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Alternative harvest strategies to alleviate predation bottlenecks: a bioeconomic modeling approach to inform adaptive management

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Abstract

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There has been increasing emphasis on using ecosystem-based management to account for the effects of trophic interactions in fisheries. However, such approaches require knowledge of ecosystem structure and function often not available to managers. I studied the Chignik salmon fishery in Alaska to explore ways to manage predator-prey interactions when predator abundance data and knowledge of interaction strengths are limited. The Chignik salmon fishery primarily targets sockeye salmon for harvest. Coho salmon are not managed or subject to directed harvest at present, but prey heavily on sockeye salmon as juveniles in the watershed. Thus, a directed coho salmon harvest may reduce predation pressure and increase productivity of the sockeye salmon fishery.

I used a Bayesian hierarchical modeling approach to estimate the annual abundance of coho salmon in the Chignik River from limited daily escapement counts, using information in years with more data to inform estimates in years with limited data. Using these estimates, I examined the relationship between sockeye salmon productivity and coho salmon escapement, and detected no strong evidence of a predation effect on sockeye salmon. Simulation models revealed that recruitment stochasticity and observation error mask even very strong predation effects and bias predation effect estimates towards zero. Simulations also revealed that active adaptive management strategies to reduce coho salmon abundance would take up to a decade before significant increases in sockeye salmon harvest were experienced by fishers, even when very strong predation effects are present.

Commercial fisheries are not executed by a single stakeholder, and each stakeholder group has different perspectives, economic constraints, and incentives. I used simulation models to examine the ecological and economic conditions under which a directed coho salmon harvest would be beneficial to fishers and seafood processors. Differential economic constraints resulted in very different outlooks for the two stakeholder groups, with processors being more limited than fishers in terms of the scenarios in which a coho salmon fishery would be beneficial over the long-term. As trade-offs are inherent to natural resource management, it is critical to consider the economic constraints and incentives of different stakeholders for management actions.

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Chapter 1. Dissertation Overview and Introduction

In natural resource management, there has been an increasing emphasis placed on shifting away from traditional selective, single-species harvest strategies towards more ecosystem-based approaches (Pikitch et al. 2004; Patrick and Link 2015). Ecosystem-based approaches to fishery management attempt to manage the impacts of harvesting on interactions between species, habitats, and diverse stakeholder groups (Link 2010). Expanding the coverage of fisheries management to account for these broader impacts of fishing requires an understanding of ecosystem structure not often available to managers. As fisheries have traditionally been managed for target species only, monitoring efforts have focused on species of commercial or conservation importance. Thus, non-target species that interact with target species typically have very limited data available with which to manage their populations, or understand how they are impacted by fisheries within an ecosystem framework.

Fisheries are inherently socio-ecological systems driven by economic decisions of stakeholders. Managers attempt to manage the biological components of the fishery (e.g., spawning biomass) by limiting or incentivizing fishing activities. However, fishery stakeholders are not primarily concerned with the amount of fish they can harvest, but with the profits they can make from their catch (Gordon 1954; Hilborn 2007). Proposals to alter management of fisheries that will result in lost income to stakeholders may face stiff political resistance to implementation. As such, attempts to enact ecosystem-based approaches to fisheries management must account for the economic impacts on actors in the fishing community.

While Alaska's salmon (*Oncorhynchus* spp.) fisheries are widely considered to be among the best managed fisheries in the world from a biological perspective, they have struggled to achieve economic objectives (Hilborn 2006). Despite large harvests of salmon in recent years, fishery value has declined due to changes in the global salmon markets (Eagle et al 2004). In remote regions of Alaska where alternative employment opportunities are limited, the reduced value of the salmon fisheries is particularly problematic.

The Chignik River watershed, located on the Alaska Peninsula, supports a commercially valuable sockeye salmon fishery. While all five species of Pacific salmon are present in the region, the fishery primarily targets sockeye salmon (*Oncorhynchus nerka*). Coho salmon (*O. kisutch*), which share juvenile rearing habitat with the sockeye salmon, enter the fishery towards the end of the sockeye salmon run and are not directly targeted for harvest due to low economic value. Previous research in the Chignik River watershed has demonstrated that juvenile coho salmon prey heavily on sockeye salmon fry in rearing lakes (Roos 1960; Ruggerone and Rogers 1992), presenting a potential predation bottleneck to sockeye salmon populations. This research suggests that a directed coho salmon harvest may reduce predation pressure on sockeye salmon populations, thereby increasing their productivity and availability to the fishery.

In a small scale fishery like Chignik, increased harvest volume would likely have little impact on the price of salmon, which is driven primarily by farmed salmon supply and larger wild harvest fisheries in Bristol Bay and the Fraser River. Therefore, increased sockeye salmon productivity resulting from a directed coho salmon harvest may provide economic opportunities to local stakeholders even though the value of the sockeye salmon fishery is driven by global market trends and coho salmon are of little direct economic value. The Chignik fishery thus likely represents a common management scenario in which switching from a single-species

approach to a multispecies approach may generate additional benefits to stakeholders, but our understanding of the ecosystem beyond the historical target species is limited. In this dissertation I examined empirical relationships and simulation models to explore the potential of alternative harvest strategies directly targeting coho salmon to increase the productivity and profitability of the sockeye salmon fishery for Chignik stakeholders.

If coho salmon predation is ultimately limiting the productivity of the sockeye salmon fishery, a negative relationship between coho salmon abundance and sockeye salmon productivity should be evident in the system. The Alaska Department of Fish and Game (ADFG) maintains an extremely high quality data set of sockeye salmon harvest, escapement, and age-composition that allows the estimation of annual recruits-per-spawner (a measure of population productivity). However, as coho salmon have been of limited commercial interest for much of the history of the Chignik fishery, ADFG has limited data available describing the abundance of coho salmon in the system. While coho salmon harvest data are available, escapement counts are much sparser due to the difference in migration timing of the two species. Salmon escapements to the Chignik River are enumerated at a seasonal weir near the mouth of the river, where all salmon migrating into the river must pass through counting gates. This enumeration method generates highly accurate daily counts throughout the sockeye salmon fishery, as the weir is in place from the end of May to the end of August. However, as coho salmon do not start entering the river until the middle of August, there are generally only two weeks of escapement counts for coho salmon before the weir is removed for the season. As the coho salmon migration continues through September and October, the first two weeks of escapement give a poor estimate of the total run size. Without knowledge of the number of coho salmon in the system, one cannot relate sockeye salmon productivity to coho salmon abundance.

Methods for estimating total escapement in a single year from incomplete daily escapement counts struggle to estimate values when there are no data from after the peak escapement date (Hilborn et al. 1999). However, if there is external information available about the average run timing and magnitude to the river, these data can be used to inform estimates in data-poor years. In Chapter 2, I used a Bayesian hierarchical modeling approach to estimate coho salmon escapement to the Chignik River (Su et al. 2001). This approach assumed that there is an overall average arrival date, standard deviation around the arrival date and total escapement for coho salmon to the river. Each of these parameters within a given year is drawn from a distribution around the river average for that parameter across all years. Fitting all years simultaneously, the model is able to use information from years in which more data are available to inform estimates in data-poor years (Adkison and Su 2001; Su et al. 2001).

I produced estimates of coho salmon escapement to the Chignik River for 33 years in which some escapement data were available (1922-1932, 1934-1936, 1995-2013). The estimates during the period of the 1920s and 1930s were more constrained than those in the more recent period, due to later operation of the weir providing more extensive daily escapement data. Estimates for years 2012-2013 were also more tightly constrained due to the availability of dual frequency identification sonar (DIDSON) data being available through the end of September. Sensitivity analyses suggest that the models require data for between one and two weeks after the peak escapement date in a given year to reduce errors in escapement estimates below 10%. This suggests that if the weir were to remain open (or the DIDSON operated) until at least the middle of September, much more reliable estimates of coho salmon escapement would be available for this system.

Knowledge of how peak escapement date varies with environmental conditions can help estimation of total annual escapement with more limited daily escapement data. As such, I extended my analysis to determine how the peak escapement date of coho salmon into the Chignik River varied with the Pacific Decadal Oscillation (PDO; Mantua and Hare 2002) index and with time. I found that the strength of these relationships depended on the assumptions about the shape of coho salmon arrival timing. Under the assumption of normally distributed arrival timing, peak escapement date was positively related to PDO index, suggesting later arrival in warm PDO years, and that there was no strong pattern across time. However, under the assumption of gamma distributed arrival timing, there was a positive trend across time, with later arrival in more recent years, and no strong relationship with the PDO index. These results suggest that there may be a relationship with both environment as well as long term trends towards later escapement, both of which have been detected in other systems in Alaska (Kovach et al. 2013; Kovach et al. 2015). However, the inconsistency of these relationships requires further examination to confirm their presence and strength.

For a directed coho salmon fishery to be able to affect the productivity of sockeye salmon stocks, a significant relationship between coho salmon escapement and sockeye salmon productivity must exist. If no relationship exists, it would suggest that predation by coho salmon does not ultimately limit sockeye salmon productivity. Alternatively, it could merely indicate that the available data are insufficient to detect an effect (Oken and Essington 2015). In Chapter 3, I examined the effect of coho salmon predation on sockeye salmon productivity by fitting a modified Ricker production function to the sockeye salmon spawner and recruit data for each stock, including a term to account for the effect of coho salmon escapement. By fitting this equation in a Bayesian framework, I obtained a distribution of plausible parameter values for the

effect of coho salmon on sockeye salmon productivity. For both the Black Lake and Chignik Lake stocks, parameter estimates included zero within the credible interval, indicating no strong evidence of a negative effect of coho predation on sockeye productivity. However, a substantial portion of the posterior distributions of these parameters were negative, suggesting that a negative effect of coho predation was plausible. The positive parameter estimates could indicate that both sockeye and coho salmon respond similarly to a common environmental condition that was not accounted for in the model.

Detection of predation effects on productivity of prey is difficult for both biological and technical reasons (Oken and Essington 2015). Environmental stochasticity can introduce substantial variability into the productivity of prey species, sufficient to mask predator effects. Additionally, observation error in predator abundance will further mask predation effects by biasing estimates towards zero (Ludwig and Walters 1981; Walters and Ludwig 1981; Fuller 2006). As both recruitment stochasticity and observation error (due to limited coho salmon escapement data) are present in the Chignik salmon data, it is possible that predation effects are present but undetectable in the data. Therefore, I employed simulation models to examine how strong of an effect of coho salmon predation could be present in the Chignik system, but remain undetectable in the data. These results indicated that recruitment stochasticity and low frequency environmental variation (such as PDO shifts) reduce the probability of detecting even strong predation effects of coho salmon on sockeye salmon. Further, observation error biased parameter estimates towards zero and, when coupled with recruitment stochasticity, often produced parameter estimates that were in the opposite direction of the true value (i.e., suggesting a positive effect of coho salmon escapement on sockeye productivity when the specified effect was negative). These results suggest that it is unlikely that an effect of coho salmon predation on

sockeye salmon productivity could be detected in the data available from Chignik, given the observation error about coho salmon escapement and recruitment stochasticity in sockeye salmon populations.

As the Chignik system is relatively simple and has some of the best available data in fisheries (i.e., the weir counts for sockeye salmon abundance), the difficulties present in detecting predation effects are likely to be enhanced in more complex marine fisheries with greater data uncertainties. Thus, managers tasked with switching to more ecosystem based approaches have to determine how to manage the species interactions in their ecosystem without fully understanding the ecosystem structure and function. Active adaptive management may be valuable in these situations and is often suggested as a method to learn about ecosystem structure and function through management experiments (e.g., Walters and Hilborn 1978; Walters 1986; Walters 2007). By using management actions as experiments, active adaptive management seeks to push ecosystems into new states that reveal relationships between ecosystem components. After determining how the system responds to management perturbations, managers adjust the management strategy, pushing the ecosystem in a different direction to again see how it responds. Such a strategy directly targeting coho salmon for harvest may be able to elucidate the strength of coho salmon predation effects on sockeye salmon productivity in Chignik. I developed simulation models to simulate a management change from incidental by-catch of coho salmon during the sockeye salmon fishery to directed harvest of coho salmon to determine how long an adaptive management program would need to be in place before any ecosystem response was detected.

Our results demonstrate that the response time of the ecosystem to an active adaptive management strategy depended upon the strength of the specified predation effect and on the

magnitude of the management change (i.e. harvest level of coho salmon). When coho salmon were managed for an escapement goal that would generate their single-species maximum sustainable yield, no appreciable effect of directed harvest on coho salmon was ever detected within the 50 year time frame of our simulations, even when predation effects were strong. When coho salmon were harvested to very low escapement goals, well below their MSY escapement levels, increases in sockeye salmon productivity were detected whenever a negative effect was truly present. However, these changes took up to a decade to become detectable in fishery harvests, even when strong predation effects were specified in the model. These results suggest that adaptive management strategies attempting to elucidate species interactions in the presence of stochastic environmental conditions will need to be enforced for extensive periods of time, often longer than the time horizons used by harvesters and managers. This is particularly important if stakeholders incur added costs under the new management strategy during the transition period.

Coho salmon are not currently targeted for harvest in Chignik primarily for economic reasons. Lack of access to fresh markets limits the wholesale value the processor is able to obtain, as frozen coho salmon products have limited markets. Thus, processors pay lower ex-vessel prices for coho salmon and are not willing to maintain operations for an extended period to harvest the late-arriving, smaller coho salmon run. Additionally, the low ex-vessel value paid for coho salmon renders coho salmon a less attractive target for the harvesting sector. However, if the different stakeholders anticipated increased productivity of the highly valuable sockeye salmon stock as a result of harvesting coho salmon, they may be willing to sacrifice profits in the short term for a long-term increase in value. The balance of short-term costs to long-term benefits will depend on ecological conditions and stakeholder-specific economic constraints.

In Chapter 4, I developed simulation models to examine the economic and ecological conditions in which a directed coho salmon harvest would be beneficial to seafood processors and fishers. The two stakeholder groups had starkly different economic outcomes from participating in a targeted coho salmon harvest. Processors would only benefit from processing a targeted coho salmon harvest under conditions of low daily operational costs, high wholesale profits-per-kg, and at least moderately strong predation effects that were alleviated by high harvest pressure on coho salmon. Conversely, fishers would benefit from a targeted coho salmon fishery under all economic conditions examined, provided that there was a negative effect of coho salmon abundance on sockeye salmon productivity and they had a market in which to sell their fish. As such, even if fishers were to desire a targeted coho salmon harvest, the processor would be more likely to choose to maintain their status quo operations, leaving the fishers without a market to sell their fish. Processors thus represent a key component of the socio-ecological system, controlling the options for harvesting strategies for fishers by controlling market access. Stakeholders in the Chignik fishery may potentially obtain greater benefits to fishery value by investing in product quality (e.g., building an extended runway for access to fresh markets, reducing fishing costs).

Taken together, the results of my dissertation demonstrate the complexities that can arise during the design of alternative management strategies aiming to shift towards more ecosystem-based approaches. As natural resources become increasingly stressed by a growing population and changing environment, managers and stakeholders will be required to make difficult decisions about trade-offs among stakeholders for use of resources. Management for different stakeholders requires an understanding of ecosystem structure and function, often at a scale more holistic than historically monitored. Revealing the structure and function of these additional

ecosystem components may require strong press manipulations for long time periods before the ecosystem responds enough to detect and understand ecosystem relationships. The economic constraints on different stakeholders need to be accounted for to understand the potential for management strategy success and failure. The management of natural resources will require long-term planning and continued monitoring as environmental conditions, economic conditions, and stakeholder values change. By addressing the concerns of multiple stakeholders at each step, management of ecosystems can more successfully achieve societal goals than by considering subsets of the system. Whether such ecosystem-based approaches will actually produce tangible benefits to people or the ecosystem remains to be seen.

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Chapter 2. Coho salmon escapement and trends in migration timing to a data poor river: estimates from a Bayesian hierarchical model¹

Introduction

Fishery managers have long recognized the importance of maintaining a sufficient stock of spawning adults to ensure the production of the next generation of individuals (e.g., Russell 1931, Beverton and Holt 1957). Statistical models relating historical spawning stock abundance to future recruitment quantify the productivity of the population at different spawning stock sizes, and allow managers to set biomass or escapement goals. Stock-assessment for many species of commercial or conservation importance relies on indices of abundance derived from a variety of information sources including size structure, age structure, biomass of previous harvests, and fishery-independent scientific surveys (Hilborn and Walters 1992). However, these data can be expensive to collect, particularly for fishery-independent data. As such, data are not available for all species, particularly those of little economic value or for stocks in remote locations where monitoring is particularly expensive. As fisheries management agencies are increasingly called upon to shift from single-species to ecosystem-based management (Pikitch et al. 2004), information on the productivity of less economically-valuable species is important for understanding the ecosystem level effects of fisheries. Further, methods to inform management from limited data will need to be increasingly applied to systems and species without long histories of stock assessment.

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Due to an anadromous life history and natal stream fidelity of spawning adults, estimating spawning stock abundance for Pacific salmon (*Oncorhynchus* spp.) is typically conducted by counting the number of adults on the spawning grounds with aerial or ground surveys, or by counting adults migrating up rivers at weirs or counting towers. By counting the number of adults entering spawning grounds, managers can obtain an estimate of spawning abundance and relate future recruitment to it. Management agencies use these relationships to set escapement goals that maximize harvest potential while ensuring sufficient spawning abundance. However, enumerating Pacific salmon escapement is an imperfect process due to incomplete counts (e.g., not counting escapement or spawner abundance every day, biased effort towards more commercially valuable species) and other sources of observation error. Estimates of salmon escapement derived from incomplete counts of spawning or migrating adults use assumptions about arrival timing to estimate total annual escapement (e.g., Hilborn et al. 1999; Su et al. 2001; Parsons and Skalski 2010). Total escapement estimates are particularly difficult to obtain in years with few data points and when data are not collected after the peak migration date (Hilborn et al. 1999).

In systems with limited data availability, a Bayesian hierarchical modeling approach provides a means for obtaining reasonable model estimates (Adkison and Su 2001) by sharing information from situations that are data-rich with situations that are data-sparse (Link and Sauer 2002). A hierarchical model structure allows for the use of all available data to inform parameter estimates, simultaneous estimation of all parameters, and assumes that parameter estimates are conditional on related parameters (e.g., Su et al. 2001; Gelman and Hill 2007). Specifically, lower level parameters (e.g., peak migration date in year i) are drawn from higher level population distributions (e.g., distribution of peak migration times for a river across all years; Su

et al. 2001). Parameters for individual years are treated as random variables drawn from a distribution common to all years. The underlying assumptions allow hierarchical models to objectively borrow information from data-rich years to inform parameter estimates in data-poor years (Adkison and Su 2001; Gelman and Hill 2007).

The number of salmon entering a fishing district or river on any given day during the migration is influenced by two primary factors: the total abundance of salmon returning to the system that year, and the timing of the run (e.g., early or late run). Variation in the timing of the run causes uncertainty for in-season fishery management actions (e.g., opening and closing the fishery), and uncertainty in total escapement estimates made from limited daily escapement counts. A year with larger than average early season escapement can either be experiencing a larger than average spawning population, or could merely be experiencing an early migration in that year. Additionally, salmon migration timing has been demonstrated to be sensitive to environmental conditions such as river discharge, temperature, sea surface temperature (Hodgson et al. 2006, Kovach et al. 2013), as well as subject to directional selection from fishery harvest (Quinn et al. 2007). The Pacific Decadal Oscillation (PDO) is a pattern of Pacific Ocean climatic variability that correlates with many marine biological dynamics including salmon productivity (Mantua and Hare 2002, Mantua et al. 1997, Schindler et al. 2005) and migration timing (Kovach et al. 2013). The direction and magnitude of the effect of environmental conditions such as the PDO on spawning migration timing varies among spawning rivers. An understanding of what causes inter-annual variation in salmon migration timing has distinct value for improving fishery management.

The Chignik Lakes watershed on the Alaska Peninsula supports two commercially, culturally and ecologically important stocks of sockeye salmon (*O. nerka*). While all five

species of Pacific salmon are harvested in the fishery, fisheries are focused on sockeye salmon (approximately 70% of returning sockeye adults are harvested annually; Clark et al. 2006), and interactions among species are not addressed explicitly in current management. Of potential interest is the effect of coho salmon (*O. kisutch*) on sockeye salmon productivity. Juvenile coho salmon have been estimated to annually consume over half of the emerging sockeye fry in Chignik Lake (one of the two sockeye salmon rearing lakes in the system; Ruggerone and Rogers 1992). Therefore, coho salmon exert substantial predation pressure on sockeye salmon populations that may limit their productivity, and thus, the potential for adult recruitment and harvest. For economic and logistic reasons (i.e., low price and late migration timing), there is no directed coho salmon harvest in the system, and coho salmon are only captured incidentally during the sockeye salmon fishery. As there is no directed harvest, coho salmon have no management goals in the Chignik Management Area and little is known about their productivity in the system.

The single-species approach to managing the sockeye salmon fishery overlooks species interactions with coho salmon populations that may have substantial effects on sockeye salmon productivity. Directed coho salmon harvest at Chignik may benefit the fishery by moving towards a more ecosystem based approach, balancing fishery harvests with ecosystem productivity (Zhou et al. 2010), as well as potentially releasing sockeye salmon from predation constraints (Ruggerone and Rogers 1992). To manage any potential directed coho salmon fishery, managers would ultimately need to understand the productivity of the Chignik Lakes system coho salmon stock. Salmon escapement is enumerated by the Alaska Department of Fish and Game (ADFG) via a weir located at the mouth of the Chignik River and operated seasonally during the sockeye salmon spawning run from the beginning of June through the end of August.

Weir removal occurs after most sockeye have migrated into the Chignik River but coincides with the onset of the coho salmon spawning migration, allowing managers to enumerate only a small portion of the coho salmon spawning migration. However, in some years, weir counts continued through the end of September, producing a combination of data-rich and data-poor years of daily migration counts from data spanning two periods: 1922-1936 and 1995-2013.

In this study, we (1) employed a Bayesian hierarchical modeling approach that shares information among data-rich and data-poor years to estimate annual coho salmon escapement to the Chignik Lakes watershed, (2) examined the influence of additional count data from dates beyond the peak escapement date for estimating annual escapement, and (3) examined the relationships between environmental conditions and peak migration timing for coho salmon. The escapement estimates derived from this model could ultimately be used in the management of any future directed coho salmon fishery at Chignik enacted to account for species interactions influencing sockeye salmon dynamics.

Methods

Study Site

The Chignik Lakes watershed, on the Alaska Peninsula, consists of two lakes, each supporting populations of sockeye salmon and coho salmon (Fig. 2.1). Black Lake, a shallow, warm and productive lake in the upper watershed, is fed primarily by the Alec River and drains into Chignik Lake via the Black River. Chignik Lake, a deep, colder, and oligotrophic lake in the lower watershed, is fed by the Black River and Clark River, and drains to Chignik Lagoon and the Gulf of Alaska via the Chignik River.

Daily counts of escapement into the Chignik watershed are made at the Chignik weir by the ADFG near the mouth of the river at the upstream end of tidal influence. Counts are made for the first ten minutes of every hour and extrapolated for the remainder of the hour. Weir counts are widely considered the most accurate method of enumerating Pacific salmon escapement, and are used by managers to make in-season fishery decisions (i.e., opening and closing the fishery). Currently, all anadromous salmonid species are counted at the weir, though historically counts focused on sockeye salmon. Since the mid-1990s, the weir has operated approximately from early June through the end of August, coinciding with sockeye salmon spawning migration timing and the sockeye salmon fishery. Coho salmon spawning runs begin to enter the river around the middle of August and is continuing to build even as the weir is removed. Daily coho escapement data are available from the Chignik Weir from 1922-1932, 1934-1936, and 1995-2013. The weir data from years in the 1920s and 1930s cover the majority of the coho salmon run, extending until the end of September. Data from 1995 until present are limited to the early portion of the run. The methods for enumerating salmon migrating past the weir have changed between the two periods, as video cameras were installed in 1994. During all periods, the fish were allowed to pass through 1-3 gates. Fish were counted and identified by technicians standing atop the weir prior to video camera installation (Owen and Price 1995). Historically, gates were closed at night and corrections were made to account for fish that would have passed overnight. Currently, gates are open at night and underwater lights allow technicians to count salmon on video monitors. We assume that any bias derived from these methodological differences is negligible (Quimby and Owen 1994). Additionally, in 2012 and 2013, ADFG operated a DIDSON sonar system 0.25 km upstream of the weir to enumerate late season escapement of sockeye and coho salmon. These data extend from late August until the end of

September. We incorporate the DIDSON data into the observed daily escapement counts for our analyses, for these most recent years. These estimates derive from daily estimates of the total number of migrating salmonids, apportioned into species based on weekly estimates from drift gill net surveys in the upper Chignik Lagoon. The data available to compare weir based escapement estimates to the DIDSON based estimates suggest that DIDSON counts reasonably reflect weir counts, but the limited amount of existing data preclude a comprehensive comparison between these two methods at present. For the purposes of our analysis, we assume that any bias was negligible.

