

Life-history diversity and its importance to population stability and persistence of a migratory fish: steelhead in two large North American watersheds

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Summary

1. Life-history strategies can buffer individuals and populations from environmental variability. For instance, it is possible that asynchronous dynamics among different life histories can stabilize populations through portfolio effects.

2. Here, we examine life-history diversity and its importance to stability for an iconic migratory fish species. In particular, we examined steelhead (*Oncorhynchus mykiss*), an anadromous and iteroparous salmonid, in two large, relatively pristine, watersheds, the Skeena and Nass, in north-western British Columbia, Canada. We synthesized life-history information derived from scales collected from adult steelhead ($N = 7227$) in these watersheds across a decade.

3. These migratory fishes expressed 36 different manifestations of the anadromous life-history strategy, with 16 different combinations of freshwater and marine ages, 7.6% of fish performing multiple spawning migrations, and up to a maximum of four spawning migrations per lifetime. Furthermore, in the Nass watershed, various life histories were differently prevalent through time – three different life histories were the most prevalent in a given year, and no life history ever represented more than 45% of the population.

4. These asynchronous dynamics among life histories decreased the variability of numerical abundance and biomass of the aggregated population so that it was > 20% more stable than the stability of the weighted average of specific life histories: evidence of a substantial portfolio effect. Year of ocean entry was a key driver of dynamics; the median correlation coefficient of abundance of life histories that entered the ocean the same year was 2.5 times higher than the median pairwise coefficient of life histories that entered the ocean at different times. Simulations illustrated how different elements of life-history diversity contribute to stability and persistence of populations.

5. This study provides evidence that life-history diversity can dampen fluctuations in population abundances and biomass via portfolio effects. Conserving genetic integrity and habitat diversity in these and other large watersheds can enable a diversity of life histories that increases population and biomass stability in the face of environmental variability.

Key-words: biocomplexity, climate change, diversity–stability, iteroparity, marine survival, portfolio effect, rainbow trout

Introduction

Environmental variability is prevalent, driving the evolution of life histories of many species (Stearns 1992). A variety of life-history strategies spread risk across

temporal variability (Stearns 1992; Wilbur & Rudolf 2006). For instance, greater longevity can buffer populations from environmental variability (Morris *et al.* 2008). Similarly, iteroparity, where individuals reproduce more than once during their lifetime, leads to buffered lifetime fitness (Orzack & Tuljapurkar 1989). Alternatively, variation in age at maturity results in individuals from the same cohort reproducing in different years, stabilizing

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populations in the face of environmental variability (Hutchings & Myers 1994). Some perennial plants exhibit prolonged dormancy, where a subset of individuals stay dormant underground (e.g. Gremer, Crone & Lesica 2012). Dormant seeds or eggs may also introduce new individuals into a population over long time-scales, or serve as a source for recolonization following extinction (e.g. Pake & Venable 1996). Given that anthropogenic climate change is thought to be increasing environmental variability (IPCC 2007), it is increasingly imperative to quantify the diversity of these various life-history traits and their role in influencing population persistence and stability.

Research on anadromous Pacific salmon (*Oncorhynchus* spp.) has increasingly emphasized the potential importance of life-history diversity to stability (Hilborn *et al.* 2003; Schindler *et al.* 2008, 2010; Healey 2009). It is thought that diversity of life histories and habitats drives asynchronous population dynamics due to different responses to climate variability (Hilborn *et al.* 2003; Rogers & Schindler 2008; Schindler *et al.* 2008). Due to this asynchrony, the dynamics of aggregations of salmon populations can be more stable than single populations (e.g. Schindler *et al.* 2010). This 'portfolio' effect of salmon biodiversity can decrease the temporal variability of catch from commercial fisheries as well as energetic intake by mobile predators that integrate across salmon populations (Payne & Moore 2006; Ruff *et al.* 2011; Schindler *et al.* 2013). Asynchrony of components of populations can also potentially facilitate metapopulation persistence (Earn, Levin & Rohani 2000; Schtickzelle & Quinn 2007). Furthermore, within a population, diverse life histories can contribute to stability (Schindler *et al.* 2010). Using population models, Hill, Botsford & Hastings (2003) suggested that higher levels of diversity of Pacific salmon ocean ages can increase predicted persistence in the face of variable ocean survival. However, there remains an incomplete understanding of how diverse life-history traits within populations contribute to temporal stability of Pacific salmonids.

Human activities have decreased salmonid diversity within and across populations (Gustafson *et al.* 2007; Moore *et al.* 2010). For instance, genetic differences across populations can be swamped by hatchery propagation (e.g. Eldridge & Naish 2007). Historically, steelhead populations in Californian rivers exhibited strong patterns of genetic isolation by distance; contemporary samples revealed genetic homogenization of these populations (Pearse, Martinez & Garza 2011). In addition, non-random extirpation of salmon populations has decreased life-history diversity within some regions (e.g. Beechie *et al.* 2006). Accordingly, dynamics of salmon populations may also be homogenized (Moore *et al.* 2010; Carlson & Satterthwaite 2011). Hatchery propagation can also reduce life-history diversity within populations (Tipping 1991). Given these widespread losses of salmon population diversity, it is increasingly important to document the extent and implications of diversity in relatively intact systems.

Steelhead (*O. mykiss*) display perhaps the most life-history diversity of any Pacific salmonid species (Thorpe 1998; Quinn 2005; Pavlov *et al.* 2008). For instance, Thorpe (1998) mentions 32 different life-history strategies of steelhead. Furthermore, some individuals are resident to freshwater habitats their whole lives (i.e. resident rainbow trout), while others migrate to the ocean and back following an anadromous life-history pattern (e.g. McPhee *et al.* 2007). In addition, steelhead are iteroparous, with the possibility of repeated spawning migrations, adding another potential different life-history trait when compared to semelparous Pacific salmon, of which all other previous research on portfolio effects have focused on (e.g. Greene *et al.* 2010; Moore *et al.* 2010; Schindler *et al.* 2010; Carlson & Satterthwaite 2011). While previous studies have observed high levels of life-history diversity in *O. mykiss* in relatively pristine watersheds (such as those in Kamchatka Peninsula, Russia; e.g. McPhee *et al.* 2007; Pavlov *et al.* 2008), there has yet to be a quantitative examination of how different elements of this diversity contribute to their stability.

We seek in this study to quantify life-history diversity and examine how different elements of this diversity contribute to population stability, defined in terms of the coefficient of variation for population abundances over time. Here, we quantified steelhead life-history diversity in the Skeena and Nass watersheds, large watersheds in northern British Columbia that are relatively intact, with few if any artificial barriers to migration and no recent hatchery propagation (Gottesfeld & Rabnett 2008; Hooton 2011). We asked two related questions: (i) What are the patterns of steelhead life-history diversity in these relatively pristine watersheds? (ii) How do these different aspects of life-history diversity contribute to population stability across years? We synthesized life-history information based on the analysis of scales collected from adult steelhead in the Skeena and Nass watersheds across a decade. This study uncovered remarkable life-history diversity and quantified how specific life-history traits increase stability via portfolio effects.

