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Authors

Jardine, SL
Sanchirico, JN

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Fishermen, markets, and population diversity

Sunny L. Jardine^{a,*}, James N. Sanchirico^{b,c}^a School of Marine Science and Policy, University of Delaware, Delaware, United States^b Department of Environmental Science and Policy, University of California, Davis, United States^c University Fellow, Resources for the Future, Washington DC, United States

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ABSTRACT

Fishing impacts biodiversity on multiple levels, potentially resulting in unintended feedbacks to the economic performance of the fishery over time. For example, targeting observable traits within a population can impact genetic diversity and targeting valuable species can impact biodiversity at the ecosystem level. The bioeconomic literature, however, has given little attention to the effect of fishing on population diversity, even though population diversity contributes to ecosystem services and estimates of population extinction rates are three orders of magnitude higher than species extinction rates. Here we develop a stochastic bioeconomic model that links the harvest of multiple salmon populations in a single commercial fishery to the trajectory of population diversity in a salmon stock complex. We parameterize our model with biological and economic data from the Copper River Chinook salmon fishery. We show that markets can incentivize the degradation of population diversity, reducing infra-marginal fishery rents, and increasing variability in economic returns. We also show that second-best management can conserve population diversity and improve welfare. Furthermore, depending on fishermen's time preferences, this management strategy is potentially self-financing.

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1. Introduction

Fishing is one type of anthropogenic selection impacting biodiversity on genetic, species, and ecosystem levels. Due to economic incentives and regulatory constraints, fishermen target specific genetic characteristics within fish populations (e.g. age at maturity), populations within species (e.g. spatial populations), and species within communities (e.g. top predators). At any of these levels, fishing can have unintended consequences for the ecological dynamics and the economic performance of the fishery over time.

The effects of fishing on genetic diversity within a fish species (reviewed in [Jørgensen et al., 2007](#)) and fishery biodiversity at the species level (e.g. [Pinnegar et al., 2000](#); [Mumby et al., 2008](#)) are well established. However, ecologists and economists have only recently given attention to the effects of fishing on biodiversity at the population level ([Luck et al., 2003](#)). Populations are groups of individuals from a single species with a high degree of genetic exchange within the group but limited genetic exchange between groups.

Understanding the welfare implications of altering population diversity within a fishery is important for a number of reasons. First, current estimates of population extinction rates are three orders of magnitude higher than species extinction

* Corresponding author.

E-mail addresses: jardine@udel.edu (S.L. Jardine), jsanchirico@ucdavis.edu (J.N. Sanchirico).

rates (Hughes et al., 1997). Second, population diversity (the existence and relative abundance of populations) provides valuable ecosystem services (Lomborg, 2001; Balmford et al., 2003; Luck et al., 2003). Finally, the unintended consequences of altering population diversity can have ripple effects throughout the ecosystem and therefore, maintenance of population diversity is important to consider when designing ecosystem-based management policies (Botsford et al., 1997; Pikitch et al., 2004).

To investigate the importance of population diversity, an emerging literature in ecology uses salmon as a prototype species (Hilborn et al., 2003; Schindler et al., 2010a; Moore et al., 2010; Carlson et al., 2011). Because salmon return to their natal spawning grounds to reproduce (a trait known as homing), a single river network can be comprised of hundreds of salmon populations that are reproductively isolated and evolve independently, adapting to local environmental conditions (Dittman and Quinn, 1996). One important finding in this literature is how independent population dynamics within a fishery can stabilize aggregate fishery returns across the complex through what is known as the “portfolio effect”. This effect is analogous to the role of asset diversity on the stability of financial portfolios.¹ As population diversity decreases, the portfolio (stock complex) becomes less diversified and potentially leads to increased variability in ecological returns over time, depending on the nature of the correlations between the populations. For example, Schindler et al. (2010b) find that recruitment to the Bristol Bay salmon complex was significantly less variable (coefficient of variation of 55%) than the recruitment of any one population (average coefficient of variation of 77%). While the ecology literature has demonstrated the existence and potential importance of the “portfolio” effect, little attention has been given to the underlying ecological, economic, and social mechanisms that could lead to a reduction in population diversity.

In contrast, a significant focus of the fisheries economics literature is on identifying the incentives that lead to changes in marine ecosystems and the associated economic returns. The literature, generally speaking, has shown how rule-of-capture incentives lead to rent dissipation often characterized as “too many boats chasing too few fish”. Recent research, however, is unraveling the rent dissipation process, revealing the multiple dimensions where it occurs, such as space, age or size, habitat, genetic diversity, etc. (see Abbott and Wilen, 2011; Smith, 2012; Reimer et al., 2014; Diekert, 2012).

Here, we identify how the rule-of-capture incentives are a potential driver of changes in population diversity and investigate whether there are feedbacks that affect the mean and variance of economic returns. At the same time, we consider how fish output markets, which can magnify the effects of ill-defined rights, can drive the within-season targeting behavior of fishermen. Specifically, we examine how seasonality in prices can create population-specific values that shift fishing effort toward higher-valued fish populations within a stock complex. The within-season shift in effort, in turn, can affect population diversity, and reduce economic returns to the fishery and, through the “portfolio” effect, reduce the stability of those returns.

The Copper River Chinook salmon fishery, in Cordova, Alaska, motivates our research questions and methodology. As with other salmon fisheries, the Copper River Chinook stock complex is comprised of multiple salmon populations (Templin et al., 2008) that have population-specific run times. Run timing is a life history trait that is genetically determined and corresponds to the time a stock migrates through the fishery on its way to its spawning grounds (Carlson and Seamons, 2008; Quinn et al., 1999; Stewart et al., 2002; Hodgson et al., 2006). Unique to the Copper River fishery, however, is that in the 1980s fishermen made investments in marketing and product quality improvements that resulted in a price premium for salmon coming from the region (Jardine et al., 2014). Additionally, the prices are highest in the beginning part of the season and subsequently fall as the season progresses (Knapp et al., 2007; Alaska Seafood, 2005). Therefore, populations migrating through the fishery early in the season are more valuable on the market.

The nature of prices for Copper River Chinook provides fishermen with incentives to target high-value early-run salmon. While the data do not exist to correlate higher prices with increased fishing effort in the early parts of the Chinook run, archival records discuss a shift in the distribution of fishing effort beginning in the 1980s just as these markets were being developed (Alaska, 2005). For example, in 1987, managers delayed the second opening of the fishery after fishermen took 20% of the total annual catch in the first opening. If left unchecked, we hypothesize that over time this selection pressure could alter population diversity with late returners making up a greater share of the Chinook stock complex. These changes in population diversity, therefore, reduce the ability of the fishermen to capture market rents from higher early-season prices, thereby reducing the returns on investments in product quality and marketing. Additionally, changes in population diversity can potentially increase the variability in economic returns to the fishery.

To examine the economics of population diversity, we couple a stochastic population dynamic model of multiple salmon populations, a model describing the seasonal effort distribution of heterogeneous fishermen, and a model describing the behavior of fishery managers. We parameterize our model with biological and economic data from the Copper River Chinook salmon fishery. With our coupled bioeconomic model, we analyze biodiversity outcomes and the mean and variance of fishery value under different market conditions including seasonal prices, where prices decline over the season due to exogenous consumer preferences, and endogenous prices that respond to fishery harvest levels. Both market scenarios are plausible depictions of the market dynamics in the Copper River fishery, which supplies some of the first wild salmon of the season when consumer demand is high (Knapp et al., 2007) and is also a branded product (Jardine et al., 2014). We examine the impacts of markets on population diversity by comparing outcomes to a baseline where prices are constant over the season.

¹ Schindler et al. (2010b) credit (Figge (2004) with establishing the term of the “portfolio” effect.

We also analyze the welfare implications of a second-best command and control policy known as in-season management (ISM), essentially fishery closures, used by Alaskan fishery managers since the 1980s to control the within-season distribution of fishing effort. Of the major wild salmon producers, only the U.S. widely practices in-season management (Sustainable, 2013). It is important to consider potential benefits from ISM as a second-best management tool, because it is a management strategy with precedent and the potential to preserve fishery biodiversity.

This paper makes several contributions to the literatures on fishery economics and population diversity. First, in contrast to the ecology literature, we examine economic drivers of changes in population diversity. Specifically, we demonstrate the role of market dynamics (i.e. price seasonality and endogeneity) in the degradation of population diversity. Increasing demand for high-quality food products and increasing niche marketing suggests that these types of market dynamics are more likely to occur in the coming years. Therefore, our analysis sheds light on the potential consequences of marketing fisheries products that are harvested in the absence of well-defined property rights.