Hierarchical Model Structure and Prior Distributions

To inform parameter estimates in years with limited escapement data, we used a hierarchical Bayesian modeling framework as described by Adkison and Su (2001). Each model of migration timing used three primary parameters, total escapement (r), peak escapement date (p), and standard deviation of migration timing (s). The hierarchical structure assumes that there is an average value for each of these parameters (μ_r , μ_p , and μ_s) in the Chignik River, with among year standard deviation (σ_r , σ_p , and σ_s). Pacific salmon migration timing is generally consistent among years within populations (Burgner 1991, Heard 1991, Sandercock 1991). As such, the assumption of normally distributed peak escapement dates around an among-year mean date is appropriate. By using data from two distinct time periods, we are assuming that the distribution of peak escapement dates, total escapement sizes, and standard deviation of migration timing are consistent between these two time periods. We examined this assumption in further analyses (*see Peak Migration Date Trends section*). The parameter values in each year j are drawn from the distributions:

$$p_j \sim N(\mu_p, \sigma_p^2),$$

$$\ln(r_j) \sim N(\mu_r, \sigma_r^2),$$

$$\ln(s_j) \sim N(\mu_s, \sigma_s^2),$$

where r_j and s_j are obtained after exponentiation after being drawn from a normal distribution on the log scale to ensure positive values. Broad, bounded prior distributions were used for all hyper-parameters because we had little information to otherwise inform them (mean values for the river and among year standard deviation; Table 2.1; Gelman 2006).

Migration timing models

We examined the fit of two alternative migration timing models to the daily escapement data, each assuming a unimodal distribution of migration timing. This assumption appears valid from a visual inspection of daily migration counts across years. In the first model, we assumed that daily coho salmon escapement timing was normally distributed (M_N) around a peak escapement date:

$$E_{i,j} = r_j e^{\left(-\frac{(d_{i,j}-p_j)^2}{2\sigma_j^2}\right)} / \psi_j, \tag{M_N}$$

$$\psi_j = \sum_{i=1}^n e^{\left(-\frac{(d_{i,j}-p_j)^2}{2\sigma_j^2}\right)},$$

where $E_{i,j}$ is coho salmon escapement on day i , year j , $d_{i,j}$ is the numeric day i of the year j , r_j is the total escapement in year j , p_j is the peak escapement date in year j , σ_j is the standard deviation in arrival timing for year j , and ψ_j is a normalizing constant which ensures that

$$\sum_{i=1}^n \left(e^{\left(-\frac{(d_{i,j}-p_j)^2}{2\sigma_j^2}\right)} \right) / \psi_j = 1,$$

where n is the last day of stream entry (Su et al. 2001). The proportion of the spawning migration passing the weir on a given day is multiplied by the total number of migrating salmon in that year to determine the number of coho salmon passing the weir that day.

As salmon daily escapement counts often demonstrate extended descending limbs, we also examined a model assuming that daily coho salmon migration timing follows a gamma distribution (M_G) around a peak escapement date:

$$E_{i,j} = r_j \left(\frac{(\beta_j)^{\alpha_j}}{\Gamma(\alpha_j)} d_{i,j}^{\alpha_j-1} e^{-\beta_j d_{i,j}} \right) / \Psi_j,$$

$$\alpha_j = p_j \beta_j + 1,$$

$$\beta_j = \frac{p_j + \sqrt{p_j^2 + 4\sigma_j^2}}{2\sigma_j^2},$$

$$\Psi_j = \sum_{i=1}^n \frac{(\beta_j)^{\alpha_j}}{\Gamma(\alpha_j)} d_{i,j}^{\alpha_j-1} e^{-\beta_j d_{i,j}},$$
(M_G)

where α_j is the gamma distribution shape parameter for year j , β_j is the gamma distribution rate parameter for year j , and all other parameters are as in model M_N . The equations for α_j and β_j are derived from the equations for the mode (here, the peak escapement date):

$$p_j = \frac{\alpha_j - 1}{\beta_j},$$

and the variance (here, the square of the standard deviation of escapement date):

$$\sigma_j^2 = \frac{\alpha_j}{\beta_j^2},$$

of the gamma distribution. The gamma model allows for the possibility of asymmetric migration timing around the peak migration date. As in model M_N , the proportion of the spawning migration passing the weir on a given day is multiplied by the total migration size in that year to determine the number of coho salmon passing the weir that day.

Likelihood Structure

The normal model (M_N) and the gamma model (M_G) were both fit to the data describing the daily escapement to the Chignik River. Daily salmon escapement counts often demonstrate higher variance during the peak of the run than at the beginning and end of the run. As such, we used a negative binomial error structure to capture over-dispersion in count data (Lindén and Mäntyniemi 2011).

$$L(\mathbf{x}|\theta) = \prod_j \prod_i \frac{\Gamma(x_{i,j} + \gamma_{i,j})}{x_{i,j}! \Gamma(\gamma_{i,j})} \rho_{i,j}^{\gamma_{i,j}} (1 - \rho_{i,j})^{x_{i,j}},$$

$$\gamma_{j,i} = \frac{E_{i,j}}{\omega - 1 + \phi E_{i,j}},$$

$$\rho_{i,j} = \frac{1}{\omega + \phi E_{i,j}},$$

where $\rho_{i,j}$ and $\gamma_{i,j}$ are the parameters of the negative binomial probability mass function for day i , year j , ϕ and ω are over-dispersion parameters (Lindén and Mäntyniemi 2011), and all other parameters are as above. Models were compared visually and by widely applicable information criterion (WAIC; Watanabe 2010), a fully Bayesian information criteria used to measure predictive accuracy of a model. WAIC uses the posterior predictive distribution to determine predictive ability, not just the posterior mean (as in deviance information criteria DIC, an alternative information criterion for Bayesian analyses), and is valid for use in hierarchical models (Hooten and Hobbs 2015). Model averaged escapement estimates were calculated from WAIC weights to account for uncertainty in model structure.

Simulated removal of post-peak data

To examine the influence of daily escapement data after the peak escapement date (i.e. when many enumeration systems are discontinued) on estimates of escapement, we generated

data sets in which daily counts were sequentially removed from the end of one year. We then reanalyzed the data with each model (assuming normally distributed M_N and gamma distributed M_G migration timing) and compared the annual escapement estimate for the year with data removed to the estimated escapement using the full dataset. The analyses were run with data from 17 days post-peak to 5 days pre-peak remaining in the data set. This analysis was run separately for years 1925, 2012 and 2013, three years for which there was escapement data for at least two weeks after the peak migration date. The percent errors of annual escapement estimates were calculated as:

$$\% \text{ error}_j = \left| \frac{E_{t-j} - E_t}{E_t} \right| \cdot 100,$$

Where j is the number of days of data removed, t is the number of dates with count data available in the data set, E_{t-j} is the predicted annual escapement using the reduced dataset, E_t is the predicted annual escapement using the full dataset. The percent error was calculated from ordered MCMC output (i.e., the lowest predicted escapement from dataset t was compared to the lowest predicted escapement from dataset $t-j$) to produce a distribution of percent errors.

Trends in Peak Migration Date

To assess whether coho salmon migration timing has undergone systematic temporal shifts or is correlated with large-scale environmental variation, we compared annual estimates of peak migration date (N=33) versus year and PDO index values. Long-term environmental datasets that cover the duration of the available coho salmon escapement data are limited, and thus we only examined the PDO index. Monthly average PDO indices were obtained for May through August (available at: jisao.washington.edu/pdo/) averaged to obtain a summer PDO index for each year in our analysis, as these are the the conditions that coho salmon would be

experiencing immediately before beginning their upstream migration. We examined the peak escapement dates estimated from our models for trends related to time (i.e., a temporal shift in peak escapement date) and PDO index (e.g., differential escapement timing related to warm or cold PDO years) with linear models. The full model examined was:

$$p_j = \beta_0 + \beta_1 Y_j + \beta_2 PDO_j + \beta_3 Y_j PDO_j,$$

Where p_j is the peak escapement date estimate for year j , Y_j is the year in year j , and PDO_j is the summer PDO index in year j . The final models were selected by AICc. These analyses were run *post hoc* for the estimated peak escapement dates from each escapement model separately (i.e., normally distributed migration timing M_N and gamma distributed migration timing M_G). We detected no evidence of autocorrelation in residuals from any of the models, except the model relating peak escapement date from M_G to only the PDO index. This model ultimately had the least support in the data and was not used further. As such, we are comfortable that autocorrelation of model errors did not influence our conclusions.

All hierarchical models were run in JAGS (Plummer 2003) and all additional calculations were carried out in the R Statistical Software Environment (R Development Core Team 2011).

Results

Escapement Estimates

The model assuming gamma distributed migration timing (M_G) had the most support by WAIC (WAIC=-89.99; 74.9% model weight), compared to the model assuming normally distributed migration timing (M_N ; WAIC = -87.81; 25.1% model weight). Both models were effective at capturing trends in daily escapement trends in data-rich years (Fig. 2.2), though, as expected, they produced more imprecise estimates in data-poor years. Estimates of total

escapement were more constrained in years with more complete data than in those years with very limited data for all models (Fig. 2.3). Each model provided similar relative estimates of total escapement between years (i.e., a year with a high escapement estimate for one model generally corresponded with high escapement estimates in the other model), although the model assuming gamma distributed arrival timing tended to produce higher estimates (Fig. 2.3; Fig. 2.4c, d). Both models predicted the highest escapement in 1927 (1.46×10^5 fish for M_N ; 1.37×10^5 fish for M_G), and the lowest escapement in 1999 (1.34×10^4 fish for M_N ; 1.84×10^4 fish for M_G ; Fig. 2.4c, d). Annual escapement estimates differed by an order of magnitude among years for both models (Fig. 2.4c, d). Median model averaged escapement estimates varied among years from a low of approximately 1.50×10^4 in 1999 to a high of approximately 1.39×10^5 in 1927 (Fig. 2.4).

Sensitivity of Escapement Estimates to Post-Peak Count Data

Simulations to test the sensitivity of annual escapement estimates to post-peak data availability demonstrated that errors were greatly reduced when including at least a week of post-peak data for the model assuming normally distributed migration timing (M_N ; Fig. 2.5). Including one week of post-peak data reduced errors to approximately 10% (median error) compared to estimates based on the entire run duration. However, as is evident from the analyses from 1925 and 2012 data, episodic escapements present difficulties to model fitting, as the percent error of estimated escapement increased as additional data can capture post-peak pulses of escapement (Fig. 2.5). The model assuming gamma distributed arrival timing (M_G) was much more sensitive to data availability and required nearly two full weeks of post-peak migration data for total escapement estimates to converge on the full-data estimate (Fig 2.5).

Trends in Peak Migration Date

Linear models relating peak escapement date estimated by the different models generally predicted a negative relationship with the PDO index, and a positive temporal trend in peak escapement date, though the relationships differed among the migration timing models (Table 2.2). The peak escapement dates estimated from the model assuming normally distributed arrival timing (M_N) demonstrate no significant temporal trend in peak escapement date, but a significant negative relationship between peak escapement date and May -August PDO index ($R^2 = 0.27$, $p = 0.002$; Table 2.2; Fig. 2.6). While the model including additive effects of year and PDO index had the lowest $AICc$ ($AICc = 167.487$), the $\Delta AICc$ between this model and the model including only PDO effects was small ($\Delta AICc = 0.18$), suggesting that there was no significant difference between the two models fit to the data. Further, a partial F-test of the change in variance explained by the two models suggested that the model including both year and PDO effects explains only a trivial amount of additional variation relative to the model including only PDO effects (partial F-test; $F_{1,30} = 3.09$, $p = 0.09$). As such, we chose the more parsimonious model including only PDO effects on peak escapement date.

The peak escapement dates estimated from the model assuming a gamma distributed migration timing (M_G) demonstrate a positive temporal trend to peak escapement timing (peak escapement date getting later over time), but no effect of PDO ($R^2 = 0.61$, $p < 0.001$; Table 2.2; Fig. 2.6). The model including only a year effect had the lowest $AICc$ value ($AICc = 194.62$), and had 69% of the model weight. As such, there is strong evidence that this model has the most support in the data, suggesting later peak escapement dates over time (approximately 1.2 [s.e. = 0.18] days later per decade).

Discussion

As fisheries management agencies face increasing calls to shift towards an ecosystem based approach, more detailed information on all species affected by or affecting the fishery are desired to inform management. There is little economic incentive to manage unexploited species (unless they are of conservation concern), and thus little urgency from management agencies to collect demographic data on these populations. However, information on non-target species may be available from monitoring efforts focused on commercially targeted species. This study estimated annual escapement of coho salmon to the river with a Bayesian hierarchical modeling approach, using data on unmanaged coho salmon collected during monitoring of economically-valuable sockeye salmon, to inform examination of potential benefits from a more ecosystem-based approach to management. Further, we estimated the value of additional data in reducing errors in escapement estimates allowing fisheries managers to weigh the costs and benefits of collecting additional data to monitor and manage coho salmon populations. Finally, we demonstrated that detection of temporal trends and climatic influences on migration timing is sensitive to the underlying model used to estimate migration timing.

Fishery productivity is often characterized by relationships between spawning stock size and production in the next generation. Estimating annual spawning stock abundance is the first step required to characterize the stock-recruit relationship for Chignik River coho salmon. The estimates of annual escapement varied by an order of magnitude among years, and some years were characterized by very low escapements. The presence of a broad range of escapement values is important for characterizing the shape of the relationship between spawning stock and recruitment; if the range of escapements observed were too limited, indications of density dependence may not be apparent in the data (Walters and Martell 2004). Management of any

future coho salmon fishery would be improved with the ability to determine sustainable escapement goals for the population.

In data-rich systems, it is possible to obtain constrained estimates of escapement model parameters from single year count data (Flynn et al. 2006). However, in data-poor systems separate estimation of parameters for individual year's results in wide confidence intervals (Hilborn et al. 1999). Hierarchical models provide a framework within which to inform the estimates of escapement in data poor systems (Adkison and Su 2001). By assuming that there is an average peak escapement date, run duration, and total escapement to the Chignik River, the model borrows information from data-rich years to inform estimates in data poor years. While both models provide qualitatively similar estimates of escapement in any given year relative to other years, the annual escapement estimates can be substantially different between models within a given year, particularly in years with very high or very low escapement relative to the mean. For example, the predicted escapement for 1936 ranged from approximately 6.50×10^4 in model M_N to approximately 1.22×10^5 in model M_G (Fig. 2.4c, d). This highlights the need to address model assumptions (i.e., uncertainty between normal or gamma distributed migration timing model structures) and use model ensemble averaging that weights the model estimates according to their fits to the data. WAIC provides a method for model averaging Bayesian hierarchical model results (Watanabe 2010), and revealed that the model assuming gamma distributed arrival had the majority of model weight (74.9% model weight), compared to the model assuming normally distributed arrival timing (25.1% model weight). This suggests that there is more support in the data for asymmetric than symmetric coho salmon migration timing to the Chignik River. Sensitivity analyses of each of the models to post-peak escapement date data demonstrate the importance of this finding for management purposes.

The ADFG removes the Chignik weir following the closure of the commercial sockeye salmon fishery and the decline in escapement of sockeye salmon in late August or early September. In doing so, the majority of the coho salmon spawning run is not observed. Our analysis demonstrates that continuing daily escapement counts for at least 1 week after the peak escapement date (approximately until September 17 from our estimates of average peak escapement date) allows hierarchical models assuming normally distributed migration timing the ability to generate much more accurate estimates of coho salmon escapement. However, models assuming gamma distributed migration timing are more sensitive to data availability and struggle to converge on estimates derived from the full season of data until nearly 2 weeks of post-peak data are available. The flexible shape of gamma distributed migration timing makes the model more sensitive to post-peak variability in daily escapement. The difference in necessary data collection to generate escapement estimates with smaller credible intervals demonstrates the importance of determining whether the coho salmon run follows an asymmetric or symmetric migration timing pattern. With few years with complete escapement data, we rely on information criteria to determine model support in the data. Additional years with complete or near complete escapement data would benefit these estimates, and inform managers of how much longer escapement should be enumerated if coho salmon escapement estimates are desired. Recently, complimentary escapement data collected by hydroacoustics were influential in informing escapement estimates based primarily on weir counts, as the inclusion of late season DIDSON sonar data in 2012 and 2013 resulted in narrow credible intervals around our coho escapement estimates. Continued collection of this data will not only help inform escapement estimates and model assumptions, but also provides a less expensive method of collecting late season

escapement estimates in the future if managers decide more effort should be made towards coho salmon management at Chignik.

By using full data sets from the 1920's and 1930's to inform daily escapement estimates in the 1990's through present, our model assumes that the factors influencing migration timing in the first data set are consistent in the second data set. While this assumption may not be strictly met (discussed below), the paucity of post-peak daily escapement counts in the second data set make it difficult to test rigorously. The use of broad priors allows years in the more recent data set which have post-peak data to drive peak escapement dates beyond the range detected in the 1920's and 1930's dataset. Our post-hoc analysis of trends in peak escapement timing allows us to examine whether any evidence for these trends exists.

Anthropogenic and natural perturbations have been shown to alter migration timing in many anadromous fish stocks. Understanding how coho salmon migration timing has changed through time and how it responds to environmental conditions would benefit estimation of the spawning run size, particularly if only incomplete escapement counts are available. Bristol Bay sockeye salmon (Quinn et al. 2007) and Columbia River sockeye salmon and American shad (Quinn and Adams 1996) have each been shown to migrate earlier than observed historically, while Columbia River early-run steelhead are migrating later than historically (Robards and Quinn 2002). Sockeye, pink, and coho salmon are migrating earlier to Auke Creek in southeast Alaska (Kovach et al 2013). Changing climate conditions and fishery related harvest pressures have been implicated in these shifts. In systems with escapement goals, managers may exert less harvest pressure in the early part of the fishing season until their escapement goals are met and then open the fishery, thus selecting for earlier migrants in the spawning population. For Chignik River coho salmon, which are harvested incidentally in the sockeye salmon fishery,

fishing pressure will be greatest on the earliest migrants and later migrants would be favored in the spawning population. As there is limited overall harvest of coho salmon in Chignik, there could be a weak effect on migration timing, providing a possible explanation for why only the model assuming gamma-distributed migration timing suggests this trend. We detected a negative effect of the PDO on peak escapement timing in Chignik River coho salmon, albeit only in the results of the model with less support from the data (M_N). Oceanic conditions may influence the migration timing of Pacific salmon by directly affecting temperature cues or by influencing inland precipitation and temperature patterns (Hamlet and Lettenmaier 1999, Keefer et al. 2008, Johnstone and Mantua 2014). Previous research detected no PDO effect on coho salmon migration timing in a southeast Alaskan stream, though a positive association with PDO was detected on sockeye salmon migration timing in the same system (Kovach et al. 2013). Further, environmental conditions associated with PDO are not uniform across the north Pacific, and local hydrology and geomorphology further refine the local expression of these broad climatic conditions experienced by populations of Pacific salmon (Lisi et al. 2013; Leppi et al. 2013). As such, these results highlight the need to consider the effects of environmental conditions in a population-, stock-, or region-specific context. Additionally, recent research has demonstrated instability in the relationship between PDO and North Pacific climatic conditions, suggesting that climate is influenced by the PDO in combination with other indices of atmospheric and oceanic conditions (e.g., Arctic Oscillation, Atlantic multidecadal oscillation; McAfee 2014).

Pacific salmon stocks exhibit many biological traits that are locally adapted to the environmental conditions of their natal streams. As stream temperature is partially controlled by air temperature, rivers in close proximity to each other are likely to have similar run timings (though see Lisi et al. 2013), and rivers at similar latitudes should be more representative of each

other than rivers at different latitudes (Hodgson et al. 2006). Previous research has suggested that incorporating information from neighboring streams to inform prior probabilities of run timing into rivers may further constrain estimates in data poor situations (Su et al. 2001). If data exist for such systems, they can provide informed prior distributions to escapement estimation in a data poor system, and thus model fits would be less influenced by single data points in small data sets (Hilborn et al. 1999). We examined the potential use of data from other southern Alaskan streams (Little Susitna River, Deshka River, Buskin Creek, Auke Creek) with weir counts of coho escapement to inform our estimates of peak escapement date. However, visual examination of the data for these streams demonstrated that the peak escapement dates were either much earlier (Deshka River, Little Susitna River) or later (Auke Creek, Buskin Creek) than was evident in data-rich years in the Chignik River. Coho salmon escapement to the Deshka and Little Susitna Rivers generally peaks at approximately the time when coho salmon begin to enter the Chignik River. Additionally, these rivers are smaller than the Chignik River and escapement may be more controlled by seasonal rain events (Sandercock 1991) or local geomorphic controls on stream thermal regimes (Lisi et al. 2013). The utility of escapement timing data from regional streams is contingent upon the comparability of the size and prevailing environmental conditions of the streams. In the case of Chignik River coho salmon, it does not appear that data from reasonable surrogate rivers exist; thus, our analyses has only used a hierarchical model structure to share data among years, rather than among sites as could be done in other situations.

As fishery managers continue to shift towards a more ecosystem based approach to fisheries management, information on the productivity of non-traditionally targeted (and thus, less well studied) stocks will be needed. As coho salmon present a potential predation bottleneck

to the commercially, culturally, and ecologically valuable sockeye salmon of the Chignik Lakes watershed (Ruggerone and Rogers 1992), knowledge of the productivity of the coho salmon stocks is required to understand the interactions between the two species at the level at which the fisheries are managed. Escapement estimates derived from the limited available data by applying Bayesian hierarchical models begin to fill this knowledge gap, allowing researchers to examine relationships between coho salmon escapement and sockeye salmon productivity, and how these interactions may affect the productivity and economics of this fishery. Additionally, the results allow for exploration of alternative harvest strategies through simulation modeling, a critical step towards implementing adaptive management strategies to account for species interactions affecting the fishery. In other systems in which there is limited data for the productivity of a historically non-target stock, a hierarchical modeling structure similar to that applied here to the Chignik coho salmon stock can inform management decisions about potential future harvest strategies.

Table 2.1. Hyper-parameter prior probabilities for Bayesian hierarchical modeling of coho salmon escapement to the Chignik River. The same prior probabilities were used for the hyper-parameters in both the model assuming normally distributed migration timing and the model assuming gamma distributed migration timing.

Parameter	Mean	SD
Peak Migration Day	$\mu_p \sim U(231,300)$	$\sigma_p \sim U(0.1, 20)$
Annual Escapement	$\mu_r \sim U(9, 13)$	$\sigma_r \sim U(0.1, 3)$
Arrival Time Variation	$\mu_s \sim U(0,3)$	$\sigma_s \sim U(0.1,1)$

Table 2.2. Linear regression results from analysis of peak migration date trends. Values represent associated slopes of predictors. Significance is denoted by asterisks: * 0.01- 0.05, ** 0.001- 0.01, *** < 0.001, -- predictor not significant by least squares regression.

