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Species and population diversity in Pacific salmon fisheries underpin indigenous food security

Holly K. Nesbitt[1]* and Jonathan W. Moore[2]

[1]*School of Resource and Environmental Management, Simon Fraser University, 8888 University Dr, Burnaby BC V5A 1S6, Canada; and* [2]*Department of Biological Sciences and School of Resource and Environmental Management, Earth to Ocean Research Group, Simon Fraser University, 8888 University Dr, Burnaby BC V5A 1S6, Canada*

Summary

1. Indigenous people are considered to be among the most vulnerable to food insecurity and biodiversity loss. Biodiversity is cited as a key component of indigenous food security; however, quantitative examples of this linkage are limited.

2. We examined how species and population diversity influence the food security of indigenous fisheries for Pacific salmon (*Oncorhynchus* species). We compared two dimensions of food security – catch stability (interannual variability) and access (season length) – across a salmon diversity gradient for 21 fisheries on the Fraser River, Canada, over 30 years, using linear regression models. We used population diversity proxies derived from a range of existing measures because population-specific data were unavailable.

3. While both population and species diversity were generally associated with higher catch stability and temporal access, population diversity had a stronger signal. Fisheries with access to high species diversity had up to 1·4 times more stable catch than predicted by the portfolio effect and up to 1·2 times longer fishing seasons than fisheries with access to fewer species. Fisheries with access to high population diversity had up to 3·8 times more stable catch and three times longer seasons than fisheries with access to fewer populations.

4. Catch stability of Chinook *Oncorhynchus tshawytscha* and sockeye *Oncorhynchus nerka* fisheries was best explained by the number of populations and conservation units, respectively, that migrate past a fishery en route to spawning grounds. Similar population diversity metrics were important explanatory variables for season length of sockeye, pink *Oncorhynchus gorbuscha*, coho *Oncorhynchus kisutch* and chum *Oncorhynchus keta* fisheries.

5. *Synthesis and applications*. We show an empirical example of how multiple scales of biodiversity support food security across a large watershed and suggest that protecting fine-scale salmon diversity will help promote food security for indigenous people. The scales of environmental assessments need to match the scales of the socio-ecological processes that will be affected by development. We illustrate that upstream projects that damage salmon habitat could degrade the food security of downstream indigenous fisheries, with implications to Canadian indigenous people and to watersheds around the world where migratory fishes support local fisheries.

Key-words: aboriginal, biodiversity, diversity–stability, First Nations, portfolio effect, rights and title, small-scale fisheries, subsistence, traditional, watershed management

Introduction

Food security, a fundamental human right, is comprised of not only the amount of food available, but also people's ability to access food and the stability of availability and access over time (FAO, IFAD & WFP 2014). There is emerging empirical evidence that links biodiversity to these different dimensions of food security. For example, population diversity stabilizes annual catches of sockeye salmon by commercial fisheries in Alaska (USA) (Schindler *et al*. 2010) through the statistical averaging of the portfolio effect (PE) (Doak *et al*. 1998). This same population diversity also impacts other dimensions of food security – these commercial sockeye salmon fisheries have

*Correspondence author. E-mail: nesbitt.holly@gmail.com

extended access to fish because they can integrate across different run-timings of different populations (Schindler *et al.* 2010). However, it is unclear how multiple levels of diversity (i.e. population vs. species) and different amounts of diversity contribute to food security.

Biodiversity loss disproportionately impacts people and cultures that rely directly on natural resources, such as many indigenous groups with subsistence diets (MEA 2005). Indigenous people are often described as the descendants of those who lived in a place prior to colonial invasion and identify as having a distinct culture from the dominant society that now occupies that place. An estimated 370 million people in the world are indigenous, making up over 5000 groups of indigenous people in 90 countries (UNPFII 2009). Traditional food systems not only support food security of indigenous people, but are also tightly linked to culture, land and self-determination (Kuhnlein *et al.* 2012). While there is general appreciation that subsistence food security rests on having a diversity of options as a safety net against interannual and seasonal resource shortages (MEA 2005; Bharucha & Pretty 2010), there remains a need to quantify how different types of diversity influence the different dimensions of indigenous food security. There is growing appreciation that multiple elements of diversity are needed to maintain ecosystem performance (Naeem, Duffy & Zavaleta 2012) and these results can likely be extended to services like subsistence food provisioning.

Indigenous salmon fisheries in western North America are an important socio-ecological system to study how diversity might influence food security. Salmon are a keystone of coastal indigenous people's diets and cultures (Garibaldi & Turner 2004). According to a recent study of traditional food use in British Columbia (BC), Canada, indigenous people consumed salmon 47 days $year^{-1}$ on average and salmon consumption represented 5·3% of protein and 45·5% of vitamin D intake (Chan *et al.* 2011). Yet 41% of indigenous households were food-insecure (Chan *et al.* 2011). Indigenous salmon fisheries are often located throughout watersheds and have access to different levels of salmon diversity based on their locations (Harris 2001; Moore *et al.* 2015). For instance, 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 salmon species and populations and thus fish from a much less diverse portfolio. In this system, biodiversity could impact both the stability and access dimensions of food security. Biodiversity may create a stabilizing effect on indigenous food security through the PE (Doak *et al.* 1998). Biodiversity may also extend fishing seasons (access) by integrating across different species and populations that migrate to their spawning grounds at different times.

