The roles of extrinsic and intrinsic factors in the freshwater life-history dynamics of a migratory salmonid

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Abstract. Key life-cycle transitions, such as metamorphosis or migration, can be altered by a variety of external factors, such as climate variation, strong species interactions, and management intervention, or modulated by density dependence. Given that these life-history transitions can influence population dynamics, understanding the simultaneous effects of intrinsic and extrinsic controls on life-history expression is particularly relevant for species of management or conservation importance. Here, we examined how life histories of steelhead (*Oncorhynchus mykiss*) are affected by weather, pink salmon abundance (*Oncorhynchus gorbuscha*), experimental nutrient addition, and density-dependent processes. We tested for impacts on the size of steelhead smolts (juveniles migrating to the sea), as well as their age and abundance across four decades in the Keogh River, British Columbia, Canada. Larger steelhead smolts were associated with warmer years and artificial nutrient addition. In addition, higher pink salmon abundance and artificial nutrient addition correlated with juvenile steelhead migrating at younger ages. While density dependence appeared to be the primary factor regulating the abundance of steelhead smolts, nutrient addition and temperature were positively and negatively associated with smolt production, respectively, prior to 1991, and pink salmon spawning abundance was positively associated with smolt production after 1990. Thus, this study provides evidence that the temporal dynamics of one species of salmon is linked to the juvenile life history of co-occurring steelhead. A complex interplay of species interactions, nutrient subsidies, density dependence, and climatic variation can control the life-history expression of species with complex life cycles.

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INTRODUCTION

Life-history transitions of organisms with complex life cycles may be influenced by multiple factors such as weather, species interactions, and management intervention (Benard 2004). Such shifts in life-history transitions can connect the conditions in the first part of the life cycle to the next part. In amphibians, for example, cues from predators, water temperatures, and density dependence can all influence the size and timing of metamorphosis and thereby influence adult fitness (Wilbur and Collins 1973, Semlitsch et al. 1988, Relyea 2007). Yet, density dependence can either exacerbate or ameliorate population-level impacts of stressors in species with complex life cycles (Hodgson et al. 2017). Understanding the potential for multiple drivers of life-history expression is particularly relevant for species of management or conservation importance as life-history shifts can alter population recovery and sustainable exploitation rates (Rowe and Hutchings 2003, de Roos et al. 2006).

Pacific salmonids are a management-relevant system for examining the simultaneous effects of intrinsic (i.e., density dependence) and extrinsic factors (e.g., climate, species interactions, and management actions) on life-history expression. Pacific salmon have complex life cycles; after a freshwater juvenile phase that can last up to several years, salmon undergo a series of physiological and morphological changes—called smoltification—prior to migrating to sea. The age and size of individuals undergoing the smoltification process can vary within and across populations (Groot and Margolis 1991, Quinn 2005), and life-history expression may respond to shifts in climate conditions (Crozier et al. 2008). However, density dependence may also affect these shifts. For example, in sockeye salmon (*Oncorhynchus nerka*) rearing lakes in Alaska, warmer years were associated with increased size of juvenile sockeye salmon (*O. nerka*) and a younger age of outmigration, but increased density decreased growth and increased age at outmigration (Schindler et al. 2005, Rich et al. 2009). Thus, life-history variation in salmon may be strongly influenced by environmental conditions and density dependence.

It is also possible that species interactions, namely from other species of salmon, could influence variation in the expression of key life-history

parameters of Pacific salmon over time. Spawning salmon, such as pink, chum (*Oncorhynchus keta*), and sockeye salmon, dislodge benthic invertebrates and release nutrient-rich eggs, which can subsidize stream salmonids by increasing prey resources (Bilby et al. 1996, Scheuerell et al. 2007, Denton et al. 2010). The carcasses of Pacific salmon also provide a source of nutrients to streams. Salmon subsidies can increase consumption and growth of stream fish (Moore et al. 2008, Bentley et al. 2012, Armstrong and Bond 2013), and this altered growth could shift the life histories of co-occurring species. For example, Nelson and Reynolds (2014, 2015) found that the density, size, and proportional age structure of coho salmon (*Oncorhynchus kisutch*) juveniles correlated with spawning chum and pink salmon densities across streams. While it has been widely hypothesized that Pacific salmon migrations benefit co-occurring salmon populations during the freshwater portion of their life cycles (Naiman et al. 2002, Achord et al. 2003, Scheuerell et al. 2005), there have been few quantifications of these potential impacts on life-history variation (but see Michael 1995). Spawning salmon could alter the size at age, age composition, or numbers of out-migrating smolts of another species (Ward and Slaney 1988), but these potential responses could be attenuated by within-species density dependence (Grant and Imre 2005, Myrvold and Kennedy 2015).

The addition of artificial nutrients to freshwater systems is one management strategy that has been employed to attempt to recreate former salmon nutrient subsidies, but there is great uncertainty regarding its efficacy and there are concerns about potential unintended consequences (Compton et al. 2006, Collins et al. 2015). Nutrient addition has generally increased individual growth rates in a variety of salmonid populations across multiple studies (Johnston et al. 1990, Wipfli et al. 2010, Collins et al. 2016). At the population level, artificial subsidies have increased juvenile fish biomass and survival in some studies of sockeye salmon (Hyatt et al. 2004), but not in other studies or locations with sockeye, or other species (Hyatt et al. 2004, Collins et al. 2016). It is worth noting that these studies were performed over relatively short periods of time (<12 yr) relative to the salmon life cycle and did not account for juvenile

density dependence. Thus, there is a need to quantify potential impacts of nutrient addition over longer time periods while accounting for density dependence.

Steelhead are one species of Pacific salmon with enormous intrapopulation life-history diversity and plasticity (Kendall et al. 2015). Thus, nutrient subsidies, density dependence, and environmental variation may cause particularly large shifts in their life history. In the juvenile portion of steelhead life history, the age and size at migration to sea are determined by a combination of growth opportunity and an individual genetically determined threshold size and growth rate (Beakes et al. 2010, Phillis et al. 2016). Given their life-history plasticity, subsidies could enable young steelhead to reach size thresholds for migration earlier, and thereby lead to smolts migrating from freshwater at younger ages. Depending on growing conditions and the timing and magnitude of subsidies, increased growth rates might also produce larger steelhead for a given age. Larger size may translate into increased survival in their subsequent marine phases, while some studies have found that larger smolts are more likely to survive the subsequent marine phase of their life cycle (Holtby et al. 1990, Bond et al. 2008, Osterback et al. 2014), other studies have failed to detect size-selective survival, or evidence that this has changed over time (Ward et al. 1989, Friedland et al. 2014). However, competition among stream-rearing salmonids can be high and density dependence may decrease juvenile steelhead size and increase mortality (Keeley 2001). Given the importance of steelhead for fisheries and the threatened status of this species in some locations (Northwest Fisheries Science Center 2015), understanding whether co-occurring salmon species or experimental nutrient addition alters their life cycles could inform management options at the ecosystem and multi-species level.

Here, we examine how four decades of variation in extrinsic (weather, a species interaction, and a management intervention) and intrinsic (density dependence) factors have influenced life-history variation in a migratory species. Specifically, we asked how temperature, precipitation, intraspecific density dependence, adult pink salmon abundance, and experimental nutrient addition correlate with the size, age, and abundance of migratory steelhead smolts. Using a long-term dataset from the Keogh River, British Columbia, Canada, we discovered that steelhead life histories appear to be influenced by multiple factors. Specifically, weather, pink salmon, and experimental nutrient addition were associated with the size, age, and production of steelhead smolts. Yet, only density dependence appeared to consistently regulate steelhead smolt production. These results provide a management-relevant example of how life-history transitions may be altered by complex environmental dynamics.

