity efficiencies indicating more selective gear). This is because the fishery removes fewer rockfish predators when rockfish are more relatively abundant. As the per capita rockfish consumption is constant, there is no compensation in rockfish consumption at high lingcod densities.

DISCUSSION

We explored the effects on rockfish of establishing a selective commercial lingcod fishery within rockfish conservation areas (RCAs) that presently restrict fishing of groundfish to protect sensitive rockfish populations and enhance their recovery. To do this, we constructed an equilibrium-based age-structured model that links rockfish abundance to their lingcod predators. We found that the fishery could avoid harming rockfish populations under a range of conditions, even with some levels of rockfish bycatch. The effect of a selective lingcod fishery on rockfish populations depends extensively on the consumption habits of lingcod; the fishery is least likely to harm rockfish when lingcod eat a large quantity of small rockfish. However, this study only serves as an initial starting point; further exploration and model development, gear testing, and experimental application may be warranted if conducted in a careful and adaptive manner. In general, this work illustrates that ecosystem-based fishery management does not always necessitate tradeoffs and tighter fishing quotas, but rather it recognizes connections among species and can lead to novel solutions that benefit both fisheries and overfished species. Although culling predators can sometimes lead to unexpected ecological outcomes (Punt and Butterworth, 1995; Yodzis, 2001), passive policies that restrict harvest of a protected species but do not additionally control predator abundances are sometimes less effective at restoring populations (Lessard *et al.*, 2005; Baskett *et al.*, 2006). Therefore, taking a flexible and creative approach towards MPAs and allowing for the harvest of abundant and productive predator species could be a socially, economically, and ecologically sustainable policy.

This work corroborates results from previous mathematical models involving rockfish and MPAs in the California Current, which generally found that considering community dynamics (both competition and predation) had a significant impact on the predicted ecological responses to management practices. (Mangel and Levin, 2005; Baskett *et al.*, 2006). Mangel & Levin (2005) found that considering community dynamics, specifically the predator-prey interaction between rockfish and lingcod, led to a completely different decision on the optimal location to place the marine reserve. We further explore the predator-prey relationship to show that its consideration should affect the regulations surrounding the MPA, not only its location. Baskett *et al*. (2006) found that the populations of larger species such as yelloweye may not recover to previous levels in the mere absence of fishing due to changes in food web interactions that result from the MPA, although since then some species have made complete recoveries, at least over large spatial scales (PFMC (Pacific Fishery Management Council), 2014). In our case, the highly abundant lingcod populations could possibly be preventing rockfish recovery, though an explicit analysis of rebuilding times is beyond the scope of this work. However, decreasing predation by lingcod *without* harvesting rockfish may improve the chances that yelloweye recover to levels that are deemed to be above safe biological limits.

We extended these previous mathematical models by incorporating an explicit and detailed age structure. The rockfish population of conservation concern in previous work was divided into juveniles and adults, but the second species (lingcod or small rockfish) was modeled as a single homogeneous population (Mangel and Levin, 2005; Baskett *et al.*, 2006). Size structure is important in accurately modeling competition and predation among fish because of the ontogenetic shifts these species undergo (Scharf *et al.*, 2000). Our finely detailed age-structure of both species of interest was crucial, as small changes in the diet size spectra of lingcod led to large qualitative shifts in model behavior, and therefore potentially sustainable levels of fishing effort. We would not have realized the importance of understanding the size distribution of lingcod diets, in addition to diet quantity, without this level of detail. Also, including explicit size structure of both rockfish and lingcod allowed us to show the robustness of our results to the age selectivity of fishing gear, and illustrated the opposite effects that changing the size of fish selected by the gear has on rockfish and lingcod.

Spatial management strategies, such as the implementations of MPAs, are valuable tools in ocean conservation, and can even increase fishery productivity (Gell and Roberts, 2003; Lester *et al.*, 2009), but need to be used thoughtfully because blanket fishing area closures are often met by pushback from local communities (Agardy *et al.*, 2003). Extensive research shows that the optimal configuration of MPAs depends on fish movement and dispersal (Botsford *et al.*, 2003) and the purpose of the MPA: biodiversity versus fishery yield (Hastings and Botsford, 2003). However, community ecology is also an important factor in setting regulations for MPAs (Gerber *et al.*, 2003). Species interactions are sometimes seen as an impetus to increase the necessary size of MPAs (Walters, 2000), but rarely to alter the fishing regulations. This work illustrates the importance of beginning with the management goal, such as rockfish recovery, rather than simply applying the tool without considering the complex food web that exists within a proposed MPA. Both the ecosystem and associated fishing communities can benefit from MPAs when they are flexible so that fishing restrictions are tailored to the system and regulations are motivated by the local ecology (Agardy *et al.*, 2003).

We found that the model was most sensitive to parameters that influence how much rockfish lingcod consume, a similar result to sensitivity analyses from multispecies age-structured stock assessments (Van Kirk *et al.*, 2015). This work showed the particular value in gaining more quantitative information on species interactions, particularly amidst the growing chorus calling for multispecies fisheries management (Pikitch *et al.*, 2004). Diet patterns generally shift through space and time as abundances of different prey species ebb and flow

(Link and Garrison, 2002). Therefore, longer time series of diets over larger spatial scales than are currently available that include sizes of both predators and prey would help elucidate trophic relationships (Szoboszlai *et al.*, 2015). Although improving precision substantially may involve collecting prohibitively large numbers of lingcod stomachs, collecting lingcod stomachs directly from a potential fishery could in fact provide an opportunity for adaptive management. In addition, because lingcod are opportunistic generalists, their diets often simply sample whatever prey assemblages are present (Link, 2004). Therefore, a more quantitative understanding of the overlap of habitat preferences between lingcod and rockfish would also help inform management (Tissot *et al.*, 2007).

This study represents an initial exploration into the potential to open rockfish conservation areas in the California Current to a selective lingcod fishery, but as with any modeling exercise, many ecological assumptions were made that may increase optimism towards the fishery. Both rockfish and lingcod shift habitat preferences as they grow, often moving from the nearshore to the offshore environments (Love *et al.*, 2002; Hamel *et al.*, 2009). Therefore, the relative abundance of juvenile rockfish in adult lingcod diets may actually be less than the relative abundance of juveniles among all benthic rockfish, although submersible surveys have shown major habitat overlap between adult lingcod and both juvenile and adult rockfish (Tissot *et al.*, 2007). This would bias our results towards finding that a potential lingcod fishery is more sustainable for rockfish than is actually true, because lingcod are able to influence rockfish dynamics more when their consumption is more targeted towards juveniles. In addition, the large-bodied rockfish modeled here engage in more anti-predator behavior than shorter-lived species (Frid *et al.*, 2012), which would result in large rockfish species being less prevalent in lingcod diets than expected, similarly biasing the results. We are hopeful that the range of diet fractions and relative abundances of rockfish and lingcod examined in the sensitivity analysis encompass actual conditions. Second, our model does not include other ecological interactions, like cannibalism in lingcod or competition of rockfish with other mesopredators, such as gadids, that may be released by lower lingcod abundances. If increased competition with mesopredators (including juvenile lingcod) effectively replaces decreased lingcod predation, rockfish would be more sensitive to the lingcod fishery (Lessard *et al.*, 2005). Increasing mesopredator populations could also cascade to lower trophic levels, decreasing abundance of their prey such as shrimp (Frid and Marliave, 2010), and therefore decreasing rockfish productivity. Although our model does not perfectly represent reality, and these assumptions are likely to impact the absolute rockfish response, the assumptions are less likely to affect the response of rockfish relative to other scenarios tested (i.e., the sensitivity analysis).

We also made several mathematical simplifications that do not necessarily bias our results, but do influence how they should be interpreted. First, many of the individual parameters tested likely covary. For example, a higher rockfish to lingcod recruitment ratio likely means that rockfish comprise a larger fraction of lingcod diets, as well. Because of this, we did not extend our sensitivity analysis to more extreme values, such as different orders of magnitude. Varying individual parameters allows us to more precisely understand the effect of each process, but we acknowledge that some realism is lost. Second, we undertook a simple equilibrium analysis even though rockfish are still recovering from an overfished state, and transient dynamics can dominate for decades after the establishment of MPAs (White *et al.*, 2013). Equilibrium analyses are useful because they are generally easy to compute, allowing for the rapid initial evaluation of many different scenarios. However, population recovery necessarily occurs during periods of transience, and whether any ecosystem ever truly reaches a “stable” equilibrium is questionable

(Simberloff, 1974). Even so, equilibrium analyses serve as important exploratory tools to begin to analyze recovery dynamics; their rapid evaluation can help to identify key parameters and general patterns that hold across many different possible situations.

Admittedly, yelloweye rockfish will always be a relatively rare species, and identifying stomach contents beyond the rockfish genus is challenging (Love *et al.*, 2002). Therefore, gaining a true understanding of the spatial intricacies concerning how lingcod consume relatively rare rockfish species will be challenging. Without more detailed knowledge about the strength of the trophic relationship between rockfish and lingcod and their place in the ecosystem, any potential fishery should be examined and established under conservative precautionary assumptions (Lauck *et al.*, 1998). This means assuming lower lingcod consumption rates over a wide range of rockfish sizes and smaller fractions of lingcod diets that are rockfish. A full management strategy evaluation accounting for uncertainty in the "state of nature" that is lingcod consumption could help quantify the amount of risk managers assume by allowing for the lingcod fishery (Smith *et al.*, 1999), and results from this current study could help to inform such an analysis. However, uncertainty in possible outcomes must also be weighed against the possible benefits to the entire social-ecological system. Despite uncertainty, these preliminary models indicate that the food web in the California Current may offer a unique policy opportunity where fishing communities can benefit beyond the status quo while also sustaining the biological community.

Table 3.1. Model parameters. When multiple values were explored for a single parameter, bold indicates the "baseline" scenario used

Symbol	Name	Value	Source
$S_{\infty,m}^{l}$	Maximum length – male lingcod	86.9 cm	Hammel *et al.* 2009
$S_{\infty,f}^{l}$	Maximum length – female lingcod	126.3 cm	Hammel *et al.* 2009
$S_{1,m}^{l}$	Length at age 1 – male lingcod	29.7 cm	Hammel *et al.* 2009
$S_{1,f}^{l}$	Length at age 1 – female lingcod	28.1 cm	Hammel *et al.* 2009
K_{m}^{l}	Von Bertalanffy K – male lingcod	0.22 yr^{-1}	Hammel *et al.* 2009
K_{f}^{l}	Von Bertalanffy K – female lingcod	0.13 yr^{-1}	Hammel *et al.* 2009
$a_{w,m}^{l}$	Weight-length intercept – male lingcod	3.953E-6 kg/cm^{b}	Hammel *et al.* 2009
$a_{w,f}^{l}$	Weight-length intercept – female lingcod	1.76E-6 kg/cm^{b}	Hammel *et al.* 2009
$b_{w,m}^{l}$	Weight-length exponent – male lingcod	3.2149	Hammel *et al.* 2009
$b_{w,f}^{l}$	Weight-length exponent – female lingcod	3.3978	Hammel *et al.* 2009
M_{m}^{l}	Natural mortality – male lingcod	0.32 yr^{-1}	Hammel *et al.* 2009
M_{f}^{l}	Natural mortality – female lingcod	0.18 yr^{-1}	Hammel *et al.* 2009
h^{l}	Steepness of lingcod Beverton-Holt relationship	0.8	Hammel *et al.* 2009
S_{∞}^{r}	Maximum length – rockfish	63.9 cm	Stewart *et al.* 2009
S_{1}^{r}	Length at age 1 – rockfish	18.4 cm	Stewart *et al.* 2009
K^{r}	Von Bertalanffy K – rockfish	0.049 yr^{-1}	Stewart *et al.* 2009
a_{w}^{r}	Weight-length intercept – rockfish	9.77E-6	Stewart *et al.* 2009
b_{w}^{r}	Weight-length exponent – rockfish	3.17	Stewart *et al.* 2009
M^{r}	Non-lingcod rockfish natural mortality	0.043 yr^{-1}	Stewart *et al.* 2009
h^{r}	Steepness of rockfish Beverton-Holt relationship	0.441, 1	Stewart *et al.* 2009
$a_{c,m}$	Lingcod consumption intercept – males	3.01	Beaudreau *et al.* 2009
$a_{c,f}$	Lingcod consumption intercept – females	3.31	Beaudreau *et al.* 2009
$b_{c,m}$	Lingcod consumption exponent – males	0.75	Beaudreau *et al.* 2009
$b_{c,f}$	Lingcod consumption exponent – females	0.77	Beaudreau *et al.* 2009
P_{6+}	Rockfish diet proportion for lingcod ages 6+	0.01, 0.02, **0.03**, 0.04	Koehn *et al.* unpublished
ϕ	Rockfish:lingcod recruitment ratio	11.4, 22.4, 33.4, 44.4, 55.2	Kaplan *et al.* 2014
ML^{l}	Minimum length caught by fishery – lingcod	40, 50, **60**, 70 cm	

ML^r	Minimum length caught by fishery – rockfish	20, **25**, 30, 35 cm	
γ_5	Slope of 5th quantile of diet size spectra	0.05	Beaudreau *et al.* 2007
γ_{95}	Slope of 95th quantile of diet size spectra	0.27, **0.29**, 0.31, 0.33	Beaudreau *et al.* 2007

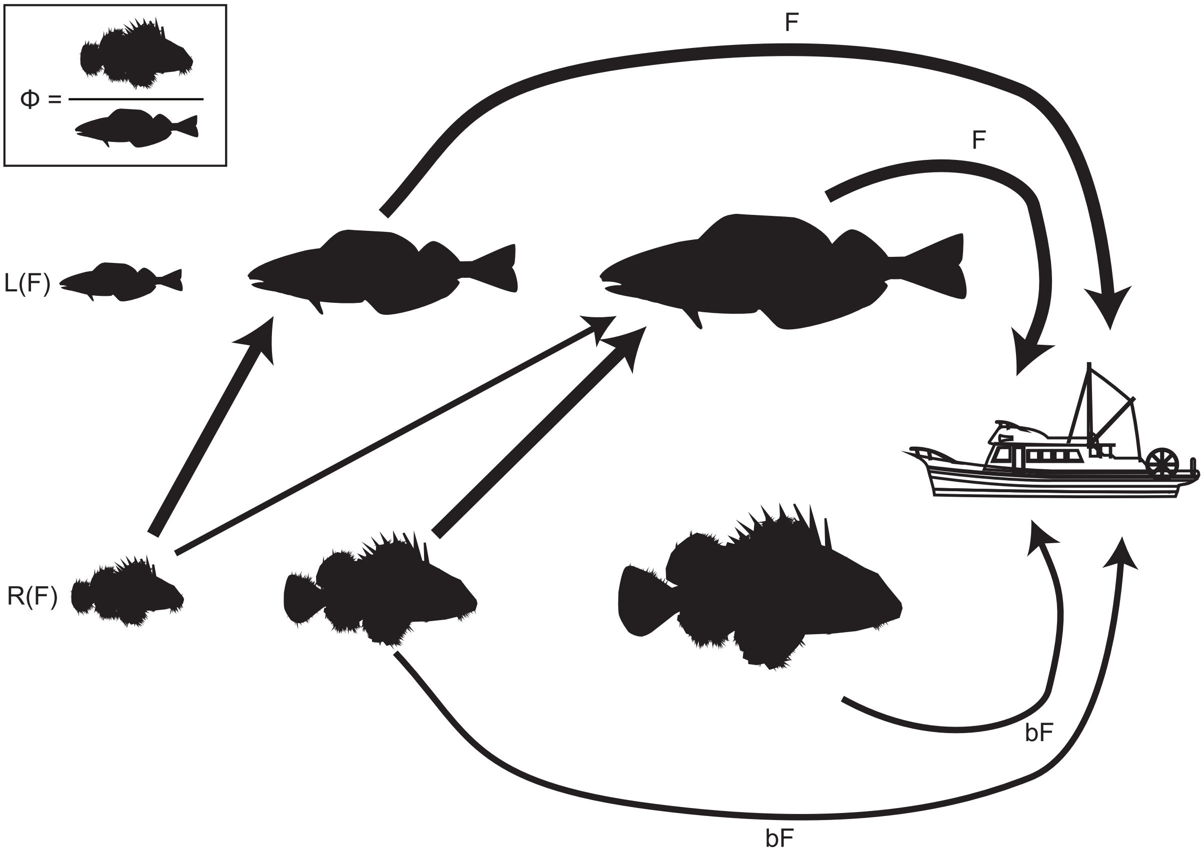

Figure 3.1. Model schematic. Top row represents lingcod dynamics and bottom row represents rockfish. Arrows represent mortality, either through fishing (arrow to boat) or consumption (arrow to lingcod), with widths approximating relative numbers of fish. The box in the upper left-hand corner represents the fixed recruitment ratio between the two groups, ϕ.

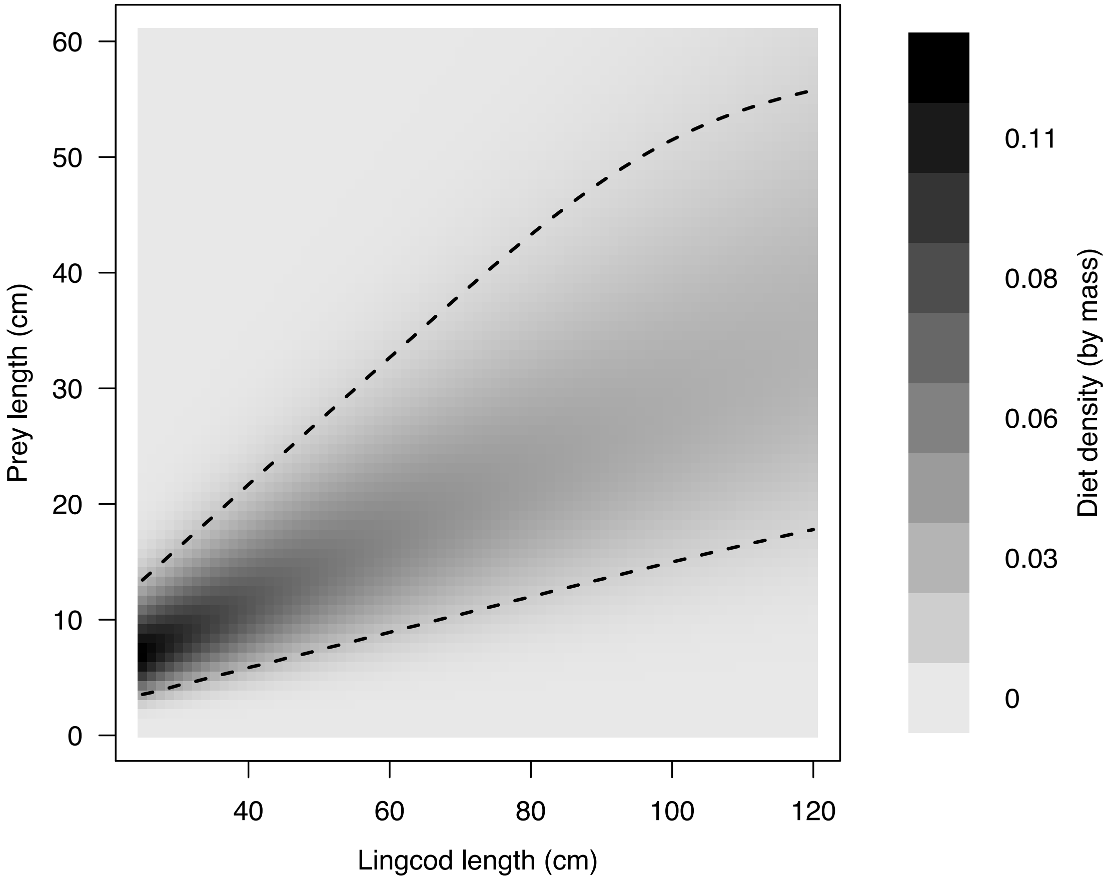

Figure 3.2. Size spectra of lingcod diets in the base case model. Each vertical slice is a probability distribution of the diet size spectrum for a given lingcod size. Darker colors indicate higher probability density. Dashed lines represent the 5th and 95th percentiles. Adapted from Beaudreau and Essington (2007).