Second, we consider populations with heterogeneous economic values. For example, price seasonality coupled with run-timing diversity implies that there are population-specific values for salmon. Previous ecology literature has focused on the value that population diversity has in stabilizing physical fishery yields (Hilborn et al., 2003; Moore et al., 2010; Schindler et al., 2010b; Carlson et al., 2011). However, when populations are valued differently on the market, population structure also has implications for the economic value of the resource.

Third, we consider how rule-of-capture incentives can lead to increased variability in the economic returns to a fish stock complex through impacts on population diversity and the “portfolio” effect. We ask what implications market dynamics have with regards to the “portfolio” effect, i.e. how do markets impact the relationship between population diversity and stability in economic returns to a fishery? While the “portfolio” effect does not necessarily have efficiency implications, risk averse fishermen or fisheries managers can benefit from the stabilizing effect of population diversity.²

We find that population diversity is degraded by fishing, that price seasonality and endogenous prices amplify biodiversity losses and, in general, fishery value declines over time. Counterintuitively, endogenous prices that respond to weekly catch totals are most likely to preserve fishery value, as the peak prices are able to shift later into the season tracking the shifting run-time distribution of the salmon complex. We also find that preserving population diversity can increase economic returns to the fishery over time. We show that the degree to which population diversity provides a variance-dampening service depends on the underlying economic structure in a fishery, i.e. the responsiveness of prices to harvest. Finally, we show that the second-best policy utilized by managers might be welfare-enhancing depending on the discount rate of fishermen, as costs are incurred initially but the persistence of early returners leads to future gains.

The article is organized as follows. We first describe the Copper River Chinook salmon fishery with special attention to the series of events starting with fishermen targeting and marketing Chinook. Next, we present a stochastic population dynamics model of multiple salmon populations within and across migratory cycles, a model of individual fishermen's behavior in a regulated limited-entry fishery, and a model of fishery management. We use our model to examine outcomes in biodiversity, fishery value, and the “portfolio” effect, under various market dynamics scenarios, as well as the political economy implications of preserving population diversity. We then discuss our findings and conclude.

2. Background

The history of the Copper River Chinook fishery is a classic example of how market forces, in the presence of ill-defined rights, can create incentives that undermine the ability of fishermen to collect a return on their investments. In this case, the negative feedbacks stem from incentives created by within-season market dynamics and the potential to degrade population diversity. Here we describe the evolution of the Copper River Chinook fishery in the 1980s and 1990s with special attention to market prices, run timing, and the distribution seasonal of fishing effort (see appendix Section 1 for more detail).

Prior to the 1980s, Chinook salmon, from the Copper River fishery and elsewhere, were not targeted by fishermen. Rather, Chinook were caught as bycatch in the commercial sockeye fishery. Most, if not all, of the salmon harvested in Alaska during this period went into markets for canned salmon (Knapp et al., 2007). During the 1980s, however, fresh and frozen salmon markets were developing in Alaska and Chinook salmon were valuable in those markets (Knapp et al., 2007), attracting added effort. Chinook salmon from the Copper River fishery were particularly valuable due to efforts of the Copper River Fisherman's Cooperative (CRFC) to improve product quality and brand salmon coming from the Copper River fishery (Jardine et al., 2014). Using a differences-in-differences analysis, Jardine et al. (2014) estimate that the CRFC increased average annual ex-vessel prices for Chinook salmon by approximately 38–57%. Additionally, Copper River Chinook prices vary dramatically over the course of the fishing season, being the highest when the season starts (see the appendix for bi-weekly price data). The pattern of Chinook salmon prices in the Copper River fishery is likely the result of seasonality in consumer demand and the timing of the run, as historically Copper River Chinook was the earliest wild salmon harvest on the market (Knapp et al., 2007), and successful marketing efforts (Knapp et al., 2007; Jardine et al., 2014).

² Other papers have examined stability in fishing profits from diversification in fishery participation (e.g. Kasperski and Holland, 2013; Sethi et al., 2014).

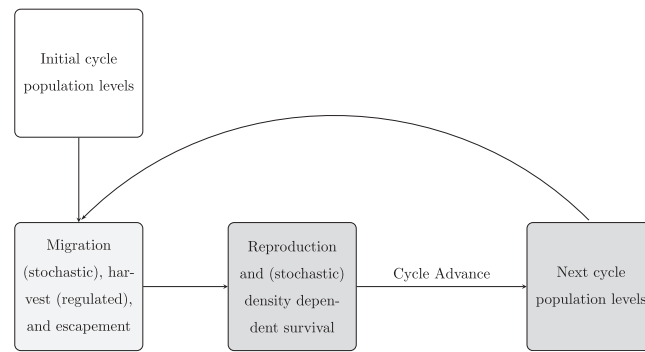


Fig. 1. Salmon model. The within-season model (timescale t) of commercial fishing effort and regulators are represented in light gray and the across-season model mapping cycle c escapement into cycle $c+1$ recruitment is represented in dark gray. The initial cycle population levels are an input and represented in white.

A limited entry program, adopted in Alaskan salmon fisheries in the 1970s, has kept the number of fishery permit holders constant over time at approximately 500 fishermen (Karpoff, 1984). However, changes in Chinook value led to changes in the total amount of effort devoted to targeting Chinook salmon (one of five species in the fishery) and the distribution of that effort over the season. In 1981, for the first time in the Copper River fishery, managers noticed fishermen targeting Chinook salmon by modifying fishing gear and fishing location choice. Managers also noticed that effort was concentrated at the beginning of the season. For example, in 1991, harvest in the first opening was 300% of projected harvest for the period while total harvest was 15% below what was anticipated, suggesting relatively greater fishing pressure on the early part of the Chinook run. In subsequent years, managers became increasingly concerned about the early portion of Chinook salmon run, but lacking historical baseline data, they were unable to assess whether there was a conservation issue (Alaska Board, 1996). In 1996 managers adopted the Copper River Chinook Salmon Management Plan to reduce total Chinook harvest by 5% and begin monitoring the stock complex in order to inform future management. In 1999, managers defined Chinook escapement goals and reduced the hours the fishery is open to fishing during the first weeks of the season, to protect the Chinook population structure.

While managers eventually adopted an ISM strategy (fishery closures) for Copper River Chinook, to limit fishing pressure on the early part of the Chinook run, the early-run escapement goals were based, in part, on escapement observations from a fishery that had already been impacted by market incentives. Therefore, it is possible that during the interim period from 1981 to 1999, incentives faced by fishermen may have led to actions that had lasting impacts on run timing and the economic returns to the Chinook stock complex. Whether fishing-induced degradation of population diversity could have happened on such a time scale, and whether or not the changes would have impacted the mean and variability in economic returns to the resource, is something we investigate with our bioeconomic model.

3. Bioeconomic model

In this section, we describe the stochastic bioeconomic model and the linkages between the biological model, the economic model, and the model of a fishery regulator (see Fig. 1). A unique feature of the bioeconomic model is the presence of two time scales (Grimsrud and Huffaker, 2006). Salmon cycles are denoted by c and span 6-year intervals, which represents the time between a spawning event of the parent population and when their offspring return to the river to spawn upstream (Alaska Department, 2013). Within each season, the availability of fish is measured on a bi-weekly time scale, represented by t , and determined by the population levels of each population as well as the populations' run-timing distributions. There are two sources of stochasticity in the model: stochasticity in salmon arrival times and stochasticity in recruitment.

3.1. Biological model

At 6 years of age, Chinook return from the open ocean to the Cooper River watershed to spawn in the stream from which they came.³ The characteristic is known as homing. The precision of salmon homing has been shown to be accurate at a fine spatial scale (Quinn et al., 1999).⁴

The spatial behavior of salmon creates distinct populations within a single species and single river system (Garant et al., 2000), where populations are groups of salmon with a high degree of genetic exchange within the group but limited genetic

³ The Copper River Chinook stock complex is dominated by salmon returning at 6 years of age although other stocks may return either earlier or later (Alaska Department, 2013).

⁴ Current science on the resolution of salmon homing abilities is limited by the ability of otolith methods to differentiate between salmon reared in streams within a close proximity (see Quinn et al., 1999).

exchange between groups. Therefore, salmon populations are defined by their spawning grounds. Additionally, each salmon population has a unique run-time distribution that is negatively correlated with the distance to the population's spawning grounds (Stewart et al., 2002; Hodgson et al., 2006). In other words, salmon populations with relatively long migration distances return to the fishery earlier than those populations that spawn closer to the mouth of the river and have relatively short migration distances.

We develop a biological model to describe multiple salmon populations that are characterized by differences in run timing. In the most general model there are S salmon populations, one for each tributary and spawning ground, with population numbers denoted by P^s where $s = 1, \dots, S$. However, the main purpose of this paper is to examine the impact of within-season market and effort dynamics on population diversity in the fishery, which can be accomplished in a two population model.⁵ In our two-population model, salmon from Population 1 are “early-run salmon”, which return in larger numbers towards the beginning of the season because their spawning grounds are farther from the mouth of the river. Population 2 salmon are “late-run salmon”.