METHODS

We analyzed four decades of steelhead smolt data from the Keogh River, a well-studied stream in British Columbia, Canada. We examined steelhead smolt size, age, and abundance and tested how these response variables may be influenced by six potential predictor variables: pink salmon spawner abundance, artificial nutrient addition, density dependence, temperature, summer precipitation, and winter precipitation. All these variables have been shown or hypothesized to affect fish growth, which in turn may have consequences for age at migration to sea and density-dependent mortality in juvenile steelhead (see Table 1 for details). Our goal was to describe the relationships between our response and predictor variables while accounting for time. We considered that our predictor variables may be important during different time intervals or time lags within the freshwater residence of juvenile steelhead. Thus, we tested two or three different time intervals for the potential linkages between predictor variables and response variables and employed temporal autocorrelation structures or random effects (where appropriate) to account for temporal patterns within our dataset. To avoid overparameterization of models, we first determined the best time interval or time lags for each predictor variable for a given response variable and then used the top time-interval variable sets for model comparison and averaging.

Site description and research history

The Keogh River is a small (31.2 km long, 130 km² watershed area) lake-headed river in northeast Vancouver Island, British Columbia, entering Northern Johnstone Strait at 50°40′43.56″

Table 1. A priori predictions for possible effects of variables on the age-specific probability of migration, smolt fork length, and smolts per wild female steelhead spawner production in the Keogh River, British Columbia, Canada.

Predictor variable	Mechanism	Metric	References
Pink salmon abundance	Pink salmon spawning can increase juvenile steelhead growth and energy reserves via a nutrient subsidy of eggs, carcass tissues, and carcass decomposition, which may increase juvenile steelhead growth and energy reserves, allowing them to reach their threshold smolting size earlier, and reducing density-dependent mortality	Log(pink salmon spawner abundance estimate)	Michael (1995), Bentley et al. (2012), Armstrong and Bond (2013), Nelson and Reynolds (2015), Phillis et al. (2016)
Nutrient addition	Nutrient addition can increase juvenile steelhead growth and energy reserves via a bottom-up nutrient subsidy, which may increase juvenile steelhead growth and energy reserves, allowing them to reach their threshold smolting size earlier, and reducing density-dependent mortality	Categorical, 0–3 nutrient addition events	Johnston et al. (1990), Hyatt et al. (2004), Phillis et al. (2016)
Density	Increased juvenile steelhead density can reduce their growth and energy reserves, which may delay juvenile steelhead reaching their threshold smolting size and increase density-dependent mortality	Total number of smolts produced by a brood year	Ward and Slaney (1993), Keeley (2001), Grant and Imre (2005), Phillis et al. (2016)
Temperature	The metabolic rate of steelhead is dependent on water temperature, controlling potential growth rates and energy reserves, which may alter the time it takes for juvenile steelhead to reach their threshold smolting size, and alter density-dependent mortality	Mean air temperature (°C) from April through October	Boughton et al. (2007), Brewitt and Danner (2014), Doctor et al. (2014), Phillis et al. (2016)
Summer precipitation	Increased summer precipitation can increase stream flow during the low flow period, increasing the amount of available habitat and drifting benthic invertebrates, which may increase juvenile steelhead growth and energy reserves, allowing them to reach their threshold smolting size earlier, and reducing mortality	Total precipitation (mm) from April through October	Brittain and Eikeland (1988), Battin et al. (2007), Courter et al. (2009), Phillis et al. (2016)
Winter precipitation	Increased winter precipitation can cause scouring events via flooding, reducing fish densities/competition via mortality, which may increase juvenile steelhead growth and energy reserves, allowing them to reach their threshold smolting size earlier	Total precipitation (mm) from November through February	Battin et al. (2007), Phillis et al. (2016)

N, 127°20′55.23″ W (Smith and Slaney 1980). The watershed is rain-dominated, receiving an average of 1910 mm of precipitation per year (Government of Canada 2015). More information on Keogh River discharge, nutrient concentrations, and the surrounding ecosystem can be found in Smith and Slaney (1980), Perrin et al. (1987), Ward and Slaney (1988), and Johnston et al. (1990). Keogh Lake has been modified with a water-control structure, allowing more water to be retained and then released later during periods of low flow (Slaney and Zaldokas 1997).

Keogh River steelhead are a winter-run ecotype and thus enter the river as adults from December to May and subsequently reproduce, with fry emerging from the gravel in early summer (Ward and Slaney 1988). Juveniles rear in the river for one to five years and then become smolts and migrate seaward in April to mid-June (Ward and Slaney 1988). Adults generally return to the river after 2 yr at sea but may stay in the ocean from 1 yr (males) up to 4 yr (Ward and Slaney 1988). Steelhead are iteroparous: Approximately 10% of adult steelhead successfully migrate back to sea and then return to reproduce again (i.e., repeat spawning; Ward and Slaney 1988).

This study builds on a strong history of research in the Keogh River by simultaneously examining the different aspects of steelhead smolt

life histories as a function of multiple potential drivers. Work has been published previously on density-dependent smolt production (Ward and Slaney 1993, Ward et al. 2008, Atlas et al. 2015), nutrient addition (Johnston et al. 1990, Ward et al. 2008), and steelhead life history (Ward and Slaney 1988, Ward et al. 1989). In addition, Ward et al. (2008) examined the effect of nutrient addition, different time periods, and stream restoration treatments on density-dependent smolt production in the Keogh River. In an analysis of 7 yr of data, they found that relative to a nearby untreated river, experimental nutrient addition in the Keogh River shifted the proportions of age-2 and age-3 smolts. Past research also found that nutrient addition influenced steelhead fry mass (Johnston et al. 1990) and showed that smolt length increased during nutrient addition (Ward et al. 2008). Here, we build on these previous studies to examine the multiple dimensions of smolt life histories (size, age, and abundance) and how they might be influenced by multiple potential drivers (species interactions, artificial nutrient subsidies, environmental conditions, and density dependence) over four decades.

Steelhead smolt sampling

Steelhead smolts were enumerated annually from 1976 to present using a counting facility that spans the full river (we focus on 1976–2014). The counting facility is in operation from approximately the end of April to mid-June and consists of a concrete sill that extends across the river, with vertical metal plates redirecting the river through the smolt trap. During high-flow events, hanging incline plane traps were used to capture smolts (Mottram 1977). Trap efficiencies were tested by marking (with fin clips) and releasing captured coho smolts above the counting facility and determining the recapture rate (Ward and Slaney 1988). Daily visual trap inspections and weekly snorkel investigations ensured that there were no gaps where smolts could escape the trap (Ward and Slaney 1988, McCubbing 2002).

Wild steelhead smolts were enumerated, and 15–20% were sampled for fork length (hereon referred to as length) and mass on a daily basis (McCubbing 2002). Fish were anesthetized (using a mixture of 10 parts clove oil to one part 95% ethanol) prior to measurements and scale sampling. Prior to release, smolts were held briefly to allow for recovery from anesthesia. Scales were aged as described in Ward and Slaney (1988). From 1976 to 1980, scales were removed from a random subsample of those fish for aging (Ward and Slaney 1988), with scales sampled posterior to the dorsal fin on the left ventral side (McLellan 2004). Smolt age classes were proportionally allocated to the total number of steelhead smolts in an outmigration year to determine how many smolts were in each age class. After 1980, scales were sampled using a stratified random design based on 10-mm length classes (Ward and Slaney 1988). For steelhead whose length was measured but were not scale-sampled (and thus not aged using scales), ages were assigned based on the size–age relationship developed from stratified age sampling. The proportions of the different ages across all sampled steelhead from each outmigration year were then multiplied by the total number of migrating smolts to determine the number of smolts in each age class. To determine the age proportions of smolts based on brood year, the age-1 to age-5 smolts from the same brood year were summed over consecutive outmigration years to calculate a total number of smolts produced by a brood year, and then, the number of smolts at a given age was divided by the total.

Adult steelhead enumeration

Adult steelhead abundance has been estimated in the Keogh River since 1972 with mark–recapture, using the combination of an adult fish weir and angling to capture adult steelhead (McCubbing 2002). Since 1997, a resistivity counter has also been used in the estimation of adult steelhead abundance (McCubbing 2002). Wild and hatchery adult steelhead abundances were estimated separately and segregated by sex. We focus on female wild steelhead as the key metric of adult steelhead abundance.

