Diversity increases stability and opportunity in First Nations salmon fisheries

by

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Abstract

Biodiversity can dampen the effects of ecosystem variability through diversification of portfolio assets providing the environmental stability that supports economies and cultures. We examined how elements of salmon biodiversity affect interannual catch stability and within-year season length (opportunity) of First Nations fisheries in the Fraser River watershed from 1983 to 2012 across 5 different species of salmon. Stability and opportunity increased in fisheries with access to increasing richness, as fisheries were closer to the ocean, in mainstem fisheries relative to tributary fisheries, and in fisheries downstream of a partial barrier. The importance of different elements of salmon biodiversity on catch stability varied by species. Richness was the most ubiquitous explanatory variable of fishing opportunity across all species. Through a novel application of spatial portfolio theory, this research quantifies the portfolio effect in fisheries across the Fraser and links basic diversity-stability theory to First Nations food security.

Keywords: Portfolio effect; diversity-stability; opportunity; First Nations fisheries; Pacific salmon; watershed management

To my family, for their support and encouragement, and to my friends "out west", for providing the community that makes BC my new home.

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Table of Contents

List of Tables

List of Figures

List of Acronyms

AICc	Akaike information criterion corrected for small sample sizes
BC	British Columbia
CV	Coefficient of variation
DFO	Fisheries and Oceans Canada
FSC	Food, social, ceremonial
GIS	Geographic Information System
gls	Generalized least squares
HG	Barrier
KM	Distance
lme	Linear mixed effects
PP	Probability of a poor year
REML	Restricted maximum likelihood
RI	Richness
TR	Tributary

Glossary

Biodiversity	From the UN Convention on Biological Diversity, “the variability among living organisms from all sources including, inter alia, terrestrial, marine, and other aquatic ecosystems and the ecological complexes of which they are part; this includes diversity within species, between species and of ecosystems.”
Coefficient of variation (CV)	The standard deviation normalized by the mean.
FSC fisheries	First Nations fisheries that have food, social, and ceremonial rights to fish according to *The Constitution Act* 1982.
Opportunity	The number of weeks a fishery is catching fish.
Probability of a poor year (PP)	The number of years with catch below half the mean at a fishery divided by the total number of years for which we have catch data at that fishery.
Stability	Low interannual variability.

1. Introduction

Integration of asynchronous population dynamics can stabilize ecosystem function over time by buffering the effects of environmental change (Doak *et al.* 1998; Tilman *et al.* 1998). Indeed, studies from multiple systems have found positive correlations between taxonomic diversity (e.g. species or population richness) and ecosystem function and stability (Den Boer 1959; Fox 2005; Duffy 2009; Greene *et al.* 2009). For example, grassland experiments have shown that among-year variability decreased with increasing species richness (Tilman 1996). This positive relationship between diversity and stability can be a result of the 'portfolio effect', where statistical averaging of the species can dampen community fluctuations (Doak *et al.* 1998) analogous to asset diversification stabilizing stock portfolios (Figge 2004). The magnitude of the portfolio effect depends on (1) the number of assets in a portfolio, (2) the variation and production of those assets and (3) the level of synchrony, or covariation in asset value (Markowitz 1952; Doak *et al.* 1998). Thus, a portfolio with an adequate number of assets and low covariation between those assets will be more stable than a less diverse portfolio despite fluctuations in some assets. Although biodiversity-stability research is a growing field, much of this research has been criticized for not being applicable to conservation as some studies have used irrelevant measures of ecosystem function and are at small spatial and temporal scales (Srivastava & Vellend 2005).

Integration of asynchronous phenologies in pulsed resources can extend feeding opportunities for mobile consumers within a season (e.g. Drent *et al.* 1978; Fryxell *et al.* 2005; Schindler *et al.* 2013), in contrast to interannual asynchrony which stabilizes ecosystem functions across years. One of the best-known examples of this is the annual migration of ungulate grazers tracking grassland productivity across the Serengeti (Mcnaughton 1985). Gazelles in the Serengeti follow grazing opportunities driven by variable rain patterns across large areas (>1600km^2) to increase the length of their foraging season (Fryxell *et al.* 2005). Phenology tracking also exists across latitudinal gradients; migratory waterfowl have been described as “surfing the green wave” of budding spring vegetation as they fly north to summer breeding grounds (Drent *et al.* 1978; van der Graaf *et al.* 2006). In a similar “silver wave”, surf scoters (*Melanitta perspecillata*) may follow the movement northwards of Pacific herring (*Clupea pallasi*) spawning events during the ducks’ annual migration to breeding grounds in northern Canada and Alaska (Lok *et al.* 2012). Thus, while windows of opportunity may be small at fine spatial scales, phenological diversity allows mobile consumers to integrate across space to extend foraging opportunities beyond individual prey populations. When phenological diversity of migration is physically constrained by migratory corridors, it is also possible that consumers could integrate across phenological diversity and have extended foraging opportunities without moving. Phenological diversity thus may increase opportunity, yet this potential ecosystem service has been less well described.

Studies of anadromous salmon have increasingly illuminated how biodiversity impacts both stability and opportunity. Because salmon return to their natal stream to spawn with high site fidelity, populations are often uniquely adapted to their local environmental conditions driving high intra-specific variability in life history traits like body size, egg size, time spent at sea, and age at spawning (Taylor 1991). These local adaptations are thought to contribute to fine-scale asynchrony of salmon population dynamics (Rogers & Schindler 2008; Schindler *et al.* 2013). In sockeye salmon from Bristol Bay Alaska, for example, diverse life history characteristics across salmon populations may contribute to stability of their aggregate stock complex (Hilborn *et al.* 2003; Greene *et al.* 2009) which supports stable fisheries (Schindler *et al.* 2010). While asynchronous population dynamics have provided year-to-year resource stability for fisheries, asynchronous spawning phenology across the region (Lisi & Schindler 2011) increases within-year opportunity of resource pulses to people and predators inland. For example, mobile consumers like gulls and grizzly bears can increase their window of feeding opportunity by two times by moving among streams and integrating across this “crimson wave” of sockeye salmon (Schindler *et al.* 2013). Thus, studies from Bristol Bay, Alaska offer an important case study of salmon biodiversity, stability, and opportunity. However, studies have yet to contrast the stability and opportunity of multiple fisheries that integrate contrasting amounts and elements of salmon biodiversity.

First Nations fisheries integrate different amounts and elements of salmon biodiversity throughout a watershed. Salmon have sustained First Nations people throughout the Pacific Rim for millennia. Historically supporting the second highest densities of aboriginal peoples in North America next to California (Ubelaker 2006), people of the northwest coast from northern California to Alaska cumulatively consumed an estimated 46 to 69 thousand tons of salmon per year in pre-contact years (Haggan *et al.* 2006), approximately equal to the average annual commercial catch of 64 thousand tons from 1901 to 2000 (Jones 2002). To First Nations in British Columbia (BC), Canada, salmon are regarded as a "cultural keystone" species (Garibaldi and Turner 2004), providing an essential food resource and representing a central element of First Nations culture and spirituality (e.g. Suttles 1960, 1987a, 1987b). First Nations' rights to fish for food, social, and ceremonial (FSC) purposes are protected by the Canadian Constitution (*The Constitution Act* 1982). While typical commercial salmon fisheries harvest salmon in the nearshore marine ecosystem, FSC fisheries are often located throughout watersheds. These watersheds are dendritic, where smaller tributaries flow into larger stream segments similar to the branching of a tree, and spatially structure the salmon diversity (Rodriguez-Iturbe *et al.* 2009; Yeakel *et al.* 2014) from which First Nations fish. Thus, FSC fisheries can integrate different amounts of salmon richness depending on their location in the watershed. For example, fisheries at the mouth of the river have access to all of the salmon that spawn throughout the entire watershed, thus integrating across the complete diversity profile of the entire river. In contrast, fisheries in the headwaters have access to fewer populations and thus fish from a much less diverse portfolio. First Nations economies and cultures depend on consistent catches (year-to-year stability) and long fishing seasons (within-year opportunity) to catch fresh fish.

The natural gradients of salmon diversity integrated by different First Nations fisheries in a large river provide an opportunity to quantify how different amounts and elements of biodiversity contribute to stability and opportunity. We examined the effect of different elements of salmon biodiversity on the stability of catch over time and fishing season length (opportunity) within the Fraser River, a large watershed (220,000 km^2) in

BC, Canada (Figure 1.1). The Fraser is an example of a dendritic watershed that varies greatly from its headwaters to its mouth, as well as from branch to branch as a function of its underlying geomorphology and local environmental conditions (Rodriguez-Iturbe *et al.* 2009). We compiled weekly and yearly catch data (1983-2012) of Chinook, chum, coho, pink, and sockeye salmon from Fisheries and Oceans Canada (DFO) on 21 FSC fishery management regions located throughout the watershed (Figure 1.1), referred to as “fisheries” from here on. We predicted that fisheries with access to greater salmon diversity would exhibit a stronger portfolio effect in their catch (i.e. more stability over time) than fisheries accessing a less diverse salmon portfolio (Table 1.1). Additionally, we predicted that fisheries with access to high salmon diversity would have longer fishing seasons, or more fishing opportunity, as they integrate across diverse run-timings (Table 1.1). We statistically examined models to determine which elements of salmon biodiversity had the greatest effect on stability and fishing opportunity. Here we show that multiple elements of salmon biodiversity are important for food security and opportunity in First Nations FSC fisheries, highlighting the importance of biodiversity-stability relationships in a management relevant context (e.g. Srivastava & Vellend 2005).

