Implications of demographic diversity for forage fish, their fisheries, and ecosystems

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Abstract

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Forage fish play a key role in marine ecosystems and fisheries worldwide. They are highly productive, and undergo dramatic fluctuations in productivity, which interact with fishing pressure and spatial dynamics to generate population variability. The mechanisms and demographic processes behind this variability are poorly understood, creating a challenge for fishery managers. In this dissertation, I address the implications of demographic diversity for forage fish ecology and management. I investigate demographic diversity in space (Chapter 1) in space and time (Chapter 2), and among different forage species (Chapters 3 and 4). In the first chapter, I demonstrate that spatial diversity in a largely unfished forage fish population (Puget Sound Pacific herring; *Clupea pallasii*) can generate portfolio effects, which stabilize their availability as prey. In the second chapter, I build a hierarchical model to address the potential processes behind these portfolio effects, distinguishing temporal variation in mortality from

spatial differences, and demonstrating that adult mortality has led to age truncation and recruitment-dominated dynamics. In the third chapter, I develop an age-structured population model and use a management strategy evaluation framework to show that demographic diversity among forage fish species (specifically, for sardine, anchovy, and menhaden-like forage species) affects management outcomes and tradeoffs. In the final chapter, I use a time series approach to investigate asynchronous dynamics in sardine (*Sardinops* spp.) and anchovy (*Engraulis* spp.), and show that although these two species are often viewed as alternating members of the forage fish guild, sardine and anchovy alone do not compose a forage portfolio that buffers fisheries and food webs from dramatic shifts in productivity. These results demonstrate the rarity of asynchronous dynamics and the importance of considering, but not relying upon, demographic diversity in forage fish populations.

TABLE OF CONTENTS

List of Figures

List of Tables

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The work herein is dedicated to Susannah Kalb and Sherril Leon Soon,

two bright stars who lit my way.

INTRODUCTION

Identifying the drivers of animal abundance has been a foundational challenge in the field of ecology. Fluctuations in abundance can be linked to shifts in demographic processes like reproduction, somatic growth, and natural mortality. These processes are influenced by the environment (Fréon 1988), as well as intraspecific and interspecific interactions like competition (Ricker 1954) and predation (Polis and Holt 1992; Hixon and Carr 1997). The combined effects of environment and biological interactions on population dynamics are particularly important when species are considered as components of a complex food web, as summarized by Charles Elton (1927): “the variation in climate affects animals and plants enormously, and since these latter are in intimate contact with other species, there are produced further disturbances which may radiate outwards to a great distance in the community.” This ecological question underpins recent movements in natural resource management from single-species approaches to an ecosystem approach, which accounts for community interactions as well as environmental factors (Slocombe 1993). Thus, ecosystem-based approaches seem particularly important for species that are highly connected to food webs and the physical environment. Identifying the demographic and environmental drivers that give rise to dynamics in these species is an essential step to building realistic models that will help us understand their ecology and potential responses to management (Plagányi *et al.* 2014).

The challenges of characterizing dynamics in highly connected animal populations is exemplified by forage species– small, schooling pelagic species that remain small and schooling throughout their lives. Forage fish are crucial components of social-ecological systems worldwide. They serve as energy conduits between lower trophic level species (phytoplankton and zooplankton) and higher trophic level predators, including seabirds, mammals and commercially valuable fish species (Fréon *et al.* 2005; Pikitch *et al.* 2012). Forage species also support valuable commercial fisheries, comprising more than 30% of global landings of marine fish (Alder *et al.* 2008). Pikitch et al. (2014) estimated that catches of forage fish are worth $5.6 billion annually and the contribution of forage fish to predator fisheries is worth $11.3 billion. Finally, they are sensitive to their environment: Multidecadal-scale fluctuations in forage fish abundance (often referred to as "regimes") have been linked to changes in boundary current flow (which is associated with upwelling and sea level changes; MacCall 2002, 2009b) and global environmental processes like the El Niño-Southern Oscillation (ENSO). These environmental patterns occur at similar frequencies to fluctuations in forage fish abundance, and have been linked mechanistically to forage fish abundance in the past (see Fréon et al. 2005 and MacCall 2009 for comprehensive reviews). Because of their important role in the food web and their sensitivity to their environment, understanding the demographic features that give rise to spatial and temporal variability in their abundance will improve ecosystem-based management of forage species.

One challenge to understanding forage species dynamics is that they undergo dramatic fluctuations in productivity. Forage fish population dynamics are characterized by high-frequency variation at a local scale and low-frequency variation on at the basin or ecosystem scale. High-amplitude interannual variation in forage fish population size is often attributed to their high degree of recruitment variability, which is in turn often linked to environmental changes (e.g., Szuwalski *et al.* 2014). However, other demographic features such as forage fish behavior and predator density may affect their abundance. Forage fish behavior (MacCall *et al.* 2017) and shifts in natural mortality (Benoît *et al.* 2011) might explain some of this characteristic variation in abundance, although both of these processes have historically been difficult to study in wild populations because of difficulties with the tagging methods often used for fish populations (Hay *et al.* 2001) and the difficulty of estimating natural mortality distinctly from fishing mortality (Vetter 1988).

The need to understand variability in forage fish populations is important because fluctuations in forage fish abundance have far-reaching impacts on dependent predators. Changes in the productivity of forage fish populations can affect the abundance and breeding success of predator populations (Crawford *et al.* 2006, 2008). Low forage fish abundance has been associated with declines in seabird breeding success (e.g., Kitaysky *et al.* 1999) and sea lion pup weights (McClatchie *et al.* 2016), and declines in the abundance of other birds and marine mammals (Smith *et al.* 2011). For forage fish predators, asynchronous or independent dynamics within or between forage fish populations might reduce variability in the overall forage available to predators, providing a buffer against variation in a single subpopulation or species. The degree and extent to which buffering occurs is important for determining the overall impact of prey dynamics on predators. An overestimation of this buffering effect could lead to management strategies for forage species that are not sufficiently sensitive to predator needs, whereas an underestimation could lead to lost catches without perceptible benefits to predators. While there are hypotheses about asynchronous dynamics in some species, they have not been characterized on a global scale.

In addition to affecting predator communities, high-amplitude, low frequency variability in forage fish populations also affect the status of forage fish fisheries, which can collapse when high fishing pressure coincides with low productivity (Essington *et al.* 2015). In the past, boom-and-bust dynamics of forage fish populations have led to unexpected fishery closures and population collapses (Radovich 1981). These collapses beg the question, do the highly variable dynamics of forage species require special management? Forage fisheries have been challenged to develop harvest strategies that are robust to biological uncertainty and the ability of surveys and assessments to capture the boom-and-bust dynamics characteristic of forage fish populations (de Moor *et al.* 2011). While certain types of variability appear to be intrinsic to forage fish populations worldwide, life history differences between species indicate that different populations will not respond similarly to the same management rules: differences in growth, mortality, and age at maturity, as well as different characteristic patterns in productivity, indicate that species may require different harvest control rules to achieve fishery and ecological objectives. Despite the large degree of life history diversity within the category "forage fish," the performance of many popular "forage fish-specific" control rules has yet to be evaluated for different life history types, leaving stakeholders to debate both management priorities and basic impacts of different harvest control rules.

Here, I present four chapters that address the demographic sources of population variability in forage fish populations and the impacts of this variability on predators and fisheries that rely on them. I address demographic variation in forage fish populations at local and global scales, using a mixture of population models, time series approaches, and simulations. Chapter 1 addresses the local-scale biomass dynamics of Pacific herring in Puget Sound, and how these relate to the availability of a key forage species for predators. In Chapter 2, I use a hierarchical, age-structured model to identify how demographic variation in space and time influences herring population dynamics in the same population. Chapters 3 and 4 expand issues of demographic diversity and population dynamics to a global scale: in Chapter 3 I use a management strategy evaluation to address the importance of considering life history differences in forage fish management, and test some commonly recommended forage fish management strategies in the face of biological and estimation uncertainty. In Chapter 4, I use time series modeling and wavelet analysis to approach the longstanding question of global asynchrony between sardine and anchovy, and identify the potential for these two important forage species to perform as a portfolio.

Chapter 1. POPULATION DIVERSITY IN PACIFIC HERRING OF THE PUGET SOUND, USA[1]

ABSTRACT

Demographic, functional, or habitat diversity can confer stability upon populations via portfolio effects that integrate across multiple ecological responses and buffer against environmental impacts. The prevalence of these portfolio effects in aquatic organisms is as yet unknown, and can be difficult to quantify; however, understanding mechanisms that stabilize populations in the face of environmental change is a key concern in ecology. Here, we examine portfolio effects in Pacific herring (*Clupea pallasii*) in Puget Sound (USA) using a 40-year time series of biomass data for 19 distinct spawning population units collected via two survey types. Multivariate auto-regressive state-space (MARSS) models show independent dynamics among spawning subpopulations, suggesting that variation in herring production is partially driven by local effects at spawning grounds or during the earliest life history stages. This independence at the level of a subpopulation confers a stabilizing effect on the overall Puget Sound spawning stock, with herring being as much as 3 times more stable to environmental perturbation than a single population unit of the same size. Herring populations within Puget Sound are highly asynchronous but share a common negative growth rate and may be influenced by Pacific Decadal Oscillation (PDO). The biocomplexity in the herring stock shown here demonstrates

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that preserving spatial and demographic diversity can increase the stability of this herring population and its availability as a resource for consumers.

Introduction

A prevailing concept in ecology is the positive relationship between biodiversity and stability (MacArthur 1955; Hooper et al. 2005). Biodiversity can be manifested as genetic, habitat, life history, phenotypic or species diversity. At a community level, species-rich communities are thought to be more stable because functionally similar species can have complementary dynamics (Lehman and Tilman 2000). At a population level, genetic heterogeneity within species can dampen the variance in abundance and prevent extinction (Agashe 2009). In addition, variation in population dynamics characterized by asynchrony, weak synchrony, or independence among individual population components can cause population stability at landscape scales. The classic example is of populations that are weakly synchronous but connected by metapopulation dynamics that increase overall population stability by providing immigrant individuals to declining or "sink" patches (Hanski 1999; McQuinn 1997). Across broad spatial scales, population dynamics variability can be produced by distinct habitats that filter regional environmental processes, by variable responses to environmental conditions, and by population stochasticity (Schindler et al. 2015). Across multiple mechanisms and scales, species and population components can fluctuate independently or asynchronously from each other, thereby dampening the aggregate community or population response to perturbation. These stabilizing dynamics are referred to as portfolio effects (Schindler et al. 2010) and can serve as an organizing concept for understanding how organisms might fare in the face of future environmental change (Schindler et al. 2015).

Portfolio effects may be important for the reliability of spatially- or temporally-structured populations, and for the stability of food webs where predators exploit prey that are spatially or temporally organized (Schindler et al. 2013). Pacific herring (*Clupea pallasii*), a major forage fish species in the eastern Pacific Ocean, are food for predators across their range (around the Pacific rim from Southern California to Korea), including marine mammals (Lance and Jeffries 2006), seabirds (Schrimpf et al. 2012), and fish (Duffy *et al.* 2010; Beaudreau and Essington 2011). During the months when herring spawn in the shallow subtidal zone, their eggs are also a food source for seabirds (Anderson et al. 2009). Pacific herring also support valuable commercial fisheries: landings of Pacific herring in the United States alone were worth $19.8 million in 2012 (NMFS 2012). Because of their ecological and economic importance, and because their life history leaves them highly vulnerable to human activities (Shelton et al. 2014), maintaining the reliability of the Pacific herring resource is a high priority in marine ecosystems where they occur.

Biocomplexity (defined here as properties emerging from complex behavioral, biological and physical interactions; Michener 2001), in marine fishes is still not widely understood, though marine fishes often exhibit subpopulation spatial and demographic diversity. While fine scale genetic diversity has been demonstrated in other marine fishes (e.g., North Atlantic cod; Hutchinson et al. 2001), recent studies have also revealed that source-sink dynamics can occur within herring populations that are genetically homogeneous (Lindegren et al. 2014). These dynamics are relevant to management decisions: population diversity can occur within groups that are managed as a single stock (Casini et al. 2011), and ignoring this complexity can result in the overfishing of sensitive subpopulations and slow recovery of overfished stocks (Hutchinson 2008). Because adult herring are highly mobile, there is little reason to suspect that there is stock structure in regional population dynamics. Conversely, because there appears to be some fidelity to spawning areas (Hay et al. 2001), it is possible that differential habitat selection is strong enough to maintain subpopulation diversity (Grabowski et al. 2011). Herring populations display differences in spawning timing and behavior, producing a situation where portfolio effects have the potential to stabilize regional abundances; however, the importance of portfolio effects for stabilizing abundance of Pacific herring has not yet been quantified.

The Puget Sound, a network of coastal waters which spans from northwestern Washington State, USA, to the southwestern tip of British Columbia, Canada, is an urbanizing estuary containing at least 21 geographically-distinct spawning groups of Pacific herring (Figure 1.1); here we refer to these spatially distinct spawning groups as "subpopulations," in the sense that they are components of the Puget Sound population. We refer to hypothesized groupings of subpopulations being tested for shared population structure as "population units." These hypothesized population units are based on the work of other scholars who have defined subpopulations according to different shared characteristics, such as microsatellite markers, muscle tissue contaminants, and geography. Puget Sound herring display several characteristics of stock structure, including differences in weight and length at age, spawn location and timing, and prespawning behavior (Chapman et al. 1941). But the consequences of this diversity for the stability of the overall Puget Sound herring resource have not been quantified.

Here, we use a time-series method for describing population structure, a multivariate autoregressive state-space (MARSS) model (Hinrichsen and Holmes 2009), incorporating data from two survey methods (described below), accounting for autocorrelation in annual abundance data and variability in error rates between the two survey methods. Using 40 years of Puget Sound herring biomass data, we address the following questions:

1. What is the population structure of Puget Sound Pacific herring? How many population units exist within Puget Sound?

2. Does the population structure of Puget Sound herring confer a stabilizing portfolio effect on the population?

Last, because previous work has shown the influence of regional environmental drivers on Puget Sound herring recruitment (Reum et al. 2011), we also include regional environmental data in our model to ask:

3. Are there environmental conditions at the regional scale that explain variation in abundance across subpopulations?

METHODS

Data Collection

We studied population structure in Puget Sound Pacific herring using time series data of adult spawner biomass from historical surveys conducted by the Washington Department of Fish and Wildlife (WDFW) from 1973-2012 on 21 Pacific herring spawning grounds (Figure 1.1). Two methods have been used historically to estimate spawning biomass: spawn deposition surveys and acoustic/trawl surveys (Stick et al. 2014). Spawn deposition surveys are conducted at each spawning site throughout the spawning season. Surveyors drag a rake attached to a line along the sea floor in subtidal to lower intertidal zones, and visually, qualitatively estimate the density of eggs attached to marine vegetation or cobble. Qualitative egg density is converted to a quantitative estimate using standard conversion factors and then extrapolated to egg abundance for the full spawning site using the length of the shoreline covered by spawn and a constant width of egg deposition (Stick et al. 2014). Beaches are surveyed once weekly during their spawning season to estimate cumulative spawn deposition. Adult spawner biomass for the site is then calculated as total egg abundance divided by a constant fecundity (eggs/g adult body mass).

Spawning adults were also historically surveyed (until 2009) using ship-based acoustics in pre-spawning holding areas, where herring aggregate 1-2 months prior to spawning. Acoustic measurements of abundance from backscatter were converted to herring biomass based on size information from paired trawl catches. For the present study, we limited our analyses to data representing only sites (1) in Puget Sound; and (2) with >10 years of historical data. This resulted in a dataset of 19 sites; hereafter reference will be made only to these 19 subpopulations.

Previous efforts to describe Puget Sound herring population trends and structure have been hampered by the fact that herring are surveyed using two different methods. The two methods estimate abundance differently over space and time (Figure 1.2): egg deposition surveys take place during the spawning season, while acoustic surveys of pre-spawning aggregations occur before the onset of spawning at each site and less frequently. It is possible that egg surveys and acoustic surveys capture different processes: non-spawning herring, or spawning herring ultimately destined for other spawning grounds, may also aggregate at pre-spawning aggregation areas, whereas egg surveys are less likely to overestimate spawning biomass. Errors in acoustic surveys are likely sensitive to the timing of surveys relative to the peak of spawning activity (Schweigert and Haegele 2001), and egg surveys could be biased by estimates of total spawning area, fecundity (Hay 2011), and skewed sex ratio. Previous comparisons of the data from both methods have indicated substantial differences in biomass estimates between acoustic and egg surveys (Burton 1990).

Because previous research has shown that early life stages of herring are correlated with regional climate drivers (Reum et al. 2011), we included the intensity of coastal upwelling (NOAA Fisheries ERD Environmental Data; available upon request from *http://oceanview.pfeg.noaa.gov/erddap/search/index.html?searchFor=upwelling+index*) and the Pacific Decadal Oscillation index (PDO; see *http://jisao.washington.edu/pdo/PDO.latest*) in the model as regional covariates of herring biomass. Since each index provided monthly data, indices were averaged over winter spawning months (January-March) to obtain an annual winter mean. Regional covariate data (winter PDO and upwelling during rearing) were available for the entire time series, and we assumed they affected all 19 subpopulations. We applied lags to the regional covariates from 2 years (the minimum number of years to maturity for Pacific herring) to 7 years (the oldest age class of herring in these subpopulations, on average) to assess the impact of juvenile growth conditions on adult spawning biomass.

Modeling Approach

We used the multivariate autoregressive state-space (MARSS) framework (Hinrichsen and Holmes 2009) to model stock structure and estimate population growth parameters in Puget Sound herring, while accounting for process variability and observation error. The MARSS framework is based on the Gompertz population growth model ($x_t = bx_{t-1} + u$, in which x_t is the log of the population size at time t, b is inversely proportional to the magnitude of density dependence, and u is the rate of exponential growth or decline). The Gompertz model describes a population experiencing density-dependent growth with stochastic population dynamics (Holmes et al. 2012). The population is driven both by environmental variation and demographic variation. The Gompertz model can be elaborated to describe a multi-stock system, and the model implies that the natural log of population size can be described by an AR-1 process. The model consists of a univariate state-space model that incorporates stochasticity in population growth (process error), as well as variation in observations due to subsampling from the whole population, differences in survey methods (i.e., acoustic survey vs. egg survey), and inaccurate counting during either survey method (observation error). The univariate state-space model is then modified to accommodate count data from multiple sites, where sites may or may not represent independent subpopulations (Hinrichsen and Holmes 2009). The basic form of the model includes a process equation that describes the autoregressive process, as

$$x_t = Bx_{t-1} + u + Cc_t + w_t \qquad w_t \sim MVN(0, Q) \tag{1.1}$$

and an observation equation,

$$y_t = Zx_t + a + v_t \qquad v_t \sim MVN(0, R) \tag{1.2}$$

which describes observations of the process. In the process model (Equation 1), x_t is an $m \times 1$ vector of the natural log of biomass for each of the m population units at time t (the values of x_t are referred to as “states”). **B** is an $m \times m$ matrix whose elements are coefficients describing the degree to which each population unit reverts to a long-term mean, u is an $m \times 1$ vector of population unit growth rates, **C** is a $m \times p$ matrix of the effects of p covariates on herring biomass and c_t represents covariate observations at time t. Process error (the vector w_t) is assumed to be uncorrelated in time and drawn randomly from a multivariate normal distribution with mean zero and variance-covariance matrix **Q**. Because the Gompertz process is linear in log-space, Gaussian errors are appropriate (Ives et al. 2003). To confirm that stationarity was an adequate assumption for our models, we used Augmented Dickey-Fuller (ADF) tests on the residuals from the states of the best-fit model (Table A1). Only three of the 19 subpopulations (Kilisut Harbor, Northwest San Juan Islands, and Wollochet Bay) had non-stationary residuals from the states, so we assumed that stationarity was an adequate assumption for our models.

In the observation model (Equation 1.2), population data from the n subpopulations enter the model as y_t, an $n \times 1$ vector of observed log adult spawning herring biomass for each of n = 19 discrete WDFW-surveyed herring subpopulations in the Puget Sound at time t. **Z** is an $n \times m$ matrix of 0s and 1s that describes which observation time series are associated with each population unit, a is an $n \times 1$ vector representing the bias between the observations and the process, and observation error (v_t) is temporally uncorrelated and drawn from a multivariate normal distribution, with variance-covariance matrix **R**.

We included the influence of environmental covariates in a subset of the models tested to determine whether environmental data improved our model fit. Matrix **C** (Equation 1.1) indicates the effect of each covariate on each state ($\boldsymbol{x}_t$). We assumed that covariate data were observed without error, so covariate states are described in the process equation as c_t. This model was used to test hypotheses about stock structure, survey error, and response to environmental factors. We used the Expectation-Maximization (EM) algorithm to obtain maximum likelihood estimates of parameters (Holmes 2014). In the EM algorithm we used 2000 iterations.

Stock Structure

To determine stock structure and estimate abundance trends of Puget Sound herring, we used data from egg deposition surveys, because they were the most complete data, and fit models modified to represent different hypotheses of stock structure (Table 1.1, Table A2; Appendix A). The basic model used to detect stock structure is given by Equations (1.1) and (1.2) without the covariate terms: a is treated as a scaling parameter (the first element sets the bias to zero, and other elements are estimated relative to the first) and **B** is an identity matrix, i.e., no interactions among subpopulations. The **Z** matrix and u vector were then modified to test hypotheses about stock structure, by changing the number of m population units according to each hypothetical population structure. Different values of m correspond to different numbers of columns in the **Z** matrix; when the populations are modeled as independent, $m = n$ and **Z** is an $n \times n$ identity matrix; when there are $m < n$ hypothesized population units, **Z** has m columns. For each model, a different **Q** ($m \times m$) and u vector ($m \times 1$) were estimated.

Although there are several possible hypothesized population structures, we chose to evaluate a subset of 9 models based on the best available information. First, we tested two "null" models; one in which all subpopulations fluctuate independently (i.e., each subpopulation follows a different process, Model 1), and one in which all subpopulations represent samples from a single underlying process (Model 4). In the two "null" models, 19 separate populations were modeled as $m = 19$ (Model 1), and one panmictic population was modeled as $m = 1$ (Model 4). We also included a model where populations were independent but covariance was equal (Model 2) and one in which populations were independent but covariance was 0 (Model 8).

We also tested four models of hypothesized population structure previously suggested based on genetic data (Small et al. 2005; Model 5), contaminant signatures (West et al. 2008; Model 7), and spatial structure (Models 3 and 6; Stout et al. 2001; Penttila 2007). The genetic structure hypothesis, based on microsatellite loci, suggests three genetic units ($m = 3$): distinct units in north Puget Sound (Cherry Point) and the south Puget Sound (Squaxin Pass), and all other subpopulations aggregated into one unit (Small et al. 2005). The contaminant hypothesis states that Puget Sound herring absorb contaminants at their feeding grounds, dividing subpopulations into three ecological units (*m* = 3; West et al. 2008). West et al. found elevated levels of polychlorinated biphenyls (PCBs) and DDTs in Puget Sound herring subpopulations south of the Cherry Point stock (in bold; Figure 1.1). Semiahmoo has lower concentrations of HCBs than the other subpopulations, and is hypothesized to be a separate population unit. The third hypothesis spatially separates all herring subpopulations into three regional units (*m* = 3; Penttila 2007): North Puget Sound, South/Central Puget Sound, and Strait of Georgia. The fourth hypothesis we tested aggregates the subpopulations into the five Puget Sound basins defined by NOAA: North Puget Sound, Whidbey, Main, Hood Canal, and South Puget Sound (*m* = 5) (Model 3; Stout et al. 2001). The subpopulations belonging in each grouping are given in Table A2. Finally, we expected that covariance might differ between pairs of stocks, so we also fit a model that estimated all elements of **Q** (Model 9).

For each of the simpler hypothesized population structures (Model 1 and Models 3-8), we assumed no covariance between groups. We also compared these population structure models under conditions where covariance was allowed between groups, to make sure that assumptions about the amount of covariance were not impacting our ability to find the structure with the best supported number of subpopulations. Because only the egg survey data were used to compare the different population structure hypotheses, we assumed that observation errors (the diagonal elements of **R**) were equal across sites. For all but one model, we estimated one parameter for the process variance (the diagonal of the variance-covariance matrix, $\mathbf{Q}_{diag}$) and one parameter for covariance between stocks (the off-diagonal of **Q,** $\mathbf{Q}_{offdiag}$). We examined residuals from the best fit models to confirm normality and determine stationarity.

Portfolio Effects

Portfolio effects (PE) in ecology can be calculated simply by comparing the temporal coefficient of variation (CV) of an aggregate population with the average CV of all the subpopulations (e.g., Schindler et al. 2010). However, CV is often size-dependent in ecological systems: as the abundance of a single subpopulation grows, its standard deviation usually increases nonlinearly according to Taylor's power law (McArdle et al. 1990), so larger populations will be less variable than expected using the average-CV PE. A second method for calculating PE accounts for this by extrapolating the mean-variance relationship to the aggregate population size, which can then be compared to the observed variability of the aggregate population. The ratio of observed to predicted variance is the mean-variance PE (Anderson et al. 2013). The mean-variance portfolio effect is calculated using the following linear regression:

$$\ln({\sigma_i}^2) = \beta_0 + z \cdot \ln(\mu_i) + \varepsilon_i \qquad (1.3)$$

where $\ln(\mu_i)$ and $\ln({\sigma_i}^2)$ are the interannual log mean and log variance of the subpopulation time series (i) from the state-space model, z is the slope of the linear regression between $\ln(\mu_i)$ and $\ln({\sigma_i}^2)$ and ε is independent and identically distributed residual error with mean 0 and an estimated variance. Equation 3 is used to predict the overall variance $\hat{\sigma}^2$ expected from a homogeneous population of the aggregated subpopulations, and the ratio of observed σ^2 to predicted $\hat{\sigma}^2$ is the mean-variance PE. PE can only be quantified when the population size is known at each time step, which is rare in long-term ecological time series. Therefore, we used

MARSS model fits from the best-fit stock structure model for each population unit as the basis for PE calculation.

We used Spearman's rank correlation to determine the strength of covariance between subpopulations, and evaluated community-wide synchrony using the index proposed by Loreau and de Mazancourt (2008):

$$\varphi_N = \frac{{\sigma_{NT}}^2}{(\sum_i \sigma_{N_i})^2} \tag{1.4}$$

where ${\sigma_{NT}}^2$ is the aggregate variance of the total biomass across all subpopulations and σ_{N_i} is the standard deviation of the biomass of each subpopulation i. This "synchrony index" varies between 0 (perfect asynchrony) and 1 (perfect synchrony). Average-CV and mean-variance PE, and synchrony index were calculated using the *ecofolio* package in R (Anderson et al. 2013).

Comparison of Survey Methods

To compare the effectiveness of each herring survey method for estimating adult spawner biomass, we modeled four potential scenarios:

1) Egg and acoustic surveys measure the same process, and observation error for each survey type does not vary by site;

2) Egg and acoustic surveys measure different processes, and observation error for each survey type does not vary by site;

3) Egg and acoustic surveys measure the same process, and observation error magnitude varies by site;

4) Egg and acoustic surveys measure different processes, and observation error magnitude varies by site;

The structure of the **Q**, **R**, **Z**, and **B** matrices were modified to test hypotheses about the process (or processes) captured by each survey type, and the error of each survey type in measuring those. Model structures tested here were informed by the best fit stock structure model: beaches were assumed to be independent and have similar process variances. We used different structures of **Q**, **R**, **Z**, and **B** to test the error associated with each survey type in estimating the underlying state process for each population unit. When comparing egg and acoustic/trawl survey data, we assumed that population growth trends (u) and process variance (Q_{diag}) were equal, and that there was no process error covariance ($Q_{offdiag} = 0$).

Environmental Effects on Herring Abundance

To test for environmental drivers of herring abundance trends, beginning with the best-fit stock structure model from the Stock Structure section (19 independent population units; referred to here as the "null model"), we added environmental data (the "full model"; data descriptions below) to see if they improved model fits of biomass time series data: regional environmental conditions (PDO and/or upwelling). If covariates explained variation in biomass, we considered the full model a better fit to the biomass data than the null model.

For regional covariates, the null model (herring biomass only) was compared to models that included PDO, upwelling, and PDO + upwelling. The spawning biomass in any given year is composed of individuals aged 2 and older; therefore the impact of regional environmental factors on spawning biomass includes impacts on eggs and larvae on spawning grounds, and impacts on adult fish in the open ocean during that year.

Model Selection

Akaike's Information Criterion (AIC) is often used to compare the difference in likelihood between an estimated model relative to the distribution of possible data from a true (unknown) process. AIC_c can underestimate the complexity penalty for MARSS models when datasets are small, favoring more complex models (Ward et al. 2010). AIC calculations include a likelihood term and a penalty for model complexity, which can be estimated using bootstrapping (AIC_b; Cavanaugh and Shumway 1997) or Monte Carlo simulation. In order to properly penalize for the number of parameters estimated and compare models with different Z matrices, we used a bootstrap AIC (AIC_b; Hinrichsen and Holmes 2009) which is designed for state space models and has been used in previous studies to compare state-space models with different Z matrices (e.g., Hinrichsen and Holmes 2009, Ward 2010). This calculation uses bootstrapping to estimate the penalty term for the number of parameters used. Models with different Z matrices do not contain different data; Z is a design matrix that specifies the relationship between the biomass time series and the hypothesized subpopulations to which they belong.

RESULTS

Synchrony, Stock Structure and Portfolio Effects

MARSS model fits indicated that that there are 19 population units of herring within Puget Sound, which behave independently (Table 1.1; Figure 1.3). The best-fit model for herring stock structure described Puget Sound herring as consisting of 19 independent population units, (i.e., **Z** was identity and m = 19), with an overall negative growth rate u (u = -0.01; 95% confidence interval (-0.03, 0.01)). Genetic, contaminant, regional, and NOAA basin population unit designations did not fit biomass time series as closely, based on AIC_b scores (Table 1).

Process variability, which was also shared by different population units, was *very large* compared to the negative deterministic trend: process variance Q_{diag} = 0.09 (0.04, 0.10) (s.d. = 0.3). The preferred model estimated no covariance across all sites ($Q_{offdiag}$ = 0), meaning that while the population units fluctuate at similar magnitudes each year (based on the Q_{diag}), they do not covary. In this analysis, because the covariance $Q_{offdiag}$ is set to the same value across all pairs of population units, it is impossible to tell whether covariance is low across all population units or whether there is covariance among some population units and not others. A model that estimated different deterministic trends (*u*) for each population unit did not improve the model fit (Model 8, Table 1.1). A model that estimated individual variance and all pairwise covariances (Model 9; Table 1.1) did not improve the model fit (variance-covariance matrix in ESM Table S3). Observation error for egg survey estimates of biomass was R_{diag} = 0.25 (0.21, 0.31). Residuals from the best-fit model appeared normal and uncorrelated.

Synchrony between population units was relatively low (Loreau and de Mazencourt synchrony index = 0.23, where 1 is a completely synchronous population and 0 is completely asynchronous; Figure 1.4). Correlations between population units were highly variable and were not dependent on geographical distance (Figure 1.4; Mantel test p = 0.69). Negative correlations were strongest between population units that were “recovering” (i.e., biomass was increasing; Holmes Harbor, Quilcene Bay, Samish/Portage Bay, and Squaxin Pass) and all other population units. The mean-variance PE calculated for Puget Sound herring was 1.92 (1.06, 3.45), meaning that the aggregate population (CV = 0.30) is 1.06 – 3.45 times more stable than one would expect from a homogeneous population with the same total biomass as the Puget Sound-wide herring metapopulation (expected CV = 0.59; Figure 1.5).

Comparison of Survey Methods

There was strong support for the hypothesis that eggs and acoustic surveys measure the same process. In comparisons of egg deposition surveys versus acoustic/trawl surveys, the best-supported model ($\Delta_{AICb} = 0$) included identical underlying processes measured by both egg and acoustic surveys (Table 1.2). There was little support for the hypothesis that eggs and acoustic surveys measure different processes, even when observation error was allowed to vary by spawning site. In the best-fit model, the observation error from egg surveys ($R_{egg\ avg} = 0.31$) was lower than the observation error from acoustic surveys ($R_{acoustics\ avg} = 0.82$).

There was also some support for the hypothesis that the two survey types vary in their accuracy depending on the beach. Survey error rates varied by beach and method; measurement error was consistently higher for biomass estimates from acoustic surveys, but was significantly higher at Semiahmoo Bay, Skagit Bay, and Quartermaster Harbor (Figure 1.6).

Effects of Regional Environmental Covariates

The inclusion of PDO as a covariate marginally improved model fits of population dynamics. The best fit model included PDO as a covariate ($\Delta_{AICb} = 0$), with an estimated coefficient of -0.0024 (-0.0042, -0.0006). Including both PDO and upwelling as covariates did not improve model fits ($\Delta_{AICb} = 2.94$). This relationship was largely the same when different lags were applied to PDO and upwelling: regardless of the lag used to relate biomass to covariates, herring-only models or models including PDO as a covariate were always best fit to biomass dynamics.

DISCUSSION

Spatially distinct population dynamics can be stabilizing for fish species, but they are difficult to measure in pelagic stocks. Multivariate state-space models provide an opportunity to use data from diverse sources to elucidate the underlying population dynamics of a dominant forage fish. Our analyses show that spatial and temporal diversity in subpopulations of Puget Sound herring produces stability in the overall population. We found a common basin-wide trend in growth, with independence among subpopulations at a fine spatial scale, suggesting that drivers at multiple scales influence Puget Sound herring dynamics. This matches what is known about their life history, which includes life stages that are tightly linked to both shorelines and pelagic environments. We show here that though herring subpopulations have similar growth rates and variability, they exhibit independent dynamics within Puget Sound. This independence could result from multiple, unknown, local processes, differences in local responses to broader scale processes, movement, or stochasticity. This complexity is ultimately an advantage, because according to our analysis, it confers a degree of stability on the Puget Sound herring resource. Our results suggest that common oceanographic processes are not strong drivers of herring biomass. Furthermore, portfolio effects may be an effective way to describe emergent dynamics in the absence of a good mechanistic population model.

Portfolio Effects, Asynchrony and Stock Structure

The independence we measured among Puget Sound spawning subpopulations has a stabilizing effect on the total Puget Sound herring population. The portfolio analysis indicated that the aggregate population is 1.1 – 3.5 times more stable than a single population of the same size (Figure 1.5). Portfolio effects can arise from a variety of mechanisms, including stochasticity, interactions among populations as in a metapopulation, and habitat-mediated or population-level variability in responses to environmental drivers (Schindler et al. 2015). Whether the portfolio effect observed here is due to genetic or environmental differences is unknown, but may be elucidated by examining differences in demographic rates between population units (Thorson et al. 2014). Regardless of the source of differences among subpopulations, our results suggest that it is important to preserve multiple spawning sites to ensure stable dynamics for Puget Sound herring and the ecosystem services they provide. Particularly for forage fish species, which demonstrate wide fluctuations in abundance, retaining some stability may be critically important for these populations' long-term prospects. Furthermore, retaining the availability of herring as a resource across a broad geographic range ensures that local drivers of decline or extinction do not cascade throughout a food web containing mobile predators that rely upon herring for prey.

In most biological systems, perfect synchrony among population components is rare. Instead, populations are often weakly synchronous to asynchronous and statistical averaging causes aggregated populations to have a lower variance. Thus, portfolio effects greater than zero are, to some extent, statistically inevitable. This statistical averaging has been used in the past to explain some of the diversity-stability relationships observed in nature (Doak et al. 1998). The properties of biological communities are also scale-dependent; communities are known to be highly variable at some scales and less variable at others (Levin 1992). However, the combination of independent population dynamics and multiple spawning subpopulations overall contribute to a more stable herring population, which is of primary importance for a resource such as a forage fish that is heavily relied upon across the ecosystem.

Even though process variance was similar across stocks, the best fit model here indicated that each egg survey time series measures a different subpopulation trajectory, suggesting that herring fluctuations vary at the local spawning site scale: good and bad years are not the same across subpopulations. The shared process variance for all subpopulations (Q_{diag} = 0.09 (0.04, 0.10)) and the absence of covariance ($Q_{offdiag}$ = 0) in the best model show that the magnitude of variability in biomass is similar throughout the Puget Sound, but that there is very little covariance between these population units, confirming the independence indicated by the MARSS model fitting exercise. The large magnitude of variance (Q_{diag}) relative to the deterministic growth trend *u* (-0.01 (-0.03, 0.01)) suggests that variability is an important component of herring biomass dynamics, and this variability is probably the largest contributor to the observed dynamics. This matches what is observed in forage fish populations globally.

There are at least two ways to measure portfolio effects from the biomass time series estimated by a MARSS model. Here, we measured PEs from the states estimated by the best-fit stock structure model. A second method involves estimating the full variance-covariance (Q) matrix, whose elements describe variability at each site and covariance between sites (Table A3). Negative covariance in the off-diagonal elements of the Q matrix in this case would indicate asynchrony between the corresponding subpopulations, and 0 covariance elements would indicate independent dynamics. Any covariance less than unity between population components could lead to a portfolio effect. Using this method also resulted in portfolio-type effects, albeit with marginally weaker estimates of interannual variability (CV = 0.28 versus 0.30) and synchrony (synchrony index = 0.16 versus 0.23), with a wider confidence interval for the portfolio effect (mean-variance PE = 1.55 (0.95, 2.53)). Regardless of method used, we found evidence of a portfolio effect in Puget Sound herring, and estimated values similar to, or larger than, PEs found in other animal populations (ranging from 0.5 to 2.0 in an empirical meta-analysis; Anderson et al. 2013). We also found that the effect was weaker (PE = 1.35 (0.732, 2.509) for the latter 20 years of our dataset than for the first 20 years (PE = 3.04 (1.678, 5.508)), and that the latter 20 years of the dataset are also more synchronous (synchrony = 0.18 versus 0.05). Although this difference is not statistically significant, it suggests that the stability of the Puget Sound herring population has changed over time.

The model selection procedure used here provides little conclusive evidence for portfolio effects arising from consistent movements between populations, such as in a metapopulation, versus those arising from independence among subpopulations. Both PE methods and the best fit MARSS model show little to no covariance among subpopulations in their biomass trends. Furthermore, we found little synchrony among subpopulations, and variable and inconsistent correlations between subpopulation pairs, all of which suggest independence among subpopulations as the source of the portfolio effect. However, it is possible for these same results to arise from movement of individuals between subpopulations, and previous work has shown that Pacific herring can change spawning beaches between years. For example, Pacific herring in British Columbia have site fidelity rates estimated between 75-96% by studies of tagged adults (Ware and Schweigert 2001). However, the tendency to return to a specific geographical area is scale-dependent and Pacific herring in British Columbia returned more often to larger geographic areas (areas must be ≥ 500 km^2 to support high fidelity; Hay et al. 2001). It is possible that the population trends estimated by the MARSS model, and variation around those trends, are associated with movement by herring among different spawning areas from year to year. If spawners consistently move between neighboring beaches, then we would expect to see negative correlations between neighboring beaches (long-term negative correlations between neighboring beaches; Figure 1.4) or negative covariance between beaches (year-to-year movements; Table A3). However, we found strong evidence for neither of these cases. While current genetic evidence shows that the bulk of the Puget Sound population units are more related to each other than to Squaxin Pass and Cherry Point, within that aggregate there is likely fine-scaled genetic structure that could identify patterns of homing, fidelity and movement. Future research to quantify the relatedness among Puget Sound herring population units will help elucidate the likely causes of observed population trends.

Stock identification is a top priority for fisheries and may benefit from the use of diverse methods. Herring stock structure is often defined on large geographical scales (e.g., across the British Columbia coast), or with the use of genetic and/or distance-based stock designations. Previous efforts to describe Puget Sound herring stock structure have hypothesized diversity in the stock based upon genetic data, spatial structure, and organic pollutants. Here, we were able to test how well these hypotheses describe biomass dynamics using MARSS models fitted to biomass data. Those tests returned the strongest support for the most fine-scale stock structure, i.e., 19 independent Puget Sound herring population units. Genetic, contaminant, and basin-wide models for population structure were poorer fits for biomass time series, suggesting that Puget Sound herring population units fluctuate at a finer scale than previously thought. We confirmed that our model selection process was capable of identifying population structure (shared dynamics between subpopulations) with time series data similar to those used here for Puget Sound herring using a simulation exercise (see Appendix S4).

This analysis suggests that at the scale of Puget Sound, herring biomass is relatively stable, but decreasing (Figure 1.3). The 95% confidence interval for the estimated trend spanned 0 (growth rate u = -0.01 (-0.03, 0.01)). The weak trend likely results from the fact that population units are fluctuating independently overall and many show opposite trends. Indeed, some subpopulations – including those at Holmes Harbor, Quilcene Bay, Samish Island/Portage Bay, and Squaxin Pass – show increasing trends, but the rest are declining. The Puget Sound-wide growth rate fitted here demonstrates the diversity in growth rates among stocks, while the variance-covariance matrix demonstrates diversity in year-to-year variation. Observation error (R_{diag}) for surveys within Puget Sound is larger than process error (Q_{diag}), meaning that observed abundance patterns in the raw survey data are not the best descriptors of population size and variability. Although the overall biomass trend is not significantly declining, the detection of a portfolio effect indicates that the number of population units is important for stability, and that efforts to prevent local extinctions are likely important for maintaining this stability.

Differences between Survey Methods

One advantage of the state-space modeling approach is that multiple data sources are used to estimate the same underlying demographic process. In doing so, we are also able to compare the accuracy of each monitoring tool in describing the underlying demographic processes, and potentially offer guidance for resource managers. In addition to providing the best support yet for Puget Sound herring population structure, the present analysis points to the use of estimated time series from an autoregressive model as a more accurate reflection of underlying states than using simple long-term means or interpolation.

We found that both herring biomass survey methods estimated the same underlying process, i.e., a decreasing but non-significant trend in the aggregate herring population. However, the two methods varied in their error rates, with egg deposition surveys having higher accuracy ($R_{egg\ avg} = 0.31$) than acoustic surveys on spawning aggregations ($R_{acoustics\ avg} = 0.82$).

Additionally, survey error rates varied by spawning site and method (Figure 1.6). This suggests that although egg surveys are more reliable overall, there may be individual sites where one survey type is more important for capturing underlying biomass trends. For example, acoustic/trawl surveys are likely more accurate at sites with rocky substrate because rake surveys undersample spawn-on-gravel. Our results match observations by local biologists: in general, the spawning sites where our model struggled to estimate herring biomass using the egg survey data matched the set of sites identified by WDFW biologists as being less amenable to egg surveys; likewise, with the acoustic survey method and estimates (K. Stick, *pers. comm.*). At present, herring are surveyed using only the egg deposition surveys, which our model identified as being the more accurate survey method, although acoustic surveys may still be useful for gathering non-biomass data relevant to life history and stock assessment.

Environmental Effects on Herring Biomass

This complex picture of Pacific herring populations – evidence for both a shared trend and independence – may be the result of herring responding to their environment at multiple scales. The common growth suggests that herring respond synchronously to shared broad-scale drivers. Despite this result and previous results linking herring abundance to environmental drivers, however, we found that regional environmental covariates were only minimally important in describing shifts in herring adult spawner biomass. Previous research by Reum et al. (2011) showed that cumulative coastal upwelling positively influences the stock recruitment of Skagit Bay herring, but we found no Puget Sound-wide effect of upwelling. Herring recruitment in the Gulf of Alaska responds strongly to winter atmospheric pressure (Zebdi and Collie 1995) and we detected a minor effect of PDO on herring spawning biomass. Shifts in PDO have been associated with changes in zooplankton range and total biomass in the northeast Pacific, with years of negative PDO resulting in decreases in the biomass of zooplankton on the West Coast (Hare et al. 1999). The effect we estimated here (-0.0024 (-0.0042, -0.0006)) may be weak because oceanic influences vary across space within Puget Sound, masking regional influences. For example, the Skagit River is closer to the Strait of Juan de Fuca whereas herring spawning in central or southern Puget Sound may be less exposed to oceanic dynamics such as upwelling. It is likely that both local and regional environmental conditions interact to influence herring abundance, and future evaluations of environmental influences on herring should include subpopulations for which both recruitment and local and regional environmental data are available.

Although we find very limited model support for covariate effects, our analyses are not exhaustive and other potential influences on abundance time series should be considered. Potential influences on herring biomass not considered here include predation, disease, spawning ground habitat availability, and a zooplankton food source that may not be linearly related to any of the covariate data tested here. For example, Puget Sound harbor seal populations have increased in recent decades, and their intense predation on herring may reduce subpopulations size, regionally or locally. Loss of nearshore habitat associated with urbanization may also impact the population at local and regional scales. These other potential influences on herring warrant future exploration.

Our results demonstrate the importance of spatial scale and subpopulation diversity in the dynamics of Puget Sound herring, and that this diversity across a broad landscape confers stability upon the aggregate herring resource. The mechanisms behind these independent dynamics were not revealed by the present analysis, and warrant future research. Because of the critical role Pacific herring play in the Puget Sound food web, and the associated importance of maintaining long-term stability in the population, resource managers and land-use planners would do well to consider the important role played by maintaining a diversity of spawning habitats in the Puget Sound, rather than focusing on a few highly productive sites.

Table 1.1. Structure and ranking of time series models.

Structure and ranking of MARSS models fitted to Pacific herring biomass time series data in the Puget Sound. For all models, process variance and observation error are equal across sites. Observation error is not correlated between sites ($R_{offdiag} = 0$). The first column indicates the way observation time series were assigned to process time series. For more detailed descriptions of model structure, see Appendix A.