Different levels and types of introductions and straying of hatchery-reared steelhead in the Keogh River have occurred. In some years in the 1980s and early 2000s, juvenile steelhead were raised in net-pens (1980s; Slaney and Harrower 1981) and then in the Quatse Hatchery (2000s; Ward 2006) and released into the Keogh River and estuary as smolts. When there were additions of hatchery smolts, numbers ranged from 3100 to 39,676 smolts. Hatchery-origin smolts

were marked using a combination of fin clips and tags and were noted as such if captured at the smolt counting facility, and thereby were excluded from our analyses. Sources of adult hatchery fish in the Keogh River include strays from the Quatse River Hatchery, and returning adults from additions of net-pen or hatchery-raised steelhead smolts during the 1980s (Slaney and Harrower 1981) and early 2000s (Ward 2006). These programs marked their juveniles prior to release, allowing hatchery adults to be identified upon return and thereby excluded from our analyses.

Pink salmon enumeration

We hypothesized that young steelhead may be positively influenced by co-occurring pink salmon. Pink salmon spawn in the river in late September and October (McCubbing et al. 1999), when their eggs may be an important source of food for young steelhead. Pink salmon fry emerge from the gravel in mid- to late April and migrate immediately to sea, and remain at sea for approximately 18 months before returning to spawn (Groot and Margolis 1991). Semelparous pink salmon die after spawning, have a fixed 2-yr life cycle, and exhibit a pronounced cycle of alternating years of high abundance (Groot and Margolis 1991). From 1976 through present, pink salmon spawner abundance in the Keogh River has been jointly enumerated by Fisheries and Oceans Canada (DFO), and the BC Provincial Government (currently managed under the Ministry of Forests, Lands, Natural Resource Operations, and Rural Development [MFLNRORD]). From 1976 to 1997, pink salmon were enumerated by DFO using stream walks and recording the peak spawner count as the escapement size (P. Van Will, *personal communication*). From 1997 to present, InStream Fisheries Research, Inc. (contracted by DFO), has been enumerating pink salmon using a resistivity counter (McCubbing et al. 1999). Resistivity counter accuracy was assessed using video validation and was incorporated into estimates of pink salmon abundance. Given that pink salmon abundance estimates from 1976 to 1997 are based on peak counts, these estimates are likely conservative. However, doubling the abundance estimates of pink salmon (which is a common correction factor for peak count data; Jones and McPherson 1997,

Jones et al. 1998) prior to 1998 did not significantly affect our results. Given that pink salmon abundance estimates over the four decades of this system ranged from less than 1000 to over 100,000, we suggest that the signal-to-noise ratio of these data are robust to potential observation error and potential bias in pink salmon abundance estimates.

Four years of pink salmon data were missing from our database: 1981, 1991, 1993, and 1994. We estimated the abundance of pink salmon in these missing years by predicting from a regression of pink salmon abundance of the nearby Cluxewe River vs. pink salmon abundance of the Keogh River with both abundances log-transformed to meet the assumptions of normality (***$P < 0.001$, $R^2 = 0.55$, $n = 36$).

Nutrient addition

Whole-river inorganic nutrient addition treatments were applied from 1983 through 1986 and from 1997 through 2004 (Johnston et al. 1990, McCubbing and Ward 1997, 1999, Ward et al. 2008, Appendix S1). Inorganic nutrients were deployed using slow-release pellets as well as liquid agricultural fertilizers (Appendix S1). The first treatment period was intended to eliminate phosphorous limitations on periphyton growth and to observe how this affected the mean mass of coho and steelhead fry (Johnston et al. 1990). The second treatment period was intended to restore depressed coho and steelhead populations in the river (McCubbing and Ward 1997). Small-scale nutrient addition experiments were also conducted in 1981 in the upper reach of the watershed (Johnston et al. 1990), but because <1 km of the river was treated, these nutrient addition experiments were not considered in our analyses. For a detailed timeline of nutrient addition events and treatments, see Appendix S1 and its associated references.

Environmental conditions

We investigated the potential effects of three environmental factors: air temperature, summer precipitation, and winter precipitation. We included these factors in our analyses because they were the best-available proxies of stream temperature and discharge that spanned our four-decade dataset. Air temperature (°C) was measured as the mean diel temperature from

April through October, and summer precipitation (mm) was measured as the total precipitation that fell from April through October. We hypothesized that these metrics of summer temperature and precipitation could be linked to growing conditions for young steelhead and thus potentially influence their size, age, and abundance (Table 1). Winter precipitation (mm) was measured as the total precipitation that fell from November through February, the period when the Keogh River is most susceptible to winter flooding which could be a source of mortality for young steelhead. All environmental conditions were measured at Port Hardy Airport, British Columbia, Canada (Government of Canada 2018), immediately adjacent to the mouth of the Keogh River.

Statistical analyses

We used a two-stage statistical modeling approach to examine the degree of support for intrinsic and extrinsic factors influencing three components of steelhead smolt outmigration (size, age, and numbers). The purpose of this approach was to create a top set of competing models and model-averaged coefficients for each response variable we analyzed, where each final group of models would contain only one time interval or lag per explanatory variable. In the first stage, for each of our response variables, we determined the best time interval or time lag of each predictor variable using Akaike information criteria corrected for small sample sizes (AIC_c; Burnham and Anderson 2002). To do this, we created a model set to compare the relative support for different potential time intervals and lags for each predictor variable, with a maximum of one time interval for each predictor. Depending on the biology of the response variable and predictor variable, we compared time intervals of lifetime, lag of one year, and lag of two years. All statistical procedures were performed using the statistical programming software R (R Core Team 2016). We competed the models using AIC_c with the MuMIn package (Bartoń 2016). From the list of top models, we selected the top time interval of each predictor variable, that is, the time interval that appeared in or nearest to the top model for a given predictor and response variable. In the second stage of modeling, we formed a global model composed of the top time

interval of each predictor variable for each response variable, and then, all possible combinations of these global models were competed using AIC_c. We model-averaged the top models with ΔAIC_c scores ≤2.

Our analyses examined multiple potential drivers of the different components of steelhead smolt life histories. We analyzed steelhead smolt age as a series of three models that represent the repeated migration decision-making process of juvenile steelhead. Mean smolt size at age and the number of smolts produced per wild female steelhead spawner were modeled with ages combined. Across the different response variables, we examined six main predictor variables: (1) intraspecific density-dependent processes as quantified by the abundance of smolts from a brood year or wild female spawner abundance, (2) pink salmon abundance, (3) nutrient addition, (4) mean air temperature during the summer, (5) total summer precipitation, and (6) total winter precipitation. All continuous variables were centered and scaled by two standard deviations (SD) to make their effect sizes comparable to categorical variables (e.g., nutrient addition and age) and to improve model interpretation (Schielzeth 2010). Where nutrient addition was used as a categorical variable, it was centered only. For a list of a priori predictions and associated mechanisms of the effects of the six predictor variables on the three sets of response variables, see Table 1.

Age.—We modeled age at outmigration as a series of decisions of whether to stay in the river or go to sea. We selected time intervals of our predictor variables based on work by Satterthwaite et al. (2009), who suggested that the absolute body size and condition of juvenile steelhead as well as rates of growth and change in body condition during a decision window interact with genetic thresholds (Phillis et al. 2016) to determine whether a juvenile steelhead migrates to sea the following spring. Thus, every year a juvenile steelhead spends in the river requires a decision on whether to migrate to sea or remain in the river and is based on two time intervals of information: lifetime history (absolute size and condition) and recent history (rates of change in size and condition). To reflect this decision-making process, we analyzed the age-specific probability of a juvenile steelhead migrating to sea with three

binary generalized linear mixed-effects models using the glmer() function in the lme4 package (Bates et al. 2017), and competed the effects of pink salmon abundance and nutrient addition at a recent time interval (outmigration year − 1) and a lifetime interval (mean of all years spent in the river). We examined the effects of our weather-related predictors at the lifetime interval because these variables tend to vary little year to year relative to pink salmon abundance and nutrient addition, thus reducing the likelihood of a meaningful difference between the effect of the lifetime interval and the effect of the year prior to migration time interval. We set migration year as a random effect given that multiple fish were sampled in each outmigration year and we wanted to account for variation common to all individuals among years.