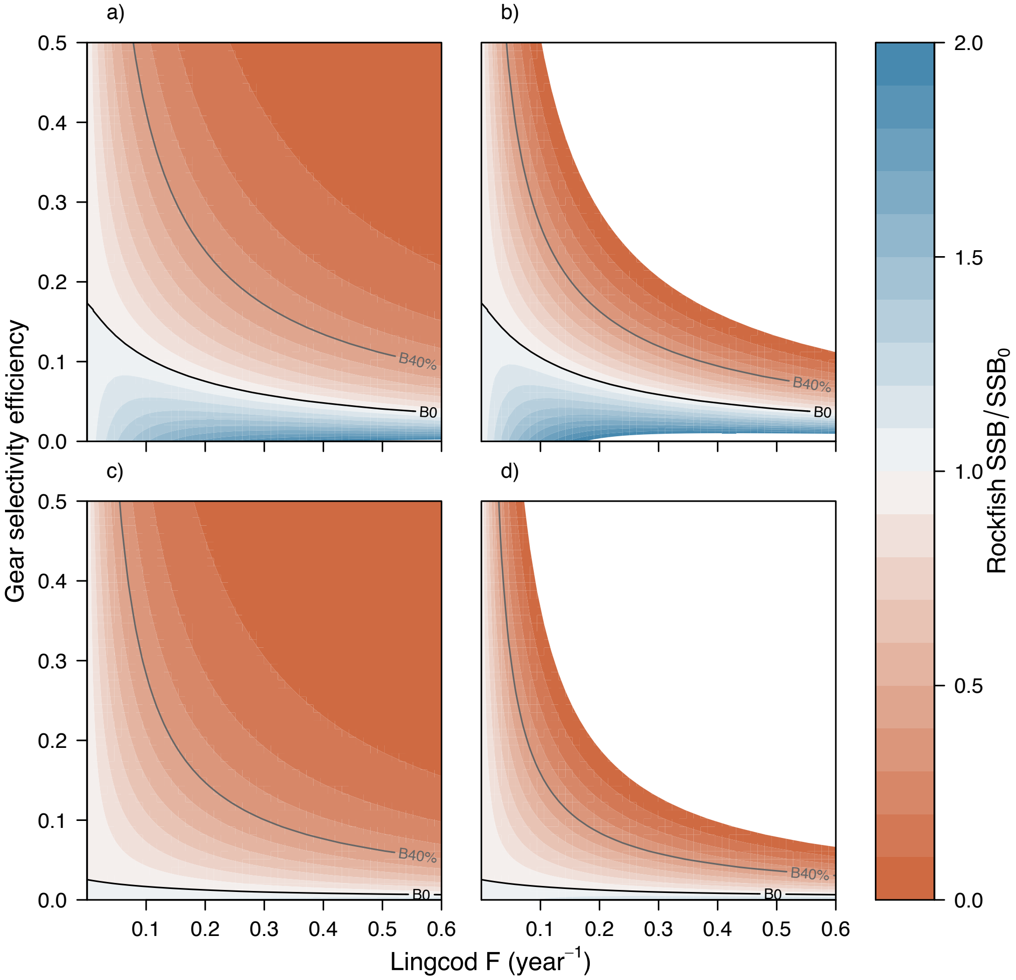

Figure 3.3. Effect of density-dependence and functional response on the rockfish spawning stock biomass (SSB) response to a potential lingcod fishery, as compared to unfished rockfish levels (SSB$_0$). Panels (a) and (b) have a constant fraction of lingcod diets composed of rockfish (saturating response) whereas panels (c) and (d) include a type I functional response. Panels (a) and (c) have constant recruitment, whereas panels (b) and (d) have a Beverton-Holt steepness for rockfish of 0.441. The contour line "B0" marks where rockfish biomass remains at the unfished level. The "B40%" contour marks where rockfish biomass remains at the management target of 40% of the unfished level. Gear selectivity efficiency (represented by *b* in equations) is the fraction of lingcod fishing mortality that rockfish experience, and indicates how effectively the gear selects against rockfish. It ranges from 0 (perfectly selective gear, zero rockfish bycatch) to 1 (indiscriminant gear, unbiased between lingcod and rockfish).

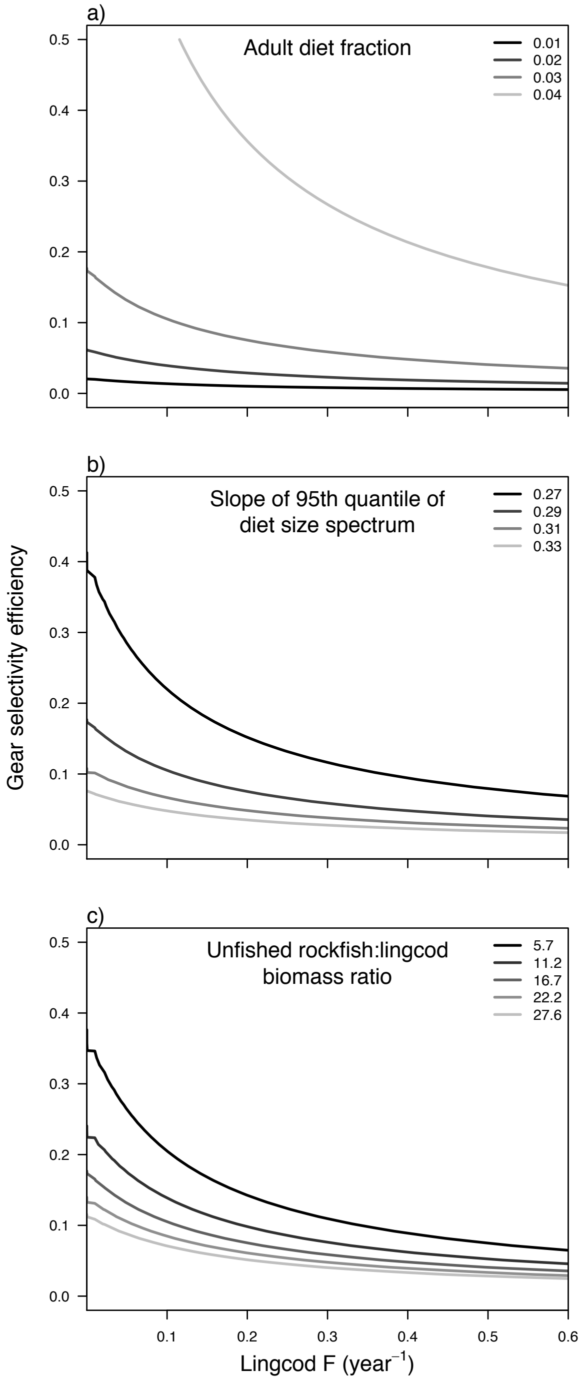

Figure 3.4. Sensitivity analysis to input model parameters. Lines represent the contour over which rockfish populations equilibrate at unfished spawning biomass. The lower the contour line, the greater the area of the plotted parameter space where equilibrium rockfish populations are below unfished biomass. The biomass ratio levels (c) are based on changing the recruitment ratio of rockfish to lingcod; however, biomass reported for interpretive purposes.

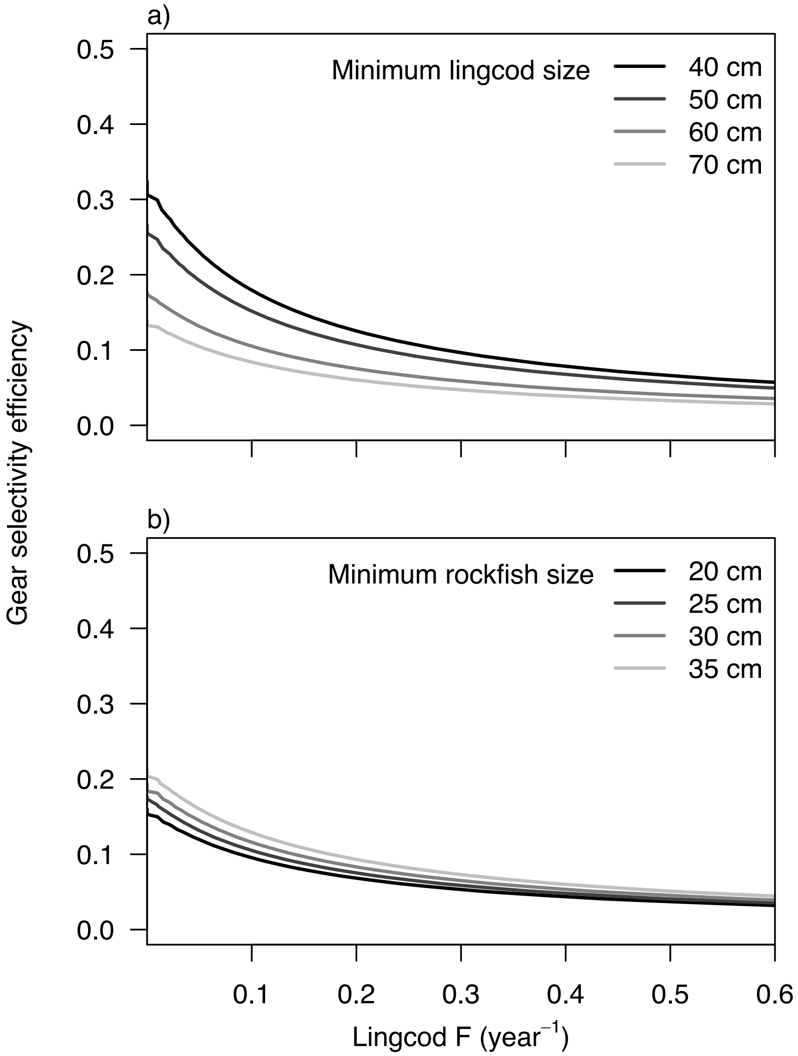

Figure 3.5. Sensitivity analysis to fishery size selectivity. Lines represent the contour over which rockfish populations equilibrate at unfished spawning biomass. The lower the contour line, the greater the area of the plotted parameter space where equilibrium rockfish populations are below unfished biomass.

Chapter 4. Uncertainty in and drivers of forest stand productivity in young growth temperate rainforests of Southeast Alaska

ABSTRACT

Young growth forests are important both for global carbon accounting and for sustainable management and logging of forest resources. However, quantifying productivity of young growth forests is challenging due to the heterogeneity of productivity among trees, stands, and landscapes, and the impracticality of directly measuring the biomass or volume of a stand. In this study, we used a long-term dataset of naturally regenerating young growth forests in the perhumid coastal temperate rainforest of Southeast Alaska, U.S.A. to identify potential drivers of productivity. Furthermore, we used data weighting to ask how propagating uncertainty caused by using proxies of productivity influences identification of drivers and the associated model estimates. Finally, we compare the relative contribution of different sources uncertainty in estimating stand biomass. We found that stand productivity was not related to any landscape-scale covariates. The lack of association implies that either other unmeasured drivers are more important, or that the covariates we used were measured at inappropriate scales. We also found that when uncertainty in stand productivity varies over stand ages – as is the case with the relationship between tree diameter and height – even small amounts of uncertainty can influence model selection and parameter estimation. Finally, uncertainty due to predicting tree biomass from field measurements is relatively large, and failing to account for this will overstate precision in productivity – environment relationships. We provide this analysis as an example of how propagating uncertainty from allometric relationships can better convey the true degree of precision, and that simple weighting schemes are sufficient to account for this uncertainty.

INTRODUCTION

Understanding patterns and drivers of productivity in young-growth forests has important global and regional implications. Young growth forests play a crucial role in natural resource management, largely because forests generally achieve their maximum productivity rates during early successional stages (Ryan *et al.*, 2004). In addition, they represent an important transfer of carbon from the atmosphere to the biosphere. This flux is of global relevance for carbon accounting, and differences in carbon accretion rates among locations can have implications for land use planning (Chazdon *et al.*, 2016; Poorter *et al.*, 2016). In addition, understanding patterns of productivity of young growth forests is important in determining what age to allow stands to reach before harvesting them, and to select which stands to harvest. This, in turn, can optimize economic and environmental benefits of timber harvest while avoiding logging of mature forests.

Quantifying productivity of young growth forests is challenging for several reasons. First, decades-long time series of plot measurements are required to understand dynamics over time scales that are relevant to forests. Second, trees in a stand can be enumerated, but it is generally not possible to directly measure variables related to productivity (i.e. biomass or volume). Instead, previously parameterized allometric relations are often used to estimate production from standard field measurements of diameter at breast height and height (Standish *et al.*, 1985; Jenkins *et al.*, 2003); however, this introduces uncertainty because allometric relations of stands or individual trees deviate from this assumed average. In addition, choosing among existing allometric relations can lead to largescale differences in conclusions (Melson *et al.*, 2011). Third, while stand age governs forest volume or biomass, other regional-scale process that vary over space and time and cause large variability among stands are also important determinants of productivity (Phillips *et al.*, 2000; D'Amore *et al.*, 2015).

In the perhumid coastal temperate rainforests (PCTR) of Southeast Alaska, U.S.A., logging operations on federally managed lands still harvest mature forests, but there is an effort to transition operations towards young growth stands that were previously logged to conserve the remaining mature forest for other ecosystem functions (USDA office of the secretary, 2013). However, as young growth stands have not yet been harvested in the region, foresters do not yet know how to ensure an economically solvent industry over the transition. One key uncertainty is at what age stands become harvestable, but because productivity varies over the landscape (D'Amore *et al.*, 2015) the optimal age at harvest is also highly variable. One major determinant of productivity in the PCTR is hypothesized to be soil drainage, though this has yet to be formally quantified (Neiland, 1971). Temperature may also be important. Inter-annual temperature variation is important on relatively short time scales in similar forests in Ireland (Saunders *et al.*, 2012), and some conifer species distributions in Southeast Alaska appear to be shifting with climate change (Caouette *et al.*, 2015). In general, a better and more precise understanding of drivers of productivity in the region can help forest managers plan the transition to young growth logging more effectively.

We make use of a long-term dataset with broad spatial coverage over Southeast Alaska, U.S.A. to quantify the effect of temperature, precipitation, and soil moisture on productivity of young growth forests in the PCTR. Furthermore, unlike most studies of forest productivity (e.g., Leighty *et al.*, 2006; Hember *et al.*, 2012; D'Amore *et al.*, 2015; Poorter *et al.*, 2016), we explore the impact of propagating uncertainty from allometric relationships on the conclusions. We ask how propagating uncertainty influences 1) which variables beyond stand age (mean annual temperature and precipitation, soil moisture, measurement year) are selected as most influential, 2) parameter estimates, and 3) predicted stand biomass and productivity. Finally, we identify the most important sources of variability by quantifying the contribution of each uncertainty source to total prediction variance.

METHODS

Data

Data come from two separate studies on young growth forests. Data collection on most plots began in 1974 and 1975, with some older plots measured beginning in 1926. Stands were initially disturbed (mainly by clear-cuts, but by windthrow in the case of some older stands) between 1826 and 1972 (median = 1941). During each plot measurement, a complete census of all trees was taken. Diameter at breast height (DBH) was measured for every tree and height was measured for a subset of trees. Stands were re-measured approximately every two years until 2000. We excluded plot measurements before stands reached 20 years of age because stand biomass increases non-linearly during that initial period (Fig. 4.2, D'Amore *et al.*, 2015). If diameters were missing but had both a previous and subsequent measurement (0.12% of the data), diameter was assumed to increase linearly in time between the two nearest available measurements. Remaining missing diameter measurements (either no previous or subsequent live measurements) were removed (only 0.03% of the data). The dominant species in the plots were western hemlock (*Tsuga heterophylla*) and sitka spruce (*Piscea sitchensis*); combined these species represented >99% of all trees. For this study, we excluded remaining species because they are not harvested for timber and their infrequent occurrence provided a limited number of height measurements. Data are described in greater detail in DeMars et al. (2000).

Environmental data came from several sources. Long-term mean annual temperature and precipitation were calculated at each plot center from ClimateWNA (Wang *et al.*, 2011). Information on soil moisture came from a compound topographic index (CTI), which uses a digital elevation map of the region to predict where water will flow and accumulate on the landscape (Creative Commons license 4.0, http://ckan.snap.uaf.edu/). Although soil wetness was ranked in the field on an ordinal scale from 1 (very poorly drained) to 5 (well drained), this was only done for a subset of the plots (34/65), and included none of the oldest plots. In addition, the field data offered limited contrast as nearly four-fifths (27/34) of plots with data fell into the "well drained" category. We used the CTI data as our indicator of soil moisture because it was available for all plots and potentially provided more detailed contrast among plots. Finally, measurement year was used as a gross indicator of temporal increases in temperature due to anthropogenic climate change. Because plots were initiated at different ages, and plots of many different ages were measured in any given year, the effects of measurement date and stand age could be separated.

Approach

The statistical modeling was divided into two parts. First, we modeled relationship between DBH and heights for trees that had direct height measurements (18% of data), used that relationship to impute missing heights, and applied previously parameterized allometric equations to estimate tree biomasses. Second we used linear models to relate plot biomass (summed over all trees) to stand age and other environmental covariates– mean annual temperature and precipitation, soil moisture, measurement year– to understand large-scale drivers of productivity, and asked how these relationships depended on which type of variance (height, biomass, both) was propagated.

Inferring height and biomass

Height was modeled with a continuous-time autoregressive process to place realistic limits on the magnitude of predicted tree height increments between plot measurement dates. A continuous time model was necessary because plot measurement dates were not evenly spaced. Height of tree i in plot j at time $t + \Delta t_{i,j,t}$, was modeled as:

$$h_{i,j,t+\Delta t_{i,j,t}} = h_{i,j,t} + \beta_{h,0}\Delta t_{i,j,t} + \beta_{h,1}(d_{i,j,t+\Delta t_{i,j,t}} - d_{i,j,t}) + \delta_{i,j,t+\Delta t_{i,j,t}} \qquad (4.1)$$

where $h_{i,j,t,}$ is the height of tree i in plot j at time t, $d_{i,j,t}$ is the DBH, $\beta_{h,0}$ is the average annual growth rate of trees across the study in the absence of any diameter growth (i.e., the intercept of the growth increment), $\beta_{h,1}$ is the additional annual height increase per meter of diameter growth, and $\delta_{i,j,t+\Delta t_{i,j,t}} \sim \mathrm{N}(0, \Delta t_{i,j,t}\sigma_h)$ is the residual for the observation; residuals were assumed independent. This formulation intentionally does not force tree height changes to be positive, as negative height changes were observed. Because we assume no observation error, we assume such decreases were due to natural events that topped the tree. The parameters $\beta_{h,0}$ and $\beta_{h,1}$, and σ_h were estimated separately for the two species. In addition to the autoregressive model, we also simultaneously estimated model parameters relating the initial tree height to height at first measurement (Fig. 1a,b). This was necessary because there is no previous height available at the first measurement of a tree so the autoregressive model cannot be used. Instead, height of tree i in plot j at the first diameter measurement (which can occur at any age) was modeled as an asymptotic function of diameter:

$$h_{i,j,0} = \alpha_0\big(1 - \exp\big(-\alpha_1 d_{i,j,0}\big)\big) + \delta_{i,j,0} \qquad (4.2)$$

where $h_{i,j,0}$ is the initial height, $\delta_{i,j,0} \sim \mathrm{N}(0, \sigma_0)$, and α_1, α_2, and σ_0 were again estimated separately for each species.