Figure 1.1. Map of the Fraser River watershed in British Columbia (BC), Canada. The downstream point of each FSC fishery region is marked with a point. Points with Roman numerals correspond to fisheries highlighted in Figure 2.1.

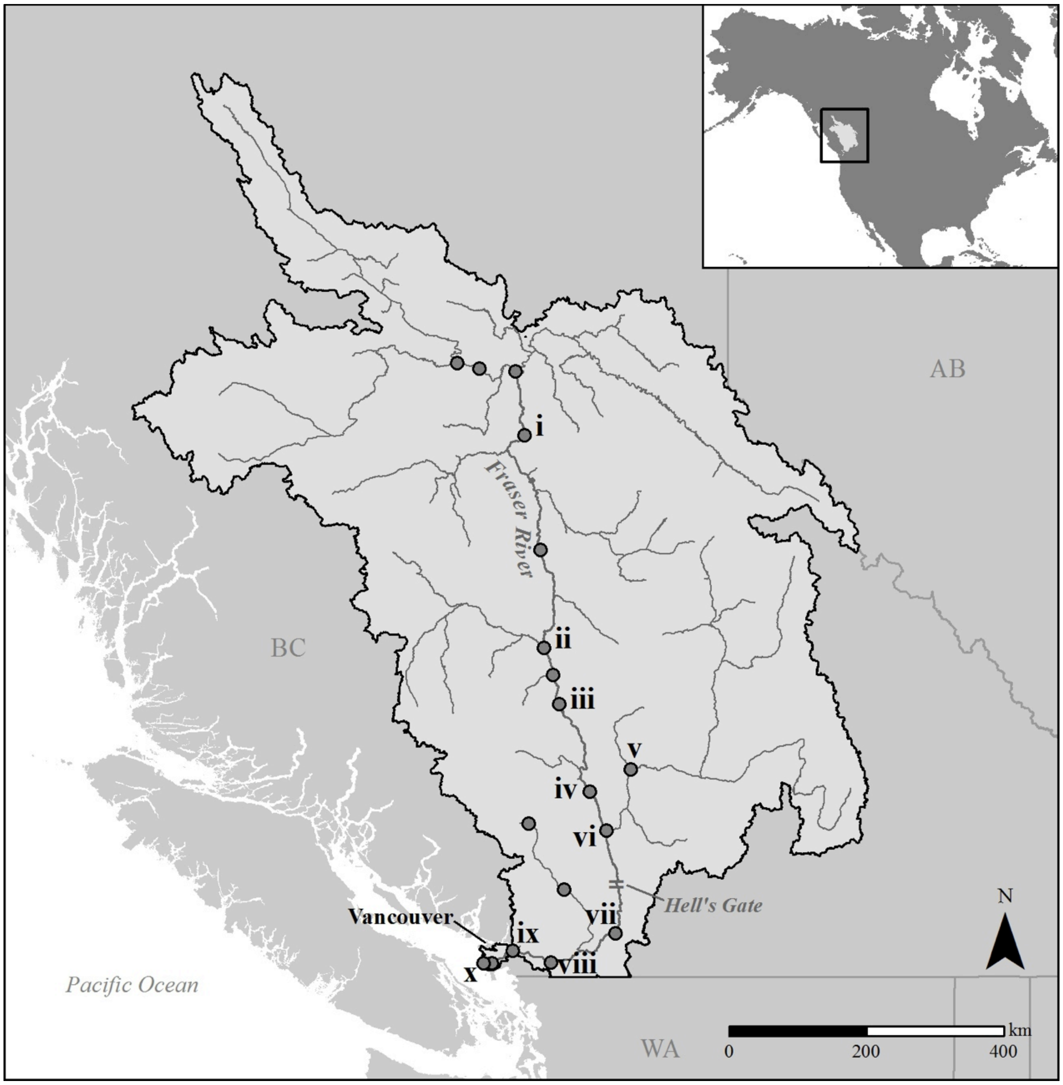


Table 1.1. **Elements of salmon biodiversity and their hypothesized impacts on catch stability and fishing opportunity**

Factor	Mechanism	Citation	Stability hypothesis	Opportunity hypothesis
Richness	Populations are uniquely adapted to their spawning and rearing grounds causing high population diversity	Markowitz 1952; Taylor 1991; Hilborn *et al.* 2003; Figge 2004; Rogers & Schindler 2008; Greene *et al.* 2009; Schindler *et al.* 2010, 2013	Fisheries that integrate across higher richness would have a greater number of assets in their portfolio compared to fisheries accessing less richness, and thus have more catch stability	Fisheries with access to more richness would integrate across more runs, thus having greater windows of fishing opportunity
Distance	Honing to natal spawning grounds causes populations to branch off of the network, reducing local richness and increasing population synchrony in reaches farther from the ocean	Olsen *et al.* 2010; Carrara *et al.* 2012; Yeakel *et al.* 2014	Fisheries near the mouth of the river would integrate across higher richness and asynchronous population dynamics, thus having higher stability compared to headwater fisheries	Fisheries near the mouth of the river would integrate across higher richness and asynchronous run-timing, thus having greater windows of opportunity compared to headwater fisheries
Tributary	Honing to natal spawning grounds causes populations to branch off of the network, reducing local richness and increasing population synchrony in tributary reaches	Olsen *et al.* 2010; Carrara *et al.* 2012; Yeakel *et al.* 2014	Mainstem fisheries would integrate across higher richness and asynchronous population dynamics, thus having higher stability compared to tributary fisheries	Mainstem fisheries would integrate across higher richness and asynchronous run-timing, thus having greater windows of opportunity compared to tributary fisheries
Barrier	Partial barriers can exclude populations and select for traits such as migration timing, causing a decrease in local richness and increasing population/run-timing synchrony	Poff 1997; Pess *et al.* 2012; Braun *et al.* In preparation	Fisheries downstream of partial barriers would integrate across higher richness and asynchronous population dynamics, thus having higher stability compared to fisheries upstream	Fisheries downstream of partial barriers would integrate across more runs and across asynchronous run-timings, thus having extended opportunity compared to fisheries upstream

2. Methods

2.1. The Fraser River watershed

The Fraser River (BC, Canada) is 1370km long, flowing from its headwaters in the Rocky Mountains to its mouth at the Pacific Ocean. The mainstem of the Fraser River is not dammed, making it the second longest dam-free salmon migration route in North America (Nilsson *et al.* 2005). Six species of anadromous Pacific salmon (*Oncorhynchus* species), including Chinook (*O. shawytscha*), chum (*O. keta*), coho (*O. kisutch*), pink (*O. gorbuscha*), and sockeye (*O. nerka*), spawn throughout the Fraser River watershed and are targeted by commercial, recreational and First Nations fisheries.

Given that stability and opportunity are influenced by richness as well as asynchronous dynamics and run timing (Doak *et al.* 1998), we examined how catch stability and opportunity are associated with the following different elements, through direct measures and proxies, of salmon biodiversity (Table 1.1):

- Richness. Richness is a direct measure of the amount of salmon taxonomic diversity. We determined richness for each fishery as the number of salmon population units that swim by a fishery en route to their spawning grounds. We hypothesized that interannual catch stability and within-year fishing opportunity would decrease with decreasing fishery access to richness (Table 1.1).
- Distance. We determined fishery distance from the ocean along the Fraser network as a proxy for salmon biodiversity; salmon richness and asynchrony decrease towards the headwaters as populations disperse throughout the watershed to spawn (Olsen *et al.* 2010). Thus we hypothesized that interannual catch stability and within-year fishing opportunity would decrease with increasing fishery distance to the ocean (Table 1.1).
- Tributary. We designated fisheries as either tributary or mainstem as a proxy for salmon biodiversity. Because tributary streams may host lower richness and more synchronized populations than mainstem streams (Olsen *et al.* 2010), we hypothesized that tributary fisheries would be less stable in their

catch across years and have less fishing opportunity within a year than mainstem fisheries (Table 1.1).