Here, we examine how species and population diversity are associated with indigenous food security in the Fraser River, BC. We focus on interannual variability as a metric of fishery stability and seasonal duration as a metric of temporal access to fresh salmon within a year. We predict that fisheries with access to greater salmon diversity exhibit a stronger PE in their catch and thus higher stability than fisheries with access to a less diverse salmon portfolio both among and within species. Additionally, we predict that fisheries with access to high salmon diversity have longer fishing seasons, as they integrate across diverse run-timings both among and within species. Given that salmon are a key part of traditional diets (Chan *et al.* 2011), the prevalence of food insecurity in Canadian indigenous households is double that of all households (Tarasuk, Mitchell & Dachner 2014) and shifts towards market foods have arguably increased chronic lifestyle diseases (e.g. diabetes, obesity) (Kuhnlein *et al.* 2004), these results have relevance to the food security and health of indigenous communities. Indigenous food, social and ceremonial (FSC) fisheries are protected by Canadian law; thus, these findings have implications for indigenous rights and title.

Materials and methods

THE FRASER RIVER WATERSHED AND FSC FISHERIES

We focused on First Nations (indigenous communities) salmon fisheries within the Fraser River watershed (Fig. 1) and the access and stability dimensions of food security. We aimed to decompose the degree to which species-level and population-level diversity underpin these aspects of food security. The mainstem of the Fraser is the second longest dam-free salmon migration route in North America (1370 km). Pacific salmon (*Oncorhynchus* species), including *Oncorhynchus tshawytscha* (Chinook), *Oncorhynchus keta* (chum), *Oncorhynchus kisutch* (coho), *Oncorhynchus gorbuscha* (pink) and *Oncorhynchus nerka* (sockeye) Walbaum, spawn throughout the watershed and are caught by commercial, recreational and First Nations fisheries.

Fraser FSC fisheries are grouped regionally and managed by First Nations and Fisheries and Oceans Canada (DFO). Catch reports are publicly available online and upon request (Fisheries and Oceans Canada 2015). Management and effort data were not consistently available; thus, we focused on catch. For each region, we acquired weekly catch totals from 1983 to 2012 for Chinook (Fig. 2), chum, coho, pink and sockeye salmon. DFO manages fisheries and catch data by species, but in most regions more than one species is caught. We perform analyses on both single-species fisheries (population-level) and multispecies fisheries by amalgamating catches across species for each region (species-level). Regional delineation changed historically, necessitating consolidation of catches across regions to make consistent comparisons. We consolidated catch if two adjacent regions were grouped in some years and not in others. Regions were removed from the analysis if there were too few years of data (<¼ of the 30 years) or if mean catch in that region was <20 fish, leaving a total of 21 regions. These regions ranged from those near the base of the watershed to those near the headwaters, thereby integrating different levels of species and population diversity. All measures for pink salmon were determined for odd years only