Model	Intercept	PDO	Year
M _N	213.79***	-1.46*	--
M _G	1.67	--	0.13***

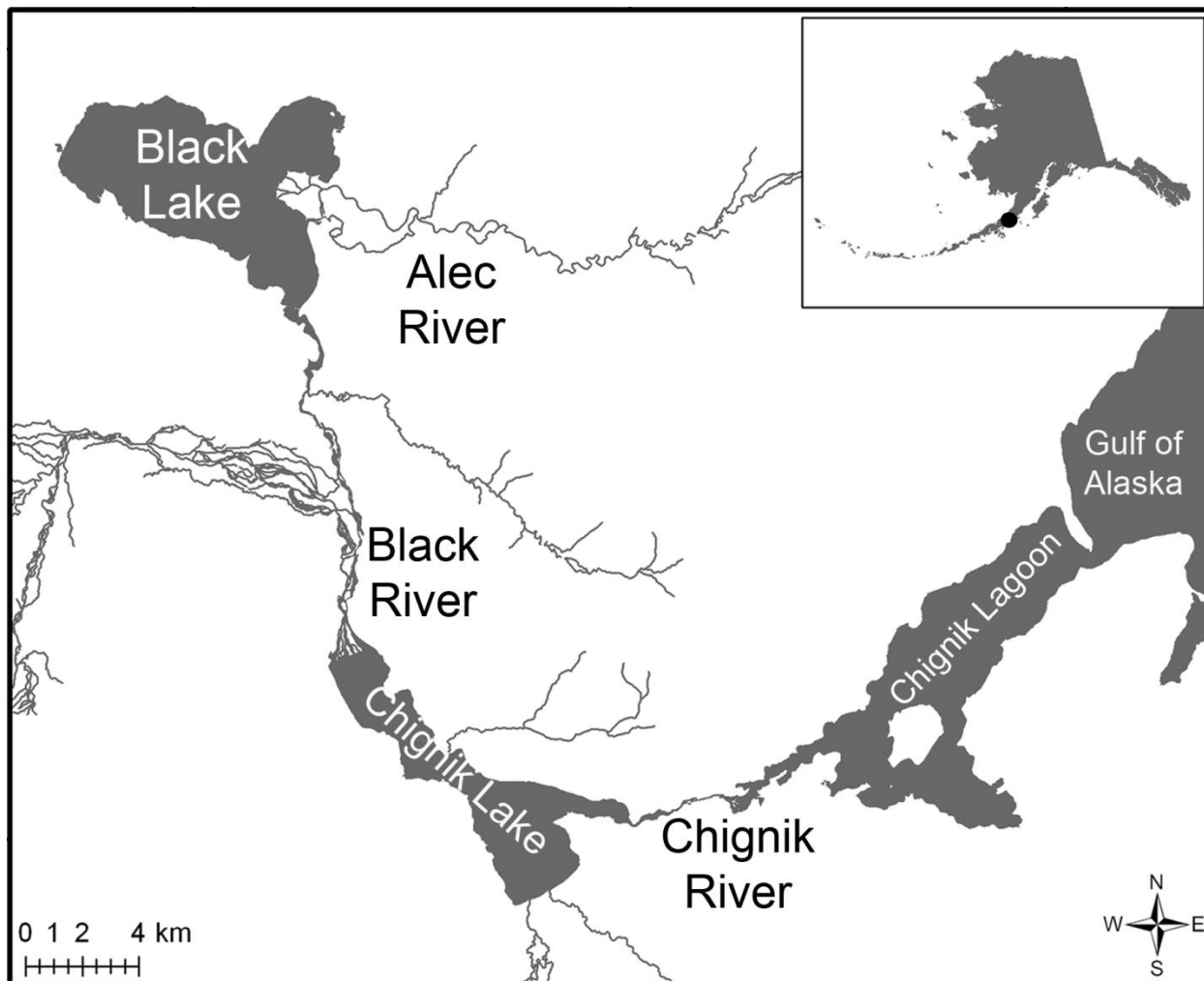


Figure 2.1. Map of the Chignik Lakes watershed. Inset shows location on Gulf of Alaska side of the Alaska Peninsula. The Chignik Weir is located between Chignik Lagoon and Chignik Lake.

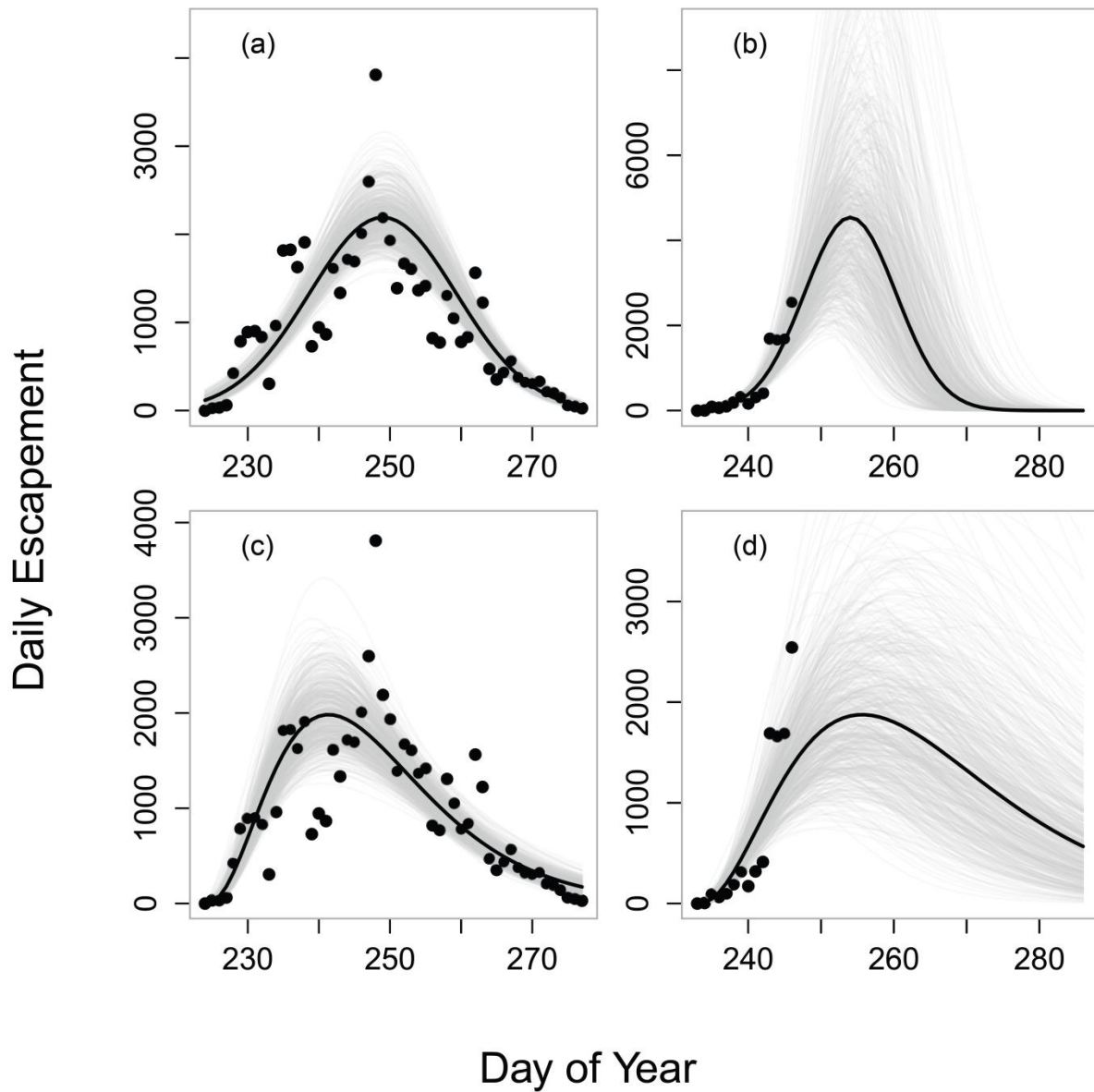


Figure 2.2. Examples of daily escapement counts (black dots) and model predicted daily escapement counts (grey lines) for data-rich (a, c) and data-poor (b, d) years with models M_N (a, b) and M_G (c, d). Black line represents the predictions using the median parameter estimates, while the thin grey lines represent individual model fits retained in the MCMC chain. Note that y-axes differ among panels.

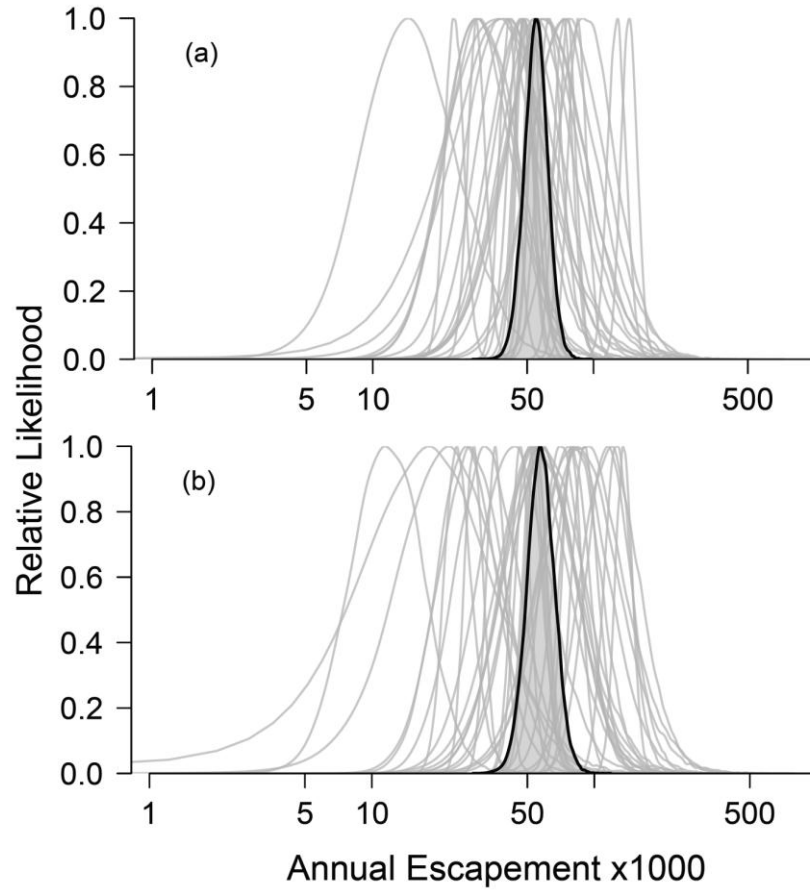


Figure 2.3. Posterior probability densities for models M_N (a) and M_G (b). Shaded region denotes the posterior density of the hyperparameter μ_r and thin lines denote posterior densities for annual escapements r_j . All distributions are scaled such that all densities are divided by the maximum likelihood value for comparison among models and years.

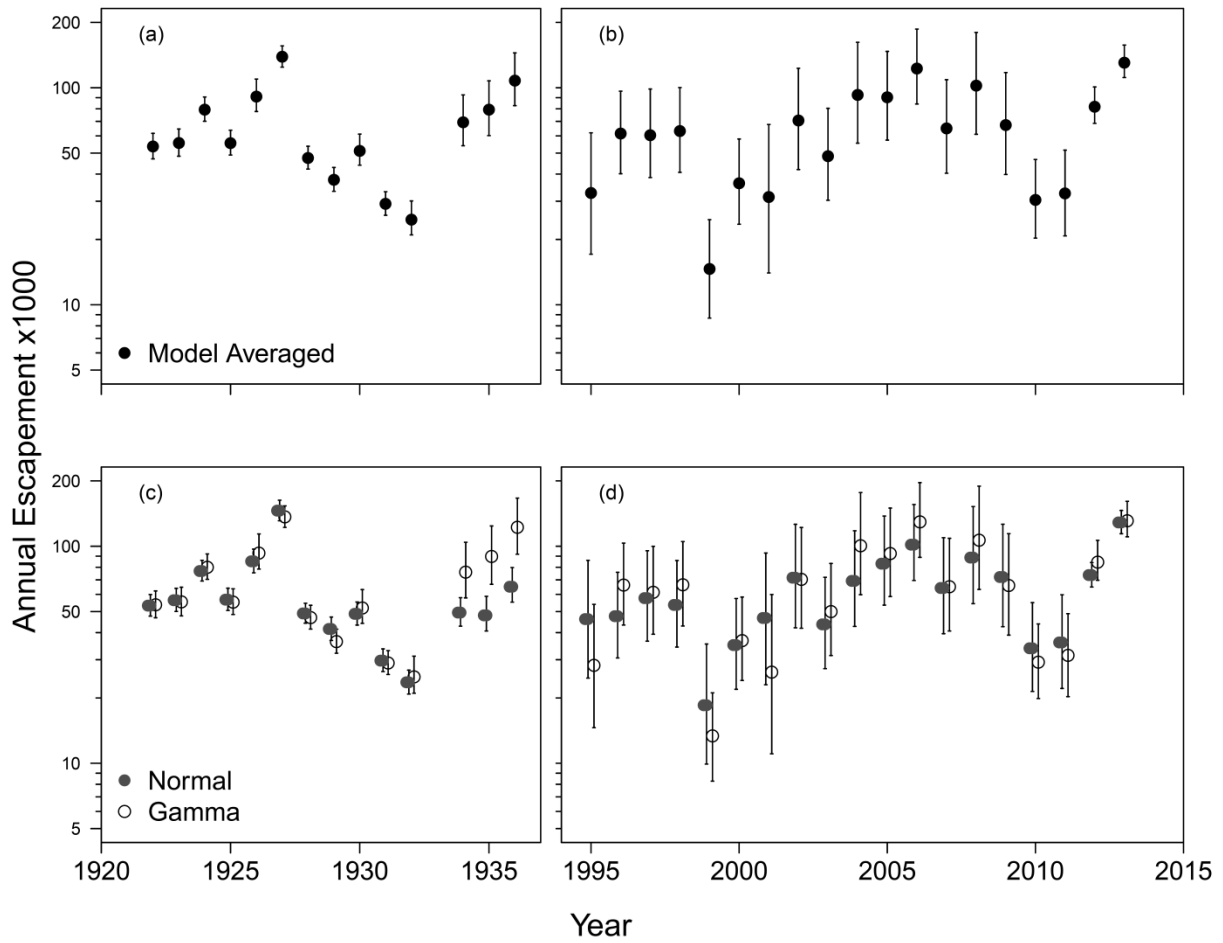


Figure 2.4. Model averaged (a,b) and individual model (c,d) annual escapement estimates by year for 1922-1936 (a,c) and 1995 – 2013 (b,d). Error bars indicate the 80% credible interval from posterior distributions. Note log scale for y-axis.

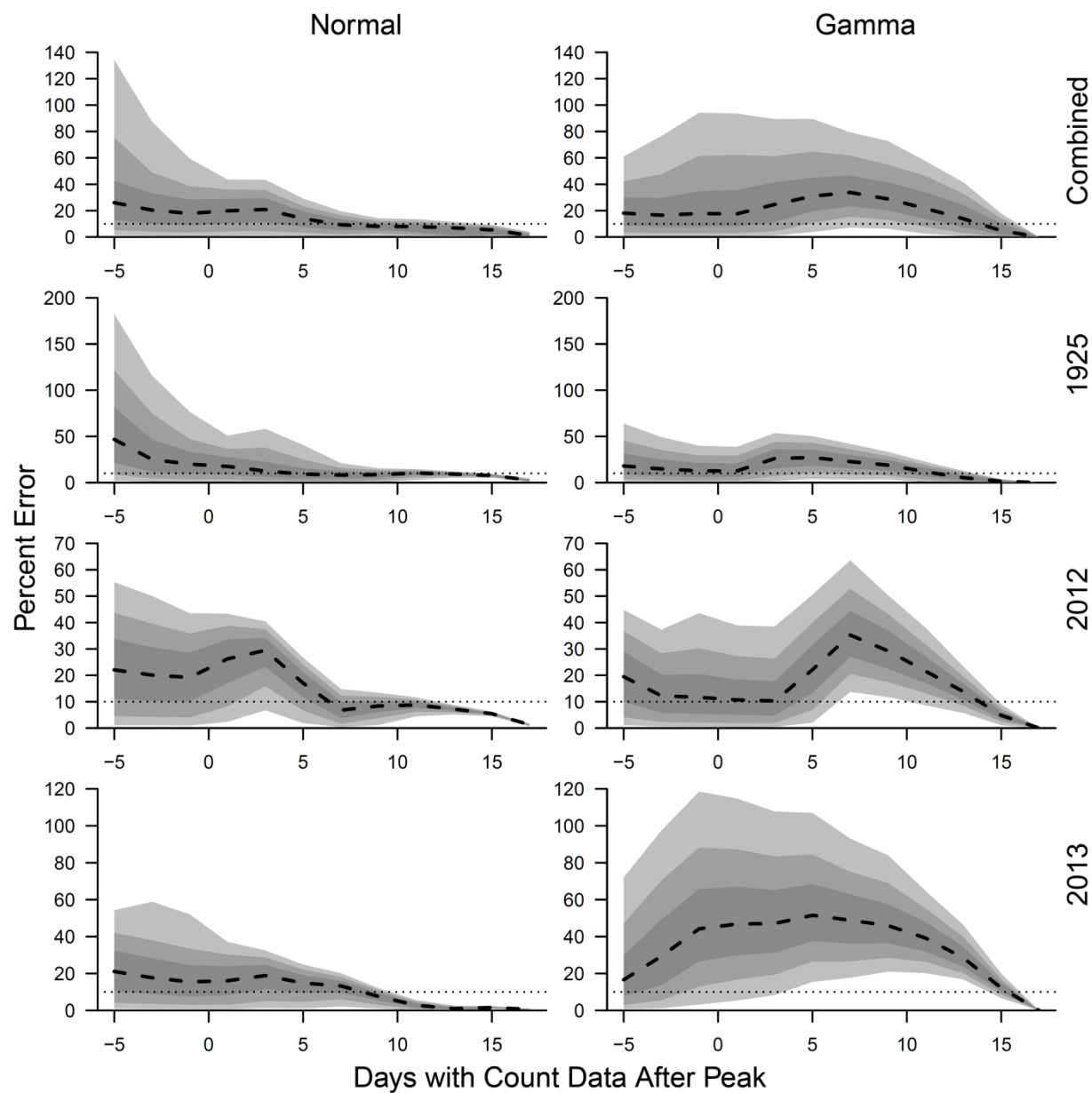


Figure 2.5. Sensitivity of annual escapement estimates to post-peak migration date data. Light grey regions encompass the 95%, medium grey the 80%, and dark grey the 50% credible intervals for percent error. The dashed line denotes the median estimate of percent error in annual escapement estimates. The dotted line indicates 10% error. The analysis was run for three years with near complete coverage of the migration, and results are presented for each year individually (denoted by year) as well as for all three years combined.

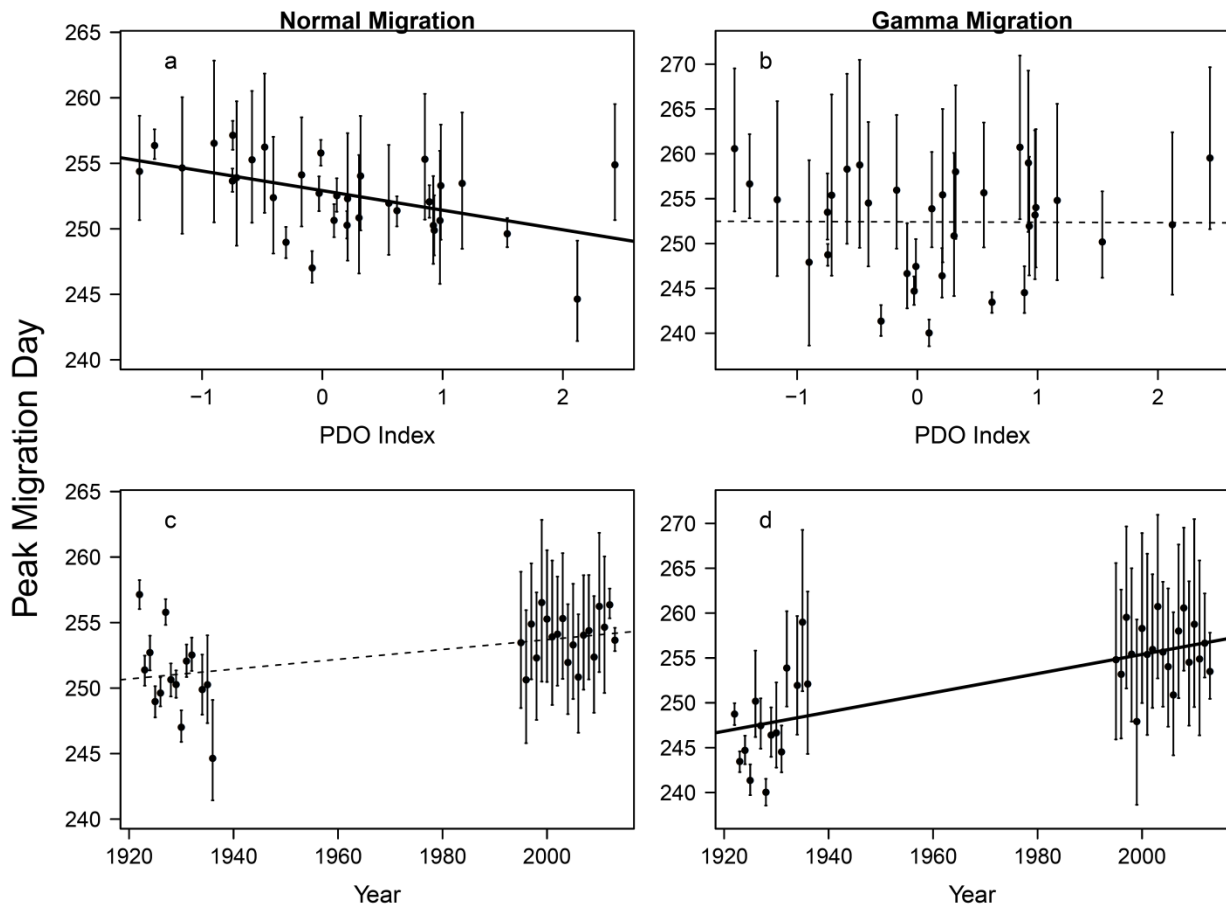


Figure 2.6. Linear regression results examining the relationship between peak migration date to environmental conditions (May-August PDO index; panels a, b) and year (panels c,d) for models assuming normally distributed migration timing (panels a, c) and gamma distributed migration timing (panels b, d). Solid black lines indicate that the predictor (PDO or year) was a significant predictor of peak escapement date, while dashed lines indicate insignificant relationships. Error bars represent the 95% credible interval of peak migration date.

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Chapter 3. Long time horizon for adaptive management to reveal predation effects in a salmon fishery

Introduction

The importance of species interactions, including predation, has become of increasing interest in the management of exploited ecosystems as traditional single-species management has sometimes resulted in surprising outcomes (e.g., collapse and lack of recovery of Newfoundland cod; Frank et al. 2005) with negative ecological, economic, and social impacts (May et al. 1979; Bax 1998). Traditional single-species management operates under assumptions that have been repeatedly criticized in the literature (Larkin 1977; May et al. 1979; Pikitch et al. 2004). Focusing management activities on a single species of interest ignores the effects of management actions on non-target species (by-catch in commercial fisheries Hall et al. 2000, mesopredator release in invasive species control (Soule et al. 1988), physical habitat (bottom-trawling Turner et al. 1999), and species interactions (e.g., cultivation-dependence Walters and Kitchell 2001; competitive release of non-target species Ruscoe et al. 2011) – or assumes that management effects on these are implicit in a successful single species approach. As such, ecologists have increasingly called for management to shift away from single-species methods towards ecosystem-based approaches (Pikitch et al. 2004). However, there remains substantial resistance to such changes among both stakeholder groups and management agencies (Patrick and Link 2015). One argument against shifting away from single-species management strategies is the complex nature of ecosystems and the species interactions that shape them hinder a scientific understanding of the important structural features of ecosystems. We usually do not know how strong these interactions are and how they change under different environmental conditions.

Models that attempt to mechanistically account for such interactions provide less accurate predictions of future conditions than non-parametric models (Perretti et al. 2013; Schindler and Hilborn 2015). As such, managers and stakeholders are often reluctant to change the management system if there is no evidence that the change will improve flows of ecosystem services. Patrick and Link (2015) argue that this is a poor reason to maintain single-species management strategies, as we know that species interactions occur and we can learn about their importance and dynamics as we manage for them.