We characterize the population run times with population-specific probability distribution functions, $\psi^1(t)$ and $\psi^2(t)$. Given the assumption on relative population run times, the corresponding cumulative distribution functions $\Psi^1(t)$ and $\Psi^2(t)$, satisfy $\Psi^1(t) \geq \Psi^2(t)$ for $\forall t$.

We model both within-season dynamics, where time steps (t) are bi-weekly openings, and across-season dynamics, where time steps (c) are the length of the salmon lifecycle or 6 years for Copper River Chinook. In the within-season model, salmon migrate into the commercial fishery, are subject to harvest, and survivors escape upstream to spawn. The across-season model maps escaping salmon in cycle c to recruits in cycle $c+1$.

3.1.1. Within-season model

Salmon in populations 1 and 2 are further distinguished by the period of arrival into the fishery τ . The number of salmon from population s that migrate into the fishery in period τ is denoted by m_τ^s and determined by population-specific distributions and population levels:

$$m_\tau^s = \psi^s(\tau)P^s. \tag{1}$$

Salmon that enter the fishery stay near the mouth of the river for a number of additional periods (ℓ) before escaping upstream to their spawning grounds. Salmon, therefore, are susceptible to fishing pressure from the time they enter the fishery to the time they head upstream. In our analysis, we set $\ell = 1$, which is true for Copper River salmon (Alaska, 2005), but our model is general and permits considering species with longer lag periods. Because of the lag time, in any period t the stock complex is comprised of salmon that have just arrived in the fishery and salmon that arrived in an earlier period ($t-1, \dots, t-\ell$), and remain near the mouth of the river.

The biological model of salmon migration is linked to an economic model through harvest and $H(t)$ is used to represent aggregate fishery harvest in period t . We assume the harvesting technology is non-selective and, therefore, the share of aggregate harvest in period t comprised of period- τ -arriving salmon from population s is equal to the fraction of period- τ -arriving salmon from population s in the total salmon stock complex $X(t)$. We use $\sigma_\tau^s(t)$ to denote the probability of harvesting a period- τ -arriving salmon from population s in each period t , where

$$\sigma_\tau^s(t) = \begin{cases} \frac{m_\tau^s}{X(t)}, & \text{if } t = \tau \\ \frac{1}{X(t)} \left[m_\tau^s - \sum_{k=\tau}^{t-1} \sigma_\tau^s(k)H(k) \right] & \text{if } (\tau < t \leq \tau + \ell) \\ 0 & \text{Otherwise.} \end{cases} \tag{2}$$

Escapement occurs at the end of each time period, implying total escapement in period t is equal to the number of salmon that entered in period $t-\ell$ that survived harvest by the commercial fishery as follows:

$$E(t) = \sum_s E^s(t) = \sum_s \left\{ m_{t-\ell}^s - \left[\sum_{k=t-\ell}^t \sigma_{t-\ell}^s(k)H(k) \right] \right\}. \tag{3}$$

The within-cycle stock dynamics evolve according to the following difference equation:

$$X(t+1) = X(t) + M(t+1) - H(t) - E(t), \tag{4}$$

where the number of salmon in the stock complex in period $t+1$ is equal to the number of salmon in the stock complex in the previous period, $X(t)$, plus the total number of migrants into the fishery, $M(t+1) = \sum_s m_{t+1}^s$, less harvest, $H(t)$, and escapement, $E(t)$.

⁵ In response to a reviewer's comment, we also developed a three-population model. We find similar qualitative results and any differences between the two and three population models depend on the relative run timing of the third population. For example, with a third population that arrives relatively early in the season, it takes longer for the positive feedback from endogenous prices to dominate (see results section for more detail). Therefore, we choose to present results from the two-population model for expositional reasons.

3.1.2. Across-season model

In each cycle, we track escapement levels for each population, which describes the trajectory of population diversity and life-history diversity in the stock complex. To close the across-season model, we map the number of salmon from population s escaping in cycle c into the number of salmon from population s that will return in the next cycle, $c+1$, based on a population-specific density dependent stock-recruitment relationship:

$$P_{c+1}^s = R\left(\sum_t E_c^s(t), \epsilon_c^s\right), \quad (5)$$

where the R function is a Ricker equation [Ricker \(1954\)](#) and ϵ is a mean-zero normally distributed error term.

Density dependence is an important feature of our model. For example, with density dependence, increasing the harvest of early-run salmon will lead to increased productivity of early-run salmon, mitigating the decline of population diversity. Modeling density dependence for populations 1 and 2 separately follows scientific evidence of local-scale density dependence in salmon (e.g. [Einum and Nislow, 2005](#)).

3.2. Economic model

We model the behavior of fishermen operating in a limited-entry fishery, because limited entry programs were adopted in the 1970s for all Alaskan salmon fisheries ([Karpoff, 1984](#)). We assume that fishermen make a number of discrete-choice decisions on whether to fish in each period of the fishing season. Discrete choice models following [McFadden \(1973\)](#) have been used in numerous empirical studies of fishing choice decisions, ranging from fishery supply under uncertainty ([Bockstael and Opaluch, 1983](#)) to fishing location choice ([Smith and Wilen, 2003](#)). The models have also been used in analytical fisheries economics research (e.g. [Smith et al., 2010](#)). Following the previous literature, we assume that fishermen are myopic and in our particular setting, we also assume that fishermen do not consider the externalities associated with degrading population diversity.

We index fishermen by $i \in \{1, \dots, N\}$ with entry capped at N permit holders. There is also a limited number of choice occasions, within a given fishing season, denoted by $t \in \{0, \dots, T\}$, where T is the maximum season length.⁶ In each period of the season (t) fishermen make a discrete choice on whether to participate in the fishery ($j=1$) or to earn an opportunity-cost wage outside of the fishery ($j=0$).

Profits from fishing are comprised of an individual-specific and time varying revenue function $p(t)q_iX(t)$ and a common cost of effort γ . Fishermen in the model are heterogeneous and the heterogeneity is captured in their catchability coefficients q_i . We assume that the q_i s follow a uniform distribution on the interval $[a, b]$. The non-fishing alternative yields value v which represents the opportunity cost of participating in the fishery.

$$\pi_{ji}(t) = \begin{cases} p(t)q_iX(t) - \gamma & \text{if } j = 1 \\ v & \text{if } j = 0. \end{cases} \quad (6)$$

In each period of the season, fishermen will select the action that offers the highest utility, i.e. they will enter the fishery when rents are positive, or $p(t)q_iX(t) - \gamma > v$. We assume that rents are dissipated in each t due to ill-defined property rights and the resulting competition among fishermen for the fish available at that time. For example, in any given period, the fishing area near the mouth of the river contains newly arriving fish and fish that arrived in the prior period. The overlapping arrivals creates a dynamic production externality where too much fishing pressure in one period can affect the available stock in the next period.

The rent dissipation process, in each period and season, is captured by fishermen entering into the fishery in order from most skilled (high q_i) to least skilled (low q_i) until rents are dissipated and there is no incentive for entry. With this assumption, in each t , aggregate effort and therefore aggregate harvest, $H(t)$, can be determined.

Ex-vessel salmon prices can either be seasonal or endogenous to fishery harvest. Exogenous seasonal ex-vessel prices best describe a small fishery with an undifferentiated product and can result from seasonality in consumer demand (e.g. [Wessells and Wilen, 1993, 1994](#)). For example, the Copper River fishery has opened each year in mid-May and historically it was the first North American wild salmon available on the market ([Knapp et al., 2007](#)). [Knapp et al. \(2007\)](#) note that prices fall as the season progresses and more Alaskan salmon is available on the market.

Endogenous prices, on the other hand, best describe a fishery with a differentiated product facing a downward-sloping demand curve. While the majority of salmon fisheries face exogenous seasonal prices (or constant prices), Copper River salmon is a branded product ([Jardine et al., 2014](#)), implying the possibility that prices are endogenous to the quantity of fishery harvest. This is illustrated by the fact that, to this day, Copper River salmon are still described as the first wild salmon on the market even though salmon harvested from the Alaskan Taku and Stikine rivers and some Washington fisheries are also available in May. The misconception is likely due to a long marketing campaign and media attention, which has focused on the beginning part of the Copper River run ([Knapp et al., 2007](#)). In what follows we model both market scenarios

⁶ Although the bioeconomic model describes outcomes across salmon reproduction cycles (denoted by c) the cycle is irrelevant to the fishermen's decisions because, in the model, fishermen are not forward looking. This means decisions made in any c are described by the same maximization problem. Therefore we suppress salmon cycle notation in this section.