Model	**Hypothesized population structure**	**Number of population units (m)**	**Covariance (Q$_{offdiag}$)**	**Δ_{AICc}**	**Δ_{AICb}**	**Relative likelihood**
1	**Each subpopulation separate (no covariance)**	**19**	**0**	**2.6**	**0.0**	**1**
2	Each subpopulation separate (covariance is equal)	19	equal	0.0	71.6	2.82 E -16
3	Basins	5	0	185.7	178.8	4.69 E -41
4	All one population (panmictic)	1	0	198.0	365.0	9.65 E -44
5	Microsatellites (Cherry Point, Squaxin, and all others)	3	0	168.8	378.7	2.20 E -37
6	Regions (North Puget Sound, South/Central Puget Sound, Straits)	3	0	199.2	393.8	5.28 E -44
7	Contaminants (Cherry Point, Semiahmoo, all others)	3	0	181.5	446.4	3.75 E -40
8	Each subpopulation separate with different trends (different trends, no covariance)	19	0	20.9	1363.8	2.82 E -05
9	Each subpopulation separate with different trends, different variance and covariance for each subpopulation	19	All different (all elements of Q estimated)	515.7	28468.9	0.000

Table 1.2 Model ranking and fits for hypotheses of different survey error structure.

Hypothesis	**ΔAIC_c**	**ΔAIC_b**
Eggs and acoustics measure the same process, observation error varies by subpopulation	**0**	**0**
Eggs and acoustics measure the same process, observation error has same magnitude in each subpopulation	79.6	22.7
Eggs and acoustics measure different processes, observation error varies by subpopulation	42.8	144.7
Eggs and acoustics measure different processes, observation error has same magnitude in each subpopulation	121.0	626.1

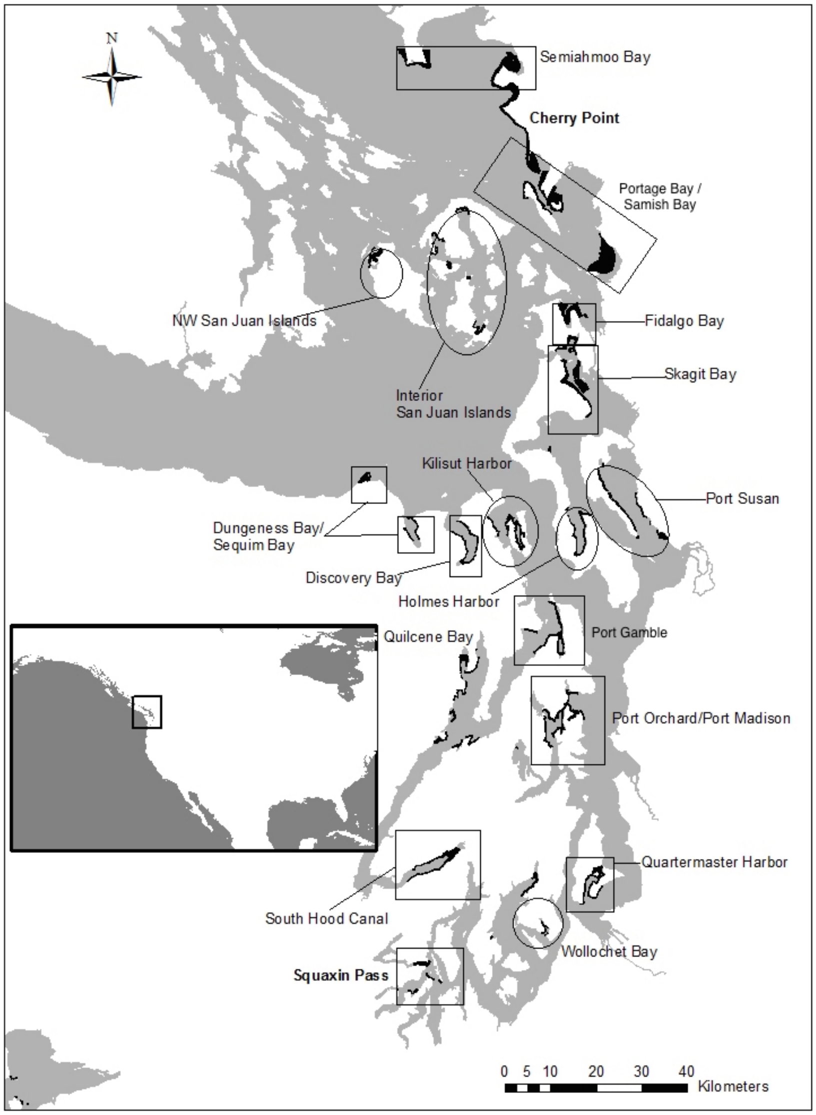

Figure 1.1: Map of Pacific herring spawning sites.

Pacific herring (*Clupea pallasii*) spawning sites in Puget Sound (black shaded areas). Cherry Point, Semiahmoo, and Squaxin Pass are often designated as separate subpopulations from the rest of the Puget Sound populations.

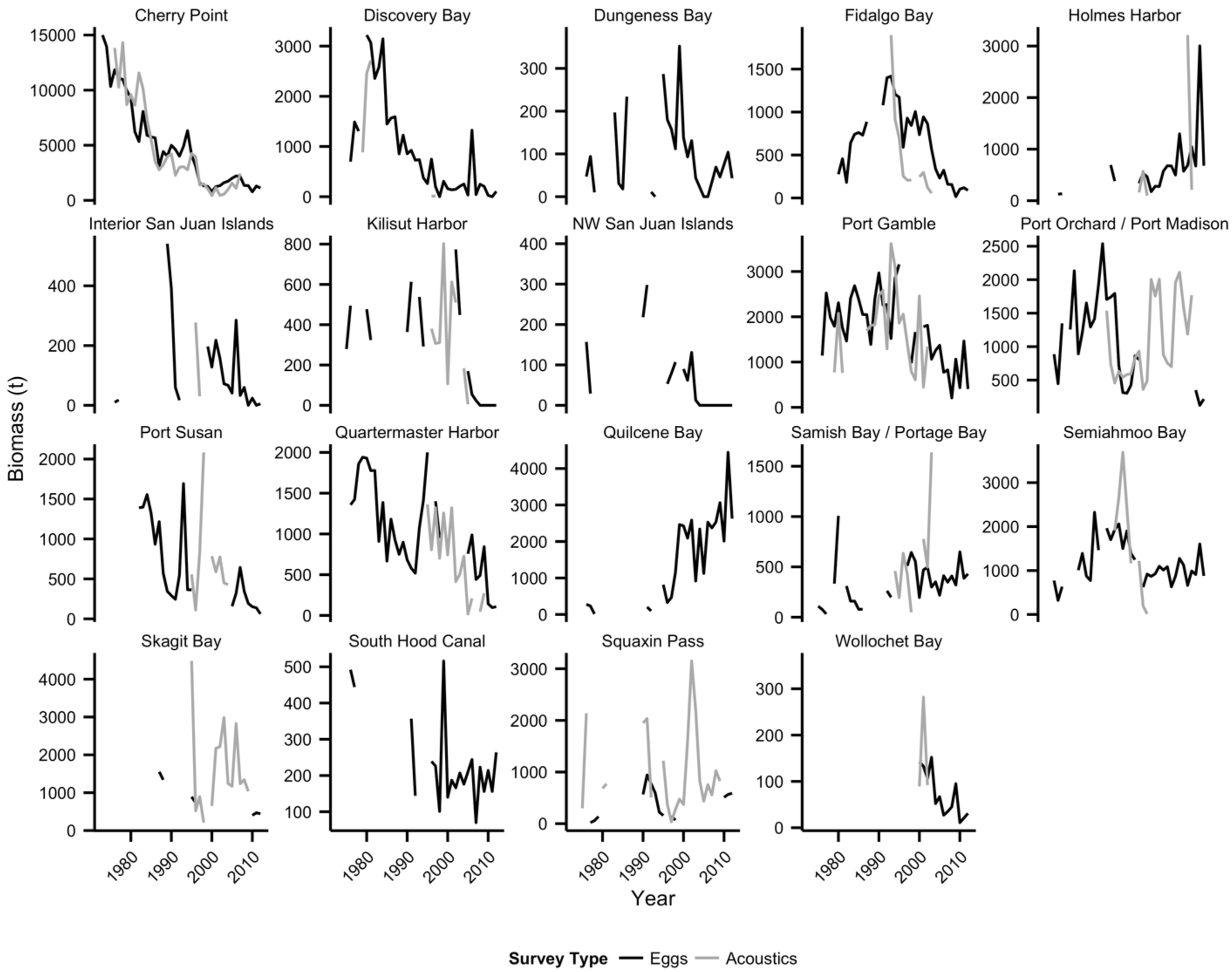

Figure 1.2 Spawner biomass estimates from WDFW surveys.

Adult herring spawner biomass estimates from egg deposition surveys (black lines) and acoustic/trawl surveys (grey lines) in Washington State (data are from Washington Department of Fish and Wildlife, 2013). Only the nineteen population units used in the analysis are shown here.

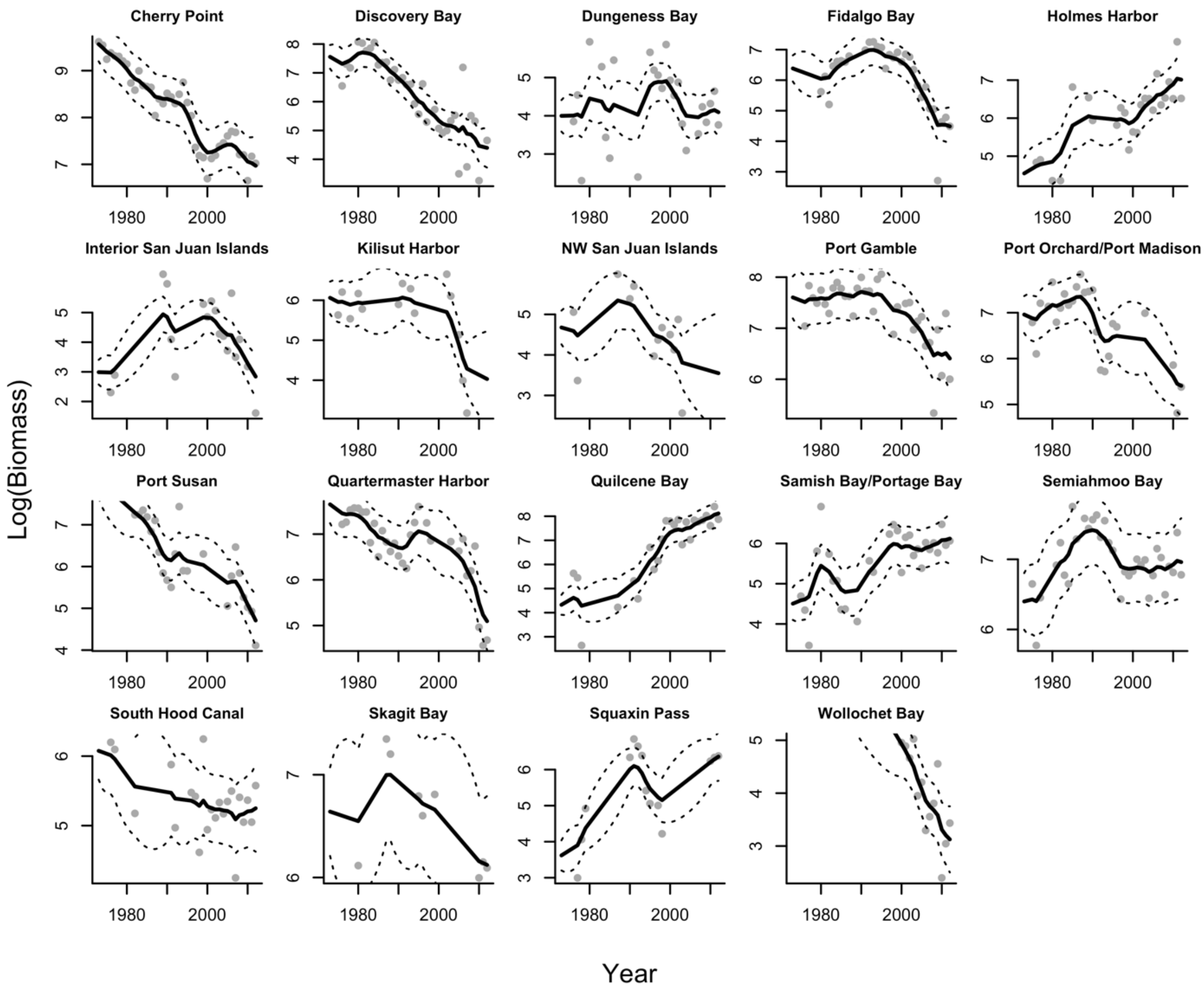

Figure 1.3 Model fits to spawner biomass.

Model fits (black lines) +/- 95% confidence intervals (dashed lines) for the best-fit stock structure model (Model 1, Table 1) of adult herring spawner biomass, based on egg survey data (grey points). Only the nineteen population units used in the analysis are shown here.

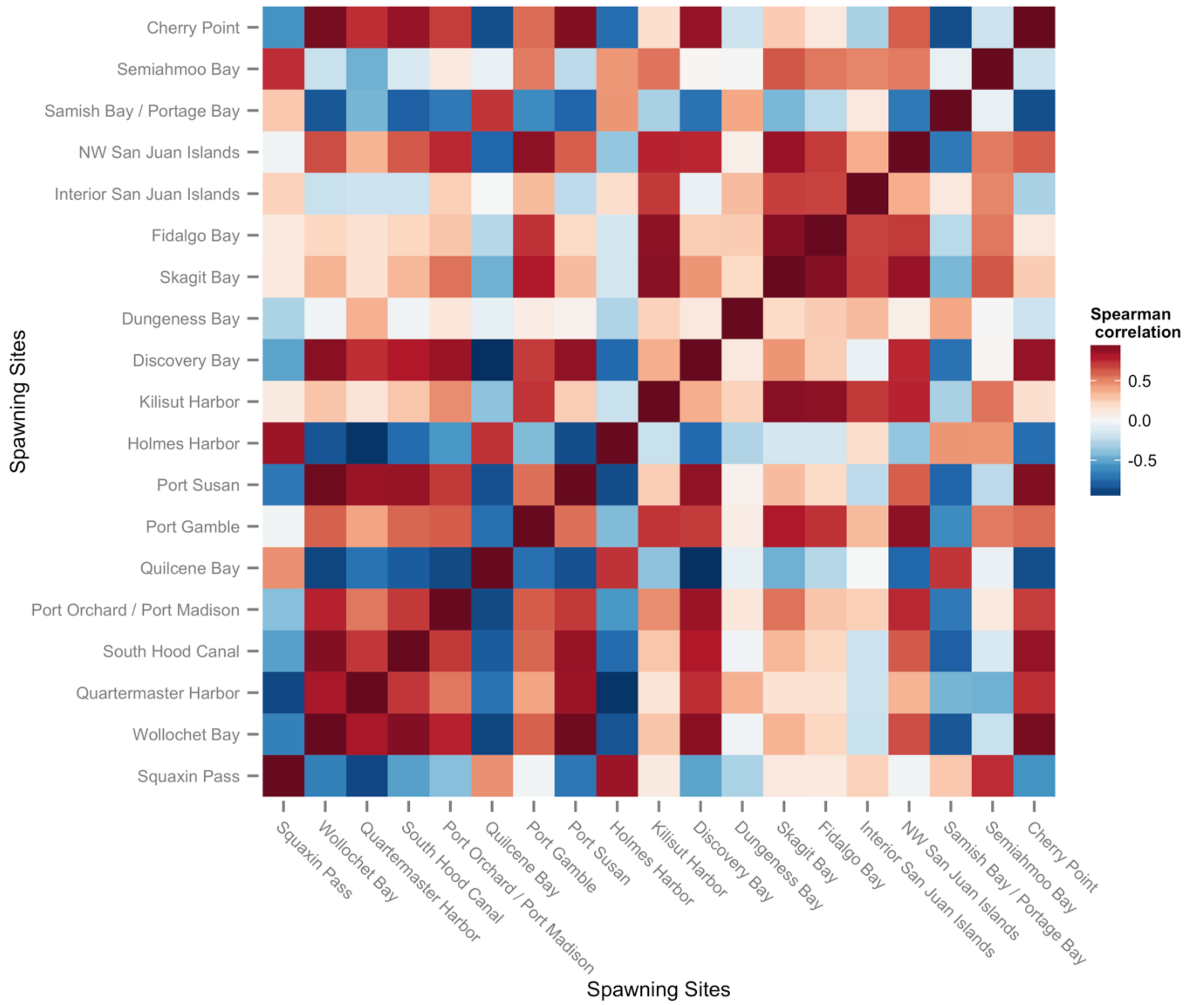

Figure 1.4 Spawning biomass correlations between sites.

Spearman's rank correlations among Puget Sound herring population units between 1973-2012, based on the best fit stock structure model (Model 1, Table 1.1). Population units are ordered from south (bottom and left) to north (top and right). The color of each square reflects the correlation coefficient (-1 to 1) calculated between a row population and a column population.

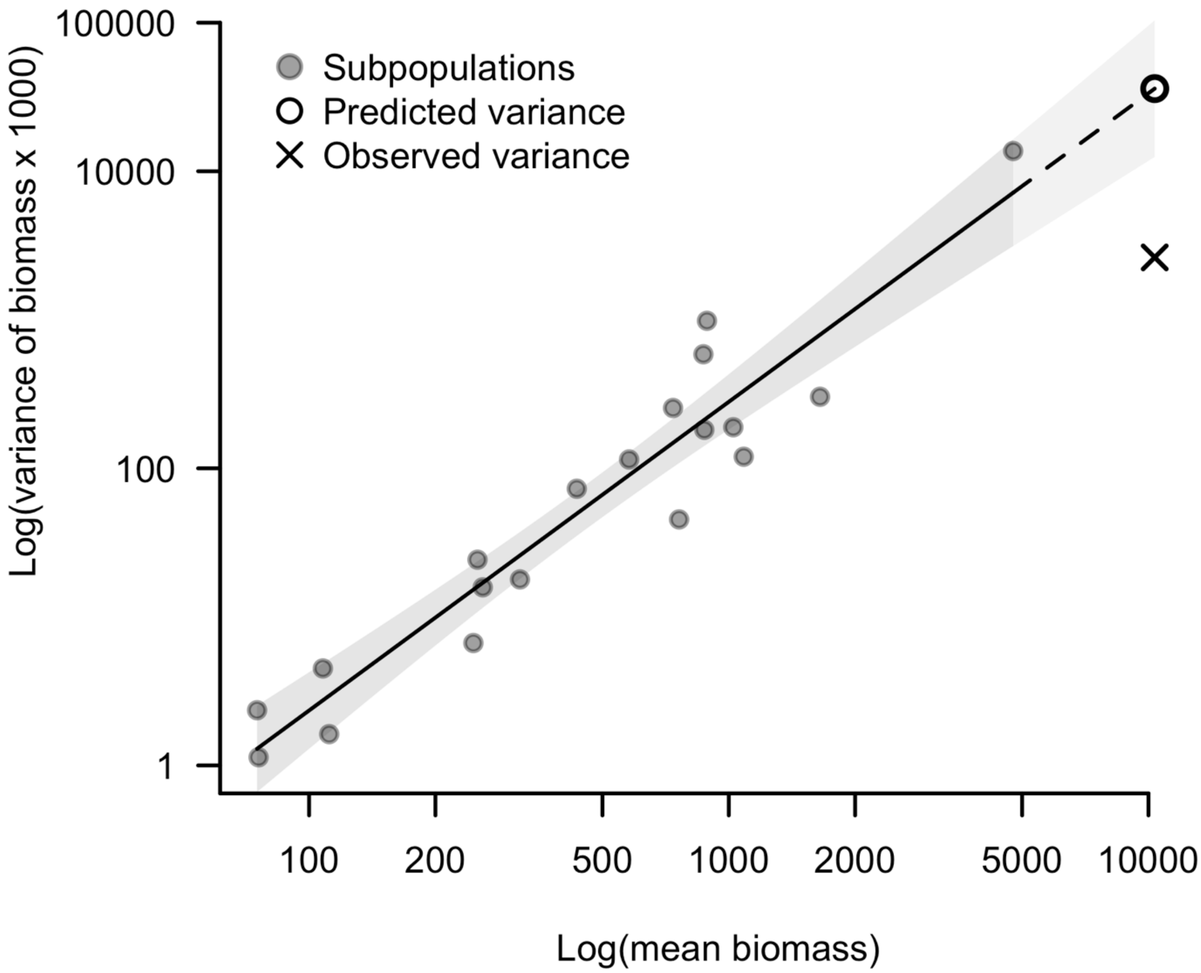

Figure 1.5 Mean-variance relationship between Puget Sound herring population units. Mean-variance relationship in Puget Sound herring population units (grey symbols). The open circle represents the variance expected for a population with the same adult spawning biomass as the aggregate Puget Sound population, based on a linear fit of the observed population mean and variance (solid line). The cross represents the observed variance for the aggregate Puget Sound population. Note the log scales on both axes.

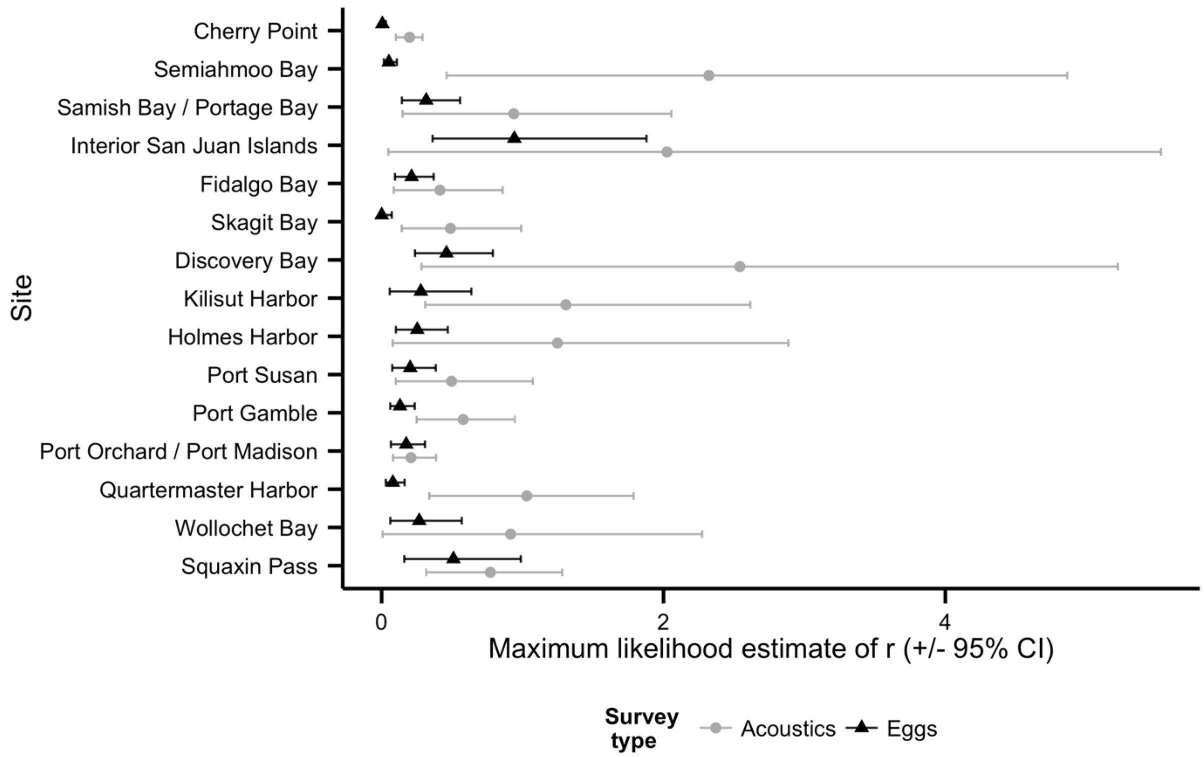

Figure 1.6 Estimated observation error for surveys.

Mean observation errors +/- 95% bootstrapped confidence intervals for acoustic (circles and grey lines) and egg (triangles and black lines) surveys at spawning sites where both survey methods were used. Dungeness Bay, Northwest San Juan Islands, Quilcene Bay, and South Hood Canal sites were removed because they had insufficient acoustic survey data.

Chapter 2. CONTRIBUTIONS OF ADULT MORTALITY TO DECLINES OF PUGET SOUND PACIFIC HERRING[2]

ABSTRACT

Forage fish undergo dramatic changes in abundance through time. Long-term fluctuations, which have historically been attributed to changes in recruitment, may also be due to changes in adult mortality. Pacific herring, a lightly exploited forage fish in Puget Sound, WA, have exhibited shifts in age structure and decreases in spawning biomass during the past 30 years. Here, we investigate changes in adult mortality as a potential explanation for these shifts. Using a hierarchical, age-structured population model, we indicate that adult natural mortality for Puget Sound Pacific herring has increased since 1973. We find that natural mortality has increased for every age class of adult (age 3+), especially age 4 fish, whose estimated mortality has doubled over the survey time period (from M=0.84 to M=1.76). We demonstrate that long-term shifts in mortality explain changes in age structure, and may explain biomass declines and failure to reach management thresholds for two spawning sites in Puget Sound (Cherry Point and Squaxin Pass). Temporal shifts in natural adult mortality could have negative implications for herring and herring predators. We demonstrate that adult mortality, in addition to recruitment variation, is an important driver for forage fish, which face exceptionally high natural mortality compared to other fishes.

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[2] This work has been published:
Siple, M.C., Shelton, A.O., Francis, T.B., Lowry, D., Lindquist, A.P. & Essington, T.E. (2017). Contributions of adult mortality to declines of Puget Sound Pacific herring. *ICES Journal of Marine Science*.

INTRODUCTION

Population fluctuations are a key feature of marine fishes (Vert-pre *et al.* 2013). These fluctuations are induced by changes in demographic rates like growth, reproduction or survival. A great deal of effort has been devoted to characterizing recruitment as an important driver of population dynamics for marine fish. However, there is mounting evidence that post-recruitment mortality also plays an important role. In exploited marine populations, the combination of fishing and natural mortality has been hypothesized to magnify population fluctuations (Shelton and Mangel 2011). Increased natural mortality can increase the importance of short-term fluctuations in determining abundance (Rouyer *et al.* 2012) and amplify the effects of impaired recruitment (Okamoto *et al.* 2016). Changes in natural mortality can therefore be important drivers of population dynamics of marine fish.

Small pelagic schooling fish species ("forage fish") like sardines (*Sardinella* spp.), anchovies (family Engraulidae), and herring (*Clupea* spp.) are well known for their high-amplitude fluctuations in abundance (Hjort 1914; Toresen and Østvedt 2000; Chavez *et al.* 2003), which occur on both short (interannual) and long (decadal) time scales. While many studies have focused on the role of recruitment variation– and climatic drivers of recruitment in particular –as the primary driver of forage fish population fluctuations (e.g., Tourre *et al.* 2007), there is increasing evidence that changes in post-recruitment mortality play an important role in population dynamics. For example, high-amplitude fluctuations in Pacific herring (*Clupea pallasii*) abundance have been attributed to changes in fishing mortality (McKechnie *et al.* 2014), environmental conditions (Nagasawa 2001), predation mortality (Walters *et al.* 1986) or some combination of the three (e.g., Schweigert *et al.* 2010). However, the influence of variable natural mortality on population fluctuations is difficult to discern because of the inherent challenge of distinguishing fishing mortality from natural mortality (Hilborn and Walters 1992).

In the north Pacific, Pacific herring are a key forage species and are heavily fished, providing economic value to large-scale fisheries in Alaska and British Columbia. They are food for predators at multiple life stages, providing a seasonal 'pulse' of marine nutrients to marine and terrestrial predators during spawning (Willson and Womble 2006) and acting as energy conduits from lower trophic levels to piscivorous predators and seabirds throughout their life span (Beaudreau and Essington 2011; Schrimpf *et al.* 2012). They are also considered a "cultural keystone species" (Thornton and Kitka, 2015; *sensu* Garibaldi and Turner, 2004) as they are the focus of indigenous harvest practices and cultural traditions. Pacific herring in Puget Sound, WA provide an excellent opportunity to study the importance of natural mortality relative to other drivers like recruitment. In this system, they experience little fishing mortality. Natural mortality is likely high because they are a preferred prey for many species in the food web (Ainsworth et al. 2008, Harvey et al. 2012) including salmonids (Duffy *et al.* 2010), seabirds (Lance and Thompson 2005), and marine mammals (Lance and Jeffries 2006). In contrast to more heavily exploited forage fish populations, including other Pacific herring populations in the Northeast Pacific, Puget Sound herring have supported only a small bait fishery in recent years (2-6% of spawning stock biomass per year between 2003-2012) (Stick *et al.* 2014). Despite very low fishing mortality rates, previous research has suggested a decline in spawning biomass (Siple and Francis 2016) and a shift in age structure (Stick et al. 2014) in Puget Sound herring. The relatively low fishing mortality provides a unique opportunity to understand variation in natural mortality in a wild forage fish population.

In addition to experiencing very low exploitation rates, herring in Puget Sound are comprised of multiple subpopulations or "stocklets" (Stick *et al.* 2014; see Siple and Francis 2016), which are defined by the spawning sites to which they return. This provides the opportunity to examine both temporal and spatial variability in recruitment, adult mortality, and abundance fluctuations. Previous work has shown that time series of spawning biomass in Puget Sound across stocklets are asynchronous, suggesting that local-scale processes might impose distinct mortality regimes (Siple and Francis 2016). Additionally, two potential mechanisms motivate examining spatial variation in adult mortality in Puget Sound: 1) tissue contaminant concentrations in adult herring, which may have deleterious sublethal effects, vary spatially (West *et al.* 2008), and 2) predators may forage more actively in some areas than others (Ward *et al.* 2012). Spatial variation in natural mortality, including different trends through time, would indicate that local processes are important for determining population dynamics. Understanding spatiotemporal variation in adult natural mortality, therefore, and its links to biomass trends, will help to elucidate the role of local processes in determining population dynamics, and suggest potential management interventions in recovery or conservation situations.

To evaluate spatial variation in natural mortality and the importance of local processes in determining population dynamics over time, we estimate temporal and spatial variation in Puget Sound herring natural mortality rates using time-series models. We then compare models to reveal the role of spatial versus temporal changes in mortality and use simulations to demonstrate the importance of natural mortality and recruitment variation in a forage fish population.

Methods

We investigated temporal changes in adult mortality in Pacific herring over 36 years (1973-2008), and assessed whether these changes are unique across a set of spatially distinct herring spawning sites (hereafter, we refer to these as "sites" and the populations that spawn at them as "stocklets"). We fitted multiple hierarchical, age-structured models, using herring trawl survey data from eight sites in Puget Sound, then used model fits to evaluate whether there was evidence for temporal and/or spatial variation in mortality. Finally, we used estimated life history parameters (initial age distribution, recruitment, and mortality) to simulate the effects of constant vs. time-varying mortality on Puget Sound Pacific herring biomass, and compared our predictions against observed abundance and management targets.

Study Site

Puget Sound is a partially mixed estuarine fjord in western North America, composed of oceanographically distinct basins separated by sills. It is connected to the coastal Pacific Ocean by the Strait of Juan de Fuca. It has a shoreline of ~2,000 km, enclosing a water area of 2,642 km^2 at mean high water. Tides are the main driving force of physical oceanographic processes in Puget Sound, and tidal range varies nearly twofold between the northern and southern parts of Puget Sound. Its maximum depth is 284 meters and average depth is ~130 m. Subtidal circulation is driven primarily by density gradients, with fresh surface water from rivers interacting with saltier marine water at the mouth of Puget Sound (Babson *et al.* 2006). Like other large estuaries, Puget Sound has an along-estuary salinity gradient (~2×10^{-5} psu m^{-1}; (Sutherland *et al.* 2011)). The basins in Puget Sound are generally well-oxygenated, although oxygen depletion is a concern in some areas (e.g., Hood Canal; Newton *et al.* 1995). Pacific herring return to beaches to spawn each winter between January and June, depending on the stocklet.

Data

We used age-specific abundance of Pacific herring in Puget Sound collected intermittently (mostly annually) between 1973 and 2008, at eight spawning sites. Numbers-at-age data were collected by the Washington Department of Fish and Wildlife (WDFW) using a midwater trawl coupled with acoustic surveys targeting pre-spawning aggregations of Pacific herring, 3-4 weeks before winter spawning in Puget Sound (Lemberg et al 1988, Stick et al. 2014). Rope trawls were used to collect samples of fish at the peak of prespawner biomass at each site (Burton 1991). Larger sites with multiple aggregating schools were split into "sub-areas." Subsamples (N=100) provided data on mean weight at age *a* ($\overline{W_a}$) and proportion at age *a* (by abundance, P_a and by weight, P_{wa}), while acoustic surveys provided data on total biomass (B_{total}). Estimates of numbers at age (N_a) in each sub-area were derived as:

$$N_a = \frac{B_a}{\overline{W}_a} \tag{2.1}$$

$$B_a = B_{total} P_{wa} \tag{2.2}$$

$$P_{wa} = P_a \frac{\overline{w}_a}{\sum_{i=1}^{n} P_i \overline{W}_i} \tag{2.3}$$

where B_a is the estimated biomass at age a and n is the number of ages.

For sites with multiple sub-areas (e.g., Port Orchard and Port Madison), proportions at age were calculated separately for each sub-area and then pooled proportionally to their contribution to the total biomass (O'Toole 1994). Age was determined from scales, with multiple scales read for each fish sampled (Stick *et al.* 2014). Because proportions at age were not available for every year and every site, we focused our analysis on eight sites for which there are more than 10 years of age-specific abundance estimates (Figure 2.1). These sites are spatially distributed throughout each of the five Puget Sound basins (Stout *et al.* 2001) (Figure 2.1). The trawls used in pre-spawning surveys only captured adults. In Puget Sound, nearly all age 3 individuals are sexually mature, but the fraction of age 2 individuals captured in the surveys that are sexually mature is unknown (Stick et al. 2014). Therefore, we only used abundance data for herring ages 3 and older.

We estimated natural mortality using an age-structured population model, consisting of a process model to estimate the parameters based on numbers-at-age data, and an observation model that relates observations (data) to the true state of nature. This state-space structure assumes that survey data are observations of an underlying process, in this case the change in age composition over time. The approach allows its user to define survey data as observations instead of exact values. This way, it is possible to acknowledge and sometimes estimate the amount of measurement error associated with the survey. In the process model, we modelled the numbers of herring in each stocklet as an age-structured population where age-specific mortality rate (M) depends on the time period (described below) or oceanographic basin. Because there are insufficient data to estimate a unique M for the very oldest age classes, we estimated unique mortality rates for ages 3-6, and a shared mortality rate among age 7-9 fish.

The number of age a adult herring in year t, at site s, $N_{a,t,s}$, given natural mortality rate M, is estimated as:

$$N_{a,t,s} = N_{a-1,t-1,s}\mathrm{e}^{-M} \quad (2.4)$$

We used this general model to explore alternative scenarios in which mortality varies in space and time. We compared seven models: M was the same for all ages, basins, and time periods (null model); M varied only by age (M_a); M varied by age and basin ($M_{a,b}$ and $M_a e^{\beta_b}$, where M_a was modified by a basin effect β_b); M varied by age and time period ($M_{a,p}$ and $M_a e^{\beta_p}$, where M_a was modified by a time period effect β_p); and M varied by basin and time period ($M_a e^{\beta_{b,p}}$; where M_a was modified by a combined basin/time period effect $\beta_{b,p}$). Numbers-at-age data were insufficient to estimate annual shifts in M, so mortality for fish of age a in year t was assumed to have the following form:

$$M_{a,t} = \begin{cases} M_{a,p=1} & if\ t < 1991 \\ M_{a,p=2} & if\ t \geq 1991 \end{cases}$$

where $p = 1$ indicates the first half of the survey time series (1973-1990) and $p = 2$ indicates the second half of the time series (1991-2008). We estimated a value for M in the first and second half of the time series separately, instead of one for each year.

Recruitment to age 3 for Puget Sound herring may vary spatially because of differences in egg loss (Shelton *et al.* 2014) or exposure of embryos to contaminants (West *et al.* 2014). We modelled age-3 abundance as a random draw from a lognormal distribution each year, with a different mean for each site. This assumes that recruitment variation is not fully explained by changes in spawning stock biomass (a common assumption for forage fish; Szuwalski and Hilborn 2015), but allows for spatial variation in recruitment. We assumed that mean recruitment to age 3 (ψ_s) was independent across sites and modelled age-3 abundance as:

$$N_{a=3,t,s} = \psi_s e^{\epsilon} \tag{2.5}$$

where $\epsilon \sim N(0, \tau^2)$ represents independent, normally distributed variation around mean recruitment and τ was the same for all sites. We note that recruitment in forage fish is often described as the number of age-0 or age-1 individuals in the population, so the recruitment patterns observed in this study may not be directly comparable to others.

We assumed lognormal observation error around numbers at age for each location and year. That is, we assumed a simple observation model:

$$\log (N_{obs\ a,t,s}) = \log (\mathrm{N}_{a,t,s}) + \varepsilon_{Obs} \tag{2.6}$$

Where ε_{Obs} is an independent and normally distributed random variable with mean 0 and standard deviation σ (see prior in Table 2.1).

Parameter Estimation

We fitted model parameters in a Bayesian framework because it allows information to be shared among frequently surveyed sites and those with less data (Punt *et al.* 2011), and because this hierarchical structure is easier to implement in a Bayesian framework than a maximum likelihood one. A Bayesian approach requires the specification of prior distributions for mortality and recruitment parameters, initial age distribution, and observation error. Parameters for which no prior information was available were given uninformative or diffuse priors (Table 2.1).

Initial numbers at age were based on recruitment to the first age class and subsequent mortality. We added a penalty to the estimation of initial age structure, based on recruitment and mortality.

The prior mean for adult mortality in this study was based on an estimate of adult Pacific herring mortality outside Puget Sound, along the Pacific coast ($M = 0.6\ yr^{-1}$; Hourston and Haegele, 1980). Since there was no available information about variation in M, we chose a variance that allowed the prior distribution to be broad and centred around this value.

We obtained posterior probabilities of parameters using Just Another Gibbs Sampler (JAGS; Plummer 2003), with three chains and 50,000 simulations, and a burn-in of 10,000 simulations. Results were examined using the R2jags and coda packages in R (Plummer *et al.* 2006; R Core Team 2017). We tested Markov Chain Monte Carlo (MCMC) chain convergence using the Gelman-Rubin diagnostic (Gelman and Rubin 1992) and chain stationarity was assessed using the Geweke statistic (Geweke 1992). We also visually examined posterior estimates to evaluate cross-correlation between variables, and performed posterior predictive checks of numbers at age to confirm that parameter estimates produced realistic population dynamics. We used Deviance Information Criteria (DIC; Spiegelhalter *et al.* 2002) to compare fitted models, using DIC.samples() in rjags (Spiegelhalter *et al.* 2002).

Model Projections

To evaluate the relative influence of adult mortality versus recruitment variation on observed biomass trends, we used mortality rates estimated by the model above to project herring populations in Puget Sound based on two alternative scenarios for herring mortality: 1) mortality increased halfway through the time series ($M_{a,1}$ changes to $M_{a,2}$ in 1991; "M time-varying"), and 2) mortality was constant throughout the time series (i.e., $M_{a,1} = M_{a,2}$; "M constant"). For comparison, we also included two recruitment scenarios, one in which mean recruitment was constant for each stocklet (ψ_s), and one in which mean recruitment varied from year to year. For scenarios where recruitment was variable, we used time series of median recruitment ψ_s and recruitment variability τ drawn randomly from the model. We projected numbers at age for each scenario using estimates of initial age distribution, recruitment variability and mortality from the process model described above (Equation 2.1).

Current management targets for Puget Sound herring are set in terms of adult spawner biomass. To describe herring stocklets in terms of biomass, we used mean weights at age (w_a; determined from trawl surveys at each site; see Supplementary Material) and numbers at age $N_{a,t,s}$ estimated by the model to calculate biomass $B_{t,s}$.

$$B_{t,s} = \sum_{a=1}^{n} N_{a,t,s} w_a \quad (2.5)$$

We did not see strong evidence that weight at age varies significantly between sites or over time so w_a was estimated from trawl survey data from all years and sites (Figures B3–B4).

RESULTS

Age truncation and structure of mortality

There was a shared pattern of age truncation (loss of older age classes) and declining biomass for Puget Sound herring over the time period 1973-2012. The maximum age observed in trawl surveys dropped in 5 of 8 stocklets over the course of the WDFW trawl survey (Figure 2.2) and older fish (>8 years) were not observed in trawl surveys at any spawning site after 2007. Even at sites where spawning biomass appears constant or increasing (e.g. Squaxin Pass), age structure has shifted such that the mean age of Pacific herring has declined over the survey time period (at Squaxin Pass, from 5.98 in 1975 to 2.0 in 2008; Figure 2.2). The degree to which older age classes were lost varies by spawning site: the proportion of the Squaxin Pass stocklet composed of age 4+ herring declined from 97% to 0% between 1975 and 2008; Cherry Point declined from 90.5% to 0% between 1973 and 2008; and Semiahmoo Bay declined from 7% age 4+ individuals in the 1988 survey to 0% in 2000. All other stocklets experienced little or no change in the number of age 4+ individuals (± 0.6 – 3% since surveys started at each site), but surveys at these sites began in the 1990s, after the percentage of older adults had already declined substantially for Cherry Point and Semiahmoo Bay. On average across all the sites in this study, the proportion of the overall Puget Sound adult herring population composed of age 3 individuals increased from an average of 49% (1973-1990) to 75% (1991-2008); in 2008, the overall Puget Sound herring population was composed of more age 3 herring than all older fish combined (Figure 2.2).

There was strong evidence for temporal changes in age-specific mortality but only weak evidence of spatial variation in mortality. The data best supported the model in which M_a varied through time, such that each age experienced a unique temporal shift in M (Age × Period; Table 2.2). The null model with age-varying mortality alone and the null model with a single M for all basins and time periods were not supported ($\Delta_{DIC} > 100$). The model where M_a varied spatially and temporally (Age + Basin × Period; $\Delta_{DIC} = 4$), was less well supported (higher Δ_{DIC}), as was the model where M increased by a common factor β_p for each age class (Age + Period; $\Delta_{DIC} = 5$). Models where M_a varied spatially (Age + Basin, $\Delta_{DIC} = 71$; Age × Basin, $\Delta_{DIC} = 87$) were better than the age-only (Age; $\Delta_{DIC} = 106$) and null models (single M; $\Delta_{DIC} = 163$), but still not as well supported as the temporal models (Table 2). Posterior predictive checks confirmed that the best fit model described realistic recruitment dynamics and changes in numbers at age (Figure 2.3; Figure B5).

Observed shifts in herring age structure were consistent with an increase in mortality of herring ages 3-6; and we further found that increases in M varied by age class (Table 2.2, Figure 2.4). Since the start of the survey, mean M increased by 35% for age 3 herring, 52% for age 4, 21% for age 5, and 14% for age 6. The model estimated a reduction in Age 7+ mortality (a 95% decline), but we note that the recent time period (1991-2008) mortality estimate is very close to the prior and there are very few data on the oldest age classes for this time period, suggesting that this value reflects the prior instead of the data.

Projections

A substantial fraction of the biomass decline in Puget Sound herring can be attributed to mortality of older age classes (age 3+), versus variation in recruitment. The scenario with increasing adult mortality and constant recruitment resulted in a nearly one-third decline in total adult biomass in Puget Sound over 36 years compared to scenarios with constant adult mortality (median -28% change in biomass across all sites between 1973-2008; Figure 2.5). The scenario with variable recruitment yielded similar results (median -40% change in biomass; Figure 2.5). For individual sites, including an increase in adult mortality resulted in biomass estimates that ranged from 2% lower (Cherry Point; 1111 t in 2008) to 58% lower (Squaxin Pass; 119 t in 2008) compared to a constant mortality scenario (Figure 2.5). Incorporating increased adult mortality resulted in biomass projections that had larger negative changes in biomass, increased variability, and were below the management targets set for Squaxin Pass (119 t of the 880 target) and Cherry Point (1154 t compared to a target biomass of 5000 t; Stick et al. 2014).

DISCUSSION

Recruitment variability, particularly resulting from changes in the environmental conditions experienced by eggs, larvae, or juvenile fish, is often considered a primary driver of forage fish dynamics (Cushing 1990; Szuwalski and Hilborn 2015). Our analysis demonstrates that changes in adult natural mortality can drive population dynamics in forage fish. We estimated high natural mortality (M) that increased nearly twofold between 1973 and 2008 (36 years), indicating that adult (age 3+) mortality is high and increasing and offering a potential explanation for profound changes in age structure. Furthermore, our model fits show that an analogous change in recruitment to age 3 could not explain the changes in age structure observed in Puget Sound herring (Table B1), excluding the possibility that depressed recruitment alone could drive herring populations.

Puget Sound herring stocklets are presently below management targets, and our results suggest that both high and increasing adult mortality and changes in recruitment may be limiting their ability to recover. Our simulations showed that an increase in natural mortality could account for up to a 28% decline in total biomass of herring across Puget Sound. When model-estimated recruitment variation was included, the increase in mortality caused a ~40% decline in biomass. Importantly, our simulations suggest that even if mortality had not increased, biomass at Cherry Point and Squaxin Pass – the two stocklets with management-defined spawning biomass targets – would be unlikely to reach those targets. Simulated 2008 biomass under constant mortality was well below management targets, suggesting that either estimated mortality at the beginning of the time series was already too high to allow recovery to target levels, or that reduced mortality alone is insufficient for recovery, and improved recruitment is also necessary. It is important to note that biomass targets include all spawning ages, which includes some unknown fraction of age-2 spawners that are not incorporated in our model. Our results illustrate the general challenge that using historical biomass targets for conservation may be problematic under changing environmental conditions. It may be impossible to reach historical abundances without correctly identifying the drivers of biomass change. This is particularly important for forage fish populations, whose historical abundances are often poorly understood in the first place.