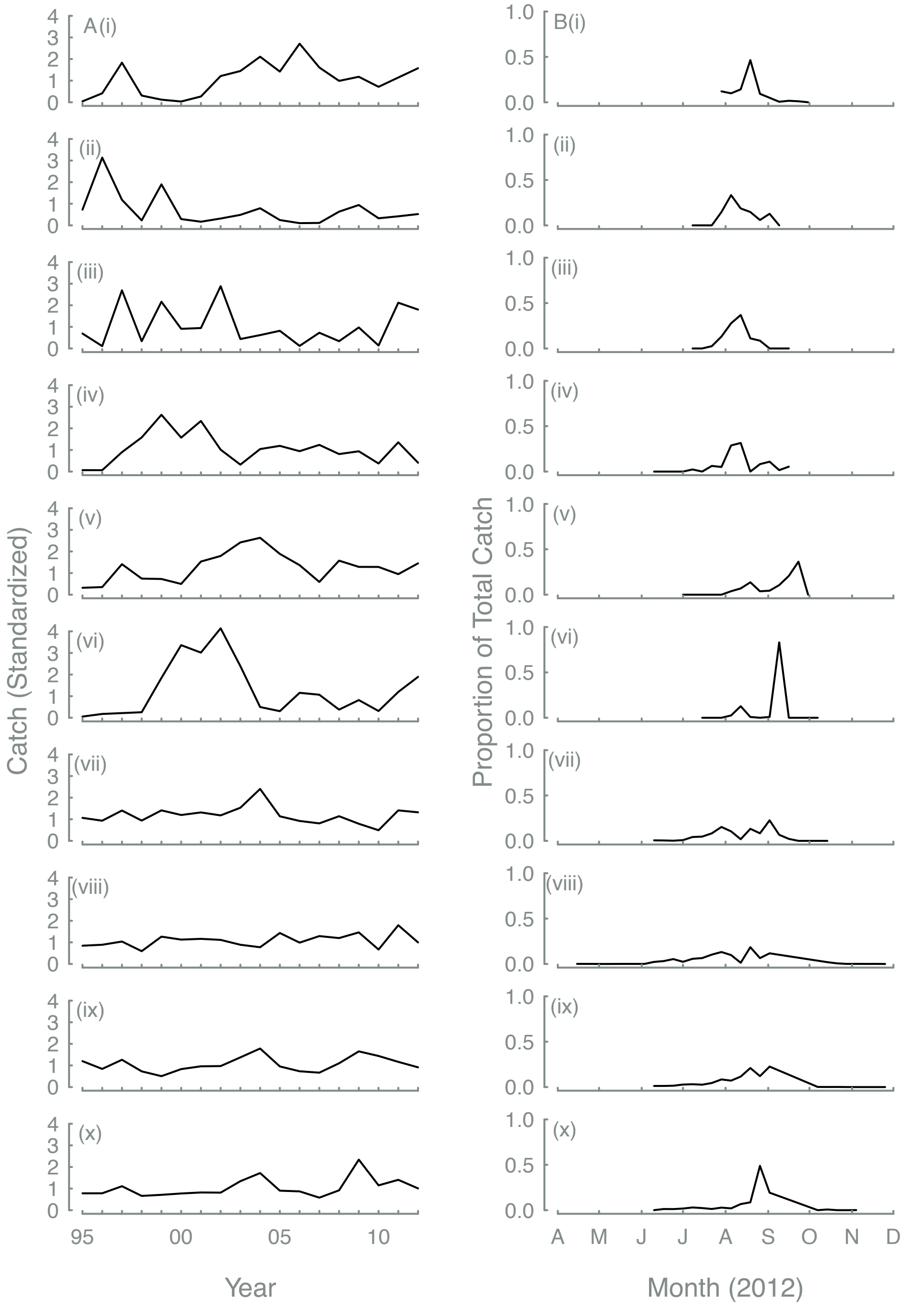
- Barrier. We designated fisheries as either up or downstream of a partial barrier, Hell's Gate, on the Fraser River as the final proxy for salmon biodiversity. Geographic and environmental barriers within a watershed can influence diversity as they can act as landscape filters that select certain traits within a species (Poff 1997) thus homogenizing the species beyond the barrier, or prevent passage entirely thus eliminating the species' presence beyond the barrier. Hell's Gate, a narrow canyon with high water velocities on the Fraser River, is a physiological barrier that acts as a bottleneck, challenging fish passage, acting as a selection pressure for certain life-histories such as asynchronous run-timing, and effectively reducing salmon diversity upstream (Braun *et al.* In preparation; Pess *et al.* 2012). Thus, we hypothesized that fisheries upstream of Hell's Gate would be less stable in their catch across years and have less fishing opportunity within a year than fisheries downstream of the barrier (Table 1.1).

2.2. Data

We quantified salmon richness as the number of salmon population units that swim by a fishery to arrive at the spawning grounds. We used the finest scale of population richness information available for each species. Chinook richness was measured as the number of populations (Mckay *et al.* In preparation) sockeye richness was measured as the number of conservation units for both lake and stream life histories (Holtby & Ciruna 2008), coho richness was measured as the number of subpopulations (Interior Fraser Coho Recovery Team 2006), pink richness was measured as the number of stocks (Mckay *et al.* In preparation), and chum richness was measured as the number of spawning locations (Salo 1991).

FSC fisheries are grouped regionally and are managed by First Nations and DFO. Fraser FSC catch reports are publicly available online and upon request through DFO. Catch is reported by species, thus we focused on catches of each salmon species separately. For each fishery along the Fraser River, we have acquired weekly and yearly catch totals from 1983 to 2012 (e.g. Figure 2.1). In some cases, fishery regions changed periodically necessitating consolidation of catches across fisheries to make consistent comparisons across the time frame. We consolidated catch if two adjacent fisheries were grouped in some years and not in others. Fisheries were dropped out of the analysis if there were too few years of data (less than ¼ of years for that fishery) or if mean catch in that fishery was less than 20 fish. All measures for pink salmon were determined for odd years only because pink salmon have a strict two-year life cycle and return to the Fraser River almost exclusively in odd years. All watershed characteristics were measured through a Geographic Information System (GIS) using ArcGIS 10.0 software.

Figure 2.1. Panel A – standardized catch at each fishery from 1995 to 2012. A fishery's catch was standardized by dividing by the mean catch across years for that fishery. Standardized catch below 1 indicates a below average year and standardized catch above 1 indicates an above average year. Each graph is a different fishery in the watershed. Graphs are ordered from farthest from the ocean at the top (i) to closest to the ocean at the bottom (x), and correspond to Roman numerals in Figure 1.1. Panel B – proportion of total Chinook catch at each site in 2012, binned by weeks.



2.3. Catch stability

We quantified the stability for each fishery with two metrics of variability. The coefficient of variation (CV) is often used as a metric of stability because it measures the variation in observations relative to the mean (e.g. Tilman 1996; Schindler *et al.* 2010). A lower CV is indicative of higher stability, or lower interannual variability. Interannual variability of each fishery was quantified with the CV. We also calculated the probability of a poor fishing year for each fishery as a more direct measurement of catch reliability. Years were considered "poor years" if catch in a given year was below half of the mean catch across years for that fishery. The probability of a poor year (PP) at a given fishery was then determined by dividing the number of poor years in a region by the total number of years for which there were data.

We examined how catch stability changed across fisheries that incorporated different elements of salmon biodiversity. To determine the variables that had the significant effects ($\alpha=0.05$) on CV and PP, we built generalized least squares (gls) models (nlme package; Pinheiro *et al.* 2011) with explanatory variables of richness (RI), distance (KM), tributary (TR), and barrier (HG) for each species (Tables 3.1, 3.2) using R (R Development Core Team 2011). Because the maximum number of observations for a species was 21, we ran one-parameter models with each of the explanatory variables for a total of 4 models per species. RI and KM were numeric vectors standardized by centering and dividing by 2 standard deviations (arm package; Gelman *et al.* 2012). HG and TR were binary factors. We logged CV to normalize its distribution. We tested for heteroskedastic variance in model fit but were unable to add variance structures due to low sample size. CVs and PPs were significantly spatially autocorrelated along the network (igraph package; Csardi & Nepusz 2006) according to Moran's I (ape package; Paradis *et al.* 2004) for Chinook fisheries, so we included a linear correlation structure using hydrological distance, selected by Akaike information criterion corrected for small sample sizes (AICc) (MuMIn package; Bartoń 2012), in those models. Parameter coefficients were estimated with restricted maximum likelihood (REML) (Tables 3.1, 3.2).