To estimate the biomass of each tree on each measurement date, we used the measured diameters, measured heights when available, and inferred heights when height was not measured. Species-specific allometric equations for large trees came from Standish et al. (1985), while a single allometric equation for small trees came from D'Amore et al. (2015). We used the same diameter cutoff points for trees to be considered "small" as D'Amore et al. (8.26 cm for hemlock, 7.14 cm for spruce). In all cases, the allometric equations took on the basic form:

$$m = a + bd^2h \tag{4.3}$$

where m is biomass and a and b are parameters from the allometric equation. We then summed all tree biomasses within a plot on a given measurement date and divided by the plot's area to obtain a tree biomass per unit area:

$$m_{j,t} = \frac{1}{A_j}\left[\sum_{i\in S_{j,t}} M\left(d_{i,j,t}, h_{i,j,t}\right) + \sum_{i\notin S_{j,t}} M\left(d_{i,j,t}, \hat{h}_{i,j,t}\right)\right] \tag{4.4}$$

Here, $S_{j,t}$ is the sample of trees with measured heights in plot j at time t (note that the sample of trees with measured heights is not the same at every re-measurement), $\hat{h}$ is the predicted height of the tree based on the fitted model (using observed values in the autoregressive formula whenever possible), A_j is the area of plot j, M is the appropriate function to calculate biomass, and $m_{j,t}$ is the biomass per hectare of plot j at time t. (Plots do not all share a uniform area.) We calculated $m_{j,t}$ at every available plot measurement time. For the first measurement of each plot, $h_{i,j,t}$ and $\hat{h}_{i,j,t}$ in equation (4.4) were replaced with $h_{i,j,0}$ and $\hat{h}_{i,j,0}$ because no previous heights were available, which are necessary in order to apply the autoregressive model.

Propagating error

To propagate error from the estimated heights and tree biomasses, we calculated the variances of stand biomass due to both of these sources or uncertainty. For height, variance of prediction induces variance in stand biomass, Var($m_{j,t}$), equal to:

$$\mathrm{Var}\left(m_{j,t}\right) = \frac{1}{A_j^2} \sum_{i \notin s_{j,t}} \left[\left(b_{i,j,t} d_{i,j,t}^2\right)^2 \mathrm{Var}\left(\hat{h}_{i,j,t}\right)\right] \tag{4.5}$$

Here, $b_{i,j,t}$ denotes the b parameter from whichever allometric equation was used for tree i in plot j at time t and Var($\hat{h}$) includes both parameter and prediction uncertainty from the autoregressive height model.

The second source of uncertainty we considered in the estimate of stand biomass was due to the use of tree heights and diameters to estimate tree biomass (equation 4.3). Residual variances for the allometric equations for large trees were calculated from values reported in Standish (1985), and for small trees were obtained from modeling the raw data in D'Amore et al. (2015). Here we accounted for only process uncertainty, because parameter uncertainty (variance of a and b in the allometric model) was not available for the equations for large trees. In this case:

$$\mathrm{Var}\left(m_{j,t}\right) = \frac{1}{A_j^2} \left[n_{PISI>c_p,j,t} \sigma_{PISI}^2 + n_{TSHE>c_t,j,t} \sigma_{TSHE}^2 + n_{small,j,t} \sigma_{small}^2\right] \tag{4.6}$$

where $n_{PISI>cp}$ represents the number of spruce trees greater than the spruce diameter cutoff, $n_{TSHE>ct}$ is the same for hemlock, n_{small} is the number of trees below their respective diameter cutoffs, and σ^2 is the residual variance for the respective allometric model for biomass.

Modeling biomass

We then fit a series of mixed-effects models to relate stand biomass to plot age, year, and landscape-level environmental predictors. All models followed the same basic form:

$$m_{j,t} = \beta_0 + (\beta_1 + \varepsilon_j)age_{j,t} + \eta_{j,t} + \delta_{j,t} \tag{4.7}$$

where $\varepsilon_j \sim N(0, \sigma_{plot})$ and $\delta_{j,t} \sim N(0, \sigma_m)$. Note that the plot random effect (ε_j) is placed on the slope with respect to age, not the intercept. This is because all plot trajectories approximately intersected at the origin (though we did estimate an intercept to reduce bias), and then diverged more as the stands grew older. Our formulation led to more uniformly distributed residuals than placing the random effect on the slope term. The value $\eta_{j,t}$ is related to uncertainty propagated from using allometric models and from the variable plot sizes; $\eta_{j,t} \sim N(0, \sigma_{prop,j,t})$, and, unlike δ, is not identically distributed. We fit this basic model under four different data weighting schemes that propagated different sources of variance into σ_{prop}: height prediction (using variance from equation 4.5), biomass prediction (using variance from equation 4.6), height and biomass (using variance from sum of equations 4.5 and 4.6), and neither ($\sigma_{prop,j}$ is inverse of plot area). We used the inverse of $\sigma_{prop,j,t}^2$ as weights in the fitting process.

We next assessed which, if any, of four additional predictors (mean annual temperature and precipitation, CTI, and measurement year) improved the base model. Plot-level predictors (all except measurement year) were included exclusively as an interaction with stand age, similar to the plot-level random effects:

$$m_{j,t} = \beta_0 + (\beta_1 + \beta_2 x_j + \varepsilon_j)age_{j,t} + \delta_{j,t} \tag{4.8}$$

where β_2 is the effect of variable x, which is only measured once per plot. Measurement year, which is unique to each re-measurement, was included as a stand-alone effect, to understand how productivity may be changing over time, separately from the effect of stand age:

$$m_{j,t} = \beta_0 + (\beta_1 + \varepsilon_j)age_{j,t} + \beta_3 t + \delta_{j,t} \tag{4.9}$$

We assessed strength of evidence for each model using the Bayesian information criterion (BIC), which is more conservative than the Akaike information criterion (AIC) at large sample sizes

(Ward, 2008), such as those found in this study. We assessed model strength under each of the four weighting schemes.

To ascertain the relative contribution of each source of variation on the uncertainty in biomass and production predictions from the model, we compared the values of standard deviations that contribute to the ultimate prediction variance for a stand that is age 45 in the year 2000. These standard deviations came from parameter uncertainty (from covariance matrix of the βs), propagated uncertainty from allometric relations (σ_{prop}), within plot uncertainty (σ_m), and among plot uncertainty (σ_{plot} multiplied by stand age). For σ_{prop}, we averaged the standard deviations due to height and biomass uncertainty among plots, using the observed value when a plot's age was closest to 45, including only stands with observed ages between 40 and 50.

All analyses were done in R version 3.3.0 (R Core Team, 2016). The height model was fit and prediction errors calculated using template model builder (Kristensen *et al.*, 2016). Mixed effects models were fit using the lme4 package (Bates *et al.*, 2015). Mixed effects models were fit using maximum likelihood estimation for model selection and restricted maximum likelihood estimation (REML) for parameter estimation (Zuur *et al.*, 2009). Residuals were examined for normality and homoscedasticity (Supplementary materials).

RESULTS

There was generally an asymptotic relationship between tree height and diameter, although the shape of this relationship differed by species (Fig. 4.1, Table 4.1). Spruce trees tend to grow wider in diameter than hemlocks across the available data range, and also show more saturation in the relationship between diameter and height. That is, spruce tree heights grow quickly and then slow, while the girth continues increasing. Hemlock trees display more consistent growth in both height and diameter. Variability in the relationship between height and diameter is not homogeneous across tree sizes, consistent with the autoregressive model that has increasing variance over time. Variability in the height-diameter relationship is low for small trees of both species and then increases, as trees grow larger (Fig. 4.1). The predictive error of autoregressive models increases through time, so our model relating tree heights to diameters captures this phenomenon.

Across entire stands, all biomass trajectories approximately intersect at the origin, increase exponentially at first, and then reach a constant growth rate (Fig. 4.2). Like the height-diameter relationship, variability among stands increases as stands age, consistent with the decision to place the random effect of plot on the effect of stand age, not the intercept. Our mixed effects model captures this because the random effect is placed on the effect of age, rather than the intercept.

The variance of stand biomass due to the two allometric relations (predicting height and biomass, equations 4.5 and 4.6) shows distinct patterns with stand age (Fig. 4.3). The variance from height predictions increases as stands age (Fig. 4.3a). Uncertainty in the biomass predictions depends on both which allometric relationship is used (small or large tree model) and how many trees are in the plot. Uncertainty in the biomass predictions first increases, as trees "grow out" of the low-variance small tree model into the high-variance large tree model; however, as the stands continue to age, the number of trees in a plot decreases, mainly due to suppression mortality, and so the uncertainty for the plot decreases (Fig. 4.3b). This rests on the assumption that residuals for the relationship between diameter and height, and biomass are homogeneous across all sizes of large trees. In both cases (height and biomass), choice of model and its associated error structure has major implications for variance that gets propagated.

The strength of evidence for the best model depends on how the variance described above is propagated. Including measurement year greatly improves the model when no prediction uncertainty is propagated and when uncertainty from only the biomass relationship is propagated (Table 4.2). Yet, measurement year is more weakly supported if uncertainty from both the height and the biomass relationships are propagated, and is not supported if height uncertainty is propagated. This is likely because when height uncertainty is included, later measurement dates are given low weight in the fitting process, particularly in the plots with the longest measurement histories. None of the landscape predictors (temperature, precipitation, and moisture) are significantly associated with stand productivity under any data weighting scheme (Table 4.2).

Parameter estimates themselves were also influenced by which sources of uncertainty were propagated, and this was particularly the case for uncertainty from height predictions (Table 4.3). The magnitude of the effect of age is higher and measurement year is lower whenever height uncertainty is propagated. (The two quantities are negatively correlated.) In particular, when height uncertainty is propagated, the measurement year effect is very close to zero, in accordance with the results from the model selection. The mean biomass at age 45 in the year 2000 is similar among all three models that propagate any uncertainty, but is lower than the estimate from the model with no weighting scheme at all.

The total uncertainty in predicting biomass was quite high, and the main source of this low precision was variability in stand biomass among plots. Standard deviations in stand biomass from potential sources of variability ranged over three orders of magnitude (Table 4.4). While variability in stand biomass among plots is the most dominant source, as expected, variability due to the use of allometric relations to estimate biomass is the second-largest source. Uncertainty in estimates of the model parameters is third highest. Variability within plots and variability due to predicting tree heights were both relatively low. This indicates that once it is known whether a stand is of high or low productivity, biomass accretes in a relatively predictable manner. However, none of our landscape factors are able to help determine how productive a stand is.

DISCUSSION

We analyzed a long-term dataset on young growth stands in the Southeast Alaska perhumid coastal temperate rainforest (PCTR) to examine what sources of uncertainty are particularly large or influential, and to ask what factors might drive productivity of the stands. Propagating error from predicted heights alters both results of model selection and the parameter estimates. In addition, uncertainty due to predicting tree biomasses from standard field measurements is the second greatest source of uncertainty after variability among stands. Combined, these results indicate that failing to propagate uncertainty from allometric relationships can have major implications for predictions and conclusions regarding drivers and estimates of productivity. We were not able to reduce uncertainty in these predictions by identifying landscape factors that determine productivity of individual stands.

Uncertainty in the measurement of the response variable, stand biomass, becomes influential when it shows a trend over stand ages, or over any other predictor. In these situations, even a small amount of uncertainty greatly influences statistical model selection, parameter estimates, and predictions, as is the case with uncertainty from predicting tree heights based on diameters. This source of uncertainty is rarely considered, despite the fact that many studies relate productivity to age, year, and environmental features to predict biomass, mainly based on DBH (e.g., Hember *et al.*, 2012; D'Amore *et al.*, 2015). We show that this source of uncertainty, while small, could still be affecting estimates as the relationship between diameter and height is consistently more predictable for smaller and younger trees. Using an autoregressive model for the height-diameter relationship, or any other model that does not assume variance is homogeneous across tree sizes, and then using the prediction variance as weights in the model for stand productivity can avoid this bias.

Uncertainty from the allometric relationship between tree biomass, and height and DBH is a large source of uncertainty that is often ignored. Predictions of stand biomass are sometimes used to determine if forests are carbon sinks or carbon sources (e.g., Phillips *et al.*, 1998; Clark, 2002; Lewis *et al.*, 2009; Pan *et al.*, 2011), and failing to account for this source of uncertainty overstates precision in those conclusions. Establishing better allometric relationships based on more trees will not decrease the inherent variability among trees, which is substantial. However, monitoring larger plots to estimate biomass can reduce this uncertainty, as the "average" allometric relationship is more likely to approximate the total biomass over a larger sample. This variability of tree biomass, coupled with the strong influence of which allometric model researchers choose to use (Melson *et al.*, 2011), lowers our confidence in the estimates of how much carbon, biomass, or wood volume forests contain.

We did not find a significant relationship between landscape factors (soil moisture, mean annual temperature and precipitation) and productivity of young growth stands. The lack or relationship could be due to several considerations. First, while soil moisture is largely thought to be a major determinant of forest productivity across the region (Neiland, 1971), moisture may not be an important driver of variation within the population of stands in this study because there is not sufficient contrast. That is, stands that are selected for logging are by definition better drained. This is supported by the fact that, for plots that had soil drainage classified in the field, nearly 80% fell into the best drained category. A second possible explanation is that we did not measure the drivers on the same scale at which they influence productivity (Levin, 1992). There is some uncertainty in the locations of plots; CTI is calculated at a 50x50m spatial resolution and temperature and precipitation were estimated at 2.5x2.5 arcminutes. In contrast, most sampled plots were less than 250 square meters. A third possible reason is that one or more unmeasured environmental variable is an important driver. For example, aspect and soil nutrient availability were only available for some, but not all, of the plots, so we did not include either; both have the potential to be contributing factors (Waring, 2000; Farrelly *et al.*, 2011). Community interactions among trees (e.g., competition) may also be an additional driver (Ford *et al.*, 2017).

Measurement year does improve the model under some weighting schemes, indicating that annual tree productivity may have increased over the course of the study. Measurement year could, potentially, be a proxy for increasing temperatures and atmospheric carbon dioxide concentrations and shifting precipitation patterns. There is a growing body of evidence that trees are becoming more productive as global temperatures warm and CO_2 concentrations increase (Graumlich *et al.*, 1989; McMahon *et al.*, 2010; Hember *et al.*, 2012; Anderson-Teixeira *et al.*, 2013). Distributions can also shift; in Southeast Alaska, distributions of several conifer species are in flux, moving both up and down slopes (Caouette *et al.*, 2015), and different species may be more or less productive. This study adds further evidence showing that dynamics in young growth forests have changed over the 20th century.

Quantifying productivity dynamics in young growth forests can help managers target stands for logging and determine at what age stands contain sufficient lumber to be profitable to harvest, but it is also important to consider uncertainty in such studies. Using variances to weight data in regressions and mixed-effects models is a relatively simple way to ensure that uncertainty from allometric relationships does not bias conclusions, and we recommend it to any researchers modeling quantities such as stand biomass, carbon, or volume. In addition, using ordinary linear or non-linear regressions to estimate allometric relationships may not accurately capture uncertainty, as variability in the response variable often increases with tree size. Because it is infeasible to directly measure forest productivity, taking advantage of allometric relationships can allow us to quantify productivity indirectly; however, it is important to remember that in utilizing these estimated relationships, we necessarily introduce uncertainty, and ignoring it can bias results and overstate precision.

Table 4.1. Estimates from the model of tree heights. See text for parameter definitions

Parameter	Estimate	Standard error
$\beta_{h,0,PISI}$	0.298	0.0064
$\beta_{h,1,PISI}$	1.44	0.37
$\sigma_{h, PISI}$	0.373	0.0033
$\beta_{h,0,TSHE}$	0.268	0.0059
$\beta_{h,1,TSHE}$	0.373	0.53
$\sigma_{h, TSHE}$	0.506	0.0044
$\alpha_{0,PISI}$	34.9	0.52
$\alpha_{1,PISI}$	3.51	0.089
$\sigma_{0, PISI}$	2.57	0.077
$\alpha_{0,TSHE}$	43.1	0.48
$\alpha_{1,TSHE}$	2.49	0.046
$\sigma_{0, TSHE}$	2.59	0.078

Table 4.2. ΔBIC under four different data weight schemes. All values are relative to the most supported model in each column, which has a ΔBIC of 0. However, BIC for each of those "best" models differs.

	No propagation	Height	Biomass	Height + Biomass
Base	56.8	0	101.6	5.0
Temperature	58.1	4.8	107.4	9.9
Precipitation	62.5	5.9	104.7	10.5
CTI	62.6	5.6	102.5	10.2
Year	0	0.9	0	0

Table 4.3. Estimate of effects of year and age, biomass at age 45 in year 2000, and residual standard deviation. All values are for model that includes both age and year. Biomass at age 45 is included instead of intercept. Estimates are included under all four data weighting schemes (± is one standard deviation)

	No propagation	Height	Biomass	Height + Biomass
Age effect	5.28 ± 0.47	8.69 ± 0.36	6.40 ± 0.47	7.77 ± 0.40
Year effect	1.27 ± 0.16	-0.31 ± 0.13	1.45 ± 0.13	0.41 ± 0.12
Mean biomass at age 45 in 2000	311 ± 13.9	291 ± 14.1	292 ± 13.4	290 ± 13.2
σ_m	3.29	4.68	4.40	2.14

Table 4.4. Variance and standard deviation of prediction of stand biomass due to five sources of uncertainty at age 45 in year 2000. Estimates obtained from model including age and year effects with data weighted in mixed effects model by both height and biomass variances. Height and biomass standard deviations are averaged among stands 40-50 years of age. Note that the standard deviation for "parameters" is the same standard error for the mean biomass at age 45 in 2000 using the model that propagates both sources of uncertainty in Table 4.3.