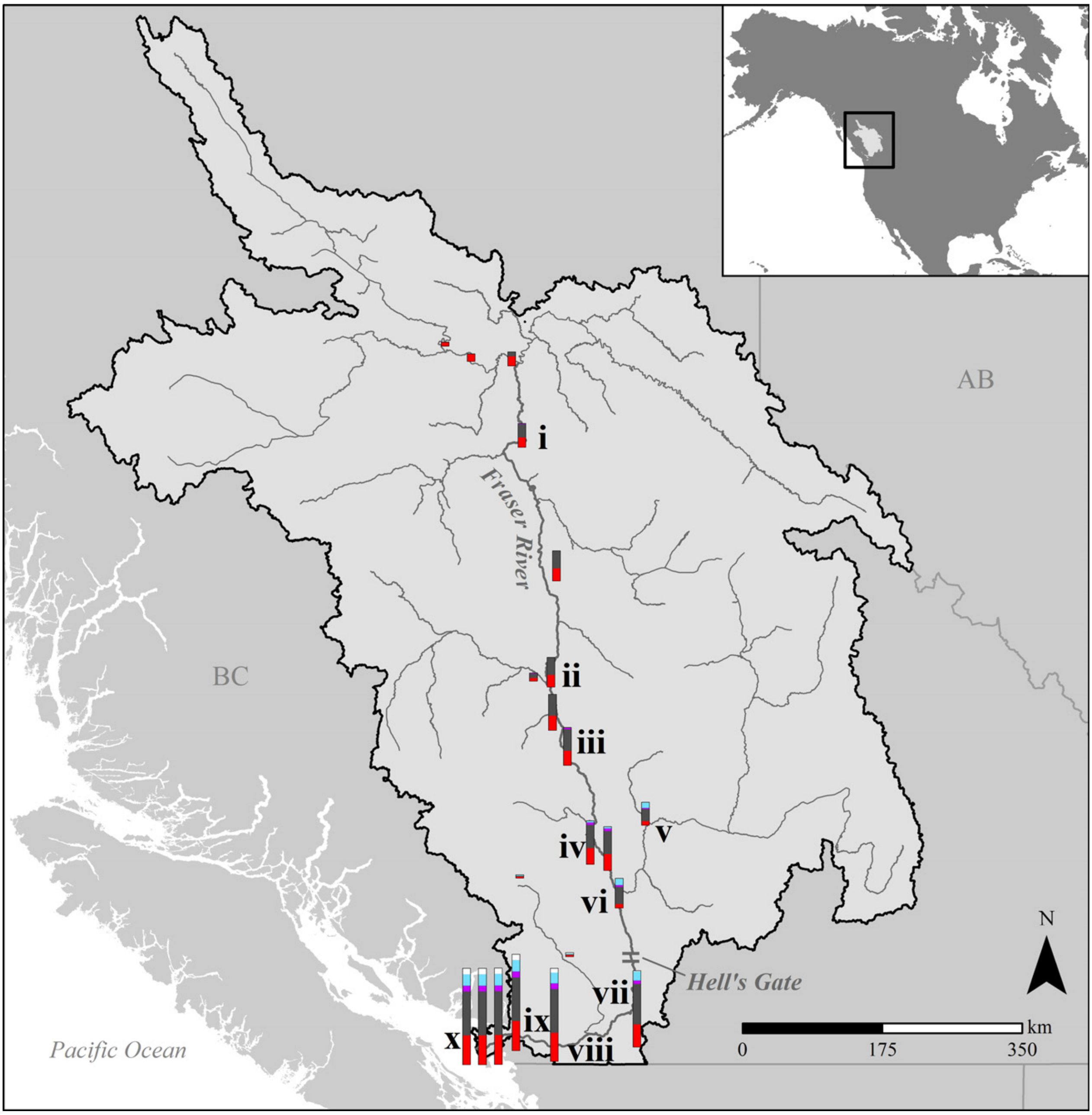

Fig. 1. The Fraser River watershed in British Columbia (BC), Canada. The downstream point of each fishery region is marked with a bar. Roman numerals (i–x) correspond to fisheries highlighted in Fig. 2. Colours are scaled to sockeye (red), Chinook (grey), pink (purple), coho (blue) and chum (white) richness (Table S2).

because pink salmon have a 2-year life cycle and return to the Fraser almost exclusively in odd years.

FOOD SECURITY OF FISHERIES

We considered the effects of species and population diversity on the food security of First Nations salmon fisheries by quantifying interannual catch stability and fishing season length. Interannual catch stability captures the consistency over time of both food availability and access, an indication of the stability dimension of food security. To measure stability, we used the coefficient of variation (CV) of interannual catch to quantify the variation in observations relative to the mean (e.g. Tilman 1996; Schindler *et al.* 2010). Season length is a metric of the access dimension of food security and was calculated as the number of weeks that fish were caught in a region. While preserving fish is feasible by drying, smoking, canning and freezing, the duration of the fish season is a metric of access to fresh fish.

SPECIES DIVERSITY

Interannual catch stability

We examined how species diversity influenced interannual catch stability by calculating the PE in each region. We defined species diversity as the number of species that a fishery caught. To

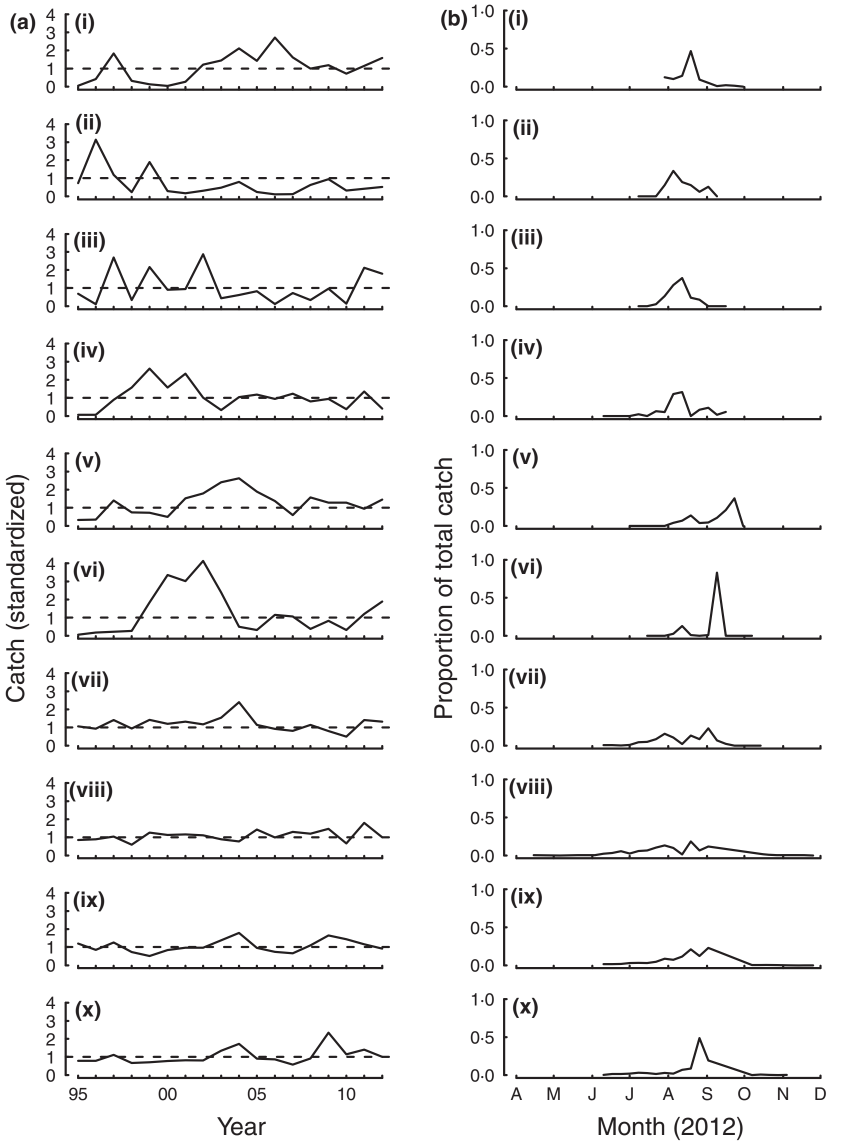

Fig. 2. (a) Standardized Chinook catch at each fishery from 1995 to 2012. A fishery's catch was standardized by dividing by the mean catch across years at each site. Standardized catch below 1 indicates a below average year and above 1 indicates an above average year. Each graph is a different fishery 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 Fig. 1. (b) Proportion of total Chinook catch at each fishery in 2012.