2.4. Fishing opportunity

In addition to catch stability, we also examined how fishing opportunity changed across fisheries that incorporated different elements of salmon biodiversity. Fishing opportunity was measured as the number of weeks that fish were caught in a region. We built linear mixed effects (lme) models to determine which explanatory variable had the greatest effect on fishing opportunity (Table 3.3). We included year as a random intercept term to account for repeated measurements over time at each region. Random slopes were included if they ranked highest through AICc (Table 3.3). Heteroskedastic variances were modeled through a variance structure selected by AICc, and were different depending on the species (Table 3.3). We tested for spatial autocorrelation in fishing opportunity but found nothing significant, thus we did not incorporate this into further models. After random effects were determined, models were ranked by AICc to determine the optimal fixed structure, parameter coefficients were estimated with REML, and coefficients from top candidate sets (ΔAICc<4) were averaged.

3. Results

3.1. Catch stability

The importance of different elements of salmon biodiversity to catch stability and probability of a poor year were examined for 5 different salmon species from 1983 to 2012 across up to 21 FSC fisheries. Different elements of salmon biodiversity were significant explanatory variables of interannual catch stability depending on the species caught (Tables 3.1, 3.2). Indeed, no one explanatory variable stands out as superior across species or across stability metrics. For example, richness was a significant explanatory variable for Chinook CV/PP and chum CV, distance was significant for Chinook PP, barrier was significant for coho PP, and tributary was significant for sockeye CV/PP (Tables 3.1, 3.2).

Interannual stability increased with increasing richness across all species and both stability metrics (Figures 3.1, 3.2), although the strength of the relationship varied. Chinook CV and PP decreased with increasing population number ($p<<<0.001$; Tables 3.1, 3.2) such that fisheries with access to maximum richness were on average 3.8 times more stable in their catch and 7.8 times less likely to have a poor catch year than fisheries that accessed only 1 population. Similarly for pink and chum fisheries, CV decreased with increasing population number ($p=0.09$, 0.05 respectively; Table 3.1) with a 1.6 and 2.5 times increase in stability respectively for fisheries accessing maximum richness. PP in sockeye and chum fisheries also increased with decreasing richness ($p=0.10$, 0.08 respectively; Table 3.2) such that fisheries accessing maximum richness were 1.4 and 3.8 times less likely to experience a poor catch year respectively.

FSC catch at the mouth was more stable and fisheries were less likely to have a poor year than the farthest upstream fisheries across all species caught except sockeye (Figures 2.1, 3.1, 3.2). For example, year-to-year variability for Chinook catch from 1995 to 2012 tended to increase in regions farther from the ocean (p=0.06; Table 3.1) (Figure 2.1A) such that fisheries at the mouth were 2.6 times more stable in their catch than fisheries in the headwaters (Figure 3.1A) and 4.5 times less likely to have a poor catch year (Figure 3.2A). This stability coincides with access to 10.6 times more population richness in fisheries at the mouth than in the headwaters. Indeed, pink, and chum fisheries CV tended to increase with increasing distance from the ocean (p=0.09, 0.06 respectively; Table 3.1) (Figure 3.1) such that fisheries at the mouth were 2.6, and 4.3 times more stable than at the headwaters respectively. Additionally, PP tended to increase with increasing distance to the ocean for chum fisheries (p=0.06; Table 3.2) (Figure 3.2E) with 3.8 times the probability of a poor catch year.

Catch stability decreased upstream of Hell's Gate across all species that are caught above the barrier but sockeye and for both stability metrics (Figure 3.1, 3.2). Coho CV and PP increased upstream of Hell's Gate (p=0.07, 0.05 respectively; Tables 3.1, 3.2) (Figure 3.2D) such that downstream fisheries were 1.7 times more stable and 1.6 times less likely to experience a poor year, than upstream fisheries. Additionally, in pink fisheries, CV increased upstream of Hell's Gate (p=0.06; Table 3.1) (Figure 3.1C) such that downstream fisheries were 1.5 times more stable than upstream fisheries.

Stability was lower on average in tributary fisheries than in mainstem fisheries for at least one metric for all species but coho. Additionally, tributary was a significant explanatory variable of catch stability in sockeye fisheries for both CV (p=0.03; Table 3.1) and PP (p=0.01; Table 3.2). Mainstem fisheries had 1.8 times more stable catch and were 1.9 times less likely to experience a poor catch year than tributary fisheries on average for sockeye.

Table 3.1. **log(CV) parameter coefficient estimates. Linear correlation structures using hydrological distance were added to Chinook models to account for spatial autocorrelation. Asterisk denotes significance ("***" <0.001, "**" <0.01, "*" <0.05, "." <0.1).**

Species	Parameter	Coefficient	SE	p	Significance
Chinook	RI	-0.93	0.10	8.13E-08	***
	KM	0.35	0.17	0.06	.
	TR	0.24	0.15	0.13	
	HG	0.01	0.12	0.97	
Sockeye	RI	-0.19	0.22	0.41	
	KM	-0.20	0.22	0.38	
	TR	0.54	0.23	0.03	*
	HG	-0.08	0.23	0.72	
Pink	RI	-0.47	0.26	0.09	.
	KM	0.48	0.26	0.09	.
	TR	0.30	0.30	0.34	
	HG	0.51	0.24	0.06	.
Coho	RI	-0.19	0.32	0.56	
	KM	0.48	0.28	0.12	
	TR	-0.12	0.33	0.73	
	HG	0.55	0.28	0.07	.
Chum	RI	-0.82	0.32	0.05	.
	KM	0.79	0.33	0.06	.
	TR	0.11	0.64	0.87	

Table 3.2. **PP parameter coefficient estimates. Linear correlation structures using hydrological distance were added to Chinook models to account for spatial autocorrelation. Asterisk denotes significance ("***" <0.001, "**" <0.01, "*" <0.05, "." <0.1).**

Species	Parameter	Coefficient	SE	p	Significance
Chinook	RI	-0.37	0.04	1.32E-07	***
	KM	0.15	0.06	0.03	*
	TR	0.04	0.06	0.48	
	HG	0.03	0.05	0.51	
Sockeye	RI	-0.11	0.06	0.10	.
	KM	-0.03	0.07	0.70	

	TR	0.19	0.07	0.01	**
	HG	0.02	0.07	0.74	
Pink	RI	-0.14	0.11	0.23	
	KM	0.14	0.11	0.25	
	TR	0.12	0.12	0.33	
	HG	0.13	0.11	0.25	
Coho	RI	-0.04	0.13	0.79	
	KM	0.18	0.12	0.16	
	TR	-0.12	0.13	0.37	
	HG	0.25	0.11	0.05	*
Chum	RI	-0.34	0.15	0.08	.
	KM	0.35	0.15	0.06	.
	TR	0.12	0.28	0.69	

Figure 3.1. The CV of catch at each management region changes with distance from the ocean for each species: Chinook (A), sockeye (B), pink (C), coho (D), chum (E). Hell's Gate (at 205km) is shown in the dotted line. Points are scaled to the proportion of salmon diversity (populations, conservation units, stocks, subpopulations, spawning locations respectively) that swims by that location.