	Variance	Standard deviation
Parameters	174	13.2
Height	18.3	4.28
Biomass	498	22.3
Within plot	4.58	2.14
Among plot	1.08E4	104
Total	**1.15E4**	**107**

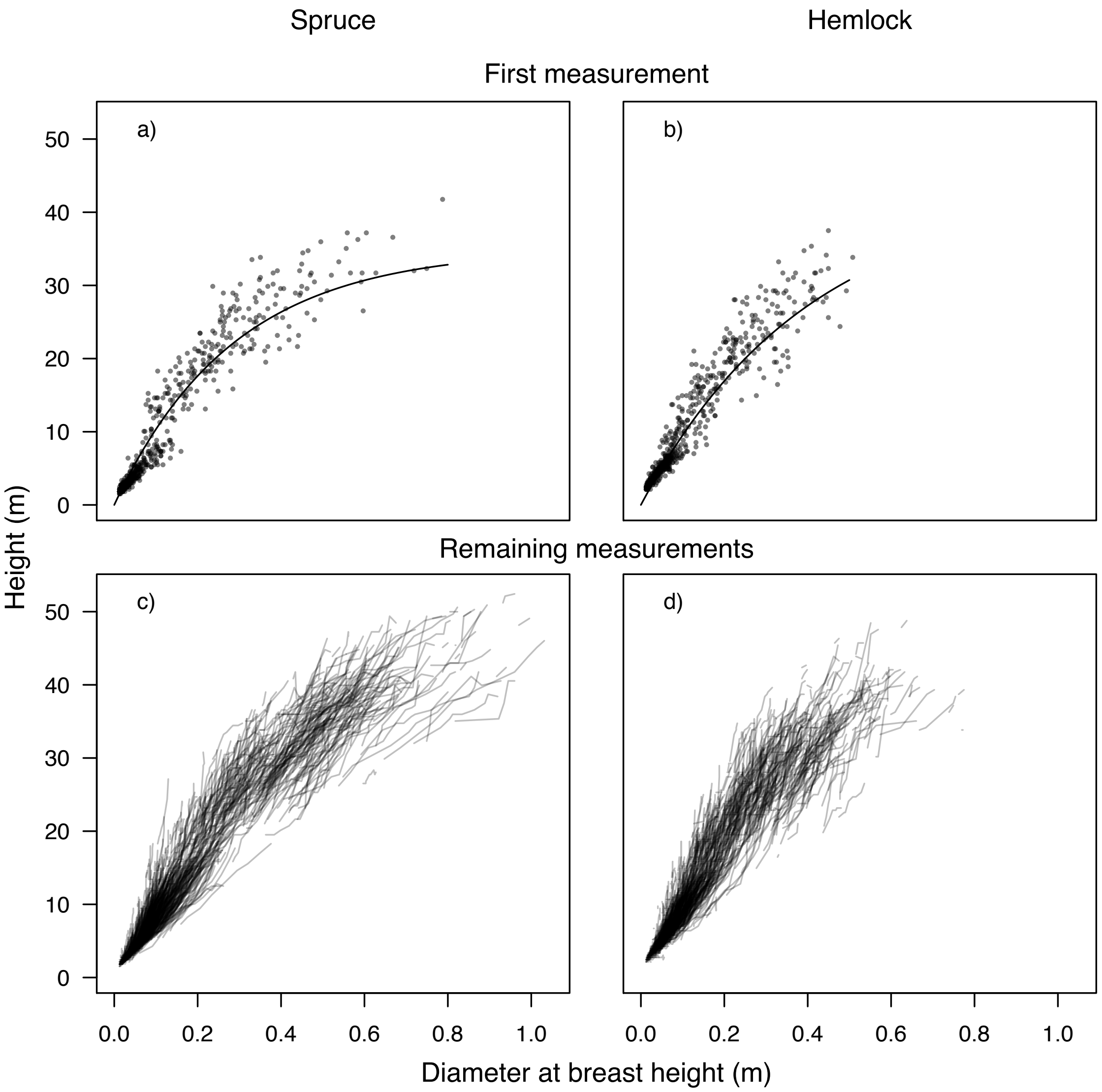

Figure 4.1. Height and diameter data by species. Panels (a) and (b) are the first measurement of a tree (initial condition) and panels (c) and (d) are trajectories of individual tress (lines) over remaining measurements.

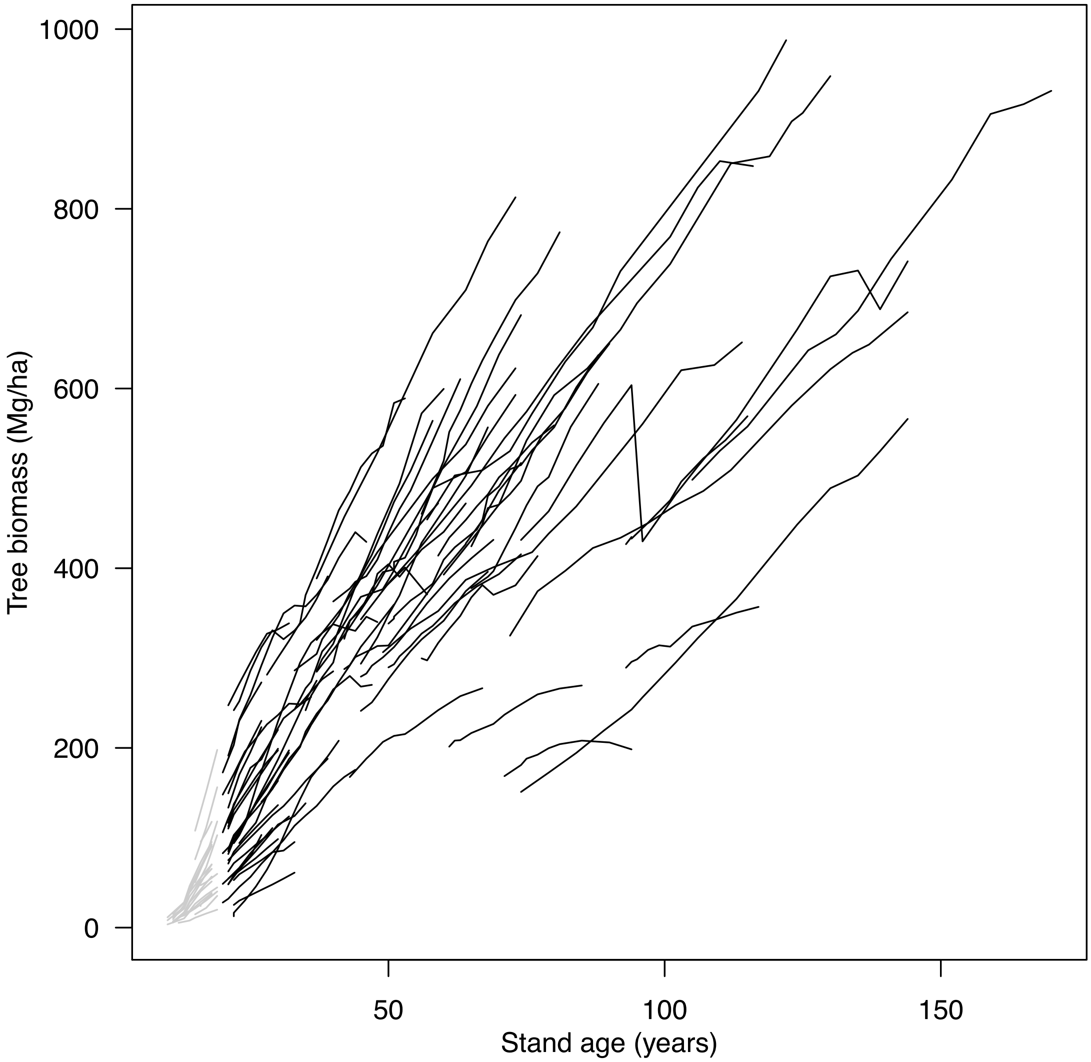

Figure 4.2. Aboveground tree biomass as a function of stand age. Lines in grey are stands less than 20 years of age and not included in the mixed-effects models. Each line represents the trajectory of an individual stand. For stands greater than or equal to 20 years of age, there are 618 points total, representing 65 different plots.

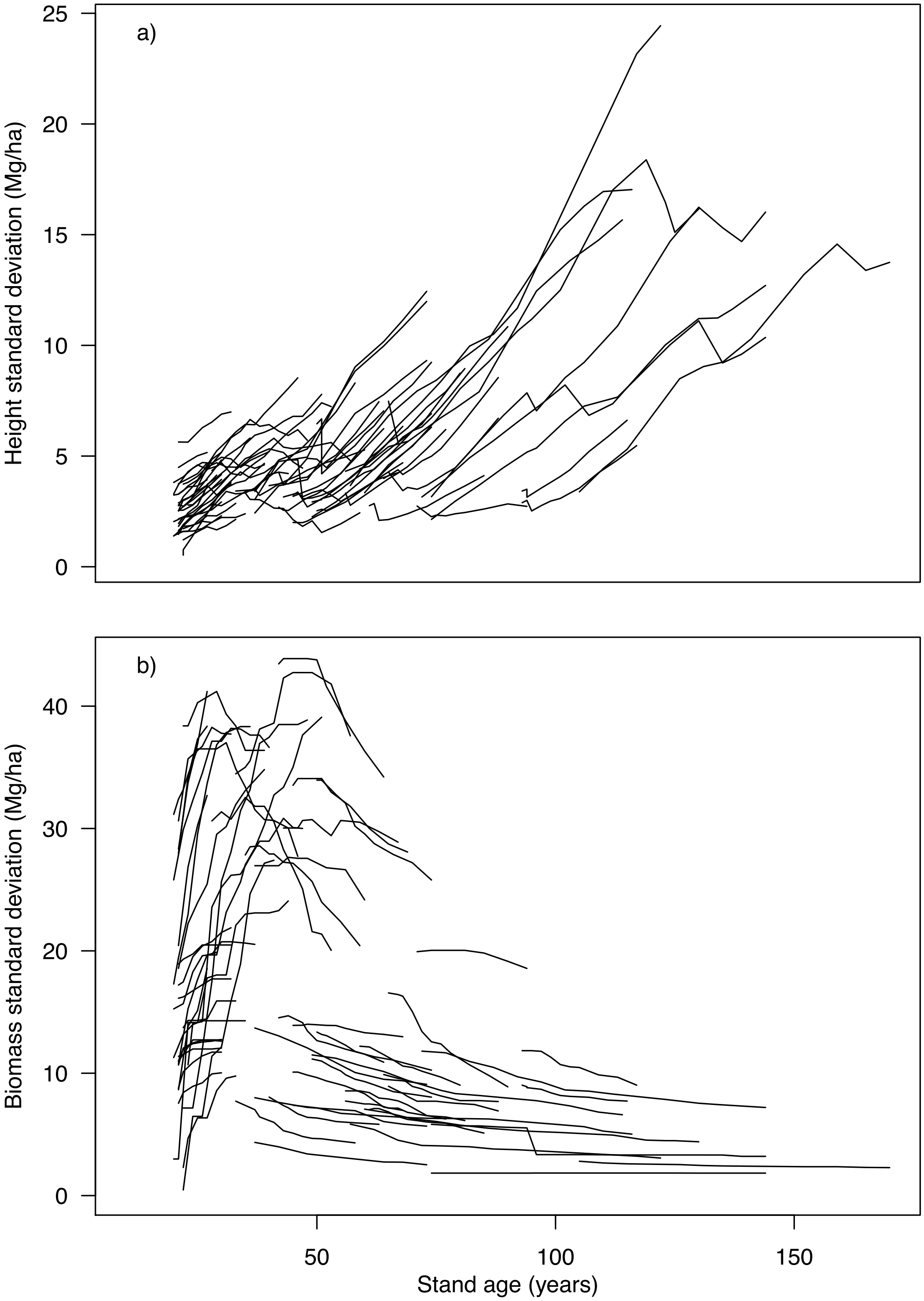

Figure 4.3. Standard deviations of plot biomass from (a) height uncertainty and (b) biomass uncertainty as a function of stand age.

Conclusions

Throughout this dissertation, I have emphasized the idea that predation is a complex process, but that is not necessarily immediately evident to a new graduate student entranced by ideas like trophic cascades, which are often presented in introductory ecology courses. Because predation is a complex process, its effects may not necessarily be evident based on the results of simple analyses. Moreover, while three of the chapters focus on predation, many of the lessons are even more general, and can be applied to any analysis of drivers of productivity, such as the final chapter on forests.

The first chapter exemplifies this dilemma, where I showed that when a process is more highly detailed than the data analyzed, your power to detect the process is not very high. Power becomes particularly low when there are other drivers of population dynamics (either measured or unmeasured), and when data are observed imperfectly, both common features of ecological data. In the second chapter, I struggled to develop a meaningful index for predation. While I was able to develop something new that improves upon previous work, it still has key drawbacks, and is realistically only a rough approximation of the predator landscape. It is unlikely that the index is precise enough to yield meaningful results from any attempt to associate it with productivity of prey populations. In the third chapter, I showed that attempts to incorporate biological processes like predation into management processes will be challenging. Without knowing the strength of the interaction between lingcod and rockfish with nearly impossible precision, it will be a challenge to accurately quantify the tradeoff between juvenile rockfish predation mortality and adult rockfish bycatch mortality. Finally, in the fourth chapter, I struggled to positively identify possible drivers of productivity, and instead found that the way in which sources of uncertainty are accounted for can impact conclusions about major drivers.

Together, these complexities may tempt researches to swing to the opposite side of the pendulum and give up, assuming the effect of predation (or any other driver) can never be properly quantified. Instead, we should strive to find a middle ground, even if doing so presents challenges. It is alright, and usually necessary, to simplify systems and processes in order to use available data and information to answer questions and test hypotheses. However, in doing so, we must carefully consider and acknowledge the limitations of our analyses. For example, a coarse index of predation may useful to answer questions about synchrony, but is unlikely to be precise enough to directly tie to prey dynamics. Knowing the exact response of rockfish to a lingcod fishery will be impossible, but we may be able to generate a probability distribution of responses that helps assess risk. While complexities certainly bring challenges, the world will always be a messy place; with creative problem solving and determination we can continue to expand our understanding of how natural systems work, in hopes of improving our management of the resources such systems provide.

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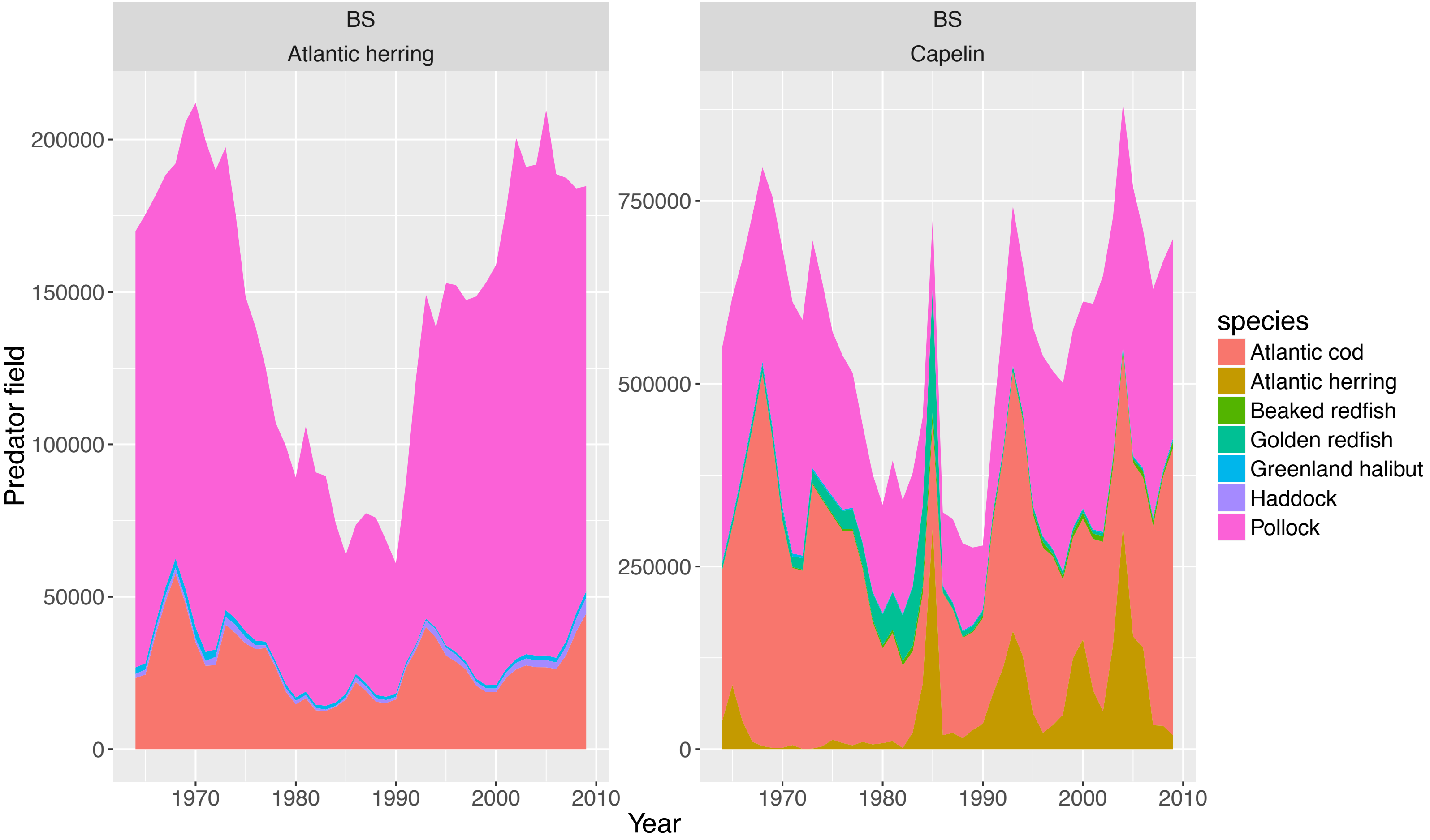
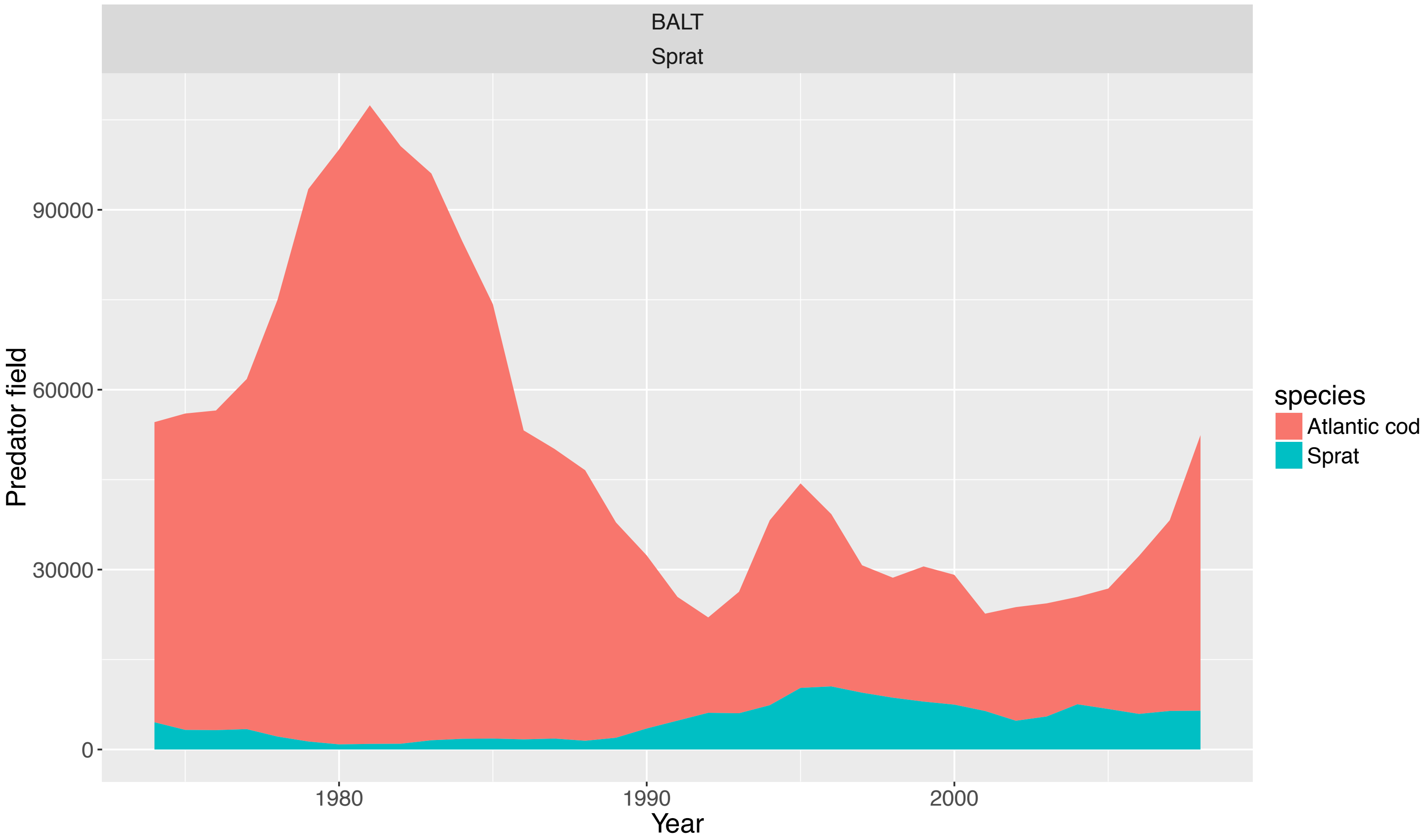
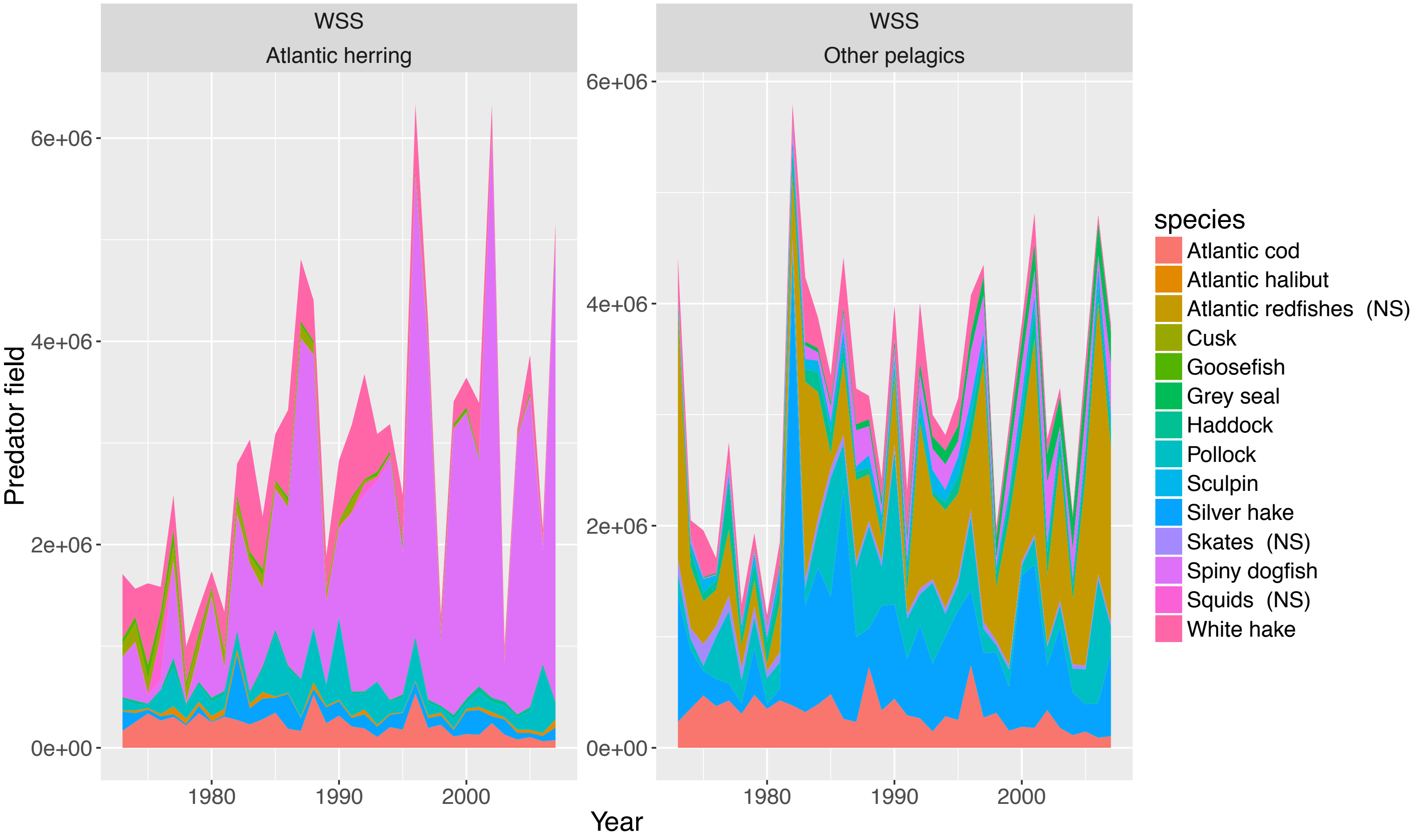
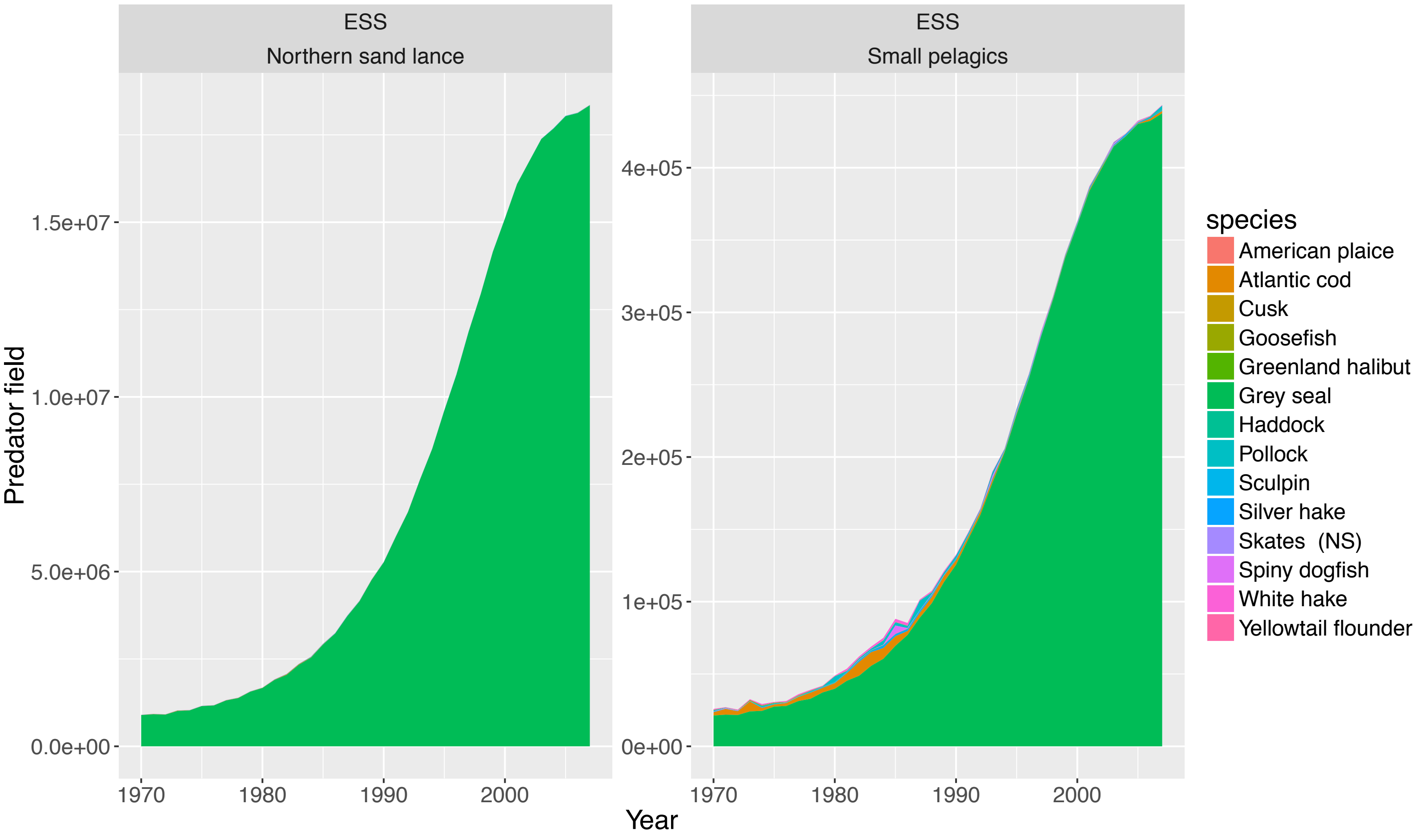
A Chapter 2