The first decision model examines the probability of juvenile steelhead migrating at age 1. All juvenile steelhead in our dataset experience this decision because it is the earliest point in time that these fish can migrate to sea. Because age-1 steelhead have only spent one year in the river, we only examined the effects of the extrinsic factors (pink salmon abundance, nutrient addition, environment) of the year prior to migration. However, because there could be both within- and across-cohort competition (intrinsic factors), we tested three different time intervals of density dependence: the abundance of smolts produced in the same brood year, the abundance of smolts produced by the previous brood year, and the sum of the same and previous brood years' smolt abundance. The abundance of smolts produced in the same brood year was the most supported time interval for predicting age-1 migration.

For subsequent age analyses, we focused on the fish that had not yet migrated to sea. Juvenile steelhead that migrated at age 1 obviously cannot migrate at age 2; thus, individuals that migrated at age 1 were removed from the dataset used to calculate the probability of migrating at age 2. The same process was repeated for the analysis of migration at age 3, where individuals that had migrated at age 1 and age 2 were excluded from the dataset used for the probability of migrating at age 3. In both analyses, the lifetime representation of nutrient addition was the proportion of years with nutrient addition over the span of time a fish had spent in the river

up to the migratory decision in question. For the age-2 analyses, the lifetime interval was the top time interval for both pink salmon abundance and nutrient addition, whereas the top time interval for the age-3 analysis was year prior to migration. The time interval best explaining the effect of density dependence (measured as total brood smolt abundance) was the previous brood year for migration at age 2, and the sum of the previous and same brood years for migration at age 3.

To perform the analyses of individual migratory decisions, we adapted our original dataset. The original dataset consisted of summary proportions of the total number of steelhead smolts produced by a brood year that migrated at age 1–5. We multiplied these smolt age proportions by the mean annual smolt-aging sample size (200 smolts) to generate representative individual-level data. Age-5 fish were rare, so we combined the age-4 and age-5 groups into the age-4$^+$ group. Based on the smolt age of an individual, we assigned 0 (no migration) or 1 (migration) for each migration window that an individual experienced. For example, an age-3 smolt was 0, 0, 1 because it failed to migrate at age 1 and age 2 but migrated at age 3.

Size.—We analyzed smolt fork length at migration to sea with a single linear model using the gls() function in the nlme package (Pinheiro et al. 2017). We set age as a fixed categorical variable and did not hypothesize interactions between age and our predictor variables. We competed the same time intervals for the same predictor variables that were used in the age-2 and age-3 probability of migration models described above, with the same rationale for restricting weather-related predictor variables to the lifetime interval only. The lifetime interval was consistently the best time interval for both pink salmon abundance and nutrient addition, and the total number of smolts produced by the previous brood year was the best time interval for density dependence. We tested for and failed to detect temporal autocorrelation in the residuals of separate, age-specific global models.

Abundance.—We examined how density dependence and extrinsic factors correlated with steelhead smolt production. Given previous evidence that there was a shift in steelhead smolt production after 1990, we analyzed production dynamics

separately in each of the two time periods (pre-1991 and post-1990). Specifically, Atlas et al. (2015) found that there was a shift in density-dependent relationships (using a linearized Ricker model) in Keogh smolt production around 1990 (Fig. 1a) associated with their spatial contraction within the watershed. We used linearized Ricker models that describe the natural log of the number of steelhead smolts produced per wild female steelhead spawner as a function of wild female steelhead spawners and other covariates. The models were fit with the gls() function from the nlme package. We tested for and failed to detect temporal autocorrelation in the global model residuals. We used a Ricker model because preliminary analyses suggested that a Ricker model fit our data better than a Beverton-Holt model, and the linearized version of a Ricker model allows for

the simple integration of additional covariates and temporal autocorrelation structures.

We examined which extrinsic factors (pink salmon abundance, nutrient addition, and weather) best explained the number of smolts produced per spawner: (1) the first year of life or (2) the mean of the first three years of life in the river. Previous work by Sogard et al. (2009) and Myrvold and Kennedy (2015) suggests that the strongest period of density-dependent mortality in juvenile steelhead may occur during the first year of life, and it also seems possible that lifetime conditions experienced by a juvenile steelhead brood could affect the total production of steelhead smolts per spawner. We averaged our extrinsic variables over the first three years juvenile steelhead may spend in the river because greater than 50% of juvenile steelhead migrate by
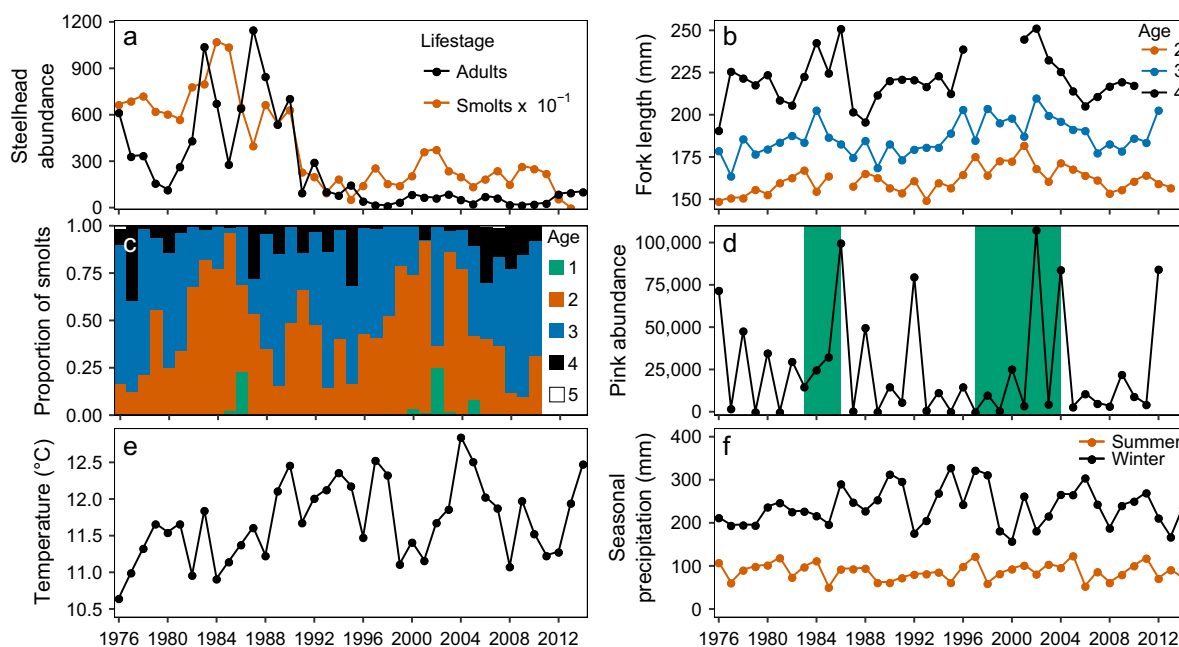

Fig. 1. Steelhead, pink salmon, nutrient addition, temperature, and precipitation data used in our analyses from 1976 to 2014 for the Keogh River, Port Hardy, British Columbia, Canada. All steelhead data are associated with brood year. (a) Steelhead smolt and wild female adult spawner abundance. Note that smolt abundance is displayed at one-tenth of total abundance for each brood year. (b) Mean steelhead smolt fork length according to smolt age. (c) Proportional steelhead smolt age composition. (d) Pink salmon spawner abundance and nutrient addition periods. The green blocks indicate the time periods when the Keogh River was treated with artificial nutrient addition. (e) Mean air temperature during the summer (from April through October). (f) Total annual summer (April through October) and winter (November through February) precipitation. Winter precipitation months span consecutive years, so total winter precipitation is assigned to the earlier year (e.g., winter precipitation in 1978 was the sum of precipitation in November–December 1978 and January–February 1979).

age 3. For our intrinsic factor (density dependence), we examined three different time intervals: the abundance of wild female steelhead spawners in the same brood year, the abundance of spawners in the previous brood year, and the sum of the same and previous brood years' spawner abundance. Lifetime was the best time interval for pink salmon abundance, temperature, and winter precipitation, whereas the brood year was the best time interval for nutrient addition, summer precipitation, and density dependence.