(seasonal and endogenous price paths) and compare the outcomes to those that result when prices are constant over the season. We assume the following functional forms for seasonal and endogenous price paths:

$$\text{Seasonal: } p(t) = p(0)\exp(-\beta t), \quad (7)$$

and

$$\text{Endogenous: } p(t) = \left(\frac{\sum_{n=0}^t H(n)}{B} \right)^{\kappa}. \quad (8)$$

These forms provide a good fit to ex-vessel prices in the Copper River fishery (see appendix for more detail). Constant prices are set equal to the mean of those in Eq. (7).

Our hypothesis is that seasonal and endogenous ex-vessel prices will unambiguously shift fishing effort in the direction of peak prices relative to a constant-price scenario. Because fishery rents ($p(t)q_iX(t) - \gamma - v$) are proportional to the size of the stock complex in the fishery, with constant prices, $\bar{p}q_i$ acts as a scalar and fishery rents peak in the same period as the number of salmon in the stock complex that are available to fishermen. With seasonal or endogenous prices, we do not find the same synchrony in run time and fishery rents.

3.3. Management model

In most salmon fisheries, especially in Alaska, fishery managers control escapement by adjusting the season length T , ensuring harvest does not exceed the total allowable catch (TAC) (North Pacific Fishery Management Council, 2012). The TAC in cycle c is the difference between the total stock size (variable from cycle to cycle) and a constant escapement goal. We assume that managers have perfect information over the total run size in each cycle before the season begins but that the TAC_c can only be imperfectly enforced because harvest cannot be perfectly controlled. In each period regulators open the fishery if cumulative harvest plus a buffer is less than the TAC_c and close the fishery otherwise. The buffer allows managers to close the fishery as harvest nears the TAC_c , preventing overharvest. Therefore, in each period managers are faced with a discrete choice of shutting the fishery down ($S=1$) or keeping it open ($S=0$), as follows:

$$S_c(t) = \begin{cases} 1 & \text{if } (\sum_{n=0}^{t-1} H_c(n)) + \text{buffer} \geq TAC_c \\ 0 & \text{Otherwise.} \end{cases} \quad (9)$$

4. Methods

Due to the complexity of our bioeconomic model, we explore the model using numerical simulations based on empirically derived parameters and we undertake sensitivity analyses to investigate the robustness of our findings.⁷ In what follows we present results under 3 market scenarios: (1) prices fall exogenously over the course of the season, (2) prices are a function of fishery harvest, and (3) prices are constant over the season.

Because effort and prices are simultaneously determined under endogenous prices, we solve the model for a Nash equilibrium where no individual fisherman can be made better off by changing their effort decision given the effort decisions of other fishermen. To obtain the solution, we undertake a number of steps: (i) pose an initial guess for the effort of each individual fisherman; (ii) calculate prices and individual profits at the initial guess; (iii) determine whether any individual is made better off by switching their effort decision; (iv) update the initial guess for fishermen that can be made better off; and (v) iterate over steps (i)–(iv) until no individual can be made better off.⁸

Our base-case results include changes in the fishery over a 60-year time period, or 10 cycles with up to 10 fishing openings in each cycle. We also present intermediate results that show outcomes by cycle. For example, outcomes from cycle 3 correspond to outcomes after 18 years.

We take several steps to calibrate our model, which are described in detail in the appendix and summarized here. First, we estimate price paths in market scenarios 1 and 2 (Eqs. (7) and (8)) and constant prices from ex-vessel price data from the 2003 to 2005 Copper River fishery (see appendix Section 4 for more detail).

Second, we estimate the population-specific run-time distributions (the $\psi^s(\tau)$ functions from Eq. 1) from data. Specifically, starting with data on the bi-weekly population composition of commercial harvest (from Seeb et al., 2009), we use a distribution fitting algorithm to select an exponential distribution and an extreme value distribution to represent early-run and late-run salmon run times, respectively. We then estimate the rate parameter for the exponential distribution and location and scale parameters for the extreme value distributions (see the appendix for more detail). Additionally, although salmon run timing is primarily determined by genetics, this life history trait also responds to changes in

⁷ The MATLAB code is available from the authors by request.

⁸ In some cases convergence requires including a margin of error. The largest margin of error is 20 fishermen or 4% of the fleet.

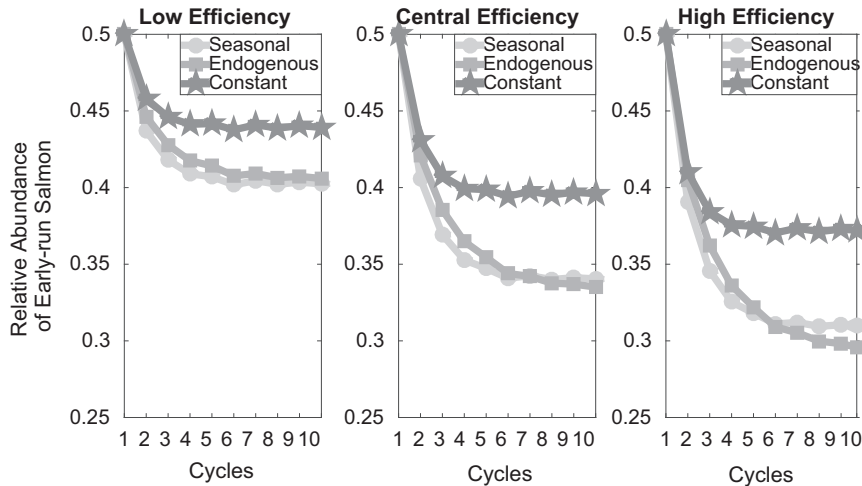


Fig. 2. Mean relative abundance of early-run salmon over 10 cycles (60 years) for low (left), central (middle), and high (right) fleet efficiency levels.

environmental conditions (e.g. a shift in the Pacific Decadal Oscillation) (Quinn, 2005). Therefore, to consider stochasticity in the run-time distributions, we assume that the rate parameter comes from a distribution that is centered around our parameter estimate and has a coefficient of variation of 0.5.

Third, we estimate parameters of the Ricker function (Eq. 5) from escapement and returns data in the Copper River Chinook salmon fishery. Additionally, we estimate the empirical error distribution in the Ricker stock-recruitment relationship and we use our estimated distribution to model stochasticity in returns (see appendix Sections (3–4)). Therefore, in each stochastic simulation we take an independent draw of the rate parameter for the early-run salmon run time distribution and independent draws of the Ricker error term for the population-specific Ricker equations. Because Ricker growth does not occur until after the first cycle, all first-cycle results are less variable than those in later cycles.

Finally, we present a sensitivity analysis over the assumed fleet efficiency levels, examining results under 3 different fleet efficiency levels: low, central, and high. We present the central fleet efficiency results as our main results. Although we lack data on actual fleet efficiency, we choose parameters to match the harvest patterns in the fishery with the central fleet efficiency assumption providing the best fit to data (see appendix Section 5).

5. Model results

Our analysis highlights how the interactions between markets, fishery characteristics, and environmental factors impact population diversity and life-history diversity in a salmon stock complex, the economic returns, and variability in those returns.

5.1. Population diversity

We examine changes in population diversity after 60 years of harvest, escapement, and recruitment. Fig. 2 shows the mean (from 10,000 stochastic simulations) relative abundance of early-run salmon in the stock complex across cycles.⁹ We assume an initial condition where all populations are equally sized, or that the relative abundance of early-run salmon is 0.5 in the first cycle.

We find that, regardless of the market scenario, the initial population structure changes over time (i.e. cycles), where there is a reduction in the relative abundance of early-run salmon. The implication is that, over cycles, there will be less early-run salmon in the stock complex and, therefore, less salmon arriving into the fishery in the beginning of the season. In other words, there is a shift in the aggregate run time of the stock complex.

The result is driven, in part, by the fact that fishery managers close the season as fleet-wide harvest approaches the TAC (predicted run size less a constant escapement goal), which effectively serves to protect late-run salmon. The result is similar to empirical findings by Quinn et al. (2007), who show evidence of shifting aggregate salmon run timing, in the Egegik and Ugashik districts of the Bristol Bay fishery, due to management policies.¹⁰

We also find, as hypothesized, that price seasonality and endogenous prices create population-specific values that lead to greater pressure on early-run salmon populations. The result holds for all fleet efficiency levels. For example, after 60 years,

⁹ While the other common measure of biodiversity is richness or a count (e.g. a count of populations), our focus is on relative abundance.

¹⁰ In these fisheries, however, managers do not open the fishery until the escapement goal has been met, favoring early-run populations (Quinn et al., 2007).