Active adaptive management allows for an ecosystem to be managed in such a way that knowledge of ecosystem structure and dynamics can be gained, and management actions adjusted as new information becomes available about ecosystem responses to management or changes in the environment (Walters and Hilborn 1978). It allows managers to test hypotheses about how the ecosystem works by manipulating key processes or species (e.g., changing harvest intensity or selectivity) to refine management strategies through time (Walters 1986). While the idea of adaptive management is attractive, the implementation of such experimental strategies is often difficult, particularly when the strategy affects species or populations of commercial or conservation importance (Gunderson 1999; Walters 2007). Learning from adaptive management is costly, both economically and politically, often requiring some stakeholders to forfeit potential harvest for at least a short duration. Additionally, it can be difficult to detect the effects of management strategies in natural systems subject to environmental stochasticity and substantial observation error on estimates of ecosystem components (Ham and Pearsons 2011). Therefore, when the system does not respond following a management change, it is difficult to determine whether the lack of change is a result of the new policy not actually affecting the ecosystem, or

whether we are merely unable to detect the effect of management due to stochasticity. Lack of appropriate reference systems makes this problem even more acute (Walters 1986).

The Chignik Lakes system, Alaska, provides an excellent situation to examine whether adaptive management could be used to understand the effects of predation and environmental stochasticity on fishery productivity. The prey species, sockeye salmon *Oncorhynchus nerka*, is highly-valued ecologically, economically, and culturally (i.e., subsistence harvest) in the area, while the predator species, coho salmon (*O. kisutch*), is less commercially and culturally valuable (Clark et al. 2006). Previous research has demonstrated juvenile coho salmon prey heavily on sockeye salmon fry in rearing lakes (Roos 1960), consuming over half of the emerging fry annually in Chignik Lake (Ruggerone and Rogers 1992), one of the primary rearing lakes for sockeye salmon. A combination of bioenergetics modeling and estimates of diet and predator digestion rates revealed that predation varied among years, ranging from 26% to 78% of sockeye salmon fry being consumed during the early summer. Thus, the biology of the system suggests that coho salmon may limit the productivity of sockeye salmon populations, and that a reduction of coho salmon in years of high abundance could increase sockeye salmon productivity (Ruggerone and Rogers 1992).

The structure of the commercial salmon fishery at Chignik may be exacerbating the effect of coho salmon predation on sockeye salmon production. While the sockeye salmon fishery is managed to achieve maximum sustainable yield, coho salmon are not subject to directed commercial harvest in the system for economic and logistic reasons and are only harvested incidentally during the sockeye salmon fishery (Clark et al. 2006). Therefore, the commercial fishery exerts asymmetric pressure on the ecosystem, potentially altering its structure in ways that depress the productivity of sockeye salmon. Further, as there is no directed coho salmon

fishery, there is limited interest in monitoring their abundance. While migrating sockeye salmon are enumerated at a seasonally-operated weir near the mouth of the Chignik River, the majority of coho salmon escapement occurs after the sockeye fishery has closed for the season, and management resources are diverted away from the weir towards other fisheries. Thus, there are excellent data regarding spawning abundance and recruitment of sockeye salmon, but the data on coho salmon escapement are limited (Walsworth and Schindler 2015).

Adaptive management requires the ability to manipulate the ecosystem to elicit a response, and the ability to sufficiently monitor the response to learn about ecosystem structure and function (e.g., Hilborn 1987). For commercial fisheries, the primary method of manipulating the ecosystem is changing fishing pressure on target species. In the case of Chignik coho salmon, while managers can begin managing for a commercial coho fishery (i.e., setting escapement goals, monitoring escapement, opening and closing fishing periods), the new management activity will require participation from the fishers. Fishers have no incentive to harvest coho salmon if they cannot make a profit, therefore making support from the fish processing industry (which sets ex-vessel prices paid to fishers) essential to any adaptive management strategy which would increase harvest of a less valuable species. As the processors may need to sacrifice profit in the short-term to realize any effects of the alternative management, they will likely want to know what effect coho salmon predation could be having on sockeye salmon production and how long they will need to incur costs before benefitting from the reduced predation pressure on sockeye salmon. Here, we examine the empirical relationship between coho salmon escapement and sockeye salmon productivity in the Chignik Lakes watershed, hypothesizing that years with increased coho salmon recruitment result in reduced sockeye salmon productivity. Additionally, as efforts to manage salmon, or any wild population,

are impaired by environmental stochasticity, observation error, and uncertainty about the underlying relationships driving productivity, we used simulation models to examine the probability of detecting coho salmon predation effects on sockeye salmon productivity in a system where the dynamics driving sockeye salmon are known. Finally, we used simulation models to examine how long an adaptive management strategy reducing coho salmon escapement would need to be implemented before any change in productivity is detected in the sockeye salmon population across a range of species interaction strengths.

Methods

Study site

The Chignik River, located on the Alaska Peninsula and draining into the Gulf of Alaska, contains two salmon rearing lakes; Black Lake in the upper watershed and Chignik Lake in the lower watershed. Each lake supports a genetically distinct stock of sockeye salmon with unique migration timings. The Black Lake stock returns to the system early in summer (June through early July), and is primarily composed of 1.3 aged fish (having spent 1 full summer in freshwater and three in the ocean), while the Chignik Lake stock returns to the system later in summer (late June through August) and is composed primarily of 2.3 aged fish. Coho salmon begin their upriver spawning migration in the middle of August and continue through September into October (Walsworth and Schindler, 2015). Commercial salmon fishing effort is concentrated in Chignik Lagoon and outside of the lagoon in Chignik Bay, and is active between early June and late August.

Data

Sockeye salmon harvest and escapement data are available through the Alaska Department of Fish and Game (ADFG). To enumerate migrating salmon passing through the fishery, ADFG operates a seasonal weir in the Chignik River at the upstream extent of tidal influence. Sockeye salmon harvest, escapement and age composition were used to generate spawning-stock and recruitment relationship for both the Chignik Lake and Black Lake stocks separately (Fig. 3.1a,b). Currently, all anadromous fish species are counted at the weir from the end of May through approximately the end of August, coinciding with the timing of the sockeye salmon fishery. Historically, escapement counts have focused primarily on sockeye salmon, limiting the availability of coho salmon escapement data. Thus, sockeye salmon escapement is enumerated with high precision, while coho salmon escapement is modeled from limited data (Walsworth and Schindler 2015) and has much lower precision (Fig. 3.1c,d).

The Pacific Decadal Oscillation (PDO) is a widely recognized pattern of low frequency environmental variability in the North Pacific Ocean that has been linked to Pacific salmon productivity. Historical PDO index data are publicly available through the Joint Institute for the Study of the Atmosphere and Oceans at the University of Washington (jisao.washington.edu).

Production Functions

Pacific salmon stock-recruitment dynamics are often assumed to follow a Ricker production function (Ricker 1954). When converted to the natural log of sockeye salmon recruits-per-spawner, the Ricker model becomes a linear regression and estimates of the effect of environmental conditions can be included. We include one environmental covariate (annual mean PDO index) and one predation covariate in the spawner-recruit relationship for both Black

Lake and Chignik Lake sockeye salmon stocks. We used a Bayesian approach with JAGS software (Plummer 2003) to fit the following model:

$$\ln\left(\frac{R_s}{S_s}\right) = \alpha_1 + \beta_1 S_s + \beta_2 P + \beta_c C_{tz},$$

$$C_{tz} = \frac{C_{\bar{t}} - \bar{C}}{\sigma_c},$$

$$C_{\bar{t}} = \ln\left(\frac{C_{t-2} + C_{t-1}}{2}\right),$$

$$C_t \sim N(\mu_t, \sigma_t),$$
(3.1)

where R_s is the number of sockeye salmon recruits from a brood year with S_s spawning adult sockeye salmon, P is the annual mean PDO index for the year in which the dominant age-class migrates to the sea (2 years after spawning for Black Lake sockeye salmon, 3 years after spawning for Chignik Lake sockeye salmon), $C_{\bar{t}}$ is the natural logarithm of the mean coho salmon escapement from two years and one year prior to the sockeye parent escapement year, \bar{C} is the mean of the natural logarithm of coho escapement across all years derived from the Bayesian hierarchical model analysis in Walsworth and Schindler (2015), σ_c is the standard deviation of annual coho salmon escapement across all years (Walsworth and Schindler 2015), C_{tz} is the z-scored value of C_t relative to the mean and standard deviation of the natural logarithm of coho salmon annual escapement (Walsworth and Schindler 2015), μ_t and σ_t are the log mean and standard deviation of the posterior distribution of coho salmon escapement estimates from Walsworth and Schindler (2015) for year t , and α_1 , β_1 , β_2 , and β_c are estimated parameters. Parameters were given broad, uniform prior distributions.

We account for two age classes of juvenile coho salmon because they spend two years in freshwater during which time they prey on sockeye fry. We used the z-scored natural logarithm of coho salmon escapement as an index of abundance to (1) normalize the predictor variable

data, and (2) to simulate density-dependent survival in the first freshwater year for coho salmon. While the natural logarithm of escapement applies strong density dependence, when scaled to have a mean of zero and a standard deviation equal to one, $\ln(\text{coho escapement})$ and absolute coho escapement generate similar values for the levels of coho salmon escapement estimated in the Chignik system and simulated in our study except at the tails of the distribution. Our assumption under-weights the effect of very high coho salmon escapement on sockeye salmon productivity and over-weights the effect of very low coho salmon escapement on sockeye salmon productivity relative to the use of coho salmon escapement as an index of predation pressure. We believe this is a reasonable assumption given density-dependent survival of coho salmon fry (Bradford 1995).

Sockeye salmon populations at Chignik are managed to achieve an escapement that produces MSY (Sagalkin et al. 2013). Spawning abundances greater than those which would produce MSY substantially increase intraspecific competition for spawning and rearing resources. This formulation of the spawner-recruit curve for sockeye salmon causes the greatest effect of coho salmon predation to occur at low sockeye salmon abundances, whereas density-dependent effects would be the primary limitation at high sockeye salmon abundance (Fig. 3.1e). More negative values of β_c correspond to larger negative effects of coho salmon predation in the expected sockeye salmon recruits-per-spawner at a given sockeye salmon escapement (Fig. 3.1f).

Adult coho salmon abundances in the watershed (escapement) were estimated with a Bayesian hierarchical model incorporating limited weir counts and late-season dual-frequency identification sonar (DIDSON) data (Walsworth and Schindler 2015). Estimates of returning coho salmon age composition (C. Russell and M. B. Loewen, ADFG *personal communication*) and annual percentage of coho salmon harvested were obtained from ADFG (Anderson et al.

2013). Using these data, the number of returning coho salmon were estimated by either (1) adding the observed harvest to the estimated escapement (for years 1995 through 2013 when data are available) or (2) by multiplying the estimated escapement by 1.11 to account for the average exploitation rate in years when harvest data are available. Coho recruitment from a given breeding year was calculated by allocating escapement by age to the breeding year. Due to data limitations, we assumed that the age composition was constant among years. Spawning stock and recruitment estimates were available for 21 years. We fit the following Ricker function to each of 30,000 random draws from the posterior distributions of annual coho salmon escapement estimates:

$$\ln\left(\frac{R_c}{S_c}\right) = \alpha_2 + \beta_3 S_c, \quad (3.2)$$

Where R_c is the number of coho salmon recruits, S_c is the number of coho salmon spawning adults, and α_2 and β_3 are fitted parameters. Fitting (3.2) to S_c values randomly drawn from the posterior distributions of coho salmon escapement (Walsworth and Schindler 2015) generates a distribution of parameter estimates. The median values of α_2 and β_3 were used in simulation analyses (*see below*). Additionally, we examined the results of all analyses with coho salmon production described by a hockey-stick model instead of a Ricker function. No changes to conclusions were drawn from this alternative formulation, so we only report results from the Ricker model analyses here.

Simulation models – Overview

To examine the potential errors in estimates of coho salmon predation on sockeye salmon productivity, we used a simulation model approach in which a known predation effect is used to generate time series of adult escapement data for both sockeye and coho salmon (conceptual

diagram Fig. 3.2). We then simulated observation error for each coho escapement estimate, and examined relationships between sockeye salmon productivity and the ‘observed’ coho salmon escapement to estimate the coho salmon predation effect using linear regression. Last, we examined the effects of changing coho salmon harvest rates on the productivity of sockeye salmon fisheries to determine how long adaptive management strategies would need to be used before detectable changes in sockeye salmon harvest manifest.

Simulation models – Population Dynamics

We used the parameters fit to eqs. (3.1) and (3.2) (results from above analysis; Table 3.1) to generate the number of sockeye salmon recruits returning from each spawning season:

$$\ln\left(\frac{R_s}{S_s}\right) = \alpha_1 + \beta_1 S_s + \beta_2 P + \beta_{c,true} C_{true,z} + \varepsilon_s,$$

$$\varepsilon_s \sim N\left(\frac{\sigma_p^2}{2}, \sigma_p^2\right), \quad (3.3)$$

$$\sigma_p^2 = \ln(cv_p^2 + 1),$$

where R_s is the number of sockeye salmon recruits from a brood year with S_s spawning adult sockeye salmon, P is the annual mean Pacific Decadal Oscillation index for the year in which the dominant age-class migrates to the sea (two years after spawning for Black Lake sockeye salmon, three years after spawning for Chignik Lake sockeye salmon), C_{true} is the z-score of the simulated ‘true’ mean coho recruitment (as C_{tz} in (3.1)), and ε_s is random error in sockeye salmon log-recruits-per-spawner. The formulation of recruitment error in (3.3) provides an expected error of zero (Hilborn and Walters 1992; Oken and Essington 2014). Trajectories of ‘future’ PDO indices were generated using an autocorrelated random walk function:

$$P_t = 0.6P_{t-1} + 0.4z_i, \quad (3.4)$$

$$z_i \sim N(0, 1.8).$$

in which the parameters for the random variable were manually selected to generate realistic periodicity and magnitude of the index (Mantua and Hare 2002). The same simulation process was used to generate coho salmon trajectories, except using the following equations:

$$\ln\left(\frac{R_c}{S_c}\right) = \alpha_2 + \beta_3 S_c + \varepsilon_c, \quad (3.5)$$

$$\varepsilon_c \sim N\left(\frac{\sigma_c^2}{2}, \sigma_c^2\right),$$

$$\sigma_c^2 = \ln(cv_c^2 + 1).$$

instead of (3.3) to simulate recruits-per-spawner and process error in recruitment. Thus, we assume that coho salmon recruitment is independent of sockeye salmon abundance. Historical data from the Chignik system suggests this to be a reasonable assumption (mean $R^2 = 0.01$, $n = 18$). Juvenile coho salmon consume other species of fish in the rearing lakes in addition to sockeye salmon (e.g., pond smelt *Hypomesus olidus*).

The recruits from each brood year were divided into age-classes by drawing from a Dirichlet distribution derived from the average age-composition of each stock (i.e., Black Lake or Chignik Lake) and species (i.e., sockeye or coho salmon; Table 3.2). Annual escapement for sockeye salmon (and coho salmon in simulation scenarios in which there was a coho salmon escapement goal) was calculated as the escapement goal multiplied by a log-normal error term fit to historic escapement data in Chignik. Harvest of each stock was then calculated as the total returns less stock specific escapement. For coho salmon under the current harvest scenario, no minimum escapement was used as they have no escapement goals under the current management strategy.

Coho salmon observation error was generated as follows:

$$\begin{aligned}
 C_{esc,obs} &= C_{esc,true} e^{\varepsilon_o}, \\
 \varepsilon_o &\sim N\left(\frac{\sigma_o^2}{2}, \sigma_o^2\right), \\
 \sigma_o^2 &= \ln(cv_o^2 + 1), \\
 C_{obs,t} &= \ln\left(\frac{C_{esc,obs,t-2} + C_{esc,obs,t-1}}{2}\right), \\
 C_{obs,z} &= \frac{C_{obs,t} - \bar{C}}{\sigma_c}.
 \end{aligned} \tag{3.6}$$

where $C_{esc,obs}$ is the observed coho salmon escapement, $C_{esc,true}$ is the true coho salmon escapement, ε_o is the observation error, σ_o^2 is the variance of the observation error, cv_o is the coefficient of variation of the observation error, $C_{obs,t}$ is the natural logarithm of the mean coho salmon escapement in years $t-1$ and $t-2$, $C_{obs,z}$ is analogous to C_{tz} in (3.1), and all other parameters are as in (3.1).

Simulation models – Scenarios of Uncertainty

Models fit to field data are subject to two sources of error; uncertainty in model structure (process error) and uncertainty in the measured data (observation error). We examined multiple scenarios with different levels of stochasticity and observation error for the ability to detect a coho predation effect on sockeye production. First, we used a range of ‘true’ coho predation effects ($\beta_{c,true}$) to project sockeye salmon populations, ranging from $-0.2 \ln(R_s/S_s)/C_z$ (very strong effect) to 0 (no effect; Fig. 3.1f). The β_c parameter can be interpreted (for the production functions used here) as an approximate reduction of $-10*\beta_c$ sockeye recruits per spawner between conditions with low coho salmon escapement (at the lower 95% credible interval as estimated in Walsworth and Schindler 2015) and high coho salmon escapement (at the upper 95% credible interval; Fig. 3.1f). We examined the ability to detect an effect of predation with

and without an effect of low frequency environmental variation, such as PDO ($\beta_2 = 0$ when no PDO effect was present). Additionally, we examined scenarios with different levels of recruitment variation (coefficient of variation $cv = 0.2, 0.8$) in sockeye salmon populations. For each of the recruitment variation scenarios, we assessed the ability to detect an effect of coho salmon predation with observation error in coho salmon escapement with $cv = 0.2$ and $cv = 0.5$.

Adult sockeye and coho salmon true and observed population trajectories were projected for 250 years and the last 50 years of data were examined for coho predation effects ($\beta_{c, est}$) using the model:

$$\ln\left(\frac{R_s}{S_s}\right) = \alpha + \beta_1 S_s + \beta_2 P + \beta_{c, est} C_{obs, z}. \quad (3.7)$$

where $C_{obs, z}$ is the z-scored natural logarithm of the mean observed coho escapement of the previous two years (3.6). All other parameters are as in (3.1). Note that besides the observation error in coho salmon escapement, this is the same model used to generate the sockeye salmon population dynamics in (3.3). The ability to detect a coho predation effect was determined by whether the p-value of $\beta_{c, est}$ was less than 0.05 for each simulation of the model, where the parameter value and p-value were estimated through ordinary least squares regression. We assumed that values greater than this would suggest to stakeholders that coho salmon do not have a statistically significant effect on sockeye salmon productivity. The model was simulated 1000 times from which we then estimated the probability of detecting a significant $\beta_{c, est}$ value by dividing the total number of simulations in which $\beta_{c, est}$ was significant by the total number of simulations. Additionally, we examined the estimates of $\beta_{c, est}$ relative to the known values of $\beta_{c, true}$ to examine bias in parameter estimates.

Simulation models – Management Scenarios

As adaptive management is often promoted as a method for understanding interactions between predators and prey (Walters 2007), we examined the ability of an active adaptive management strategy to detect a change in prey (sockeye salmon) abundance over time after initiating a directed harvest of the predator species (coho salmon). For these simulations, we ran the model for 50 years under the current harvest strategy (targeted harvest of sockeye salmon, incidental low harvest of coho salmon), and then switched the management strategy to either (a) managing both sockeye salmon and coho salmon for escapement levels that would produce maximum sustainable yield (calculated for each species separately) or (b) managing sockeye salmon for maximum sustainable yield and reducing coho salmon escapements well below the value that would supply maximum sustainable yield. Hereafter, these strategies will be referred to as the (a) “MSY” strategy and the (b) “heavy exploitation” strategy. Sockeye salmon harvests after the harvest strategy change were compared to the previous 50 years after a period of years ranging from 3 to 50 years after implementation of the new coho salmon harvest regime, under different known levels of coho salmon predation effects on sockeye salmon productivity. Current sockeye salmon escapement goals were used as the escapement that would lead to MSY (Sagalkin et al. 2013). Coho salmon MSY escapement levels were calculated as follows:

$$\hat{\alpha} = \alpha_2 + \frac{\sigma^2}{2}, \tag{3.8}$$

$$S_{MSY} = \frac{\hat{\alpha}}{-\beta_3} (0.5 - 0.07\hat{\alpha}).$$

where σ^2 is the residual mean squared error of the coho salmon Ricker spawner-recruitment function (3.2), and all other parameters are as in (3.2) (Hilborn and Walters 1992). As (3.2) resulted in a distribution of parameter estimates for the coho salmon spawner-recruitment curve,

we used the median estimate of S_{MSY} for the coho salmon MSY harvest scenario. A significant increase in sockeye salmon harvest was defined as at least 80% of simulations demonstrating an increase in harvest after the management change. All analyses were conducted in the R Statistical Computing Environment (R Core Team 2015).

Results

Spawning Stock and Recruitment Relationships

Sockeye salmon from Black Lake had a lower median baseline productivity estimate (Ricker $\alpha_1 = 1.59$ [0.13 SD]; Table 3.1) than the Chignik Lake stock ($\alpha_1 = 1.80$ [0.09 SD]). However, median parameter estimates suggest that Black Lake sockeye salmon have weaker density-dependence ($\beta_1 = -1.75 \times 10^{-6}$ [2.38×10^{-7} SD]) than does the Chignik Lake stock ($\beta_1 = -2.22 \times 10^{-6}$ [1.95×10^{-7} SD]). Both the Black ($\beta_2 = 0.21$ [0.10 SD]) and Chignik Lake ($\beta_2 = 0.18$ [0.06 SD]) sockeye salmon stocks were positively related to the PDO index, demonstrating greater productivity during warm phases. The distributions of β_c estimates varied widely and the credible intervals spanned zero for both the Chignik Lake ($\beta_c = 0.26$ [0.14 SD]) and Black Lake ($\beta_c = 0.04$ [0.21 SD]) sockeye salmon stocks (Fig. 3.3a,b). The coho salmon stock had lower median estimates of baseline productivity (median $\alpha_2 = 1.39$ [0.17 SD]) and higher density dependence (median $\beta_3 = -1.65 \times 10^{-5}$ [3.12×10^{-6} SD]) than either sockeye salmon stock.

Simulation Model - Detecting Predator Effects

When the ‘true’ state of the ecosystem included low recruitment variability for sockeye salmon ($cv = 0.2$) and there was no low frequency variation associated with the PDO (i.e., $\beta_2 = 0$), a coho predation effect was detected in nearly 100% of simulations in which an effect was present (Fig 3.4a). However, when more recruitment variability was added to the system ($cv = 0.8$), the ability

to detect a predation effect was reduced, with relatively large predation effects (e.g., $\beta_c = -0.1$) being detected in less than 50% of simulations (Fig. 3.4a). With the addition of low frequency recruitment variation associated with the PDO to the model (i.e., $\beta_2 =$ fitted values), a predation effect was still detected greater than 99% of the time when there were strong coho predation effects ($\beta_c \leq -0.1$) and low recruitment variability (recruitment $cv = 0.2$; Fig. 3.4b). However, detection probabilities decreased sharply at weaker β_c values, notwithstanding low recruitment stochasticity (Fig. 3.4b). The addition of low frequency recruitment variability had less of an effect on the probability of detecting predation effects under conditions of high recruitment stochasticity ($cv = 0.8$), though detection probabilities were marginally lower for all levels of β_c (Fig. 3.4b).

There was little bias in estimates of the predation effect strength under conditions of low observation error (Fig. 3.4c), but substantial bias towards zero in scenarios with greater observation error (Fig. 3.4d). Further, individual simulation estimates of predation effect strengths were highly variable around the ‘true’ value in both low and high observation error scenarios (Fig. 3.4c,d).

Simulation Model – Adaptive Management Scenarios

As expected, no change in sockeye salmon harvest was detected under either adaptive management strategy when no coho salmon predation effect was present in the model (Fig. 3.5). Additionally, no effect of coho salmon predation on sockeye salmon productivity was ever detected (in the 50 year monitoring period) in models simulating an MSY harvest strategy on coho salmon, even when there were strong predation effects ($\beta_c = -0.2$; Fig. 3.5). In models simulating heavy exploitation of coho salmon, an increase in sockeye salmon productivity was detected in all scenarios in which an effect existed. However, under intermediate predation

effect levels, no difference in sockeye salmon harvest was detected until 15 years ($\beta_c = -0.10$) after the harvest strategy change. Even in scenarios of strong predation effects, nearly a decade of targeted coho salmon harvest was required before a significant increase in sockeye salmon production was detected (Fig. 3.5).