Materials and methods

STUDY SYSTEM

This study focused on anadromous *O. mykiss* in the Skeena and Nass watersheds in north-western British Columbia. These two watersheds originate in an area known as the 'sacred headwaters' at approximately 2500 m elevation and then curve west and drain into the Pacific Ocean (Fig. 1). Compared to other large salmonid-bearing watersheds in North America, these two watersheds are relatively intact. While there are historical, ongoing and proposed land uses such as timber harvest, road systems, mining and other extractive land use changes, human population densities are relatively low and dispersed, there are no major dams, and little history of hatchery propagation of steelhead (Gottesfeld & Rabnett 2008; Walters *et al.* 2008). Both watersheds are large; the Skeena is 54 432 km² and the Nass is 20 839 km².

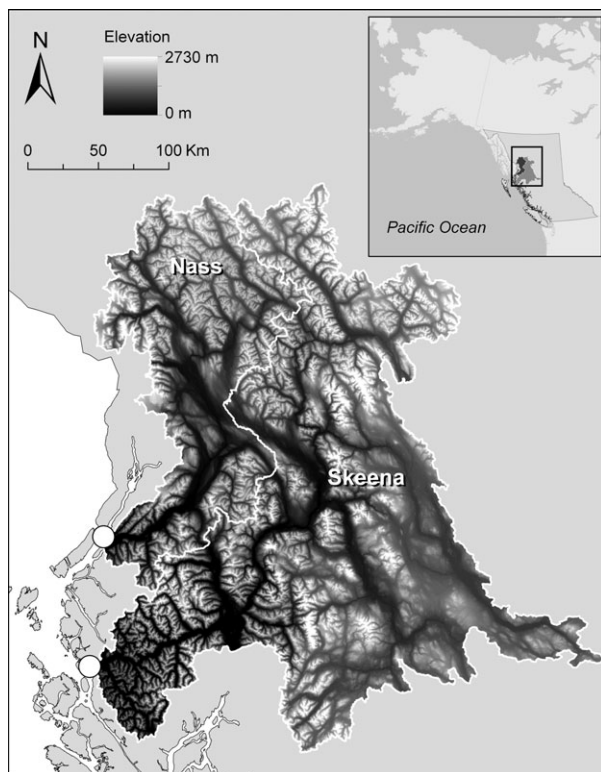


Fig. 1. Map of the Skeena and Nass River watersheds. Lighter colours indicate higher elevations, indicating the geographical diversity within these large watersheds. Circles indicate where the rivers flow into the Pacific Ocean. White lines indicate watershed boundaries.

Anadromous *O. mykiss*, steelhead, are an iconic fish in these watersheds (Hooton 2011). These fish are caught as bycatch in commercial salmon fisheries (predominantly sockeye, *O. nerka*), First Nation food, social, or ceremonial fisheries, and recreational fisheries that are currently catch-and-release (Hooton 2011). We focus on summer-run steelhead that return from the Pacific Ocean to their natal system from June to October, overwinter, and then spawn in the spring (May to June). As in other watersheds, steelhead in the Skeena and the Nass have been characterized as having fine-scale population genetic structure, with significant genetic differentiation among steelhead from major tributaries within these large watersheds (Heath, Pollard & Herlinger 2001; Beacham *et al.* 2012; Wellband *et al.* 2012). These molecular tools have also helped illuminate life-history diversity in these fishes, for example, different populations of steelhead also return to spawn at different times of the year (Beacham *et al.* 2012). We focused on quantifying the life-history diversity that underpins temporal stability in annual steelhead returns. Temporal stability of abundance of steelhead would support more stable fisheries. Temporal stability of total biomass of spawning steelhead would provide an index of the stability of total offspring production, presumably important to population persistence.

DATA

We analysed life-history information obtained from scale analyses of returning adult steelhead. In the Skeena, scales were predominantly collected from in-migrating summer steelhead caught

during the Tye test fishery that occurs at the mouth of the Skeena. This fishery uses a multipanel and multimesh-sized gillnet. In the Nass, scales were collected from in-migrating summer steelhead sampled at fish wheels that operate in the lower mainstem of the river. Thus, these scale samples serve as a reasonably representative sample of steelhead population that returns to spawn in these two watersheds. Total lengths were also collected from the fish at the time of scale sampling. It is possible that fish were not sampled in an entirely random way by both sampling procedures; for example, relatively smaller fish that only spend 1 year in the ocean might be underrepresented to a limited extent in the Tye test fishery. Scales, or their impressions, were viewed at magnification (35.5-fold to 250-fold), to quantify years spent rearing in freshwater, duration of ocean life and number of spawning migrations made by an individual fish. All of the scale analyses over the multiple years of sampling were completed by Carol Lidstone of Birkenhead Scale Analysis, providing consistency in technique. Scale reading was performed without information on size to avoid bias. Scale-reading techniques were standardized among other leading scale readers to increase repeatability. We discarded any individuals from analysis if any portion of their life history was deemed to be uncertain due to regeneration, poor condition, resorption or unreadable. This left us with $N = 7227$ scales. Of these scales, 1188 were from the Skeena (from 2008, 2010 and 2011) and 6039 were from the Nass from 9 years: 2000 ($N = 382$), 2001 ($N = 1175$), 2004 ($N = 502$), 2005 ($N = 84$) and 2007–2011 ($N = 135, 675, 1394, 928$ and 764, respectively). We use standard notation for referring to life histories, with the first number being the number of winters in freshwater and the second number being the years in saltwater. Thus, a 2.2 fish was born in early summer, migrated from freshwater habitat to the ocean 2 years later in spring, spent 2 years in the ocean and then migrated back to fresh waters in summer/fall.

In the Nass watershed, where there were 9 years of scale data, there are corresponding adult steelhead abundance estimates that were collected as part of a collaborative monitoring effort between Nisga'a First Nation and the Ministry of the Environment (Alexander *et al.* 2013; Nisga'a Fisheries 2013). Abundance estimates were generated via a combination of mark-recapture estimates from fish wheels that operate in the mainstem of the Nass River and tributary resampling as well as fish wheel catch index techniques (Alexander *et al.* 2013; Nisga'a Fisheries 2013).

ANALYSES

We quantified the prevalence of different life histories in steelhead across these two watersheds. We considered different combinations of ages in any part of the life history as a unique life-history realization of the general anadromous life-history strategies. The steelhead life histories of the two watersheds were visualized using graphical networks, where link thickness denotes the proportional abundance of that life history; dotted links represent trajectories with proportional abundance <20%. It is important to note that the observed life histories represent successful life histories of fish that returned back to spawn. The distribution of life histories of fish that did not survive could be quite different from those that survive.