RESULTS

Keogh River steelhead adult and smolt abundances varied across an order of magnitude between 1976 and 2010, with a notable decline in abundance of both life stages after 1990 (Fig. 1a). In contrast, mean steelhead smolt length by brood year, smolt ages, and pink salmon spawner abundance varied greatly over the period without any clear long-term change in pattern after 1990 (Fig. 1b–d). The even-year pink salmon population averaged 6.4 times more abundant than the odd-year population (Fig. 1d); thus, there was biennial change in salmon-derived food for young steelhead. On average, odd-year steelhead broods produced greater proportions of age-4 smolts, and even-year broods produced greater proportions of age-3 smolts (Fig. 1; Appendix S2) in the absence of artificial nutrient addition. The spikes in the proportion of age-2 steelhead smolts coincide with years when nutrients were added to the whole river (Fig. 1c, d). Mean temperature from April through October increased over time by approximately 0.021°C/yr (95% confidence interval [CI] 0.005–0.037). Annual summer and winter precipitation varied from year to year but did not show a consistent trend through time.

Probability of migration at age

Age 1.—Age-1 migration in Keogh River steelhead was rare but positively associated with increased nutrients and pink salmon. The top predictors of the probability of a juvenile steelhead migrating at age 1 were nutrient addition (in all top models) and pink salmon abundance (in six of seven top models; Figs. 2a, 3a;

Appendix S3). Nutrient addition during the brood year increased the odds ratio of migrating at age 1 by 2.4 units (95% CI 0.5–4.2; Fig. 3a), and pink salmon during the autumn of the brood year increased the mean odds ratio of migrating at age 1 by 2.1 units (95% CI −0.03–4.2; Fig. 3a) for every ~4-unit increase in log pink salmon abundance. In other words, nutrient addition increased the mean probability of migrating at age 1 from 0.0005 (95% CI 0.0001–0.003) to 0.006 (95% CI 0.0002–0.15) and increasing pink salmon abundance from ~7000 fish (mean abundance) to ~400,000 fish (mean + 2 SD) increased the mean probability to 0.004 (95% CI 0.0001–0.15). The other covariates tested (density, temperature, and precipitation) appeared in less than three of the top models, and all had effects with 95% CIs that spanned zero (Fig. 3a; Appendix S3).

Age 2.—The probability of an age-2 juvenile steelhead migrating was higher in years of nutrient addition and high pink salmon abundance. Both mean nutrient addition and mean log pink salmon abundance were in all models with AIC_c ≤2 (Figs. 2b, 3b; Appendix S3). The proportion of years of nutrient addition increased the mean odds ratio of smolts that did not migrate at age 1 migrating at age 2 by 1.5 units (95% CI 0.9–2.1; Fig. 3b) for every 0.9-unit (2 SD) increase in the proportion of years with nutrients added, and mean log pink salmon abundance during the first and second autumns since brood year hatching increased the mean odds ratio of smolts migrating at age 2 by 0.7 units (95% CI 0.06–1.4; Fig. 3b) for every ~2-unit (2 SD) increase in mean log pink salmon abundance. In other words, increasing nutrient addition from 1 to 2 yr increased the mean proportion of smolts that did not migrate at age 1 and migrated at age 2 from 0.50 (95% CI 0.20–0.78) to 0.68 (95% CI 0.37–0.90), and increasing mean pink salmon abundance from ~6700 fish (mean abundance) to ~48,300 fish (mean + 2 SD) increased the mean proportion of smolts that did not migrate at age 1 and migrated at age 2 from a mean of 0.45 (95% CI 0.38–0.53) to 0.63 (95% CI 0.40–0.82). All other covariates tested only appeared in one of the five top models, and all had effects with 95% CIs that spanned zero (Fig. 3b; Appendix S3).

Age 3.—The top predictors for the probability of a juvenile steelhead migrating at age 3 that had not migrated at age 1 or age 2 were nutrient
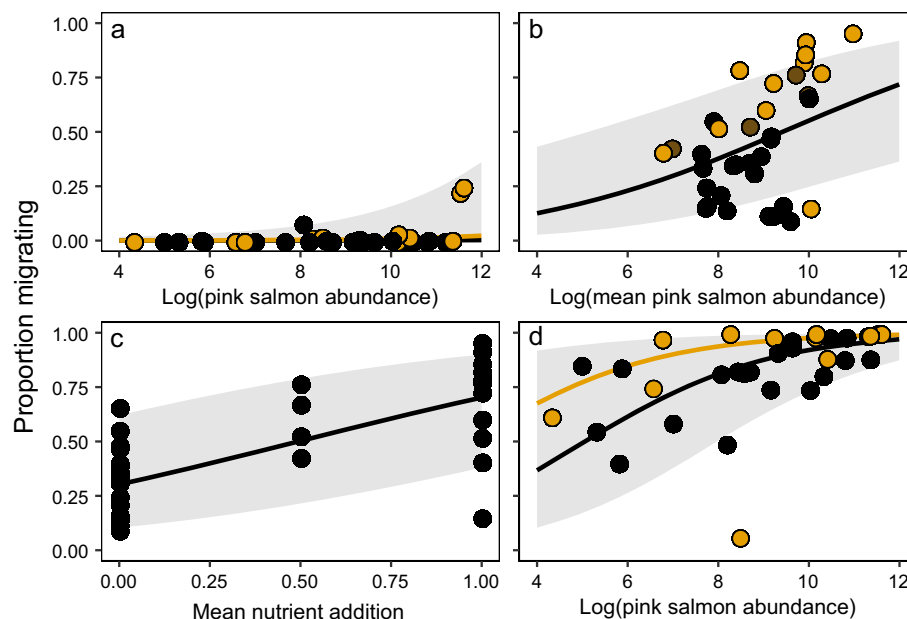
Fig. 2. Plots illustrating the age-specific proportion of juvenile steelhead migrating to sea given that they did not migrate in a previous year. Points represent raw proportions of steelhead that went to sea on a given year, lines represent mean proportions of steelhead migrating to sea under different levels of nutrient addition, and light-gray areas represent the combined 95% confidence intervals of all lines in the plots. (a) Probability of migration at age 1. The black and the yellow points and lines represent no nutrient addition and nutrient addition during the brood year, respectively. Pink salmon abundance is measured during the fall of the brood year. (b) Effect of log mean pink salmon abundance over the two autumns spent in the river on the probability of migrating at age 2. Darker points denote less nutrient addition. (c) Effect of the mean proportion of years of nutrient addition on the probability of migrating at age 2. (d) Probability of migration at age 3. The black and the yellow points and lines represent no nutrient addition and nutrient addition, respectively, in the year prior to migration. Pink salmon abundance was measured during the autumn prior to migration.

addition and pink salmon abundance (both in all top models; Figs. 2c, 3c; Appendix S3). Log pink salmon abundance during the third autumn since brood year hatching increased the mean odds ratio of smolts that did not migrate at age 1 or age 2 migrating at age 3 by 2.1 units (95% CI 1.2–3.1; Fig. 3c) for every ~4-unit increase in log pink salmon abundance, and nutrient addition in the autumn before migration increased the mean odds ratio of smolts that did not migrate at age 1 or age 2 migrating at age 3 by 1.3 units (95% CI 0.3–2.3; Fig. 3c). In other words, increasing pink salmon abundance from ~7000 fish (mean abundance) to ~400,000 fish (mean + 2 SD) increased the mean probability of migration at age 3 (given no previous migration) from a mean of 0.86 (95% CI 0.79–0.92) to 0.98 (95% CI 0.92–1.00), and nutrient addition in the autumn before migration

increased the mean probability of migration at age 3 to 0.96 (95% CI 0.83–0.99). All other covariates tested were not present in more than three of seven top models and had effects with 95% CIs spanning zero (Fig. 3c; Appendix S3).