compare across species, we converted catch from numbers to kilograms of fish using average masses for each species (Ricker 1981). The PE is the degree to which diversity decreases variability (Schindler *et al.* 2010; Anderson, Cooper & Dulvy 2013) and was calculated for each region (i) as the difference between the predicted CV assuming no asynchronous asset dampening [equivalent to the weighted average of the CVs for each species (CV_j), weighted by their proportional catch biomass (X_j)] and the observed CV (CV_{obs}) of total catch biomass (all species combined):

$$PE_i = \sum_{j=1}^{n} X_j \mathrm{CV}_j - \mathrm{CV}_{obs}$$

Accordingly, PE is the additional stability conferred to the aggregate than would otherwise be expected based on the sum of its component parts. When PE is >0, the predicted CV is higher than the observed, evidence that asynchronous dynamics are stabilizing the aggregate.

We examined the hypothesis that the PE would be more positive in fisheries that were closer to the ocean and that integrated more species diversity. We compared two linear and two broken-stick models (SiZer package; Sonderegger 2012) with explanatory variables of fishery distance from the ocean or species diversity using R (R Development Core Team 2011) (five models including the null). A linear relationship would suggest that any incremental diversity change influences the PE, while the broken-stick relationship (slope differs before and after a change point) could suggest that biodiversity-benefits asymptote (Tilman 1996; Doak *et al.* 1998). We did not find significant spatial autocorrelation in these data. Models were compared based on differences in the Akaike Information Criterion corrected for small sample sizes (ΔAIC_c); the probability of a model being the best out of those examined was determined with Akaike weights (w_i) (Burnham & Anderson 2002).

Fishing season length

We examined how species diversity influenced temporal access to salmon, measured as the fishing season length. Specifically, we calculated the impact of species diversity on season length (D) in each region (i) by comparing the difference between the mean number of weeks that salmon, aggregated across all species, were caught in each region (A_{tot}) to the maximum mean number of weeks across individual species that fish were caught in each region (A_i):

$$D_i = A_{tot} - \max(A_i)$$

Because we had multiple years, we used the average season length across years for both A_i and A_{tot}. To prevent skews in the average across years, we removed years where there should have been more than two species caught in that region but there was only one due to missing data. Following our approach with PE, we examined how distance from the ocean and species richness affected the impact of species diversity on season length, comparing linear, broken-stick and null models. We did not find significant spatial autocorrelation in these data.

POPULATION DIVERSITY

We examined how population diversity contributes to stability and seasonal duration of fisheries within specific salmon species. Because dynamics of the component populations are unknown, we were not able to quantify PEs within salmon species. Instead, we examined how catch stability and temporal access are associated with the proxies/drivers of population diversity below (see Table S1, Supporting Information) because populations are often uniquely adapted to their local habitats driving variability in life-history traits (Taylor 1991) and asynchronous dynamics (Braun *et al.* 2015).

1. Richness. We determined how much population diversity each fishery could access using the finest scale of information available and defined this proxy as ‘richness’. Chinook, sockeye, coho, pink and chum salmon richness were measured as the number of populations (Parken *et al.* 2008), conservation units (Holtby & Ciruna 2008), subpopulations (Interior Fraser Coho Recovery Team 2006), stocks (Northcote & Larkin 1989) and major spawning locations (Salo 1991) upstream of a fishery, respectively. For example, Chinook richness at a fishery was measured as the number of populations that migrate past that fishery en route to spawning grounds. We hypothesized that interannual catch stability and within-year fishing season would decrease with decreasing fishery access to richness.

2. Distance. We determined fishery distance from the ocean along the Fraser network. Salmon richness and run-timing diversity decrease towards the headwaters as populations disperse throughout the watershed to spawn (Olsen *et al.* 2010). We hypothesized that interannual catch stability and within-year fishing season would increase in fisheries closer to the ocean because they integrate across the diversity of the entire watershed.

3. Tributary. We designated fisheries as either tributary or mainstem. 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 a smaller fishing season within a year than mainstem fisheries.

4. Barrier. We designated fisheries as either up or downstream of a partial barrier, Hell’s Gate, on the Fraser to examine how a landscape filter can alter diversity and fisheries (e.g. Poff 1997). Hell’s Gate is a narrow canyon with high water velocities which can create challenges to upstream salmon migration during high flow periods and acts as a selection pressure for certain life histories such as run-timing (Pess *et al.* 2012). We hypothesized that fisheries upstream of Hell’s Gate would be less stable in their catch across years and have smaller fishing seasons than fisheries downstream of the barrier.

We predicted that these elements of population diversity would vary by species in their importance due to differences in species life histories and physiology.

Interannual catch stability

We examined how catch stability changed across fisheries that incorporated different proxies/drivers of population diversity. We quantified fishery stability by its CV. Threshold metrics of stability, based on the probability of a poor fishing year, were similar to the CV analysis and so are not shown. To determine the elements that had an effect on CV, we compared generalized least squares models (nlme package; Pinheiro *et al.* 2011) with explanatory variables of richness, distance, tributary and barrier for each species. Because the maximum number of observations for a species was 21 (fishery regions), we compared one-parameter models with each of the explanatory variables for a total of five models per species, including the null model. Richness and distance were numeric vectors standardized by centring and dividing by two standard deviations. Barrier and tributary were binary factors. We log-transformed CV to normalize its distribution. We tested for heteroscedastic variance in model fit but were unable to add more specific variance structures due to sample size. CV residuals were significantly spatially autocorrelated according to Moran’s I for Chinook fisheries, so we included a linear correlation structure using hydrological distance, selected by the highest support from AIC_c, in those models. Parameter coefficients were estimated with restricted maximum likelihood (REML), models were ranked with ΔAIC_c, and the probability of a model being the best out of those examined was determined with Akaike weights (w_i) (Burnham & Anderson 2002).