We linked steelhead life-history diversity through time to abundance and biomass in the Nass River. We focused on the Nass River because of the longer time series for scales and the available corresponding abundance estimates. We generated

annual life-history-specific estimates of abundance by multiplying the total run estimate by the proportional frequency of each life history. We estimated confidence intervals around the proportional contribution of each life history, treating the different life-history categories as classes in a multinomial distribution. For this, we used the R package 'MultinomialCI', which considers the sample sizes and number of categories. We also generated annual life-history-specific estimates of biomass. Given that the number of eggs and size of eggs both increase as a function of length (Quinn 2005), we consider estimated spawning biomass as an index of the potential production of offspring. We estimated mass for each individual based on observed lengths and the best estimate of length–weight parameters from FishBase ($g = 0.00824 \text{ cm}^{3.09}$) (Froese & Pauly 2011). For the small subset of fish for which lengths were not available ($N = 13$ out of 6039), we used the average length for that ocean age. These individual biomass estimates were averaged for each year and life history and then multiplied by the previously calculated abundance estimates to generate an estimate of the biomass of spawning steelhead from each life history over time in the Nass River.

We subsequently examined patterns of temporal correlation in abundance (numerical and biomass) among specific life histories in the Nass River. These analyses were performed in order to investigate the life histories that contribute to the asynchrony that underpins diversity–stability relationships. We used Mantel tests to examine patterns of correlations of age-class dynamics for Nass fish. Mantel tests can statistically compare two matrices; in this case, one matrix was the correlation matrix in population dynamics of different Nass life histories, and the other matrix described whether life histories were similar or not. We examined how two elements of life history could contribute to patterns of correlation. First, we examined the possibility that diversity in ocean entry was contributing to asynchrony. Given that these analyses focused on return year, life histories with the same year of ocean entry will have the same ocean age. Thus, we statistically tested the hypothesis that age classes with different ocean ages (e.g. 4.3 vs. 4.2) were less correlated than age classes that shared the ocean age (e.g. 4.2 vs. 5.2). For the shared ocean entry analysis, we aggregated rare life histories into groups that shared ocean-entry years (e.g. aggregated all other 1-year ocean life histories, 'other.1'). Secondly, we examined the possibility that diversity in year born was contributing to asynchrony. Thus, we statistically tested the hypothesis that age classes with different total ages (e.g. 4.1 vs. 4.2) were less correlated than age classes with the same total age (e.g. 4.1 vs. 3.2). For the shared birth year analysis, we aggregated rare life histories into groups that shared total age (e.g. aggregated all other 7 year total age life histories). We removed repeat spawners for all Mantel tests, reasoning that their population dynamics would be driven also by other environmental factors. We performed Mantel tests with the EcoDist package in R (Goslee & Urban 2007).

The Nass data allowed us to examine how different life histories contribute to the stability of abundance and biomass of steelhead from the entire river system. We calculated the coefficient of variation (CV) of annual numerical and biomass abundance as an index of stability (or instability). CV normalizes the standard deviation by the mean. Thus, it is important to note that changes in CV can be driven also by changes in mean (if the variability does not scale with the change). We compared the CV of individual life histories to the observed CV of the entire watershed. We used the weighted average CV of the specific life histories as an estimate of the predicted CV of the entire return to the watershed

if life-history returns were synchronous. We thus took the sum of the products of the proportional contributions of each life history and their CV. The difference between the variability of the predicted and observed whole watershed returns was used as an index of the portfolio effect – the degree to which diversity increases stability (e.g. Schindler *et al.* 2010).

We examined whether years with smaller sample sizes (e.g. 2005 with 84 scales and 2007 with 135 scales) were biasing results due to the potential for sampling error. Thus, we re-ran all the Nass River analyses after omitting one or both of these years. We used R version 2.15.2 for all analyses (R Development Core Team 2012).

SIMULATIONS

We also used simulations to examine how different elements of life-history diversity contribute to population fluctuations and the probability of extinction. These stochastic simulations examined how different compositions of life-history diversity respond to three different scenarios of environmental conditions: (i) good ocean conditions, (ii) medium ocean conditions and (iii) autocorrelated ocean conditions. These scenarios were chosen to reflect the different aspects of variability of ocean survival, as evidenced by previous studies (Beamish *et al.* 2000; Smith & Ward 2000; Mantua & Francis 2004; Scheuerell, Zabel & Sandford 2009). Ocean conditions change according to a transition probability matrix, where the transition probabilities control the proportion of time steps that the system stays in a good or bad period for a given simulation. In the good ocean scenario, we set the probability of a good year following a good year, $\text{pr}(G \rightarrow G)$, to be 0.8, and the probability of a bad year following a bad year, $\text{pr}(B \rightarrow B)$, to be 0.2. Accordingly, when conditions are good, they are likely to stay good; when conditions are bad, they are likely to change. In contrast, for the medium ocean scenario, we set $\text{pr}(G \rightarrow G)$ to 0.8 and $\text{pr}(B \rightarrow B)$ to 0.4, and in the autocorrelated ocean scenario, we set both $\text{pr}(G \rightarrow G)$ and $\text{pr}(B \rightarrow B)$ to be 0.8. In the latter scenario, there can be strings of bad (or good) years. By bootstrapping observed life-history trajectories from the Nass and Skeena Rivers (with replacement), population dynamics were simulated with recruitment at the next time-step, $R(t+1)$, dependent on the density of spawning adults at the current time, $S(t)$, which was determined with the Beverton–Holt stock–recruitment function $R(t+1) = aS(t)/(1+bS(t))$, where we set the parameters $a = 8$ and $b = 1/80$ (cf. Ward 2000).

Traditional age-structured population models concern quantifying probability matrices for the transition from one life stage to another. Given that our data describe only surviving individuals (such that we do not have age-specific mortality rates), we focus instead on exploring the impacts of different observed life-history trajectories in the face of environmental variability and stochastic mortality. Accordingly, an entire life-history trajectory was assigned to an individual at the recruit stage, with survival from one year to the next dependent on (i) the length of the randomly drawn life-history trajectory including the number of repeat spawning events and (ii) stochastic mortality during the initial freshwater-to-ocean transition (determined as a function of ocean conditions: good, bad or autocorrelated). Population dynamics were thus simulated as a Markov chain with life stages bootstrapped from the recorded Nass and Skeena river populations, with density-dependent recruitment, and stochastic mortality dependent on life stage and ocean conditions.

Simulated individuals experienced mortality only during the initial transition from the freshwater to oceanic environment. During good years, the probability of freshwater-to-ocean mortality was set to 0.80, and during bad years the probability of freshwater-to-ocean mortality was set to 0.95. Simulated populations were iterated for 500 time-steps with the initial population size set to 100 individuals during good ocean conditions; time-steps 1 to 200 were discarded to avoid the influence of transient dynamics. Fifty simulation replicates were generated for each ocean condition scenario.