Discussion

Here, we highlight the challenges inherent in adaptive management strategies designed to illuminate predator effects on prey that arise due to the often mismatched time-scales of ecosystem dynamics and the political will to test hypotheses. In our study system, in which diet data suggest strong predation limitation of juvenile life-stages of a prey species, we did not consistently detect a negative effect of predator abundance on prey productivity. Additionally, simulation models in which a known process was used to both generate the data and examine model observations demonstrated limited ability to detect predation effects. Further, estimates of a predation effect were substantially and systematically biased towards zero. Finally, we demonstrated that even for relatively short lived species such as salmon, adaptive management experiments designed to reveal ecosystem structure and function through press manipulations require substantial time to detect an effect of predation, even in simple simulated ecosystems with strong predator effects. In a management environment that is increasingly shifting towards ecosystem-based management approaches (e.g., Pikitch et al. 2004; Patrick and Link 2015) it can be attractive to stakeholders to account for species interactions in exploited ecosystems. However, ecosystem complexity and inertia coupled with stakeholder impatience could derail any potentially successful strategy before the ecosystem has responded sufficiently to detect effects masked by process and observation errors.

While empirical biological evidence suggests a strong effect of predation on sockeye salmon productivity in the Chignik Lakes watershed (Roos 1960; Ruggerone and Rogers 1992), regressions of sockeye salmon productivity against coho salmon escapement did not reveal a significant relationship. As the data available to test the effects of predation are adult abundances, all of the different sources of mortality that occur throughout the lifetime of the individuals are integrated. Even if predation mortality due to coho salmon predation is substantial, potential ecological mechanisms exist which could explain the lack of detection in the adult abundance data (e.g., subsequent life-stages may experience stronger survival bottlenecks, predation could alleviate density-dependence within sockeye salmon populations thereby compensating for predation effects). Alternatively, data limitations (e.g., short time series, observation error) can mask even strong drivers of ecosystem dynamics (e.g., Walters and Ludwig 1981; Oken and Essington 2014).

Simulation models revealed that, even in a system where the true structure of the ecosystem is known, the ability to detect an effect of predation on prey productivity is limited when environmental stochasticity affects recruitment, and observation error is present in the adult abundance data. We should expect these conditions to be ubiquitous in fisheries (Hilborn and Walters 1992). Our results are potentially an optimistic estimate of the ability to detect predation effects in this system because the errors in sockeye escapement and catch are assumed to be negligible, a reasonable assumption given that sockeye salmon abundances at Chignik are enumerated via an intensive weir program and commercial harvests are carefully reported. Our results agree with the findings of Oken and Essington (2014), in which they find that predator effects are easily masked by ecological or sampling processes that introduce variability for age-structured populations. In particular, they found that predators that target sub-adult life-stages

are particularly difficult to detect. As coho salmon predation affects the fry life-stage of sockeye salmon, the likelihood of detecting an effect of coho salmon predation in adult sockeye salmon abundance data is limited. Our results suggest that the effect of coho predation would need to cause a decrease of more than one recruit-per-spawner (under a scenario of high coho salmon recruitment vs. low coho salmon recruitment) before there is a greater than 50% chance of detecting the predator effect in adult salmon data. Stochastic recruitment at levels observed in natural systems can easily mask any influence of even strong predation.

In addition to high-frequency, interannual environmental variability, the influence of low frequency environmental variation (e.g., PDO, North Pacific Gyre Oscillation, North Atlantic Oscillation) is increasingly appreciated in the ecological literature (Mantua and Hare 2002; Stenseth et al. 2002; Di Lorenzo et al. 2008). Many Alaskan fisheries experienced large increases in productivity following the 1977 PDO shift, though some species experienced reduced productivity (Hare et al. 1999). The addition of low-frequency variation to prey recruitment further masked the effect of predation in our simulations. While small predator effects were easily detected in the absence of a simulated PDO effect under scenarios with low interannual recruitment stochasticity, these same predator effects were much less likely to be detected when a PDO signal was included. This highlights the importance of considering longer-term variation in environmental conditions when examining species interactions. Traditional examinations of ecosystem dynamics assume static relationships between ecosystem components, which is increasingly recognized to be inappropriate (e.g., Deyle et al. 2016). Short-term studies may capture transient dynamics as productivity regimes switch, and therefore may not detect the true relationships between species that have important consequences within the context of the broader productivity regimes.

Modeling efforts to explore the responses of ecosystem-based management are sensitive to the parameter values used in models, as small changes in parameter values can lead to large changes in our understanding of ecosystem state. Observation error is ubiquitous in ecological monitoring and presents an ongoing challenge for the accurate estimation of important parameters in population or ecosystem models (Walters and Ludwig 1981). Measurement errors have long been recognized as problematic for regression analyses (Fuller 2006), and can result in biased conclusions about the system being managed, potentially rendering historical data of little use for examining relationships between recruitment and explanatory variables (Ludwig and Walters 1981). Our simulations demonstrate that observation error biases parameter estimates of the effects of predators on prey towards zero, suggesting only weak effects of predators on prey population dynamics. Many of the estimates of predation effects in our simulations were positive (i.e., greater coho salmon escapement resulted in increased sockeye salmon productivity), when the true relationship was negative. These results suggest that the effect of predation could often be much stronger and in the opposite direction of what is detected in studies of predation from empirically measured indices of adult abundances. As coho salmon escapement estimates from the Chignik salmon fishery are modeled from incomplete count data (Walsworth and Schindler 2015), the positive correlation measured between observed coho salmon escapement and sockeye salmon productivity could be a result of recruitment stochasticity and observation error masking the true relationship. Even in situations with extensive investment in monitoring, such as at Chignik, these problems will be difficult, if not impossible, to avoid.

We chose to examine the effect of predation on sockeye salmon productivity by examining dynamics in the adult returns to the system as this is the level at which management and fishers interact. Managers set escapement goals and fishery openings in response to the

number of adults returning to the system, and fishers reduce the number of fishes escaping to the watershed to spawn by harvesting surplus individuals. As the actions of fishers and managers influence escapement, an alternative harvest and management framework would likely be enacted through changes to escapement goals for sockeye or coho salmon. However, the evidence of a predation effect on sockeye salmon survival (Roos 1960, Ruggerone and Rogers 1992) is derived at relatively small scales. Predation occurs within the freshwater rearing lakes, while adult return data encompass sockeye salmon mortality from multiple sources and in multiple habitats throughout their lives. Life-cycle models attempt to examine the effects of mortality sources at multiple life-stages, thus revealing important sources of mortality to the overall productivity of populations (e.g., Scheuerell et al. 2006, Battin et al. 2007). Such models are effective at examining the potential responses of populations to different ecosystem changes. However, developing appropriate models relies on good data and understanding of the relationships between species and their environment. As such, life-cycle models attempting to incorporate coho salmon predation effects on sockeye productivity in Chignik would suffer from the same uncertainty regarding abundance of coho salmon, in addition to having greater uncertainty in the sockeye salmon fry and smolt abundance data.

Despite increased calls for managers to shift towards an ecosystem based approach to management, most Alaskan salmon fisheries remain managed under a single-species framework with no explicit consideration of species interactions in the management of any given species. Management typically focuses on achieving escapement goals (i.e., number of adults that escape the fishery to reach their natal rivers) that on average provides MSY (Sagalkin et al. 2013). Coho salmon in the Chignik management area are not managed, and thus do not currently have an escapement goal. Were coho salmon to be directly managed to reduce predation pressure on

sockeye salmon populations, one escapement goal managers could enact would be to reduce escapement to a level that would produce coho salmon MSY. While such a strategy would be consistent with historic management actions for Alaska's salmon fisheries, our simulations suggest that there would be no measurable effect on sockeye salmon harvest, except under circumstances where predation effects are very strong ($\beta_c = -0.2$). Even under very strong coho salmon predation effects, multiple decades of sustained harvest would be required to detect an effect on the harvest of sockeye salmon. This is driven by the assumption of density-dependent mortality in the first year of the coho salmon life-cycle, prior to the size-classes at which they prey upon sockeye salmon. Density-dependence in the first year is supported for many coastal coho salmon populations, where productivity is limited by pool habitat suitable for overwintering in the first year of life (e.g., Quinn and Peterson 1996) or by territorial aggressive behavior limiting densities within habitats (reviewed by Sandercock 1991). Managing coho salmon escapement for MSY maintains high coho salmon recruitment, on average, and likely does little to reduce predation pressure on sockeye salmon. To reduce predation pressure on sockeye salmon fry, coho salmon escapement would need to be managed well below their single-species MSY spawning stock. This highlights the importance of considering species interactions when determining management targets in multi-species framework (May et al. 1979), and the importance of understanding the life-histories of the species being managed.

Adaptive management is widely promoted as a method for learning about ecosystem structure and function through active manipulation of different ecosystem components (Walters 1986). It is also suggested that we can begin managing under an ecosystem management framework in the presence of great uncertainty if we use adaptive management to learn about the ecosystem as we manage (Patrick and Link 2015). However, adaptive management strategies

often require substantial support and sacrifice from stakeholders (Walters 2007), producing pressure to realize a benefit of the management change over short time periods. Models used to examine the potential effects of alternative management strategies that could be used in an adaptive management framework often focus on the equilibrium dynamics of the system following the management changes. The transition time between equilibrium states is of critical importance in a world of limited management resources and economic consequences to stakeholders. In our simulations, even in scenarios with very strong predation effects on prey populations, it would take at least nearly a decade before any substantial change in prey productivity was detectable. Testing multiple hypotheses sequentially with an adaptive management framework could thus take a quarter century or more to learn about two separate hypotheses, assuming the results of each take as long to manifest, and that there are no other fundamental changes to the ecosystem that would mask these effects. This time-scale is longer than the tenure of most managers, the economic time horizon of most fishers, and political cycles, which can all reduce the likelihood of maintaining an adaptive management strategy long enough to experience the potential benefits (Walters 1997). Adaptive management as a tool to learn about ecosystems as we shift towards ecosystem based management is challenged by the mismatch of time-scales of learning from ecosystem response to manipulation and the political will to maintain what may be initially costly strategies. It is critical for stakeholders and managers to understand the time-scale at which ecological responses to management changes may take in order to weigh the costs and potential benefits of adaptive management (Bearlin et al. 2002). Would stakeholders be willing to sacrifice for multiple years before experiencing any benefit from the change? If not, any adaptive management strategy will be doomed to fail, even if the ecological effect would have ultimately have been beneficial to stakeholders.

Shifting towards ecosystem based approaches to management will require continued learning about ecosystem structure and function. For the Chignik salmon fishery, while predation by coho salmon may be limiting the productivity of sockeye salmon populations, as suggested by diet data and bioenergetics modeling (Ruggerone and Rogers 1992), it would be extremely difficult to detect and accurately characterize any predation effect from adult return data, even if predation effects were very strong. Further, adaptive management strategies aimed at revealing predator-prey interactions in the system would take a long time to demonstrate an effect, and the management strategy employed (i.e., coho salmon escapement target) would determine if and when an effect could be discerned. It is critical for future studies to examine not only the ecological consequences of potential alternative harvest regimes that could be enacted in an adaptive management framework, but also the socioeconomic consequences of strategies that may take a long time to produce benefits for stakeholders. More broadly, consideration of transition times between ecosystem states must be acknowledged when presenting adaptive management simulations to stakeholders and managers. If long transition periods are not acknowledged and stakeholders observe no measurable effect of the new management regime, but have experienced economic or social costs because of the new policy, the political support for testing alternative strategies would disappear well before any benefit could be realized.

Table 3.1. Parameter estimates for the stock-recruitment curves for each sockeye salmon stock and the coho salmon stock.

Species	Stock	Ricker Parameters							
		α		β_1		β_2		β_c	
		Median	SD	Median	SD	Median	SD	Median	SD
Sockeye Salmon	Black Lake	1.59	0.13	-1.75E-06	2.38E-07	0.21	0.10	0.04	0.14
	Chignik Lake	1.80	0.09	-2.22E-06	1.95E-07	0.18	0.06	0.26	0.21
Coho Salmon		1.39	0.17	-1.65E-05	3.12E-06	--	--	--	--

Table 3.2. Age-class distributions for each salmon stock used in simulation models to generate returning adult salmon abundances from multiple brood years.

Species	Stock	Age Class							
		1.1	1.2	2.1	1.3	2.2	3.1	1.4	2.3
Sockeye Salmon	Black Lake	--	0.07	--	0.6	0.05	--	0.02	0.26
	Chignik Lake	--	0.05	--	0.35	0.11	--	--	0.49
Coho salmon		0.28	--	0.69	--	--	0.03	--	--

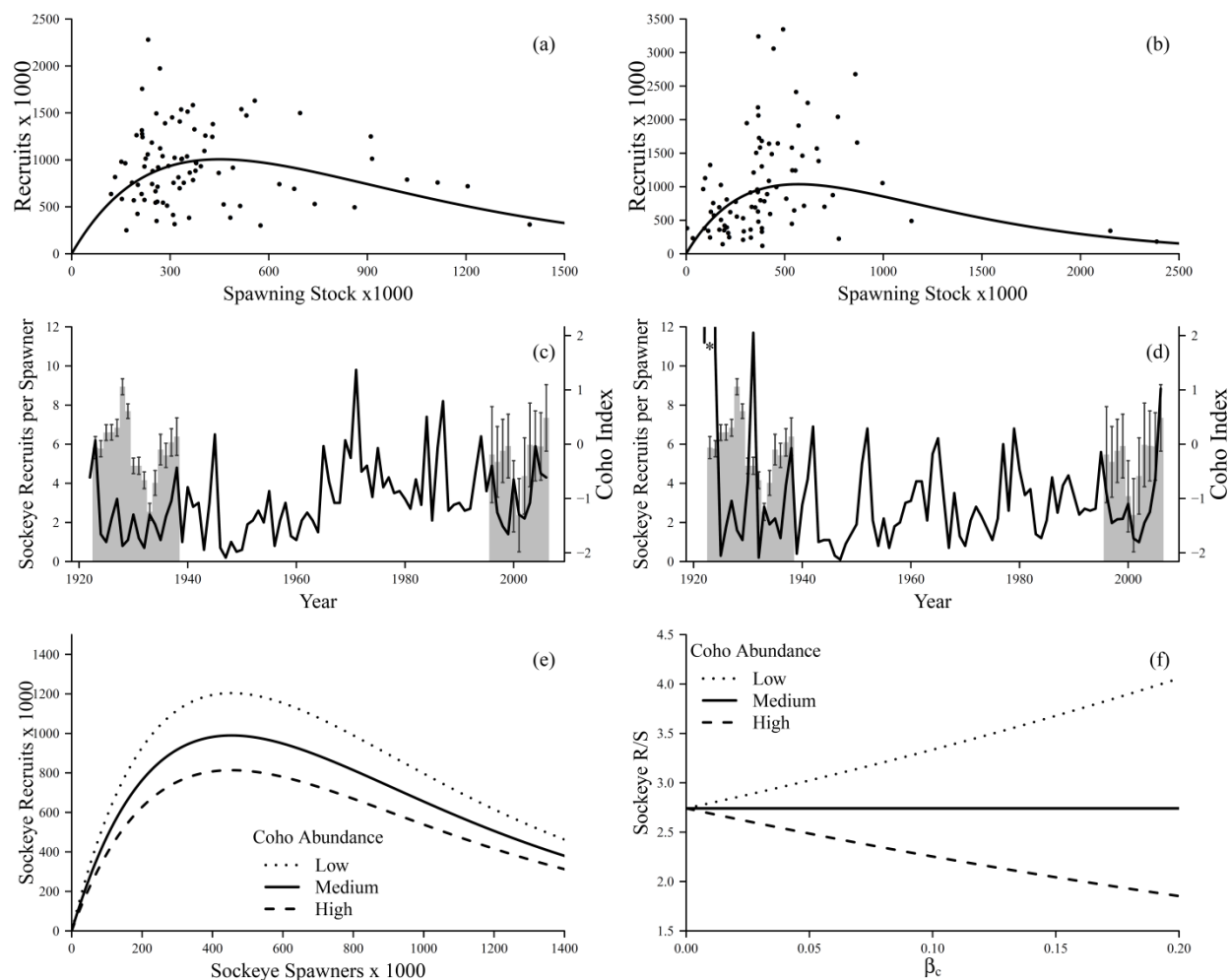


Figure 3.1. Sockeye salmon spawning stock and recruit relationships for Chignik Lake stock (a) and Black Lake stock (b), time-series of sockeye salmon recruits-per-spawner (solid lines) and coho salmon abundance indices (grey bars) for Chignik Lake (c) and Black Lake (d), example production functions (e) and effects of coho predation on recruits-per-spawner for Chignik Lake sockeye salmon at their current escapement goal under different levels of coho abundance (median, upper, and lower bounds of the 95% credible interval of coho salmon escapement; f). Black Lake recruits-per-spawner for 1923 ($R/S = 81.9$, noted with * in panel (d)) are significantly higher than any other value and are thus not plotted. Error bars on coho index denote ± 1 SD.

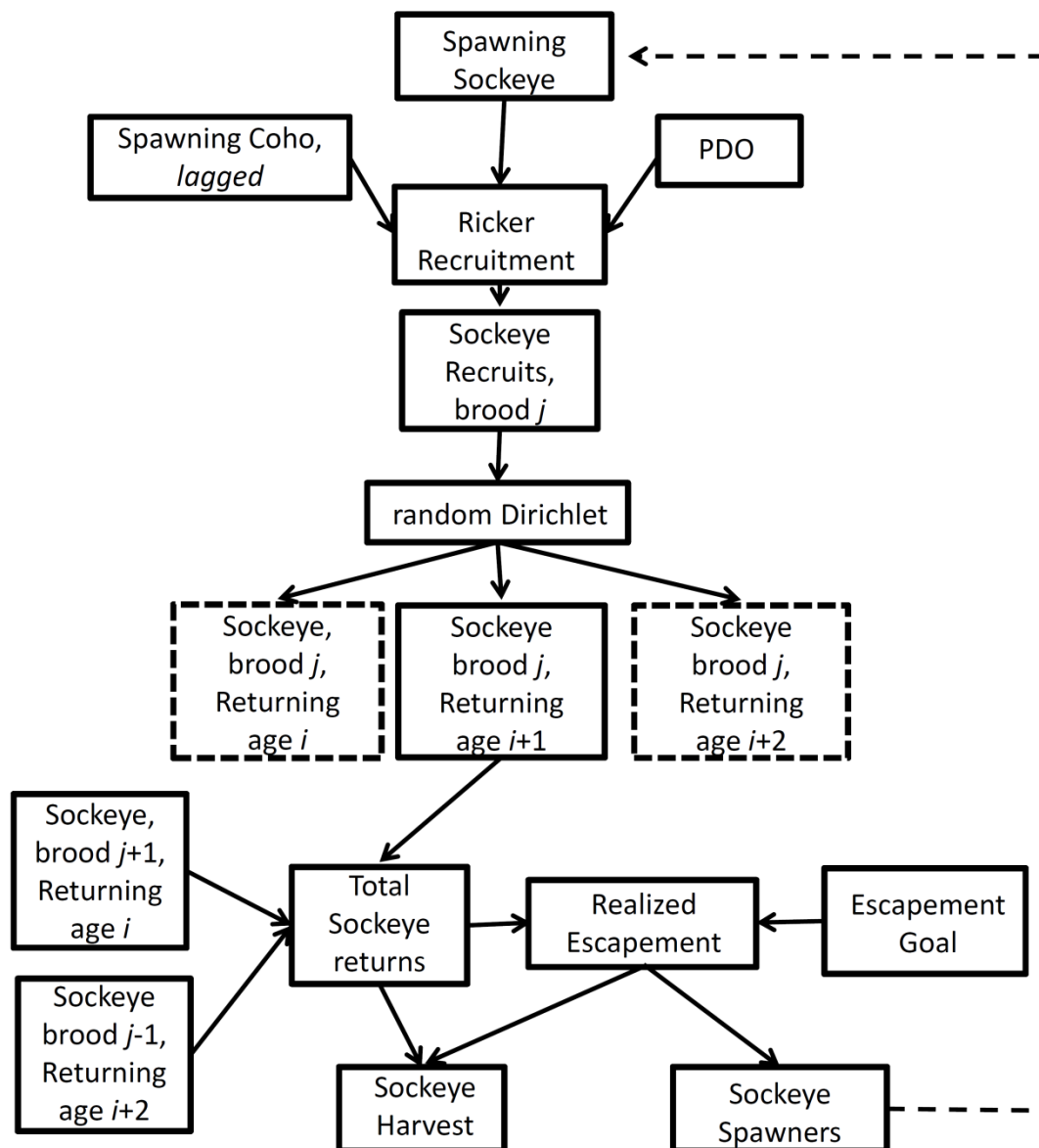


Figure 3.2. Conceptual diagram of the simulation modeling strategy for sockeye salmon populations. Recruits are determined from a Ricker spawner-recruit curve with parameters for spawning sockeye salmon, coho salmon recruits in the lakes, and an environmental signal of the Pacific Decadal Oscillation. The resultant recruits are then divided into returning age classes with a Dirichlet distribution derived from observed age composition data. The sum of the recruits from different brood years returning in a given year determines the total sockeye returns for a year. The number of salmon escaping to the rivers to spawn was determined from the stock-specific escapement goal with log-normal error fit to historic escapement data. The number of harvested sockeye is determined by subtracting the escapement from the total returns.

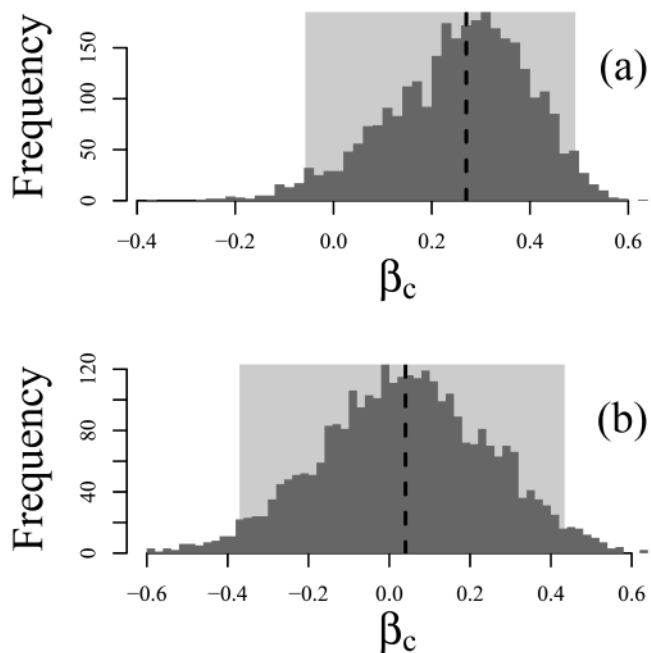


Figure 3.3. Coho salmon predation effect estimate posterior distributions for Chignik Lake (e) and Black Lake (f) from Bayesian analysis of historic catch and escapement data. Dashed black line represents the median value and light grey polygon encompasses the 95% credible interval.