We predict that the truncated age structure in herring could have major implications for population dynamics going forward, for three main reasons. First, age truncation can remove the buffering effect of older age classes on years with poor growth or recruitment, causing population variability to more closely follow high-frequency environmental signals (Warner and Chesson 1985). In an urbanized estuary like Puget Sound where nearshore conditions are highly diverse on small spatial scales (Simenstad *et al.* 2011), temporal and spatial changes in environmental drivers of recruitment may become even more influential to a population dominated by younger individuals. Second, age truncation may also have behavioural impacts: in a study of Pacific herring in on the British Columbia coast, Hourston (1959) found more consistent homing in fish tagged as adults than fish tagged as juveniles (82% of adults returned to spawning beaches where they were tagged after 2 years at large, compared to 52% of herring tagged as juveniles, after adjusting for natural mortality). "Learned migration" was proposed by McQuinn (1997) to explain how herring migration patterns change or disappear under fishing. If homing behaviour in Puget Sound Pacific herring is similarly influenced by older fish, age truncation could lead to unexpected shifts in future spawn timing or location (Francis et al. *unpublished data*). Recruitment made more variable by these changes would compound the effects of age truncation on older age classes, causing population dynamics to track an increasingly variable set of environmental signals.

The absence of spatial effects indicates that drivers of adult mortality operate at an across-basin scale, and that asynchronous biomass dynamics among sites may be driven by differences in recruitment (as in Thorson *et al.* 2014) or growth instead of adult mortality. Thus, asynchronous biomass dynamics observed at a local (spawning site) scale shown by Siple and Francis (2016) are likely due to spatial differences in other demographic rates like juvenile survival, instead of differences in M. Spatial differences in adult mortality are still an important consideration, but require higher resolution survey data to detect.

Although we found adult mortality to be a dominant driver of population dynamics in herring, we expect survival through early life history to be important in Puget Sound during other regimes. Forage fish experience large swings in productivity based on the availability of planktonic food sources for newly emerged larvae (Cushing 1990), the retention of larvae and transport to areas with planktonic prey (e.g., in the Kuroshio Current Ecosystem; Yatsu *et al.* 2013), and changes in sea surface temperature that affect growth and recruitment. Herring recruitment, influenced by environmental conditions, is often the source of large fluctuations in productivity as well (Saetre *et al.* 2002). Finally, age-0 to age-3 herring experience high and variable natural mortality, which can dampen or exacerbate changes in year-class strength (de Barros and Toresen 1998). In our model, recruitment occurs to age 3, so the "recruitment" estimated by the model includes both environmental impacts on early life history (predation and starvation during first feeding larval and early juvenile stages) as well as effects on age-1 and age-2 mortality. A dependency on recruitment may appear as spatial differences in population dynamics; in Puget Sound, predation on herring eggs (Anderson *et al.* 2009) and juvenile herring (Beaudreau and Essington 2011) generate spatial difference in early life history survivorship. Therefore, age truncation may give way to spatial differences in early life history survival if this pattern persists.

Our results demonstrate that adult herring in Puget Sound have high and increasing rates of natural mortality. Higher susceptibility of older adults to pathogens and bioaccumulation of contaminants are two plausible sources of mortality for older herring in Puget Sound. Older herring are more susceptible to certain infectious diseases and parasites; for example, *Ichthyophonus hoferi* infection rate and parasite load both generally increase with age (Hershberger *et al.* 2015). Diseases can also act synergistically, exacerbating the effects of other stressors (Hershberger *et al.* 2006). Lipophilic contaminants such as PCBs, which tend to bioaccumulate in older individuals, are particularly relevant in highly urbanized estuaries like Puget Sound. Tissue PCB concentrations are higher for Puget Sound resident fish (in this case, Chinook salmon) than oceanic migrants (West *et al.* 2008; O'Neill and West 2009) and have not declined in Puget Sound Pacific herring since 1990 (West and O'Neill 2007). Contaminants and disease may also make herring more susceptible to other sources of mortality such as predation via sublethal effects. Age truncation occurred across sites, suggesting that the observed changes were not simply due to movement of adults between sites. This is supported by genetic evidence, which indicates little or no mixing of spawning adults between Washington and British Columbia stocks (Beacham *et al.* 2008).

There is conflicting evidence that the observed increase in adult mortality could have resulted from increased predator abundance. Abundances of some herring predators in Puget Sound are not consistent with this possibility: Chinook salmon, for example, have declined to less than half of their estimated historical run size (Good *et al.* 2005), and several species of seabirds that consume adult herring are also in decline (Western grebes have declined by 95% in Puget Sound since 1975; surf scoters at some locations have declined by 97.5%; Puget Sound Action Team 2007; Pearson and Hamel 2013). Exceptions to this general decline in seabird abundance are double-crested and pelagic cormorants, which are main seabird predators of herring in Puget Sound and have increased 97 and 87%, respectively, between 1978 and 2005 (Bower 2009). In contrast, pinniped populations (sea lions and harbor seals) regularly consume herring (NMFS 1997) and have increased exponentially in abundance (harbor seal abundance increased 7-10 fold between 1970-2003; Jeffries *et al.*, 2003 Steller sea lions increased 3–4 fold between 1979-2010; Wiles, 2015). If the high consumption rates of Chinook salmon by pinnipeds (Chasco *et al.* 2017) are comparable to predation pressure on herring, predation mortality could be an important factor.

Incorporating changes in vital rates into population assessments will be an ongoing challenge to managing fish and wildlife in a changing climate. For exploited fish populations, accurately identifying temporal changes in natural mortality influence is essential to understanding drivers of abundance (e.g., Predator-driven Allee effects; Kuparinen and Hutchings 2014; Swain and Benoît 2015) and accurately assessing population status (Johnson *et al.* 2015; Thorson *et al.* 2015). Changes in natural mortality have also been documented in Atlantic cod (Swain 2011), winter skates (Swain *et al.* 2009), and white hake (Benoît *et al.* 2011). Our findings add to the growing body of evidence that changes in natural mortality are an important consideration for assessing population trends and ecology. Although high natural mortality is expected for forage fish relative to other marine fishes because of predation, the pattern of increasing M with age is contrary to most models of mortality in marine fish, which often assume that survival increases with size because predators are gape-limited (Sogard 1997). In most fished populations, fishing mortality increases with age, but the bait fishery for Puget Sound herring selects younger individuals, so fishing mortality does not explain the differences in M observed here. Increases in natural mortality can remove the buffering effect of adult survival on population size, making fish populations more sensitive to recruitment variation. Here we demonstrate temporal changes in natural mortality in a key forage species. These changes are sufficiently large to cause long term declines in biomass, in combination with other demographic changes. Long-term shifts in adult mortality, although challenging to detect in heavily exploited populations, should be considered a possibility for forage species and incorporated in population assessments, as should particularly high rates of adult mortality.

Table 2.1 Estimated parameters.

Parameters estimated by the age-structured model, their definition, and the priors used to specify their distribution. The prior for mean recruitment was the same for each site, but was estimated separately for each site.

Parameter	Definition	Prior distribution
ε	Observation error associated with trawl surveys	$\varepsilon \sim N(0, \sigma)$
σ	Standard deviation of log(Observations)	$\sigma \sim \Gamma(0.5, 0.75)$
ψ_s	Mean recruitment to site *s*	$\psi_s \sim N(11, 3)$
ϵ	Recruitment error	$\epsilon \sim N(0, \tau)$
τ	Standard deviation of log(Recruitment)	$\tau \sim \Gamma(0.5, 0.75)$
M	Mortality rate of herring, where subscripts indicate age (*a*), time period (*p*) or basin (*b*). Prior mean is based on estimates for herring mortality outside Puget Sound (m=0.6; Hourston and Haegele 1980).	$\ln(M_{a,p}) \sim N(-0.5, 0.5)$

Table 2.2 Life history model fits.

Comparison of life history models with spatial and temporal differences in adult mortality. *e* indicates the base of the natural logarithm (ΔDIC is the difference in Deviance Information Criterion; DIC; between each model and the best fit model).

Model	**Form**	**ΔDIC**
Age × Period	$M_{a,p}$	0
Age + Basin × Period	$M_a e^{\beta_{b,p}}$	4
Age + Period	$M_a e^{\beta_p}$	5
Age + Basin	$M e^{\beta_b}$	71
Age × Basin	$M_{a,b}$	87
Age	M_a	106
Null	M	163

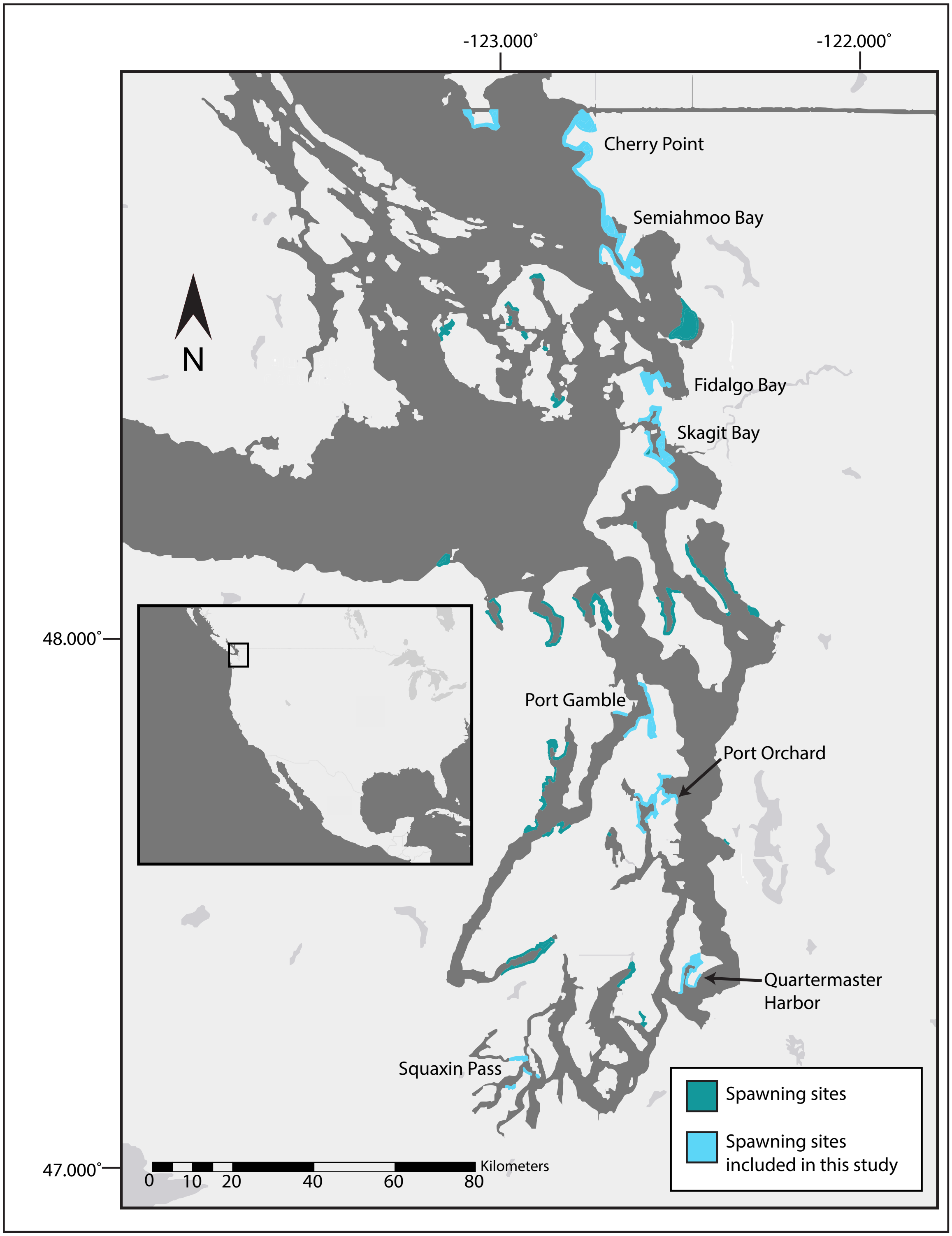

Figure 2.1 Map of spawning sites.

Herring spawning sites in Puget Sound (coloured areas). The group of fish returning to each site is referred to as a "stocklet." Map modified from Stick & Lindquist (2014).

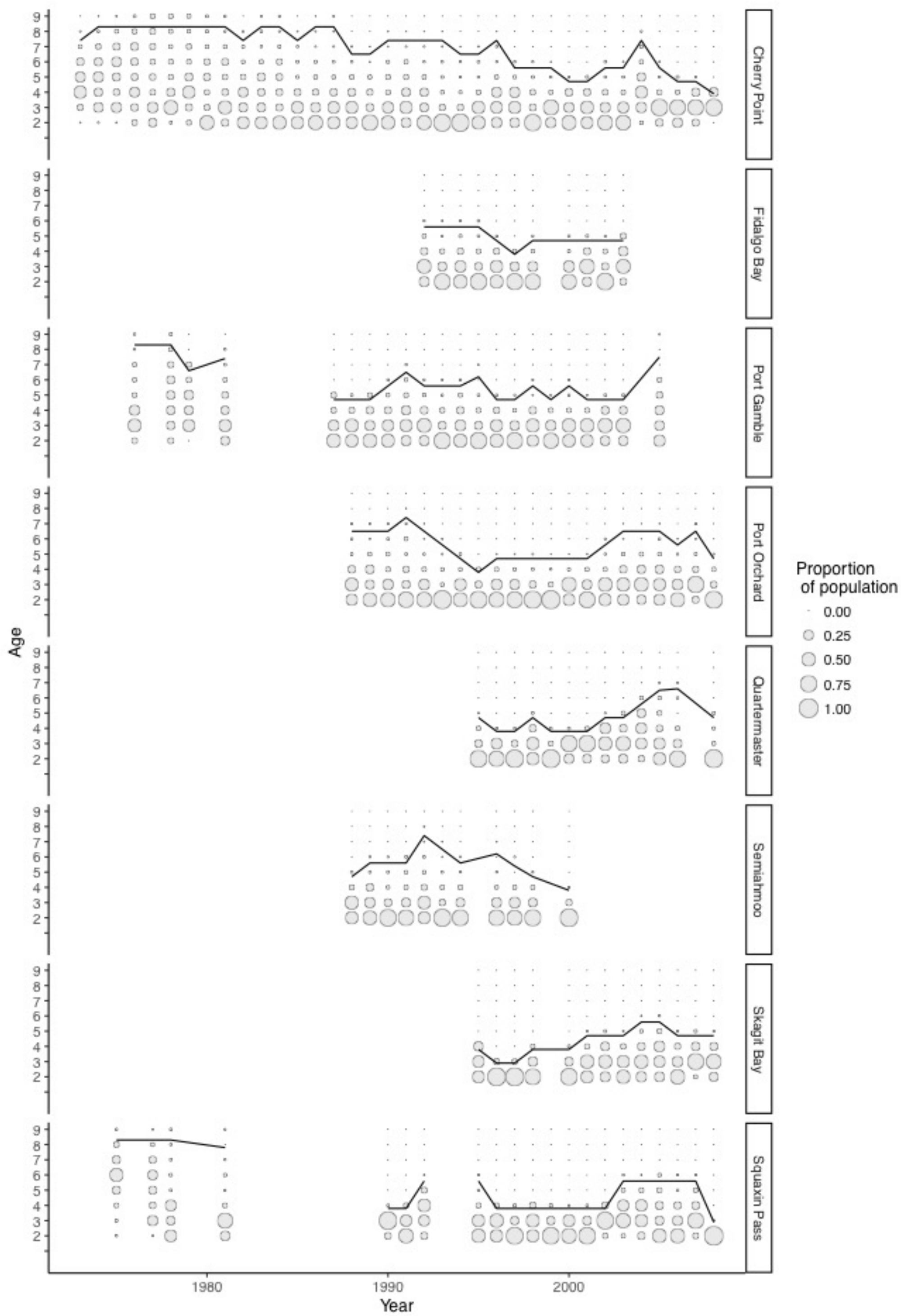

Figure 2.2 Proportions at age since the start of the survey.
The dark line represents the 90th percentile of age over time.

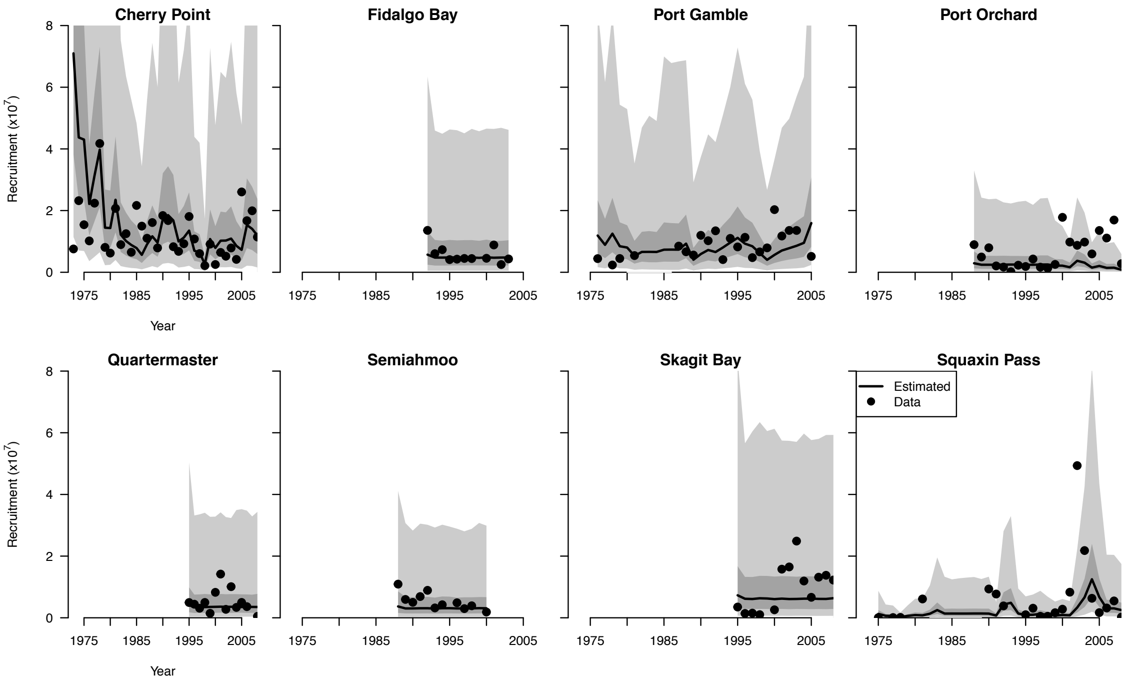

Figure 2.3 Recruitment to age 3.

Recruitment to age 3 estimated by the best fit model (median, black line; with 50% and 95% credible intervals shaded) and observed recruitment to age 3 (points) at each site.

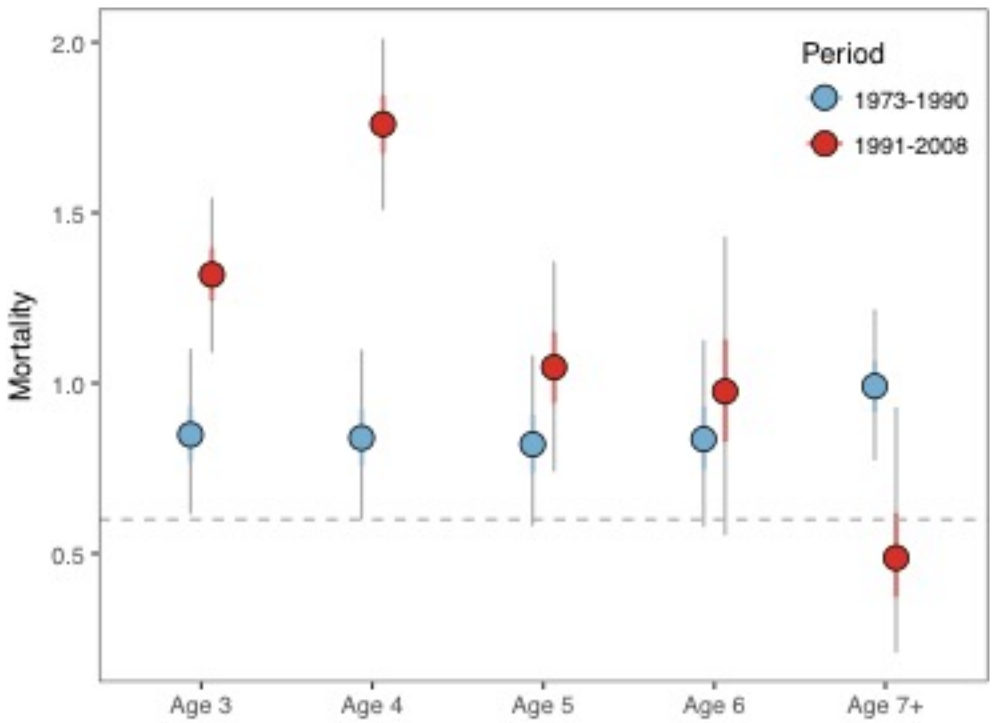

Figure 2.4 Posterior distributions for mortality.

Posterior distributions of $M_{a,p}$ where p represents the time period (first or second half of the survey time series) and a represents age. Vertical bars indicate 50% and 95% quantiles. The average M previously estimated for Pacific herring on the Pacific Coast, and the mean of the prior used for all $M_{a,p}$ (M = 0.6; Hourston and Haegele 1980) is represented by a dashed line.

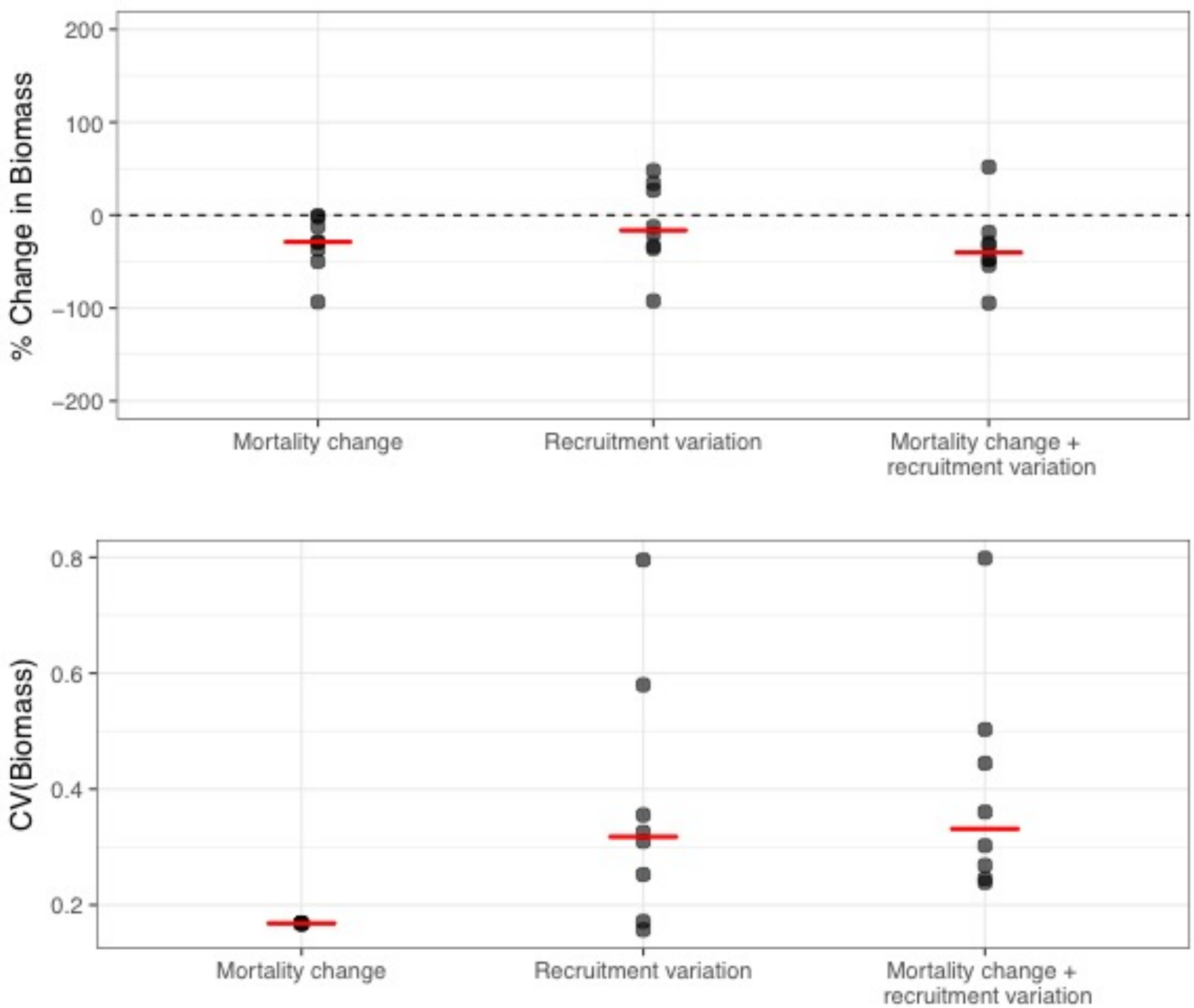

Figure 2.5 Percent change and CV(Biomass) based on mortality changes.

Simulated percent change in biomass and CV(Biomass) over the survey time period, based on simulations with mortality changes and recruitment variation estimated from the model. Each point represents one site; red bars indicate the median across all sites.

Chapter 3. FORAGE FISH FISHERIES MANAGEMENT REQUIRES A TAILORED APPROACH TO BALANCE TRADEOFFS[3]

Abstract

Ecosystem-based fishery management requires considering the effects of actions on social, natural and economic systems. These considerations are important for forage fish fisheries, because these species provide ecosystem services as key prey in food webs and support valuable commercial fisheries. Forage fish stocks fluctuate naturally, and fishing may make these fluctuations more pronounced. Harvest strategies intended to ameliorate these effects might adversely affect fisheries and communities. Here, we evaluate trade-offs among a diverse suite of management objectives by simulating outcomes from several harvest strategies on forage fish species. We demonstrate that some trade-offs (like those between catches and minimizing collapse length) were universal among forage species and could not be mitigated by the use of different control rules. We also demonstrate that tradeoffs vary among forage fish species, with strong tradeoffs between stable, high catches and high-biomass periods ("bonanzas") for menhaden- and anchovy-like fish, and counterintuitive tradeoffs for sardine-like fish between shorter collapses and longer bonanzas. We find that harvest strategies designed to maintain stability in catches will result in more severe collapses. Finally, we show that the ability of assessments to detect rapid changes in population status greatly affects control rule performance and the degree and type of tradeoffs, increasing the risk and severity of collapses and reducing catches. Together, these results demonstrate that while default harvest strategies are useful in

[3] This work is currently in review for publication; coauthors are T.E.E. and Éva Plagányi (CSIRO).

data poor situations, management strategy evaluations that are tailored to specific forage fish may better balance trade-offs.

INTRODUCTION

A central tenet of ecosystem-based fishery management (EBFM) is that management decisions should consider not only the direct effects of extraction, but also the indirect effects that fisheries have on natural, economic, and social systems. Developing strategies for EBFM involves interdisciplinary, often computationally intensive approaches to complex adaptive systems (Berkes 2012). Many issues are not technically resolvable, requiring tradeoffs among diverse management objectives (see references in Link and Browman 2017) that arise in interconnected natural, social and economic systems (Charles 2001). Identifying the many tradeoffs associated with fisheries management decisions requires information about population dynamics, ecological interactions, and the needs of diverse stakeholders. When this information is not available, ecosystem-based management strategies must be robust to uncertainty.

The challenges of EBFM are manifested in forage species—small, schooling species like anchovies, sardines, and herring—which often play key roles in marine food webs, transferring energy from lower trophic levels to valued predators. Forage fish also support large commercial fisheries worldwide (Pikitch *et al.* 2014) and provide social and cultural benefits (Thornton *et al.* 2010; Levin *et al.* 2016). As such, they have been the focus of recent efforts to incorporate food web dynamics into fishery management (Garcia *et al.* 2003; Plagányi 2007; Kaplan *et al.* 2017). This presents a challenge to fishery managers, who seek to satisfy the needs of human communities (Thornton *et al.* 2010; Levin *et al.* 2016)– including a valuable fishing industry (Alder *et al.* 2008)– and the requirements of marine food webs.

Quantifying tradeoffs between different human priorities for forage fish is complicated by the fact that forage fish dynamics are highly variable and hard to predict. Forage fish characteristically undergo high-amplitude fluctuations in their productivity. These fluctuations occur in the absence of fishing (Chavez *et al.* 2003; McClatchie *et al.* 2017) but can be amplified by fishing when productivity drops rapidly and management fails to respond (Dickey-Collas *et al.* 2010; Essington *et al.* 2015). Regardless of their cause, collapses in forage fish abundance affect livelihoods for those involved in fishing and processing, and can cause shifts in predator diet, abundance and reproductive success (e.g., Francis *et al.* 1998; Kitaysky *et al.* 1999; Punt *et al.* 2016b; Kaplan *et al.* 2017). Rapid increases in abundance, on the other hand, are a boon for predators and provide opportunities for additional catches. Slow detection of these increases could potentially lead to lost fishing opportunities and revenue (Dickey-Collas *et al.* 2010).

Despite this shared characteristic of highly variable productivity, forage fish are a highly diverse group that vary significantly in their life history, drivers of productivity, and resulting patterns of abundance (see Dickey-Collas *et al.* 2014; Essington *et al.* 2015), presenting an additional challenge for management. For example, low-frequency variation is a dominant pattern for sardines (Baumgartner *et al.* 1992), whereas other species (like menhaden) exhibit high-frequency variation in productivity (Stenseth *et al.* 2005). Survey time series may not be long enough to capture full cycles of productivity, especially when low-frequency variation may occur on the scale of 60-100 years (Baumgartner *et al.* 1992). The presence of regime-like shifts in productivity has led to recommendations that forage fish be managed in synchrony with environmental changes (Fréon *et al.* 2005). The challenge of coping with long-term variability in forage fish productivity has inspired a diverse suite of forage fish management recommendations that are adaptable and resilient to changes in productivity, and explicitly consider uncertainty.

Recommendations for managing forage species globally tend towards approaches that can adapt to fluctuations in productivity. These recommendations include directly incorporating regime shifts in harvest rules (e.g., "regime-specific harvest rates"; King 2005), adaptive approaches that detect and respond to productivity shifts interannually (MacCall 2002; Jacobson *et al.* 2005), precautionary measures that maintain a buffer so that stocks can be resilient to changes in productivity (Cury *et al.* 2011; Pikitch *et al.* 2012), and highly adaptive rules that involve in-season adjustments. These have been implemented in several fisheries. In populations where forage fish are sensitive to environmental fluctuations, harvest strategies can account for productivity shifts by modifying allowable catches directly based on environmental conditions (e.g., sea surface temperature in Pacific sardine; Hill *et al.* 2014). The Pacific sardine and Peruvian anchoveta fisheries both have control rules with lower biomass thresholds that reduce or suspend catches when biomass is low (Fréon *et al.* 2008). The primary justification for these approaches is to buffer the population and the fishery against changes in productivity. A precautionary approach is also justified as a buffer for predators against variation in forage species (e.g., Antarctic krill; CCAMLR 2015). Finally, some fisheries have developed highly adaptive approaches that involve some combination of tradeoff analysis and adaptive management, including in-season adjustments and simulation analysis to negotiate tradeoffs with stakeholders (de Moor *et al.* 2011), as in the South African operational management procedure

(OMP) for sardine and anchovy (De Oliveira and Butterworth 2004). Despite the popularity of adaptive and precautionary measures, there is also some support for simpler control rules: constant harvest rate strategies can be robust to estimation errors and avoid overcapitalization (Barange 2009). Although diverse harvest approaches are available for forage fish given their importance to predators and their penchant for variability, there is reason to believe that the effectiveness of these approaches will vary among forage species and fisheries.

Harvest control rule performance may differ among species with different life history characteristics, particularly those with differences in maximum age and the amount of variability in productivity (Wiedenmann *et al.* 2013). Forage fish vary significantly in their longevity; for example, Atlantic menhaden live to a maximum age of 6 years (Atlantic menhaden; SEDAR 2015), whereas sardine can be up to 15 years old (Pacific sardine; Hill *et al.* 2014). Longer-lived fish with variable productivity could be expected to sustain more consistent catches if older individuals survive low-productivity years (i.e., through storage effects), whereas shorter-lived species could suffer collapses when consecutive low-productivity years are longer than the spawning age. The scale of recruitment variability likely interacts with life history to affect control rule performance: species with lower-frequency changes in recruitment like sardine, which notoriously fluctuate on the scale of ~ 60 years (MacCall 2009; Lindegren *et al.* 2013), might benefit from lower biomass limits (the biomass level at which the fishery is closed) that would protect the stock during lower-productivity periods, whereas less precautionary rules with little or no lower biomass limit might generate sustainable populations for highly variable species such as menhaden or anchovy.

Harvest strategy performance is likely also dependent on the ability of surveys and assessments to detect changes in biomass. Constant harvest rate strategies, in which fishing removes a constant fraction of the biomass, can in theory cope with the inherent uncertainty in highly variable fish populations (Walters and Parma 1996). However, in practice the effectiveness of constant harvest strategies is contingent on the accuracy of stock assessments, and additional harvest restrictions at low biomass can buffer against collapses when forecasts are inaccurate (Tommasi *et al.* 2017). Therefore, low, constant harvest rate strategies may perform well in general for forage species but poorly when observation errors lead to overestimated biomass, leading to overfishing when biomass is low. “Hockey-stick” rules, in which fishing mortality is constant above a target biomass and zero below a biomass limit (Pikitch *et al.* 2012) may also fail to buffer the population from collapse when changes are hard to detect, or depending on the delay, lead to unnecessarily lower catches when there is a lag between estimated and actual increases in biomass.

Despite this expected variation among forage species and the potential impact of survey accuracy on management performance, the “default” rules for forage fish have not been tested with a variety of forage fish types or using a broad array of social, ecological, and economic management objectives. Choosing among control rules requires one to understand the underlying trade-offs in the fishery (Link 2010) as well as key uncertainties that affect both trade-offs and performance (Punt *et al.* 2016a). A direct comparison of basic approaches should illuminate some tradeoffs between multiple objectives that are shared across strategies, and identify strategies that are most robust to uncertainty.

Here, we evaluate several alternative harvest control rules for distinct forage fish types, to compare their performance across a wide range of ecological, social and economic performance measures. The performance of each harvest control rule depends on stakeholder objectives; here we use management strategy evaluation (MSE; Butterworth and Punt 1999; Rademeyer *et al.* 2007; Punt *et al.* 2016a) to evaluate decision rules for management, using some common key stakeholder objectives identified in other studies. We show that a single "rule of thumb" approach may not work uniformly well for all forage fish, and that the performance of control rules for forage fish depends on their life history and the ability of stock assessments to detect rapid changes in biomass.

METHODS

We evaluated the performance of six harvest control rules for each of three forage fish types (anchovy/herring, menhaden, and sardine) according to a set of ecosystem and fishery objectives, and evaluated the tradeoffs among objectives under different biological and management scenarios. We simulated stocks of each of three life history types, based on generic life-history parameters from sardine, anchovy/herring, and menhaden populations. Recruitment deviations drove population dynamics in an age-structured operating model implemented in R (R Core Team 2017), in which recruitment deviations drive population dynamics, and catches were based on harvest control rules relating biomass to fishing rate.

Performance Measures

To describe the extent to which each control rule fulfilled management objectives, we identified a set of fishery performance measures (Table 3.1). These were intended to measure a broad range of priorities, including ecological needs for predators and the needs of fishers and fishery-dependent stakeholders such as processors.

Ecosystem objectives for forage fish biomass are notoriously hard to identify because predator needs are variable in time (Willson and Womble 2006) and space (Wolf and Mangel 2008; Plaganyi and Butterworth 2012), and predator numerical responses to prey depletion are poorly known (Abrams and Ginzburg 2000). We defined two thresholds based on unfished dynamics of the population biomass with recruitment variation: collapses and bonanzas. Collapses, which we define as biomass falling below 20% of mean unfished biomass, impose risk to predators because predator sensitivity to forage fish abundance increases when food is scarce (Cury et al. 2011). Extended collapses, in which collapse periods last at least two years and are preceded and followed by recovered periods, could have prolonged impacts on predators. Thus, avoiding collapses reduces the risk of adverse effects on predators and industry.

To quantify the ecological benefits of exceptionally high biomass, we introduce a new term, "bonanzas," defining years where biomass is above 80% of mean unfished biomass. Though empirical evidence for the benefits of bonanzas for predators is not strong, ecological theory suggests that predators may benefit during "bonanza" periods because when prey is abundant, forage populations will often expand their spatial ranges (MacCall 1990). In addition, species that share predators with forage fish might benefit from predators switching foraging tactics.

Control rules

We tested five harvest control rules that prioritize different performance measures (Table 2). Three control rules were modifications of a "hockey-stick" rule, where the fishing rate F was zero when biomass was below a limit threshold (referred to as B_{lim}) and increased linearly from 0 to Fmax when biomass is between B_{lim} and B_{target} (sometimes described as $B_{trigger}$ in ICES-managed stocks), and is constant at F_{max} above B_{target} (Figure 3.1). These modifications consisted of three hockey-stick control rules which represent a basic hockey stick, a case where B_{lim} is low relative to the base case ("Low B_{lim}") and one in which F_{max} is high ("High F_{max}") relative to the base case. Control rules with higher B_{lim} and lower F_{max} might be expected to minimize collapses or increase mean biomass. A fourth modification to the hockey-stick rule limited the extent to which the total catch could change from the previous year: while biomass was above B_{lim}, F was calculated such that total catch did not change by more than 15% from the previous year. This "Stability-favoring" rule was intended to reduce variation in catches. Finally, two constant-rate fishing rules were included at F = F_{MSY} and F = $0.5F_{MSY}$.

Model Framework

Each simulation comprised four steps: (1) Population dynamics simulated from an age-structured model; (2) annual biomass estimated from some assessment method; (3) Annual catch specified based on estimated biomass and harvest control rule. We describe each in turn, as well as key uncertainties in each that formed the basis of the MSE.

Population Model

The population was represented by an age-structured model, in which dynamics are driven by deviations from the stock-recruitment relationship (see "Recruitment Deviations" below).

$$N_{t+1,1} = R_{t+1} \quad \text{(age 0)} \tag{3.1}$$

$$N_{t+1,a} = N_{t,a-1}e^{-M-s_{a-1}F_t} \quad \text{(age 1+)} \tag{3.2}$$

$$N_{t+1,x} = N_{t,x-1}e^{-M-s_{x-1}F_t}+N_{t,x}e^{-M-s_xF_t} \quad \text{(plus group)} \tag{3.3}$$

where $N_{t,a}$ is the population size in year *t* and age *a*, s_a is the selectivity of the fishery on age *a*, F_t is the fishing mortality in year *t*, *M* is natural mortality, and *x* is the plus-group age.

Recruitment R_{t+1} was modelled as a Beverton-Holt stock-recruit relationship.

$$R_{t+1} = \frac{S_t}{\alpha+\beta S_t}e^{\varepsilon_t} \tag{3.4}$$

$$\alpha = SBPR_0 * \left(\frac{1-h}{4h}\right);\ \beta = \frac{5h-1}{4hR_0}$$

$$SBPR_0 = \sum_{a=1}^{x} N_a\, m_a$$

Where S_t is the spawning biomass in year t, α and β describe the initial slope and asymptote of the stock-recruit curve respectively, ε_t is the recruitment deviation in year *t*, $SBPR_0$ is the unfished spawning biomass per recruit, R_0 is the unfished recruitment, N_a are the numbers at age and m_a is the proportion mature at age a. α and β were parameterized from estimated unfished spawning biomass per recruit and steepness, the proportional reduction in recruitment from unfished equilibrium to 20% of unfished levels (Mace and Doonan 1988). Lower steepness indicates that more spawning stock is required to replenish the population when population size is low, i.e., that a forage fish stock must maintain high population sizes to avoid collapse. Forage fish steepness is often assumed to be high in stock assessments but low steepness could have serious implications for collapses, recovery from fishing, and population variability. We assume each forage fish type had distinct characteristics for ε (standard deviation and autocorrelation).

Annual catch of a fish aged *a* is calculated from the Baranov catch equation:

$$C_{t,a} = \frac{w_a s_a F_t}{M + s_a F_t} N_{t,a} (1 - e^{-M - s_a F_t}) \tag{3.5}$$

Where w_a is the weight at age of the fish.

Key biological uncertainties

An essential step in MSE development is to identify key uncertainties about the biology of the natural resource, the fishery, and the management system (Punt *et al.* 2016a). We identified uncertainties that might be particularly important for forage species: the stock effect on recruitment, and frequency of variation in productivity. We identified three forage fish life history "types," which bracket the range of life history variation found in fished stocks. These types vary in their productivity patterns and life history traits, including natural mortality, maximum age, and age at maturity. Life history parameters were taken from stock assessments and literature on stocks within each group, and productivity patterns were estimated from stocks in each category from time series of estimated recruitment in the RAM legacy database (Ricard et al. 2013; Table C1).

We sought to generate recruitment patterns similar to those observed in each of the forage fish types. We estimated time series characteristics (spectral β and standard deviation) of existing forage fish recruitment time series for each of three forage fish "types," and generated autocorrelated recruitment deviations based on a moving average model as follows:

$$\varepsilon_t = \rho\varepsilon_{t-1} + \omega_t \tag{3.7}$$

$$\varepsilon_{t=1} = 1$$

$$\omega_t \sim N(0, \sigma\sqrt{1-\rho})$$

Where values of ρ and σ define the autocorrelation and variability of recruitment deviations respectively (Figure 3.3). These recruitment deviations generated dynamics similar to those of recruitment time series estimated in real populations (Figures C4–C6), and generated collapse frequencies similar to those expected in wild stocks, when recruitment from the stock assessment were used in the operating model (Figure C7).

Recruitment estimates from stock assessments may be heavily influenced by fishing, especially in heavily exploited populations. Time series properties of simulated recruitment time series resembled those estimated from stock assessments (Figures C2–C4), and the number of collapses were similar in simulated populations to populations in the RAM legacy database (Ricard *et al.* 2013; Figure C5).

Observation Model

Observation error impacted the assumed accuracy of observations of total biomass. Observations of total biomass were used with the control rule to determine the proposed fishing rate. That fishing rate and the observed biomass were used to determine the total catch each year.

We assumed that annual estimates of population biomass are a function of true biomass plus observation error. We adopted a common error structure used in MSEs to represent observation error, as a simpler alternative to embedding a full assessment model within the MSE. Specifically, the estimated biomass in year t, $\hat{I}_t$, equals the true biomass (B_t) times a multiplicative error term:

$$\hat{I}_t = B_t e^{\epsilon_t - 0.5\varphi_t} \tag{3.8a}$$

$$B_t = \sum_{a=1}^{x} w_a N_{t,a}$$

The observation error at time *t*, ϵ_t, is based on the observation error in the previous time step ϵ_{t-1}, an autocorrelation parameter ϕ, and random log-errors φ_t around the true biomass:

$$\epsilon_t = \phi\epsilon_{t-1} + \sqrt{1-\phi^2}\varphi_t \tag{3.8b}$$

$$\varphi_t \sim N(0, \sigma_s{}^2) \tag{3.8c}$$

Here, we use ϕ = 0.5 and $\sigma_s = 0.3$. This simplified model adequately describes basic observation error for a variety of stocks. However, errors may have more structure for species that have unique dynamics. In forage species, these errors could be related to the magnitude of change in the true population size: if assessments are not able to predict or detect large changes in abundance, observation error could lead to a lag in responsiveness of assessment. Therefore, to explore this possibility as an uncertainty analysis, we developed a novel model that simulates an assessment or survey that is resistant to accepting dramatic changes in biomass.

Uncertainties in Observation Model

A unique challenge to the accurate assessment of forage species abundance is that assessments may not detect large and rapid changes in biomass. These large changes can be detrimental for the fishery, if the assessment underestimates biomass in particularly productive years. They can also be detrimental with respect to ecological objectives, if the survey or assessment does not predict large declines in biomass, overestimating the biomass in a collapse year and leading to overfishing (Essington et al. 2015). We used this novel observation model to simulate the condition where assessments lag true changes in biomass.

This estimator resembles a case where the analyst or the assessment model is reluctant to predict large changes in biomass from one year to the next. Its mathematical roots are based in Bayes theorem, where there is a prior expectation regarding the magnitude of interannual change in biomass. There is random error in estimated biomass each year, plus a bias towards predicting small changes as determined by prior expectation on the mean annual change. The prior expectation is described by a normal distribution, with a mean 0 and variance ${\tau_0}^2$. High variance implies a weak prior belief such that the assessment more closely tracks true population change, whereas small variance in the prior implies a strong prior belief that interannual changes should be small, leading to shrinkage towards the prior mean of 0 change from one year to the next (Gelman 2014).