We evaluated the impact of different elements of life-history diversity on the relative size of fluctuations (measured as the CV of a time series) and the probability of extinction (measured as the proportion of replicate simulations resulting in extinction). It is important to note that these do not reflect predicted extinction rates for the study populations, but are rather intended as another component of variability. Using these stability indices, we examined how different elements of observed steelhead diversity contribute to stability and persistence. Specifically, we quantified stability indices across different life-history compositions: (i) repeat spawners: 0x, 0.5x, 1x, 2x, 5x, all, where 'x' denotes 'times observed prevalence'; (ii) freshwater maturation: observed vs. all with 3 years in freshwater (the most common freshwater duration), which we denote as '3._'; (iii) ocean maturation:

observed vs. all with 2 years in the ocean following the first migration (also the most common duration), which we denote as '_2'. We explored a large range of different potential contributions of the repeat spawner class to the population, from 0% contribution up to 100% contribution. Although such extrema are unrealistic in natural populations, they serve to illustrate the theoretical maximum and minimum influence that repeat spawning can have on population-level stability. Moreover, we excluded repeat spawners from the freshwater and ocean maturation scenarios to avoid results that overlapped with manipulations of the proportion of repeat spawners. Thus, the simulations examine, in a simplistic framework, how different steelhead life-history diversity contributes to population stability.

Results

LIFE-HISTORY DIVERSITY

We observed 36 different life-history trajectories among Nass and Skeena steelhead, all different expressions of the anadromous life history (Fig. 2). Individuals varied in the number of years they spend in fresh water, from 2 to 6 years, with 3 and 4 years being most common

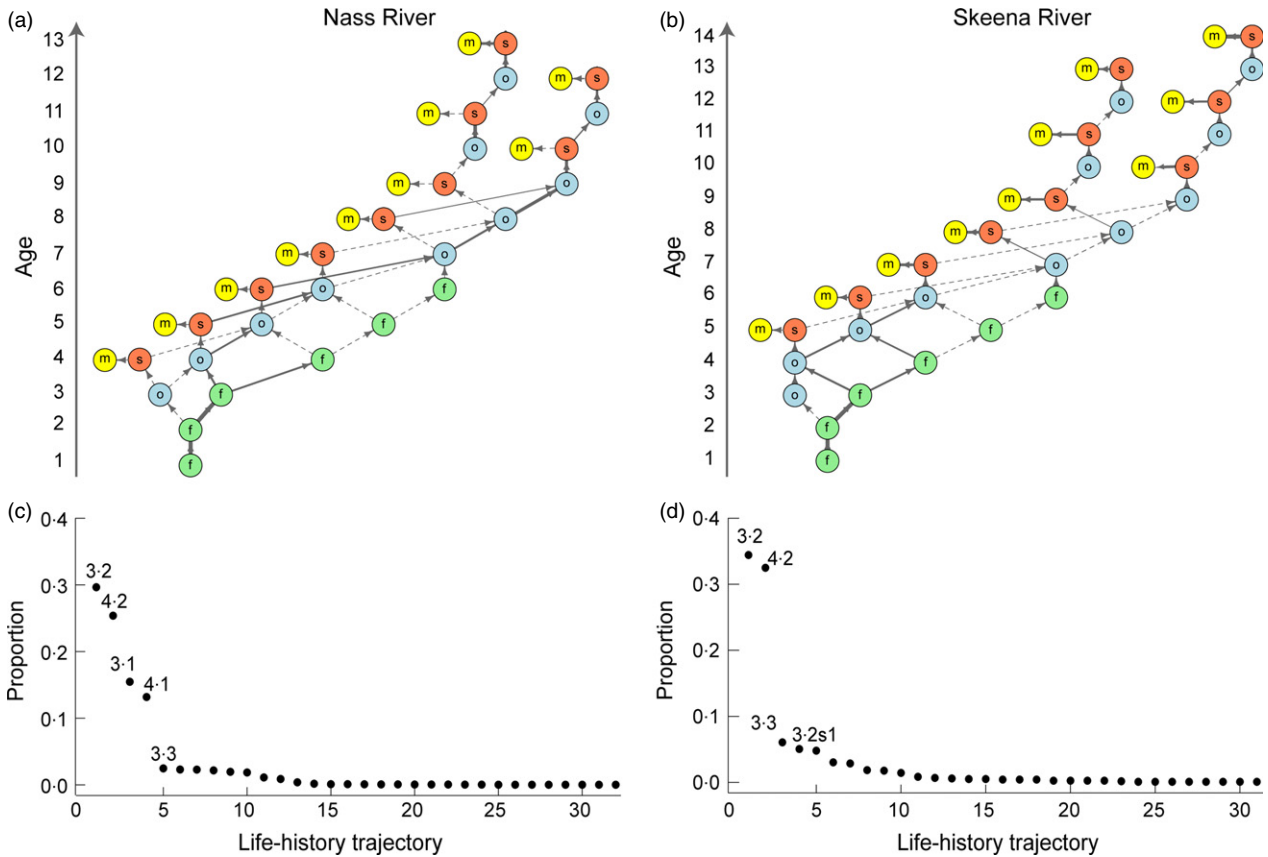


Fig. 2. Life-history diversity of Skeena and Nass River steelhead. Networks illustrating the different life-history strategies for (a) Nass and (b) Skeena steelhead. For each year, link thickness is weighted to the relative frequency of that life-history. Dashed arrows denote frequencies <0.20. The life stage of the fish is abbreviated with a letter and colour (f = freshwater, o = ocean, s = returning to freshwater to spawn, m = inferred mortality). Note that some fish exhibit repeated migrations to spawn. The age of the fish is denoted with a number. These are the life histories of the successful fish that return to spawn. (c, d) The relative proportions of each unique life-history strategy, ranked by order of frequency, for steelhead returning to the two watersheds across all years and individuals. The most common life-history trajectories are identified, with 's' signifying a single repeat spawning event. The y-axis is the relative proportion of each unique life history.

(Table 1). In addition, individuals varied in the number of years they spent in the ocean before migrating back to spawn, from 1 to 4 years (Table 1). Furthermore, some individuals made repeat spawning migrations (Table 1). An extreme example from the Skeena River is a female that spent 4 years in freshwater, 2 years in the ocean, migrated to spawn, migrated out to the ocean for another year, migrated again to spawn, back to the ocean for another year and so on for a total of four spawning migrations and a total age of 12 years (Fig. 2). The Nass had more evenness of the life histories. In the Nass, 3·2, 3·1, 4·2 and 4·1 fish all represented at least 12% of the population.

NASS RIVER STEELHEAD DIVERSITY AND STABILITY

Nass steelhead abundances fluctuated during 2000–2011 (Fig. 3a). From 2000 to 2003, abundances were relatively intermediate (11 500–15 000), followed by 4 years of low population abundance (4000–7200), with a rebound in abundance in 2008. Over this time series (2000–2011), the observed CV of total Nass summer-run steelhead abundance was 0·50. A diversity of steelhead life histories with different temporal dynamics contributed to the Nass adult steelhead population (Fig. 3b). Across years, no single life history ever contributed more than 45% of the population. Three different life histories were the most prevalent in any given year: 3·2 fish were most prevalent in 5 out of 9 years, 4·2 fish were the most prevalent in 3 out of 9 years, and 3·1 were the most prevalent in 1 year. Some life histories exhibited large shifts in relative contribution (e.g. 3·1), while others were more stable. The biomass of Nass River steelhead showed similar temporal dynamics (Appendix S1).