Fishing season length

We examined how fishing season duration changed across fisheries that incorporated different elements of population diversity. Season length was measured as the number of weeks that fish were caught in a region. We built linear mixed-effects models (nlme package; Pinheiro *et al.* 2011) to determine which explanatory variables had an effect on season length. Models contained all combinations of the proxies/drivers of population diversity for a total of 10 models for chum and 16 models for each of the other species, including the null models (no interactions). Richness and distance were highly correlated for pink, coho and chum ($r = -0{\cdot}86$, $-0{\cdot}83$ and $-0{\cdot}98$, respectively); thus, it was difficult for those models to differentiate between these two variables. We included year as a random intercept term to account for repeated measurements over time at each fishery. Random slopes were included if those models had the highest support through AIC_c ranking (Table S2). Heteroscedastic variances in residuals were modelled through a variance structure selected by highest AIC_c support (Table S2). We did not find significant spatial autocorrelation in these data. Models were ranked by ΔAIC_c, parameter coefficients were estimated with REML and averaged across top models ($\Delta AIC_c < 4$), and relative variable importance was determined with Akaike weights (w_{ip}) (Burnham & Anderson 2002).

Results

SPECIES DIVERSITY

Interannual catch stability

Species diversity substantially stabilized FSC catch in downstream fisheries that integrated several salmon species (Fig. 3a). The PE decreased as fisheries were farther from the ocean and integrated fewer salmon species (Fig. 3a). This relationship was best explained by the linear model with distance as the explanatory variable (w_i = 0·43, adjusted r^2 = 0·39), which was similar to the distance broken-stick model (w_i = 0·35) and better than the other models (w_i < 0·2) (Tables 1 and S3). Fisheries with access to all five species of salmon had CVs that were up to 1·4 times more stable than predicted (PE as high as 0·28), whereas fisheries with access to fewer species had a smaller stabilizing PE.

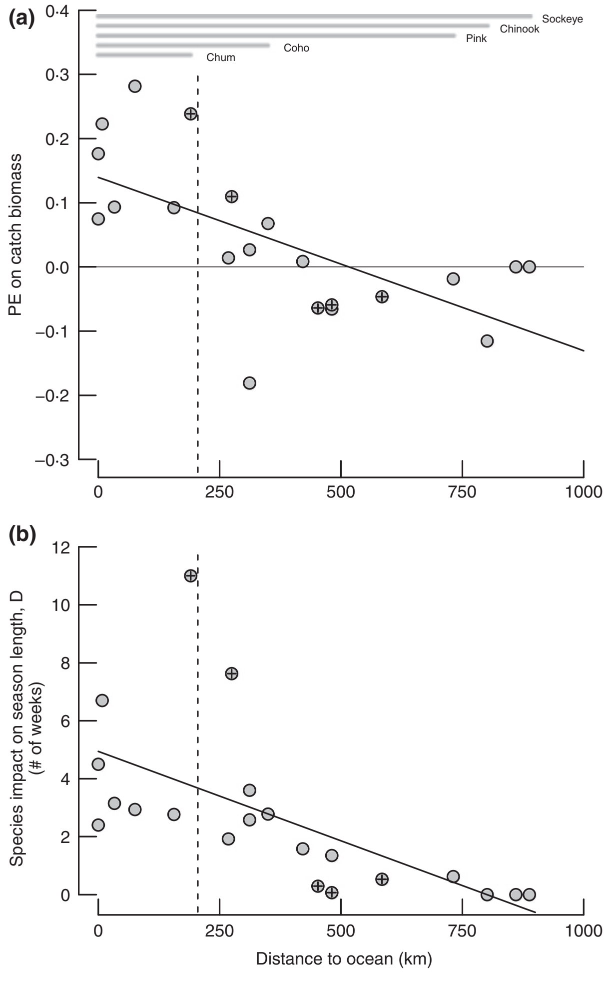

Fig. 3. Species diversity effects on the stability of catch biomass, portfolio effect (a), and fishing season length, D (b), at each fishery. Grey horizontal bars at the top of the figure indicate the spatial distribution of species in the catch record (e.g. chum were not caught above Hell's Gate, while sockeye were caught the farthest upstream). Hell's Gate (at 205 km) is shown in the dotted line. Pink were not caught at fisheries denoted with a cross, although were caught farther upstream.

Fishing season length

Season length (mean weeks) for all salmon species was higher at all fisheries for the aggregated fishing season than for the individual species seasons but the difference decreased as fisheries got farther from the ocean and species diversity declined (Fig. 3b). Fisheries aggregating across all five species were up to 1·2 times longer than the maximum season length for an individual species. Fisheries in the headwaters progressively had access to fewer species such that the difference between the length of the aggregate and species-specific fishing season declined to 0. The relationship between the impact of species on season length and distance to ocean was best explained by the linear model with distance as the explanatory variable (w_i = 0·75, adjusted r^2 = 0·35), which performed better than the other models (w_i < 0·2) (Tables 1 and S2).