We denote biomass in year *t* as B_t, and the estimated biomass the previous year as $\hat{I}_{t-1}$. We introduce y_t as the log-ratio of $B_t/\hat{I}_{t-1}$:

$$y_t = \log\left(\frac{B_t}{\hat{I}_{t-1}}\right) \quad (3.9)$$

We assume that observations of $\log(B_t)$ are normal with mean $\log(B_t)$ and some observation error, ${\sigma_0}^2$. The variance of the prior mean of y is denoted ${\tau_0}^2$, which governs the degree to which assessment-based estimates track true populations. When τ_0 is large, the analyst believes the "data" and estimates changes that track true changes closely. When τ_0 is small, the analyst discounts the data and predicts population abundance in year *t* that is more similar to $\hat{I}_{t-1}$ (Figure 3.4).

$F(y_t)$ is the posterior probability distribution describing the expected change in biomass based on the log-ratio y_t and the prior belief about whether big changes in biomass are believable, $\left(\frac{1}{{\tau_0}^2}\right)$ (Gelman 2014):

$$\hat{I}_t = \begin{cases} B_t e^{\varepsilon};\ \varepsilon \sim N(0, {\sigma_0}^2) & t = 1 \\ E_{t-1} e^{F(y_t)} & t \geq 2 \end{cases} \tag{3.10}$$

$$F(y_t) \sim N(y_t - y_t\left(\frac{{\sigma_0}^2}{{\tau_0}^2 + {\sigma_0}^2}\right), {\tau_1}^2) \tag{3.11}$$

Where:

$${\tau_1}^2 = \left(\frac{1}{{\tau_0}^2} + \frac{1}{{\sigma_0}^2}\right)^{-1}$$

The key difference in this model compared to the base model is that is that the mean of the observation errors is not 0, depending instead on the prior and the rate of change in the population. Thus, E_t is based on E_{t-1} and on the true biomass, as opposed to the true biomass and the observation error in the previous year. We specified values of τ_1 and τ_0 based on the amount of error in the base model, and the degree to which we thought assessments might be resistant to estimate large changes in biomass, respectively. σ_0 and σ_s (from the base model) were selected so that each observation model generated observations with a similar error structure.

Management Model

$\hat{I}_t$ was translated into F_t using each of the control rules in Table 3.1. Each year, a total allowable catch was set based on F_t and $\hat{I}_t$, and this catch was removed from the population after recruitment occurred.

RESULTS

Base Case

We found a small set of tradeoffs that were consistent across forage fish type, but a broader pattern of tradeoffs varying by life history type. Unsurprisingly, we found that tradeoffs between catches and mean biomass were universal among forage fish types and could not be mitigated by the use of different control rules (Figure 3.5). Likewise, it was not possible to maximize catches while also maximizing catch stability or bonanza length, or minimizing the probability of a collapse. These tradeoffs were consistent across scenarios and forage fish life history types: even when steepness was high, there were strong tradeoffs between maximizing catches and having fewer collapses or longer bonanza periods (Figures 3.5–3.7; Figures C8-C10). Larger catches were inherently more variable, introducing an unavoidable tradeoff between overall stability and total amount of catches. Control rules that minimized years with zero catch performed most poorly in terms of minimizing the length and severity of collapses and vice versa.

Whereas we found some consistent tradeoffs across life history types and scenarios, it was also true that life history type affected which tradeoffs were most pronounced. For example, the low B_{lim} rule was able to minimize collapse length and closures for menhaden, ensuring low but stable catches. However, no control rule performed similarly for sardine and anchovy, indicating that having fewer closures necessarily led to longer collapses for sardine- and anchovy-like fish, regardless of the control rule. A low, constant fishing rate maximized bonanza length while maintaining high biomass, minimizing closures and stabilizing catches for sardine and anchovy, while the Low B_{lim} rule did the same for menhaden (Figure 3.5, left panel). The best-performing rule for some metrics varied across forage fish types as well. The rule that minimized collapse length was different for each fish type: Low B_{lim} and High F_{max} were best for menhaden, Basic hockey stick for anchovy, and the stability-favoring rule for sardine (Figures 3.5–3.7).

Sardine-like fish had some distinguishing properties from the other forage fish types. A tradeoff between maximizing bonanza length and minimizing collapse length was apparent for sardine but not for other types (Figure 3.5; Figure C10). Finally, there were strong tradeoffs between catch stability and ecological metrics (minimizing the probability of a collapse, and minimizing the length and severity of those collapses) for sardine, but a low constant fishing rate ($F = 0.5F_{MSY}$) simultaneously minimized closures, maximized biomass, and maximized bonanza length. The stability-favoring rule overcame tradeoffs between maximizing catches and minimizing collapse length for sardine-like fish, but for other species was either not effective at those two management goals or was outperformed by a hockey-stick rule (Basic hockey stick, Low B_{lim}, or High F_{max}).

The control rule intended to stabilize catches was generally successful at stabilizing catches, but caused longer, more severe collapses and led to greatly reduced catches relative to other control rules. The "stability-favoring" rule, which is essentially a hockey-stick control rule that stipulates total catches must not change by more than 15%, had high catch stability overall (Figure 3.5, all three panels). However, the stability stipulation resulted in a fishery that was not adaptable to changes in productivity, unable to take advantage of short-term increases in productivity, and causing catastrophic collapses when sudden decreases in productivity corresponded with higher catches. The overall result of the stability favoring rule was low catches for long stretches– resulting in high mean biomass and longer bonanzas than other control rules– followed by long, severe collapses when catches were high relative to biomass (Figure 3.5). The stability-favoring rule did not perform as intended when accounting for differences in average catch; across all forage fish types the CV of catches was 2.2–2.3 for the stability-favoring rule and 0.6–0.8 for the low, constant fishing rate. Other control rules maximized catches better than the stability-favoring rule in every scenario (Figures 3.5–3.7), with the hockey-stick rules (Basic hockey stick, Low B_{lim}, and High F_{max}) consistently outperforming the stability-favoring rule by at least 30% (Figures 3.5–3.7). The next best rule for stabilizing catches was a rule with low, constant fishing ($F = 0.5\ F_{MSY}$) anchovy and sardine, and two hockey-stick rules (Basic hockey stick and Low B_{lim}) for menhaden. The stabilization afforded by more conservation-based strategies for menhaden came at the cost of lower mean catches, and more fishery closures.

With respect to conservation objectives, hockey-stick rules expected to preserve ecological functions (Basic hockey stick, Low B_{lim}, and High F_{max} control rules) achieved these goals for all forage fish types, resulting in higher long-term mean biomass and shorter, less severe collapses (Figure 3.5). This result was robust to different steepness, but sensitive to the ability of the survey to detect changes in biomass (Figures 3.5–3.7; Tables C3–C5). The low, constant F rule led to slightly (1-2 years) longer bonanzas for anchovy and sardine but the Basic hockey stick rule led to the longest bonanzas in menhaden. In general, the high biomass and shorter, less severe collapses came at a cost to catches, leading to more closures than other control rules and thus lower long-term catches. However, among years when the fishery was open, catches for all forage species were maximized by the High F_{max} rule. This result changed in the delayed detection scenario, with the stability-favoring rule maximizing nonzero catches when large changes were difficult to detect.

Ability to detect changes

We found that control rule performance was sensitive to the ability of the assessment or survey to detect large changes in biomass, with negative consequences especially with respect to total catches and collapses. For all forage fish, delayed detection of peaks reduced catches by 2-45%, with a corresponding reduction in catch variability (Figure 3.8). Collapse severity increased for sardine and anchovy forage species (2-58%; with the strongest impacts on anchovy), and length of collapses increased by up to 57% across all forage fish types. The probability of a longer (five-year) fishery closure increased or remained the same among forage fish types between the base case and the delayed detection scenario.

The negative impacts of delayed detection on collapses and bonanzas varied by life history type and were in some cases mitigated by the use of more ecologically precautionary control rules. Across performance metrics, anchovy was impacted the most strongly by a delayed detection scenario. An inability to anticipate rapid changes in biomass resulted in higher probability of collapse (+30-83%), and longer, more severe collapses for anchovy, regardless of the control rule (Figure 3.8). Under some control rules (Low B_{lim}, or High F_{max}), there was also a higher probability of a five-year closure for anchovy. For all forage species, delayed detection of changes in biomass led to an increase in the length of bonanzas (1-2 years longer), but nearly twice as severe collapses (a 58% increase) when they occurred (Figure 3.8). Collapses for all species were the same length or longer when there was delayed detection of changes in biomass (Figure 3.8).

Some of the negative effects of delayed detection were mitigated by the use of different harvest control rules, and the rules that best mitigated these effects depended on the life history type. For example, collapse severity actually decreased slightly when the basic hockey-stick and High F_{max} rules were used for menhaden, as opposed to the 10-58% increases in severity under other control rules (Figure 3.8). Populations could also be 'rescued' from long collapses: when the basic hockey stick rule was used for anchovy and sardine, negative impacts were minimized. This also occurred when the High F_{max} rule was used for sardine.

The extent to which tradeoffs were affected by delayed detection also differed among life history types: Although performance on individual measures changed (Figure 3.8), tradeoffs for menhaden were not strongly affected by the delayed detection scenario (Figure 3.7), and only noticeably affected tradeoffs for anchovy by diversifying the performance of control rules with respect to the probability of a 5-yr closure. For sardine, however, tradeoffs between ecological objectives (minimizing the number, severity, and probability of collapses occurring) and minimizing catch stability were also enhanced in the delayed detection scenario relative to the base case. The stability-favoring rule performed particularly poorly in a delayed detection scenario for sardine, causing a higher probability of collapse and longer collapses under delayed detection, relative to other control rules (Figure 3.7).

DISCUSSION

We found that inherent tradeoffs between management objectives cannot be resolved by a single harvest control rule for all forage fish; rather the management approach that works best to resolve tradeoffs is life history- and context-dependent. We also found that tradeoffs are sensitive to biological uncertainty (mainly, the stock effect on recruitment) and observation uncertainty (whether or not large changes are detectable by the survey or assessment). Because of their importance in marine food webs, marine fisheries, and industries that rely on forage fish for feed, forage fish stocks are at the nexus of several, sometimes conflicting, human priorities for management. Our results suggest that while some tradeoffs are unavoidable regardless of forage fish life history or harvest strategy, others can be mitigated if management decisions account for their different productivity patterns.

Recommendations for forage fish management often focus on risk mitigation for ecological needs or to maximize catches, with the implicit assumption that mitigating impacts on predator growth, survival and reproduction will come at a cost to fishery catches. We found that some of these tradeoffs were unavoidable with conventional harvest strategies: maximizing catch, for example, always came at the cost of longer collapses, lower mean biomass, and shorter bonanzas regardless of life history or productivity patterns. While some of these tradeoffs are expected based on basic properties of fisheries (like the tradeoff between catches and catch stability; Smith 1994), others are less intuitive. Risks to predators may depend on the availability of certain size or age classes of prey (Sogard 1997) or the availability of prey in certain locations (Plaganyi and Butterworth 2012), and our metrics for ecological scenarios are based on total biomass. Therefore, it is possible that tradeoffs will be less strong for predators that either specialize on sizes not selected by the fishery, feed in locations where forage populations contract in times of low density, or can switch prey when some forage fish are not available. Our results highlight that some tradeoffs will consistently emerge among the diverse forage fish and fishery types, and resources may be better invested in adapting to these accepted tradeoffs than in devising more complex control rules.

Although there were some common tradeoffs across species and scenarios, we found a broader pattern of tradeoffs being dependent on forage fish life history: sardine-like species in particular exhibited different tradeoffs than anchovy- and menhaden-like fish. For example, HC3, a rule with a high F_{max} mitigated a strong tradeoff between minimizing longer closures and maximizing biomass for sardine. Were this rule applied to menhaden, it would lead to shorter collapses, but a high probability of closures occurring. Recommendations for forage fish management can be broad in order to mitigate risk (Cury *et al.* 2011; Pikitch 2015) or they are tailored to specific stocks, based on the biology of a specific system (Punt *et al.* 2016b). Here, we show that the “best” rule for maximizing performance of forage fish stocks might be one tailored to the life history of the species, the tradeoffs involved in the fishery, and stock-specific uncertainties.

Because of the high degree of variability in forage fish populations, stabilizing catches might be an important performance measure when processors are involved. The “stability-favoring rule,” in our study achieved its intended purpose at great cost to the fishery and ecosystem (Figures 3.5–3.7). This control rule resulted in low, stable catches much of the time, but caused long, severe collapses when catches were not more adaptable to rapid changes in productivity. This is particularly evident in the case of menhaden, the forage fish type with the highest amount of interannual variation in productivity (Figure 3.3; Figure 3.7). This result suggests that processors must choose between adapting to highly variable catches, or sacrificing total fish meal and production for a consistent supply. Hockey-stick rules were better able to enhance catch stability while also enhancing catches (Figure 3.5). Among the control rules not designed specifically for catch stability, the low-constant F rule stabilized catches best for anchovy and sardine, indicating that simpler rules might be sufficient for achieving this objective. Walters and Parma (1996) found that fixed exploitation rate strategies can lead to nearly-optimum yields, as long as there is some interannual correlation in environmental influences (in this case, changes in recruitment) or an ability to anticipate large changes in productivity. Here, we found that although a low, constant exploitation was effective with respect to many performance measures, constant fishing rate strategies were sensitive to delays in the detection of large changes in biomass and to steepness (Figures 3.5–3.7). Thus, the benefits of maximizing multiple objectives with constant F rates must be balanced with the risks of collapse and low biomass. Upper catch limits might also reduce price pressure and improve outcomes for multiple countries in cases where the stock moves between territorial waters of multiple countries.

In terms of improving basic ecological metrics for control rule success, we found that rules with a lower biomass limit were indeed effective for reducing the risks of collapse and the severity of collapses when they occur (Figures 3.5–3.7). These "stop-loss" rules have been recommended for forage species previously (Pikitch *et al.* 2012; Pikitch 2015) for these reasons. We found that they did come at a long-term cost to catches relative to other control rules, but that catches were high among years when the fishery was open, suggesting that a highly adaptable fishery might be able to take advantage of erratic catches while still minimizing the risk and severity of a collapse. This result is consistent with previous research that suggests hockey stick and other rules with biomass thresholds can achieve similar long term yields but at the cost of high interannual variation in catches (Smith *et al.* 2011). Regardless of the survey error scenario, hockey-stick rules performed best for minimizing collapses and collapse severity. Under circumstances with an accurate, adaptable assessment or management plan, rules with a biomass limit may yield long-term catches similar to more aggressive control rules.

There is reason to believe that the ability to detect large changes is an influential factor in determining an appropriate control rule. A poorer ability to detect big changes could have both ameliorating or exacerbating effects on a population: If the assessment underestimates the actual biomass, annual catch levels may be less than those prescribed by the harvest control rule. On the other hand, delayed detection may exacerbate the issue in populations that are heavily fished, if the biomass is overestimated and unintentional overfishing occurs. We found that delayed detection reduced catches, and increased the severity and duration of collapses, especially for anchovy. Anchovy have strong interannual variability but less autocorrelated productivity. When declines in abundance occurred in the delayed detection scenario, assessments would be slow to respond, allowing a high fishing rate even when stocks were declining. This was in contrast to menhaden populations, for which delayed detection of large changes had a dampening effect on fishery extractions (Figures 3.5–3.7); and sardine, which generally seemed to sustain more severe impacts when there were delays in detection. Our analysis indicates that populations managed with hockey-stick rules would be more resilient to the negative impacts of delayed detection than those managed with other control rules (Figures 3.5–3.7).

More adaptive, responsive control rules are one solution to the challenge of detecting changes in forage fish biomass. Our analysis indicates that managers may have to make a choice between investing in faster responses and losing catch by being more precautionary. The fact that tradeoffs changed for sardine but less so for the other fish under delayed detection demonstrates that management should consider survey uncertainty in balancing tradeoffs, especially for species with low-frequency variation in abundance.

The pattern of delayed anticipation of peaks is not characteristic of all management plans or assessments. In-season surveys of juvenile abundance in some fisheries are used to adjust the quota within the fishing season (e.g., in South African sardine and anchovy fisheries; Coetzee et al. 2008; de Moor et al. 2008). Within-season quota adjustments are also used to cope with rapid changes in abundance. Our results demonstrate that fishing and processing industries stand to benefit from improvements in detecting or adapting to rapid changes in biomass, especially stocks with stronger low-frequency variation like sardine. When changes are difficult to detect, conservative control rules perform better than harsher rules for sardine-like species, underscoring the importance of control rules that are tailored to these unique productivity patterns.

Although we have attempted to bracket the range of control rules used and/or suggested for forage species, we have also demonstrated control rule performance and tradeoffs with relatively data-rich strategies, and tailoring them requires a relatively strong knowledge of life history and stock status. As information about stock status and life history is reduced, more precautionary measures such as lower catch rates are likely needed (Pikitch *et al.* 2012). Increasing catches in data-poor situations can significantly increase risk unless there is also investment in data collection to improve the precision of biomass estimates (Little *et al.* 2016). Data-poor approaches (see review in Dowling *et al.* 2015) are sensitive to the manner in which trends in CPUE or biomass are linked to changes in the total allowable catch, so we have not included them here. Data-poor approaches may be a viable avenue for forage fish management but should be tested extensively before being recommended for forage species.

This analysis highlights the possibility that some tradeoffs will consistently emerge among diverse forage fish and fishery types, and resources may be better invested in adapting to these accepted tradeoffs than in devising more complex control rules. However, other control rules will perform better when they are tailored to the life history and productivity patterns of specific forage species. We do not intend that these results be used to guide specific management decisions, but to demonstrate the inherent tradeoffs involved in managing forage species and the importance of life history diversity in decision-making. In addition to considering the role of forage species in the ecosystem and the spatial distribution of the fishery relative to predator needs, decision-making for real forage stocks should incorporate uncertainty in life history and recruitment dynamics, including specific patterns of potential changes in growth or mortality. Moreover, practitioners should consider control rules that are feasible given data availability and current management strategies.

Table 3.1 Performance measures and their definitions.

Performance metric	Definition
Maximize average catch	Mean long term catches
Minimize catch variability	Standard deviation of annual catches
Maximize years with nonzero catches	Number of years with nonzero catch
Minimize probability of a 5-year closure	Probability of a 5-year closure given that a closure of some length has occurred
Maximize bonanza length	Mean number of years in a bonanza period (when $B_t > 80\% B_0$)
Minimize collapse length	Mean number of years in a collapse period (when $B_t < 20\% B_0$)
Minimize probability of collapse	Annual probability of a collapse occurring
Minimize collapse severity	Among collapse periods, severity = $1 - B_{collapse} / 0.2B_0$
Minimize the number of sustained **collapses**	Number of collapse periods longer than two years, preceded and followed by 4 years of non-collapsed "recovery" state

Table 3.2 Harvest control rules tested in this study.

	B_{lim}	B_{target}	F_{max}	**Other**	**Citation**
Basic hockey stick rule	$0.4B_0$	$0.8B_0$	0.5M	-	Consistent with proposed default control rules from Lenfest and MSC guidelines (Pikitch et al. 2012 p. 100)
Low B_{lim}	$0.1B_0$	$0.8B_0$	0.5M	-	Basic hockey stick rule with lower B_{lim}
High F_{max}	$0.4B_0$	$0.8B_0$	F_{MSY}	-	Basic hockey stick rule with higher F_{max}
Stability-favoring[4]	$0.5B_{MSY}$	B_{MSY}	$F = F_{MSY}$	Additional step: if biomass is above biological limits, catch cannot change by >15%	Loosely based on the Common Fisheries Policy (European Commission Brussels, May 30 2008)
Constant F - High	-	-	-	$F = F_{MSY}$	-
Constant F - Low	-	-	-	$F = 0.5F_{MSY}$	-

[4] This control rule is loosely based on the Common Fisheries Policy (CFP) guideline that catch should not change by more than 15% from one year to the next. In this rule, potential catch is determined from the harvest control rule. If that potential catch is more than 15% different than the previous year's catch, the catch is set to 15% away from (either more or less than) the previous year's catch.

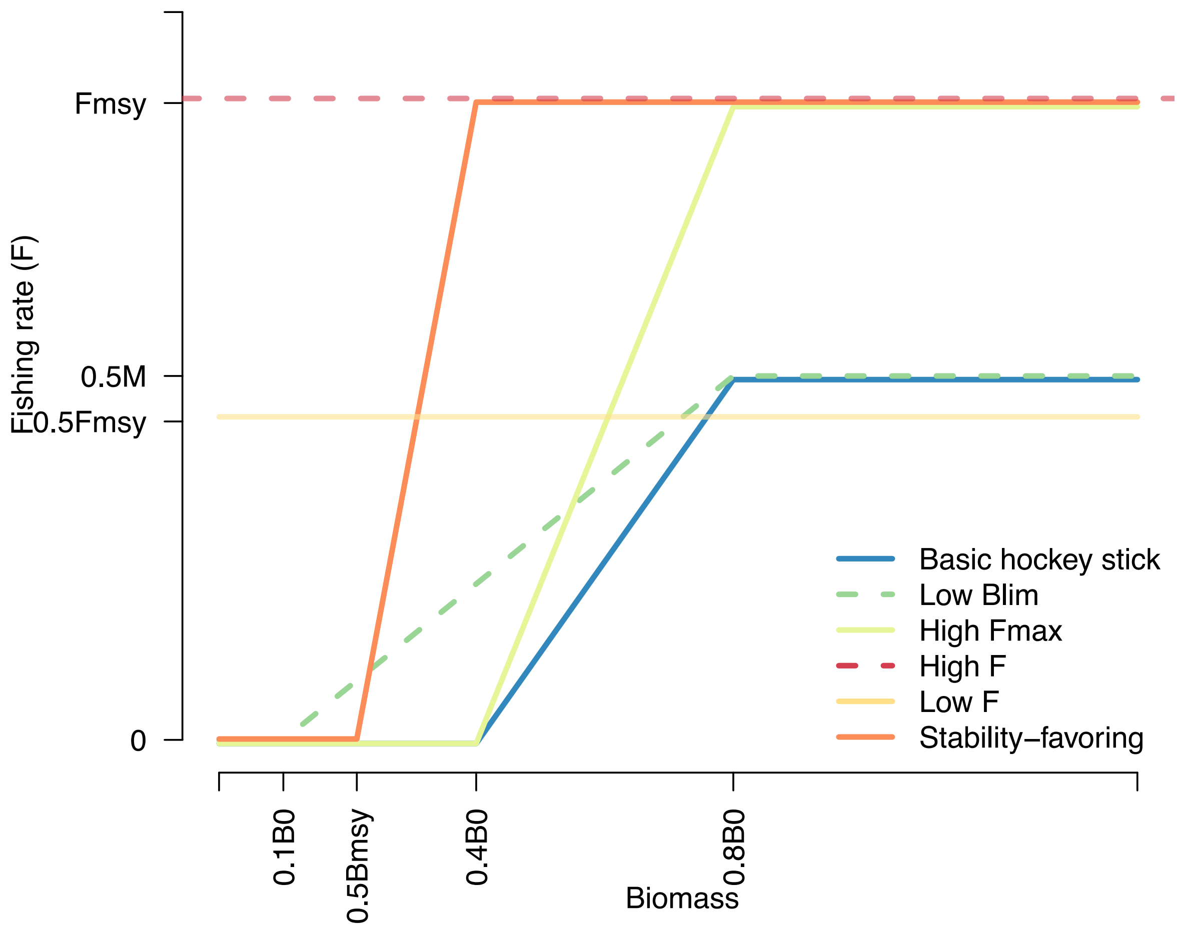

Figure 3.1 Harvest control rules.

Harvest control rules used in this study. The “stability favoring” rule has an additional qualification that catch cannot change by more than 15%.

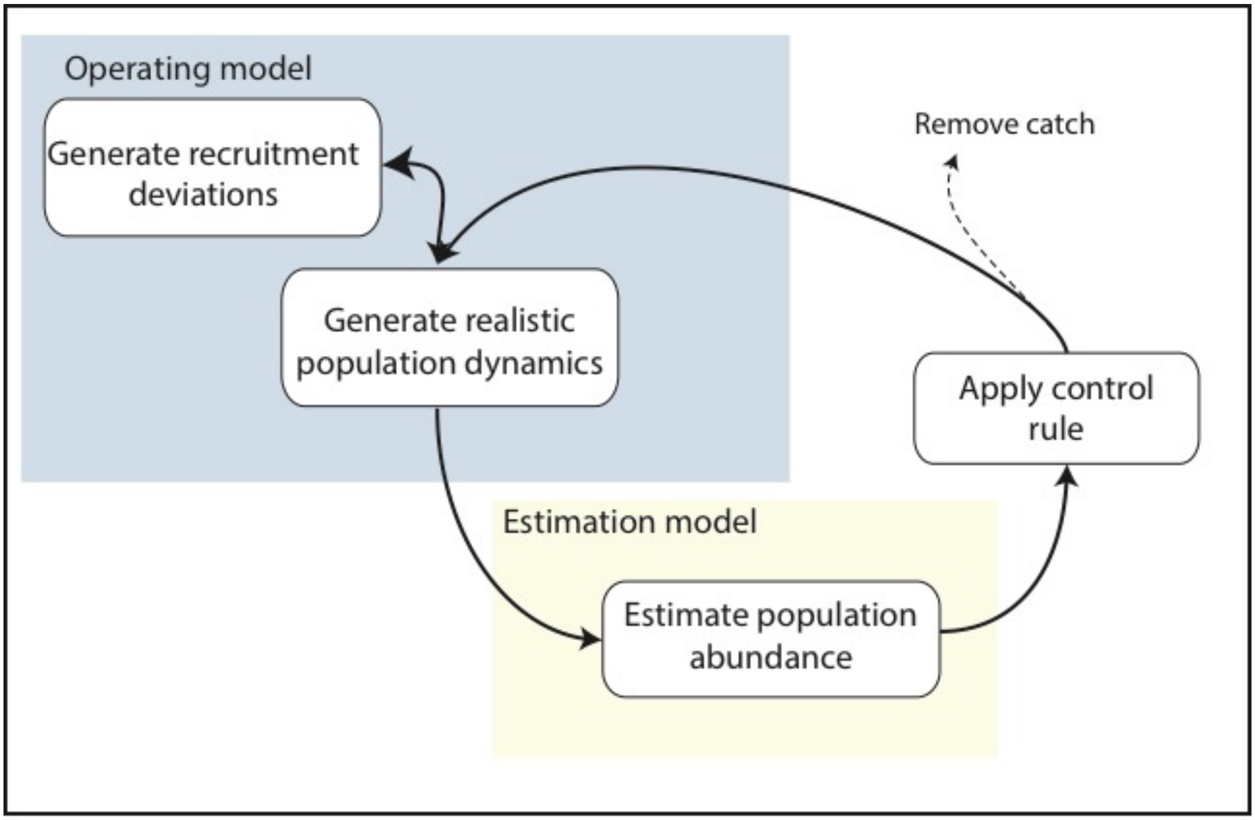

Figure 3.2 Management strategy evaluation structure.

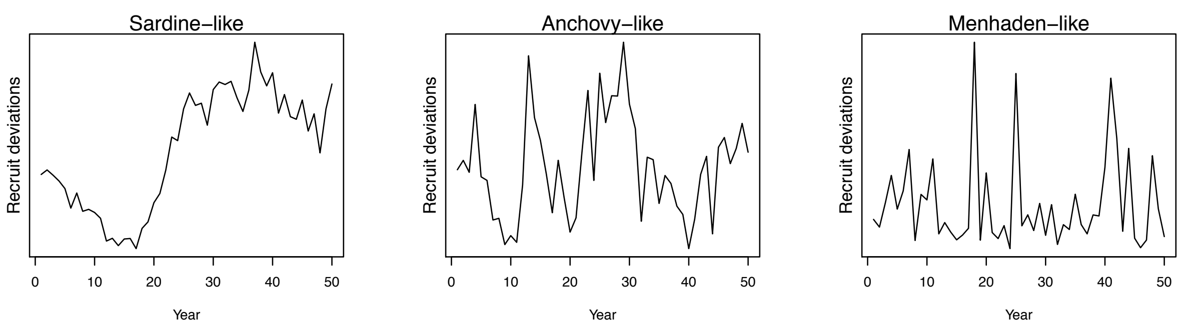

Figure 3.3 Simulated recruitment deviations

Examples of deviations around Beverton-Holt recruitment for (a) Sardine-like (b) Anchovy-like and (c) Menhaden-like life history types. Recruitment deviations are based on basic time series properties of recruitment for each forage fish type.

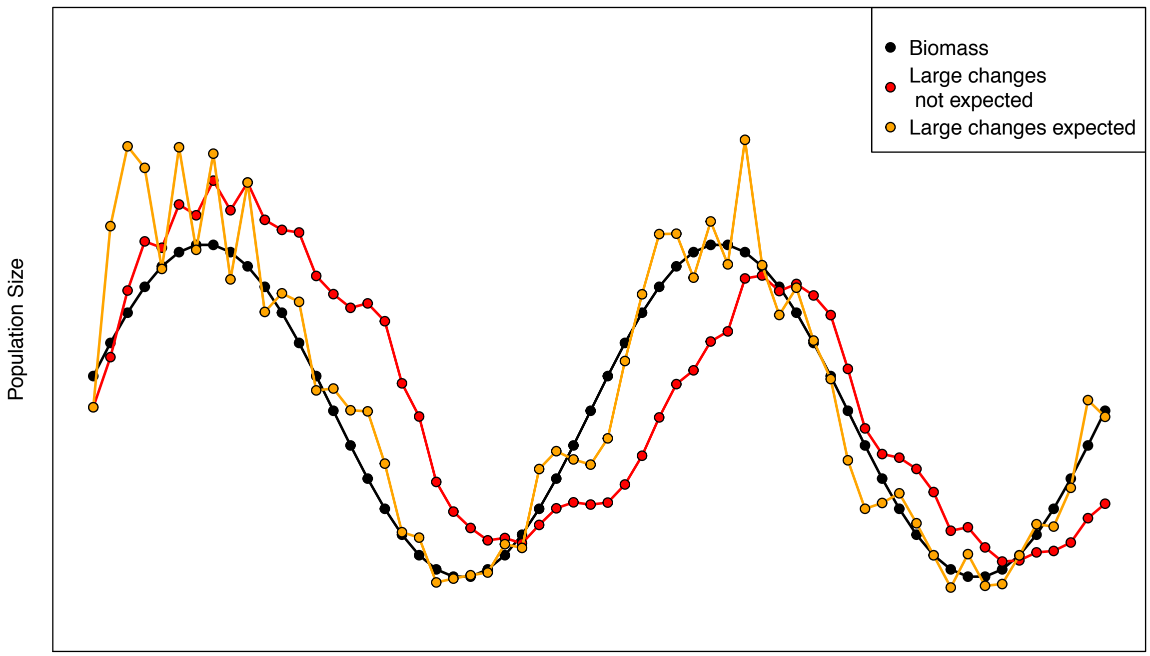

Figure 3.4 Delayed detection model

The “delayed detection” model under low (τ_0 = 0.1; red points) and high (τ_0 = 1000; orange points) expectation of large interannual population changes. Black points represent the true biomass. When τ_0 is low, this estimator represents a case where the analyst or the assessment model is reluctant to estimate large changes in biomass from one year to the next.

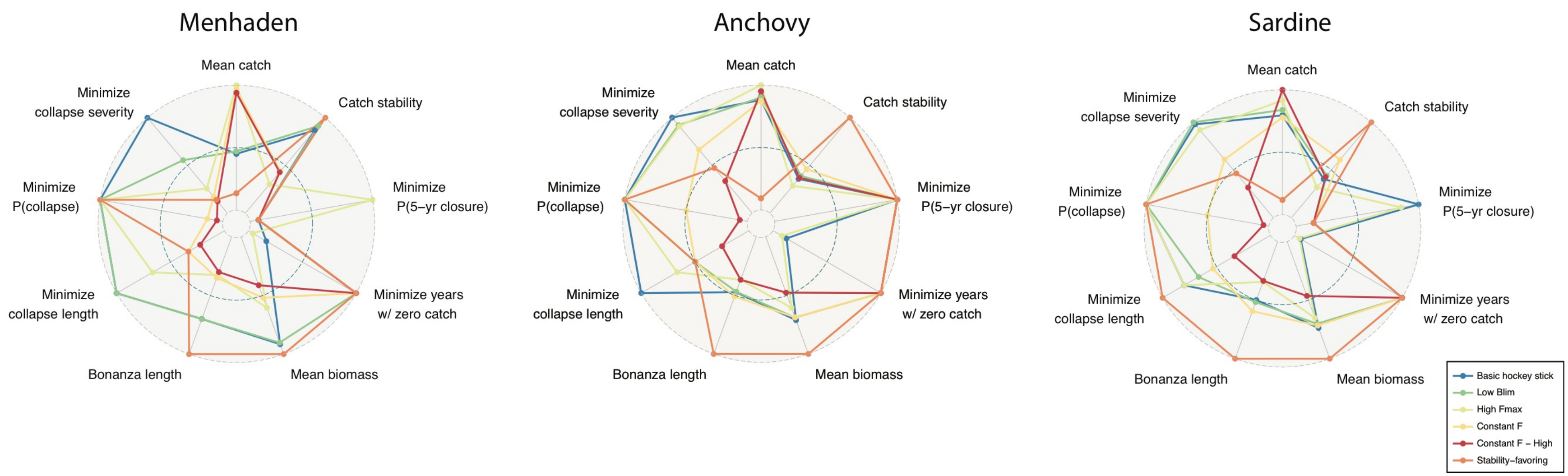

Figure 3.5 Tradeoffs in base case.

Tradeoffs between control rules for menhaden, anchovy, and sardine, in the **base case** (autocorrelated observation error; h = 0.6). Performance is scaled so that 1 = best performance. These tradeoff plots assume equal weighting in evaluating performance scores, which is important to keep in mind when interpreting them.

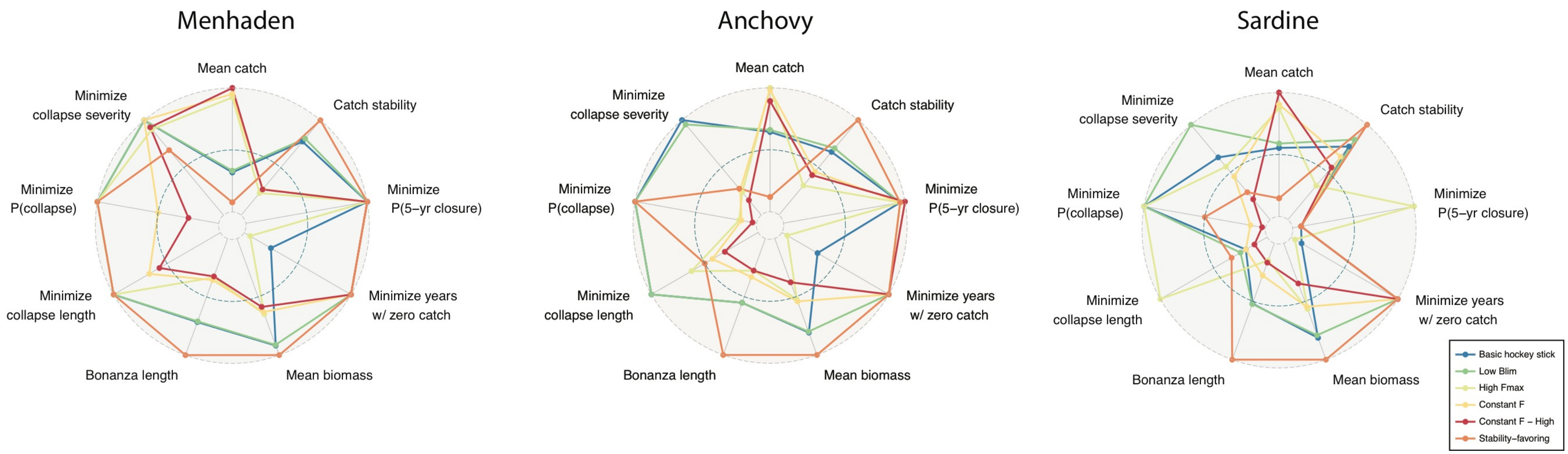

Figure 3.6 Tradeoffs in high-steepness case

Tradeoffs between control rules for menhaden, anchovy, and sardine, in the **high-steepness case** (autocorrelated observation error; h = 0.9). Performance is scaled so that 1 = best performance.

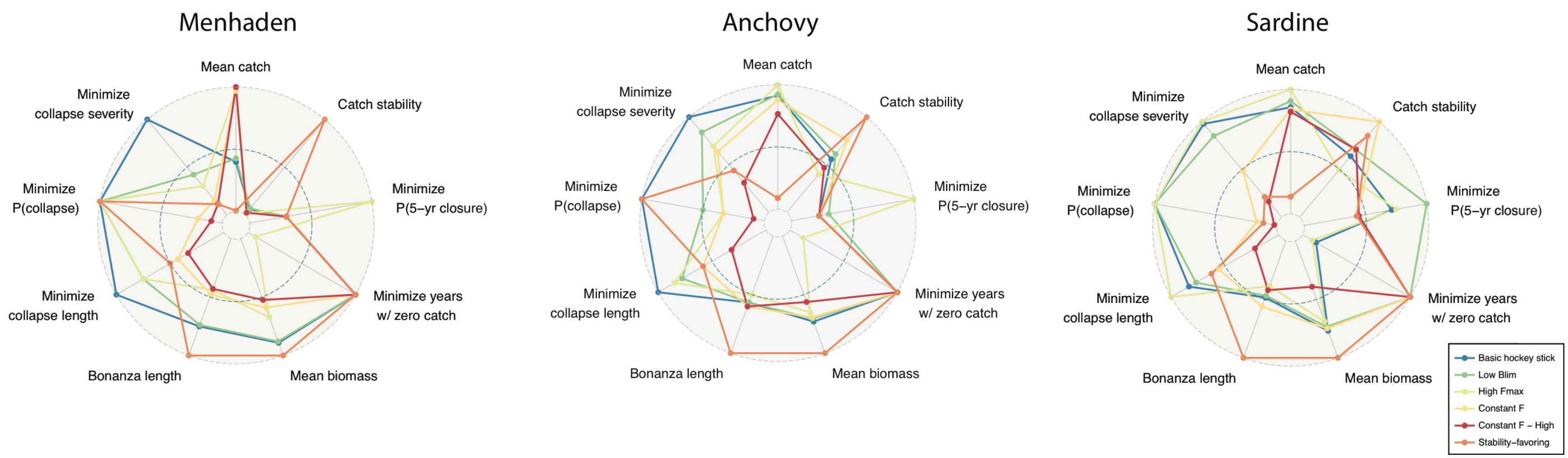

Figure 3.7 Tradeoffs in delayed detection scenario

Tradeoffs between control rules for menhaden, anchovy, and sardine, in the case where large changes in biomass are hard to detect ("**delayed detection**"; h = 0.6). Performance is scaled so that 1 = best performance.

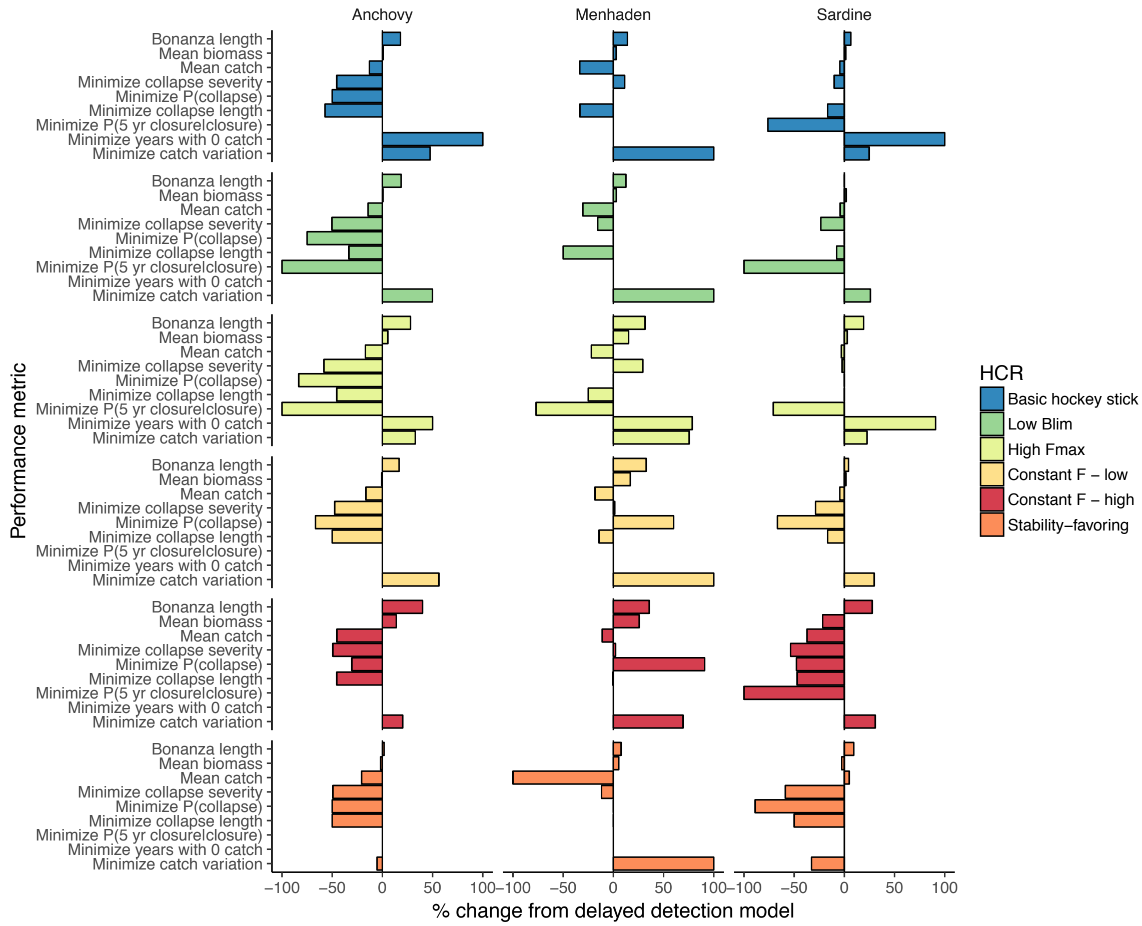

Figure 3.8 Effects of delayed detection on performance metrics

Percent change in performance metrics when assessment is slow to detect population change.

Chapter 4. EVALUATING ASYNCHRONY AND REPLACEMENT BETWEEN SARDINE AND ANCHOVY[5]

ABSTRACT

Sardine (*Sardinops* spp.) and anchovy (*Engraulis* spp.) are globally distributed genera that co-occur in upwelling ecosystems worldwide. Sardine and anchovy are hypothesized to have asynchronous dynamics on short (interannual) and longer (decadal) time scales, creating the impression that they might replace one another as key forage species in upwelling ecosystems. Using several time series of landings, biomass, and recruitment estimates, we show that anchovy and sardine are not replaceable in terms of total biomass (peak biomass differs between 22–230% between sardine and anchovy, and median biomass differs between 2–160%) or landings (a 3–189% difference in maximum landings and 46–133% difference in median landings), indicating that even if the dynamics of the two species were asynchronous, low productivity for the dominant species cannot be fully compensated for by high productivity of the other species. We use wavelet analysis and a time series approach to demonstrate that patterns of asynchrony in sardine and anchovy are generally not detectable at interannual or longer time scales (appearing in only the two of five large marine ecosystems), and that patterns of asynchrony at these time scales may instead be a statistical relic of observing short time series with low-frequency fluctuations. Finally, we use a simulation approach to show that power to detect asynchronous patterns at long time scales is poor, generally requiring 100-200 years of observations to detect decadal-scale asynchrony. Together, these results suggest that asynchrony does not necessarily buffer food webs and fisheries from

[5] When this chapter is submitted for publication, coauthors will be T.E.E. and Lewis A. K. Barnett.

variability and that perceived patterns of asynchrony from short time series should be interpreted with caution.

Introduction

Forage fish management is challenged by the apparent sensitivity of forage fish to the environment and by the unpredictable nature of shifts in productivity. One consequence of the sensitivity of productivity to environment has been the replacement of species in communities as the environment shifts to favor one species over another. This has been most widely documented for sardine (*Sardinops* spp.) and anchovy (*Engraulis* spp.) (Kawasaki and Nihon 1991; Lluch-Belda *et al.* 1992; Schwartzlose *et al.* 1999; Chavez *et al.* 2003; Alheit and Bakun 2010). populations, two genera that contribute 50% or more of total marine fishery landings (Fréon *et al.* 2005) and are important prey for a number of marine predators (Crawford *et al.* 2008; Cury *et al.* 2011). They are often predominant forage species where they occur, as one of a few mid trophic level species occupying the "wasp waist" of highly productive marine ecosystems (Vasconcellos *et al.* 1997; Cury *et al.* 2000; Shannon *et al.* 2000).

Decadal-scale alternations between sardine and anchovy have appeared in several of the world's large marine ecosystems (Kawasaki 1983). Evidence that sardine and anchovy populations are asynchronous includes rapid increases in anchovy abundance when sardine abundance is declining (Lluch-Belda *et al.* 1989, 1992; Schwartzlose *et al.* 1999), corresponding oceanographic changes that suggest anchovy and sardine benefit from different environmental conditions (Chavez *et al.* 2003), and changes in ecosystem structure, which have been termed "ecological regime shifts" because of the long-term nature of the changes and the combination of intrinsic and extrinsic factors driving sardine and anchovy abundance (Alheit et al. 2009). Extrinsic factors that occur at similar timescales to sardine and anchovy dynamics include mixed layer depth (in the Kuroshio-Oyashio Current), sea-surface temperature (in the Humboldt Current Ecosystem), the depth of the thermocline (in the California Current), and changes in dissolved oxygen and primary production (in the Benguela Current) (Alheit et al. 2009). These changes are sometimes linked to larger-scale patterns of flow, leading to hypotheses about teleconnections between different LMEs (Alheit and Bakun 2010).