Different steelhead life histories had different patterns of abundance (Appendix S1). There was a wide range in pairwise correlations among the abundance dynamics of different life histories. Correlation coefficients ranged

Table 1. Proportional frequency of life histories of steelhead in the Nass and Skeena Rivers. Shown are three different components of life-history diversity: number of years spent in freshwater prior to out-migration, number of years spent in the ocean prior to spawning, and the number of repeat spawning migrations. Note that there is one full year in the ocean between each bout of repeat spawning

Years	Freshwater		Ocean		Repeat spawning	
	Nass	Skeena	Nass	Skeena	Nass	Skeena
1	NA	NA	0·334	0·087	0·069	0·134
2	0·005	0·003	0·617	0·805	0·003	0·017
3	0·512	0·501	0·048	0·107	<0·001	0·002
4	0·434	0·423	0·001	0·001		
5	0·048	0·070				
6	0·000	0·003				

'NA' indicates no individuals of this life history were sampled.

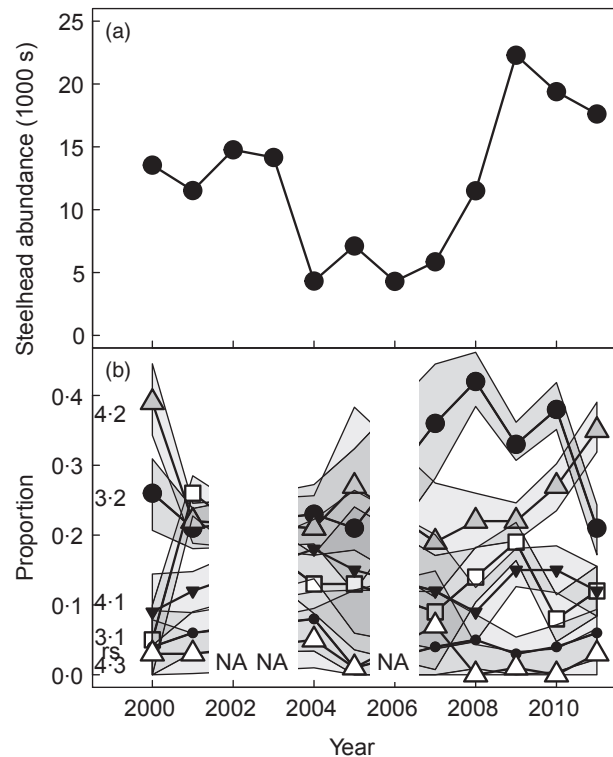


Fig. 3. Population dynamics of Nass steelhead. (a) Total estimated abundance of returning adult steelhead to the Nass watershed from 2000 to 2011. (b) Proportions of different steelhead life histories in the Nass from 2000 to 2011. Shaded regions indicated the 95% confidence intervals based on the sample size of scales and a multinomial distribution (see Materials and methods). Years 2002, 2003 and 2006 are marked with 'NA' as there were no age structure data available. We focus on the six most abundant life histories for ease of viewing: grey triangles were 4·2, large black circles were 3·2, small black triangles were 4·1, white squares were 3·1, small black circles were repeat spawners ('rs'), and white triangles were 4·3.

from strongly positive ($r = 0·88$) to negative ($r = -0·41$), with a median correlation coefficient of 0·34 (excluding the diagonal). Thus, different life histories are associated with different patterns of synchrony and asynchrony.

Specific life-history traits were associated with different population dynamics (Fig. 4). We used Mantel tests to examine how specific life-history traits influenced correlation structure. Life histories that were the same total age and thus born on the same year (for example, 5·2 and 4·3) were not significantly more correlated with each other than other pairs of life histories (Mantel $r = 0·16$, $P = 0·57$). In contrast, life histories that entered the ocean the same year (for example, 5·2 and 4·2; noting that these were based on return year not brood year) were significantly more correlated with each other than other pairs of life histories (Fig. 4, Mantel $r = 0·30$, $P = 0·038$). The median correlation coefficient of life histories that entered the ocean at the same time was high ($r = 0·51$), 2·5 times higher than the median pairwise coefficient of life histories that entered the ocean at different times ($r = 0·21$) (Fig. 4). Even when years with smaller sample sizes were

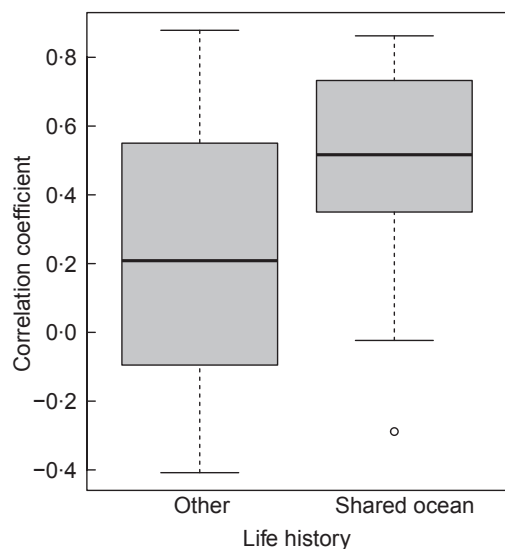


Fig. 4. Box plot of correlation coefficients of spawning abundances for pairs of life histories that shared the same year of ocean entry (i.e. 2.2 vs. 3.2) vs. life histories that had different years of ocean entry (e.g. 2.3 vs. 3.2). The box plot shows the median value, the interquartiles and the whiskers approximate a 95% confidence interval of the data. Repeat spawners are omitted from this plot (see Materials and methods).

removed from the analyses, life histories that entered the ocean the same year were significantly more correlated than the other pair of life histories (2005 omitted: Mantel $r = 0.30$, $P = 0.039$; 2005 and 2007 omitted: Mantel $r = 0.334$, $P = 0.036$). Also consistent, shared birth year remained insignificant when years with smaller sample sizes were removed from analyses (2005 omitted: Mantel $r = 0.20$, $P = 0.20$; 2005 and 2007 omitted: Mantel $r = 0.25$, $P = 0.30$). Thus, life histories with different years of ocean entry had more asynchronous population dynamics (Fig. 4).

Different life histories exhibited different patterns of stability of numerical abundance in the Nass (Fig. 5). The coefficient of variation of estimated numerical abundance for 12 categories of life histories ranged from repeat spawners, which were relatively stable with a CV of 0.54, to the 3-1 life history with a CV of 0.75. Other year-/age-specific life histories had CVs that ranged from 0.54 to 0.90. Asynchrony between different life histories contributed to numerical stability of Nass steelhead abundance (Fig. 5). The predicted CV, based on the weighted average CV of the specific life histories, was 0.63. In contrast, the observed CV of abundance was 0.50, > 20% less variable, evidence of a substantial 'portfolio effect'. The total biomass of returning spawning steelhead was also stabilized via portfolio effects among life histories (Appendix S1). The size of the portfolio effect for spawning biomass was of a similar large magnitude; the observed CV of biomass of returning spawners was 0.48, while the weighted average of the component life histories was 0.62. These patterns were robust to removing years with smaller sample sizes (Appendix S1).