POPULATION DIVERSITY

Interannual catch stability

There were strong signals of different components of population diversity contributing to catch stability for different salmon species (Fig. 4). Support for different population diversity models varied by species (Table S4) – no one model stood out as superior across species. Richness was the best-approximating model for Chinook CV (w_i = 1·0; Tables 1 and S4). Chinook CV decreased with increasing population number (Fig. 4a) such that fisheries with access to maximum richness were on average 3·8 times more stable in their catch than fisheries that accessed only one population. Tributary was the best-approximating model for sockeye CV (w_i = 0·55; Tables 1 and S4) but was not well supported for other species. Mainstem sockeye fisheries had 1·8 times more stable catch than tributary fisheries on average. For pink, coho and chum, support was low for population diversity models, at least partly due to low sample sizes (n = 14, 12 and 7, respectively).

Fishing season length

Richness and other elements of population diversity were strong explanatory variables of fishing season length, but their importance varied depending on the species (Fig. 5; Table 1). Richness was the most ubiquitous explanatory variable of season length, having a positive effect on season length and high relative variable importance for sockeye, pink, coho and chum (w_{ip} = 0·9, 1·0, 0·85 and 1·0, respectively; Table 1). Fisheries with access to maximum richness had 1·8, 3, 1·1 and 1·6 times longer seasons on average than fisheries accessing minimum richness for sockeye, pink, coho and chum fisheries, respectively (Fig. 5).

Table 1. Model outputs for top models in each of the species- and population-level analyses. For population-level season length outputs, average coefficients (avg coefficient) and Akaike weights for variable importance (w_{ip}) are shown for models with ΔAICc < 4

Level	Dimension of food security	Response variable	Explanatory variable(s)	n	Coefficient (avg coefficient)	SE	w_i (w_{ip})
Species	Interannual catch stability	PE (linear model)	Distance	21	−0·15	0·04	0·43
	Fishing season length	D (linear model)	Distance	21	−3·51	1·02	0·75
Population	Interannual catch stability	Chinook CV	Richness	19	−0·93	0·1	1
		Sockeye CV	Tributary	21	0·54	0·23	0·55
	Fishing season length	Chinook weeks	Barrier	19	−21·24	1·18	1
			Tributary		−1·42	0·97	0·7
			Distance		−0·31	1·57	0·64
			Richness		−2·44	1·99	0·57
		Sockeye weeks	Barrier	21	−3·28	0·43	1
			Distance		2·39	0·63	0·9
			Richness		4·63	0·95	0·9
			Tributary		0·02	1·28	0·47
		Pink weeks	Richness	14	4·01	1·36	1
			Barrier		−1·78	1·13	0·72
			Distance		0·38	0·95	0·43
			Tributary		−0·08	0·79	0·36
		Coho weeks	Distance	12	−2·61	1·21	0·9
			Richness		1·88	0·93	0·85
			Barrier		−1·17	1·17	0·61
		Chum weeks	Distance	7	5·96	1·94	1
			Richness		7·45	1·9	1
			Tributary		−5·15	1·25	1

CV, coefficient of variation; D, the impact of species diversity on season length; PE, portfolio effect.

The Hell's Gate partial barrier was also a consistently strong explanatory variable for season length; fisheries located downstream of this barrier had longer season lengths for all species but chum, which are not caught above the barrier (Fig. 5). Fisheries downstream of Hell's Gate had 3, 1·5, 2·5 and 2·8 times longer seasons on average than fisheries upstream for Chinook, sockeye, pink and coho fisheries, respectively (Fig. 5). Furthermore, Hell's Gate was the most supported explanatory variable of fishing season length for Chinook and sockeye models (w_{ip} = 1·0 and 1·0, respectively; Table 1).

Other explanatory variables of season length were not as ubiquitous across species, but had importance for individual species. Fishery distance from the ocean had a negative effect on fishing season length for Chinook and coho models (w_{ip} = 0·64 and 1·0, respectively; Table 1 and Fig. S1). Chinook and coho fisheries near the mouth of the river (Figs 2b (x) and 5) had 5·4 and 6·1 times longer mean fishing season than the most upstream fisheries for each species (Figs 2b (i) and 5). Additionally, season length was 2·2, 2·3 and 1·6 times longer in mainstem than in tributary fisheries for Chinook, pink and chum species (w_{ip} = 0·7, 0·36 and 1·0, respectively; Table 1).

Discussion

Our comparative study provides evidence of how biodiversity supports the food security of indigenous fisheries throughout a watershed. We illustrate that species and population diversity contribute to interannual catch stability and intra-annual fishing season length for First Nations salmon fisheries in the Fraser watershed. While factors other than diversity likely contribute to stability and season length, we generally found that population diversity had a greater signal on fisheries than species diversity. Our results suggest that different metrics of population diversity vary in importance to different dimensions of this ecosystem service and for different species. These findings extend recent research; ecosystem function increases across multiple elements of diversity, including taxonomic, functional and genetic (Naeem, Duffy & Zavaleta 2012). While it is generally appreciated that biodiversity supports the food security, culture, health and well-being of indigenous people around the world (Kuhnlein *et al.* 2012), our results provide rare quantitative evidence of this linkage.