Mean smolt length

The strongest predictors of mean smolt fork length were age, nutrient addition, and temperature (Figs. 3d, 4a, b). Not surprisingly, older smolts were larger: On average, age-3 smolts were 24 mm longer than age-2 smolts (95% CI 47–54), and age-4 smolts were 60 mm longer than age-2 smolts (95% CI 82–89). Nutrient addition was associated with an increase in mean smolt length by 8 mm (95% CI 3–12; Fig. 3b) when moving from no nutrient addition to 50% of years with nutrient addition, and smolt length increased by
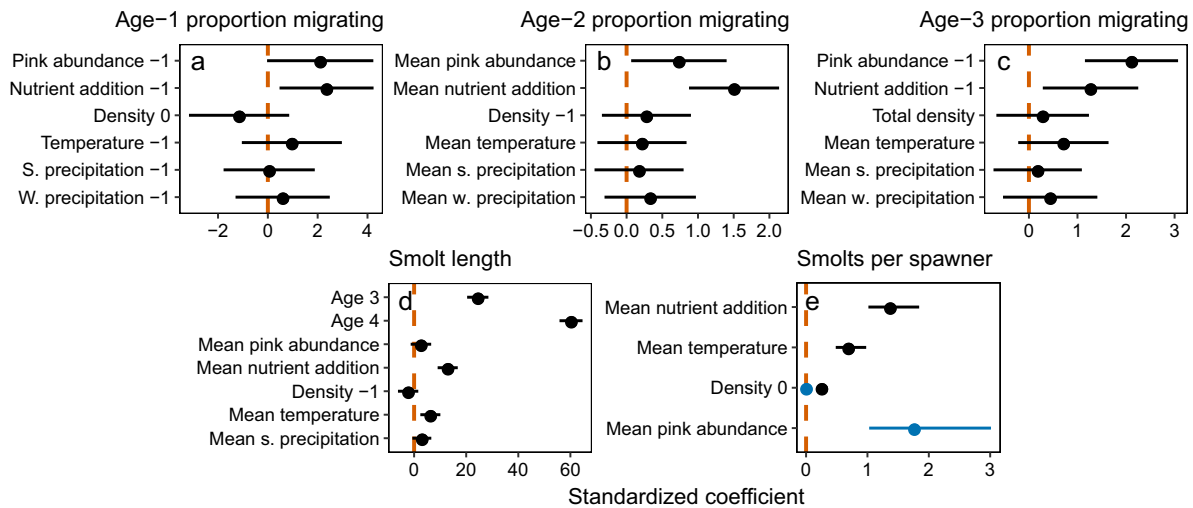
Fig. 3. Plots of standardized Akaike information criteria corrected for small sample sizes model-averaged coefficients with 95% confidence intervals describing the effects of pink salmon abundance, whole-river nutrient addition, density dependence, temperature, and precipitation (s., summer; w., winter) on measurements of probability of migration to sea (a, b, c), steelhead smolt length (d), and abundance (e). Density refers to the total number of steelhead smolts produced by a given brood year(s), except for plot (e), where density refers to wild female steelhead spawner abundance. In plot (e), the black coefficients represent results from the 1976 to 1990 model, and the blue coefficients represent results from the 1991 to 2010 model. Numbers following predictor variables denote time lags, where −1 refers to the growing season or winter prior to migration (except density, where −1 means the previous brood year), and 0 refers to the brood year. For the "mean" of predictor variables, such as pink salmon abundance and nutrient addition in panel (d), this refers to the mean value of that predictor over the lifetime of the fish.
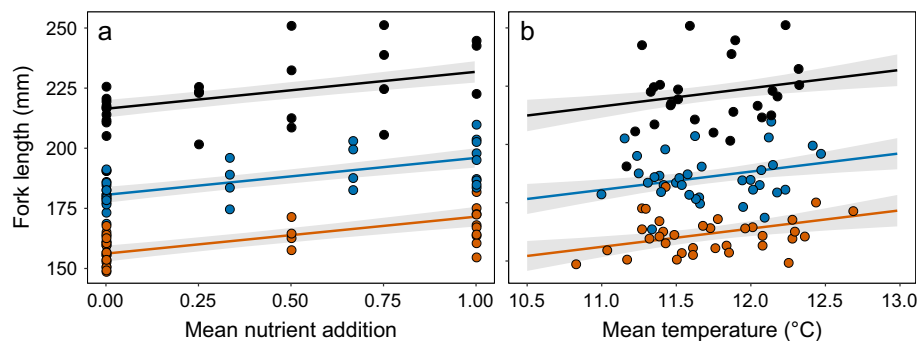

Fig. 4. Plots of smolt fork length (mm) vs. (a) mean proportion of years of nutrient addition, (b) mean temperature over the summers (April–October) each age class had spent in the river. Light-gray areas represent 95% confidence intervals for each line, and points represent raw data. Orange, blue, and black points and lines represent smolt ages 2–4, respectively.

6 mm (95% CI 2–10) for every 0.80°C (2 SD) increase in mean temperature. All other predictor variables tested either had weak effects (pink salmon, summer precipitation, density) with 95% CIs that spanned zero or did not appear in the top model set (winter precipitation).

Brood smolt abundance

The number of steelhead smolts produced per wild female steelhead spawner was negatively density-dependent and best predicted by wild female steelhead spawner abundance in both the 1976–1990 and 1991–2010 time periods (Figs. 3e, 5a–c;

Appendix S3). In the earlier time period, the top extrinsic predictors of steelhead smolt production were nutrient addition and temperature, whereas pink salmon abundance was the best extrinsic predictor in the later time period. From 1976 to 1990, the average number of smolts produced per spawner was 27 (at an average spawning density of 545 female steelhead) and decreased by a factor of 0.25 (95% CI 0.18–0.35; Fig. 3e) for every ~625 (2 SD) additional wild female steelhead spawners in a brood year. Smolts produced per spawner were associated with a decrease by a factor of 0.69 (95% CI 0.48–0.98; Fig. 3e) for every ~0.7°C (2 SD) increase in mean temperature and increase by a factor of 1.16 (95% CI 1.14–1.18; Fig. 3e) when moving from zero years of nutrient addition to 3 yr (100%) of nutrient addition. From 1991 to 2010, the average number of smolts produced per spawner was 3 (at an average spawning density of 73 females) and decreased by a factor of 0.00056 (95% CI 0.000039–0.0083; Fig. 3e) for every ~625 (2 SD) additional wild female steelhead spawners in a brood year. Smolts produced per spawner increased by a factor of 1.76 (95% CI 1.03–3.01; Fig. 3e) for every additional ~40,000 pink salmon (2 SD increase in mean pink salmon abundance). All other predictor variables tested did not appear in the top model sets (summer and winter precipitation).

Discussion

We discovered that multiple extrinsic (species interactions, artificial nutrient addition, and warming temperatures) and intrinsic (density-dependent) factors are linked to the freshwater life histories in a migratory fish with a complex life cycle. Through analyses of a four-decade time series of steelhead smolts, we found that the age and size of juvenile steelhead appeared to be primarily influenced by extrinsic factors: temperature, experimental nutrient addition, and pink salmon abundance. In contrast, the intrinsic factor of conspecific density was the only consistent predictor of the number of juvenile steelhead produced per spawning female. However, warmer temperatures were associated with fewer smolts per female, whereas nutrient addition and higher pink salmon abundances were associated with more smolts per female, depending on the time period (before or after 1990). Thus, our study provides evidence that steelhead life-history
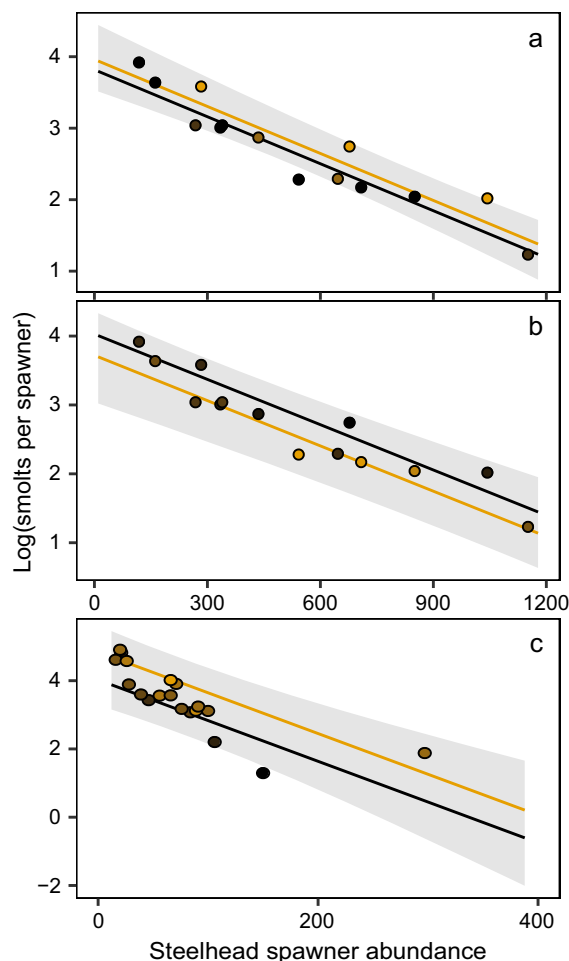