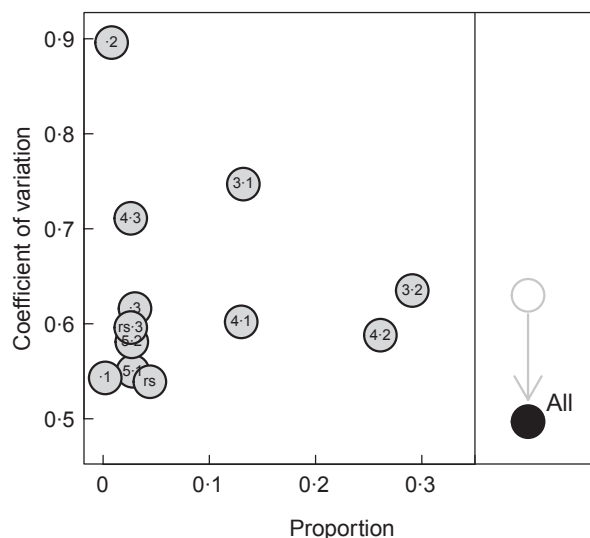


Fig. 5. Diversity and stability in Nass steelhead. Each grey-filled black circle represents the coefficient of variation (CV) of abundance across years as a function of proportion contribution each life history. We focus on 12 most abundant life-history groups. We aggregated repeat spawners into those that spent a total of 3 years in the ocean ('rs.3') and other repeat spawners ('rs'). We also aggregated a suite of less common freshwater life histories into those that spent one ('.1'), two ('.2') and three ('.3') years into the ocean. Shown to the right is the measured CV of the entire Nass population (filled black circle). Also shown to the right (grey outline white-filled circle) is the estimated CV of the population based on the weighted average of the CVs of the different life histories. The difference between the observed and predicted CV is a metric of the portfolio effect, the degree to which diversity decreases variability.

SIMULATIONS

Our simulation scenarios showed that the prevalence of repeat spawners had a large impact on the relative magnitude of population fluctuations (CV), and this impact was greater for moderate levels of autocorrelation among bad years (Fig. 6). For good ocean conditions ($\text{pr}(G \rightarrow G) = 0.8$ and $\text{pr}(B \rightarrow B) = 0.2$), and when the proportion of repeat spawners in a population was less than observed, the CV increased from 0.16 ± 0.04 (Nass) and 0.16 ± 0.03 (Skeena) to 0.19 ± 0.03 (Nass) and 0.17 ± 0.04 (Skeena) for half as many repeat spawners and 0.21 ± 0.04 (Nass) and 0.21 ± 0.05 (Skeena) when repeat spawners were eliminated (reported as mean values ± 1 standard deviation). In contrast, CV decreased to 0.15 ± 0.03 (Nass) and 0.13 ± 0.02 (Skeena), and 0.12 ± 0.02 (Nass) and 0.09 ± 0.02 (Skeena) when repeat spawners were 2 \times and 5 \times more prevalent than expected, respectively. For the (unlikely) extreme of a population entirely composed of repeat spawners, CV decreased further to 0.07 ± 0.01 (Nass and Skeena). We observed a similar trend for medium ocean conditions ($\text{pr}(G \rightarrow G) = 0.8$ and $\text{pr}(B \rightarrow B) = 0.4$). The number of extinctions was negligible for both good and medium ocean

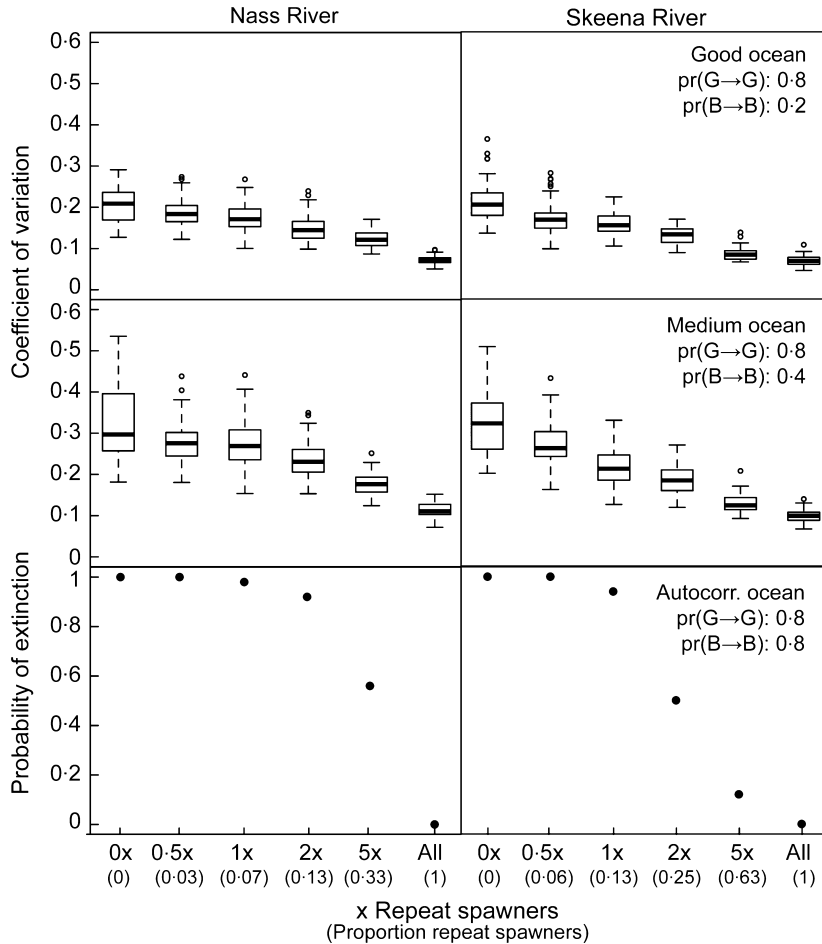


Fig. 6. Stability for different proportions of repeat spawners. Shown are the coefficients of variation for simulation results of populations with different life-history diversities. We altered the number of repeat spawners from that observed in the Nass and Skeena rivers (0x, 0.15x, 1x, 2x and 5x) and across good, medium and autocorrelated ocean conditions. The probability of extinction – instead of CV – is shown for autocorrelated ocean conditions due to the difficulty in measuring CV for simulations with high extinction probabilities. These box plot shows the median value, the interquartiles and the whiskers approximate a 95% confidence interval of the data.

conditions and are not shown. autocorrelated ocean conditions ($\text{pr}(G \rightarrow G) = 0.8$ and $\text{pr}(B \rightarrow B) = 0.8$) resulted in high probabilities of extinction such that measures of CV were difficult to obtain. We show that the probability of extinction decreased similarly for both the Nass and Skeena as the proportion of repeat spawners was increased (Fig. 6).