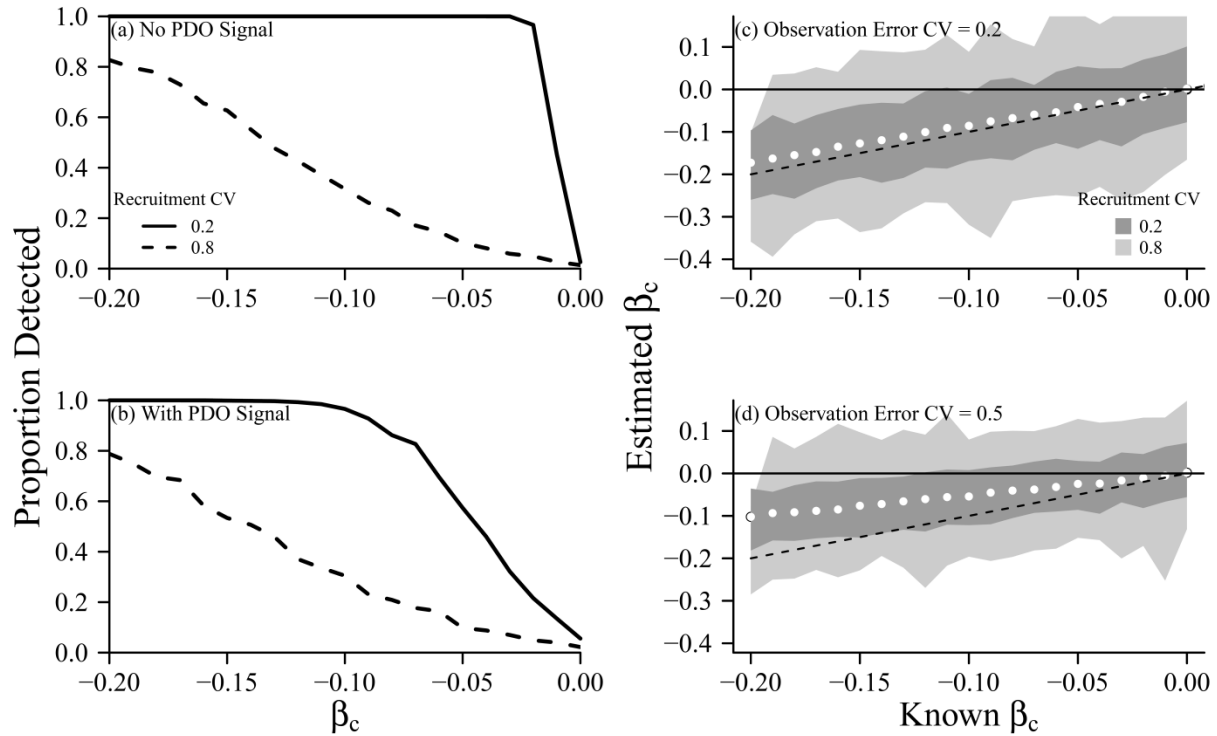


Figure 3.4. Proportion of simulations in which an effect of coho salmon predation on sockeye salmon productivity was detected by linear regression under scenarios without (a) and with (b) low frequency environmental variation, such as PDO, and bias in estimates of predation effect magnitude with low ($cv = 0.2$; c) and high ($cv = 0.5$; d) observation error. The effects of recruitment stochasticity on detection probabilities (a,b) are shown with solid (recruitment $cv = 0.2$) and dashed (recruitment $cv = 0.8$) lines, and its effects on parameter estimate bias (c,d) are shown with dark grey (recruitment $cv = 0.2$) and light grey (recruitment $cv = 0.8$) polygons. White points (c,d) represent median estimated parameter values. The solid and dashed lines in (c,d) denote the zero and 1:1 line, respectively.

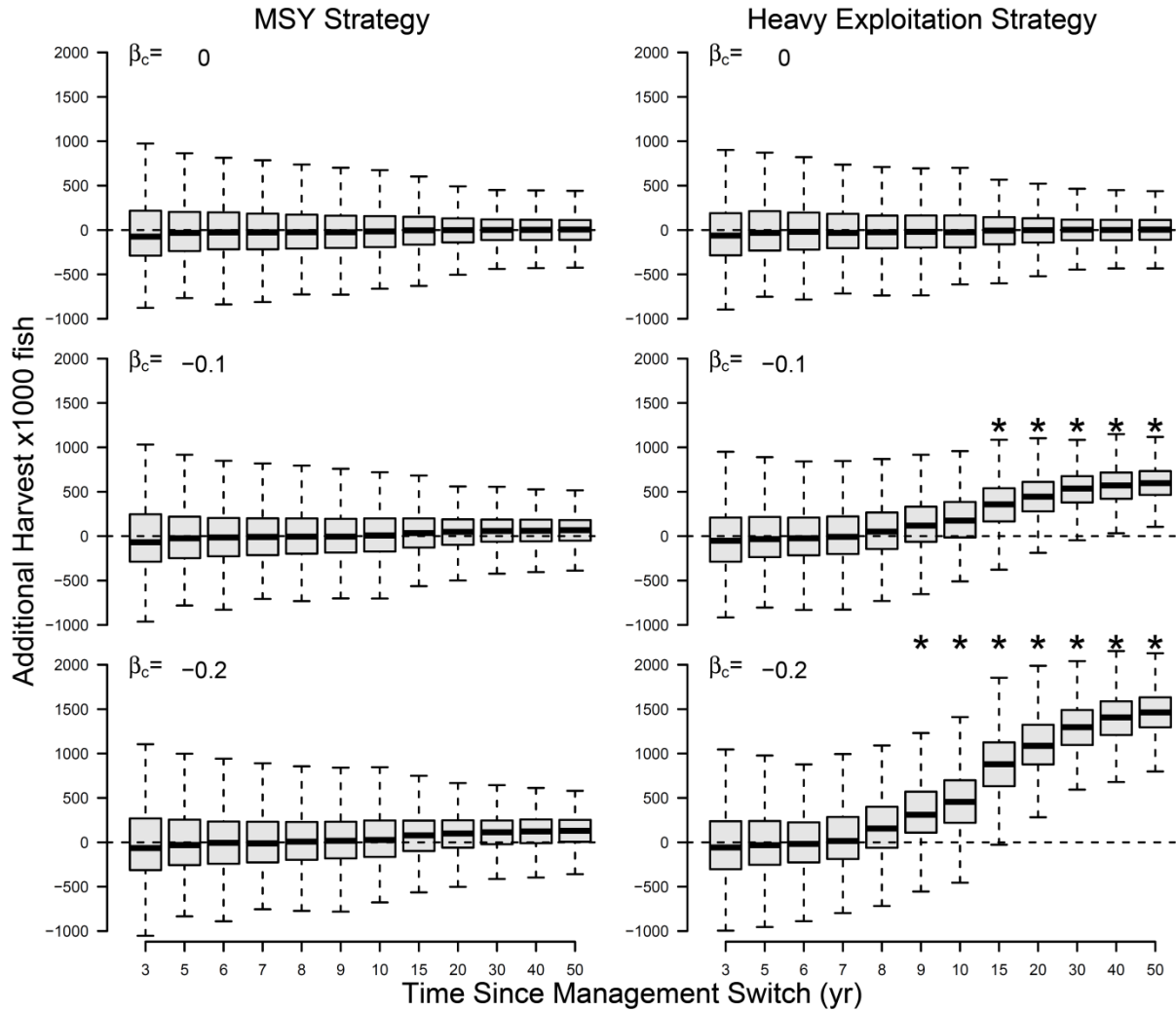


Figure 3.5. Change in sockeye salmon harvest following implementing directed harvest off coho salmon to escapement levels equal to the single species MSY (left column) and to levels far below MSY (right column). Asterisks indicate scenarios in which a significant increase in harvest was detected.

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Chapter 4. Constrained by markets: processing costs limit potential for managing predator-prey interactions in a commercial fishery

Introduction

Resource management agencies are increasingly called upon to shift towards more ecosystem-based approaches to managing renewable resources (Pikitch *et al.* 2004; Patrick & Link 2015). Ecosystem-based approaches explicitly consider the trade-offs among different ecosystem components and stakeholders (Link 2010). Ecosystem-based approaches therefore are concerned with linkages among biological components, such as among species or between habitats and populations. In addition to “natural” components, ecosystem-based approaches explicitly consider human systems and the distinct values and objectives of the diversity of stakeholders in a typical social-ecological system. Integrating multiple economic and ecological components into models used for management planning allows for assessments of holistic management of ecosystems.

Ecological and economic constraints can drive a fishery to exert asymmetric pressure on ecosystem components, selectively removing some species while having little direct effect on other species. Selective harvest strategies may indirectly limit the overall productivity of the aggregate fishery, as species interactions may limit the productivity and abundance of valuable species (e.g., Carpenter, Kitchell & Hodgson 1985; Link 2002). For example, harvesting species that consume or compete with target species may, in some cases, result in increased fishery productivity (Larkin 1963; May *et al.* 1979). Multi-species harvest strategies may reveal novel approaches to achieving maximum economic and social benefits that would not be found in

single-species strategies. However, whether such a multi-species harvest approach makes sense in a given fishery depends on many ecological and economic constraints (e.g., the ability to influence predation effect through adult predator harvest (Rieman & Beamesderfer 1990; Beamesderfer 2000; Yodzis 2001), the economic structure of the fishery (Clark 2010), or temporal delays in population response to change in harvest strategy (Frank *et al.* 2011; Walsworth & Schindler *unpublished data*)).

Fisheries are integrated social-ecological systems in which managers attempt to indirectly manage the biological components of the system by managing human behaviors for desired social outcomes (Gordon 1954; Rosenberg 2003; Hilborn & Walters 1992). Achieving new management goals can be difficult without consideration for the economic effects of management across a range of stakeholders. Rational economic behavior may produce unanticipated dynamics in the social-ecological ecosystem (Gordon 1954), or political resistance to proposed changes may inhibit their implementation (Matulich, Mittlehammer & Reberte 1996; Rosenberg 2003). Many ecosystem-based management models incorporate bioeconomic components to assess alternative management strategies for both conservation of biodiversity and generation of economic and social benefits from harvest. The bioeconomic analyses typically incorporated into fisheries management focus primarily on the economic effects of management on the harvesters in the fishery (e.g., Sanchirico & Wilen 2001; Clark 2010). However, in many fisheries the fish processing sector is distinct from the harvesting sector (Matulich, Mittlehammer & Reberte 1996), having different and often independent constraints on their operations and, therefore, cost and revenue structures. Thus, management changes will likely affect processing sectors differently than harvesting sectors. Consideration of multiple

sectors within the broader commercial fishery can be critical for assessing the economic and ecological effects of alternative management strategies.

Alaska's Pacific salmon (*Oncorhynchus spp.*) fisheries are widely considered among the best managed fisheries in the world from a biological perspective, as large commercial harvests have been sustained for over a century from multiple river systems. While these fisheries are biologically sustainable and productive, economic issues continue to plague them (Hilborn 2006; Eagle, Naylor & Smith 2004). Over-capitalization of fleets limits the overall profitability of these fisheries, and global market changes have created serious challenges to Alaska's salmon fisheries (Eagle, Naylor & Smith 2004; Asche *et al.* 2005). Salmon prices have dropped markedly in recent decades, driven by the increase in production of farmed salmon worldwide (Eagle, Naylor & Smith 2004; Asche *et al.* 2005; Knapp, Roheim & Anderson 2007). Thus, even with recent large harvests, fishers in Alaska have struggled economically due to low prices. Reduced salmon prices raise issues beyond the commercial fishery, particularly in remote villages with limited opportunity for alternative employment (Eagle, Naylor & Smith 2004). Salmon fishery dependent communities thus have an interest in exploring options to increase the viability of their fishing activities, while still maintaining ecological sustainability.

The Chignik Lakes watershed, on the Alaska Peninsula, supports a relatively low volume, but high value sockeye salmon (*O. nerka*) fishery. The watershed supports multiple highly productive runs of sockeye salmon that support commercial and subsistence fishing activities (Clark *et al.* 2006). Additionally, Chignik sockeye salmon demand a higher market price than many other Alaskan sockeye salmon fisheries due to the use of purse seine gear which produces a high quality product compared to the more common gillnet fisheries. While harvest and management efforts in Chignik focus on sockeye salmon, all five species of Pacific salmon are

present in the system, including a population of coho salmon (*O. kisutch*) that use the same freshwater habitats as the sockeye salmon for juvenile rearing. Coho salmon are not currently targeted for commercial harvest due to economic and logistical reasons. Coho salmon do not demand as high of a price from consumers, so processors pay fishers lower ex-vessel prices for this species. The low value of coho salmon in the Chignik fishery is partly due to a lack of access to fresh markets from the remote region. Additionally, the smaller run size of coho salmon limits the potential overall benefit from harvesting coho salmon, when considered in a single-species context.

Previous research in the watershed showed that juvenile coho salmon prey heavily on sockeye salmon juveniles (Roos 1960), consuming over half of the emerging fry annually (Ruggerone & Rogers 1992). Thus, predation by coho salmon may limit the productivity of sockeye salmon populations, thereby limiting the profitability of the commercial fishery (Ruggerone & Rogers 1992). This would make a compelling case for alleviating the predation pressure not accounted for in the current selective fishery harvest. While diet and bioenergetics data demonstrate strong predation pressure (Ruggerone & Rogers 1992), coho salmon abundance in the watershed and sockeye salmon recruitment are not strongly associated (Walsworth & Schindler *unpublished data*). However, estimated predation impacts are hindered by substantial recruitment stochasticity in sockeye salmon and observation error in coho salmon abundance estimates, making it difficult to detect even strong predation effects in the system (Oken & Essington 2014; Walsworth & Schindler *unpublished data*).

Here, we examine ecological and economic conditions under which an active adaptive management strategy directly targeting coho salmon for harvest could be beneficial to stakeholders in the Chignik salmon fishery. With limited ability to detect the effect of predation

on fishery productivity in the available data, managers may wish to enact an active adaptive management strategy to explore how the system responds to increased coho salmon harvest (Walters 1986; Walters 1997). Simulations of active adaptive management strategies to detect increased productivity of sockeye salmon resulting from increased harvest of coho salmon suggest that long time frames would be needed to detect all but the strongest effects of coho salmon predation (Walsworth & Schindler *unpublished data*). The ecological and economic performance of the fishery during the extended transition period thus becomes critical in determining the viability of alternative harvest strategies and stakeholders' willingness to participate. We use a bioeconomic simulation model across multiple ecological and economic scenarios to determine the relative net present value of directed coho salmon harvest to both fishers and processors.

Materials and Methods

Overview

We employed a simulation modeling approach (Fig. 4.1) to assess the ecological and economic conditions under which directed harvest of coho salmon would be beneficial for fishers and processors in Chignik. We compared multiple potential future harvesting strategies attempting to alleviate predation on juvenile sockeye salmon by coho salmon to determine which would be beneficial to stakeholders under different economic and ecological conditions. One scenario assumed that coho salmon were only harvested incidentally during directed sockeye salmon fishing, a continuation of the current situation. The other scenarios had an escapement goal established for coho salmon and assumed that fishers (processors) extended their operating seasons and harvested (processed) coho salmon returning in excess of the escapement goal. We

examined directed harvest scenarios with coho salmon escapement goals ranging from 5000 (harvest rate = 0.73) to 25000 (harvest rate = 0.62).

In addition to the multiple harvesting strategy scenarios, we simulated the fishery across different values of six parameters: strength of the coho salmon predation effect β_c , variable cost to fishers v_f , base daily operating cost to processors b_p , processor profit-per-kg of sockeye salmon p_{sp} , sockeye salmon ex-vessel value p_{sf} , and coho salmon escapement goal G_c (Table 1). The predation effect strengths are within the range of plausible estimates from Walsworth and Schindler (2015) for this ecosystem. This analysis allows us to examine which combinations of ecological and economic conditions need to be present for an extended fishing season targeting coho salmon to be beneficial to fishers and stakeholders. Directed coho salmon harvest strategies were considered economically advantageous when the NPV of the directed coho salmon harvest strategy was greater than the NPV of the current harvest strategy. Thus, we report the relative difference between NPV of the directed coho salmon harvest strategy and NPV of the current harvest strategy (incidental catch of coho salmon) for each ecological and economic scenario. As we examined all of these scenarios under stochastic recruitment dynamics, we report the percent of simulations in which an increase in NPV was detected under a directed coho salmon harvest.

Study Site

The Chignik River salmon fishery is located on the south side of the Alaska Peninsula, approximately 400 km SW of Kodiak, AK (Fig. 4.2). While the fishing district is further divided into 5 sub-districts, the majority of sockeye salmon harvests occur in the Bay and Central districts. Many coho salmon harvested outside of the Bay district are of unknown origin (i.e., it is not known whether they are from a population which spawns in the Chignik River) and are

potentially migrating along the coast. As such, we have limited our consideration of historical coho salmon harvest to those in the Bay district.

The Alaska Department of Fish and Game (ADFG) manages the fishery for escapement to produce sustainable yields from each of two sockeye salmon stocks that spawn in the Chignik watershed. The sockeye salmon fishery typically opens in early June and continues through the end of August. Coho salmon are not directly targeted in the fishery, and therefore are not managed (i.e., no escapement goals are present for Chignik coho salmon). Because coho typically migrate into the Chignik River after the sockeye salmon migration is largely over, current exploitation rates on coho salmon are low.

Approximately 100 limited entry permits are present in the fishery, though not all permits participate every season. Historically, multiple processing companies operated in Chignik, though the majority of salmon are processed by one processor, currently. The processor operates a floating processor ship, brought to the region each year during the salmon fishery.

Data

Sockeye salmon spawner abundance, recruitment, and harvest data are available from weir counts from 1922 – present. Coho salmon spawner abundance and recruitment data are taken from a prior analysis of limited escapement data (Walsworth & Schindler 2015). From these data, stock-specific Ricker production functions were developed to relate the number of returning fish to the number of spawners that produced those individuals (Walsworth & Schindler *unpublished data*). Ex-vessel prices for sockeye salmon and coho salmon were obtained from annual fishery reports distributed by ADFG. Due to the confidential nature of cost and profit data in commercial fisheries, all operating costs were simulated across a range spanning potential values.

Simulation Model – Production Functions

Salmon population dynamics were generated from Ricker production functions fit to either empirical data (for sockeye salmon) or model estimates (for coho salmon; Walsworth & Schindler 2015) from the Chignik system. Each sockeye salmon stock had a unique production function of the form:

$$\ln\left(\frac{R_s}{S_s}\right) = \alpha_1 + \beta_1 S_s + \beta_2 P + \beta_c C_z, \quad (4.1)$$

Where α is the baseline productivity of the population, S_s is the spawning abundance, P is an index of low frequency productivity shifts (e.g., similar to those produced by the PDO; Mantua & Hare 2002), and C is the z-scored mean of the natural logarithm of coho salmon escapement from years t-1 and t-2 (the age classes of coho salmon which would prey upon juvenile sockeye salmon). At intermediate abundances of sockeye salmon, the effect of coho salmon predation has a greater effect than at higher sockeye salmon spawning abundances, when density-dependence has a greater effect on the population productivity (Fig. 4.4).

Coho salmon were produced from a similar Ricker production function:

$$\ln\left(\frac{R_c}{S_c}\right) = \alpha_2 + \beta_3 S_c, \quad (4.2)$$

Where S_c is the spawning abundance of coho salmon and all other parameters are as in (4.1). We assumed that coho salmon are not limited by sockeye salmon, an assumption validated from limited historical data (mean correlation = 0.01, N=18).

Simulation Model – Harvest and Escapement

Because sockeye salmon mature at different discrete ages, proportions of recruits returning at each age were assigned from a Dirichlet distribution parameterized from historical

age data for each stock. All fish of each stock returning in a given year were summed across brood years to compose a year's returns. As the Chignik salmon fishery is a terminal fishery, the fleet is very effective at harvesting when the fishery is open. However, there is implementation error in the harvest policy, with realized escapements often higher, and occasionally lower, than the escapement goal. We modeled annual escapement as the escapement goal with log-normal error:

$$E_{st} = G_s \varepsilon_{Est}, \quad (4.3)$$

$$\varepsilon_{Est} \sim \text{LN}(\text{mean} = 0.229, \text{sd} = 0.240),$$

where E_{st} is the escapement for stock s in year t , G_s is the escapement goal for stock s , and ε_{Est} is the error in annual escapement for stock s in year t . The mean and standard deviation parameters for the log-normal distribution were fit to escapement data for both Black and Chignik Lake sockeye salmon stocks from 1980 to 2015 using the R package `fitdistrplus` (Delignette-Muller & Dutang 2015).

For coho salmon harvest under the current scenario, where they are captured incidentally during the sockeye salmon fishery, we randomly drew a harvest rate from a right skewed beta distribution, with harvest then calculated as:

$$H_t = h_t R_t, \quad (4.4)$$

$$h_t \sim \text{Beta}(\alpha = 0.945, \beta = 3.712),$$

where H_t is the harvest in year t , h_t is the harvest rate in year t , and R_t is the total return in year t . Beta distribution parameters α and β were fit to Chignik fishery coho salmon harvest data. After calculating escapement, all remaining salmon were harvested by the fishery.

Simulation Model – Economics

Fishing effort (boat days) was calculated from a regression between harvest rate and the number of active permits fit to empirical data from the Chignik fishery. Fishing costs were calculated as:

$$C_{ft} = v_f B_t d_t + F_{sf} B_t, \quad (4.5)$$

where d_t is the total number of days fished in year t , B_t is the average number of boats fishing per day, v_f is the variable cost to fishers (i.e., daily operating costs), and F_f is the fixed cost to fishers. Variable costs for fishers are comprised primarily of fuel and grocery prices, while fixed costs include permit costs, off-season maintenance, and insurance. Costs to fishers were estimated from interviews with Chignik salmon fishers (McDowell Group, in Knapp 2007).

Fishers receive a substantially lower ex-vessel value for coho salmon than for sockeye salmon in the Chignik fishery. We used a range of ex-vessel prices for sockeye and coho salmon encompassing recent observed prices in the Chignik fishery. We assumed that future salmon prices were constant in each scenario. We assumed a constant weight of each species throughout all simulations (3.2 kg for sockeye and 4.1kg for coho salmon). Fishers' annual profit was calculated as:

$$\pi_{pt} = \left(\sum_i p_{fi} H_{it} w_i \right) - C_{ft}, \quad (4.6)$$

where H_{it} is the harvest (round) of species i in year t , w_i is the round weight for species i , p_{fi} is the ex-vessel value paid by processors for species i , C_{ft} is the cost of fishing in year t , and π_{ft} is the profit to the fishing fleet in year t .

Processor effort was defined as the number of days from when the floating processor arrived in the region until it stopped purchasing fish. As the coho salmon run occurs after the sockeye salmon runs, we assumed that the processors operated from June 4 to August 27 when

no directed coho salmon fishery was present and from June 4 to September 30 when a directed coho salmon fishery was present. Variable costs to the processor involved a base rate (e.g., food and housing for employees, electricity, maintenance, and management and administration costs) as well as a cost of processing fish which scaled linearly with kg processed per day. Revenue was considered as the first wholesale value minus the ex-vessel value paid to fishermen. We assumed that processors made a constant profit-per-kg of salmon processed.

$$\begin{aligned}
 v_{pt} &= b_p + c_p \frac{H_t}{d_t}, \\
 c_p &= r_{sp} - p_{sp}, \\
 C_{pt} &= v_{pt}d_t + F_p, \\
 r_{cp} &= r_{sp} - 1.
 \end{aligned} \tag{4.7}$$

where v_p is the daily cost of operating for the processor, b_p is the base daily operating cost, c_p is the cost of processing each kg of salmon, r_{sp} is the revenue-per-kg of sockeye salmon processed (minus ex-vessel value paid to fishers), p_{sp} is the profit-per-kg of sockeye salmon processed, F_p is the annual fixed cost of operating for the processor, and r_{cp} is the revenue-per-kg of coho salmon processed (minus ex-vessel value paid to fishers). We assumed constant variable and fixed costs for both processors and fishers throughout the duration of each simulation, and we assumed no opportunity costs to either stakeholder group for continuing to fish or coho salmon.

Fish mass is lost during processing, as heads, guts, etc. are discarded. We assumed a constant percent retention of mass for each species (74% for sockeye salmon, 75% for coho salmon; Knapp, Roheim & Anderson 2007). The annual profit to the processing firm was calculated as:

$$\pi_{pt} = \left(\sum_i p_{pi} H_{it} \rho_i \right) - C_{pt}, \tag{4.8}$$

where H_{it} is the harvest (round) of species i in year t , ρ_i is the percentage of round weight for species i that is retained after processing, p_{pi} is the profit-per-kg sold by processors for species i , C_{pt} is the cost of processing in year t , and π_{pt} is the profit to processors in year t .

We calculated the net present value (NPV) of the fishery for each stakeholder in each simulation:

$$NPV_s = \sum_t^Y \frac{\pi_{st}}{(1 + \delta)^t}, \quad (4.9)$$

where NPV_s is the net present value of the fishery for stakeholder s , π_{st} is the annual profit to stakeholder s in year t , δ is the discount rate, and Y is the final year of the simulation. We assumed an annual discount rate of 0.05. We use the term ‘risk’ to describe the percent of simulations of a given scenario in which stakeholders achieve a reduced NPV under a directed coho salmon harvest than under the current strategy. All simulations and analyses were conducted in the R Statistical Programming Environment (R Core Development Team 2015).