There are several potential explanations for asynchrony in sardine and anchovy populations. Under an "equilibrium" view, sardine and anchovy are ecologically equivalent, and the ecosystems they inhabit cannot simultaneously sustain high abundances of both species. Sardines and anchovy would share a food resource, and switch in numerical dominance when fishing or failed recruitment reduces the dominant species, but the total abundance of forage fish would not vary significantly (this has been referred to as the "biological regimes hypothesis"). However, the current consensus is that there are few direct interactions between sardine and anchovy, as they tend to use different spawning areas (anchovy nearshore, sardine offshore; MacCall 2009b) and can consume different diets (sardines are capable of filtering smaller particles with their gillrakers, and thus are able to meet energetic requirements with smaller zooplankton; Van Der Lingen *et al.* 2006; Rykaczewski and Checkley 2008).

Alternatively, because oceanic processes occur at similar timescales to shifts in the dominance of sardines vs. anchovy (Lluch-Belda *et al.* 1989; Chavez *et al.* 2003), a newer theory posits that sardine and anchovy alternate in abundance when physical conditions are more favorable for one or the other. Generally, warm temperatures are favorable for sardine, and anchovy dominate when temperatures are cooler. This is illustrated well in the Peru-Humboldt large marine ecosystem (LME), where anchoveta fare poorly during El Niño episodes but sardines persist (Bakun and Broad 2003). Patterns in cyclic dominance sometimes occur simultaneously in distant systems, which has inspired attempts to identify large-scale climatic fluctuations that affect multiple sardine and anchovy populations simultaneously across large geographical areas (Schwartzlose *et al.* 1999; Alheit and Bakun 2010).

Finally, MacCall (2009) proposed a framework for a theory that links sardine and anchovy abundance to low frequency variability in boundary current flows, of which temperature happens to be an indicator. In this framework, sardine larvae risk being flushed downstream in major boundary currents before they gain swimming capacity. Therefore, when currents are strong, they are restricted to nearshore areas and productivity is low. Anchovy, however, are always restricted to nearshore regions and their abundance is influenced mainly by upwelling and coastal productivity. Because changes in boundary current flows often occur at the same time as SST anomalies, this framework is in agreement with earlier studies relating sardine productivity to SST anomalies. The patterns and hypothesized processes behind sardine-anchovy asynchrony have been addressed extensively in the literature, so for further discussion we refer the reader to several reviews and analyses of sardine and anchovy dynamics (Lluch-Belda *et al.* 1989; Schwartzlose *et al.* 1999; Chavez *et al.* 2003; Alheit and Bakun 2010; Lindegren *et al.* 2013). Despite the diversity of theories explaining asynchrony, there have been surprisingly few attempts to characterize the extent and time scales of asynchrony across multiple ecosystems.

Relatively short time series have hampered efforts to distinguish sardine-anchovy asynchrony and its consequences for fisheries and ecosystems. Statistically robust measures of correlation between these two species might be rare because a single time series might only contain 1-2 cycles of low-frequency variation, and thus the number of independent data points is limited. Most time series used to identify asynchrony and replacement in biomass are relatively short (~30-60 years; MacCall, *pers. comm*), and correlations are sensitive to the length of the time series.

There are two components of sardine and anchovy co-dynamics that correspond to their causes and consequences: replaceability and asynchrony. The first, replaceability, refers to the possibility that sardine and anchovy are ecologically or economically **replaceable** (Lluch-Belda *et al.* 1992). This is particularly important for predators and fisheries of forage fish, which may need to shift their diets or catch according to the prey community that is available. The second component is whether **asynchrony** is present. This asynchrony may have different interpretations depending on the variable in which it occurs.

Replaceability

If sardine and anchovy replace each other as the 'wasp-waist' component of marine ecosystems where they co-occur, predators and fisheries should be able to sustain a more stable supply of food or catches by switching across species. Evidence for replaceability includes alternating but similar catches of sardine and anchovy (Moloney and Wickens 1985) and evidence that dependent predators rely on one species in years when the other is not available (e.g., in South Africa, where cape gannets and snoek diet proportions are thought to reflect changes in relative biomass (Cury and Shannon 2004; and references within).

Asynchrony

Asynchrony in sardine and anchovy dynamics governs, in part, the importance of replaceability for predators and fisheries. This is because asynchronous compensatory dynamics stabilize the portfolio of sardine and anchovy. That is, if sardine and anchovy are asynchronous, there will be a dampening of variation in forage resources available for predators, to the degree that they are also replaceable. Evidence for asynchrony includes rising anchovy biomass when sardine biomass is decreasing (Lluch-Belda *et al.* 1992) and declines in the productivity of one species following large year classes in the other (Schwartzlose *et al.* 1999).

The time scale of asynchrony and the population metric in which it appears are important to our understanding of sardine and anchovy dynamics and their causes: Asynchronous landings represent changes in resource use and benefits to human communities, whereas biomass should reflect changes in resources available to predators. Recruitment should more closely reflect the sensitivity of sardine and anchovy to their environment (Lluch-Belda *et al.* 1991; Jacobson and MacCall 1995), so asynchrony in recruitment will likely reveal environmental mechanisms that affect both species. The time scale of asynchrony is important for detecting it and for assigning possible mechanisms (i.e., processes on <5-year vs. multidecadal time scales). We expect that asynchrony will be most robustly detectable on short time scales and less so at longer time scales.

In this paper, we quantitatively test the hypothesis that anchovies and sardines are both replaceable and asynchronous in marine coastal ecosystems. Specifically, we ask:
1) Is one species frequently replaced by the other in a given large marine ecosystem (LME)? In which LMEs are sardine and anchovy ecologically replaceable? Using simulated time series based on parameters from existing populations, we also ask:

2) Given the spectral characteristics of sardine and anchovy time series, what is the probability of observing a pattern of asynchrony at random?
3) If anchovy and sardine were truly asynchronous, how many years of data would be needed to detect asynchrony?

We address (2) and (3) at multiple temporal scales, as asynchrony can be present at short (interannual) to much longer (70–100 year) frequencies and detectability is likely to depend on the timescale of fluctuation. For cases where data might be insufficient for quantifying synchrony or asynchrony, we estimate the statistical power to detect these patterns across a range of potential strengths of covariance.

METHODS

We collated sardine and anchovy time series from all available global databases to assemble the longest and most complete datasets available. We used simple metrics to determine the extent to which sardine and anchovy might be replaceable in each of five large marine ecosystems (LMEs). We also estimated covariance between sardine and anchovy to quantify asynchrony on an interannual scale, and used a randomization approach to test whether the observed degree of asynchrony in each LME and at each timescale was stronger than what one would expect by chance. Finally, to determine the roles of time series length and low-frequency variation in generating apparent short-term asynchronous dynamics, we simulated sardine and anchovy with known covariance and quantified the probability of observing asynchrony at the same time scales, given different lengths of time series.

We collected sardine and anchovy time series from five large marine ecosystems (LMEs; Sherman 1995): the Kuroshio-Oyashio Current, California Current, Humboldt Current, Northeast Atlantic and Benguela Currents (Table 4.2). All are upwelling ecosystems except for the Kuroshio-Oyashio Current (a western boundary current) and the Northeast Atlantic, which is a shelf ecosystem. Time series data were compiled from the RAM legacy database and several European stock assessments and individual scientists, compiled in Barange et al. (2009) (Figure 4.1).

We assessed **replaceability** (the potential for one forage species to functionally replace the other) by comparing the landings, biomass, and recruitment of each species in each basin during periods of high abundance, and defined cases where sardine and anchovy were replaceable as cases where the long-term peak biomass for one species was within +/- 25% of the other. We assessed **asynchrony** using two approaches: (1) a time series approach, in which the strength and sign of the covariance were estimated by fitting a multivariate autoregressive (MAR) model, and (2) a wavelet approach, which decomposes time series into different frequencies and can be used to quantify asynchrony or negative correlation at each frequency (Rouyer *et al.* 2008). Specifically, the wavelet modulus ratio provides a measure of asynchrony at multiple frequencies. This approach has been used to analyze compensatory dynamics in ecological communities in the past (e.g., Vasseur *et al.* 2014). Both time series and wavelet approaches can be used to generate time series with similar properties to perform significance tests (Rouyer *et al.* 2008).

To estimate covariance, we fit a MAR model to log-transformed sardine and anchovy time series from each LME. We compared covariances across LMEs and time series type (landings, biomass, or recruitment). The MAR model was fit using the MARSS package in R (Holmes *et al.* 2012; R Core Team 2017). The model consists of a state equation:

$$x_t = \mathbf{B}x_{t-1} + u + w_t \qquad w_t \sim MVN(0, Q) \qquad (4.1)$$

and an observation equation,

$$y_t = Zx_t + v_t \qquad v_t \sim MVN(0, R) \qquad (4.2)$$

which describes observations of the process (sardine and anchovy dynamics are assumed to be two observation time series estimating two separate processes). In the process model (Eq. 1), x_t is an $m \times 1$ vector of the natural log of biomass for sardine and anchovy at time t. **B** is an $m \times m$ matrix containing autocorrelation parameters on the diagonal and 0 elsewhere, and u is an $m \times 1$ vector of population growth rates. Process error (the vector w_t) is assumed to be uncorrelated in time and drawn randomly from a multivariate normal distribution with mean zero and variance-covariance matrix **Q**. Values of **Q**, u, and **R** are estimated; the off-diagonal value of **Q** (q_{sa}) is the covariance between sardine and anchovy.

Detecting asynchrony can be viewed as an issue of Type I vs. Type II statistical error. To determine whether sardine and anchovy were more asynchronous than expected by chance (i.e., the chances of a Type I error), we generated 1,000 surrogate time series with the same spectral properties as the observations (landings, biomass, and recruitment), but without phase information (i.e., information about synchrony was not included). We calculated the continuous wavelet transform at several scales for each sardine-anchovy time series:

$$w_k(t,s) = s^{-1} \int_{-\infty}^{\infty} \psi\left(\frac{t-\tau}{s}\right) x_k(\tau) d\tau \qquad (4.3)$$

Where s is the scale of the analysis (the scale at which the wavelet transform is sampled, or the "scale localization"), ψ_τ is the wavelet function and $x_k(\tau)$ is the biomass of the kth species at time τ (Keitt 2008).

We then calculated the localized wavelet modulus ratio (ρ) as described in Keitt (2008):

$$\rho(t,s) = \frac{\Lambda_{t,s}(|\sum_k w_k(\tau,s)|)}{\Lambda_{t,s}(\sum_k |w_k(\tau,s)|)} \tag{4.4}$$

Where $\Lambda_{t,s}(\cdot) = \int_{-\infty}^{\infty} e^{-\frac{1}{2}(\frac{t-\tau}{s})^2}(\cdot)d\tau$ (a Gaussian localization function in time *t*) and $|\cdot|$ is the complex modulus (Keitt 2008). The numerator is the modulus of the sum of the wavelet transform, and thus is lower when species have compensatory or asynchronous dynamics. The denominator, the sum of the moduli of sardine and anchovy, is the maximum possible amplitude if the phases of both species were perfectly aligned. Thus, $\rho(t,s)$ is bounded between 0 and 1, with lower values are characteristic asynchronous or compensatory dynamics, and higher values are characteristic more synchronous dynamics (Keitt 2008; Vasseur *et al.* 2014), and intermediate values are characteristic of independent dynamics. Surrogate time series were generated using the fractal package and wavelet modulus ratios were calculated using the mvcwt package in R (Keitt 2014; Constantine and Percival 2016).

The empirical distribution for the WMR for the surrogate time series was used to generate an expectation for the amount of asynchrony one would expect with no relationship between the two species (Figure 4.2). We determined a cutoff for the wavelet modulus ratio based on simulated, negatively covarying time series, choosing a cutoff below which dynamics tended to be asynchronous (WMR = 0.7; Figure D1). The choice of WMR = 0.7 as a cutoff is arbitrary and used to reduce dimensionality in WMR density (another study used a cutoff of WMR = 0.5; Vasseur *et al.* 2014). The cumulative density of values less than 0.7 was used as a one-sided test for the probability of observing asynchrony. Surrogate time series with no phase information were used to create a “null expectation” for the amount of synchrony that might be detected between sardine and anchovy if the two species’ dynamics are unrelated to one other.

Finally, to estimate the number of years of survey data necessary to detect asynchrony (minimize Type II error), we simulated time series with similar autocorrelation and error to real forage fish populations, with known covariance. We then measured asynchrony within a sample time window (from 20 to 200 years) and compared those to the true covariance.

Covarying time series were simulated as follows:

$$\eta_t = \boldsymbol{\rho_{sim}} \eta_{t-1} + \varepsilon \quad (4.5)$$

$$\varepsilon \sim MVN(0, \boldsymbol{\sigma}^2)$$

Where $\boldsymbol{\rho_{sim}}$ is a matrix containing sardine and anchovy autocorrelation (ρ_s and ρ_a), which were previously estimated for sardine and anchovy biomass (see Chapter 3). The variance-covariance matrix for sardine and anchovy $\boldsymbol{\sigma}$ contains the variance of each time series and σ_{sa} sets the strength and direction of covariance:

$$\boldsymbol{\sigma} = \begin{bmatrix} \sigma_s & \sigma_{sa} \\ \sigma_{sa} & \sigma_a \end{bmatrix}$$

Where σ_{sa} is the degree of covariance. At each sample size (n = 20–200 years) and each level of covariance (ϕ = ±0.99, 0.75, 0.5 and 0, as a fraction of σ_a), we simulated 1,000 sardine and anchovy time series, quantified asynchrony at three timescales (<5 years, 5-10 years, and 10+ years), and measured the probability of detecting a significant amount of asynchrony as the frequency at which simulated WMR was <0.7 (Figure 4.2).

RESULTS

We found no consistent pattern of replaceability in landings between sardine and anchovy across LMEs. Each of the five LMEs had one dominant forage species by landings, with differences of up to 189% between anchovy and sardine (in the Humboldt Current). Anchovy had the maximum long-term landings in the Humboldt and Benguela currents, and sardine were dominant in the Northeast Atlantic, Kuroshio-Oyashio, and California currents (Figure 4.3). Sardine and anchovy landings were replaceable by our definition (max value within 25% of the other) in the California Current, where anchovy peak long-term landings were only 3.4% lower than peak sardine landings (Figure 4.2). The same was true when median biomass and landings were used to assess replaceability: sardine and anchovy biomass were replaceable in the Benguela and California currents (Figure 4.3b).

Finally, there was weaker evidence for replaceability (larger differences between maximums) in biomass compared to landings (Figure 4.3). Biomass in each of the five LMEs had one dominant forage species, with differences in maximum biomass of up to 230% (Humboldt Current, dominated by anchoveta) and differences in median biomass of up to 158% (Northeast Atlantic, dominated by sardine). Sardine and anchovy were most replaceable in the California Current, where the median biomass of sardine was only 16% lower than the median biomass of anchovy, according to data from Barange et al. (2009). These results were consistent among datasets (Figure D2).

We did not find strong evidence for negative covariance between sardine and anchovy landings at the interannual timescale – instead, covariance was weak and varied across LMEs. The LME with the strongest negative covariance in landings was the California Current (q_{sa} = -0.288; 95% CI [-0.53, 0.08]). In the Kuroshio-Oyashio Current, landings covaried positively (0.24 [0.01, 0.470]). The maximum likelihood estimate for covariance was positive in the Benguela Current (0.07 [-0.10,0.18]) but this confidence interval spanned zero, so it is possible that q_{sa} was zero. Covariance in landings was near zero in the Humboldt Current (-0.13 [-0.36, 0.12]) and Northeast Atlantic (0.01 [-0.01, 0.04]) LMEs. The strongest covariance between sardine and anchovy (both negative and positive) appeared in landings (Figure 4.4).

Covariance in biomass was less strong than covariance in landings, and occurred in the same direction as covariance in landings in every LME except the Northeast Atlantic (positive covariance in biomass; 0.03 [0.001,0.044] but zero in landings; 0.03 [0.001, 0.044]). The confidence intervals of estimated covariance overlapped with estimates from other ecosystems, suggesting that if landings, biomass or recruitment differed in the extent to which they are asynchronous, these differences were not strong at interannual time scales (Figure 4.4).

We found a general trend towards asynchrony at longer time scales, but this pattern was not universal nor was it consistently stronger than expected by chance.

Randomization tests with similar time series reveal that observed levels of decadal asynchrony in landings were only significantly different from levels expected by chance in the Humbolt Current, which was also significantly asynchronous at other time scales. Otherwise, changes in landings tended to be or more synchronous than expected by chance (Figure 4.5). Landings in the California Current, Kuroshio-Oyashio Current, and Northeast Atlantic LMEs were more synchronous than expected by chance at short (<5 year) time scales (Figure 4.5). This was consistent with the positive covariance described above for the Kuroshio-Oyashio Current and Northeast Atlantic.

Biomass was generally less asynchronous than landings: All LMEs except the Northeast Atlantic had synchronous biomass at some timescale, with stronger synchrony than expected by chance at shorter timescales (1-10 years) and no support for asynchronous dynamics. In the Benguela and Kuroshio-Oyashio currents, there was synchrony in biomass (Figure 4.5) consistent with the positive covariance described above. Biomass was strongly asynchronous in the Northeast Atlantic compared to other LMEs.

In the Humboldt Current and Northeast Atlantic, we found contrasting patterns of synchrony. Landings were highly asynchronous in the Humboldt Current, whereas biomass was synchronous (significantly so at the <5-year scale according to randomization tests; Figure 4.5) suggesting that asynchrony could be enhanced/exaggerated by changes in the species targeted by the fishery, rather than changes in the relative abundance of species. In contrast, the Northeast Atlantic had much more asynchronous biomass than landings (Figure 4.5), a pattern that suggests that fishing patterns buffered a high degree of asynchrony in biomass. A steady decline in sardine landings while anchovy had high interannual variability was likely influential in this estimate (Northeast Atlantic; Figure 4.1). Lower resolution in biomass estimates than landings could also result in a false positive for synchrony in biomass at short time scales.

In all LMEs, patterns of synchrony and asynchrony were generally shared across timescales. Levels of synchrony/asynchrony that were stronger than expected at random were more commonly found at shorter time scales, supporting the hypothesis that the ability to find asynchrony is scale-dependent and compensatory dynamics may not be detectable with the amount of data currently available.

We found statistical power to detect asynchrony at decadal scales to be low. Our power analysis indicates that if sardine and anchovy underwent low-frequency fluctuations, detecting a significant amount of asynchrony at long time scales could take several more decades of data than are currently available. In highly autocorrelated time series (for example, when both sardine and anchovy have ρ=0.9), 50-60 years of data are sufficient for detecting asynchrony at short time scales (>50% detection probability for asynchrony occurring on a <5-year time scale; Figure 4.6). This was consistent with our ability to detect a significant degree of synchrony or asynchrony at shorter time scales (Figure 4.5). However, detecting asynchrony on longer time scales (5-10 years) can take at least 100 years, even with very strong negative covariance between sardine and anchovy (covariance is -0.99 times the variance of anchovy biomass or landings). Finally, detecting this strong asynchrony at much longer (10+ year) time scales would take at least 100 years of data and more than 200 years of data when covariance is less strong (covariance is -0.75 times anchovy variance; Figure 4.6).

DISCUSSION

In ecosystems with multiple forage species, the impacts of boom and bust forage fish dynamics on fisheries and predators could be buffered by compensatory patterns in biomass or landings. These compensatory patterns require both replaceability (the potential for one species to provide a similar amount of resource to predators and human communities) and asynchrony (the potential for species to provide resources at times when the other species is not available). Overall, we found that sardine and anchovy were not replaceable in marine food webs over the time series that we observed; i.e., one species tended to be dominant in terms of both landings and biomass in each ecosystem. We also found that asynchronous dynamics were present but not a dominant pattern across ecosystems, and that alternations in abundance are not detectable at the relatively short time periods for which we have data. These results indicate that there is limited potential for sardine and anchovy to effectively replace each other as key forage species in the ecosystems where they occur.

The lack of replaceability we found here suggests that alternations in anchovy and sardine abundance will impact human needs (via fishing) and ecosystem needs proportionally to the availability of the dominant forage species (in the Benguela and Humboldt Currents, anchovy; and in the Kuroshio-Oyashio Current, Northeast Atlantic, and California Current, sardine; Figure 4.3). Especially in places where one species is much more abundant than the other and sardine are not strongly asynchronous (e.g., the Humboldt Current and Kuroshio-Oyashio Current), fluctuations in the dominant species are likely to have a larger impact on the needs of predators and fisheries. The low potential for replacement indicates that even highly asynchronous dynamics will not be sufficient to stabilize the availability of forage fish for fisheries or predators.

In general, we found stronger asynchrony and more potential for replacement in landings more than biomass, suggesting that fishery-dependent data may exaggerate patterns of variation that exist in natural populations. A shift of fishing effort between sardine and anchovy within the same ecosystem could lead to a high degree of negative covariance in landings. This would be consistent with a pattern of risk-mitigation in which fishermen shift among target species as they are available and/or profitable (as in Cline *et al.* 2017). Asynchronous landings at longer time scales were a particularly strong pattern in the Humboldt Current (Figure 4.5), an ecosystem where fishing effort might shift to sardine when anchoveta are less available: For example, the collapse of the anchoveta fishery in 1972 was followed by a southern expansion of sardine and a newly available fishery for them; (MacCall 2009a) Figure 4.1). Shifts in fishing pressure likely result from changes in biomass, but paint a picture of more asynchronous dynamics than do biomass estimates.

Overall, we found synchronous dynamics to be more common than asynchronous ones at interannual and longer time scales (Figure 4.4–4.5). This is in contrast to a large body of literature about asynchrony in Japanese sardine and anchovy (Lluch-Belda *et al.* 1989; Schwartzlose *et al.* 1999; Takasuka *et al.* 2008; Takahashi *et al.* 2009). Positive covariance in landings might be expected in the context of a mixed fishery, in cases where sardine and anchovy are caught together and habitats overlap (e.g., in the Benguela Current; Checkley *et al.* 2000; De Oliveira 2002), during periods of fishery development and expansion. Synchrony in biomass is counterintuitive given the bulk of literature on contrasting environmental conditions in which both species flourish.

Besides a true lack of asynchrony, there are several reasons why it may be difficult to detect a strong, statistically significant pattern: according to our power analysis, one of these limitations may be the significant data requirements for detecting asynchrony at long timescales (Figure 4.7). Other explanations include the spatial resolution of survey data and the LME-scale aggregation of data. However, there is also reason to believe that asynchrony may not be the characteristic pattern between sardine and anchovy. Long-term (2000-yr) paleosedimentary studies in the Santa Barbara Basin in Southern California do not support asynchronous dynamics (Soutar and Isaacs 1969, 1974; Baumgartner *et al.* 1992; McClatchie *et al.* 2017). Similar cores from the North Pacific (British Columbia) do not contain high enough densities of sardine scales to quantify asynchrony (Holmgren 2001). Because there are also few mechanistic explanations for the pattern of asynchrony (MacCall 2009b), our results indicate that perceived global asynchrony may instead be a relic of low-frequency, strongly autocorrelated biomass of both species, which can randomly generate asynchronous dynamics 50-75% of the time, depending on the ecosystem (Figure 4.5). The appearance of asynchronous dynamics can arise randomly when there are time series with low-frequency fluctuations like sardine and anchovy (Figure 4.5). The results of this study indicate not that asynchrony is not ecologically reasonable, but that it is difficult to detect.

This study is the first to examine asynchrony from multiple perspectives (biomass in addition to landings) and quantify the robustness of observed asynchrony at multiple temporal scales. Our results show that sardine and anchovy rarely fulfill the requirements of replaceability and asynchrony that would cause them to function as part of a fully compensatory forage portfolio for fisheries and ecosystems. Furthermore, we have shown that that asynchrony in landings and biomass could be a relic of low-frequency fluctuations in both species, that our ability to detect significant asynchrony is limited by the length of the time series available, and that asynchrony, when present, is unlikely to buffer the forage fish population for fisheries and predators. In cases where dynamics are synchronous, the assumption of asynchrony is particularly risky for managers to make, even if previous long-term patterns show that decreases in one species usually coincide with increases in the other. Forage fish management occurs at much shorter time scales and waiting to get information about synchrony from existing time series is unrealistic at the time scale of management decisions. Thus, while long-term ecological time series continue to accumulate, diagnosing asynchrony requires robust statistical approaches and conservative assumptions.

Table 4.1 Data

Data collected for this study from the RAM legacy database, and Barange et al. 2009.

Region	Data source	Dominant anchovy stock*	Dominant sardine stock
NE Atlantic	Barange	Bay of Biscay anchovy	European sardine
California	Barange	California anchovy	California sardine
Humboldt	Barange	Humboldt anchovy – Central Peru	Humboldt sardine – South Peru N Chile
Kuroshio-Oyashio	Barange	Japanese anchovy	Japanese sardine
Benguela	Barange	Southern Benguela anchovy	Northern Benguela sardine
NE Atlantic	RAM	Anchovy ICES VIII	European pilchard ICES VIIIc-Ixa
Benguela	RAM	Anchovy South Africa	Sardine South Africa
Kuroshio-Oyashio	RAM	Japanese anchovy Tsushima Strait	NA
California	RAM	N Anchovy E Pacific	Pacific sardine Pacific Coast
Humboldt	RAM	Peruvian anchoveta North-Central Peru	NA

*Dominant stocks are defined by the sardine or anchovy stock with the maximum spawning stock biomass for that region and data source.

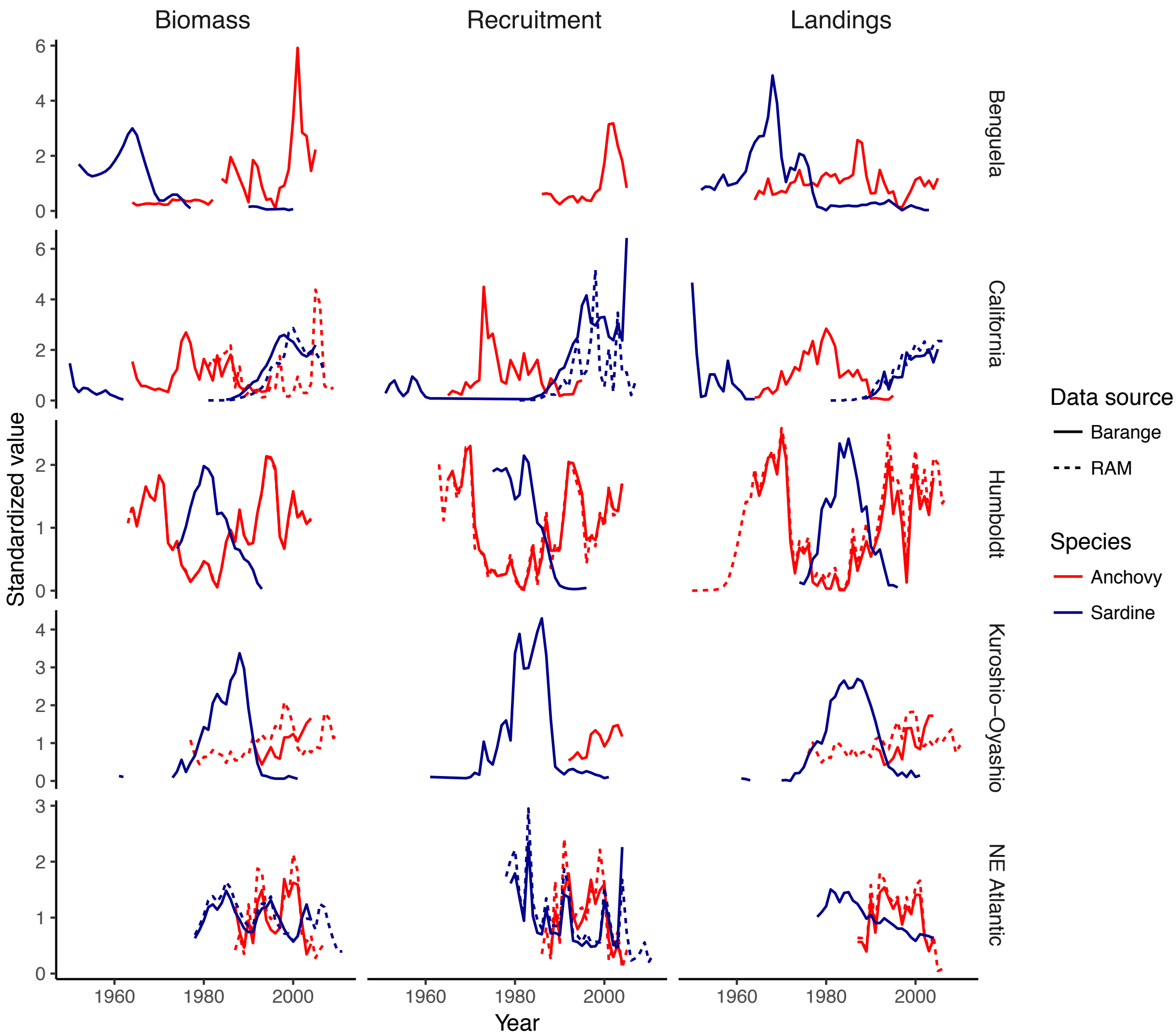

Figure 4.1 Time series of sardine and anchovy biomass.

Time series of dominant sardine and anchovy stocks (by biomass) in each LME included in this study. Values are standardized by dividing by the long-term mean. SSB indicates spawning stock biomass.

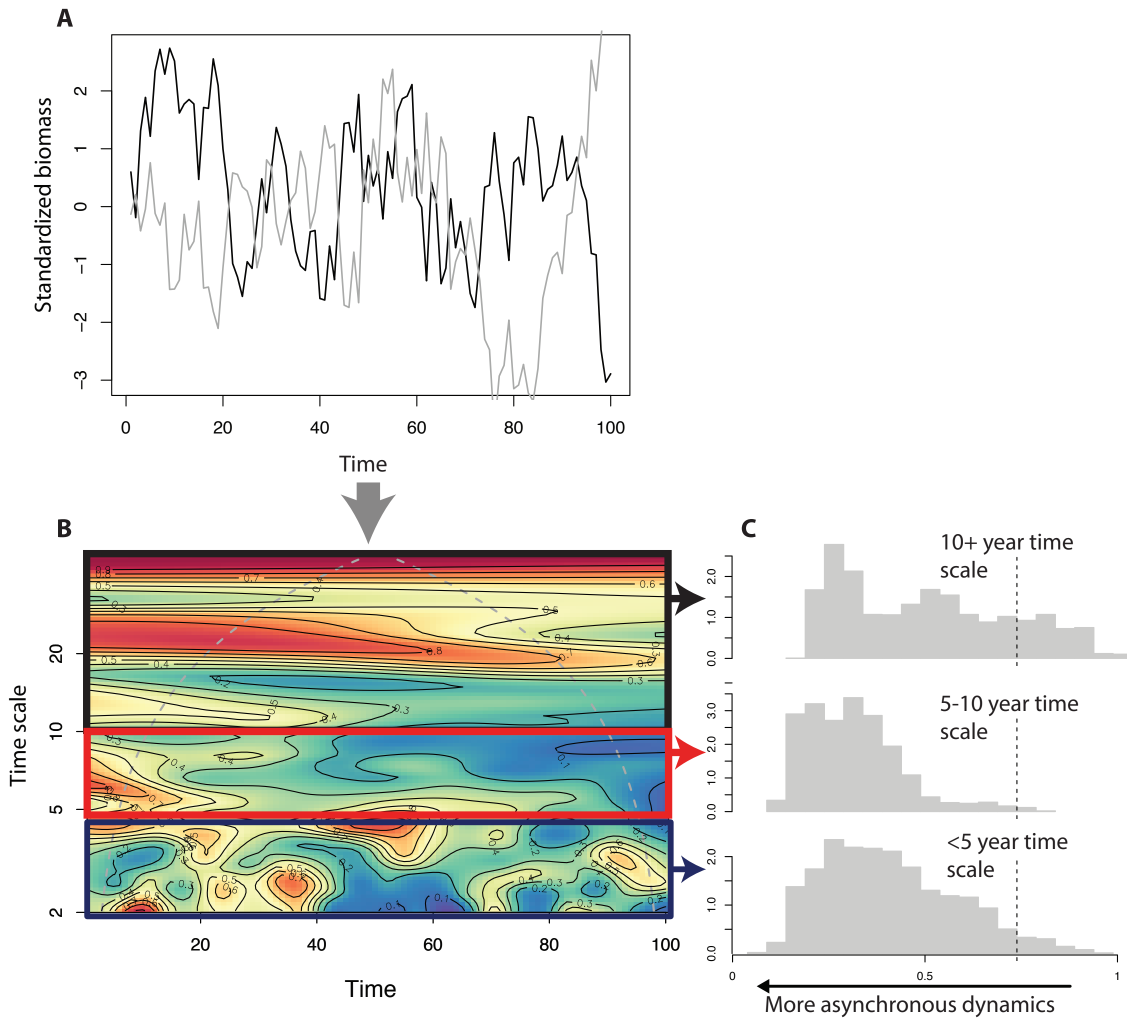

Figure 4.2 Method for analyzing asynchrony.

Method for quantifying asynchrony at each time scale. (A) Hypothetical time series of sardine and anchovy (B) Wavelet analysis gives the wavelet modulus ratio at several time scales. Only values within the “cone of influence” are included in the analysis (values outside the cone of influence are subject to edge effects; Torrence and Compo 1998) (C) The density of wavelet modulus ratio values at each time scale can be used to quantify the degree of asynchrony and compare across variables.

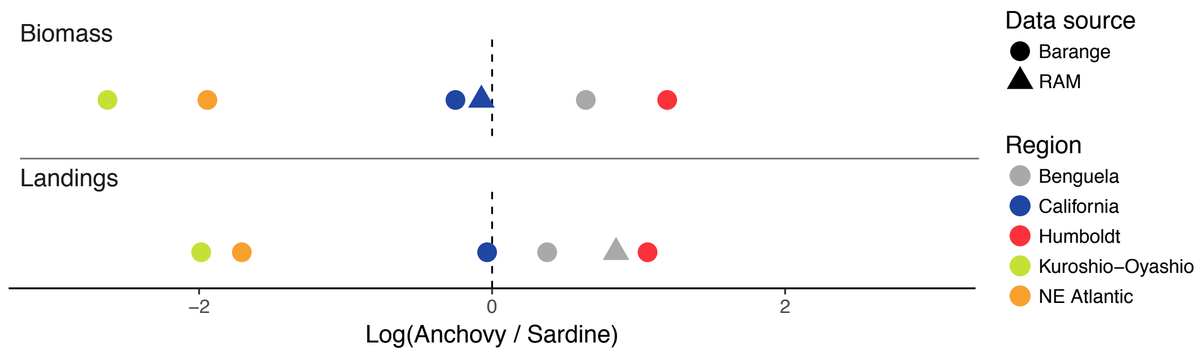

Figure 4.3a Log-ratio of anchovy to sardine maximum landings and biomass. The dotted line indicates a log-ratio of zero, where points would fall if the two species were fully replaceable. Points to the left of the dotted line are LMEs where sardine are dominant.

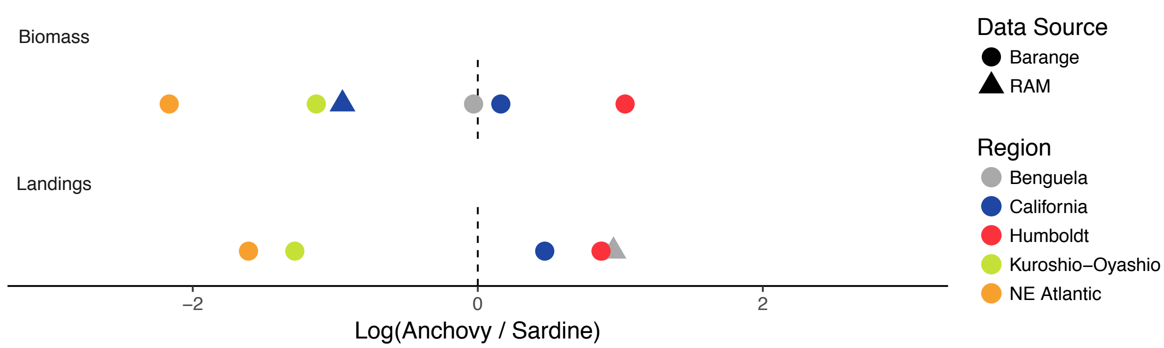

Figure 4.3b Log-ratio of anchovy to sardine median landings and biomass.

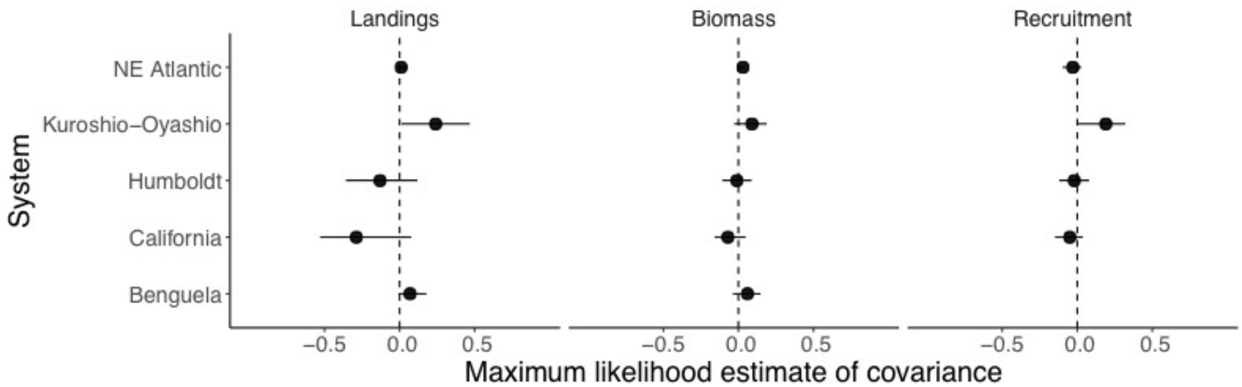

Figure 4.4 Estimated covariance between sardine and anchovy.

Covariance between sardine and anchovy in each region using data from Barange et al. (2009), estimated with MARSS models.

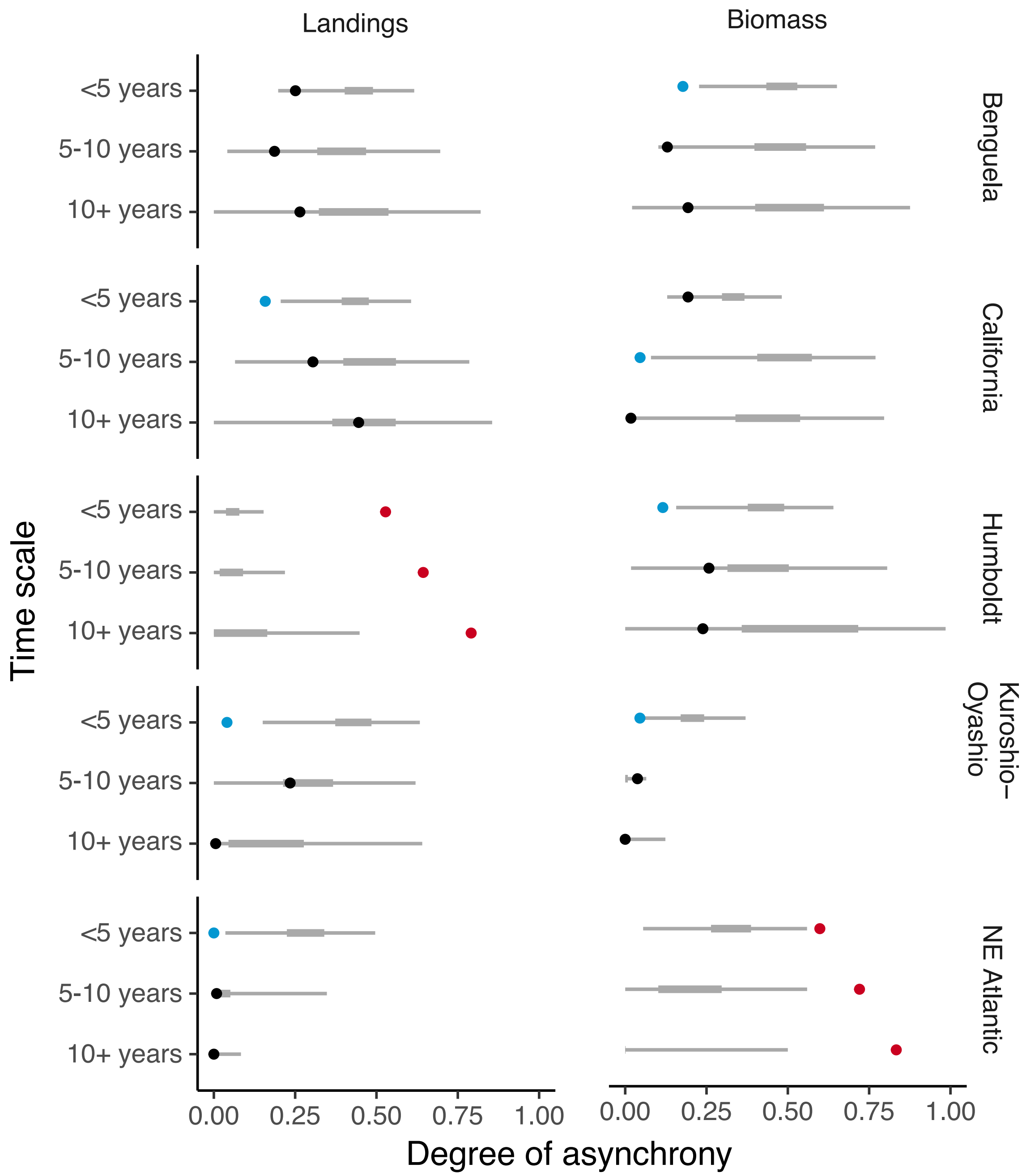

Figure 4.5 Estimated synchrony/asynchrony in each large marine ecosystem. Expected degree of asynchrony based on surrogate time series with similar properties (measured as density of WMR<0.7; grey bars) and the observed degree of asynchrony at each time scale in each ecosystem. Thicker bars indicate 50% quantiles, thinner bars represent 95% quantiles. Colored points indicate time scales and variables where sardine and anchovy have more asynchronous (red) or more synchronous dynamics (blue) than expected.

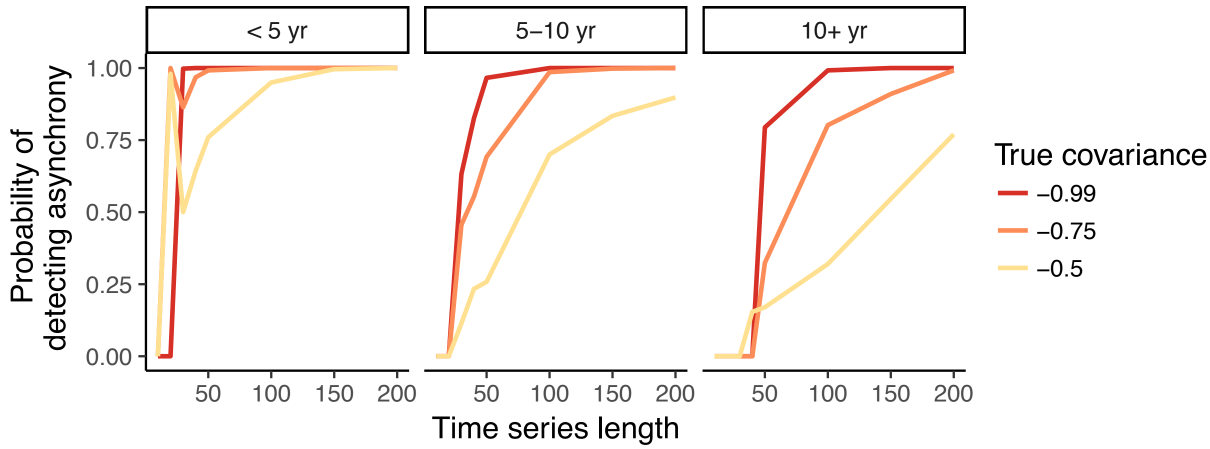

Figure 4.6 Power analysis.

Probability of detecting asynchrony with asynchronous time series of different lengths, based on simulations. Autocorrelation in both species is high ($\rho_s = \rho_a = 0.9$). Results were similar when sardine and anchovy were less highly autocorrelated ($\rho_s = \rho_a = 0.8$).

SYNTHESIS

This dissertation represents an exploration of the unique population dynamics of forage fish and how those dynamics might influence management. I have sought to determine the consequences, and some of the causes, of the dramatic shifts in productivity that are considered characteristic of forage fish populations. Investigating these questions has given me some broader insights about the ecological processes that lead to emergent patterns at different scales. First, forage fish, which are often lumped together as one trophic group, contain a remarkable degree of diversity, from intraspecific diversity in behavior to interspecific diversity in the guild of forage species available to predators. The fluctuations in abundance of diverse subpopulations and species generate buffering effects for predators and fisheries. Second, the mechanisms generating this diversity may be behavioral as well as biological. Finally, forage fish exist at the nexus of several, often conflicting stakeholder priorities, and the value of understanding the mechanisms behind forage fish dynamics is context-dependent and I predict will be an ongoing debate in fisheries.