Simulation scenarios where we manipulated the residence time for freshwater and ocean life stages (in the absence of repeat spawners) illustrated that these elements of life-history diversity also contributed somewhat to predicted stability (Fig. 7). For both good and medium ocean conditions, CV increased marginally relative to values for the observed life-history diversity. If repeat spawners were excluded, the CV for the observed life-history diversity was 0.18 ± 0.04 (Nass) and 0.21 ± 0.05 (Skeena) in good ocean conditions, and 0.31 ± 0.11 (Nass) and 0.32 ± 0.10 (Skeena) for medium ocean conditions. For the freshwater scenario (where individuals were restricted to remain in freshwater for exactly 3 years), CV increased to 0.23 ± 0.04 (Nass) and 0.25 ± 0.05 (Skeena) in good ocean conditions, and 0.33 ± 0.08 (Nass) and 0.43 ± 0.15 (Skeena) for medium ocean conditions. For the ocean duration scenario (where individuals were restricted to remain in the ocean for exactly 2 years after the first migration), CV again increased to 0.24 ± 0.06 (Nass) and

0.23 ± 0.05 (Skeena) in good ocean conditions, and 0.38 ± 0.12 (Nass) and 0.38 ± 0.12 (Skeena) in medium ocean conditions. Results are not shown for the autocorrelated ocean conditions, as the probability of extinction was near unity for all scenarios.

Discussion

This study quantifies high diversity of life histories of migratory steelhead in two large and relatively pristine watersheds in northern British Columbia: the Skeena and the Nass. In the Nass River, life histories were differently prevalent across time. Furthermore, different life histories within populations of steelhead displayed different patterns of variation through time. Repeat spawners were especially stable in numerical abundance and biomass. The temporal dynamics of different life histories were variably correlated, with some life histories being strongly correlated and others being negatively correlated. Life histories that entered the ocean at the same year were significantly more positively correlated than life histories that entered the ocean in different years, illustrating how diversity of this life-history trait can provide the asynchrony that buffers populations from annual variation in early-ocean mortality. We estimate that portfolio effects due to these asynchronous life histories decreased varia-

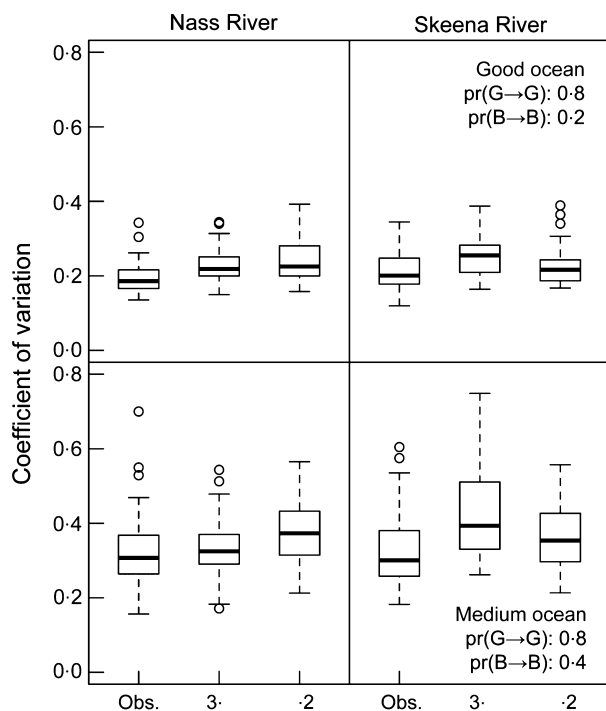


Fig. 7. Stability for freshwater and ocean life-history components. Shown are the coefficients of variation for simulation results with constrained residence in freshwater (3 years) and ocean environments during the first migration (2 years), corresponding to the most common residence times observed in these habitats. Repeat spawners are excluded from the simulations for all scenarios. The autocorrelated ocean condition is not shown due to negligible survival across all scenarios.

tion in aggregate Nass steelhead abundance and biomass by > 20%. Simulation models based on observed life histories further illustrated how different components of life-history diversity contributed to population stability.

Anadromous *O. mykiss* in these large and relatively pristine watersheds exhibited remarkable life-history diversity. These migratory fishes expressed 36 different life-history trajectories. Thus, there are many different specific stochastic realizations of the general anadromous life-history strategy. It is also important to note that *O. mykiss* also express resident life histories (e.g. Zimmerman & Reeves 2000; McPhee *et al.* 2007; Pavlov *et al.* 2008). Thus, *O. mykiss* undoubtedly possess more life-history diversity in these watersheds than we quantified, perhaps even further buffering these populations from environmental variability. Steelhead are known for their life-history diversity; Thorpe (1998) previously described 32 different life histories, focusing on different combinations of freshwater and ocean ages. This remarkable diversity of life histories has presumably evolved due to historic variability in environmental conditions and disturbances (Waples, Pess & Beechie 2008).

The observed diversity of life histories in *O. mykiss* is likely due to a combination of locally adapted life histories within these watersheds, plastic responses to environmental conditions or habitat accessibility, and differen-

tial survival driven by environmental variability (Quinn 2005; Satterthwaite *et al.* 2010, 2012). Previous studies have observed genetic differentiation among these watersheds and subwatersheds (Heath, Pollard & Herlinger 2001), and there is evidence of heritability of life-history traits in salmonids (Carlson & Seamons 2008). The study watersheds are large and include multiple habitats with diverse flow regimes, temperatures, growing conditions and other selective pressures (Gottesfeld & Rabnett 2008). Environmental variability across space and time also can influence the expression of the different life histories. *Oncorhynchus mykiss* have notoriously plastic life-history responses to environmental conditions; for example, water temperature and freshwater growing conditions may influence the duration of freshwater rearing (Jonsson & Jonsson 1993; Satterthwaite *et al.* 2010; Mills *et al.* 2012). While we did not examine the potential role of sex-specific life-history trajectories, different sexes of *O. mykiss* also can have different life-history trajectories which may influence population stability; for example, reproductive contributions from non-anadromous male *O. mykiss* likely stabilizes the effective population sizes of steelhead (Seamons, Bentzen & Quinn 2004; Araki *et al.* 2007). Stochastic processes also contribute to the different expressions of anadromy. For example, while certain populations may have genetic underpinnings that favour the possibility of repeat spawning, the fact that some fish made up to three repeat spawning migrations is partly due to the randomness of survival during spawning and migration in variable environments with predators such as seals and anglers. Regardless of the underlying mechanisms, there was high life-history diversity in these iconic fish.