Results

Simulation examples

The fishery model parameterized to simulate current conditions produced salmon abundance and harvest trajectories representative of the dynamics observed historically. Black Lake sockeye salmon returns and harvest were more variable than those of Chignik Lake sockeye salmon, driven by higher recruitment stochasticity in the Black Lake stock (Fig. 4.3a,b). Sockeye salmon harvests and profits were higher in a given year under directed coho salmon harvest strategies (example shown has $G_c = 5000$) than under the current harvest strategy, but

only after a delay of about 10 years (Fig. 4.3d,e,g). Coho salmon returns ranged between approximately 2.0×10^5 and 2.2×10^5 under the current harvest strategy (Fig. 4.3c), and harvests were low in each year (Fig. 4.3f). Under a directed coho salmon harvest strategy with a very low coho salmon escapement goal ($G_c = 5000$), coho salmon harvest was very high for a short period before declining to levels near what was harvested under incidental harvest scenarios as the stock became limited by spawner abundance (Fig 4.3f). The annual value of the coho salmon harvest was always positive during incidental harvest (as the processor was already processing sockeye salmon and incurred no additional costs to process coho salmon). However, under directed coho salmon harvest, the value of the coho salmon harvest was always negative to the processor (Fig. 4.3h).

Fisher Net Present Value Across Scenarios

The change in NPV to fishers resulting from directly targeting coho salmon for harvest was generally positive across all ranges of parameters considered in these simulations (Fig. 4.4). Only when β_c , the effect of coho salmon predation on sockeye salmon, was equal to zero were directed coho salmon harvest strategies less valuable to fishers than the current strategy. The effect of fisher's variable cost (v_f) was strongest at weak predation effect (β_c) levels, as additional profits from sockeye salmon harvests swamped out minor increases in costs to harvest coho when β_c values were large (Fig. 4.4). The effects of sockeye salmon ex-vessel prices (p_{sf}) and coho salmon escapement goal on change in NPV to fishers were greatest under strong predation effects (Fig. 4.4). Similar patterns of benefit were detected at equilibrium conditions (Fig. 4.5). Examining the distribution of simulation results allows examination of the likelihood of fishers experiencing a benefit in NPV from directly targeting coho salmon. If fishers were unlikely to

risk a greater than 10% chance of reduced NPV, the potentially beneficial scenarios became more limited than when examining the median change in NPV (Fig. 4.6).

Processor Net Present Value Among Scenarios

The change in NPV to the processor demonstrated more variable responses to alternative harvest strategies than for fisher NPV (Fig. 4.7). Directed coho salmon fisheries were never beneficial to the processor when β_c was equal to zero (no predation effect). The benefit of alternative harvesting strategies to processors increased with more negative β_c values (stronger predation), decreasing coho salmon escapement goals, decreasing variable costs (b_p), and increasing wholesale profit-per-kg (p_{sp}). When variable costs were high, a directed coho salmon fishery could be beneficial to the processor when there was a strong predation effect and either low coho salmon escapement or high wholesale profit-per-kg for sockeye salmon (Fig. 4.7). When variable costs were low, processors could benefit from a directed coho fishery under any level of predation strength (β_c) examined, though the benefit still depended on wholesale profit-per-kg and the coho salmon escapement goal (Fig. 4.7). Under conditions of very strong coho salmon predation effects (β_c) on sockeye salmon productivity, the processor could benefit from a directed coho salmon fishery at any variable cost (v_p) examined in this study, depending on coho salmon escapement goal and wholesale profit-per-kg of sockeye salmon (Fig. 4.7). At equilibrium, a wider range of conditions were beneficial to processors than when considering the transient dynamics (Fig. 4.8). The risk of reduced NPV processors were willing to accept determined where potentially beneficial conditions exist, as lower probability of reduced NPV required lower coho salmon escapement goals, stronger predation effects, lower variable costs, or greater wholesale profit-per-kg of sockeye salmon than would be required given the median predicted values (Fig. 4.9). For example, at a given coho salmon escapement goal, predation

effect, and variable cost, processors would need to increase their wholesale profit-per-kg by approximately \$0.45 to have 10% chance of reduced NPV relative to a 50% chance of reduced NPV.

Discussion

We demonstrate how selective harvest in a predator-prey system can limit the overall profitability of a multi-species fishery, but also that transition dynamics and stakeholder-specific economic constraints ultimately limit the overall economic performance. By implementing a directed coho salmon fishery to alleviate predation pressure on valuable sockeye salmon stocks, harvesters are predicted to realize economic benefits under any scenario in which predation has a negative effect on sockeye productivity. Additionally, we demonstrate the importance of considering multiple stakeholders when considering changing harvest strategies in fisheries, as the processor is much more limited in its ability to realize economic benefits. Processors have higher variable costs than fishers, and due to the low market value of coho salmon, require substantial increases in sockeye salmon productivity to offset the additional cost of extending their operating season to purchase coho salmon. Thus, the processor decision of whether or not to buy into the alternative harvest strategy would likely be the step in which a decision to maintain status quo harvesting strategies is made.

Bioeconomic analyses of fisheries management strategies have historically focused primarily on the economics of harvesters (Clark 2006; *but see* Clark & Munro 1980; Weninger 1999). Had we only considered the economics of the harvesting sector, the results would have suggested that a targeted coho salmon harvest would benefit the fishery under any scenario in which coho predation negatively affects recruitment of sockeye salmon. Our estimates of benefits accrued to fishers may be conservative, as fewer boats than estimated may be able to

harvest enough coho salmon to reduce predation pressure. We developed our effort relationship from sockeye salmon harvest data, when more fishers than would be strictly necessary to harvest the fish are operating (Knapp 2008; Deacon, Parker & Costello 2013). Reducing the number of boats fishing each day during the coho salmon fishery would reduce the costs to fishers. As the Chignik salmon fishery is a terminal fishery, a small number of boats could harvest the vast majority of the coho salmon run by fishing at the mouth of the river (Knapp 2008). If sufficiently few boats could harvest coho salmon at a high enough exploitation rate to reach the alternative escapement goals, fishers could profit even without subsequent increases in sockeye salmon productivity (Deacon, Parker & Costello 2008; Knapp 2008; Deacon, Parker & Costello 2013).

Harvesting and processing sectors have distinct constraints and incentives in commercial fisheries (e.g., Clark & Munro 1980; Weninger 1999). In our simulations, while fishers are likely to profit from an alternative harvesting strategy if coho salmon predation does reduce sockeye salmon productivity, the processor has more complex responses. Processor profitability depends on how much profit the processors make per unit of sockeye salmon sold, daily operational costs, strength of the predation effect on sockeye salmon and the coho salmon escapement goal. Due to the late seasonal arrival of coho salmon to the fishery at Chignik, processing fish from a directed coho salmon fishery would require the processor to pay daily operational and maintenance costs for an additional month beyond the harvest current scenario, while processing low volumes of low value fish. Additional profit gained from eventual increases in sockeye salmon production must outweigh these losses from processing coho salmon in order for the processor to benefit from directly targeting coho salmon. If the processor does not anticipate benefitting from continuing operations to process coho salmon, fishermen would not be able to sell their catch. Therefore, both processors and harvesters would need to anticipate a benefit for any alternative

harvest strategy to be attempted. Further, expected equilibrium benefits suggest that alternative harvest strategies would benefit processors under a broader range of scenarios than when accounting for transient dynamics with net present value. When stakeholders are likely to sacrifice benefits in the short term, it is critical to consider the influence of short-term dynamics on the overall value of potential alternative management strategies (Clark 1973; Smith *et al.* 2010).

Much of the uncertainty in whether a directed coho salmon fishery will increase the value of the overall fishery derives from uncertainty about the strength of the relationship between coho salmon abundance in the watershed and sockeye salmon productivity (Walsworth & Schindler *unpublished data*). Fishers exploit the abundance of sockeye salmon that have survived multiple sources of mortality, of which predation from coho salmon is among the earliest. If there is a subsequent, stronger source of mortality, or if sockeye salmon survival is strongly density-dependent, reducing coho salmon predation pressure on sockeye salmon fry may have little noticeable effect sockeye salmon recruitment to the fishery. Obtaining accurate estimates of the coho salmon predation effect is difficult in natural populations due to stochastic processes effecting recruitment and observation errors in coho salmon escapement masking the true effects of predation (Oken & Essington 2015; Walsworth & Schindler *unpublished data*). Reducing this uncertainty requires long-term, accurate data collection, which is expensive to fisheries managers. From a societal stakeholder perspective, it would be important to consider the benefits to the fishery from a better characterization of predation effects relative to the increased management and monitoring costs required to obtain the estimate. This study could be extended to account for the costs of managing the extended duration of commercial fishing in Chignik.

Economic analyses of predator-prey fisheries often find that if the prey species is more valuable than the predator, the optimal management strategy for the harvesting sector is to eradicate the predator, releasing prey species from top-down control (Clark 2010). While such strategies would be legally and politically impossible to implement, strategies in which predators are harvested to reduced abundance may be more tenable for stakeholders. Watershed stakeholders could be included in the analysis by assuming an increase in the marginal value of coho escapement as coho escapement decreases. When coho escapement is low, the marginal value of each coho salmon to watershed stakeholders value is higher than when coho salmon escapement is high. While beyond the scope of this study, were a directed coho salmon fishery to be implemented, it would be beneficial to incorporate watershed stakeholders when determining the coho salmon escapement goal (e.g., Levi *et al.* 2012).

While an important first step in discerning the potential value of alternative harvest strategies in the Chignik salmon fishery, this study has several limitations. The importance of the transient dynamics that make the short-term losses outweigh long-term gains depends on the discount rate chosen (Brown, Abdullah & Mumby 2015). We assumed a discount rate of 5% for both fishers and processors, a value within the range commonly used in the fisheries literature. Fishers are often thought to use higher discount rates than processing firms, given lower capital availability to weather poor fishery performance in the short-term. A higher discount rate would reduce the benefit realized by fishers from switching to a directed coho salmon harvest. As such, fewer economic and ecological scenarios would be beneficial to fishers if a higher discount rate were used. Additionally, fish processors are often limited by their capacity to process fish during peaks of runs (Hilborn 2006). In our model we assumed unlimited processing capacity, and that processing costs were constant. Limiting processing capacity in our model could reduce the

benefit realized by processors from larger sockeye returns. However, if processors expected additional sockeye salmon to be available, they could invest in greater processing capacity, relaxing this constraint.

As stakeholders in the Chignik area consider how to ensure the sustainability of their communities, they will need to consider the drivers and constraints on different stakeholder groups. The approach taken in this study allows multiple stakeholders to consider their individual costs and revenues to determine whether it is worth changing harvest strategies to potentially increase profits. Additionally, stakeholders can determine which variables they can influence through innovation or behavioral changes to make the fishery more valuable. In the presence of ecological uncertainty, it may be more beneficial for all stakeholders to work to improve the value of their product or reduce the costs of harvesting and processing than to attempt to increase the productivity of the exploited stocks. As management strategies for fisheries resources continue to move towards more ecosystem based approaches, it is critical to consider how management changes will affect behavior of multiple stakeholder groups. Such considerations can reveal unexpected outcomes before the onset of costly implementation procedures.

Table 4.3. Parameter values used in different simulation scenarios; coho salmon predation effect strength (β_c , units = $\ln(R_s/S_s)/C_z$), wholesale profit-per-kg of sockeye salmon (p_{sp} , US\$/kg), sockeye salmon ex-vessel value (p_{sf} , US\$/kg), processor base daily operation cost (b_p , US\$/day), fishers' daily operation cost (v_f , US\$/day), and coho salmon escapement goal (G_c , salmon). All combinations of parameters were simulated, resulting in 3125 unique scenarios.

Parameter	Value
β_c	(-0.2, -0.15, -0.1, -0.05, 0)
p_{sp}	(0.44, 0.88, 1.32, 1.76, 2.20)
p_{sf}	(1.76, 2.31, 2.87, 3.42, 3.97)
b_p	(5000, 15000, 25000, 35000, 45000)
v_f	(200, 400, 600, 800, 1000)
G_c	(5000, 10000, 15000, 20000, 25000)

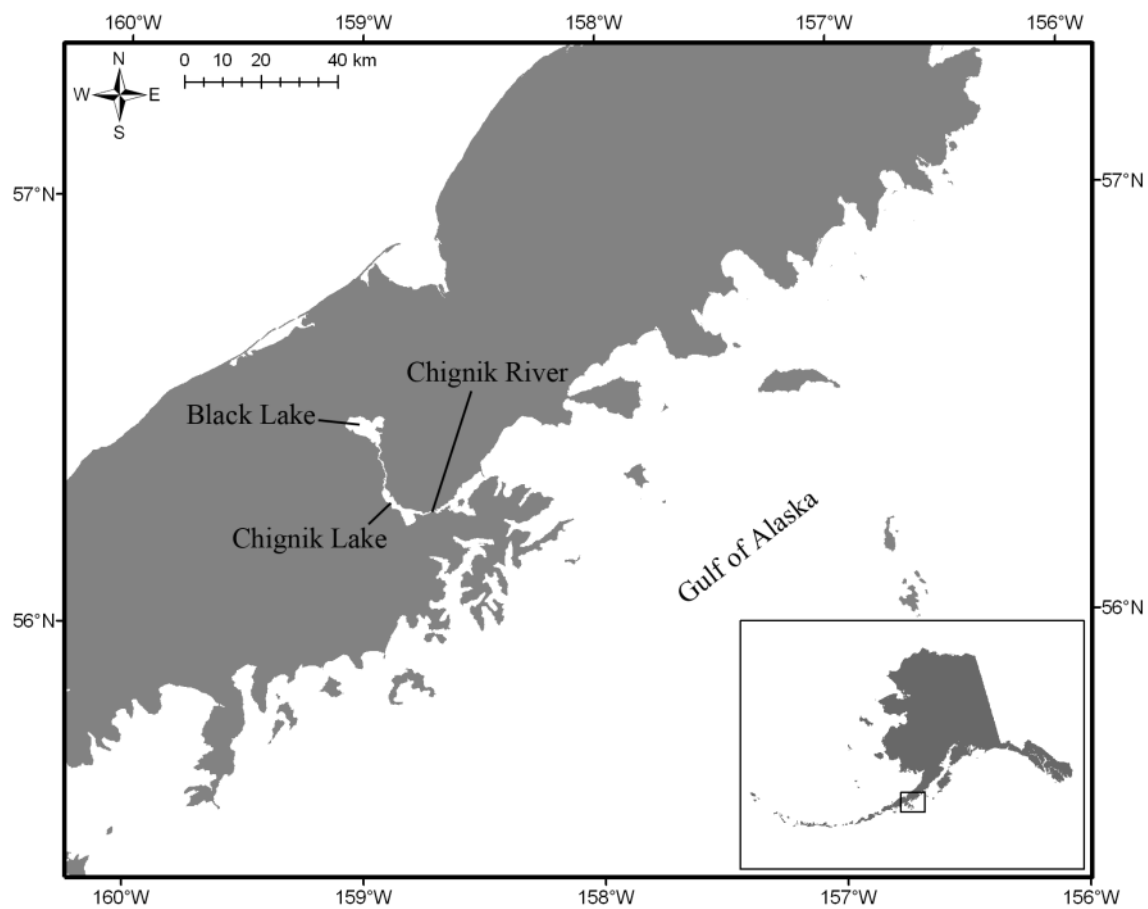


Figure 4.1. Map of the Chignik Management Area on the Alaska Peninsula. The Chignik River and the two sockeye salmon rearing lakes (Black and Chignik Lakes) are labeled.

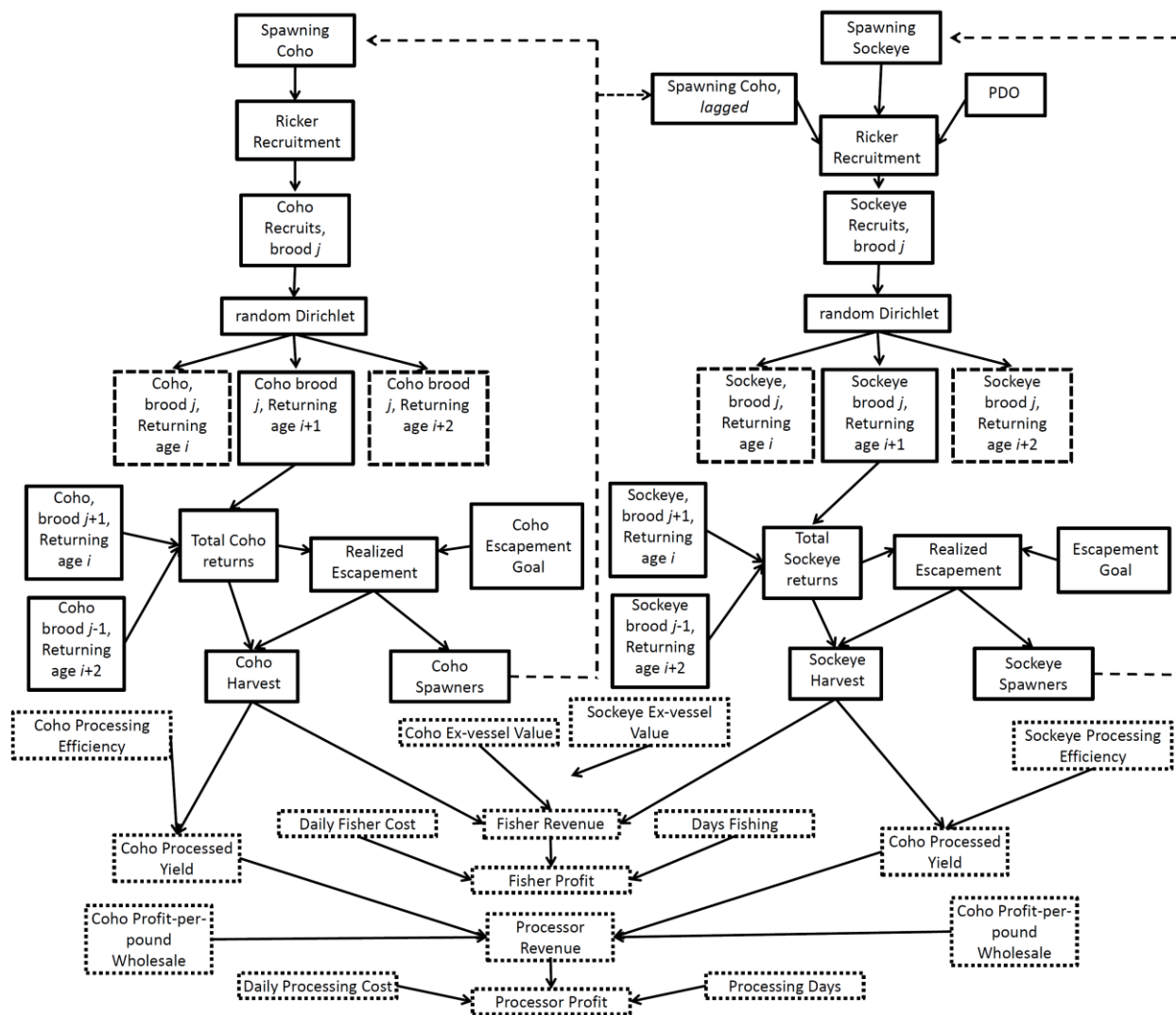


Figure 4.2. Conceptual diagram of the modeling approach taken in this study

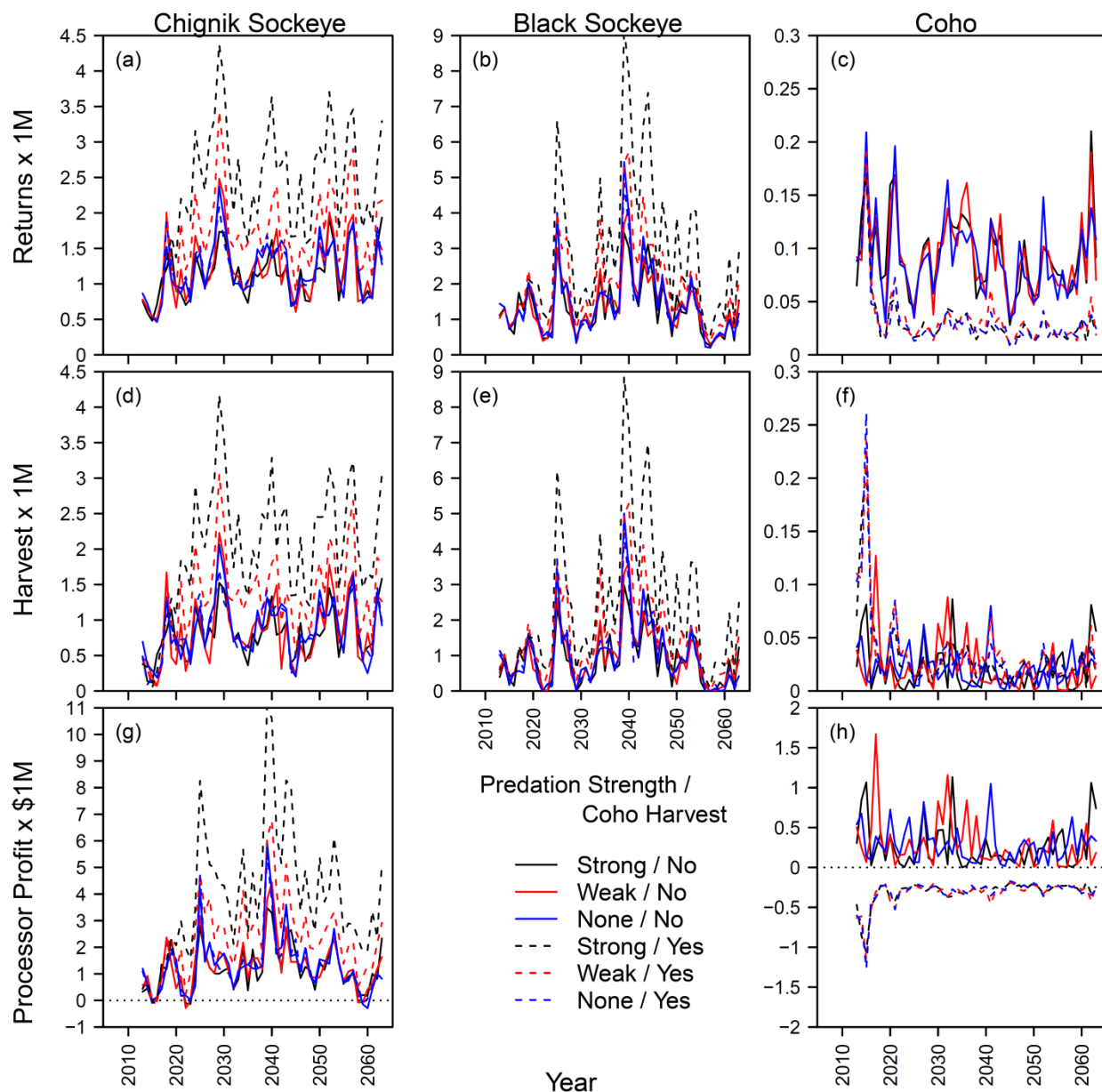


Figure 4.3. Example salmon return (a,b,c), harvest (d,e,f), and processor profit (g,h) trajectories from fishery simulation models for Black Lake sockeye salmon (a,d,g), Chignik Lake sockeye salmon (b,e,g), and coho salmon (c,f,h). Each of the simulations used to generate these trajectories had $b_p = 10,000$, processor profit per kg sockeye sold $p_{sp} = 0.44$, and a coho salmon escapement goal $G_c = 5000$ when coho salmon were directly targeted. Trajectories from six scenarios are presented in each panel, with strong, moderate, or no effect of coho salmon on sockeye salmon productivity, and either directed coho salmon harvest or only incidental coho salmon harvest. Line labels are presented as ‘predation strength scenario / directed coho salmon

harvest scenario' (e.g., the solid blue line labeled 'None / No' represents a scenario with no effect of coho salmon predation on sockeye salmon productivity and no directed coho salmon fishery).