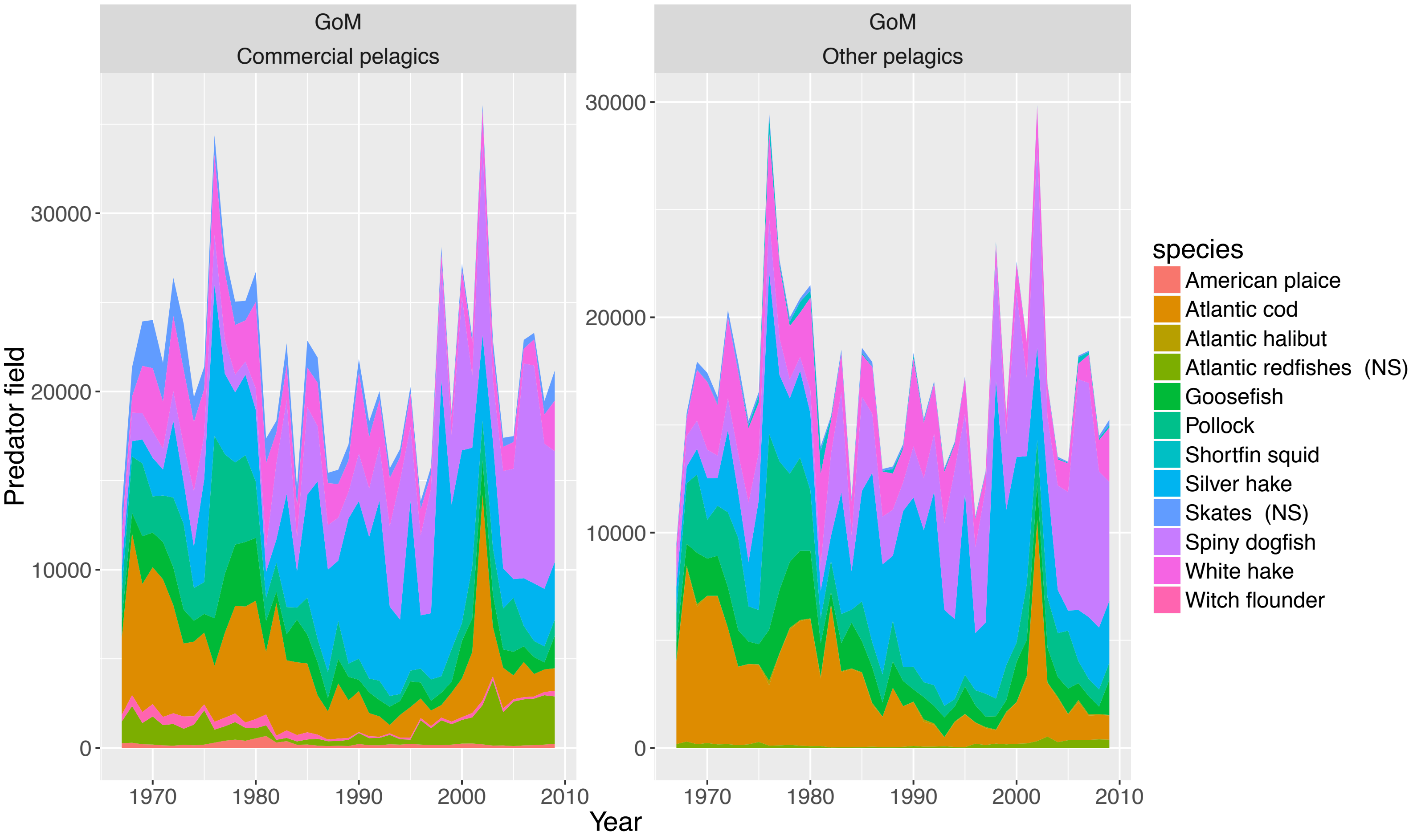
Figures A1-A10: Time series of predator index (top ten predator species), by region, with each species labeled

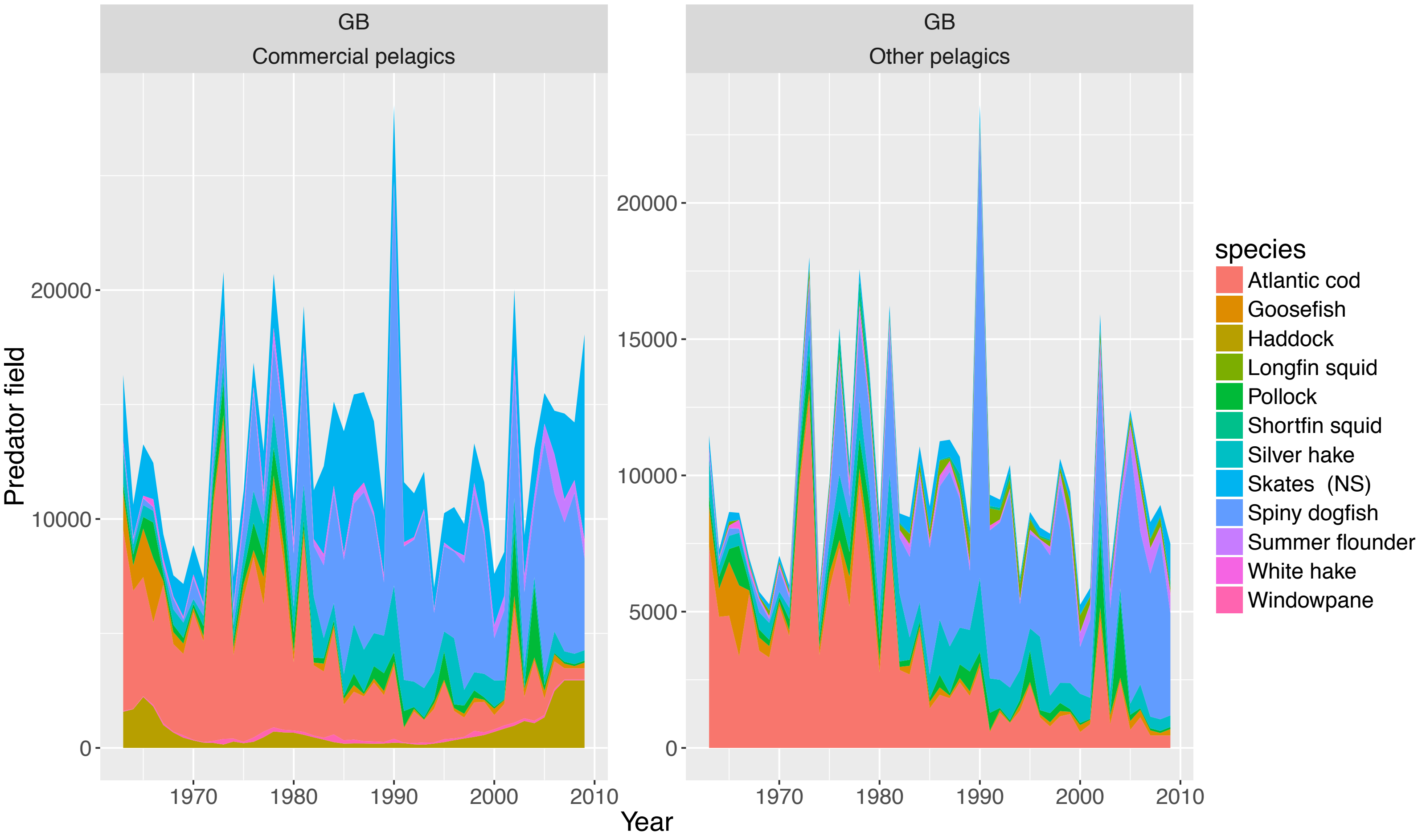

BS
Atlantic herring
BS
Capelin
Predator field
200000
150000
100000
50000
0
750000
500000
250000
0
1970
1980
1990
2000
2010
Year
species
Atlantic cod
Atlantic herring
Beaked redfish
Golden redfish
Greenland halibut
Haddock
Pollock

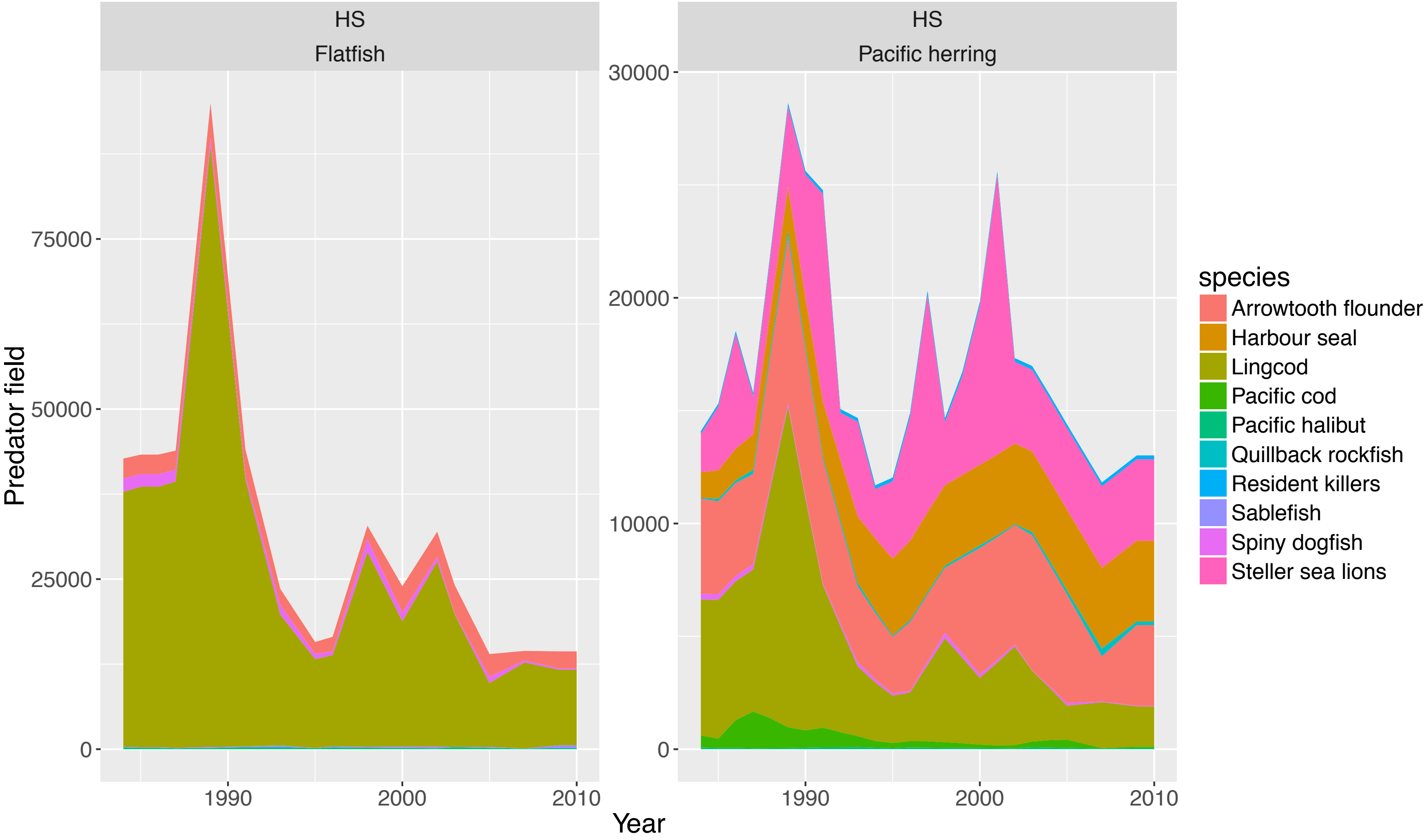

BALT
Sprat
Predator field
90000
60000
30000
0
1980
1990
2000
Year
species
Atlantic cod
Sprat