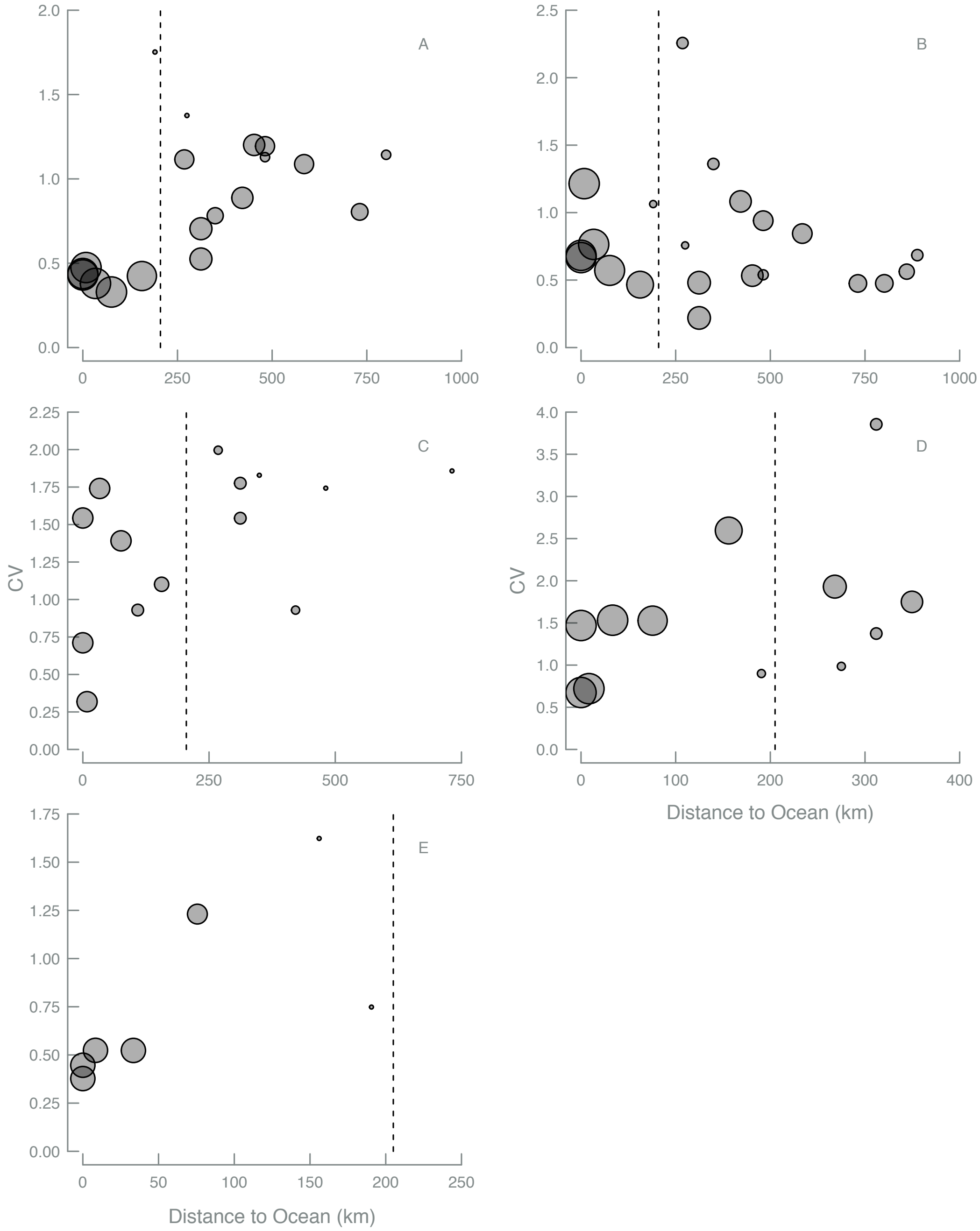
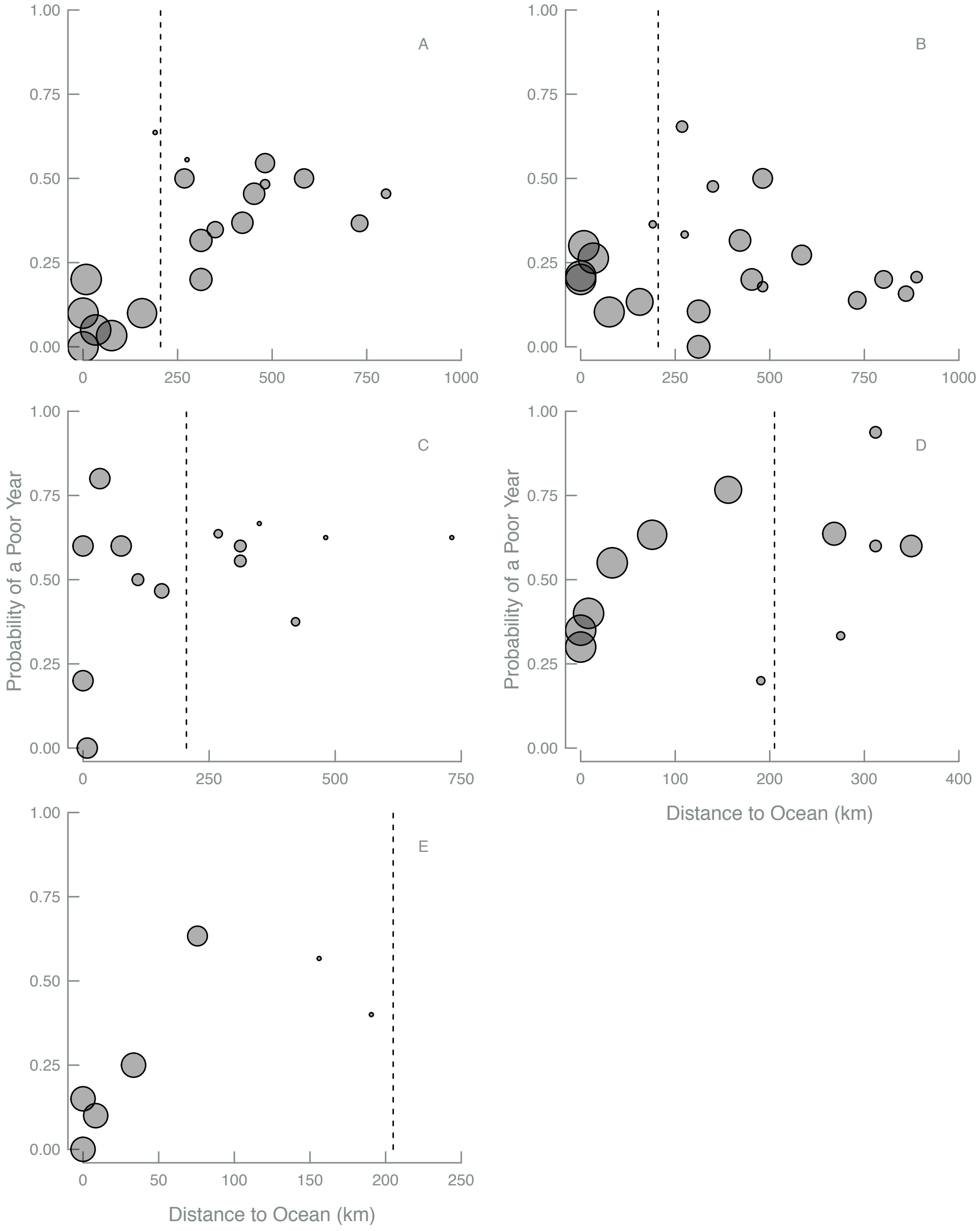


Figure 3.2. The probability of a poor year (PP) at each fishery changes with distance from the ocean for each species: Chinook (A), sockeye (B), pink (C), coho (D), chum (E). Hell's Gate (at 205km) is shown in the dotted line. Points are scaled to the proportion of salmon diversity (populations, conservation units, stocks, subpopulations, spawning locations respectively) that swims by that location.



3.2. Fishing opportunity

Richness and other elements of salmon biodiversity – distance, tributary, and barrier – were significant explanatory variables of FSC opportunity but their significance varied depending on the species (Table 3.3). Richness was the most ubiquitous significant explanatory variable of opportunity, having a significant positive effect on fishing opportunity for sockeye ($p<<<0.001$), pink ($p=0.003$), coho ($p=0.04$), and chum fisheries ($p<0.001$) (Table 3.3). Indeed, fisheries with access to maximum richness had 3.9, 1.8, 3, 1.1, and 1.6 times more mean fishing opportunity than fisheries accessing minimum richness for Chinook, sockeye, pink, coho, and chum fisheries respectively (Figure 3.3).

Fishing opportunity in regions farther from the ocean decreased across all species (Figures 2.1B, 3.3). For example, Chinook fisheries near the mouth of the river (Figures 2.1B(x), 3.3A) had 5.4 times longer mean fishing season than fisheries in the headwaters (Figures 2.1B(i), 3.3A). This trend is true across all species examined: sockeye, pink, coho, and chum fisheries at the mouth of the Fraser had 1.9, 4.2, 6.1, and 2 times the opportunity than the most upstream fisheries for each species (Figure 3.3). For example, opportunity decreased with increasing distance to the ocean for coho fisheries ($p=0.03$; Table 3.3). Although opportunity decreased as richness decreased throughout the watershed, models predicted increasing opportunity with increasing distance for sockeye and chum fisheries ($p<0.001$, $p=0.003$ respectively; Table 3.3).