Although forage fish are defined by their trophic role as forage for predators, the category of forage fish is incredibly diverse in its own right. Not only are forage species taxonomically diverse (Koehn *et al.* 2016), and genetically diverse within species (e.g., McPherson 2001) but forage fish also exhibit considerable behavior and life history diversity. Thus, although highly productive ecosystems may appear to be destabilized by the presence of just a few forage species in mid-trophic level roles (Cury *et al.* 2000), these species appear to have several stabilizing mechanisms beyond species richness. I have approached diversity within forage fish at several scales: spatial diversity and changes through time within a population, demographic variation among species, and variation between the same species in different ecosystems. I have realized that this diversity is often an important consideration for management, whether because it has a stabilizing effect (Chapter 1), because demographic rates may vary in space and/or time (Chapter 2; Siple *et al.* 2017) or because life history types require different management approaches (Chapter 3).

The low species diversity in the official "forage fish" category has led to a hypothesis that highly productive marine ecosystems are "wasp-waisted," with a diverse set of predators relying on a relatively small number of forage species. If this food web structure were true, low species richness in forage species would render generalist predators highly sensitive to changes in the abundance of any one forage species. After studying the dynamics of these species for nearly five years, I recognize that although there are some shared traits among forage species (highly productive, important in the diets of several predators, and exhibiting large dramatic fluctuations in productivity), the group of fish that occupy a "forage-like" ecological role is quite a bit more diverse, including juveniles of predator species, invertebrates, and bathypelagic species such as myctophids. Thus, categorizing ecosystems that have a few dominant forage species as necessarily wasp-waisted would be inaccurate. The concept of a diverse forage category has already been demonstrated using ecosystem models (Fréon *et al.* 2009), and I have come to similar conclusions about the diversity of dynamics in these species: with enough independence between subpopulations (Chapter 1) or species (Chapter 4), buffering effects can protect predators from changes in the abundance of a single prey species. With a speciose forage category like that found in the California Current (Koehn *et al.* 2016), responses of generalist predators to changes in the abundance of a single species might be weaker still. After studying forage fish dynamics at multiple scales, I recognize that predator responses to changes in forage fish abundance should depend on the diversity of the prey field as well as the dynamics of the species within it. For fisheries, it is already clear that there are long-term benefits to targeting a diverse portfolio of species (Cline *et al.* 2017); my research has suggested to me that predators of forage fish should benefit similarly.

Are buffering effects in forage species caused by behavior or by biology? Traditionally, "diversity" within populations is understood as genetic diversity, which can stabilize populations in the long-term and improve resilience. My first chapter found that portfolio effects can be generated at relatively local scales, among subpopulations that do appear to be genetically diverse at a local scale. Forage fish are difficult to distinguish genetically with the currently available tools, but show remarkable diversity and plasticity in behavior, including movement (MacCall 2012). It remains to be seen whether these behaviors arose as adaptations to a highly variable coastal environment, or are merely emergent properties of highly sensitive fish with complex responses to environmental fluctuations (Levin *et al.* 2016). Either way, this work has shown me that persistence in forage fish populations can arise from sources other than traditional metapopulation dynamics. This pattern, while encouraging for forage fish conservation, should also not be relied upon in the context of managing marine food webs (Chapter 4).

As research on forage fisheries moves forward, I believe a continuing challenge will be identifying when additional data and more complex models can be useful, and to which stakeholders. For example, in Chapter 3, I found that conservative approaches generally seem to achieve "ecological" objectives (maintaining higher long-term biomass for predators and reducing the probability of a collapse), even when information about population dynamics is poor. In this case, developing a relatively risk-averse control rule is sufficient for maximizing one type of objective, but presents a tradeoff with fishery objectives like maximizing long-term catches. Thus, the value of additional ecological information is not only a modeling issue but a management issue as well. The exercise of identifying important uncertainties in forage fish biology and management has given me an appreciation for the interactions between biology, management, and modeling capabilities (Siple and Koehn 2017). While it would be a grandiose career goal to fully understand any one of these elements, I am inspired to use their interaction as a framework for understanding fisheries as social-ecological systems.

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Appendix A: Chapter 1

Matrix model descriptions
Stock structure

October 19, 2017

All models have the following structure:

$$x_t = Bx_{t-1} + u + w_t; w_t \sim MVN(0, Q) \tag{1}$$

$$y_t = Zx_t + a + v_t; v_t \sim MVN(0, R) \tag{2}$$

In the process model, (Equation 1), x_t is an $m \times 1$ vector of the natural log of biomass for each population unit m at time t (the values of x_t are referred to as 'states'). **B** is an $m \times m$ matrix whose elements are coefficients describing the degree to which each population unit m reverts to a long-term mean and u is an $m \times 1$ vector of population unit growth rates. Process error (the vector w_t) is assumed to be uncorrelated in time and drawn randomly from a multivariate normal distribution with mean zero and variance-covariance matrix **Q**. In the observation model (Equation 2), **Z** is an $n \times m$ matrix that describes which observation time series are associated with each state time series, a is an $n \times 1$ vector representing the bias between the observation and the process, and observation error (v_t) is temporally uncorrelated and drawn from a multivariate normal distribution, with variance-covariance matrix **R**. Here, I_n refers to an $n \times n$ identity matrix, and e_n refers to a vector of 1's of length n.

1: All subpopulations independent (n = 19, m = 19)

Z is a 19 x 19 identity matrix

$$Z = I_{19} \tag{3}$$

a is a vector with 19 elements:

$$a = \begin{bmatrix} 0 \\ \vdots \\ 0 \end{bmatrix} \tag{4}$$

R is a 19 x 19 diagonal matrix:

$$R = rI_{19} \tag{5}$$

$$B = I_{19} \tag{6}$$

$$U = ue_{19} \tag{7}$$

Q is a 19 x 19 diagonal matrix:

$$Q = qI_{19} \tag{8}$$

2: All subpopulations independent but have equal covariance

This model is the same as (1) except for the Q matrix:

$$Q = \begin{bmatrix} q & c & c & \cdots & c \\ c & q & c & \cdots & c \\ c & c & q & \cdots & c \\ \vdots & \vdots & \vdots & \ddots & c \\ c & c & c & c & q \end{bmatrix} \tag{9}$$

3: Subpopulations divided by NOAA basins ($n = 19$, $m = 5$)

$$Z = \begin{bmatrix} 1 & 0 & 0 & 0 & 0 \\ 1 & 0 & 0 & 0 & 0 \\ 1 & 0 & 0 & 0 & 0 \\ 1 & 0 & 0 & 0 & 0 \\ 0 & 1 & 0 & 0 & 0 \\ 1 & 0 & 0 & 0 & 0 \\ 0 & 0 & 1 & 0 & 0 \\ 1 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 1 & 0 \\ 0 & 0 & 1 & 0 & 0 \\ 0 & 1 & 0 & 0 & 0 \\ 0 & 0 & 1 & 0 & 0 \\ 0 & 0 & 0 & 1 & 0 \\ 1 & 0 & 0 & 0 & 0 \\ 1 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 1 & 0 \\ 0 & 1 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 1 \\ 0 & 0 & 0 & 0 & 1 \end{bmatrix} \tag{10}$$

a is a vector:

$$a = \begin{bmatrix} 0 \\ a_{DiscoveryBay} \\ a_{DungenessBay} \\ a_{FidalgoBay} \\ 0 \\ a_{InteriorSanJuans} \\ 0 \\ a_{NWSanJuans} \\ 0 \\ a_{PortOrchard/PortMadison} \\ a_{PortSusan} \\ a_{QuarterMasterHarbor} \\ a_{QuilceneBay} \\ a_{SamishBay/PortageBay} \\ a_{SemiahmooBay} \\ a_{SouthHoodCanal} \\ a_{SkagitBay} \\ 0 \\ a_{\text{WollochetBay}} \end{bmatrix} \tag{11}$$

R is a 19 x 19 diagonal matrix:

$$R = rI_{19} \tag{12}$$

$$B = I_5 \tag{13}$$

u is a vector with 5 elements:

$$u = \begin{bmatrix} u_{NorthPugetSound} \\ u_{WhidbeyBasin} \\ u_{MainBasin} \\ u_{HoodCanal} \\ u_{SouthPugetSound} \end{bmatrix} \tag{14}$$

Q is a 5 x 5 matrix:

$$Q = qI_5 \tag{15}$$

As with all other models, D, C, d, and c are all equal to zero.

4: Herring belong to one large population (m=1) Z is a vector of ones with 19 elements:

$$Z = e_{19} \tag{16}$$

a is a vector:

$$a = \begin{bmatrix} 0 \\ a_{DiscoveryBay} \\ a_{DungenessBay} \\ a_{FidalgoBay} \\ a_{HolmesHarbor} \\ a_{InteriorSanJuans} \\ a_{KilisutHarbor} \\ a_{NWSanJuans} \\ a_{PortGamble} \\ a_{PortOrchard/PortMadison} \\ a_{PortSusan} \\ a_{QuartermasterHarbor} \\ a_{QuilceneBay} \\ a_{SamishBay/PortageBay} \\ a_{SemiahmooBay} \\ a_{SouthHoodCanal} \\ a_{SkagitBay} \\ a_{SquaxinPass} \\ a_{WollochetBay} \end{bmatrix} \tag{17}$$

R is a 19 x 19 diagonal matrix as in (1).

B = 1

U = u

Q = q

5: Herring are separated by microsatellites (Small et al. 2005) (m=3)

Z is a 19x3 matrix:

$$Z = \begin{bmatrix} 1 & 0 & 0 \\ 0 & 0 & 1 \\ \vdots & \vdots & \vdots \\ 0 & 0 & 1 \\ 0 & 1 & 0 \\ 0 & 0 & 1 \end{bmatrix} \tag{18}$$

a is a vector:

$$a = \begin{bmatrix} 0 \\ 0 \\ a_{DungenessBay} \\ a_{FidalgoBay} \\ a_{HolmesHarbor} \\ a_{InteriorSanJuans} \\ a_{KilisutHarbor} \\ a_{NWSanJuans} \\ a_{PortGamble} \\ a_{PortOrchard/PortMadison} \\ a_{PortSusan} \\ a_{QuartermasterHarbor} \\ a_{QuilceneBay} \\ a_{SamishBay/PortageBay} \\ a_{SemiahmooBay} \\ a_{SouthHoodCanal} \\ a_{SkagitBay} \\ 0 \\ a_{WollochetBay} \end{bmatrix} \quad (19)$$

R =

$$I_{19} \quad (20)$$

as in (1).

$$B = I_3 \quad (21)$$

u is a vector with 3 elements:

$$u = \begin{bmatrix} u_{CherryPoint} \\ u_{SquaxinPass} \\ u_{allothers} \end{bmatrix} \quad (22)$$

Q is a 3 x 3 matrix:

$$Q = qI_3 \quad (23)$$

6: Herring are separated by regions (North Puget Sound, South Puget Sound, Strait of Juan de Fuca; m=3)

Z is a 19 x 3 matrix. The first column identifies North Puget Sound subpopulations, the second gives Strait of Juan de Fuca subpopulations, and the last column is South Puget Sound subpopulations:

$$Z = \begin{bmatrix} 1 & 0 & 0 \\ 0 & 1 & 0 \\ 0 & 1 & 0 \\ 1 & 0 & 0 \\ 0 & 0 & 1 \\ 1 & 0 & 0 \\ 0 & 0 & 1 \\ 1 & 0 & 0 \\ 0 & 0 & 1 \\ 0 & 0 & 1 \\ 0 & 0 & 1 \\ 0 & 0 & 1 \\ 0 & 0 & 1 \\ 1 & 0 & 0 \\ 1 & 0 & 0 \\ 0 & 0 & 1 \\ 0 & 0 & 1 \\ 0 & 0 & 1 \\ 0 & 0 & 1 \end{bmatrix} \tag{24}$$

a is a vector:

$$a = \begin{bmatrix} 0 \\ 0 \\ a_{DungenessBay} \\ a_{FidalgoBay} \\ 0 \\ a_{InteriorSanJuans} \\ a_{KilisutHarbor} \\ a_{NWSanJuans} \\ a_{PortGamble} \\ a_{PortOrchard/PortMadison} \\ a_{PortSusan} \\ a_{QuartermasterHarbor} \\ a_{QuilceneBay} \\ a_{SamishBay/PortageBay} \\ a_{SemiahmooBay} \\ a_{SouthHoodCanal} \\ a_{SkagitBay} \\ a_{SquaxinPass} \\ a_{WollochetBay} \end{bmatrix} \tag{25}$$

R is

$$rI_{19} \tag{26}$$

as in (1).

$$B = I_3 \tag{27}$$

u is a vector with 3 elements:

$$u = \begin{bmatrix} u_{NorthPugetSound} \\ u_{StraitofJuandeFuca} \\ u_{SouthPugetSound} \end{bmatrix} \tag{28}$$

Q is a 3 x 3 matrix:

$$Q = qI_3 \tag{29}$$

7: Herring are separated by contaminants (Cherry Point, Semiahmoo Bay, all others; m=3)
Z is a 19 x 3 matrix. The first column identifies the Cherry Point subpopulation, the second is the Strait of Juan de Fuca, and the last column is all other subpopulations:

$$Z = \begin{bmatrix} 1 & 0 & 0 \\ 0 & 0 & 1 \\ 0 & 0 & 1 \\ 0 & 0 & 1 \\ 0 & 0 & 1 \\ 0 & 0 & 1 \\ 0 & 0 & 1 \\ 0 & 0 & 1 \\ 0 & 0 & 1 \\ 0 & 0 & 1 \\ 0 & 0 & 1 \\ 0 & 0 & 1 \\ 0 & 0 & 1 \\ 0 & 0 & 1 \\ 0 & 1 & 0 \\ 0 & 0 & 1 \\ 0 & 0 & 1 \\ 0 & 0 & 1 \\ 0 & 0 & 1 \end{bmatrix} \tag{30}$$

a is a vector:

$$a = \begin{bmatrix} 0 \\ 0 \\ a_{DungenessBay} \\ a_{FidalgoBay} \\ a_{HolmesHarbor} \\ a_{InteriorSanJuans} \\ a_{KilisutHarbor} \\ a_{NWSanJuans} \\ a_{PortGamble} \\ a_{PortOrchard/PortMadison} \\ a_{PortSusan} \\ a_{QuartermasterHarbor} \\ a_{QuilceneBay} \\ a_{SamishBay/PortageBay} \\ 0 \\ a_{SouthHoodCanal} \\ a_{SkagitBay} \\ a_{SquaxinPass} \\ a_{WollochetBay} \end{bmatrix} \tag{31}$$

R is a 19 x 19 diagonal matrix as in (1).
B is a 3 x 3 identity matrix:

$$B = I_3 \tag{32}$$

u is a vector with 3 elements:

$$u = \begin{bmatrix} u_{CherryPoint} \\ u_{SemiahmooBay} \\ u_{allothers} \end{bmatrix} \tag{33}$$

Q is a 3 x 3 matrix:

$$Q = qI_3 \tag{34}$$

8: This model is the same as (1) but with different growth rates allowed for each subpopulation (m=19)

All matrices have the same structure as in (1) but u is a vector.

$$u = \begin{bmatrix} u_{CherryPoint} \\ \\ u_{DiscoveryBay} \\ u_{DungenessBay} \\ u_{FidalgoBay} \\ u_{HolmesHarbor} \\ u_{InteriorSanJuans} \\ u_{KilisutHarbor} \\ u_{NWSanJuans} \\ u_{PortGamble} \\ u_{PortOrchard/PortMadison} \\ u_{PortSusan} \\ u_{QuartermasterHarbor} \\ u_{QuilceneBay} \\ u_{SamishBay/PortageBay} \\ u_{SemiahmooBay} \\ u_{SouthHoodCanal} \\ u_{SkagitBay} \\ u_{SquaxinPass} \\ u_{WollochetBay} \end{bmatrix} \tag{35}$$

9: This model is the same as (8), but Q is completely unconstrained: variances q and growth rates u are unique for each population, and covariances are unique for each pair of populations (m=19)

All matrices have the same structure as in (8) but **Q** is fully estimated.

$$Q = \begin{bmatrix} q_1 & \cdots & \cdots & \cdots & \cdots \\ c_{21} & q_2 & \cdots & \cdots & \cdots \\ c_{31} & c_{32} & q_3 & \cdots & \cdots \\ \vdots & \vdots & \vdots & \ddots & \cdots \\ c_{n1} & \cdots & \cdots & \cdots & q_n \end{bmatrix} \tag{36}$$

Where 1:n are the subpopulations, q_1 is the variance of subpopulation 1, and c_{12} is the covariance of subpopulations 1 and 2.

How well can MARSS models detect populations with similar dynamics?

In order to confirm that model selection with MARSS can detect shared dynamics, we did a simulation experiment on a simplified set of populations (n = 5).

For each simulation, we did the following:

- Generate 50-year time series (annual time steps) for 5 autocorrelated subpopulations, with known levels of correlation to one another (correlation varied between 0 and 0.99; Figure 1.2).
  Fit MARSS models to the simulated time series, using 3 hypothesized population structures as reflected in 3 different Z matrix structures:
  1) 1 panmictic population (m = 1, Z has dimension 5 ×1)
  2) Subpopulations are grouped into 3 groups (m = 3, Z has dimensions 5 × 3)
  3) Populations are fully independent (m = 5, Z has dimensions 5 × 5)
- As in our herring study, use AIC_b to determine which of these three models best described the population

We then repeated this exercise 100 times at each level of correlation, and tallied the number of times that each model was selected as the best fit to ask, how often does the model selection process (in 100 runs) correctly identify the population structure? In other words, for simulated time series using correlation = 0, how often does the MARSS model correctly select m = 5 as the best model? Likewise, for simulated time series using correlation = 0.99, how often does the MARSS model correctly select m = 1 as the best model? We confirmed that model selection using different Z structures and a time series roughly the same length as the herring time series can detect differences in the correlation between autoregressive time series (Figure 1.3).

The results of this exercise indicate that 32% of the time, when there is no correlation among populations, model selection chooses a simple, panmictic stock structure (i.e., false negative), but the chance of choosing an independent population model is very low at 0.5 correlation, and zero when populations have very similar dynamics.

This procedure is not as complex as the series of models that we tested for herring in Puget Sound but may be used as a framework to further explore the use of MARSS models to describe population structure.

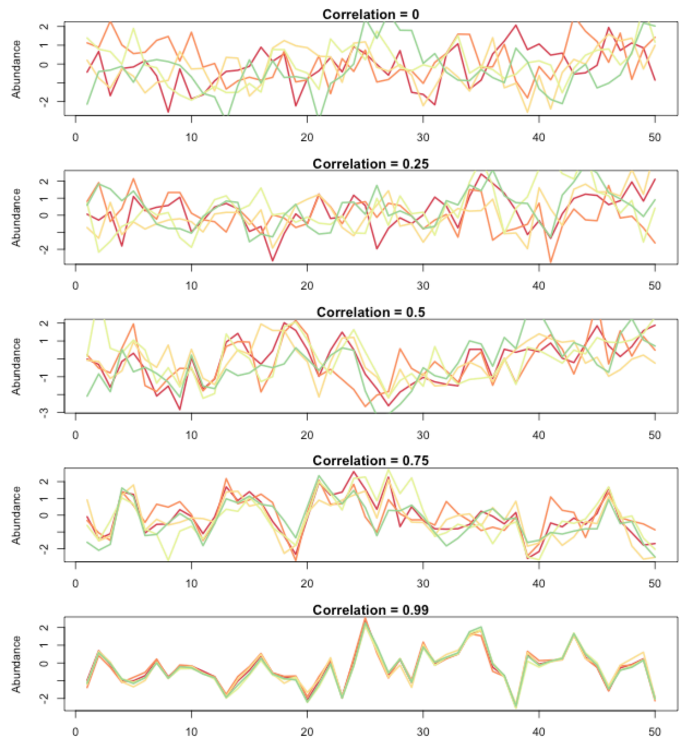

Figure A1. Examples of simulated subpopulations used to test our ability to detect population structure using different structures of the Z matrix with model comparison.

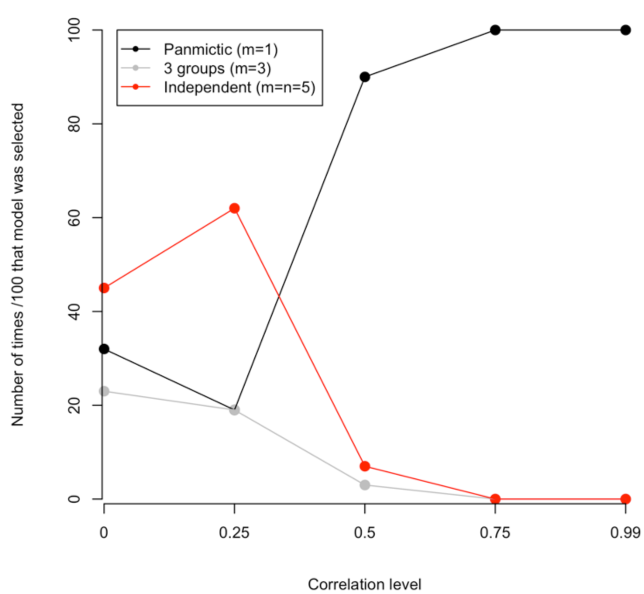

Figure A2. The number of times each model was selected as the best fit model, under on 5 levels of induced correlation. Model selection chose the "independent" model the majority of the time when correlation was <0.5.

Table A1. Stationarity test results

Subpopulation	ADF test statistic for residuals	P-value
Cherry Point	-5.5663	0.01
Discovery Bay	-4.8523	0.01
Dungeness Bay	-4.0195	0.02258
Fidalgo Bay	-4.6136	0.01
Holmes Harbor	-4.6622	0.01
Interior San Juan Islands	-3.6304	0.04783
Kilisut Harbor	-2.2621	**0.4725**
Northwest San Juan Islands	-2.2942	**0.4603**
Port Gamble	-7.4744	0.01
Port Orchard / Port Madison	-5.2946	0.01
Port Susan	-5.4819	0.01
Quartermaster Harbor	-5.3351	0.01
Quilcene Bay	-4.718	0.01
Samish Bay / Portage Bay	-6.5873	0.01
Semiahmoo Bay	-5.4611	0.01
South Hood Canal	-5.0918	0.01
Skagit Bay	-4.0511	0.02147
Squaxin Pass	-5.1114	0.01
Wollochet Bay	-2.6859	**0.3111**

Table A2. Classifications for each subpopulation under each hypothesized stock structure.

Subpopulation	*Stock structure hypothesis*					
	Each subpopulation separate (Model 1; m=19)	*NOAA basins (Model 3; m=5)*	*All one population (panmictic; Model 4; m=1)*	*Microsatellites (Model 5; m=3; Small et al. 2005)*	*Regions (Model 6; m=3)*	*Contaminants (Model 7; m=3; West et al. 2008)*
Cherry Point	Cherry Point	North Puget Sound	Puget Sound	Cherry Point	North Puget Sound	Cherry Point
Discovery Bay	Discovery Bay	North Puget Sound	Puget Sound	other	Strait of Juan de Fuca	other
Dungeness Bay	Dungeness Bay	North Puget Sound	Puget Sound	other	Strait of Juan de Fuca	other
Fidalgo Bay	Fidalgo Bay	North Puget Sound	Puget Sound	other	North Puget Sound	other
Holmes Harbor	Holmes Harbor	Whidbey	Puget Sound	other	South Puget Sound	other
Interior San Juan Islands	Interior San Juan Islands	North Puget Sound	Puget Sound	other	North Puget Sound	other
Kilisut Harbor	Kilisut Harbor	Main	Puget Sound	other	South Puget Sound	other
NW San Juan Islands	NW San Juan Islands	North Puget Sound	Puget Sound	other	North Puget Sound	other
Port Gamble	Port Gamble	Hood Canal	Puget Sound	other	South Puget Sound	other
Port Orchard/Port Madison	Port Orchard/Port Madison	Main	Puget Sound	other	South Puget Sound	other
Port Susan	Port Susan	Whidbey	Puget Sound	other	South Puget Sound	other
Quartermaster Harbor	Quartermaster Harbor	Main	Puget Sound	other	South Puget Sound	other
Quilcene Bay	Quilcene Bay	Hood Canal	Puget Sound	other	South Puget Sound	other
Samish Bay/Portage Bay	Samish Bay/Portage Bay	North Puget Sound	Puget Sound	other	North Puget Sound	other
Semiahmoo	Semiahmoo	North Puget Sound	Puget Sound	other	North Puget Sound	Semiahmoo
Skagit Bay	Skagit Bay	Whidbey	Puget Sound	other	South Puget Sound	other
South Hood Canal	South Hood Canal	Hood Canal	Puget Sound	other	South Puget Sound	other
Squaxin Pass	Squaxin Pass	South Puget Sound	Puget Sound	Squaxin Pass	South Puget Sound	other
Wollochet Bay	Wollochet Bay	South Puget Sound	Puget Sound	other	South Puget Sound	other

Table A3. Standard deviations of biomass for each subpopulation (in bold, on the diagonal) and correlations between subpopulations.

	Cherry Point	Discovery Bay	Dungeness Bay	Fidalgo Bay	Holmes Harbor	Interior San Juan Islands	Kilisut Harbor	NW San Juan Islands	Port Gamble	Port Orchard/ Port Madison	Port Susan	Quartermaster Harbor	Quilcene Bay	Samish Bay/ Portage Bay	Semiahmoo Bay	South Hood Canal	Skagit Bay	Squaxin Pass	Wollochet Bay
Cherry Point	**0.2**																		
Discovery Bay	0.21	**1.04**																	
Dungeness Bay	-0.07	0.23	**1.16**																
Fidalgo Bay	-0.19	0.03	0.26	**0.64**															
Holmes Harbor	0.64	0.01	-0.14	0.08	**0.53**														
Interior San Juan Islands	-0.03	0.47	0.83	0.3	-0.05	**0.94**													
Kilisut Harbor	-0.54	-0.07	-0.14	0.5	-0.38	-0.08	**0.48**												
NW San Juan Islands	-0.25	-0.1	0.33	0.92	0.22	0.34	0.4	**0.89**											
Port Gamble	0.47	-0.28	0.2	-0.14	0.43	0.05	-0.09	-0.1	**0.31**										
Port Orchard/ Port Madison	-0.12	0.63	0.62	-0.1	-0.39	0.8	0.04	-0.15	0	**0.52**									
Port Susan	-0.17	0.06	-0.29	0.35	0.13	-0.1	0	0.24	-0.33	-0.29	**0.59**								
Quartermaster Harbor	0.33	0.6	0.27	-0.3	-0.02	0.43	-0.14	-0.38	0.22	0.62	0.03	**0.4**							
Quilcene Bay	0.04	0.04	0.63	0.07	0.23	0.55	-0.15	0.37	0.12	0.26	-0.46	0.12	**0.79**						
Samish Bay/ Portage Bay	-0.29	0.21	0.23	0.47	-0.57	0.07	0.27	0.23	-0.43	0.08	0.38	0.04	-0.31	**0.54**					
Semiahmoo Bay	0.35	0.3	0.48	0.58	0.59	0.57	-0.15	0.6	0.29	0.17	0.07	-0.04	0.29	-0.08	**0.2**				
South Hood Canal	0.03	0.59	0.74	0.07	-0.25	0.68	0.06	0.07	0.01	0.77	-0.62	0.34	0.54	0.13	0.3	**0.49**			
Skagit Bay	-0.1	0.48	0.35	0.81	0.11	0.56	0.3	0.69	-0.15	0.31	0.39	0.01	-0.03	0.39	0.75	0.28	**0.38**		
Squaxin Pass	0.09	0.42	-0.01	0.58	0.1	0.16	0.12	0.36	-0.23	0.06	0.3	-0.26	-0.42	0.36	0.61	0.1	0.79	**0.54**	
Wollochet Bay	-0.02	0.02	-0.55	-0.58	0.13	-0.44	0.11	-0.54	0.19	-0.1	0.13	0.38	-0.26	-0.42	-0.5	-0.38	-0.45	-0.46	**0.63**

Appendix B: Chapter 2

Natural mortality in other populations

Here we found a high mortality rate for adult Pacific herring relative to other populations. Mortality rates estimated for herring worldwide (*M* = 0.35-0.51; Lemberg et al. 1997) are lower than those estimated by this study: Atlantic herring on average have a lower mortality rate ($M_{average}$ = 0.18 yr^{-1}) than Pacific herring ($M_{average}$ = 0.52; McGurk 1993). This average value for Pacific herring is lower than the *M* estimated for Puget Sound herring by Stick and Lindquist (*M* = 1.27; 2014) and by this study (*M* = 0.82 – 1.7; 2008-2012). The *M* estimated here is nearly twice that estimated for adult Pacific herring outside of Puget Sound (nearly twice as high; Hourston and Haegele 1980). We also found that for some age classes, *M* increased with age (in period 1: median $M_{a=1,p=1}$=0.85; $M_{a=5,p=1}$ =0.99; in period 2: $M_{a=1,p=2}$ = 1.32; $M_{a=2,p=2}$ = 1.75). Tanasichuk (2000) found a similar pattern of higher *M* for older herring in Southern British Columbia, and attributed the increase in *M* with age to the inability of older herring to meet the energetic demands of reproduction.

Time-varying mortality vs. time-varying recruitment

In some cases, mortality and recruitment can be confounded, such that a decrease in recruitment might be interpreted as an increase in natural mortality. To make sure that M and recruitment were differentiable, we tested an additional model with constant, age-varying mortality and mean recruitment that was estimated separately for the first and second half of the survey time series. If either case fit the data similarly to models where *M* changed, then it would be difficult to distinguish an increase in adult mortality from a decrease in recruitment.

Weights at age used in simulations

To get weights at age for simulations (w_a), we used unpublished data from WDFW on herring length and weight at age in trawls adjacent to each site.

Von Bertalanffy growth parameters (L_{inf}, k, t_0 and sigma) were estimated from length at age data in trawl surveys using optim() in R. We examined residuals from the age-length relationship by site and by year to see whether it would be reasonable to include the effects of site or year on growth. Because we did not find strong evidence for systematic changes in size at age over time or consistent differences between sites, the mean lengths at age used to generate biomass in the simulations were estimated from all sites and years.

Mean lengths at age were converted to weights at age using the relationship between length and weight for all Puget Sound Pacific herring ($W = aL^b$; a = 7.774145e-06; b = 3.1188).

Estimated von-Bertalanffy growth parameters (Figure B2)

L_{inf} = 203.36 mm

k = 0.339

t_0 = 1.542

A. Penalty on initial numbers at age

We added a penalty to the estimation of initial age structure at each site, based on recruitment and mortality. This is specified in JAGS as follows:

$$N_{a,1,s} \sim \text{LogNormal}\left(\psi_s - \sum_{x=3}^{a} m_{x,p}\, , \tau^2\right)$$

where τ^2 is recruitment variance.

We compared draws from this distribution against one another and against the initial numbers at age data to confirm that this was realistic.

Table B1. Fits for models where mortality changed (in grey) and then where recruitment changed instead (in black).

Model	Form	ΔDIC
Age × Period	$M_{a,p}$	0
Age + Basin × Period	$M_a e^{\beta_{b,p}}$	4
Age + Period	$M_a e^{\beta_p}$	5
Age + Basin	$M e^{\beta_b}$	71
Age × Basin	$M_{a,b}$	87
Age	M_a	106
Null	M	163
Site × Period (Mean recruitment changes instead of mortality; age-specific adult mortality is constant at M_a)	$\psi_{s,r}$	166

Table B2. Cross-correlation matrix among posterior estimates

	$m_{r=1,a=3}$	$m_{r=1,a=42}$	$m_{r=1,a=5}$	$m_{r=1,a=6}$	$m_{r=1,a=7+}$	$m_{r=2,a=3}$	$m_{r=2,a=4}$	$m_{r=2,a=5}$	$m_{r=2,a=6}$	$m_{r=2,a=7+}$	ε	$\psi_{s=1}$	$\psi_{s=2}$	$\psi_{s=3}$	$\psi_{s=4}$	$\psi_{s=5}$	$\psi_{s=6}$	$\psi_{s=7}$	$\psi_{s=8}$	τ
$m_{r=1,a=3}$	1.00	-0.31	-0.10	-0.06	-0.07	-0.04	-0.02	0.00	0.00	0.02	0.13	0.64	0.06	0.39	0.08	0.07	0.04	0.06	0.49	-0.27
$m_{r=1,a=4}$	-0.31	1.00	-0.29	-0.10	-0.09	0.01	0.01	-0.04	-0.02	-0.01	-0.10	0.12	0.00	0.09	0.01	0.00	0.03	0.01	0.09	-0.03
$m_{r=1,a=5}$	-0.10	-0.29	1.00	-0.26	-0.07	0.02	0.00	0.03	-0.05	-0.01	-0.07	0.03	0.01	0.02	0.01	0.00	-0.01	0.00	0.03	-0.01
$m_{r=1,a=6}$	-0.06	-0.10	-0.26	1.00	-0.31	0.02	-0.01	0.00	0.04	-0.03	-0.04	0.02	0.00	0.04	0.00	-0.01	0.01	-0.01	0.02	0.00
$m_{r=1,a=7+}$	-0.07	-0.09	-0.07	-0.31	1.00	-0.01	0.00	0.00	0.02	0.01	-0.04	0.03	0.00	0.04	0.01	0.02	-0.02	0.01	0.03	-0.03
$m_{r=2,a=3}$	-0.04	0.01	0.02	0.02	-0.01	1.00	-0.43	0.00	0.01	0.00	-0.15	0.00	-0.01	-0.03	-0.05	-0.02	-0.03	-0.03	-0.04	0.18
$m_{r=2,a=4}$	-0.02	0.01	0.00	-0.01	0.00	-0.43	1.00	-0.40	0.00	-0.01	0.01	-0.01	-0.01	-0.01	0.01	0.01	0.00	-0.01	-0.01	0.00
$m_{r=2,a=5}$	0.00	-0.04	0.03	0.00	0.00	0.00	-0.40	1.00	-0.32	-0.02	-0.02	-0.01	0.00	-0.01	0.01	0.00	-0.01	0.01	-0.01	0.02
$m_{r=2,a=6}$	0.00	-0.02	-0.05	0.04	0.02	0.01	0.00	-0.32	1.00	-0.14	-0.04	0.00	0.00	0.00	-0.01	-0.02	0.00	-0.01	-0.01	0.00
$m_{r=2,a=7+}$	0.02	-0.01	-0.01	-0.03	0.01	0.00	-0.01	-0.02	-0.14	1.00	0.04	0.00	0.00	0.00	0.01	0.00	0.01	0.00	0.01	-0.01
ε	0.13	-0.10	-0.07	-0.04	-0.04	-0.15	0.01	-0.02	-0.04	0.04	1.00	-0.06	-0.01	-0.05	0.02	0.00	0.01	0.00	0.02	-0.04
$\psi_{s=1}$	0.64	0.12	0.03	0.02	0.03	0.00	-0.01	-0.01	0.00	0.00	-0.06	1.00	0.09	0.44	0.10	0.07	0.08	0.07	0.53	-0.33
$\psi_{s=2}$	0.06	0.00	0.01	0.00	0.00	-0.01	-0.01	0.00	0.00	0.00	-0.01	0.09	1.00	0.07	0.06	0.04	0.05	0.05	0.08	-0.22
$\psi_{s=3}$	0.39	0.09	0.02	0.04	0.04	-0.03	-0.01	-0.01	0.00	0.00	-0.05	0.44	0.07	1.00	0.09	0.07	0.07	0.08	0.35	-0.33
$\psi_{s=4}$	0.08	0.01	0.01	0.00	0.01	-0.05	0.01	0.01	-0.01	0.01	0.02	0.10	0.06	0.09	1.00	0.06	0.06	0.07	0.10	-0.28
$\psi_{s=5}$	0.07	0.00	0.00	-0.01	0.02	-0.02	0.01	0.00	-0.02	0.00	0.00	0.07	0.04	0.07	0.06	1.00	0.06	0.04	0.08	-0.22
$\psi_{s=6}$	0.04	0.03	-0.01	0.01	-0.02	-0.03	0.00	-0.01	0.00	0.01	0.01	0.08	0.05	0.07	0.06	0.06	1.00	0.05	0.07	-0.21
$\psi_{s=7}$	0.06	0.01	0.00	-0.01	0.01	-0.03	-0.01	0.01	-0.01	0.00	0.00	0.07	0.05	0.08	0.07	0.04	0.05	1.00	0.08	-0.22
$\psi_{s=8}$	0.49	0.09	0.03	0.02	0.03	-0.04	-0.01	-0.01	-0.01	0.01	0.02	0.53	0.08	0.35	0.10	0.08	0.07	0.08	1.00	-0.33
τ	-0.27	-0.03	-0.01	0.00	-0.03	0.18	0.00	0.02	0.00	-0.01	-0.04	-0.33	-0.22	-0.33	-0.28	-0.22	-0.21	-0.22	-0.33	1.00

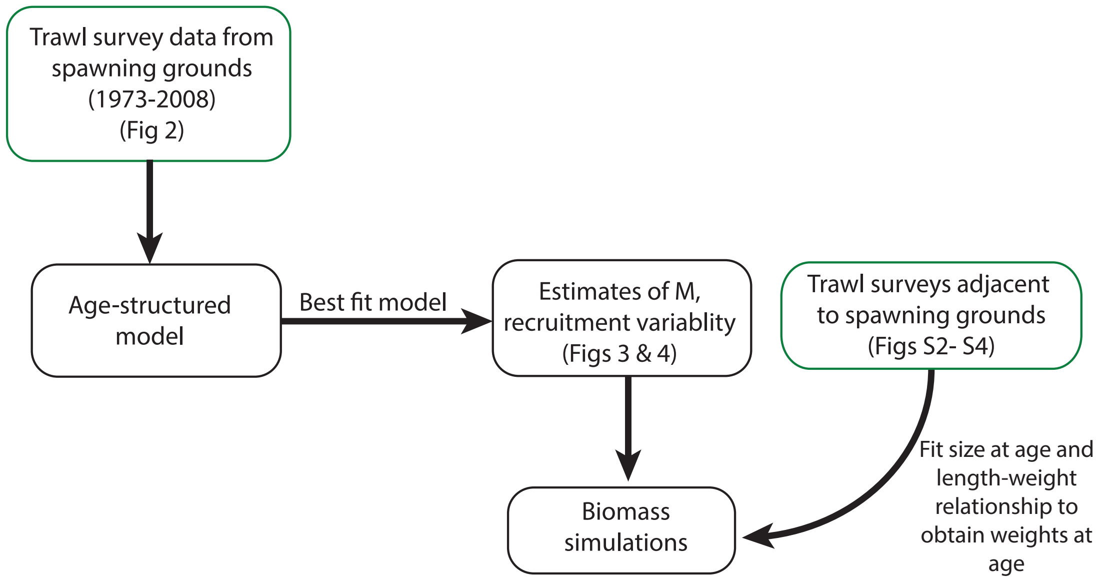

Figure B1. Steps in the modeling and simulation process. Data are shown in green boxes.

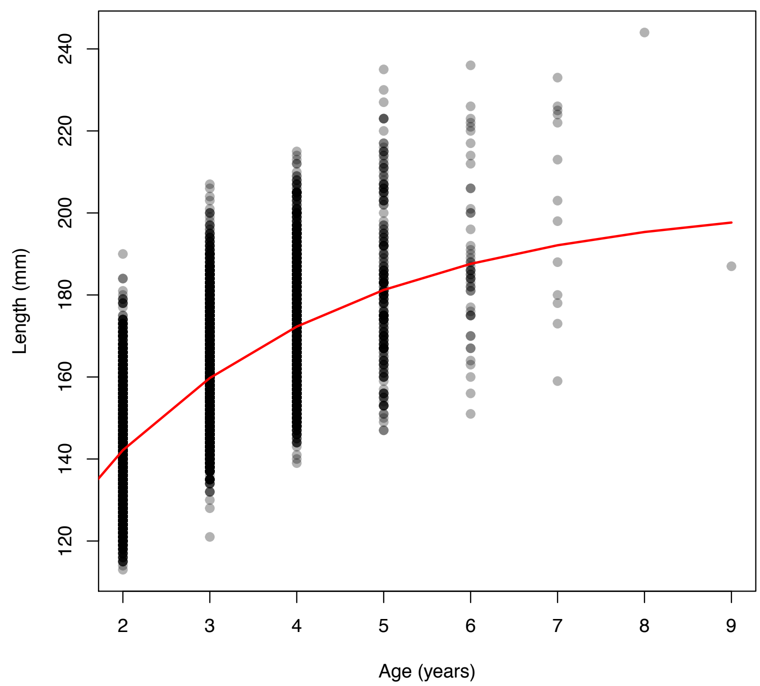

Figure B2. von Bertalanffy growth for herring caught in trawls adjacent to each site in this study between 2001-2011. Length is fork length.

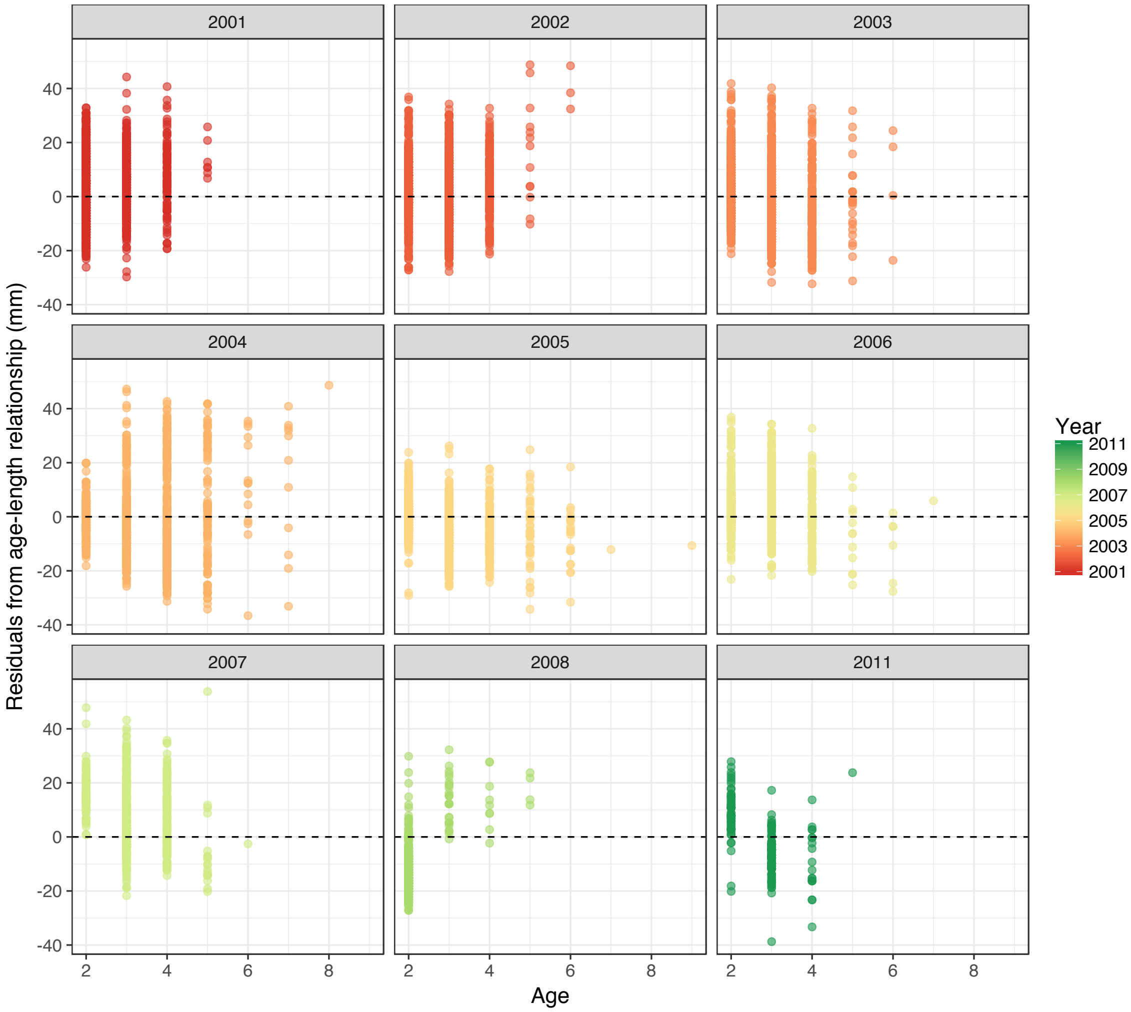

Figure B3. von Bertalanffy growth residuals for each year with trawl data, based on trawl surveys by WDFW.