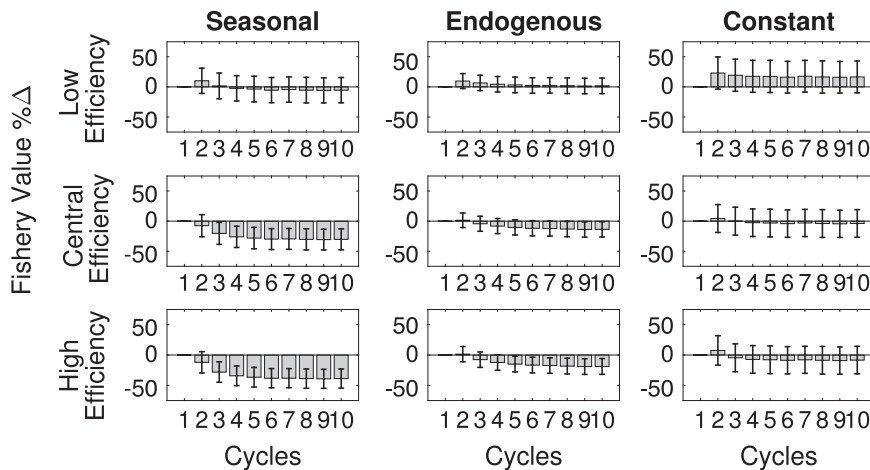


Fig. 3. Mean (bars) and standard deviation (lines) of the percentage change in fishery value from the initial cycle, by cycle, for low (top row), central (middle row), and high (bottom row) fleet efficiency levels and seasonal (left column), endogenous (middle column) and constant (right column) prices.

in our central fleet efficiency case, the relative abundance of the early-run population is 6% smaller when prices are seasonal rather than constant (see Fig. 2). Interestingly, the population-specific values lead to the greatest impacts on biodiversity (relative to constant prices) in the first 3 cycles, suggesting the possibility of fishing-induced degradation of population diversity in the Copper River Chinook fishery between 1981 and 1999.

Comparing different market scenarios, we find that eventually endogenous prices lead to the greatest changes in population diversity. Prices that are endogenous to aggregate harvest introduce both negative and positive feedbacks in the model and it is not clear *a priori* which type of feedback will dominate. Negative feedbacks arise from prices falling as too many early-run salmon are harvested, potentially leading to reduced levels of effort in the early part of the season. This reduction in effort can maintain population diversity. On the other hand, over cycles any decline in early run salmon population levels (which occurs in all market scenarios) restricts the ability of fishermen to supply salmon early in the season, driving prices up when they are endogenous and drawing even more effort into the fishery by making the last remaining early-run salmon even more valuable. Therefore, positive feedbacks can incentivize harvest even when individual early-season catch levels are low due to the declines in early-run salmon population levels.

The dynamics of these feedbacks can be seen in Fig. 2 (the feedback dynamics are explored further in appendix Section 7). For example, in our central efficiency case, in cycles 1–7, the negative feedbacks dominate when prices are endogenous. However, after the seventh cycle, the relative abundance of early-run salmon is lower when prices are endogenous, i.e. the positive feedbacks dominate. We find that eventually the positive feedback effect dominates in our setting, based on price elasticities estimated from data, although the result can vary in other settings.

Finally, we see that biodiversity losses are increasing in fleet efficiency. For example, after 60 years with seasonal prices the decline in the relative abundance of early-run salmon is roughly 16% at central fleet efficiency levels and about 19% in our high fleet efficiency case.

5.2. Fishery value

We showed that markets can degrade population diversity in a salmon stock complex. An important question is how these changes impact economic returns in the fishery (if at all). To explore this question, we compare the total inframarginal rents earned in the fishery across cycles under different market scenarios and for different fleet efficiency levels. Specifically, in our model, the marginal fisherman earns (approximately) zero rents while all inframarginal fishermen earn positive rents. Therefore, we define the fishery value as the total amount of inframarginal rents earned in the fishery, which is the sum of individual fishermen's profits in each cycle under the various scenarios.

In our central fleet efficiency case, the mean fishery value declines relative to the initial-cycle level under all market conditions (middle panel of Fig. 3).¹¹ Specifically, after 60 years the mean value falls by roughly 30% when prices are seasonal, roughly 14% when prices are endogenous, and about 4% when prices are constant. Even though endogenous prices lead to the greatest changes to biodiversity (Fig. 2), the resulting reduction in fishery value is less than when prices are seasonal (Fig. 3). Endogenous prices allow inframarginal rents to be maintained even when aggregate run timing in the fishery shifts later into the season over cycles. In other words, with changes in the aggregate run time, high prices follow. Therefore, we find that endogenous ex-vessel prices can attenuate losses in fishery value from the changing population diversity in the salmon stock complex (middle row of Fig. 3).

¹¹ While the escapement goal has not been selected optimally, based on our model, if fishing pressure was equal across the two populations, there would be a 4% increase in the number of salmon in the stock complex. Therefore, there is the ability for fishery value to grow over cycles.

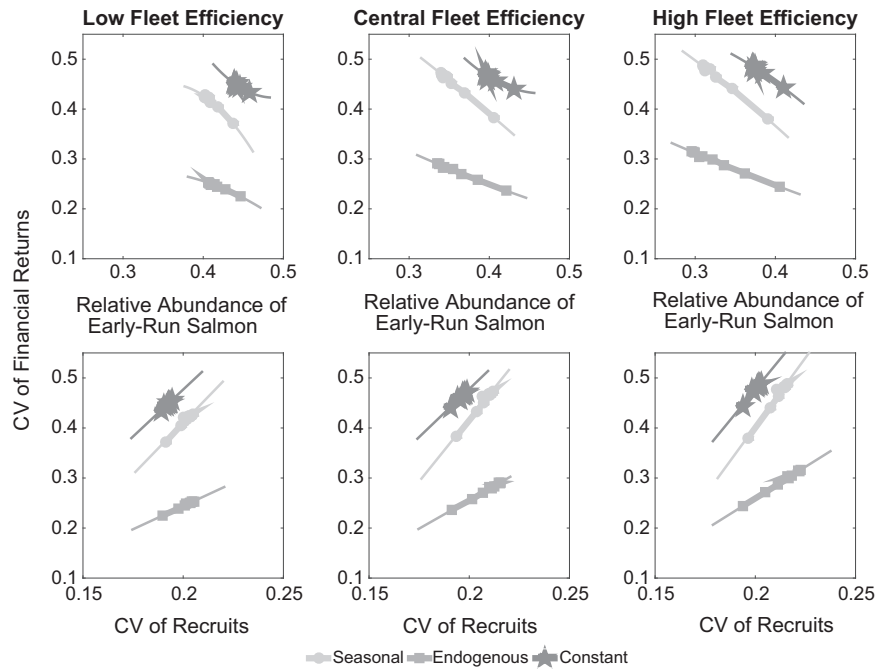


Fig. 4. Top panel: relative abundance of early-run salmon (population diversity) plotted against the coefficient of variation in financial returns to the fishery, by fleet efficiency and market scenario. Data are from cycles 2–10. Bottom panel: the coefficient of variation in total recruits to the stock complex (ecological stability) plotted against the coefficient of variation in financial returns to the fishery (economic stability), by fleet efficiency and market scenario. Data are from cycles 2–10.

5.3. The “Portfolio” effect

In this section, we explore the relationship between market incentives and the “portfolio” effect. First we examine the relationship between population diversity and economic returns to the fishery. Fig. 4 (top panel) plots the coefficient of variation in financial returns against the mean relative abundance of early-run salmon in cycles 2–10.¹² In each market scenario and fleet efficiency case, we find a reduction in the relative abundance of early-run salmon and an increase in the coefficient of variation of financial returns to the fishery. Initially constant prices display the greatest variability in financial returns. Over the years and salmon cycles, however, fishing drives a reduction in the early-run population size, the harvest of late-run salmon increases, and economic returns under seasonal prices become the most variable in the central and high fleet efficiency cases. On the other hand, we find surprisingly that endogenous prices result in the lowest variability in economic returns, due to increased price responsiveness and higher prices buffering the negative shocks to the early-run recruits.

Next we investigate the relationship between variability in recruits to the salmon stock complex and variability in economic returns. While current literature in ecology has focused on the relationship between population diversity and physical yield (Hilborn et al., 2003; Schindler et al., 2010a; Moore et al., 2010; Carlson et al., 2011), it is unlikely that there will be a one-to-one mapping between physical and economic yield. Fig. 4 (bottom panel) plots the coefficient of variation in financial returns (economic stability) against the coefficient of variation in recruits to the stock complex (ecological stability). We find that increasing variability in returns to the stock complex leads to the greatest impact on variability in economic returns when prices are seasonal (slope ≈ 5) and has the smallest impact on variability in economic returns when prices are endogenous (slope ≈ 2). The result suggests that the economic implications of traditional measures of the “portfolio” effect depend on market dynamics and the economic structure of the fishery.