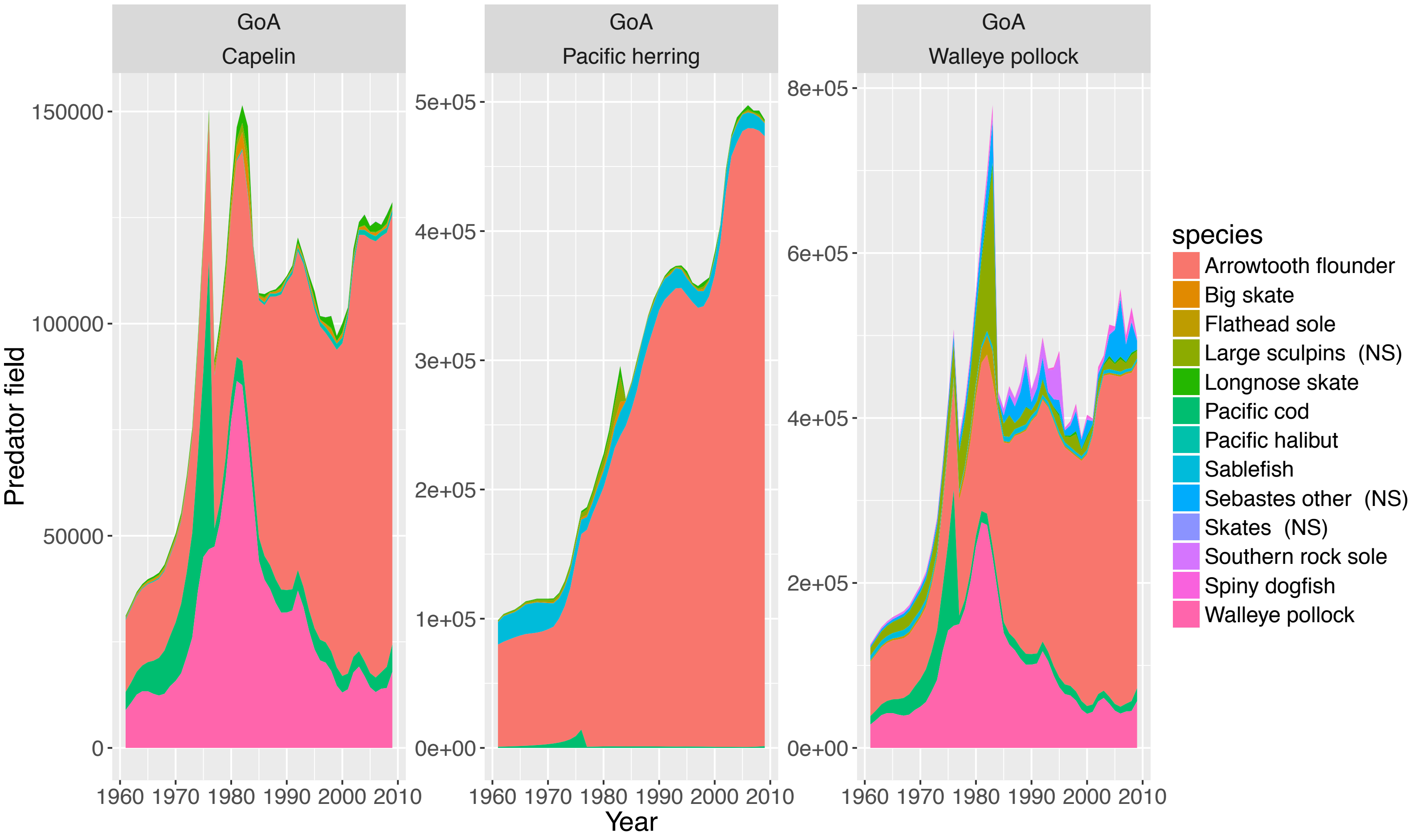

WSS
Atlantic herring
WSS
Other pelagics
Predator field
Year
0e+00
2e+06
4e+06
6e+06
1980
1990
2000
species
Atlantic cod
Atlantic halibut
Atlantic redfishes (NS)
Cusk
Goosefish
Grey seal
Haddock
Pollock
Sculpin
Silver hake
Skates (NS)
Spiny dogfish
Squids (NS)
White hake

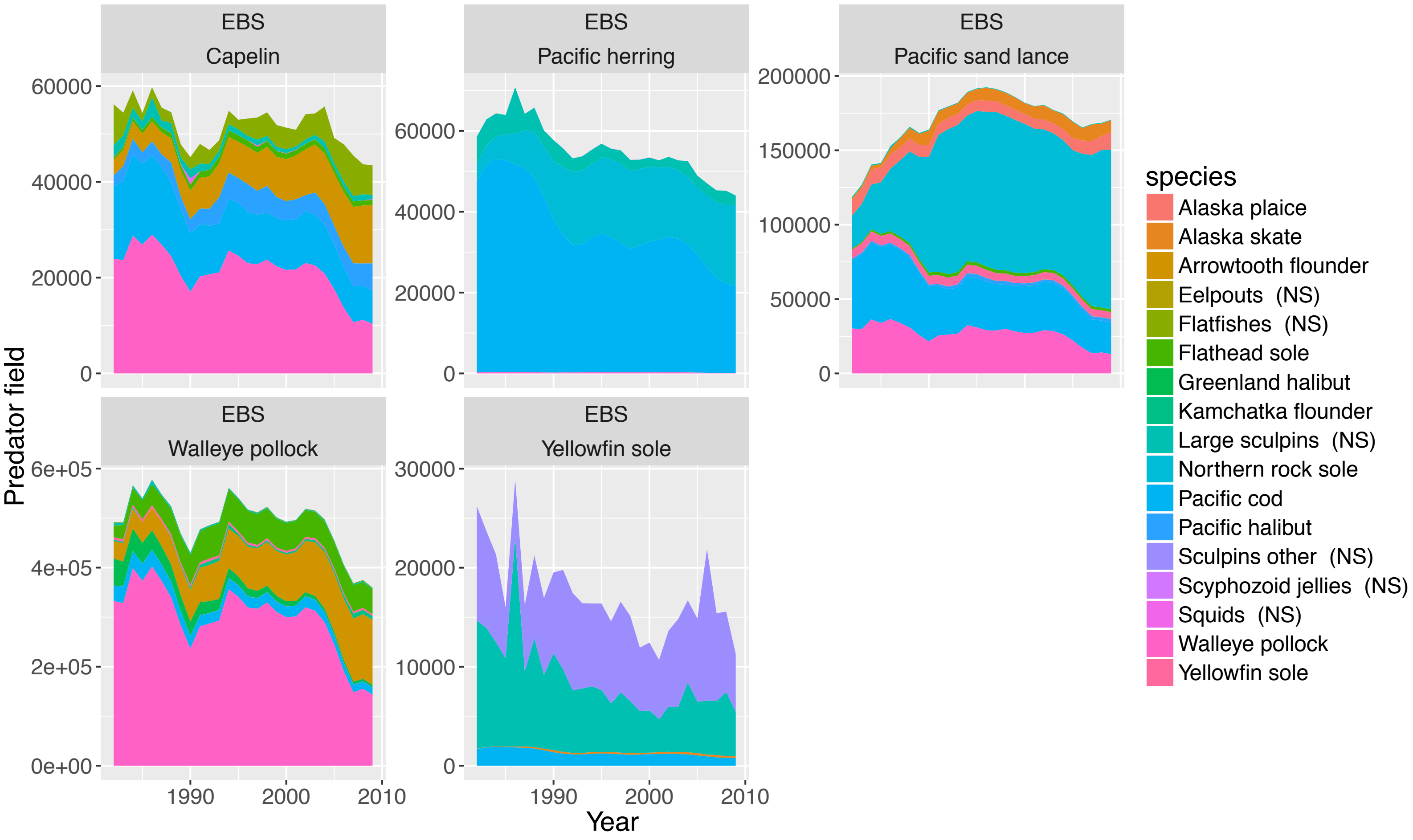

ESS
Northern sand lance
ESS
Small pelagics
Predator field
Year
0.0e+00
5.0e+06
1.0e+07
1.5e+07
0e+00
1e+05
2e+05
3e+05
4e+05
1970
1980
1990
2000
species
American plaice
Atlantic cod
Cusk
Goosefish
Greenland halibut
Grey seal
Haddock
Pollock
Sculpin
Silver hake
Skates (NS)
Spiny dogfish
White hake
Yellowtail flounder


GoM
Commercial pelagics
GoM
Other pelagics
Predator field
Year
0
10000
20000
30000
1970
1980
1990
2000
2010
species
American plaice
Atlantic cod
Atlantic halibut
Atlantic redfishes (NS)
Goosefish
Pollock
Shortfin squid
Silver hake
Skates (NS)
Spiny dogfish
White hake
Witch flounder


GB
Commercial pelagics
GB
Other pelagics
Predator field
Year
0
10000
20000
0
5000
10000
15000
20000
1970
1980
1990
2000
2010
species
Atlantic cod
Goosefish
Haddock
Longfin squid
Pollock
Shortfin squid
Silver hake
Skates (NS)
Spiny dogfish
Summer flounder
White hake
Windowpane


HS
Flatfish
HS
Pacific herring
Predator field
0
25000
50000
75000
0
10000
20000
30000
1990
2000
2010
Year
species
Arrowtooth flounder
Harbour seal
Lingcod
Pacific cod
Pacific halibut
Quillback rockfish
Resident killers
Sablefish
Spiny dogfish
Steller sea lions


GoA
Capelin
GoA
Pacific herring
GoA
Walleye pollock
Predator field
Year
150000
100000
50000
0
5e+05
4e+05
3e+05
2e+05
1e+05
0e+00
8e+05
6e+05
4e+05
2e+05
0e+00
1960
1970
1980
1990
2000
2010
species
Arrowtooth flounder
Big skate
Flathead sole
Large sculpins (NS)
Longnose skate
Pacific cod
Pacific halibut
Sablefish
Sebastes other (NS)
Skates (NS)
Southern rock sole
Spiny dogfish
Walleye pollock


EBS
Capelin
EBS
Pacific herring
EBS
Pacific sand lance
EBS
Walleye pollock
EBS
Yellowfin sole
Predator field
Year
60000
40000
20000
0
60000
40000
20000
0
200000
150000
100000
50000
0
6e+05
4e+05
2e+05
0e+00
30000
20000
10000
0
1990
2000
2010
1990
2000
2010
species
Alaska plaice
Alaska skate
Arrowtooth flounder
Eelpouts (NS)
Flatfishes (NS)
Flathead sole
Greenland halibut
Kamchatka flounder
Large sculpins (NS)
Northern rock sole
Pacific cod
Pacific halibut
Sculpins other (NS)
Scyphozoid jellies (NS)
Squids (NS)
Walleye pollock
Yellowfin sole

B Chapter 3

B.1 Calculating the D matrix

We assumed that an age a lingcod's preference for different sizes of prey is defined by a gamma distrubtion, gamma(α_a, β_a), where β is a scale parameter. This gamma distribution represented lingcod preferences by number of prey consumed (not mass) and measures prey (rockfish) sizes in standard length in order to utilize previous research on lingcod diets. We furthermore assumed that the 5th and 95th quantiles of the gamma distribution increase linearly with lingcod size. This means that the distribution for lingcod of age a is gamma$(\alpha, \beta S_a^l)$, where the parameters α and β are constant across lingcod size, and S_a^l is the size of age a lingcod.

We then wished to use this distribution to calculate a given lingcod's relative preference for each age class of rockfish. To do this, we defined an interval of prey sizes for each rockfish age class, where the interval breakpoints were halfway between the length-at-age of consecutive rockfish age classes. We then integrated the gamma distribution over each of these size-at-age bins to obtain initial diet preferences for each age class of rockfish (Fig. B.1). Because the size-at-age bins did not cover the entire domain of the gamma distribution (which is all positive numbers), we normalized these weights so that they summed to one. If Δ is the array of relative (unnormalized) lingcod diet preferences by number (as opposed to mass), then Δ_{a_r,a_l} is calculated as follows:

$$\Delta_{a_r,a_l} = \int_{(S^r_{a_{r-1}}+S^r_{a_r})/2}^{(S^r_{a_{r+1}}+S^r_{a_r})/2} f_{\alpha,\beta S^l_{a_l}}(s)\, ds = F_{\alpha,\beta S^l_{a_l}}\left[(S^r_{a_{r+1}} + S^r_{a_r})/2\right] - F_{\alpha,\beta S^l_{a_l}}\left[(S^r_{a_{r-1}} + S^r_{a_r})/2\right] \tag{1}$$

where f and F are the PDF and CDF respectively of the gamma distribution with parameters noted in the subscript, and S_a is the size at age with an l superscript for lingcod sizes (total length) and an r superscript for rockfish (standard length).

To convert the size spectra so that they accounted for lingcod preferences by mass, instead of by number, we multiplied the relative preference in each length bin by the associated weight of a rockfish in that length bin, and then re-normalized the vector.

In doing this, we generated a vector of diet weights with one entry for each rockfish age class. This process of obtaining relative diet weights for each rockfish age class was done for each lingcod size-at-age and for both lingcod sexes. We used these vectors to populate an array D, of two $r \times l$ matrices where r is the number of rockfish age classes and l is the number of lingcod age classes. There is one matrix for each lingcod sex, and each column of both matrices of D sums to one.

B.2 Derivation of equation 3.5: consumption with linear functional response

Without loss of generality, let us ignore lingcod sex. Then without the linear functional response, the per capita consumption of rockfish for age a_l lingcod is $P_{a_l} C_{a_l}$. We wish for this quantity, which we define as RC_{a_l} to scale with rockfish biomass, while also accounting for the lingcod diet size preferences. In other words:

$$0.5RC_{a_l} = \alpha_{a_l} \sum_{a_r=0}^{r} D_{a_r,a_l} R_{a_r}(F) W_{a_r} \tag{2}$$

where α_{a_l} is the constant of proportionality or slope of the functional response and the one-half appears because we wish to only account for consumption of females. This means that the per lingcod consumption of age a_r rockfish biomass by age a_l lingcod is $\alpha_{a_l} D_{a_r,a_l} R_{a_r}(F) W_{a_r}$.

To determine the slope, α_{a_l}, we define that $RC_{a_l} = P_{a_l} C_{a_l}$ from the constant functional response when $F = 0$. That is:

$$0.5P_{a_l} C_{a_l} = \alpha_{a_l} \sum_{a_r=0}^{r} D_{a_r,a_l} R_{a_r}(0) W_{a_r} \tag{3}$$

$$\alpha_{a_l} = \frac{0.5P_{a_l} C_{a_l}}{\sum_{a_r=0}^{r} D_{a_r,a_l} R_{a_r}(0) W_{a_r}} \tag{4}$$

We use this α_{a_l} as the slope of the functional response for consumption of each rockfish age class. Therefore:

$$\begin{aligned} Q_{a_r}(F) &= \sum_{a_l=0}^{l} \frac{0.5RC_{a_l,a_r} L_{a_l}(F)}{W_{a_r}} && (5) \\ &= \sum_{a_l=0}^{l} \alpha_{a_l} D_{a_r,a_l} R_{a_r}(F) L_{a_l}(F) && (6) \\ &= \sum_{a_l=0}^{l} \frac{0.5P_{a_l} C_{a_l} D_{a_r,a_l} R_{a_r}(F) L_{a_l}(F)}{\sum_{i=0}^{r} D_{i,a_l} R_i(0) W_i} && (7) \end{aligned}$$

To calculate the consumption for the plus group, age r, we use equation (3). For simplicity of notation, we define $\exp[-(M + vbF)]$ as a constant c. Then:

$$\begin{aligned} R_r(F) &= \frac{cR_{r-1}(F) - Q_{r-1}(F) - Q_r(F)}{1 - c} && (8) \\ &= \frac{cR_{r-1}(F) - Q_{r-1}(F) - R_r(F) \sum_{a_l=0}^{l} \alpha_{a_l} D_{a_r,a_l} L_{a_l}(F)}{1 - c} && (9) \end{aligned}$$

$$R_r(F) \left(\frac{1 - c + \sum_{a_l=0}^{l} \alpha_{a_l} D_{a_r,a_l} L_{a_l}(F)}{1 - c} \right) = \frac{cR_{r-1}(F) - Q_{r-1}(F)}{1 - c} \tag{10}$$

$$R_r(F) = \frac{cR_{r-1}(F) - Q_{r-1}(F)}{1 - c + \sum_{a_l=0}^{l} \alpha_{a_l} D_{a_r,a_l} L_{a_l}(F)} \tag{11}$$

B.3 Allowing a free ratio of lingcod to rockfish recruitment

We wished to test the model assumption that lingcod and rockfish have a fixed recruitment ratio. To do this, we used the previously fixed recruitment ratio as the ratio for the equilibrium unfished condition. This allowed us to calculate the two separate stock-recruit relationships, with steepness values as reported in the age-structured stock assessments (Table 1). Then, to calculate the base model under the full range of fishing mortality rates and gear selectivity efficiencies tested, we first calcuted the equilibrium lingcod age structures, which allowed us to generate vectors quantifying the consumed rockfish for each rockfish age class. (Note that for this analysis, only the constant functional response was considered.) We then iterated the rockfish population model until it stabilized, the population went extinct, or 500 iterations were reached. Results indicated a similar shape for the unfished contour, although it intersected the y-axis at a higher gear selectivity efficiency (0.24 versus 0.17), leading to a larger region where rockfish abundance exceeds unfished levels, indicating the assumption of a fixed ratio was conservative (Fig. B.2). The transient dynamics were somewhat concerning, as the population tended to crash to extinction at fishing intensities slightly above those that fell along the unfished maintenance curve. This is an artifact of the simple manner in which the two species were trophically linked in the model where lingcod do not decrease their consumption of rockfish when rockfish are at low abundances, thus extirpating rockfish populations rather easily when abundances fall below the unfished equilibrium.