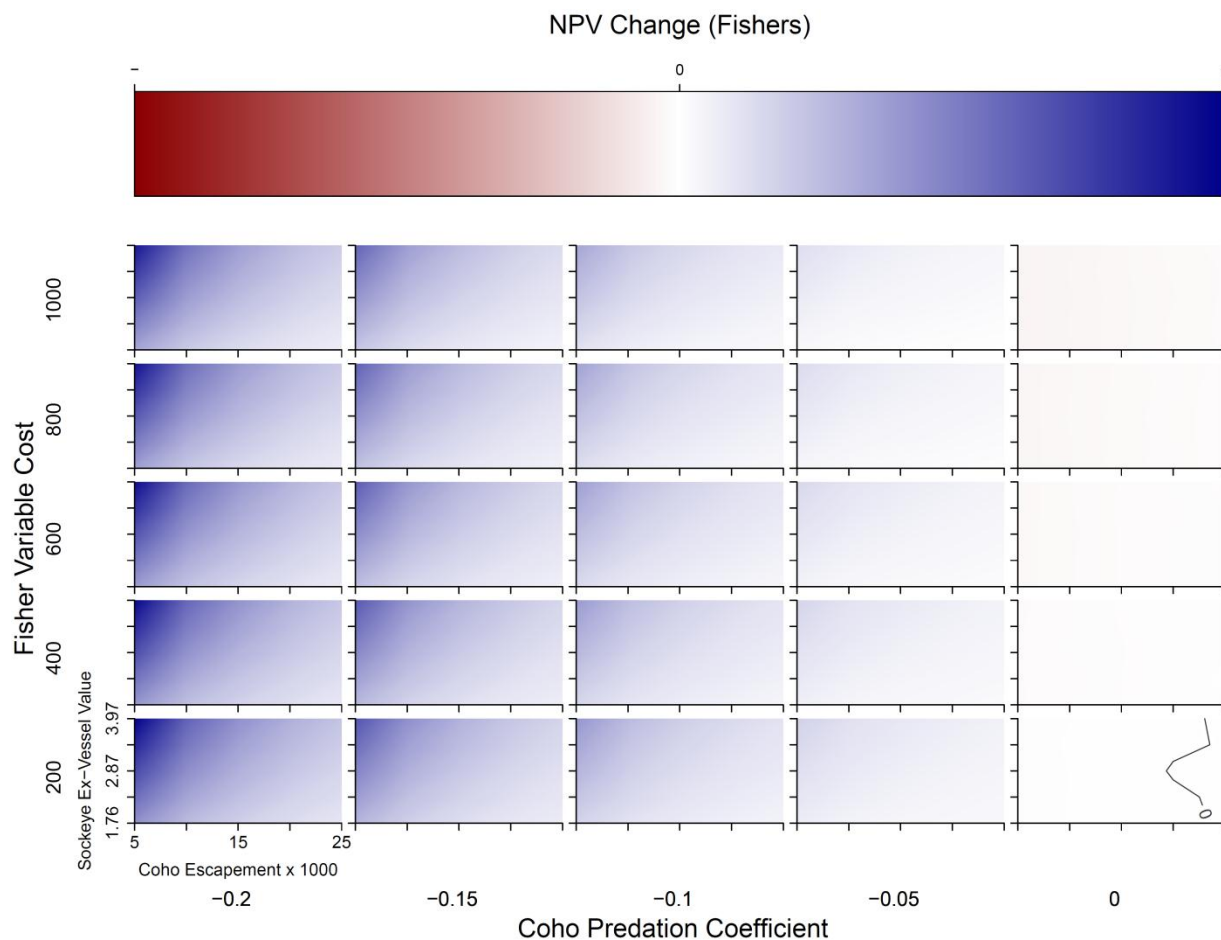


Figure 4.4. Median relative change in net present value to fishers between the current harvesting scenario and alternative scenarios with directed coho salmon fishing. Red values indicate conditions in which directly targeting coho salmon would result in lower NPV for fishers, blue shades indicate conditions in which fishers would expect higher NPV from directly targeting coho salmon, and white areas indicate no change from current. Contour line denotes zero difference between fishery value under current harvest strategies and directed coho harvesting.

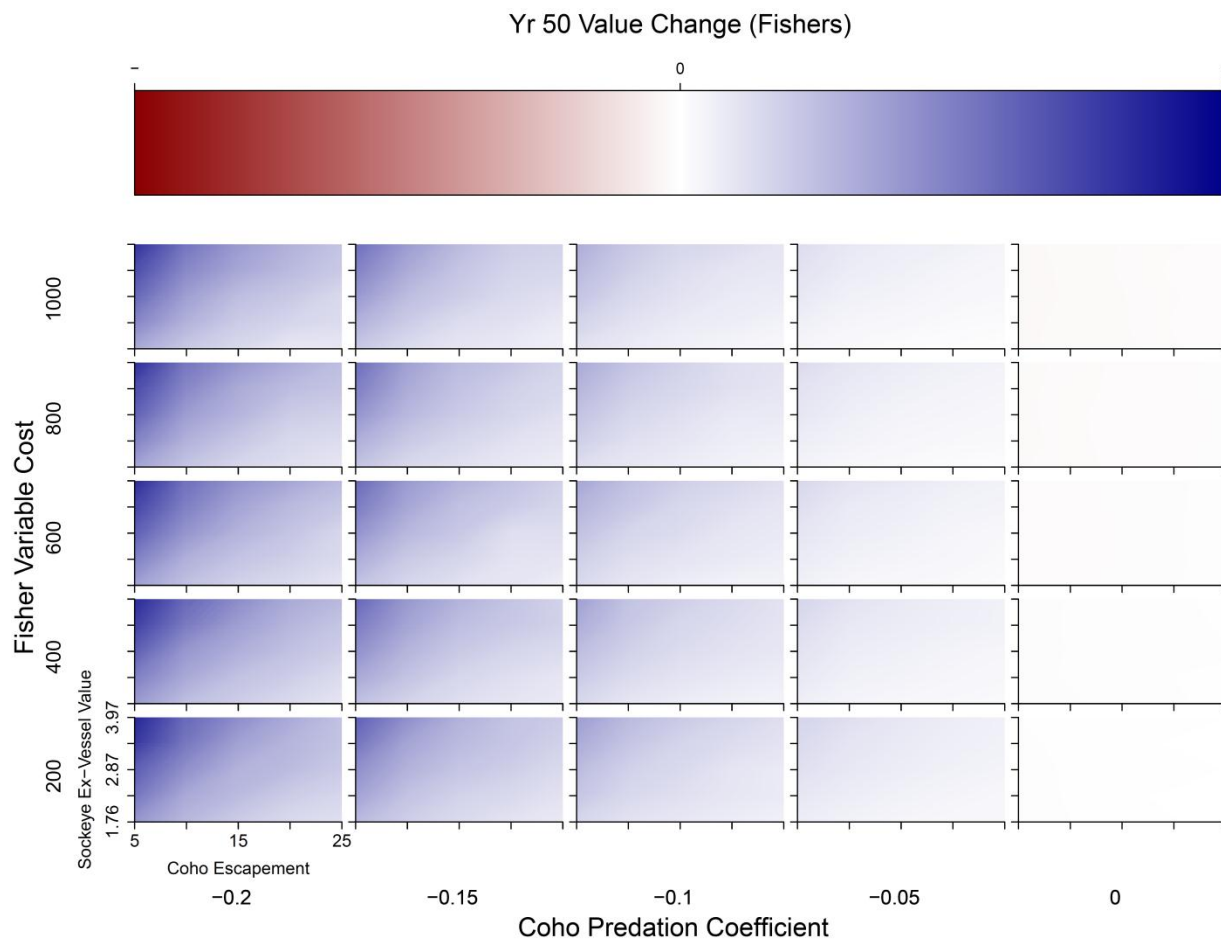


Figure 4.5. Change in value at year 50 between current harvest strategy and alternative harvest strategies for fishers. Red values indicate conditions in which directly targeting coho salmon would result in lower value at year 50 for fishers, blue shades indicate conditions in which fishers would expect higher value at year 50 from directly targeting coho salmon, and white areas indicate no change in value at year 50 from the current strategy. Contour line denotes zero difference between fishery value under current harvest strategies and directed coho harvesting.

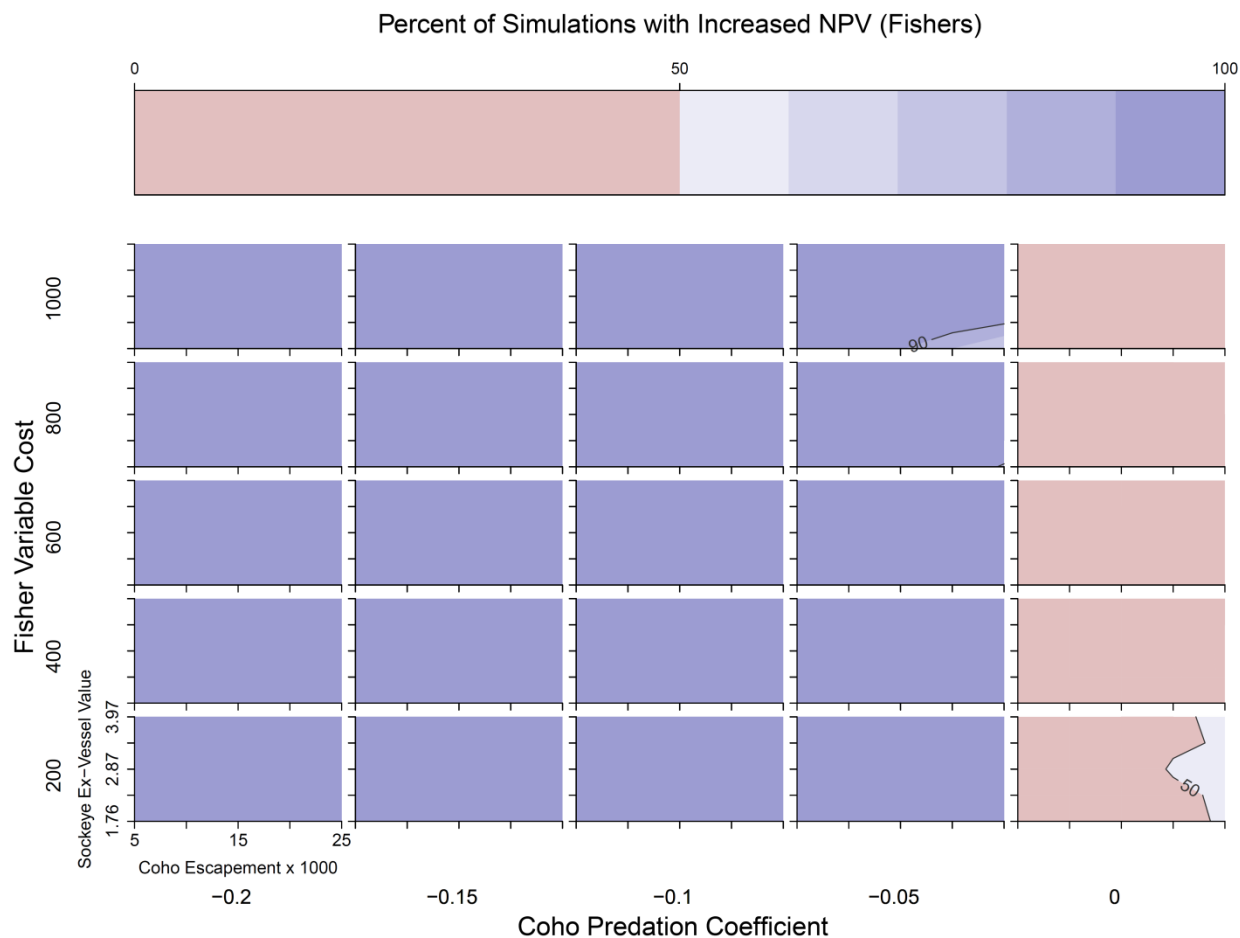


Figure 4.6. Percent of simulations in which fishers would experience an increase in NPV with a harvesting strategy directly targeting coho salmon relative to the current harvest strategy. Red shade indicates conditions in which less than half of simulations predict a benefit to fishers from targeting coho salmon. Blue shades indicate scenarios in which more than half of simulations predict targeting coho salmon would benefit fishers' NPV, with darker shades indicating progressively more certainty of benefit.

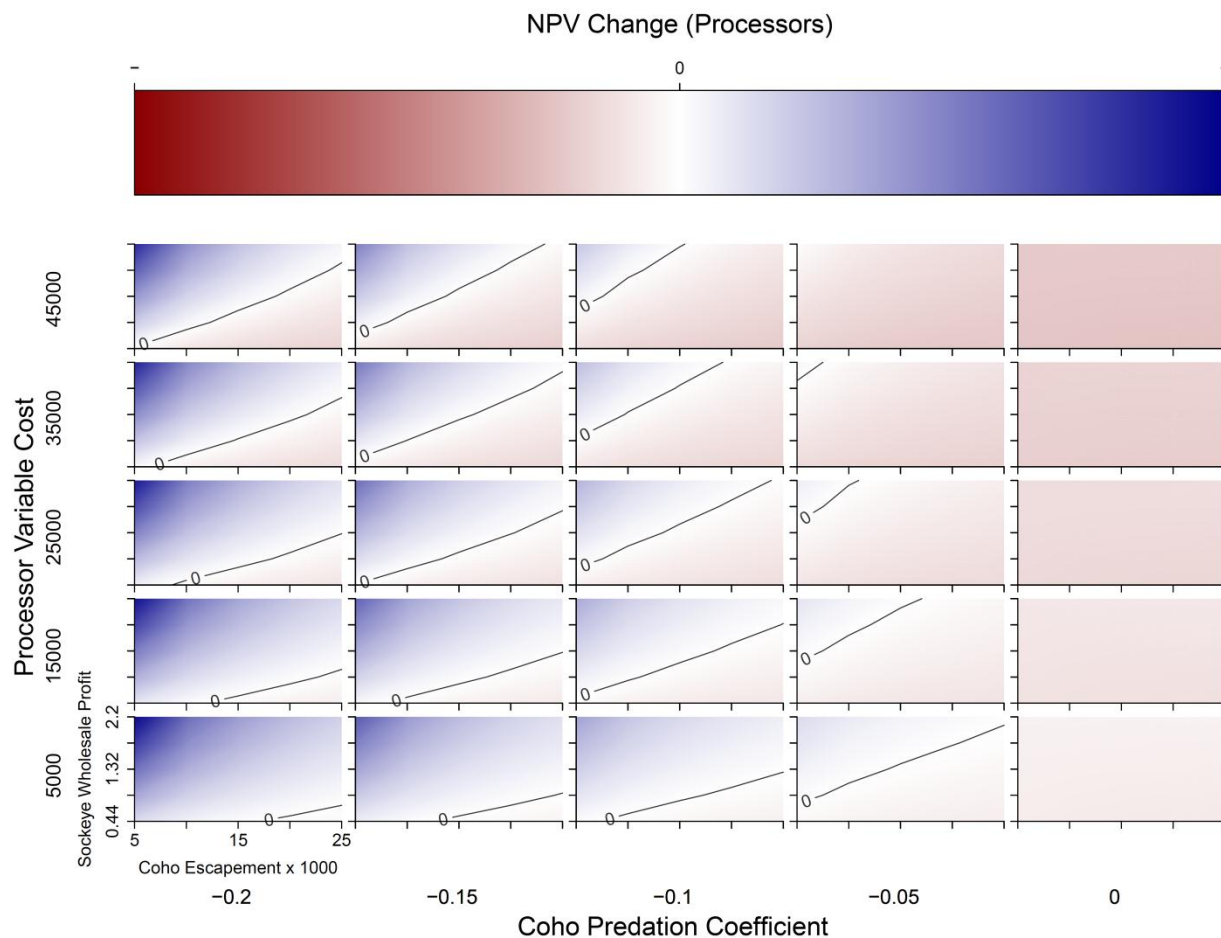


Figure 4.7. Median simulated relative change in net present value to processors between the current harvesting scenario and alternative harvesting scenarios with directed coho salmon fishing. Red values indicate conditions in which directly targeting coho salmon would result in lower NPV for fishers, blue shades indicate conditions in which fishers would expect higher NPV from directly targeting coho salmon, and white areas indicate no change from current. Contour line denotes zero difference between fishery value under current harvest strategies and directed coho harvesting.

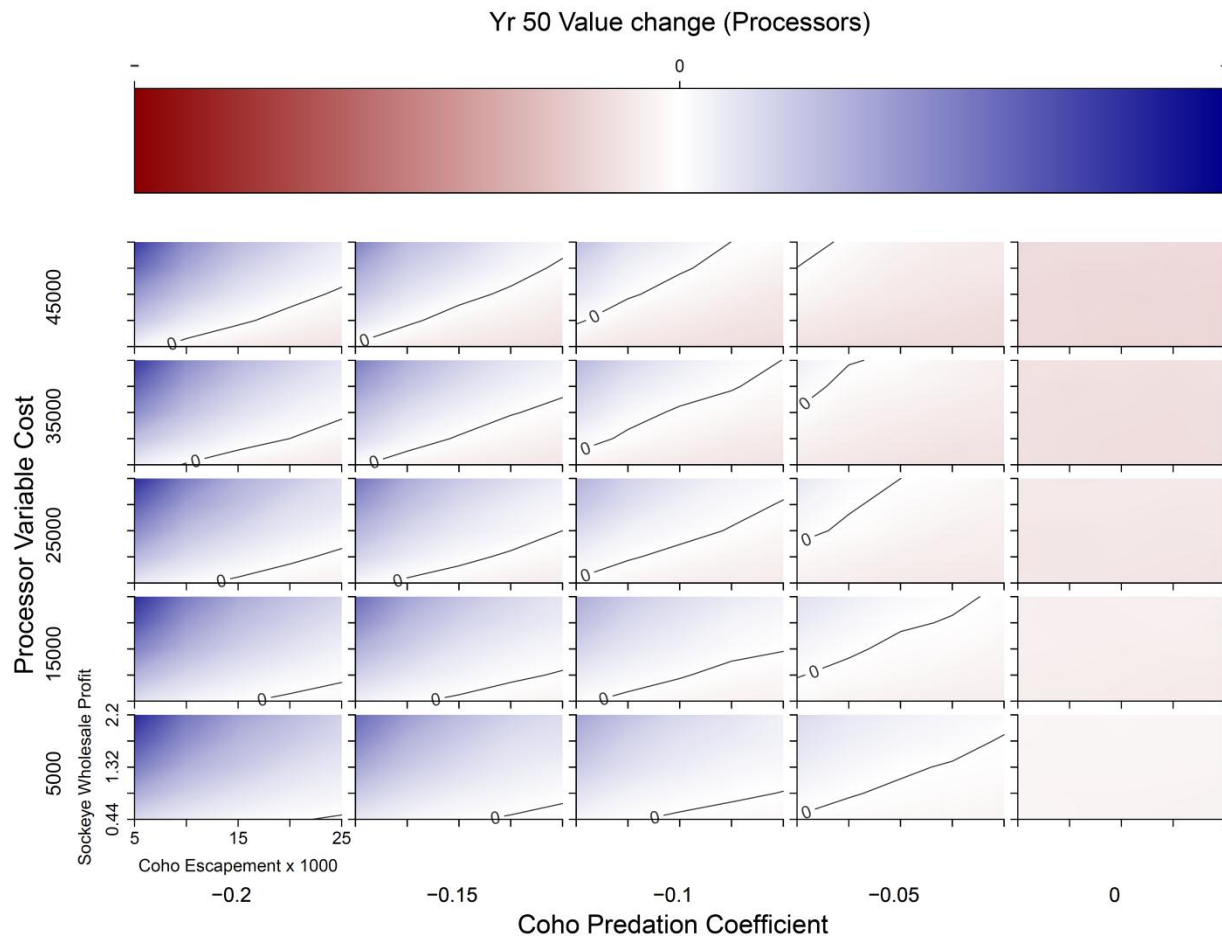


Figure 4.8. Change in value at year 50 between current harvest strategy and alternative harvest strategies for the processor. Red values indicate conditions in which directly targeting coho salmon would result in lower value at year 50 for the processor, blue shades indicate conditions in which processor would expect higher value at year 50 from directly targeting coho salmon, and white areas indicate no change in value at year 50 from the current strategy. Contour line denotes zero difference between fishery value under current harvest strategies and directed coho harvesting.

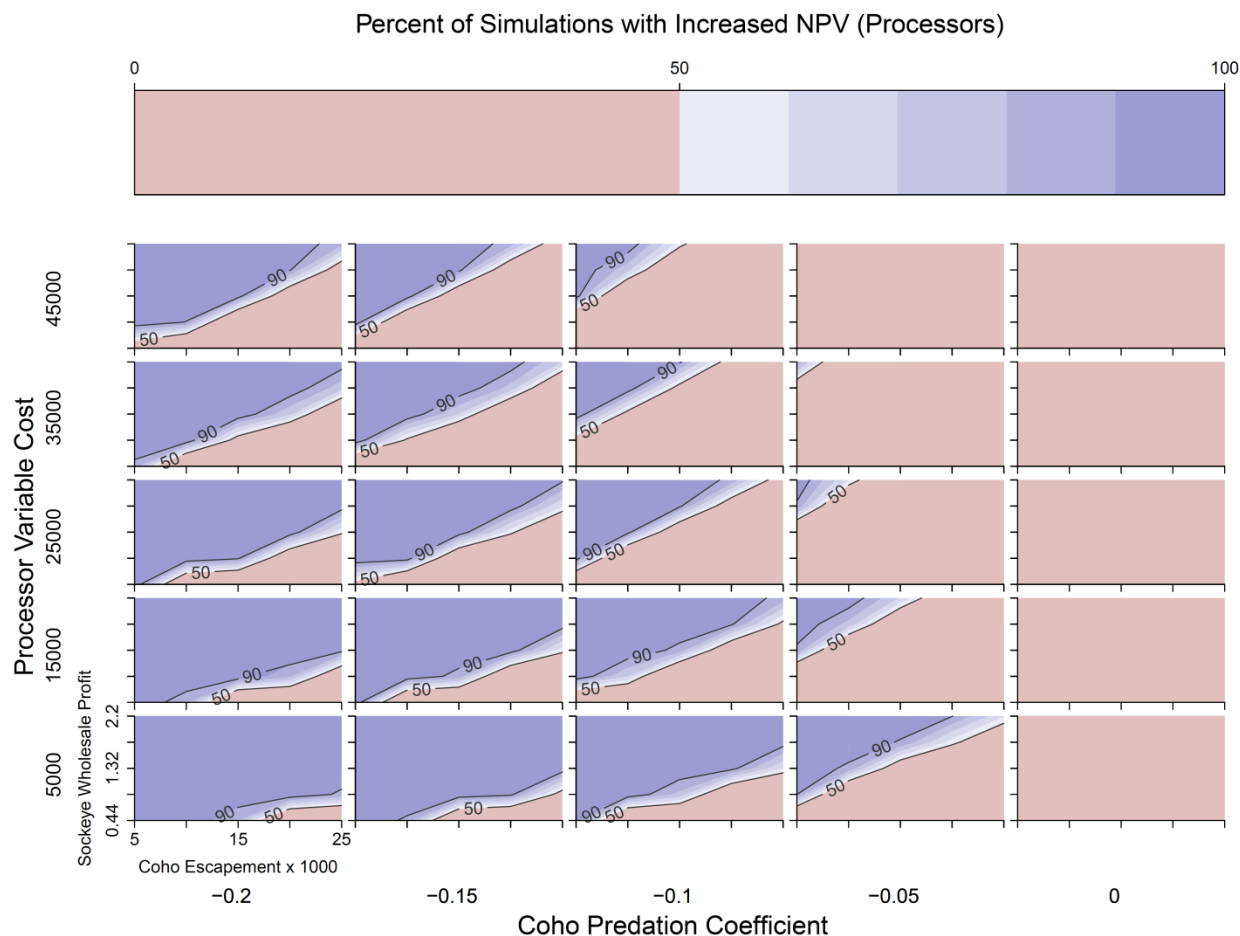


Figure 4.9. Percent of simulations in which processors would experience an increase in NPV with a harvesting strategy directly targeting coho salmon relative to the current harvest strategy. Red shade indicates conditions in which less than half of simulations predict a benefit to the processor from targeting coho salmon. Blue shades indicate scenarios in which more than half of simulations predict targeting coho salmon would benefit the processor's NPV, with darker shades indicating progressively more certainty of benefit.

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Chapter 2

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Chapter 3

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Chapter 4

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