5.4. Gains from ISM

In 1999 managers in the Copper River fishery adopted ISM for Chinook salmon to protect the early portion of the Chinook run by restricting fishing time in the beginning of the season with timed closures. In this section, we assess this second-best across two dimensions. First, we examine the willingness to pay (WTP) for ISM. Second, we explore the relationship between ISM and the “portfolio” effect. While the actual implementation of ISM in the Copper River fishery is somewhat

¹² Because each of the stochastic simulations starts with a constant number of salmon in both populations, the only variability in financial returns in cycle 1 are from stochasticity in the early-run salmon run time distribution. Therefore, plotting data from cycle 1 would convey a false level of stability associated with equally sized populations.

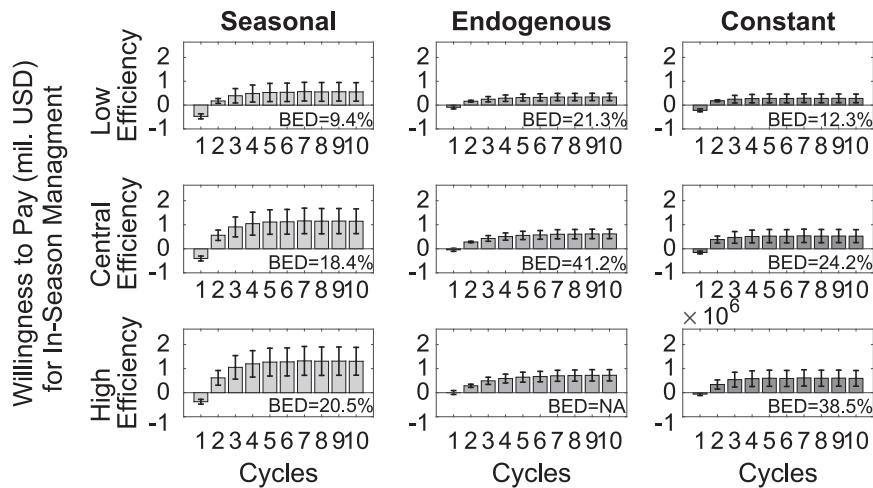


Fig. 5. Mean (bars) and standard deviation (lines) of willingness to pay for in-season management by cycle, for low (top row), central (middle row), and high (bottom row) fleet efficiency levels and seasonal (left column), endogenous (middle column), and constant (right column) prices. The break-even discount rate (BED) sets fishery NPV over 10 cycles (60 years) to zero.

complicated, we explore the simple case where the fishery is closed to fishing in the second period. Our simple model of ISM performs quite well in maintaining population diversity over cycles, e.g. in our central fleet efficiency case the relative abundance of early-run salmon changes by less than 4.5% after 60 years in all market scenarios compared to roughly a 20% reduction when ISM is not implemented.

We define the WTP for ISM as the difference in infra-marginal rents earned when ISM is implemented in the first cycle (and for every subsequent cycle) and when ISM is not implemented. When WTP is negative it means that closing the fishery in the second week reduces infra-marginal fishery rents. Our WTP assessment is similar to the approach taken by [Smith et al. \(2010\)](#) who evaluate the WTP for the creation of marine reserves.¹³

[Fig. 5](#) summarizes the results for different fleet efficiency levels and market scenarios. In almost every case the WTP for ISM is negative in the first cycle (the exception is when prices are endogenous and there is a high level of fleet efficiency). Fishermen are unable to harvest salmon in the second period and the restriction reduces infra-marginal rents. However, in each case the WTP becomes positive over cycles and, as expected, the WTP is greatest when prices are seasonal.

Under low fleet efficiency levels, there is a positive WTP for ISM over cycles, which implies that fishery value can increase (top panel of [Fig. 5](#)). Interestingly, the positive WTP occurs even though the fishery value is relatively constant across cycles (top panel of [Fig. 3](#)). In other words, even though the decrease in fishery value from reduced population diversity may be small, the losses may be substantial when compared to a scenario in which biodiversity is preserved. The results demonstrate how population diversity is another dimension where fishery rents can be dissipated, and that ISM can be effective in maintaining both population diversity and fishery value.

Because in most cases there are temporary losses in fishery value and the benefits occur in the future, whether ISM is a welfare-enhancing policy depends on fishermen's time preferences. For the relevant cases (when WTP switches from negative to positive) we calculate the discount rate that sets the 60-year fishery NPV to zero. We call this the "break even" discount rate or BED. For example, we find in our central case with seasonal prices that fishermen who discount future profits at 18.4% annually will be indifferent to ISM. All BEDs are recorded in [Fig. 5](#). A high BED implies that there is potentially more industry support for ISM, because fishermen with relatively higher discount rates still benefit from ISM. In other words, if fishermen discount future profits below the BED, then they benefit from ISM. Although in all cases our calculated BEDs are higher than the market interest rates (e.g. the interest rate on a 10-year US Treasury note), in many cases they are low compared to empirical estimates of fishermen's discount rates (in [Hannesson et al., 1996](#); [Asche, 2001](#); [Curtis, 2002](#)), which often exceed 30%, implying potential opposition to ISM.

In addition to increasing the mean annual value in the fishery over time, we find the protection of early-run salmon provided by ISM also maintains the "portfolio" effect. For example, in our central fleet efficiency case without ISM the coefficient of variation goes from 0.38 in cycle 2 to 0.47 in cycle 10 and with ISM the coefficient of variation goes from 0.35 in cycle 2 to 0.37 in cycle 10. Therefore, ISM can potentially stabilize the mean and variance of economic returns over time.

6. Conclusion

We explore the economic and biological factors that contribute to the degradation of population diversity in a salmon stock complex, and the associated changes in the mean and variance in economic returns and willingness to pay for ISM. We

¹³ The definition assumes that fishermen are risk neutral.

parameterize our model with biological and economic data where possible and perform sensitivity analyses over the parameter values for which data do not exist.

We find that market dynamics can drive changes in population diversity and also determine how changes in population diversity map into changes in the mean and variance of economic returns to the fishery. Therefore, in order to quantify the value of ecosystem services provided by population diversity, it is necessary to understand market dynamics and the economic structure of a fishery. For example, the economic implications of the stabilizing effect of population diversity on physical fishery yields can vary widely depending on the nature of fish prices.

While our primary focus is on the impact of population diversity on economic returns from fishing, there are other values associated with salmon population diversity not considered here. For example, salmon are a keystone species serving the important ecological role of transferring ocean nutrients upstream, which provides food for both aquatic and terrestrial species (see Cederholm et al., 1999 for a review of this literature). Because salmon populations exhibit breeding site fidelity and the breeding sites are spatially discrete, altering the salmon population structure may have ecosystem impacts through altering the spatial distribution of ocean nutrients in the terrestrial upstream ecosystem. Additionally, there are cultural values for salmon population diversity in the Copper River area. For example, the Ahtna people have occupied the Copper River Valley for at least a millennium (Workman, 1977) and have strong cultural connections to salmon populations in the area (see Simeone et al., 2007). Considering the complete set of values of population diversity is important and is left for future work.

Additionally, several important questions remain including: How do outcomes, both with and without ISM, compare to outcomes under optimal harvest when externalities on biodiversity are internalized? In other words, how would a sole owner balance the costs and benefits of maintaining population diversity when populations are valued differently on the market? The optimal harvest strategy could be used to quantify rents that are being dissipated through rule-of-capture incentives. Another question is, what are the implications of a reduction in life-history diversity on the robustness of salmon populations to potential changes in environmental conditions due to climate change? With the increasing frequency of extreme weather events, addressing the impacts of fishing on relative population abundance levels may become even more important to maintaining populations from future extinction. Finally, what is the empirical magnitude of economic losses due to degraded population diversity induced by markets? Carefully controlled natural experiments could potentially be employed to measure these losses. We leave these questions for future work.

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Appendix A. Appendix to fishermen, markets, and population diversity

This appendix describes how model parameters are estimated from data, when possible, and assumptions on the remaining model parameters. The appendix is organized as follows:

- I. Historical Management Detail
- II. Price Paths
- III. Population-specific Run-time Distributions
- IV. Local-scale Density Dependence
- V. Fishing Costs and Fleet Efficiency
- VI. Initial Values
- VII. Price Feedbacks

I. Historical management detail: Table 1 summarizes the history of development and management in the Copper River Chinook salmon fishery.

II. Price paths: The three price paths (seasonal, endogenous, and constant) used in the model simulations are parameterized with ex-vessel Chinook price data collected in the Copper River fishery by Alaska (2005) in 2003–2005 (Table 2).

The seasonal and endogenous price paths (Eqs. (7) and (8)) are estimated, respectively, with the following two econometric models:

$$\log[p(t)] = \alpha - \beta t + \mu(t),$$

$$\log[p(t)] = \alpha + \kappa \log \left[\sum_{n=0}^t H(n) \right] + e(t),$$

Table 1

Selected records from archival fisheries management reports (paraphrased).