Interannual catch stability of Fraser FSC salmon fisheries increased with increasing species and population diversity (Figs 3a and 4). Fisheries with larger catchment areas were buffered from year-to-year catch variability presumably through access to increased species/population diversity and asynchronous dynamics (the PE). However, Chinook and sockeye salmon fisheries were the only species where interannual catch stability was explained by population diversity, perhaps because, of the five species examined, Chinook and sockeye are thought to stray less from their natal spawning grounds and exhibit relatively high levels of genetic and life-history diversity (Waples *et al.* 2001). This study provides further evidence of the linkages between salmon diversity and stability (Hilborn *et al.* 2003; Schindler *et al.* 2010), extending empirical

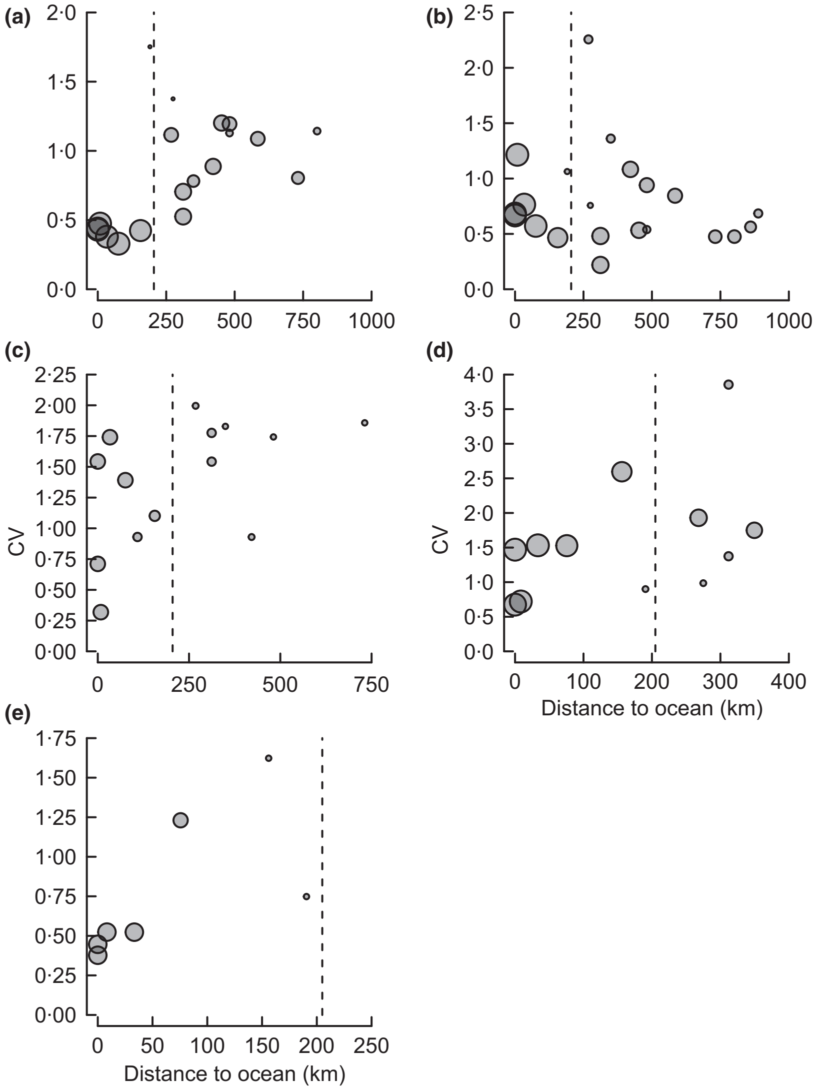

Fig. 4. The coefficient of variation of catch at each fishery changes with distance from the ocean for each species: Chinook (a), sockeye (b), pink (c), coho (d) and chum (e). Hell's Gate (at 205 km) is shown in the dotted line. Points are scaled to the proportion of salmon richness to which that fishery has access (populations, conservation units, stocks, subpopulations and spawning locations upstream of a fishery, respectively).

support for the diversity–stability relationship in a management-relevant system to compare different types of diversity (species and population) along a gradient for multiple species. We show that fine-scale diversity supports aggregate stability throughout a vast river network, and suggest that habitat protection is critical for the stability of this ecosystem service.

Season length of fisheries within a year also increases with biodiversity for FSC fisheries throughout the Fraser watershed (Figs 3b and 5). While mobile consumers like bears prolong feeding seasons by tracking patterns in the phenological diversity of ephemeral resources (Deacy *et al.* 2016), we show that salmon fisheries at the mouth of the river can integrate across the phenological diversity throughout the watershed because these ephemeral salmon runs are funnelled through the mouth of the river. Alternatively, season length is shorter for fisheries in areas of the watershed that host much less diversity, that is in headwaters, tributaries and above partial barriers. We found that season length was strongly linked to both salmon richness and the Hell's Gate barrier, depending on the species. For species that possess disparate run-timings, such as Chinook and sockeye, the barrier was the best explanatory variable of season length. This result demonstrates the importance of landscape filters on driving asynchrony and thus extending fishery seasons. Phenological diversity may be a critical component of diversity–ecosystem functions for time-sensitive processes such as seasonally pulsed resource waves (Armstrong *et al.* 2016).

While our study found evidence of biodiversity underpinning fisheries stability and season length, some cases did not match predictions, providing insight into situations where diversity may not confer increased stability or season length. Our species-level examination shows that some fisheries exhibited a negative PE (Fig. 3a), implying that the observed stability of the aggregate was less than predicted. In these cases, sockeye made up >95% of the total catch biomass, driving down the effect of other species in the predicted CVs relative to the observed CVs. This result highlights the importance of evenness among asset size (i.e. species catch biomass) in driving the magnitude of the PE (Doak *et al.* 1998). Abundance may be