Fig. 5. Log(steelhead smolts per wild female steelhead spawner) vs. wild female steelhead spawner abundance (density 0) from (a, b) 1976 to 1990, and from (c) 1991 to 2010. Points represent raw data, and lines represent a linearized Ricker. (a) The yellow line represents smolt production when all years experience nutrient addition, and the black line represents smolt production in the absence of nutrient addition. Darker points represent a lower proportion of years of nutrient addition. (b) The yellow line represents smolt production when the mean temperature is 2 standard deviation (SD) above normal, and the black line represents smolt production when the mean temperature is 2 SD below normal. Darker points represent cooler mean temperatures. (c) The yellow line represents smolt production when pink salmon abundance is 2 SD above normal, and the black line represents smolt production when pink salmon abundance is 2 SD below normal. Darker points represent lower mean pink salmon abundances.

dynamics are influenced by a variety of extrinsic and intrinsic factors that can vary substantially over time.

Long-term studies such as this allow insights into complex ecological dynamics that would likely be missed by shorter-term studies (Hughes et al. 2017). Our study system underwent major biological and environmental changes over the last four decades. Across the four decades of data, wild female steelhead abundance decreased from an average of 533 adult female wild steelhead (pre-1990) to an average of 75 adults after 1990. This pattern of decreased abundance mirrors larger-scale trends in regional salmon abundance; southern populations of many salmon species have tended to decline over the last several decades (Mueter et al. 2002, Malick and Cox 2016, Kendall et al. 2017). In contrast, pink salmon returns have a strong biennial pattern, but their trends have been relatively stable or increasing in their southern range and did not exhibit a large post-1990 regime shift in abundance (Malick and Cox 2016). With respect to climatic variability, precipitation did not consistently increase or decrease over time, but temperature increased by an average of 0.021°C/yr, tracking patterns of climatic warming. Thus, although our data come from only one intensively monitored watershed (Bennett et al. 2016), this system experienced many of the larger-scale trends observed in streams across the Pacific Northwest.

Nutrient addition

Whole-river nutrient addition was associated with an increase in the mean size of smolts, an increase in the probability of juvenile steelhead migrating to sea at a younger age, and an increase in the number of smolts produced per wild female steelhead spawner prior to 1991. These results fit well within the proposed mechanisms that drive smoltification (Beakes et al. 2010, Satterthwaite et al. 2009, Phillis et al. 2016), where smolt age is determined by a combination of growing conditions and a genetically determined growth rate and size threshold. Artificial nutrient addition presumably increased steelhead growth and thereby reduced the time that was required for individuals to meet their threshold size to begin smoltification, resulting in a portion of smolts leaving at least one year earlier than normal. Nutrient addition was also associated

with greater smolt numerical production in the earlier portion of the time series but not during the later period of the time series. Indeed, previous studies of juvenile salmon responses to artificial nutrient addition have found that they only sometimes appear to have a positive numerical response (Hyatt et al. 2004, Collins et al. 2016). The lack of a numerical response after 1990 aligns with previous analyses from the Keogh River (Ward 2000, Ward et al. 2008) and those observed from other long-term studies of nutrient-enriched streams where initial increases in the individual growth of fish or macroinvertebrate predators failed to persist through time (Slavik et al. 2004, Davis et al. 2010). Our findings mirror the results of a synthesis by Collins et al. (2015), where they showed that while nutrient addition was commonly associated with individual-level responses, population-level effects remain uncertain.

Pink salmon

Pink salmon abundance was positively associated with steelhead smolts migrating to sea in the following year and greater numbers of steelhead smolts produced per steelhead spawner after 1990. Thus, high abundances of pink salmon should be associated with shorter generation times and higher abundances of steelhead smolts in the current regime. Given that generation time is linked to population growth rate, if steelhead have a positive population growth rate (which they currently do not in the Keogh River), then higher abundances of pink salmon could increase the rate of population increase of steelhead, assuming all other things being equal.

Our results provide an important critical test of the hypothesis that salmon beget more salmon (Bilby et al. 1998). We observed linkages between pink salmon abundance and steelhead smolt age and abundance; however, it appears that pink salmon abundance only affected smolt production after an apparent shift in the ecosystem around 1990 (Atlas et al. 2015). After 1990, it appears that there was spatial contraction of steelhead in the Keogh River toward the lower reaches of the watershed (Atlas et al. 2015); these lower reaches are also the areas of the river used by pink salmon for spawning. In the earlier portion of the time series, there was no statistical evidence that pink salmon abundance was associated with steelhead smolt production. Importantly, pink

salmon abundance was positively correlated with steelhead smolt production in the current regime. It is possible that this positive relationship between pink salmon and steelhead smolt abundance became apparent because of the spatial alignment of pink salmon spawning and steelhead within the watershed. Regardless of the mechanism, our results suggest that a 2 SD increase in log pink salmon abundance may approximately double steelhead smolt production per spawner.

Despite the effect of pink salmon on the probability of migrating to sea and the number of smolts produced per female steelhead spawner, pink salmon did not appear to affect steelhead smolt size. Mechanistically, pink salmon likely influenced steelhead life history by providing pulsed and energy-rich food resources. Steelhead could be subsidized through direct consumption of pink salmon eggs and carcass tissues (Bilby et al. 1998, Moore et al. 2008), or indirectly through increased invertebrate prey that have fed on pink salmon carcasses (Wipfli et al. 2010) or have been dislodged during pink salmon spawning (Scheuerell et al. 2007, Harding et al. 2014). We hypothesize that some of the increased growth in young steelhead due to high pink salmon returns could have manifested itself as shifted age structure toward a younger age at migration. Alternatively, given that recent changes in body condition are one of the factors controlling the decision to smolt in steelhead (Satterthwaite et al. 2009), we hypothesize that the pulsed nature of pink salmon spawning may cause an increase in body condition without affecting smolt length, improving survival and driving juvenile steelhead to smolt earlier. Our results align with the general paradigm where faster growth will confer survival advantages in stream salmonids (Quinn and Peterson 1996, Zabel and Achord 2004).

Other studies within freshwater that have compared across streams with different salmon densities have found that high abundances of one species of salmon (e.g., sockeye, pink, or chum salmon) are associated with larger sizes of co-occurring stream-rearing salmon like coho (Nelson and Reynolds 2015, Smits et al. 2016). Many papers have speculated that one population of salmon can benefit another co-occurring population by increasing growth and thus

survival (Bilby et al. 1996, Wipfli et al. 1998), and this appears to be the case with steelhead and pink salmon in the Keogh River after 1990. Our results align with those of Michael (1995), who found that higher returns of pink salmon were associated with more coho smolts produced per spawner in the Skagit River. Our research adds to the growing appreciation for the ecological impacts of pink salmon, which are increasing in many locations (Malick and Cox 2016). For example, there is a growing body of evidence that pink salmon in the marine ecosystem are important competitors, and years with high abundances are associated with decreased survival and size in sockeye salmon and nesting seabirds (Ohlberger et al. 2018, Springer et al. 2018). Here, we provide rare evidence that the temporal dynamics of one species of salmon is linked with the life history of a co-occurring salmonid during the freshwater phase of their life and that it may directly translate into increased per capita productivity.