Year	Management records
1981:	Fishermen are targeting Chinook for the first time.
1985:	Chinook harvest was unexpectedly high and the escapement index was 1/3 of historical levels.
1986:	A dockside survey suggests 15% of the fleet is targeting Chinook. Managers put a maximum mesh size restriction to protect Chinook.
1987:	Fishermen take 20% of total annual anticipated Chinook harvest in the first opening so managers delay the second opening.
1991:	Managers delay the season opening to protect Chinook. In the first period fishermen harvest 300% of anticipated harvest for that week. For the season, Chinook harvest was 15% below anticipated.
1996:	Managers adopt a temporary Chinook management plan to reduce commercial, personal use, and sport harvest by 5% each. They also use area closures and time restrictions to protect the early part of the run. Chinook monitoring begins to assess whether there is a conservation issue for the Chinook salmon stock complex.
1999:	Managers renew the Chinook management plan to set escapement goals and the goal of protecting the early part of the run.

Source: Alaska Department of Fish & Game 1981–1999.

Table 2

Copper River ex-vessel Chinook prices by season opening (2013 USD per pound).

Opening	Year		
	2003	2004	2005
First	\$6.33	\$7.71	\$7.04
Second	\$5.63	\$6.47	\$7.28
Third	\$4.43	\$5.86	\$4.89
Fourth	–	\$5.92	\$4.77
Fifth	\$3.48	–	\$4.89

Source: Alaska Department of Fish & Game (Alaska, 2005).

where $p(t)$ is the ex-vessel price per fish, t represents fishery openings, $\mu(t)$ is a mean zero normally distributed an error term in the seasonal price equation, $H(t)$ is aggregate harvest (in numbers), and $e(t)$ is a mean zero normally distributed error term in the endogenous price equation.

The price data are per-pound ex-vessel prices adjusted for inflation to 2013 USD and converted to price per fish using the average pounds of a Chinook salmon caught in the 2003–2005 seasons (approximately 22 pounds per fish Alaska, 2005). Harvest data, in numbers per opening from 2003 to 2005, are taken from management reports (Alaska, 2005).

The seasonal price path was estimated using OLS and the endogenous price path was estimated using two-stage least squares (2SLS) with lagged aggregate harvest, from the same opening in the previous year, serving as an instrumental variable for current-year aggregate harvest.

Tables 3 and 4 report OLS and 2SLS results respectively. Reduced-form estimates (Table 4) are used to calculate the structural parameters in Eq. (8) as follows: $\kappa = \hat{\kappa}$ and $B = \exp(-\hat{\alpha}/\hat{\kappa})$. Finally, we use the average value of the fitted seasonal prices (from estimates in Table 3) to calculate the constant price.

III. Population-specific run-time distributions: We use population-specific harvest data collected by Seeb et al. (2009) to estimate the population-specific run-time distributions. Seeb et al. (2009) conducted a genetic analysis of samples from commercial Chinook harvest in Cordova Alaska collected in 2005 in 10 bi-weekly openings. With the genetic analysis Seeb et al. (2009) categorized the bi-weekly commercial harvest into 4 regional population groups (see Seeb et al., 2009 for more detail). We use two of these groups, the Upper Copper River and Lower Copper River Chinook, to represent our early-run and late-run populations, respectively. Table 5 summarizes commercial fishery harvest by opening, and the fraction of each population in the harvest as estimated by Seeb et al. (2009). Although it is possible that each regional group is comprised of multiple populations, regional groups are the finest scale population structure data available for this fishery.

To estimate the run time distributions from the contribution data in Table 5, we assume that total harvest is the same fraction of the stock size in every week.¹⁴

Of the several distributions considered, we select an exponential distribution for the Upper population (representing our early-run population) and an extreme value distribution for the Lower population (representing our late-run population), as

¹⁴ Our run time distribution estimates also fit the data well when we assume that the stock is the same in each opening and that harvest only varies within the season due to the effort distribution over openings in the season. This enables us to estimate of the number of fish from each population caught in each opening and the fraction of aggregate bi-weekly harvest from each population. The distributions are then estimated in a two-step process: (i) we identify the class of population density functions that fits the data for each of the two groups (using the distribution fitting tool in MATLAB); and (ii) we estimate parameters for each distribution (using the distribution fitting tools in MATLAB).

Table 3

Seasonal price path parameter estimates.

Parameter	Estimate	Robust Std. Error
α	5.041	0.050**
β	–0.126	0.030**
Number of observations	13	
R-squared	0.639	

*denotes parameter estimates significant at 5% levels.

** denotes parameter estimates significant at 1% levels.

Table 4

Endogenous price path parameter estimates.

First Stage Estimates		
Variable	Estimate	Robust Std. Error
Lagged H (t)	0.634	0.170**
Constant	3.530	1.661*
Number of Observations	13	
F-statistic	13.89	
Second Stage Estimates		
Parameter	Estimate	Robust Std. Error
α	8.533	0.739**
κ	–0.385	0.078**
Number of Observations	13	
R-squared	0.756	

* denotes parameter estimates significant at 5%.

** denotes parameter estimates significant at 1% level.

Table 5

Copper River Chinook population estimates, by opening, from Seeb et al. (2009).

Opening	Commercial Harvest Harvest	Upper Contribution	Lakes Contribution
1	7500	0.371	0.253
2	4191	0.286	0.289
3	3717	0.220	0.353
4	3404	0.117	0.455
5	3356	0.013	0.740
6 [†]	2400	NA	NA
7	1675	0.039	0.748
8	2364	0.009	0.844
9	2096	0.009	0.876
10	1105	0.000	0.922

[†] Data were not collected from the 6th opening.

they provide the closest fit to our data. The exponential distribution is characterized by a single parameter, the rate parameter, and the extreme value distribution is characterized by location and scale parameters. Estimates of these parameters are provided in Table 6 and Fig. 6 shows population-specific run time histograms along with our fitted distributions.

IV. *Local-scale density dependence*: We assume that the escapement-recruitment relationship, for each salmon population, follows a Ricker (1954) process:

$$P_{c+1}^s = \alpha E_c^s \exp(-\beta E_c^s) \exp(\epsilon_c^s)$$

where P_{c+1}^s is the number of population s salmon recruits in $c+1$, E_c^s is the total number of population s salmon that escape in cycle c , and ϵ_c^s is a mean-zero normally distributed error term.

Biological parameters α and β are estimated from escapement and returns data for Copper River Chinook salmon from 1980 to 2007 collected by Fair et al. (2008). We assume that of the total number of returns and spawners (escaped salmon)

Table 6
Run time distribution parameter estimates.

Parameter	Estimate
Rate parameter for early-run distribution	0.511
Location parameter for late-run distribution	6.81
Scale parameter for late-run distribution	2.47

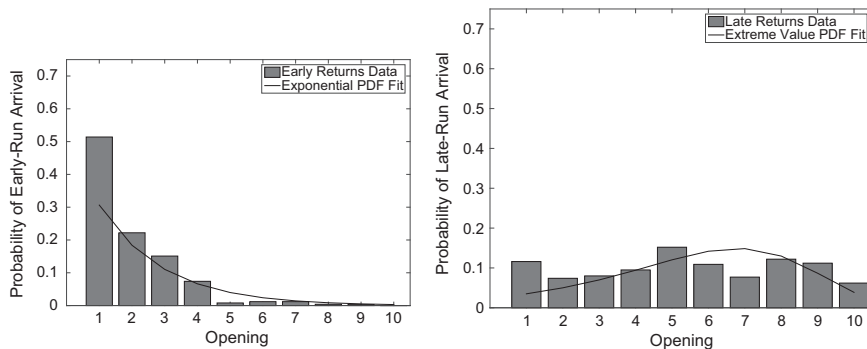


Fig. 6. Run time histograms and fitted distributions for the Upper and Lakes Copper River Chinook populations

Table 7
Ricker growth equation parameter estimates.

Parameter	Estimate	Standard Error
λ	1.72	0.13**
β	4.65e-05	9.17e-06**
Number of observations	28	
R-squared	0.4973	

*denotes parameter estimates significant at 5%.