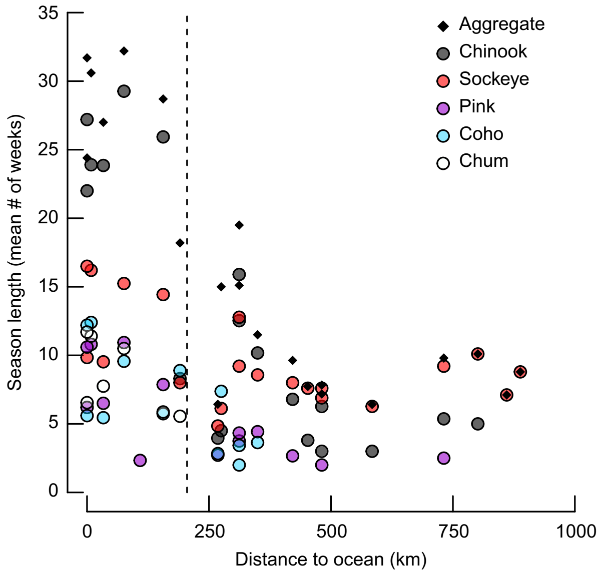

Fig. 5. The mean number of fishing weeks (season length) at each fishery changes with distance from the ocean for each species. The number of fishing weeks at each fishery, averaged across years, is shown in circles for each species. The aggregate number of fishing weeks at each fishery, aggregated across species and averaged across years, is shown in diamonds.

another important driver in the relationships shown here because, although abundance data are not available, catch (kg) as a proxy for abundance is correlated with species diversity, PE and D (r = 0·53, 0·59 and 0·57, respectively). For our population-level examination, catch (#) is also correlated with richness for Chinook and sockeye (r = 0·62 and 0·56, respectively), with CV for Chinook (r = −0·59) and with season length for Chinook and coho fisheries (r = 0·68 and 0·55, respectively). Additionally, we acknowledge that we were unable to measure population diversity directly. We also found that sockeye and chum fisheries did not exhibit strong evidence of season length decreasing with increasing distance from the ocean – we found the opposite. For sockeye salmon, this relationship might be caused by unequal spatial and temporal distributions in population abundance. For example, the Stuart catchment (888 km from the ocean at its mouth) hosts separate sockeye runs in June and August (English *et al.* 2011); thus, these fine-scale population differences can lengthen the fishing season despite its upstream location in the watershed.

Salmon have sustained indigenous people throughout the Pacific Rim for millennia. Historically supporting 200–300 thousand indigenous people, cumulative salmon consumption in BC was an estimated 46–69 thousand tonnes year^{-1} in pre-contact years (230 kg year^{-1} per person) (Haggan *et al.* 2006). This cultural stability has likely in part arisen from the integration of salmon biodiversity (Lepofsky *et al.* 2005), as shown here for communities near the coast, but also through trade and cultural practices that helped offset the effects of shorter seasons or local resource scarcity (Campbell & Butler 2010). Resource use and the associated settlement patterns corroborate our findings. Northwest coastal people could integrate across a diverse resource portfolio, which conferred stability and enabled them to live in large permanent villages, whereas where portfolios were less diverse farther inland, smaller groups of people moved throughout the watershed to integrate across greater diversity (Muckle 2006). Our research builds on these anthropological studies to illustrate the quantitative linkage between salmon biodiversity and First Nations fisheries stability and season length.

Our results have specific regional and broad management implications for watershed management. First, protecting multiple aspects of salmon diversity at fine scales, through conservation of local populations, habitats and connectivity, will help protect the biodiversity that maintains indigenous food security. In BC, 41% of First Nations are food-insecure and 91% state that they want to consume more traditional foods like salmon. Lack of availability was cited as one of the top five barriers to consuming more traditional foods (Chan *et al.* 2011). Secondly, our analyses illustrate that fish habitat and biodiversity underpin the stability and duration of fisheries that are 100s of km away. Upstream projects that damage salmon habitat could degrade the security of downstream indigenous fisheries. Given that FSC rights are protected in Canada, these findings have regional implications for environmental decision-making and indigenous rights and title. For instance, decision-makers should consider fine-scale diversity, not just species richness, and how proposed projects may impact stability and fishing opportunities, not just abundance. Further, fishery rights of downstream First Nations need to be considered when evaluating potential risks of headwater projects, and *vice versa*, because migratory salmon can transmit impacts to fisheries throughout the watershed (Moore 2015). These findings have implications for management of rivers and their local fisheries around the world. For example, large hydropower projects proposed for the Mekong, Amazon and Congo may not have adequately considered risks to fish biodiversity and local fisheries. These three river systems contain one-third of the world's freshwater fish species and provide food and livelihood for a substantial portion of the people living in their basins (Béné *et al.* 2009; Coomes *et al.* 2010; Mekong River Commission 2010); yet small-scale fisheries are often overlooked in project impact assessments (Winemiller *et al.* 2016). We recommend that the geographic scale of environmental assessments matches the socio-ecological processes that will be affected by development. In some cases, like that shown here for food security, this means that people throughout the watershed should be able to participate in decision-making through collaborative planning approaches (Gregory & Failing 2002), especially those who are most vulnerable to biodiversity change (Díaz *et al.* 2006).

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Data accessibility

Fraser River FSC catch reports are available at http://www.pac.dfo-mpo.gc.ca/fm-gp/fraser/archives-a-eng.html#First_Nations (Fisheries and Oceans Canada 2015). Data can be accessed at http://dx.doi.org/10.5061/dryad.ng8pf (Nesbitt & Moore 2016).

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Supporting Information

Additional Supporting Information may be found in the online version of this article.

Fig. S1. Population diversity – fishing season length interannual variability.

Table S1. Proxies and drivers of salmon population diversity.

Table S2. Population diversity – fishing season length top candidate models.

Table S3. Species diversity – PE and D models.

Table S4. Population diversity – interannual catch stability model outputs.