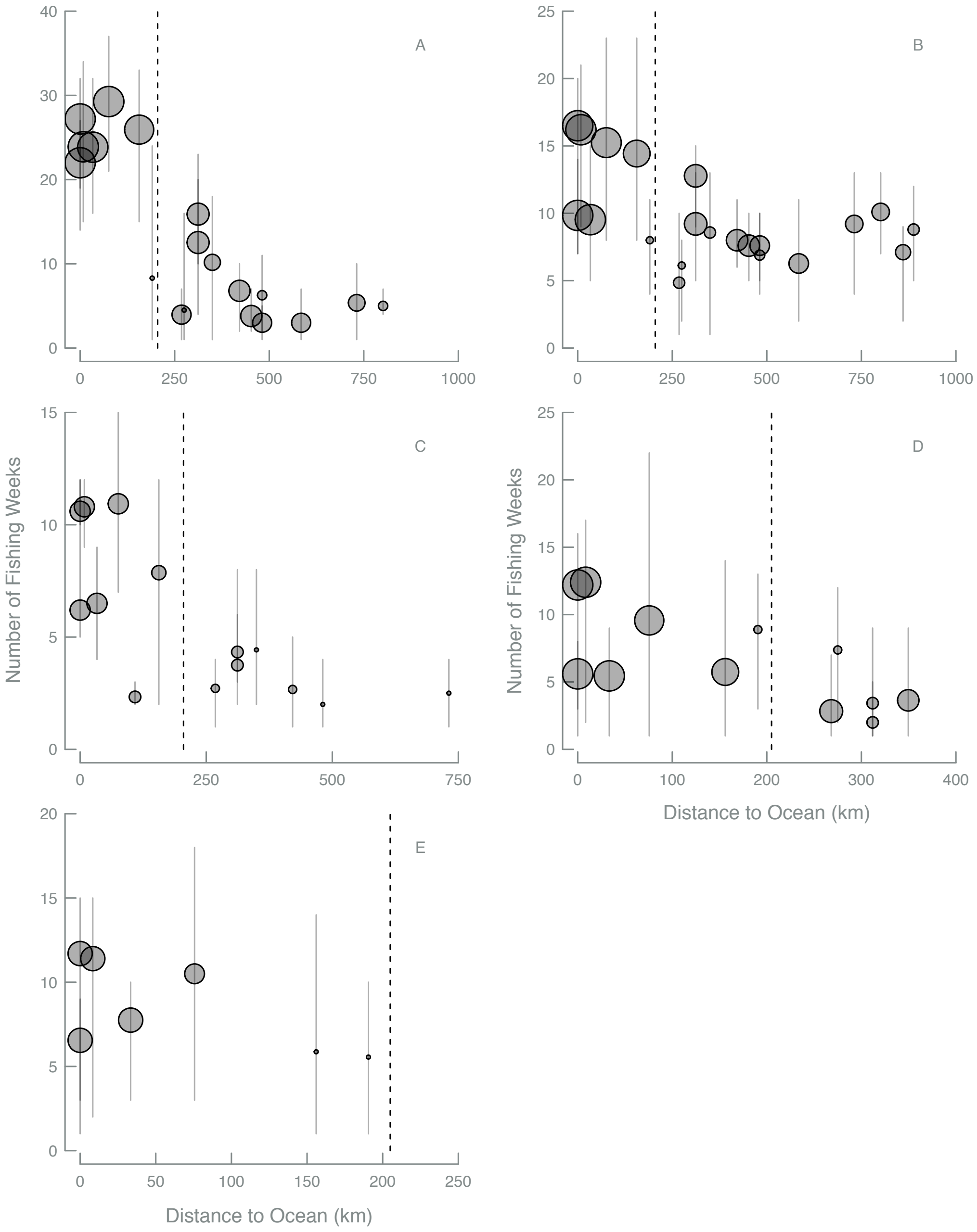
Opportunity decreased upstream of Hell’s Gate for all fisheries but chum which are not caught above the barrier (Figure 3.3). Hell’s Gate was a significant explanatory variable of fishing opportunity for Chinook and sockeye fisheries having a large negative significant effect on opportunity upstream of the barrier ($p<<<0.001$; Table 3.3). Furthermore, fisheries downstream of Hell’s Gate had 3, 1.5, 2.5, and 2.8 times more mean opportunity than fisheries upstream for Chinook, sockeye, pink, and coho fisheries respectively (Figure 3.3).

Opportunity was lower in tributary fisheries than in that of the mainstem for all species. For example, mean opportunity was significantly lower in tributaries relative to the mainstem for chum fisheries (p<<<0.001; Table 3.3). Indeed, mainstem fisheries had 1.6 times the mean fishing opportunity than tributary fisheries for chum.

Table 3.3. Parameter coefficient estimates were averaged for opportunity models with ΔAICc<4. Asterisk denotes significance ("*" <0.001, "**" <0.01, "*" <0.05, "." <0.1).**

Species	Parameter	Avg coefficients	SE	p	Significance
Chinook	intercept	26.61	1.05	<2.00E-16	***
	RI	-2.44	1.99	0.22	
	KM	-0.30	1.56	0.85	
	TR	-1.42	0.97	0.15	
	HG	-21.23	1.18	<2.00E-16	***
Sockeye	intercept	11.86	0.40	<2.00E-16	***
	RI	4.62	0.95	1.30E-06	***
	KM	2.38	0.63	1.59E-04	***
	TR	-2.78E-03	1.29	1.00	
	HG	-3.28	0.43	<2.00E-16	***
Pink	intercept	6.67	0.65	<2.00E-16	***
	RI	4.01	1.35	3.41E-03	**
	KM	0.38	0.95	0.69	
	TR	-0.08	0.78	0.92	
	HG	-1.78	1.13	0.12	
Coho	intercept	6.38	0.70	<2.00E-16	***
	RI	1.88	0.93	0.04	*
	KM	-2.61	1.21	0.03	*
	HG	-1.17	1.17	0.32	*
Chum	intercept	8.28	0.59	<2.00E-16	***
	RI	7.45	1.90	1.76E-04	***
	KM	5.96	1.94	2.79E-03	**
	TR	-5.15	1.25	7.94E-05	***

Figure 3.3. Fishing opportunity changes with distance from the ocean for each species: Chinook (A), sockeye (B), pink (C), coho (D), chum (E). Hell's Gate (at 205km) is shown in the dotted line. Points represent mean fishing opportunity at each fishery and are scaled to the proportion of salmon diversity (populations, conservation units, stocks, subpopulations, spawning locations respectively) that swims by that location. Lines through points show the range across years of opportunity at that fishery.



4. Discussion

Our study illustrates that salmon biodiversity is strongly related to catch stability and opportunity in First Nations FSC salmon fisheries on the Fraser River, one of the largest remaining free-flowing rivers in the world. Year-to-year catch stability increased with at least one element of salmon biodiversity – either increasing salmon richness, decreasing distance to the ocean, in mainstem fisheries relative to tributaries, or downstream of Hell's Gate (Figure 3, 4) – for both metrics of stability across all species but pink PP. Opportunity decreased with decreasing richness across all species (Figure 5) and richness was the most consistent significant explanatory variable of opportunity for sockeye, pink, coho, and chum salmon. In general, catch stability and opportunity decreased with decreasing richness, with distance from the ocean, in tributaries relative to the mainstem, and upstream of Hell's Gate. These results suggest that diversity, and different types of diversity, are critical for stability and opportunity in a real world context.

Salmon biodiversity drives catch stability across all salmon species fished by FSC fisheries throughout the Fraser River watershed. Because fisheries integrate across varying degrees of branch complexity and the associated asynchrony in dynamics, we hypothesized that catch stability would be conferred to fisheries that were in areas of the Fraser watershed that could integrate across large amounts of diversity through the portfolio effect. Indeed, we found that the strength of the portfolio effect increases along gradients of salmon biodiversity, e.g. with richness and other elements. Catch stability increases in fisheries that can integrate across high amounts of diversity, presumably due to the buffering effects of richness and asynchrony. This compliments other works on ecological portfolio theory in Bristol Bay nicely; not only does biodiversity drive population stability at long time scales (Hilborn *et al.* 2003; Greene *et al.* 2009) and fisheries stability at a large spatial scale (Schindler *et al.* 2010), it also drives fishery stability across different elements of salmon biodiversity and at increasing scales. Using fisheries as integration points of different amounts of biodiversity, we were able to show that portfolio effects are important to fisheries of economical and cultural value (Srivastava & Vellend 2005).

Salmon biodiversity also drives within-year fishing opportunity across all salmon species fished by FSC fisheries throughout the Fraser River watershed. We hypothesized that fisheries integrating across higher richness and asynchronous run-timing would have longer fishing seasons and increased access to fresh fish. While mobile consumers prolong feeding seasons by tracking patterns in the phenological diversity of ephemeral resources (e.g. Mcnaughton 1985; Schindler *et al.* 2013), we show here that salmon fisheries at the mouth of the river can integrate across all of the phenological diversity throughout the watershed because these ephemeral resource pulses are funnelled through the mouth of the river. Alternatively, windows of opportunity are small for fisheries in areas of the watershed that host much less diversity, i.e. in headwaters, tributaries, and above partial barriers. Indeed, we found that fishing opportunity was strongly linked to both salmon population richness as well as the Hell's Gate barrier, depending on the species. For species that possess strongly disparate run-timings, such as Chinook and sockeye salmon (Mckay *et al.* In preparation), the barrier was a significant explanatory variable of fishing opportunity. For the other species, with arguably more subtle differences among populations in run-timing, more general metrics of salmon population diversity were significant explanatory variables of opportunity. Opportunity within a year, an ecosystem function not often examined but of large importance to food security at smaller time scales, also increases with biodiversity.

While our study found strong evidence of biodiversity underpinning fisheries stability and opportunity, some species did not match predictions, providing insight into situations where diversity may not confer increased stability or opportunity. Specifically, sockeye and chum fisheries did not exhibit strong evidence of opportunity decreasing with increasing distance from the ocean – we found the opposite. For sockeye, this relationship might be caused by unequal spatial and temporal distributions in population abundance. For example, the Stuart watershed (888 km from the ocean at its mouth) hosts separate runs in June and in August and the Thompson watershed (268 km from the ocean at its mouth) hosts separate runs in August and September-October (English *et al.* 2011), lengthening the fishing season despite the higher location in the watershed.