Comparing the subsidies

This study offers the opportunity to consider how two different types of nutrient subsidies (artificial nutrients and pink salmon spawning) simultaneously affect steelhead, a migratory species with a complex life cycle. Both nutrient addition and pink salmon tended to shift juvenile steelhead toward earlier migration and were positively associated with greater smolt production in some time periods. However, pink salmon abundance did not substantially alter smolt size, while nutrient addition did tend to increase the length of migrating smolts. This difference in impact between pink salmon abundance and artificial nutrient addition is likely because these two subsidies differed substantially in their distribution across space and time as well as their potential pathways of incorporation. From a spatial perspective, artificial nutrients increased the ambient nutrient concentrations of the whole river, whereas pink salmon spawning is restricted to the lower 15 km of the river. Thus, steelhead smolts from the upper parts of the watershed would not experience elevated growth potential from pink salmon. Nutrient addition and pink salmon also differ in the timing and duration of potential increases in steelhead food. Nutrient addition could potentially increase food availability throughout the growing season

through bottom-up processes (Johnston et al. 1990). In contrast, pink salmon provide more contracted sources of nutrients and energy to young steelhead, with eggs and dislodged benthic invertebrates being available in the fall (Scheuerell et al. 2007, Moore et al. 2008), then their fry become a potential food source in the early spring, and carcasses subsidize steelhead through bottom-up processes (Naiman et al. 2002). Across years, the pink salmon signal was primarily an even–odd-year pattern (Appendix S2), whereas nutrient addition occurred in several multi-year blocks. Our study adds to the growing scientific appreciation that artificial nutrient addition impacts stream ecosystems differently than salmon (Compton et al. 2006, Wipfli et al. 2010).

Climatic variation

Warmer temperatures were associated with larger smolt sizes, and prior to the regime shift, higher temperatures were correlated with less steelhead smolts produced per wild female steelhead spawner. Increased temperatures may have increased growth rates of juvenile steelhead through bioenergetics (Boughton et al. 2007, Brewitt and Danner 2014), and increased the per capita energy demand of juvenile steelhead, thereby reducing the number of individuals that could survive summer stream temperatures. In addition, increased summer precipitation (our proxy for discharge of the Keogh River) tended to increase the size of smolts and the numbers of smolts per spawner, but both responses were uncertain. More summer precipitation could translate into increased amounts of habitat and increase benthic invertebrate availability (Battin et al. 2007, Courter et al. 2009). We note that we had to use nearby air temperatures and precipitation measures as proxies for stream temperature and flow, which likely introduced error into these potential relationships. Regardless, there is evidence that ongoing climatic variability can influence steelhead smolts.

Caveats

While our study provides insights on how long-term ecological dynamics influence juvenile steelhead life histories, it is important to discuss the limitations of our study. In the Keogh River, different nutrient concentrations and methods for artificial nutrient addition were used for each treatment block, but we considered these treatments as similar. Despite this potential source of variability, there were measurable effects of whole-river nutrient addition on steelhead smolt age, size, and abundance. Another important biological reality of this system is that pink salmon spawning only occurs in the lower 15 km of the watershed, with spawning densities increasing closer to the mouth of the river. Thus, juvenile steelhead had unequal access to pink salmon subsidies, depending on what part of the river they reared in. We also note that our study focused on a single (albeit long-term) study system and these dynamics may operate differently in other systems and regions. For instance, the Keogh River is nutrient-poor (Johnston et al. 1990) and thus is a system where nutrient addition may have particularly large effects. Further, although our study did account for weather variability in terms of air temperature and precipitation, these are indirect proxies for stream conditions. There were also a series of habitat manipulations that have been performed in the Keogh River, such as placement of large woody debris and installation of the water storage structure that occurred during the time series that could have contributed to unexplained variance in steelhead life-history dynamics. Our study did not examine other potential drivers of steelhead smolt characteristics and numbers, processes such as competition with other fishes such as coho salmon. Coho are the numerically dominant stream-rearing salmonid in the Keogh River and may compete for space and food resources (Hartman 1965, Young 2004). Thus, coho could affect juvenile steelhead life histories, which should be investigated in future work. We also acknowledge that hatchery practices could be contributing to unexplained variation in the dynamics of this population through several potential mechanisms. First, outgoing hatchery smolts can residualize (fail to migrate to sea and become river residents; Slaney and Harrower 1981) and may contribute to in-river density dependence (Ward 2006). Records from 1980 and 1981 indicate that the majority of artificially reared smolts emigrated from the river (68.2–92.6%; Slaney and Harrower 1981), and those that failed to migrate to sea but survived and became river residents only occupied the lower 3 km of the Keogh River (Slaney and Harrower

1981). Thus, the effect of residualized hatchery fish on the juvenile wild steelhead population in the Keogh River was likely minimal. Second, hatchery adults that spawned in the Keogh River could have contributed to the numbers of smolts in the following years. However, previous studies have found that adult hatchery steelhead usually produce much fewer smolts than wild steelhead (from 4% to 88%; Araki et al. 2008). We also acknowledge that we fit a Ricker model rather than a Beverton-Holt or hockey stick model even though previous work has commonly used Beverton-Holt models for steelhead (Ward 2000, Moore et al. 2014), and overescapement seems biologically unlikely. We did so for two reasons. First, a Ricker model fit the data better (data not shown). Second, for every parameter fitted in a linearized Ricker model, one must fit two parameters in the equivalent Beverton-Holt model, which reduces statistical power. Collectively, while there are many important realities to this system and analyses, our study does provide insight into the dynamics of juvenile steelhead through analyses of the longest-term dataset on steelhead life histories of which we are aware.

Potential management implications

Our study quantifies how two potential management levers, population abundance of co-occurring salmon and artificial nutrient addition, can alter the life cycle of a depressed population of steelhead. Wild steelhead are targeted by catch-and-release fisheries in British Columbia (MFLNRORD 2017) that likely impart little mortality (<6%; Nelson et al. 2005) and are intercepted to varying degrees in commercial salmon fisheries (MFLNRORD 2016). Thus, it is difficult for harvest rates of wild steelhead in British Columbia to be modified for conservation objectives. In contrast, other salmon species such as pink salmon are harvested both commercially and recreationally. Where salmon populations are depressed, nutrient addition has been used as an enhancement option (Stockner and MacIsaac 1996, Ashley and Slaney 1997). However, we found that while nutrient addition increased the numbers of smolts produced per female steelhead spawner before the regime shift, we detected no effect of nutrient addition on smolt abundance after the regime shift. We did detect a

positive effect of pink salmon abundance on the number of smolts produced per steelhead spawner after the regime shift. Further, we found that increased nutrient addition and pink salmon abundance were linked with juvenile steelhead migrating to sea at a younger age, which should decrease the generation time of steelhead and could increase their productivity in periods of positive population growth.

It is possible that the impacts of pink salmon and artificial nutrient addition on the size and age of migrating steelhead smolts could have carryover effects (sensu O'Connor et al. 2014) and alter subsequent marine survival and numbers of returning adults. On the one hand, our work discovered that nutrient addition was associated with larger smolts of a given age and previous research has found that larger steelhead and Atlantic salmon (*Salmo salar*) smolts can have a greater probability of surviving the marine portion of their life cycle to return to spawn in some studies (Antonsson et al. 2010, Osterback et al. 2014), but not others (Keogh River; Friedland et al. 2014). On the other hand, increased pink salmon abundance and artificial nutrient addition were associated with younger ages of outmigration and younger smolts are generally smaller. Indeed, the difference in length between smolt ages was on average ~2–3 times greater than the effect of artificial nutrient addition on smolt length. Thus, carryover effects from pink salmon and artificial nutrient addition might actually reduce the probability of smolts surviving the marine environment due to migrating to sea at a younger age as smaller fish. Regardless of these freshwater dynamics, there have been dramatic declines in steelhead production in many parts of their southern range over the last several decades, including British Columbia, which appear to be predominantly influenced by climate-driven ocean conditions (Welch et al. 2000, Kendall et al. 2017).

Through analyses of four decades of steelhead data, a species with a complex life cycle and of conservation concern, we discovered considerable temporal variation in the size and age of individuals when they migrate from freshwater to the ocean. These variations in life history were linked with a combination of extrinsic variables: nutrient subsidies in the form of species interactions and management intervention and climatic

variation. These individual life-history shifts did not consistently scale up to contribute to juvenile population abundances over time. Instead, abundance of out-migrating steelhead smolts was consistently regulated by an intrinsic variable: density dependence. This demonstrates that a complex interplay of species interactions, nutrient subsidies, density dependence, and climatic variation can control the life-history expression of species with complex life cycles.

ACKNOWLEDGMENTS

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