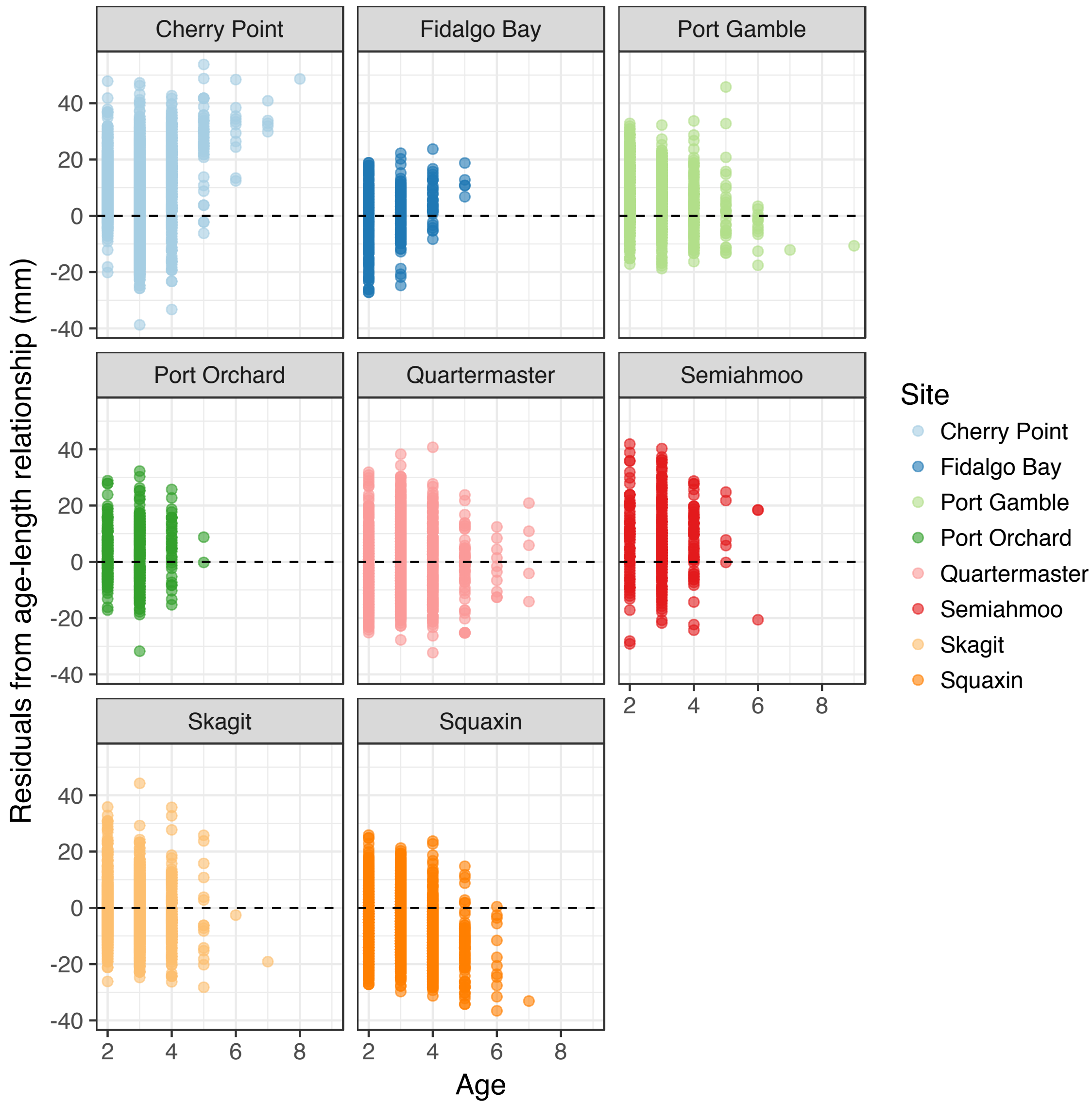

Figure B4. von Bertalanffy growth residuals by site, based on data from trawl surveys by WDFW.

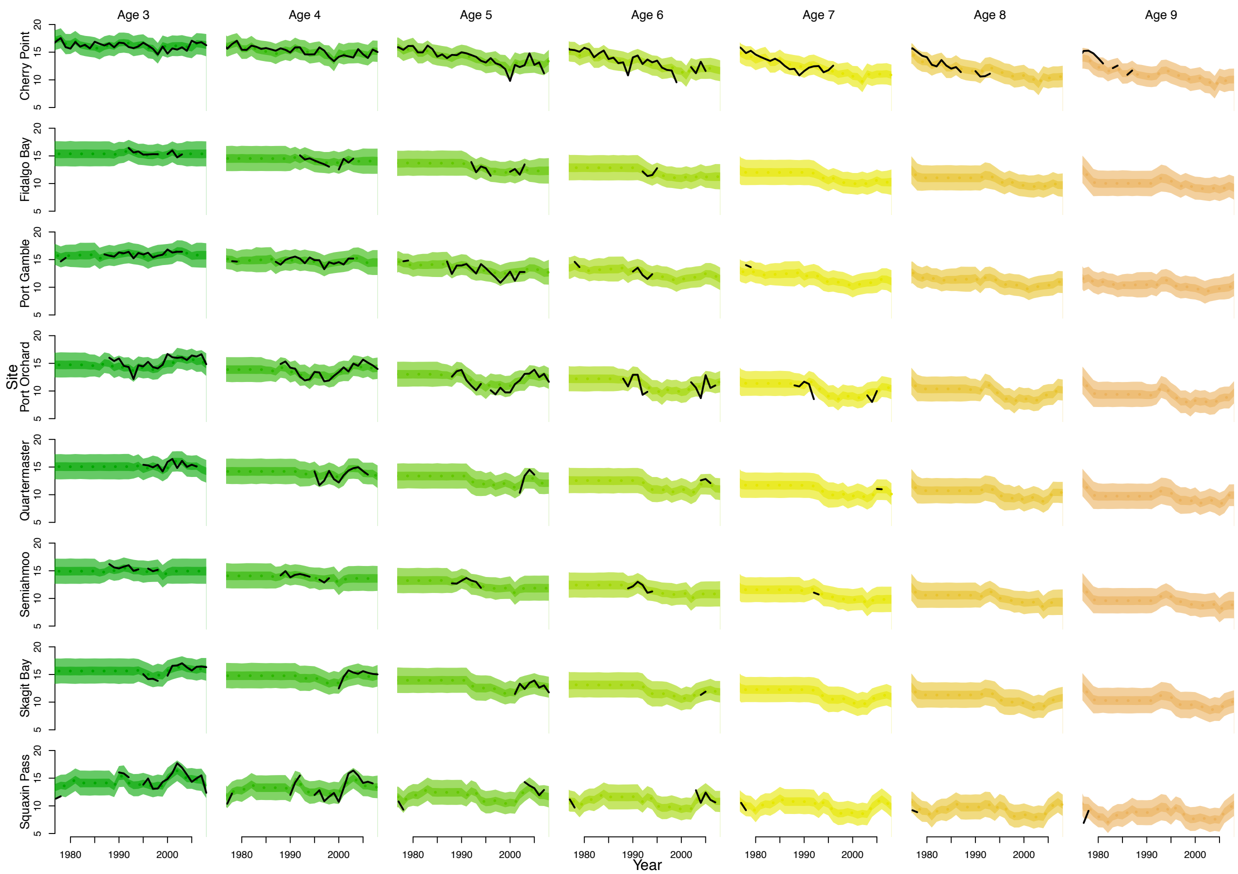

Figure B5. Posterior predictive projections for Log(N) at age based on the model where age-specific mortality changes and recruitment is variable. Shaded colored areas are 50% and 95% prediction intervals for projections with medians shown as dotted lines, and black lines are observed numbers at age.

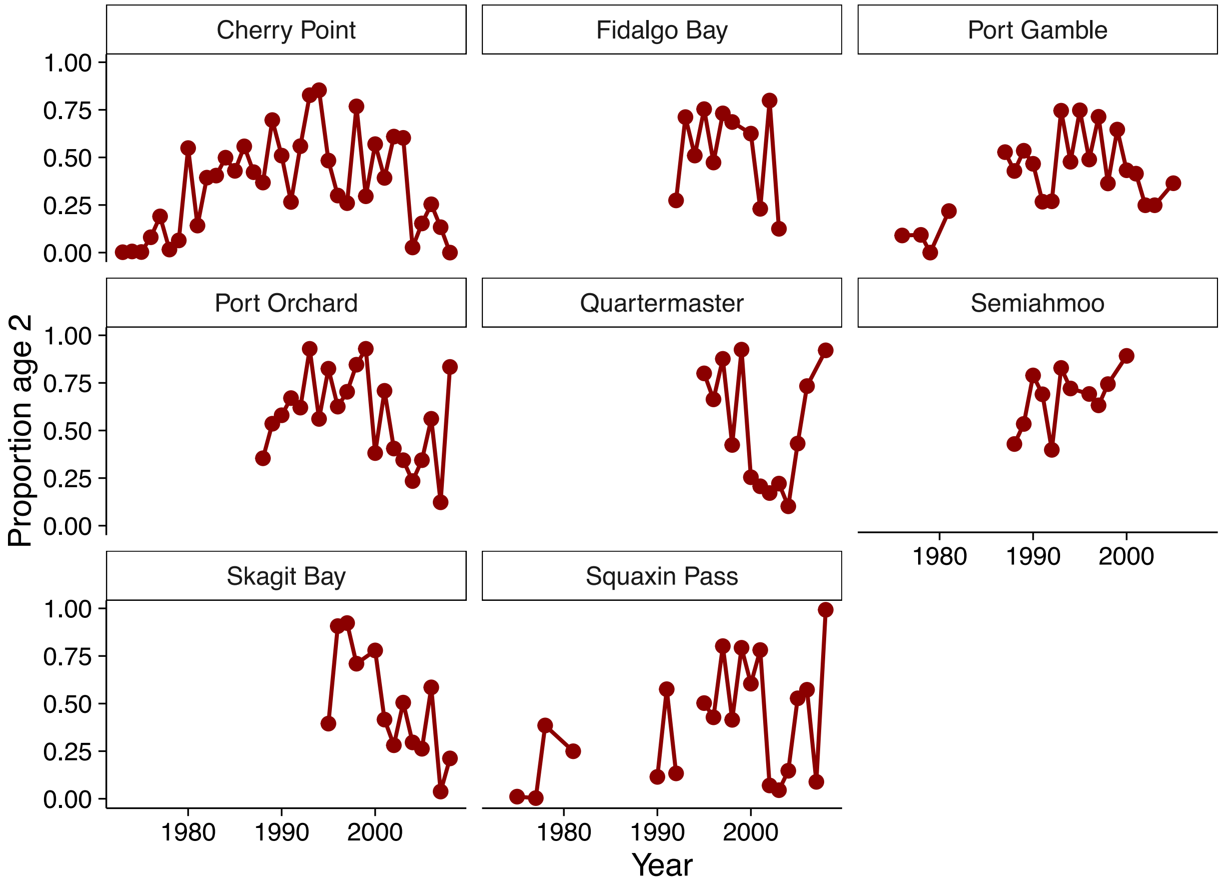

Figure B6. Proportion of the population composed of age 2 fish, according to trawl surveys of pre-spawning aggregations.

Appendix C: Chapter 3

Table C1. Life history parameters used for different forage fish life history types

Forage fish type	Life span (years)	Natural mortality (M)	Length at age (cm)		Fishery selectivity		Weight at age or length-weight relationship		Maturity		Primary source of life history parameters
		1.09			Age	Selectivity			Age	Proportion mature	
			Age	Length (cm)	0	0			0	0	
		(MacCall 1974)	0	10.8	1	0.6			1	0.4	
			1	14	2	1			2	0.85	
Anchovy-like	0:06		2	16.3	3	1	a = 1.015; b = 3 (FishBase)		3	0.99	Northern anchovy (CA)
			3	17.8	4	1			4	1	
			4	18.9	5	1			5	1	
			5	19.6	6	1			6	1	
			6	20	(Methot 1989)						
		0.5			Age	Selectivity	Age	Weight at age in 2013 (kg)	Age	Proportion mature (from NEAMAP)	
			Age	Length (cm)	0	0.004	0.5	0.0569	0	0	
		(Atlantic menhaden assessment, Table 3.6.1)	0	8	1	0.143	1	0.1281	1	0.13	
			1	16.66	2	0.994	2	0.2317	2	0.53	Atlantic menhaden
Menhaden-like	0:06		2	21.74	3	0.84	3	0.3285	3	0.83	
			3	25.13	4	0.191	4	0.3711	4	0.98	
			4	26.98	5	0.024	5	0.5371	5	1	
			5	30.22	6	0	6+	0.4481	6	1	
			6+	28.87	("domed" selectivity for reduction fishery; Butterworth et al. 2012)		(Atlantic menhaden stock assessment; Table 3.3.3)		7	1	
									8	1	
			Age	Length (cm)	Age	Selectivity	Age	Weight (kg)	Age	Proportion mature	
			0	4	0	0.263	0	0.014	0	0	
			1	5.6	1	1	1	0.02506667	1	0.4	
			2	7.2	2	1	2	0.03613333	2	0.85	
			3	8.8	3	0.669	3	0.0472	3	0.99	
			4	10.4	4	0.471	4	0.05826667	4	1	
			5	12	5	0.39	5	0.06933333	5	1	
			6	13.6	6	0.358	6	0.0804	6	1	
			7	15.2	7	0.345	7	0.09146667	7	1	
			8	16.8	8	0.339	8	0.10253333	8	1	Pacific sardine (CA)
Sardine-like	0:15	0.4	9	18.4	9	0.335	9	0.1136	9	1	
			10	20	10	0.333	10	0.12466667	10	1	
			11	21.6	11	0.332	11	0.13573333	11	1	
			12	23.2	12	0.332	12	0.1468	12	1	
			13	24.8	13	0.331	13	0.15786667	13	1	
			14	26.4	14	0.331	14	0.16893333	14	1	
			15	28	15	0.331	15	0.18	15	1	
			(Hurtado-Ferro & Punt 2014)								
					(Hill et al. 2012 sardine stock assessment)						

Table C2. Spectral properties of recruitment estimates for each forage fish "type." Data are from RAM Legacy Database and Barange et al. 2009

Sardine-like:

	Data source	Rec Length	σ_R	β_R	lowerCI	upperCI	SE(β_R)
California sardine	1	55	1.40	3.05	1.89	4.21	0.58
European sardine	1	26	NA	NA	NA	NA	NA
Humboldt sardine – N Central Peru	1	32	0.66	5.15	1.01	9.30	2.04
Japanese sardine	1	41	1.34	3.73	2.36	5.10	0.68
Pacific sardine Pacific Coast	2	27	1.21	-0.48	-4.01	3.04	1.72
European pilchard ICES VIIIc-IXa	2	34	0.64	0.75	-1.05	2.56	0.89

1: Barange et al. 2009
2: RAM Legacy database

Anchovy-like:

	Data source	Rec Length	σ_R	β_R	lowerCI	upperCI	SE(β_R)
Anchovy South Africa	2	27	0.84	1.39	-1.39	4.16	1.35
Herring ICES 25-32	2	38	0.45	1.63	-0.08	3.34	0.85
Herring ICES 30	2	39	0.67	-1.01	-2.24	0.22	0.61
Herring NAFO 4R spring spawners	2	40	1.33	-0.46	-1.95	1.03	0.75
Herring NAFO 4T fall spawners	2	30	0.59	0.85	-1.48	3.17	1.14
Herring NAFO 4T spring spawners	2	30	0.82	-1.03	-4.60	2.55	1.76
Herring Scotian Shelf and Bay of Fundy	2	42	0.83	1.38	-0.16	2.92	0.77

Pacific herring Central Coast	2	54	0.98	-1.28	-2.13	-0.42	0.43
Herring Northern Irish Sea	2	50	0.65	1.29	0.28	2.31	0.51
Herring North Sea	2	52	0.63	2.34	1.18	3.50	0.59
Atlantic herring Northwestern Atlantic Coast	2	47	0.89	0.77	-0.07	1.61	0.42
Pacific herring Prince Rupert District	2	54	0.67	0.06	-0.73	0.85	0.40
Pacific herring Queen Charlotte Islands	2	54	1.54	-0.38	-1.03	0.26	0.32
Herring ICES 28	2	35	0.62	0.99	-0.87	2.85	0.92
Herring ICES VIIa-g-h-j	2	53	0.60	1.45	0.58	2.31	0.44
Pacific herring Sitka	2	27	1.05	-3.84	-6.75	-0.93	1.42
Pacific herring Straight of Georgia	2	54	0.43	0.37	-0.88	1.63	0.63
Herring ICES VIa	2	54	1.10	0.31	-0.54	1.16	0.43
Pacific herring West Coast of Vancouver Island	2	54	0.56	-0.11	-0.98	0.76	0.44
Japanese anchovy Pacific Coast of Japan	2	28	0.76	0.32	-2.08	2.73	1.18
California anchovy	1	31	0.92	1.53	-1.12	4.18	1.30
Humboldt anchovy - Central Peru	1	40	0.66	2.57	1.36	3.78	0.60

Menhaden-like:

	Data source	Rec Length	σ_R	β_R	lowerCI	upperCI	SE(β_R)
Gulf menhaden Gulf of Mexico	2	41	0.37	0.06	-1.08	1.20	0.57

Atlantic menhaden Atlantic	2	57	0.83	1.95	1.11	2.80	0.43

Table C3. Performance of control rules for anchovy-like fish, for (A) the base case (h = 0.6, autocorrelated observation error), (B) high steepness (h = 0.9), and (C) delayed detection of changes.

C3.A. Anchovy – base case

h	*Observation error*	*HCR*	*LT mean catch*	*SD(Catch)*	*Probability of 5-yr closure*	*Years w/ zero catch*	*LT mean biomass*	*Bonanza length*	*Collapse length*	*Probability of collapse*	*Collapse severity*	*Sustained collapses*
0.60	Autocorrelated (AC)	Stability-favoring	148.89	393.43	0.00	0	15189.38	8.17	2.00	0.01	0.19	0
0.60	AC	Constant F	1410.37	857.55	0.00	0	10440.47	4.17	2.00	0.02	0.13	0
0.60	AC	Basic hockey	1424.58	1098.81	0.00	8	10802.32	3.87	1.00	0.01	0.09	0
0.60	AC	Low Blim	1456.12	1016.31	0.00	0	10468.48	3.83	2.00	0.01	0.10	0
0.60	AC	High Fmax	1615.45	1380.75	0.00	12	9204.38	3.00	1.50	0.01	0.10	0
0.60	AC	Constant F - High	1535.99	1064.86	0.00	0	7240.59	3.00	4.00	0.16	0.26	1

C3.B: Anchovy – high steepness

h	*Observation error*	*HCR*	*LT mean catch*	*SD(Catch)*	*Probability of 5-yr closure*	*Years w/ zero catch*	*LT mean biomass*	*Bonanza length*	*Collapse length*	*Probability of collapse*	*Collapse severity*	*Sustained collapses*
0.90	AC	Stability-favoring	319.41	773.47	0.00	0	15327.35	7.25	2.00	0.01	0.22	0
0.90	AC	Constant F	2635.95	1701.45	0.00	0	8284.27	2.40	2.33	0.08	0.23	1
0.90	AC	Basic hockey	1726.90	1164.03	0.00	3	12389.13	4.00	1.00	0.01	0.06	0
0.90	AC	Low Blim	1771.55	1099.83	0.00	0	12260.36	4.00	1.00	0.01	0.06	0
0.90	AC	High Fmax	2680.54	2497.56	0.00	20	8008.53	2.00	1.60	0.07	0.25	1
0.90	AC	Constant F - High	2395.26	1842.53	0.96	0	5769.84	2.00	3.20	0.30	0.39	2

C3.C: Anchovy – delayed detection of changes

h	*Observation error*	*HCR*	*LT mean catch*	*SD(Catch)*	*Probability of 5-yr closure*	*Years w/ zero catch*	*LT mean biomass*	*Bonanza length*	*Collapse length*	*Probability of collapse*	*Collapse severity*	*Sustained collapses*
0.60	Delayed detection of changes (DD)	Stability-favoring	123.33	415.52	0.00	0	14925.38	8.31	4.00	0.02	0.37	0
0.60	DD	Constant F	1211.93	548.63	0.00	0	10372.44	5.00	4.00	0.06	0.25	0
0.60	DD	Basic hockey	1261.38	744.65	0.00	1	10908.58	4.71	2.33	0.02	0.16	0
0.60	DD	Low Blim	1274.45	678.11	0.74	0	10531.79	4.71	3.00	0.04	0.19	0
0.60	DD	High Fmax	1381.61	1039.67	0.23	8	9732.23	4.17	2.75	0.06	0.23	1
0.60	DD	Constant F - High	1057.07	885.63	0.00	0	8409.01	5.00	7.33	0.23	0.52	1

Table C4. Performance of control rules for menhaden-like fish, for (A) the base case, (B) high steepness, and (C) delayed detection of changes.

C4.A: Menhaden – base case

h	*Observation error*	*HCR*	*LT mean catch*	*SD(Catch)*	*Probability of 5-yr closure*	*Years w/ zero catch*	*LT mean biomass*	*Bonanza length*	*Collapse length*	*Probability of collapse*	*Collapse severity*	*Sustained collapses*
0.60	AC	Stability-favoring	5246.21	13752.97	0.00	0	400526.20	10.00	3.00	0.01	0.23	0
0.60	AC	Constant F	37866.32	31312.63	0.00	0	207815.06	3.50	3.00	0.08	0.19	1
0.60	AC	Basic hockey	17582.44	15820.35	0.00	6	366630.34	7.00	1.00	0.01	0.03	0
0.60	AC	Low Blim	18372.47	15048.52	0.00	0	361433.08	7.00	1.00	0.01	0.06	0
0.60	AC	High Fmax	39044.67	45424.30	0.07	25	242221.65	3.25	1.50	0.01	0.12	0
0.60	AC	Constant F - High	36681.00	32002.65	0.00	0	165150.47	3.00	4.46	0.21	0.26	2

C4.B: Menhaden – high steepness

h	*Observation error*	*HCR*	*LT mean catch*	*SD(Catch)*	*Probability of 5-yr closure*	*Years w/ zero catch*	*LT mean biomass*	*Bonanza length*	*Collapse length*	*Probability of collapse*	*Collapse severity*	*Sustained collapses*
0.90	AC	Stability-favoring	4684.85	12822.92	0.00	0	424853.96	9.86	1.00	0.01	0.21	0
0.90	AC	Constant F	57636.69	46818.24	0.00	0	267654.58	3.50	1.50	0.02	0.14	0
0.90	AC	Basic hockey	19331.44	16548.45	0.00	4	390086.54	7.06		0.01		0
0.90	AC	Low Blim	20116.01	15890.64	0.00	0	387559.86	7.00		0.01		0
0.90	AC	High Fmax	55919.34	55055.42	0.00	18	275184.22	3.29	1.00	0.01	0.16	0
0.90	AC	Constant F - High	60519.04	47344.34	0.00	0	249041.54	3.20	1.75	0.04	0.15	0

C4.C: Menhaden – delayed detection of changes

h	*Observation error*	*HCR*	*LT mean catch*	*SD(Catch)*	*Probability of 5-yr closure*	*Years w/ zero catch*	*LT mean biomass*	*Bonanza length*	*Collapse length*	*Probability of collapse*	*Collapse severity*	*Sustained collapses*
0.60	DD	Stability-favoring	244.67	424.77	0.00	0	423184.55	10.83	3.00	0.01	0.26	0
0.60	DD	Constant F	32001.56	15284.90	0.00	0	249999.93	5.20	3.50	0.05	0.18	0
0.60	DD	Basic hockey	13168.39	7312.69	0.00	0	377285.74	8.14	1.50	0.01	0.03	0
0.60	DD	Low Blim	14090.47	6310.44	0.00	0	372323.84	8.00	2.00	0.01	0.07	0
0.60	DD	High Fmax	32024.63	25882.54	0.30	14	285478.61	4.75	2.00	0.01	0.10	0
0.60	DD	Constant F - High	33004.22	18889.91	0.00	0	222407.21	4.67	4.50	0.11	0.25	1

Table C5. Performance of control rules for sardine-like fish, for (A) the base case, (B) high steepness, and (C) delayed detection of changes.

C5.A: Sardine – base case

h	*Observation error*	*HCR*	*LT mean catch*	*SD(Catch)*	*Probability of 5-yr closure*	*Years w/ zero catch*	*LT mean biomass*	*Bonanza length*	*Collapse length*	*Probability of collapse*	*Collapse severity*	*Sustained collapses*
0.60	AC	Stability-favoring	3902.44	9916.98	0.00	0.00	495446.55	19.33	4.00	0.01	0.21	0
0.60	AC	Constant F	25883.73	16301.04	0.00	0.00	355336.78	11.50	7.50	0.02	0.16	0
0.60	AC	Basic hockey	26441.84	24479.74	0.14	17.00	365552.28	9.67	5.00	0.01	0.10	0
0.60	AC	Low Blim	27883.66	22410.50	0.00	0.00	347743.45	10.00	6.00	0.01	0.10	0
0.60	AC	High Fmax	30407.45	31153.61	0.17	21.00	323365.00	6.67	5.00	0.01	0.11	0
0.60	AC	Constant F - High	33240.05	23185.37	0.00	0.00	230133.76	6.50	12.00	0.23	0.31	1

C5.B: Sardine – high steepness

h	*Observation error*	*HCR*	*LT mean catch*	*SD(Catch)*	*Probability of 5-yr closure*	*Years w/ zero catch*	*LT mean biomass*	*Bonanza length*	*Collapse length*	*Probability of collapse*	*Collapse severity*	*Sustained collapses*
0.90	AC	Stability-favoring	7959.05	19039.09	0.00	0.00	485495.73	18.00	3.00	0.02	0.24	0
0.90	AC	Constant F	49005.98	28627.72	0.00	0.00	265002.89	5.00	5.00	0.08	0.15	0
0.90	AC	Basic hockey	29995.19	24690.59	0.00	10.00	394681.84	9.33	5.00	0.01	0.11	0
0.90	AC	Low Blim	31901.95	22564.09	0.00	0.00	383821.70	9.42	4.00	0.01	0.07	0
0.90	AC	High Fmax	47236.40	53178.67	0.07	26.00	274628.02	2.67	1.00	0.01	0.12	0
0.90	AC	Constant F - High	54201.63	34618.23	0.00	0.00	168018.83	3.00	8.40	0.35	0.32	2

C5.C: Sardine – delayed detection of changes

h	*Observation error*	*HCR*	*LT mean catch*	*SD(Catch)*	*Probability of 5-yr closure*	*Years w/ zero catch*	*LT mean biomass*	*Bonanza length*	*Collapse length*	*Probability of collapse*	*Collapse severity*	*Sustained collapses*
0.60	DD	Stability-favoring	4102.57	14735.97	0.00	0.00	482421.98	21.33	8.00	0.09	0.51	0
0.60	DD	Constant F	24753.47	12565.14	0.00	0.00	361168.30	12.00	9.00	0.06	0.23	0
0.60	DD	Basic hockey	25294.91	19629.85	0.60	8.00	371058.98	10.33	6.00	0.01	0.11	0
0.60	DD	Low Blim	26757.75	17792.04	0.43	0.00	354233.64	10.00	6.50	0.01	0.13	0
0.60	DD	High Fmax	29527.83	25412.51	0.57	11.00	332908.79	8.25	5.00	0.01	0.11	0
0.60	DD	Constant F - High	24224.01	17726.85	0.96	0.00	189215.61	9.00	22.67	0.44	0.67	1

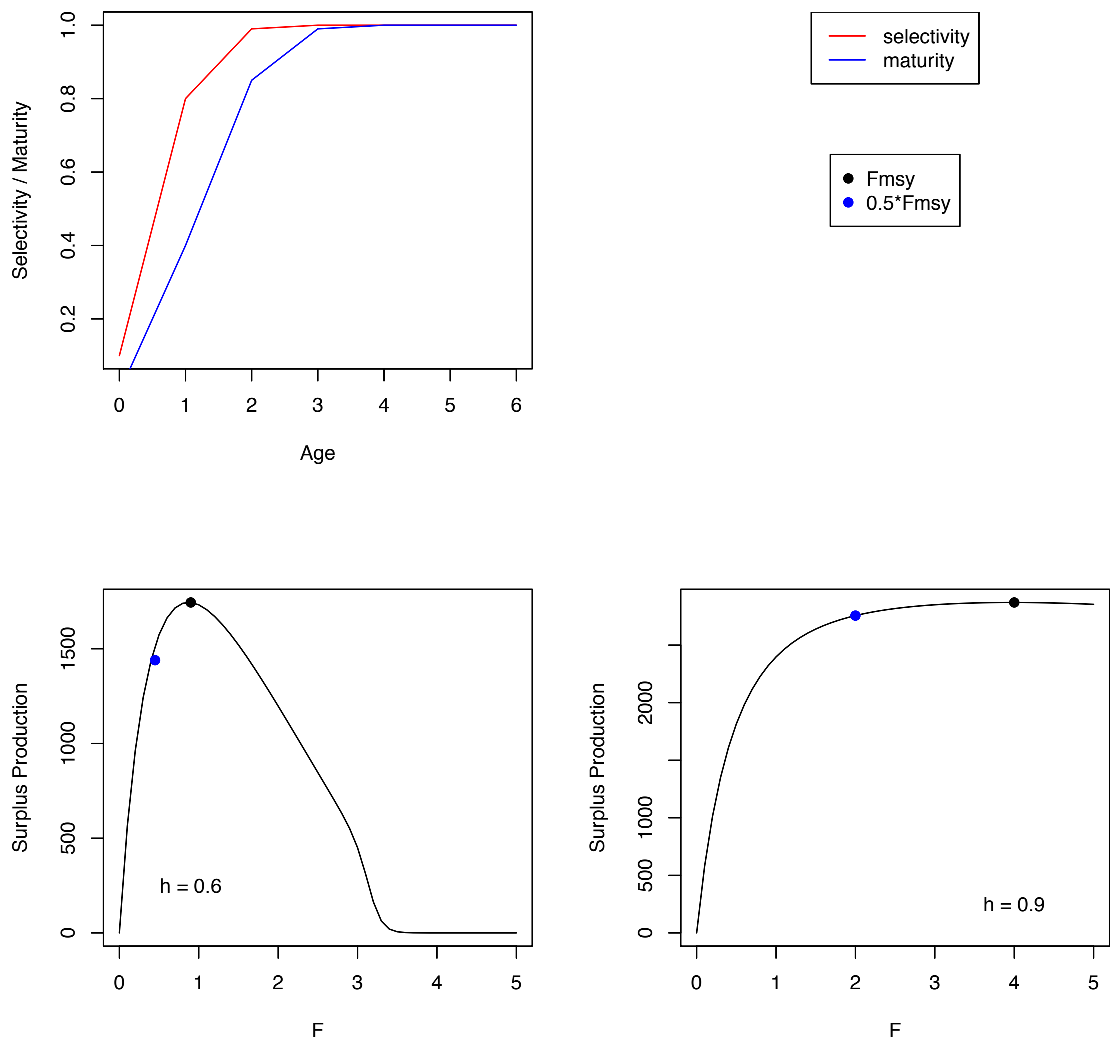

Figure C1. Selectivity, maturity, and yield curves for anchovy-like forage fish.

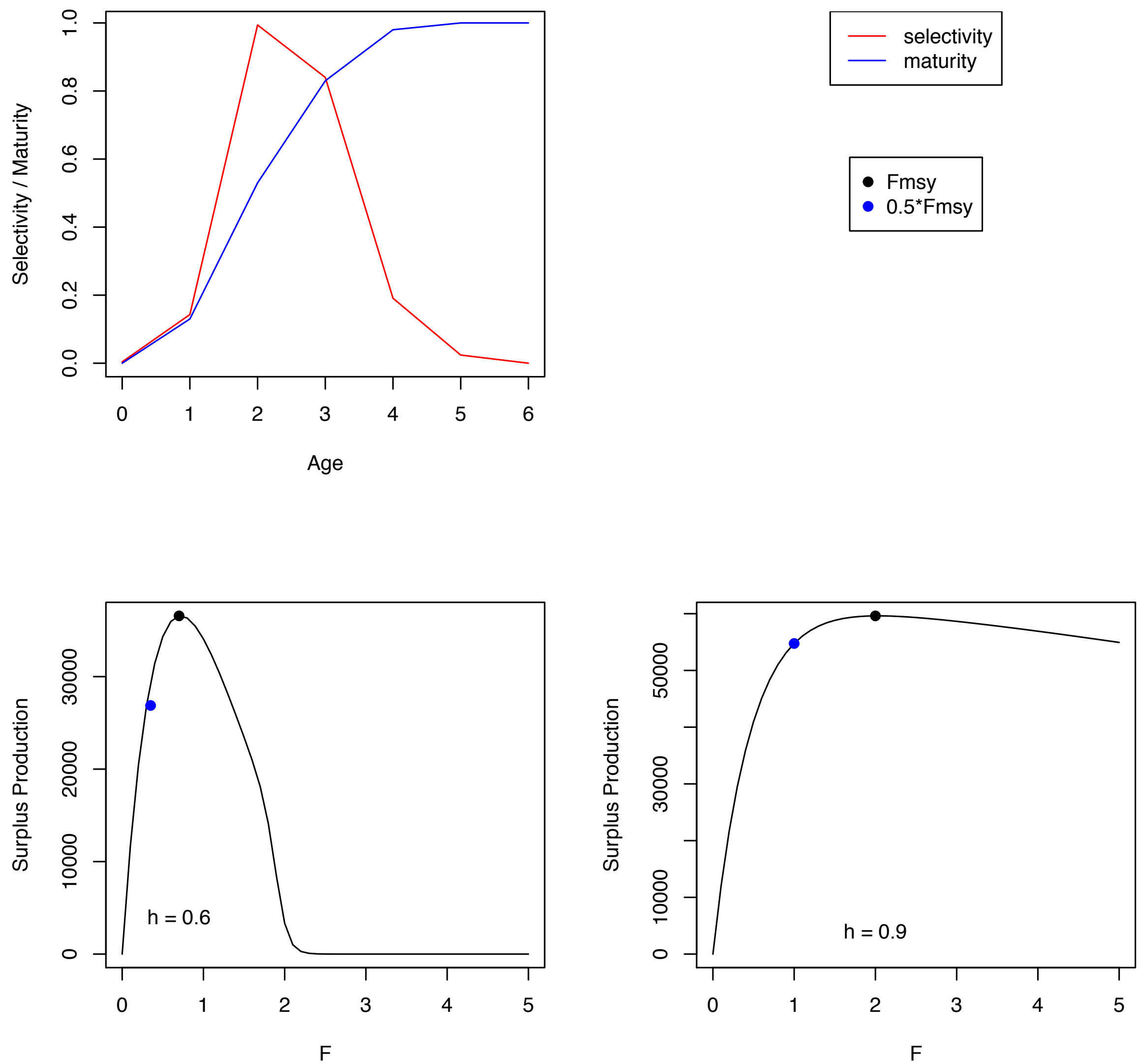

Figure C2. Selectivity, maturity, and yield curves for menhaden-like forage fish.

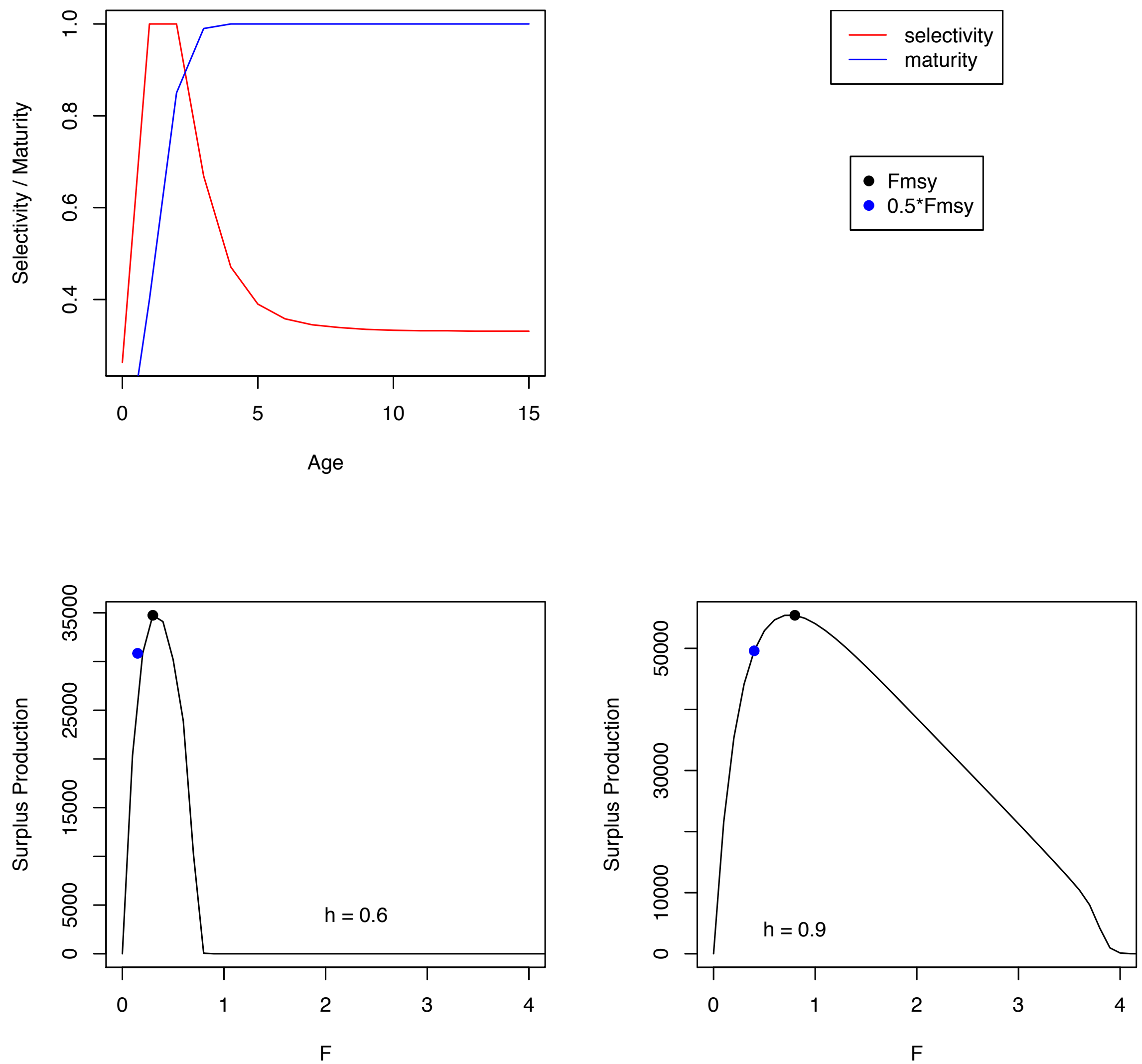

Figure C3. Selectivity, maturity, and yield curves for sardine-like forage fish.

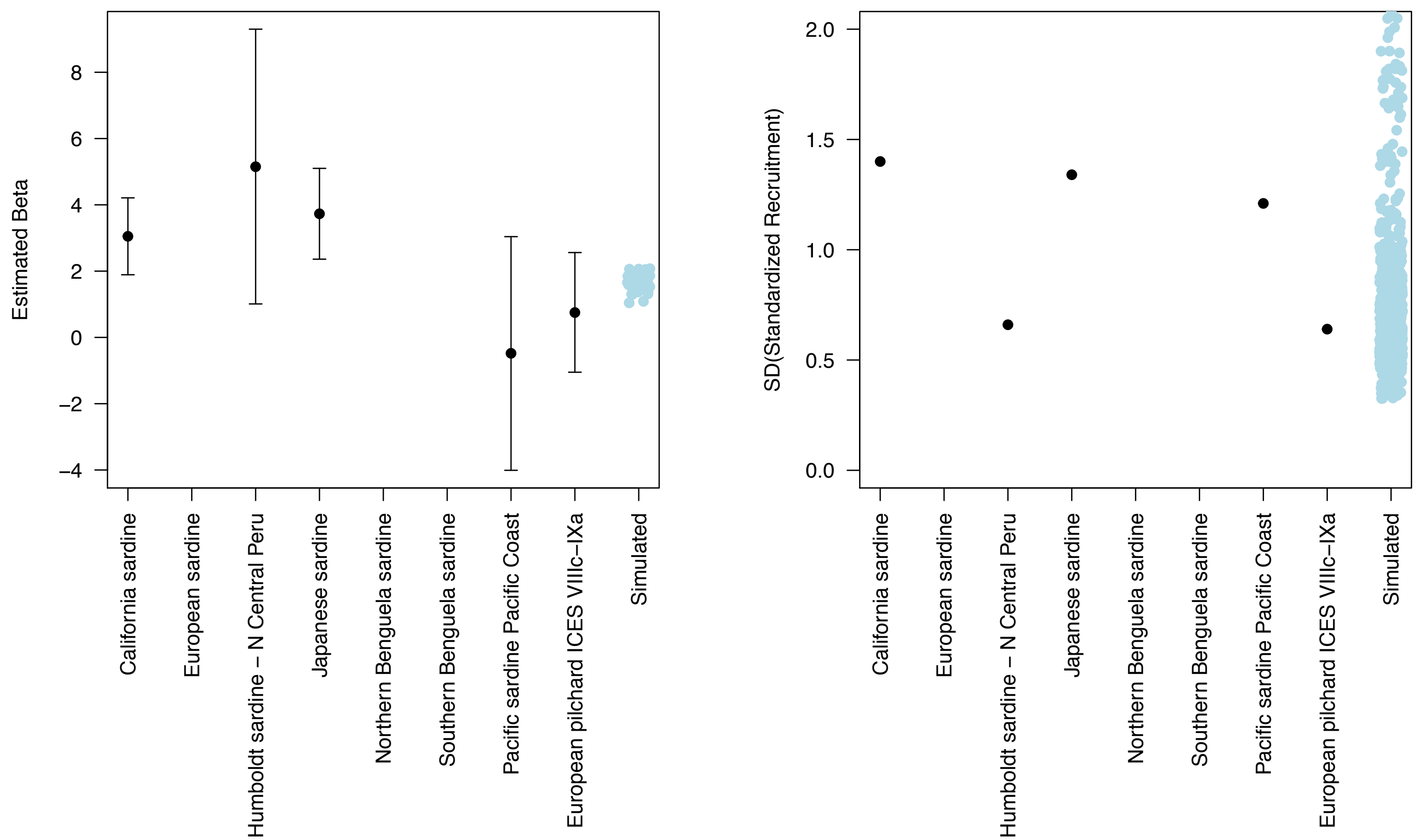

Figure C4. Comparison between beta (estimated, +/- 95% CIs) and SD between time series of recruitment estimates from sardine stocks, and spectral beta/SD of the simulated recruitment time series (blue). All time series of recruitment estimates were standardized before beta/SD were measured.

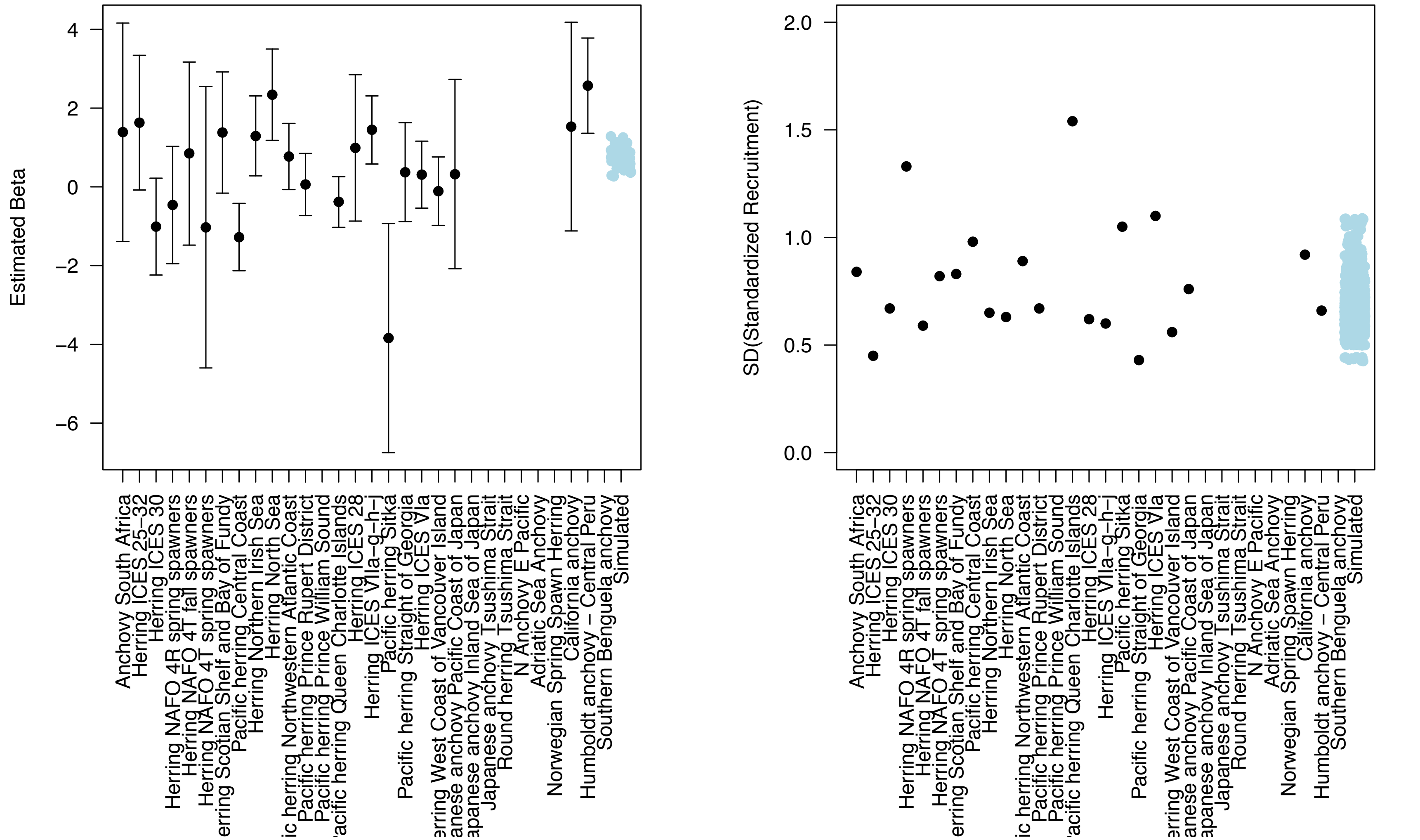

Figure C5. Comparison between beta (estimated, +/- 95% CIs) and SD between time series of recruitment estimates from herring and anchovy stocks, and spectral beta/SD of the simulated recruitment time series (blue).