Additionally, fishery restrictions and closures downstream to allow fish passage to the spawning grounds might cause an overall decrease in the fishing season for downstream fisheries relative to those farther upstream. For example, DFO restricts and closes fisheries to meet escapement targets of threatened populations; fisheries are restricted downstream of Vedder River (flowing into the Fraser at km 90) to reach targets for Cultus Lake sockeye farther upstream in August and September and non-retention and time/area closures occur to reach conservation targets for Lower and Interior Fraser coho through September and mid-October (Fisheries and Oceans Canada 2013). Although all of our diversity-stability predictions were supported, diversity might not track catch variability in situations where returns are so high that fisheries become saturated and catch data are not representative of population numbers. Indeed, FSC fisheries have similar functional responses to Type II predators, where a higher percentage of the fish population is caught at low abundances and catch asymptotes at a given salmon population size (Peterman 1980), likely a function of handling time and search efficiency limitations (Holling 1959). Because this study uses data from a real-world setting, amounts and elements of salmon biodiversity could not be controlled, introducing possible confounding factors like those mentioned above.

Biodiversity increases both stability and opportunity, but to this point these processes have yet to be explicitly linked. Our results suggest that fisheries with access to high amounts of salmon biodiversity have both increased year-to-year catch stability and within-year opportunity to fish. Further, phenological diversity allows downstream fisheries to integrate across the season, which not only extends their windows of opportunity beyond individual salmon populations but potentially buffers against weeks with poor catches. So while fisheries that integrate across a small watershed might experience instability and poor opportunity, fisheries that integrate across larger watersheds can increase their stability and opportunity by increasing the diversity in their portfolios. However, different elements of salmon biodiversity apparently drive year-to-year stability and within-year opportunity. Specifically, explanatory variables of stability varied in their significance by species, yet richness was the most consistent significant explanatory variable of opportunity across all species.

The stability of salmon fisheries likely contributes to the cultural stability of Fraser River First Nations. This cultural stability has likely arisen in part from the integration of salmon biodiversity, as shown here, but also through trade and cultural practices that further diversified their natural resource portfolios (Campbell & Butler 2010). The resilience of this salmon-people relationship has been attributed to a combination of resource flexibility through switching target species depending on seasonal availability and complex social institutions like harvest regulations, potlatches, and trade that helped hedge against resource scarcity (Campbell & Butler 2010). In other words, people maintained a stable resource portfolio by offsetting decreased windows of opportunity or local resource scarcity through trade and food sharing via family ties (Suttles 1960). For example, Ray (1991) tells how the collapse of a salmon run in their local tributary caused one community to transcend the watershed divide and ask for help from a neighbouring watershed with the understanding that the favour would be returned in the future. Trosper (2003) suggests that trade/sharing across large scales was required for this "buffering system" to work because bad run years occurred throughout a watershed. While anthropologists have examined this relationship qualitatively, there has never been a quantitative linkage between salmon biodiversity and First Nations fisheries stability and opportunity until now.

Our study provides key evidence that riverine structure, and its associated diversity, may strongly influence stability (Moore *et al.* Submitted). The dendritic nature of the Fraser watershed structures the spatial variability of salmon diversity that fisheries integrate across and thus controls the inherent stability of their portfolios. Because watersheds are spatially constrained along a network pathway, the factors that control population presence and synchrony are influenced by fragmentation of the corridor and directionality of water flow and biotic movement (Fagan 2002; Carrara *et al.* 2012). For example, ecological diversity increases with proximity to the outlet (Carrara *et al.* 2012), or as integration across branch complexity increases. Integrating across increased branching complexity confers inherent stability due to aggregation of populations, asynchrony in their dynamics, and the statistical inevitability of averaging the aggregate (Doak *et al.* 1998; Yeakel *et al.* 2014). Indeed, FSC fisheries on the Fraser with the most stable portfolios were in locations that allowed them to integrate across greater richness and interannual asynchrony, e.g. downstream of greater branching complexity.

This study provides critical evidence of the importance of fine-scale salmon biodiversity to food security and cultural stability. As such, scales of conservation need to occur at a fine level to preserve high levels of variability (e.g. Wild Salmon Policy, Fisheries and Oceans Canada 2005). Here we focus on how diversity within fisheries provides a stabilizing effect; however, mixed stock fisheries are fundamentally challenging to manage to avoid wiping out the very diversity that maintains them. Given recent changes in Canadian environmental protection (Favaro *et al.* 2012; Hutchings & Post 2013), there are increasing threats to biodiversity such as the salmon biodiversity that underpins First Nations' fisheries stability and opportunity. Analyzing trade-offs between impacts to ecosystems and fisheries will become increasingly important.

There is growing appreciation that multiple elements of diversity are needed to maintain ecosystem performance (Pasari *et al.* 2013). Our results suggest that different metrics of diversity vary in importance to different ecosystem services (stability and opportunity) and to different species. This conclusion agrees with other recent research; ecosystem function increases across multiple elements of diversity (Naeem *et al.* 2012), including taxonomic (Tilman 1996), functional (Schleuter *et al.* 2010), phylogenetic (Connolly *et al.* 2011), and genetic (Latta *et al.* 2010). Furthermore, multiple ecosystem functions increase simultaneously at high levels of biodiversity (Zavaleta *et al.* 2010). Our results represent an important example that is arguably rare (Srivastava & Vellend 2005) of the importance of biodiversity to stability on a management-relevant topic and scale. Conservation of multiple elements of fine-scale diversity – populations, life histories, habitats – will help maintain the stability of culturally important ecosystem services such as fisheries.

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Appendix A.

Supplemental table

Table A1. **Top candidate sets (ΔAICc<4) for opportunity models.**

Species	Top Models (ΔAICc<4)	Random	Variance	AICc	ΔAICc	Weight
Chinook	HG + KM + RI + TR	1 + HG + RI | year	varIdent (form = ~ 1 | RI)	1873.8	0.00	0.32
	HG + TR + RI			1874.8	1.05	0.19
	HG + KM			1875.1	1.38	0.16
	HG + KM + RI			1876.1	2.32	0.10
	HG			1876.4	2.68	0.08
	HG + RI			1876.5	2.75	0.08
	HG + TR + KM			1877.6	3.81	0.05
Sockeye	HG + KM + RI	1 + RI | year	varIdent (form = ~ 1 | fishery	1835.1	0.00	0.49
	HG + KM + RI + TR			1835.9	0.78	0.33
	HG + TR			1838.3	3.18	0.10
Pink	HG + RI	1 + RI | year	varPower (form = ~ KM)	482.2	0.00	0.27
	HG + KM + RI			482.9	0.72	0.19
	HG + TR + RI			483.5	1.31	0.14
	HG + KM + RI + TR			483.9	1.66	0.12
	RI			484.0	1.77	0.11
	KM + RI			485.0	2.78	0.07
	TR + RI			485.4	3.19	0.05
	TR + KM + RI			485.8	3.61	0.04
Coho	HG + TR + KM	1 + HG | year	none	885.9	0.00	0.44
	TR + KM			886.6	0.68	0.31
	HG + KM			889.0	3.05	0.10
	TR			889.4	3.49	0.08
	HG + TR			889.5	3.58	0.07
Chum	TR + KM + RI	1 | year	varIdent (form = ~ 1 | RI)	620.2	0.00	0.99

Appendix B.

First Nations fisheries on the Fraser: A brief historical and legal context, management now and future implications

Historical context

Salmon have sustained aboriginal people throughout the Pacific Rim for millennia. Historically supporting the second highest densities of aboriginal peoples in North America next to California (Ubelaker 2006), people of the northwest coast from northern California to Alaska cumulatively consumed an estimated 46 to 69 thousand tons of salmon per year in pre-contact years (Haggan et al. 2006), approximately equal to the average annual commercial catch of 64 thousand tons from 1901 to 2000 (Jones 2002). The resilience of this salmon-people relationship has been attributed to a combination of resource flexibility through switching target species depending on seasonal availability and complex social institutions like harvest regulations, potlatches, and trade that helped hedge against resource scarcity (Campbell & Butler 2010). In other words, people maintained a stable resource portfolio by offsetting decreased windows of opportunity or local resource scarcity through trade and food sharing via family ties (Suttles 1960). For example, Ray (1991) tells how the collapse of a salmon run in their local tributary caused one community to transcend the watershed divide and ask for help from a neighbouring watershed with the understanding that the favour would be returned in the future. Trosper (2003) suggests that trade/sharing across large scales was required for this "buffering system" to work because bad run years occurred throughout a watershed.