In this study, we quantified the different pathways by which life-history diversity contributed to stability. Nass steelhead abundance and biomass was relatively stable over the observed time series, with a CV of approximately 0.50. Stability is a product of the weighted average of the specific life histories as well as the covariation among the life histories (Doak *et al.* 1998). Thus, the stability we observed was due to two main mechanisms: (i) certain life histories were relatively stable and (ii) asynchrony among different life histories enabled a stabilizing portfolio effect. These two mechanisms are discussed in turn below. First, the stability of specific life histories can stabilize the aggregate. This stability is conferred to the aggregate, proportional to its relative abundance. For instance, abundance of repeat spawners was relatively stable with a CV of 0.54. Repeat spawners are longer-lived and are therefore predicted to be relatively buffered from climatic variability (Morris *et al.* 2008). In addition, there were many different manifestations of the 'repeat spawner' group. Our simulation results confirmed the relationship between the proportion of repeat spawners in the population, and the stability and persistence of steelhead populations. Higher frequencies of repeat spawning individuals serve to increase the distribution of individual ages, staggering mortality and spawning events such that the over-

all fluctuations of the population trajectory were dampened, thus lowering the CV. Furthermore, because repeat spawners spawn repeatedly and may be larger, they can contribute more offspring over their lifetime (Seamons & Quinn 2010), pushing the population towards the carrying capacity, which could contribute to decreased variability. Thus, repeat spawners may stabilize population dynamics via multiple mechanisms.

Stability of the aggregate population was also driven by asynchrony among different life histories, allowing for the stabilizing portfolio effect (Doak *et al.* 1998; Tilman, Lehman & Bristow 1998; Thibaut & Connolly 2013). In the Nass watershed, where there were 9 years of scale data and corresponding population estimates, we found that unique life histories were differently prevalent through time – three life histories were dominant for a single year across the short time series, and no life history ever represented more than 45% of the population. The stability of Nass steelhead abundance and biomass was > 20% higher than it would be in the absence of these asynchronous life-history returns (Fig. 5). Simulations showed slight increases to CV when life histories were constrained to the most common number of years in freshwater or years in the ocean following first migration (Fig. 7). Moreover, predictions of increased CV were more exaggerated with increased oceanic mortality. Asynchrony was most pronounced for pairs of life histories that had different years of ocean entry.

Diversity in the year of ocean entry was thus a key life-history trait that contributed to the stability of steelhead. The first year in freshwater and the first year in the ocean are the two key life stages for anadromous salmonids, during which enormous mortality occurs (Smith 2000; Quinn 2005). Life histories that were born the same year (for example, 3-2 and 4-1) were not significantly more correlated than life histories born in different year, implying that early-life freshwater variability was not driving return patterns. In contrast, life histories that entered the ocean at the same year (for example, 5-2 and 4-2) had population dynamics that were 2.5 times more positively correlated than life histories with different ocean-entry years (Fig. 4). Thus, life histories with different ocean-entry years have more different dynamics, and this asynchrony is likely driven by variability in survival during the first year of marine life. It is important to note that this is based on variability of returning fish; if the analysis had focused on variability of production based on brood year, freshwater age-class diversity would likely have been also important source of asynchrony. For instance, if there is a bad ocean year where few out migrating fish would survive, variable freshwater ages will ensure that the brood year contributes to recruitment in future generations. Alternatively, variable ocean ages mean that returning fish from outmigration years with good ocean survival are spread throughout multiple years. Indeed, ocean survival can unpredictably range from > 20% to <1% in stream-rearing species such as coho salmon (*O. kisutch*) and steel-

head (Beamish *et al.* 2000; Smith & Ward 2000; Mantua & Francis 2004; Scheuerell, Zabel & Sandford 2009). Large-scale climate oscillations, such as the Pacific Decadal Oscillation, can drive these large swings in ocean survival on yearly and decadal scales (Mantua *et al.* 1997; Welch *et al.* 2000; Mueter, Pyper & Peterman 2005). This study illustrates that in steelhead, life-history diversity buffers populations from oceanic variability.

This study adds to previous research on Pacific salmon about potential linkages between life-history diversity and stability. In particular, Hill, Botsford and Hastings (2003) parameterized population models with data from Chinook and coho salmon and found that modelled ocean age diversity can increase the probability of persistence given variable ocean conditions. Other previous research on this subject predominantly comes from studies of sockeye salmon in Bristol Bay, Alaska. Schindler *et al.* (2010) found that the variation of specific ocean ages was 42–69% higher than the variability of the observed sockeye populations, thereby stabilizing of the commercial sockeye salmon fisheries that integrate across this diversity. Greene *et al.* (2010) also found that life-history diversity was correlated with temporal stability of sockeye salmon production in Bristol Bay. Life-history diversity within Pacific salmon populations can stabilize their populations. Life-history diversity across salmon population can stabilize processes that integrate across this diversity, such as the persistence of meta-populations or the stability of fisheries (Moore *et al.* 2010; Schindler *et al.* 2010). More generally, our study follows recommendations to move beyond the somewhat nebulous concept of stability to examine underlying mechanisms and processes (McCann 2000; Ives & Carpenter 2007; Loreau & de Mazancourt 2013).

Most studies have focused on how species diversity contributes to stability of communities. For example, Tilman, Wedin and Knops (1996) found a strong saturating relationship between grassland plant diversity and the stability of plant community biomass through time. Statistical models indicate the stability should be a function of the asynchrony, evenness and richness of species (Doak *et al.* 1998; Loreau & de Mazancourt 2013; Thibaut & Connolly 2013). There is also increasing appreciation that other scales of biodiversity can also confer stability. For example, eelgrass with higher genetic diversity were more stable in response to a perturbation (Hughes & Stachowicz 2004). Given that rates of population diversity loss exceed that of species loss by three- to eightfold (Hughes, Daily & Ehrlich 1997), studies such as ours represent key evidence of existing diversity and resultant stability that is being rapidly lost in many species and many regions.

MANAGEMENT IMPLICATIONS

Across the world, most large river systems are dammed (Nilsson *et al.* 2005), blocking migrations of migratory fishes such as steelhead. Twenty-nine per cent of steelhead

and salmon populations have been extirpated in their southern range (Gustafson *et al.* 2007). Furthermore, through widespread hatchery propagation and habitat degradation, there has likely been underappreciated loss of genetic or life-history population diversity within remaining populations (e.g. Tipping 1991; Moore *et al.* 2010; Carlson & Satterthwaite 2011; Pearse, Martinez & Garza 2011). This study provides a rare example of life-history diversity and its importance in large, relatively pristine watersheds. While there is a vast body of literature focusing on predicting how species will respond to directional climate change, perhaps just as important is understanding how species will cope with climate variability. Here, we illustrate the linkages between specific elements of life-history diversity and stability in the face of variability. This type of diversity will provide 'climate insurance' (*sensu* Mantua & Francis 2004). We echo suggestions from recent papers (e.g. Hilborn *et al.* 2003; Mantua & Francis 2004; Schindler *et al.* 2008; Healey 2009; Moore *et al.* 2010; Yeakel *et al.* 2014) that preserving diverse habitats and genetic integrity in these large watersheds will allow for the processes and local adaptations that facilitate the expression of a diversity of life histories that will confer stability through time.

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Data accessibility

Data and supporting information is archived on Dryad digital archive, doi: 10.5061/dryad.q7vk2 (Moore *et al.* 2014).

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Supporting Information

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

Appendix S1. Additional supplemental analyses on temporal dynamics and stability.