** denotes parameter estimates significant at 1% level.

50% are early-run and 50% are late run salmon. We estimate the parameters with an OLS regression as follows:

$$\begin{aligned} \log\left(\frac{P_{c+1}^S}{E_c^S}\right) &= \log(\alpha) - \beta E_c^S + \epsilon_c^S \\ &= \lambda - \beta E_c^S + \epsilon_c^S. \end{aligned}$$

Table 7 contains the Ricker parameter estimates, and associated standard errors. Fitted residuals from the model $\hat{\epsilon}_c$ are used to model stochasticity in the Ricker equation. Specifically, we fit a normal distribution, to the empirical residuals ϵ_c^S . The fitted normal distribution has a mean of $-2.85e-16$ and a standard deviation of 0.26. We then use independent random draws from this distribution for our stochastic simulations. Assuming the Ricker error terms are i.i.d. across populations and cycles follows (Schindler et al., 2010a) who find that the sockeye salmon populations are only “weakly synchronous” and that assuming the returns to each population were uncorrelated would only “marginally” impact their results. Fig. 7 shows the estimated empirical error distribution.

V. fishing costs and fleet efficiency: Lacking data on fleet efficiency, we assume that fishermen's catchability coefficients q_i follow a uniform distribution on the interval [a,b] and assume 3 different values for the distribution parameters (a and b) to explore model results under a wide range of assumptions. Additionally, we assume a value for the opportunity cost of effort. Fishing cost estimates are from a survey conducted in 2001 in the Bristol Bay salmon fishery by Carlson (2002), which implies a trip cost of about \$296 (2013 USD) (see Jardine et al., 2014 for more detail).

The fleet efficiency and opportunity cost parameters were chosen so that modeled first-period harvest levels in the initial cycle approximates actual first-period harvest levels in the fishery. We use data from the 1988 to 2005 fishing seasons and

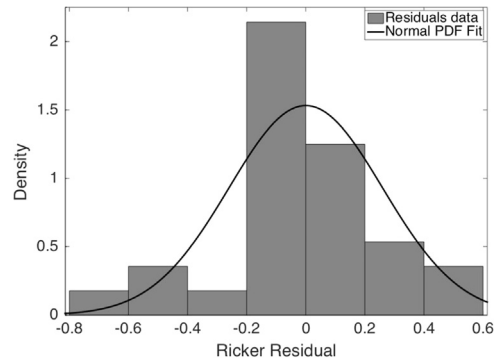


Fig. 7. Residuals from the Ricker OLS model and the fitted distribution

Table 8

Modeled first-period harvest in the initial cycle, by fleet efficiency (rows) and market scenario (columns).

Fleet Efficiency	Modeled harvest Seasonal prices	Modeled harvest Endogenous prices	Modeled harvest Constant prices
Low	0.989e+04	0.984e+04	0.892e+04
Central	1.106e+04	1.098e+04	1.010e+04
High	1.151e+04	1.140e+04	1.056e+04

Table 9

Fleet efficiency parameters

Parameter	Description	Value	Source
a^L	Low efficiency q is are $\sim U(a^L, b^L)$	1.25e-05	Assumed
b^L	Low efficiency q is are $\sim U(a^L, b^L)$	2.5e-03	Assumed
a^M	Central efficiency q is are $\sim U(a^M, b^M)$	1.5e-05	Assumed
b^M	Central efficiency q is are $\sim U(a^M, b^M)$	2.6e-03	Assumed
a^H	High efficiency q is are $\sim U(a^H, b^H)$	1.75e-05	Assumed
b^H	High efficiency q is are $\sim U(a^H, b^H)$	2.7e-03	Assumed
γ	Fishing trip cost	296	(Carlson, 2002)
ν	Opportunity cost of a Chinook fishing trip	1204	Assumed

adjust for differences in opening lengths by multiplying catch per hour by 24 h, the most common season length in the data. The median of normalized first-period catch was 10, 779 (min 2984, max 22, 878).

Table 8 summarizes modeled harvest levels in the initial cycle for each fleet efficiency level and market scenario, showing that our model's predicted first-period harvest levels are a good fit to actual median first-period harvest levels. Table 9 summarizes the parameters that characterize the fleet efficiency distributions in our low, central, and high fleet efficiency cases and the cost parameters.

VI. Remaining parameters and initial conditions: Remaining model parameters and initial conditions are, for the most part, taken from fisheries management reports. These parameters and initial conditions are recorded in Table 10, and described here. The Chinook escapement goal (adopted in 1999) is 24,000 salmon and average escapement from 1981 to 1998 was roughly 26,000 (Fair et al., 2008) suggesting that escapement met the goal before it was adopted. Harvest from 1991 to 2005 was roughly 50,000 salmon. Based on this data, we assume that the initial size of the stock complex is 74,000 salmon. While the actual buffer managers use to target the TAC is unknown, using a 5% buffer in our model prevents harvest from going over the TAC. We also assume that each population comprises 50% of the total stock.¹⁵

VII. Price Feedbacks: Endogenous prices can create both positive and negative feedbacks. Negative feedbacks occur when the harvest of early-run salmon depresses prices, reducing equilibrium effort and biodiversity impacts. Positive feedbacks

¹⁵ To check the sensitivity of our results to the assumption regarding the share of the two populations, we conducted a sensitivity analysis, setting the initial fraction of early-run salmon in the stock complex to 0.25, 0.4, 0.6, and 0.75. In general, we find that our biodiversity results do not change qualitatively, when the early run population comprises less than 60% of the stock complex. When the early-run population comprises more than 60% of the stock complex, however, we find that seasonal prices lead to the greatest biodiversity changes. The result stems from high early-season catches that lead to lower prices and to lower equilibrium effort levels. In other words, the larger early-run population is never degraded enough to introduce positive feedbacks in the model.

Table 10
Remaining parameters and initial conditions.

Initial condition/parameter	Description	Value	Source
$X(c=1)$	Salmon stock in the initial cycle	74,000	(Fair et al., 2008)
EG	Escapement goal	24,000	ADF & G [1]
TAC	Total allowable catch	Run-24,000	ADF & G [1]
$P^1(c=1)$	Population 1 stock in the initial cycle	$0.5 \times 74,000$	Assumed
$P^2(c=1)$	Population 2 stock in the initial cycle	$0.5 \times 74,000$	Assumed
Buffer	Managers target TAC-Buffer	5% of the TAC	Assumed
N	Number of fishermen in the fishery	500	CFEC

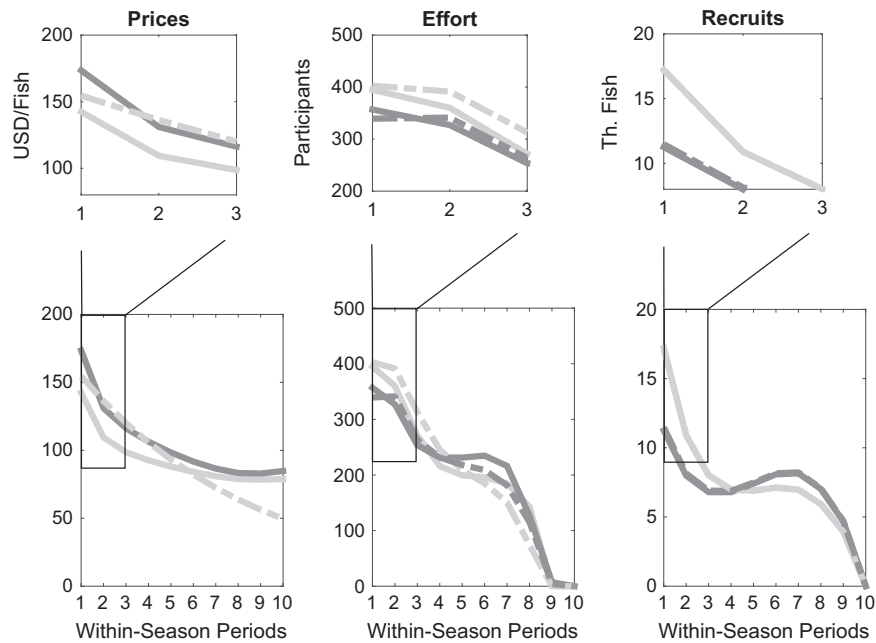


Fig. 8. Within-season prices, effort, and recruits. Values from the initial cycles are represented in light gray and values from the final cycles are represented in the dark gray. Results under endogenous prices are represented by a solid line and results under seasonal prices are represented by a dashed line. The top panel shows results from the first 3 periods in the season and the bottom panel shows results from the entire season (10 periods).

occur when degraded population diversity reduces the supply of salmon early in the season, increasing prices, and drawing effort into the fishery.

Comparing the within-season results from the initial cycle and the terminal cycle (after 60 years) illustrate this point. Fig. 8 presents within-season results for central fleet efficiency assumptions. The figure shows that early-season endogenous prices in the terminal cycle are higher than in the initial cycle (left panels); early-season effort in the terminal cycle remains high relative to effort levels when prices are seasonal (middle panels); and early-run salmon recruits fall in the terminal cycle for both market scenarios, but fall slightly more when prices are endogenous. Therefore, when prices are endogenous the biodiversity impacts lead to higher early-season prices and sustain relatively higher levels of early-season effort.

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