Table B.1: Yelloweye female weight-at-age, from Taylor & Wetzel, 2011

Age	Female weight (kg)	Age	Female weight (kg)
0	0.01	51	4.28
1	0.11	52	4.32
2	0.16	53	4.37
3	0.21	54	4.41
4	0.27	55	4.45
5	0.34	56	4.48
6	0.41	57	4.52
7	0.49	58	4.55
8	0.58	59	4.59
9	0.67	60	4.62
10	0.76	61	4.65
11	0.86	62	4.68
12	0.96	63	4.71
13	1.07	64	4.73
14	1.17	65	4.76
15	1.28	66	4.78
16	1.39	67	4.81
17	1.50	68	4.83
18	1.61	69	4.85
19	1.72	70	4.87
20	1.83	71	4.89
21	1.94	72	4.91
22	2.05	73	4.93
23	2.16	74	4.94

24	2.26	75	4.96
25	2.37	76	4.98
26	2.47	77	4.99
27	2.57	78	5.01
28	2.67	79	5.02
29	2.77	80	5.03
30	2.86	81	5.05
31	2.95	82	5.06
32	3.04	83	5.07
33	3.13	84	5.08
34	3.21	85	5.09
35	3.29	86	5.10
36	3.37	87	5.11
37	3.45	88	5.12
38	3.52	89	5.13
39	3.59	90	5.14
40	3.66	91	5.14
41	3.73	92	5.15
42	3.79	93	5.16
43	3.86	94	5.17
44	3.92	95	5.17
45	3.97	96	5.18
46	4.03	97	5.18
47	4.08	98	5.19
48	4.14	99	5.20
49	4.19	100	5.21
50	4.23		

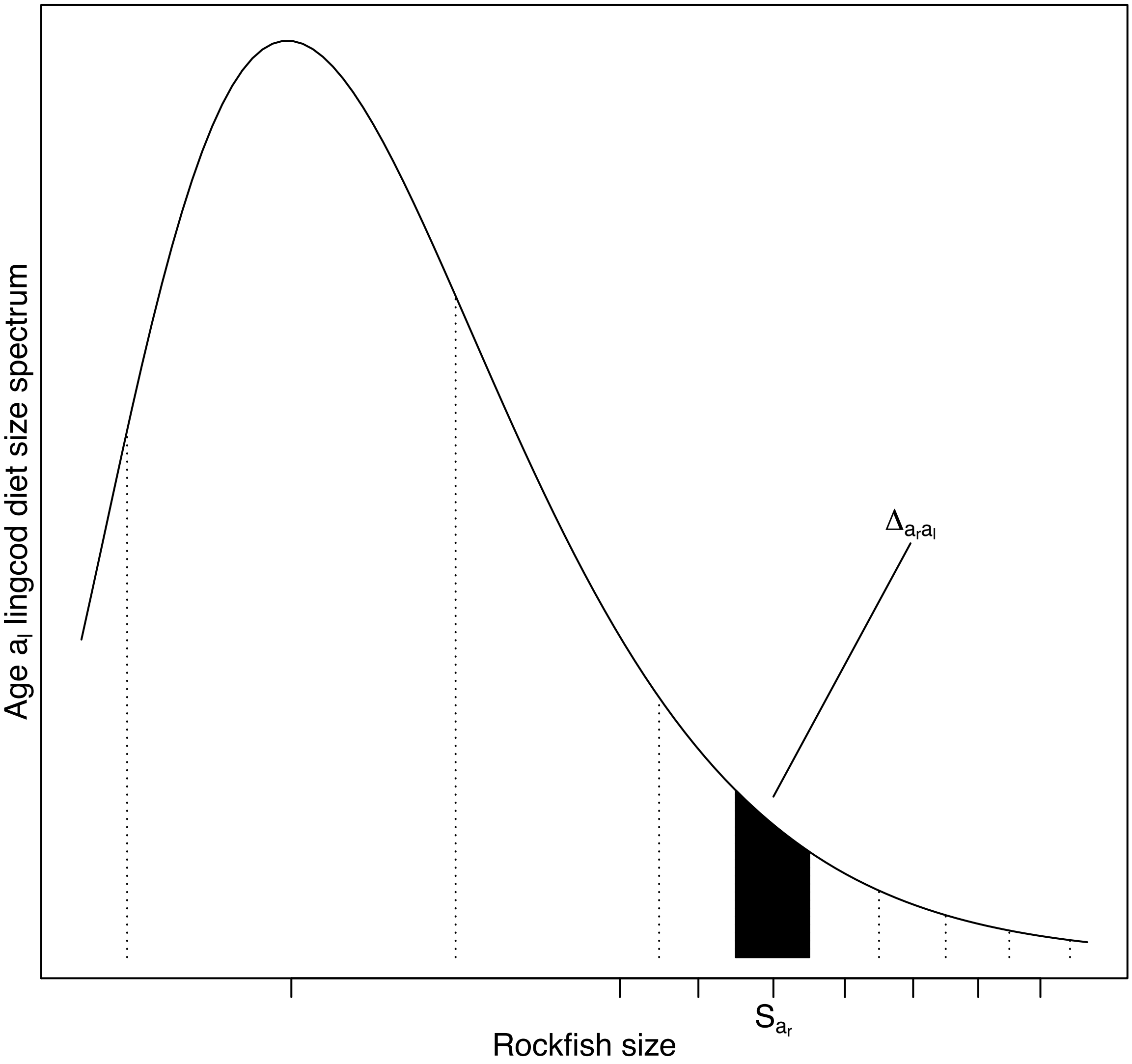


Figure B.1: Schematic of calculating the diet weights in the D matrix. Ticks represent rockfish standard lengths-at-age. Dotted vertical lines represent bin breakpoints, between which the size spectrum distribution (solid line) is integrated (e.g., black vertical slice) to calculate the initial diet weights (Δ) for each age of rockfish. The initial weights are then adjusted to calculate the actual weights, D. This process is then repeated for every length-at-age of lingcod.

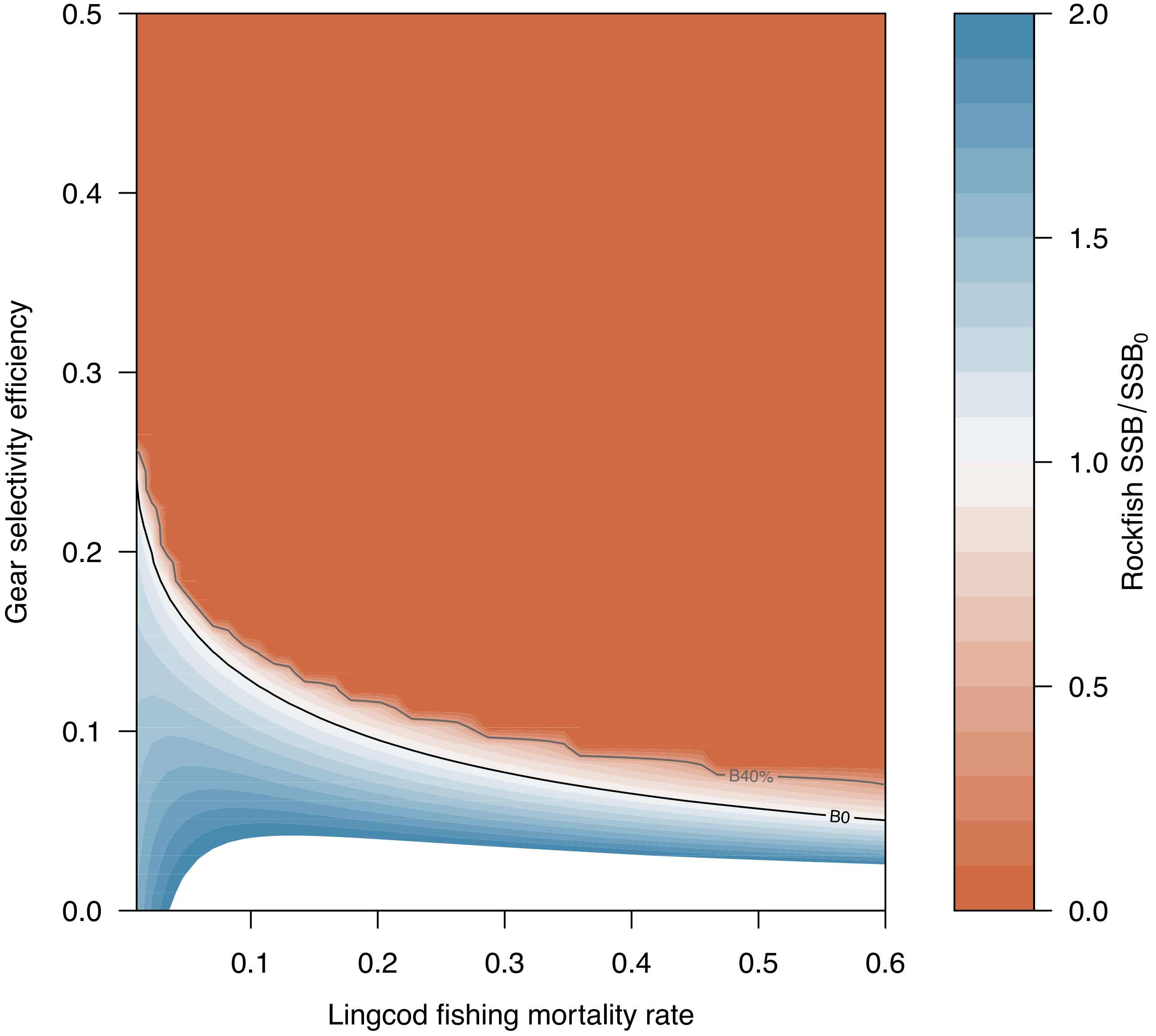
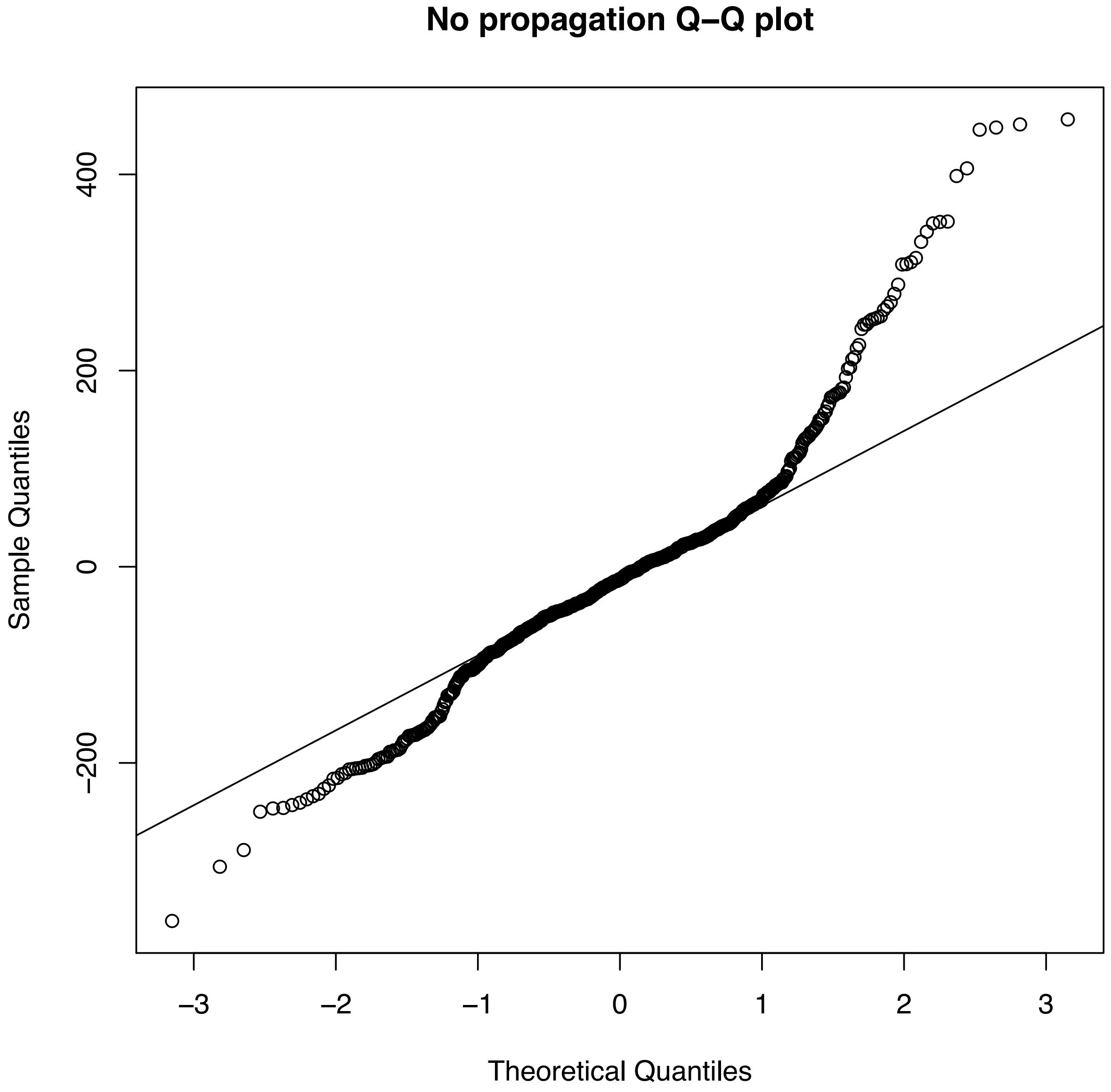
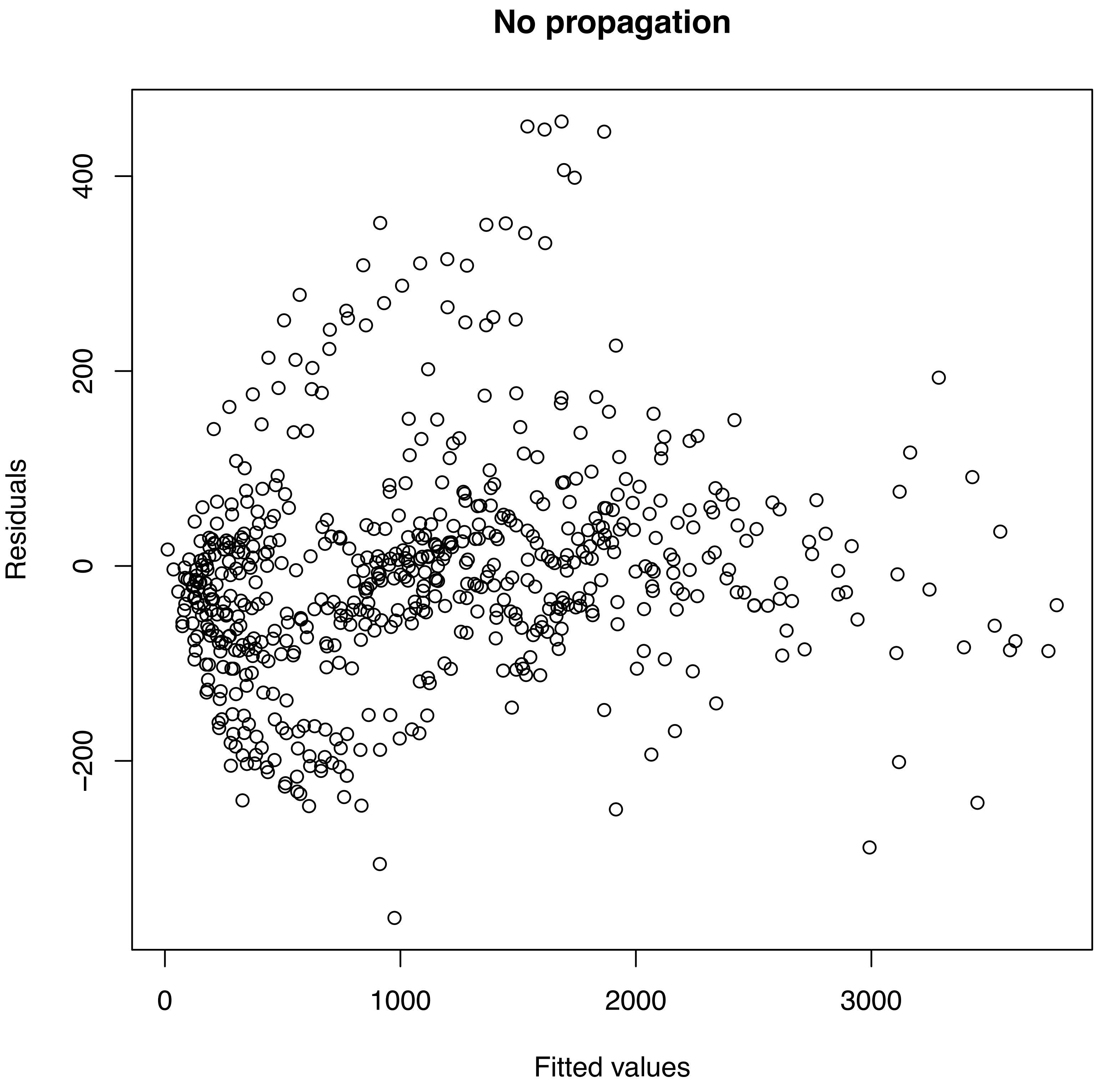


Figure B.2: Baseline scenario with unfixed lingcod:rockfish recruitment ratio. Functional response is constant and both species have Beverton-Holt stock recruit relationships (i.e., steepness < 1).

C Chapter 4

Figures C1-C8: Model diagnostics for model without any additional predictors (i.e., age only) under four different weighting schemes