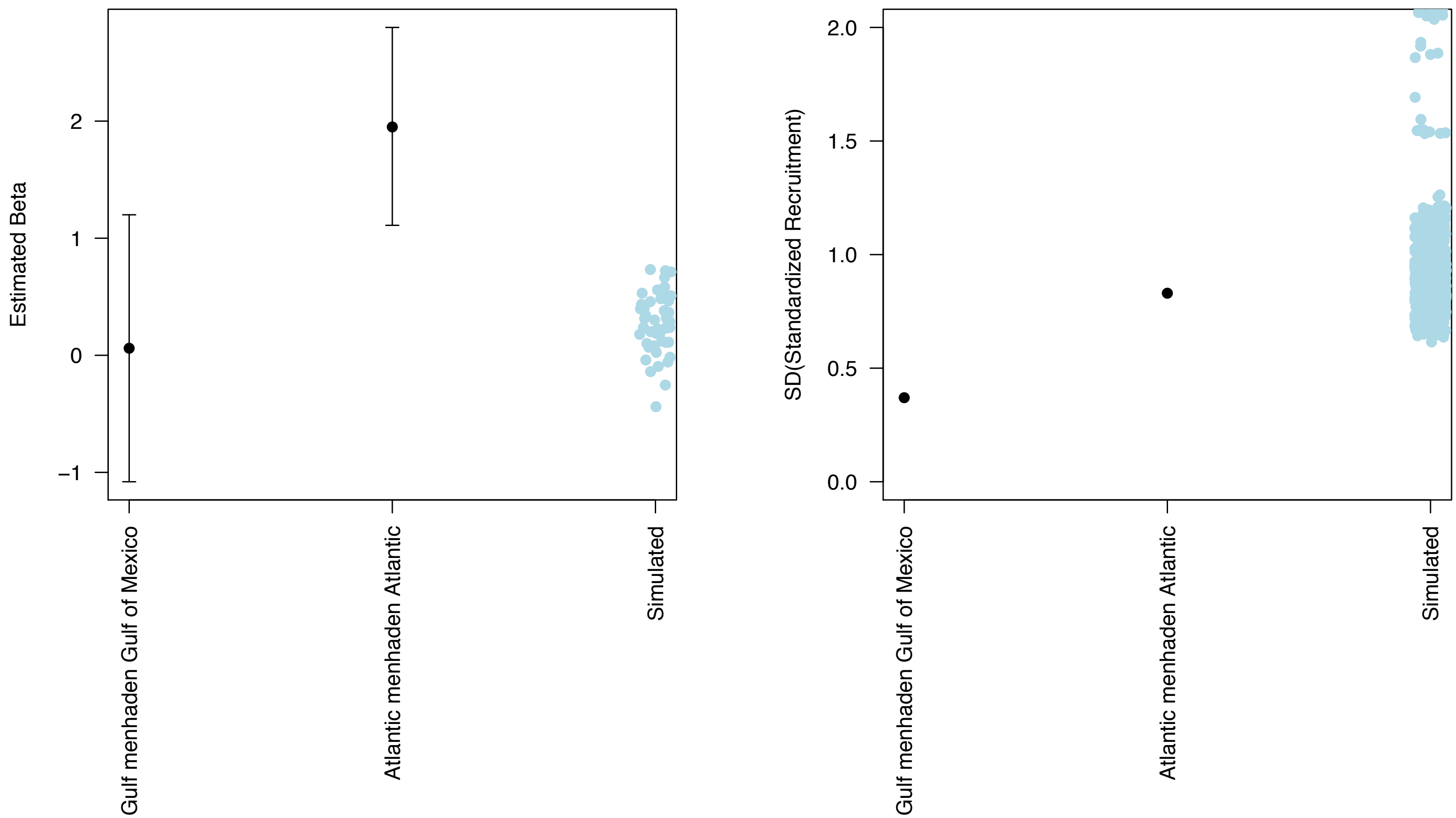

Figure C6. Comparison between beta (estimated, +/- 95% CIs) and SD between time series of recruitment estimates from menhaden stocks, and spectral beta/SD of the simulated recruitment time series (blue).

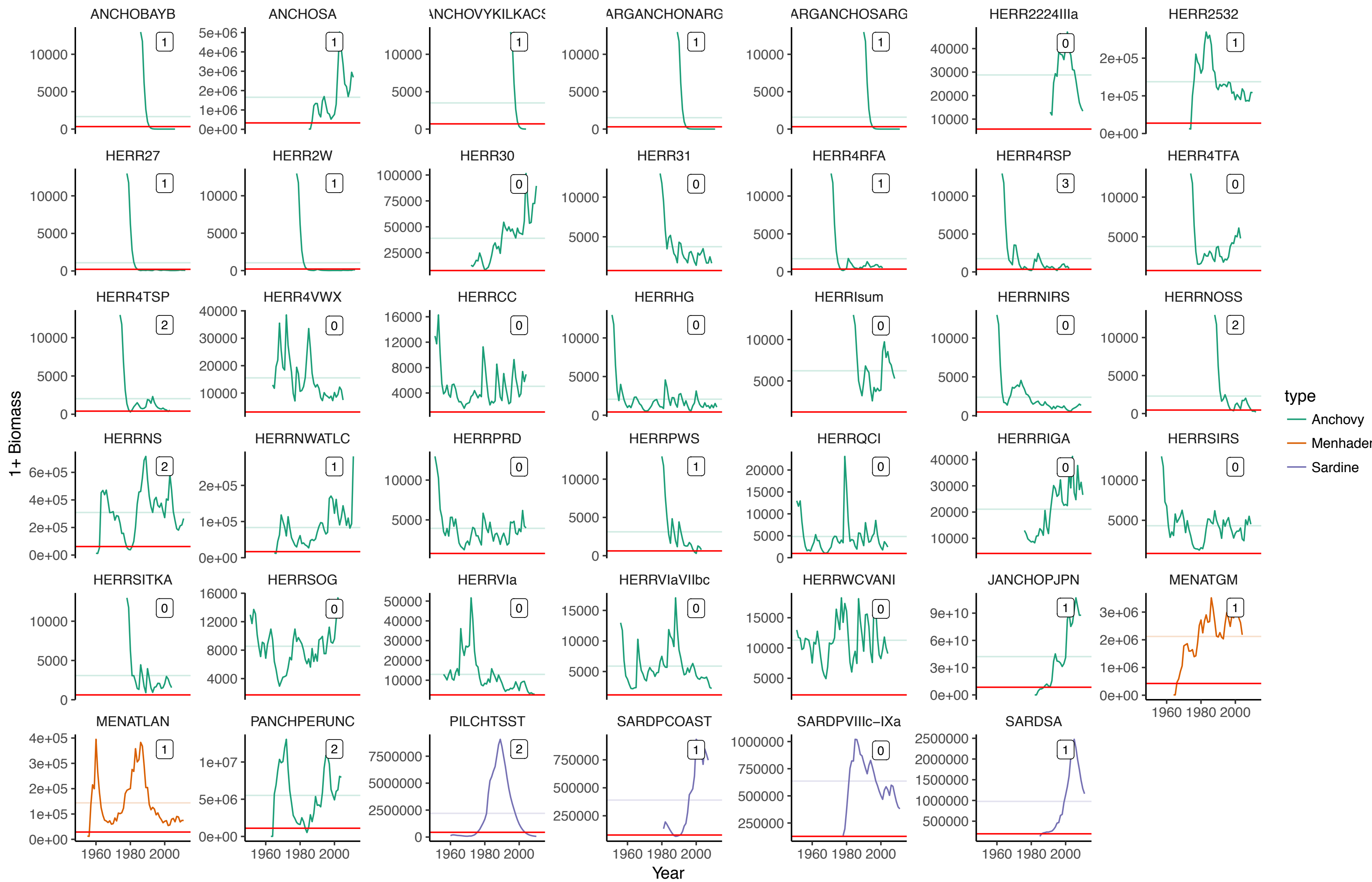

Figure C7. 1+ biomass when recruitment estimates from RAM were used directly in the operating model. The red line represents 20% of long term mean unfished biomass, our threshold for collapse. Numbers in each plot indicate the number of times each population would be collapsed, according to our definition

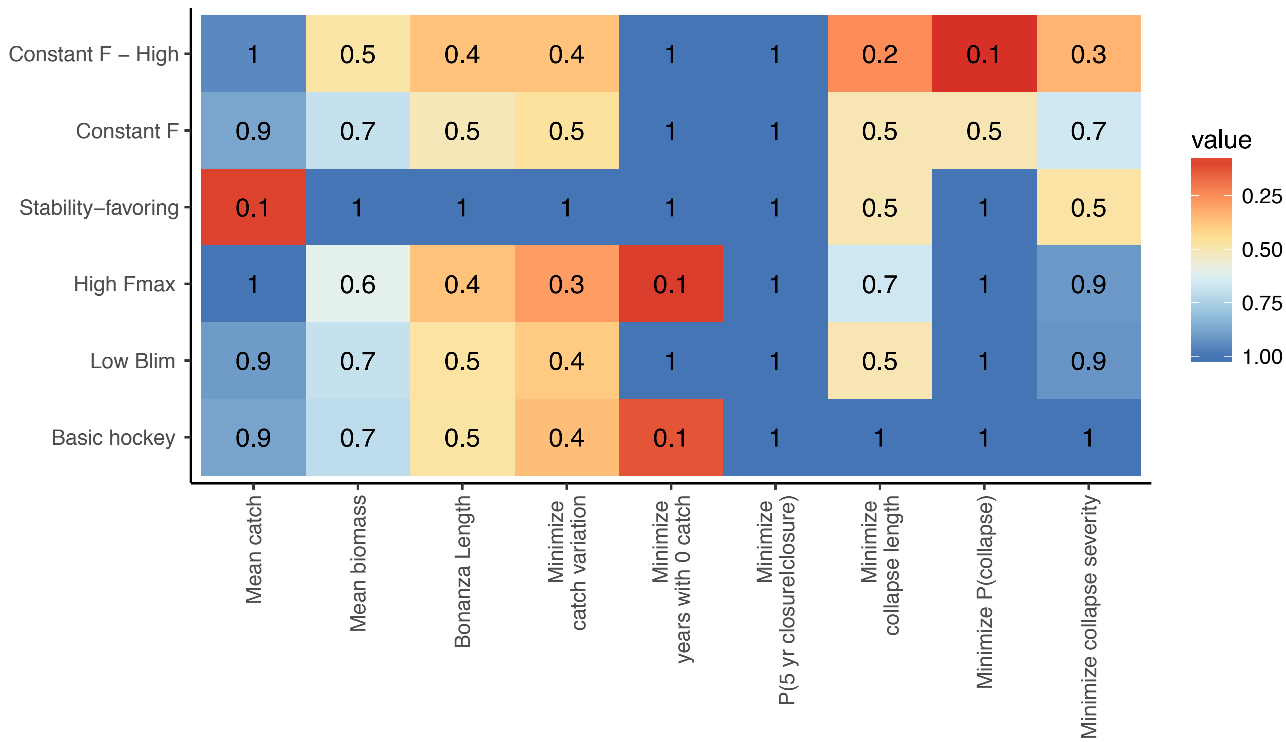

Figure C8. Tile plots showing the performance of each control rule for **anchovy**, scaled to the rule that performs best for each performance measure (1 = blue = best performance). These results are for the base case (autocorrelated observation error; h = 0.6).

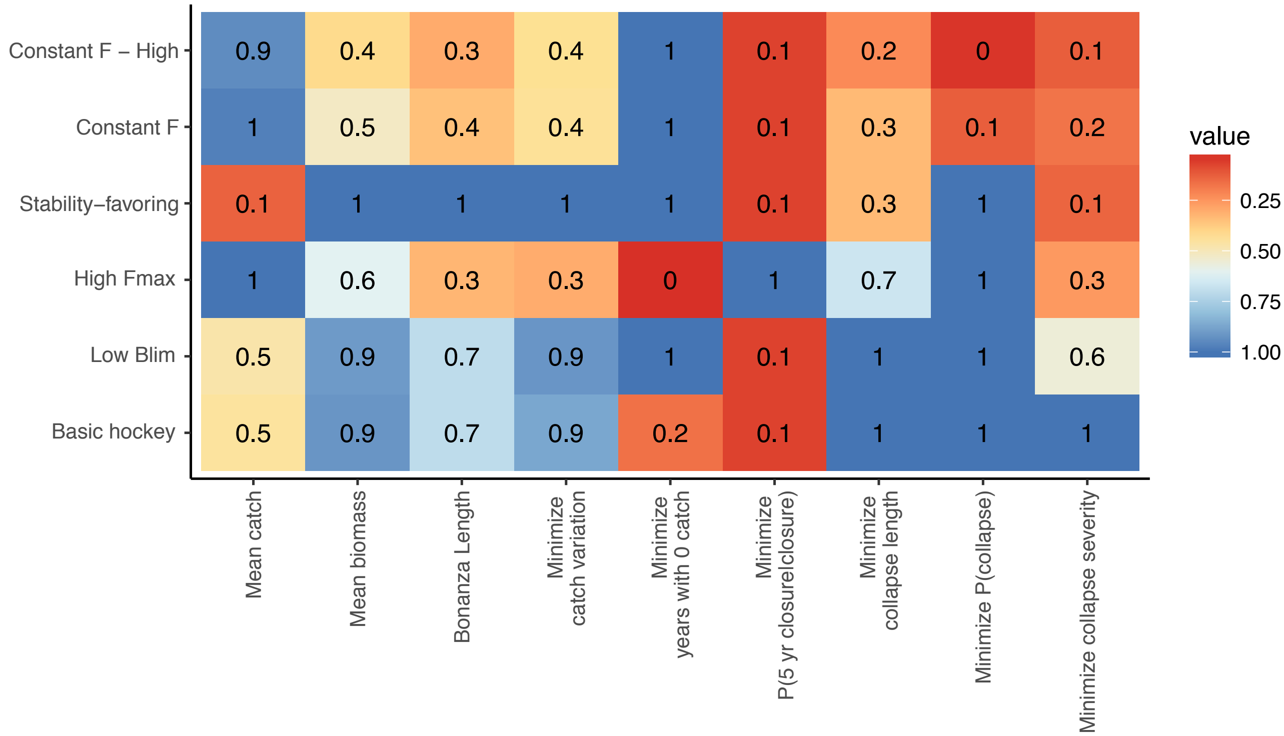

Figure C9. Tile plots showing the performance of each control rule for **menhaden**, scaled to the rule that performs best for each performance measure (1 = blue = best performance). These results are for the base case (autocorrelated observation error; h = 0.6).

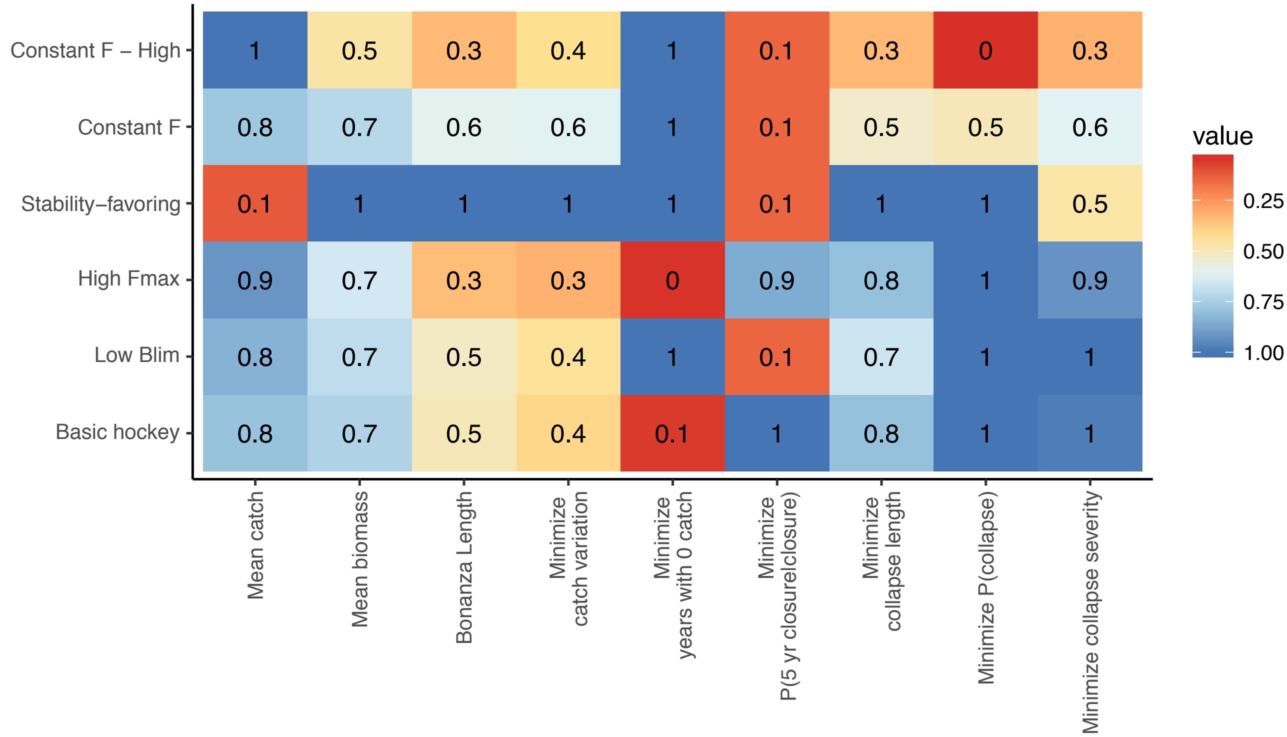

Figure C10. Tile plots showing the performance of each control rule for **sardine**, scaled to the rule that performs best for each performance measure (1 = blue = best performance). These results are for the base case (autocorrelated observation error; h = 0.6).

Time-varying natural mortality

Forage fish can undergo shifts in natural mortality due to changes in predator abundance (Swain and Benoît 2015), disease dynamics (e.g., Muradian et al. 2017), density dependent competition for food, and sometimes cannibalism and intraguild predation (Engelhard et al. 2013). These changes can have strong impacts on population dynamics and age structure (Siple et al. 2017).

We tested scenarios where natural mortality was constant over time, when it was time-varying (as a random walk) and when it increased permanently by 25% halfway through the time series.

In the scenario where M was time-invariant, M was set to the published mortality rate from literature or the stock assessment. We tested two simple scenarios where M was time-varying. In the first, mortality was simulated as a random walk:

$$M_y = \bar{M}e^{\eta_y - {\sigma_M}^2/2} \qquad \text{(Eq. i)}$$

$$\eta_y = \rho_M \eta_{y-1} + \sqrt{1 - {\rho_M}^2}\tau_y \qquad \text{(Eq. ii)}$$

$$\tau_y \sim N(0, {\sigma_M}^2)$$

Where $\bar{M}$ is mean recruitment, η_y are annual deviations in mortality, ρ_M is the extent of autocorrelation in M, and ${\sigma_M}^2$ is the standard deviation of annual deviations in M. For all simulations, ρ_M=0.6 and ${\sigma_M}^2 = 0.2$, and $\bar{M}$ is set to the value of M used in constant M scenarios.

In the second, natural mortality underwent a “regime shift” from average to high natural mortality:

$$M_y = \begin{cases} \bar{M}, & y < \text{midpoint} \\ 1.25\bar{M}, & y \geq \text{midpoint} \end{cases}$$

where the “midpoint” is the midpoint of the time series used to calculate performance metrics (in our analysis, the midpoint of the last 100 years of the simulation).

Performance was affected by different forms of mortality; tradeoffs did not change significantly when mortality was time-varying as a random walk, but did change significantly when there was a “regime shift” of a 25% increase in mortality. These changes included lower catches, lower biomass, and longer collapses.

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Siple, M.C., Shelton, A.O., Francis, T.B., Lowry, D., Lindquist, A.P. & Essington, T.E. (2017). Contributions of adult mortality to declines of Puget Sound Pacific herring. *ICES J. Mar. Sci.*

Swain, D.P. & Benoît, H.P. (2015). Extreme increases in natural mortality prevent recovery of collapsed fish populations in a Northwest Atlantic ecosystem. *Mar. Ecol. Prog. Ser.*, 519, 165–182.

Appendix D: Chapter 4

Table D1. Data collected for this study.

Region	Current type	Subregion	Species	Scientific name	Landings	Biomass or SSB	Recruitment
Benguela Current	Eastern boundary current (EBC)		Anchovy	*Engraulis encrasicolus*	B*, RAM	B, RAM	B
		all	Sardine	*Sardinops sagax*	RAM	RAM	na
		Northern Benguela	Sardine	*Sardinops sagax*	B	B	na
		Southern Benguela	Sardine	*Sardinops sagax*	B	B	B
California Current	EBC	all	Anchovy	*Engraulis mordax*	B	B, RAM	B
			Sardine	*Sardinops sagax*	B, RAM	B, RAM	B
Humboldt Current	EBC	all	Anchovy	*Engraulis ringens*	RAM	RAM	na
		Central Peru	Anchovy	*Engraulis ringens*	B	B	B
		South Peru-North Chile	Anchovy	*Engraulis ringens*	B	B	B
		Central Peru	Sardine	*Sardinops sagax*	B	B	B
		South Peru-North Chile	Sardine	*Sardinops sagax*	B	B	B
			Sardine	*Strangomera bentincki*	B	B	B

Region	Current type	Subregion	Species	Scientific name	Landings	Biomass or SSB	Recruitment
Kuroshio/ Oyashio	Western boundary current	all	Anchovy	*Engraulis japonicus*	B	B	B
		Northwest Pacific	Anchovy	*Engraulis japonicus*	RAM	RAM	na
		Inland Sea of Japan	Anchovy	*Engraulis japonicus*	RAM	RAM	na
		Tsushima Strait	Anchovy	*Engraulis japonicus*	RAM	RAM	na
			Sardine	*Sardinops sagax*	B	B	B
Northeast	Shelf	Bay of Biscay	Anchovy	*Engraulis*	B	B	B

Atlantic			*encrasicolus*			
	Adriatic Sea	Anchovy	*Engraulis encrasicolus*	B	B	B
	Black Sea	Anchovy	*Engraulis encrasicolus*	B	B	B
	ICES VIII	Anchovy	*Engraulis encrasicolus*	RAM	RAM	na
		Sardine	*Sardina pilchardus*	B	B	B
	ICES VIIIc-Ixa	Sardine	*Sardina pilchardus*	na	RAM	na

***B = Barange et al. 2009**

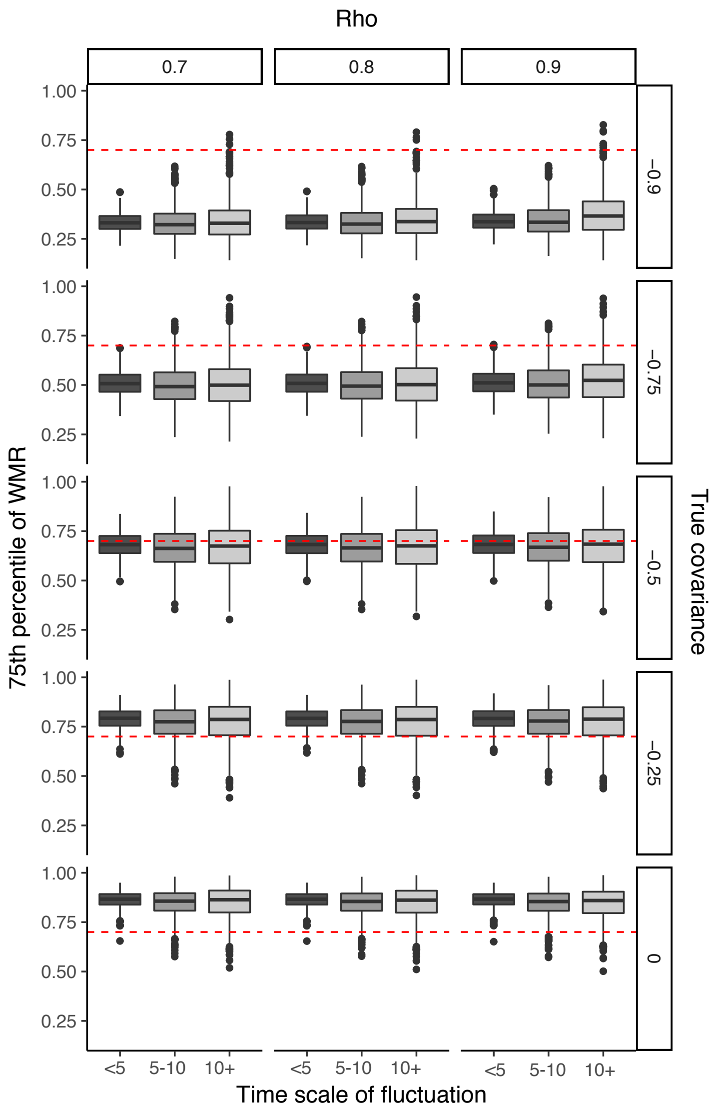

Figure D1. Simulations of sardine and anchovy time series with set covariance and autocorrelation (ρ).

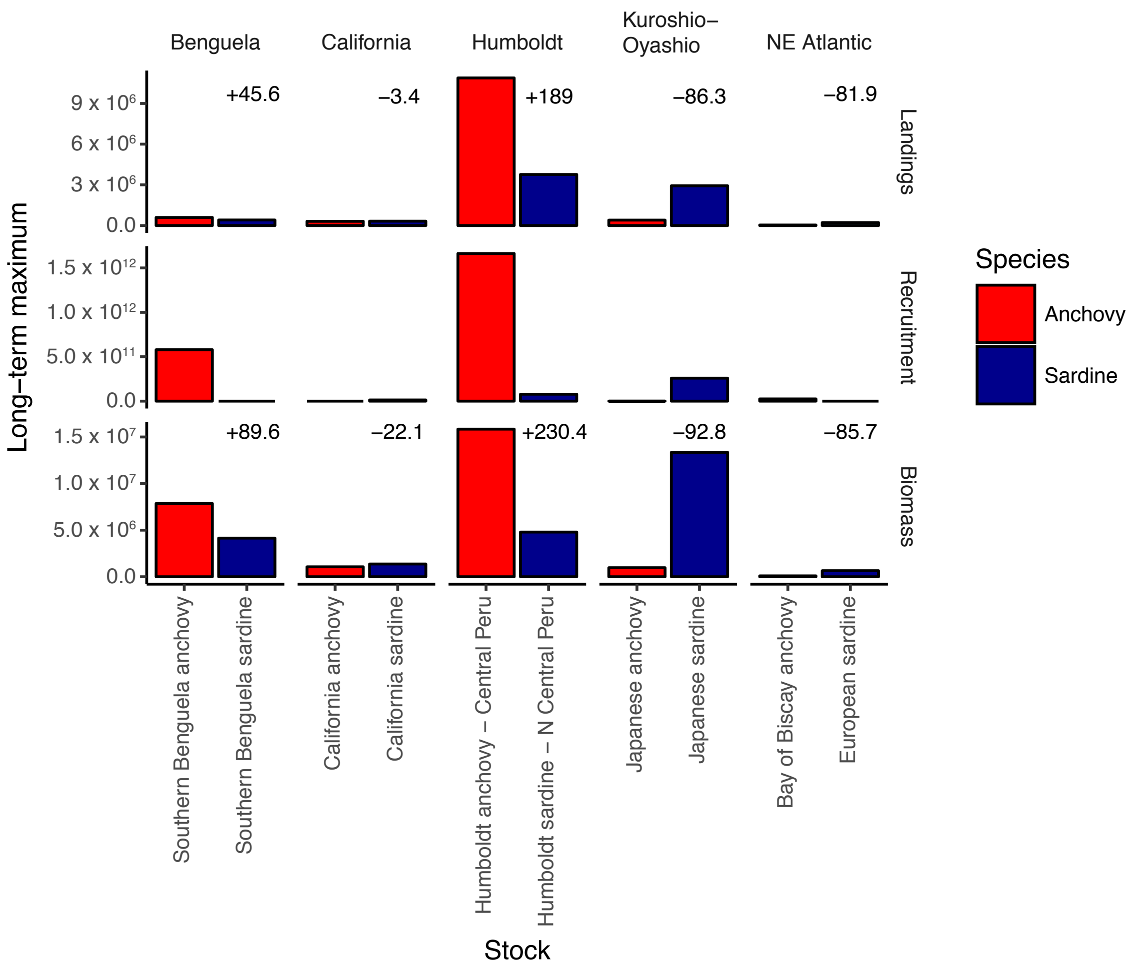

Figure D2. Peak landings, biomass, and recruitment for sardine and anchovy in each LME, based on data from Barange et al. (2009).

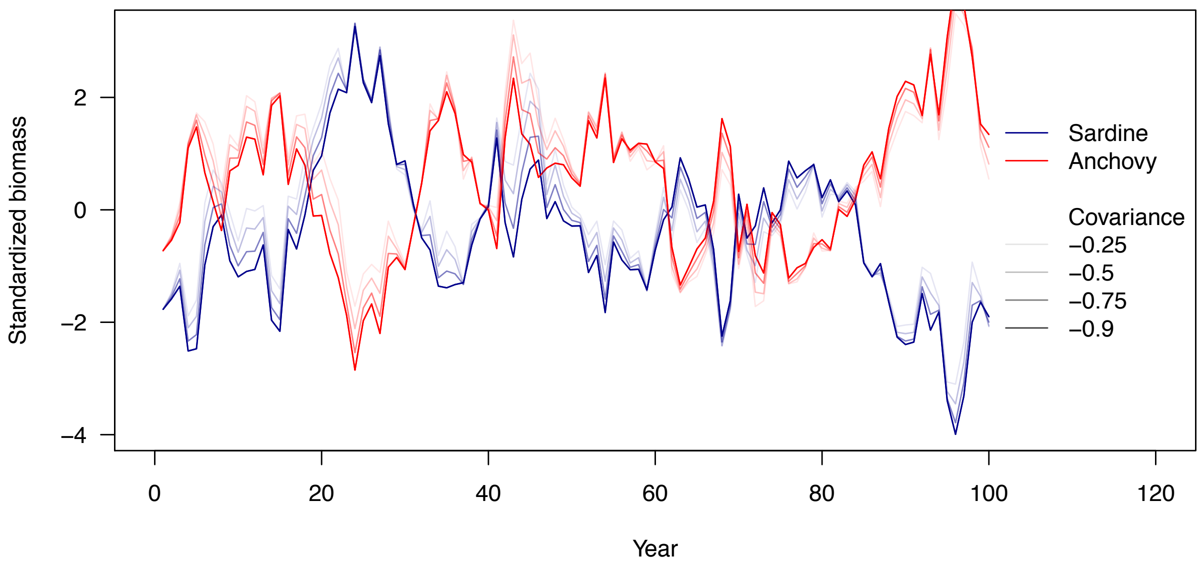

Figure D3. Example of simulations generated for power analysis.

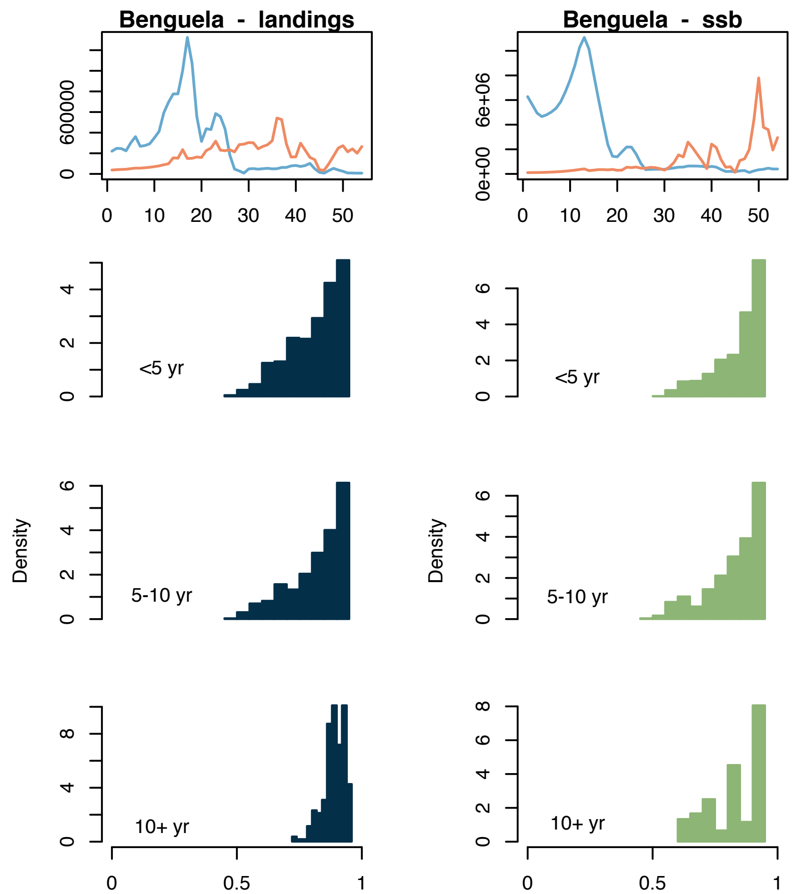

Figure D4. Wavelet modulus ratios for the Benguela Current (data from Barange et al. 2009).

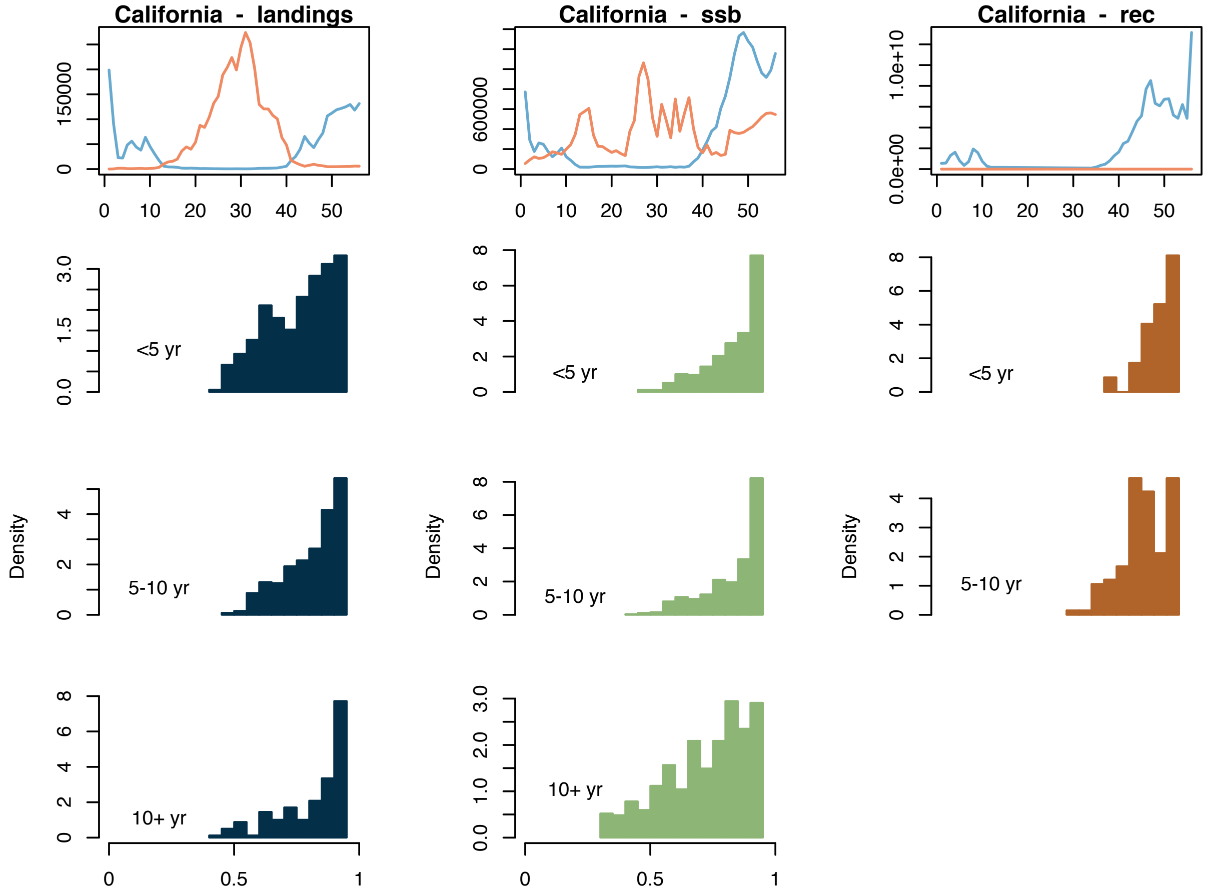

Figure D5. Wavelet modulus ratios for the California Current (data from Barange et al. 2009).

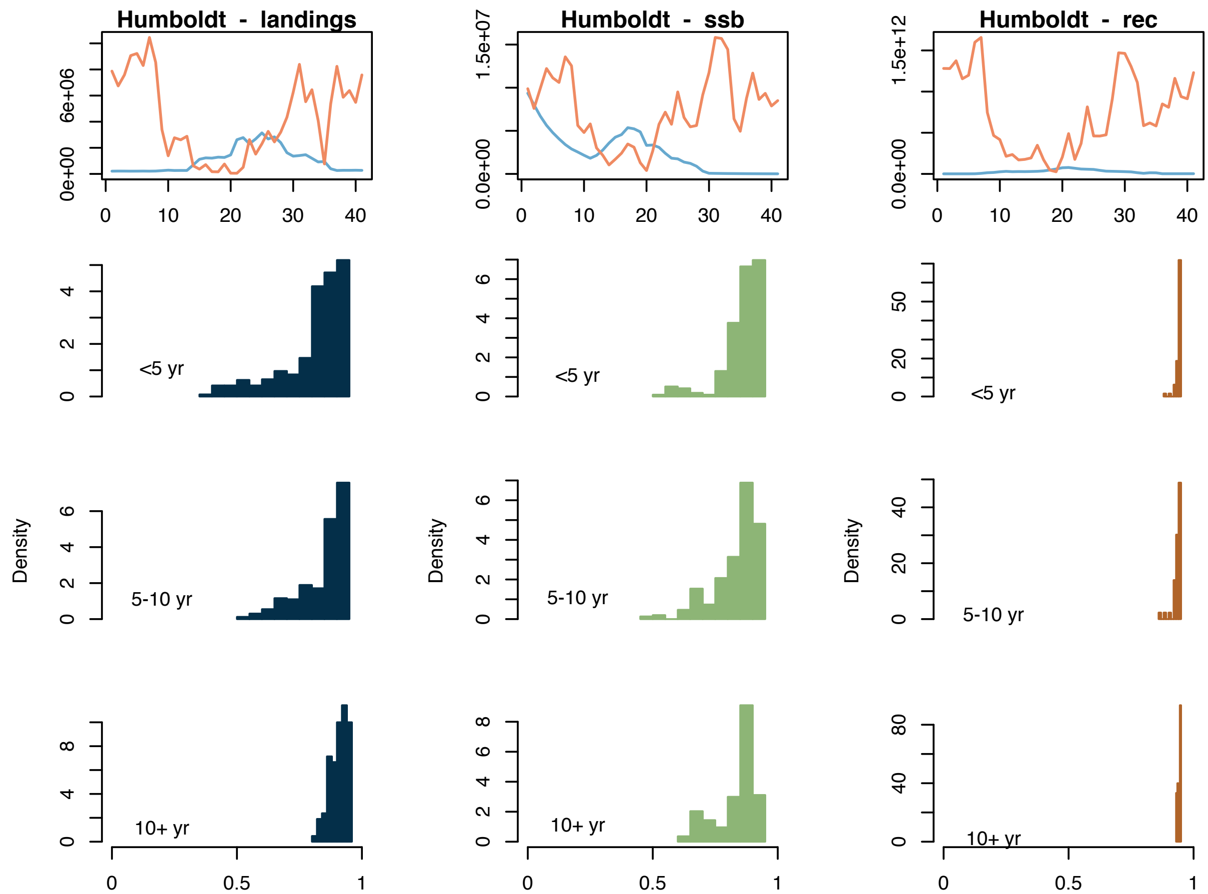

Figure D6. Wavelet modulus ratios for the Humboldt Current (data from Barange et al. 2009).

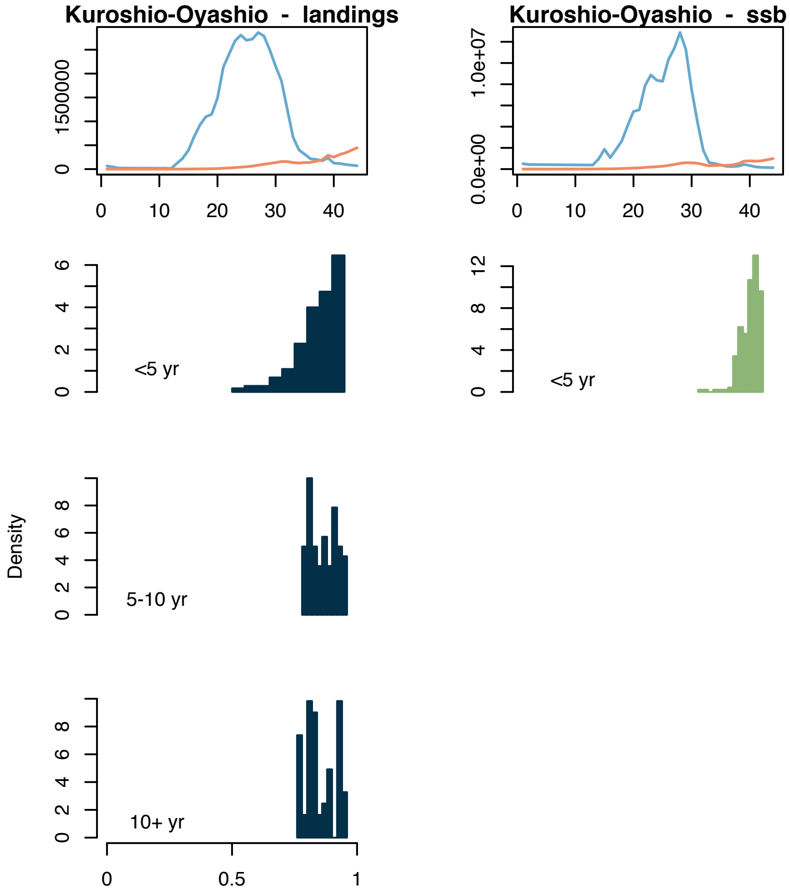

Figure D7. Wavelet modulus ratios for the Kuroshio-Oyashio current (data from Barange et al. 2009).

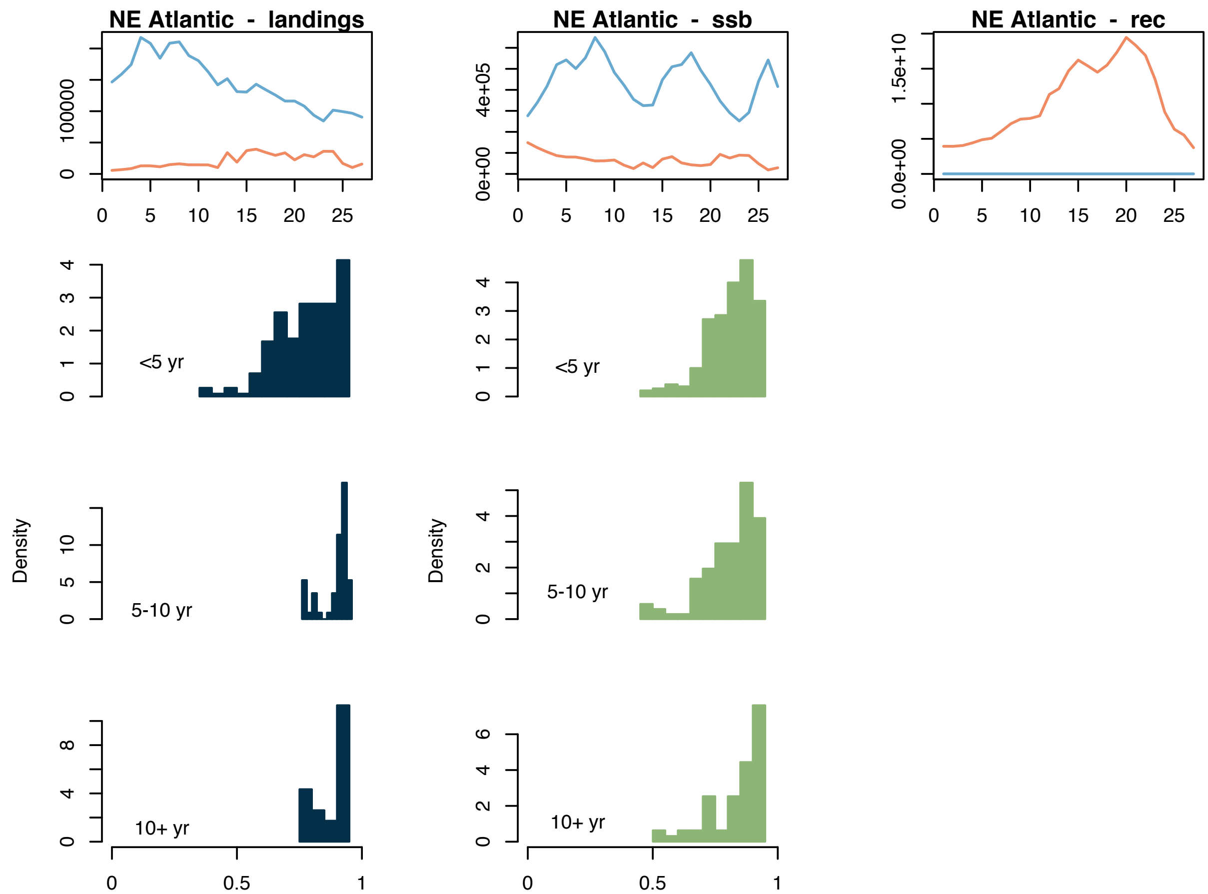

Figure D8. Wavelet modulus ratios for the Northeast Atlantic (data from Barange et al. 2009).

VITA

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