Aboriginal fisheries have changed substantially since European contact. Prior to the arrival of Europeans, individuals, families, or entire tribes had informal property rights to fish in the river using weirs and traps (Higgs 1982; Schwindt 1995; Weinstein 2000). With the arrival of European fishers came new fishing technology which allowed fishers to move farther out to sea in small boats, essentially "leapfrogging" aboriginal fisheries and effectively reducing the ability of aboriginals to catch fish (Schwindt 1995). By the late 1800s, the commercial fishery was dominated by small boats in the sea or mouth of the Fraser and it was clear that open access was a serious problem for both fishers (who were/are competitively excluding one another) and salmon populations (which were/are declining) (Fraser 1977). Because of these problems and others like them across Canada, the Department of Marine and Fisheries (now known as Fisheries and Oceans Canada) was created in 1867 as the federal regulating body responsible for marine fisheries management. Since then, federal regulators have been attempting to address the social, economic, and biological complications of these fisheries using tools like entry restrictions and gear limitations on both commercial and aboriginal fisheries. So although fisheries on the Fraser were initially sustainable for millennia despite high fishing pressure, aboriginal ability to catch fish was out-competed through small-boat fisheries leapfrogging traditional river fishing, and when that was deemed unsustainable, fisheries management was subsequently controlled by top-down approaches – approaches that are currently being questioned for their lack of effectiveness today.

Legal context

"Sea Coast and Inland Fisheries" are under federal jurisdiction according to section 91 of the *Constitution Act*, 1867. Fisheries and Oceans Canada (DFO) is a federal agency that has been appointed to manage ocean and inland fisheries. The authority of the DFO Minister stems from the *Fisheries Act*, by which he or she is granted discretionary powers to regulate and enforce fisheries policies and practices, while being held accountable for the protection of fish resources and habitat. In addition to the *Fisheries Act*, the Minister is also enabled through the *Species at Risk Ac*t (SARA), the *Oceans Act*, the *Canadian Environmental Assessment Act* (CEAA), the *Canadian Environmental Protection Act* (CEPA), and several other pieces of legislation.

Policies and practices of DFO must be in accordance with Section 35 of the *Constitution Act*, 1982, "Rights of the Aboriginal Peoples of Canada", which recognizes and affirms aboriginal rights and title. Following *R. v. Sparrow*, 1990 SCR 1075, the Supreme Court of Canada found that aboriginal groups have the right to fish for food, social, and ceremonial (FSC) purposes and that this right is second only to conservation. In response to this judgment, DFO developed the Aboriginal Fisheries Strategy (AFS) in 1992 to manage, in order of priority, the conservation of fish, FSC fisheries, and commercial and recreational fisheries. Additionally, according to *Haida Nation v. British Columbia (Minister of Forests)*, 2004 SCC 73, there is a constitutional obligation, in the "honour of the Crown," to consult with First Nations when the outcome of a decision has the potential to impact aboriginal rights and title.

Until recently, FSC fisheries have not been permitted to sell or trade their catch, restricted to using catch for mostly subsistence purposes. However, First Nations have argued that this restriction infringes on their constitutional right of culture. In particular, five First Nations on Vancouver Island (together known as the Nuu-chah-nulth) have made the legal case that because trade of marine commodities existed in their culture and supported their economies long before European contact, they should have the right to sell their catch in a commercial fishery. After 10 years of litigation, the Nuu-chah-nulth have recently had their economic fishing rights recognized by Canadian law. The original ruling by the BC Supreme Court in 2009, relying on historic trade records and accounts, found that the bands "have aboriginal rights to fish for any species of fish in the environs of their territories and to sell fish" (*The Ahousaht et al. v. The A.G.of Canada*, 2009 BCSC 1673). BC Supreme Court Justice Nicole Garson concluded "that the plaintiffs have proved that Canada's fisheries regulatory regime infringes their aboriginal rights to fish and to sell fish by their preferred means, both legislatively and operationally" but that First Nations do not have unrestricted commercial rights. She added that DFO is still the regulating body of all fisheries and urged First Nations to negotiate fisheries management and commercial sales practices. The Supreme Court of Canada upheld her judgement – that the bands have aboriginal rights to a commercial fishery – on January 30, 2014 through the dismissal of the federal government's appeal (*Attorney General of Canada v. Ahousaht Indian Band et al*., 2014 SCC 3511*)*.

Management now

DFO manages aboriginal fisheries under the AFS. The AFS only applies to fisheries that are not managed by other land claim agreements – thus in the case of BC the AFS applies to most aboriginal fisheries. The objectives of the AFS are:

- To provide a framework for the management of fishing by Aboriginal groups for food, social and ceremonial purposes.
- To provide Aboriginal groups with an opportunity to participate in the management of fisheries, thereby improving conservation, management and enhancement of the resource.
- To contribute to the economic self-sufficiency of Aboriginal communities.
- To provide a foundation for the development of self-government agreements and treaties.
- To improve the fisheries management skills and capacity of Aboriginal groups.

With these objectives, DFO and a First Nation negotiate the management and regulation plans of a fishery. In cases where an agreement is reached, DFO issues communal fishing licences for FSC fisheries in accordance with the Aboriginal Communal Fishing Licences Regulations. In cases where an agreement is not reached, DFO issues licences with provisions that the Minister deems consistent with Canadian law. Although most licences issued are for FSC fisheries, some economic opportunity licences are also issued (Fisheries and Oceans Canada 2012).

Implications for future management

This work shows that biodiversity promotes stability and opportunity in FSC fisheries on the Fraser River. From that conclusion, there appear to be two major implications: 1) conservation of fine-scale biodiversity is critical for this culturally important ecosystem service and using guidelines set out in the Wild Salmon Policy will likely help meet sustainability objectives, and 2) alternative management strategies are needed to buffer the social effects of access to low salmon biodiversity.

The current spatial structure of most fisheries makes them inherently challenging to manage for maintaining fine-scale biodiversity. Because most salmon fisheries are in the ocean or at the mouth of the river, they have access to all of the salmon populations that spawn throughout the watershed. This method results in “mixed-stock” fisheries where multiple stocks of fish are being caught at one time, in one place (Paulik et al. 1967). Efficient for catching a lot of fish over long seasons, the downside of these mixed stock fisheries is that it is challenging to reduce fishing impacts on threatened populations because fishing pressure is not specific to any one population (Hilborn 1975). So while these fisheries might have access to high amounts of salmon biodiversity, they can in fact decrease the salmon biodiversity from which they reap the benefits.

Conservation of fine-scale diversity may require a fundamental shift in fisheries spatial arrangement and management. For example, in an attempt to mitigate for the impacts of mixed-stock fisheries, a commercial fishery in the Skeena River (BC) was moved farther upstream to better target specific populations and reduce by-catch of threatened populations. Recognizing that this movement to more terminal locations in the watershed limits a fishery’s interannual catch stability and within-year fishing opportunity, policies are being discussed to permit catch trade as a method of buffering against resource scarcity. In this way, biodiversity conservation is maintained by physically moving fisheries to places where management is more population specific and stability/opportunity is maintained through trade. Thus, long-term resource scarcity is buffered through biodiversity conservation and short-term resource scarcity is buffered through social institutions like trade. An effective solution, this strategy is nothing new. It reflects the structure of aboriginal fisheries historically, which were located in-river and where local shortages were supplemented through trade and reciprocity across the region.

Alternative aboriginal fisheries management strategies across BC are possible in this current social climate. The recently upheld judgement of *The Ahousaht et al. v. The A.G.of Canada* case might set a precedent for aboriginal commercial fisheries in regions other than those on Vancouver Island, as pre-contact aboriginal trade was quite extensive across all of BC (the most famous trade routes being the eulachon “grease trails”). In the Skeena, this verdict means linking terminal aboriginal fisheries with trade might be legally possible – a win-win for both biodiversity and culture. This coupled strategy might be useful in other watersheds also, like that of the Fraser. If this coupled strategy moves forward, managing subsistence and commercial aboriginal fisheries separately will be counterintuitive because catch from subsistence fisheries could be commercially traded in some years and not others depending on the need at that location and in other locations throughout the watershed. As such, community licence negotiations should consider not only catch allocation, but also interannual catch stability/within-year fishing opportunity at their location. In this way, they will better anticipate trading networks and needs. Furthermore, community licence negotiations would be much more effective if they were done at the watershed scale, because of the spatial relationship of catch amounts, stability, and opportunity, rather than between individual communities and DFO. Although it is certainly challenging to negotiate across such a large and diverse stakeholder group, it is possible and the feasibility of which is worth investigating.

Here we show that biodiversity and fisheries stability/opportunity are linked and suggest that management strategies also reflect that coupled structure through biodiversity prioritization actions like movement to terminal fisheries and buffering actions like legal trade. Returning to historical management systems that were resilient for millennia might be an effective management solution in this time of biodiversity loss and resource uncertainty (Trosper 2003).

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