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Residuals
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200
0
−200
Fitted values
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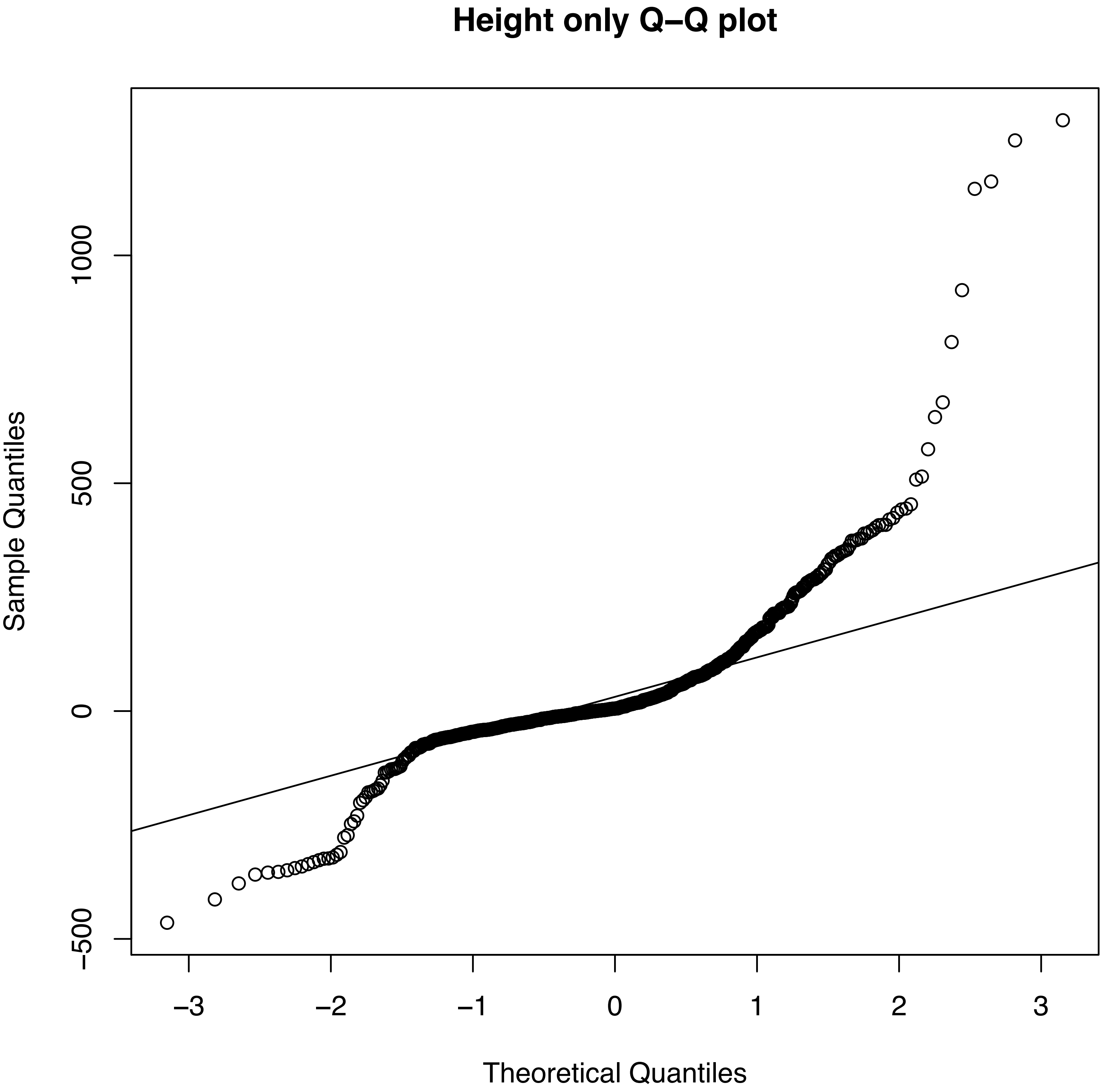
1000
2000
3000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0
500
1000
Theoretical Quantiles
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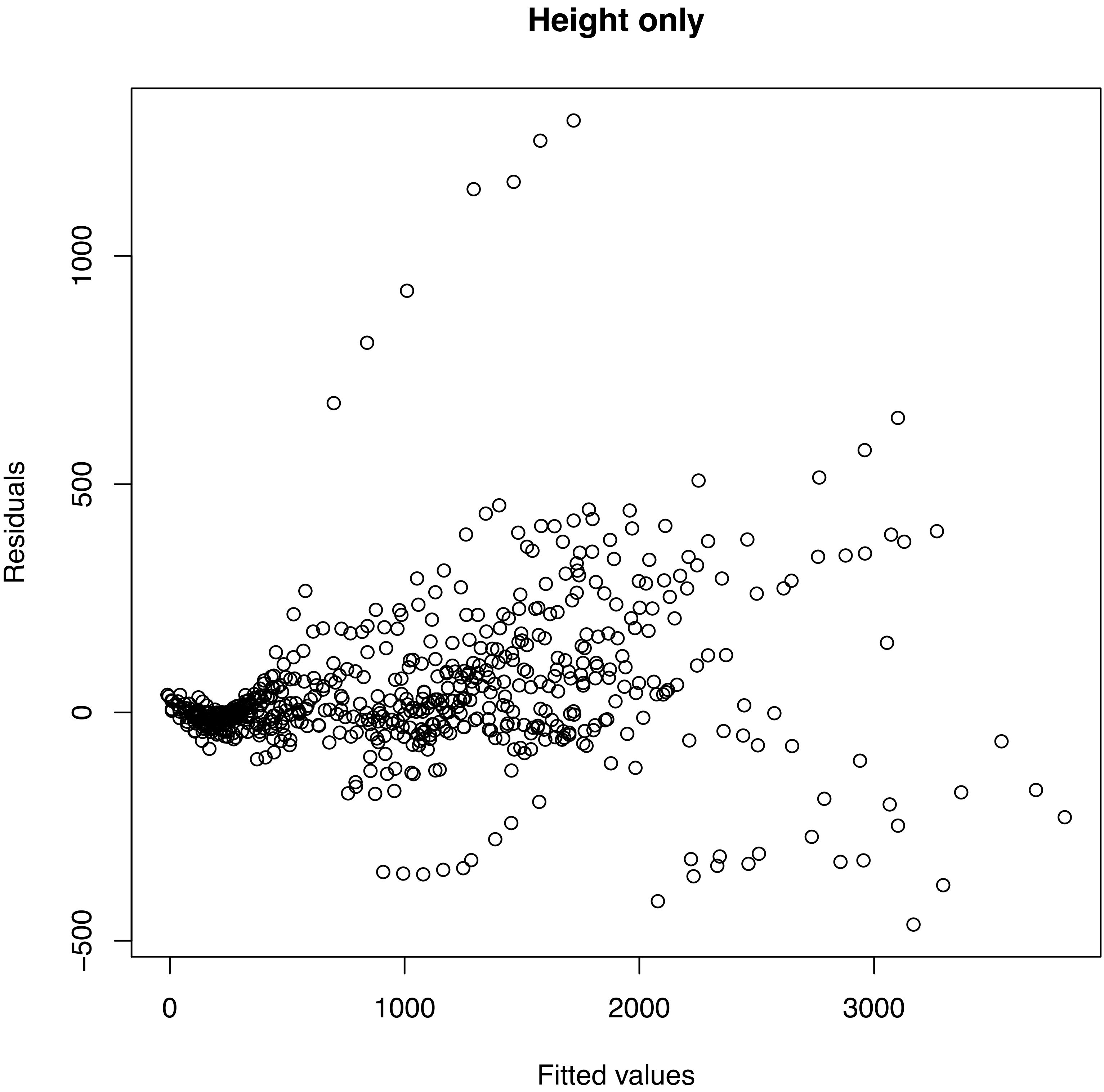
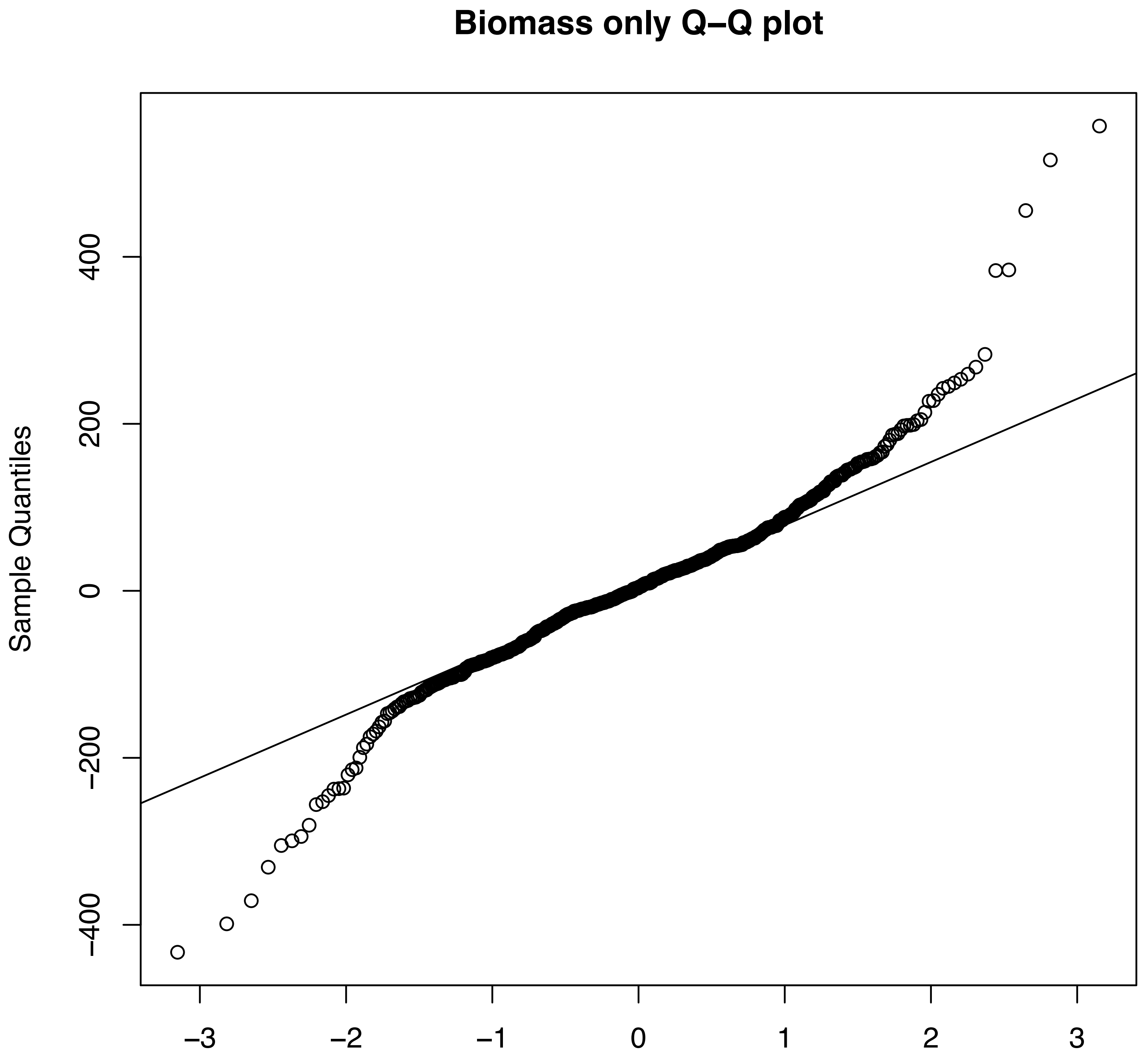
−2
−1
0
1
2
3


Height only
Residuals
Fitted values
1000
500
0
−500
0
1000
2000
3000


Biomass only Q–Q plot
Sample Quantiles
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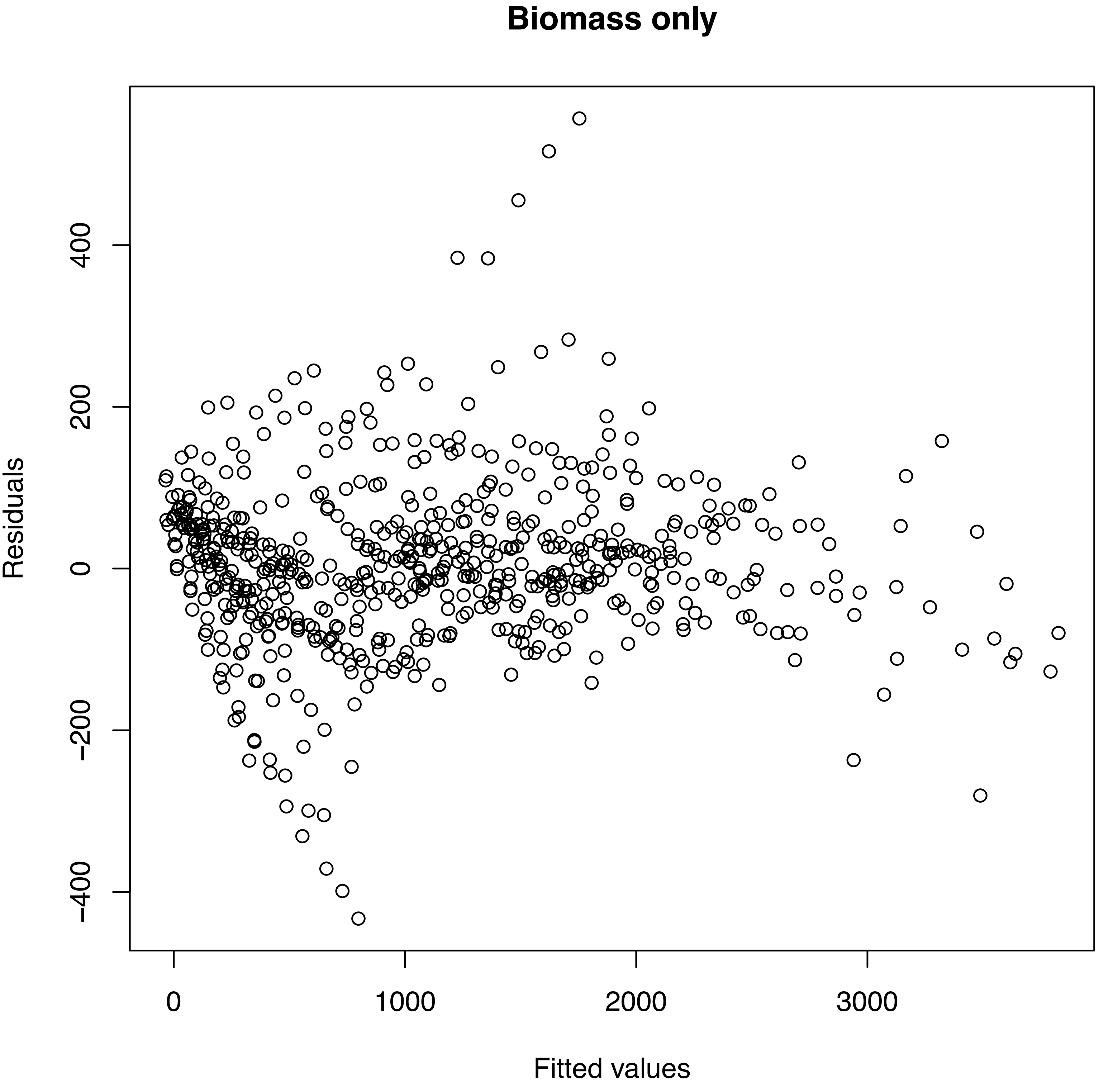
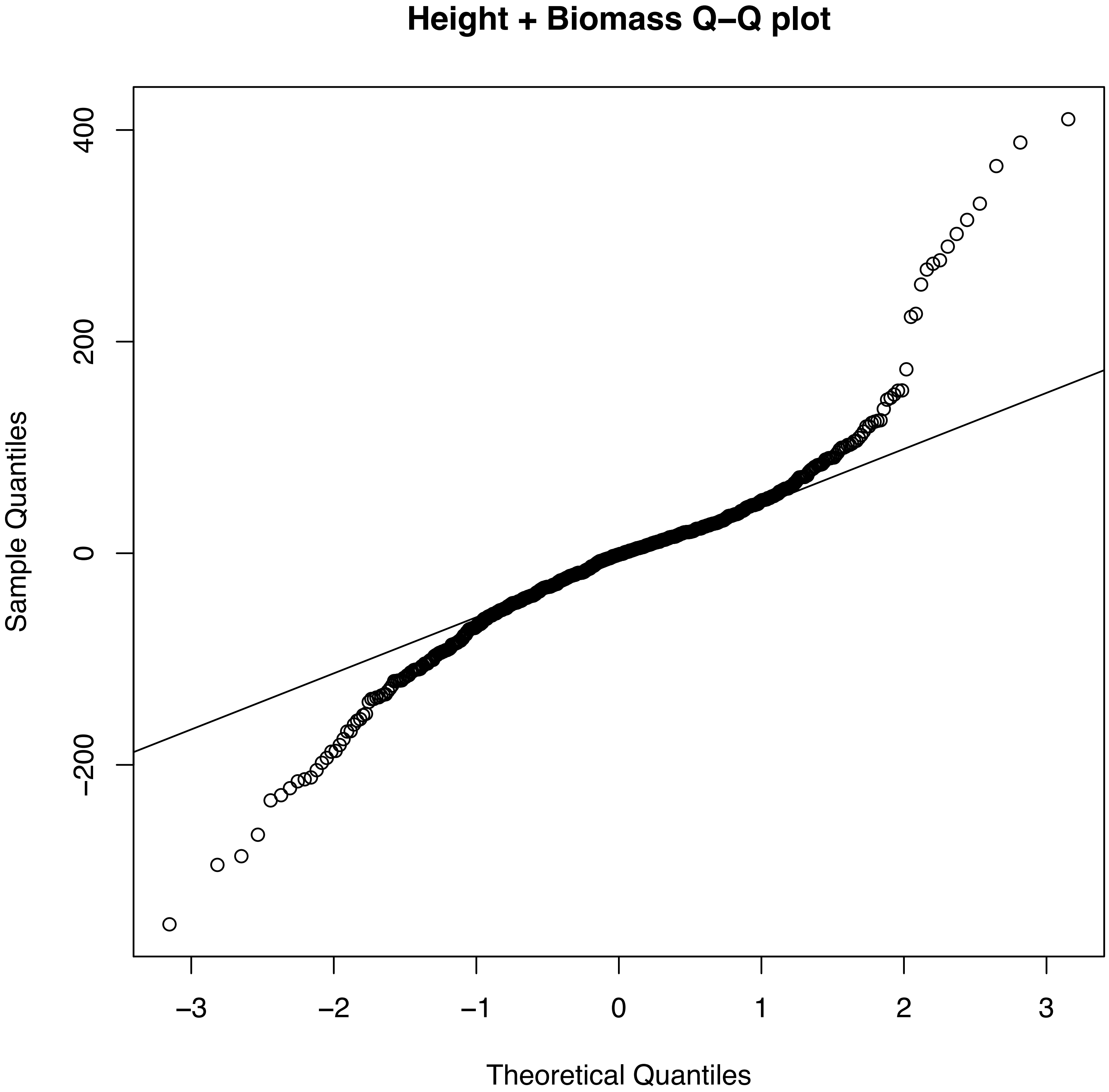
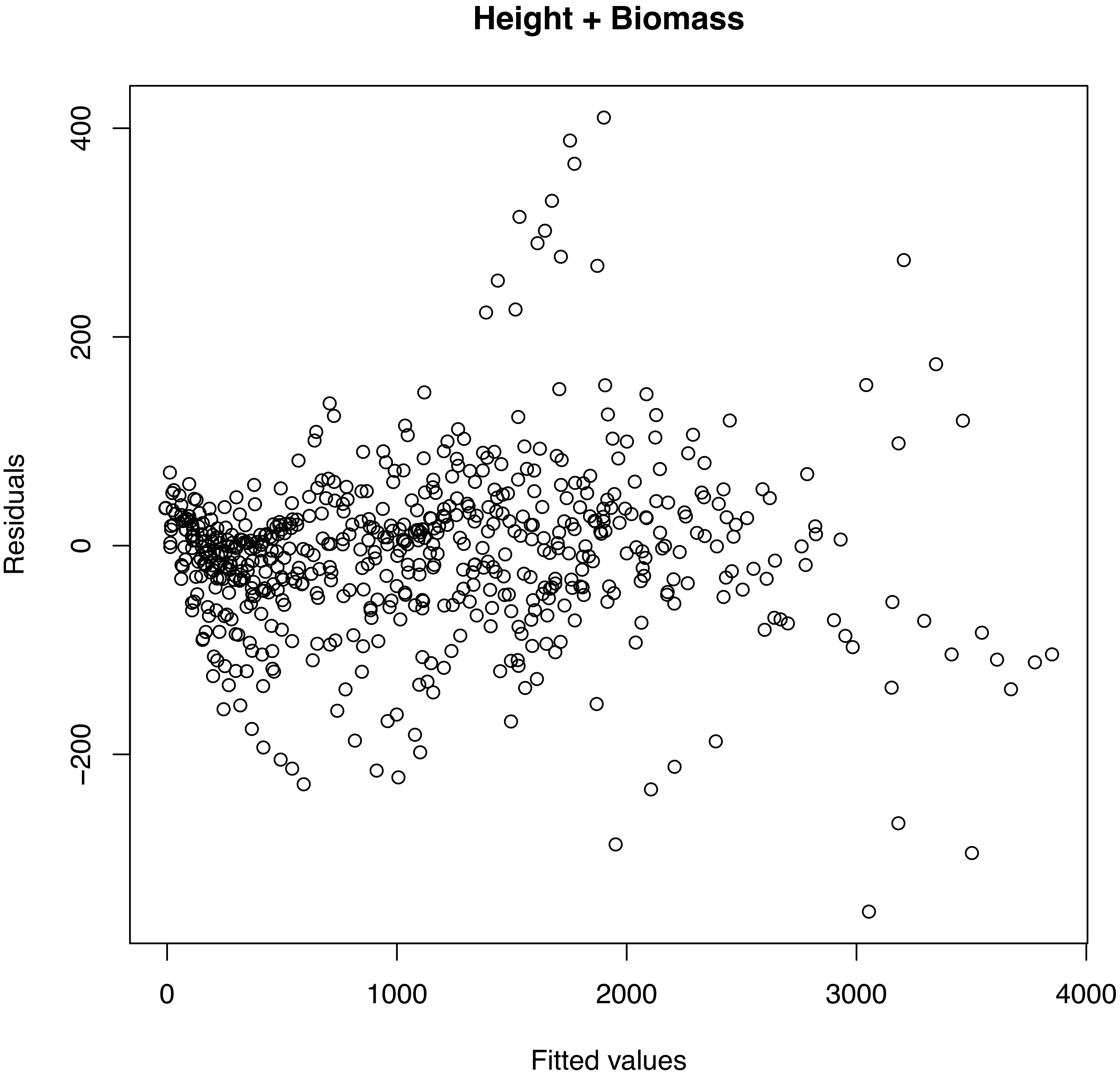
−200
0
200
400
Theoretical Quantiles
−3
−2
−1
0
1
2
3



Biomass only
Residuals
Fitted values
400
200
0
−200
−400
0
1000
2000
3000


Height + Biomass Q–Q plot
Sample Quantiles
400
200
0
−200
Theoretical Quantiles
−3
−2
−1
0
1
2
3


Height + Biomass
Residuals
Fitted values
400
200
0
−200
0
1000
2000
3000
4000

VITA

Kiva Laren Oken is originally from Portland, Oregon. She grew up fostering an early love the outdoors with frequent family trips to the Oregon coast and annual father-daughter backpacking trips. In high school, volunteering as a student leader for Portland's Outdoor School program piqued her interest the environmental sciences. She earned her undergraduate degree at Carleton College in Northfield, Minnesota in 2010, graduating Magna cum Laude and phi beta kappa, and majoring in math while also completing a concentration in environmental studies. As an undergraduate, she spent two summers doing research at Oregon State University and Woods Hole Oceanographic Institution. Prior to graduate school, Kiva earned an NSF graduate research fellowship which she used to attend the Quantitative Ecology and Resource Management program at the University of Washington in 2011. She earned her PhD in 2016. Her dissertation focused broadly on understanding and quantifying different drivers of productivity in exploited ecosystems, exploring the impact of predation in marine ecosystems, and other landscape and climatic factors in Southeast Alaska forests.